

## THE SHAPES OF BIRDS' EGGS

BY F. W. PRESTON

The usual way of describing a bird's egg is to report its length and maximum diameter. The latter is not the diameter at the mid-point of the length, as a rule, because most eggs are bigger at one end than the other. A statement of length and maximum diameter is not a complete description therefore, and the question arises whether a complete description *can* be given, and, if so, how many measurements are needed to define it. Obviously, it requires at least three, but it may take more. In fact, it will be shown in what follows that most avian eggs require four measurements or "constants" (that is, two in addition to length and breadth), and that some require five. The problem then becomes one of finding a general equation suitable for *all* eggs, of expressing the facts in the simplest, most logical, and most convenient way, and of devising apparatus for measuring the eggs and deducing the constants.

This investigation was not undertaken primarily as a mathematical amusement. It seems likely that it may throw some light on several biological and ecological problems, but the present paper concerns itself merely with the broad question of what *is* the shape of a bird's egg. The mathematics may conceivably show something of the physiology and mechanics of egg-laying, since the shape of the egg is a response to the forces exerted by the oviduct during shell-formation (Mallock, 1925; D'Arcy Thompson, 1943). These biological problems are perhaps more interesting than the purely geometrical one of defining egg shape. Thompson (*op. cit.*: 936, footnote) seems to throw up his hands in the belief that egg shape is indescribable, particularly if it happens to be a guillemot's (= murre's). Romanoff and Romanoff (1949: 88) are more explicit: "The numerous variations in the contour of individual eggs obviously cannot be expressed in mathematical terms." It seems to me that, on the contrary, nothing can be more obvious than that, as a matter of theory, any such shape should be readily described; and, as a matter of fact, they take very little describing, and the results appear interesting. The present paper will, therefore, be confined to a logical development of the mathematical aspects, leaving the biological and other problems, for which they may provide a solution, for later papers.

Since this paper was completed and accepted by the A.O.U., I have received through the kindness of Professor Bartels and Dr. Storer, both of Ann Arbor, Michigan, a reprint of a paper by Jun-ichi Okabe ("On the Forms of Hens' Eggs" Reports of Research Institute

for Applied Mechanics, Kyushu University, Vol. 1, No. 1, 1952) in which the shape of eggs is treated as a problem in the forces that mold that shape, as D'Arcy Thompson would have wished, and the shape is then used to deduce the forces involved. This is a problem in mechanics, and even in its approximate form, leads to some striking conclusions, biological and otherwise. It differs entirely in treatment, and in purpose, from this present paper, which is purely geometrical and descriptive in nature, and aims to discover with accuracy what *is*

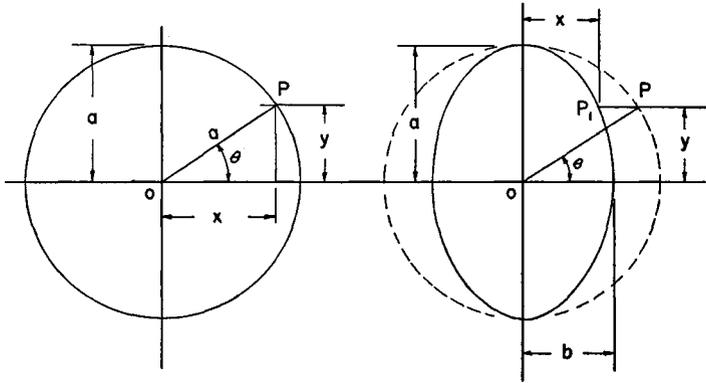


FIGURE 1 (*left*). Parametric equation of a circle in terms of the eccentric angle.  
FIGURE 2 (*right*). Parametric equation of an ellipse.

the shape of an egg before, or without, attempting an analysis of the forces necessary to produce that shape. It seems logical to assume that it may be possible to establish a connection between the "constant" or parameters of Jun-ichi Okabe and the present writer, but this is not yet certain.

A still more recently received paper (Bradfield, J. R. G., Radiographic studies on the formation of the hen's egg shell, *Journ. Exper. Biol.*, 28: 125-150, 1951) greatly clarifies the mechanism of shell formation, and makes it unnecessary to pursue further this aspect of the problem.

A circle may be defined by the parametric equation (cf. fig. 1)

$$\begin{aligned} y &= a \sin \theta \\ x &= a \cos \theta. \end{aligned} \tag{1}$$

Here *a* is the "radius vector" drawn from the center *O* to a point *P* on the perimeter, and  $\theta$  is the angle this radius makes with the *x* axis.

A circle may be otherwise defined. For instance, in polar coordinates, by the simple equation

$$r = a \text{ (where } a \text{ is a constant),}$$

or in Cartesian coordinates by

$$x^2 + y^2 = a^2 .$$

For our purpose, however, the parametric equation is the most useful, because we can gradually elaborate on it till it describes all conceivable forms of eggs.

The first step in the elaboration is to develop the parametric equation for an ellipse (fig. 2). If the circle be imagined as pivoted along its  $y$  axis, and then rotated around this so that it makes an angle with respect to the paper, the circle will appear "foreshortened" and will look like an ellipse. All  $x$ -coordinates will be shortened in the same ratio, say  $b/a$ , all  $y$  coordinates will remain unaltered, and our parametric equation becomes

$$\begin{aligned} y &= a \sin \theta \\ x &= b \cos \theta . \end{aligned} \tag{2}$$

Here  $a$  is the semi-major axis,  $b$  the semi-minor axis, and  $\theta$  has become what is called the "eccentric angle." It is not the angle which the radius vector to a point on the *ellipse* makes with the  $x$  axis, but the angle to the corresponding point on the original, circumscribing, circle.

The ellipse may be described in various other ways; for instance, in Cartesian coordinates, it is given by

$$\frac{x^2}{b^2} + \frac{y^2}{a^2} = 1 .$$

However, we need the parametric form.

Now, the first and most obvious thing about a typical egg is that it is always *somewhat* elongated: an ellipsoid is a closer approximation than a sphere, and for some eggs an ellipse may be a sufficient approximation. The ordinary method of describing eggs, with two constants only, amounts mathematically to saying that this is good enough. However, the great majority of eggs are clearly larger at one end than at the other, and all of them prove to be so when measured. In all that follows we shall imagine that the egg has its long axis vertical and the big end uppermost.

The simplest parametric equation we can use to describe an egg in this position is then

$$\begin{aligned} y &= a \sin \theta \\ x &= b \cos \theta (1 + c_1 \sin \theta) \end{aligned} \tag{3}$$

where  $c_1$  is a "dimensionless" constant that may vary from egg to egg, but is constant for any particular specimen. This equation represents what I shall call the "simple" or "perfect" ovoid. By introducing this one new constant,  $c_1$ , we can describe all eggs to a very fair approximation, but not always to the limits of experimental accuracy. To show the degree of approximation graphically, figure 3 has been prepared. It shows the effect of changing the ratio of  $b/a$  and of varying  $c_1$ . It will be immediately obvious that a whole family of egg forms can thus be developed and that they do not depart a great deal from the known forms of eggs.

That equation (3) is the simplest and most logical form of an ovoid may be seen as follows: our objective is to make the top half of the egg wider than the bottom half, while taking care to keep the left-hand side symmetrical with the right-hand. It is a case of dilating the top and constricting the bottom while requiring the curve to pass through the points marking the ends of the major and minor axes of the ellipse. These conditions can be met only by postulating a correction term, for the  $x$  coordinate, which is a function of  $\sin \theta$  and of nothing else. The advantage of the parametric form of the equation is that it permits us to write this fact down in mathematical form by mere inspection.

Careful comparison of actual eggs with this equation shows, however, that though it represents some eggs very well, it is not quite right for the majority. We may, therefore, develop the mathematics generally. Any egg, as we have seen, must conform to the equation

$$\begin{aligned} y &= a \sin \theta \\ x &= b \cos \theta \cdot \varphi(\sin \theta) \end{aligned} \quad (4)$$

where  $\varphi(\sin \theta)$  is some function of  $\sin \theta$  yet to be discovered experimentally.

We may reasonably assume that  $\varphi(\sin \theta)$  can be expanded in series, so that

$$\varphi(\sin \theta) = c_0 + c_1 \sin \theta + c_2 \sin^2 \theta + c_3 \sin^3 \theta + \dots \quad (5)$$

and obviously, from what we have seen already,  $c_0 = 1$ , and in most eggs the other coefficients are much less than unity, and most often are a rapidly declining series.  $c_1$  will always be positive, because we have said the big end of the egg is to be uppermost, but  $c_2$  and  $c_3$  may be negative. In nearly all the cases so far examined  $c_2$  is negative. This has the effect of making both ends of the egg slightly more conical than in the Simple Ovoid. We may therefore call this the Biconical Term and refer to eggs having only  $c_1$  and  $c_2$  terms as the Standard Avian Egg-Shape, for  $c_3$  is usually zero or negligible.

In a few cases  $c_3$  is not negligible. Since it is attached to a term of  $\sin \theta$  which is an odd power (the cube of  $\sin \theta$ ), the effect of a non-negligible  $c_3$  is to emphasize the attenuation of one end of the egg and the blunting of the other, whereas the coefficients of even terms ( $c_2$  for instance) attenuate, or blunt, both ends equally. To date I have found sizeable values of  $c_3$  only in the murre and their allies, and a few others, so an ovoid in which  $c_3$  is important may be called an Alcid Ovoid.

Except in a very few eggs, I have not found  $c_2$  negligible. It has apparently a maximum value in the plover and gull groups, so that it characterizes the charadriid and larid ovals; it is also important in the ostrich group.

In no case to date have I found it necessary to consider terms higher than  $\sin^3 \theta$ .

Therefore, the general equation of birds' eggs is finally

$$\begin{aligned} y &= a \sin \theta \\ x &= b \cos \theta (1 + c_1 \sin \theta + c_2 \sin^2 \theta + c_3 \sin^3 \theta) \end{aligned} \quad (6)$$

which, except in the case of the Alcids, reduces to

$$\begin{aligned} y &= a \sin \theta \\ x &= b \cos \theta (1 + c_1 \sin \theta + c_2 \sin^2 \theta). \end{aligned} \quad (6a)$$

For a few eggs

$$\begin{aligned} y &= a \sin \theta \\ x &= b \cos \theta (1 + c_1 \sin \theta), \end{aligned} \quad (6b)$$

and for a few others, whose two ends are virtually alike, we may have

$$\begin{aligned} y &= a \sin \theta \\ x &= b \cos \theta (1 + c_2 \sin^2 \theta). \end{aligned} \quad (6c)$$

In a later section (table 5) we compare the observed and calculated values for a number of representative eggs of a wide variety of species belonging to different orders. It is necessary first to consider how the observed values may best be ascertained and the constants computed.

*Methods of Observation.*—When, in the early stages of this investigation, it seemed probable that equation (6b), that for the Simple Ovoid, adequately represented actual eggs, it was logical to believe that a measurement of the curvature of each end, together with a measurement of the length and the maximum diameter, would give all the information required. As a matter of fact, it would theoretically give more than this, for it would give four measurements to determine three constants, and so one measurement would be redundant, or

could be used as a check on the others. This was tried first on eggs of the domestic fowl (*Gallus gallus*), both pullets and adults. Very often the results were remarkably close. The length of the egg and the curvatures at the two ends were used to predict the maximum diameter, and frequently did so to less than 1 per cent. This is an exceedingly severe test, using minute areas near each end to predict the shape of the whole egg. For this purpose a special spherometer was devised.

This method has much to recommend it, but only if the egg is a Simple Ovoid. But most eggs are Standard Avian (Biconical) or Alcid.

A better method would seem to be to measure the diameters of the egg at various places along the length. If we divide the length  $l$  ( $2a$  in fig. 2) of the egg into eight equal parts, the "latitudes" of these subdivisions, when referred to the circumscribing circle, are the values of the parameter  $\theta$  such that:

$$\sin \theta = 0, \pm \frac{1}{4}, \pm \frac{1}{2}, \pm \frac{3}{4}, \pm 1.$$

The positive values in this set correspond to the "north latitude" or big end of the egg, and the negative values to the "south latitude;" the value 0 corresponds to the "equator," and the values  $\pm 1$  to the "poles." These values for the  $\sin \theta$  are simply the values of  $y/a$  at the points of subdivision. At each of these points we may measure the "diameter" of the cross-section of the egg. These measurements represent the values of  $2x$  for the corresponding latitudes  $\theta$  (or  $\sin \theta$ ).

The value of  $2x$  at the poles is zero, so that no information pertaining to the coefficients  $c_1$ ,  $c_2$ , and  $c_3$  in the formulae (6) can be derived from these points. The value of  $2x$  at the equator is  $2b$ . Note that in general the maximum diameter is greater than  $2b$  and occurs north of the equator. In the computation of the value of  $2x$  at the other latitudes in the set chosen above we make use of the values in the following table:

$\sin \theta$	$\sin^2 \theta$	$\sin^3 \theta$	$\cos \theta$
$\pm 1/4$	1/16	$\pm 1/64$	0.968
$\pm 1/2$	1/4	$\pm 1/8$	0.866
$\pm 3/4$	9/16	$\pm 27/64$	0.661

With this information and the measured values of the diameters,  $2x$ , we can determine optimum values for the constants  $c_1$ ,  $c_2$ , and  $c_3$ .

The real problem is, how should we measure the diameters at the various latitudes selected? It is particularly desirable to get accurate estimates of diameters at  $\sin \theta = \pm \frac{3}{4}$ , *i. e.*, fairly close to the poles,

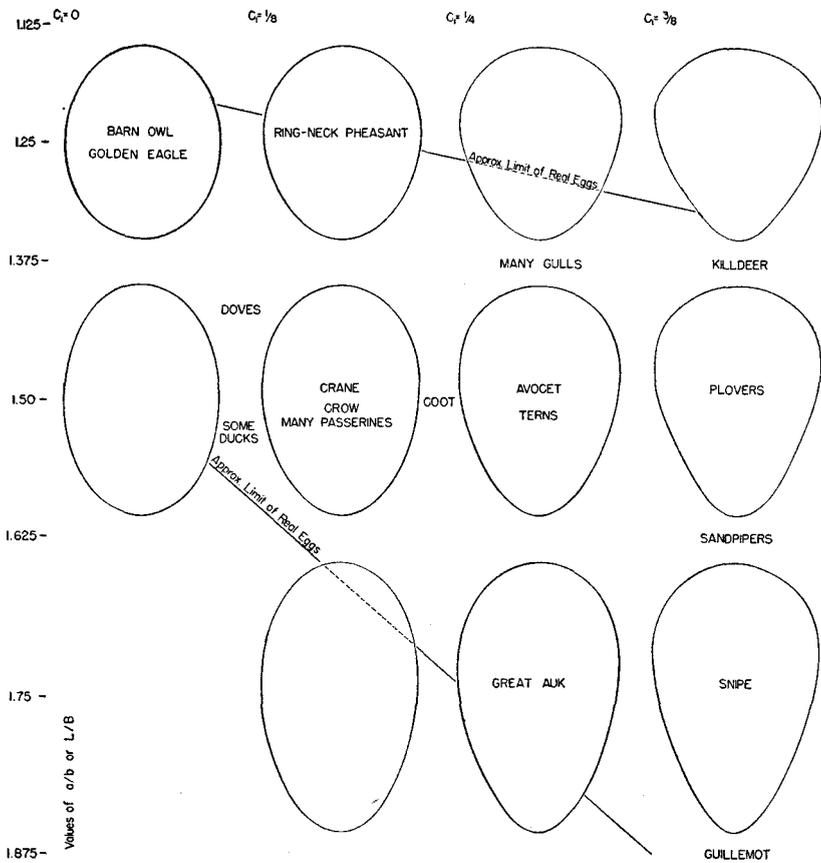


FIGURE 3. "Simple" ovals over the range of values of elongation ( $a/b$ ) and of ovalness ( $c_1$ ) found among real eggs. [Note: the  $c_2$  and  $c_3$  terms are assumed to be zero in making this drawing.]

but here the egg is tapering off so rapidly that measuring the solid egg needs special techniques. We have so far found it preferable to use a profile diagram of the egg, representing a longitudinal, or "meridian," section.

This can be done approximately by photography. Mallock (1925) used a pinhole camera. Dresser (1910) has a whole volume of very fine photographic plates. It is in fact from this work that the positions of characteristic eggs are plotted on our figure 3. However, this did not prove entirely satisfactory, for several reasons. The margin of an egg in a photograph is always slightly fuzzy and exact diameters are hard to measure. More important, perhaps, is the fact that an egg does not lie with a meridian plane horizontal. The pointed end

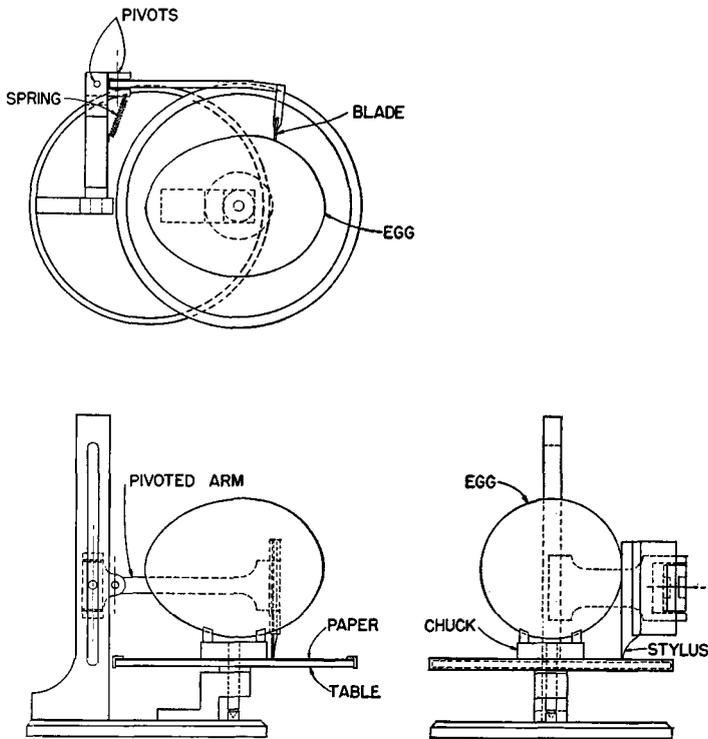


FIGURE 4. Profile-copying machine.

is always lower. By propping up the small end of the egg a satisfactory photograph might be obtained, but the process is in any case cumbersome, and the film and photographic paper may shrink or expand with processing. Further, with large eggs, the aperture of the lens may not permit it to "see" the meridian plane, which lies "below the horizon."

We therefore used a profile-copying machine of our own devising which was much quicker, more accurately represented the desired section, and permitted easier measurements (see fig. 4).

*Description of profile-transfer* (fig. 4).—The apparatus consists of a circular table, mounted on tight-fitting ball-bearings and free to rotate on a vertical axis. On this table is placed a sheet of typewriter carbon paper, face up, and on top of this a sheet of thin white paper, face down. The papers are held down at the rim by a simple retaining ring that slips over them and fits the edge of the table. A "chuck" to hold the egg is mounted concentrically with the table and above it; it has three, or four, prongs or fingers faced with pressure-sensitive

tape, sensitized on both sides, so that one side sticks to the prongs and the other to the egg. The egg is laid on them so that its axis is horizontal and parallel to the table, is gently pressed into place so that the tape adheres, and, if necessary, is kept under gentle finger pressure while its profile is traced.

A pivoted arm is mounted on a vertical axis beyond the edge of the table, and is drawn up to the egg by a light spring, so that the egg acts as a cam controlling the arm as "cam-follower." The follower bears on the egg by means of a vertical blade-edge carrying a stylus at the bottom, and the stylus bears on the white paper by its own weight. In order to keep this constant, a horizontal pivot is provided in the arm near the vertical one. The pressure of the stylus causes the carbon paper to mark the under side of the white paper with a very sharply defined line. We usually go twice around the egg, to make sure there has been no movement.

The white paper is inserted and removed readily by providing it in the center with a hole that slips over the chuck. The carbon paper does not need to be removed.

Examples of the tracings or profilings are shown in figure 5, 5/9 natural size. These show the varieties of shapes and indicate that extreme forms were included and are readily "graduated" with equations of the type we have been discussing.

We believe that observational and computational errors, in our present work dealing with large eggs and with profiles measured without the benefit of travelling microscopes or other special devices, are normally about 0.1 to 0.2 mm., at times a little more. Consequently, we consider the observed shape to be accurately represented within the limits of experimental error when the computed values do not differ from the observed ones by a residuum which greatly exceeds this figure. A tenth of a millimeter is four-thousandths of an inch, and about twice the diameter of a human hair. The extent of agreement will be obvious from the tabular matter.

*Fitting Measurements by "Least Squares."*—If we know that an egg is a true ellipsoid, it is sufficient to measure its length and its diameter at any known "latitude," preferably at the "equator." Any further measurements are redundant, and cannot be used unless there are experimental errors in the measurements, or unless the actual shape is not a true ellipsoid and we agree to compromise on an "ellipsoid of best fit" for descriptive purposes. In such a case the accepted method is the method of least squares, that is, the minimizing of the sum of the squares of all the "errors," which are defined as the differences between observed and calculated values.

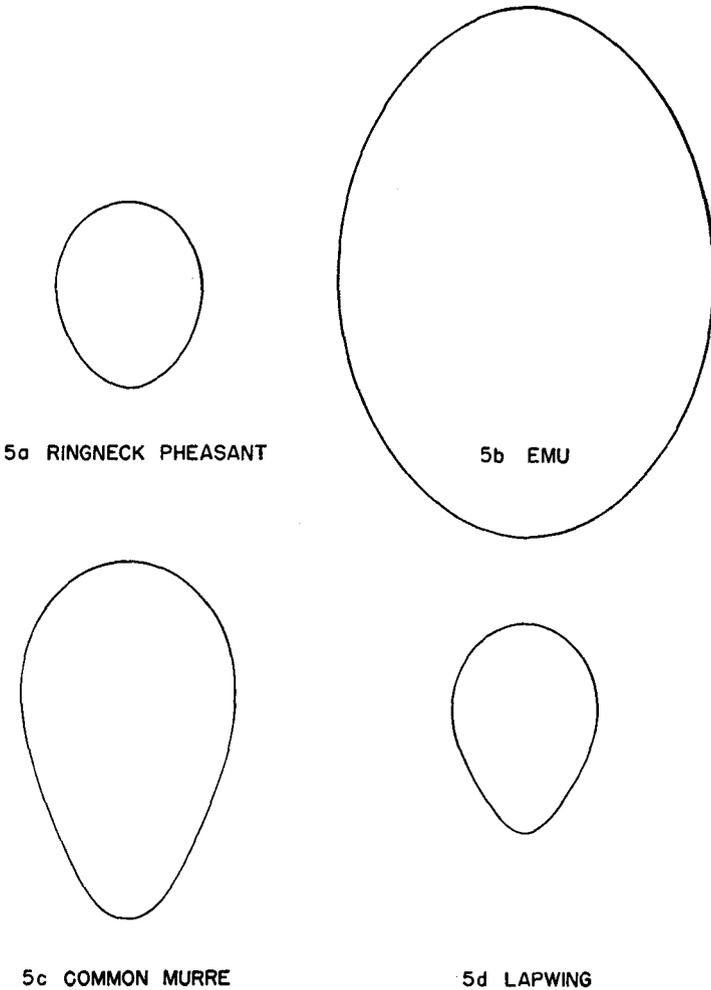


FIGURE 5. Representative Egg Shapes.. All eggs in Preston Collection.  
5a. *Ring-necked Pheasant* (England). An approximation to a "simple" oval. The  $c_1$  term is moderately large, the  $c_2$  term rather small, and  $c_3$  negligible. Some eggs of the Domestic Fowl, the Common Loon, and the Golden Eagle are equally good representatives of the simple oval. 5b. *Emu*. An approximation to the biconical form. The egg is *not*, as might be thought at first sight, a good ellipse. This egg is, in effect, the reverse of 5a, in that the  $c_2$  term is substantial and the  $c_1$  term very small. The Tinamou's egg is even more extreme than this. 5c. *Common Murre* (Wales). In this egg  $c_1$  is very high,  $c_3$  very high (but negative, of course), and  $c_2$  (the biconical element) very small. This is the typical Alcid egg, just as the Tinamou's is the typical biconical. 5d. *Lapwing* (England). Here both  $c_1$  and  $c_2$  are large, while  $c_3$  is negligible. This is the characteristic plover egg.

Similarly, if we assume that the egg is a "simple oval," adequately defined by its length, equatorial diameter, and the constant  $c_1$  that defines the amount of ovateness, then we cannot measure more than three experimental values, say the length and two diameters at different latitudes, without redundancy.

A normal avian egg, however, is found by experience to contain the  $c_2$  term. In fact, in struthious birds, including the tinamous, the  $c_2$  term is more important than the  $c_1$  term. The egg is more biconical (in the sense of the present author, not necessarily in Dresser's sense) than it is ovate. Thus, to describe the egg we need, theoretically, the length and three diameters, neither more nor less. This will permit us to assign values to both  $c_1$  and  $c_2$ , even though one of them may be zero.

Finally, in the case of the Alcids (guillemots, murre, Great Auk, and a few others like the Red-throated Loon and some gulls) it is necessary or at least advisable, if great accuracy is required, to take measurements at four diameters, but in no case is it necessary to use more, though I have used an equation for Dresser's *photograph* (1910: pl. 102, fig. 1) of a Great Auk's egg, involving the equivalent of five measured diameters.

However, when a contour has been obtained, it is easy and convenient to measure the diameter at seven places (nine including the two "poles" where the diameter is zero) equally spaced along the polar axis. We then have a considerable excess of measurements, and their proper use involves fitting by least squares. This is standard practice in statistical work, but it is not often that an egg-shaped curve, or one as complicated, is fitted in this manner, and some interesting points come out. Other methods of fitting are permissible, but this method has the advantage that it eliminates all personal equation and automatically produces a result in which we can have considerable confidence. It has two disadvantages. First, the computations are, superficially, a little formidable, and second, the assumption is made that errors of measurement are likely to be equally as great at one diameter as at another.

The great advantage is that the proceedings can be reduced to a very simple routine, and turned over to the operator of a calculating machine. The process of boiling it down to this routine is what looks formidable, but actually it is merely tedious once, and forever after there is nothing to it.

A considerable simplification is effected if the diameters that are measured are symmetrically distributed above and below the equator or mid-point in the length. Then for every  $\sin \theta$  there is a  $\sin (-\theta)$ ,

which is numerically equal to it but opposite in sign and cancels it out in such summations as involve odd powers of  $\sin \theta$  like  $\Sigma \sin \theta$ ,  $\Sigma \cos \theta \sin \theta$ ,  $\Sigma \cos \theta \sin^3 \theta$ , etc. (but not in terms involving measured diameters  $k$ , like  $\Sigma k \sin \theta$ ,  $\Sigma k \cos \theta \sin^3 \theta$ ; see below).

A second great simplification is introduced by agreeing that we will always divide the length into eight equal parts, never more and never less, so that we have a numerical value of purely trigonometric functions  $\Sigma \cos \theta$ ,  $\Sigma \sin \theta \cos \theta$ , etc., which is the same throughout our work on all eggs. It is this which boils the whole procedure down to a simple routine.

It is necessary to decide first what equation we are going to fit to our observational data. We may try a simple ellipsoid, a simple oval, a biconical oval, or an alcid equation. A good deal of experience suggests that for any egg but the extreme form, the most convenient choice is the biconical, but for a few it is better to use the alcid.

Let us suppose for a moment, however, that we had decided to use the simplest of all, the ellipse.

Its equation, for the abscissa, is  $x = b \cos \theta$ . (8)

This is more conveniently written  $2x = B \cos \theta$ , where  $B = 2b$ . (8a)

Now what we measure at latitude  $\theta$  is a diameter, which we may call  $k$ , to distinguish it from the theoretical diameter  $2x$ .

The "error" or "residuum" is  $(2x - k) = (B \cos \theta - k)$ , and its square is  $(B \cos \theta - k)^2$ .

The "least squares" method involves summing the squares of the residuals at the several values of  $\theta$ , for which we have experimental values  $k$ , and making the sum a minimum.

That is,  $\Sigma (B \cos \theta - k)^2$  or  $\Sigma (B^2 \cos^2 \theta - 2Bk \cos \theta + k^2)$  is to be a minimum.

$\Sigma k^2$  cannot be changed, and so this becomes

$B^2 \Sigma (\cos^2 \theta) - 2B \Sigma (k \cos \theta)$  is to be a minimum.

Differentiating with respect to  $B$  and setting the result equal to zero gives

$$2B \Sigma (\cos^2 \theta) - 2 \Sigma (k \cos \theta) = 0$$

or

$$B = \frac{\Sigma (k \cos \theta)}{\Sigma (\cos^2 \theta)}. \quad (9)$$

This gives us the optimum value of  $B$ , which is the only "unknown" for a simple ellipse.

When we come to egg shapes proper, we get more complicated equations, and have to differentiate with respect not only to  $B$ , but

to  $c_1$ ,  $c_2$ , and  $c_3$ , or as many of them as we assume to be present in our equations. The procedure is just the same as before, but the equations get increasingly complex. Since we differentiate with respect to all of our adjustable factors we necessarily end up with as many simultaneous equations as there are adjustables. We can, therefore, solve for all of our unknowns.

TABLE 1  
SUMMARY OF EQUATIONS FOR BEST FITTING CURVES

Best Fitting *Ellipse*. One unknown, viz.  $B$  ( $= 2b$ )

$$B = Z_{01} / T_{02}$$

Best Fitting *Simple oval*. Two unknowns, viz.  $B$  and  $c_1$

$$B [T_{02} + c_1^2 \cdot T_{22}] = [Z_{01} + c_1 \cdot Z_{11}]$$

$$c_1 = \frac{1}{B} \cdot \frac{Z_{11}}{T_{22}}$$

Best Fitting *Standard Avian Oval*. Three unknowns, viz.  $B$ ,  $c_1$ , and  $c_2$

$$B [T_{02} + (c_1^2 + 2c_2) T_{22} + c_2^2 T_{42}] = [Z_{01} + c_1 \cdot Z_{11} + c_2 \cdot Z_{21}]$$

$$c_1 = \frac{1}{B} \cdot \frac{Z_{11}}{T_{22}} \quad (\text{same as for Simple Oval})$$

$$c_2 = \frac{1}{B} \left[ \frac{Z_{21}}{T_{42}} \right] - \frac{T_{22}}{T_{42}}$$

Best Fitting *Alcid Oval*. Four unknowns, viz.  $B$ ,  $c_1$ ,  $c_2$ , and  $c_3$

$$B [T_{02} + (c_1^2 + 2c_2) T_{22} + (2c_1 c_3 + c_2^2) T_{42} + c_3^2 T_{62}] = [Z_{01} + c_1 Z_{11} + c_2 Z_{21} + c_3 Z_{31}]$$

$$c_1 = \frac{1}{B} \left[ \frac{Z_{11} T_{62} - Z_{31} T_{42}}{T_{22} T_{62} - (T_{42})^2} \right]$$

$$c_2 = \frac{1}{B} \left[ \frac{Z_{21}}{T_{42}} \right] - \frac{T_{22}}{T_{42}} \quad (\text{same as for Standard Avian Oval})$$

$$c_3 = \frac{1}{B} \left[ \frac{Z_{31} \cdot T_{22} - Z_{11} \cdot T_{42}}{T_{22} \cdot T_{62} - (T_{42})^2} \right]$$

The resulting equations are none the less somewhat elaborate-looking. In order to condense them it will be convenient to develop a sort of mnemonic or shorthand.

Let us write  $\Sigma (\sin^m \theta \cos^n \theta)$  as  $T_{m n}$ , and

$$\Sigma (k \sin^m \theta \cos^n \theta) \text{ as } Z_{m n}.$$

Here  $T$  means that the function is purely trigonometric, while  $Z$  means that the measured value  $k$ , at each latitude  $\theta$ , is involved.

If  $m = 0$ ,  $\sin^m \theta = 1$ , so that  $T_{0n}$  is  $\Sigma (\cos^n \theta)$ , and our equation (9) above becomes

$$B = Z_{01}/T_{02}$$

In all that follows it is assumed, as previously mentioned, that for every diameter we measure north of the equator there is another measured at the same distance south of the equator. This causes a few terms to cancel out which would be present if we did not have a symmetrical arrangement of measuring points. Subject to this symmetry, the tabulation above (table 1) does *not* require that the latitudes be equally spaced, or that there be eight, or any other particular number of levels for measuring.

These equations are somewhat general, as above mentioned, and now a further simplification can be introduced if we agree that we will always divide the polar axis into eight equal parts, and measure the diameters at the places where  $\sin \theta = 3/4, 1/2, 1/4, 0, -1/4, -1/2,$  and  $-3/4$ . Under these circumstances, all the  $T$  functions become simple numerical values. These values are given in table 2 below.

TABLE 2  
NUMERICAL VALUES OF THE "T" FUNCTIONS

$T_{02} = \Sigma \cos^2 \theta = 5.25$
$T_{22} = \Sigma \sin^2 \theta \cos^2 \theta = 0.984375$
$T_{42} = \Sigma \sin^4 \theta \cos^2 \theta = 0.377930$
$T_{62} = \Sigma \sin^6 \theta \cos^2 \theta = 0.179626$
$(T_{42})^2 = 0.142831$

Substituting these numerical values in the formulae of table 1 greatly simplifies those formulae so far as  $c_1, c_2,$  and  $c_3$  are concerned. The equation for  $B$ , however, remains a cubic, and therefore complicated. A further simplification is therefore greatly to be desired. We find this in the fact that, while we have no idea in advance what the values of  $c_1, c_2,$  and  $c_3$  are going to be, we *do* know that  $B$  is going to come out very close to the observed value  $k_0 (= 2x_0)$ , the measured equatorial diameter.

In practice we have found it satisfactory to assume that  $B$  can be replaced by the observed value  $k_0$ , which should be measured with care, and fortunately is usually the easiest of all the diameters to measure with precision.

A better approximation than that obtained by simply setting  $B$  equal to  $k_0$  could be obtained by setting  $B = k_0 + \Delta k_0$ , where the unknown "correction"  $\Delta k_0$  to the simpler estimate for the value of  $B$  is assumed to be so small that its square and cube can be neglected.

When this is valid we can replace  $B^2$  and  $B^3$  by their approximates  $k_0^2 + 2k_0 \cdot \Delta k_0$  and  $k_0^3 + 3k_0^2 \cdot \Delta k_0$ , respectively. We thus obtain a linear equation in the correction  $\Delta k_0$ . But the task of formulating this equation, though linear and readily soluble, is tedious. We have not found that it is worth the trouble.

We therefore proceed to assume that  $B = k_0$  and that the equations for the "c" values are those of table 3, where numerical values from table 2 are substituted in the formulae of table 1. We confine table 3 to Standard Avian and Alcid types.

TABLE 3  
FORMULAE FOR COMPUTING THE "c" VALUES OF EGG SHAPES

*Standard Avian Oval*

$$c_1 = \frac{1}{k_0} (1.0159 Z_{11})$$

$$c_2 = \frac{1}{k_0} (2.6460 Z_{21}) - 2.6046$$

$$(B = k_0)$$

*Alcid Oval*

$$c_1 = \frac{1}{k_0} (5.2850 Z_{11} - 11.1195 Z_{31})$$

$$c_2 = \frac{1}{k_0} (2.6460 Z_{21}) - 2.6046 \quad (\text{Same as for Standard Avian})$$

$$c_3 = \frac{1}{k_0} (28.9624 Z_{31} - 11.1195 Z_{11})$$

$$(B = k_0)$$

It is now possible to eliminate the last traces of trigonometric functions, because we use only a limited number of positions of  $\theta$ , for which  $\sin \theta$ ,  $\cos \theta$ , and more complicated ones like  $\sin^2 \theta \cdot \cos \theta$  have stock values. This permits us to write down the  $Z$ -values as simple linear functions of the observed diameters. This is done in table 4 below.

The process of computing now becomes very simple, and is as follows:

On a profile of the egg, divide the polar axis into eight equal parts, corresponding to "latitudes" given by  $y/a = \sin \theta = \frac{3}{4}, \frac{1}{2}, \frac{1}{4}, 0$  (the "equator"),  $-\frac{1}{4}, -\frac{1}{2},$  and  $-\frac{3}{4}$ . Measure the diameter at each latitude, and call these *measured* diameters,  $k_{3/4}, k_{1/2}, \dots, k_{-3/4}$ .

From table 4 compute  $Z_{11}$  and  $Z_{21}$ , and if the egg is believed Alcid in type, compute also  $Z_{31}$ .

From table 3, using these values of  $Z$ , compute the "c" values.

We now have the "best fitting" mathematical equation of our egg, and it describes the whole contour of the egg, *i. e.*, its shape.

If now we want to see how good a fit we have, we use the equation to compute the diameters at the standard latitudes, and compare these computed diameters with the observed ones.

TABLE 4  
THE Z-VALUES

$[Z_{01} = 0.6614 (k_{3/4} + k_{-3/4}) + 0.8660 (k_{1/2} + k_{-1/2}) + 0.9682 (k_{1/4} + k_{-1/4}) + k_0]$	Not used in Standard Avian or Alcid types.
$Z_{11} = 0.4961 (k_{3/4} - k_{-3/4}) + 0.4330 (k_{1/2} - k_{-1/2}) + 0.2421 (k_{1/4} - k_{-1/4})$	
$Z_{21} = 0.3720 (k_{3/4} + k_{-3/4}) + 0.2165 (k_{1/2} + k_{-1/2}) + 0.0605 (k_{1/4} + k_{-1/4})$	
$[Z_{31} = 0.2790 (k_{3/4} - k_{-3/4}) + 0.1083 (k_{1/2} - k_{-1/2}) + 0.0151 (k_{1/4} - k_{-1/4})]$	Used only in Alcid types.

Since the murrees are commonly regarded as having the most extreme forms of eggs, I have tabulated the computed and observed values of these eggs first, in table 5, section A. Then follow a variety of examples, most of which are adequately "graduated" by a Standard Avian type of equation. Finally, in section C, I have included Dresser's figure of the egg of the Great Auk, carried out to the term involving  $\sin^4 \theta$ .

In table 4, for ease of reference, are given the "c" values of these eggs.

It should not be assumed that in a given species these "c" values are constants. They are not even constants for a given individual bird, the eggs of a clutch differing markedly one from another, which is a useful and perhaps important biological phenomenon, and will be the subject of a second communication.

*Discussion.*—Perhaps the most interesting thing is that the shape of even extreme eggs can be so well represented with so few terms and constants. The next is the almost universal presence of the  $c_2$  or biconical term. This is related to the physiology of the oviduct, and in some species changes during the progress of the clutch, and so may have useful ecological implications. The ingenuity of the murre in fitting its egg so well to an equation which may well seem quite formidable to a mere seafoal is to be commended. The skill of the lapwng in eliminating the  $c_3$  term while retaining a high value of the  $c_2$  term is also noteworthy.

Another interesting point is the importance in struthious birds of the  $c_2$  term compared with the  $c_1$  term. The two ends of the egg are very much alike, but the egg is not elliptical. It is biconical, the  $c_2$  term being relatively large.

However, for ordinary descriptive purposes it is likely that orni-

thologists or oologists will not wish to compute terms beyond the first. The unassisted eye will not normally be able, unless well educated, to detect the existence of further terms, but the existence of  $c_1$  will nearly always be very obvious. If profiles are all reduced, or enlarged to a standard size, they can be compared with the chart of figure 3 and reasonably close values of  $b/a$  and of  $c_1$  can be assigned without measurement. This will permit a description of the shape with very fair accuracy, and will give a much better picture than the present conventional methods.

A couple of points of mathematical interest may be noted. The  $c_2$  term is independent of the  $c_1$  and  $c_3$  terms, but the  $c_1$  and  $c_3$  terms are not independent of one another. The differential equations, in the form in which they are first obtained (though not shown in this present text), express these coefficients explicitly one in terms of the other. The present text reports them in a later stage when this complication has been eliminated, for purposes of computation. However, the interdependence persists, and if we assume that the egg is Standard Avian, *i. e.*, that  $c_3 = 0$ , we shall get a different value of  $c_1$  from that which will obtain on the assumption that the egg is Alcid, *i. e.*, that  $c_3$  is not zero. As previously indicated,  $c_2$  will not be affected in the slightest by our choice of assumptions in this particular, but it would be affected by the assumption that a  $c_4$  term is present. The reason is that the odd terms,  $c_1$  and  $c_3$ , both tend to make the egg large at one end and small at the other, while the even terms affect both ends equally, as mentioned at the outset. It might be expected that an egg of "extreme" type, such as a murre's, would have a positive value of  $c_3$  and that  $c_3$  would partially replace the more moderate term  $c_1$ . In practice that is not what happens. The  $c_3$  term is always negative, apparently, thus permitting  $c_1$  to assume a very high value. A positive value of  $c_3$  would tend to flatten the big end of the egg, and this end always shows a somewhat hemispherical character.

Table 6 indicates the effect on  $c_1$  of assuming the zero or non-zero value of  $c_3$  for several species of birds.

In practically all eggs so far examined  $c_2$  is negative unless it is very nearly zero.

Finally, it should not be thought that the equations we have been using are restricted to representing conventional "egg" shapes. They will equally well represent pears, peg-tops, figures of eight, dumb-bells, and numerous others still more complicated. Egg shapes are merely those in which all coefficients are rather small, and are generally confined to the first two or three. It is, therefore, not remarkable that egg shapes are rather readily represented by our equations.

TABLE 5

SECTION A

Family Alcidae *Uria aalge* Common Murre (Preston Collection)

$$L = 2a = 85.2 \quad y = a \sin \theta \quad 2x = 47.5 \cos \theta \quad (1 + 0.374 \sin \theta - .041 \sin^2 \theta - .127 \sin^3 \theta)$$

<i>k</i>	$\frac{3}{4}$	$\frac{1}{2}$	$\frac{1}{4}$	0	$-\frac{1}{4}$	$-\frac{1}{2}$	$-\frac{3}{4}$
2x (calc.)	37.8	47.8	50.1	47.5	41.7	33.7	23.6
2x (obs.)	37.8	47.8	50.0		41.7	33.6	23.6
calc. - obs.	0	0	+0.1	0	0	+0.1	0

Family Alcidae *Uria lomvia* Brünnich's Murre (Carnegie Museum)

$$L = 2a = 75.1 \quad y = a \sin \theta \quad 2x = 47.1 \cos \theta \quad (1 + .3816 \sin \theta - .0842 \sin^2 \theta - .1111 \sin^3 \theta)$$

2x (calc.)	37.1	47.1	49.6	47.1	41.1	32.7	22.2
2x (obs.)	37.1	47.2	49.6		41.0	32.8	22.2
calc. - obs.	0	-0.1	0	0	+0.1	-0.1	0

Family Gaviidae *Gavia stellata* Red-throated Loon (Carnegie Museum)

$$L = 2a = 79.9 \quad y = a \sin \theta \quad 2x = 43.1 \cos \theta \quad (1 + .1963 \sin \theta + .0693 \sin^2 \theta - .1151 \sin^3 \theta)$$

2x (calc.)	32.4	41.1	43.9	43.1	39.9	34.8	26.8
2x (obs.)	32.5	41.0	43.8		39.9	34.7	26.9
calc. - obs.	-0.1	+0.1	+0.1	0	0	+0.1	-0.1

TABLE 5

SECTION B

Family Dromiceidae *Dromiceius novaehollandiae* Emu (Preston Collection)

$$L = 2a = 127.4 \quad y = a \sin \theta \quad 2x = 89.2 \cos \theta \quad (1 + .014 \sin \theta - .078 \sin^2 \theta)$$

<i>k</i>	$\frac{3}{4}$	$\frac{1}{2}$	$\frac{1}{4}$	0	$-\frac{1}{4}$	$-\frac{1}{2}$	$-\frac{3}{4}$
2x (calc.)	57.0	76.3	86.2	89.2	85.6	75.2	55.8
2x (obs.)	56.7	76.6	86.6		85.7	75.3	55.8
calc. - obs.	-0.3	-0.3	-0.4	0	-0.1	-0.1	0

Family Rheidae *Rhea americana* Rhea (Carnegie Museum)

$$L = 2a = 123.3 \quad y = a \sin \theta \quad 2x = 90.3 \cos \theta \quad (1 + .0312 \sin \theta - .0884 \sin^2 \theta)$$

2x (calc.)	58.2	77.7	87.6	90.3	86.3	75.3	55.4
2x (obs.)	57.9	78.0	88.0		86.4	75.7	55.1
calc. - obs.	+0.3	-0.3	-0.4	0	-0.1	-0.4	+0.3

Family Tinamidae *Rhynchotus rufescens* Tinamou (Carnegie Museum)

$$L = 2a = 56.4 \quad y = a \sin \theta \quad 2x = 45.7 \cos \theta \quad (1 + .0061 \sin \theta - 0.1399 \sin^2 \theta)$$

2x (calc.)	28.0	38.3	43.9	45.7	43.8	38.1	27.7
2x (obs.)	28.0	38.3	43.9		43.9	37.9	27.8
calc. - obs.	0	0	0	0	-0.1	+0.2	-0.1

TABLE 5

## SECTION B (Continued)

Family Spheniscidae *Spheniscus demersus* Cape Penguin (Carnegie Museum)

$$L = 2a = 84.3 \quad y = a \sin \theta \quad 2x = 54.4 \cos \theta \quad (1 + .064 \sin \theta - .0027 \sin^2 \theta)$$

$k$	$\frac{3}{4}$	$\frac{1}{2}$	$\frac{1}{4}$	0	$-\frac{1}{4}$	$-\frac{1}{2}$	$-\frac{3}{4}$
2x (calc.)	37.7	48.6	53.5	54.4	51.8	45.6	34.2
2x (obs.)	37.8	48.4	53.5		51.9	45.5	34.2
calc. - obs.	-0.1	+0.2	0	0	-0.1	+0.1	0

Family Cariamidae *Cariama cristata* Seriama (Carnegie Museum)

$$L = 2a = 62.2 \quad y = a \sin \theta \quad 2x = 46.7 \cos \theta \quad (1 + .1056 \sin \theta - .0523 \sin^2 \theta)$$

2x (calc.)	32.4	42.0	46.3	46.7	43.9	37.8	27.5
2x (obs.)	32.4	42.0	46.1		43.5	37.4	27.9
calc. - obs.	0	0	+0.2	0	+0.4	+0.4	+0.4

Family Gaviidae *Gavia immer* Common Loon (Carnegie Museum)

$$L = 2a = 94.3 \quad y = a \sin \theta \quad 2x = 54.9 \cos \theta \quad (1 + .1257 \sin \theta - .0149 \sin^2 \theta)$$

2x (calc.)	39.4	50.4	54.8	54.9	51.4	44.4	32.6
2x (obs.)	39.1	50.6	55.0		51.1	44.2	32.9
calc. - obs.	+0.3	-0.2	-0.2	0	+0.3	+0.2	-0.3

Family Pelecanidae *Pelecanus erythrorhynchos* White Pelican (Carnegie Museum)

$$L = 2a = 86.3 \quad y = a \sin \theta \quad 2x = 56.0 \cos \theta \quad (1 + .0690 \sin \theta - .0747 \sin^2 \theta)$$

2x (calc.)	37.4	49.3	54.9	56.0	53.0	45.9	33.6
2x (obs.)	37.2	49.5	55.1		52.9	46.3	33.4
calc. - obs.	+0.2	-0.2	-0.2	0	+0.1	-0.4	+0.2

Family Anatidae *Branta canadensis* Canada Goose (Preston Collection)

$$L = 2a = 85.2 \quad y = a \sin \theta \quad 2x = 60.0 \cos \theta \quad (1 + .127 \sin \theta - .070 \sin^2 \theta)$$

2x (calc.)	41.9	54.3	59.7	60.0	56.0	47.7	34.3
2x (obs.)	42.0	54.3	59.5		56.0	47.6	34.4
calc. - obs.	-0.1	0	+0.2	0	0	+0.1	-0.1

Family Accipitridae *Aquila chrysaetos canadensis* Golden Eagle  
(Carnegie Museum)

$$L = 2a = 74.4 \quad y = a \sin \theta \quad 2x = 57.6 \cos \theta \quad (1 + .1115 \sin \theta - .0163 \sin^2 \theta)$$

2x (calc.)	40.9	52.5	57.3	57.6	54.2	46.9	34.6
2x (obs.)	41.0	52.2	57.3		53.7	46.6	34.9
calc. - obs.	-0.1	+0.3	0	0	+0.5	+0.3	-0.3

Family Pandionidae *Pandion haliaëtus carolinensis* Osprey  
(Carnegie Museum)

$$L = 2a = 62.1 \quad y = a \sin \theta \quad 2x = 43.6 \cos \theta \quad (1 + .1070 \sin \theta - .0207 \sin^2 \theta)$$

2x (calc.)	30.8	39.6	43.3	43.6	41.0	35.5	26.2
2x (obs.)	30.6	39.8	43.3		40.8	35.4	26.4
calc. - obs.	+0.2	-0.2	0	0	+0.2	+0.1	-0.2

TABLE 5

SECTION B (Continued)

Family Phasianidae		<i>Phasianus colchicus</i> Ring-necked Pheasant (Preston collection)						
$L = 2a = 44.0$	$y = a \sin \theta$	$2x = 33.3 \cos \theta (1 + .1050 \sin \theta - .041 \sin^2 \theta)$						
$k$	$\frac{3}{4}$	$\frac{1}{2}$	$\frac{1}{4}$	0	$-\frac{1}{4}$	$-\frac{1}{2}$	$-\frac{3}{4}$	
2x (calc.)	23.2	30.0	33.0	33.3	31.3	27.1	19.8	
2x (obs.)	23.2	30.0	33.0		31.1	27.2	19.8	
calc. - obs.	0	0	0	0	+0.2	-0.1	0	
Family Phasianidae		<i>Gallus gallus</i> Domestic Fowl (Preston Collection)						
$L = 2a = 51.8$	$y = a \sin \theta$	$2x = 40.5 \cos \theta (1 + .0797 \sin \theta - .0349 \sin^2 \theta)$						
2x (calc.)	27.9	36.2	39.9	40.5	38.3	33.4	24.7	
2x (obs.)	27.9	36.2	39.8		38.3	33.6	24.5	
calc. - obs.	0	0	+0.1	0	0	-0.2	+0.2	
Family Gruidae		<i>Grus canadensis</i> Sandhill Crane (Carnegie Museum)						
$L = 2a = 93.6$	$y = a \sin \theta$	$2x = 62.0 \cos \theta (1 + .1135 \sin \theta - .0296 \sin^2 \theta)$						
2x (calc.)	43.8	56.3	61.6	62.0	58.2	50.2	36.8	
2x (obs.)	43.8	56.3	61.7		58.3	50.0	37.0	
calc. - obs.	0	0	-0.1	0	-0.1	+0.2	-0.2	
Family Haematopodidae		<i>Haematopus palliatus</i> Oyster-catcher (Carnegie Museum)						
$L = 2a = 58.2$	$y = a \sin \theta$	$2x = 38.5 \cos \theta (1 + .1253 \sin \theta - .1750 \sin^2 \theta)$						
2x (calc.)	25.2	34.2	38.1	38.5	35.8	29.9	20.5	
2x (obs.)	25.4	34.0	38.0		35.7	29.8	20.6	
calc. - obs.	-0.2	+0.2	+0.1	0	+0.1	+0.1	-0.1	
Family Charadriidae		<i>Vanellus vanellus</i> Lapwing (Preston Collection)						
$L = 2a = 40.7$	$y = a \sin \theta$	$2x = 33.3 \cos \theta (1 + .252 \sin \theta - .161 \sin^2 \theta)$						
2x (calc.)	24.2	31.3	33.9	33.3	29.9	24.0	15.9	
2x (obs.)	24.2	31.3	33.9		30.0	23.8	16.0	
calc. - obs.	0	0	0	0	-0.1	+0.2	-0.1	
Family Laridae		<i>Larus fuscus</i> Lesser Black-backed Gull (Preston Collection)						
$L = 2a = 65.0$	$y = a \sin \theta$	$2x = 45.7 \cos \theta (1 + .163 \sin \theta - .068 \sin^2 \theta)$						
2x (calc.)	32.8	42.1	45.9	45.7	42.3	35.7	25.4	
2x (obs.)	32.6	42.3	45.8		42.1	35.3	25.7	
calc. - obs.	+0.2	-0.2	+0.1	0	+0.2	+0.4	-0.3	
Family Laridae		<i>Larus argentatus</i> Herring Gull (Preston Collection)						
$L = 2a = 72.0$	$y = a \sin \theta$	$2x = 45.0 \cos \theta (1 + .244 \sin \theta - .024 \sin^2 \theta)$						
2x (calc.)	34.8	43.5	46.2	45.0	40.8	34.0	23.9	
2x (obs.)	34.6	43.6	46.2		40.4	33.7	24.3	
calc. - obs.	+0.2	-0.1	0	0	+0.4	+0.3	-0.4	

TABLE 5

SECTION B (*Continued*)

Family Laridae <i>Larus canus</i> European Common Gull (Preston Collection)								
$L = 2a = 58.6 \quad y = a \sin \theta \quad 2x = 42.0 \cos \theta \quad (1 + .185 \sin \theta - .119 \sin^2 \theta)$								
$k$	$\frac{3}{4}$	$\frac{1}{2}$	$\frac{1}{4}$	0	$-\frac{1}{4}$	$-\frac{1}{2}$	$-\frac{3}{4}$	
2x (calc.)	29.8	38.7	42.2	42.0	38.5	31.9	22.1	
2x (obs.)	29.5	39.0	42.5		38.8	32.0	22.0	
calc. - obs.	+0.3	-0.3	-0.3	0	-0.3	-0.1	+0.1	
Family Laridae <i>Rissa tridactyla</i> Kittiwake (Carnegie Museum)								
$L = 2a = 56.1 \quad y = a \sin \theta \quad 2x = 42.2 \cos \theta \quad (1 + .1634 \sin \theta - .0881 \sin^2 \theta)$								
2x (calc.)	30.0	38.7	42.3	42.2	39.0	32.8	23.1	
2x (obs.)	29.9	38.9	42.5		38.9	32.8	23.3	
calc. - obs.	+0.1	-0.2	-0.3	0	+0.1	0	-0.2	
Family Corvidae <i>Corvus corone</i> European Carrion Crow (Preston Collection)								
$L = 2a = 41.7 \quad y = a \sin \theta \quad 2x = 28.9 \cos \theta \quad (1 + .177 \sin \theta - .085 \sin^2 \theta)$								
2x (calc.)	20.7	26.7	29.1	28.9	26.6	22.3	15.7	
2x (obs.)	20.5	27.0	29.2		26.5	22.5	15.6	
calc. - obs.	+0.2	-0.3	-0.1	0	+0.1	-0.2	+0.1	

TABLE 5

## SECTION C

Family Alcidae <i>Pinguinus impennis</i> Great Auk (Dresser, 1910, pl. 102, fig.1)								
$L = 2a = 115 \text{ mm.} \quad y = a \sin \theta \quad 2x = 66.1 \cos \theta \quad (1 + 0.320 \sin \theta - 0.074 \sin^2 \theta - 0.152 \sin^3 \theta + 0.159 \sin^4 \theta)$								
$k$	$\frac{3}{4}$	$\frac{1}{2}$	$\frac{1}{4}$	0	$-\frac{1}{4}$	$-\frac{1}{2}$	$-\frac{3}{4}$	
2x (calc.)	51.78	64.82	68.72	66.1	58.77	48.68	34.42	
2x (obs.)	51.8	64.8	68.6	66.2	58.8	48.6	34.4	
calc. - obs.	0.0	0.0	+0.1	-0.1	0.0	+0.1	0.0	

It will be obvious that in many cases the residual divergences between calculated and observed values are extremely small, well inside the experimental errors. In a few cases they fall just outside the strictly observational errors, and the reasons will usually be obvious on inspection. For instance, in the case of the Emu, since all residues are negative, we could get more perfect agreement by retaining the "c" values but increasing the  $k_0$  value (observed equatorial diameter) by 0.2 mm., which would give a more probable value of  $B$  (calculated equatorial diameter) and would increase all the other calculated diameters.

In the case of the Serriama, a reduction of  $k_0$  by 0.2 mm. would produce closer agreement, and there is some evidence that a tiny  $\sin^3$  term may be present, since the errors are not symmetrical about the equator.

TABLE 6  
VALUES OF *C*

<i>Bird</i>	<i>Standard Avian</i>		<i>Alcid</i>		
	<i>c</i> <sub>1</sub>	<i>c</i> <sub>2</sub>	<i>c</i> <sub>1</sub>	<i>c</i> <sub>2</sub>	<i>c</i> <sub>3</sub>
<i>A</i>					
Red-throated Loon	0.1520	0.0691	0.1966	0.0691	-0.1162
Common Murre	0.325	-0.0415	0.3747	-0.0415	-0.1291
Brünnich's Murre	0.3388	-0.0844	0.3824	-0.0844	-0.1136
<i>B</i>					
Emu	0.014	-0.0784	0.0222	-0.0784	-0.0213
Rhea	0.0312	-0.0886			
Tinamou	0.0061	-0.1400			
Cape Penguin	0.0640	-0.0029			
Seriama	0.1056	-0.0525			
Common Loon	0.1257	-0.0151			
White Pelican	0.0690	-0.0749			
Canada Goose	0.127	-0.0702			
Golden Eagle	0.1115	-0.0165			
Osprey	0.1070	-0.0209			
Ring-necked Pheasant	0.102	-0.0414			
Domestic Fowl	0.0797	-0.0351			
Sandhill Crane	0.1135	-0.0298			
Oyster-catcher	0.1253	-0.1752			
Lapwing	0.252	-0.1613			
Lesser Black-backed Gull	0.163	-0.0683	0.1835	-0.0683	-0.0524
Herring Gull	0.244	-0.0241	0.2718	-0.0241	-0.0729
European Common Gull	0.185	-0.1194	0.1928	-0.1194	-0.0204
Kittiwake	0.1634	-0.0883			
European Carrion Crow	0.177	-0.0853	0.1912	-0.0853	-0.0371
<i>C</i>					
Great Auk			0.3181	-0.0038	-0.1479

As previously mentioned, the "*c*" values are not fixed in a given species, or even in a given individual, but there are none the less certain general principles that may be noted. Most birds (species or individuals) have a negligible *c*<sub>3</sub> term and may be graduated as standard avians. The murre group have a very high *c*<sub>1</sub> and substantial *c*<sub>3</sub> term, but a very modest *c*<sub>2</sub>. Struthious birds vary greatly in elongation or ellipticity (*b/a* ratio), generally have the two ends of the eggs so nearly alike that it is hard to guess which is the big end (*c*<sub>1</sub> very small), but the *c*<sub>2</sub> term is quite large, reaching an exceptional value in the Tinamou. This is obvious on mere inspection of the eggs of the last species.

On the other hand, it is not so obvious on mere inspection of the eggs of the Lapwing (say) that the *c*<sub>2</sub> term is even higher than in the Tinamou, because the characteristic plover shape, with one end of the egg enormous compared with the other, due to a high *c*<sub>1</sub> term, somewhat thoroughly disguises the biconical element.

Murres, which also have one very big and one very small end to their eggs, do not have this excessive *c*<sub>2</sub> component.

Many birds have so low a *c*<sub>2</sub> value (less than 0.050) that they may be regarded as virtually "simple ovals." Such species are the domestic fowl, Ring-necked Pheasant, Golden Eagle, Osprey, and Sandhill Crane.

The queer shape of the egg of the Red-throated Loon is due to a substantial *positive* *c*<sub>2</sub> term. In all other species so far examined, if *c*<sub>2</sub> is not negligible, it is negative.

In table 6, there are sometimes indicated optional ways of graduating the observations, using either the Standard Avian or Alcid formula. The formula actually used for comparison purposes in table 5 is indicated in that table.

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*Summary.*—The meridian section or profile of eggs can be represented very easily and very accurately by an analytical expression. In the present paper we make use of a form of equation involving the "eccentric angle." In order of increasing complexity the forms described by this equation are the circle (sphere), ellipse (ellipsoid), simple oval, standard avian oval, and Alcoid oval. The appropriate equations are derived, and a method of estimating the "adjustable constants" or parameters by the use of "Least Squares" on a practical basis is worked out. A comparison of observed and calculated values is tabulated for a considerable variety of species. Biological implications are left for a later paper.

A sequel to this paper, dealing with the variation of the shape of eggs according to their position in the clutch sequence, by F. W. and E. J. Preston, will appear later this month in the *Annals of the Carnegie Museum*.

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