THE SHAPES OF BIRDS' EGGS:
MATHEMATICAL ASPECTS

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ABSTRACT.—In the *Handbook of North American birds* the description of egg sizes, and more particularly of egg shapes, proceeds on somewhat different lines from those of previous works. The present paper explains the methods of measuring and methods of "reducing" the observations. The elements actually measured are the conventional average length and breadth, plus the (unconventional) radii of the blunt and pointed ends. The standard deviations of each of these are estimated from the sample. From these measurements, all of which in effect are measurements of size, certain dimensionless quantities are derived hereinafter referred to as asymmetry, bicone, and elongation. These are specifications of shape independent of size. This paper sets forth the theory, modifies the theory to achieve maximum practical utility, and gives reasons for believing the results valid and adequate. In addition methods of sampling are discussed, and a new procedure of sampling is given for getting somewhat more representative results than heretofore.

THE only figures usually given for the size of an egg are its length and its maximum diameter, hereinafter called its breadth. The older texts, such as the *Catalog of eggs in the British Museum* (1901) or Seebohm (1896), give the extreme values that have been encountered for these figures in some survey or other, and this specifies the "range" of lengths or breadths within which the dimensions of another egg of the same species may reasonably be expected to fall. In the *Handbook of British Birds* (Witherby *et al.*, 1938), in Bent (1919), and in some other more recent texts the *average* value of length and breadth is given, together with the extreme values. Neither method is entirely satisfactory, for even if a hundred eggs were examined to obtain these extremes, it is obvious that if we examine another hundred, half the extremes may be exceeded. Still more recently, some authors have adopted the more useful procedure of giving the averages and the standard deviations rather than the average and the extreme values. Then, provided that the "sample" is drawn from a "normal" or "Gaussian" population of eggs—and Van Bree (1957) has shown that at least for the population he examined this assumption is sound—we can estimate the probability that an egg will depart by any given amount from the average.

There is one precaution that has not normally been observed. Measurements should be strictly independent and on unbiased samples. As it has been shown (Preston and Preston, 1953) that parentage has a significant effect on egg size, a valid sample, if it is to represent a species, should have equal numbers of eggs from each parent, and indeed it would be best to have as many *parents* represented as possible. In the case of a human population, for example, it would not be wise, in estimating the average

TABLE 1
Average Measurements of all Eggs in a series Compared with Those of a Single Egg from each Clutch

	Length (mm)	Breadth (mm)	$R_B{}^1$ (mm)	$R_P{}^2$ (mm)	E^3
Northern Red-shouldered Hawk, 73 eggs in 22 clutches (Carnegie Museum Collection)					
Average of 73 eggs	54.01	43.32	18.20	14.60	1.25
Average of 22 eggs, one per clutch	53.94	43.27	17.90	14.60	1.25
Spotted Sandpiper, 122 eggs in 31 clutches (Carnegie Museum Collection)					
Average of 122 eggs	32.08	23.76	10.84	5.45	
Average of 31 eggs, one per clutch	32.07	23.63	10.70	5.45	
Ring-billed Gull, 75 eggs in 25 clutches (from a single colony, at one time, in Lake Ontario)					
Average of 75 eggs	58.59	41.55	17.61	9.49	1.41
Average of 25 eggs, one per clutch	58.60	41.88	17.61	9.49	1.40
Eastern Kingbird, 51 eggs in 13 clutches (Carnegie Museum Collection)					
Average of 51 eggs	23.92	17.78	7.23	5.03	
Average of 13 eggs, one per clutch	23.86	17.64	7.07	4.81	
House Wren, 62 eggs in 11 clutches (Preston Collection)					
Average of 62 eggs	16.50	12.81	5.64	3.88	
Average of 11 eggs, one per clutch	16.42	12.82	5.71	3.85	

[1] Radius of curvature of blunt end.

[2] Radius of curvature of pointed end.

[3] Elongation (length/breadth).

height of the men of a tribe or of a town, to measure simply the heights of 10 brothers. This requirement is most easily met by using only one egg from a clutch. Some species lay only one egg, and the requirement is then automatically met, but others lay a dozen. We might get a false idea of the variability of eggs in such a species by measuring all the eggs of a few clutches, and certainly we could not effect any comparison of the variability of one species with another if one lays a dozen eggs and the other a single egg. Further, within a given species if one individual presents us with four eggs and another with eight, and we measure all the eggs, we have a sample that is biased in favor of the bigger clutch. After some experimentation we found that what is important is not the number of eggs measured, but the number of clutches or "sets," and if we use one egg, chosen by strictly random methods, from each of 20 clutches, the standard deviation will probably represent the species better.

The first point, that one egg per clutch is as good as the whole clutch, was established for several species, viz. Red-Shouldered Hawk (*Buteo lineatus lineatus*), Spotted Sandpiper (*Actitis macularia*), Ring-billed Gull (*Larus delawarensis*), Eastern Kingbird (*Tyrannus tyrannus*), and House Wren (*Troglodytes aedon*) as shown in Table 1. There is no reason to doubt that the same results would be obtained with other species.

THE SHAPES OF EGGS

In all the older texts that give only length and breadth, the shape of the egg remains indeterminate. Length and breadth are sufficient to specify with exactness the shape, as well as the size, of an ellipsoid, but eggs are not ellipsoids. Therefore a number of terms have been devised to describe the shape, such as "oval," "ovate," "subspherical," and so on. These are somewhat qualitative, but an attempt has been made in the *Handbook* to give them more precise meanings. Unfortunately while this terminology can take account, in a rough way, of the extent to which one end of the egg is bigger than the other, it does not take account of the extent to which both ends are more pointed or more blunt than would be expected. When the egg is fairly symmetrical from end to end, both ends may be conspicuously pointed as in the tinamous, or they may both be conspicuously blunt as in the hummingbirds. The first situation has resulted in the eggs being called "biconical." I am not clear that the other condition has been named, though it could be called "subcylindrical." However, the biconical condition may be present in eggs that are highly unsymmetrical or pyriform, and then it is generally overlooked by the casual observer, though its amount may be large.

It seemed desirable therefore to devise a method of measuring eggs, and a method of reducing the observations, that would give a quantitative measure of the amount of asymmetry and the amount of bicone. This was done by measuring not only the length and breadth of an egg, but also the curvatures of the two ends, and reducing the observations by the methods described later in this paper.

In practice the great majority of eggs tend to be somewhat more pointed than might be expected. This is the true "biconical" shape. The mathematical treatment results in this shape having a negative sign, and this is not inappropriate, as the egg then has less volume than if it had zero bicone: something has been subtracted. A few families, such as the hummingbirds and albatrosses, give "positive bicone;" that is, they have more volume than a zero value would give.

As a rule an egg has both asymmetry and bicone, and the values of these, plus the values for length and breadth, really define shape and size with virtual completeness. We have included one other figure, the ratio of length to breadth, and called it "elongation." Some eggs are notably elongated and others notably lacking in elongation.

Measurement.—The measuring of length and breadth presents no problem in principle. In the past calipers have been used. To get greater accuracy, so that the statistical treatment is justified, we have used dial indicators, and for small and frail eggs have tried to arrange for a minimum pressure to be exerted (Preston, 1957), but the principle is the same.

The other quantities we have measured are the curvatures of the two ends. This calls for a spherometer of some sort. The spherometers we have used have been described by Gemperle and Preston (1955).

Reduction of the measurements to shape specifiers.—By shape specifiers we mean asymmetry, bicone, and elongation. The last of these presents no problem, and has been dealt with above. The theory of the first two follows.

We have seen elsewhere (Preston, 1953) that any egg ought to be describable to any desired degree of precision by the "parametric" equation

$$Y = a \sin \theta$$

$$x = b \cos \theta \, (1 + c_1 \sin \theta + c_2 \sin^2 \theta + c_3 \sin^3 \theta + c_4 \sin^4 \theta + \ \ . \ .) \ (1)$$

where a is the half length (L/2), b is half the breadth at the "equator" or mid-point of the length, θ is the "eccentric angle," and c_1, c_2, c_3, etc. are constants peculiar to the individual egg. Note that b is *not* half the *maximum* breadth, though it may be, and usually is, very close to it. Unfortunately with the more extreme-shaped eggs, the difference is substantial, and this has been the deciding point in our treatment of the subject for the *Handbook*. For while it is easy to measure the maximum diameter, hereinafter called B, it is much less simple to measure b or 2b, the equatorial diameter.

The equation for x above is a "power" series, not a Fourier series, which also is capable of describing an egg completely, but the power series has the advantage that it "converges" rapidly in practice, or, more precisely expressed, the shape of an egg can be described with great accuracy by using only the first two or three terms.

The reason for this calls for care when we come to considering the curvatures of the ends. It is: $\sin \theta$ can range only from -1 to $+1$, corresponding to $\theta = -90°$ and $+90°$. Until we get close to the "poles," or ends of the egg, $\sin \theta$ must have a value less than 1. The higher powers of $\sin \theta$ are thus very small fractions indeed. But this is not true at the pole itself where (at the north pole) $\sin^n \theta = \sin \theta = 1$, no matter how large n may be.

Now if R_B is the radius of curvature of the blunt end and R_P that of the pointed end, it can be shown that

$$R_B = \frac{b^2}{a} \, (1 + c_1 + c_2 + c_3 + \ldots)^2$$

$$R_P = \frac{b^2}{a} \, (1 - c_1 + c_2 - c_3 + \ldots)^2$$

(2)

It follows that at the "poles" of the egg, the value of c_{15} (say) is just as important as c_1, while it is utterly unimportant for the shape of the egg all the way from the equator to the immediate neighborhood of the pole.

Taking the square roots of each side of equation (2) we have

$$\sqrt{R_B} = \frac{b}{\sqrt{a}} \cdot (1 + c_1 + c_2 + c_3 + \ldots)$$

(3)

$$\sqrt{R_P} = \frac{b}{\sqrt{a}} \cdot (1 - c_1 + c_2 - c_3 \ldots)$$

Subtracting the two equations gives

$$(\sqrt{R_B} - \sqrt{R_P}) \sqrt{a}/2b = (c_1 + c_3 + c_5 + c_7 + \ldots)$$ (4)

and adding them gives

$$(\sqrt{R_B} + \sqrt{R_P}) \sqrt{a}/2b = (1 + c_2 + c_4 + c_6 + \ldots)$$ (5)

These two equations may be more usefully written

$$c_1 + c_3 + c_5 + c_7 + \ldots = (\sqrt{R_B} - \sqrt{R_P}) \sqrt{a}/2b$$ (6)

$$c_2 + c_4 + c_6 + c_8 + \ldots = \{(\sqrt{R_B} + \sqrt{R_P}) \sqrt{a}/2b\} - 1$$ (7)

In other words, the sum of all the coefficients that contribute to the asymmetry is given by equation (6) while the sum of all the terms that contribute to the bicone is given by equation (7). We might therefore logically define the right hand side of these equations as the asymmetry and the bicone respectively. This would be, in principle, the right thing to do, because the odd and even subscripts of the "c"s are completely separated and there is no effect of bicone on asymmetry or vice versa.

PRACTICAL CONSIDERATIONS

With the special spherometer previously described we can measure R_B and R_P with very good accuracy. Nonetheless the result is not theoretically perfect because we do not measure a mathematical point at the poles, but a finite, though small, area around it. On a true sphere this would not matter, but on an egg the curvature is changing slightly even on a small area.

A more important point is the one we mentioned earlier, that it is not easy to measure 2b, the equatorial diameter. What we are given is the maximum diameter, B. The relation between B and 2b is discussed briefly in another paper (Preston and Preston, 1953), but it is not a simple one.

For those eggs where 2b is very nearly equal to B—and there are very many such eggs—we could write our equations in the form:

$$\text{Asymmetry} = (\sqrt{R_B} - \sqrt{R_P}) \frac{\sqrt{L}}{\sqrt{2}} \cdot \frac{1}{B}$$ (8)

$$\text{Bicone} = \{(\sqrt{R_B} + \sqrt{R_P}) \frac{\sqrt{L}}{\sqrt{2}} \cdot \frac{1}{B}\} - 1$$ (9)

However in view of the fact that with some eggs the approximation would be rather rough and confusion could result, we have decided not to

use these formulae at all, but to dispense with all the square roots and write, quite usefully though a little arbitrarily, for the purposes of the *Handbook*,

$$\text{Asymmetry} = (R_B - R_P) \cdot L/B^2 \tag{10}$$

$$\text{Bicone} = \{(R_B + R_P) \cdot L/B^2\} - 1 \tag{11}$$

The logic of this procedure may be seen thus:

If we were dealing with a true ellipsoid, the radius of curvature at each end would be given by

$$R = B^2/2L \tag{12}$$

In a real egg the average curvature of the two ends is given by

$$(R_B + R_P)/2 \tag{13}$$

The *ratio* of this average curvature of the two ends of a real egg to the curvature of the ellipsoid is therefore

$$(R_B + R_P) \cdot L/B^2 \tag{14}$$

If this ratio is equal to unity, we should say we have no bicone, because the egg is either a true ellipsoid (if $R_B = R_P$) or a "simple oval" produced by introducing asymmetry ($R_B \neq R_P$) without introducing bicone. We therefore define bicone as

Bicone $= \{(R_B + R_P) \cdot L/B^2\} - 1$, which is equation (11) above.

A similar argument shows the logic of the definition of asymmetry in equation (10).

If we use the derivation of the last few paragraphs, we do not depend at all on the theory of the parametric equation, but that theory does warn us that in eggs possessing both asymmetry and bicone, and substantial amounts of both, we may have some slight contamination of each by the other when using the simplified version, or equation, just given. In the present state of our knowledge this does not appear to be a matter of any consequence and, if our definition contains a slight element of arbitrariness, this would seem to be offset by the practical convenience of having definitions that involve only easily measured quantities and operating on these by the simplest and most logical means.

It should be emphasized, perhaps, that the new or practical definition does *not* produce figures for asymmetry and bicone that approximate to the figures given by the "ideal" formula. Both formulae agree in making both asymmetry and bicone zero for an ellipsoid, which is as it should be. It can be shown mathematically that when asymmetry or bicone or both are present, then the "practical" formulae (10) and (11) give numerical values that are roughly twice those obtained by the ideal formulae or their approximations (8) and (9). This is convenient, for it is better unless an approximation is a good one, to have no approximation at all; it might result in confusion in later work.

It may also be established experimentally, of course, that (10) and (11)

give figures about twice those of (8) and (9). Take the case of a tinamou egg (*Tinamus major zuliensis*, from Columbia) where we have a very high biconical term and a very modest asymmetry. The experimental or measured values are $L = 57.13$ $B = 46.90$ $R_B = 16.49$ $R_P = 15.26$, all dimensions in millimeters.

The practical formulae give   Bicone $= -0.17$ Asymmetry $= 0.032$
The ideal formulae give   Bicone $= -0.093$ Asymmetry $= 0.017$

This shows that the one method gives figures roughly twice that of the other.

In the *Handbook* the "practical" formulae are used throughout.

How Do We Get a "Representative" Sample?

This question is tied up with the question what should the statistics in the *Handbook* represent? For a species that breeds over a considerable area, we should probably prefer to collect eggs from all over that area. We might even like to adjust our sampling so that we sample densely where the population is heavy and lightly where the population is sparse. If the distribution is notably disjunct, we might like to sample the disjunct communities separately, but if not, we should like all the various disjunct groups to be represented. With inbreeding communities or gentes, as apparently exhibited by the clones of Canada Geese, the problem of what constitutes a representative sample becomes particularly difficult. With colonially nesting species, the rate of gene flow between colonies may be limited, and we might prefer to quote the properties of a "type locality" rather than mix together a number of localities.

But the properties of even a well-defined colony in a single locality are not constant; they vary from year to year. It has been established for a number of species that the size of the eggs varies with the age of the parent (for a summary of the evidence see Preston, 1958). But the age-composition of a given colony can fluctuate widely from time to time either by reason of direct human interference (Andersen, 1957) or the success, or lack of success, of recent breeding seasons (Richdale, 1957: 157). Thus a sample that is representative of a colony one year may be unrepresentative of some other years or of the secular average.

The possibility also exists that with some species second nestings may differ from first nestings and that renestings may differ from first nestings.

Manifestly eggs are simple things compared with birds. In particular they are rigid and their dimensions can be measured with more precision than the dimensions of a bird. The measurements should therefore lend themselves to statistical treatment with more certainty. But there are some offsetting factors. Indeed the basic question "what constitutes an egg?" seems to be subject to rather more uncertainty than "what constitutes a bird?".

The Romanoffs (1949, Chapter V, "Anomalies") figure a number of monstrosities that clearly cannot be used at all for measurements of the kind discussed in the present paper. Jacobs (1896) describes a number of freak eggs of wild birds, some or all of which we might likewise feel should be excluded. In domestic poultry we come across double-yolked eggs and yolkless eggs, and these also, for some purposes, should be excluded. In general we might decide that nonviable eggs should be excluded, but it is not always easy to decide whether or not an egg is viable.

Dixon (1937) has described a female Golden Eagle (*Aquila chrysaëtos canadensis*) that year after year laid eggs of outstanding size, and these never hatched; but could we ascertain this by mere inspection of the shells in a museum? Again some eggs are infertile and therefore not viable, but the shells do not seem to differ from fertile ones in size or shape and presumably should not be excluded. A fair proportion of museum specimens may represent infertile eggs.

The difficulty is not limited to eggs. A bird that has lived for some months is, by some definitions, viable, but I once had a Redhead Duck (*Aythya americana*) that lived many months, yet grew to only half the size of its fellow hatchlings. While it lived it was just as active as the others. Should the measurements of such a bird be included in statistical work?

It would seem that the only course is to exclude eggs (or birds) known to be pathological, to exclude with discretion eggs suspected of being pathological, and to include unusual eggs, so long as no very certain stigma attaches to them. The decisions will not always be right, but we may hope they will generally be so.

In one sense this discussion is at present moot. The eggs we must measure are those that happen to be available in museums. We have tried to use only clutches authenticated as to locality and identifiable on the original worksheets by museum and catalog number. The localities are indicated in the *Handbook* or in the summary sheets in the *Handbook* office at Albany, New York. Because Bent relied heavily on the National Museum in Washington, we have tried to avoid that collection as much as possible in order to have an independent appraisal. We have preferred, when we had the choice, to use clutches collected within the limits of North America as defined in the *Handbook*. This, of course, is not possible for all species. For some species or subspecies it is very difficult, and for a few impossible, to assemble 20 clutches from all the museums and private collections put together. As it seems now that all or nearly all the egg measurements for the *Handbook* have been made that can be made, this paper is offered to explain some of the problems encountered and how they were dealt with.

TABLE 2

CALIFORNIA MURRE EGGS FROM ALASKA

	Length (mm)	Breadth (mm)	$R_B{}^1$ (mm)	$R_P{}^2$ (mm)
All 66 eggs	83.70	51.11	21.05	9.61
First random group of 20 eggs	83.34	51.23	21.05	9.34
Second random group of 20 eggs	83.84	51.18	21.05	9.54
Third random group of 20 eggs	83.53	50.99	20.82	9.54

[1] Radius of curvature of blunt end.

[2] Radius of curvature of pointed end.

ADEQUATE SAMPLING

We still have to establish how many eggs constitute an adequate sample. This depends on how much confidence we wish to feel in our "means" or averages, and this is describable in terms of the "standard error of the mean." This figure is given for each species or subspecies in the original reports filed with the editor but will not be quoted in the Handbook, as it is simply the standard deviation (s) divided by $\sqrt{n}$ where n is the number of eggs in the sample and these two figures will be given in each case. For this purpose n should be the number of parents so that the measurements are independent and not partially correlated.

Now the standard deviation when expressed as a percentage of the means, i.e. as a "coefficient of variation," tends to be around 3 or 4 per cent for the classic measurements, that is for length and breadth. It is generally substantially more for the curvatures of the two ends.

We should like the standard error of the mean to be not much more than 0.5 per cent. This would call for 40 or 50 clutches of each species, and for only a relatively few species is it possible to assemble this number. If we have 10 clutches, the standard error of the mean will be around 1 per cent, often a little more. This seems a rather rough sort of measurement. We have compromised on an effort to get 20 clutches and to measure one egg from each of these clutches. This reduces the standard error of the mean to about 0.7 per cent for a great many species. This is not sufficient, in general, to decide whether two local populations are significantly different and similar questions, for which 60 or 100 clutches are desirable. It does represent a target to aim at and a systematic procedure.

In order that this conclusion might not be arrived at solely on a theoretical basis, we tested it on a series of 66 eggs (and therefore 66 clutches) of the California Murre (*Uria aalge californica*) in the collection of Sidney B. Peyton of Fillmore, California, to whom we are indebted for the loan of the eggs. They were obtained on Forrester Island, Alaska, in 1920. Undoubtedly they were not strictly a random sample, but chosen to illustrate the notoriously wide variations in color and pigmentation that prevail

among murre eggs. There is no reason to suppose they were chosen to show the variations in shape or size that occur, but there is naturally some reason to suspect, or at least to imagine, that if they exhibit great variations in color and pigmentation they are less likely to be uniform in size and shape than eggs of very similar color and pigmentation. Thus the test we are about to describe may be more severe than a strictly randomized sample would provide. We first measured all the eggs in detail. Then we picked three groups of 20 eggs, each a "random" group from the whole 66 (with replacement) and came up with the information of Table 2. Thus our proceedings appear to be justified by the results.

In the present paper we are concerned only with methods of describing the shapes of eggs in quantitative terms, in discussing the theoretical and practical aspects of such methods, and in justifying and explaining the particular procedures we adopted for the *Handbook*. We have indicated that for many species the biconical aspect of eggs is not properly to be ignored.

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