

THE VOLUME OF AN EGG

F. W. PRESTON

IN MEMORIAM, FRANCIS JOSEPH ASHBY, 1895-1972
with whom I collected my first birds' eggs June 8, 1906, in central
England, shared my first seafoal eggs from North Wales a little
later, and with whom I went birding and bird's-nesting for 60 years.

RECENTLY I have received several inquiries as to how one calculates the volume of an egg from its "dimensions," and by dimensions is meant the length and the maximum breadth. The answer is that it cannot be done with any real accuracy on the basis of only two measurements. I have shown (Preston 1969) that the "shape," i.e. the longitudinal contour, of an egg and its size can be described with a high order of accuracy by means of four parameters, length, breadth, asymmetry, and bicone, and that it cannot usually be described with less. The contour determines the volume, and hence volume cannot be estimated from two measurements only.

In cross section an egg is remarkably circular. It is therefore legitimate to consider an egg as a "surface of revolution," and this assumption is always made. An egg lies between two simple geometrical figures, a cylinder and a true bicone.

In Figure 1A, we show a cylinder of length L ($= 2b$) and diameter B ($= 2a$). Its volume is $(\pi/4) \cdot LB^2$ or $2\pi ba^2$.

An ellipsoidal egg of length L and diameter B would lie entirely inside the cylinder, touching the centers of both ends and making contact with the cylindrical surface on a circle.

In Figure 1B, we show a bicone. Its volume is $(\pi/12) \cdot LB^2$. Our egg would lie entirely outside the surfaces of the bicone, and, if symmetrical, it would pass through the apices of the two cones and would touch the bases of the cones all the way round.

If our egg is asymmetrical, it would touch the same points and places of the bicone in Figure 1C, whose volume is still $(\pi/12) \cdot LB^2$.

We may surmise therefore that in real eggs, which lie between Figures 1A and 1C, asymmetry (the extent to which one end is bigger or blunter than the other) makes little difference to volume, but bicone makes a great deal, the coefficient of LB^2 varying somewhat but lying between $(\pi/4)$ and $(\pi/12)$.

The preliminary assumption of the early writers is that the egg is, to a first approximation, an ellipsoid of revolution. If so, its volume would be $(\pi/6) \cdot LB^2$. The approximation is sometimes quite good, and taking $\pi = (22/7)$, the formula becomes

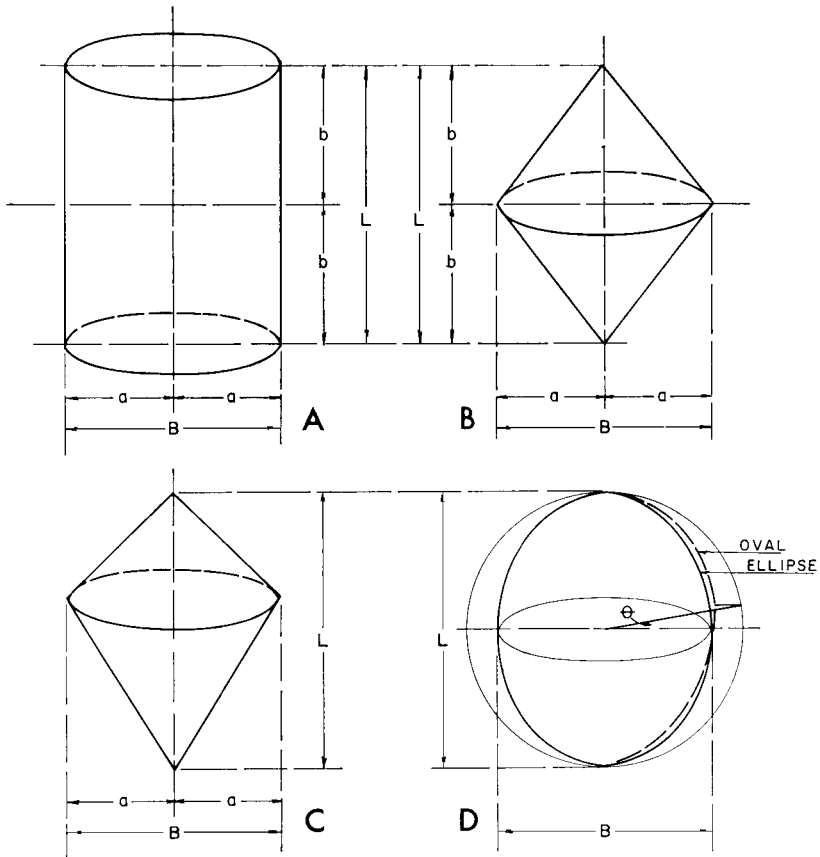


Figure 1. A, a cylinder of length $L (= 2b)$ and diameter $B (= 2a)$ may be regarded as circumscribing any egg, even a hummingbird's. B, a bicone (two cones base to base) will lie inside any egg, even a tinamou's, which will circumscribe it. C, the two cones do not need to be identical in height, though they must have the base in common. D, a circle circumscribes an ellipse, touching only at the ends or poles. The "eccentric angle" defines a parameter in terms of which the x and y coordinates of the ellipse, or of the oval, can be expressed.

$$V = \frac{11}{21} \cdot LB^2 \tag{1}$$

a formula used by some earlier writers.

However the approximation is sometimes not good. The hummingbirds (see figure in Preston 1969) lay blunt-ended eggs halfway between the ellipsoid and the cylinder, so the coefficient of LB^2 is much higher than $11/21$, while the grebes and tinamous lay eggs between the ellipsoid and

the bicone, i.e. they are pointed at both ends like an American or Rugby football, so the coefficient is less than $(\pi/6)$ ($= 11/21$). For a more detailed discussion of the inadequacies of various proposed formulae see Barth (1953).

The question therefore is, in the formula $V = kLB^2$, what is the appropriate value of k ? Obviously there is no one value that will fit all species. Indeed a single value will not fit all species of a single family, and in some clutches I have seen it will not fit all eggs of a single clutch.

Below I give a mathematical treatment in more detail.

As in Figure 1D, draw a circle circumscribing the egg, i.e. touching the two ends of the egg. From the center of the circle draw any radius of the circle, making an angle $(90^\circ - \theta)$ with the long axis of the egg, till it meets the periphery of the circle at a point P_1 (shown but not marked in Figure 1D). From P_1 draw a horizontal line to meet the oval or ellipse at point P_2 (again, shown but not marked in Figure 1D). Then the coordinates (x, y) of P_2 can be specified in terms of the angle θ , which is called the "eccentric angle," (see Preston 1953) and of the length and (equatorial) breadth of the egg.

DIGEST

The parametric equation of the longitudinal section of an egg may be taken (v. Figure 1D) as

$$\left. \begin{aligned} y &= b \sin \theta \\ x &= a \cos \theta (1 + c_1 \sin \theta + c_2 \sin^2 \theta + \text{etc.}) \end{aligned} \right\} \text{ (see Preston 1953)} \quad (2)$$

where θ is the "eccentric angle," a is the semidiameter at the true equator (i.e. halfway between the two ends of the egg), b is the half-length of the egg, c_1 and c_2 are coefficients that vary from egg to egg and have to be found experimentally, and the terms labelled "+ etc." can usually be neglected. c_1 and c_2 are usually quite small, so that c_1^2 , c_2^2 , and c_1c_2 can be neglected.

Slicing the egg parallel to the equator (perpendicular to the long axis of the egg) into small thicknesses dy , gives us various elements of volume

$$dV = \pi x^2 \cdot dy$$

and the total volume of the egg is

$$V = \int_{-b}^b \pi x^2 dy \quad (3)$$

Ignoring terms that include negligible coefficients, we have

$$x^2 = a^2 \cos^2 \theta (1 + 2c_1 \sin \theta + 2c_2 \sin^2 \theta)$$

and of course we have

$$dy = b \cos \theta \cdot d \theta$$

So

$$V = \pi a^2 b \int_{-\pi/2}^{\pi/2} \cos^3 \theta (1 + 2c_1 \sin \theta + 2c_2 \sin^2 \theta) d \theta \quad (4)$$

The complete integral from $-\pi/2$ to $+\pi/2$ of the middle term vanishes (being $-\cos^4 \theta$) and the integral reduces to

$$V = \pi a^2 b \int_{-\pi/2}^{\pi/2} (\cos^3 \theta + 2c_2 \cos^3 \theta \sin^2 \theta) d \theta \quad (4a)$$

and by writing $\cos^3 \theta = \cos \theta (1 - \sin^2 \theta)$, this integrates to

$$V = \frac{4\pi}{3} a^2 b \left(1 + \frac{2}{5} \cdot c_2 \right) \quad (5)$$

If the length of the egg is $L (= 2b)$ and its equatorial (not necessarily maximum) breadth is $B (= 2a)$ this equation takes the form

$$V = \frac{\pi}{6} \cdot LB^2 \left(1 + \frac{2}{5} c_2 \right) \quad (5a)$$

If c_2 is zero this reduces to $V = (\pi/6) \cdot LB^2$, the volume of an ellipsoid of revolution, and it does not depend on c_1 at all, provided we were justified in assuming c_1 is comparatively small and c_1^2 negligible. c_2 can be either positive or negative. With most species and individual parents, c_2 is negative, so the volume of the egg is less than the volume of the circumscribing ellipsoid. But with hummingbirds and some others it is positive, and the volume is then more than that of the ellipsoid.

EFFECT OF USING B_{\max} INSTEAD OF $B_{\text{equatorial}}$

$$\left. \begin{aligned} \text{in the parametric equation } y &= b \sin \theta \\ x &= a \cos \theta (1 + c_1 \sin \theta + c_2 \sin^2 \theta) \end{aligned} \right\}$$

the maximum value of x is obtained when dx/dy (*not* dy/dx) is zero, or, what is just as good, when $dx/d\theta = 0$.

Let θ_m be the value of θ that makes x a maximum. If $c_1 = c_2 = 0$, the equation of an ellipse, we get

$$\frac{dx}{d\theta} = -a \sin \theta, \text{ and this is zero when } \theta = 0: \quad (6)$$

and this is a correct solution.

Now let $c_2 = 0$ but let c_1 be non-zero. Then, remembering that $\sin \theta_m$ is assumed small and therefore that $\cos \theta_m$ is very near unity, we get

$$\sin \theta_m = \frac{-1 + \sqrt{1 + 4c_1^2}}{2c_1} \quad (7)$$

Remembering that c_1 is much less than unity, the square root term is very nearly $(1 + 2c_1^2)$, so that

$$\sin \theta_m = c_1 \text{ very nearly.} \quad (7a)$$

If c_1 and c_2 are both non-zero, but $\cos \theta_m$ is very near unity ($\sin \theta_m$ being small), we get a cubic equation for $\sin \theta$ as follows:

$$c_2 \sin^3 \theta_m + c_1 \sin^2 \theta_m + (1 - 2c_2) \sin \theta_m - c_1 = 0 \quad (8)$$

This can be solved exactly, but if $\sin \theta_m$ is small (it is often less than 0.1), we can neglect the term in $\sin^3 \theta_m$ and get a simple quadratic, whose solution is

$$\sin \theta_m = \frac{-(1 - 2c_2) + \sqrt{(1 - 2c_2)^2 + 4c_1^2}}{2c_1} \quad (8a)$$

We may note that when c_1 and c_2 are small (and c_1 tends to average about 0.1 and c_2 about -0.1)

$$\sin \theta_m \text{ tends to be about } c_1, \text{ independently of the value of } c_2. \quad (9)$$

This locates the *position* of the maximum diameter. The *value* of that diameter is

$$\begin{aligned} B_{\max} &= 2x_{\max} = 2a \cos \theta_m (1 + c_1 \sin \theta_m + c_2 \sin^2 \theta_m) \\ &= 2a \cdot \sqrt{1 - c_1^2} \cdot (1 + c_1^2 + c_2 c_1^2) \end{aligned}$$

or

$$\frac{B_{\max}}{B} = \left(1 - \frac{c_1^2}{2}\right) (1 + c_1^2)$$

ignoring $c_2 c_1^2$ as very small, and so, remembering our previous comment on the square root term,

$$\frac{B_{\max}}{B} = 1 + \frac{c_1^2}{2} \quad (10)$$

For instance if $c_1 = 0.1$, B_{\max} exceeds B by about one-half of one per cent.

ERRORS IN ESTIMATING VOLUME FROM THE TWO DIMENSIONS, L and B_{\max}

If an experimenter measures the length and maximum diameter of an egg and calculates its volume by the ellipsoidal formula as

$$V = \frac{\pi}{6} \cdot LB_{\max}^2$$

he will overestimate the volume in the ratio $(B_{\max}/B)^2$, that is (from equation 10) in the ratio

$$\left(1 + \frac{c_1^2}{2}\right)^2 \text{ or } 1 + c_1^2 \text{ approximately} \quad (11)$$

and if $c_1 = 0.1$, the error is 1%, while if $c_1 = 0.2$ (a value it reaches in only a few families) the error will be 4%.

But this is not the most serious error.

A more important error is that due to the bicone term. Since this is usually negative, it will again produce an overestimate, of value $(2/5)c_2$. Thus if $c_2 = 0.1$, the overestimate is 4%. In the case of the Oystercatcher of Preston 1953 the error would be 7%. In the case of the hummingbird or albatross of Preston 1969 (p. 259), the error would be a very substantial underestimate.

Worth (1940) considers that it is close enough to assume, for any egg, that its volume is 15% less than that given by the ellipsoidal formula, and this I cannot concede.

It is no use trying to refine the estimate of the volume of an egg by modifying arbitrarily the coefficient k in the expression

$$V = k LB^2_{\max}$$

from its ellipsoidal value of $\pi/6$. Errors of 5% or more can readily occur. They arise from assuming that the shape of an egg is simpler than it really is. There are not enough data or parameters in the equation.

THE INTERNAL AND EXTERNAL VOLUMES OF AN EGG

Some writers are concerned with the overall (or external) volume of an egg (i.e. including the shell) and some are concerned more with the internal volume, excluding the shell.

Stonehouse (1966) is concerned with the total, external, volume, and with how far it departs from the ellipsoidal volume $V = 0.524 LB^2$. For a number of seabirds' eggs he found an average of $V = 0.51 LB^2$, and just about the same for the Australian Black Swan, *Cygnus atratus*. This is about 3% less than the ellipsoidal value, and is due chiefly to the "negative bicone," the eggs being "somewhat more pointed at the ends" than a true ellipsoid. Even in a single species, the swan, the degree of pointedness varied and the deficiency of volume of course varied with it.

Coulson (1963) was interested in estimating the internal volume from the external measurements, and concluded that the internal volume averaged about $0.487 LB^2$, which is about 9.3% less than the (external) ellipsoidal formula would give. If we assume that the bicone accounts for about 3%, there remains about 6% that must be due to the shell thickness.

It is easily shown that if the egg shell thickness is t and the average external diameter of the egg is d , where $d = \sqrt[3]{LB^2}$, then the internal volume falls short of the external volume by approximately $600 t/d$ percent.

I measured one egg of the *Gallus gallus*, the domestic fowl, and found d to be about 1.9" (= 48 mm) and the shell thickness average about 0.015" (= 0.38 mm) so that $600 t/d$ is about 4.7%.

I also measured one egg of *Numida meleagris*, the crowned or helmeted guinea fowl, a species whose eggs are notoriously thick-shelled. This was a domestic specimen, the egg apparently a trifle less in breadth, though not in length, than the average wild egg in South Africa. I found d to be about 1.62" (41 mm) and t averaged about 0.022" (0.56 mm), so $600 t/d = 8.2\%$.

Coulson's Kittiwake eggs were therefore intermediate, in relative shell thickness, between *Gallus* and *Numida*.

Coulson was interested in estimating the age composition of a colony of gulls by noting that older birds tended to lay bigger, that is more voluminous eggs, but I think he could have used the breadth as effectively as the volume.

Worth (1940) was interested in the problem as to whether one could estimate the length of the incubation period if given the volume of the egg. Lack (1968) discussed this point and concluded that the correlation is poor, and this agrees with my own, less extensive, computations.

ACKNOWLEDGMENTS

I am indebted to A. Robert Shott for a preliminary check on the algebra, and in particular for checking by actual solution of the equations that, assuming $c_1 = 0.1$ and $c_2 = -0.1$, the cubic equation (8) and the quadratic (8a) give virtually identical answers. I am indebted also to J. L. Glathart for looking over the paper. I did not ask either of them to check every detail. I am also in the debt of Lloyd F. Kiff and Charles H. Blake for several comments and suggestions.

LITERATURE CITED

- BARTH, E. K. 1953. Calculation of egg volume based on loss of weight during incubation. Auk 70: 151-159.
- COULSON, J. C. 1963. Egg size and shape in the Kittiwake (*Rissa tridactyla*) and their use in estimating age composition of populations. Proc. Zool. Soc. London 140: 211-227
- LACK, D. 1968. Ecological adaptations for breeding in birds. London, Methuen & Co., Ltd.
- PRESTON, F. W. 1953. The shapes of birds' eggs. Auk 70: 160-182.
- PRESTON, F. W. 1969. Shapes of birds' eggs: extant North American families. Auk 86: 246-264.
- STONEHOUSE, B. 1966. Egg volumes from linear dimensions. Emu 65: 227-228.
- WORTH, C. B. 1940. Egg volumes and incubation periods. Auk 57: 44-60.

Box 49, Meridian Station, Butler, Pennsylvania 16001. Accepted 15 May 1973.