The stomach contained three lepidopteran larvae 2 cm long.

I am very grateful to Elsie and Walter Fiala and to Andrew Williams for their assistance in the field and permission to include their records here. C. Collins, T. Howell, F. G. Stiles, and, especially, E. Eisenmann examined various specimens and offered helpful comments. My field work and that of the Fialas and Williams was supported by the Western Foundation of Vertebrate Zoology.

LITERATURE CITED

ARNOLD, K. A. 1966. Distributional notes on Costa Rica birds. Wilson Bull. 78:316–317.

COLLINS, C. T. 1968. Distributional notes on some Neotropical swifts. Bull. Brit. Ornithol. Club 88: 133–134.

EISENMANN, E. 1955. The species of Middle American birds. Trans. Linnean Soc. of N.Y. Vol. 7.

EISENMANN, E. 1971. Range expansion and population increase in North and Middle America of the White-tailed Kite (*Elanus leucurus*). Amer. Birds 25:529–536.

ORIANS, G. H., AND D. R. PAULSON. 1969. Notes on Costa Rican birds. Condor 71:426–431.

RIDGWAY, R. 1911. The birds of North and Middle America. Bull. U.S. Natl. Mus. No. 50, 859 p.

RUSSELL, S. M. 1964. A distributional study of the birds of British Honduras. A.O.U. Monogr. No. 1, 195 p.

SLUD, P. 1964. The birds of Costa Rica. Distribution and ecology. Bull. Amer. Mus. Nat. Hist. 128:1–430.

WETMORE, A. 1968. The birds of the Republic of Panamá. Pt. 2. Smithsonian Misc. Coll. 150 (2).

WOLF, L. L. 1966. Notes on Costa Rican birds. Condor 68:400–401.

Accepted for publication 12 November 1973.

THE SURFACE AREA OF AN EGG

A. R. SHOTT

AND

F. W. PRESTON

Meridian Research Center
Box 49, Meridian Station
Butler, Pennsylvania 16001

IN MEMORIAM
(1897–1964)

Air Vice-Marshall D. V. Carnegie, C.B.E., birds' nester extraordinary and a life-long friend of one of us, Chief of the Coastal Command (Scotland), and Chief of the New Zealand Air Force, who learned camouflage from the birds and insects and taught the British how to disguise their airfields in the Battle of Britain.

The surface area of an egg is occasionally desired or needed for computations of shell permeability or probable period of incubation. It is not easily measured directly, and cannot be computed from measurements of length and (maximum) breadth without possible errors of several percent. This could be done if an egg were a true ellipsoid, i.e., a prolate spheroid, to which it is a rough, and sometimes a close, approximation. An indirect method is to measure the volume of the egg, for instance, by total immersion in water or other liquid of known density, and hence to estimate the surface area since there is a relation between area and volume. This can usually come within 1 or 2%. A still more indirect method is to weigh the egg, assume a density for it, and hence estimate the volume, and from the volume estimate the area.

This paper considers these indirect methods and their probable accuracy.

If we have a number of solids of identical shape but of different sizes, there is necessarily a relation between surface area (A) and volume (V) of the form

$$A = kV^{2/3} \qquad (1)$$

where k is a "dimensionless" constant for the series. For a different series (i.e., for a different shape), we shall have a different constant. Thus for cubes $k = 6$: for spheres $K = \sqrt[3]{36\pi} = 4.836$.

Many eggs approximate to prolate spheroids, that is, ellipsoids generated by rotating an ellipse around its major axis. Let the length of the major axis be $2a$, and of the minor be $2b$, and let the ratio b/a be called p. Then p is the reciprocal of what Preston has elsewhere called the "elongation" (e.g., Auk 86:246, 1969).

The volume V of such an ellipsoid is given by

$$V = 4\pi/3 \cdot b^2 a = 4\pi/3 \cdot p^2 a^3 \qquad (2)$$

so that

$$V^{2/3} = 2.598\ p^{4/3} \cdot a^2 \qquad (2a)$$

The surface area (A) of a prolate spheroid is

$$A = 2\pi\ b^2 + (2\pi\ a\ b \cdot \sin^{-1} \epsilon)/\epsilon \qquad (3)$$

where $\epsilon = c/a$, c being half the distance between the two foci of the ellipse, so

$$\epsilon = \sqrt{1 - b^2/a^2} = \sqrt{1 - p^2}$$

while $\sin^{-1} \epsilon$ is the number of radians in an angle whose sine is ϵ.

The surface area of the spheroid is then

$$A_e = 2\pi\ a^2\ (p^2 + p/\epsilon \cdot \sin^{-1} \epsilon)$$
$$= 2\pi\ a^2\ \{p^2 + (p/\sqrt{1-p^2}) \cdot \sin^{-1} \sqrt{1-p^2}\} \qquad (4)$$

The surface area of the circumscribed sphere, A_s, $= 4\pi\ a^2$ so that the ratio

$$A_e/A_s = 1/2\ \{p^2 + (p/\sqrt{1-p^2}) \cdot \sin^{-1} \sqrt{1-p^2}\} \qquad (5)$$

and we can plot this for various values of p, i.e., of b/a, and see how the area contracts as the minor axis contracts.

We are here, however, more concerned with the constant k in equation (1) above, where $k = A_e/V^{2/3}$, and this is given by

$$k = 2\pi/2.598 \cdot 1/p^{4/3} \cdot (p^2 + p/\sqrt{1 - p^2} \cdot \sin^{-1} \sqrt{1-p^2}.) \qquad (6)$$

We may note in passing that when p is nearly unity, $(\sin^{-1} \sqrt{1 - p^2})/\sqrt{1 - p^2}$ is unity, though both numerator and denominator are zero, and the expression is superficially ambiguous or "indeterminate." Then $k = 4\pi/2.598 = 4.836$, the correct value for a sphere.

No avian egg, however, is spherical. The elongations a/b have a range from about 1.19 to about 1.64 (Preston, op. cit.), so that p ranges from about 0.61 to 0.84, with a pronounced concentration in the approximate range 0.7 to 0.75.

Substituting numerical values for k in equation (6), we get

$$\left.\begin{array}{l} \text{For } p = 0.6,\ k = 5.04 \\ \text{''}\quad p = 0.7,\ k = 4.95 \\ \text{''}\quad p = 0.8,\ k = 4.85, \text{ while for} \\ \quad p = 1.0 \text{ (a sphere)},\ k = 4.836, \\ \qquad \text{as we have seen.} \end{array}\right\} \quad (7)$$

Thus for most eggs, for which p is near 0.7, k should be about 4.95, and as expression (7) shows, k varies only slowly with p.

It is therefore a fair guess that though eggs are, many of them, not ellipsoids but ovoids, with some asymmetry and some bicone, the ratio k will remain within 2 or 3% of its value for a sphere. Since a sphere has the least possible surface area per unit volume of any solid, an egg must have a slightly higher value, roughly 4.95 vs. 4.836, as mentioned above.

Since such a great change of shape as that from a sphere to an ellipsoid whose length is 1.67 times its breadth produces so little change in the k value, we may surmise that bicone and asymmetry will produce very little change, too, since they are, so to speak, minor perturbations of the basically ellipsoidal shape; and though bicone, for instance, can raise or lower the volume by several percent, the change in surface area changes in the same direction, so that the ratio changes very little.

It follows that if we measure the volume of an egg, we generally can assess its surface area thereby to within $\pm 1\%$, and this is much easier than trying to measure the surface area directly. Further, since the density of most fresh eggs is 1.00 within about 2%, a measurement of weight gives the volume and therefore the surface area. This estimate is close enough for many purposes.

Let us make a rough calculation for a hummingbird's egg which departs strikingly from the ellipsoidal form.

If we cut a sphere of diameter D $(= 2r)$ into two hemispheres, move them apart, and insert a cylinder of diameter D and length l between them, we have a sausage of idealized shape, of overall length $D + l$. Its elongation is $(D + l)/D = 1 + l/D = 1 + l/2r$. If the length l is nr, the overall length is $(2 + n)r$ and the elongation is $(1 + n/2)$.

If n is small, of the order 1.5 (say), we have a shape that closely approximates some hummingbird eggs. See, for instance, the enlarged photograph of an egg of *Stellula calliope* (Preston, op. cit., fig. 6). In figure 1 herewith, the broken line is an enlarged tracing of that photograph, while the solid line is the cartouche or sausage shape that caricatures the photograph. We think it will be obvious that the two figures, in their three-dimensional form, will have nearly the same volume and nearly the same surface area.

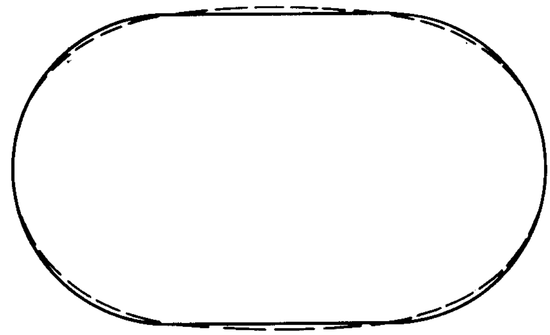

FIGURE 1. The shape of a Hummingbird's (*Stellula calliope*) egg, broken line, and a short sausage, consisting of two hemispheres joined by a cylinder as a "caricature." Actually the real egg fits the two hemispheres slightly closer than in the figure; the difference has been deliberately exaggerated or it might scarcely be perceptible on this scale.

The volume (V) of our sausage is $\pi r^2\,(4r/3 + l)$ and its surface area (A) is $2\pi\, r(2r + l)$. We are interested in the ratio R defined as $A/V^{2/3}$.

This is

$$R = (2)\cdot(3^{2/3})\ \pi^{1/3}\ (2 + n)/(4 + 3n)^{2/3} \quad (8)$$

or

$$R = 6.092\ (2 + n)/(4 + 3n)^{2/3}. \quad (8a)$$

$$(\text{For a sphere, } n = 0, \text{ and } R = 4.836.) \quad (9)$$

For $n = 1.47$, the egg we have chosen to caricature, $R = 5.11$ (10)

which is about 3% greater than the typical value of 4.95 for ellipsoidal eggs.

Referring to the figure once more, it is clear that the surface area of the real egg is not much more than we have computed, while the volume is slightly greater than the caricature's, so the error is probably somewhat less than 3%.

These hummingbird eggs have a quite exceptional positive bicone, and if any eggs at all should be expected to produce a ratio R far from 4.95, these should be they. We think we may be satisfied that most eggs will have $R = 4.95$ within about 1%.

This note is intended simply as an aid to those who are working on the shapes and behavior of eggs. It is concerned solely with the geometrical properties of certain three-dimensional surfaces and is not itself concerned with the structure, strength, permeability, incubation properties or periods, or any physiological or even physical matters, though we hope it may be useful to those workers who are so concerned.

Accepted for publication 14 September 1973.