THE EFFECT OF SHAPE ON THE SURFACE-VOLUME RELATIONSHIPS OF BIRDS' EGGS

DONALD F. HOYT

Ornithologists have rarely succeeded in demonstrating any functional significance of the differences in the shapes of birds' eggs. Presumably, egg shape is the result of natural selection. If so, differences in shape must reflect adaptations to different environmental conditions, and an understanding of the selective advantages of different egg shapes would provide some broader insights into avian biology.

Surface-volume relationships are of widespread functional significance in biological systems, and one might intuitively expect that shape would affect the surface-volume relationships of birds eggs. Besch et al. (1968) summarized the literature on the estimation of egg surface area and presented the details of an accurate new method for its measurement. Utilizing a semi-automated version of this method, Paganelli et al. (1974) conducted a comparative study of the surface areas and volumes of the eggs of 29 species of birds. The relationship between surface area and volume which they reported was:

$$\text{Surface Area} = 4.951 \text{ Volume}^{.666} \quad (r = .99997) \tag{1}$$

As a check of the accuracy of equation (1), they compared the surface areas predicted with it for four eggs of divergent shapes with the surface areas they had measured. They found a maximum error of less than three percent; and this, as well as the extremely high correlation coefficient, certainly indicates that shape does not have a profound effect on the surface-volume relationship. However, since the comparison made on these four eggs was their only check of the effect of shape, we cannot exclude the possibility that some systematic relationship does exist.

A method of quantifying and comparing egg shapes is necessary for a systematic study of its effect on the surface-volume relationship. Preston (1953) described a method for defining the shape of eggs mathematically. He later derived three dimensionless shape "specifiers" and published the values of these specifiers for the eggs of 63 families of North American birds (Preston 1968, 1969). In the present study, I have systematically investigated the effect of shape on the surface-volume relationship of birds' eggs. Having discovered a systematic effect of shape, I have improved the accuracy with which egg surface area can be predicted from simple measurements. Additionally, I have developed a simple and accurate device for measuring volume.

THEORY

VOLUME AND SURFACE AREA

Assuming that the shape of an egg can be represented by the surface of revolution generated by revolving a curve about the egg's axis of symmetry, its volume and surface area can be determined from standard equations of calculus. If the curve is represented by the function $y = f(x)$, the equation for volume is:

$$\text{Volume} = \pi \int y^2 \, dx \tag{2}$$

The equation for the area of a surface of revolution can be solved only in special cases. If the function, $f(x)$, is known, a close approximation can be made by using a computer to simulate the integration by solving the equation:

$$\text{Surface Area} = \Sigma \, 2 \, \pi \, f(x) \cdot (1 + (f'(x))^2)^{1/2} \, \triangle X \tag{3}$$

The error involved in the approximation is small if $\triangle x$ is small.

SURFACE-VOLUME INDEX

The equation specifying the surface area of an object in terms of its volume has the form:

$$\text{Surface Area} = K \cdot \text{Volume}^{2/3} \tag{4}$$

This can be rearranged so that the constant is specified in terms of the surface area and volume:

$$K = \text{Surface Area}/\text{Volume}^{2/3} \tag{5}$$

The constant, K, expresses the relative amounts of surface area and volume and, being dimensionless, allows the direct comparison of objects of different sizes. For the purposes of this study, the constant defined by equation (5) will be called the Surface-Volume Index (symbolized by K_i).

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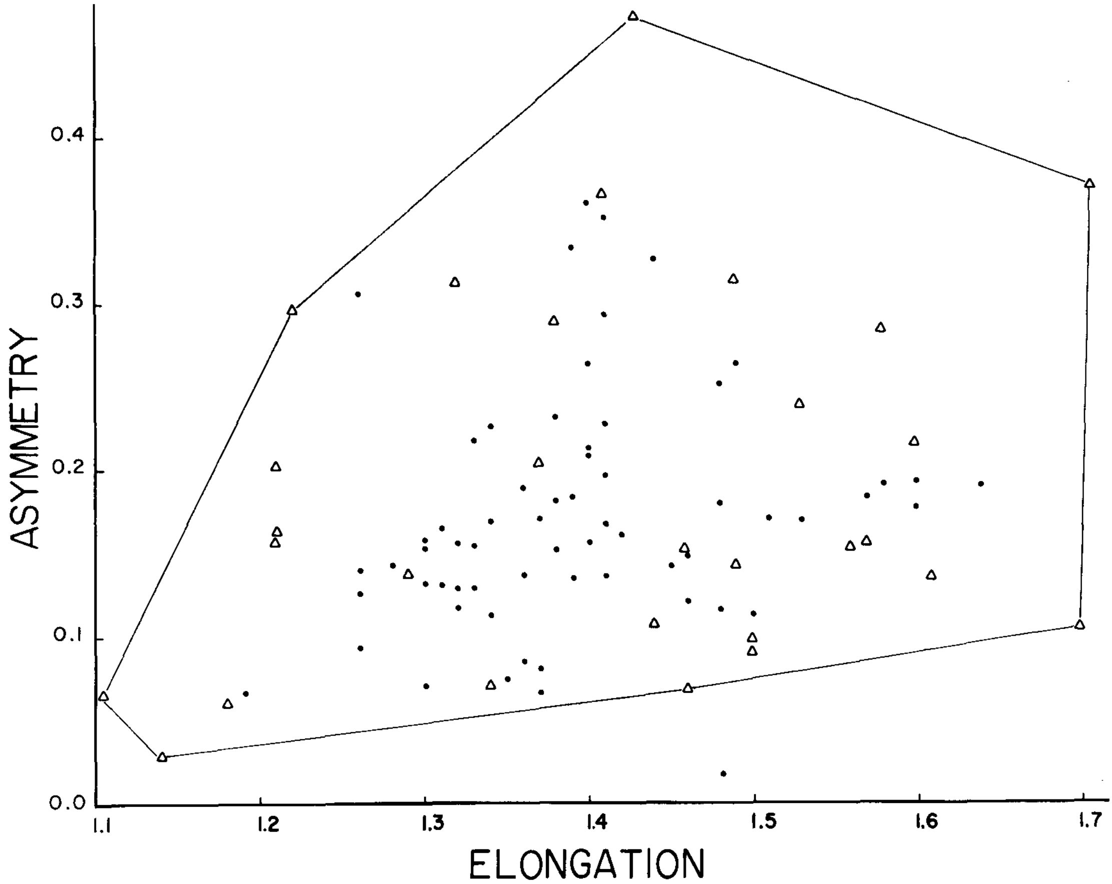

FIGURE 1. A scatter diagram showing the means (solid circles) for 63 families of North American birds (from Preston 1969) and the values measured from the eggs used in the present study (triangles). 98% of the family means are enclosed within the polygon connecting the outlying values for the eggs in the present study.

EGG SHAPE SPECIFIERS

Preston (1968) defined three dimensionless egg shape specifiers in terms of the length (L), breadth (B), the radius of curvature of the broader end (R_B), and of the more pointed end (R_P). The shape specifiers are:

$$\text{Elongation} = L/B \quad (6)$$

$$\text{Asymmetry} = (R_B - R_P) \cdot (L/B^2) \quad (7)$$

$$\text{Bicone} = [(R_B + R_P) \cdot (L/B^2)] - 1 \quad (8)$$

Elongation is self-explanatory. Asymmetry specifies the extent to which one end is more pointed than the other, and Bicone specifies the extent to which the average curvature of the two ends deviates from the curvature of an elipsoid with major axis equal to L/2 and minor axis equal to B/2.

METHODS

EGGS

The eggs used in this study were provided by the Western Foundation of Vertebrate Zoology. With the aid of Preston's (1969) values of the egg shape specifiers for the families of North American birds, I attempted to select a group of eggs which exhibited the fullest possible diversity of egg shapes (figure 1).

STATISTICS

Regressions were calculated by the method of least squares. Because the existence of measuring bias is of primary interest in this study, all errors are presented as mean percents, plus or minus a 95% confidence interval. A test was considered significant if $P < 0.05$.

MEASUREMENT OF VOLUME BY WATER DISPLACEMENT

Egg volume was measured in a series of specially-adapted plastic beakers in which the water level was automatically regulated by a glass spout (figure 2). When the water level in the beaker was raised above the regulated level, water drained from the spout until the water in the beaker returned to the regulated level. The blown eggs were filled with water and sealed with a one-centimeter square piece of plastic tape so that they would sink when placed in the beaker. The volume of an egg was then determined by weighing the water (to the nearest

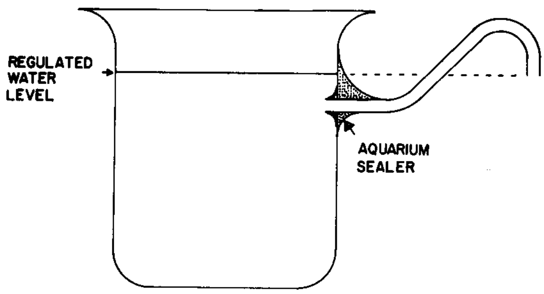

FIGURE 2. Diagram of the type of beaker used for the determination of egg volume. The glass spout was sealed in place with aquarium sealer.

0.01 gm) which drained from the spout when the egg was placed in the beaker. Because the precision of the volume determination was a function of the cross-sectional area of the beaker, five different-sized beakers were used; and each egg was measured in the smallest possible beaker. For the smallest eggs, I improved the precision by substituting isopropyl alcohol for the water because its lower surface tension reduced the size of drops falling from the spout. The volumes reported are the means of four replicate measurements. Fluid densities were corrected for temperature.

I checked the accuracy of this method by measuring the volumes of pieces of machined aluminum rod in the beakers. The actual volumes of the rods were determined by measuring their length and diameter with calipers, and they were checked against the volumes predicted by weight and density. The volumes of the rods determined by these two methods differed by less than 0.05%. All five beakers yielded volumes which were reproducible within one percent, and none of them had a systematic error.

COMPUTER MEASUREMENT OF SURFACE AREA AND VOLUME

The function, f(x), used to determine the surface area and volume with equations (2) and (3) was a third order polynomial fitted to a series of points defining the profile of half of the egg. These points were measured as radii from the axis of symmetry on a high contrast enlargement from a 35mm negative. At least 25 radii, recorded to the nearest 0.2mm, were measured on each egg, using a piece of semi-transparent graph paper (Keuffel & Esser #46–1513) symmetrically placed over the image of the egg. The distance between successive radii was smallest near the ends of the egg, but never exceeded one centimeter.

The accuracy of this method, obviously, depends on the accuracy with which the polynomial fits the points. Since the entire half-profile of most eggs cannot be accurately approximated by a third-order polynomial, the egg was divided into nine segments along its length; and a different polynomial was fitted to each segment. The fit achieved in this way was exceptionally good, the line appearing to pass through every point and having a very smooth curvature between the points. This meant that the portion of the egg profile between the points did not have to be approximated by a straight line, as was the case with the method of Besch et al. (1968). Once f(x) was determined for each segment, equations (2) and (3) were solved; and the surface

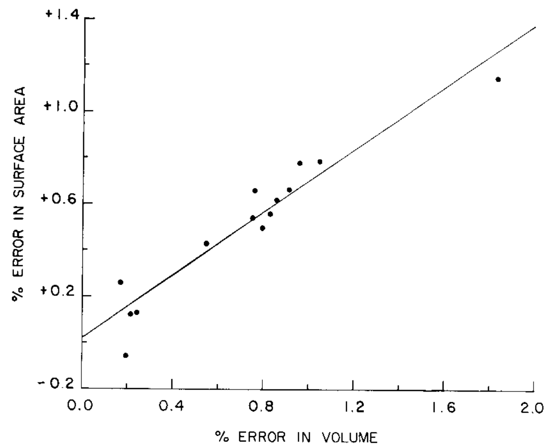

FIGURE 3. A regression of the percent error in surface area on the percent error in volume for the "Geometric Eggs."

areas and volumes of the segments were summed. Finally, I corrected these values for the enlargement of the photograph by a scaling factor determined by measuring the length and breadth of the eggs and comparing these measurements with those taken from the photographs.

ACCURACY OF SURFACE AREA MEASUREMENTS

The accuracy of the method was checked by comparing predicted and known surface areas and volumes of fourteen figures representing extreme egg shapes. Drawings, composed of sections of circles and frustra of right cones tangent to the circles, were treated in the same way as the egg photographs. The only data required to calculate the surface area and volume of one of these "geometric eggs" were the distances between the centers of the circle and their radii. (For full details, see Appendix I.) The mean difference between the predicted and known volumes and surface areas were: +.72% ± 0.26 and +.51% ± 0.18. This indicated that there was a small but statistically significant bias in the method which should be corrected. The relation between percent error in surface area (E_{Surf}) and the percent error in volume (E_{Vol}) (figure 3) is:

$$E_{Surf} = 0.2 + 0.68\ E_{Vol} \quad (9)$$

($r = 0.955$; Standard error of the estimate is 0.098)

This relationship was used to correct the surface areas predicted by the computer for the real eggs. The percent errors in the computer-predicted volumes were determined by comparing them with the corresponding volumes determined by water displacement. The computer-predicted surface areas were then corrected by the percent errors predicted by equation (9). The mean error in the computer-predicted volumes was +0.66% ±0.25, and this was very similar to the error in the volumes predicted by the computer for the geometric eggs (0.72%).

DETERMINATION OF EGG SHAPE SPECIFIERS

The calculation of the values of the egg shape specifiers required the measurement of the radii of

TABLE 1. Surface areas, volumes and shape specifiers.

Species	Predicted Volume (cm^3)[a]	Observed Volume (cm^3)[b]	Surface Area (cm^2)[c]	Elongation[d]	Asymmetry[d]
Struthio camelus	1100.68	1087.30	513.84	1.180	0.060
Podilymbus podiceps	21.58	21.53	38.47	1.501	0.098
Diomedea nigripes	299.17	298.13	222.14	1.491	0.142
Oceanodroma melania	10.21	10.15	23.17	1.443	0.107
Morus bassanus	95.71	94.62	104.13	1.609	0.135
Phalacrocorax pelagicus	35.83	35.47	54.08	1.574	0.156
Ardea herodias	72.21	71.09	84.91	1.464	0.068
Phoenicopterus ruber	146.36	144.83	139.51	1.702	0.106
Olor columbianus	312.09	308.60	228.16	1.563	0.153
Branta canadensis	157.69	157.28	145.41	1.527	0.238
Anas platyrhynchos	43.73	43.41	61.27	1.466	0.149
Falco peregrinus	47.83	47.61	63.91	1.210	0.156
Bonasa umbellus	17.59	17.51	33.01	1.294	0.137
Phasianus colchicus	24.14	24.26	40.82	1.213	0.201
Lophortyx californicus	8.45	8.37	20.11	1.221	0.295
Meleagris gallopavo	73.56	72.93	86.00	1.371	0.203
Numenius americanus	84.78	84.46	94.77	1.315	0.311
Calidris alpina	8.81	8.93	21.39	1.434	0.471
Himantopus mexicanus	21.93	21.63	38.59	1.408	0.364
Uria aalge	83.76	82.90	97.61	1.708	0.369
Aethia pusilla	15.64	15.44	30.81	1.491	0.313
Coccyzus erythropthalmus	6.95	6.90	17.80	1.344	0.071
Tyto alba	22.69	22.49	38.80	1.212	0.163
Otus asio	18.55	18.49	33.91	1.140	0.029
Bubo virginianus	63.34	62.91	76.65	1.096	0.064
Calypte anna	0.46	0.45	2.93	1.503	0.090
Corvus corax	30.55	30.35	48.81	1.583	0.283
Corvus brachyrhynchos	14.43	14.40	29.20	1.383	0.288

[a] Predicted by computer.
[b] Measured by water displacement.
[c] Corrected, as described in text.
[d] Measured from photograph.

curvature of the ends of the egg. These were approximated with the radii of circles which fitted the terminal six millimeters of the eggs in the enlargements. (For details see Appendix II.) The values derived in this way correlate well with Preston's (pers. comm.) corresponding species means ($r = 0.972$ and 0.979 for R_B and R_P respectively).

RESULTS

Table 1 summarizes the data obtained in this study. The relation between surface area and volume is:

$$\text{Surface Area} = 4.928\ \text{Volume}^{.668} \qquad (10)$$

($r = 0.9999$; For the log transformed data the standard error of the estimate is 0.0061)

The relation between surface area and volume reported by Paganelli et al. (1974) is:

$$\text{Surface Area} = 4.951\ \text{Volume}^{0.666} \qquad (11)$$

The mean difference between the surface areas measured for the eggs in this study and those predicted for them with equation (11) is −.15% ± 0.53. This indicates that there are no systematic differences between the method of estimating surface area in the present study and that of Paganelli et al. (1974). Since the data of Paganelli et al. (1974) are based on mean values of surface area and volume for species, the best estimate of the relation between surface area and volume is probably derived, not by combining the two sets of data, but by averaging the two equations. The average value of the two constants is 4.940. Since the average of the exponents in the two equations is 0.667, and this is the same as the theoretical value for the relation between surface area and volume, the best approximation of the relation between surface area and volume is:

$$\text{Surface Area} = 4.940\ \text{Volume}^{2/3} \qquad (12)$$

As is intuitively expected, there is a systematic effect of shape on the surface-volume relationship. The Surface-Volume Index, K_i, is highly correlated with Elongation. The relation between K_i and Elongation (figure 4) is:

$$K_i = 4.393 + 0.394\ \text{Elongation} \qquad (13)$$

($r = 0.968$; Standard error of the estimate is 0.017)

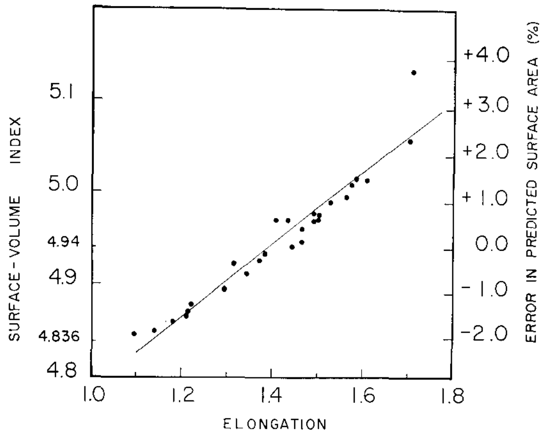

FIGURE 4. A regression of the Surface-Volume Index (K_i) on Elongation. See text for definitions.

A multiple regression of K_i on Elongation, Asymmetry, and Bicone indicates that K_i is significantly correlated with both Elongation and Asymmetry ($P < .01$ for both variables). The multiple regression of K_i on Elongation and Asymmetry yields the following relationship:

$$K_i = 4.395 + 0.382 \text{ Elongation} + 0.080 \text{ Asymmetry} \quad (14)$$

($R = 0.976$; Standard error of the estimate is 0.015)

An egg with Elongation equal to one, and Asymmetry equal to zero would be a sphere and would have the minimum possible K_i. Equation (13) predicts a K_i of 4.787 for such an egg, and this is significantly different from the K_i of a sphere (4.836). An examination of Figure 4 suggests that this discrepancy is due to a non-linear relationship between K_i and elongation for low values of elongation. For eggs with elongation less than 1.15, it is probably best to assume that K_i is equal to 4.836.

Because the error in the surface area predicted for an egg with equation (12) is proportional to the differences between the K_i of the egg and the constant (4.940) in the equation, it is possible to improve the estimate of the surface area from volume by using the value of K_i predicted with either equation (13) or (14) in the general equation:

$$\text{Surface Area} = K_i \text{ Volume}^{2/3} \quad (15)$$

The ordinate on the right side of figure 4 indicates the error in the surface areas predicted with equation 12, where the effect of elongation on K_i is not accounted for. This figure can be used to predict the error involved in using equation 12 for any egg of known elongation. Table 2 reports the errors involved in predicting surface area from volume with the various equations derived in this study. The eggs used in this table were selected because they exhibit extremes of shape. The egg of the Common Murre (*Uria aalge*) is very elongate and highly asymmetrical. The egg of the Flamingo (*Phoenicopterus ruber*) is also very elongate but has very low asymmetry and the egg of the Great Horned Owl (*Bubo virginianus*) is nearly round (Elongation = 1.096) and has very low asymmetry. As can be seen in Table 2, Equation 12 predicts surface areas which are, on average, in error by about 1% but surface areas may be over-estimated by as much as about 2% or underestimated by nearly 4%. Equation 13 is useful when dealing with elongate eggs and, in fact, yields smaller errors for 26 of the 28 eggs in this study. Equation 14 adds little to the accuracy available with equation 13.

TABLE 2. Errors involved in predicting surface area from volume.

	Equation 12	Equations 13 & 15	Equations 14 &15
Mean Absolute Error	1.09	0.22	0.19
Common Murre	–3.78	–1.33	–1.11
Flamingo	–2.34	+0.10	–0.10
Great Horned Owl	+1.95	–0.43	–0.55

DISCUSSION

It remains an article of faith that the shape of an egg is the result of selective pressures relating to functional aspects of the egg. Since pore area, pore density and shell thickness, the factors which determine the respiratory parameters of the shell (Ar et al. 1974 and Wangensteen et al. 1970/71), are independent of surface area, there would appear to be no effect of shape on respiratory physiology. The effect of the small variability in surface area on heat exchange would seem to be insignificant when compared with the effects of nest insulation, microhabitat selection and incubation patterns. Therefore, it seems likely that the functional significance of the variation in the shapes of birds' eggs is not related to physiological exchanges with the environment.

SUMMARY

The surface areas and volumes of 29 birds' eggs were determined with the aid of a computer, and a new accurate method of mea-

suring volume by water displacement was developed. The relationship between shape and surface area was studied with the aid of a newly defined parameter, the Surface-Volume Index (K_i). The relation between surface area and volume found in the present study corresponds closely with that of Paganelli et al. (1974). However, the use of either equation may lead to estimated surface areas in error by nearly four percent. This error can be reduced by using the relationship established between K_i and Elongation, an easily determined specifier of egg shape.

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APPENDIX I

As can be seen from the shaded triangle in figure 5, the angle theta is defined by the distance between the centers of the circles (D1) and the difference in their radii ($R_1 - R_2$). Once theta is determined, all of the values necessary for the calculation of the surface areas and volumes of the segments of the geometric eggs can be readily determined (Table 3). Four of the fourteen geometric eggs were composed of two spheres and one frustrum as in figure 6. The remaining ten were made of three spheres and two frustra

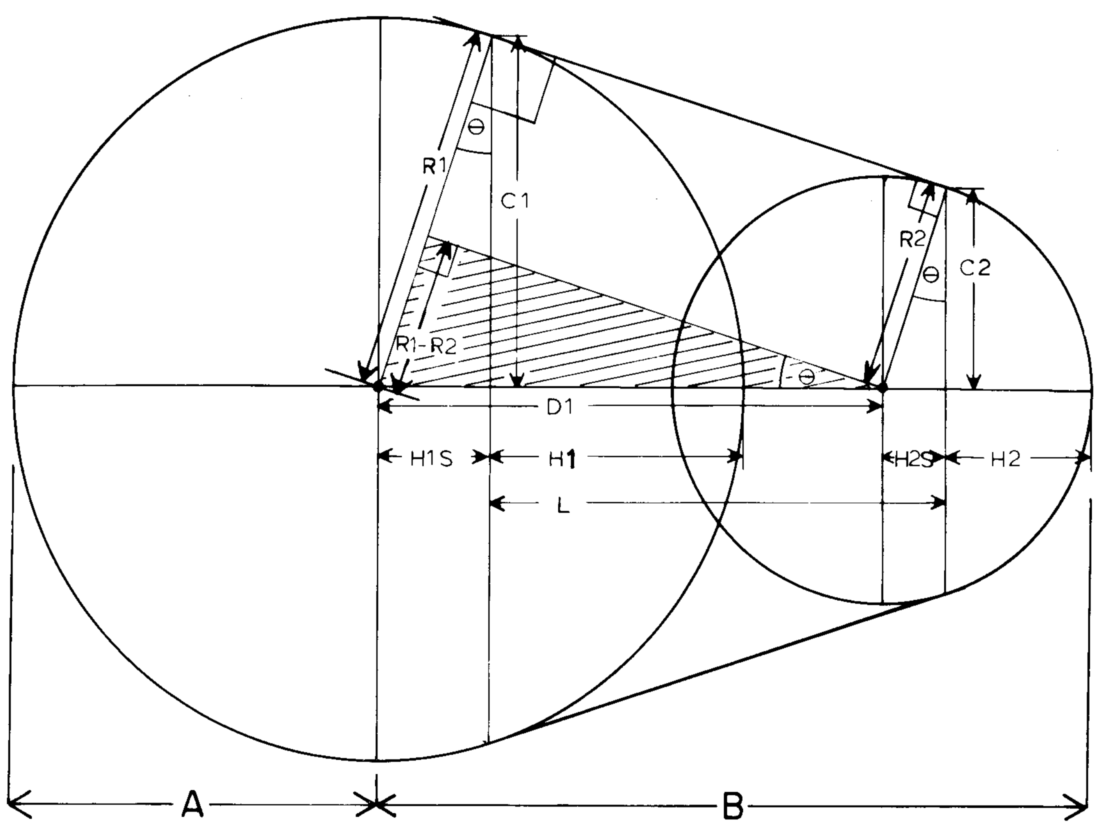

FIGURE 5. A generalized diagram of a "Geometric Egg."

TABLE 3. Equations used for Geometric Eggs:

$\sin \theta = (R1 - R2) \div D1$
$H1S = R1 \cdot \sin \theta$
$H1 = R1 - H1S$
$H2S = R2 \cdot \sin \theta$
$H2 = R2 - H2S$
$C1 = R1 \cdot \cos \theta$
$C2 = R2 \cdot \cos \theta$
$L = D1 + H2S - H1S$
Surface of Hemisphere $= 2 \pi Ri^2$
Surface of Spherical Segment $= 2 \pi RiHi$
Surface of Frustrum of a Cone $= \pi (C1 + C2) (L^2 + (C1 - C2)^2)^{1/2}$
Volume of Hemisphere $= (2/3) \pi Ri^3$
Volume of Spherical Segment $= (1/3) \pi Hi^2 (3Ri - Hi)$
Volume of Frustrum of Cone $= \pi (L/3) (C1^2 + C1 \cdot C2 + C2^2)$

by replacing part A (figure 5) with a second set of shapes analogous to part B.

APPENDIX II

If it is assumed that the terminal segment of the egg from A to B (figure 6) can be approximated by the arc of a circle, then the radius of curvature of the end of the egg equals the radius of the circle (R_c). From the Pythagorean Theorem, it is obvious that:

$$R_c = (R^2 + (R_c - L)^2)^{1/2}$$

rearranging:

$$R_c = (R^2 + L^2) - 2L$$

It is easy to determine the radius of curvature of the end of the egg by simply measuring the radius of the egg (R) on the photograph at some predetermined distance (L) from the

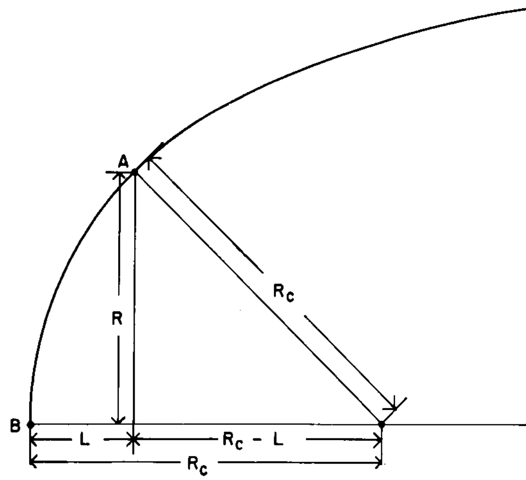

FIGURE 6. A diagram showing how the radius of curvature of the end of an egg can be determined from the radius of the egg at a known distance from the end of the egg.

end of the egg. To the extent that the end of the egg is not a perfect sphere, the radius of curvature determined in this way will be a function of L. To have data comparable to Preston's, it was, therefore, necessary to carefully select the value of L to be used. For five eggs of different sizes I empirically determined that Preston's corresponding species means could be approximated most closely by the radius of curvature of the terminal six millimeters, and this was the value of L used for all the eggs used in this study.

Department of Biology, University of California, Los Angeles, California 90024. Accepted for publication 26 February 1976.