THE AVIAN EGG: SURFACE AREA, VOLUME, AND DENSITY

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INTRODUCTION

The surface area of the avian egg through which the developing embryo must exchange heat, metabolic gases, and water vapor is a variable of prime importance for quantitation of the permeability of the egg shell to these substances. Surface-area measurements are necessary if one is to compare the permeability properties of shells ranging in size from less than 0.5 g in hummingbirds, to 1.5 kg in the Ostrich (*Struthio camelus*), and to more than 10 kg in the extinct *Aepyornis*. In the course of experiments designed to measure and compare the water vapor permeability of eggs of many species (Ar et al. 1974), we found it necessary to develop a method of measuring surface area that was both convenient and accurate.

The problem of surface-area measurement in eggs is complicated by the fact that eggs come in a variety of shapes, few of which can be described by simple, analytic functions. Shapes vary from the nearly spherical eggs of owls to the sharply pointed eggs of murres and gulls. In their classic text, Romanoff and Romanoff (1949) reviewed many of the empirical and theoretical formulas for calculating surface area and volume of eggs. Although a mathematical description of surface area and volume was developed by Carter (1968) for the hen's egg, we required a method which would be applicable to eggs of any shape, as long as there was circular symmetry about an axis of rotation. Once such a method was developed, it was used to establish allometric relations between surface area and egg weight and volume. Correlative data provided by Schönwetter (1960–71) enabled us to define additional relations between egg weight (as the independent variable), and shell weight, shell density, and egg density (as dependent variables).

THEORY

Our approach to the problem of surface-area measurement was derived directly from that of Besch et al. (1968), which depends on

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making a tracing of the profile of an egg, dividing the tracing into segments, and estimating the surface area generated as each segment is rotated about the long axis of the egg. We used a photographic technique in conjunction with a hybrid analog-digital computer to facilitate collection and treatment of the data. Assuming that an egg shell is a surface of revolution generated by revolving a curve $y = f(x)$ about the x-axis (in our case the long axis of the egg), the surface area A is given by:

$$A = 2\pi \int_a^b y \left[1 + \left(\frac{dy}{dx} \right)^2 \right]^{1/2} dx \qquad (1)$$

where a and b are limits of integration as shown in figure 1. If the functional relation $y = f(x)$ is an analytical function, it may be possible to perform the integration directly. In our case, since we do not in general know y as a function of x, we resort to an approximation.

As suggested by figure 2, when the curve formed by the profile of the egg shell is revolved about the x-axis, the chords AB, BC, etc., generate the lateral areas of the frustra of right circular cones. The sum of these lateral areas approximates the surface of the shell and approaches it with increasing closeness as Δx becomes very small. The lateral area generated by the chord AB is given by:

$$A_i = \pi (y_{i-1} + y_i)(\Delta x_i^2 + \Delta y_i^2)^{1/2}$$

Thus the surface area A of the egg shell will be approximately given by:

$$A \cong \sum_{i=1}^{n} A_i = \pi \sum_{i=1}^{n} (y_{i-1} + y_i)(\Delta x_i^2 + \Delta y_i^2)^{1/2} \qquad (2)$$

The volume V of the egg is given by:

$$V \cong \sum_{i=1}^{n} V_i = \frac{\pi}{3} \sum_{i=1}^{n} [y_{i-1}^2 + y_i^2 + (y_{i-1}^2 \cdot y_i^2)^{1/2}] \Delta x_i \qquad (3)$$

Equation (3) contains the formula for the volume of the frustrum of a right circular cone whose bases have areas of πy_{i-1}^2 and πy_i^2, and whose height is Δx_i. Knowledge of the (x, y) co-ordinates of n points on the pro-
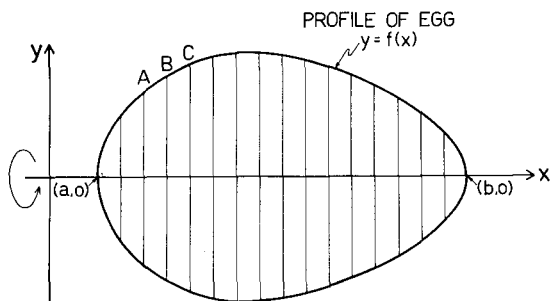
FIGURE 1. Profile of egg showing division into 16 segments. The direction of rotation is shown by the arrow. The points A, B, and C refer to the two segments shown on an expanded scale in figure 2.

FIGURE 3. Regression of egg shell surface area (cm²) on fresh egg weight (g) on log-log scale. Points represent means; the dotted lines enclose ±2 SE, and represent 95% confidence limits for log of surface area.

file of the shell permits calculation of the approximate surface area and volume of the shell. The larger the value of n, of course, the closer will be the approximation to the true surface area and volume.

For example, Eq. (2) yields a value of $A = 112.5$ cm² for a sphere whose radius is 3 cm (roughly the size of a chicken egg), with $n = 17$ (16 equal intervals). The actual area of the sphere is 113.1 cm², a difference of about 0.5%.

MATERIALS AND METHODS

Measurements were made on 225 eggs of 29 species of wild and domestic birds collected from local and foreign sources (table 1, species arranged in order of increasing initial weight). A positive transparency was made of each egg with Polaroid 146-L film, and its long axis measured with a micrometer caliper to ±0.002 SD cm. Special care was taken to align the long axis of the egg parallel to the film plane. From this transparency, an enlarged tracing of the egg in profile was made on 11 × 17-inch graph paper, which was then placed on the bed of an X-Y recorder. The pen of the X-Y recorder was positioned sequentially at 17 equally spaced points (16 equal intervals) on the upper half of the profile of the egg by two potentiometers whose voltage outputs were
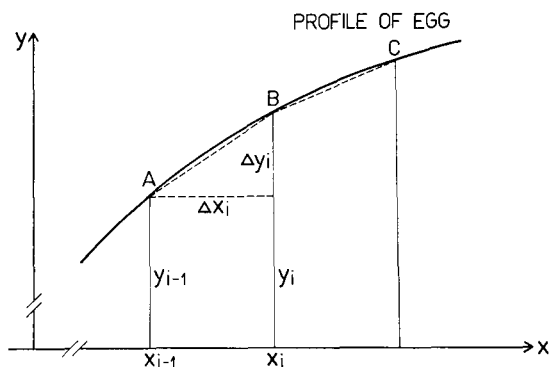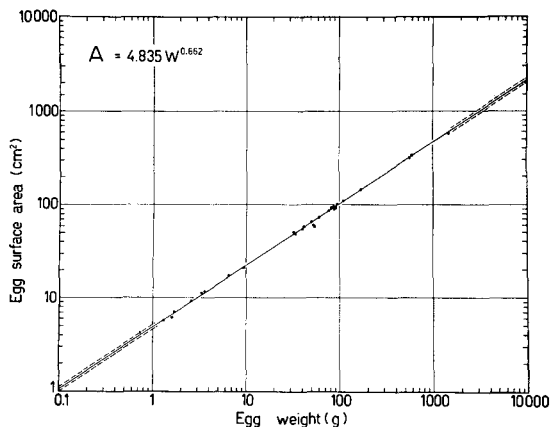
digitized and transmitted to a PDP-12 computer (Digital Equipment Corp., Maynard, Mass.). In this manner, each point on the half-profile was represented by a pair of voltages corresponding to the (x, y) co-ordinates of the point. The voltage-pairs and a scale factor relating the long axis of the egg in centimeters to the length of the long axis of the tracing permitted calculation of the surface area and volume of the egg from Eq. (2) and (3), respectively. Since eggs are seldom perfect solids of revolution, both top and bottom half-profiles of the tracings were measured twice. Thus, four values each of surface area and volume were obtained from each tracing, from which averages were calculated.

The accuracy of our measurement technique was tested by photographing a sphere of 3 cm radius and determining its surface area and volume. In a series of 10 replicate measurements, these were underestimated systematically by about 1% and 2%, respectively. The precision of measurement was checked for both large and small eggs in two separate series of 10 replicate determinations. For a hen's egg, $A =$
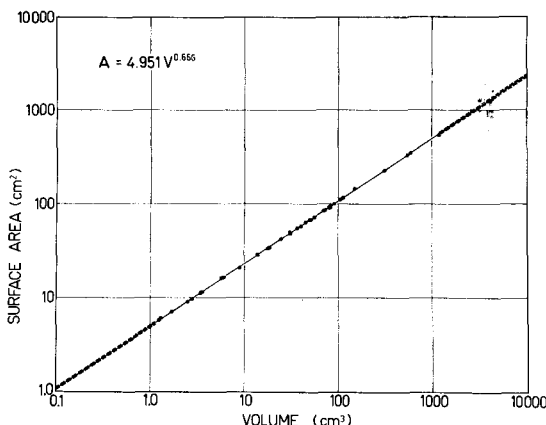

FIGURE 2. Enlarged portion of egg profile showing the geometrical relations involved in approximating the surface area. Δx_i, Δy_i, etc., refer to the quantities given in Eqs. (2) and (3) of the text.

FIGURE 4. Regression of egg shell surface area (cm²) on egg volume (cm³) on log-log scale. Points represent means; the dotted lines enclose ±2 SE, and represent 95% confidence limits for log surface area.

TABLE 1. Surface areas and volumes of eggs, measured as described in text.

Species	No. eggs	Initial wt. (g) ± SD	Length of eggs (cm) ± SD	Area (cm²) ± SD	Volume (cm³) ± SD
Troglodytes aedon (House Wren)	27	1.32 ± 0.13	1.62 ± 0.06	5.73 ± 0.44	1.27 ± 0.13
Dendroica petechia (Yellow Warbler)	3	1.60 ± 0.09	1.73 ± 0.04	6.11 ± 0.42	1.33 ± 0.24
Iridoprocne bicolor (Tree Swallow)	5	1.72 ± 0.07	1.89 ± 0.03	7.08 ± 0.15	1.71 ± 0.06
Passer domesticus (House Sparrow)	21	2.62 ± 0.15	2.15 ± 0.11	9.18 ± 0.33	2.53 ± 0.13
Molothrus ater (Brown-headed Cowbird)	7	3.33 ± 0.40	2.31 ± 0.08	11.22 ± 0.93	3.45 ± 0.44
Agelaius phoeniceus (Red-winged Blackbird)	18	3.59 ± 0.39	2.29 ± 0.18	11.44 ± 0.75	3.46 ± 0.47
Quiscalus quiscula (Common Grackle)	3	6.29 ± 0.03	2.69 ± 0.34	16.51 ± 0.07	6.08 ± 0.06
Turdus migratorius (American Robin)	6	6.46 ± 0.08	2.83 ± 0.12	16.40 ± 0.16	5.88 ± 0.10
Coturnix coturnix (Japanese Quail)	12	9.62 ± 0.66	3.09 ± 0.10	20.91 ± 1.04	8.80 ± 0.67
Pluvialis apricaria (Eurasian Golden Plover)[a]	3	32.64 ± 0.05	5.18 ± 0.13	49.69 ± 0.26	31.45 ± 0.45
Phasianus colchicus (Ring-necked Pheasant)	12	33.84 ± 2.34	4.61 ± 0.19	48.05 ± 2.23	30.81 ± 2.05
Lophura nycthenerus (Chinese Silver Pheasant)	3	39.94 ± 0.98	5.15 ± 0.06	54.74 ± 1.32	37.18 ± 1.33
Haematopus ostralegus (European Oystercatcher)[a]	2	41.45 ± 0.40	5.59 ± 0.18	58.10 ± 2.74	40.12 ± 2.79
Phalacrocorax auritus (Double-crested Cormorant)[b]	8	49.88 ± 3.37	6.19 ± 0.21	64.37 ± 2.70	45.87 ± 2.75
Numenius phaeopus (Whimbrel)[a]	4	53.46 ± 0.40	6.21 ± 0.06	68.46 ± 0.28	50.87 ± 0.16
Gallus gallus (Domestic Chicken)	12	53.89 ± 2.13	5.67 ± 0.16	68.00 ± 8.51	50.95 ± 11.40
Fratercula arctica (Common Puffin)[a]	6	59.65 ± 3.43	6.22 ± 0.23	72.55 ± 3.15	55.85 ± 3.44
Larus canus (Mew Gull)[a]	8	76.20 ± 4.48	6.76 ± 0.20	85.79 ± 3.92	72.51 ± 5.11
Cairina moschata (Muscovy Duck)	4	80.20 ± 7.61	6.27 ± 0.19	91.59 ± 2.41	81.36 ± 3.82
Anas boscas (Pekin Duck)	11	82.34 ± 5.61	6.51 ± 0.37	90.65 ± 8.47	79.46 ± 11.60
Larus fuscus (Lesser Black-backed Gull)[a]	6	84.90 ± 4.27	6.92 ± 0.25	91.96 ± 3.40	80.16 ± 4.46
Meleagris gallopavo (Turkey)	11	87.76 ± 4.32	6.69 ± 0.15	93.04 ± 2.81	82.15 ± 3.73
Larus argentatus (Herring Gull)[b]	3	88.16 ± 3.97	7.09 ± 0.12	94.91 ± 3.77	83.70 ± 4.91
Catharacta skua (Great Skua)[a]	6	95.47 ± 5.41	7.19 ± 0.26	100.09 ± 4.28	91.04 ± 5.53
Larus marinus (Great Black-backed Gull)[a]	9	110.80 ± 12.07	7.49 ± 0.37	110.17 ± 8.22	105.11 ± 11.43
Anser domesticus (Embden Goose)	11	170.21 ± 10.00	9.01 ± 0.32	146.15 ± 7.08	158.74 ± 10.95
Dromiceius novae-hollandiae (Emu)[c]	1	577.62 –	13.33 –	319.09 –	514.07 –
Rhea americana (Rhea)[c]	2	609.26 ± 80.86	13.22 ± 1.33	337.70 ± 48.64	566.94 ± 118.73
Struthio camelus (Ostrich)[c]	1	1480.03 –	17.07 –	582.46 –	– –

Lengths were measured on the long axis of the eggs. The values are means of the number of eggs shown in the table ± one standard deviation (SD). The letters indicate geographical origin or source of egg: a = Faeroe Islands, N.E. Atlantic Ocean; b = Mt. Desert Island, Maine; and c = San Diego Biological Gardens. No letter indicates that eggs were from Buffalo, New York area.

64.9 ± 0.3 SD cm², and $V = 47.4 ± 0.3$ SD cm³, while for a wren's egg, $A = 6.33 ± 0.07$ SD cm² and $V = 1.47 ± 0.03$ SD cm³. The largest random errors in the measurement technique (those for small eggs) are about 1% for surface area and about 2% for volume. Both systematic and random errors are small compared with the natural variation of egg sizes within every given species (table 1). The averages in the table were not corrected for systematic error for this reason.

RESULTS

Table 1 gives the values of surface area and volume of the eggs measured. The regressions of the logarithm of surface area on the logarithm of both initial weight and volume were calculated by the method of least squares, and the resulting graphs are shown in figures 3 and 4. The relation between area and weight is as follows:

$$A = 4.835 \ W^{0.662} \qquad (4)$$

or $\log A = \log 4.835 + 0.662 \log W ± 0.010$ (Standard error of estimate, SE); $r = 0.9998$, where A = area in cm²,

W = egg weight in g,

r = correlation coefficient.

The relation given by Besch et al. (1968) for hen's eggs is $A = 4.76 \ W^{0.658}$, which is quite close to Eq. (4), especially when one considers the variety of egg shapes which are included in Eq. (4).

A   B   C   D
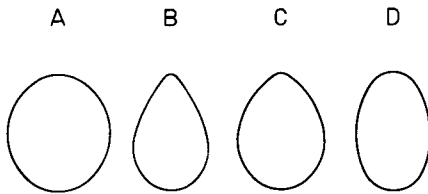
Length , cm	5.9	8.0	6.4	1.3
Measured Area, cm²	87.6	105.6	74.2	3.30
Calculated Area, cm²	88.9	103.4	74.1	3.28

FIGURE 5. Comparison of measured and calculated surface areas of birds eggs of disparate shapes. A: Great Horned Owl (*Bubo virginianus*); B: Common Murre (*Uria aalge*); C: Domestic Chicken (*Gallus domesticus*); D: Ruby-throated Hummingbird (*Archilochus colubris*). The volume and area of each egg were measured as described in the text; the measured volume was then used to obtain the calculated area shown in the figure from Eq. (5).

The equation relating area and volume is:

$$A = 4.951 \ V^{0.666} \qquad (5)$$

or log A = log 4.951 + 0.666 log V ± 0.004 SE; $r = 0.99997$,
where V = egg volume in cm³.

DISCUSSION

AREA AND VOLUME RELATIONSHIPS

To test the general applicability of Eq. (5) to eggs of disparate shapes, we chose four types of eggs (shown in fig. 5) which were not used originally in deriving Eq. (5). Their volumes and surface areas were measured as described above. The measured areas were then compared with the surface areas calculated from Eq. (5). The agreement in area is better than 3% in all cases.

The general form of the relation between surface area and volume for objects of similar shape but different size is $A = aV^{2/3}$. For spheres, $a = 4.836$ is the minimal value possible. Equation (5) shows that, for eggs, the value of a will have a range of 4.9 to 5.0 SE. On the average, eggs will have a surface area larger than a sphere of the same volume by a factor of 4.951/4.835 = 1.024. In practice, then, area can be determined simply by measuring egg volume (e.g., by water displacement, computing the surface area of a sphere of that volume, and multiplying the area so obtained by 1.024. This simplified calculation yields areas which are in error by about 1% for the smallest eggs (House Wren, *Troglodytes aedon*), and by less than 0.5% for the largest (Ostrich), in our series. These errors are small compared with actual errors associated with measurement of volume.

AREA AND EGG WEIGHT RELATIONSHIPS

Equation (4) provides a practical way to calculate surface area when initial egg weight is known. It replaces the measurement of egg dimensions with a simple weighing, which can be done quickly and accurately.

EGG DENSITY AND EGG WEIGHT RELATIONSHIPS

To obtain an expression for egg density ρ_e (g cm⁻³), which is simply defined as W/V, Eqs. (4) and (5) can be combined to eliminate A, and from the resulting expression, ρ_e is obtained as a function of W:

$$\rho_e = 1.038 \ W^{0.006} \qquad (6)$$

Thus, egg density has only a slight dependence on egg weight. For example, a 1-g egg will have a density of 1.038, whereas the density of a 1000-g egg is 1.082. The density of fresh hen's egg contents is 1.033 (Romanoff and Romanoff 1949). If one assumes that the contents of bird's eggs in general have this density regardless of weight, then Eq. (6) suggests that the fractional weight of the shell must increase with egg weight.

SHELL WEIGHT AND EGG WEIGHT RELATIONSHIPS

An empirical relation between shell weight (W_{sh} in g) and egg weight was obtained from data presented by Schönwetter (1960–71), and is shown in figure 6. Our measurements of egg weight are in close agreement with those given in Schönwetter (see fig. 7). The regression of shell weight on egg weight for 368 species has the form:

$$W_{sh} = 4.82 \times 10^{-2} \ W^{1.132} \qquad (7)$$

The SE in log W_{sh} is ± 0.0805; the correlation coefficient $r = 0.995$. Equation (7) shows clearly that the percentage of shell weight increases with whole egg weight, a relation shown in figure 8. For example, one of the smallest eggs recorded in Schönwetter (1960–71) is that of the hummingbird (*Chlorostilbon canivetii*), whose weight averages 0.3 g in two specimens; its shell weighs 0.017 g, or 5.7% of the egg weight. Equation (7) predicts that on the average a 0.3-g egg will have a 0.012-g shell, or 4% of egg weight, in close agreement with the actual figure. At the other end of the scale, Schönwetter gives calculated egg weights which average 9130 g for 23 specimens of shells of the extinct bird, *Aepyornis*. For an egg of this weight, Eq. (7) predicts a shell weight of 1470 g, or 16% of egg weight, a fourfold increase over the percentage figure for the hummingbird. The
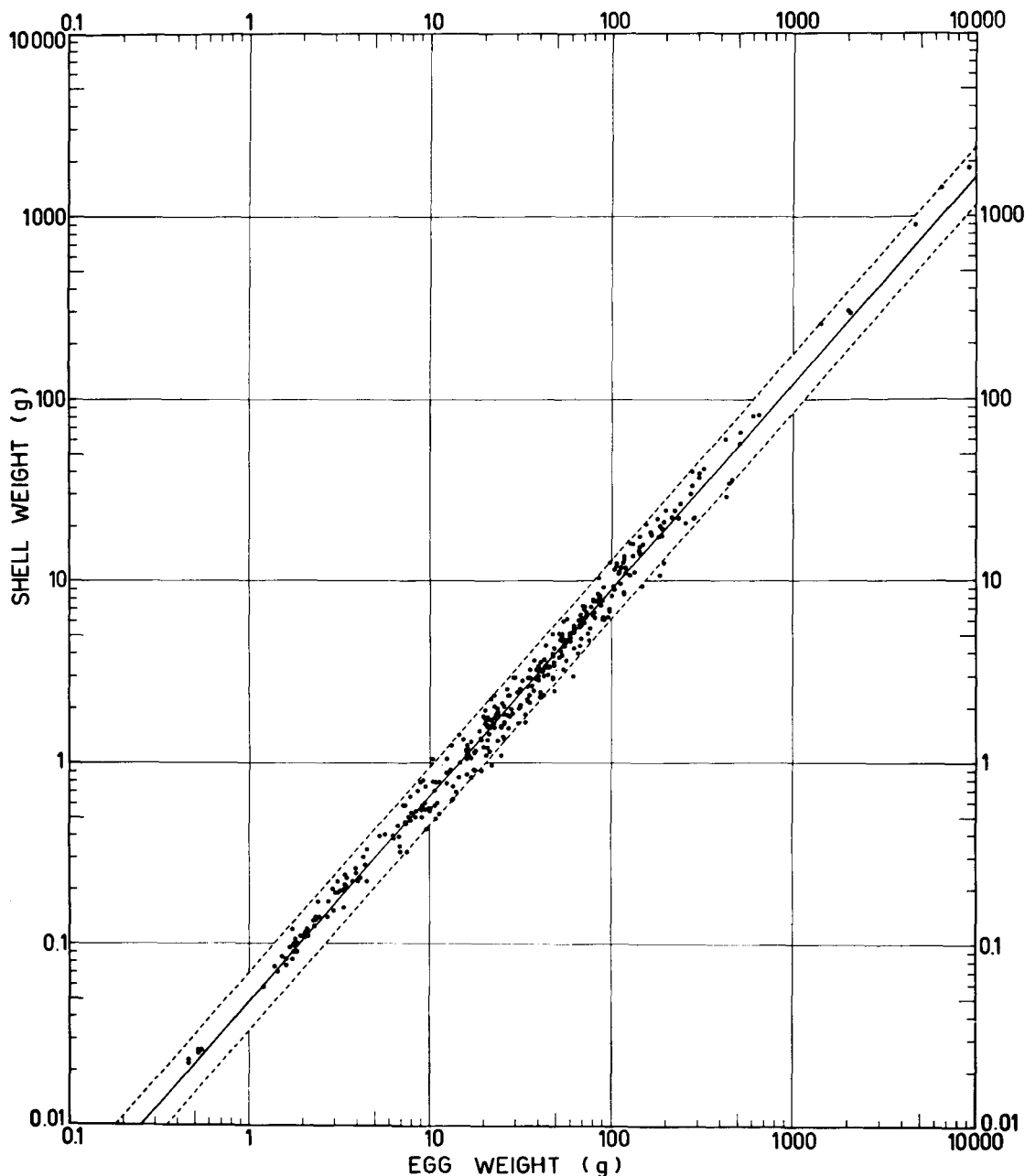
FIGURE 6. Regression of egg shell weight (g) on egg weight (g) on log-log scale. Data obtained from Schönwetter (1960–71). Points represent mean values for a given species; the dotted lines enclose ±2 SE, and represent 95% confidence limits for log shell weight, $n = 368$.

average shell weight for the same 23 *Aepyornis* shells is actually 1833 g, in fair agreement with the predicted value.

SHELL DENSITY AND EGG WEIGHT

Shell density (ρ_{sh} in gm cm^{-3}) as a function of egg weight can be derived from Schönwetter's data on shell thickness (L in cm) and egg weight, which together with shell area can be used to calculate shell volume. From Ar et al. (1973):

$$L = 5.126 \times 10^{-3} \ W^{0.456} \tag{8}$$

The volume (V_{sh}) of the shell is simply $L \times A$; from Eqs. (4) and (8), we have:

$$V_{sh} = 2.48 \times 10^{-2} \ W^{1.118} \tag{9}$$

Shell density is now expressed as W_{sh}/V_{sh}, or, from Eqs. (7) and (9):

$$\rho_{sh} = 1.945 \ W^{0.014} \tag{10}$$

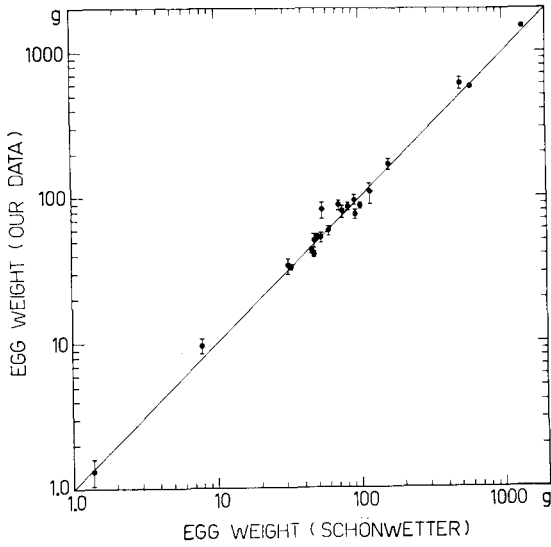Equation (10) represents the trend to be ex-

FIGURE 7. Regression of average fresh egg weight (g), taken from the present measurements, on average egg weight (g) for the same species found in Schönwetter (1960–71), on a log-log scale.

pected in density over a large range of egg weights. Experimental verification of this trend using single eggs should prove quite difficult. As an example, there is variation in diet within species. Additionally, the slight dependence on weight may be masked by specific adaptation within a given species. The cumulative error in Eq. (10) creates a further uncertainty of ± 30% in prediction of density. However, if Eq. (10) is valid in general, one should find a growing ratio of inorganic to organic material in the shell as the egg grows larger.

As in the case of egg density, one would predict that the density of shell material increases only slightly as egg weight increases.
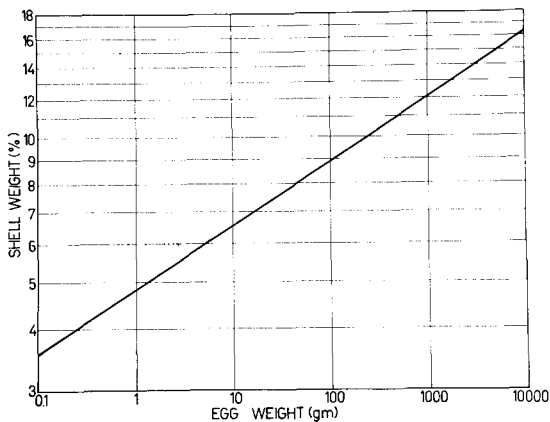

FIGURE 8. Data from figure 6 plotted on log-log scale as percentage of shell weight (weight of shell/weight of egg) × 100 vs. egg weight (g).
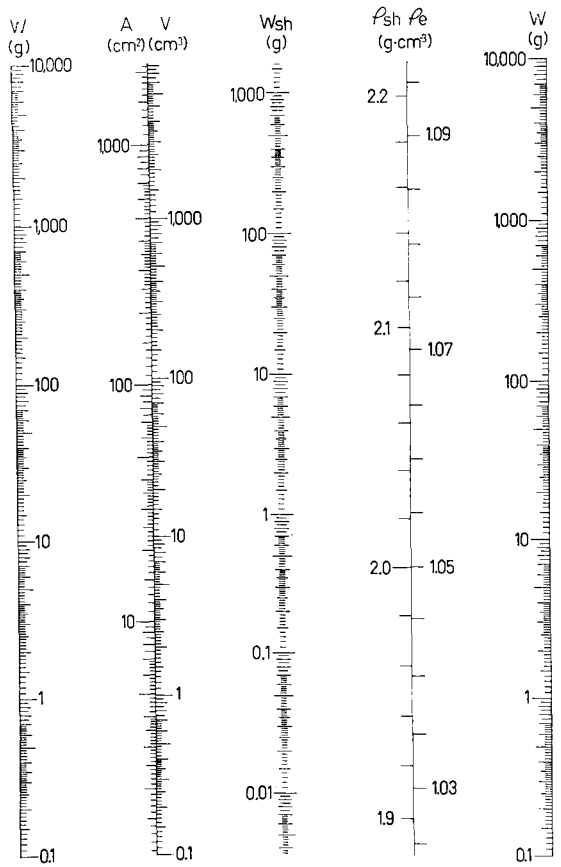

FIGURE 9. Alignment chart showing relations among egg weight W (g) as the independent variable and shell area A, egg volume V, weight of shell W_{sh}, density of shell ρ_{sh}, and density of egg ρ_e as dependent variables. To use the chart, align a straight edge with a given egg weight on the two edges of the chart and read the variables of interest at the intersection of the straight edge with the appropriate columns.

For example, the change in shell density between one-gram and thousand-gram typical eggs is only 0.2 g cm^{-3}, or about 10%.

SUMMARY

Measured surface areas and volumes for bird eggs of different weights yield allometric relations between weight (or volume) on the one hand and area on the other. Data from the literature on shell weight and thickness enable us to derive allometric relations between these variables and egg weight. Finally, combining the allometric relations leads us to predictions of how egg density and shell density should vary with egg weight. The alignment chart shown in figure 9 summarizes the relationships among egg weight, shell area, egg volume, shell weight, and shell and egg density in a compact form.

The allometric equations developed in the present analysis are collected below.

(1) Area (A, cm^2) vs. egg weight (W, g):
$A = 4.835 \ W^{0.662}$

(2) Area vs. egg volume (V, cm^3):
$A = 4.951 \ V^{0.666}$

(3) Egg density (ρ_e, g cm^{-3}) vs. egg weight:
$\rho_e = 1.038 \ W^{0.006}$

(4) Shell weight (W_{sh}, g) vs. egg weight:
$W_{sh} = 4.82 \times 10^{-2} x \ W^{1.132}$

(5) Shell density (ρ_{sh}, g-cm^{-3}) vs. egg weight:
$\rho_{sh} = 1.945 \ W^{0.014}$

(6) Shell volume (V_{sh}, cm^3) vs. egg weight:
$V_{sh} = 2.48 \times 10^{-2} \ W^{1.118}$

ACKNOWLEDGMENTS

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