CALCULATION OF EGG VOLUME BASED ON LOSS OF WEIGHT DURING INCUBATION

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The volume of an egg (inclusive of shell) is an important parameter exact determination of which is of great value in certain ornithological problems. Since eggs show different shapes, the volume is not a onevalued function of the lengths of the axes; likewise the weight is variable and has meaning only in newly-laid eggs.

The volume can be determined exactly by any method using the principle of displacement of water, or flotation. Many of these methods require special apparatus, particularly if the egg has been incubated for some time and does not sink. Blowing-out an egg and subsequently filling the shell with a liquid of known specific gravity is also a cumbersome procedure.

In the present paper a method will be offered that demands a minimum of mechanical equipment, viz: a small ordinary balance and a container of any kind to make a water test. The method is therefore particularly suited for determinations in the field. Observations were made chiefly at Heröy, Norway, on eggs of the Common Gull (*Larus canus*), which nests along the entire coast of southern Norway.

The derived formula is independent of the axial lengths and shape of the egg and is based on the observed loss of weight during the time of incubation. The formula can therefore be used for computing volumes from literature data of the weight of newly-laid eggs.

REVIEW OF LITERATURE

An egg that has been incubated for a few days weighs less than the newly-laid egg. Heinroth (1922) showed a method of determining the original weight. He took the egg and, after having blown out its contents, filled it with water. According to Heinroth, the weight of the egg filled with water is practically the same as that of the egg before incubation. Groebbels and Möbert (1927b) held that, by adding about 2.5 - 3.0 per cent of the weight, the most correct results are to be found.

Groebbels (1927) presented observations on the decrease of the specific gravity of the egg during the course of incubation and gave a brief summary of the previous works on this subject. I therefore do not include these earlier papers in the present bibliography.

Groebbels weighed the eggs, found their volumes by observing the quantity of water displaced in a specially constructed vessel, and examined their contents. But only in a few instances did he follow the time/weight curve of the individual egg. All eggs without exception were, for at least some time, put into an incubator, or in some other way taken out of their natural environment. In another paper Groebbels and Möbert (1927a) presented data on the loss of weight in eggs of 17 different species of birds, and found that the results differed in the different species. Horton (1932) gave the loss of weight of domestic duck eggs. Pringle and Barott (1937) have shown that small eggs generally have comparatively greater losses of weight than do large ones. Small eggs have greater surface in proportion to their mass; consequently they have potentialities for a comparatively greater evaporation and loss of weight.

Groebbels (1937) quoted various older papers dealing with shape, surface, and volume of eggs. Formulas have been proposed showing the relations of these data, but all include the lengths of the axes, thus introducing a degree of uncertainty and invalidating the results.

Szielasko (1920) introduced the so-called "symmetry factor" as a measure of the shape, and Grossfeld (1933) tried to use Szielasko's data in computing egg volumes, but found it impracticable because of the complexity of the equations. Grossfeld therefore applied the formula for an ellipsoid of rotation— $0.524 L B^2$ modified to $0.519 L B^2$ —to obtain the volume. Romanoff and Romanoff (1949) reported that a number of different constants have been used in this equation. They thought that an error of less than two per cent could be obtained for hens' eggs of various sizes and shapes by using 0.526.

Schönwetter (1925) used the formula of the ellipsoid to compute the weights of newly-laid eggs. Bergtold (1929) used a similar method and proposed the equation, $w = 11/21 \ L \ B^2 \ S$, where S is the specific gravity. The fraction, 11/21 = 0.5238, is identical with the constant in the formula for the ellipsoid. Bergtold also experimented with filling empty egg-shells with various liquids and recommended chloroform as the most suitable. Westerskov (1950) used Bergtold's simplified formula, $V = 0.51 \ L \ B^2$. Worth (1940) has proposed the formula $V = 0.85 \ \left(\frac{\pi \ L \ B^2}{6}\right)$.

NEW OBSERVATIONS ON Larus canus

A water-test is made by putting the egg into water. (Water from nearby ponds and streams was used. This water carries a surprisingly small amount of soluble matter, and approaches the qualities of distilled water; the specific gravity can be taken as equal to 1.) If the egg is newly-laid, it will sink; after having been incubated a few days, its rounded end will rise a little from the bottom. A little more than a week's incubation will make it stand straight up in the water, the pointed end barely touching the bottom. After about nine days' incubation, the egg shows a tendency to rise from the bottom, and after 10 to 11 days, it will settle directly under the surface. The loss of weight continues; after about two weeks' incubation, the rounded end of the egg protrudes above the water. As time goes on, its long axis becomes more and more oblique in the water, because the air-filled compartment, which lies in the rounded end of the egg, grows steadily larger, and moves obliquely down towards the pointed end of the egg. At the stage when it barely floats (or more correctly, when it remains suspended in the water), the specific gravity of the whole egg is one.

As distinct from other workers, I have systematically studied the eggs in their natural environment, except for the short time taken to make flotation tests, and I have followed each egg during the whole incubation period. A total of 65 eggs from 31 different clutches was observed. Their average weight was 52.0 gm., newly-laid. When the young bird first cracked open its shell, the eggs averaged 42.5 gm., and at the concluding stage of hatching the average weight was 41.0 gm. The chick usually starts working at the egg shell, trying to pierce it, 3.5 days before it is fully-hatched. Before this period, the rate of the loss of weight per unit of time is constant as showed by repeated weighings. After the egg is cracked, the rate steadily in-When the chick starts breathing with its lungs, the rate of creases. the excretion of water increases. The more intensely the chick works to get out of the shell, the greater is the loss of weight. More and more cracks become visible on the egg shell, and about 24 hours before hatching there are definite holes in the shell. At this point the rate of the loss of weight increases still more; during the last 24 hours the average egg reduces its weight by as much as 1.5 gm.

Forty-one eggs were used for a methodical study of the water-test. For these eggs I have accurate observations for the time of the development of the embryo, and for the time of the eggs floating up. Table 1 gives the arithmetical mean weights for these 41 eggs, together with the median deviation and the extremes of the observations. The median deviations, *m*, are worked out by the equation $m = \pm \sqrt{\frac{(b-A)^2}{n}}$ where *b* is each separate observation, *n* the number of observations (= number of eggs), and *A* the arithmetical mean for the *n* observations.

The eggs float up after being incubated on the average for 42.4 per cent of total time of development, and the total loss of weight in

per cent of weight of newly-laid eggs averages 21.8. Two of the carefully studied eggs (not recorded in the tables) had decided cracks in their shells, and as a consequence showed an exceptionally great loss of weight. Nevertheless, the embryos developed and hatched.

TABLE 1

AVERAGE DATA ON 41 EGGS OF Larus canus

(The average time of development is 25 days)

Weight in grams	Arithmetic Mean and Median Deviation	Greatest Variation from arithmetic Mean	Observed Range
Weight of newly-laid egg, (w_0)	53.3 ± 4.3	8.3	45.0-61.5
Number of days before floating up Time before floating up in percentage of total time of	10.6 ± 1.5	2.6	8 -13
development	42.4		32.0-52.0
Weight when just floating			
up (v)	49.3 ± 3.9	7.3	42.0 -56.5
Loss of weight before			
floating up	4.0 ± 0.5	1.0	3.0-5.0
Loss of weight per day			
before floating up (k)	0.38 ± 0.07	0.18	0.25-0.56
Total loss of weight in per- cent of weight of newly-laid egg	21.8		17.3-35.0
Specific gravity of newly- laid egg $(d_0 = w_0/v)$	1.081 ± 0.0075	0.017	1.068-1.098

All these eggs floated 8 to 13 days after they had been laid. If we put each day in a category by itself, the results are as given in table 2.

Small eggs lost weight more rapidly than large ones. This is shown in table 2 by combining the first three categories (8 to 10 days before floating, average weight 52.3 gm.) and the last three (11 to 13 days before floating, average weight 54.4 gm.). It is not possible, however, to use this as a definite rule. Small eggs may float late, and large eggs may float early.

At that point in the incubation period when the egg's specific gravity (shell + contents) is one, then the figure for the total weight in grams is the same as that for the volume in cubic centimeters. This gives a possibility for an exact determination of the volume of eggs. The method is based on the buoyancy, and is therefore *independent of the shape of the egg.* All equations for calculating the volume based on the axes of the eggs will give great errors. To look at an egg as an ellipsoid of rotation will in a few instances be correct. In the Laridae

the shape of the egg varies greatly even within the same species. Two eggs may have the same length and breadth and still have different volumes. The extremes are represented by those shaped like pears. By weighing such eggs, it is immediately possible to distinguish the great difference in their mass, even though their axes are the same. For this reason it is important that the equation for the volume does not contain the figures for the axes.

TABLE	2
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Correlation between Time of Floating and Weight of Eggs

		Average weight, newly-laid egg	Number eggs	Average weight, newly-laid egg	
4	8	50.6 gm.)			
4	9	53.8	21	52.3 gm.	
13	10	52.5			
7	11	54.5			
8	12	54.3	20	54.4 gm.	
5	13	54.4			
Total 41			41		

GENERAL FORMULAE

The following relation defines the volume: V = w/d, where w is the weight and d is the specific gravity. If the egg is newly-laid we put: $V = w_0/d_0$.

From table 1 we find $d_0 = 1.081$; hence

 $V = 0.925 w_0$ for *L*. canus.

During the incubation period the weight decreases regularly by an amount, k grams per day, until the chick starts pecking at the shell. After n days we have: $w_n = Vd_0 - kn$, or $V = w_n + kn/d_0$; w_n (or w_0) is found by weighing each time; d_0 and k must be determined empirically for each species. Table 1 shows that, in L. canus, k = 0.38, and $d_0 = 1.081$; consequently, V = 0.925 ($w_n + 0.38n$) for L. canus.

If *n* is unknown, a water test can approximate it. The median error and maximum error of the volume thus computed are ± 0.3 cc. and ± 0.7 cc., respectively. (These figures correspond to the median deviation and maximum deviation in d_0 as listed in table 1.)

According to my observations, the eggs of few kinds of birds vary as greatly in size, shape, and quality of the shell, as those of the gull. The range of the variation of d_0 and k should be smaller therefore for birds other than the Laridae.

For other kinds of birds average values for d_0 and k are now being computed. As examples, some preliminary figures are given in table 3. (For comparison, the data of *L. canus* are repeated.)

April 1953] If weight and specific gravity of the shell are known, the internal volume of an egg can be computed. My data demonstrate that the weight of the empty shell of eggs of *L. canus* is close to 3.0 gm., and Schönwetter has determined that the specific gravity approximates 2.0. Thus the average internal egg volume is $V' = 0.925 w_0 - 3/2 = 47.8$ cc. for *L. canus*.

TABLE 3

			Volume		
Species	Weight of newly-laid egg (w ₀) <u>f</u> in grams	weight br. day (k)		Specific gravity of newly-laid egg (d ₀)	newly-laid egg, and for
•	vn grums	in grums	meters	egg (u0)	
Larus argentatus	97.0	0.50	90.99	1.066 {	$V = 0.938 w_0$ $V = 0.938 (w_n + 0.50 n)$
Larus fuscus	} 76.7	0.37	71.48	1.073 {	$V = 0.932 w_0$ V = 0.932 (w _n + 0.37 n)
Larus canus	} 53.3	0.38	49.3	1.081 {	$V = 0.925 w_0$ V = 0.925 (w _n + 0.38 n)
Haematopus ostralegus	} 43.5	0.32	39.02	1.087 {	$V = 0.920 w_0$ V = 0.920 (w _n + 0.32 n)
Sterna hirundo	21.0	0.167	19.49	1.078 {	$V = 0.928 w_0$ V = 0.928 (w _n + 0.167 n)
Tringa totanus	} 21.0	0.118	19.70	1.066	$V = 0.938 w_0$ V = 0.938 (w _n + 0.118 n)
Turdus pilaris	8.0	0.10	7.40	1.081	$V = 0.925 w_0$ V = 0.925 (w _n + 0.10 n)
Delichon urbica	} 1.91	0.02	1.81	1.056	$V = 0.947 w_0$ $V = 0.947 (w_n + 0.02 n)$
Phylloscopus trochilus	} 0.95	0.0125	0.90	1.056	$V = 0.947 w_0$ V = 0.947 (w _n + 0.0125 n)

AVERAGE DATA ON EGGS OF VARIOUS BIRDS

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Comparison of Methods

I have mentioned that Groebbels and Möbert computed the egg volume by adding not more than 3 per cent to the weight of the egg filled with water. Let us use this method on my material listed in table 1. The average egg of *L. canus*, filled with water, will weigh 47.8 + 1.4 = 49.2 gm. The correct value is, however, 53.3 gm.; the Groebbels-Möbert method thus gives values that are about 8 per cent too low.

The equation for the volume of a hen's egg, given by Grossfeld, is: $V = 0.519 L B^2$, where, as stated previously, L is the egg's long axis, and B its short axis. Through measuring 382 eggs from L. canus, I have found the following averages: L = 5.74 cm., B = 4.10 cm., and weight when newly-laid $(w_0) = 51.8$ gm. Grossfeld's equation gives here: $V = 0.519 \cdot 5.74 \cdot 4.10^2 = 50.1$ cc. My equation, $V = 0.925 w_0$, gives: $V = 0.925 \cdot 51.8 = 47.9$ cc. Thus the values of Grossfeld's are about 4.5 per cent too large. Grossfeld thinks that his formula can be used to determine the volume of eggs in collections (blown-out eggs). This may, however, lead to serious errors.

An almost identical formula, $V = 0.51 L B^2$, was given by Bergtold (1929) and used by Westerskov (1950) on pheasants' eggs. Worth uses, $V = 0.85 \left(\frac{\pi L B^2}{6}\right)$, which may be reduced to 0.445 L B².

Measurements carried out on the 41 eggs listed in table 1 give, as average values, L = 5.819 cm. and B = 4.126 cm. Used on this material, Grossfeld's formula and Bergtold's and Westerskov's formula give volumes that are respectively 2.1 cc. and 1.2 cc. too large, whereas Worth's formula results in a volume that is 5.2 cc. too small.

Johannes Erstad (1945) has examined hens' eggs, and weighed 83 of them. Further, he has calculated the volume of the eggs by immersion in water. He also has determined the specific gravity and measured the long and short axes for all the eggs. In tabular form he has made a comparison between his own calculations of the volume, and the volumes he arrived at by using Grossfeld's equation (see above). When using this equation, the results usually give large errors, especially for the distinctly pear-shaped and spherical eggs.

From the specific gravity of all eggs tabulated by Erstad, I have arrived at the following relation for the volume: $V = 0.930 w_0$ for hens' eggs.

Table 4 shows the volume relation of eggs that, according to Erstad, are of abnormal shape. The calculated volumes, according to the methods of Grossfeld, Bergtold and Westerskov, and of myself, are compared with the correct volumes as directly measured by Erstad.

Eggs No. 3, 11, and 22 must have been shaped like pears because the earlier authors' formulae give figures which are too large. Nos. 49 and 72 must have been almost spherical, giving figures which are too small. By the use of Worth's formula still greater discrepancies will result. These calculations demonstrate the fundamental inadequacy of any volume formula based on measurement of the axial length of an egg.

The use of Heinroth's method for determining the weight of newlylaid eggs, in connection with Erstad's tables, gives good results by adding about 2 per cent to the weight of the water-filled egg shells, as Groebbels and Möbert have pointed out. For L. canus I have shown that one must add about 8 per cent to the weight of the water-filled shell to get the correct result. The reason for this difference is chiefly due to weight of the shell which is much greater for eggs of domestic chickens than for those of L. canus.

TABLE 4

VOLUME RELATIONS OF HENS' EGGS ACCORDING TO VARIOUS AUTHORS (All data in cubic centimeters)

Table of Erstad, egg no.	Correct volume, according to Erstad	Volume calculated after Grossfeld	Variation from correct volume	Volume calculated after Bergtold and Westerskov	Variation from correct volume	Volume calculated after Barth	Variation from correct volume
3	59.99	64.8	+4.8	63.73	+ 3.74	59.38	- 0.61
11	57.43	62.0	+5.0	60.97	+ 3.54	57.33	- 0.10
22	62.69	65.2	+2.5	64.05	+1.36	62.99	+0.30
49	48.21	46.1	- 2.1	45.29	- 2.92	48.41	+0.20
72	68.58	65.6	- 3.0	64.47	- 4.11	68.89	+ 0.31

CONCLUSIONS

The known formulae for computing the volume of eggs are unsatisfactory because they are based on measurements of the length of the axes of the eggs.

A new formula which is independent of the shape of the egg and which is usable for eggs of all species is offered for consideration. It is based on the general relation—V = w/d—where V is the volume, w the weight, and d the specific gravity of an egg.

The specific gravity of a newly-laid egg has a characteristic value for each kind of bird; for *Larus canus*, $d_0 = 1.081$ and consequently $V = 0.925 w_0$ for *L. canus*, where w_0 is the weight of the newly-laid egg. After *n* days of incubation the weight, w_n , shows the following relation:

 $w_n = Vd_0 - kn$, where k is a constant denoting the loss of weight suffered by the egg per day. Consequently, $V = (w_n kn)/d_0$, or V = 0.925 ($w_n + 0.38n$) for L. canus.

For L. canus, values of d_0 and k have been found statistically, and preliminary values have been calculated for some other kinds of birds (see table 4). The value of w_0 (or w_n) must be determined by weighing each time.

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