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Accurate calculation of the content volume, density and original weight of museum curated eggs

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Worldwide museums hold collections of eggshells representing material for descriptive studies. However, an obstacle to this is the lack of information about the original contents and weight of the entire egg (*W*). This study aimed to fill this gap though development of a methodological mechanism for calculating the volume of the egg interior (*Vi*), its density (*Di*) and *W*. To determine *Vi*, it is sufficient to measure four geometric dimensions of the egg and shell thickness. The *Di* value depends on the surface area-to-volume ratio (*S*/*V*) and can be calculated from an empirical relationship. For its derivation, data on 454 eggs from 447 avian species, 95 families and 13 orders were used. Imputing data on the contents and shell weight (*Ws*), we proposed a theoretical relationship for calculating *W*. We found a negative correlation between *Di* and *S*/*V* (which reflects the egg metabolism level) and suggest that a female in most species maintains the duration of egg incubation at a constant level that has practically an unchanged value for the respective species. A mathematical algorithm for calculating the *Di* value depending on the *S*/*V* ratio provides the missing link in calculating *W* of a whole egg from archived collection material.

Keywords Museum bird eggshells, Egg weight, Egg contents, Density of egg interior, Surface area-to-volume ratio, Egg metabolic rate

The enduring popularity of investigations into the density of bird eggs' interior (D_i)[1–3] is mostly due to the fact that D_i can be an indirect indicator of quality, particularly important for poultry species[3]. The value of D_i may even be used to estimate the sex of the embryo, which would be useful for poultry management technologies, if applied widely[4,5]. The use of destructive methods for examining eggs of wild bird species is, of course, unacceptable in view of current environmental protection agenda, ethical issues and conservational concerns. The possibility, therefore, of non-invasive assessment of D_i for non-domesticated species could allow for a new wave of ornithological applications to study its relationship with offspring survival, sex ratio, ecological impact, evolutionary principles and many other factors.

The earlier works of authors who explored the structure, physical and biological interdependencies of egg contents are especially relevant, particularly a large number of allometric studies describing the relationship between various parameters of bird eggs and their weight (W). Most were derived by a group of scientists led or coordinated by an American Professor Hermann Rahn (1912–1990; see the respective biographical memoir by Pappenheimer[6]). In spite of those, D_i remained without an appropriate description in terms of mathematical dependencies. Rahn and Paganelli[2], examining the variability of this parameter, suggested using a constant value of 1.031 g/cm^3 for all eggs by demonstrating the adequacy of this value for eggs of both domestic and wild species.

In our previous work[3], we demonstrated a theoretical relationship between D_i and other egg parameters as follows:

$$D_i = \frac{W - W_s}{V - V_s}, \quad (1)$$

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where D_i is density of the egg contents (in g/cm^3), W is egg weight (in g), W_s is shell weight (in g), V is egg volume (in cm^3), and V_s is shell volume (in cm^3).

For further calculations, we used the Paganelli et al.[1] allometric relationships regarding W_s and V_s, as well as V, with the latter being obtained from the formula for egg density (D) presented by those authors:

$$W_s = 0.0482W^{1.132}, \tag{2}$$

$$V_s = 0.0248W^{1.118}, \tag{3}$$

$$V = 0.963W^{0.994}, \tag{4}$$

where V_s and V are measured in cm^3, and W_s and W are measured in g.

Substituting Eq. 2 to 4 into (1), we can derive the following formula:

$$D_i = \frac{W - 0.0482W^{1.132}}{0.963W^{0.994} - 0.0248W^{1.118}}. \tag{5}$$

Substituting the W values from 0.5 to 1000 g (which approximately corresponds to the entire series of eggs existing in nature) into Eq. 5, the resultant calculation of D_i allowed us to obtain the graphical dependence presented in Fig. 1.

The nature of the resultant dependence in Fig. 1 does not fit into the framework of the usual allometric relationship, i.e., power function, which invoked the Rahn and Paganelli[2] decision to recommend taking the value D_i in the form of a constant in calculations.

In our preliminary work[3], we dwelled in some detail on methods for non-destructive assessment of the D_i value. The results obtained turned out to be quite promising, but were purely empirical in nature. Experimental studies were carried out on chicken eggs using destructive assessment methods, suggesting a set of parameters that most accurately predict D_i. The resultant computation formulae, however, cannot automatically be transferred to eggs of other species. That is, interspecific trends in the variability of this parameter need to be taken into account. This is because they can, firstly, be pivotal for understanding evolutionary processes. Secondly, they can serve as an impetus for other oological studies limited by a lack of data and. Most importantly, however, we cannot derive real world data for D_i of wild bird eggs due to the need to use destructive measurement methods to establish them.

In order to develop a universal methodology for calculating the D_i value among multiple avian species, museum collections of eggs (see, for an example, Fig. 2), of which millions of pieces have been accumulated in various storage facilities[7,8], provide a most useful resource. Most often, a researcher examining such collections can only deal with the shell remaining from a once whole egg, and reliable information about its W is a thing of the distant past. Knowledge of the D_i value of a particular egg that can, nonetheless, contribute to the calculation

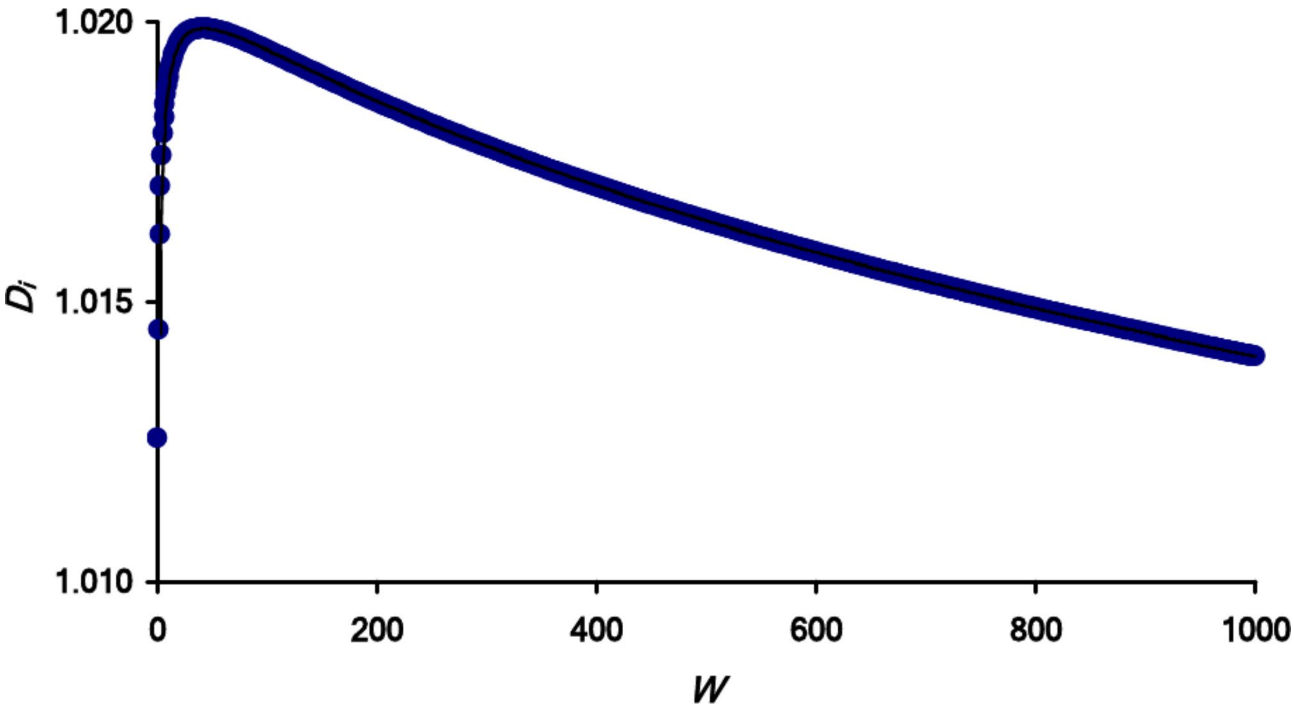

Fig. 1. Graphical visualization of Eq. 5 for density of egg contents (D_i) depending on egg weight (W).

Fig. 2. Example of the shell of a Kākāpō (*Strigops habroptilus*) egg from the collection of the Auckland Museum, New Zealand (https://commons.wikimedia.org/wiki/File:Strigops_habroptilus_(AM_LB14427-1).jpg , by Fæ; CC-BY-4.0).

of the W value of these eggs. From a mathematical point of view, such restoration of a disappeared parameter is relatively straightforward.

Transforming Eq. 1 into the following formula:

$$W = (V - V_s)D_i + W_s. \tag{6}$$

The V value of an egg can be quite easy to determine. Our oological group alone has proposed about seven different approaches for calculating this indicator based on simplified, more complex and most accurate dependencies[9–16]. W_s can be easily obtained by weighing museum exhibits. With respect to V_s, the question is somewhat more complicated since museum rules prohibit immersing exhibits in water to prevent possible damage. Previously, we laid down theoretical approaches to calculating this parameter non-invasively[17,18]. However, given the variety of bird egg shapes that exist in nature, the calculation of the V_s value requires some improvement (see below).

Theoretical approaches to calculating V_s.

Using the theoretically derived formula for a mathematical description of the shape of any bird egg[19], we defined the following calculated relationship for determining V of such an ovoid[16]:

$$V = \frac{\pi}{128}\left[\left(8.917 - 29.998\frac{w}{L}\right)\left(\frac{D_p}{B}\right)^2 + \left(2.459 + 88.647\frac{w}{L}\right)\frac{D_p}{B} - 36.26\frac{w}{L} + 12.453\right]LB^2 \tag{7}$$

where L is egg length, B is its maximum breadth, w is the parameter that shows the distance between two vertical lines conforming to B and the half length of the egg ($L/2$), and D_p is diameter measured at a point distant from the pointed end of the egg by $L/4$.

Transforming Eq. 7 into the following form:

$$V = (0.219L - 0.736w)D_p^2 + (0.06L + 2.176w)D_pB + (0.306L - 0.89w)B^2. \tag{8}$$

Similar to the course of mathematical transformations presented by us in the study by Narushin et al.[18], we find the volume of egg contents (V_i), correspondingly reducing the geometric dimensions in Eq. 8 by twice the shell thickness (T), except for the parameter w, the value of which remains unchanged, as was demonstrated in our previous investigation[17].

$$V_i = [0.219(L-2T) - 0.736w]\,(D_p-2T)^2 + [0.06(L-2T) + 2.176w]\,(B-2T)(D_p-2T) + [0.306(L-2T) - 0.89w]\,(B-2T)^2 \quad (9)$$

The mathematical transformation of Eq. 9 resulted in the following equation:

$$\begin{aligned} V_i &= (0.219L - 0.736w)D_p^2 + (0.06L + 2.176w)BD_p + (0.306L - 0.89w)B^2 \\ &- \big[0.438D_p^2T + 4T(0.219L - 0.736w - 0.438T)(D_p - T) \\ &+ 0.121BD_pT + 2T(0.06L + 2.176w - 0.121T)(B + D_p - 2T) \\ &+ 0.611B^2T + 4T(0.306L - 0.89w - 0.611T)(B - T)\big] \end{aligned} \quad (10)$$

Considering that V of a bird's egg can be represented as the sum of V_i and V_s, analysis of Eqs. 8 and 10 suggests that:

$$\begin{aligned} V_s = 4T\,\big\{&0.11\left[D_p^2 + 2(L - 3.361w - 2T)(D_p - T)\right] \\ &+ 0.03\left[BD_p + (L + 36.267w - 2T)(B + D_p - 2T)\right] \\ &+ 0.153\left[B^2 + 2(L - 2.908w - 2T)(B - T)\right]\big\} \end{aligned} \quad (11)$$

Thus, to determine the V_s value, one needs to measure the geometric parameters of the egg (B, L, w and D_p) and T. Most often, T values in museum collections (e.g., Fig. 2) can be measured directly or using a special micrometer with an extended pin. For small museum eggs or for shells with very small holes, ultrasonic thickness gauges can be used that are common in many industries (e.g., Deis and Allen[20]), including commercial poultry production[21–23]. As a result, the D_i value (Eq. 6) is the only parameter that impedes the recalculation of W and thereby accurate information about what museum ostraca, sherds and shells were like before they became exhibits.

A promising criterion that seems to be very informative in assessing the correlation relationships with the D_i value may be the ratio of the egg surface area to its volume (S/V). Based on the results of studies that analyzed the influence of this index on the indicators of various biological mechanisms (e.g., Cohen et al.[24], Cragg[25], Harris and Theriot[26], Lewis[27]), the S/V value may prove to be very relevant for predicting the parameters of the egg contents.

The goal of the current studies was to develop a method for non-destructive prediction of the density of the contents in various bird species eggs (i.e., D_i) depending on their physical and geometric features.

Materials and methods

As part of the research, on the one hand, we used the published results of other researchers who have performed such experiments previously (e.g., Rahn and Paganelli[2]). On the other, it was important for us to develop our own approach to calculating D_i using data from oological measurements of other parameters of bird eggs. Although, among these parameters, there is no direct information on D_i, the available other characteristics allow us to judge the D_i value indirectly.

The most extensive source of oomorphological data is the reference book by Schönwetter[28], used by Paganelli et al.[1] when deriving their allometric dependencies. It was especially important for this study that Schönwetter[28], in addition to oomorphological parameters, also placed many images of bird eggs, whose data was included here in the reference information. This enabled us to measure all the geometric egg parameters required not only to calculate V_s (Eq. 11), but also V (Eq. 7), as well as S according to the formula from Narushin et al.[16]:

$$S = \pi BL\left(0.389 + 0.188\frac{B}{L} - 0.063\frac{w}{L} + 0.365\frac{D_p}{B} + 0.114\frac{D_p}{L} - 0.168\frac{w}{L}\cdot\frac{B}{L} + 0.46\frac{w}{L}\cdot\frac{D_p}{B} + 0.484\frac{w}{L}\cdot\frac{D_p}{L}\right). \quad (12)$$

We described the procedure for measuring images of bird eggs in detail in the results of our previous studies[29,30]. Briefly, the egg image was measured in pixels using an electronic ruler in Microsoft Office Picture Manager. The pixel measurements were then converted to centimeters according to the eggs' metric data for L and B given in the tables of Schönwetter[28]. Schematically, the measurements of images of bird eggs are presented in Fig. 3.

Schönwetter[28] in his oological reference book presented images of 434 eggs belonging to 433 avian species. Despite the large array of data obtained, the drawback of their analysis was the relatively low W range of eggs with available images, i.e., from 1 to 100 g. For a more complete analysis, we lacked data on birds laying eggs of greater W values. In this respect, we used the numerical values of such eggs from the reference book Schönwetter[28], while relying on images of these eggs obtained from other sources, e.g., the digitized collection of images of bird eggs from the Natural History Collections of the Museum Wiesbaden[31]. As a result, a total of 454 eggs belonging to 447 avian species, 95 families and 13 orders were represented. The entire list of avian species whose eggs were used in the current study can be found as Supplementary Table S1 online.

The second stage of our experimental analysis of D_i values was based on data presented in Rahn and Paganelli[2]. Their results were based on data from some earlier findings by Roca et al.[32], in which the authors studied the density, weight and chemical structure of the main components the egg contents, i.e., albumen and yolk. Although these investigations were carried out on eggs of only 14 bird species representing six families and five orders, they provided invaluable material for a more in-depth analysis and derivation of relationships with those egg parameters, the measurement of which can be performed non-invasively even during field studies.

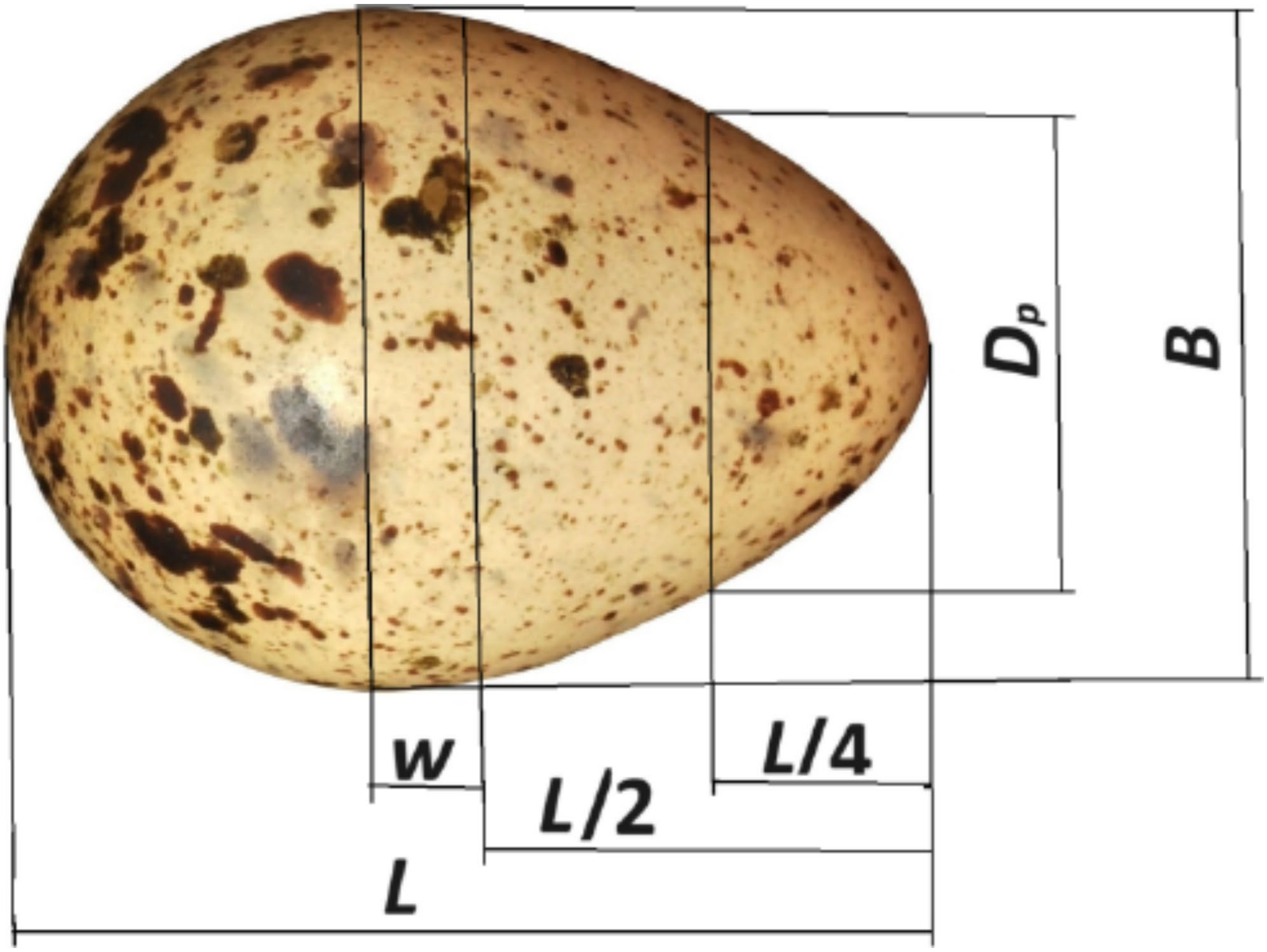

Fig. 3. Schematic representation of the measured geometric parameters using the example of the Common Sandpiper egg image (*Actitis hypoleucos*). (Image source: https://commons.wikimedia.org/wiki/File: Actitis_hypoleucos_MWNH_0255.JPG, by Klaus Rassinger and Gerhard Cammerer, 2012; CC-BY-SA-3.0[31]).

Images for computing geometric characteristics in this group of eggs were obtained from the Natural History Collections of the Museum Wiesbaden[31] and the Muséum de Toulouse[33].

When performing the experimental procedure, we encountered one undermentioned constraint related to the definition of the concept embedded in the value of the parameter D_i. On the one hand, the D_i value can be determined by the density of the main components of the contents: albumen and yolk. This is the approach undertaken by Roca et al.[32] Perhaps it is applicable when examining freshly laid eggs in which the air cell has not yet formed. However, in practice, this is extremely difficult to achieve, if at all possible.

In our opinion, the contents should include the values of W (and/or V) of the egg after subtracting W_s (and/or V_s) of the shell. That is, this calculation should take into account the fact that if the air cell weight is conditionally equal to 0, its volume can be very significant, especially during the process of hatching or even storing eggs (e.g., Narushin et al.[34]). In this context, when calculating D_i, a certain process naturally occurs that depends on the time elapsed between laying and weighing an egg. Despite this error, a larger array of analyzed data will not greatly distort the eligibility and general trend of possible dependencies.

The next assumption in our calculations was the fact that the shell membrane was classified as a component of the shell. This assumption was also adhered to by Schönwetter[28] who placed data on T and W_s in his reference materials. Moreover, the shell membrane is present in the composition of the shell in museum collections, which was the fundamental factor in combining these membranes into a single structural component of the egg used in further calculations here.

To process the results, statistical and mathematical algorithms were used that are available in the STATISTICA 5.5 program (StatSoft, Inc./TIBCO, Palo Alto, CA, USA), as well as applications to the Microsoft Excel program. Thereby, the validity of the obtained relationships was assessed by the value of the Pearson correlation coefficient (R) and regression models using the coefficient of determination (R^2) with confirmation of their significance at the level of $p < 0.05$.

Results and discussion

As a result of the analysis of experimental data, we found a significant, although relatively lower, correlation between the D_i value and the S/V ratio ($R = -0.277$, $p < 0.05$). A negative sign of the correlation coefficient was indicative of an inverse relationship between these values as also demonstrated by the graphical interpretation of this dependence (Fig. 4).

The S/V value is an indirect criterion for reflecting the level of embryonic metabolism that was examined in detail by us in a number of our recent studies[16,35,36]. Thus, it can be assumed that eggs with denser contents have a lower metabolic rate. This assumption was accepted by us as a working hypothesis requiring at least a logical justification.

According to various authors[32,37], the density of the yolk is slightly higher than that of the albumen. Thus, eggs with greater yolk content also appear to have higher D_i values. Taking into account the fact that the yolk contains the main nutritional components necessary for the developing embryo[37], it is quite logical to assume that embryo's maturation occurs at a slightly slower pace, which is regulated by a decrease in the metabolic rate (S/V). This fact can be confirmed by the results of our previous studies[30], in which we demonstrated an inverse relationship between incubation time and S/V value using a large interspecific sampling of bird eggs. In other words, in species whose eggs have a relatively lower level of metabolism, hatching periods will be expected to be longer.

We asked the question whether the existence of such a relationship between D_i and S/V is possible due to the high level of differences in the weight fractions of oomorphological parameters included in the computation equation used to recalculate the D_i value (Eq. 1). To answer this question, we decided to isolate from the general sampling, and analyze separately, eggs of the order Passeriformes characterized by relatively similar values of W and weights of egg's structural components. For example, within the framework of our current research, the W value of Passeriformes eggs was in the range of 0.5 to 11 g. The results of this analysis are presented in Fig. 5.

Dependence analysis in Fig. 4 also suggests a similar negative relationship between these parameters, although with a slightly lower but significant correlation coefficient ($R = -0.101$, $p < 0.05$). That is, the nature of this relationship remained unchanged in general.

An analysis of the relationship between the D_i value and the S/V ratio was also carried out on the data presented by Roca et al.[32] The correlation between these indicators was $R = -0.358$, although it was statistically non-significant, probably due to a limited sampling of bird eggs ($n = 14$). A visualization of the resulting relationship is presented in Fig. 6 and is fully consistent with our results for a more representative sampling (Figs. 4 and 5).

In order to completely remove questions about the relationship between D_i and S/V, we decided to carry out such an analysis on the eggs of birds of the same species. This experiment could only be carried out on poultry eggs. Considering that we previously performed a study on calculating the morphological parameters of goose eggs[38], we used the measurements taken as part of that work (Fig. 7).

The resultant relationship was fully concordant with our hypothesis about a decrease in the level of embryonic metabolism in eggs with denser contents. The correlation between the parameters D_i and S/V was at the level of -0.122, but turned out to be insignificant.

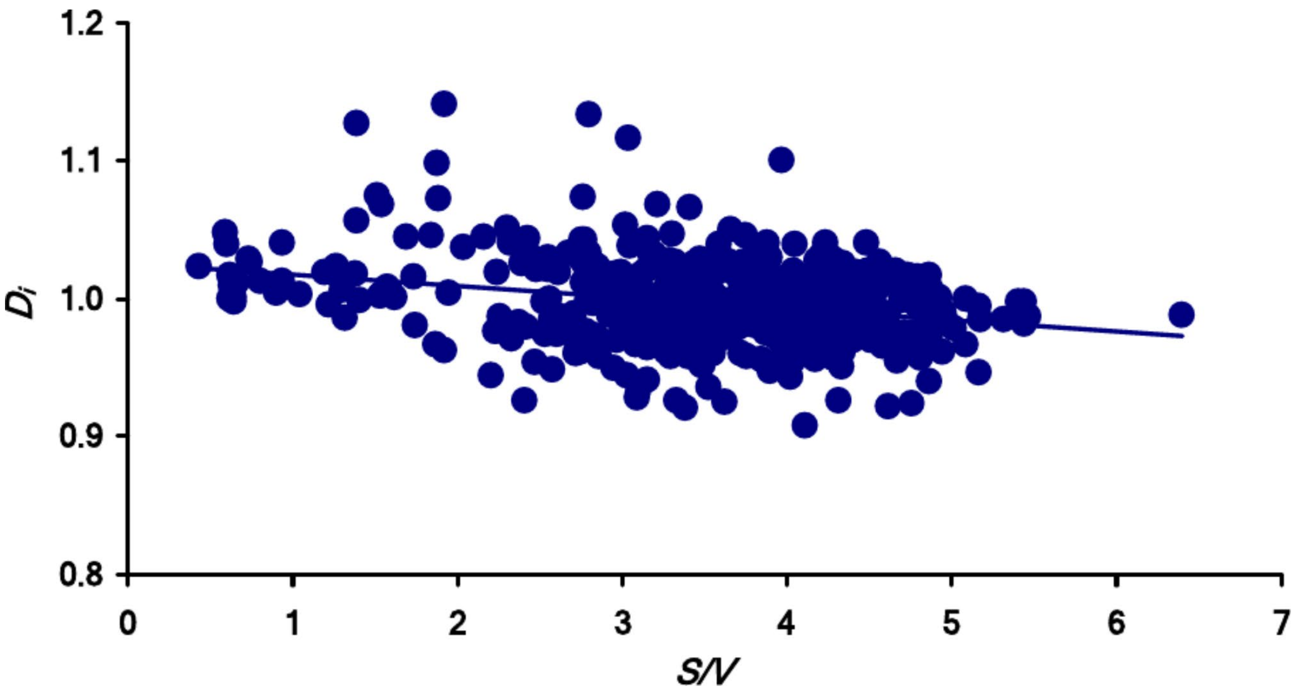

Fig. 4. Graphical visualization of the relationship between D_i and S/V.

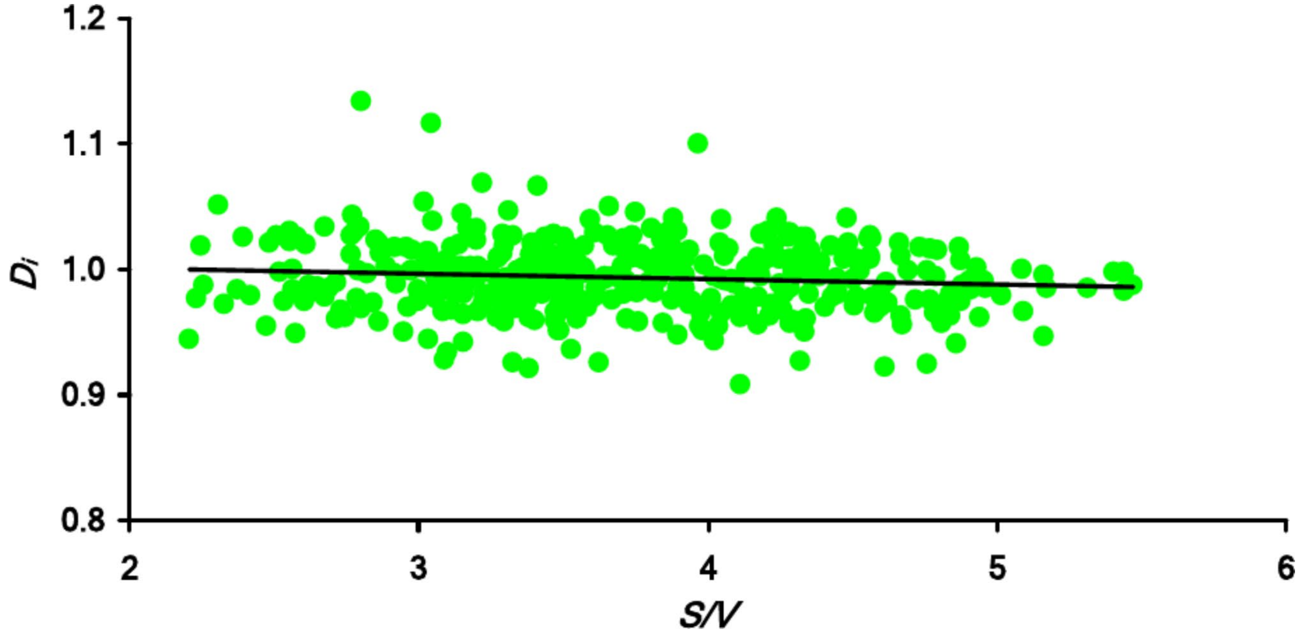

Fig. 5. Graphical visualization of the relationship between D_i and S/V in eggs of the order Passeriformes.

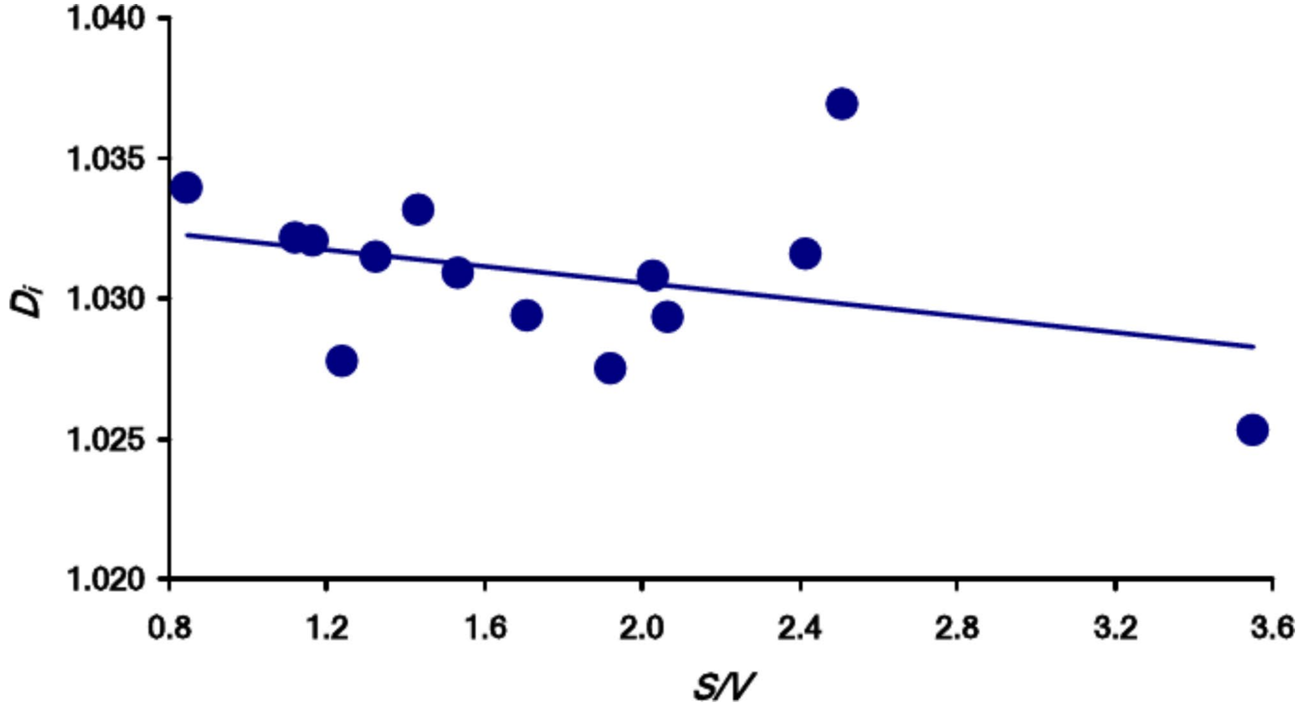

Fig. 6. Graphical visualization of the relationship between D_i and S/V calculated from the data by Roca et al.[26].

Based on the free energy minimization principle (e.g., Karl[39]), including minimized costs of reproduction, the mother bird very clearly, even at the species level, invests into the interaction between the size of the yolk that she managed to produce and the parameters V and S of the entire egg. Thereby, she maintains the duration of incubation of her offspring at a constant level that has practically an unchanged value for the respective species.

Since one of the fundamental factors that served as an impetus for carrying out these studies was the possibility of restoring museum shell remains into a full-fledged, albeit virtual, analogue of a whole egg, we need to be able to recalculate the value of D_i for these purposes. Based on our present research, the most convenient and logical

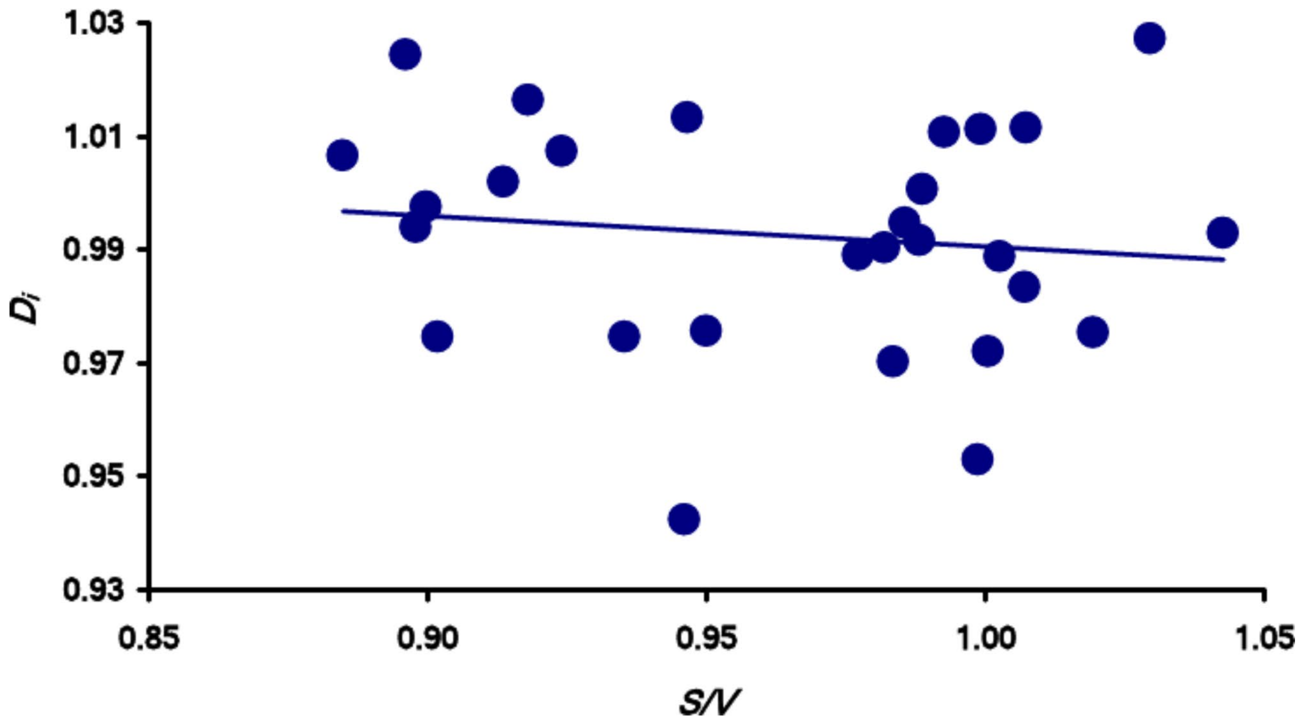

Fig. 7. Graphical visualization of the relationship between D_i and S/V in goose eggs.

parameter for carrying out such a calculation turned out to be the S/V ratio. Mathematical approximation of data in Fig. 4 allowed us to obtain the following dependence:

$$D_i = 1.0258 - 0.0083\frac{S}{V}, \quad (13)$$

with $R^2 = 0.077$ ($p < 0.05$),

where D_i is measured in g/cm^3, V in cm^3, and S in cm^2.

Despite of a lower value of R^2, its meaning appeared to be significant and thus can be used for the corresponding recalculations of D_i.

Within the set of the studied eggs, the values of the S/V ratio varied from 0.4 to 6.4, due to which the resultant calculated D_i (Eq. 13) had a range of approximately 5% (i.e., 0.973 to 1.022). Naturally, the final calculation of the initial W value (Eq. 6) would provide an even smaller value of accuracy variation. However, considering that any study assumes the provision of the most accurate result that can be accepted as a final solution, we suggest following the proposed calculation of D_i (Eq. 13). In cases where preference is given to simplicity and/or speed of predicting, one can use the average D_i value that, within the data we analyzed, was 1.00 g/cm^3.

Thus, we suggest that the process of restoring the lost W value of a whole museum egg should, methodically, consist of the following stages:

1. A shell from a museum collection is weighed (W_s), its T and geometric dimensions (B, L, w and D_p) are measured.
2. The V value of the egg is calculated using Eq. 7, its S using Eq. 12 and V_s using Eq. 11.
3. The D_i value is computed using Eq. 13.
4. The W value of the whole egg is calculated using Eq. 6.

Conclusions

As an outcome of the current study and its results obtained therein on non-destructive prediction of D_i in various bird species eggs in relation to their physical/geometric features, two undermentioned postulates can be formulated. Firstly, an evolutionary feature of the bird egg is the inverse relationship between its D_i and embryonic metabolism expressed by the S/V ratio. Secondly, a mathematical algorithm for calculating the D_i value depending on the S/V ratio provides the missing link in calculating the initial W of a whole egg (Eq. 13), the value of which has hitherto not been available for the extensive collection material of shell membranes stored in the world's museums.

Author contributions statement.

Conceptualization, data curation, formal analysis, methodology, resources, investigation, software, visualization: VGN. Writing – original draft: VGN and MNR. Writing – review & editing: VGN, MNR, NAM, and DKG. Project administration: MNR. Supervision: DKG.

Competing interests statement The authors have no relevant financial or non-financial interests to disclose.

Ethics statement This study involved only images of the eggs from the electronic sources. No live animals or natural eggs were used. No compliance with ARRIVE or other relevant guidelines were needed.

Supplementary Information The online version contains supplementary material available at https://doi.org/.

Data availability
The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

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Conceptualization, data curation, formal analysis, methodology, resources, investigation, software, visualization: VGN. Writing – original draft: VGN and MNR. Writing – review & editing: VGN, MNR, NAM, and DKG. Project administration: MNR. Supervision: DKG.

Declarations

Competing interests

The authors declare no competing interests.

Additional information

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