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Original Article

Mathematical progression of avian egg shape with associated area and volume determinations

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Development of nondestructive techniques for estimating egg parameters requires a comprehensive approach based on mathematical theory. Basic properties used to solve theoretical and applied problems in this respect are volume (V) and surface area (S). There are respective formulae for calculating V and S of spherical, ellipsoidal, and ovoid eggs in classical egg geometry; however, the mathematical description and calculation of these parameters for pyriform eggs have remained elusive. In the present study, we derived the appropriate formulae and established that this would be not only applicable and valid for the category of pyriform eggs, but also universal and explicit for all other naturally occurring avian egg shapes. Thus, we have demonstrated "mathematical progression" of this natural object, considering the egg as a sequence of geometric figures that transform from one to another in the following sequence of shapes: sphere → ellipsoid → ovoid (whose profile corresponds to Hügelschäffer's model) → pyriform ovoid.

Keywords: egg shape geometry; egg volume; surface area; nondestructive measurement; mathematical progression

Introduction

Since the middle of the 20th century, there have been continual attempts to derive a mathematical model for the contours of a bird's egg. The starting point can be considered the work of Preston,[1] who proposed the basic approaches to the development of such equations. Although Preston[1] mentioned that his "investigation was not undertaken primarily as a mathematical amusement," he did state the more important aim that his contribution may eventually "throw some light on several biological and ecological problems." Carter,[2] when creating his model of an egg-shaped ovoid, pointed out that these mathematical developments are necessary primarily for the derivation of the basic geometric parameters of the egg, that is, volume and surface area.

We recently developed a theoretical formula that can be used to describe the contours of any standard bird egg found in nature:[3]

$$y = \pm \frac{B}{2}\sqrt{\frac{L^2 - 4x^2}{L^2 + 8wx + 4w^2}} \cdot$$

$$\left[1 - \frac{\sqrt{5.5L^2 + 11Lw + 4w^2} \cdot (\sqrt{3}BL - 2D_{L/4}\sqrt{L^2 + 2wL + 4w^2})}{\sqrt{3}BL(\sqrt{5.5L^2 + 11Lw + 4w^2} - 2\sqrt{L^2 + 2wL + 4w^2})}\right.$$

$$\left.\left(1 - \sqrt{\frac{L(L^2 + 8wx + 4w^2)}{2(L - 2w)x^2 + (L^2 + 8Lw - 4w^2)x + 2Lw^2 + L^2w + L^3}}\right)\right]$$

$$(1),$$

where B and L are the maximum breadth and length of the egg, w is a measure of the displacement of the B axis from the center of the egg, and $D_{L/4}$ is the egg diameter at the point corresponding to $\frac{1}{4}$ of its length from the pointy end. A schematic
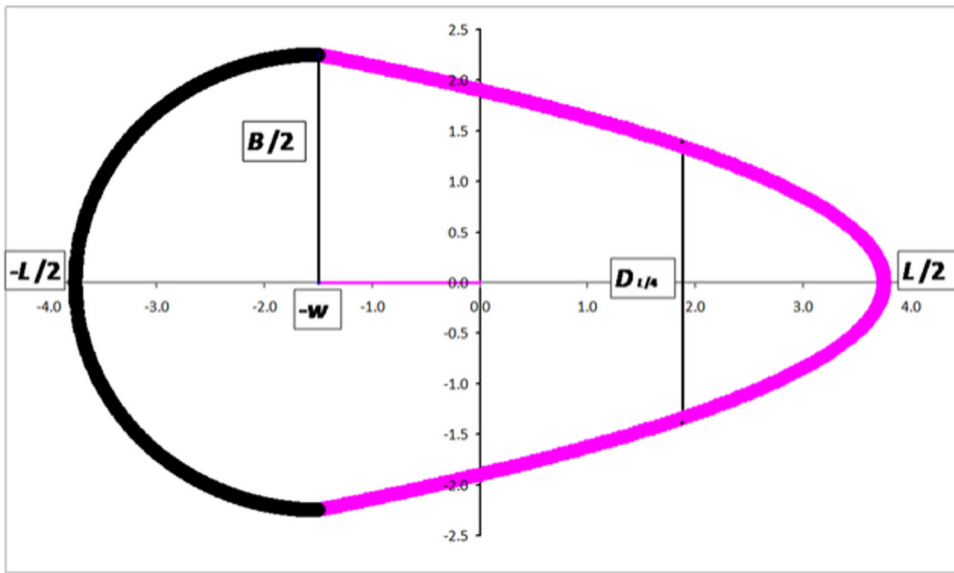
Figure 1. The geometry of the pyriform egg (adapted from Narushin *et al.*[19]).

representation of each of these parameters is shown in Figure 1.

Fully agreeing with opinions of previous researchers[1,2] that such dependencies, in addition to satisfying scientific interest, should also have a certain applied value, we aimed to continue the work of Preston[1] targeting derivation of mathematical dependencies for main geometrical egg parameters.

In the poultry industry, breeding, and ornithology, not only egg production traits, but also egg quality, including egg volume, V, and surface area, S, are considered as the most important characteristics. This is because the size of both table and breeder eggs can be used to judge egg weight,[4–7] air exchange,[8–10] incubation properties,[11] shell thickness and strength,[12,13] and egg content quality.[14] Most often, these indicators are targeted in research relevant to the poultry industry, and therefore, the calculation formulae for defining the egg volume and surface area, as derived in previous studies, were based both on empirical data[4,5,15] and theoretical computation.[16–19] Theoretically inferred formulae are of particular research and practical interest, since they do not depend either on the number of measurements or on the sample of eggs used in an experiment. As a result, their adequacy is not questioned as, for example, the theoretical formulae for finding V and S of an ellipsoid or a sphere. When deriving such theoretical dependencies concerning

the egg characteristics, the following fundamental formulae of integral geometry can be employed:

$$V = \pi \int_a^b y^2 dx \qquad (2),$$

$$S = 2\pi \int_a^b y\sqrt{1 + \left(\frac{dy}{dx}\right)^2}\, dx \qquad (3),$$

where a and b are the limits of integration of the function y, which describes the contour of the egg.

Despite the well-developed mathematical apparatus for integral calculations, it is sometimes quite difficult to carry out this operation, even using approximate calculation methods. We encountered this obstacle when deriving a formula for S_H of chicken eggs, the profile of which is described quite accurately by Hügelschäffer's model,[18,19] named after the German mathematician, engineer, and inventor Fritz Hügelschäffer.[20] Only using simulation methods and the minimum step in division of the integrated function enabled us to obtain an accurate result.[21]

Formula (1) is so complex to integrate that even approximate methods do not allow for mathematical transformations (2) and (3) to derive theoretical formulae that could be used to compute the volume
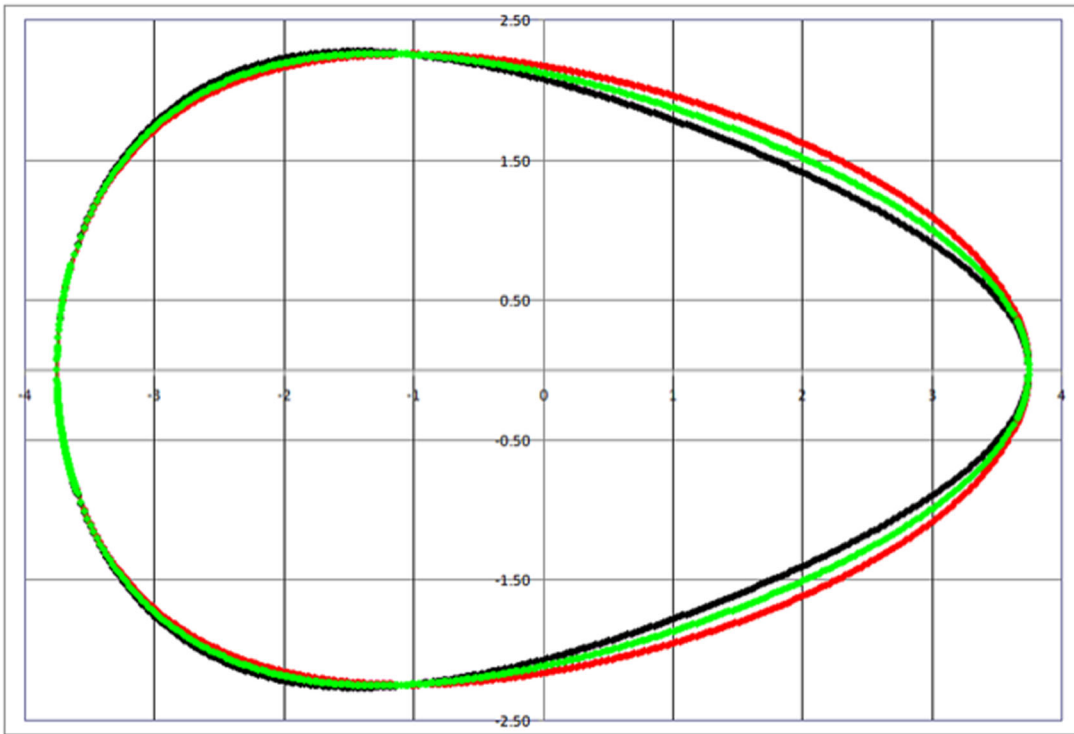
Figure 2. Possible egg contours (adapted from Narushin *et al.*[19]): black line, conical egg (parabola + Hügelschäffer's model); red line, usual ovoid egg (Hügelschäffer's model); green line, an egg whose profile lays just between the pyriform and ovoid contours.

and surface area for eggs of any shape, especially for not quite typical ones found in the poultry industry, that is, the so-called pyriform (pear-shaped) eggs.

In our previous study on deriving Eq. (1),[3] we assumed the progression of mathematical shapes of bird eggs from the simpler, spherical to the most complex, pyriform ones through the intermediate stages of ellipsoidal and ovoid shapes, the latter of which corresponds to Hügelschäffer's model.[21] Here, the availability of calculation formulae for V_H and S_H is limited to the first three forms, that is, spherical, ellipsoidal, and ovoid. Whereas calculation of spheres and ellipsoids is given in geometric reference books, to obtain adequate dependences for ovoids, whose shape obeys Hügelschäffer's model, we carried out a series of theoretical and experimental studies[18,19,21] that resulted in the following formulae:

$$V_H = \frac{\pi B^2}{256 w^3} \left(4wL(L^2 + 4w^2) - (L^2 - 4w^2)^2 \cdot \ln\left|\frac{L + 2w}{L - 2w}\right| \right) \quad (4),$$

$$S_H = \pi BL \left[\left(0.043 \frac{w}{L} + 0.292 \right) \frac{B}{L} - 0.061 \frac{w}{L} + 0.704 \right] \quad (5).$$

Thus, the problem was narrowed down to obtaining the calculated dependences V_{pyr} and S_{pyr} for pyriform eggs. As we showed earlier,[3] the boundary shape for such eggs is the combination of the paraboloid at the pointy end and the ovoid of Hügelschäffer's model at the blunt end (Fig. 1).

We further conditionally distinguish this subcategory of the pyriform shape as a separate one and call it conical.

As was also shown in our previous study,[3] between the contours of conical eggs and the profiles of all other types of eggs existing in nature and described with sufficient accuracy using Hügelschäffer's model, there are combinations of some intermediate contours corresponding to the green line in Figure 2 (taken from Ref. 3).

These eggs corresponding to the intermediate contours (green line in Fig. 2) are referred to below as pyriform.

With the above in mind, the objective of this study was to derive the theoretical dependencies V_{pyr} and S_{pyr} for pyriform eggs (based on conical to ovoid ones), as well as establish their mathematical adaptation for universal use in any bird's eggs found in nature.

Methodology

We proceed from the premise that theoretically derived formulae are to be preferred to empirically obtained formulae, since the accuracy of the latter may be adversely affected by small sample sizes and the materials or tools used. In this work, we, therefore, focus on theoretical investigations only.

Currently, a large amount of data have been accumulated on the size, shape, and variability of avian eggs in specific bird groups and for a broad diversity of the avian world. In our previous investigations,[3,21] we already substantiated possible variations in the ratios of basic geometric egg parameters: B/L and w/L, which made it possible to use simulation methods to create a virtual series of eggs with a full range of their geometric sizes. A similar methodological approach has been used here when performing these studies.

Since the derivation of theoretical dependences for calculating the egg volume and surface area was based on the classical equations of integral geometry (2) and (3), we also exploited a numerical method in MS Excel, as was proposed elsewhere.[22]

The accuracy of the obtained equations was tested using a classical statistic of the percentage error, ϵ, that equals the ratio of the difference between the predicted and actual data to the latter one, taken as a percentage.[23]

Theory and results

Conical eggs

Considering the subcategory of conical eggs (Fig. 1), egg volume, V_{con}, and surface area, S_{con}, can be conventionally represented as a sum of the respective parameters for two egg constituent parts, a paraboloid (i.e., solid of revolution of the parabola) at the pointy end and an ovoid (i.e., solid of revolution of the Hügelschäffer's model ovoid) at the blunt side. Let us consider below the derivation of formulae for each part separately.

Volume at the pointy end. To describe the pointy end of a conical egg, the following formula of the parabola was deduced by Narushin *et al.*:[3]

$$y = \pm \frac{B}{2} \cdot \sqrt{\frac{L - 2x}{L + 2w}} \tag{6}.$$

Considering Eq. (6) and the interval for x of this parabolic part of the egg as $[-w, L/2]$ (Fig. 1), the volume of the conic egg at the pointy end, $V_{con(p)}$, is determined using Eq. (2) as follows:

$$V_{con(p)} = \frac{\pi B^2}{4} \int_{-w}^{\frac{L}{2}} \frac{L - 2x}{L + 2w} dx \tag{7}.$$

Integration of Eq. (7) gives the following outcome:

$$V_{con(p)} == \frac{\pi B^2 (L + 2w)}{16} \tag{8}.$$

The respective integration steps are presented in more detail in File S1.1 (online only).

Surface area at the pointy end. When determining the surface area of the conical egg at the pointy end, $S_{con(p)}$, the interval for x will be similar, that is, $[-w, L/2]$. Then, using Eq. (3), the value of $S_{con(p)}$ can be determined as follows:

$$S_{con(p)} = 2\pi \int_{-w}^{\frac{L}{2}} \frac{B}{2} \cdot \sqrt{\frac{L - 2x}{L + 2w}} \sqrt{1 + \frac{B^2}{4(L + 2w)(L - 2x)}} dx \tag{9}.$$

This results in the following final equation:

$$S_{con(p)} = \pi B \cdot \frac{\sqrt{\left(4(L + 2w)^2 + B^2\right)^3} - B^3}{24(L + 2w)^2} \tag{10}.$$

The solution to integral (9) is detailed in File S1.2 (online only).

Volume at the blunt end. The blunt end of the pyriform (conical) egg can be described with the formula of Hügelschäffer's model, as was presented in Narushin *et al.*:[18]

$$y = \pm \frac{B}{2} \sqrt{\frac{L^2 - 4x^2}{L^2 + 8wx + 4w^2}} \tag{11}.$$

Considering the interval for x of the egg blunt end as $[-L/2, -w]$ (Fig. 1), the volume of this part of

the egg, $V_{con(b)}$, can be defined using the following classic formula of the integral geometry:

$$V_{con(b)} = \frac{\pi B^2}{4} \int\limits_{-\frac{L}{2}}^{-w} \frac{L^2 - 4x^2}{L^2 + 8wx + 4w^2} dx \qquad (12).$$

Integration of Eq. (12) leads to the following final formula:

$$V_{con(b)} = \frac{\pi B^2 (L - 2w)}{128w^2}$$

$$\left(L^2 + 2Lw + 8w^2 - \frac{(L - 2w)(L + 2w)^2}{4w} \cdot \ln \left| \frac{L + 2w}{L - 2w} \right| \right)$$

$$(13).$$

The integration steps are given in more detail in File S1.3 (online only).

Surface area at the blunt end. Considering the integration interval for x at the egg blunt end as $[-L/2, -w]$ (Fig. 1) and the original equation for y following Hügelschäffer's model (11), Eq. (3) for the blunt part of the egg will be rewritten as:

$$S_{con(b)} = 2\pi \int\limits_{-\frac{L}{2}}^{-w} y \sqrt{1 + \left(\frac{dy}{dx} \right)^2} dx \qquad (14).$$

Previously, we faced certain difficulties when trying to solve such an integral for the eggs defined per Hügelschäffer's model.[18,19] In our follow-up article,[21] we used numerical methods for solving this integral to derive an improved formula for recalculating S. In this regard, the same algorithm was taken as the basis for solving Eq. (14), which leads to the following result:

$$S_{con(b)} = \pi BL$$

$$\left[\left(0.2051 \frac{w}{L} + 0.1452 \right) \frac{B}{L} - 0.7066 \frac{w}{L} + 0.3531 \right]$$

$$(15).$$

A detailed analysis of the integration process is demonstrated in File S1.4 (online only).

Final formulae for conical eggs. To infer the final formulae for V_{con} and S_{con} of conical eggs, the volume and surface area of the whole egg are considered as a sum of the corresponding egg constituents, that is, its pointy and blunt ends, which will be equal to $V_{con} = V_{con(p)} + V_{con(b)}$ and

$S_{con} = S_{con(p)} + S_{con(b)}$, respectively. Hence,

$$V_{con} = \frac{\pi B^2}{16} \left[L + 2w + \frac{L - 2w}{8w^2} \left(L^2 + 2Lw + 8w^2 \right. \right.$$

$$\left. \left. - \frac{(L - 2w)(L + 2w)^2}{4w} \cdot \ln \left| \frac{L + 2w}{L - 2w} \right| \right) \right] \qquad (16),$$

$$S_{con} = \pi B \left(\frac{\sqrt{\left(4(L + 2w)^2 + B^2 \right)^3} - B^3}{24(L + 2w)^2} \right.$$

$$\left. + 0.2051 \frac{B}{L} w + 0.1452 B - 0.7066 w + 0.3531 L \right) \qquad (17).$$

Pyriform eggs
As we mentioned in the Introduction, we mean by the pyriform type of eggs all possible contours between the conical profile and the ovoid one, whose shape corresponds to Hügelschäffer's model (Fig. 2).

It should be noted that for all types of eggs, the blunt end shape corresponds to Hügelschäffer's model.[3] That is, keeping the same principle of assigning subscript indices we have adopted, the volume and surface area at the blunt end of pyriform eggs are denoted by $V_{pyr(b)}$ and $S_{pyr(b)}$, which will be identical to $V_{con(b)}$ (Eq. 13) and $S_{con(b)}$ (Eq. 15).

Therefore, our task has been reduced to finding only the volume and surface area at the sharp end of pyriform eggs, that is, $V_{pyr(p)}$ and $S_{pyr(p)}$, respectively.

Volume at the pointy end. The boundary contours of the sharp end of the pyriform egg are the conical shape on the one side, and Hügelschäffer's model, on the other side. For the conical profile, we derived the calculation formula of $V_{con(p)}$ (Eq. 8). This value reflects the minimum possible volume of a pyriform egg. The maximum value is obtained when the outline of the pyriform egg reaches the ovoid profile in Hügelschäffer's model (see the red line in Fig. 2). Then, our further theoretical calculations were aimed at defining the calculated dependences for $V_{H(p)}$, that is, the volume at the sharp end of ovoid eggs described by Hügelschäffer's model.

The calculated formula for $V_{H(p)}$ will be similar to the initial one in Eq. (12), only with different

integration intervals corresponding to the contour of the pointy end (Fig. 1):

$$V_{H(p)} = \frac{\pi B^2}{4} \int_{-w}^{\frac{L}{2}} \frac{L^2 - 4x^2}{L^2 + 8wx + 4w^2} dx \qquad (18).$$

As a result of the integration of Eq. (18), the following computation formula is produced:

$$V_{H(p)} = \frac{\pi B^2 (L + 2w)}{128 w^2}$$

$$\left(L^2 - 2Lw + 8w^2 - \frac{(L - 2w)^2 (L + 2w)}{4w} \cdot \ln \left| \frac{L + 2w}{L - 2w} \right| \right) \quad (19).$$

The integration process is presented in File S2.1 (online only).

Having the calculated formula for the volume at the sharp end of ovoid eggs corresponding to Hügelschäffer's model, that is, $V_{H(p)}$ (Eq. 19), and conical eggs, that is, $V_{con(p)}$ (Eq. 8), we can proceed to deriving the volume $V_{pyr(p)}$ of intermediate forms (Fig. 1, green line).

Earlier, as a defining indicator of the contour of eggs of any shape, we justified the use of the diameter $D_{L/4}$ of the egg at the point corresponding to $\frac{1}{4}$ of its length, that is, taken at a distance of $L/4$ from the pointy end of the egg.[3] At the same time, $D_{L/4}$ for an ovoid egg corresponding to Hügelschäffer's model will be determined as twice the value of y from formula (11) after substituting the value $x = L/4$. $D_{L/4}$ for a conical egg will be similarly defined as twice the value of y from formula (6) after the same appropriate substitution.

Then, keeping the indexing adopted by us for the eggs of the respective shape, the following equations can be produced:

$$D_{H(L/4)} = \frac{\sqrt{3}BL}{2\sqrt{L^2 + 2wL + 4w^2}} \qquad (20),$$

$$D_{con(L/4)} = B \sqrt{\frac{L}{2(L + 2w)}} \qquad (21).$$

The next step was to find the relationship between the difference in the volume of the pointy part of the egg when changing from its "primary," conical shape to the "final" one that is consistent with the principles of Hügelschäffer's model. To do this, we established the functional dependence of the difference in volumes of the abovementioned

boundary shapes on the respective difference in diameters at the point $L/4$:

$$\Delta V_p = V_{H(p)} - V_{con(p)} \qquad (22),$$

$$\Delta D_{L/4} = D_{H(L/4)} - D_{con(L/4)} \qquad (23).$$

Let us rewrite Eq. (22) using Eqs. (19) and (8), and Eq. (23) using Eqs. (20) and (21), respectively. Then:

$$\Delta V_p = \frac{\pi B^2 (L + 2w)}{16}$$

$$\left[\left(\frac{L^2 - 2Lw + 8w^2}{8w^2} - \frac{(L - 2w)^2 (L + 2w)}{32 w^3} \cdot \ln \left| \frac{L + 2w}{L - 2w} \right| \right) - 1 \right]$$

$$(24),$$

$$\Delta D_{L/4} = B\sqrt{L} \cdot \frac{\sqrt{6L(L + 2w)} - 2\sqrt{L^2 + 2wL + 4w^2}}{2\sqrt{2(L + 2w)(L^2 + 2wL + 4w^2)}} \quad (25).$$

To determine the dependence of ΔV_p on $\Delta D_{L/4}$, we looked for the ratio of Eqs. (24) and (25). As a result of simplifications and transformations detailed in File S2.2 (online only), the following functional dependence is obtained:

$$\Delta V_p = 0.91 \Delta D_{L/4} \cdot BL \left[\left(\frac{w}{L} \right)^2 + 0.84 \frac{w}{L} + 0.44 \right] \qquad (26).$$

If we operate with a certain measured diameter $D_{L/4}$ at the point $L/4$, it can be represented as:

$$D_{L/4} = D_{con(L/4)} + n \cdot \Delta D_{L/4} \qquad (27),$$

where n is a certain coefficient ranging from 0 to 1. The value $n = 0$ will mean that the egg meets the conical criterion, that is, its pointy end is conical and parabolic, while for $n = 1$, the contour of the egg will correspond to Hügelschäffer's model. Based on (27), the following equation is obtained:

$$n = \frac{D_{L/4} - D_{con(L/4)}}{\Delta D_{L/4}} \qquad (28).$$

Therefore, to expand formula (26) to all "intermediate" egg profiles between the parabola and Hügelschäffer's model (green line, Fig. 2), instead of $\Delta D_{L/4}$, its product by the value of the coefficient n, that is, $n\Delta D_{L/4}$, will be used, and to avoid confusion, the value of the difference in volumes will be denoted by $\Delta V_{pyr(p)}$. This will match the difference in the volume at the pointy end of the egg, whose contours are described by Hügelschäffer's model, that is, $V_{H(p)}$, and, accordingly, the volume of any

of the intermediate shapes of the pyriform profile (green line, Fig. 2), that is, $V_{pyr(p)}$.

Hence, like our approach expressed by formula (27), the real volume of the sharp part of the pyriform egg, that is, $V_{pyr(p)}$, can be written as:

$$V_{pyr(p)} = V_{con(p)} + \Delta V_{pyr(p)} \quad (29).$$

In this case, $\Delta V_{pyr(p)}$ is determined from (26) as:

$$\Delta V_{pyr(p)} = 0.91n \cdot \Delta D_{L/4} \cdot BL\left[\left(\frac{w}{L}\right)^2 + 0.84\frac{w}{L} + 0.44\right] (30).$$

Considering formulae (8), (21), (23), (26), (27), and (28), the following equation can be obtained:

$$V_{pyr(p)} = \frac{\pi B^2(L + 2w)}{16} + 0.91BL$$

$$\left(D_{L/4} - B\sqrt{\frac{L}{2(L + 2w)}}\right)\left[\left(\frac{w}{L}\right)^2 + 0.84\frac{w}{L} + 0.44\right]$$

$$(31).$$

A detailed derivation of formula (31) is shown in File S2.3 (online only).

Volume of the pyriform egg. Taking into consideration the obtained expression (31) for the volume at the pointy end and Eq. (13) at the blunt one, the total volume of all combinations of the pyriform egg, V_{pyr}, is determined as the sum of these equations, which results in the following formula:

$$V_{pyr} = 0.992B^2L\left[\left(\frac{D_{L/4}}{B} - 0.426\right)\frac{w}{L} + 0.396\frac{D_{L/4}}{B} + 0.182\right](32).$$

A detailed derivation of formula (32) can be seen in File S2.4 (online only).

Surface area at the pointy end. To find an algorithm for calculating the surface area at the pointy end of a pyriform egg, that is, $S_{pyr(p)}$, the same method was used as for determining its volume, that is, the relationship between the difference in the surface area of the pointy part of the egg when changing from a conical shape to Hügelschäffer's model and the difference in diameters at the L/4 point.

Similar to Eq. (22), the following equation can be formulated:

$$\Delta S_p = S_{H(p)} - S_{con(p)} \quad (33).$$

If we consider an egg, whose contours correspond to Hügelschäffer's model, the surface area at its pointy end, $S_{H(p)}$, can be found as the difference between the surface areas of the entire egg, S (Eq. 5), and its blunt end, $S_{con(b)}$ (Eq. 15). As mentioned

above, when deriving formulae for calculating the volumes of various parts of an egg, following our theoretical studies to determine a universal formula for the mathematical description of the profile of bird eggs,[3] the blunt end is the same for both conical eggs and those whose contours obey Hügelschäffer's model, and therefore, the areas of their surfaces are also identical.

If $S_{con(b)}$ (Eq. 15) is subtracted from S_H (Eq. 5), the following formula can be obtained:

$$S_{H(p)} = \pi BL\left[\left(0.1468 - 0.1621\frac{w}{L}\right)\frac{B}{L} + 0.6456\frac{w}{L} + 0.3509\right](34).$$

Then, considering Eq. (10), Eq. (33) takes the following form:

$$\Delta S_p = BL\left[\left(0.0902\left(\frac{B}{L}\right)^2 - 0.245\frac{B}{L} - 0.123\right)\frac{w}{L}\right.$$

$$\left. - 0.1784\left(\frac{B}{L}\right)^2 + 0.3274\frac{B}{L} + 0.0848\right] \quad (35).$$

A detailed derivation of formula (35) is presented in File S2.5 (online only).

Next, we determined the dependence of ΔS_p on $\Delta D_{L/4}$ by determining the ratio of Eqs. (25) and (35). As a result of simplifications and transformations detailed in File S2.6 (online only), the following functional dependence is obtained:

$$\Delta S_p = L \cdot \Delta D_{L/4} \cdot$$

$$\left[\left(-9.6025\left(\frac{B}{L}\right)^2 + 14.845\frac{B}{L} + 1.7629\right)\left(\frac{w}{L}\right)^2\right.$$

$$\left. + \left(-0.9759\left(\frac{B}{L}\right)^2 + 1.5087\frac{B}{L} + 0.1793\right)\frac{w}{L}\right.$$

$$\left. - 1.1068\left(\frac{B}{L}\right)^2 + 2.0284\frac{B}{L} + 0.5231\right] \quad (36).$$

The actual surface area of the pointy part of a pyriform egg, $S_{pyr(p)}$, can be written similarly to Eq. (29):

$$S_{pyr(p)} = S_{con(p)} + \Delta S_{pyr(p)} \quad (37),$$

where, by analogy with Eq. (30):

$$\Delta S_{pyr(p)} = L \cdot n \cdot \Delta D_{L/4} \cdot$$

$$\left[\left(-9.6025\left(\frac{B}{L}\right)^2 + 14.845\frac{B}{L} + 1.7629\right)\left(\frac{w}{L}\right)^2\right.$$

$$+ \left(-0.9759 \left(\frac{B}{L} \right)^2 + 1.5087 \frac{B}{L} + 0.1793 \right) \frac{w}{L}$$

$$- 1.1068 \left(\frac{B}{L} \right)^2 + 2.0284 \frac{B}{L} + 0.5231 \Bigg] \qquad (38).$$

Taking into consideration formulae (10), (21), (23), (27), (28), and (38):

$$S_{pyr(p)} = \pi B \cdot \frac{\sqrt{\left(4(L + 2w)^2 + B^2 \right)^3} - B^3}{24(L + 2w)^2}$$

$$+ L \left(D_{L/4} - B \sqrt{\frac{L}{2(L + 2w)}} \right)$$

$$\left[\left(-9.6025 \left(\frac{B}{L} \right)^2 + 14.845 \frac{B}{L} + 1.7629 \right) \left(\frac{w}{L} \right)^2 \right.$$

$$+ \left(-0.9759 \left(\frac{B}{L} \right)^2 + 1.5087 \frac{B}{L} + 0.1793 \right) \frac{w}{L}$$

$$- 1.1068 \left(\frac{B}{L} \right)^2 + 2.0284 \frac{B}{L} + 0.5231 \Bigg] \qquad (39).$$

A detailed derivation of formula (39) is given in File S2.7 (online only).

Surface area of the pyriform egg. In view of the obtained formula (39) for the surface area at the pointy end, $S_{pyr(p)}$, and Eq. (15) for the blunt end, $S_{pyr(b)}$, the total surface area of all combinations of the pyriform eggs, S_{pyr}, can be determined as the sum of these equations, which results in the following formula:

$$S_{pyr} = 0.2447 BL$$

$$\left\{ \left(\frac{B}{L} - 0.0838 \right) \frac{w}{L} + 3.5039 \frac{B}{L} + 8.3032 \right.$$

$$- 39.2419 \left(\frac{D_{L/4}}{B} + 0.5165 \frac{w}{L} - 0.7016 \right)$$

$$\left[\left(\frac{B^2}{L^2} - 1.546 \frac{B}{L} - 0.1836 \right) \left(\frac{w}{L} + 0.1016 \right) \frac{w}{L} \right.$$

$$+ 0.1153 \left(\frac{B}{L} \right)^2 - 0.2112 \frac{B}{L} - 0.0545 \Bigg] \Bigg\} \qquad (40).$$

A detailed derivation of formula (40) is presented in File S2.8 (online only).

Mathematical progression of avian egg shape

In our previous article,[3] when concerning the main types of geometric shapes for all observed varieties of bird eggs in nature, we proposed a concept of *mathematical evolution*. Nevertheless, the use of this term may raise questions and even a certain objection regarding its appropriateness among researchers working in egg-related studies. Therefore, in the present investigation, we suggested to change the term *mathematical evolution* to *mathematical progression*. The meaning of this concept and its formulation is that each subsequent shape contains the characteristics of the previous one with a potential of a further simple, stepwise transformation. These egg shape types can be represented by the following sequence: sphere → ellipsoid → ovoid (with the profile described by Hügelschäffer's model) → pyriform ovoid. At each stage of the transition from one shape to the next one, we can see that a shape transforms from the previous one, and then into the subsequent one by adding one more key parameter to describe this shape mathematically. For a sphere, this key parameter is its diameter, that is, in our case, the maximum breadth of the egg, *B*. Another parameter is added to its formulae for the ellipsoid description, which is the egg length, *L*. Furthermore to describe the ovoid with Hügelschäffer's model, we need to determine the value of the parameter *w*, and for the pyriform egg, its diameter at the point corresponding to $\frac{1}{4}$ the length of the egg, that is, $D_{L/4}$.

To test how this theory of the mathematical change in the egg shape works with our formulae for the egg volume, V_{pyr}, and surface area, S_{pyr}, that describe the pyriform profile, we carried out a step-by-step transformation from a pyriform ovoid to a sphere using the obtained formulae (32) and (40). This stepwise transformation also enabled checking possible calculated errors when using the formulated mathematical relationships for eggs of various profiles.

Mathematical progression of egg volume. If we assume that the derived formula (32) is universal for all types of eggs, it should be transformed into Eq. (16) after substituting Eq. (21) instead of $D_{L/4}$, making it possible to calculate the volume of conical eggs as the boundary shape of a pyriform profile.

Verification of this assumption results in the following formula:

$$V_{con(Eqn32)} = B^2 L \left(0.46 - 0.0542 \frac{w}{L} \right) \qquad (41),$$

which was comparable with the formula similarly transformed from Eq. (16):

$$V_{con(Eqn16)} = B^2 L \left(0.46 - 0.0543 \frac{w}{L} \right) \qquad (42).$$

A detailed derivation of both Eqs. (41) and (42) is demonstrated in File S3.1 (online only).

Based on Eqs. (41) and (42), we can calculate the percent error, ϵ, resulting from using Eq. (32) instead of Eq. (16) when defining the volume of conical eggs:

$$\varepsilon = \left| \frac{V_{con(Eqn32)} - V_{con(Eqn16)}}{V_{con(Eqn16)}} \right| \cdot 100\%$$

$$= \left| \frac{0.0001 \frac{w}{L}}{0.46 - 0.0542 \frac{w}{L}} \right| \cdot 100\% \qquad (43).$$

Knowing the value of possible variations in the ratio $w/L \in [0, 0.25]$, the determined maximum error does not exceed 0.006%.

The next test was to check the validity of Eq. (32) when computing the volume of classical ovoid eggs, the shape of which corresponds to Hügelschäffer's model. In this case, it is necessary to substitute its calculated formula, that is, Eq. (20), instead of $D_{L/4}$ into Eq. (32), and compare the resulting expression with the classical computation formula (4) for eggs of this type.

As a result of transformations like those performed for conical eggs, the following equation is produced:

$$V_{H(Eqn32)} = B^2 L \left(0.5269 - 0.1081 \frac{w}{L} \right) \qquad (44),$$

which can be compared to the classical but pretransformed Eq. (4):

$$V_{H(Eqn4)} = B^2 L \left(0.5273 - 0.1084 \frac{w}{L} \right) \qquad (45).$$

A comprehensive derivation of both Eqs. (44) and (45) is provided in File S3.2 (online only).

Based on Eqs. (44) and (45), the percent error, ϵ, was found that results from using Eq. (32) instead of Eq. (4) when calculating the volume of ovoid eggs, whose shape corresponds to Hügelschäffer's

model:

$$\varepsilon = \left| \frac{V_{H(Eqn32)} - V_{H(Eqn4)}}{V_{H(Eqn4)}} \right| \cdot 100\%$$

$$= \left| \frac{0.0003 \frac{w}{L} - 0.0004}{0.5273 - 0.1084 \frac{w}{L}} \right| \cdot 100\% \qquad (46).$$

Using the value of possible variations in the ratio $w/L \in [0, 0.25]$, the estimated maximum error will not exceed 0.076%.

The next step in testing Eq. (32) included its use to calculate the volume of elliptical and spherical eggs. Here, we need to substitute $D_{L/4}$ in Eq. (32) with its value that would be similar to that for the ellipsoid and/or the sphere, and also equate w to 0.

In Supplementary Material S2.4 (online only), the $D_{L/4}$ value for the sphere is determined as follows:

$$D_{sph(L/4)} = \frac{\sqrt{3}}{2} B \qquad (47).$$

Let us proceed similarly with the calculation of $D_{L/4}$ for ellipsoids. The appropriate formula for an ellipse adapted to the basic geometric egg dimensions, L and B, will be deduced using the following mathematical expression:

$$\frac{x^2}{(L/2)^2} + \frac{y^2}{(B/2)^2} = 1 \qquad (48),$$

which can be transformed to the more suitable form:

$$y = \frac{B\sqrt{L^2 - 4x^2}}{2L} \qquad (49).$$

Substituting the value $x = L/4$ and doubling y, the following equation is produced:

$$D_{ell(L/4)} = \frac{\sqrt{3}}{2} B \qquad (50).$$

We can conclude that the $D_{L/4}$ value is the same for both ellipsoidal (Eq. 47) and spherical (Eq. 50) shapes. Finally, substituting Eq. (47) into Eq. (32) and taking $w = 0$, the obtained result can be compared with the classical formulae for calculating the volume of an ellipsoid, V_{ell}, and a sphere, V_{sph}:

$$V_{ell(Eqn32)} = 0.5207 B^2 L \qquad (51),$$

$$V_{ell} = 0.5236 L B^2 \qquad (52),$$

$$V_{sph(Eqn32)} = 0.5207 B^3 \qquad (53),$$

$$V_{sph} = 0.5236B^3 \qquad (54).$$

A step-by-step derivation of formulae (51)–(54) is presented in File S3.3 (online only).

Computation of the percent error, ϵ, resulting from using Eq. (32) instead of the classical geometric formulae, that is, Eqs. (52) and (54), when calculating egg volume of eggs, whose shape corresponds to an ellipsoid and/or a sphere, showed an estimate of 0.55%.

Thus, the obtained Eq. (32) for calculating the volume of pyriform eggs can be considered universal concerning the volume of eggs of any shape, as supported by a minimum calculation error. Depending on the $D_{L/4}$ value, this formula is transformed into the respective dependencies for calculating the volume of ovoids, ellipsoids, and spheres, thereby confirming the principle of mathematical progression that we proposed for the geometry of birds' eggs.

Mathematical progression of egg surface area.
In considering the correspondence of the principles of mathematical progression for the surface area of bird eggs, we used a similar approach that we applied when analyzing the formulae for calculating their volumes.

In the case of surface area, the initial equation is Eq. (40) that we first compared with Eq. (17) for S_{con}. If formula (40) is universal for all types of eggs, after substituting $D_{L/4}$ in it with Eq. (21), it should be transformed into Eq. (17) to calculate the volume of conical eggs.

Verification of this assumption makes it possible to obtain the following formula:

$$S_{con(Eqn40)} = BL$$
$$\left[\left(0.2452\frac{B}{L} - 0.0127 \right) \frac{w}{L} + 0.8574\frac{B}{L} + 2.0309 \right]$$
$$(55),$$

which is further compared with that one similarly transformed from Eq. (17):

$$S_{con(Eqn17)} = BL$$
$$\left[\left(0.2447\frac{B}{L} - 0.0205 \right) \frac{w}{L} + 0.8574\frac{B}{L} + 2.0318 \right]$$
$$(56).$$

A thorough derivation of both Eqs. (55) and (56) is shown in File S3.4 (online only).

Based on the generated Eqs. (55) and (56), we can compute the percent error, ϵ, resulting from using Eq. (40) instead of Eq. (17) when calculating the surface area of conical eggs:

$$\varepsilon = \left| \frac{S_{con(Eqn40)} - S_{con(Eqn17)}}{S_{con(Eqn17)}} \right| \cdot 100\%$$
$$= \left| \frac{\left(0.0005\frac{B}{L} + 0.0078 \right) \frac{w}{L} - 0.0009}{\left(0.2447\frac{B}{L} - 0.0205 \right) \frac{w}{L} + 0.8574\frac{B}{L} + 2.0318} \right|$$
$$\cdot 100\% \qquad (57).$$

Because of the value of possible variations in the ratio $w/L \in [0, 0.25]$ and $B/L \in [0.5, 1]$, the calculated maximum error does not exceed 0.045%.

The next stage in our testing was to check the conformity of using Eq. (40) to calculate the surface area of classical ovoid eggs, whose shape obeys Hügelschäffer's model. In this case, it is necessary to substitute $D_{L/4}$ in Eq. (40) with its calculation formula per Eq. (20) and compare the resulting expression with the classical calculation formula (5) for eggs of this type.

As a result of the transformations, the following equation is obtained:

$$S_{H(Eqn40)} = BL$$
$$\left[\left(0.1358\frac{w}{L} + 0.917 \right) \frac{B}{L} - 0.188\frac{w}{L} + 2.2114 \right]$$
$$(58).$$

A complete derivation of Eq. (58) is presented in File S3.5 (online only).

Based on the obtained Eq. (58), we calculated the percent error, ϵ, resulting from using Eq. (40) instead of Eq. (5) when computing the surface area of eggs whose profile matches Hügelschäffer's model:

$$\varepsilon = \left| \frac{S_{H(Eqn40)} - S_{H(Eqn5)}}{S_{H(Eqn5)}} \right| \cdot 100\%$$
$$= \left| \frac{\left(0.0008\frac{w}{L} - 0.0003 \right) \frac{B}{L} + 0.0036\frac{w}{L} - 0.0003}{\left(0.135\frac{w}{L} + 0.9173 \right) \frac{B}{L} - 0.1916\frac{w}{L} + 2.2117} \right|$$
$$\cdot 100\% \qquad (59).$$

Considering the value of possible variations in the ratio $w/L \in [0, 0.25]$ and $B/L \in [0.5, 1]$, the calculated maximum error does not exceed 0.021%.

At the final verification step, the applicability of Eq. (40) is evaluated for identifying values of

the surface area of eggs of elliptical and spherical shapes. Here, we would require substituting $D_{L/4}$ in Eq. (40) with its value, which corresponds to the analogous value for the ellipsoid and/or the sphere and equating w to 0. As we found out earlier, the $D_{L/4}$ value is the same for ellipse and circle, as can be seen from Eqs. (47) and (50). Therefore, substituting any of them into Eq. (40) and taking $w = 0$, the obtained result can be compared with the classical formulae for calculating the surface area of an ellipsoid, S_{ell}, and a sphere, S_{sph}:

$$S_{ell} = \frac{\pi BL}{2} \left(\frac{\arcsin \sqrt{1 - \frac{B^2}{L^2}}}{\sqrt{1 - \frac{B^2}{L^2}}} + \frac{B}{L} \right) \qquad (60),$$

$$S_{sph} = \pi B^2 \qquad (61).$$

As a result of the appropriate transformations, the following expressions are produced:

$$S_{ell(Eqn40)} = BL \left(0.9178 \frac{B}{L} + 2.2149 \right) \qquad (62),$$

$$S_{sph(Eqn40)} = 3.1267 B^2 \qquad (63).$$

At the same time, for the convenience of comparing Eq. (62) with Eq. (60), the latter can be transformed to the following form:

$$S_{ell} = BL \left(0.9153 \frac{B}{L} + 2.2167 \right) \qquad (64).$$

A step-by-step derivation of Eqs. (62)–(64) is provided in File S3.6 (online only).

Computation of the percent error, ϵ, resulting from using Eq. (40) instead of the classical formula (60), when calculating the surface area of elliptical eggs, shows the following result:

$$\varepsilon = \left| \frac{S_{ell(Eqn40)} - S_{ell}}{S_{ell}} \right| \cdot 100\%$$

$$= \left| \frac{0.0025 \frac{B}{L} - 0.0018}{0.9153 \frac{B}{L} + 2.2167} \right| \cdot 100\% \qquad (65).$$

Knowing the value of possible variations in the ratio $B/L \in [0.5, 1]$, the estimated maximum error does not exceed 0.022%.

For spherical eggs, the corresponding percent error calculated from Eqs. (61) and (63) was 0.48%.

Thus, the produced calculation formula for surface area of pear-shaped eggs, that is, Eq. (40),

can be suggested as a universal one for computing the surface area of eggs of any shape with a minimum calculation error. Depending on the $D_{L/4}$ value, this equation can be transformed into the respective dependencies for computing the surface area of ovoids, ellipsoids, and spheres, which verifies the concept of mathematical progression we postulated for the geometry of bird eggs.

Discussion

The mathematical description of egg shape, including formulae for volume and area, has both pure mathematical interest and application value. In the poultry industry, calculating the egg's geometric parameters has relevance for breeding and the incubation and storage of eggs. In other words, the efficiency of the poultry industry is highly dependent on egg quality characteristics.[24–27] For example, egg quality parameters can be instrumental in developing nondestructive techniques for hatchability improvement,[28–32] *in ovo* sex identification,[33–36] and embryo growth modeling.[37,38] Because an increasing number of different domesticated bird species are currently used, there is a wide variability in the shape of eggs produced in poultry houses, aviaries, and free-range farms, similarly to what can be seen in wildlife. This shape variation ranges from round eggs, like in the African ostrich, to elliptical ones, for example, in emu, and from the classic ovoid, like in chickens, to elongated eggs, for example, in some species of waterfowl. Given the fact that a whole army of breeders is working on creating various poultry crosses, we could not exclude the prospect that in the foreseeable future, commercially used avian species may appear that carry even conical eggs. Perhaps this might increase the occupancy rate of incubators or, for example, improve their air exchange. Or it would create some marketing advantage of conical eggs with such an exotic look, in comparison with ordinary table eggs. Thus, our theoretical research can have direct practical application not only for ornithology, including oomorphology as its separate subdiscipline, and evolutionary biology, but also for the practical needs of commercial poultry farming.

In this study, we provided an explicit and universal formulation for the key egg quality parameters, that is, the volume and surface area, and demonstrated their concordance with the concept of mathematical progression of avian egg shape (see

further discussion in File S4, online only). Our theoretical studies are also of an applied nature. Using the mathematical apparatus, we obtained the theoretical formulae for calculating the egg volume (Eq. 32) and surface area (Eq. 40) that are valid for computing these parameters in eggs of any shape, provided their profile meets the condition of symmetry. Herewith, the initial key parameters of such a calculation are four basic geometric egg measurements: (1) the length, L; (2) the maximum diameter (breadth), B; (3) the value of the displacement of the maximum diameter from the central axis, w; and (4) the egg diameter at the point corresponding to $\frac{1}{4}$ of the length from its sharp end, that is, $D_{L/4}$.

The importance of the generated formulae lies in the fact that for the first time, we were able to derive mathematical relationships not only for key geometric figures that help describe the shape of a bird's egg (e.g., a sphere, an ellipsoid, etc.) but also for intermediate profiles that mainly account for the so-called pyriform types of eggs (Fig. 2). In our previous work,[3] we demonstrated that the boundary geometric shape for eggs of this type is a summation of a parabola and an ovoid described by Hügelschäffer's model. Further transformation of this profile that we conditionally called conical leads to a shape fitting Hügelschäffer's ovoid that we described in detail and examined its features in the previous studies of chicken eggs.[18,19,21] This summation of possible egg profiles between the conical one and Hügelschäffer's ovoid falls under the category of pyriform eggs. The latter shape caused the most difficulties and gave the maximum calculation error in the earlier investigations.[39,40]

The merit of the formulae we have derived is their explicitly theoretical grounding, meaning that the results of our research rely on a solid mathematical basis. Our approach advantageously differs from other studies that were based on the use of empirical data, albeit a large but still limited set of research material.

We have also shown that the formulae for calculating the volume and surface area of pyriform eggs can be easily converted into classical calculation expressions for other well-known geometric figures, whose shape also corresponds to eggs of various types, that is, a sphere, an ellipsoid,[41] and an ovoid, as supported by a very small calculation error. Thus, we can confidently rewrite Eqs. (32) and (40), without using the subscript index *pyr* we

assigned, considering their adequacy in calculating any bird's egg, as follows:

$$V = 0.992B^2L$$
$$\left[\left(\frac{D_{L/4}}{B} - 0.426\right)\frac{w}{L} + 0.396\frac{D_{L/4}}{B} + 0.182\right]$$
(66),

$$S = 0.2447BL$$
$$\left\{\left(\frac{B}{L} - 0.0838\right)\frac{w}{L} + 3.5039\frac{B}{L} + 8.3032\right.$$
$$- 39.2419\left(\frac{D_{L/4}}{B} + 0.5165\frac{w}{L} - 0.7016\right)$$
$$\left[\left(\frac{B^2}{L^2} - 1.546\frac{B}{L} - 0.1836\right)\left(\frac{w}{L} + 0.1016\right)\frac{w}{L}\right.$$
$$\left.\left. + 0.1153\left(\frac{B}{L}\right)^2 - 0.2112\frac{B}{L} - 0.0545\right]\right\}$$
(67).

Conclusion

In this study of the egg volume and surface area, we have considered the concept of the mathematical progression of the two major parameters of avian eggs in the explicit and universal formulation. However, we do not assume that we have the right to draw any analogies regarding the sequence of evolutionary variability in the shape of bird eggs and, accordingly, did not set out to address the following questions: (1) whether this process was carried out from a simpler, mathematical point of view, spherical object to a more complex, pear-shaped one; and (2) how logical it would be to assume that the biological laws of such a modification would correspond to mathematical principles. There are four fundamental geometric shapes of bird eggs that exist in nature.[42,43] This variability can be traced not only in the evolutionary variability of the mathematical functions describing these shapes,[3] but also in the calculating formulae characterizing their main geometric parameters, which we have demonstrated in these studies. The proposed formulae can be conducive to further developing technological solutions in poultry industry and research.

Author contributions

V.G.N.: conceptualization, methodology, validation, formal analysis, investigation, and data curation. V.G.N. and M.N.R.: writing—original

draft preparation. V.G.N., M.N.R., D.K.G., and B.M.: writing—review and editing. M.N.R. and D.K.G.: supervision. M.N.R., D.K.G., and B.M.: project administration. All authors read and agreed to the published version of the manuscript.

Supporting information

Additional supporting information may be found in the online version of this article.

File S1. Formulae for conic eggs.

File S2. Formulae for pyriform eggs.

File S3. Formulae for mathematical evolution.

File S4. Extended discussion on mathematical progression.

Competing interests

The authors declare no competing interests.

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