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===================== **MATHEMATICAL MODELING** =====================

Eggs from the Baker: Simplifying and Improving on an Under-appreciated Oological Model

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***Abstract*.** Biologists have been baffled by the reasons behind, and evolutionary and ecological implications of, interspecific variations in avian egg shape. In this respect, Douglas E. Baker's mathematical model of bird eggs has been largely under-appreciated because a) the author never wrote another paper on it, b) at the time of its publication (2002) several other models were in widespread use, and c) it typically requires eight different egg measurements. Thus, the current study aimed to reduce Baker's model to a more convenient form in terms of its parameters, number of initial measurements required, compliance with the principles of geometric laws, and, finally, its mathematical transformation to a form that warrants such compliance. An experimental comparison of three modifications of the model with the contours of actual eggs that have oval, conical and pyriform shapes was performed. Results allowed us to present a new standard geometric solid of revolution of an ovoid shape, for the description of which three key egg parameters are required: length, L, maximum breadth, B, and the value of the vertical axis shift from the centre, w. In addition to the minimum set of initial measurements, this modification of Baker's model complies with the principles of the main axiom of the mathematical formula of the bird's egg and demonstrates acceptable accuracy (< 10 %) in describing the contours of real eggs. The adoption of the simplified and improved Baker model is essential for ecological and evolutionary research involving birds and their egg shapes, as well as for egg-inspired engineering.

Key words: *avian eggs, egg geometry, Baker model, standard egg shape, main axiom of the mathematical formula of the bird's egg*

INTRODUCTION

At the time of the publication of Douglas E. Baker's paper [1], in which the author described his approach to deriving a mathematical model describing a bird's egg, the scientific oological world was already using a number of formulae for similar purposes (e.g., [2–8]). Such an preponderance of alternative models did not help widespread dissemination of Baker's model, nor did the fact that it necessitated carrying out a large number of initial egg measurements. Baker himself, consequently, did not publish another study, neither on its use in applied oological research, nor on a more in-depth analysis of the obtained mathematical expression and the model was left without due attention. Fifteen years after its publication, however, the Baker model has recently come to the attention of oologists owing to the fundamental research of Stoddard et al. [9], who demonstrated that the flight characteristics of a bird are directly related to the shape of its eggs. Hereby, as characteristics of the egg shape, Stoddard et al. [9] used two coefficients, for ellipticity and asymmetry, the values of which are included in the Baker model [1]:

$$y = T(1+x)^{\frac{1}{1+\lambda}}(1-x)^{\frac{\lambda}{1+\lambda}} \quad (1)$$

The coefficients T and λ in Eqn1 were explained by Baker [1] so that an egg's asymmetry is measured by λ, while its reciprocal equatorial elongation is measured by T.

Stoddard et al. [9] caused scientific controversy among oologists (e.g., [10–12]) while, correspondingly, testing the Baker model. Emphasising importance and difficulty of accurately quantifying the shape of birds' eggs, Biggins et al. [10] noted that biologists have been perplexed by the reasons behind, and evolutionary and ecological implications of, interspecific variations in avian egg shape. Furthermore, Biggins et al. [13] came to the conclusion that accuracy of the Baker model was clearly insufficient and that the model itself was similar in structure to the earlier Preston [2] model. It is also reasonable to suggest that the Baker model remains not fully understood, and, indeed, the identity of Douglas E. Baker himself is somewhat shrouded in mystery, due to the fact that he did not present any other publications on this topic to the scientific world. Another fact that arouses interest in the Baker model (Eqn1) is an unusual approach to its derivation. Baker applied the path curves method used by Edwards [14] to describe mathematically the geometric shape of buds in various plants. Herewith, Edwards [14] shed some light on the personality of Douglas Baker, noting in his book: "*I was very happy, years later, when my friend Douglas Baker, mathematics teacher in Connecticut, offered to undertake a more thorough research into this whole field of the eggs*."

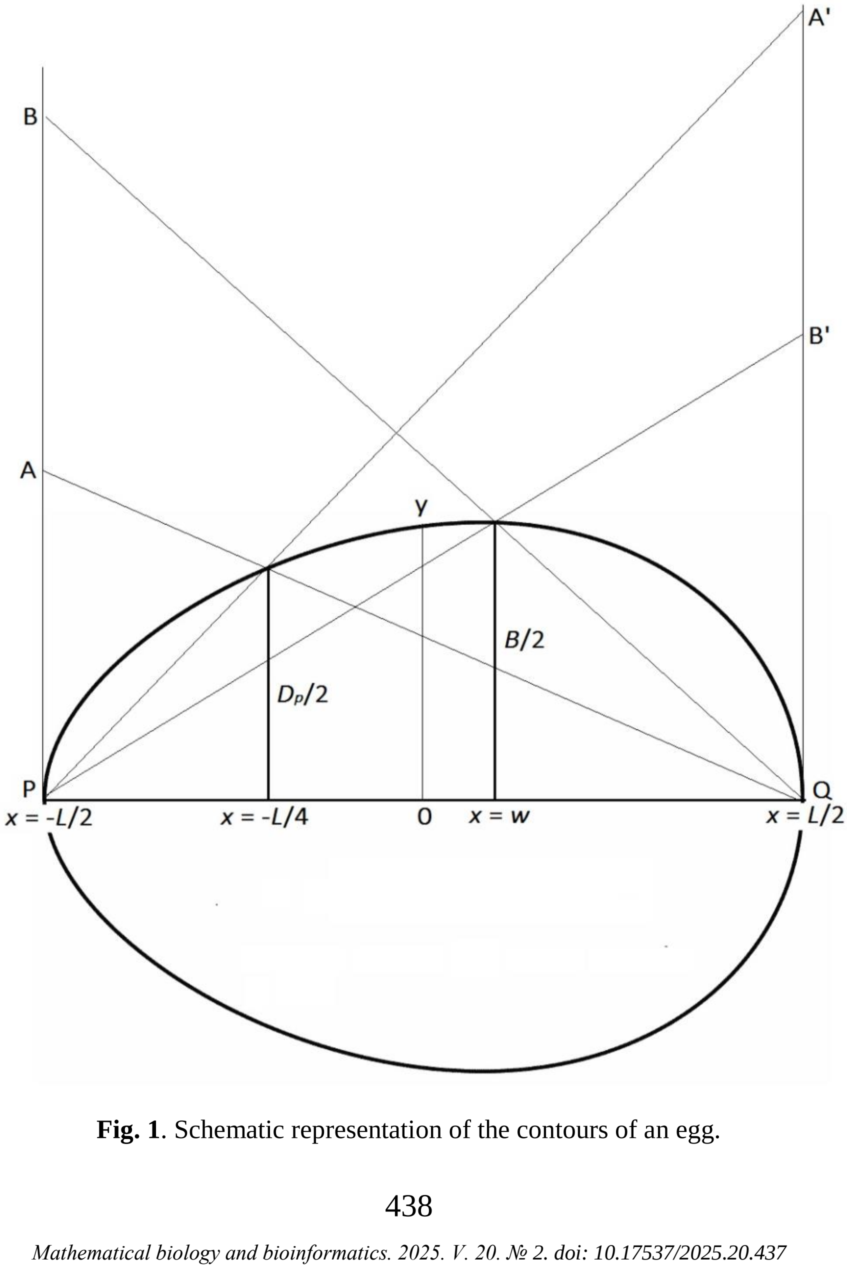


Fig. 1. Schematic representation of the contours of an egg.

The paucity of research into the Baker model lies in the limited study of its compliance with geometric laws. We [15] proposed a new unique approach to defining a certain geometric standard of the egg-shaped ovoid, as a result of which a geometric criterion was introduced to which mathematical models describing egg shapes must conform. This criterion was called the "*Main Axiom of the Mathematical Formula of the Bird's Egg*" (hereinafter the "Main Axiom"). This axiom basically states that the extremum of the function defining the contour geometry of the egg should be equal to half of the egg's maximum diameter ($B/2$). The reason why the compliance of mathematical models, describing a body, with geometric laws so important, is because such compliance can warrant the maintenance of the accuracy and predictability of the calculation. It can aid in the understanding and interpretation of the results, and also ensure the unification of mathematical knowledge.

Moreover, Baker's model has a number of assumptions, e.g., the fact that the ratios r_1 and r_2 are geometric sequences (Fig. 1,A in [1]). Even if one of these ratios (r_1 or r_2) could be constructed based on the rules of geometric progression, this does not mean that the second ratio would correspond to the same principles.

The difficulty using Baker's model in practical terms is the need to measure eight parameters: seven radii of the egg at different points, plus its length. Furthermore, Baker [1] used not the actual egg dimensions, but those reduced to a conventional length equal to 2 ($x = -1$ … 1). With this in mind, we resolved to examine more closely Baker's model and his approach using more familiar designations of egg parameters and their interrelations. The purpose of this work, therefore, was a more in-depth analysis of the Baker model, both from the viewpoint of its compliance with geometric laws, as well as the possibility and expediency of practical applications for the mathematical description of the shape of actual eggs.

THEORY

For context, here, we introduce into the Baker model (Eqn1) more familiar designations of the main egg parameters that we formulated earlier in our works [15–17], providing them schematically in Fig. 1. Akin to how it was presented by Baker [1], we place the image of the egg between two vertical axes with the image of path curves, the practical use of which is given below.

Now, we represent the contours of the egg in a coordinate system such that the horizontal x-axis coinciding with the egg length, L, and the vertical y-axis passes through the middle of L. That is, in contrast to the conventional boundary frames of the egg length $[-1, 1]$ adopted by Baker [1], the egg, in our case, is located on the segment of the x-axis = $[-L/2, L/2]$. The maximum breadth of the egg, B, is shifted from the central vertical y-axis by a certain value $x = w$. In Figure 1, we also depicted the diameter of the egg, D_p, at a point located from the pointed end by ¼ of its length ($x = -L/4$), the meaning of which will be explained below.

$$y = \pm T\left(\frac{L}{2}+x\right)^{\frac{1}{1+\lambda}}\left(\frac{L}{2}-x\right)^{\frac{\lambda}{1+\lambda}}. \tag{2}$$

In order to determine the values of the parameters T and λ, Baker [1] suggests measuring the radii of the egg at seven points uniformly spaced along its length. However, this approach does not guarantee that the resultant model complies with the principles of the Main Axiom. In this regard, based on the principle of the necessity of matching the extremum point of function (2) to the point $x = w$, we find the following derivative of Eqn2:

$$\frac{\partial y}{\partial x} = \frac{T}{1+\lambda}\left[\left(\frac{\frac{L}{2}-x}{\frac{L}{2}+x}\right)^{\frac{\lambda}{1+\lambda}} - \lambda\left(\frac{\frac{L}{2}+x}{\frac{L}{2}-x}\right)^{\frac{1}{1+\lambda}}\right]. \tag{3}$$

After equating this to zero and taking into account that $x = w$, we determine the value of the parameter λ:

$$\lambda = \frac{L-2w}{L+2w}. \quad (4)$$

Baker [1] characterised the value of the parameter T as the scaled equatorial radius of the egg. This statement is quite logical, since, to determine T, it is sufficient to substitute the value $x = 0$ into Eqn1. In our case, using Eqn2 as the base, the calculation of T became somewhat more complicated. However, the main difficulty of such a mathematical approach is that in this case it was necessary to introduce another measured parameter, i.e., the diameter (or radius) of the egg at the point $x = 0$. Any extra measurement complicates the process of using the mathematical model and, therefore, we decided to use a pair of traditional parameters characterising the geometric features of the egg, i.e., B and w. When $x = w$, $y = B/2$. Then, substituting these equalities into Eqn2, we obtain:

$$T = \frac{B}{2}\cdot\frac{1}{\left(\frac{L}{2}+w\right)^{\frac{1}{1+\lambda}}\left(\frac{L}{2}-w\right)^{\frac{\lambda}{1+\lambda}}}. \quad (5)$$

From our experience in analysing various bird egg shape models [15–17], we know that one of the key parameters that significantly increases the accuracy of describing their geometric contours is the D_p value that we already mentioned above (Fig. 1).

To introduce the D_p value into the Baker model, we define the relationship between the parameters λ and D_p. We will use the "path curves" principle developed by Edwards [14] and successfully applied by Baker [1] in deriving his model. According to Baker [1], λ is $\ln(r_2)/\ln(r_1)$. The values of r_1 and r_2 are geometric sequences, for finding which Baker [1] proposed measuring the radii of the egg at seven points, similar to how Edwards [14] used it to mathematically describe plant buds. One of our goals was to reduce the number of measured parameters.

Earlier [15, 17], we showed that the contour of any egg can be defined using four key dimensions: L, B, w and D_p. Thus, we will proceed from this fact when upgrading Baker's model. To find the values of r_1 and r_2, we only need two points on the upper part of the egg contour. Moreover, examples of calculating r_1 and r_2 using two points on the path curve are given in a number of publications describing this method (e.g., [18–20]). Let us choose as such the points corresponding to the egg diameters at $x = -L/4$, i.e., D_p, and at $x = w$, i.e., B (Fig. 1). Since r_1 = PA/PB and r_2 = QA'/QB' [1], we should, following Baker [1], consider the triangles PAQ, PBQ, PA'Q and PB'Q. Using the principles of similarity, we write:

$$\mathrm{AP} = \frac{2}{3}D_p, \quad (6)$$

$$\mathrm{BP} = \frac{BL}{L-2w}, \quad (7)$$

$$\mathrm{A'Q} = 2D_p, \quad (8)$$

$$\mathrm{B'Q} = \frac{BL}{L+2w}. \quad (9)$$

Thus,

$$r_1 = \frac{2D_p(L-2w)}{3BL}, \quad (10)$$

$$r_2 = \frac{2D_p(L+2w)}{BL}. \quad (11)$$

In order to distinguish the values of the parameters λ (Eqn4) and T (Eqn5) obtained using the Main Axiom principles from those calculated using the four basic parameters of the egg (L, B, w and D_p), we will conventionally call them (new) λ' and T'. Then,

$$\lambda' = \frac{\ln \dfrac{2D_p(L+2w)}{BL}}{\ln \dfrac{2D_p(L-2w)}{3BL}}. \tag{12}$$

Now, let us determine the value of the parameter T', similar to what we did when deriving Eqn5. The only thing is, in this case, we substitute the values $x = -L/4$, $y = D_p/2$ into Eqn2. Then,

$$T' = \frac{2}{3^{\frac{\lambda'}{1+\lambda'}}} \cdot \frac{D_p}{L}. \tag{13}$$

It is possible that the use of the values of the parameters λ' (Eqn12) и T' (Eqn13) in Eqn2 may lead to a violation of the Main Axiom principles. However, this fact is easier to verify by experimental studies.

As a basis for comparing the described Baker model modifications obtained theoretically, we will use the results of calculations of the parameters λ and T proposed by Baker [1], i.e., implementing measurements of seven radii of the egg along its longitudinal axis. Considering that the basic form of the Baker model (Eqn2) was somewhat modified by us in comparison with the classical one (Eqn1), we will also have to modify the corresponding calculation of the parameters included in it, which, again, in order to avoid confusion, we will designate as λ'' and T''. We depict in Figure 2 path curves conforming to seven equally spaced diameters, which we name according to their coordinate on the x-axis: $D_{-3L/8}$ ($x = -3L/8$), $D_{-L/4}$ ($x = -L/4$), $D_{-L/8}$ ($x = -L/8$), D_0 ($x = 0$), $D_{L/8}$ ($x = L/8$), $D_{L/4}$ ($x = L/4$) and $D_{3L/8}$ ($x = 3L/8$). The diameters in Figure 2 are shown as radii, that is, divided by 2.

Using the path curves diagram in Figure 2, and acting similarly to the principle used in deriving Eqns 6 to 12, while averaging the results of the ratios BP/AP, CP/BP, DP/CP, EP/DP, FP/EP, GP/FP to find r_1 and, accordingly, B'Q/A'Q, C'Q/B'Q, D'Q/C'Q, E'Q/D'Q, F'Q/E'Q, G'Q/F'Q to find r_2, we obtain:

$$\lambda'' = \frac{\ln\left(\dfrac{D_{-L/4}}{12D_{-3L/8}} + \dfrac{D_{-L/8}}{9D_{-L/4}} + \dfrac{D_0}{8D_{-L/8}} + \dfrac{2D_{L/8}}{15D_0} + \dfrac{5D_{L/4}}{36D_{L/8}} + \dfrac{D_{3L/8}}{7D_{L/4}}\right)}{\ln\left(\dfrac{7D_{-L/4}}{36D_{-3L/8}} + \dfrac{D_{-L/8}}{5D_{-L/4}} + \dfrac{5D_0}{24D_{-L/8}} + \dfrac{2D_{L/8}}{9D_0} + \dfrac{D_{L/4}}{4D_{L/8}} + \dfrac{D_{3L/8}}{3D_{L/4}}\right)}. \tag{14}$$

The value of T'' is quite easy to determine from the Baker model (Eqn2) after substituting the value $x = 0$. In this case, the value of y corresponds to $D_0/2$. Then,

$$T'' = \frac{D_0}{L}. \tag{15}$$

Substituting the values of the parameters λ'' (Eqn14) и T'' (Eqn15) into Eqn2, we obtain the desired egg profile.

As a result of this theoretical research, we obtained three modifications of the Baker model (Eqn2), which we will conventionally denote as: (i) BM^{MA}, which implies the use of parameters λ (Eqn4) and T (Eqn5), which obviously satisfy the requirements of the Main Axiom; (ii) BM', which uses the values of λ' (Eqn12) and T' (Eqn13); and (iii) BM'', in which the parameters λ'' and T'' are calculated according to the appropriate Eqn14 and Eqn15.

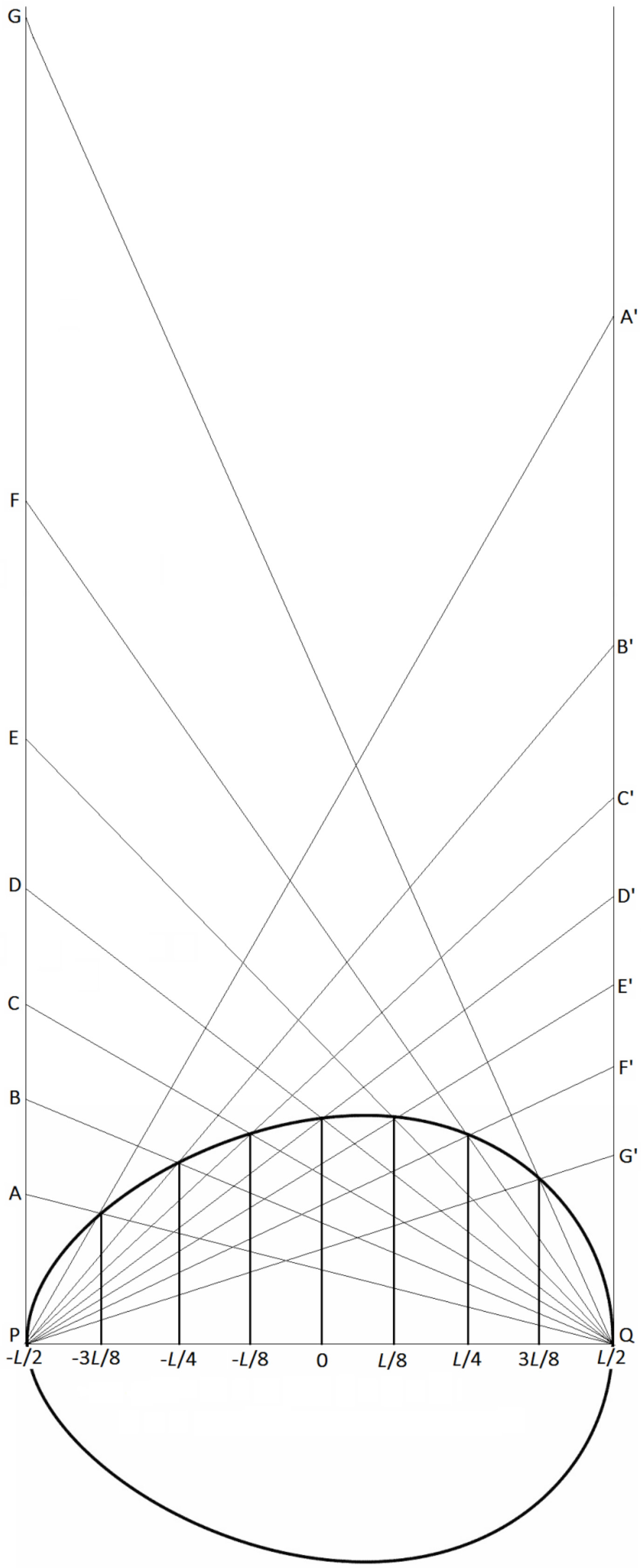


Fig. 2. Constructing the egg contours using path curves.

The accuracy of each model, as well as the verification of their compliance with the Main Axiom, was carried out by conducting an experimental procedure as outlined below.

MATERIALS AND METHODS

The study of Baker's model is not the first investigation of mathematical formulae developed to describe egg contours. Previously, we [21, 22] thoroughly examined and, where possible, improved the Preston [2] and Smart [4] models. While it was not possible to bring the Preston model to a form conforming to the Main Axiom principles [21], the Smart model was successfully modified [22]. The use of three initial egg measurements, i.e., B, L and w, substituted into the derived formula, made it possible to ensure the accuracy of defining the main types of egg profiles at the level of 3.6–7.2 %. Since the primary goal of the current Baker model study is to find and analyse the parameters that ensure compliance with the Main Axiom requirements, we decided to use the same digital profiles of bird eggs as in Narushin et al. [22] to compare these studies. The quantitative data of the used digital profiles were taken from our previous works [15–17, 23, 24] as shown in Figure 3. These were a chicken (*Gallus gallus*) egg, conforming to the shape of a classic ovoid; a razorbill (*Alca torda*) egg, the profile of which is a representative of pear-shaped (pyriform) eggs; and a common sandpiper (*Actitis hypoleucos*) egg, the geometric features of which can be characterised as conical, i.e., a kind of "symbiosis" of the first and second egg shape types. Herewith, some eggs are presented in pixels and some in centimetres, observing actual geometric proportions.

Chicken (*Gallus gallus*) egg. Source: Woodlands Farm, Canterbury and Staveleys Eggs Ltd, Coppull, UK

Common sandpiper (*Actitis hypoleucos*) egg. Source: https://commons.wikimedia.org/wiki/File:Actitis_hypoleucos_MWNH_0255.JPG (by Klaus Rassinger and Gerhard Cammerer, 2012; Category: Eggs of the Natural History Collections of the Museum Wiesbaden; CC-BY-SA-3.0)

Razorbill (*Alca torda*) egg. Source: https://www.flickr.com/photos/blackcountrymuseums/5237094139/ (by the Black Country Living Museum, Dudley, UK, 2010; CC-BY-NC-SA 2.0)

A B C

Fig. 3. Three eggs of characteristic shapes: ovoid (A), conical (B) and pyriform (C), used in the experiment.

For each egg, its geometric shape was generated using the three presented Baker model modifications (BM^{MA}, BM' and BM'') and compared with the respective actual digital profile. The approximate mean percentage error, ε (e.g., [25]), was used to evaluate how closely each theoretical egg profile matched the actual one:

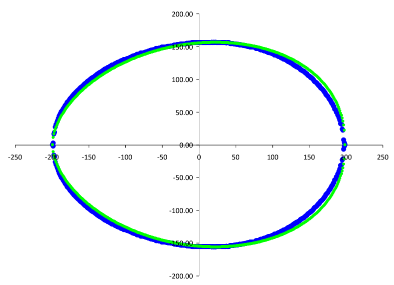
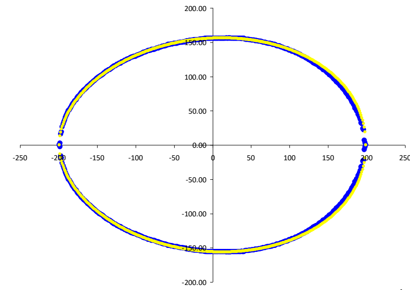
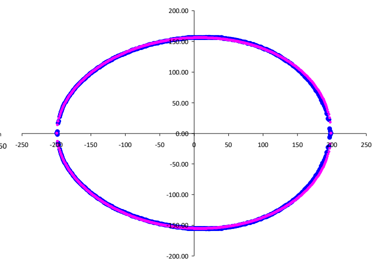
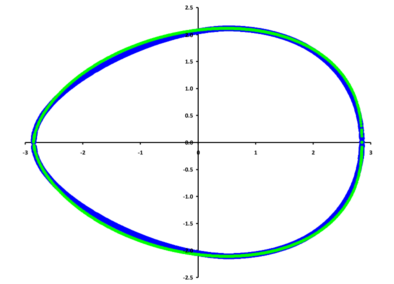
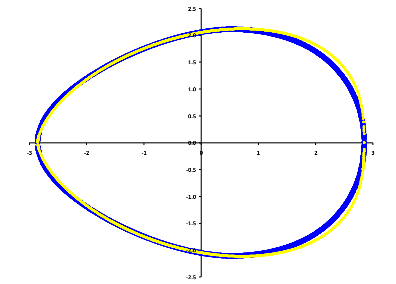
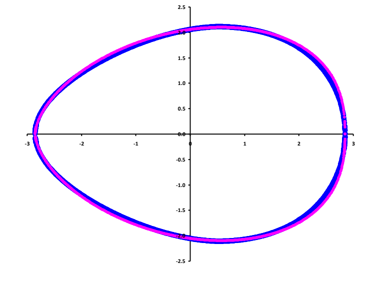
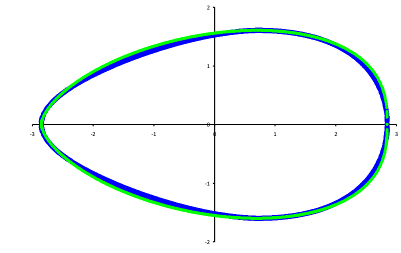
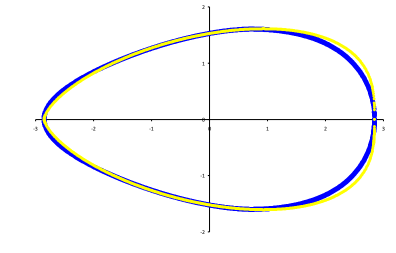
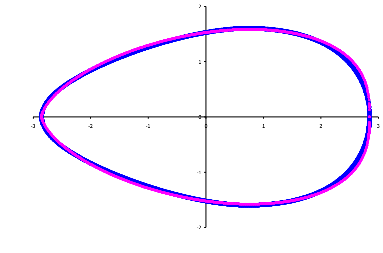
$$\varepsilon = \frac{1}{k} \cdot \sum_{1}^{n} \left| \frac{v_1 - v_2}{v_1} \right| \cdot 100\,\%, \tag{16}$$

where k represents a number of x points on the horizontal axis, and v_1 and v_2 represent the pertinent values of y that were obtained, respectively, from (1) a direct measurement of the egg profile and (2) calculation using the appropriate Baker model modification.

RESULTS AND DISCUSSION

The results of the visualisation of geometric profiles obtained using various modifications of Baker models (BM^{MA}, BM' and BM'') in comparison with real contours of three types of bird eggs are presented in Table 1. Each profile is accompanied by the appropriate ε value (in %).

Table 1. Visualisation results for geometric profiles obtained using three different Baker model modifications (green line for BM^{MA}, yellow line for BM’, and purple line for BM’’) in comparison with actual contours of three types of bird eggs (blue line)

BM^{MA}	**BM’**	**BM’’**
Chicken (*Gallus gallus*) egg		
		
ε = 8.7%	ε = 5.3%	ε = 4.7%
Common sandpiper (*Actitis hypoleucos*) egg		
		
ε = 6.6 %	ε = 11.0 %	ε = 7.4 %
Razorbill (*Alca torda*) egg		
		
ε = 8.6 %	ε = 12.8 %	ε = 8.9 %

In his book, Edwards [14], describing the mathematical interpretation results for profiles of 55 plant species and varieties, noted that about 55 % falls within a 10 % accuracy interval, and 36 % falls between 10 % and 20 %. Baker [1], when describing 250 eggs of various shapes, used a somewhat unusual accuracy indicator: “*the path curve regression error, which is the measure used to accept or reject the least-squares path curve fit to any egg oval and is based on the standard regression error formula for the sum of square deviations between the path curve radius and the actual egg radius at each of the seven diameter levels*.” This indicator of the goodness-of-fit of the path curve to an actual egg oval allowed us to conclude that the profile of real eggs was described quite accurately. In this case, both authors used data from eight initial measurements, i.e., length and seven radii, which conforms to our BM" model.

As a result of our experimental verification, this BM" model also demonstrated a fairly high accuracy in comparison with other modifications, which was especially noticeable when describing eggs of a regular ovoid shape that is typical for chicken eggs. However, such a number of initial measurements can be a certain obstacle for using this model, both in the laboratory and industrial applications. Why do we pay such attention to minimising the number of measured parameters? We tried to generalise the answers to this question in the form of the following provisions:

- *Reduction of model complexity.* The fewer parameters and data that need to be taken into account, the simpler and faster the calculation becomes. This is especially important for computationally complex models, where redundant data can slow down the process and require more resources.
- *Improving the interpretability of the obtained results.* With a large amount of initial data, the model becomes complex and difficult to analyse. Limiting the variables helps to understand how each of them affects the result. This approach simplifies the analysis and interpretation of the obtained data.
- *Reducing the risk of overfitting, say, when using Deep Learning principles.* If a model uses too much data, it can adjust to noise and random dependencies in the source data, losing its ability to generalise. Reducing the number of variables helps avoid overfitting and improves the predictive capabilities of the model.
- *Reduced data collection costs.* Each measurement requires time, resources and, accordingly, financial investments. Limiting their number allows you to reduce these costs and focus only on key parameters.
- *Easier data verification and fewer errors*. The less data, the easier it is to verify its correctness and accuracy. This reduces the likelihood of errors due to noise and measurement errors.

It was with respect to the above provisions that our efforts were concentrated on modifying the Baker model in the direction of reducing the number of measurements. As a result, the BM' modification was proposed. The accuracy of describing the selected egg contours using the BM' model was practically not inferior to BM" for ovoid eggs (ε = 5.3 % vs. 4.7 %) but was clearly insufficient to create theoretical profiles that are more complex in mathematical expression, i.e., conical and pyriform eggs (ε = 11.0 % and 12.8 %, respectively). Nevertheless, both models (BM' and BM") demonstrated their inconsistency with the Main Axiom principle: the extrema of these functions were shifted away from the required location, i.e., $x = w$. At the same time, the shift of the extrema, both for the BM' and BM" models, was quite significant (20 ... 47 % and 10 ... 60 %, respectively). At the same time, some violations also occurred in the value of the maximum breadth of the theoretical egg profiles (B). Although the degree of such deviations did not exceed 0.5 % of the B value for an actual egg, even a small discrepancy, nevertheless, is capable of violating the ratio of the geometric parameters of the egg.

The results of using the BM^{MA} modification were somewhat unexpected for us. The accuracy of its conformation to actual profiles was the lowest when describing ovoid eggs (ε = 8.7 %); however, the results were the best when mathematically interpreting eggs of complex geometric shape (respectively ε = 6.6 % for conical eggs and ε = 8.6 % for pyriform eggs). In addition, the presence of such advantages as usage of only three initial measurements and absolute compliance with the Main Axiom requirements further enhances the significance and expediency of the practical use of this modification. The basis for the possible application of BM^{MA} may be the theoretical display of a certain standard geometric figure of an egg-shaped form. In our previous studies [15, 17], we considered the possible advantages of its use as a method for assessing the deviation of a particular egg from a certain egg standard inherent in a given bird species and/or, directly, the egg being assessed. The quantitative value of these deviations can serve as a criterion for the nutritional, incubation or physiological properties of the egg being studied or the embryo developing in it. Thus, the presence of a geometric standard can give impetus to a new round of applied research aimed at finding and analysing such relationships.

A comparative assessment of the accuracy of describing the contours of eggs of different shapes using the Baker model modification that complies with the Main Axiom principles (i.e., BM^{MA}) and a similar version of the Smart model that also adhered to these principles [22] demonstrated some advantage of the latter: 8.7 % vs. 7.2 % for ovoid eggs, 6.6 % vs. 4.1 % for conical eggs, and 8.6 % vs. 3.6 % for pyriform eggs. Despite this, both models can have practical application without contradicting, but, on the contrary, complementing each other, since we are talking about an egg-shaped standard geometric figure designed to characterise the deviations in the contours of an actual egg and not about an exact copy of its profile.

CONCLUSION

In this study, we have explored an under-appreciated oological model introduced by Baker [1]. A modification of the Baker model (Eqn2), the parameters λ and *T* of which are determined from the conditions of compliance with the Main Axiom criteria and calculated in accordance with Eqns 4 and 5, can be a good alternative to creating a standard oviform geometric figure, the shape of which varies from an elongated pyriform egg to a classic ovoid. This model is quite easy to use and requires measuring only three initial parameters, i.e., egg length, *L*, maximum breadth, *B*, and the value of the vertical axis shift from the centre, *w*. The standard figure can serve as a basis for comparing possible deviations in the geometric dimensions of an actual egg, which makes it possible to search for correlations with its quality characteristics and/or incubation properties. Simplifying and improving on the Baker model of egg shape is instrumental for its use in ecological and evolutionary studies in birds as well as in egg-inspired engineering and artificial intelligence-assisted technologies (e.g., [26, 27]).

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