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**Egg and Math: Introducing a Universal Formula for Egg
Shape**

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4 2 Egg and Math: Introducing a Universal Formula for Egg Shape
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27 13 **Short title:** Avian egg shape universal formula
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Abstract

Egg as one of the most traditional food products has been attracting mathematicians', engineers' and biologists' attention from analytical point of view since long ago. As a main operand in oomorphology, the shape of a bird's egg has, to date, escaped a universally applicable mathematical formulation. Analysis of all egg shapes can be laid in four geometric figures: sphere, ellipsoid, ovoid, and pyriform (conical or pear-shaped). The first three have a clear mathematical definition, each derived from expression of the previous, but a formula for the pyriform profile has yet to be inferred. To rectify this, we introduced an additional function into the ovoid formula. The subsequent mathematical model fits a completely novel geometric shape that can be characterized as the last stage in the evolution of the sphere—ellipsoid—Hügelschäffer's ovoid transformation applicable to any egg geometry. Required measurements are the egg length, maximum breadth, and diameter at the terminus from the pointed end. These mathematical analysis and description represent the sought-for universal formula and is invariably a significant step in understanding not only the egg shape itself, but how and why it evolved, thus making widespread biological and technological applications theoretically possible.

Introduction

Described as “the most perfect thing”,¹ the egg was always considered as a major food source in the human history and nutrition. It is also one of the most recognizable shapes in nature and an example of evolutionary adaptation to the most diverse environmental conditions and situations. These include extremes of heat and humidity, incubated with and without body heat, in or out of nests and/or from clean to highly infected environments. Moreover, the practical issues of evolving a shape that is large enough to incubate an embryo, small enough to exit the body in the most efficient way, not roll away once laid, and be structurally sound enough to bear weight, are all primary considerations of a remarkable structure that is a feature of over 10,500 extant bird species including those used for egg production and consumption by people. The recent appreciation that birds are living dinosaurs also opens up a whole new line of enquiry in studies of the most well-known of extinct species. The egg shape is thus, most worthy of a full mathematical analysis and description. Despite this, an expression of “oviform” or “egg-shaped” (a term used in common parlance) that is universally applicable to all birds has belied accurate description by mathematicians, engineers and biologists.² Various attempts to derive such a standard geometric figure in this context that, like many other geometric figures, can be clearly described by a mathematical formula are nonetheless over 65 years old.³ Such a universal formula potentially would have applications in biological science, physics, engineering and technology where oomorphology (i.e., the study of egg shape)⁴ is an important aspect of research and development in disciplines such as food quality, food engineering, poultry breeding and farming, ornithology, genetics, species adaptation, evolution, systematics, architecture and artwork.

We believe that a universal mathematical egg model would be a prerequisite and an important breakthrough for widespread applicability for many other investigations in corresponding fields of science and technology, such as (1) comprehensive scientific definition of this biological object, (2) accurate and simple calculation of its physical characteristics, and (3) bionics.⁵

According to Nishiyama,⁶ all profiles of eggs can be described in four main shape categories *circular*, *elliptical*, *oval* and *pyriform* (conical or pear-shaped) (Fig. 1A–D). A circular profile indicates a spherical egg; elliptical an ellipsoid; oval an ovoid and so on. Precise mathematical formulae have hitherto only been achieved for the simpler (e.g., spherical, elliptical, etc.) forms, however.

Many researchers have identified to which shape group a particular egg can be assigned, and thus developed various indices to help make this definition more accurate. Historically, the first of these indices was the shape index (*SI*) Romanoff and Romanoff,⁷ which is a ratio of maximum egg breadth (*B*) to its length (*L*). *SI* has been mainly employed in the poultry breeding industry to evaluate the shape of chicken eggs and sort them thereafter. Its disadvantage is that, according to this index, one can only judge whether or not an egg falls into the group of circular shape. With each subsequent study, there have been more and more other devised indices. That is, while the early studies⁸ limited themselves to the usefulness of such egg characteristics as asymmetry, bicone and elongation, the later ones increased the number of indices to seven,⁴ and even to ten.⁹ The purpose of the current

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2 67 study was to take this research to its ultimate conclusion to present a universal formula for calculating the shape
3 68 of any egg based on revising and re-analysis of the main findings in this area.

8 70 **Theory**

10 71 In parallel to the process of developing various egg shape indices, a broader mathematical insight into
11 72 comprehensive and optimal description of the natural diversity of oviform warrants further study. The definition of
12 73 the groups of circular and elliptical egg shapes (Fig. 1A and B) is relatively straightforward since there are clear
13 74 mathematical formulae for the circle and ellipse. To describe mathematically oval and pyriform shapes (Fig. 1C
14 75 and D) however, new theoretical approaches are necessary.

18 76 Preston³ proposed the ellipse formula as a basis for all egg shape calculations. Multiplying the length of its vertical
19 77 axis by a certain function $f(x)$ (which he suggested to express as a polynomial) Preston showed that most of the
20 78 eggs studied could be described by a cubic polynomial, although for some species, a square or even linear
21 79 polynomial would suffice. This mathematical hypothesis turned out to be so effective that most of the further
22 80 research in this area was aimed solely at a more accurate description of the function $f(x)$. Most often, this function
23 81 was determined by directly measuring the tested eggs, after which the data was subjected to a mathematical
24 82 processing using the least squares method. As a result, a function could be deduced that, unfortunately, would be
25 83 adequate only to those eggs that were involved in an experiment.¹⁰⁻¹² Some authors^{13,14} applied the circle equation
26 84 instead of ellipse as the basic formula, but the principle of empirical determination of the function $f(x)$ remained
27 85 unchanged. Several attempts were made to describe the function $f(x)$ theoretically in the basic ellipse formula;^{15,16}
28 86 however, for universal and practical applicability to all eggs (rather than just theoretical systems), it is necessary
29 87 to increase the number of measurements and the obtained coefficients.

36 88 The main problem of finding the most convenient and accurate formula to define the function $f(x)$ is the difficulty in
37 89 constructing graphically the natural contours corresponding to the classical shape of a bird's egg.¹⁷⁻¹⁹ Indeed, all
38 90 the reported formulae have a common flaw; that is, although these models may help define egg-like shapes in
39 91 works of architecture and art, they do not accurately portray "real life" eggs for practical and research purposes.
40 92 This drawback can be explained by the fact that the maximum breadth of the resulting geometric figure is always
41 93 greater than the breadth (B) of an actual egg, as the B value is measured as the egg breadth at the point
42 94 corresponding to the egg half length. This drawback has been reviewed in more detail in our previous work.⁵ In
43 95 order, therefore, for the mathematical estimation of the egg contours not to be limited by a particular sample used
44 96 for computational purposes, but to apply to all egg shapes present in nature, further theoretical considerations are
45 97 essential. One such tested and promising approach is Hügelschäffer's model.²⁰⁻²²

51 98 The German engineer Fritz Hügelschäffer first proposed an oviform curve, shaped like an egg, by moving one of
52 99 concentric circles along its x -axis constructing an asymmetric ellipse as reviewed elsewhere.²³⁻²⁵ A theoretical
53 100 mathematical dependence for this curve was deduced elsewhere,^{20,21} which was later adapted by us in relation to

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2 101 the main measurements of the egg (i.e., its length, L , and maximum breadth, B) and carefully reviewed as applied
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4 102 to chicken eggs.⁵

$$y = \pm \frac{B}{2} \sqrt{\frac{L^2 - 4x^2}{L^2 + 8wx + 4w^2}}, \quad (\text{Eqn1})$$

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15 106 where B is the egg maximum breadth, L is the egg length, and w is the parameter that shows the distance between
16 107 two vertical lines corresponding to the maximum breadth and the half length of the egg.

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18 108 Hügelschäffer's model works very well for three classical egg shapes, i.e., circular, elliptical and oval (Fig. 2A–D).
19 109 Indeed, when $L = B$, the shape becomes a circle and when $w = 0$ it becomes an ellipse. Therefore, the majority of
20 109 egg shapes can be defined by the formula above (Eqn1). Unfortunately, Hügelschäffer's model is not applicable
21 110 in estimating the contours of pyriform eggs (Fig. 2E). For instance, it is obvious even from visual inspection that
22 111 the theoretical profile of the Brünnich's guillemot egg does not resemble its actual "real world" counterpart. Thus,
23 111 Hügelschäffer's model has some limitations in the description of the eggs, and one of those is a limited range of
24 112 possible variations of the w value.⁵
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29 115 Based on the analysis of various formulae accumulated and available in the arsenal of egg geometry
30 116 researchers,¹⁴ one can admit a problem of a mathematical definition of pyriform (or conical) eggs to be the most
31 116 difficult in comparison with all other egg shapes. With this in mind, the goal of this work was research aimed at
32 117 developing a mathematical expression that would be able to accurately describe pyriform eggs and at devising a
33 118 universal formula for eggs of any shape.
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40 121 **Methods**

41 122 To verify if the Hügelschäffer's model (Eqn1) previously applied by us to chicken eggs⁵ is valid to all possible egg
42 122 shapes of various birds, we tested it on the following species: Ural owl (*Strix uralensis*) as a representative of
43 123 circular eggs (Fig. 2A), emu (*Dromaius novaehollandiae*) representing elliptical eggs (Fig. 2B), song thrush (*Turdus*
44 124 *philomelos*) and osprey (*Pandion haliaetus*) for oval eggs (Fig. 2C and D), and Brünnich's guillemot (*Uria lomvia*)
45 125 for pyriform eggs (Fig. 2E).
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49 127 In trying to establish if the novel formula of the pyriform contours (Eqn3) and the universal Eqn5 we developed
50 127 here are valid for describing a variety of pyriform shapes, we applied them to the following species: Brünnich's
51 128 guillemot (*Uria lomvia*; Fig. 3A), great snipe (*Gallinago media*; Fig. 3B), and king penguin (*Aptenodytes*
52 129 *patagonicus*; Fig. 3C).
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2 131 For mathematical and standard statistical calculations, Microsoft Excel and STATISTICA 5.5 (StatSoft, Inc./TIBCO,
3 132 Palo Alto, CA, USA) programmes were exploited. As a part of our broader research project to develop more
4 133 theoretical approaches for non-destructive evaluation of various egg characteristics,² we did not handle eggs from
5 134 wild birds or any valuable egg collection in this study. Where needed, we substituted actual eggs with their images
6 135 and mathematical representational counterparts. To make it clear, we have considered a standard hen's egg as
7 136 represented by Romanoff and Romanoff⁷ and used their data of numerous egg measurements to deduce a formula
8 137 for recalculation of w (see Supplementary Material S1).

138 139 **Results**

140 As a first step, we employed the data of numerous egg measurements represented by Romanoff and Romanoff⁷
141 for a standard hen's egg, and produced the following formula for recalculation of w (see details in Supplementary
142 Material S1):

$$143$$

$$144 \quad w = \frac{L - B}{2n} \quad (\text{Eqn2})$$

145 in which n is a positive number.

146 Inputting different numbers in Eqn2 and substituting the value of w into Eqn1, we can design different geometrical
147 curves that resemble egg contours of other species (Fig. 4A–C).

148 Thus, the principal limitation for Hügelschäffer's model is the fact that n cannot be less than 1, which means that
149 the maximum value of w is $(L-B)/2$. Otherwise, the obtained contour does not resemble the shape of any egg (Fig.
150 4D–F). This fact was investigated and well explained elsewhere.²²

151 Such limitations explain why Hügelschäffer's model cannot be used to describe the contours of pyriform eggs. The
152 only way to make the shape of the pointed end of such eggs more conical is to use the n values less than 1, but
153 in this case the obtained contours do not resemble any egg currently appearing in nature. In a series of
154 mathematical computations, we deduced a formula for the pyriform egg shape (see details in Supplementary
155 Material S2):

$$156$$

$$157 \quad y = \pm \frac{B}{2} \cdot \sqrt{\frac{(L^2 - 4x^2)L}{2(L - 2w)x^2 + (L^2 + 8Lw - 4w^2)x + 2Lw^2 + L^2w + L^3}} \quad (\text{Eqn3})$$

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2 159 If we place both contours, the pyriform Eqn3 and Hügelschäffer's Eqn1 ones, together onto the same diagram
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4 160 (Fig. 5), the presence of white area between them allows to arise a peculiar question: what to do with those eggs
5 161 whose contours are tracing within this zone?

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7 162 If we choose any point on the x -axis within the interval $[-w...L/2]$ corresponding to the white area between two
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9 163 models, there is obviously some difference, Δy , between the values of the functions recalculated according to
10 164 Hügelschäffer's model, y_H (Eqn1), and the pyriform one, y_c (Eqn3), that tells how conical the egg is:

$$15 \ 166 \ \Delta y = y_H - y_c \quad (\text{Eqn4})$$

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20 168 The subscript index 'c' was added only to designate that this function is related to its classic pyriform (conic) profile
21 169 according to Eqn3 (y_c does not differ from y in Eqn3). Maximum values of Δy mean that the egg contour is related
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23 170 to its classic pyriform profile and can be expressed with Eqn3. When $\Delta y = 0$, the egg shape has a classic ovoid
24 171 profile (Hügelschäffer's model) and is defined mathematically with Eqn1.

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26 172 To fill this gap (Δy) between the egg profiles according Eqn1 and Eqn3, the mathematical calculations were
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28 173 undertaken (see Supplementary Material S3) being resulted in the final universal formula applicable for any egg:

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32 \ 175 \ 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})} \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) \quad (\text{Eqn5})$$

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38 177 where $D_{L/4}$ is egg diameter at the point of $L/4$ from the pointed end (Fig. 5).

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41 178 Both Eqn3 and Eqn5 were tested using pyriform eggs of different shape index (SI) and w to L ratio, and their
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43 179 validity were explicitly verified (Fig. 3).

44 45 180 46 47 181 Discussion

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49 182 Historically, the egg has represented a traditional food product and a natural object laid by birds that has a
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51 183 remarkable and unique shape. The common perception of "egg-shaped" is an oval, with a pointed end and a blunt
52 184 end and the widest point nearest the blunt end, somewhat like a chicken's egg. As we have demonstrated however,
53 185 things can be far simpler (as in the case of the spherical eggs seen in owls, tinamous and bustards) or far more
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55 186 complicated (as in the case of pyriform eggs, e.g., seen in guillemots, waders and the two largest species of

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2 187 penguin). Evidence suggests²⁶ that egg shape is determined before the shell forms and by the underlying
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4 188 membranes. Why, in evolutionary terms, an egg is the shape that it is, is surprisingly under-studied. That is,
5 189 although there are some previous investigations in the field of egg shape evolution,^{27–30} we do not know how
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7 190 exactly this process occurred. In this context, it is the pyriform eggs (the ones that, in this study, we have
8 191 incorporated in order to make the formula universal) that have attracted the most attention. In common sandpipers
9 192 (and other waders) the pyriform shape is an adaptive trait ensuring that the (invariably) four eggs “fit together” in
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11 193 a nest (pointed ends innermost) to ensure maximum incubation surface against the mother’s brood patch
12 194 (Hewitson, 1831–1838).³¹ In guillemots, the relative benefits of the pyriform shape to prevent eggs rolling off cliff
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14 195 edges have been much debated, however, to the best of our knowledge, this is far from certain.¹ The selective
15 196 advantage to being “oviform” rather than spherical is, according to Birkhead,¹ three-fold: First, given that a sphere
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17 197 has the smallest surface area to volume ratio of any geometric shape, there is a selective advantage to being
18 198 roughly spherical as any deviation could lead to greater heat loss. Equally, non-spherical shapes are warmed
19 199 more quickly and thus an egg may represent compromise morphology for most birds. A second consideration may
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21 200 well be, as in common sandpipers, related to “packaging” of the eggs in the brood, and the third could be related
22 201 to the strength of the shell. In this final case, the considerations are that the egg needs to be strong enough so as
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24 202 not to rupture when sat on by the mother (a sphere is the best bet here), but weak enough to allow the chick to
25 203 break out. As a compromise between two, a somewhat elongated shape (be in elliptical, oval or pyriform) may
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27 204 represent a selective advantage.

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29 205 In this study, we observed that applications of a mathematical apparatus in the area of oomorphology⁴ and egg
30 206 shape geometry have developed from more simple formulae to more complex ones. In particular, the equation for
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32 207 the sphere would come first, being, then, modified into the equation for the ellipse by transforming the circle
33 208 diameter into two unequal dimensions. Hügelschäffer’s model represented a mathematical approach to shift a
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35 209 vertical axis along the horizontal one. Finally, through the universal formula (Eqn5) we have provided here would
36 210 allow to consider all possible egg profiles including the pyriform ones. For this, we would need only to measure
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38 211 the egg length, L , the maximum breadth, B , the distance w between the two vertical lines, corresponding to the
39 212 maximum breadth and the half length of the egg, and the diameter, $D_{L/4}$, at the point of $L/4$ from the pointed end.
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41 213 While we have provided evidence that our formula is universal for the overall shape of an egg, not every last
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43 214 contour of an egg may fit into the strict geometric framework of Eqn5. This is because natural objects are much
44 215 more diverse and variable than mathematical objects. Nevertheless, generally speaking, we accept that the
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46 216 mountains are pyramidal, and the sun is round, although, in reality, their shapes only approximately resemble
47 217 these geometric figures. In this regard, a methodological approach to assessing the shape of a particular bird egg
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49 218 would be to search for possible differences between the tested egg and its standard geometric shape (Eqn5).
50 219 These distinctive criteria can (and should) be different for various purposes and specific research tasks. Perhaps,
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52 220 this would be the radius of the blunt and/or pointed end, or the skewness of one of the sections of the oval, or
53 221 something else. The key message is that by introducing the universal egg shape formula we have expanded the
54 222 arsenal of mathematics with another geometric figure that can safely be called a “real world” egg. The
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2 223 mathematical modelling of the egg shape and other egg parameters that we have presented here will be useful
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4 224 and important modus operandi for further stimulating the relevant theoretical and applied research in the fields of
5 225 mathematics, engineering and biology.²
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9 227 **Conclusion**

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12 228 Here, a universal mathematical formula for egg shape has been proposed that is based on four parameters: egg
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14 229 length, maximum breadth, shift of the vertical axis, and the diameter at one quarter of the egg length. This formula
15 230 can theoretically describe any bird's egg that exists in nature. Mathematical description of the sphere, the ellipsoid
16 231 and the ovoid (all basic egg shapes) have already found numerous applications in a variety of disciplines including
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18 232 food research, mechanical engineering, agriculture, biosciences, architecture and aeronautics. We propose that
19 233 this new formula will, similarly, have widespread application. We suggest that biological evolutionary processes
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21 234 such as egg formation are amenable to mathematical description, and may become the basis for the
22 235 methodological concept of research in evolutionary biology.
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24 236 In the course of the present analysis and search for the optimal mathematical approximation of oomorphology,
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26 237 i.e., the egg contours, we showed that our approach is as accurate as possible for the egg shape prediction. Based
27 238 on the results of exploring the egg shape geometry models, we postulate here for the first time the theoretical
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29 239 formula that we have found as a universal equation solution for determining the egg contours. Our findings can be
30 240 applied in a variety of fundamental and applied disciplines including food and poultry industry, and serve as an
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32 241 impetus for the further development of scientific investigations using eggs as a research object.
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34 242

36 243 **Author contributions**

37 244 V.G.N.: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Validation, Visualization,
38
39 245 Writing – original draft, Writing – review & editing. M.N.R.: Conceptualization, Writing – original draft, Writing –
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41 246 review & editing. D.K.G.: Conceptualization, Project administration, Supervision, Writing – original draft, Writing –
42 247 review & editing.
43 248

44 249 **Supporting information**

46 250 Additional supporting information may be found in the online version of this article.
47

48 251 **Supplementary Material S1.** Recalculation of w .
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50
51 252 **Supplementary Material S2.** Mathematical description of pyriform eggs.
52

53 253 **Supplementary Material S3.** Inferring a universal formula for an avian egg.
54

Competing interests

The authors have no conflict of interest to declare.

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Figure legends

Figure 1. Basic egg shape outlines based on Nishiyama:⁶ (A) circular, (B) elliptical, (C) oval, and (D) pyriform

Figure 2. The images of eggs of the four main shapes from the following species: (A) Ural owl (*Strix uralensis*), circular (https://commons.wikimedia.org/wiki/File:Strix_uralensis_MWNH_0642.JPG); (B) emu (*Dromaius novaehollandiae*), elliptical (https://commons.wikimedia.org/wiki/File:Dromaius_novaehollandiae_MWNH_0009.JPG); (C) song thrush (*Turdus philomelos*), oval (https://commons.wikimedia.org/wiki/File:Turdus_philomelos_MWNH_2235.JPG); (D) osprey (*Pandion haliaetus*), oval (https://commons.wikimedia.org/wiki/File:Pandion_haliaetus_MWNH_0705.JPG); and (E) Brünnich's guillemot (*Uria lomvia*), pyriform (https://commons.wikimedia.org/wiki/File:Uria_lomvia_MWNH_2182.JPG); with their theoretical contours (on the right graphs) plotted using the Hügelschäffer's model (Eqn1). All egg images were taken by Klaus Rassinger and Gerhard Cammerer, 2012, are distributed under the terms of a CC-BY-SA-3.0 license and available in Wikimedia Commons (Category: Eggs of the Natural History Collections of the Museum Wiesbaden), and their dimensions do not correspond to actual size due to scaling

Figure 3. The images and their theoretical profiles of pyriform eggs of different shape index (*SI*) and *w* to *L* ratio: (A) a Brünnich's guillemot's (*Uria lomvia*) egg (https://commons.wikimedia.org/wiki/File:Uria_lomvia_MWNH_2182.JPG), $SI = 0.58$, $w/L = 0.17$; (B) a great snipe's (*Gallinago media*) egg (https://commons.wikimedia.org/wiki/File:Gallinago_media_MWNH_0193.JPG), $SI = 0.69$, $w/L = 0.10$; and (C) a king penguin's (*Aptenodytes patagonicus*) egg (https://commons.wikimedia.org/wiki/File:Manchot_royal_MHNT.jpg), $SI = 0.07$, $w/L = 1.8$. The egg dimensions do not correspond to actual size due to scaling. The egg images are available in Wikimedia Commons and distributed under the terms of a CC-BY-SA-3.0 license, and were taken by Klaus Rassinger and Gerhard Cammerer, 2012 (A and B; Category: Eggs of the Natural History Collections of the Museum Wiesbaden) and by Didier Descouens, 2011 (C; Category: Bird eggs of the Muséum de Toulouse)

Figure 4. The egg contours plotted using Eqn1 and Eqn2 if: (A) $n = 2$, (B) $n = 1.3$, (C) $n = 1$, (D) $n = 0.8$, (E) $n = 0.5$, and (F) $n = 0.3$.

Figure 5. The contours of the egg plotted using the pyriform model according to Eqn3 (inner line) and the Hügelschäffer's model according to Eqn1 (outer line).

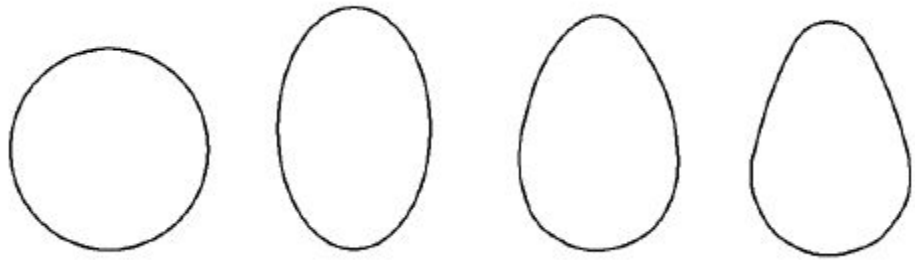
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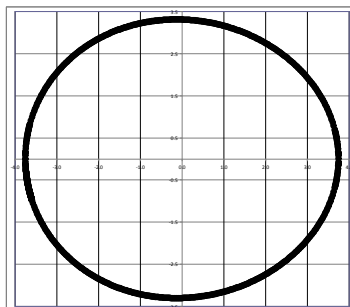
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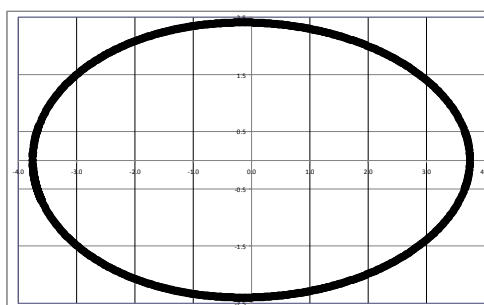
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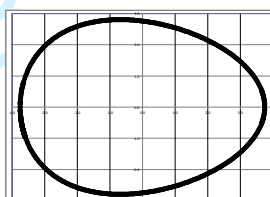
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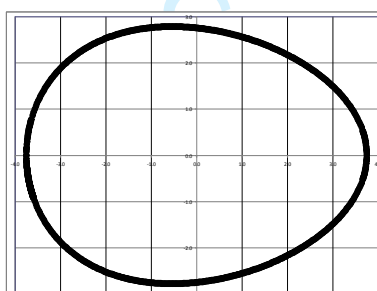
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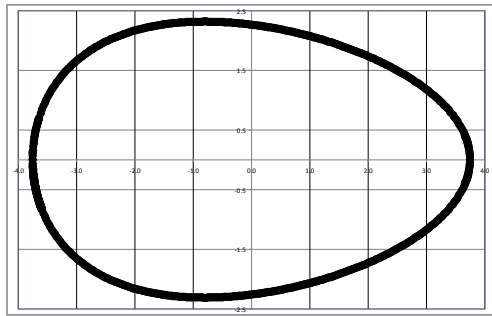
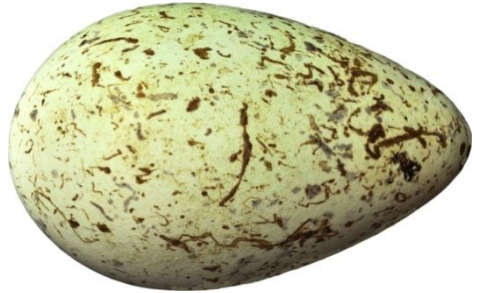


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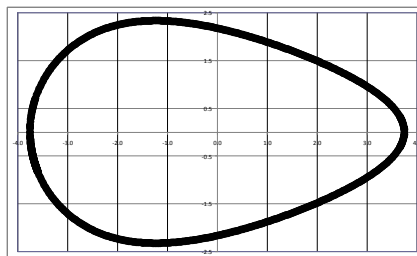
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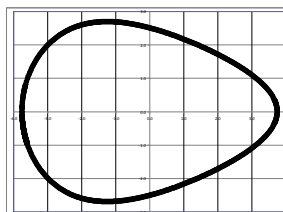
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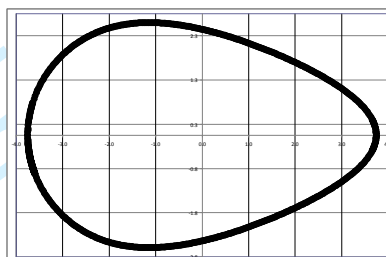
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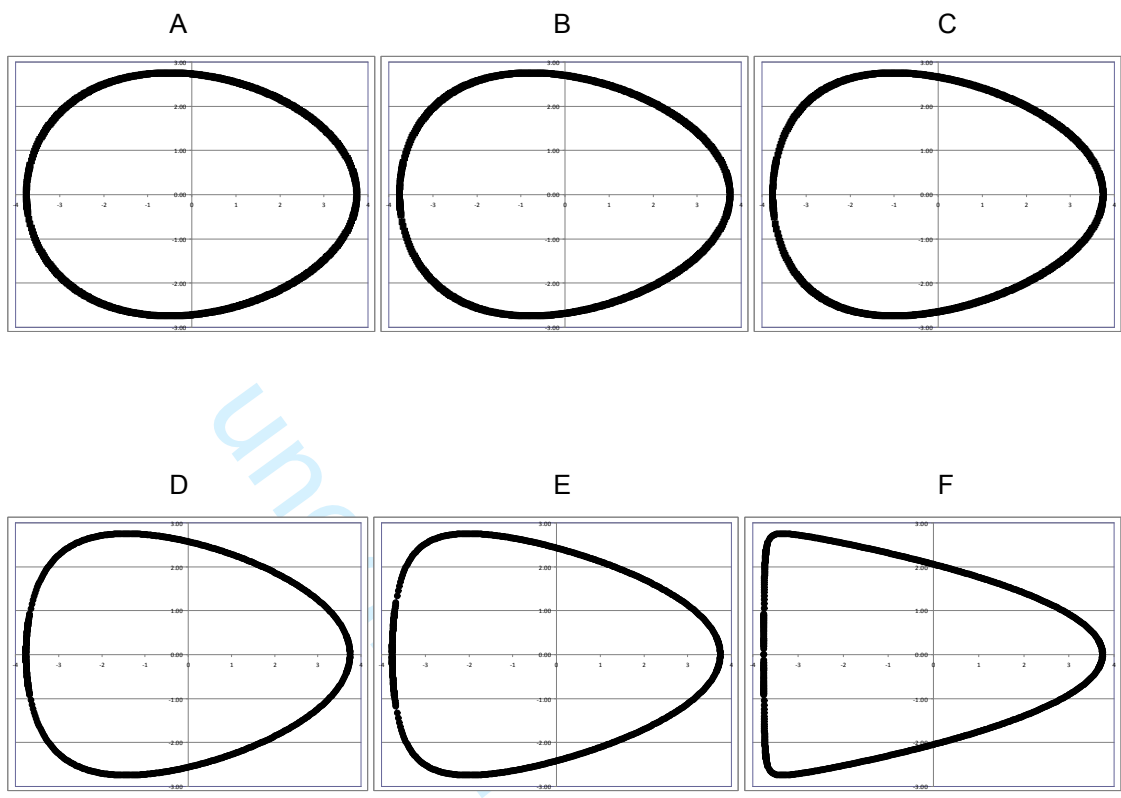
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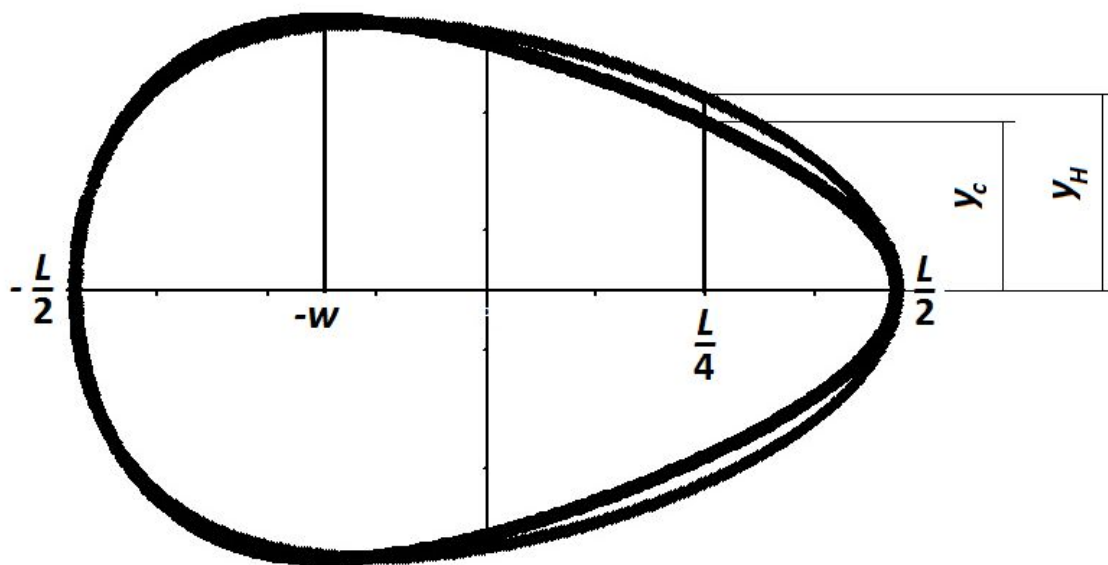


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