Egg equation

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Contents

Chicken egg (stock image).Credit: © yuthana Choradet / stock.adobe.com; modified from (1)

(1) A universal equation for the shape of an egg

Date:

August 31, 2021

Source:

University of Kent

Summary:

Researchers have discovered a universal mathematical formula that can describe any bird's egg existing in nature -- a significant step in understanding not only the egg shape itself, but also how and why it evolved, thus making widespread biological and technological applications possible.

Researchers from the University of Kent, the Research Institute for Environment Treatment and Vita-Market Ltd have discovered a universal mathematical formula that can describe any bird's egg existing in nature, a feat which has been unsuccessful until now.

Egg-shape has long attracted the attention of mathematicians, engineers, and biologists from an analytical point of view. The shape has been highly regarded for its evolution as large enough to incubate an embryo, small enough to exit the body in the most efficient way, not roll away once laid, is structurally sound enough to bear weight and be the beginning of life for so many species. The egg has been called the "perfect shape."

Analysis of all egg shapes used four geometric figures: sphere, ellipsoid, ovoid, and pyriform (conical or pear-shaped), with a mathematical formula for the pyriform yet to be derived.

To rectify this, researchers introduced an additional function into the ovoid formula, developing a mathematical model to fit a completely novel geometric shape characterized as the last stage in the evolution of the sphere-ellipsoid, which it is applicable to any egg geometry.

This new universal mathematical formula for egg shape is based on four parameters: egg length, maximum breadth, shift of the vertical axis, and the diameter at one quarter of the egg length.

This long sought-for universal formula is a significant step in understanding not only the egg shape itself, but also how and why it evolved, thus making widespread biological and technological applications possible.

Mathematical descriptions of all basic egg shapes have already found applications in food research, mechanical engineering, agriculture, biosciences, architecture and aeronautics. As an example, this formula can be applied to engineering construction of thin walled vessels of an egg shape, which should be stronger than typical spherical ones.

This new formula is an important breakthrough with multiple applications including:

1. Competent scientific description of a biological object. Now that an egg can be described via mathematical formula, work in fields of biological systematics,

optimization of technological parameters, egg incubation and selection of poultry will be greatly simplified.
2. Accurate and simple determination of the physical characteristics of a biological object. The external properties of an egg are vital for researchers and engineers who develop technologies for incubating, processing, storing and sorting eggs. There is a need for a simple identification process using egg volume, surface area, radius of curvature and other indicators for describing the contours of the egg, which this formula provides.
3. Future biology-inspired engineering. The egg is a natural biological system studied to design engineering systems and state-of-the-art technologies. The egg-shaped geometric figure is adopted in architecture, such as London City Hall's roof and the Gherkin, and construction as it can withstand maximum loads with a minimum consumption of materials, to which this formula can now be easily applied.

Darren Griffin, Professor of Genetics in the University of Kent and PI on the research, said: "Biological evolutionary processes such as egg formation must be investigated for mathematical description as a basis for research in evolutionary biology, as demonstrated with this formula. This universal formula can be applied across fundamental disciplines, especially the food and poultry industry, and will serve as an impetus for further investigations inspired by the egg as a research object."

Dr Michael Romanov, Visiting Researcher at the University of Kent, said: "This mathematical equation underlines our understanding and appreciation of a certain philosophical harmony between mathematics and biology, and from those two a way towards further comprehension of our universe, understood neatly in the shape of an egg."

Dr Valeriy Narushin, former visiting researcher at the University of Kent, said: "We look forward to seeing the application of this formula across industries, from art to technology, architecture to agriculture. This breakthrough reveals why such collaborative research from separate disciplines is essential."

The paper "Egg and math: introducing a universal formula for egg shape" is published in *Annals of the New York Academy of Sciences* (Valeriy G. Narushin, Research Institute for Environment Treatment and Vita-Market Ltd, Ukraine; Dr Michael N. Romanov, University of Kent; Professor Darren K. Griffin, University of Kent).

Story Source: Materials provided by **University of Kent**. Original written by Sam Wood. *Note: Content may be edited for style and length.*

Journal Reference:

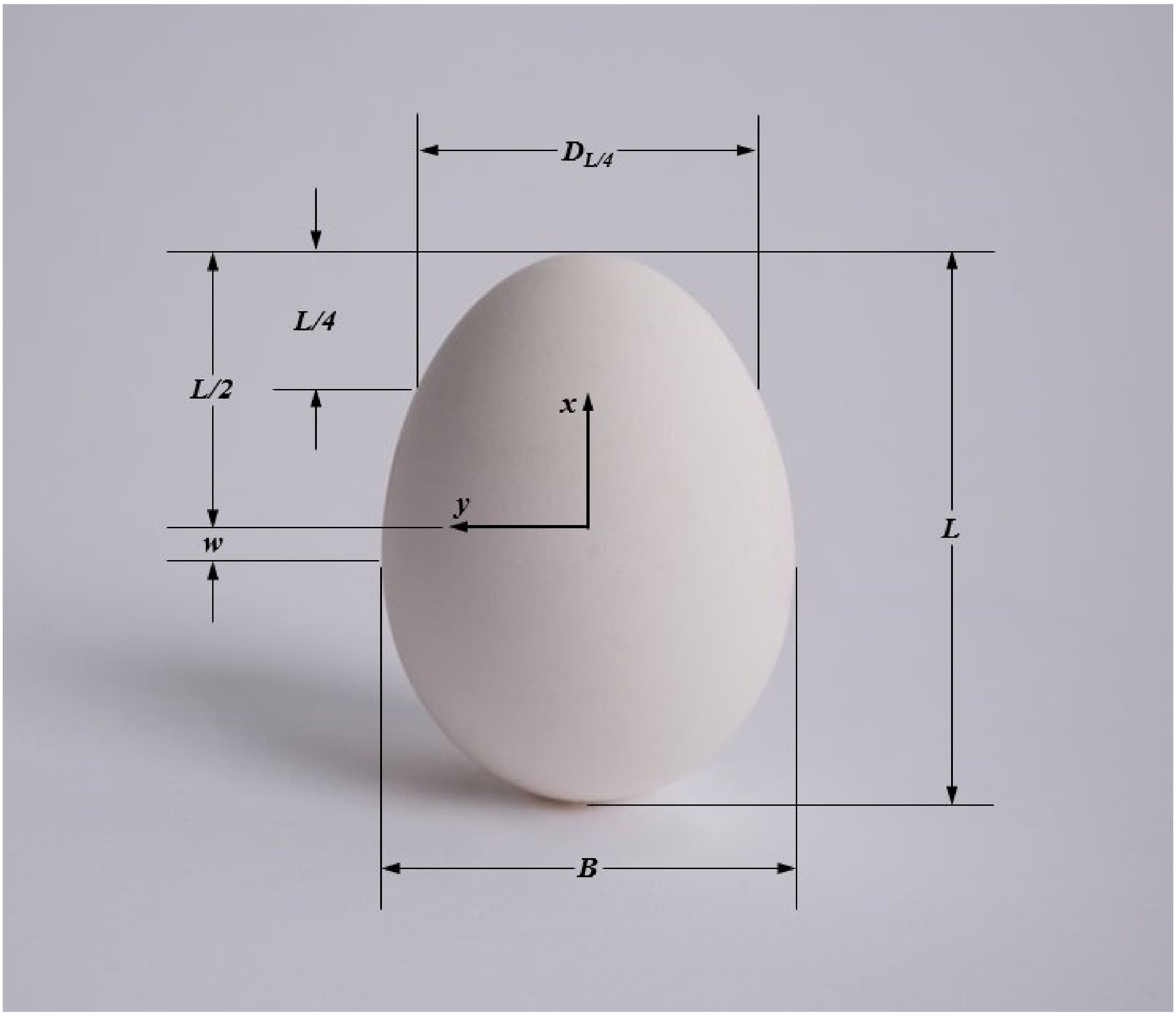
1. Valeriy G. Narushin, Michael N. Romanov, Darren K. Griffin. **Egg and math: introducing a universal formula for egg shape**. *Annals of the New York Academy of Sciences*, 2021; DOI: 10.1111/nyas.14680

(2) The Mathematically Defined Egg

10 September 2021

We're marking a unique achievement today, the development of which has eluded mathematicians, biologists, and fowl farmers for centuries: a universal formula for avian eggs!

Here's a diagram we created to mark the occassion, followed by the formula presented in a recently published paper by Valeriy G. Narushin, Michael N. Romanov, and Darren K. Griffin.



$$y = \pm\frac{B}{2}\sqrt{\frac{L^2-4x^2}{L^2+8wx+4w^2}}\cdot\left(1-\frac{\sqrt{5.5L^2+11Lw+4w^2}\cdot\left(\sqrt{3}BL-2D_{L/4}\sqrt{L^2+2wL+4w^2}\right)}{\sqrt{3}BL\left(\sqrt{5.5L^2+11Lw+4w^2}-2\sqrt{L^2+2wL+4w^2}\right)}\right)\cdot\left(1-\sqrt{\frac{L(L^2+8wx+4w^2)}{2(L-2w)x^2+(L^2+8Lw-4w^2)x+2Lw^2+L^2w+L^3}}\right)$$

The press release issued by the University of Kent explains what's now possible because of the development of a universal formula for bird eggs:

> This new formula is an important breakthrough with multiple applications including:
>
> 1. Competent scientific description of a biological object. Now that an egg can be described via mathematical formula, work in fields of biological systematics, optimization of technological parameters, egg incubation and selection of poultry will be greatly simplified;
> 2. Accurate and simple determination of the physical characteristics of a biological object. The external properties of an egg are vital for researchers and engineers who develop technologies for incubating, processing, storing and sorting eggs. There is a need for a simple identification process using egg volume, surface area, radius of curvature and other indicators for describing the contours of the egg, which this formula provides;
> 3. Future biology-inspired engineering. The egg is a natural biological system studied to design engineering systems and state-of-the-art technologies. The egg-shaped geometric figure is adopted in architecture, such as London City Hall's roof and the Gherkin, and construction as it can withstand maximum loads with a minimum consumption of materials, to which this formula can now be easily applied.

The "Gherkin" is the nickname of a visually distinctive building at 30 St. Mary Axe in London. The next time any architects want to make a building that looks like an egg, they'll finally have the math to make it happen!

References

Valeriy G. Narushin et al, Egg and math: introducing a universal formula for egg shape, *Annals of the New York Academy of Sciences* (2021). DOI: 10.1111/nyas.14680. Ungated Preprint: BioRxiv (PDF Document).

Image Credit: Photo by Jasmin Egger on Unsplash, to which we added the dimensional annotations.

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Original Article

Egg and math: introducing a universal formula for egg shape

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The egg, as one of the most traditional food products, has long attracted the attention of mathematicians, engineers, and biologists from an analytical point of view. As a main parameter 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 done using four geometric figures: sphere, ellipsoid, ovoid, and pyriform (conical or pear-shaped). The first three have a clear mathematical definition, each derived from the expression of the previous, but a formula for the pyriform profile has yet to be derived. To rectify this, we introduce 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, and it is applicable to any egg geometry. The required measurements are the egg length, maximum breadth, and diameter at the terminus from the pointed end. This mathematical analysis and description represents the sought-for universal formula and is a significant step in understanding not only the egg shape itself, but also how and why it evolved, thus making widespread biological and technological applications theoretically possible.

Keywords: egg geometry; egg shape; pyriform ovoid; Hügelschäffer's model; oomorphology; universal formula

Introduction

Described as "the most perfect thing,"[1] the egg has always been considered a major food source in 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 range of environmental conditions and situations. These include extremes of heat and humidity, incubation with or 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, a geometric characterization of "oviform" or "egg-shaped" (a term used in common parlance) that is universally applicable to the eggs of 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

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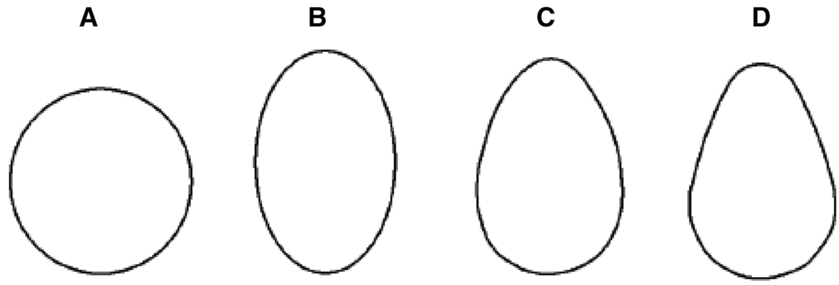

Figure 1. Basic egg shape outlines based on Nishiyama:[6] (A) circular, (B) elliptical, (C) oval, and (D) pyriform.

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*) of Romanoff and Romanoff,[7] which is the ratio of maximum egg breadth (B) to egg length (L). *SI* has been mainly employed in the poultry breeding industry to evaluate the shape of chicken eggs and sort them. 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 indices that have been devised. That is, while the early studies[8] 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 10.[9] The purpose of the current study was to take this research to its ultimate conclusion to present a universal formula for calculating the shape of any egg based on reviewing and reanalysis of the main findings in this area.

Theory

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

Preston[3] proposed the ellipse formula as a basis for all egg shape calculations. Multiplying the length of its vertical axis by a certain function $f(x)$ (which he suggested to be expressed as a polynomial), Preston showed that most of the eggs studied could be described by a cubic polynomial, although for some species, a square or even linear polynomial would suffice. This mathematical hypothesis turned out to be so effective that most of the further research in this area was aimed solely at a more accurate description of the function $f(x)$. Most often, this function was determined by directly measuring the tested eggs, after which the data were subjected to a mathematical processing using the least squares method. As a result, a function could be deduced that, unfortunately, would be adequate only to those eggs that were involved in the experiment.[10–12] Some authors[13,14] applied the circle equation instead of ellipse as the basic formula, but the principle of empirical determination of the function $f(x)$ remained unchanged. Several attempts were made to describe the function $f(x)$ theoretically in the basic ellipse formula;[15,16] however, for universal and practical applicability to all eggs (rather than just theoretical systems), it is necessary to increase the number of measurements and the obtained coefficients.

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

The German engineer Fritz Hügelschäffer first proposed an oviform curve shaped like an egg by moving one of two concentric circles along its x-axis, constructing an asymmetric ellipse, as reviewed elsewhere.[23–25] A theoretical mathematical dependence for this curve was deduced elsewhere,[20,21] which was later adapted by us in relation to the main measurements of the egg (i.e., its length, L, and maximum breadth, B) and carefully reviewed as applied to chicken eggs:[5]

$$y = \pm\frac{B}{2}\sqrt{\frac{L^2 - 4x^2}{L^2 + 8wx + 4w^2}}, \qquad (1)$$

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

Obradović *et al.*[22] demonstrated possible transformations of the egg-shaped ovoid by introducing some modifications to Hügelschäffer's model. In this regard, we consider the Hügelschäffer's model described by Eq. (1) as the standard one.

The standard Hügelschäffer's model works very well for three classical egg shapes, that is, circular, elliptical, and oval (Fig. 2A–D). Indeed, when $L = B$, the shape becomes a circle, and when $w = 0$, it becomes an ellipse. Therefore, the majority of egg shapes can be defined by the above formula (Eq. 1). Unfortunately, Hügelschäffer's model is not applicable for estimating the contours of pyriform eggs (Fig. 2E). For instance, it is obvious even from visual inspection that the theoretical profile of the Brünnich's guillemot egg does not resemble its actual real-world counterpart. Thus, Hügelschäffer's model has some limitations in the description of eggs, and one of those is a limited range of possible variations of the w value.[5] Use of other models that mathematically describe the shape of a bird's egg is complicated by the fact that these equations only allow the creation of geometric profiles that resemble an egg. However, this would result in a violation of the size of the described egg,[5] which is quite acceptable in architecture and fine arts but absolutely unacceptable in biological research.

On the basis of analysis of various formulae available to egg geometry researchers,[14] one can admit that the problem of a mathematical definition of pyriform (conical) eggs is the most difficult in comparison with all other egg shapes. With this in mind, the goal of this research was aimed at developing a mathematical expression that would be able to accurately describe pyriform eggs and at devising a universal formula for eggs of any shape.

Methods

To verify if the standard Hügelschäffer's model (Eq. 1) previously applied by us to chicken eggs[5] is valid for all the possible egg shapes of various birds, we tested it on the following species: Ural owl (*Strix uralensis*) as a representative of circular eggs (Fig. 2A); emu (*Dromaius novaehollandiae*) representing elliptical eggs (Fig. 2B); song thrush (*Turdus philomelos*) and osprey (*Pandion haliaetus*) for oval eggs (Fig. 2C and D); and Brünnich's guillemot (*Uria lomvia*) for pyriform eggs (Fig. 2E).

In trying to establish if the novel formula of the pyriform contours (Eq. 3) and the universal formula (Eq. 5) we developed here are valid for describing a variety of pyriform shapes, we applied them to the following species: Brünnich's

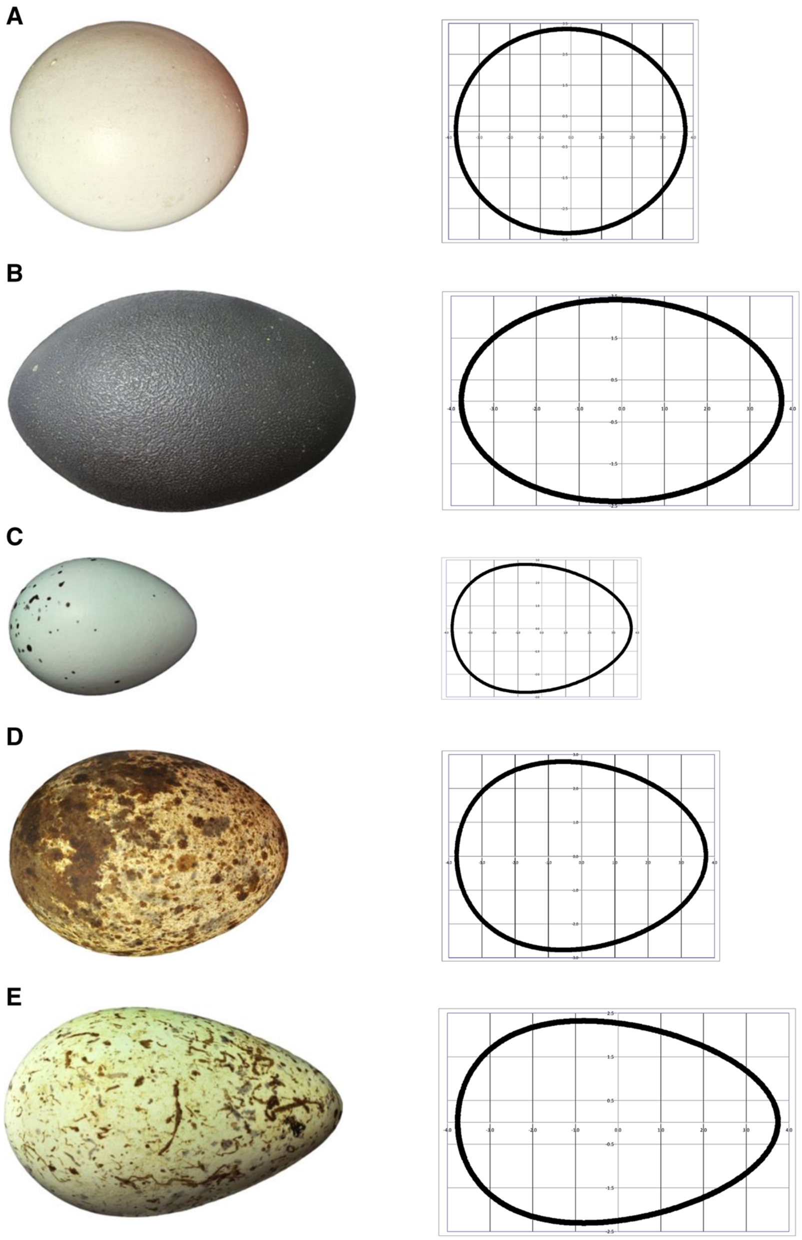

Figure 2. The images of eggs of the four main shapes from the following species: (A) Ural owl (*Strix uralensis*), circular (https://commons.wikimedia.org/wiki/File:Strix_uralensis_MWNH_0642.JPG). (B) Emu (*Dromaius novaehollandiae*), elliptical (https://commons.wikimedia.org/wiki/File:Dromaius_novaehollandiae_MWNH_0009.JPG). (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). (E) Brünnich's guillemot (*Uria lomvia*), pyriform (https://commons.wikimedia.org/wiki/File:Uria_lomvia_MWNH_2182.JPG). The graphs on the right show the theoretical contours plotted using Hügelschäffer's model (Eq. 1). 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 because of scaling.

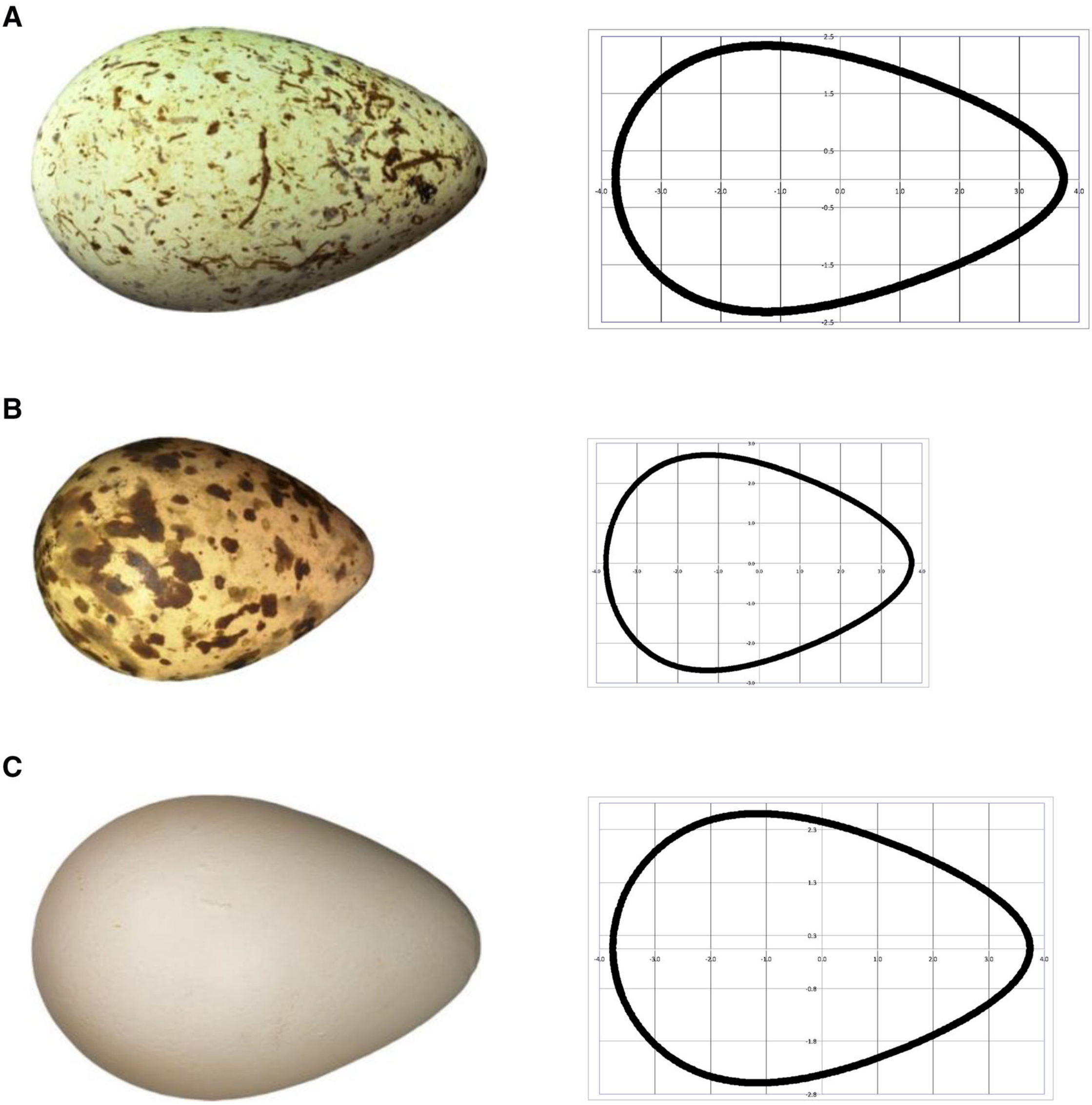

Figure 3. **The images and corresponding theoretical profiles of pyriform eggs of different shape indices (*SI*) and *w* to *L* ratios. (A) A Brünnich's guillemot's (*Uria lomvia*) egg (https://commons.wikimedia.org/wiki/File:Uria_lomvia_MWNH_2182.JPG), $SI = 0.58$, $w/L = 0.17$. (B) A great snipe's (*Gallinago media*) egg (https://commons.wikimedia.org/wiki/File:Gallinago_media_MWNH_0193.JPG), $SI = 0.69$, $w/L = 0.10$. (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 because of 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).**

guillemot (*Uria lomvia*; Fig. 3A), great snipe (*Gallinago media*; Fig. 3B), and king penguin (*Aptenodytes patagonicus*; Fig. 3C).

For mathematical and standard statistical calculations, Microsoft Excel and STATISTICA 5.5 (StatSoft, Inc./TIBCO, Palo Alto, CA) were used. As a part of our broader research project to develop more theoretical approaches for nondestructive evaluation of various egg characteristics,[2] we did not handle eggs from wild birds or any valuable

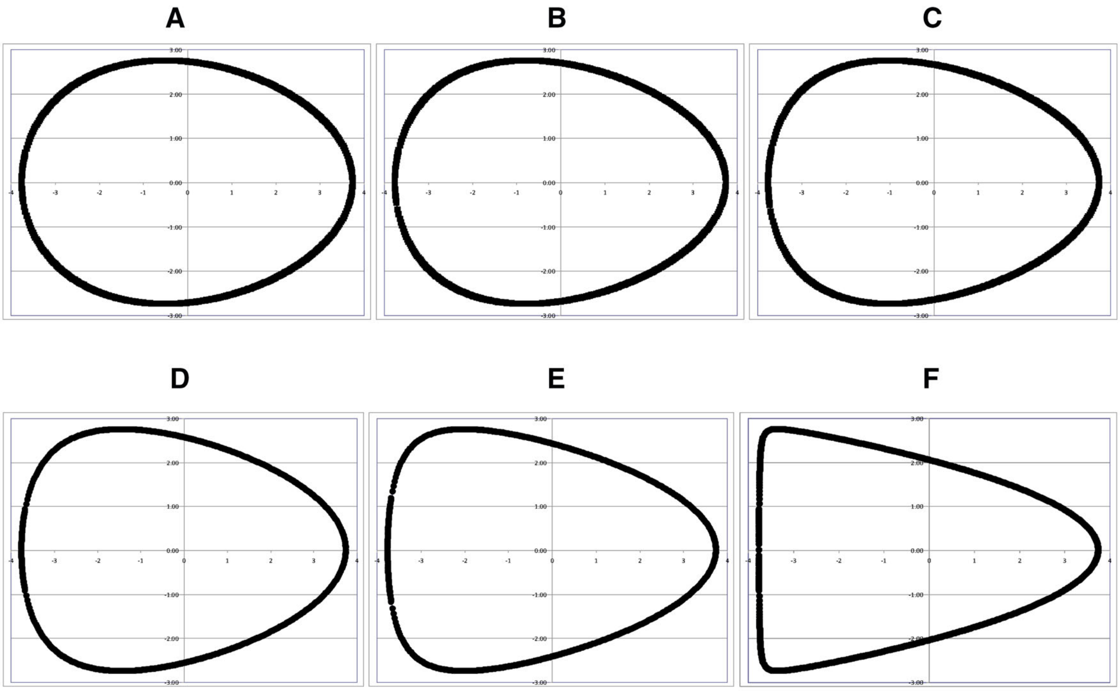

Figure 4. The egg contours plotted using Eqs. (1) and (2) if (A) $n = 2$, (B) $n = 1.3$, (C) $n = 1$, (D) $n = 0.8$, (E) $n = 0.5$, and (F) $n = 0.3$.

egg collection in this study. Where needed, we substituted actual eggs with their images and mathematical representational counterparts. To make it clear, we have considered a standard hen's egg as represented by Romanoff and Romanoff[7] and used their data of numerous egg measurements to deduce a formula for recalculation of w (see Supplementary Material S1, online only).

Results

As a first step, we employed the data of numerous egg measurements obtained by Romanoff and Romanoff[7] for a standard hen's egg, and produced the following formula for the recalculation of w (see details in Supplementary Material S1, online only):

$$w = \frac{L - B}{2n} \quad (2),$$

in which n is a positive number.

Inputting different numbers in Eq. (2) and substituting the value of w into Eq. (1), we can design different geometrical curves that resemble the egg contours of other species (Fig. 4A–C).

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

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

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

If we place both contours, the pyriform (Eq. 3) and Hügelschäffer's (Eq. 1) ones, together onto the same diagram (Fig. 5), the presence of white area

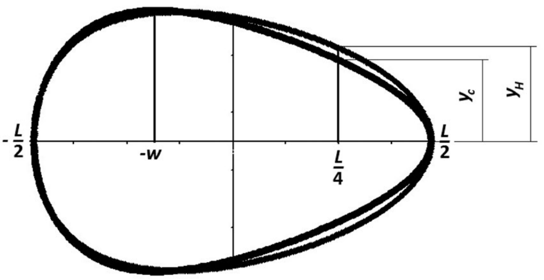

Figure 5. The contours of the egg plotted using the pyriform model according to Eq. (3) (inner line) and Hügelschäffer's model according to Eq. (1) (outer line).

between them raises the peculiar question: what to do with those eggs whose contours are tracing within this zone?

If we choose any point on the x-axis within the interval $[-w \ldots L/2]$ corresponding to the white area between two models, there is obviously some difference, Δy, between the values of the functions recalculated according to the standard Hügelschäffer's model, y_H (Eq. 1), and the pyriform one, y_c (Eq. 3), that tells how conical the egg is:

$$\Delta y = y_H - y_c \quad (4).$$

The subscript index c was added only to designate that this function is related to its classic pyriform (conic) profile according to Eq. (3) (y_c does not differ from y in Eq. 3). Maximum values of Δy mean that the egg contour is related to its classic pyriform profile and can be expressed with Eq. (3). When $\Delta y = 0$, the egg shape has a classic ovoid profile (the standard Hügelschäffer's model) and is defined mathematically with Eq. (1).

To fill this gap (Δy) between the egg profiles according to Eqs. (1) and (3), mathematical calculations were carried out (see Supplementary Material S3, online only), which resulted in the final universal formula applicable for any egg:

$$y = \pm\frac{B}{2}\sqrt{\frac{L^2-4x^2}{L^2+8wx+4w^2}} \times \left(1-\frac{\sqrt{5.5L^2+11Lw+4w^2}\times\left(\sqrt{3}BL-2D_{L/4}\sqrt{L^2+2wL+4w^2}\right)}{\sqrt{3}BL\left(\sqrt{5.5L^2+11Lw+4w^2}-2\sqrt{L^2+2wL+4w^2}\right)}\times\left(1-\sqrt{\frac{L(L^2+8wx+4w^2)}{2(L-2w)x^2+(L^2+8Lw-4w^2)x+2Lw^2+L^2w+L^3}}\right)\right) \quad (5),$$

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

Both Eqs. (3) and (5) were tested using pyriform eggs of different shape indices (SI) and w to L ratios, and their validity was explicitly verified (Fig. 3).

Discussion

Historically, the egg has represented a traditional food product and a natural object laid by birds that has a remarkable and unique shape. The common perception of "egg-shaped" is an oval, with a pointed end and a blunt end and the widest point nearest the blunt end, somewhat like a chicken's egg. As we have demonstrated, however, things can be far simpler (as in the case of the spherical eggs seen in owls, tinamous, and bustards) or far more complicated (as in the case of pyriform eggs, e.g., seen in guillemots, waders, and the two largest species of penguin). Evidence suggests[26] that egg shape is determined by the underlying membranes before the shell forms. Why, in evolutionary terms, does an egg have the shape that it does is surprisingly understudied. That is, although there are some previous investigations in the field of egg shape evolution,[27–30] we do not know how exactly this process occurred. In this context, it is the pyriform eggs (the ones that we have incorporated in this study in order to make the formula universal) that have attracted the most attention. In common sandpipers (and other waders), the pyriform shape is an adaptive trait ensuring that the (invariably) four eggs "fit together" in a nest (pointed ends innermost) to ensure maximum incubation surface against the mother's brood patch.[31] In guillemots, the relative benefits of the pyriform shape to prevent eggs rolling off cliff edges have been much debated; however, to the best of our knowledge, this is far from certain.[1,32] The selective advantage to being oviform rather than spherical is, according to Birkhead,[1] three-fold: First, given that a sphere has the smallest surface area to volume ratio of any geometric shape, there is a selective advantage to being roughly spherical as any deviation could lead to greater heat loss. Equally, nonspherical shapes are warmed more quickly, and thus an egg may represent compromise morphology for most birds. A second consideration may well be, as in common sandpipers, related to the packing of the eggs in the brood, and the third could be related to the strength of the shell. In this final case, the considerations are that the egg needs to be strong enough so as not to ruptured when sat on by the mother (a sphere is the best bet here), but weak enough to allow the chick to break out. As a compromise between the two, a somewhat elongated shape (be it elliptical, oval, or pyriform) may represent a selective advantage.

In this study, we observed that the applications of a mathematical framework for the study of oomorphology[4] and egg shape geometry have developed from more simple formulae to more complex ones. In particular, the equation for the sphere would come first, being, then, modified into the equation for the ellipse by transforming the circle diameter into two unequal dimensions. The standard Hügelschäffer's model represented a mathematical approach to shift a vertical axis along the horizontal one. Finally, the universal formula (Eq. 5) we have provided here would allow the consideration of all possible egg profiles, including the pyriform ones. For this, we would need only to measure the egg length L, the maximum breadth B, the distance w between the two vertical lines corresponding to the 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.

While we have provided evidence that our formula is universal for the overall shape of an egg, not every last contour of an egg may fit into the strict geometric framework of Eq. (5). This is because natural objects are much more diverse and variable than mathematical objects. Nevertheless, generally speaking, we accept that the mountains are pyramidal and the sun is round, although, in reality, their shapes only approximately resemble these geometric figures. In this regard, a methodological approach to assessing the shape of a particular bird egg would be to search for possible differences between the tested egg and its standard geometric shape (Eq. 5). These distinctive criteria can (and should) be different for various purposes and specific research tasks. Perhaps, this would be the radius of the blunt and/or pointed end, or the skewness of one of the sections of the oval, or something else. The key message is that by introducing the universal egg shape formula, we have expanded the arsenal of mathematics with another geometric figure that can safely be called a real-world egg. The mathematical modeling of the egg shape and other egg parameters that we have presented here will be useful and important for further stimulating relevant theoretical and applied research in the fields of mathematics, engineering, and biology.[2]

Conclusion

Here, a universal mathematical formula for egg shape has been proposed that is based on four parameters: egg length, maximum breadth, shift of the vertical axis, and the diameter at one quarter of the egg length. This formula can theoretically describe any bird's egg that exists in nature. Mathematical descriptions of the sphere, ellipsoid, and ovoid (all basic egg shapes) have already found numerous applications in a variety of disciplines, including food research, mechanical engineering, agriculture, biosciences, architecture, and aeronautics. We propose that this new formula will, similarly, have widespread application. We suggest that biological evolutionary processes, such as egg formation, are amenable to mathematical description and may become the basis for research in evolutionary biology.

In the course of the present analysis and search for the optimal mathematical approximation of oomorphology, we showed that our approach is as accurate as possible for egg shape prediction. On the basis of the results of exploring egg shape geometry models, we postulate here for the first time the theoretical formula that we have found is a universal equation solution for determining egg contours. Our findings can be applied in a variety of fundamental and applied disciplines, including food and poultry industry, and serve as an impetus for further scientific investigations using eggs as a research object.

Author contributions

V.G.N. was involved in conceptualization, data curation, formal analysis, investigation, methodology, validation, visualization, writing, and editing. M.N.R. was involved in conceptualization, writing, and editing. D.K.G. was involved in conceptualization, project administration, supervision, writing, and editing.

Supporting information

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

Supplementary Material S1. Recalculation of *w*.

Supplementary Material S2. Mathematical description of pyriform eggs.

Supplementary Material S3. Inferring a universal formula for an avian egg.

Competing interests

The authors declare no competing interests.

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(4) Supplementary Material S1: Recalculation of *w*

Let's consider a standard hen's egg as represented by Romanoff & Romanoff[1] using their data of numerous egg measurements (Fig. S1).

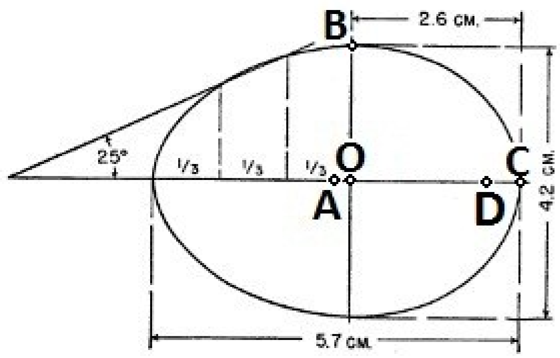

Figure S1. A standard (or "ideal") chicken egg.[1]

In this example, we selected the following five points on the egg image (Fig. S1): A) a midpoint of the egg length, *L*/2; B) a point at the egg maximum breadth (*B)*; C) the utmost distant point of the blunt end of the egg; D) a point at a radius of an inner circle with the center in the O point, (where O is a cross point of the egg maximum breadth and length) so that the distances **OB** and **OD** are equal.

Then, we can state that **AO** = *w*, **OB** = **OD** = *B*/2, and

$$\mathbf{DC} = \frac{L}{2} - \frac{B}{2} - w \qquad \text{(EqnS1.1)}$$

Taking into consideration that:

$w = \frac{5.7}{2} - 2.6 = 0.25$ and **DC** = 2.6 – 2.1 = 0.5, it is possible to conclude that **DC** = 2*w*. Then, EqnS1.1 can be rewritten as:

$$2w = \frac{L}{2} - \frac{B}{2} - w$$

$$w = \frac{L - B}{2 \cdot 3} \quad \text{(EqnS1.2)}$$

For common usage of the Hügelschäffer's formula, we could rewrite EqnS1.2 as:

$$w = \frac{L - B}{2n} \quad \text{(EqnS1.3)}$$

in which *n* is a positive number.

Reference

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Supplementary Material S2: Mathematical description of pyriform eggs

By sequentially sorting out the classical functions of the curves, we determined that the image of the pointed end of the guillemot egg (Fig. 2E) shows that it is complied with contours of a square parabola. A parabola is a plane curve, which is mirror-symmetrical and is approximately U-shaped and perfectly described the sharp end of pyriform eggs. If our assumption is correct, a blunt end of the pyriform egg will have a classic egg contour according to Hügelschäffer's model. The pointed end however should have a form of a parabola whose vertex lays on the *x*-axis, and the lines are rested against the extreme points of the egg maximum breadth (Fig. S2-1).

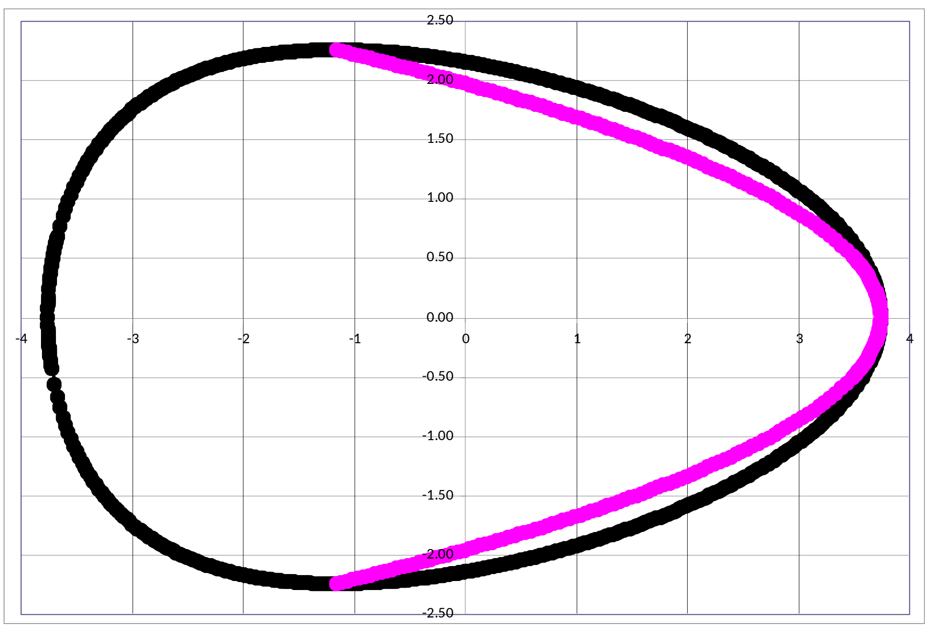

Figure S2-1. Graphic representation of the guillemot egg profile using a parabola (pink line) and Hügelschäffer's model (black line).

Thus, the objective of our study was the theoretical definition of the pyriform egg with mathematical terms and plotted using both the Hügelschäffer's model and the parabola. Similar to Petrović & Obradović,[1] where principles of Newton's hyperbolism were used and the function $t(x)$

$$t(x) = 1 + \frac{2wx + w^2}{(L/2)^2} \quad \text{(EqnS2.1)}$$

was added into the equation of the ellipse, obtaining a formula for a classic egg contour (or the Hügelschäffer's model):

$$\frac{x^2}{(L/2)^2} + \frac{y^2}{(B/2)^2} \cdot \left(1 + \frac{2wx + w^2}{(L/2)^2}\right) = 1 \quad \text{(EqnS2.2)}$$

we assumed to follow the same principle for a pyriform profile, so another function that we conditionally defined as *p*(*x*) and called a 'pyriform function' was used in the EqnS2.2 instead of *t*(*x*):

$$\frac{x^2}{(L/2)^2} + \frac{y^2}{(B/2)^2} \cdot p(x) = 1 \quad \text{(EqnS2.3)}$$

Wherefrom:

$$p(x) = \frac{B^2}{4} \cdot \frac{L^2 - 4x^2}{y^2 L^2} \quad \text{(EqnS2.4)}$$

According to our assumption, a vertex of the parabola that corresponds to the pointed end of the classic egg contour (Hügelschäffer's model) lays on the *x*-axis at $x = L/2$ and the lines are rested against the extreme points of the egg maximum breadth, *B*, which is shifted from the *y*-axis at the value of $x = -w$, while the blunt end has the form of Hügelschäffer's model (Fig. S2-2).

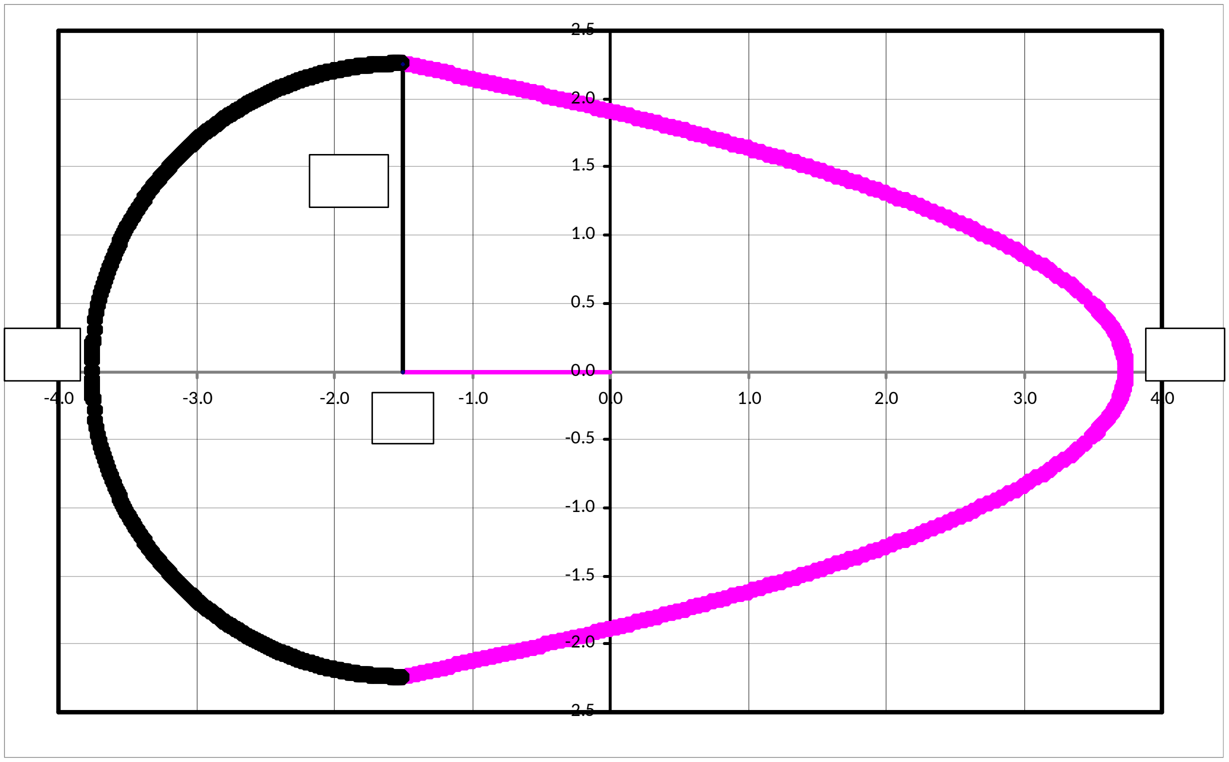

Figure S2-2. Geometry of the pyriform egg.

Taking into account that a vertex of a horizontal parabola is located on the *x*-axis, thus grounding upon theoretical principles for the following function as reviewed elsewhere[2] and the data which follows from Fig. S2-2, when $y = 0$, $x = L/2$; and when $x = -w$, $y = B/2$, we obtained the functional dependence of the parabolic end of the pyriform egg contour:

$$y_p = \pm \frac{B}{2} \cdot \sqrt{\frac{L - 2x_p}{L + 2w}} \qquad \text{(EqnS2.5)}$$

Considering that the pyriform egg contour consists of two geometrical figures, the parabola and Hügelschäffer's model, the values *x* and *y* of the pointed and blunt ends are different, so the subscript index '*p*' would correspond to the meanings of *x* and *y* of the parabolic part, and the ones for the Hügelschäffer's part would have the subscript index '*H*'. Thus, the interval for x_p is $[-w, L/2]$ and the one for x_H is $[-L/2, -w]$.

Inputting EqnS2.5 into EqnS2.4 we inferred the pyriform function $p(x_p)$ for the parabolic part of the egg:

$$p(x_p) = \frac{(L + 2x_p)(L + 2w)}{L^2} \qquad \text{(EqnS2.6)}$$

Then, the pyriform function $p(x_H)$ for Hügelschäffer's part of the egg is expressed accordingly from EqnS2.1 thus:

$$p(x_H) = \frac{L^2 + 8wx_H + 4w^2}{L^2} \qquad \text{(EqnS2.7)}$$

To produce a universal formula for recalculating the pyriform multiplier $p(x)$, we would need to unite the both equations for $p(x_p)$ and $p(x_H)$ into one. For this, each EqnS2.6 and EqnS2.7 were transformed as follows:

$$p(x_p) = \left(1 + 2 \cdot \frac{x_p}{L}\right) \cdot \left(1 + 2 \cdot \frac{w}{L}\right) \qquad \text{(EqnS2.8)}$$

$$p(x_H) = 1 + 8 \cdot \frac{w}{L} \cdot \frac{x_H}{L} + 4 \cdot \left(\frac{w}{L}\right)^2 \qquad \text{(EqnS2.9)}$$

If we express the values of x in terms of the egg length L as $x = aL$, wherefrom $a = x/L$, then, for the parabolic part of the egg the values of a_p would be within the interval a_p = [$-w/L$; 1/2], and for the Hügelschäffer's one within a_H = [$-1/2$; $-w/L$] (Fig. S2-2), so EqnS2.8 and EqnS2.9 were rewritten as follows:

$$p(x_p) = (1 + 2a_p) \cdot \left(1 + 2 \cdot \frac{w}{L}\right) \quad \text{(EqnS2.10)}$$

$$p(x_H) = 1 + 8a_H \cdot \frac{w}{L} + 4 \cdot \left(\frac{w}{L}\right)^2 \quad \text{(EqnS2.11)}$$

The united function $p(x)$ should satisfy both EqnS2.10 and EqnS2.11 within the whole interval of a = [–1/2; 1/2]. Prior to start an approximation procedure of such combination, we defined possible variations of the meanings of w/L. In accords with the Hügelschäffer's model, w cannot be less than 0. In this case, the egg image just revolves for 180° over the x-axis and, thus, the minimum possible value for w is 0. When w = 0, the classic egg contour transforms into the ellipse.[1] As above mentioned, the maximum possible meaning of w is $(L–B)/2$. Thus, the minimum possible value of w/L is 0, and the maximum one is:

$$\frac{w_{\max}}{L} = \frac{L - B}{2L} = \frac{1 - SI}{2} \quad \text{(EqnS2.12)}$$

where SI is the egg shape index (maximum breadth to length ratio). Then, the maximum value of w would be when the value of SI is minimal. We found that the mostly elongated eggs, i.e., with the least shape index (0.55 to 0.57), are inherent in the maleos (*Macrocephalon maleo*) and long-tailed sylph (*Aglaiocercus kingii*).[3,4] Nevertheless, the similar approach to describing oomorpholgy can be used not only for avian species. For example, the eggs of American crocodiles and some dinosaurs[5] have the shape index values close to 0.5, so we assumed this as a minimal value for SI. Then, as follows from EqnS2.12, $w_{\max}/L$ = 0.25, and performing the approximation procedure, we should deal with the interval of w/L = [0; 0.25], dividing it into five equal subintervals of the length 0.05 with the following subinterval endpoints: 0, 0.05, 0.1, 0.15, 0.2 and 0.25.

The meanings of $p(x_H)$ and $p(x_p)$ (EqnS2.10 and EqnS2.11) were recalculated by inputting the correspondent values of *a* for the Hügelschäffer's part of the egg, a_H = [–1/2; –*w*/*L*], and for the parabolic one, [–*w*/*L*; 1/2]. As a result, the diagram in Fig. S2-3 was plotted.

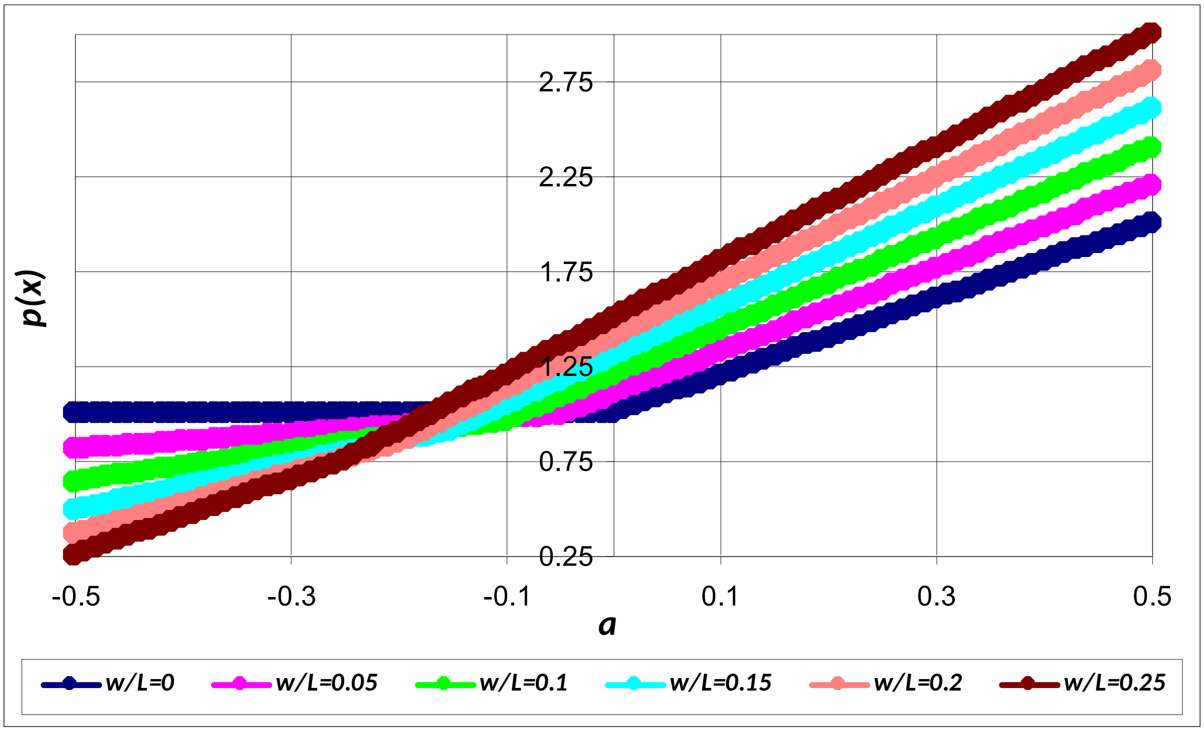

Figure S2-3. The curves of *p*(*x*) as a function of *a* according to EqnS2.10 and EqnS2.11 for the values of *w*/*L* ranged between 0 and 0.25.

The functions of *p*(*x*) in Fig. S2-3 are related to piecewise functions,[6] so we can unite these into one using a numerical procedure.

At first, we intended to define an approximating function that would double the combination of the obtained curves (Fig. S2-3) as accurate as possible. Taking into account that the curves consist of two linear functions (EqnS2.10 and EqnS2.11), principles of linear algebra[7] were used for this approximation. The most accurate results were obtained using the following formula:

$$p(x) = \frac{c_1 + c_2 a + c_3 a^2}{c_4 + c_5 a + a^2} \quad \text{(EqnS2.13)}$$

in which $c_1 \ldots c_5$ are constant coefficients to be defined.

The results of the approximation with EqnS2.13 are shown in Fig. S2-4.

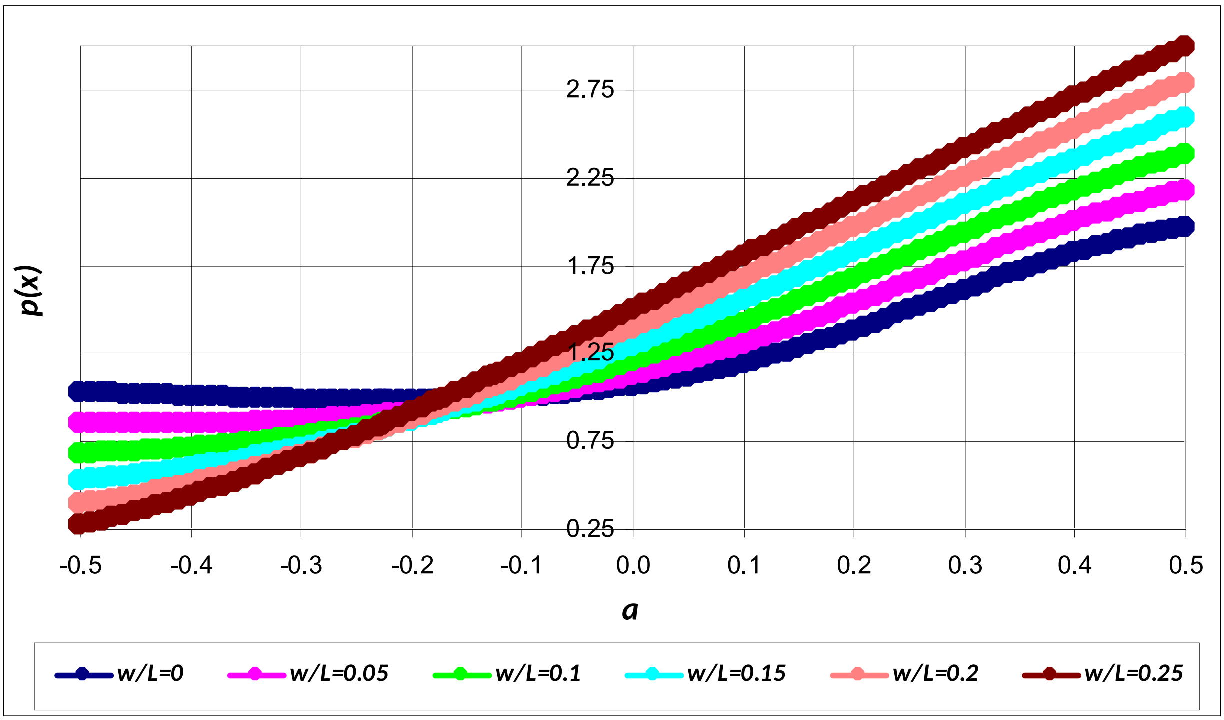

Figure S2-4. The approximated curves *p*(*x*) using EqnS2.13.

The obtained coefficients for each meaning of *w*/*L* are presented in Table S2-1 together with the coefficient of determination (R^2) between the results calculated using EqnS2.13 and EqnS2.10 or EqnS2.11, respectively.

Table S2-1. Meanings of the coefficients $c_1 \ldots c_5$ in EqnS2.13.

w/*L*	c_1	c_2	c_3	c_4	c_5	R^2

0	0.316	-0.320	1.493	0.297	-0.556	0.9962
0.05	0.517	0.024	1.415	0.461	-0.609	0.9979
0.10	0.851	0.814	1.548	0.711	-0.537	0.9988
0.15	1.447	2.484	2.286	1.124	-0.221	0.9994
0.20	2.617	6.128	4.612	1.886	0.635	0.9997
0.25	5.171	14.714	11.246	3.467	2.828	0.9999

To make EqnS2.13 valid for all meanings of *w*/*L* (Fig. S2-4), each coefficient *c* was defined as a function *c* = *f*(*w*/*L*) and, then, approximated with relevant equations (Fig. S2-5).

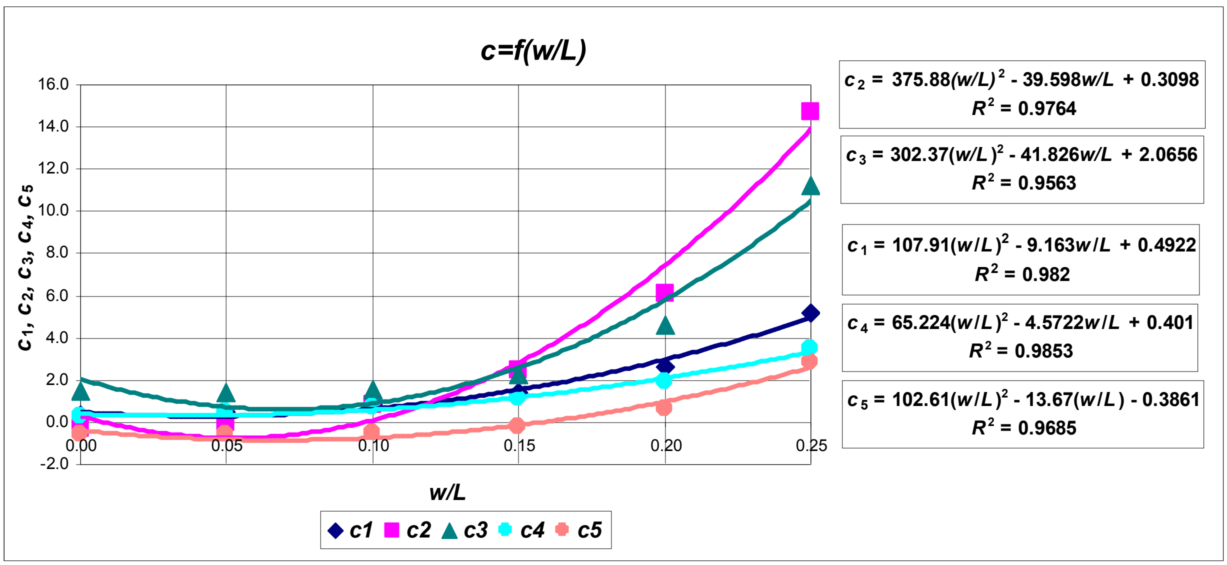

Figure S2-5. The approximation of the coefficients $c_1 \ldots c_5$ with square polynomials.

As a result, the final approximating formula was defined as follows:

$$p(x) = \frac{107.91 \cdot \left(\frac{w}{L}\right)^2 - 9.16 \cdot \frac{w}{L} + 0.49 + \left(375.88 \cdot \left(\frac{w}{L}\right)^2 - 39.6 \cdot \frac{w}{L} + 0.31\right) \cdot \frac{x}{L} + \left(302.37 \cdot \left(\frac{w}{L}\right)^2 - 41.83 \cdot \frac{w}{L} + 2.07\right)}{65.22 \cdot \left(\frac{w}{L}\right)^2 - 4.57 \cdot \frac{w}{L} + 0.4 + \left(102.61 \cdot \left(\frac{w}{L}\right)^2 - 13.67 \cdot \frac{w}{L} - 0.39\right) \cdot \frac{x}{L} + \left(\frac{x}{L}\right)^2}$$

(EqnS2.14)

Considering EqnS2.3, the function that defines the contours of the pyriform eggs can be represented as:

$$y = \pm \frac{B}{2} \cdot \sqrt{\frac{L^2 - 4x^2}{L}} \cdot \sqrt{\frac{65.22 \cdot \left(\frac{w}{L}\right)^2 - 4.57 \cdot \frac{w}{L} + 0.4 + \left(102.61 \cdot \left(\frac{w}{L}\right)^2 - 13.67 \cdot \frac{w}{L} - 0.39\right) \cdot \frac{x}{L} + \left(\frac{x}{L} \ldots\right.}{107.91 \cdot \left(\frac{w}{L}\right)^2 - 9.16 \cdot \frac{w}{L} + 0.49 + \left(375.88 \cdot \left(\frac{w}{L}\right)^2 - 39.6 \cdot \frac{w}{L} + 0.31\right) \cdot \frac{x}{L} + \left(302.37 \cdot \left(\frac{w}{L}\right)^2 - 41 \ldots\right.}}$$

(EqnS2.15)

Judging from the appropriate graphic (Fig. S2-6) and further theoretical analysis of the obtained equation EqnS2.15, it showed a considerable drawback: at the point of $x = -w$, y should be equal to $B/2$.

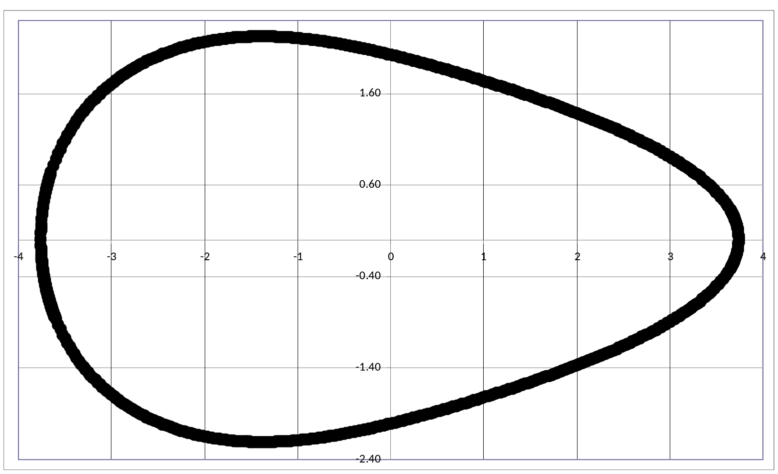

Figure S2-6. The contour of an actual guillemot egg plotted using EqnS2.15.

This principle was thoroughly described in our previous paper[8]. Apart from looking very similar to the actual guillemot egg contour, the maximum value of y that is supposed to be equal to $B/2$ = 2.25 cm in our case, equals to 2.21 cm. This discrepancy would require a further detailed revisit of EqnS2.15 as follows:

if $x = -w$, $y_{max} = B/2$, and considering EqnS2.15, that is valid when

$$\sqrt{\frac{L^2 - 4w^2}{L}} \cdot \sqrt{\frac{65.22 \cdot \left(\frac{w}{L}\right)^2 - 4.57 \cdot \frac{w}{L} + 0.4 - \left(102.61 \cdot \left(\frac{w}{L}\right)^2 - 13.67 \cdot \frac{w}{L} - 0.39\right) \cdot \frac{w}{L} + \left(\frac{w}{L}\right)^2}{107.91 \cdot \left(\frac{w}{L}\right)^2 - 9.16 \cdot \frac{w}{L} + 0.49 - \left(375.88 \cdot \left(\frac{w}{L}\right)^2 - 39.6 \cdot \frac{w}{L} + 0.31\right) \cdot \frac{w}{L} + \left(302.37 \cdot \left(\frac{w}{L}\right)^2 - 41.83 \cdot \frac{w}{L}\right.}}$$

(EqnS2.16)

The obtained equation EqnS2.16 demonstrated a bias and was not true for the whole possible interval of *w*/*L* meanings. Numerical methods in adjusting EqnS2.16 enabled us to stipulate that the main error occurs when the results of the approximated calculations do not coincide with the initial ones at three basic points *p*(–*L*/2), *p*(–*w*) and *p*(*L*/2), or when *a* = –1/2, *a* = –*w* and *a* = 1/2. Thus, to circumvent this obstacle, we undertook another approach. For each meaning of *w*/*L* chosen previously, we determined the meanings at three basic points (Table S2-2), which were recalculated from EqnS2.10 and EqnS2.11 accordingly.

Table S2-2. The meanings of *a* and *p*(*x*) at three basic points *p*(–*L*/2), *p*(–*w*) and *p*(*L*/2).

w*/*L	***a* = –1/2**	***a* = –*w***	***a* = 1/2**	***p*(–*L*/2)**	***p*(–*w*)**	***p*(*L*/2)**
0	–0.5	0.00	0.5	1.00	1.00	2.00
0.05	–0.5	–0.05	0.5	0.81	0.99	2.20
0.10	–0.5	–0.1	0.5	0.64	0.96	2.40
0.15	–0.5	–0.15	0.5	0.49	0.91	2.60
0.20	–0.5	–0.2	0.5	0.36	0.84	2.80
0.25	–0.5	–0.25	0.5	0.25	0.75	3.00

The results of the approximation of the data from Table S2-2 are given graphically in Fig. S2-7.

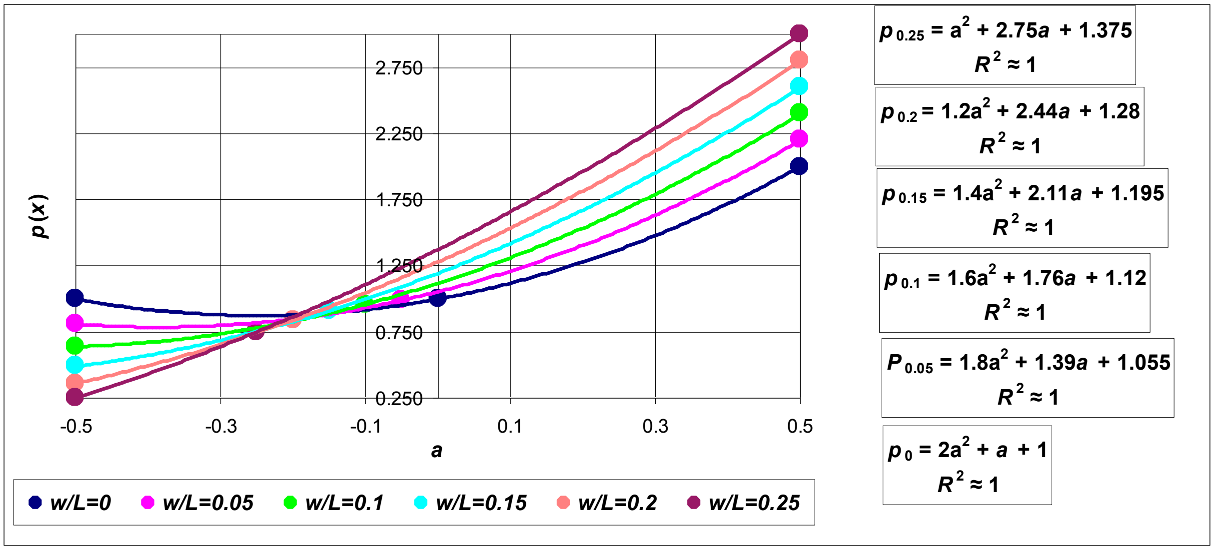

Figure S2-7. The results of the approximation of the data from Table S2-2.

All the curves showed very accurate results expressed with square polynomials. Similar to the previous approximating approach, to make the results valid for all meanings of *w*/*L* (Fig. S2-7), each coefficient *c* was defined as a function $c = f(w/L)$, where coefficients $c_1 \ldots c_3$ correspondingly fit the following condition:

$$p_{w/L} = c_1 \cdot \left(\frac{w}{L}\right)^2 + c_2 \cdot \frac{w}{L} + c_3 \qquad \text{(EqnS2.17)}$$

in which $p_{w/L}$ means the value of $p(x)$ (EqnS2.10 and EqnS2.11) for the respective value of *w*/*L*.

The results of the coefficients approximations are shown graphically in Fig. S2-8.

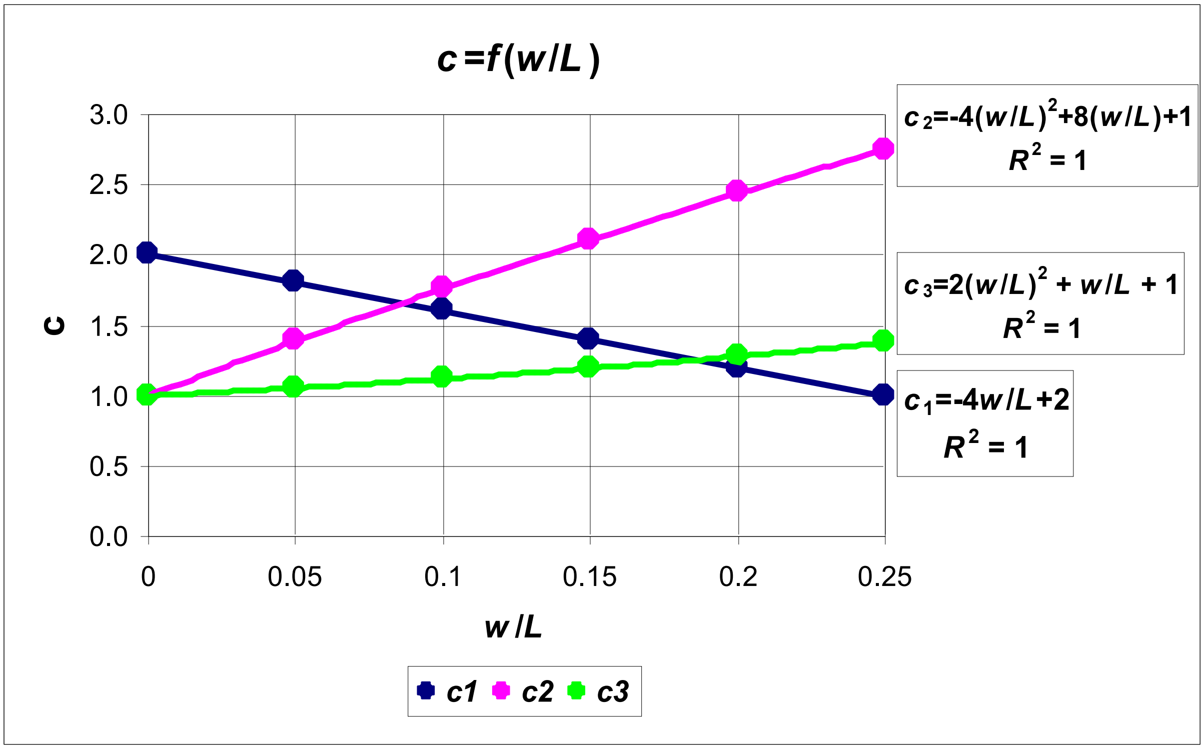

Figure S2-8. The results of the approximation of the coefficients $c_1 \ldots c_3$ in the equations of Fig. S2-5.

Then, the penultimate approximating formula was defined as follows:

$$p(x) = \frac{2(L-2w)x^2 + (L^2 + 8Lw - 4w^2)x + 2Lw^2 + L^2w + L^3}{L^3} \qquad \text{(EqnS2.18)}$$

And finally, the function that should satisfy the geometrical description of the pyriform eggs can be inferred after substituting EqnS2.18 into EqnS2.3 as follows:

$$y = \pm\frac{B}{2}\cdot\sqrt{\frac{(L^2-4x^2)L}{2(L-2w)x^2 + (L^2+8Lw-4w^2)x + 2Lw^2 + L^2w + L^3}} \qquad \text{(EqnS2.19)}$$

The undertaken test of substituting $x = -w$ into EqnS2.19 demonstrated that the meaning of $y_{max} = \pm B/2$, and EqnS2.19 fully satisfies the basic condition for the universal geometrical description of avian eggs:

$$\sqrt{\frac{(L^2 - 4w^2)L}{2(L-2w)w^2 + (L^2 + 8Lw - 4w^2)w + 2Lw^2 + L^2w + L^3}} = 1 \qquad \text{(EqnS2.20)}$$

$$L^3 - 4Lw^2 - 2Lw^2 + 4w^3 + L^2w + 8Lw^2 - 4w^3 - 2Lw^2 - L^2w - L^3 = 0$$

(EqnS2.21)

A graphical representation of EqnS2.21 (or Eqn3) for the images of typical representatives of the pyriform eggs of different variations in the values of their shape index and *w*/*L* ratio also showed its validity (Fig. 3).

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Supplementary Material S3: Inferring a universal formula for an avian egg

For enabling us to express the contours between these two classic models, the pyriform one (EqnS2.21, or Eqn3) and the ovoid one (Eqn1), we assumed that the pyriform function *p*(*x*) (EqnS2.20) can be represented as a product of the Hügelschäffer's function, *t*(*x*), (EqnS2.1) and some multiplier, M_p, that we coined as a *pyriform multiplier*:

$$p(x) = t(x) \cdot M_p \qquad \text{(EqnS3.1)}$$

Then, as follows from (EqnS2.3)

$$y_H = \frac{B}{2L} \cdot \sqrt{\frac{L^2 - 4x^2}{p(x)}} \qquad \text{(EqnS3.2)}$$

the formula for the conic shapes can be expressed accounting EqnS3.1 as follows:

$$y_c = \frac{B}{2L} \cdot \sqrt{\frac{L^2 - 4x^2}{t(x) \cdot M_p}} \qquad \text{(EqnS3.3)}$$

wherefrom considering (Eqn4):

$$\Delta y = y_H \cdot \left(1 - \frac{1}{\sqrt{M_p}}\right) \qquad \text{(EqnS3.4)}$$

As follows from EqnS2.20 and EqnS2.1, the pyriform multiplier is defined as follows:

$$M_p = \frac{2(L-2w)x^2 + (L^2+8Lw-4w^2)x + 2Lw^2 + L^2w + L^3}{L(L^2+8wx+4w^2)} \qquad \text{(EqnS3.5)}$$

Then, considering EqnS3.4:

$$\Delta y = y_H \cdot \left(1 - \sqrt{\frac{L(L^2+8wx+4w^2)}{2(L-2w)x^2 + (L^2+8Lw-4w^2)x + 2Lw^2 + L^2w + L^3}}\right) \qquad \text{(EqnS3.6)}$$

As follows from Eqn4 and EqnS3.6, the classic pyriform (conic) shape can be expressed with the following equation:

$$y_c = y_H \sqrt{\frac{L(L^2+8wx+4w^2)}{2(L-2w)x^2 + (L^2+8Lw-4w^2)x + 2Lw^2 + L^2w + L^3}} \qquad \text{(EqnS3.7)}$$

If to substitute the formula for y_H (Eqn1), as expected EqnS3.7 is identical to EqnS2.21 (or Eqn3).

If an egg profile is located just between Hügelschäffer's and pyriform curves, we would need in this case to take only a respective part of Δ*y*, which can be defined as some coefficient *k*. Then, if we express a mathematical function of such eggs as $y_{H/c}$:

$$y_{H/c} = y_H - k \cdot \Delta y \qquad \text{(EqnS3.8)}$$

or

$$y_{H/c} = y_H \left(1 - k\left(1 - \sqrt{\frac{L(L^2+8wx+4w^2)}{2(L-2w)x^2 + (L^2+8Lw-4w^2)x + 2Lw^2 + L^2w + L^3}}\right)\right)$$

(EqnS3.9)

The meanings of k are within the interval [0…1]. When $k = 0$, the egg shape is expressed with the Hügelschäffer's model. If $k = 1$, then, it appears to be of classic pyriform (conic) one, so (EqnS3.9) can be considered as **the universal formula for any avian egg.**

Independent validation of the universal formula

To check if (EqnS3.9) is valid, let us assume that $k = 0.5$. The graphic representations of the egg contours (Fig. S3) with $k = 0$, 0.5 and 1 suggested that (EqnS3.9) can be used for practical calculations of these egg profiles.

Figure S3. The egg contours according to (EqnS3.9) with *k* = 0 (red); *k* = 0.5 (green) and *k* = 1 (black).

An additional question that required further resolution was how to determine the value of k for any tested egg. For this purpose, we considered a characteristic point at $x = L/4$ (Fig. 4D–F) that can be measured directly. As found in our previous study,[1] this point was one of the mostly informative in predicting the parameter w in Hügelschäffer's formula. Then, inputting $x = L/4$ into Hügelschäffer's model (Eqn1) and the pyriform formula (EqnS2.21, or Eqn3), we derived the meaning of $y_{L/4}$ at this point respectively for both models:

$$y_{H_{L/4}} = \frac{\sqrt{3}BL}{4\sqrt{L^2 + 2wL + 4w^2}} \quad \text{(EqnS3.10)}$$

$$y_{c_{L/4}} = \frac{\sqrt{3}BL}{2\sqrt{5.5L^2 + 11Lw + 4w^2}} \quad \text{(EqnS3.11)}$$

Consequently, the difference between EqnS3.10 and EqnS3.11 leads to the meaning of $\Delta y_{L/4}$ at the point of $x = L/4$:

$$\Delta y_{L/4} = \frac{\sqrt{3}BL}{4} \cdot \frac{\sqrt{5.5L^2 + 11Lw + 4w^2} - 2\sqrt{L^2 + 2wL + 4w^2}}{\sqrt{(L^2 + 2wL + 4w^2)(5.5L^2 + 11Lw + 4w^2)}} \quad \text{(EqnS3.12)}$$

The value $y_{r_{L/4}}$ of an actual egg can be recalculated from direct measurements of the egg diameter, $D_{L/4}$, at the point of $L/4$ using a caliper as proposed, for example, elsewhere,[2] machine vision[1,3] or any other proper technique. Taking into consideration that:

$$y_{r_{L/4}} = \frac{D_{L/4}}{2}, \quad \text{(EqnS3.13)}$$

$$\Delta y_{r_{L/4}} = y_{H_{L/4}} - \frac{D_{L/4}}{2} = \frac{\sqrt{3}BL}{4\sqrt{L^2 + 2wL + 4w^2}} - \frac{D_{L/4}}{2} \quad \text{(EqnS3.14)}$$

in which $\Delta y_{r_{L/4}}$ is the difference of the *y* values at the point of *x* = *L*/4 of Hügelschäffer's model and an actual egg. Then, the value of the coefficient *k* can be determined using a division of EqnS3.14 and EqnS3.12:

$$k = \frac{\Delta y_{r_{L/4}}}{y_{H_{L/4}}} = \frac{\sqrt{5.5L^2 + 11Lw + 4w^2} \cdot (\sqrt{3}BL - 2D_{L/4}\sqrt{L^2 + 2wL + 4w^2})}{\sqrt{3}BL(\sqrt{5.5L^2 + 11Lw + 4w^2} - 2\sqrt{L^2 + 2wL + 4w^2})} \qquad \text{(EqnS3.15)}$$

Finally, inputting EqnS3.15 into EqnS3.9, we can state that we have obtained the universal model applicable for any avian egg as follows:

$$y = \pm y_H \left(1 - \frac{\sqrt{5.5L^2 + 11Lw + 4w^2} \cdot (\sqrt{3}BL - 2D_{L/4}\sqrt{L^2 + 2wL + 4w^2})}{\sqrt{3}BL(\sqrt{5.5L^2 + 11Lw + 4w^2} - 2\sqrt{L^2 + 2wL + 4w^2})} \cdot \left(1 - \sqrt{\frac{L(L^2 + 8wx + 4w^2)}{2(L - 2w)x^2 + (L^2 + 8Lw - 4w^2)x + 2Lw^2 + L^2w + L^3}}\right)\right) \qquad \text{(EqnS3.16)}$$

or expressing y_H with Eqn1

$$y = \pm \frac{B}{2}\sqrt{\frac{L^2 - 4x^2}{L^2 + 8wx + 4w^2}} \cdot \left(1 - \frac{\sqrt{5.5L^2 + 11Lw + 4w^2} \cdot (\sqrt{3}BL - 2D_{L/4}\sqrt{L^2 + 2wL + 4w^2})}{\sqrt{3}BL(\sqrt{5.5L^2 + 11Lw + 4w^2} - 2\sqrt{L^2 + 2wL + 4w^2})} \cdot \left(1 - \sqrt{\frac{L(L^2 + 8wx + 4w^2)}{2(L - 2w)x^2 + (L^2 + 8Lw - 4w^2)x + 2Lw^2 + L^2w + L^3}}\right)\right) \qquad \text{(EqnS3.17)}$$

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