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Measurement of the neutral axis in avian eggshells reveals which species conform to the golden ratio

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Abstract

Avian eggs represent a striking evolutionary adaptation for which shell thickness is crucial. An understudied eggshell property includes the neutral axis, a line that is drawn through any bent structure and whose precise location is characterized by the k -factor. Previous studies have established that, for chicken eggs, mean k corresponds to the golden ratio ($\Phi = 1.618$, or 0.618 in its reciprocal form). We hypothesized whether such an arrangement of the neutral axis conforms to the eggshell of any bird or only to eggshells with a certain set of geometric parameters. Implementing a suite of innovative methodological approaches, we investigated variations in k of 435 avian species, exploring which correspond to Φ . We found that mean k is highly variable among birds and does not always conform to Φ , being much lower in spherical and ellipsoid eggs and higher in pyriform eggs. While 21 species had k values within 0.618 ± 0.02 (including four falcon species) and the Falconinae subfamily (six species) revealed a mean of 0.618 , it is predominantly domesticated species (chicken, ducks, and geese) that lay eggs whose neutral axis corresponds to the golden ratio. Thus, the study of the mathematical secrets of the eggshell related to the golden ratio of its neutral axis suggests its species-specific signatures in birds.

KEYWORDS

avian egg, eggshell, evolution, golden ratio, neutral axis

INTRODUCTION

In the evolution of terrestrial vertebrates, one of the most striking adaptations is the formation, laying, brooding, and hatching of calcified avian eggs. Essentially, the bird's egg needs to have a series of characteristics for which its shape, parameters, and thickness are crucial. It needs to be large enough to incubate an embryo but small enough, and of the right shape, to exit the body. It needs to be strong enough to survive the rigors of incubation (i.e., not break when sat on or moved) but fragile enough to allow the chick to hatch. Other shape- and thickness-

related properties essential for its survival are related to temperature and humidity modulation (either in isolation or in relation to other eggs in the clutch) and the ability to stay put once laid. While the role of egg shape variation (i.e., oomorphology¹) in these adaptations has been studied in a range of birds,²⁻⁴ hitherto understudied properties include shell thickness and the role of the neutral axis.⁵

To visualize the concept of the neutral axis, imagine a wooden beam with a rectangular cross-section and a length l . It is relatively straightforward to calculate its volume by multiplying the dimensions of the rectangular cross-section with l . Let us now suppose that we bent

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this beam to a profile of specific interest. Here, the measurement of l becomes more complex as the outer part of the beam is somewhat stretched, and the inner part shrunken. The true value of l , therefore, is somewhere in between these extremes. These problems are not new for engineers, materials scientists, builders, and so on, and the calculation of such a midline is called the neutral axis.⁵ The neutral axis corresponds to an imaginary line that has the same length before the beam was bent.⁶ Moreover, its precise location is characterized by the so-called k -factor, a ratio of the neutral axis location compared to the material thickness. In other words, the formula is $k = t/T$, with t being the neutral axis position and T being the material thickness.⁷ Crucially, the neutral axis is not always at the exact middle of T , that is, k is not always equal to 0.5. Rather, k depends on the bend radius and material thickness,⁸ on the properties and composition of the material,⁹ and finally on the forces applied to bend the beam.¹⁰ In other words, the neutral axis is an imaginary line in a beam or other structure subjected to a bending action in which the fibers are neither stretched nor compressed, or where the longitudinal stress is zero.

Imagine now a scenario where no force was applied to the material, but, rather, it was already formed curved. In nature, one such example is the shell of a bird's egg, which is typically spherical, ellipsoid, ovoid, or pyriform in shape.¹¹ Knowledge of its various internal and external parameters has wide applications in ornithological curation, the poultry industry, and ecological studies. Rahn and Paganelli¹² stated that no studies have yet been able to obtain accurate shell density estimates using oological collections as they usually rely on only approximate calculation methods. To the best of our knowledge, this holds true over 20 years later. Such detailed calculations are also relevant for the food industry, that is, in commercial poultry farming, when it is necessary to calculate the volume of the shell and, accordingly, the contents of the egg. In a recent study,¹³ we established that the nondestructive calculation of the shell volume is much more accurate if we use the exact value of the k -factor and not an approximate value of 0.5, as is conventionally accepted. Indeed, most previous studies that considered oomorphology assume the neutral axis to be at the midline, that is, $k = 0.5$. The purpose of this study was to challenge this notion and thereby calculate k for a range of eggs spanning the phylogenetic class Aves. In order to do this, we developed the theoretical prerequisites as outlined in File S1.

Expressing k from the obtained Equation (S1.18) (see File S1) is a laborious task, so in this context, we analyzed it using numerical methods, substituting into Equation (S1.18) various sets of parameters characteristic, say, for chicken eggs. In addition to the already clarified variety of values for $L/T = [120 \dots 230]$, we needed to decide on the nature of changing B/L and w/L . The former is no more than the so-called shape index proposed by Romanoff and Romanoff¹⁴ that, according to their data, varies for chicken eggs in the range of $[0.65 \dots 0.82]$. This was also confirmed by the data of our previous experiments.^{15–21}

The w/L ratio is not an index as commonly known as B/L , and, therefore, we could only rely on our data produced by measuring these parameters.²¹ Although in another work,³ we demonstrated, through theoretical research, the possible range of variation of this ratio as $[0 \dots 0.25]$, which corresponds to the entire possible variety of bird

eggs in nature, for chicken eggs alone, it was much more modest, that is, $[0.001 \dots 0.05]$. Furthermore, substituting all possible values of $L/T = [120 \dots 230]$, $B/L = [0.65 \dots 0.82]$, and $w/L = [0.001 \dots 0.05]$, and by dividing each ratio range into subcategories, we generated 378 different combinations, thus obtaining 378 cubic equations based on Equation (S1.18). Solving each of them using Cardan's formulae,²² we obtained different variations in k values from 0.327 to 0.959, with an average value of 0.618. It was this number, which also reflects the location of the neutral axis in the shell of chicken eggs, that made us examine it more closely. The reason is that the value of k exactly corresponded to the value of the so-called golden ratio.²³

The golden ratio ($\Phi = 1.618$, or 0.618 in its reciprocal form) is well described in mathematics, science, architecture, and the arts and is otherwise known as the golden section, golden mean, or divine proportion. It can be traced back to Euclid and is defined as "the ratio of a line segment cut into two pieces of different lengths such that the ratio of the whole segment to that of the longer segment is equal to the ratio of the longer segment to the shorter segment."²⁴ With the golden ratio in mind, we tested here the hypothesis that such a unique arrangement of the neutral axis corresponds typically the shell of any bird, the alternative being that it only applies to the shells of eggs with a certain set of geometric parameters. To do this, we implemented the methodological approaches described in the Methods section.

METHODS

The generation of all possible combinations of characteristics to encompass the entire variety of bird eggs is an unfeasible task. For this reason, we decided to rely, as a starting point, on the previously adopted model species and its eggs, that is, the chicken, which is the most widespread and useful, both in terms of variability and broad experimental applications.²⁵ The study of the influence of the geometric dimensions of eggs on the position of the shell's neutral axis was carried out by the method of correlation analysis. For this, we used the statistical and mathematical algorithms available in the STATISTICA 5.5 program (StatSoft, Inc./TIBCO, Palo Alto, CA, USA), as well as computation applications in Microsoft Excel.

We also focused on examining the data available for the shells of various wild bird species. Data cards for some museum collections of avian eggs are somewhat patchy;²⁶ however, the most complete, both in terms of species diversity and availability of a set of oomorphological data, is likely to be the Schönwetter²⁷ oological handbook. While it has been established that there are some inaccuracies and assumptions taken by the author when compiling it,²⁸ it is the only reasonably reliable open source from which we were able to glean data for identifying all three indices that we use to calculate the values of k . While the data on the values of B , L , and T are provided for practically all the species presented in this reference book, to determine the values of w , we used the photographs available there. A total of 434 suitable eggs were employed from the Schönwetter²⁷ oological handbook that represented 11 extant avian orders and 83 families from the infraclass Neognathae.

Along with the various egg images, Schönwetter²⁷ also presented information about 23 eggs of the extinct elephant bird (genus

Aepyornis, infraclass Palaeognathae—increasing our species count by one, to 435) that, in addition to the sizes B , L , and T that were of interest to us, included data on their volumes, V . Considering the formula we derived earlier for recalculating w from V as follows:¹

$$w = 0.00415L + \frac{\sqrt{1.1675L^2B^2 - 2.2311LV}}{B}, \quad (1)$$

indicators for this species were also used for the analyses.

Recalculation according to Equation (1) made it possible to obtain rational w values only for a sample of 11 eggs, which was due to some inaccuracies in Schönwetter's²⁷ determination of actual egg volumes. Thus, to the set of 434 images of bird eggs, the values of the parameters for the 11 *Aepyornis* eggs were also added.

The development of various mathematical relationships based on oological data from the Schönwetter²⁷ handbook is not new. A number of formulae have stood the test of time and thorough reviews by the scientific community, for example, allometric dependences for calculating various morphological parameters of eggs depending on their mass.^{12,29}

Each egg image was analyzed as follows. Measurements of geometric parameters were carried out in pixels using the Microsoft Office Picture Manager program. First, sizes B and L were measured. Thereafter, the egg radiuses were measured at points corresponding to the $L/4$ length, respectively, from the sharp and blunt edges, which we will denote as $y_{L/4}$ (measured from a sharp edge) and $y_{-L/4}$ (measured from a blunt edge). Narushin et al.³ showed that the shape of an egg can be classified as a classical ovoid, corresponding to the Hügelschäffer model, if the radius of the egg at a point distant from the sharp edge by the value of $L/4$ is not lower than $y_{L/4}$ calculated by the following formula:

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

Accordingly, at $y_{L/4} = \sqrt{3B}/4$, the ovoid will match a sphere, and if $y_{L/4}$ is less than that calculated by Equation (2), the egg falls into the pyriform (pear-shaped) category.⁴ If the measured value of $y_{L/4}$ is equal to the value of $y_{-L/4}$, then the shape of such an egg will correspond to an ellipsoidal one.

Narushin et al.²¹ demonstrated that even using 2-D digital methods, it is quite difficult to measure the value of w , and therefore, we proposed a method for recalculating it through the measured values of $y_{L/4}$ and $y_{-L/4}$:

$$w = \frac{L}{8} \left(\frac{\sqrt{3B^2 - 12y_{L/4}^2} - 2y_{L/4}}{y_{L/4}} + \frac{2y_{-L/4} - \sqrt{3B^2 - 12y_{-L/4}^2}}{y_{-L/4}} \right). \quad (3)$$

This calculation formula of Equation (3) was used in our present studies to determine the values of w from the data obtained after processing photographic images of egg profiles.

To estimate the divergence time of any two taxa, TimeTree,³⁰⁻³² a web tool and a public knowledge base for information on the evolutionary timescale of life, was employed.

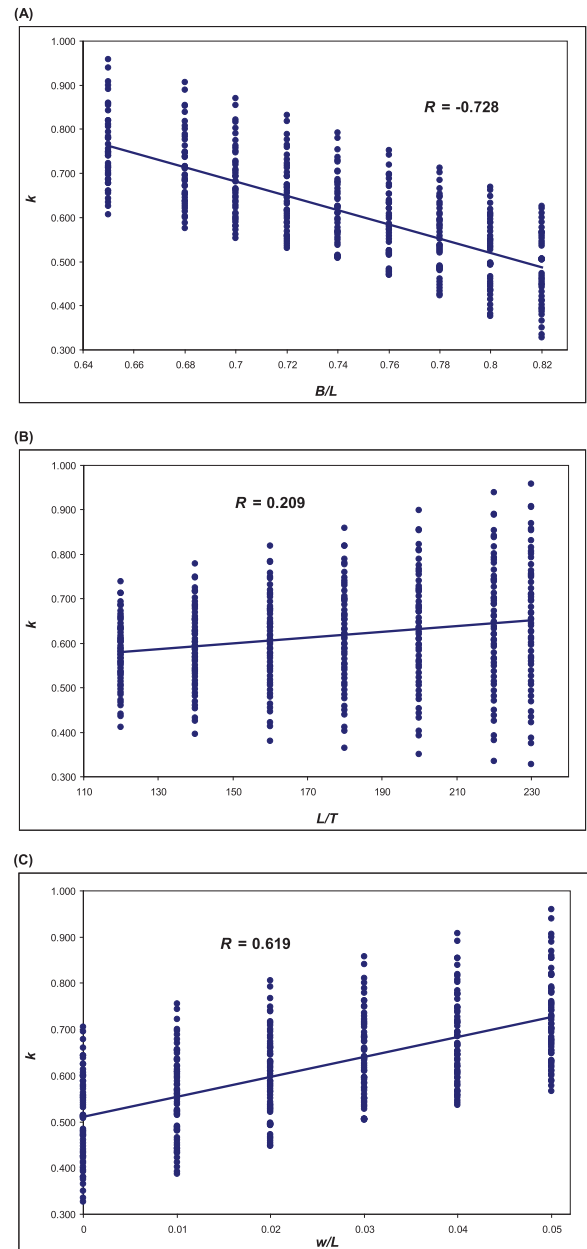


FIGURE 1 Graphical dependences of the coefficient k on the indices: (A) B/L , (B) L/T , and (C) w/L .

RESULTS

Classical egg-shaped ovoid

The classification of eggs according to their profile was reasonably well established. In our previous work;³ in this study, and as mentioned in the Introduction, we used the gradation of Nishiyama,¹¹ who proposed dividing the shape of eggs into four main geometric groups: spherical, ellipsoidal, ovoid, and pyriform (conical). Since chicken eggs can be considered the classic representatives of eggs with an ovoid profile,³ we chose this group for a more detailed analysis of the location of the neutral axis of their shell. Using the resulting database of 378 generated chicken egg sizes, we derived an empirical dependence for calculating k

that was more convenient and simpler than the theoretical Equation (1) (see the Methods):

$$k = 0.02235 + 1.403518 \frac{B}{L} + 0.00682 \frac{L}{T} - 3.10721 \frac{w}{L} - 0.00916 \frac{B}{L} \cdot \frac{L}{T} + 4.12025 \frac{B}{L} \cdot \frac{w}{L} + 0.02446 \frac{L}{T} \cdot \frac{w}{L} - 1.01509 \left(\frac{B}{L} \right)^2 + 0.18445 \left(\frac{w}{L} \right)^2, \quad (4)$$

with $R^2 = 0.9998$.

Also, using the generated data, we estimated the degree of influence of each of the three indices on the value of the coefficient k , as presented in the form of graphical dependencies (Figure 1).

It seemed to us a very interesting property of ovoid shells that the indices containing only the external parameters (B , L , and w) have a much greater effect on their internal characteristic (k) than the index that only includes the direct internal parameter, the shell thickness (T). We thus carried out the further analysis in such a way as to find an answer to the question: at what parameters of the three egg indices does the coefficient k have the value of the golden ratio, 0.618? For this purpose, we introduced the golden ratio value into Equation (4):

$$1.403518 \frac{B}{L} + 0.00682 \frac{L}{T} - 3.10721 \frac{w}{L} - 0.00916 \frac{B}{L} \cdot \frac{L}{T} + 4.12025 \frac{B}{L} \cdot \frac{w}{L} + 0.02446 \frac{L}{T} \cdot \frac{w}{L} - 1.01509 \left(\frac{B}{L} \right)^2 + 0.18445 \left(\frac{w}{L} \right)^2 - 0.59568 = 0. \quad (5)$$

Thus, Equation (5) enables an understanding of what the set of the three main indices of the egg and/or its four key geometric parameters should be in order for the neutral axis of the shell to conditionally divide it according to the principle of the golden ratio. Equation (5) also turned out to be useful for answering the next question: if nature has laid down that, in an ideal ovoid egg, the neutral axis of the shell should correspond to the golden ratio, then what parameters can be varied and, in what ranges, to ensure this location? To address this question, we transformed Equation (5) into three possible versions:

$$\frac{B}{L} = 2.0295 \frac{w}{L} - 0.00451 \frac{L}{T} + 0.69133 + \sqrt{\left(0.00451 \frac{L}{T} - 2.0295 \frac{w}{L} - 0.69133 \right)^2 + 0.00672 \frac{L}{T} - 3.06102 \frac{w}{L} + 0.0241 \frac{L}{T} \cdot \frac{w}{L} + 0.18171 \left(\frac{w}{L} \right)^2 - 0.586825}, \quad (6)$$

$$\frac{L}{T} = \frac{1.403518 \frac{B}{L} - 3.10721 \frac{w}{L} + 4.12025 \frac{B}{L} \cdot \frac{w}{L} - 1.01509 \left(\frac{B}{L} \right)^2 + 0.18445 \left(\frac{w}{L} \right)^2 - 0.59568}{0.00916 \frac{B}{L} - 0.02446 \frac{w}{L} - 0.00682}, \quad (7)$$

$$\frac{w}{L} = 8.42291 - 11.16902 \frac{B}{L} - 0.066305 \frac{L}{T} + \sqrt{\left(11.16902 \frac{B}{L} + 0.066305 \frac{L}{T} - 8.42291 \right)^2 + 5.50333 \left(\frac{B}{L} \right)^2 + 0.04966 \frac{B}{L} \cdot \frac{L}{T} - 7.60921 \frac{B}{L} - 0.03697 \frac{L}{T} + 3.22949}. \quad (8)$$

In each of the above equations (i.e., Equations 6–8), we substituted different sets of combinations of the indices L/T , B/L , and w/L typical for chicken eggs, and 1080 possible virtual eggs were generated. After that, we discarded those combinations that were impossible in nature either due to the presence of negative values, or very small or large values, for example, less than 100 or more than 300 for L/T . Finally, using these suitable and plausible sets of parameters, we obtained all 1080 combinations for the B/L index, 925 for w/L , and 504 for L/T . From this, we concluded that the L/T ratio is the most critical index, having fairly stable intraspecific values varying in a very narrow range. In contrast, the B/L shape index turned out to be the most variable. Thus, it is possible to reimagine the desired position of the neutral axis by changing it accordingly. Any set of combinations of the other two indices had absolutely no effect on the possible outliers of B/L values outside the natural variation found in nature. At the same time, the index w/L occupies an intermediate state, being positioned according to its variability between two other indices, and facilitating natural processes, along with the shape index, to influence the correction of the L/T values. However, although this analysis is suitable for the principles of targeted selection and modeling, we need to address the question of whether it actually happens in nature.

Analysis of eggshells based on a reference

To test the above hypothesis, and also in view of the fact that, despite the wide intraspecific variability of the simulated parameters, they still remain typical for the group of chicken eggs, we proceeded to the analysis of other bird species, the egg sizes of which were obtained by measuring their images from the oological reference book by Schönwetter.²⁷ The results of the measurements and the corresponding calculations are presented in Table 1.

According to the data in Table 1, the mean value of k does not correspond to the value of the golden ratio (0.618), exceeding it by a factor of ~ 1.5 (Table 1, bottom row, penultimate figure, 0.91). If the variations in the B/L and w/L indices could be considered relatively expected and even, to some extent, conforming to chicken eggs, then the L/T values that we actually observed came as a surprise. A deeper analysis

TABLE 1 Data of measuring and recalculating the variables of all the investigated eggs from Schönwetter²⁷

Indices	Max. value	Min. value	Mean	Standard deviation
B/L	0.96	0.58	0.74	0.04
L/T	389.2	78.3	265.6	51.1
w/L	0.14	0	0.06	0.03
k	1.64	0.35	0.91	0.25

TABLE 2 Data of measuring and recalculating the variables of the investigated eggs from Schönwetter²⁷ for three taxonomic groups

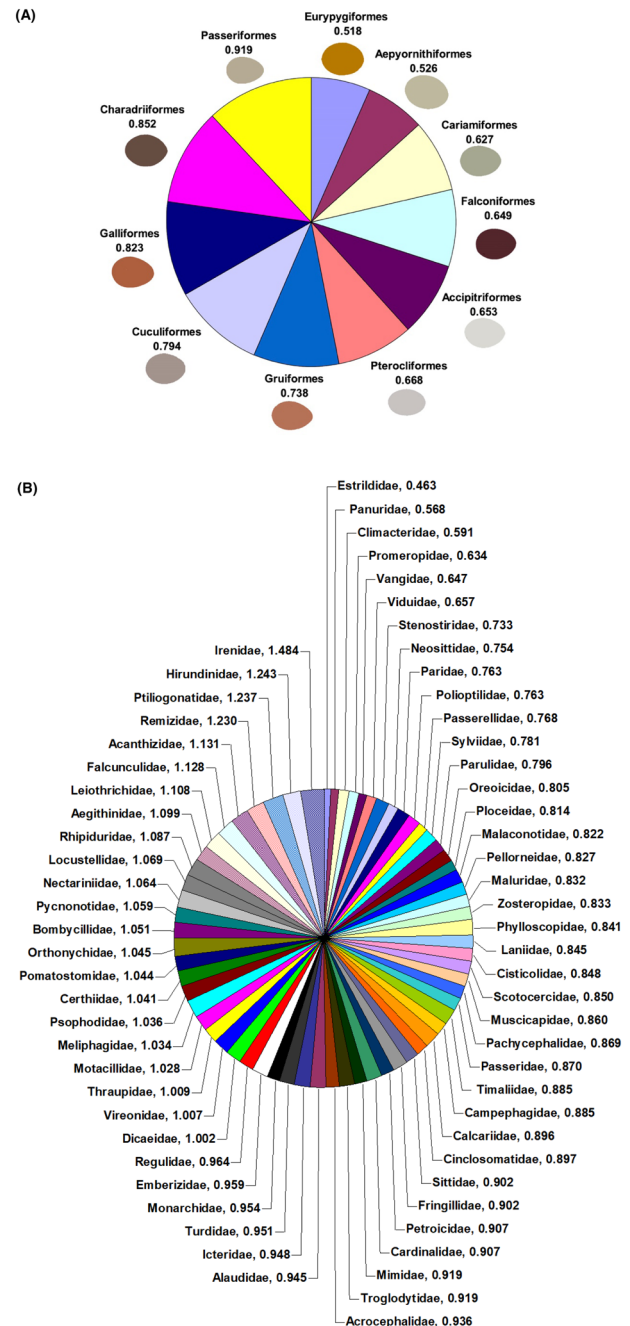
Indices	Max. value	Min. value	Mean	Standard deviation
<i>Aepyornis</i>				
B/L	0.77	0.66	0.73	0.03
L/T	99.7	78.3	88.2	7.2
w/L	0.015	0.003	0.007	0.003
k	0.58	0.49	0.53	0.23
Non-passerine species				
B/L	0.96	0.62	0.75	0.06
L/T	338.0	157.6	207.9	43.4
w/L	0.10	0.01	0.05	0.03
k	1.14	0.39	0.74	0.19
Passerine species				
B/L	0.86	0.58	0.73	0.04
L/T	389.2	158.9	275.6	38.4
w/L	0.14	0	0.06	0.02
k	1.64	0.35	0.93	0.24

made it possible to distinguish several groups of the studied eggs, and we divided those into *Aepyornis* (a ratite bird), passerines (songbirds), and non-passerine species. Their measurement results are presented in Table 2.

A further subdivision of birds led to more detailed information on mean *k* variations for eggs of all studied orders (Figure 2A) and separately for passerine families (Figure 2B).

Of these, only 21 species approximated the golden ratio (Table 3). Notably, four of these were in the order Falconidae and three of the same genus (*Falco*). Further analysis of all seven Falconidae species in the dataset, including *Falco subniger* (black falcon), *Falco biarmicus* (lanner falcon), *Daptrius ater* (black caracara), *Polihierax semitorquatus castanonotus* (pygmy falcon), *Falco cuvieri* (African hobby), *Falco punctatus* (Mauritius kestrel), and *Falco novaeseelandiae* (New Zealand falcon) revealed a mean *k* value of 0.649. When considering only the Falconinae subfamily (same list minus *Daptrius ater* [black caracara], i.e., true falcons only), the *k* value was then exactly 0.618.

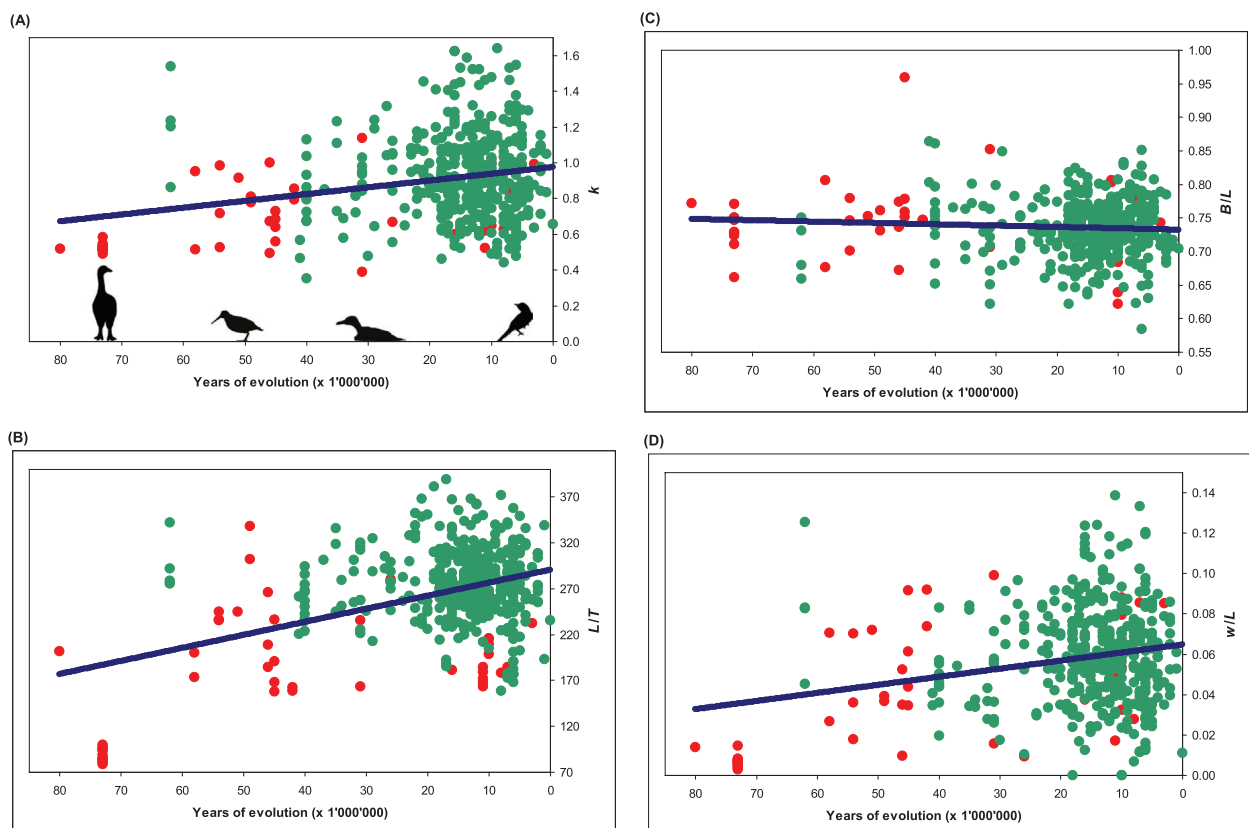
The values of *B/L* and *w/L*, if not completely coinciding, are very close to one another. However, the value of the *L/T* index demonstrates a certain tendency for the thinning of the shell relative to the size of the

**FIGURE 2** Diagrams for mean *k* values. The avian taxa shown include: (A) 11 orders studied, and (B) 65 Passeriformes families.

egg, when comparing the three taxonomic groups, that is, *Aepyornis*, passerines, and non-passerines. In particular, *Aepyornis* had a thicker shell than non-passerines, whereas passerines turned out to be the most thin-shelled. Since the group of passerines is most recent in evolutionary terms,³³ we attempted, for each index, to track any possible dynamics of this process. For this, using the TimeTree web tool^{30–32} that enabled us to judge the approximate date of origination and divergence of a particular taxon, we plotted graphical dependences shown in Figure 3A–D.

TABLE 3 List of species whose k value fell within 0.02 of the golden ratio

Order	Linnean name	Common name	k value
Falconidae	<i>Polihierax semitorquatus castanonotus</i>	Pygmy falcon (castanonotus)	0.60
Muscicapidae	<i>Monticola rupestris</i>	Cape rock-thrush	0.60
Laniidae	<i>Lanius isabellinus</i>	Isabelline shrike	0.60
Icteridae	<i>Molothrus bonariensis minimus</i>	Shiny cowbird (minimus)	0.60
Thraupidae	<i>Microspingus melanoleucus</i>	Black-capped warbling-finch	0.60
Parulidae	<i>Protonotaria citrea</i>	Prothonotary warbler	0.60
Cisticolidae	<i>Cisticola galactotes</i>	Rufous-winged cisticola (galactotes)	0.61
Cisticolidae	<i>Prinia rufescens</i>	Rufescent prinia	0.61
Icteridae	<i>Lamprosar tanagrinus guianensis</i>	Velvet-fronted grackle (guianensis)	0.61
Falconidae	<i>Falco subniger</i>	Black falcon	0.62
Troglodytidae	<i>Microcerculus marginatus squamulatus</i>	Southern nightingale-wren (squamulatus)	0.62
Cariamidae	<i>Chunga burmeisteri</i>	Black-legged seriema	0.63
Parulidae	<i>Setophaga delicata</i>	St. Lucia warbler	0.63
Falconidae	<i>Falco cuvierii</i>	African hobby	0.63
Muscicapidae	<i>Ficedula ruficauda</i>	Rusty-tailed flycatcher	0.63
Paridae	<i>Melaniparus niger</i>	Black tit (niger)	0.63
Falconidae	<i>Falco novaeseelandiae</i>	New Zealand falcon	0.63
Parulidae	<i>Setophaga pitiayumi elegans</i>	Tropical parula (elegans)	0.63

**FIGURE 3** Dynamics in the process of avian evolution for the four indices: (A) k , (B) L/T , (C) B/L , and (D) w/L . For a better visibility, we colored the circles corresponding to the passerine group in green and all the others (*Aepyornis* and non-passerines) in red. The trend lines in panels A, C, and D are significant, with respective correlation coefficients of -0.23 , -0.41 , and -0.24 . The trend line in panel B is insignificant, with $R = 0.06$.

As we have already noted, the shape of all bird eggs can be divided into four main categories.¹¹ The spherical shell can be defined, theoretically, with relative ease, as we have done above in the introduction section of this work. However, among eggs of various shapes considered in our analysis, there were a few attributed to an ellipsoidal shape and a limited number of pyriform ones. We explore these below in more detail.

Ellipsoid

Eggs of this shape are relatively common in nature. How will the neutral axis behave in the shell of ellipsoidal eggs? It was not difficult to address this question, and for this, we took the value of $w/L = 0$ in Equation (S1.8) (see File S1), since the central vertical axis of the ellipsoids is not displaced and runs along its maximum width. Then, Equation (S1.8) can be rewritten as:

$$k^3 - \left(0.647\frac{B}{L} + 0.853\right)\frac{L}{T} \cdot k^2 + \left(\left(0.331\frac{B}{L} - 0.011\left(\frac{B}{L}\right)^2 + 0.177\right)\left(\frac{L}{T}\right)^2 + \left(0.337\frac{B}{L} + 0.169\right)\frac{L}{T} - 0.337\right)k + 0.005\left(\frac{B}{L}\right)^2 \cdot \left(\frac{L}{T}\right)^3 - 0.004\frac{B}{L} \cdot \left(\frac{L}{T}\right)^3 - 0.169\frac{B}{L} \cdot \left(\frac{L}{T}\right)^2 - 0.084\left(\frac{L}{T}\right)^2 + 0.169\frac{L}{T} = 0. \quad (9)$$

Substituting into Equation (9) the intervals of values $L/T = [100 \dots 280]$ and $B/L = [0.62 \dots 0.88]$ that are typical for eggs of a wide variety of wild bird species, we obtained an average value of $k = 0.49$, with a range from 0.16 to 0.77. In a sample of ellipsoidal eggs from the oological reference book by Schönwetter,²⁷ we were able to select only six eggs, for which the average value of k corresponded to 0.53, with a range from 0.46 to 0.61.

Pyriform (conical) ovoid

Using a similar, already established methodology for calculating the coefficient k for passing the neutral axis in the shell of conical eggs, we applied the calculated formulae derived by us⁴ to determine their volume, V_{con} , and surface area, S_{con} :

$$V_{con} = B^2L \left(0.46 - 0.054\frac{W}{L}\right), \quad (10)$$

$$S_{con} = BL \left(\left(0.2447\frac{B}{L} - 0.0205\right)\frac{W}{L} + 0.8574\frac{B}{L} + 2.0318\right). \quad (11)$$

Performing transformations similar to our theoretical studies for spherical and ovoid eggs, we produced a cubic equation for calculating k (see its detailed derivation presented in File S2):

$$k^3 - \frac{L}{T} \left(0.6484\frac{B}{L} + 0.8516 + 0.0388\frac{W}{L}\right)k^2 + \left(\left(\frac{L}{T}\right)^2 \left(0.3408\frac{B}{L} + 0.0593\frac{B}{L} \cdot \frac{W}{L} - 0.0018\frac{W}{L} - 0.0054\left(\frac{B}{L}\right)^2 + 0.1758\right)\right)$$

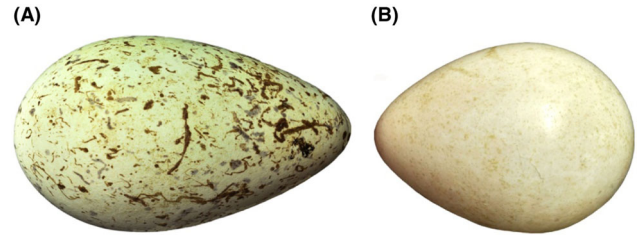


FIGURE 4 Images of pyriform eggs: (A) a Brännich's guillemot (*Uria lomvia*) egg (https://commons.wikimedia.org/wiki/File:Uria_lomvia_MWNH_2182.JPG) and (B) a Chukar partridge (*Alectoris chukar*) egg (https://commons.wikimedia.org/wiki/File:Alectoris_chukar_MWNH_1084.JPG). Both images were changed from the original photographs taken by Klaus Rassinger and Gerhard Cammerer, 2012; available in Wikimedia Commons, Category: Eggs of the Natural History Collections of the Museum Wiesbaden; and distributed under the terms of the CC-BY-SA-3.0 license).

$$+ \frac{L}{T} \left(0.3184\frac{B}{L} - 0.0187\frac{W}{L} + 0.1592\right) - 0.3184\right)k + \left(\frac{L}{T}\right)^3 \left(0.0027\left(\frac{B}{L}\right)^2 - 0.0083\frac{B}{L} - 0.0085\frac{B}{L} \cdot \frac{W}{L} - 0.0106\frac{W}{L} \cdot \left(\frac{B}{L}\right)^2\right) + \left(\frac{L}{T}\right)^2 \left(0.0094\frac{W}{L} - 0.1592\frac{B}{L} - 0.0796\right) + 0.1592\frac{L}{T} = 0. \quad (12)$$

Pyriform eggs are variable in nature (Figure 4). For example, a guillemot (*Uria lomvia*) egg has indices $B/L = 0.59$ and $w/L = 0.13$, and a Chukar partridge (*Alectoris chukar*) egg has $B/L = 0.74$ and $w/L = 0.08$.

Assuming that the possible parameters of variation are higher than those of the given examples of eggs, say, $B/L = [0.55 \dots 0.80]$ and $w/L = [0.05 \dots 0.15]$, and choosing the interval of the third index typical for the whole variety of bird eggs, that is, $L/T = [120 \dots 274]$, as calculated from the data of Paganelli et al.,³⁴ Ar et al.,³⁵ Rahn and Paganelli,¹² and Peterson et al.,³⁶ we generated 378 different combinations, thus obtaining 378 cubic equations based on Equation (12). Solving each of them, we obtained variations for k values characteristic of pyriform ovoids, that is, from 1.75 to 4.72, with an average value of 3.139, which was very far from the golden ratio.

Among the sample of eggs from the oological reference book,²⁷ we found 13 eggs conforming to the conical category. Calculation of the k values for them resulted in the range of [2.93 ... 5.40], with an average value of 4.14. The results obtained were slightly different from the simulated ones, which was possibly due to the small sample size, but the extent of their values was the same and just as far from the value of the golden ratio. Thus, it appears that only eggshells whose shape corresponds to the classical ovoid, as mathematically described by the Hügelschäffer formula,²¹ and that have a very limited range of values of the three indices B/L , w/L , and L/T can validate the hypothesis about the location of the neutral axis such that the k -factor corresponds to the golden ratio.

DISCUSSION

The study herein presented represents the largest and most comprehensive overview of the neutral axis of bird eggshells to date. Despite

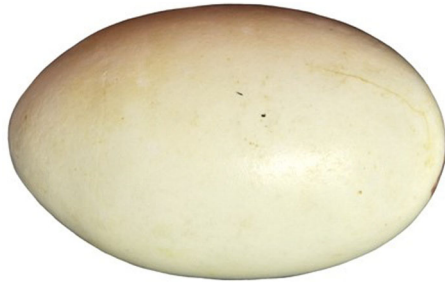


FIGURE 5 An image of a greater white-fronted goose (*Anser albifrons*) egg with a B/L golden ratio equal to 0.618 (https://commons.wikimedia.org/wiki/File:Anser_albifrons_MWNNH_0945.JPG; an altered image originally taken by Klaus Rassinger and Gerhard Cammerer, 2012; available in Wikimedia Commons, Category: Eggs of the Natural History Collections of the Museum Wiesbaden; and distributed under the terms of the CC-BY-SA-3.0 license).

initial findings indicating a mean k value of 0.618 (the golden ratio) among domesticated birds, such as chickens, ducks, and geese (see Introduction), we reject the hypothesis that such a figure is typical of avian eggs in general. Rather, the k value is highly variable, much lower in spherical and ellipsoid eggs and higher in pyriform eggs, varying considerably even among passerine birds. The golden ratio for the neutral axis, therefore, only applies to domesticated species, such as chickens, ducks, and geese, plus the handful of species indicated in the study for whom an approximate value of 0.618 was found (Table 3). One possible exception might be falcons (subfamily Falconinae) for whom (in six examples) the mean k value was exactly 0.618.

Attempts to link the parameters of bird eggs with the golden ratio have been made many times. Both the egg and the golden ratio are important objects in architecture and art, and also have a certain touch of mystery^{23,37-42} that is presumably the stimulus for a number of researchers to try and correlate them. Of course, the first thing that could be tied into this relationship is the ratio of egg length and maximum breadth, that is, the basic index B/L , called the shape index.¹⁴ Although it is not difficult to find an egg with the ratio of these parameters equal to 0.618, the average values of this index are slightly higher. As our studies of the eggs of wild bird species have shown, on average, it corresponds to 0.74 and differs little from this value when divided into main shape groups (Tables 1 and 2). Since, in general, our perception of the shape of a bird's egg correlates with that of a chicken egg, as the most common in everyday life, the index of their shape, as we have already mentioned several times in the framework of these studies, is in the range of [0.65... 0.82]. This is confirmed by the psychological experiments of Kimber,⁴³ who experimented with her students, giving them the task of drawing an egg profile in the hope of proving that the golden ratio is such an elegant shape that, in the imagination of an ordinary person, the contour ratio would be just that. However, she invariably received an average result with a clearly overestimated value.⁴³ In point of fact, in nature, the most common B/L ratio equal to 0.618 is found in geese (see an example in Figure 5). Perhaps not without reason that the famous Aesop's fable⁴⁴ referred to "the goose that

laid the golden egg," although there are other versions of the fable that refer to a chicken rather than a goose.⁴⁵

Mytiai and Matsyura⁴⁶ also found in some species that the ratio of blunt and pointed ends radiuses can be described with the golden ratio. Petrović and Obradović⁴⁷ considered in their work many options for plotting the contours of eggs, using as a basis for such a design a combination of various parameters, the ratio of which corresponds to the golden ratio. Levine⁴⁸ and later Nagy⁴⁹ obtained egg profiles by substituting different values of n in the basic equation $x^n + y^n = 1$ so that n conforms to the value of the golden ratio raised to a certain power. Some of the profiles obtained did indeed resemble an egg, although most were far from the classic ovoids. Considering these studies together, it seems that attempts to link together the golden ratio and egg geometry are somewhat artificial. Indeed, choosing measurements of certain parameters, the ratio of which is 0.618, is quite simple, both for a variety of natural and manmade objects, by virtue of the fact that, with such a large sample size, some are bound to conform by chance alone (Table 3). We thus do not exclude the possibility that our study case is probabilistic; however, when the probability consistently repeats itself, it is reasonable to hypothesize that this may be a pattern. Such a constancy has only been noted in the case of parameters corresponding to chicken eggs, and possibly eggs of other poultry species. In this context, we can rely on the data based on measurements of duck eggs⁵⁰⁻⁵² and goose eggs.⁵³⁻⁵⁶ In other words, only those eggs of bird species intensively domesticated by humans appear to conform, notwithstanding the 21 species found in this study (Table 3) and the possible associations with falcons. Why falcons should conform to this ratio and no other wild birds is not clear at this stage.

Given that the neutral axis golden ratio applies predominantly to species domesticated by humans over many generations, it seems reasonable to suggest that it was directed artificial selection that contributed to the production of ovoids with these "golden" geometric parameters. It is highly unlikely, of course, that poultry breeders deliberately targeted this criterion when domesticating poultry. Nonetheless, it prompts the question of whether the achievement of other optimal egg indicators from the point of view of economically important properties (say, improving hatchability, safety, shell strength, etc.)^{5,57-61} might be best facilitated by conforming to the golden ratio in terms of the neutral axis. But why, then, is this phenomenon not widely observed in wild species?

Judging from the graph in Figure 2A, it is possible that at the stage of their evolution, the parameters of the earliest eggs corresponded to this "golden" principle. However, with each evolutionary leap, the neutral axis ran lower and lower, that is, the value of k increased steadily. This fact was due to a relative decrease in shell thickness, that is, an increase in the L/T index (Figure 2B). This becomes particularly apparent after the appearance of the passerine species. Similar results were obtained by Rahn and Paganelli,¹² who, like us, used data from the oological reference book.²⁷ They derived two different allometric relationships for calculating the shell thickness for non-Passeriformes and Passeriformes, since in the latter, with a similar egg mass, the shell thickness was always less. Perhaps, it was one of several specific features of passerines that contributed to their widespread distribution

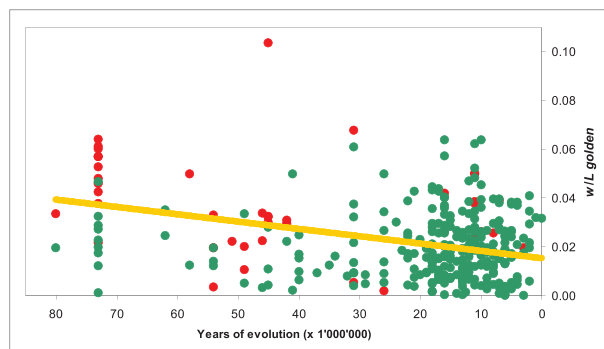


FIGURE 6 Predictive dynamics in the evolution of the w/L values that would conform to the value of $k = 0.618$. Green circles correspond to the passerine group and the red ones to *Aepyornis* and non-passerines. The trend line is significant, with $R = 0.34$.

on the planet. Evolution toward a decrease in the thickness of the shell could facilitate reducing the energy consumption of the mother's body for the formation and subsequent incubation of eggs and enable even weaker embryos to hatch better, thereby improving reproduction. Therefore, the protection of eggs from possible damage was implemented by developing the process of nesting and laying eggs in hard-to-reach places, as can be observed among various passerines.

Why then did the evolutionary process not go further, adjusting other parameters in such a way that, despite the value of T being out of the standard, the result of calculating k would still approach the golden ratio value of 0.618? Either this number does not play any role at all in the optimal structure of egg ovoids, or the process of egg evolution has not yet been completed. If the latter hypothesis is correct, then the more variable indices w/L and B/L should come into play, with the aid of which the natural regulation of the optimal value of k takes place. However, the question is obviously not solved as simply as in the mathematical model. Judging from the B/L relationship change over 80 million years of evolution (Figure 2C), this indicator, on average, has remained practically unchanged, that is, approximately equal to 0.74. The same can be observed in chicken eggs because this ratio is well known for a standard chicken egg, the dimensions of which were provided by Romanoff and Romanoff¹⁴ based on numerous measurements. It is likely that this ratio is much more critical than shell thickness for embryonic development and, accordingly, the survival of the offspring. Indeed, according to research by Deeming,⁶² egg shape is influenced not only by the pelvis size and shape but also by the egg content, in particular, the proportion of yolk.

As for the third index, w/L , its value gradually increases (Figure 2D), and it is possible that this ratio is intended to equalize the values of k , bringing them closer to the "golden" value. Using Equation (8), we recalculated the w/L values with unchanged B/L and L/T data. As a result, a linear trend was obtained, as shown in Figure 6, as a golden line. Herein, we have also plotted what the w/L ratio values would be in the passerine group (green circles), and *Aepyornis* and non-passerines (red circles) if, leaving the B/L and L/T values unchanged, the neutral axis would run along the golden ratio of their shells.

Thus, to ensure that the value of k corresponded to the golden ratio, the evolutionary process of changing w/L would have to go in the opposite direction, that is, by decreasing the value of the parameter w and, respectively, approaching the geometric shape of the egg toward the ellipsoid. However, in reality, this has not happened. Surely, the relationship of the oomorphological parameters is much deeper than the attempt to provide the location of the neutral axis of the eggshell. We can suggest that a more compact laying of eggs in the nest depends on the size w ,^{63–65} and, consequently, their optimal air and temperature exchange and, as a result, incubation success. In any event, it seems that if the golden ratio of the shell plays a particular role for bird eggs (see File S3 for further discussion), then this factor is clearly inferior to other egg quality characteristics (e.g., shape^{2–4}) that are no less important and relevant.

Importantly, our study is a useful finding given that the golden ratio has been asserted in numerous contexts in earlier studies, despite the fact that those assertions were not always accurate (indeed, they were frequently false). Some of them^{66,67} argued the existence of the golden ratio in self-replicating systems, but this is not particularly unique in view of various other existing mathematical constants. Others^{68,69} believed that it is simple to find non-golden ratios in many natural systems. Therefore, our study offers crucial information to help resolve such contradictions in the context of eggshells.

CONCLUSION

Collectively, the present study exemplifies an original attempt to look nondestructively inside the eggshell, revealing its characteristics and secrets using the appropriate mathematical apparatus only. Moreover, we have for the first time designed, described, and successfully applied a method to easily recalculate the location of the neutral axis in any geometrical object. A few novel indices have been introduced to characterize avian eggs comprehensively in relation to their evolutionary adaptation. Our findings contribute to developing a conception of how the mathematical secrets of eggshells can reveal new evolutionary signatures in birds.

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AUTHOR CONTRIBUTIONS

Conceptualization, investigation, methodology, and software: V.G.N. Data curation: A.W.G. Formal analysis: D.K.G. Project administration: M.N.R. Supervision: D.K.G. Validation: V.G.N. and D.K.G. Visualization, V.G.N. and M.N.R. Writing—original draft: V.G.N. and A.W.G. Writing—review and editing, M.N.R. and D.K.G.

COMPETING INTERESTS

The authors declare no competing interests.

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