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Comparison of two polar equations in describing the geometries of domestic pigeon (*Columba livia domestica*) eggs

Lin Wang ,[*] Darren K. Griffin,[†,‡] Michael N. Romanov ,[†,‡,§,1] and Johan Gielis[‖]

[*]Key Laboratory of Bio-Resource and Eco-Environment of Ministry of Education, College of Life Sciences, Sichuan University, Chengdu 610065, China; [†]School of Biosciences, University of Kent, Canterbury, Kent CT2 7NJ, United Kingdom; [‡]Animal Genomics and Bioresource Research Unit (AGB Research Unit), Faculty of Science, Kasetsart University, Chatuchak, Bangkok 10900, Thailand; [§]L. K. Ernst Federal Research Center for Animal Husbandry, Dubrovitsy, Podolsk Municipal District, Moscow Oblast, 142132, Russia; and [‖]Department of Biosciences Engineering, University of Antwerp, Antwerp B-2020, Belgium

ABSTRACT Two-dimensional (**2D**) egg-shape equations are potent mathematical tools, facilitating the description of avian egg geometries in their applied mathematical modelling and poultry science implementations. They aid in the precise quantification of avian egg sizes, including traits such as volume (***V***) and surface area (***S***). Despite their potential, however, polar coordinate egg-shape equations have received relatively little attention for practical applications in oomorphology. This may be attributed to their complex model structure and the absence of explicit geometric interpretations for the equation parameters. In the present study, 2 distinct polar equations, namely the Carter-Morley Jones equation (**CMJE**) and simplified Gielis equation (**SGE**), were used to fit the profile geometries of 415 domestic pigeon (*Columba livia domestica*) eggs based on nonlinear least squares regression methods. The adequacy of goodness-of-fit for each nonlinear egg-shape equation was evaluated through the adjusted root-mean-square error (**$\mathbf{RMSE_{adj}}$**), while relative curvature measures of nonlinearity were utilized to assess the nonlinear behavior of equations. All of the $RMSE_{adj}$ values of the 2 polar equations were lower than 0.05, which demonstrated the validity of CMJE and SGE in depicting the shapes of *C. livia* egg profiles. Moreover, the 2 egg-shape equations showed good nonlinear behavior across all 415 *C. livia* eggs. Wilcoxon signed rank tests relative to $RMSE_{adj}$ values between CMJE and SGE revealed that CMJE displayed inferior fits to empirical data when compared to SGE. CMJE, however, had a better linear approximation performance than SGE at the global level. At the individual parameter level, all of the parameters of CMJE or SGE exhibited good close-to-linear behavior. This study provides an instrumental mathematical tool for the practical application of polar egg-shape equations, such as nondestructively estimating *V* and *S* of avian eggs. Additionally, it offers valuable insights into assessing nonlinear regression models for accurately describing the geometries of 2D egg profiles.

Key words: Pigeon egg, close-to-linear behavior, goodness of fit, linear approximation and nonlinear regression, polar egg-shape equation

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INTRODUCTION

Birds' eggs have been of great interest to the scientific community through the centuries as they have long been a major food source in the history of human nutrition (Romanov et al., 2009). The added interest for ecological modelling (Narushin and Romanov, 2000; Heming and Marini, 2015; Biggins et al., 2018; Duursma et al., 2018), conservation (Henderson, 2007; Moula et al., 2009) and developmental biology studies (Narushin et al., 1997, 2016, 2023b; Narushin and Romanov, 2001; 2002a,b), as well as hobbyists such as bird watchers and breeders (Preston, 1953; Todd and Smart, 1984; Baker, 2002; Troscianko, 2014; Biggins et al., 2022) widen their appeal for a range of scientific disciplines including poultry science. As such, egg shapes and sizes have been subject of many studies, and numerous mathematical equations to describe the oomorphology, i.e., the profiles of bird eggs (Narushin et al., 2021a, 2023a), have been proposed. For example, these include Preston's universal formula (Preston, 1953) and the polar formula proposed by Carter and

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[1]Corresponding author: m.romanov@kent.ac.uk

Morley Jones (1970), henceforth denoted as CMJE. Todd and Smart's re-expression of Preston's universal formula (Todd and Smart, 1984), Baker's equation (Baker, 2002), Troscianko's equation (Troscianko, 2014), the Hügelschäffer model (Narushin et al., 2020, 2021b, 2022), the 4-diameter equation introduced by Biggins et al. (2022), and the simplified Gielis' equation (Shi et al., 2022a), denoted hereafter as SGE, are more recent examples. Among the above models, the 5-parameter CMJE and the 3-parameter SGE models stand out as they are created in a polar coordinate system.

Previous studies demonstrated the efficacy of numerous egg-shape models in accurately representing avian egg shapes based on empirical data (Biggins et al., 2018, 2022; Shi et al., 2022a). However, comparatively few studies have focused on the polar coordinate egg-shape models, perhaps due to the lack of explicit geometric interpretations for the parameters within the polar equations. They do, nonetheless, possess certain unique advantages: CMJE features a generalized linear structure, making it conducive to parameter estimation through multiple linear regression methods. Conversely, the complex equation structure of SGE, also a polar coordinate equation, renders linear regression methods unsuitable for parameter estimation. In such cases, nonlinear optimization serves as a viable alternative, albeit with lower efficiency. Our previous findings (Shi et al., 2022a; Wang et al., 2022a) support this observation. Moreover, when estimating parameters of a nonlinear model, optimization methods generally offer greater flexibility and achieve superior goodness of fit (Shi et al., 2023b). A comparison between equations of the same type often yields more equitable evaluation results. Biggins and colleagues' study assessed the fitting effects of various egg-shaped equations, including CMJE (Biggins et al., 2018). However, their study encompassed both rectangular and polar equations, utilizing "error about y" as a criterion for fitting effects. This approach may unfairly bias against polar equations that adopt "error about r" as the criterion. Exploring the use of polar equations for modeling bird egg shapes thus warrants further investigation as the 2-dimensional contour of bird eggs invariably forms a closed curve, aligning with the rotation of the pole radius around the pole in polar equations for closed curves.

Generally, polar egg-shape equations have been derived from fundamental geometric shapes such as a circle or ellipse, or from trigonometric series. For example, CMJE in this context involves 9 measurements of an egg, including its length (***L***) and maximum breadth (***B***), utilized to obtain an equation describing the profile of the egg in polar coordinates, as a sum of cosine and sine terms up to third order (analogous to the Preston (1953) equation). The Gielis equation is an extension of circle and ellipse, 2 of the 4 classic conic sections (Gielis, 2003, 2017) and prior studies have affirmed its efficacy in depicting a wide range of actual biological geometries relevant to applied mathematical modelling, among other applications (Shi et al., 2015, 2020; Lin et al., 2016; Tian et al., 2020; Li et al., 2022; Wang et al., 2022a). Recently, SGE (Shi et al. 2022a) was employed to fit the boundary geometries of eggs from 9 bird species, achieving superior goodness of fit compared to a complex egg-shape model. Nevertheless, research focusing on polar equations (including CMJE and SGE) for describing avian egg profiles, particularly in quantifying extensive empirical egg data, remains limited. Consequently, a comparative assessment of the effectiveness of different polar egg-shape equations in capturing egg features is noticeably lacking, despite its potential to yield valuable insights into physiological and mechanical factors influencing egg-shape formation. In this respect, it is noted that 1 advantage of the polar equations is that development from a pole (center) can be modelled. This has also led to highly efficient methods for solving boundary value problems using the original Fourier Projection method by generalizing the Laplacian (Natalini et al., 2008; Example 2 in this reference is an egg shape).

To address this gap in our knowledge, we used here the 2 polar egg-shape equations (CMJE and SGE) to fit the profile shapes of 415 eggs of domestic pigeon (*Columba livia domestica*). This species was of particular interest to us as they have general egg-shaped characteristics specific to most other species; they are easy to obtain and thus ensure the sufficient amount of data used in an experiment in addition to being a reasonably well-known foodstuff.

In this study, the root-mean-square error and the relative curvature measures of nonlinearity were used to determine which 1 of the 2 egg-shape models referred provided the best description of the shapes of 2-dimensional (**2D**) pigeon egg contours. The objective of this study was therefore twofold: first, to ascertain the validity of employing relative curvature measures of nonlinearity within nonlinear regression analyses; and second, to introduce a novel methodology for the future assessment of avian egg-shape models relevant to poultry science and other disciplines.

MATERIALS AND METHODS

Data Acquisition

A total of 415 fresh *C. livia* eggs were collected in October 2022, from a commercial pigeon breeding farm located at the county of Zhengding (38°8′38.3″ N, 114° 33′47.7″ E), Hebei, China, as the main validation data for this study, mainly due to the availability of the eggs in large numbers. Importantly, this species of bird has a typical, representative egg shape. Figure 1 shows an example *C. livia* egg image. An adjustable tabletop phone mount was employed to hold a smartphone (Huawei P30Pro, Huawei, Dongguan, China) to photograph eggs. In order to make the mid-line of the egg as parallel to the horizontal desktop as possible, we used a concave base to support eggs, such as a test tube rack (Figure 1A), before placing the egg for imaging (Shi et al., 2023a). In addition, to calibrate the deviation of the image size of each egg from its actual size, we measured L of the egg using a vernier caliper (zero to 150 mm; Shanghai Accurate Measuring Tools Co. Ltd., Shanghai, China; measure

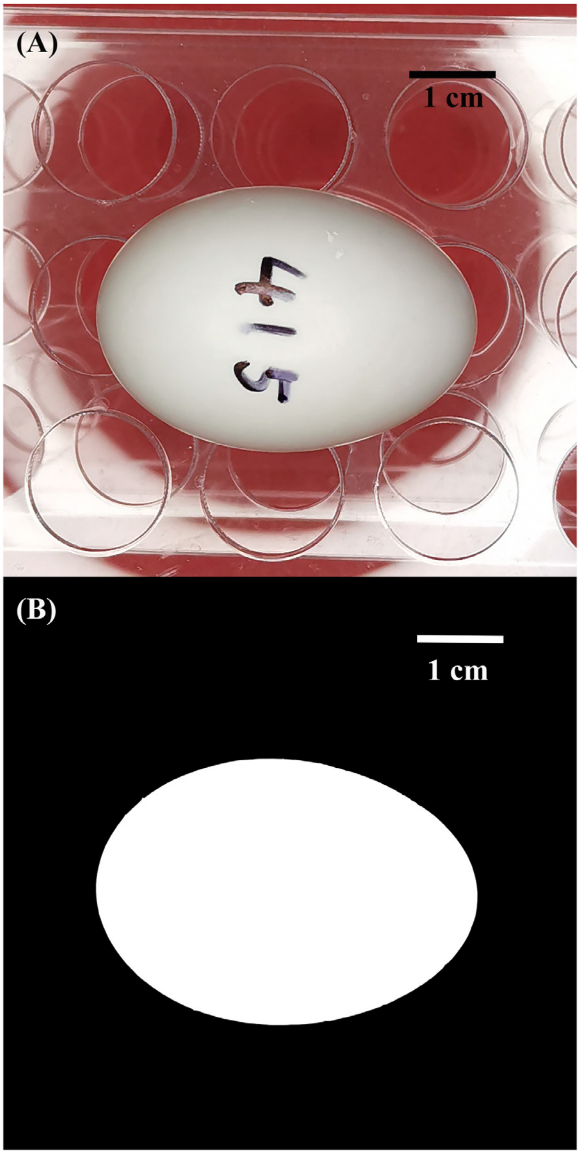

Figure 1. An example *C. livia* egg image (A) and the extracted 2D egg profile (B).

accuracy: 0.02 mm). Adobe Photoshop CS2 (version 9.0; Adobe, San Jose, CA) was used to convert the egg images into black and white bitmap files at a resolution of 600 dpi (see Figure 1B). The MATLAB (version 2009a; MathWorks, Natick, MA, USA) procedures developed by Shi et al. (2018) and Su et al. (2019) were used to extract the planar coordinates of each egg profile. Then, the function adjdata in the biogeom package (version 1.4.3; Shi et al. 2022b) based on R (version 4.2.1; R Core Team, 2022) was utilized to obtain 2000 approximately equidistant data points from the boundary coordinate data (Supplementary Table S1).

Models

The empirical data of 2D egg profiles were subsequently fitted using the following equations:

(i) The 5-parameter CMJE model (Carter and Morley Jones, 1970):

$$r = K_1 + K_2\cos 2\varphi + K_3\left(-\cos^3\varphi\right) + K_4\left(-\sin^2 2\varphi\right) + K_5\sin^3 2\varphi, \quad (1)$$

where r and φ are the polar radius and polar angle, respectively; and K_1, K_2, K_3, K_4, and K_5 are constants to be estimated. Carter and Morley Jones (1970) pointed out that for a given egg-shape curve generated by CMJE, the line $\varphi = 0$ corresponds to the long axis of the egg and the line $\varphi = \pi/2$ corresponds to the line of B. Therefore, L and B can be calculated as:

$$L = 2(K_1 + K_2),\quad B = 2(K_1 - K_2). \quad (2)$$

Given values of the constants of K_1, K_2, K_3, K_4, and K_5, the value of r can be calculated for any value of φ. Conversely, for sufficient number of points of egg profile in the Euclidean coordinate system, the values of r and φ for each point can be obtained through the transformation of coordinates $x = r\cos(\varphi), y = r\sin(\varphi)$, and then the values of the parameters K_1, K_2, K_3, K_4, and K_5 can be estimated by multiple regression of r on cos 2φ, $-\cos^3\varphi$, $-\sin^2 2\varphi$, and $\sin^3 2\varphi$:

$$r \sim K_1 + K_2 m_1 + K_3 m_2 + K_4 m_3 + K_5 m_4 + \varepsilon, \quad (3)$$

where $m_1 = \cos 2\varphi$, $m_2 = -\cos^3\varphi$, $m_3 = -\sin^2 2\varphi$, and $m_4 = \sin^3 2\varphi$; and ε is an additive random error representing errors of measurement.

(ii) The 3-parameter SGE model (Shi et al., 2022a):

$$r = a\left(\left|\cos\frac{\varphi}{4}\right|^{n_2} + \left|\sin\frac{\varphi}{4}\right|^{n_2}\right)^{-\frac{1}{n_1}}, \quad (4)$$

where r and φ are the polar radius and polar angle, respectively; and a, n_1, and n_2 are parameters to be estimated. Similarly, the abscissa and ordinate of egg shape in the Euclidean coordinate system can be calculated as $x = r\cos(\varphi)$ and $y = r\sin(\varphi)$, respectively. Based on the theoretical study of the Gielis equation by Wang et al. (2022b), L can be obtained as follows:

$$L = a\left(1 + 2^{-\frac{1}{n_1}}\left(\frac{\sqrt{2}}{2}\right)^{-\frac{n_2}{n_1}}\right). \quad (5)$$

In general, the parameters a, n_1, and n_2 within SGE were estimated by the nonlinear regression protocols. Additionally, Shi et al. (2022a) introduced 3 location parameters x_0, y_0, and θ into SGE when performed the nonlinear regression. Herewith, x_0 and y_0 represent the coordinates of the polar point of SGE in the Euclidean coordinate system, and θ represents the angle between the scanned egg length axis and the x-axis. Therefore, a total of 6 parameters, including 3 model parameters a, n_1, and n_2 and 3 location parameters x_0, y_0, and θ, need to be estimated within the SGE model.

Data Fitting and Model Assessment

The 2 egg-shape models, namely CMJE and SGE, were used to fit the 2D egg profiles based on the empirical data. The Nelder−Mead optimization algorithm (Nelder and Mead, 1965) was employed to minimize the fitting criterion of nonlinear regression. The parameters within egg-shape models were estimated by minimizing the residual sum of squares (RSS) between the actual distances from the polar point to the data points on the scanned perimeter of the egg shape and the distances from the polar point to the data points on the predicted perimeter of the egg shape:

$$\mathrm{RSS} = \sum_{i=1}^{n} (r_i - \hat{r}_i)^2, \tag{6}$$

where r_i represents the observed distance from the polar point to the i-th point on the scanned perimeter of egg shape; $\hat{r}_i$ represents the predicted distance from the polar point to the i-th point on the predicted perimeter of egg shape based on the CMJE or SGE; and n represents the number of data points on the scanned perimeter of egg shape.

Additionally, the adjusted root-mean-square error (**$\mathbf{RMSE_{adj}}$**) was then used to measure the goodness of fit between the observed and predicted data points:

$$\mathrm{RMSE_{adj}} = \sqrt{\frac{\mathrm{RSS}/(n-p)}{A/\pi}}, \tag{7}$$

where p represents the number of parameters to be estimated within each egg-shape equation, A represents the area of the scanned egg profile. The $\mathrm{RMSE_{adj}}$ represents the ratio of the mean absolute deviation (between the observed and predicted radii from the polar point to the egg profile) to the radius of a hypothetical circle whose area equals to that of the 2D egg profile, which can standardize the prediction error regardless of the egg profile size. As a rule of thumb, an $\mathrm{RMSE_{adj}}$ value less than 0.05 usually indicates a good fit, i.e., the mean absolute deviation between the observed and predicted polar radius does not exceed 5% of the hypothetical radius. In addition, the smaller the $\mathrm{RMSE_{adj}}$ value, the better the model fits. Wilcoxon signed rank test (Wilcoxon, 1945) with a 0.05 significance level was employed in the present study to determine whether there were significant differences among $\mathrm{RMSE_{adj}}$ values derived from different egg-shape models.

In utilizing least squares methods to fit a mathematical model, it is crucial to incorporate a stochastic assumption. This assumption precisely defines the variability of the error term, which in this context represents the discrepancies between the observed and predicted polar radii as a function of changes in the polar angle. Theoretically, assuming the error term adheres to an independent and identically distributed normal distribution, the least squares estimators for parameters in a linear regression model are unbiased, jointly normally distributed, and exhibit minimum variance among estimators within the class of regular estimators (Ratkowsky and Reddy, 2017). However, in the scenario of a nonlinear regression model, estimators obtained via least squares methods do not retain these advantageous properties, especially when contending with a small sample size. Only when the sample size is expanded to a sufficiently large scale, these least squares estimators begin to approach the esteemed asymptotic qualities. Fortunately, 2000 approximately equidistant data points from the boundary coordinate data of each 2D egg profile were selected as our test data points. This meant that the sample size for each egg was sufficient enough in the present study. However, evaluating the assumptions of the 2 nonlinear models remain an essential step in the analytical process.

Ratkowsky (1983) classified "close-to-linear" models as nonlinear models whose least squares estimators closely approached the mentioned asymptotic properties. Conversely, "far-from-linear" nonlinear models lacked these desirable asymptotic properties. In point of fact, the foundation of algorithms used for computing least squares estimates relies on a local linear approximation, which attained through the first-order Taylor expansion. This approximation hinges on 2 key assumptions: the planar assumption and the uniform coordinate assumption, as elucidated by Bates and Watts (1980, 1988). Geometrically, the planar assumption suggests that the solution locus (Box and Lucas, 1959) is approximated by a tangent plane. Meanwhile, the uniform coordinate assumption entails the imposition of a linear coordinate system on this approximating tangent plane. Numerous measures of nonlinearity have been proposed to shed light on the adequacy or inadequacy of the linear approximation (Beale, 1960; Box, 1971; Bates and Watts, 1980; Hougaard, 1985). For instance, Bates and Watts (1980, 1988) introduced the root-mean-square relative curvature, which included the root-mean-square relative intrinsic curvature (γ^N_{RMS}) and the root-mean-square relative parameter-effects curvature (γ^T_{RMS}). These measures provide a global assessment to ascertain whether a nonlinear model leans towards being "close-to-linear" or "far-from-linear". The 2 root-mean-square relative curvatures γ^N_{RMS} and γ^T_{RMS} were evaluated by the critical curvature (K_c), defined as $1/\sqrt{F(p, n-p; \alpha)}$, where F represents the F-distribution, p is the number of the model parameters, n is the number of data points, and α is the confidence level equal to 0.05 (Bates and Watts, 1988). In the present study, the ratio of the root-mean-square relative curvature to the critical curvature was employed to determine the adequacy of the linear approximation. The expressions are as follows:

$$\delta^N = \frac{\gamma^N_{\mathrm{RMS}}}{K_c}, \tag{8}$$

and

$$\delta^T = \frac{\gamma^T_{\mathrm{RMS}}}{K_c}. \tag{9}$$

Here, a value of δ^N not exceeding 1 suggests that the planar assumption can be confidently acceptable. Meanwhile, if δ^T is smaller than 1, then the uniform coordinate assumption holds true. Furthermore, the smaller the values of δ^N and δ^T, the more close-to-linear the nonlinear model is (Bates and Watts, 1980, 1988). We used Wilcoxon signed rank test (Wilcoxon, 1945) with a 0.05 significance level to compare δ^N (or δ^T) values derived from the 2 egg-shape models in this study.

Nevertheless, γ^N_{RMS} and γ^T_{RMS} cannot provide substantial insights into individual model parameter performance on the linear approximation. In the present study, the percentage bias (**P_b**) of each parameter, as suggested by Box (1971) and Ratkowsky (1983), was used to evaluate the nonlinear behavior of the specific parameter within a nonlinear model. As a rule of thumb, an absolute value of P_b less than 1% indicates that the nonlinear model is close-to-linear. This illustrates that the estimators of parameters exhibit several asymptotic properties mentioned above, including proximity to unbiasedness, normal distribution, and minimization of variance (Ratkowsky, 1990).

The function lm in the stats package (version 4.4.0) and the function fitGE in the biogeom package (version 1.4.3; Shi et al. 2022b) were utilized to estimate the model parameters within CMJE and SGE, respectively. The functions curvIPEC and biasIPEC in the IPEC package (version 1.1.0; Shi et al., 2024) were used to calculate the involved curvature measures of nonlinearity, γ^N_{RMS}, γ^T_{RMS}, K_c, and P_b. All calculations and figures were accomplished based on R (version 4.2.1; R Core Team, 2022).

RESULTS

Figure 2 illustrates the fitting of the egg profile using the 2 polar equations for 1 egg among the 415. For the fitted results of all *C. livia* eggs, the $\mathrm{RMSE_{adj}}$ values ranged from 0.002 to 0.033 with a median of 0.011 for CMJE, and from 0.002 to 0.012 with a median of 0.004 for SGE (Tables S2 and S3, Figure 3). The results of Wilcoxon signed rank test revealed that the $\mathrm{RMSE_{adj}}$ values of SGE were significantly lower compared to CMJE ($W = 164866$, $P < 0.001$), which indicated that SGE displayed better goodness of fit than CMJE.

The global nonlinearity of the nonlinear models was assessed by δ^N and δ^T. The values of δ^N of the 2 egg-shape models for 415 *C. livia* eggs were all consistently far below 1 (Supplementary Tables S2 and S3, Figure 4), which demonstrated exceptional adherence to the planar assumption. Meanwhile, all of the values of δ^T of the 2 egg-shape models applied to 415 *C. livia* eggs were far less than 1 (Supplementary Tables S2 and S3, Figure 4), indicating that the uniform coordinate assumption could be confidently acceptable for the 2 models. These results emphasize that the 2 polar egg-shape models exhibited good linear approximation.

The results of Wilcoxon signed rank test, however, revealed that the values of δ^N derived from SGE were significantly higher compared to those derived from CMJE on a log-log scale ($W = 0$, $P < 0.001$) (Figure 4),

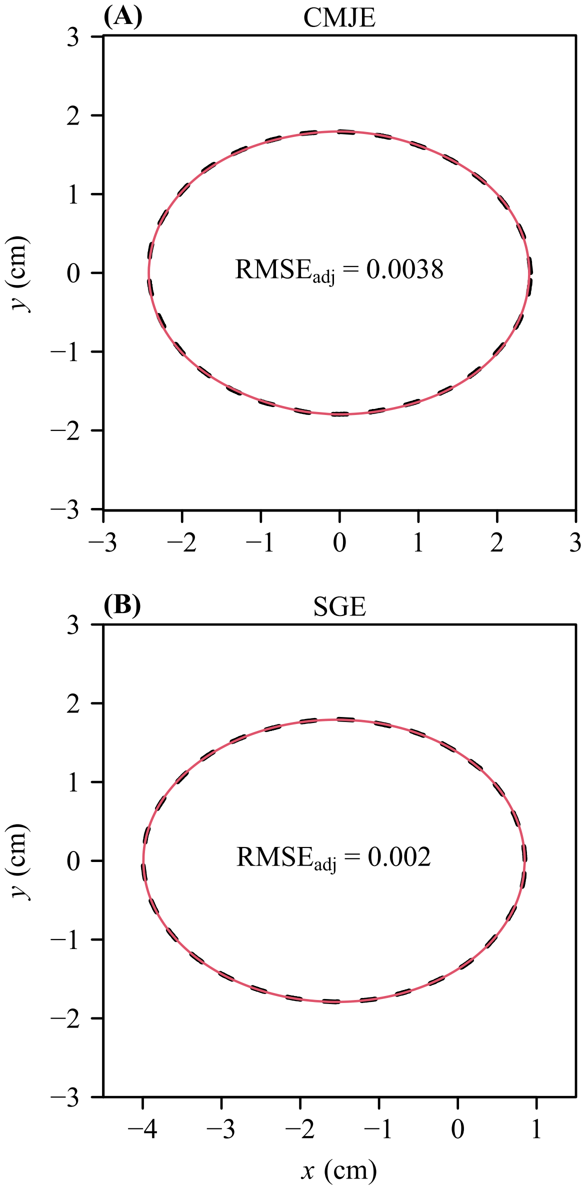

Figure 2. The observed (dashed curves in black) and predicted (solid curves in red) boundary geometries of the representative egg (see Figure 1) simulated using the 2 polar equations CMJE and SGE. $\mathrm{RMSE_{adj}}$ in each panel represents the adjusted root-mean-square error between the observed and predicted r values.

and the values of δ^T derived from SGE were also significantly higher than CMJE on a log-log scale ($W = 0$, $P < 0.001$) (Figure 4). The results indicated that CMJE had a better close-to-linear behavior compared to SGE at the global level.

When considering the nonlinear behavior at the individual parameter level, analyzing the percentage bias (P_b) of each parameter within the nonlinear models can yield valuable insights. For CMJE, all of the absolute values of P_b for parameters K_1, K_2, K_3, K_4, and K_5 were far below 1% (Supplementary Table S2); and for SGE, all of the absolute values of P_b for a, n_1, and n_2 were also far less than 1% (Supplementary Tables S3). The results revealed that the 2 tested nonlinear egg-shape models exhibited good close-to-linear behavior at the individual parameter level.

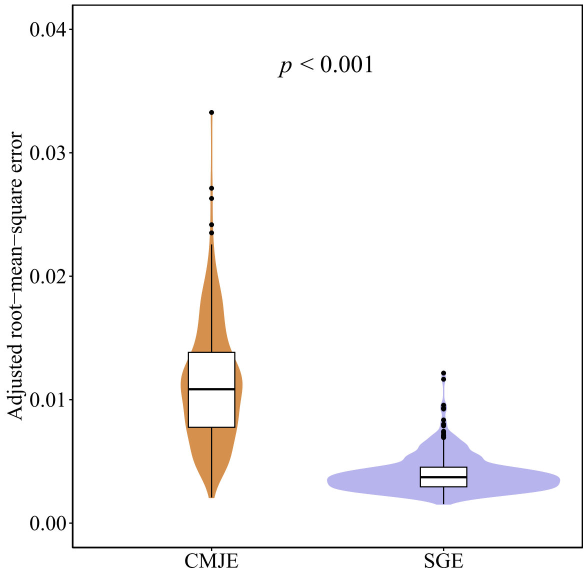

Figure 3. Violin plot showing the distribution of the adjusted root-mean-square error values calculated based on the 2 polar equations CMJE and SGE. Horizontal bars within boxes denote medians; bottoms and tops of boxes represent 25th and 75th percentiles, and lines extend to the 1.5-fold interquartile range. The letter $P < 0.001$ indicates significant difference among the 2 groups using the 2-sided Wilcoxon test at the 0.05 significance level.

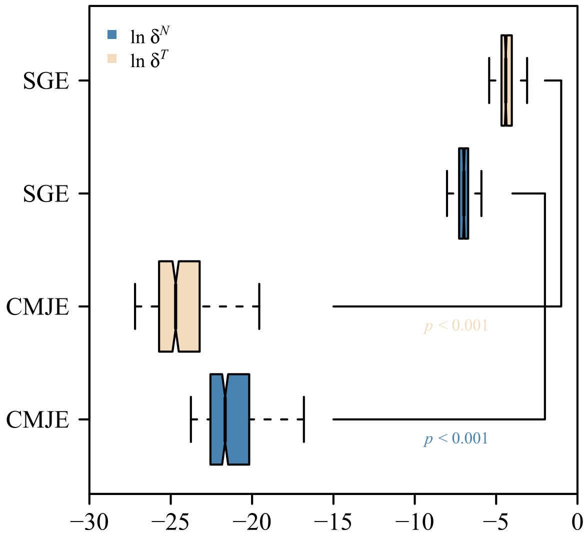

Figure 4. Boxplot of the natural logarithm of δ^N in Eq. (8) and the natural logarithm of δ^T in Eq. (9) compared between the 2 polar equations CMJE and SGE. Significant differences between the 2 polar equations using the 2-sided Wilcoxon test at 0.05 significance level were found for both δ^N and δ^T ($P < 0.001$). The vertical solid line in each box represents the median; the left and right of each box represent 25th and 75th percentiles, and whiskers extend to the 1.5-fold interquartile range.

DISCUSSION

The Application of Polar egg-Shape Equations on Egg Volume and surface Area Estimation

The notion that avian eggs possess rotational symmetry around their longest axis, i.e., the line connecting the egg's 2 ends, is widely acknowledged and supported by numerous observations. Additionally, a previous study has proved that eggs are solids of revolution (Shi et al., 2023b), thus, egg volume ($\boldsymbol{V}$) and surface area ($\boldsymbol{S}$) can be approximated through revolving the 2D egg profiles. The calculation formulae for V and S are as follows:

$$V = \frac{2}{3}\pi \int_0^{\pi} r^3(\varphi)\sin(\varphi)\, d\varphi, \tag{10}$$

and

$$S = 2\pi \int_0^{\pi} \sin(\varphi) r(\varphi) \sqrt{r^2(\varphi) + \left(\frac{dr(\varphi)}{d\varphi}\right)^2}\, d\varphi, \tag{11}$$

where r and φ are the polar radius and polar angle respectively in Eqs. (1) and (4).

In actual fact, the curve derived from CMJE is not bilaterally symmetrical about x-axis, i.e., $r(-\varphi) \neq r(\varphi)$ within Eq. (1). This lack of symmetry can lead to inaccuracies in estimating both V and S of the avian egg when using Eqs. (10) and (11) based on CMJE. Fortunately, the source of this bilateral asymmetry is solely attributed to the term of $K_5 \sin^3 2\varphi$ within Eq. (1), in other words, when the absolute value of K_5 is small, there is an approximation of $r(-\varphi) \approx r(\varphi)$. The fitted results in our study reveal that the range of values of parameter K_5 is from -0.035 to 0.051(Table S2), suggesting that the term $K_5 \sin^3 2\varphi$ exerts a minimal effect on CMJE, especially in the V and S calculations using Eqs. (10) and (11). However, we did not compare the actual and predicted values of V or S because the study did not obtain actual measurements of the volume and surface area of 415 *C. livia* eggs. As a result, the application of polar egg-shape equations for estimating V and S remained theoretical. Nevertheless, recent studies (Shi et al., 2023b; Lian et al., 2024) have provided reliable evidence supporting the hypothesis that bird eggs are solids of revolution, suggesting that the use of polar coordinate equations is promising for these estimations.

The Significance of Relative Curvature Measures of Nonlinearity for Model Comparison

In the majority of prior studies pertaining to 2D egg-shape modelling, the assessment of the model has predominantly centered on the goodness of fit (Biggins et al., 2018, 2022; Shi et al., 2022a, 2023a). Nevertheless, our findings underscore that such a focus is inadequate. Beyond the fitting for the empirical data, a robust nonlinear model should guarantee that each parameter demonstrates close-to-linear behavior, thereby ensuring that their least squares estimators are nearly unbiased, conform to a normal distribution, and embody estimators with minimal variance (Ratkowsky and Reddy, 2017). Therefore, it is imperative to scrutinize thoroughly the nonlinear behavior in the egg-shape equations.

The results of our study showed that SGE has better fits to the empirical data compared to CMJE (Figure 3). However, CMJE surpasses SGE in its ability to achieve superior close-to-linear behavior at the global level

(Figure 4). One plausible explanation could be that CMJE exhibits a closer alignment with linearity in its model structure (see Eq. [3]), specifically, CMJE functions as a linear function of parameters K_1, K_2, K_3, K_4, and K_5. On the contrary, SGE exhibits a nonlinear function of parameters a, n_1, and n_2.

It is worth noting that all of the values of root-mean-square relative intrinsic curvature (or the root-mean-square relative parameter-effects curvature) were far less than the corresponding critical curvature for the 2 polar equations scrutinized (Supplementary Tables S2 and S3, Figure 4). Moreover, the absolute values of percentage bias of the parameters for CMJE and SGE were far below 1% for all of the 415 *C. livia* eggs (Supplementary Tables S2 and S3). This outcome can be attributed in part to the utilization of approximately 2000 sample points for each egg during the fitting process, thereby enhancing the efficacy of linear approximation within nonlinear regression analysis. To ascertain the influence of sample size on the attainment of close-to-linear behavior of nonlinear models, we used the 2 polar equations to fit the geometries of 415 *C. livia* egg profiles based on varying sample sizes ranging from 50 to 2,000 (i.e., 50, 100, 200, 300, 400, 500, 750, 1,000, 1,250, 1,500, 1,750, and 2,000). The fitted results are detailed in Tables S4 and S5. We proceeded to calculate the medians of measures of nonlinearity, i.e., δ^N, δ^T, and P_b, based on the corresponding each sample size. Subsequently, all the median values were interconnected by smooth curves (Figure 5). For CMJE, both the root-mean-square relative curvatures and the absolute value of each parameter's percentage bias consistently remained small, exhibiting a notable declining pattern with the increasing of sample size (Supplementary Table S4, Figures 5A, C). For SGE, as the number of sample points increased, there was a reduction in the values of the root-mean-square relative curvatures and the absolute value of each parameter's percentage bias (Supplementary Table S5, Figures 5B, D). These findings highlight that the nonlinear behavior of CMJE and SGE demonstrates a notable correlation with changes in the number of samples. The 2 polar equations mentioned above tend to exhibit better close-to-linear behavior as the sample size increase.

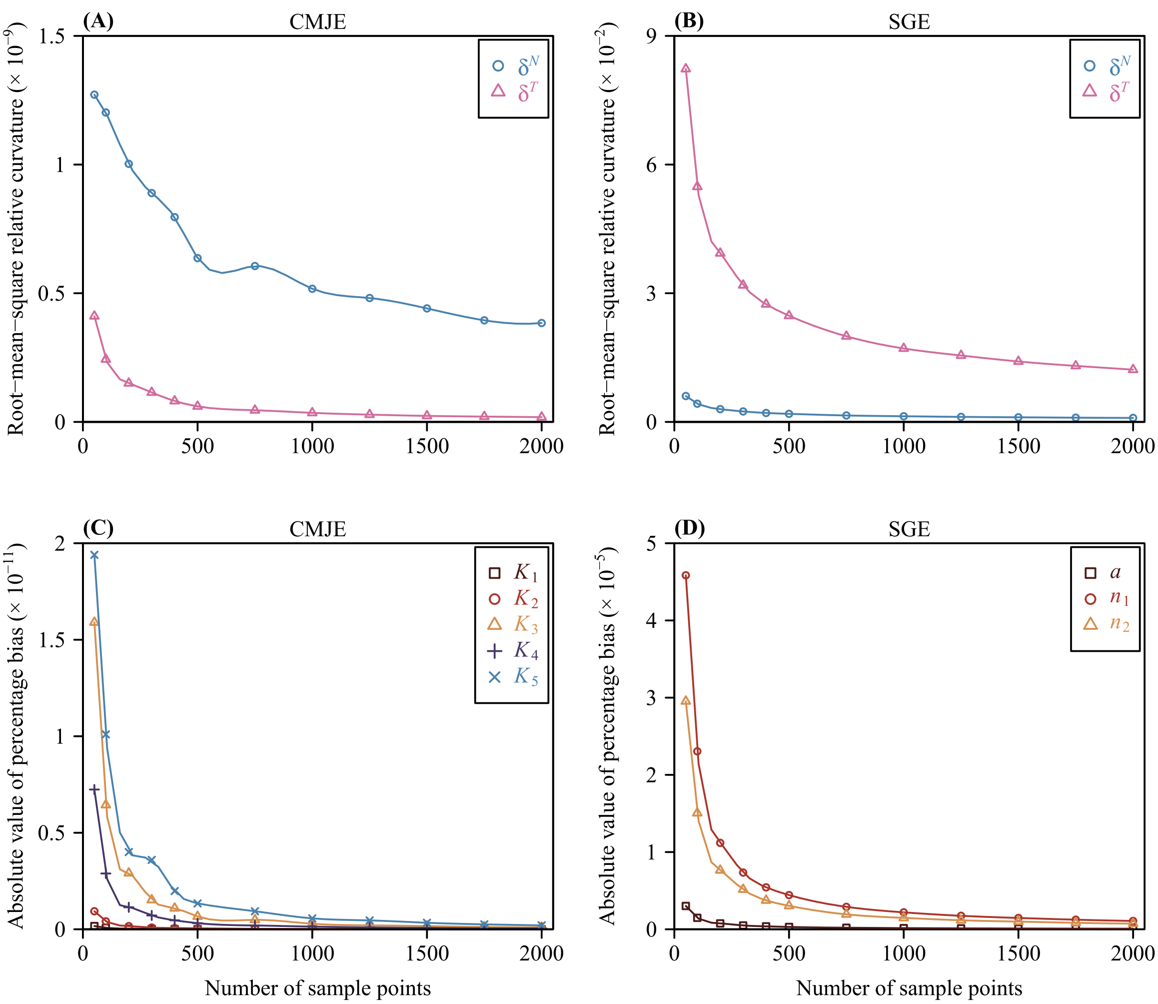

Figure 5. The relationship between close-to-linear behavior of egg-shape equations and sample size. (A) Changes manifest in both δ^N and δ^T for CMJE as the sample size increases; (B) changes manifest in both δ^N and δ^T for SGE as the sample size increases; (C) changes manifest in parameters K_1, K_2, K_3, K_4, and K_5 within CMJE as the sample size increases; and (D) changes manifest in parameters a, n_1, and n_2 within SGE as the sample size increases. Each panel displays data points corresponding to sample sizes of 50, 100, 200, 300, 400, 500, 750, 1,000, 1,250, 1,500, 1,750, and 2,000, respectively. In each panel, each data point represents the median value derived from 415 *C. livia* eggs based on the corresponding sample size.

CONCLUSIONS

In summary, 2 polar equations, i.e., CMJE and SGE, were used to fit the 2D egg-shape profiles of 415 *C. livia* eggs. Among them, CMJE exhibited poor goodness of fit for the empirical data compared to SGE. CMJE, however, had the better linear approximation performance across the pooled data at the global level. In terms of individual parameter level, each parameter within CMJE and SGE provided good close-to-linear behavior. One limitation of this study is that it involved only a single species, thus neglecting the impact of interspecific variation in egg-shape on the use of polar equations for 2D egg-shape modeling across a broad range of bird species. Consequently, further investigation is warranted to assess the applicability of polar equations to a diverse array of egg shapes. This study offers valuable insights into the criteria guiding the assessment of egg-shape models, which were used to describe the geometries of 2D egg profiles. Going beyond description, polar descriptions allow for connecting description and the solution of classic boundary value problems (e.g., Laplace and Helmholtz) with various boundary conditions via the classical Fourier projection methods (Caratelli and Ricci, 2009; Ricci and Gielis, 2022). Our results have the potential to serve as the theoretical and practical basis for a large body of additional study in the related fields of poultry science, oomorphology and applied mathematical modeling (Gielis et al., 2022).

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Data availability: The datasets for this study are accessible in the Supplementary Tables S1−S5.

DISCLOSURES

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

SUPPLEMENTARY MATERIALS

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.psj.2024.104196.

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