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A New Program to Estimate the Parameters of Preston's Equation, a General Formula for Describing the Egg Shape of Birds

Peijian Shi [1,]*, Lin Wang [1], Brady K. Quinn [2] and Johan Gielis [3]

[1] Bamboo Research Institute, College of Science, Nanjing Forestry University, Nanjing 210037, China
[2] Biological Effects Section, St. Andrews Biological Station, Fisheries and Oceans Canada, St. Andrews, NB E5B 0E4, Canada
[3] Department of Biosciences Engineering, University of Antwerp, B-2020 Antwerp, Belgium
* Correspondence: pjshi@njfu.edu.cn

Abstract: Preston's equation is a general model describing the egg shape of birds. The parameters of Preston's equation are usually estimated after re-expressing it as the Todd-Smart equation and scaling the egg's actual length to two. This method assumes that the straight line through the two points on an egg's profile separated by the maximum distance (i.e., the longest axis of an egg's profile) is the mid-line. It hypothesizes that the photographed egg's profile is perfectly bilaterally symmetrical, which seldom holds true because of photographic errors and placement errors. The existing parameter estimation method for Preston's equation considers an angle of deviation for the longest axis of an egg's profile from the mid-line, which decreases prediction errors to a certain degree. Nevertheless, this method cannot provide an accurate estimate of the coordinates of the egg's center, and it leads to sub-optimal parameter estimation. Thus, it is better to account for the possible asymmetry between the two sides of an egg's profile along its mid-line when fitting egg-shape data. In this paper, we propose a method based on the optimization algorithm (optimPE) to fit egg-shape data and better estimate the parameters of Preston's equation by automatically searching for the optimal mid-line of an egg's profile and testing its validity using profiles of 59 bird eggs spanning a wide range of existing egg shapes. We further compared this method with the existing one based on multiple linear regression (lmPE). This study demonstrated the ability of the optimPE method to estimate numerical values of the parameters of Preston's equation and provide the theoretical egg length (i.e., the distance between two ends of the mid-line of an egg's profile) and the egg's maximum breadth. This provides a valuable approach for comparing egg shapes among conspecifics or across different species, or even different classes (e.g., birds and reptiles), in future investigations.

Keywords: bilateral symmetry; bird eggs; multiple linear regression; optimization method; root-mean-square error

1. Introduction

It is widely accepted, and common experience, that eggs have rotational symmetry about their longest axis (the line joining the two ends of the egg), resulting in circular cross-sections perpendicular to that mid-line. Thus, the shape of the egg is fully determined by the two-dimensional cross-section in a plane containing its mid-line, and this cross-section will exhibit bilateral symmetry. The boundary of such a cross-section is referred to as the egg's profile. The rotational symmetry of the egg entails that all such profiles for a particular egg are essentially the same, which justifies modeling just one such profile to capture the egg's shape. The modeling of the shape of these profiles goes back at least to Preston [1], who proposed an egg-shape model and several simplified versions thereof. The shape of an egg can be modeled based on a suitable photograph of the egg, which records a two-dimensional cross-section. It is important to develop a parametric model for

quantifying egg shape, and the parameter(s) of such a model can potentially be used to compare the intra- or inter-specific variation in egg shapes, and even that between classes. Recently, Narushin et al. [2] proposed a general egg-shape equation that can describe many extant egg shapes of birds, which is referred to as the Narushin–Romanov–Griffin equation (NRGE) hereinafter, but they did not use this equation to fit actual egg-shape data. Shi et al. [3] tested the validity of the NRGE using the actual egg-shape data of nine species of birds and found that the NRGE worked well. However, they also found that a simplified version of the polar coordinate equation proposed by Gielis [4] could describe the shapes of these nine eggs well, and even attained better goodness-of-fit for most eggs.

In fact, there are many mathematical models used to describe the shapes of birds' eggs, and many investigators have claimed that their models are general (see ref. [5] and references therein). Among these general models, the equation proposed by Preston [1] might be the best because it can obtain the best goodness of fit [5,6]; this equation is expressed as:

$$y_P = a \sin \zeta$$
$$x_P = b \cos \zeta \left(1 + c_1 \sin \zeta + c_2 \sin^2 \zeta + c_3 \sin^3 \zeta\right),$$

$\hspace{10cm}$ (1)

where x_P and y_P are the abscissa and ordinate coordinates in the plane of an arbitrary point on an egg's boundary; a, b, c_1, c_2, and c_3 are constants to be estimated, among which a and b represent half the egg's length and approximately half the egg's maximum breadth, respectively; and ζ is an angle ranging from 0 to 2π. We refer to Equation (1) as Preston's equation (PE) for convenience hereinafter. There is a need to note that the mid-line of a simulated egg by the PE is aligned to the y-axis on which the egg base is uppermost and the egg tip is lowermost (Figure 1). The PE is flexible enough to produce curves representing a wide variety of egg shapes by setting different combinations of values to its parameters (Figure 1), and the x and y coordinates on the curve plotted by the PE can be known at a given value of ζ. Nevertheless, ζ is not a polar angle, and this means that $\tan \zeta \neq y_P/x_P$. To estimate the parameters of the PE, Todd and Smart [7] re-expressed the PE as:

$$y = \pm\sqrt{1 - x^2}\left(d_0 + d_1 x + d_2 x^2 + d_3 x^3\right) \hspace{2cm} (2)$$

where $x = y_P/a$ and $y = x_P/a$, and the two variables represent the abscissa and ordinate coordinates in the plane of an arbitrary point on an egg's profile scaled by $1/a$; and $d_0 = b/a$, $d_1 = c_1(b/a)$, $d_2 = c_2(b/a)$, and $d_3 = c_3(b/a)$. Because a is half the egg's length, the two endpoints of the egg's length axis in this re-expressed formula are located at $(-1, 0)$ and $(1, 0)$ in the plane, respectively. Equation (2) can be further re-written as:

$$y = d_0 z_0 + d_1 z_1 + d_2 z_2 + d_3 z_3 \hspace{2cm} (3)$$

where $z_0 = \pm\sqrt{1 - x^2}$, $z_1 = x z_0$, $z_2 = x^2 z_0$, and $z_3 = x^3 z_0$. For the image of an egg, the x_P and y_P can be obtained by digitizing the image, and the maximum distance between two points on the egg's profile is regarded as the egg's length. In this case, the numerical value of a is known, as it then equals half of the maximum distance between the two points. This then allows the variables z_0 to z_3 to be calculated. The parameters d_0 to d_3 can be estimated using a multiple linear regression procedure based on ordinary (or weighted) least-squares, with the intercept set to 0 [5,6]. We refer to Equation (3) as the Todd-Smart equation (TSE).

Biggins et al. [5] fit egg-shape data from 50 bird species with two types of egg shape (25 pyriform and 25 other) with the TSE and its simplified version corresponding to the simplified versions of Preston's Equation (6) in ref. [1], as well as the NRGE, the simplified Gielis equation, and other models, and found that the TSE had the smallest prediction error. However, when using the multiple linear regression method to estimate the parameters of the TSE, there is an implicit hypothesis that the egg is perfectly bilaterally symmetrical. The planar projection of an egg's profile (in side view) is seldom perfectly bilaterally symmetrical. This can occur because of (i) photographic errors caused by the deviation of the angle from the vertical line through an egg's center perpendicular to the horizontal mid-

line of the egg, (ii) placement errors caused by the deviation of the angle of the horizontal mid-line of the egg from the placed horizontal plane, and (iii) other errors caused by abiotic and biotic factors, e.g., an accidental physical pressure on an immature egg's surface in the oviduct and inter-individual variation in egg shape. If the camera lens is exactly focused on the center of an egg and the horizontal mid-line is exactly parallel to the placed horizontal plane, the photographed egg's profile tends to be perfectly bilaterally symmetrical without considering the influences of other factors. However, in practice, it is difficult to accurately determine where the egg's center is, and it is also difficult to render the horizontal mid-line of the egg parallel to the placed horizontal plane. In addition to the influences of other abiotic and biotic factors, the photographed egg's profile thus usually deviates from a perfectly bilaterally symmetrical geometry.
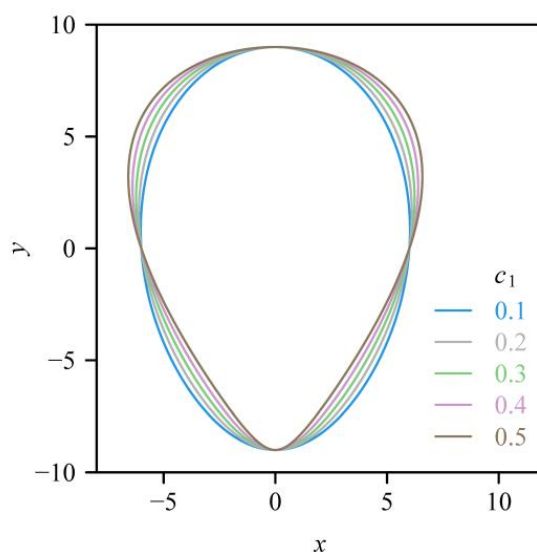
Figure 1. Egg shapes simulated using Preston's equation (PE). Here, $a = 9$, $b = 6$, $c_2 = -0.04$, $c_3 = 0.02$, and c_1 ranges from 0.1 to 0.5, in 0.1 increments. The x and y coordinates of the Preston curves are obtained when ζ ranges from 0 to 2π.

To decrease prediction errors, Biggins et al. [6] considered an angle of deviation for the mid-line from the straight line through the two points on an egg's profile separated by the maximum distance (i.e., the longest axis of an egg's profile) via setting different candidate values for the angle of deviation to minimize the residual sum of squares between the observed and predicted y values based on Equation (3). However, rotating the longest axis of the egg's profile cannot ensure that the mean of the x values and that of the y values of the egg's profile are exactly located at the center of an egg. In other words, this method cannot provide an accurate estimate on the coordinates of the egg's center, and it leads to sub-optimal parameter estimation. This means that the existing data-fitting method based on multiple linear regression does not reasonably consider the potential asymmetry between the two sides of an egg along the mid-line. Therefore, it would be better to add a parameter to quantify the deviation of the actual mid-line of an egg's profile from the x-axis to account for such possible asymmetry, as suggested by the authors of [3,8].

In this study, we developed a function based on the optimization method to directly estimate the parameters of an explicit mathematical expression of the PE and compared the goodness of fit achieved using this method with that of the multiple linear regression method using the actual shape data of 59 eggs. Considering that the optimization method can account for the differences of boundary coordinates in bilateral symmetry about the mid-line in a digitized egg's profile and automatically search for the mid-line, we expected that the optimization method would be able to obtain a better fit to the egg-shape data than the multiple linear regression method that does not reasonably determine the mid-line of an egg's profile based on the rotation of the longest axis of the egg's profile [5,6].

2. Materials and Methods

2.1. Egg Samples and Image Processing

We used the eggs of nine species of birds (including seven from [2] and an additional two from [3]) to visually exhibit the fitted results of the tested equations, given that these nine eggs comprise representatives of the existing range of egg shapes in birds. The boundary coordinates of these nine eggs have been included as a dataset named 'eggs' in the R package 'biogeom' (version 1.3.5) [9]. In addition, we used the set of 50 species' egg-shape data in [5] in our analyses; the images of these 50 eggs are available in the online repository Dryad [10]. The 50 eggs were used by Biggins et al. [5], and they selected 50 out of 965 eggs along the morphospace defined by three egg characteristics (elongation, polar asymmetry, and pointedness) (See Figure SF1 in ref. [5]). In other words, the 50 eggs can represent a wide range of morphological variations in avian egg shapes. The 50 egg-shape images were saved as black-and-white .bmp files, and their planar coordinates were extracted using Matlab (version $\geq$ 2009a; MathWorks, Natick, MA, USA) M-file developed by [11,12].

2.2. Models and Data-Fitting Approaches

The TSE (i.e., Equation (3), a re-expression of the PE) was fit to egg-shape data using the multiple linear regression procedure to estimate the parameters of this equation [5,6]. We refer to this procedure as lmPE hereinafter.

We developed a new approach based on the optimization method to directly fit data and estimate the parameters of an explicit mathematical expression of Preston's equation [13]:

$$y = \pm b \cdot \sqrt{1 - \left(\frac{x}{a}\right)^2} \cdot \left(1 + c_1\left(\frac{x}{a}\right) + c_2\left(\frac{x}{a}\right)^2 + c_3\left(\frac{x}{a}\right)^3\right), \tag{4}$$

where $x = y_P/a$ and $y = x_P/a$; and the other parameters are the same as those of Equation (1). On the right side of Equation (4), the positive sign corresponds to the upper part of an egg's profile, and the negative sign corresponds to the lower part of the egg's profile, which are divided by the mid-line. We refer to Equation (4) as the explicit Preston equation (EPE) to distinguish it from Equation (1). The y-coordinate of the midpoint of the egg's length is 0, and the x-coordinate of the midpoint of the egg's maximum breadth is 0 in the EPE. The mid-line of the egg's profile is aligned to the x-axis, which is defined as the major axis in the EPE. For the digitized egg image boundary data, the center of the egg is usually not located at the origin, and there is an angle between the mid-line and the x-axis. Therefore, we defined the coordinates of the egg's center as (x_0, y_0), and the angle between the mid-line and the x-axis as θ, which then formed the three location parameters for curve-fitting [3,8]. There are then five model parameters to be estimated for the EPE: a, b, c_1, c_2, and c_3. The Nelder–Mead optimization method [14] was used to minimize the residual sum of squares (RSS) between the observed and predicted y values on the egg's profile. We refer to this method as optimPE hereinafter.

To be able to directly compare the goodness of fit among the optimPE and lmPE methods, we calculated the root-mean-square errors (RMSEs) of the two methods. To reduce the influence of egg size on the RMSE, we took the adjusted RMSE to quantify prediction errors, which is equal to RMSE divided by half of the egg's maximum breadth, and the adjusted RMSE can represent the ratio of the mean absolute deviation (between the observed and predicted y values) to half the egg's maximum breadth. For the 50 egg-shape data sets from [5], the paired t-test was used to test whether the adjusted RMSEs significantly differed between the two methods, optimPE and lmPE. RMSEs were compared qualitatively among methods for each of the additional nine data sets from [2,3]. The additional nine eggs of nine species of birds were used for visually comparing the fitted results between the two methods without being used to carry out the paired t-test, so there was no need to use the adjusted RMSE values.

The R package 'biogeom' (version 1.3.5) [9] based on R software (version 4.2.0) [15] was used to fit data and estimate the parameters of the PE and EPE. In the 'biogeom' package (version 1.3.5) [9], the 'fitEPE' function was used to carry out optimPE, and the 'lmPE' function was used to estimate the parameters of the TSE (i.e., re-expression of the PE) based on the multiple linear regression procedure. R software (version 4.2.0) [15] was used to carry out all calculations and to draw figures.
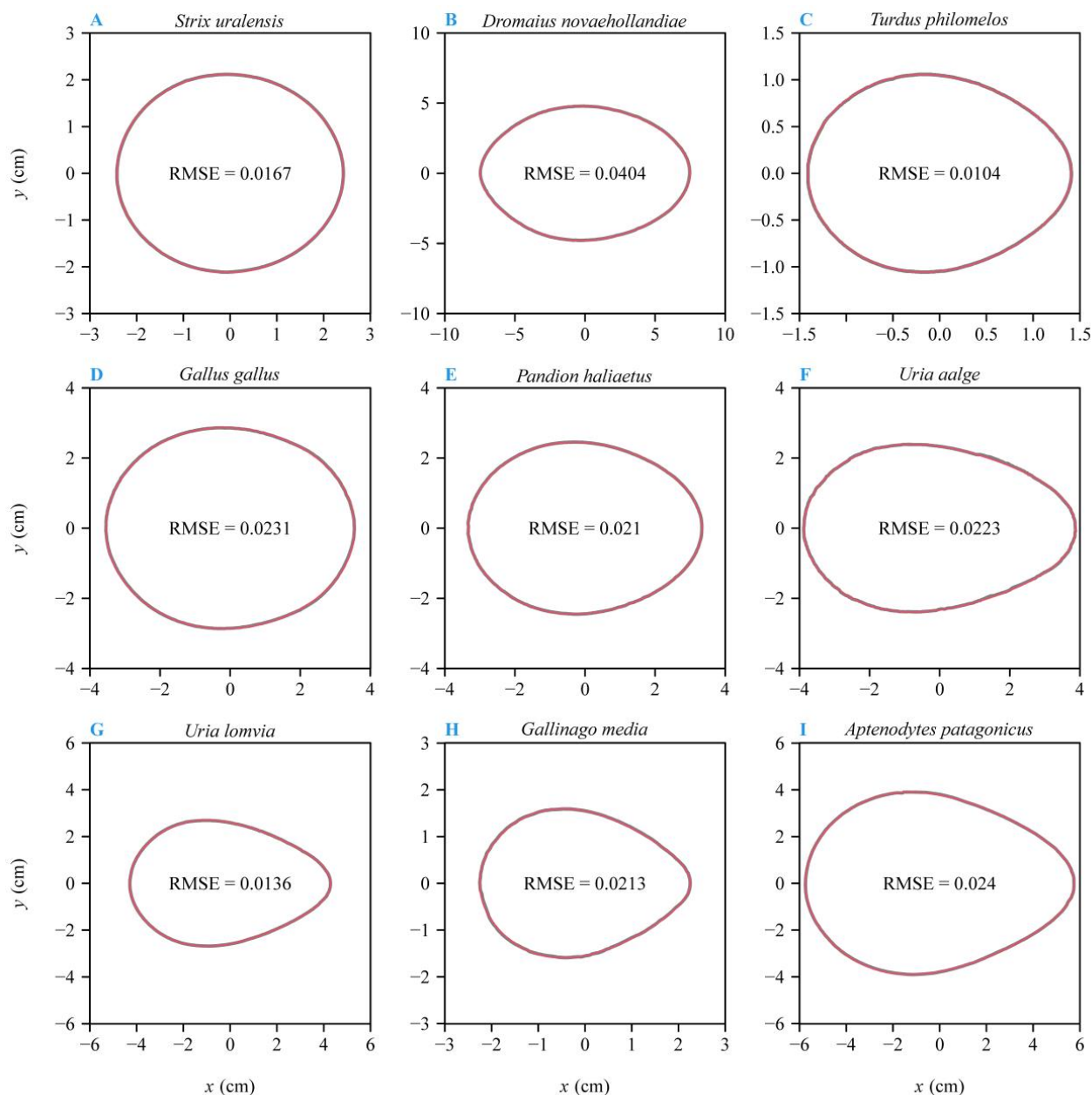
3. Results

For each of the nine species' egg boundary coordinate data sets from [2,3], the optimPE, and lmPE methods both fit the data very well (Figures 2 and 3). In comparisons between the optimPE and lmPE methods, each of the nine RMSEs for optimPE were smaller than those for lmPE, which suggests that optimPE was able to attain a better goodness of fit than lmPE.

For the 50 species' egg-shape data sets from [5], the conclusions were similar to those for the nine egg-shape data sets described above. For either pyriform or other egg shapes, optimPE obtained better goodness of fit than lmPE for each type of egg shape (Figure 4).
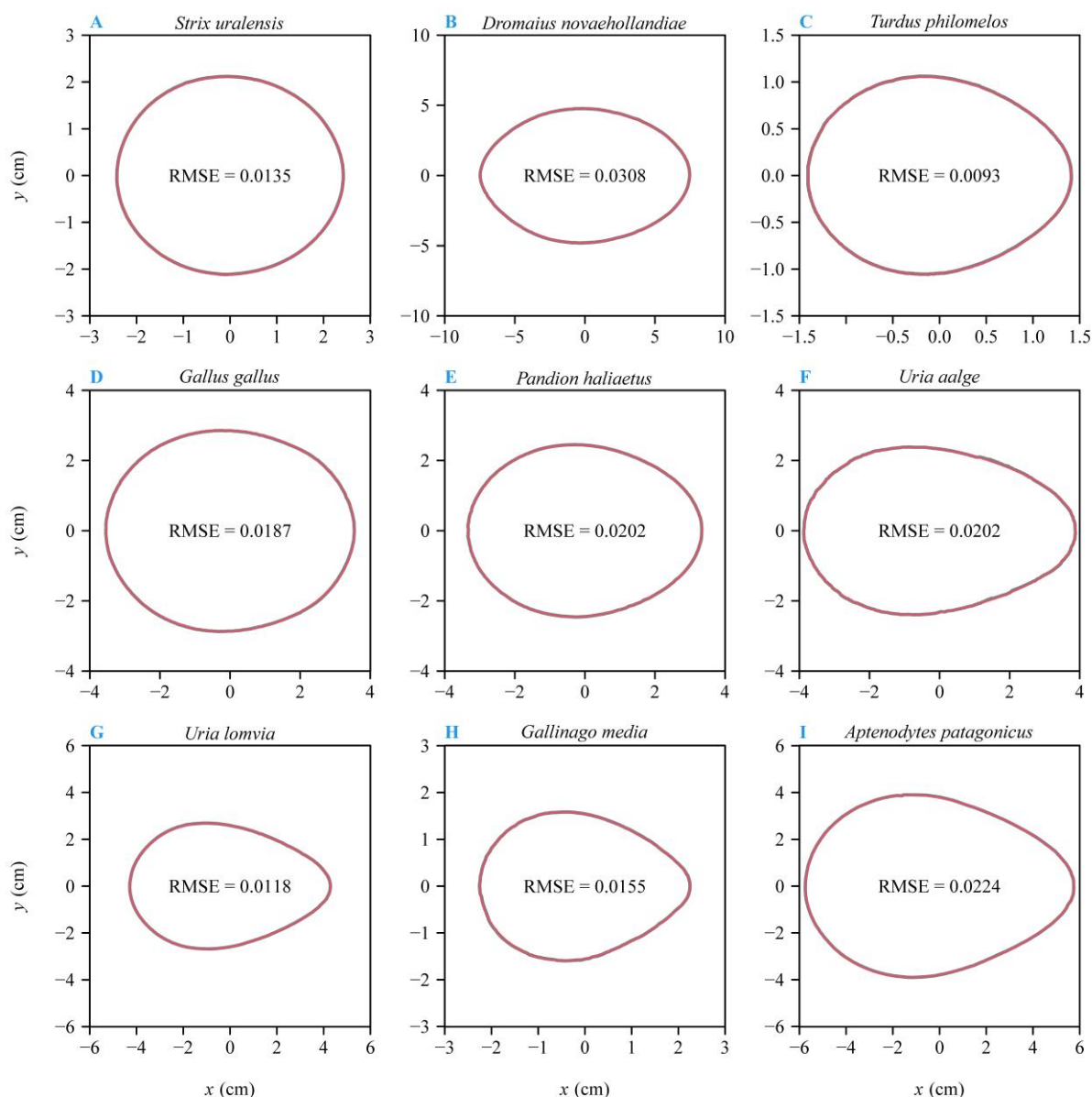

Figure 2. Results of fitting the egg boundaries of nine species of birds using the explicit Preston equation (EPE) with the Nelder–Mead optimization method (optimPE). Panels (**A**–**I**) represent the

fitted results for the nine representative species of birds. In each panel, the gray curve represents the observed egg perimeter, and the red curve represents the egg perimeter predicted by the explicit Preston equation fit using the optimization method. RMSE is the root-mean-square error between the observed and predicted y values.

Figure 3. Results of fitting the egg boundaries of nine species of birds using the Todd-Smart equation (TSE) (i.e., the re-expression of Preston's equation) with the multiple linear regression method (lmPE). Panels (**A**–**I**) represent the fitted results for the nine representative species of birds. In each panel, the gray curve represents the observed egg perimeter, and the red curve represents the egg perimeter predicted by the Todd-Smart equation (re-expressed Preston's equation) based on the multiple linear regression method. Note that the coordinates were scaled by *a* to compare the goodness of fit achieved using this method with the goodness of fit using the explicit Preston equation and the optimization method (see Figure 2). RMSE is the root-mean-square error between the observed and predicted y values.
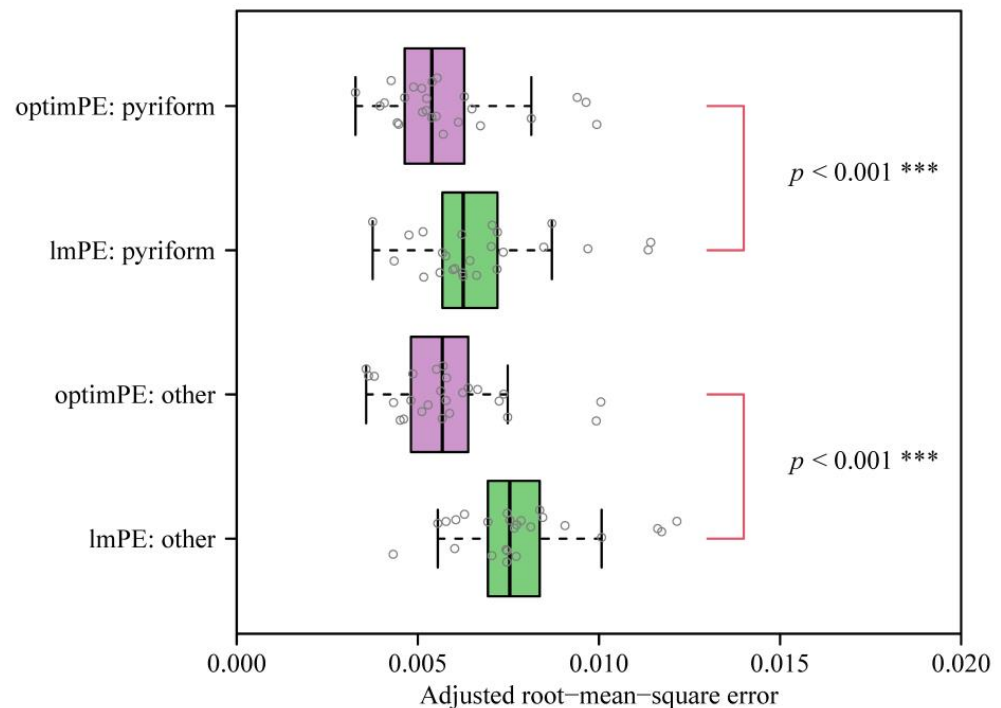
Figure 4. Boxplot of the root-mean-square errors (RMSEs, adjusted by dividing by half the egg's maximum breadth) compared between two methods (optimPE, and lmPE) for the 50 egg-shape data sets from [5]. Here, optimPE represents the explicit Preston equation fit based on the Nelder–Mead optimization method; and lmPE represents the Todd-Smart equation (i.e., the re-expression of the Preston equation) fit based on the multiple linear regression method. The 50 eggs were divided into two types: pyriform and other shapes (n = 25 each), as in [5]. Significant differences between the two methods using the paired t-test at the 0.05 significance level were found for both types of egg shape. The vertical solid line in each box represents the median; the whiskers extend to the most extreme data point, which is no more than 1.5 times the interquartile range from the box. The three asterisks represent $p < 0.001$.

4. Discussion

4.1. The Optimization Versus Multiple Linear Regression Method for Estimating Parameters of Preston's Equation

Although parameter estimation for the EPE based on the optimization method (optimPE) can obtain a lower RMSE than that for the TSE based on the multiple linear regression method (lmPE), the two methods both have their strengths and drawbacks. A disadvantage of using optimPE is that suitable initial values for parameters need to be provided; otherwise, it will be fairly time-consuming to obtain the globally optimized solutions for the target parameters using this method. The optimPE method has two main advantages: (i) it can account for the lack of symmetry between the two sides of an egg's profile (as extracted from its scanned or photographed images) along the mid-line; and (ii) it can directly provide the egg's length and maximum breadth values via the optimization method rather than the method used by [5,6]. In contrast, lmPE largely ignores the deviation from bilateral symmetry between the two sides of an egg caused by the photographic and placement errors. However, it does not need initial values for parameter estimation. Based on ordinary (or weighted) least-squares, the parameters can be quickly estimated using lmPE, and the corresponding standard deviation, confidence interval, and significance for each parameter can also be determined. Relative to the nonlinear least-squares method, that using linear least-squares is highly effective for parameter estimation, especially in terms of shortening the running time of calculations. In addition, the estimated values of parameters of Preston's equation by lmPE can be used as the initial values for the parameters when subsequently using optimPE (see the relationships of the parameters in the TSE and PE

listed below Equation (2)). This means that we can combine the advantages of optimPE and lmPE when estimating the parameters of Preston's equation. However, to obtain a higher prediction accuracy, we recommend using the parameters estimated by lmPE to calculate the initial values of the parameters in the EPE (i.e., Equation (4)) for carrying out an optimization algorithm. Even when using lmPE, the following method is recommended: to consider an angle of deviation for the mid-line from the longest axis of an egg's profile (whose length is scaled to two), which can be obtained by minimizing the residual sum of squares between the observed and predicted y values for the scaled egg's profile among different candidate values [6]. Relative to the maximum distance method, this method can largely reduce prediction errors for the egg images, even without them being photographed well. For each of the 59 studied eggs, the goodness of fit achieved using the longest axis rotation method was better than that obtained using the maximum distance method. The reason for this is simply that, if using the former method cannot obtain a better goodness of fit relative to using the latter method, then the prediction errors of using the two methods are at least the same, which corresponds to the case in which the rotation angle equals 0 for the former method.

4.2. The Potential Extension of Preston's Equation to Other Egg Shapes

The shape of reptile eggs is similar to that of birds [16,17], and they are both approximately bilaterally symmetrical. Thus, we are confident that PE can also be applied to modeling the egg shape of reptiles. However, the egg shape of arthropods, including insects and crustaceans, has greater variation. For instance, many insect eggs are not bilaterally symmetrical [18]. Introducing a deformation function to the EPE provides a promising avenue to potentially extend the EPE to use in representing other egg shapes, e.g., of arthropods. Figure 5 shows an example of transforming a perfectly bilaterally symmetrical egg to a deformed egg using a parabolic deformation function. The lmPE method cannot be extended to a deformed egg shape because this method implicitly assumes that an egg has perfect bilateral symmetry. However, optimPE can be further modified to apply to a deformed egg shape by introducing a deformation function. It is feasible, at least in theory, that the additional parameters in the deformation function can also be estimated by the optimization method. For example, Huang et al. [19] introduced a linear deformation function to the superellipse equation to describe the shape of the culm cross-section of a species of square bamboo. The application of such methods to deformed egg shapes thus merits further investigation.
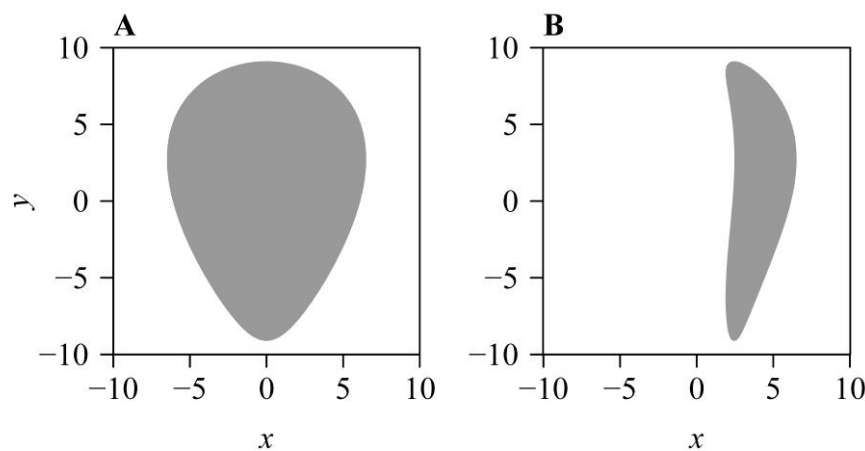
Figure 5. An insect egg shape simulated using the explicit Preston equation and its deformed shapes generated with the parabolic deformation function. In panel (**A**), the parameters in the explicit Preston equation are $\theta = \pi/2$, $a = 9$, $b = 6$, $c_1 = 0.4$, $c_2 = -0.04$, and $c_3 = 0$. In panel (**B**), the parameters are the same as those in panel (A), but there is an additional parabolic deformation function as follows: $x' = x + 0.05(7 - x)^2$, and $y' = y$, where x' and y' are the coordinates of the deformed egg shape.

4.3. Recommendations for Field Biologists

There are some special requirements for photographing eggs. To obtain clear egg images, an investigator should use a digital camera with a resolution ≥ 6 megapixels or a smartphone with a shooting function, and take photos of eggs alongside a ruler or an irregular geometrical object (e.g., a square) whose actual size is known. It is better to have a higher resolution digital camera or smartphone if an egg's color makes it difficult to distinguish it from its nest. While photographing an egg, we recommend using a mount for holding the camera or smartphone to render the lens to (approximately) pass the vertical line through the egg's center (see Figure 1 published in ref. [20]). In our recent study, we also used an adjustable tabletop phone mount to hold the smartphone to take photos of 2221 eggs of six species of poultry [13], which helped us to use a constant scale to calculate the actual eggs' sizes. It is important to focus the camera lens on an egg's center, which can be roughly determined as the midpoint of the mid-line. Before placing the egg for imaging, one needs to prepare a concave base to support it, such as a test tube rack or a small beaker, to make the mid-line of the egg as parallel to the horizontal desktop as possible. In addition, it is better to use appropriate lens distortion correction software. However, the same camera (or the same smartphone) and lens distortion correction software need to be used consistently in the same experiment to reduce the potential influences of differences in these methodologies on the profiles of eggs. In general, the surface of a ruler needs to be rendered to show the scales to be aligned to the mid-line of an egg. Nevertheless, it is inconvenient to adjust the height of the ruler's surface while photographing a large number of eggs. The intraspecific difference in egg size tends to be smaller than the interspecific difference in egg size, so the ruler's surface does not need to be moved. To correct the measurement error caused by the inappropriate placement of the ruler around the egg being photographed, one should measure the actual value of the egg's maximum length and scale the egg size when the egg's maximum length extracted from the photo seriously deviates from its actual value.

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