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Reference:
Shi Peijian, Gielis Johan, Niklas Karl J..- Comparison of a universal (but complex) model for avian egg shape with a simpler model
Annals of the New York Academy of Sciences / New York Academy of Sciences - ISSN 1749-6632 - 1514:1(2022), p. 34-42
Full text (Publisher's DOI): https://doi.org/10.1111/NYAS.14799
To cite this reference: https://hdl.handle.net/10067/1884700151162165141

ANNALS of THE NEW YORK ACADEMY OF SCIENCES

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Journal:	*Ann NY Acad Sci*
Manuscript ID	annals--115
Manuscript Type:	Commentary
Date Submitted by the Author:	24-Feb-2022
Complete List of Authors:	Shi, Peijian; Nanjing Forestry University, Bamboo Research Institute, College of Science, GIELIS, Johan; University of Antwerp, Biosciences Engineering Niklas, Karl J.; Cornell University, School of Integrative Plant Science
Keywords:	goodness-of-fit, model structure, Narushin- Romanov-Griffin equation, simplified Gielis equation, symmetry

Comparison of a recently published universal model for avian egg shape with a simpler model

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Short title: Comparison of two egg shape models

Keywords: goodness-of-fit; model structure; Narushin- Romanov-Griffin equation, simplified Gielis equation; symmetry; universality

Abstract

Recently a universal model, called NRGE, was proposed to describe the shape of avian eggs. It can simulate the shape of spherical, ellipsoidal, ovoidal, and pyriform eggs. However, the predictions of NRGE were not tested against actual data. Here, we tested the validity of NRGE by fitting actual data of egg shapes, and compared it with the predictions of a simpler model for egg shape (denoted as SGE). The eggs of nine bird species were sampled for this purpose. NRGE was found to fit the empirical data of egg shape well, but it did not define the egg length axis (i.e., symmetric axis) which significantly affected the prediction accuracy. The egg length axis in NRGE is defined as the maximum distance between two points on the scanned perimeter of the egg's shape. In contrast, SGE fitted the empirical data better, and had a smaller root-mean-square error than NRGE for each of the nine eggs. Based on its mathematical simplicity and goodness of fit, SGE appears to be a reliable and useful model for egg shape.

Introduction

Bird eggs manifest excellent axial symmetry, i.e., their shapes are perfectly symmetric along a well-defined length axis. Yet, avian eggs are asymmetric along their maximum width axis, which has attracted the attention of many scientists interested in modelling natural shape.[1-3] For example, Stoddard et al.[1] proposed two biologically relevant parameters, asymmetry and ellipticity, to quantify diverse egg shapes. The concept of asymmetry is a relative measure for the extent of the deviation from a circle or an ellipse in one direction since all eggs share bilateral symmetry in their top-down cross-section. In a recent publication,[2] a universal equation (denoted henceforth as **NRGE)** for simulating different shapes of eggs was proposed by Narushin, Romanov and Griffin who substantially extended Hügelschäffer's formula to render their new equation to describe the shape of pyriform eggs:

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

where x and y represent the abscissa and ordinate of the egg shape in the Euclidean coordinate system, L represents the egg's length, B represents the egg's maximum width, w is $(L–W) / 2k$, where k is a positive number to be estimated, and $D_{L/4}$ is the egg's diameter at the distance of $L/4$ from the tip of the egg.

Narushin *et al.*[2] simulated different egg shapes by adjusting the numerical value of parameter w, and compared the simulations with seven actual egg shapes. In this important and seminal work, NRGE is transformed to deal with the basic ovoid forms (i.e., spherical, ellipsoidal, and Hügelschäffer's ovoid), which can be deemed as a 'mathematical evolution' from the simplest shape (i.e., sphere) to the most complex (i.e., Hügelschäffer's ovoid). However, they did not provide the results of fitting the empirical data of egg shape. They only demonstrated the feasibility of NRGE in depicting the diversity of egg shape by simulation. Thus, there is a need to test whether NRGE can effectively approximate actual egg shapes and to evaluate the goodness-of-fit. In addition, although Eq. (1) is described as being 'universal' in simulating the shape of avian eggs, its applied scope is limited to a certain class of shapes.

It is also necessary to consider alternative equations for the purpose of simulating egg shape, as for example the equation proposed by Johan Gielis,[4] which describes many organic shapes especially symmetric ones:

$$r(\varphi) = a\left(\left|\cos\left(\frac{m}{4}\varphi\right)\right|^{n_2} + k\left|\sin\left(\frac{m}{4}\varphi\right)\right|^{n_3}\right)^{-1/n_1}, \tag{2}$$

where r is the polar radius at the polar angle φ, where a, k, n_1, n_2 and n_3 are parameters to be estimated, and m is a positive integer, which determines the number of angles of the curve generated by Eq. (2) within $[0, 2\pi]$. This is a generalization of the Pythagorean Theorem and of the superellipse equation.[4] When $n_2 = n_3$, Eq. (2) produces bilaterally symmetric shapes, and when $n_2 = n_3$, $k = 1$ and $m > 1$, Eq. (2) produces radial symmetric shapes. Many classical geometries such as circles, ellipses, squares, rectangles, diamonds, triangles, and pentagrams can be generated by Eq. (2). The simplified Gielis equation has been used to successfully fit the empirical outline data of bamboo leaves, sea stars, seeds, and tree rings.[5-9]

Prior work on a variety of organic shapes (e.g., the seeds of *Ginkgo biloba*, the Maidenhair tree)[9] indicates that Eq. (2) can be simplified further when dealing with objects manifesting near perfect bilateral symmetry (e.g., $m = 1$), i.e.,

$$r(\varphi) = a\left(\left|\cos(\varphi/4)\right|^{n_2} + \left|\sin(\varphi/4)\right|^{n_2}\right)^{-1/n_1}, \tag{3}$$

which has only three parameters, a, n_1, and n_2. Note that 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. Eq. (3) is denoted as SGE (simplified Gielis equation) hereafter.

Here, we compare the ability of NRGE and SGE to fit the empirical data of the egg shapes of nine species of birds spanning the full range of egg shapes to determine which of these two models is more successful at fitting the empirical data.

Data Acquisition and Parameter Estimation

We used the shapes of seven eggs appearing in Ref. 2, and added two additional egg shapes (see Fig. 1 for details). The protocols proposed by Su *et al.*[10] were subsequently used to extract the planar coordinates of these shapes to obtain 2000–3000 data points for each the perimeter of the egg's shape.

Because the planar coordinates of the scanned images usually deviated from those generated by SGE (Fig. 2), three additional location parameters were introduced, i.e., x_0, y_0, and θ,[5-9] where (x_0, y_0) represents the coordinates of the polar point of SGE in the Euclidean coordinate system, and θ represents the angle between the scanned egg length axis (i.e., the major axis) and the x-axis. The value of θ was defined as a positve number when the major axis rotated counterclockwise from the x-axis, and it was defined as a negative number when the major axis rotated clockwise from the x-axis. To estimate the parameters of SGE, we minimized the residual sum of squares between the actual distances from the polar point to the data points on the scanned the perimeter of the egg's shape and the distances from the polar point to the data points on the predicted perimeter of the egg's shape using the Nelder-Mead optimization method.[11]

Due to the complexity of the mathematical structure of NRGE, the Nelder-Mead optimization method failed to estimate the parameters. Because three out of four parameters of NRGE have clear biological and geometric meanings (i.e., L, B and $D_{L/4}$), their values could be estimated by means of numerical calculation. After obtaining the numerical values of the three parameters, the optimization method was used to estimate w. Because of the failure of using the optimization method to estimate the major axis and model parameters of NRGE, it was difficult to define the egg length axis, although it is essential for calculating L, B and $D_{L/4}$. For this reason, two methods were used to obtain the major axis: the maximum distance method, and the SGE major axis approximation method. In the first method, the straight line through two points forming the maximum distance on the perimeter of the egg's shape is defined as the major axis. In the second method, the major axis predicted by SGE was directly used as the major axis of NRGE, because SGE balances the goodness-of-fit of the model and the bilateral symmetry of the curve. Because the direction from the egg base to the egg tip predicted by SGE is the reverse of that predicted by NRGE, the angle between the major axis of NRGE and the x-axis is equal to the sum of the estimated θ of SGE and π.

Once the major axis is established, the distance of the major axis can be calculated as the estimate of L. Using the maximum distance method, L equals the maximum distance. Using the SGE major axis approximation method, L may be slightly smaller than the true distance. After rotating the major axis to make it overlap with the x-axis, a large number of equidistant rectangles can be used[12] (e.g., 2000) from the egg base to egg tip to intersect the perimeter of the egg's shape. This methodology makes it easy to obtain the maximum egg width (i.e., B) and $D_{L/4}$. The residual sum of squares (RSS) between the observed and predicted y values can be minimized using the optimization method to estimate w. Despite the complex structure of NRGE [see Eq. (1)], the optimization method for estimating the remaining parameter w becomes feasible after the other three parameters were numerically estimated.

The root-mean-square error (RMSE) between the observed and predicted ordinate coordinates, y_i and $\hat{y}_i$, respectively, was used to determine the goodness-of-fit of any of the two models:

$$\mathrm{RMSE} = \sqrt{\sum_{i=1}^{N}(y_i - \hat{y}_i)^2/N}, \tag{4}$$

where the subscript i represent the ith data point on the egg's edge, and N represents the number of data points on the egg's edge. As a rule of thumb, a ≤ 0.05 RMSE indicates a satisfying goodness-of-fit of a model, thereby validating a model's ability to fit the data. We compared NRGE with SGE based on their RMSE values. If SGE has a smaller RMSE, it can be concluded that SGE is superior in its goodness-of-fit and its model simplicity.

The software R (version 4.1.2)[13] was used to carry out all calculations and data fitting.

Results and Discussion

Analyses indicated that the RMSE values obtained using SGE are smaller than 0.05 for each of the nine egg shapes investigated (Fig. 3 and Table S1 in online supplementary material). There are two methods to define the major axis of NRGE (i.e., the maximum distance method and the SGE major axis approximation method) that can be used to numerically calculate the model's parameters. The RMSE of NRGE based on the first method was higher than the RMSE of NRGE based on the second method (Figs. 4 and 5; Tables S2 and S3). Therefore, the SGE major axis approximate method is better to find the major axis of the egg shape generated by NRGE, which can improve the goodness-of-fit. However, the two methods are only for the use of NRGE. The RMSE values of the two methods for NRGE were both higher than the RMSE values obtained using SGE for each of the nine egg shapes (Tables S2 and S3 vs. Table S1). The maximum distance method obtained a large prediction error for the egg of *Uria aalge* (i.e., RMSE = 0.1821), whereas RMSE = 0.0335 using the SGE major axis approximation method. These results support the validity of NRGE in light of empirical data for egg shape once the major axis was properly identified. However, as can be seen, the selection of the major axis relies on the predictions of SGE. It should be noted that we were unable to directly find the optimal major axis of NRGE based on the optimization method due to the complexity of model's structure. To directly use the straight line associated with the maximum distance between two points on an egg-edge was infeasible for several egg shapes. In addition, we found that the estimates of parameter *w* in NRGE obtained negative numbers for several eggs (see Tables S2 and S3), which was inconsistent with how *w* was originally defined in NRGE (i.e., *k* is considered to be a positive number to be estimated).[2]

The NRGE has revealed a mathematical 'evolution' from the simplest shape (i.e., sphere) to the most complex (i.e., Hügelschäffer's ovoid), and the predicted curves exhibited a good axi-symmetry and covered the ovoid geometries of interest. Given the morphological similarity between reptilian eggs and bird eggs, NRGE also applies to both types, and it is likely applicable for describing the shape of some insect eggs. However, although SGE has fewer parameters, its goodness-of-fit is better than that of NRGE. In general, the fewer the number of parameters, the more concise a model and the greater the 'close-to-linear' behavior in the relevant nonlinear regression, i.e., the greater the convergence in the parameter space using fewer data points.[14-16] In our study, Akaike information criteria or Bayesian information criteria (which consider the trade-off between the goodness-of-fit and the complexity of model's structure[17]) were not used to compare SGE with NRGE, because the mathematical simplicity of SGE with fewer parameters clearly obtains smaller RMSE values than NRGE. Overall, from the viewpoint of the conciseness of model structure and goodness-of-fit, SGE offers advantages over NRGE. It is also necessary to point out that the purported universality of NRGE is constrained regarding its range of egg geometries. By relaxing the limitation for m = 1 in Eq. (3), the four-parameter SGE with the same number of parameters as NRGE can describe a broader range of geometries including triangles, rectangles, pentagrams, and others, i.e., the 'universality' of SGE is greater than that of NRGE.

It is useful to point out that it is not feasible to use a one-parameter model to adequately describe the shape of eggs. Indeed, a two-parameter SGE was required to describe the shape of bamboo leaves, i.e.,[5,6,18]

$$r(\varphi) = a\left(\left|\cos(\varphi/4)\right| + \left|\sin(\varphi/4)\right|\right)^{-1/n_1}, \tag{5}$$

where the parameters a and n_1 were empirically found to represent leaf length and width, which implies that Eq. (5) can be considered as a function of leaf length and width.[10, 18] Although Eq. (5) was shown to be valid for fitting the empirical data of bamboo leaves,[5,6,18] it cannot be extended to other ovate or lanceolate leaf shapes.[18] We explored the use of Eq. (5) to fit the actual data of the egg shapes shown in Fig. 1, but failed to confirm its universality across all of the nine egg shapes (results not shown because of the space limitations). However, a two-parameter SGE can reflect a limited spectrum of egg shapes by setting n_2 to be a constant (as done in Eq. [5]) whose numerical value relies on the morphological characteristics of the class of egg shapes of interest. However, it is clear that such a two-parameter SGE cannot serve as a universal formula for egg shape. In fact, the length and width of a planar projection of a biological object with a certain intra-variation in morphology can estimate the area of the projection, by multiplying the product of length and width with a parameter to be estimated.[19, 20] This suggests to us that the parameter can be potentially regarded as an index to quantify shape by checking the extent of deviation from a rectangle or an ellipse.[21] However, this parameter does not reflect the extent of symmetry for the shape of interest.[1] Therefore, any viable 'universal' model for egg shape must consider the extent of the deviation from a given geometry (e.g., an ellipse) and that of symmetry or asymmetry. In that case, a truly universal model for egg shape requires three or more parameters.

Conclusion

The validity of the Narushin-Romanov-Griffin equation (NRGE) with four parameters was confirmed for fitting the empirical data of nine species of bird eggs representing the full spectrum of avian egg shapes. However, the prediction accuracy of NRGE depends on whether the major axis (i.e., the egg length axis) can be correctly determined. Because of the complexity of the NRGE model, the parameters of NRGE cannot be directly estimated using optimization methods. A simplified Gielis equation with three parameters (SGE) was proposed to describe the shape of avian eggs, and its validity was confirmed. Specifically, the goodness-of-fit of SGE is greater than that of NRGE for each of the nine egg shapes. Given the conciseness of SGE model and its lower root-mean-square errors relative to NRGE, SGE is advocated as a better 'universal' model for egg shape. In addition, if we add an additional parameter *m* in SGE, it can generate a broader spectrum of geometries than NRGE. After using the predicted major axis by SGE, the prediction error of NRGE was greatly decreased relative to that using the straight line identified by the maximum distance between two points on the perimeter of the egg's shape as the major axis. The future application of NRGE would benefit by using SGE to predict the major axis. Although NRGE and SGE both provide feasible tools for describing and fitting the actual shape of avian (and non-avian) eggs, SGE is more concise and more flexible in its curve-fitting capacity.

Author contributions

P.S. and J.G. were both involved in conceptualization, formal analysis, investigation, methodology, and writing. J.G. was also involved in supervision. K.J.N. was involved in formal analysis, investigation, and editing.

Acknowledgements

We thank Valerity G. Narushin for his valuable discussion on the main results of this work, and Yirong Li for her helpful image processing work. We also thank Dr. Douglas Braaten for encouraging us to submit this work for publication.

Supporting information

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

Table S1. Fitted results using the simplified Gielis equation (SGE) to the nine eggs

Table S2. Fitted results using the Narushi-Romanov-Griffin equation (NRGE) based on the maximum distance method to the nine eggs

Table S3. Fitted results using the Narushi-Romanov-Griffin equation (NRGE) based on the SGE major axis approximation method to the nine eggs

Competing interests

The authors declare no competing interests.

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Figure legends

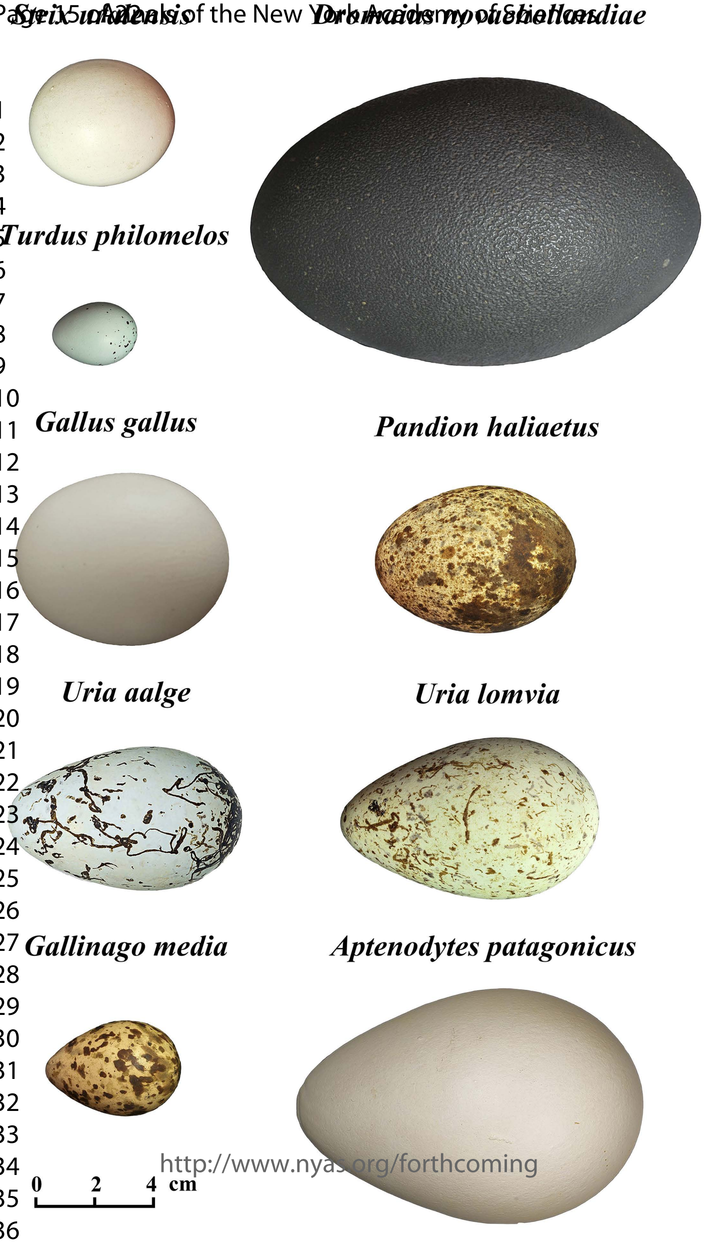
Figure 1. Nine eggs used to assess modeling capability. The egg of *Gallus gullus* was photographed by Peijian Shi; a common murre egg came from the website (https://www.penbaypilot.com/article/kristen-lindquist-everyday-miracle-bird-egg/117278); the others came from the websites reported in Ref. 2. The actual size of each was calculated using the scale in the corresponding original image.

Figure 2. Comparison between the coordinates of a scanned egg shape with those of the egg shape generated by the simplified Gielis equation. The polar coordinates of the scanned egg shape are (–1, 1) and $\theta = -\pi/4$. The major axis (red straight line) of the scanned egg shape can be considered as a result of a straight line on the *x*-axis rotating clockwise $\pi/4$.

Figure 3. Comparison between the scanned egg shape and that predicted by the simplified Gielis equation (SGE) with three parameters to the nine egg examples. RMSE represents the root-mean-square error; the gray curve is the scanned egg shape (i.e., actual egg's shape); the red curve is the predicted egg shape by the model.

Figure 4. Comparison between the scanned egg shape and that predicted by the Narushi-Romanov-Griffin equation (NRGE) with four parameters, based on the maximum distance method, to the nine egg examples. RMSE represents the root-mean-square error; the gray curve is the scanned egg shape (i.e., actual egg shape); the red curve is the predicted egg shape by the model.

Figure 5. Comparison between the scanned egg shape and that predicted by the Narushi-Romanov-Griffin equation (NRGE) with four parameters, based on the SGE major axis approximation method, to the nine egg examples. RMSE represents the root-mean-square error; the gray curve is the scanned egg shape (i.e., actual egg shape); the red curve is the predicted egg shape by the model.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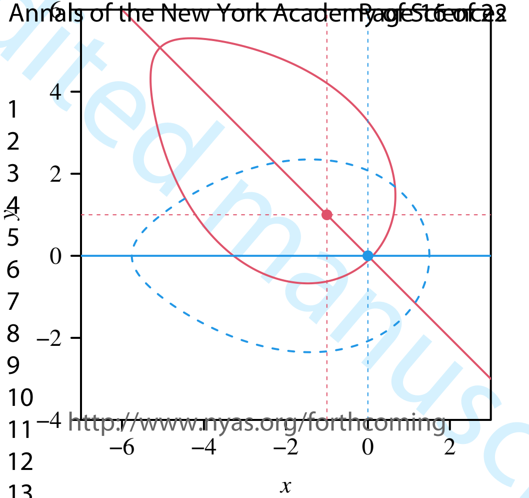
Dromaius novaehollandiae
Turdus philomelos
Gallus gallus
Pandion haliaetus
Uria aalge
Uria lomvia
Gallinago media
Aptenodytes patagonicus
0 2 4 cm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−6
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x
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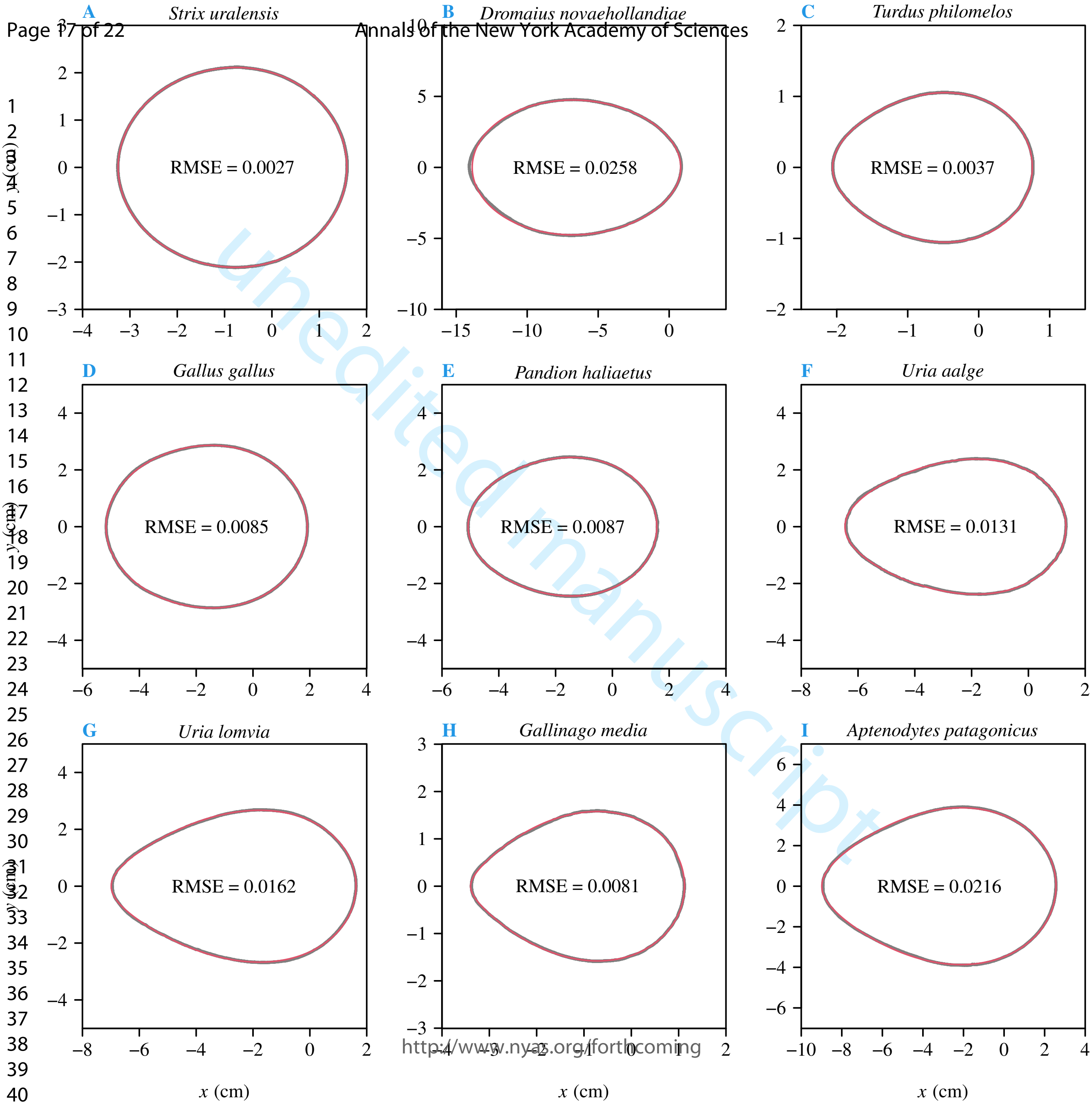
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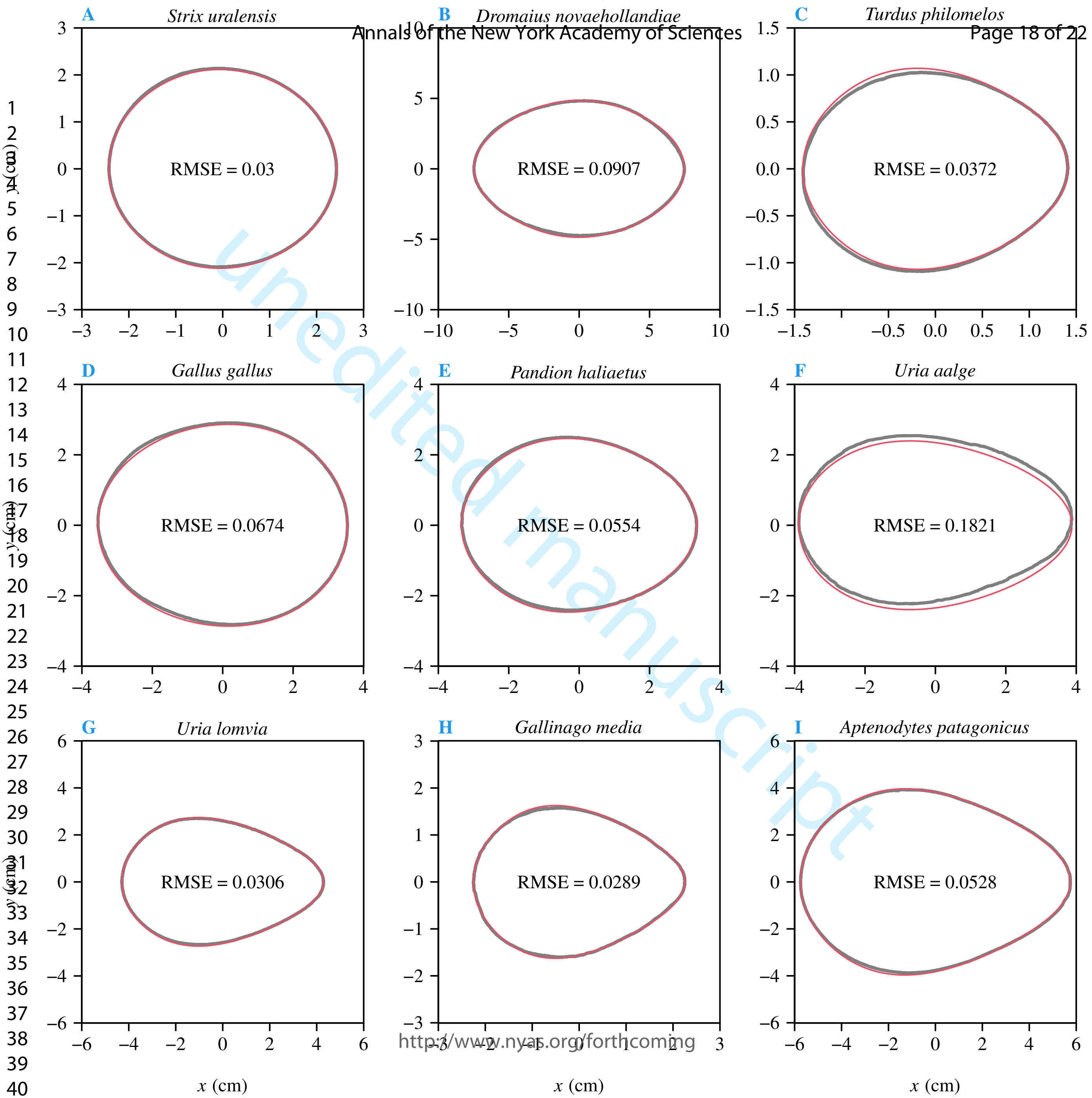
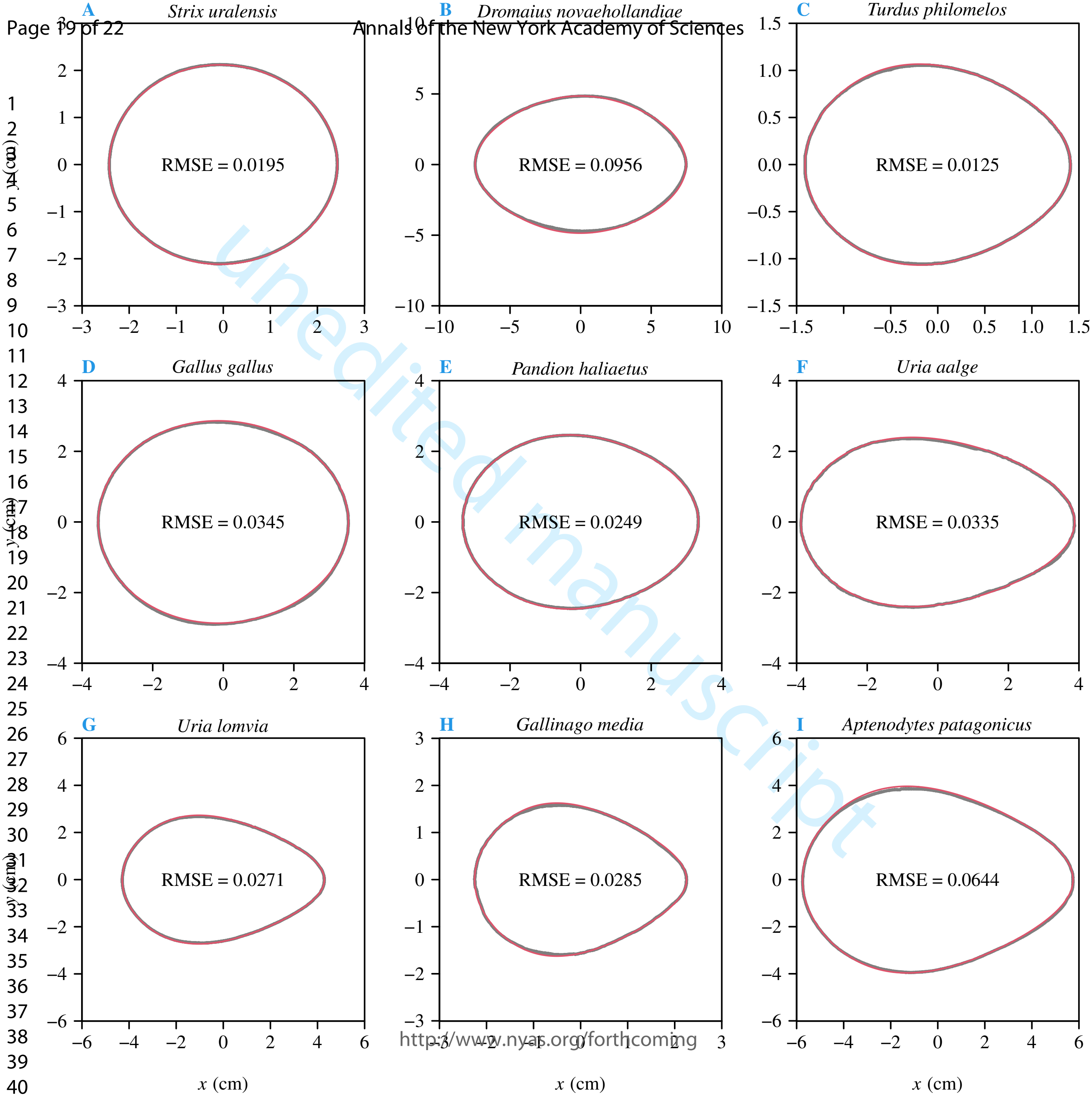
RMSE = 0.0027
B
Dromaius novaehollandiae
RMSE = 0.0258
C
Turdus philomelos
RMSE = 0.0037
D
Gallus gallus
RMSE = 0.0085
E
Pandion haliaetus
RMSE = 0.0087
F
Uria aalge
RMSE = 0.0131
G
Uria lomvia
RMSE = 0.0162
H
Gallinago media
RMSE = 0.0081
I
Aptenodytes patagonicus
RMSE = 0.0216
y (cm)
x (cm)


A Strix uralensis
RMSE = 0.03
B Dromaius novaehollandiae
RMSE = 0.0907
C Turdus philomelos
RMSE = 0.0372
D Gallus gallus
RMSE = 0.0674
E Pandion haliaetus
RMSE = 0.0554
F Uria aalge
RMSE = 0.1821
G Uria lomvia
RMSE = 0.0306
H Gallinago media
RMSE = 0.0289
I Aptenodytes patagonicus
RMSE = 0.0528
y (cm)
x (cm)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RMSE = 0.0195
B Dromaius novaehollandiae
RMSE = 0.0956
C Turdus philomelos
RMSE = 0.0125
D Gallus gallus
RMSE = 0.0345
E Pandion haliaetus
RMSE = 0.0249
F Uria aalge
RMSE = 0.0335
G Uria lomvia
RMSE = 0.0271
H Gallinago media
RMSE = 0.0285
I Aptenodytes patagonicus
RMSE = 0.0644
y (cm)
x (cm)

Table S1. Fitted results using the simplified Gielis equation (SGE) to the nine eggs

Species	x_0	y_0	θ	a	n_1	n_2	Length	Width	Area	RSS	N
Strix uralensis	19.0838	19.0105	3.8352	1.5836	2.2409	6.6471	4.8505	4.2351	16.0189	0.0217	2996
Dromaius novaehollandiae	44.9468	42.5071	3.9444	0.8104	0.5398	6.4232	14.9470	9.5761	108.9956	1.9919	2999
Turdus philomelos	9.7020	9.6087	3.9332	0.7548	5.2122	17.0839	2.8212	2.1175	4.5517	0.0290	2075
Gallus gallus	29.5917	25.7853	6.2615	1.9101	2.0557	7.9118	7.0920	5.7293	31.8526	0.2183	2999
Pandion haliaetus	22.0227	21.4504	3.9467	1.5644	2.8869	11.8125	6.6750	4.9101	25.2994	0.2261	2990
Uria aalge	30.6614	23.9197	0.0096	1.3204	4.5965	23.0556	7.7560	4.7776	28.3091	0.5147	2997
Uria lomvia	26.4530	25.4271	3.9511	1.6239	8.6162	38.2804	8.5816	5.3748	34.3207	0.7850	2999
Gallinago media	14.7791	14.7885	3.9306	1.1246	14.8388	49.3067	4.5062	3.1801	10.5849	0.1976	2999
Aptenodytes patagonicus	35.1851	35.6391	3.9365	2.5630	8.5660	33.0040	11.4956	7.8058	66.9549	1.4039	2997

Table S2. Fitted results using the Narushi-Romanov-Griffin equation (NRGE) based on the maximum distance method to the nine eggs

Species	θ	L	B	w	$D_{L/4}$	Length	Width	Area	RSS	N
Strix uralensis	0.7286	4.8523	4.2315	-0.0227	3.6050	4.8523	4.2315	16.0189	2.6885	2996
Dromaius novaehollandiae	0.8088	14.9473	9.5693	-1.1107	8.1660	14.9473	9.5693	108.9956	24.6551	2999
Turdus philomelos	0.7387	2.8235	2.1191	0.0160	1.6509	2.8235	2.1191	4.5517	2.8735	2075
Gallus gallus	0.0215	7.0924	5.7284	-0.1211	5.0786	7.0924	5.7284	31.8526	13.6214	2999
Pandion haliaetus	0.8433	6.6789	4.9097	0.0136	3.9787	6.6789	4.9097	25.2994	9.1708	2990
Uria aalge	3.1301	7.7560	4.7714	0.4136	3.6339	7.7560	4.7714	28.3091	99.3389	2997
Uria lomvia	0.8151	8.5818	5.3736	0.4044	3.7727	8.5818	5.3736	34.3207	2.8120	2999
Gallinago media	0.7781	4.5062	3.1799	0.1242	2.2262	4.5062	3.1799	10.5849	2.5102	2999
Aptenodytes patagonicus	0.8023	11.4959	7.8037	0.4571	5.5542	11.4959	7.8037	66.9549	8.3699	2997

* Note: Here θ was estimated to be the angle between the straight line associated with the maximum distance between two points on the egg edge and the x-axis.

Table S3. Fitted results using the Narushi-Romanov-Griffin equation (NRGE) based on the SGE major axis approximation method to the nine eggs

Species	θ	*L*	*B*	*w*	$D_{L/4}$	Length	Width	Area	RSS	*N*
Strix uralensis	6.9767	4.8505	4.2337	-0.0095	3.5993	4.8505	4.2337	16.0189	1.1362	2996
Dromaius novaehollandiae	7.0860	14.9470	9.5685	-1.0963	8.1588	14.9470	9.5685	108.9956	27.3804	2999
Turdus philomelos	7.0748	2.8212	2.1166	0.0369	1.6498	2.8212	2.1166	4.5517	0.3257	2075
Gallus gallus	9.4031	7.0920	5.7291	0.0802	4.8449	7.0920	5.7291	31.8526	3.5727	2999
Pandion haliaetus	7.0883	6.6750	4.9082	0.0365	3.9757	6.6750	4.9082	25.2994	1.8499	2990
Uria aalge	3.1512	7.7560	4.7713	0.4008	3.6390	7.7560	4.7713	28.3091	3.3581	2997
Uria lomvia	7.0927	8.5816	5.3729	0.4057	3.7722	8.5816	5.3729	34.3207	2.2072	2999
Gallinago media	7.0721	4.5062	3.1798	0.1242	2.2291	4.5062	3.1798	10.5849	2.4286	2999
Aptenodytes patagonicus	7.0781	11.4956	7.8030	0.4449	5.5605	11.4956	7.8030	66.9549	12.4250	2997

* Note: Here θ is equal to the estimated θ of SGE + π.