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УДК 598.293.1

© Amurian zoological journal. VII(2), 2015. 166-174

Published: 30.06. 2015

GEOMETRIC MODELLING OF EGG VARIABILITY IN CORVIDAE

I.S. Mityay¹, A.V. Matsyura²

[¹Митяй И.С., ²Мацюра А.В. Геометрическое моделирование оологической вариабельности у врановых птиц] ¹National University of Life and Environmental Sciences of Ukraine, Heroyev Oborony str. 15, 03041, Kiev, Ukraine. E-mail: oomit@mail.ru

²Altai State University, Lenina str. 61, 656049, Barnaul, Russia. E-mail: amatsyura@gmail.com

¹Национальный университет биоресурсов и природопользования, ул. Героев Обороны 15, 03041, Киев, Украина. E-mail: oomit@mail.ru

²Алтайский государственный университет, ул. Ленина 61, 656049, Барнаул, Россия. E-mail: amatsyura@gmail.com

Key words: ovoids, Corvidae, species-specific egg shapes

Ключевые слова: овоид, врановые, видоспецифические формы яиц

Summary. We analyzed the egg shape in bird family Corvidae using a polynomial model and a compound ovoid model. We constructed a geometric model that reflects the relationship between cloacal and infundibular arcs, and the length and the diameter of the egg. Specifically, we quantified the shape of the egg via seven indices: the traditional index of elongation and six novel indices. Morphological parameters of bird eggs within three genera of Corvids (*Corvus, Pica,* and *Garrulus*) revealed that although there was overlap with their minimum and maximum values, the mean values remained different. Cluster analysis, using suggested indices and polynomial equations based on the absolute length and diameter of eggs, demonstrated different values within three main groups: the Hooded Crow, Carrion Crow, and Common Raven group, the European Jackdaw and Eurasian Jay group, and the Rook and Eurasian Magpie group. This is best explained by the variation in the elongation indices, suggesting that spheroid eggs are the optimal for clutches of 1-2 eggs or more than 5 eggs. Geometrical schemes, formulas of compound ovoid, and polynomial equations generated for seven species of corvids are supplied, which provide evidence of species-specific patterns of egg shapes.

Резюме. Нами были проанализированы формы яиц врановых птиц с помощью полиномиальной модели и модели составного овоида. Для каждой из форм была построена геометрическая модель, которая отражает взаимосвязь между клоакальной и инфундибулярной зоной, длиной и диаметром яйца. Количественные описание овоидов проводили по семи показателям: традиционному индексу удлиненности и шести оригинальным индексам. Анализ морфологических параметров яиц птиц трех родов (*Corvus, Pica* и *Garrulus*) показал, что их минимальные и максимальные значения перекрываются, но существуют выраженные различия в средних значениях. Был установлен кластер «серая ворона, черная ворона, ворон – галка, сойка – грач, сорока» относительно семи индексов и предложенных уравнений, базирующихся на значениях абсолютной длины и диаметра яиц, и отражающих изменение удлиненности яиц. Это может быть объяснено тем, что сфероподобные яйца вероятно являются наиболее оптимальными в кладках из одного-двух и из более чем пяти яиц. Для проверки этой гипотезы потребуется дополнительное исследование. Геометрические схемы, формулы и полученные полиномиальные уравнения для семи видов врановых птиц предложены нами в качестве исходных величин для видоспецифичных моделей форм яиц, которые могут быть использованы в систематике и филогении.

INRODUCTION

The shell of bird egg plays an important role in providing the essential conditions for the development of the embryo. It acts as a barrier from outside conditions and simultaneously provides an area for the embryo to develop [Alabi et al., 2012; Deeming, Ruta, 2014a; Demming, Ruta, 2014b; Gamauf, Haring, 2004; Hoyt, 1968; Zelenitsky et al., 2011]. The efficacy of mechanical properties of an eggshell depends on the degree of its curvature and its thickness. A perfect sphere will have maximum strength with a minimal shell thickness. However, birds typically do not produce perfect spherical eggs and thus must create a compromise between the curvature and thickness of their eggs and strength [Andersen et al., 2014; Barta, Székely, 1997; Livezey, Zusi, 2007; Richter, Wirkner, 2014]. In addition to its mechanical functioning, a shell allows gas exchange, transpiration, and thermoregulation during incubation. All these processes are associated with the egg surface. Ultimately, these properties vary by morphometric parameters of the egg, namely, its shape and quantitative indicators. The description of the last is in many ways problematic [Alabi et al., 2012; Andersen et al., 2014; Barta, Székely, 1997; Hoyt, 1968; Livezey, Zusi, 2007; Preston, 1968; Troscianko, 2014].

The underlying issue in bird eggs, Corvidae eggs in particular, is that there is no holistic approach of describing an egg that takes into consideration its form, geometrical diagrams and their accompanying quantitative calculations. In doing so, it would allow one to highlight the ideal shapes for any bird species, analyze their relationship with certain aspects of the process of incubation, and the suitability of egg form to ensure the optimal development of the embryo in variable environmental conditions [Alabi et al., 2012; Barta, Székely, 1997; Deeming, Ruta, 2014a; 2014b; Zelenitsky et al., 2011].

The purpose of this research was to analyze the eggs of certain species in the family Corvidae and to identify their species-specific shapes by geometric models and compare them with the actual egg shapes.

METHODS

Data (raw measurements and pictures) was collected in the field as well as in museums in Ukraine and Russia: National Science and Natural History Museum of National Academy of Sciences of Ukraine (Kiev), the Zoological Museum of Kiev, National Taras Shevchenko Museum of Zoology (Kiev), Lviv National Ivan Franko University, State Museum of Natural History of National Academy of Sciences of Ukraine (Lviv), the Nature Museum of Kharkiv National University, Cherkassy Regional History Museum, the Zoological Museum of Moscow State University (Russian Federation) – see Table 1. Index ($I_{iz} = r_i / D$), lateral area Index ($I_{lz} = r_i / D$), and cloacal area Index ($I_{sz} = r_c / D$); Index of asymmetry ($I_{as} = r_c / r_i$), Equatorial Index ($I_{eq} = b = L-(r_c + r_i)$ and Complementarity Index $I_{com} = (r_c + b) (r_i + b) bL$, where $b = L-(r_c + r_i)$, L - egg length , D - egg diameter, r_c , r_i , $r_i - the radii of the areas.$

All parameters were developed with our novel approach (Fig. 1) stemming from digital pictures of eggs with the help of computer programs developed by B. Trotsenko and C. Shelestyuk on equations of piecewise continuous curve.

In addition to the above-mentioned model of the composite ovoid, the Polynomial model was used which reflects the physical nature of the eggs. A computer program calculating four-degree polynomial has been kindly offered by L.I. Frantsevich [2015]. Statistical processing was performed by Statistica 9.0 and Microsoft Excel 2010.

RESULTS AND DISCUSSION

Eggs differed in diameter (D), length (L), and arc radius of the polar (r_1, r_3) , and lateral zones (r_1) . We ultimately did not utilize the minimal variation

Table	1
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Species	Egg number	Length, mm	Diameter, mm	Weight, g
Corvus corax	87	49.5±0.241	33.7±0.123	28.9±0.232
Corvus corone	13	43.5±0.578	30.0±0.193	_
Corvus cornix	98	41.5±0.221	29.5±0.106	18.9±0.167
Corvus frugilegus	100	40.1±0.249	28.0±0.094	16.6±0.119
Corvus monedula	100	34.9±0.120	25.1±0.079	11.3±0.077
Pica pica	294	33.0±0.126	23.5±0.056	9.5±0.072
Garrulus glandarius	96	31.0±0.093	22.8±0.064	8.6±0.069

The volume of initial data of Corvidae eggs

We processed the data from 788 eggs of the Corvidae. Data processing was realized by methods previously described in [Mityay, 2003; 2008]. To compare the characteristics of the shapes of Corvidae eggs we used a model of a composite ovoid. According to this model all the variety of shapes are obtained by drawing (combination, pairing, and smoothing) of arcs adequate to the curvature of ovoid areas [Hoyt, 1968; Preston, 1968; Troscianko, 2014]. For each of the shapes we constructed the geometric model that reflects the relationship between cloacal and infundibular arcs, along with the length and the diameter of the ovoid.

Quantified description of ovoids was performed via seven indices: a traditional index of elongation I_{el} (egg length/diameter ratio), and six proposed novel indices.

The six novel area indices are: infundibular area

of the latter index in the egg description, and thus our results were limited to the four former indices. Moreover, these parameters are closely united in a single system where the length serves as the whole, while the diameter and radius of the polar zones are the components. This approach makes it possible to deduce the formulas of eggs, build basic geometric models, and numerically characterize the minimum number of parameters (length, diameter, and one of the polar radii) – see Fig. 2.

Our classification was based on these settings. All the forms were divided into ovoids ($r_i = 0.5$ D), symmetric and asymmetric pseudoovoids due to equality or inequality of infundibular and cloacal radii [Mityay, Degtyarenko, 2012].

The analysis of empirical data showed that the eggs of Corvidae are predominantly asymmetric pseudoovoids (81.5 %) and ovoids (14.9 %). This



Fig. 1. Schemes of measurements from different type of eggs: a, c – symmetric and asymmetric pseudoovoids; b – ovoids Рис. 1. Схемы снятия промеров с различных типов яиц: a, c – симметрических и асимметрических псевдоовоидов; b – овоидов

ratio varies in different species. Eggs of Common Raven are dropping-shaped pseudoovoids of type 13 and 14: Group 1 (8.2 %), Group 2 (17.11 %), Group 3 (25.57 %), Group 4 (15.79 %), Group 5 (14.29 %), and Group 6 (10.53 %), see Fig. 3.

24.0 % of Hooded Crow eggs are typical ovoids (type 9-10), the other – the typical pseudoovoids of type 9-10: Group 2 (6 %), Group 3 (22 %), Group 4 (18 %), Group 5 (8 %), Group 6 (22 %) – see Fig. 4.

10.25 % of Eurasian Magpie eggs are teardropshaped ovoids (type 13-15) and pseudoovoids of type 13-14: Groups 1-4, respectively 12.4, 14.73, 40.31, and 22.31 % (Fig. 5).

13.13 % of European Jackdaw eggs are blunt and normal ovoids of type 8-9. The pseudoovoids of type 13-14 were also selected: Group 2 (19.19 %), Group 3 (16.17 %), Group 4 (22.22 %), Group 5 (22.22 %), and Group 6 (7.07 %) – Fig. 6.

14.6 % of Eurasian Jay eggs are ovoids, rest are the pseudoovoids, between them 3.61 % of Group 2; 4.82 % of Group 3; 15.66 % of Group 4; 46.99 % of Group 5; and 28.92 % of Group $6 - \sec$ Fig. 7.

Using these indices and the polynomial coefficients we have implemented a comparison of the egg shapes at the level of genera and species of the Corvidae family. Analysis of morphological parameters of bird eggs of three genera (*Corvus*, *Pica*, and *Garrulus*) showed that their minimum and maximum values overlap, but there are differences in the mean values (Table 2).

The eggs of all three species were significantly different in length (t = 34.5, -37.0, 18.7; $t_{a,v} = 1.653$; $\alpha = 0.05$) and diameter (t = 30.1, 35.1, 13.1, $t_{a,v} = 1.653$; $\alpha = 0.05$). Genera *Corvus* and *Pica* also significantly differ in the indices of the lateral (t= 10.5; $t_{a,v} = 1.653$; $\alpha = 0.05$), infundibular (t = 7.1; $t_{a,v} = 1.653$; $\alpha = 0.05$) zones, the equatorial Index (t = -4.2; $t_{a,v} = 1.653$; $\alpha = 0.05$), and all the polynomial coefficients (t = -12.8,

9.2, 7.0, -2.2; $t_{a,v} = 1.653$; $\alpha = 0.05$).

These data indicate that the egg shapes in the genus Corvus have larger radius lateral edges and smaller angle of inclination. They have a greater distance between the centers of the infundibular and cloacal arcs together with smaller infundibular radius and diameter of the egg meridian (k_0) . The genera *Corvus* and Garrulus have significant differences in the radius of infundibular arc to the distance between the centers of the arcs of infundibular and cloacal areas and the two polynomial coefficients (k_2, k_3) . European Jay eggs are closer to ovoid shape in all the parameters. They have higher infundibular and cloacal radius, but the distance between them is lesser. They also have a shorter diameter of egg meridian (k_0). Genera *Pica* and Garrulus have differences only in the lateral arc radius and polynomial coefficient of the first degree. Thus, the majority of morphological parameters of Corvidae eggs at genera level is species-specific.

Our further studies were related to the certain types of shapes in Corvidae eggs. Most of the literature sources indicate the species-specific shape of eggs, but the evidence showing the benefit of this is almost non-existent. In general, each species of Corvus genera is characterized by a specific set of egg shapes, the parameters of which overlap to varying degrees, and the mean values differ. Some egg shapes are more regular providing a base for oological databank of bird species. Less distributed egg shapes are the abnormalities on the one hand, and on the other - the original surplus variation as a potential material for natural selection. To determine the degree of similarity of eggs of different species of Corvidae we conducted a cluster analysis by seven egg shape indices and four polynomial coefficients (Fig. 8).

For each of the clusters we made the additional comparison by the shape index (Table 3), the coefficients of the polynomial (Table 4), and geometric



Fig. 2. Basic forms and geometric diagrams of Corvidae eggs. Here 1-4 – Corvus corax; 5-8 – C. corone; 9-14 – C. cornix; 15-17 – C. monedula; 18-21 – Garrulus glandarius; 22-24 – C. frugilegus; 25-30 – Pica pica (the size of rectangle inside the schemes corresponds to the diameter of eggs, the points are the centers of the corresponding circles, horizontal and vertical lines correspond to half of the ovoid, the circles outline the contours of the polar circle zones of the egg) Рис. 2. Основные формы и геометрические схемы яиц врановых птиц: 1-4 – Corvus corax; 5-8 – C. corone; 9-14 – C. cornix; 15-17 – C. monedula; 18-21 – Garrulus glandarius; 22-24 – C. frugilegus; 25-30 – Pica pica (прямоугольник внутри схем по размерам соответствует диаметру яйца, точки – центры соответствующих окружностей, горизонтальная и вертикальная линии соответствуют половине овоида, окружности очерчивают контуры полярных зон яйца)

Fig. 3. Shape and indices of Common Raven eggs Рис. 3. Формы и индексы для яиц ворона

Fig. 4. Egg shapes and indices of Hooded Crow Рис. 4. Формы и индексы для яиц серой вороны

Fig. 5. Egg shapes and indices of Eurasian Magpie Рис. 5. Формы и индексы для яиц сороки обыкновенной

constructions (Fig. 7). The last one arranged so that the radius of the polar area, the length, and diameter of the egg expressed by the dependence on each other and are reflected in the compound ovoid formula. Besides, the polynomial equation was calculated for each shape type.

Eggs in the transition pattern 'Common Raven – Hooded Crow' are very similar in shape (Fig. 7), but the significant differences on most of the indices and polynomial coefficients were found. These differenc-

Fig. 6. Egg shapes and indices of European Jackdaw Рис. 6. Формы и индексы для яиц галки

Fig. 7. Egg shapes and indices of Eurasian Jay Рис. 7. Формы и индексы для яиц сойки

es were observed only for the length, diameter, and elongation index (t = 1.87 t_{av} = 1,70; α = 0,05).

A formula of compound ovoid egg of Common Raven:

$$\begin{split} L &= 2r_i + 2r_c; (r_i = LD; r_c = (2D-L/2); \\ L &= 2r_i + 3r_c; (r_i = L/4; r_c = L/6); \\ L &= 2r_i + 4r_c; (r_i = L/4; r_c = L/8). \\ \text{The same for the Hooded crow:} \\ L &= 2r_i + 2r_c (r_i = LD; r_c = (2D-L/2); \\ L &= 2r_i + 3r_c (r_i = LD; r_c = (2D-L/3); \\ L &= 2r_i + 4r_c; (r_i = L/4; r_c = L/8). \\ \text{Generalized polynomial equation:} \\ y(x) &= 0.681 + 0.004(1 + 0.128 + 0.006x - 0.027 + 0.004x^{2+} \\ 0.103 + 0.003x^{3})Z \\ \text{For the Hooded Crow:} \\ y(x) &= 0.688 + 0.004(1 + 0.13 + 0.006x - 0.036 + 0.004x^{2+} \\ 0.1 + 0.003x^{3})Z \end{split}$$

(Z-value here and below is: $Z = (1-x^2)^{0.5}$).

$z = \sqrt{1 - x^2}$

There was a significant difference in the cluster 'Hooded Crow – European Jackdaw – Eurasian Jay' in absolute length (t = 23.74, 42.34, 17.31; $t_{a,v} = 1.66$; $\alpha = 0.05$) and diameter (t = 38.66, 51.41, 21.15; $t_{a,v} = 1.66$; $\alpha = 0.05$). Eggs of Hooded Crow and European Jackdaw are different in the lateral area index, the index of elongation, and polynomial coefficients of zero, first and third degree (t = -3.25, 1.73, 1.78, 3.15, -2.14; $t_{a,v} = 1.66$; $\alpha = 0.05$).

The Hooded Crow and Eurasian Jay differed in the indices of infundibular area and polynomial coefficients of the second and third degree, the other differences were also significant (t = -3.22, -3.79, -3.1, 5.16, -3.18, 4.29, -4.77, 3.4; $t_{av} = 1.66$; $\alpha = 0.05$).

The Hooded Crow and Eurasian Jay had no dif-

Fig. 8. Tree diagram of Corvidae egg shapes

Рис. 8. Диаграмма сходства формы яиц Врановых

Table 2

Egg shape indices and polynomial coefficients of three Corvidae genera

Indox	Corvus (n=473)				Pica (n	=295)	Garrulus (96)		
nuex	min	Max	M±m	min	max	M±m	min	max	M±m
K ₀	0.07	0.95	0.68±0.005	0.62	0.61	0.72±0.003	0.65	0.81	0.74±0.003
k ₁	-0.01	0.31	0.12±0.003	0.001	0.28	0.08±0.003	0.03	0.76	0.22±0.03
k ₂	-0.19	0.17	-0.03 ± 0.002	-0.15	0.06	-0.06 ± 0.003	-0.001	0.26	0.09±0.005
	-0.11	0.82	0.11±0.006	-0.04	0.18	0.10±0.002	-0.11	0.14	0.04±0.004

Indices of Corvidae egg shapes

Table 3

Doromotor	Corvus (n=473)			<i>Pica</i> (n=295)			Garrulus (96)		
Parameter	min	max	M±m	min	max	M±m	min	max	M±m
L, mm	29.3	55.5	41.2±0.2	26.2	40.8	33.3±0.1	28.2	34.1	31.0±0.09
D, mm	22.4	36.1	28.9±0.1	20.0	26.2	23.7±0.1	21.1	24.2	22.8±0.06
I _{cz}	0.2	0.4	0.2±0.002	0.1	0.4	0.2±0.003	0.2	0.4	0.3±0.005
I _{lz}	0.7	1.8	0.9±0.008	0.7	1.4	0.9±0.007	0.7	1.6	0.9±0.014
I	0.3	0.5	0.5±0.001	0.3	0.5	0.5±0.002	0.4	0.5	0.5±0.002
I _{as}	0.2	0.9	0.5±0.005	0.3	0.9	0.6±0.008	0.3	1.0	0.6±0.011
I _{eq}	0.3	1.1	0.7±0.005	0.3	0.9	0.7±0.01	0.4	0.8	0.6±0.008
I _{el}	1.2	1.7	1.4±0.004	1.2	1.6	1.4±0.005	1.2	1.5	1.4±0.005
I _{com}	1.0	1.5	1.1±0.002	1.0	1.5	1.1±0.007	1.1	1.4	1.2±0.005

Table 4

The polynomial coefficients of Corvidae eggs

Species	N	k ₀	k ₁	k ₂	k ₃
Corvus corax	87	0.68	0.13	-0.03	0.10
Corvus corone	13	0.69	0.13	-0.04	0.10
Corvus cornix	98	0.71	0.13	-0.03	0.08
Corvus frugilegus	100	0.69	0.16	-0.02	0.07
Corvus monedula	100	0.72	0.10	-0.04	0.09
Pica pica	294	0.72	0.09	-0.06	0.10
Garrulus glandarius	96	0.74	0.10	-0.04	0.09

Table 5

Indices of bird egg shape									
Species	n	I _{cz}	I _{lz}	I _{iz}	I _{el}	I _{as}	I _{com}	I _{eq}	
Corvus corax	87	0.23	1.05	0.47	1.47	0.49	1.10	0.77	
Corvus corone	13	0.23	1.00	0.47	1.45	0.49	1.10	0.75	
Corvus cornix	98	0.24	0.96	0.47	1.39	0.51	1.12	0.69	
Corvus frugilegus	100	0.23	1.06	0.48	1.43	0.49	1.12	0.72	
Corvus monedula	100	0.24	0.89	0.47	1.38	0.52	1.13	0.67	
Pica pica	294	0.24	0.89	0.46	1.39	0.52	1.12	0.69	
Garrulus glandarius	96	0.26	0.88	0.47	1.35	0.55	1.15	0.62	

ference in the indices of the lateral and infundibular area and polynomial coefficients of first and second degree. The remaining differences are authentic.

Formula of composite ovoid of Hooded Crow:

$$\begin{split} & L = 2r_i + 2r_c; r_i = L - D; r_c = (2D - L)/2. \\ & L = 2r_i + 2r_c; r_i = L - D; r_c = (D - L)/2. \\ & L = 2r_i + 3r_c; r_i = L - D; r_c = (2D - L)/3. \\ & L = 2r_i + 3r_c; r_i = D/2; r_c = (2D - L)/4. \\ & L = r_i + 4r_c; r_i = 2D - L; r_c = (L - D)/2. \\ & \text{The same for European Jackdaw:} \\ & L = 2r_i + 2r_c; r_i = 2L/3; r_c = L/6. \\ & L = 2r_i + 3r_c; r_i = (3D - 2L)/2; r_c = L - D. \\ & \text{For Eurasian Jay:} \\ & L = 2r_i + 2r_c; r_i = L/4; r_c = 3L/16; L = 2r_i + r_c; r_i = D/2; r_c \\ & = L - D. \end{split}$$

Polynomial equation for egg shape of Hooded Crow: $y(x) = 0,71\pm0,004(1+0,133\pm0,006x-0,027\pm0,004x^2+0,103\pm0,003x^3)Z.$

The same for European Jackdaw:

 $y(x) = 0.72\pm0.004$ (1+0.099±0.006x-0.045±0.004x² +0.103±0.098x³)Z.

For Eurasian Jay:

 $y(x) = 0,74\pm0,003(1+0,222\pm0,025x+0,097\pm0,004x^{2}-$

$0,037\pm0,003x^{3})Z.$

All the parameters were significantly different in the cluster 'Rook – Magpie'.

Formula of composite ovoid for the Rook:

$$\begin{split} L &= 2r_i + 2r_c; \quad r_i = 2L/3; \quad r_c = L/6; \quad L = 2r_i + 3r_c; \quad r_i = L/4; \\ r_c = L6; \quad L = r_i + 4r_c; \quad r_i = L/4; \quad r_c = 3L/8. \\ \text{For Eurasian Magpie:} \\ L &= 2r_i + 2r_c; \quad r_i = L-D; \quad r_c = (2D-L)/2; \quad L = 2r_i + 2r_c; \quad r_i = (2D-L)/2; \quad r_c = L/6; \quad L = r_i + 2r_c; \quad r_i = D/2; \quad r_c = L/6; \quad L = r_i + 2r_c; \quad r_i = D/2; \quad r_c = L/6; \quad L = r_i + 2r_c; \quad r_i = D/2; \quad r_c = L/6; \quad L = r_i + 4r_c; \\ r_i = L-D; \quad r_c = (2D-L)/2. \\ \text{Polynomial equation for the Rook:} \\ y(x) &= 0, 72 \pm 0,004 \quad (1 + 0,099 \pm 0,006x - 0,045 \pm 0,004x^2 + 0,103 \pm 0,098x^3)Z. \\ \text{For Eurasian Magpie:} \\ y(x) &= 0, 74 \pm 0,003(1 + 0,222 \pm 0,025x + 0,097 \pm 0,004x^2 - 0,037 \pm 0,003x^3)Z. \end{split}$$

CONCLUSIONS

We suggested that each of the corvid species has typical egg shape with a set of parameters that are overlapped at some extent. Moreover, the average values of such parameters have significant differences. This contributes to the species specificity of egg shapes. We also determined that some egg shapes occur most frequently from the whole set making the basis of species oological fund. Less distributed egg shapes are the deviations from the norm on one hand and sort of variation surplus as a potential material for natural selection on other hand.

Our data testified that the use of an integrated approach for eggs description, which includes names, geometric diagrams, standards, and quantitative characteristics presents a significant opportunity for entirely new research. This could allow to diagnose the egg shapes, to carry out a variety of comparisons towards literary data and associate each egg shape with relevant biological information.

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