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A simple way to calculate the volume and surface area of avian eggs

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1 **A simple way to calculate egg volume and surface area: Proof of concept using six**
2 **avian species**

3

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23

24 **Running title:** Egg volume and surface area

25

26 **Abstract**

27 The incubation period of avian eggs is constrained by egg surface area, volume, and
28 therefore geometry and shape. The geometries of eggs can be described using Preston's
29 equation, but it has been seldom used to calculate the volume (V) and surface area (S) of
30 eggs to explore S vs. V scaling relationships. Here, we provide a re-expression of Preston's
31 equation (designated as EPE) to calculate V and S , assuming that an egg is a solid of
32 revolution. The side profiles of >2200 eggs of six species of poultry were digitized, and
33 RPE was used to describe each egg profile. The volumes of 360 eggs predicted by EPE
34 were compared with those obtained using water displacement in graduated cylinders. There
35 was no significant difference in V between the two methods, which verified the utility of
36 EPE and the hypothesis that eggs are solids of revolution. The data also indicated that V
37 was proportional to the product of egg length (L) and maximum width (W) squared with a
38 proportionality coefficient of 0.511, i.e., $V = 0.511LW^2$. A 2/3-power law relationship
39 between S and V for each species was also observed such that S is proportional to $(LW^2)^{2/3}$
40 with a proportionality coefficient 3.14, i.e., $S = 3.14(LW^2)^{2/3}$. These results can be extended
41 to describe the shapes of the eggs of other species to study the evolution of avian (and
42 perhaps reptilian) eggs.

43

44 **KEYWORDS**

45 asymmetry, definite integral, egg shape, scaling relationship, solid of revolution

46

47 **INTRODUCTION**

48 The shapes of avian and reptilian eggs have received considerable attention because of their
49 deviation in symmetry from an ellipse above and below their maximum width along their
50 longitudinal axis (Stoddard et al., 2017). As a consequence, many mathematical models
51 have been proposed to describe the shapes of bird and reptile eggs, and most are related to
52 the 2-D egg profile (Preston, 1953; Troscianko, 2014; Biggins et al., 2018, 2022; Narushin
53 et al., 2021; Shi et al., 2022a). This generic approach is based on the assumption that an
54 egg is a solid of revolution, such that its 3-D shape can be generated by revolving the 2-D
55 egg profile by π . Although this assumption has not been rigorously tested, it appears to be
56 reasonable given the peristalsis-like conveyance of an ovoid or pyriform shaped egg in the
57 oviduct compared with the movement of a cuboid solid. Based on what is known
58 empirically about avian and reptilian egg shapes, it is also reasonable to assume that the 2-
59 D egg profile can be used to generate the 3-D shape (and size) of the same egg, which
60 would provide a nondestructive method for calculating egg surface area and volume.

61 In recent studies, the equation and its simplified versions proposed by Preston (1953)
62 have been found to be the best among all existing egg-shape models (Biggins et al., 2022;
63 Shi et al., 2023). Preston's equation takes the form

64
$$\begin{cases} y_p = a \sin \theta \\ x_p = b \cos \theta (1 + c_1 \sin \theta + c_2 \sin^2 \theta + c_3 \sin^3 \theta), \end{cases} \quad (1)$$

65 where x_p and y_p represent the x - and y -coordinates of a 2-D egg profile in the plane, θ is
66 called the "eccentric angle", a is one-half of the egg length, b is approximately one-half of
67 the egg maximum width, and c_1 , c_2 and c_3 are parameters to be estimated. For some eggs,
68 Equation (1) can be simplified by removing one or more of the c_1 , c_2 and c_3 parameters
69 (Preston, 1953). In his seminal paper, Preston (1953) suggested setting c_1 to be a positive
70 number, such that the egg base is uppermost and the egg tip is lowermost (Figure 1A).

71 However, Equation (1) does not provide an explicit relationship between y_P and x_P , i.e.,

72 $y_P = f(x_P)$. Todd and Smart (1984) suggested another form of Preston's equation:

73
$$y_{TS} = \pm \frac{b}{a} \sqrt{1 - x_{TS}^2} (1 + c_1 x_{TS} + c_2 x_{TS}^2 + c_3 x_{TS}^3), \quad (2)$$

74 where $x_{TS} = y_P/a$ and $y_{TS} = x_P/a$. In this case, the egg length axis overlaps the x -axis,

75 and the two endpoints of egg length are located at $(-1, 0)$ and $(1, 0)$. The positive and

76 negative signs of the right-handed side of Equation (2) indicate the upper tip part and lower

77 base part of the egg about the x -axis (i.e., the mid-line of the egg profile), respectively

78 (Figure 1B).

79 Note that it is sometimes convenient to neglect the expression of the lower part, when

80 the upper part is symmetrical to the lower part about the x -axis. Given this simplification

81 of Equation (2), Biggins et al. (2018) re-wrote Preston's equation as

82
$$y_{TS} = d_0 z_0 + d_1 z_1 + d_2 z_2 + d_3 z_3, \quad (3)$$

83 where $z_0 = \sqrt{1 - x_{TS}^2}$, $z_1 = x_{TS} \sqrt{1 - x_{TS}^2}$, $z_2 = x_{TS}^2 \sqrt{1 - x_{TS}^2}$, and $z_3 = x_{TS}^3 \sqrt{1 - x_{TS}^2}$, and

84 where d_0 to d_3 are parameters to be estimated, i.e., $d_0 = b/a$, $d_1 = c_1(b/a)$,

85 $d_2 = c_2(b/a)$, and $d_3 = c_3(b/a)$. The parameters in Equation (3) can be estimated using

86 multiple linear regression protocols based on (weighted) least-squares for data drawn from

87 the eggs of the same or different species using the numerical values of d_0 and d_1 in each

88 case. Nevertheless, Equation (3) cannot explicitly express the relationship between the

89 vertical and horizontal coordinates (y and x) of an egg's empirical profile. Yet, it is

90 important to have an explicit expression relating x and y , which can then be used to directly

91 calculate the volume (V) and surface area (S) of an egg (Narushin et al., 2022) employing

92 the Equations (4) and (5):

93
$$V = \pi \int_{-a}^a y^2 dx, \quad (4)$$

94 and

95
$$S = 2\pi \int_{-a}^a y \sqrt{1 + \left(\frac{dy}{dx}\right)^2} dx, \quad (5)$$

96 where $y = x_p$, $x = y_p$, a is one-half of egg length [as in Equation (1)], and dy/dx is the
97 derivative of y with respect to x .

98 When considering the volume of an egg, empirical studies report that V is proportional
99 to the product of egg length (L) and maximum width squared (W^2), i.e., $V \propto LW^2$ (Hoyt,
100 1979; Narushin et al., 2022). Preston (1974) provided a mathematical proof for this
101 proportional relationship. However, his derivation is based on Equation (1) with the
102 simplification that $c_3 = 0$. His proof also lacks an explicit mathematical expression relating
103 y and x . Consequently, the volume formula in Preston's (1974) proof is based on a vaguely
104 defined "eccentric angle" θ . In addition, as will be shown, the neglected parameter c_3 can
105 play an important role in estimating egg shape. Indeed, all of the parameters from c_1 to c_3
106 are required to achieve a high degree of accuracy.

107 Despite the limitations of Preston's (1974) proof, as noted, the proportional
108 relationship $V \propto LW^2$ has been demonstrated empirically to hold true (Hoyt, 1979;
109 Narushin et al., 2022). Consequently, there have been many attempts to improve the
110 prediction accuracy of V using other mathematical expressions of L and W (Narushin, 2005;
111 Sedghi and Ghaderi, 2022).

112 The important of egg surface area and volume cannot be too overstated. Indeed, the
113 scaling of biological surface areas and volumes has been intensely studied both
114 theoretically and empirically [see Niklas (2015) and references therein]. This focus is based
115 on the fact that the surface area and volume of a cell or multicellular organism can provide
116 insights into metabolic rates because S reflects the ability to exchange mass and energy
117 with the external environment, whereas V reflects the metabolic demands for external
118 resources (von Bertalanffy, 1957). In the case of a fertilized egg, S is important for

119 respiration and the conduction of heat, whereas V provides an expression of the quantity of
120 nutrients available during gestation, e.g., the metabolic resources for sustained respiration.
121 Likewise, the quotient of cell or organismic mass and surface area can influence the
122 efficiencies of respiration and the conduction of heat (Lourens et al., 2006). When the
123 density of an organism is invariant with respect to size (i.e., $\rho \propto M/V$), its mass is
124 proportional to its volume (i.e., $M \propto V$). Provided that an egg's surface area is proportional
125 to the 2/3-power of volume (Paganelli et al., 1974), it follows that S will be proportional to
126 the 2/3-power of M (i.e., $S \propto M^{2/3}$). Because respiration is usually proportional to surface
127 area, it also follows that respiration (R) will be proportional to the 2/3-power of M (i.e., R
128 $\propto M^{2/3}$) (von Bertalanffy, 1957). However, the scaling of cell surface area to cell volume
129 is often non-Euclidian for cells with rigid walls (e.g., diatoms and unicellular green algae)
130 and can manifest a 3/4-scaling relationship (Niklas, 2015). Likewise, the densities of many
131 organisms are not (even approximately) 'invariant' with increasing body size.
132 Consequently, the scaling exponent of respiration with respect to mass often deviates from
133 a 2/3-power law. Nevertheless, the scaling relationship between S and V of avian eggs does
134 conform to the 3/4-power rule, despite having a rigid wall and being unicellular (see
135 Paganelli et al. 1974) such that S can be estimated reliably using the $V \propto LW^2$ relationship
136 (Preston, 1974; Hoyt, 1979). However, this expectation has not been tested empirically in
137 priori studies. In addition, the calculation of an egg's volume and surface area is based on
138 the hypothesis that an egg is a solid of revolution (Preston, 1974; Narushin et al., 2022),
139 which has also not been tested using experimental data.

140 To address these concerns, we photographed >2200 eggs of six species of
141 domesticated birds and fitted the 2-D profiles using an explicit Preston's equation
142 (designated as EPE) to answer the following four questions: (i) does the re-expressed
143 Preston equation fit egg profiles sufficiently well?, (ii) can an egg typically be treated as a

144 solid of revolution?, (iii) is there a significant and robust scaling relationship between S
145 and V at the species level and across species, and if so, is it governed numerically by a 2/3-
146 power rule?, and (iv) do both V and S scale as the product of L and W^2 , and if so, is there a
147 strong log-log linear relationship between V (or S) and LW^2 ? These questions were
148 motivated to evaluate non-destructive ways to calculate V and S , which can inform our
149 understanding of avian (and potentially reptilian) evolution.

150 **MATERIALS AND METHODS**

151 *Egg samples*

152 We selected six species of poultry for study because of the availability in large numbers of
153 their eggs: two Anatidae species (*Anas platyrhynchos domesticus*, and *Anser cygnoides*
154 *domesticus*), and four Phasianidae species (*Alectoris chukar domesticus*, *Coturnix japonica*
155 *domesticus*, *Gallus gallus domesticus*, and *Phasianus colchicus domesticus*). Figure 2
156 shows six representative eggs for the investigated species. For each species, >350 eggs
157 were selected for detailed study (see Table 1 for details). In passing, it was important to use
158 a large sample size of eggs for each studied species to obtain a statistically robust scaling
159 relationship between S and V . Unfortunately, this was not practical in the case of wild
160 species, many of which are strictly protected. The six poultry species used in this study
161 were selected because (i) large numbers eggs from each species were commercially
162 available, and (ii) the shapes and sizes of the eggs of these species spanned a broad
163 spectrum of the egg morphospace (Figure 2). Although the eggs from domestic birds were
164 used in this study, there is no evidence to show that the egg shape of domestic bird species
165 deviates from that of wild bird species.

166

167 *Photographing and Egg-shape data acquisition*

168 We used an adjustable tabletop phone mount to hold one smartphone (Huawei P30Pro,

169 Huawei, Dongguan, China) to photograph *A. platyrhynchos*, *A. cygnoides*, *C. japonica*, and
170 *G. gallus*), and another smartphone (Redmi K40S, Xiaomi, Kunshan, China) to photograph
171 *A. chukar*, and *P. colchicus*). Over 2200 eggs of each of the six species were photographed
172 at constant scale to determine the representative 2-D egg profiles of each species. To focus
173 the camera on the center of each egg, we estimated the midpoint of the length of each
174 profile. In addition, we prepared a test tube rack and a small beaker as a concave base to
175 support each egg to make the mid-line of each profile orthogonal to tabletop phone mount.
176 In addition, we measured each egg's length to provide a correction for the actual size from
177 its image size.

178 The egg images were converted to black and white .bmp files with Photoshop (version
179 13.0; Adobe, San Jose, CA, USA). The procedures of Matlab (version $\geq 2009a$; MathWorks,
180 Natick, MA, USA) developed by Shi et al. (2018) and Su et al. (2019) were used to extract
181 the planar coordinates of each egg profile. Each egg profile was characterized by 2000
182 approximately equidistantly spaced coordinates using the 'adjdata' function of the
183 'biogeom' package (version 1.3.5) (Shi et al., 2022b) in R (version 4.2.0) (R Core Team,
184 2022).

185

186 *Explicit Preston equation and data fitting*

187 Using Equation (2), Preston's equation can be re-expressed in a more explicit form (Shi et
188 al., 2023), which will be referred to as EPE hereinafter:

$$189 \quad y = b \cdot \sqrt{1 - \left(\frac{x}{a}\right)^2} \cdot \left(1 + c_1 \left(\frac{x}{a}\right) + c_2 \left(\frac{x}{a}\right)^2 + c_3 \left(\frac{x}{a}\right)^3\right), \quad (6)$$

190 where $y = x_p$ and $x = y_p$. Equation (4) can be used to obtain an analytical solution of the
191 volume formula based on Equation (6):

192
$$V = \frac{4}{315} \pi ab^2 (105 + 21c_1^2 + 42c_2 + 9c_2^2 + 18c_1c_3 + 5c_3^2)$$

$$\approx \frac{1}{630} \pi LW^2 (105 + 21c_1^2 + 42c_2 + 9c_2^2 + 18c_1c_3 + 5c_3^2).$$

(7)

193 Equation (7) indicates that the volume of an egg is approximately but not exactly
 194 proportional to the product of egg length (L) and the maximum egg width squared (W^2).
 195 For pyriform eggs, the numerical value of c_2 plays an important role in affecting the
 196 proportionality coefficient. However, because parameters c_1 , c_2 , and c_3 are all very small
 197 for non-pyriform eggs, Equation (7) can be simplified for these species to take the form:

198
$$V \approx \frac{420}{315} \pi ab^2 \approx \frac{1}{8} \cdot \frac{420}{315} \pi LW^2 \approx 0.52LW^2.$$

(8)

199 Because each egg profile was characterized by 2000 data points, the ‘fitEPE’ function
 200 in the ‘biogeom’ package was used to fit the data points to estimate the values of a , b , c_1 ,
 201 c_2 , and c_3 by minimizing the residual sum of squares (RSS) between the observed and
 202 predicted y -values using the Nelder-Mead optimization method (Nelder and Mead,
 203 1965). The adjusted root-mean-square error (RMSE) was then used to measure the
 204 goodness of fit between observed and predicted data (Shi et al., 2023):

205
$$\text{RMSE}_{\text{adj}} = \frac{\sqrt{\text{RSS}/N}}{W/2},$$

(9)

206 where N represents the number of data points on an egg profile, and W represents the egg
 207 maximum width. Because the 2-D egg-profile parameters are known, Equations (4) and (5)
 208 can be used to calculate the V and S for a solid of revolution.

209

210 *Testing the solid of revolution hypothesis*

211 Provided that the calculated values for V and S using Equations (4) and (5) and the
 212 hypothesis of the solid of revolution are statistically indistinguishable (or nearly so) from
 213 the empirical values V and S , the solid of revolution hypothesis must hold true. However,
 214 it is extremely difficult to measure the S of most eggs with great accuracy. In contrast, V is

215 easy to measure by submerging an egg into a graduated cylinder and measuring the
216 displacement of water. If Equation (6) fits an egg profile, the calculated V based on the 2-
217 D equation is approximately equal to that using the water displacement method, which
218 would also support the solid of revolution hypothesis. We therefore measured the V of 120
219 *A. cygnoides* eggs using a 1000 mL glass graduated cylinder with a diameter 6.7 cm, and
220 the V of 366 *P. colchicus* eggs using a 250 mL glass graduated cylinder with a diameter 4
221 cm.

222

223 *Statistical methods*

224 The Tukey's honestly significant difference (HSD) test with a 0.05 significance level (Hsu,
225 1996) was used to test whether there were significant differences in the egg size and shape
226 among the six species of poultry. We used the V and S as a measure of egg size, and the
227 ratio of the distance on the mid-line of an egg profile from the egg base to a point associated
228 with B to egg length (i.e., L_W/L) as a descriptor of egg shape. When $L_W/L = 1/2$, the egg is
229 nearly elliptical in outline. Larger value of L_W/L correspond to greater deviations from
230 'ellipticalness'.

231 Reduced major axis protocols (Niklas, 1994; Quinn and Keough, 2002) were used to
232 estimate the intercept and slope of S vs. V on a log-log scale. We fitted the data of V versus
233 LW^2 to test whether V is proportional to LW^2 as predicted by Equation (7). If S scales with
234 V with a scaling exponent $2/3$, it has a $S \propto (LW^2)^{2/3}$ scaling relationship. Thus, we fitted
235 the data to determine the scaling exponent of the S vs. LW^2 relationship. In addition, we
236 also used reduced major axis protocols to fit the observed and predicted volumes of two
237 species of eggs. We also used the paired t -test to test to determine whether there is a
238 significant difference between the observed and predicted volumes for each species of eggs.

239 The statistical software R (version 4.2.0; R Core Team, 2022) and the specific package

240 'biogeom' (version 1.2.5) was used to carry out data extraction, analysis and to make
241 figures.

242

243 **RESULTS**

244 The adjusted RMSE values for the 2221 eggs ranged from 0.0028 to 0.90 with a median
245 value of 0.0063, which indicates a good fit for each egg profile (Figure 3). A comparison
246 between the observed and predicted egg profiles for each egg example is provided in Figure
247 4.

248 There were significant differences in both egg size and shape among the six species
249 (Figure 5). The eggs of *A. platyrhynchos*, *A. cygnoides*, and *G. gallus* are larger (Figure
250 5A,B) and more elliptical (Figure 5C,D) than the other three species.

251 There was no statistically significant difference between the volumes predicted by
252 Equation (7) and those empirically determined using graduated cylinders, i.e., the 95%
253 confidence interval (CI) of predicted V vs. observed V for each species included 1 (Figure
254 6). In addition, the results of paired t -tests showed that there was no significant difference
255 between predicted and observed egg volumes ($t = -1.3308$, $df = 119$, $P = 0.1858 > 0.05$ for
256 *A. cygnoides*, $t = -1.0271$, $df = 365$, $P = 0.3051 > 0.05$ for *P. colchicus*).

257 The 95% CIs of S vs. V for four of the six species included 2/3, and the lower bounds
258 of the 95% CIs for the remaining two species were approximately 2/3 (Figure 7). The V vs.
259 S scaling relationships for all of the species were statistically very robust, i.e., the six
260 coefficients of determination were all greater than 0.99. The V vs. LW^2 scaling relationships
261 were also statistically robust (Figure 8), as was the S vs. LW^2 relationship (Figure 9). As
262 expected for the three species producing pyriform eggs (Figure 8C,D,F), Equation (8) did
263 not predict the numerical values of the slopes exceptionally well, as shown for the pooled
264 data (Figure 10). In summary, the data indicate that (i) S is approximately proportional to

265 the 2/3-power of V , (ii) V is proportional to LW^2 with a proportionality coefficient 0.51, and
266 (iii) S is proportional to $(LW^2)^{\frac{2}{3}}$ with a proportionality coefficient 3.14.

267

268 **DISCUSSION**

269 The results based on >2200 eggs of six species validates the predictions of the explicit
270 Preston equation (EPE) using the egg 2-D profile and solid of revolution hypothesis. Thus,
271 EPE can be used to calculate egg volume (V) and surface area (S). The data also show that
272 S scales as the 2/3–power of V on a log-log scale both at the species level and for the pooled
273 data. In addition, the extensive data set used in this study further validates that V is
274 proportional to the product of the egg length (L) and maximum profile width squared (LW^2).
275 These and other assertions are discussed in detail, but only after considering the important
276 issue of measurement error.

277

278 *Measurement error of egg volume using graduated cylinders*

279 The use of graduated cylinders and water displacement to measure egg volume invariably
280 introduces errors resulting from measuring the increase in overall volume. The degree of
281 error depends on the size of an egg in relation to the diameter of the graduated cylinder.
282 This phenomenology is illustrated in Figure 6. For example, in panel B of this figure,
283 several groups of data points deviate from the regression curve. These data were gathered
284 using the smallest graduated cylinder (i.e., 250 mL, with a 2 mL level of accuracy), which
285 provided a 1.0 mL error in visualizing the level of displacement. Nevertheless, we believe
286 that the regression statistics using data gathered from the water displacement method are
287 sufficiently robust to support the conclusions of this study.

288

289 *Is there a better egg-shape model than Preston's equation*

290 We used a re-expression of Preston's equation (Preston, 1953) to predicted egg surface area,
291 volume, and shape. However, there are other egg-shape models (e.g., Troscianko, 2014;
292 Biggins et al., 2018, 2022; Narushin et al., 2021; Shi et al., 2022a). Biggins et al. (2022)
293 found that the prediction errors of Troscianko's equation and Preston's equation are the
294 smallest among existing prior egg-shape models, and Preston's equation had a slightly
295 better goodness-of-fit than Troscianko's equation for each of the 50 eggs they investigated
296 (Biggins et al., 2022). Shi et al. (2023) used an optimization approach to replace the
297 multiple linear regression approach proposed by Biggins et al. (2018, 2022), and obtained
298 a lower prediction error than the latter for each of 50 eggs. The present study, which took
299 the same optimization approach as Shi et al. (2023) to estimate the parameters of Preston's
300 equation, shows that the prediction error of each of 2221 eggs was <2% of the egg half
301 maximum width, with a median prediction error of 0.63%. Based on these results, we argue
302 that the explicit Preston equation is sufficient to describe the 2-D and 3-D geometries of
303 eggs and that additional refinements are not required for this purpose.

304

305 *The 2/3-power law relationship between S and V*

306 For many classical (Euclidian) 3-D geometries, such as a cuboid, cylinder, cone, and sphere,
307 S is easily shown to be proportional to $V^{\frac{2}{3}}$ for any series geometric form that does not
308 change in shape while increasing in size (Thompson, 1917). However, if either shape or
309 geometry changes within a series of objects increasing in size (i.e., a non-Euclidian series),
310 it is difficult to predict a power-law relationship between surface area and volume.
311 Fortunately, the results reported here show unequivocally that at both the species level and
312 for the pooled data, the surface area of an avian egg scales approximately as the 2/3-power
313 law, i.e., $S \propto V^{\frac{2}{3}}$, which is in accordance with the results reported by Paganelli et al. (1974).
314 As a consequence of this power law relationship, the S of an egg becomes easy to estimate

315 because of the previously reported $V \propto LW^2$ scaling relationship (Preston, 1974; Hoyt,
316 1979; Narushin et al., 2022), which is confirmed by our data (Figure 10B). Thus, $S \propto$
317 $(LW^2)^{\frac{2}{3}}$.

318

319 *Can the results be extended to other bird species*

320 We explored the egg morphospace presented by Biggins et al. (2022), which consisted of
321 965 bird species and three egg morphometrics (i.e., elongation, polar asymmetry and
322 pointedness) [see Figure SF1 in Biggins et al. (2022)]. Using 50 egg-shapes out of the 965
323 species occupying diverse positions within the egg morphospace, we determined that for
324 these 50 egg-shapes the numerical value of the scaling exponent of the S vs. V relationship
325 is approximately $2/3$, and that there is a statistically robust log-log linear relationship
326 between V and LW^2 and S and LW^2 (Figure 11). Importantly, 25 out of the 50 eggs are
327 pyriform, which yielded a proportionality coefficient for the pooled data that deviated
328 slightly from a numerical value of 0.52 (Figure 11B). However, this deviation does not
329 affect the proportional relationship between V (or S) and LW^2 , which provides a convenient
330 way to estimate V and S in a simple way.

331

332 **CONCLUSIONS**

333 Using morphometric data derived from >2200 eggs of six bird species, we show that the
334 explicit Preston equation (EPE) provides the most robust method to predict egg volume
335 using digitized 2-D egg profiles. The data also show that avian eggs can be modelled as a
336 solid of revolution. In addition, a robust log-log linear relationship exists for S vs. V
337 governed by a $2/3$ -power law, and, V is also shown to be proportional to the product of egg
338 length (L) and maximum width squared (W^2). The data show that egg shape plays a
339 significant role in determining proportionality (normalization) coefficients of log-log S vs.

340 V scaling relationships. For non-pyriform eggs, coefficients are approximately 0.52. For
341 pyriform eggs, the proportionality coefficient is approximately 0.51. The corresponding
342 proportionality coefficient is approximately 3.14 for the pooled data. The methods and
343 results presented here provide further insights into interspecific and intraspecific
344 differences avian egg morphometrics and can be potentially extended to explore the
345 evolution of non-avian eggs.

346

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351

352 **COMPETING INTERESTS**

353 The authors declare no competing interests.

354

355 **AUTHOR CONTRIBUTIONS**

356 All authors contributed integrally to the construction of all the points of the manuscript,
357 giving their consent for its publication; P.S., J.G., and K.J.N. designed this work; L.C., K.Y.,
358 Q.M., X.G., and M.L. carried out the experiment; P.S., and K.J.N. wrote the initial draft;
359 and B.K.Q., and J.G. commented on and revised the final manuscript.

360

361 **DATA AVAILABILITY STATEMENT**

362 The raw egg-shape data for 2221 eggs will be published in Dryad when this manuscript is
363 accepted.

364

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TABLES

Table 1. Information of egg samples

Family	Latin name	Location	Arrival date
Anatidae	<i>Anas platyrhynchos domesticus</i>	Hanshan, Ma'anshan, Anhui Province, China	22nd May, 2022
Anatidae	<i>Anser cygnoides domesticus</i>	Shouguang, Weifang, Shandong Province, China	26th May, 2022
Phasianidae	<i>Alectoris chukar domesticus</i>	Liyang, Changzhou, Jiangsu Province, China	22nd, October, 2022
Phasianidae	<i>Coturnix japonica domesticus</i>	Hanshan, Ma'anshan, Anhui Province, China	22nd May, 2022
Phasianidae	<i>Gallus gallus domesticus</i>	Hanshan, Ma'anshan, Anhui Province, China	22nd May, 2022
Phasianidae	<i>Phasianus colchicus domesticus</i>	Shanghe, Jinan, Shandong Province, China	12nd, October, 2022

FIGURE LEGENDS

FIGURE 1 Simulated egg shapes by Preston's equation (A) and the Todd-Smart equation (B).

FIGURE 2 Representative eggs for the six investigated species.

FIGURE 3 The adjusted root-mean-square errors (RMSEs) for the egg profiles using the explicit Preston equation. $RMSE_{adj}$ represents the adjusted root-mean-square-error (RMSE), which is the RMSE between the observed and predicted y -values divided by half of an egg's maximum breadth. (A) The frequency distribution of the natural logarithm of the adjusted RMSEs. (B) The comparison of the natural logarithm of the adjusted RMSEs across the six avian species. The numbers above the whiskers represent the coefficients of variation (%). The horizontal solid lines represent the medians, and the asterisks within boxes represent the means.

FIGURE 4 Observed (gray) and predicted (red) geometries (boundary coordinates) of the six egg examples. The red curves were obtained using the explicit Preston equation. $RMSE_{adj}$ represents the adjusted root-mean-square-error (RMSE), which is the RMSE between the observed and predicted y -values divided by half the egg's maximum breadth.

FIGURE 5 Interspecific comparisons of the surface area (S), volume (V), the quotient of an egg's maximum breadth (W) and egg length (L), and the quotient of the distance from the egg base to the point on the mid-line of the egg's profile associated with W , L_W , and egg length. The numbers above the whiskers represent the coefficients of

variation (%). The horizontal solid lines represent the medians, and the asterisks within boxes represent the means.

FIGURE 6 Linear fit to the data of the observed and predicted egg volume. The intercept was insignificant ($P > 0.05$), so it was removed from the linear regression. The reduced major axis protocols were used because the observations of the volumes using graduated cylinders had larger variances than those using the equation of the solid of revolution based on the re-expressed Preston equation (Equation (4)). Here, y denotes the predicted volume by Equation (4) based on the re-expressed Preston equation, and x denotes the observed volume using measuring cylinders; CI represents the 95% confidence interval of the slope.

FIGURE 7 Fitted scaling relationships between egg surface area and volume at the species level. Here, y denotes the natural logarithm of an egg's surface area, and x denotes the natural logarithm of an egg's volume; CI represents the 95% confidence interval of the slope; r^2 represents the coefficient of determination; n represents the sample size (i.e., the number of eggs); the straight line represents the regression line, and the marks around the straight line are the predicted egg surface area and volume using the explicit Preston equation.

FIGURE 8 Fitted proportional relationships between an egg volume and LW^2 at the species level. Here, y denotes the natural logarithm of an egg's volume, and x denotes the natural logarithm of the product of an egg's length and maximum breadth squared; K_V represents the proportionality coefficient; CI represents the 95% confidence interval

of the proportionality coefficient; r^2 represents the coefficient of determination; n represents the sample size (i.e., the number of eggs); the straight line represents the regression line, and the marks around the straight line are the predicted egg volume using the explicit Preston equation and the observations of LW^2 on a log-log scale. The dashed line in each panel denotes $y = 0.52x$.

FIGURE 9 Fitted scaling relationships between an egg's surface area and LW^2 at the species level. Here, y denotes the natural logarithm of an egg's surface area, and x denotes the natural logarithm of the product of an egg's length and maximum breadth squared; K_S represents the proportionality coefficient; CI represents the 95% confidence interval of the proportionality coefficient; r^2 represents the coefficient of determination; n represents the sample size (i.e., the number of eggs); the straight line represents the regression line with a given slope $2/3$, and the marks around the straight line are the predicted egg's surface area using the explicit Preston equation and the observations of LW^2 on a log-log scale.

FIGURE 10 Fitted scaling relationships for the pooled data of the six avian species. (A) The scaling relationship between egg surface area and volume. (B) The proportional relationship between egg volume and LW^2 . (C) The scaling relationship with a constant scaling exponent $2/3$ between egg surface area and LW^2 .

FIGURE 11 Fitted scaling relationships for the 50 egg-shape data from Biggins et al. (2022). (A) The scaling relationship between egg surface area and volume. (B) The proportional relationship between egg volume and LW^2 . (C) The scaling relationship with a constant scaling exponent $2/3$ between egg surface area and LW^2 .

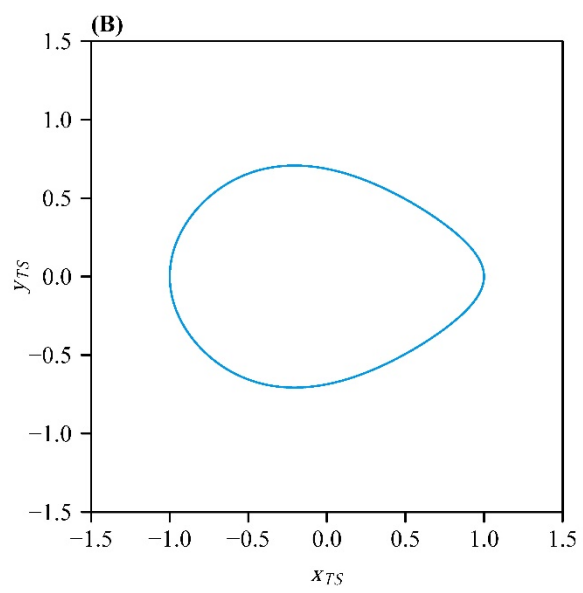
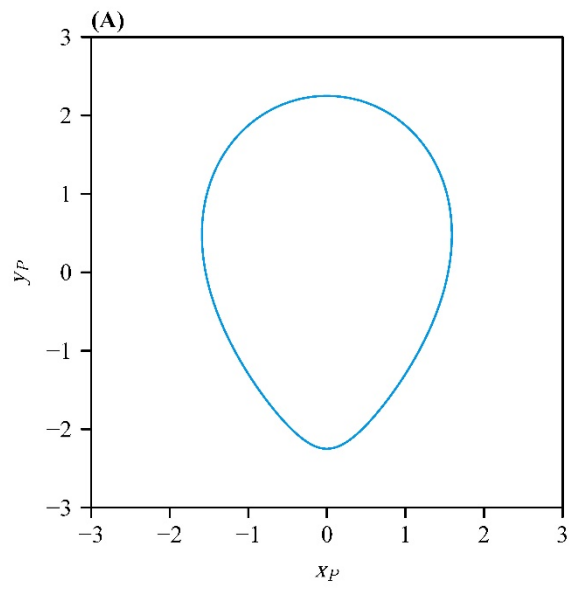


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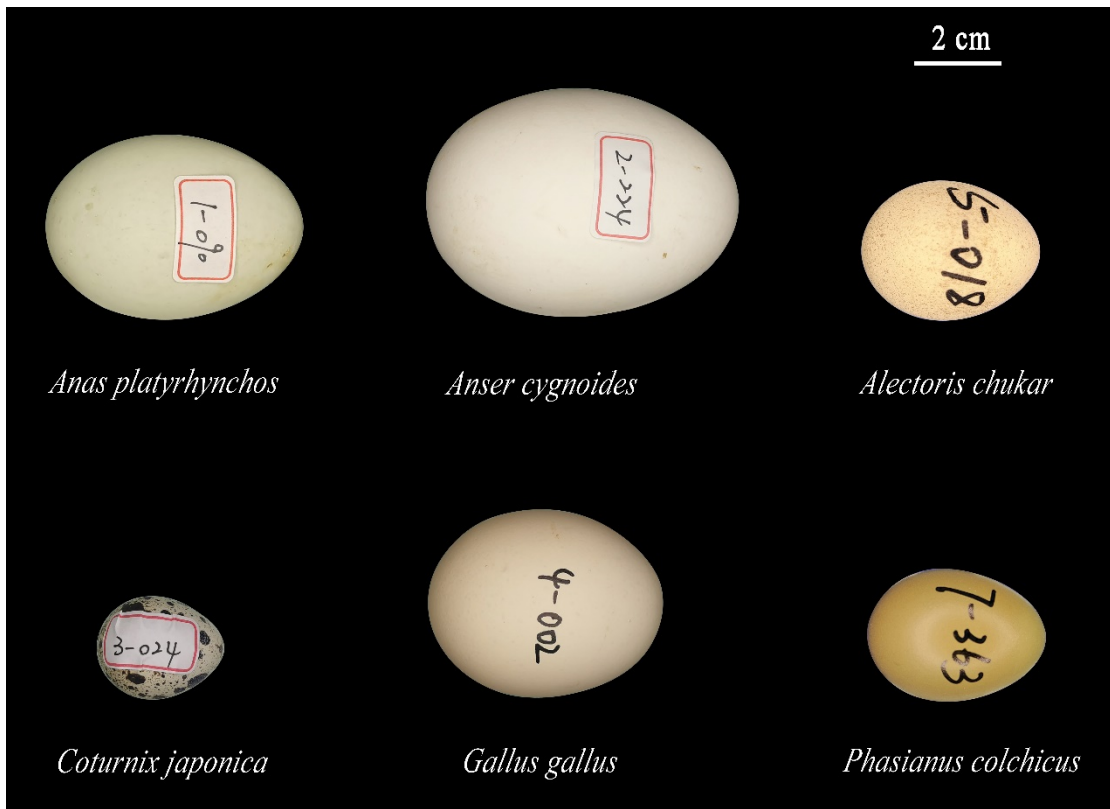


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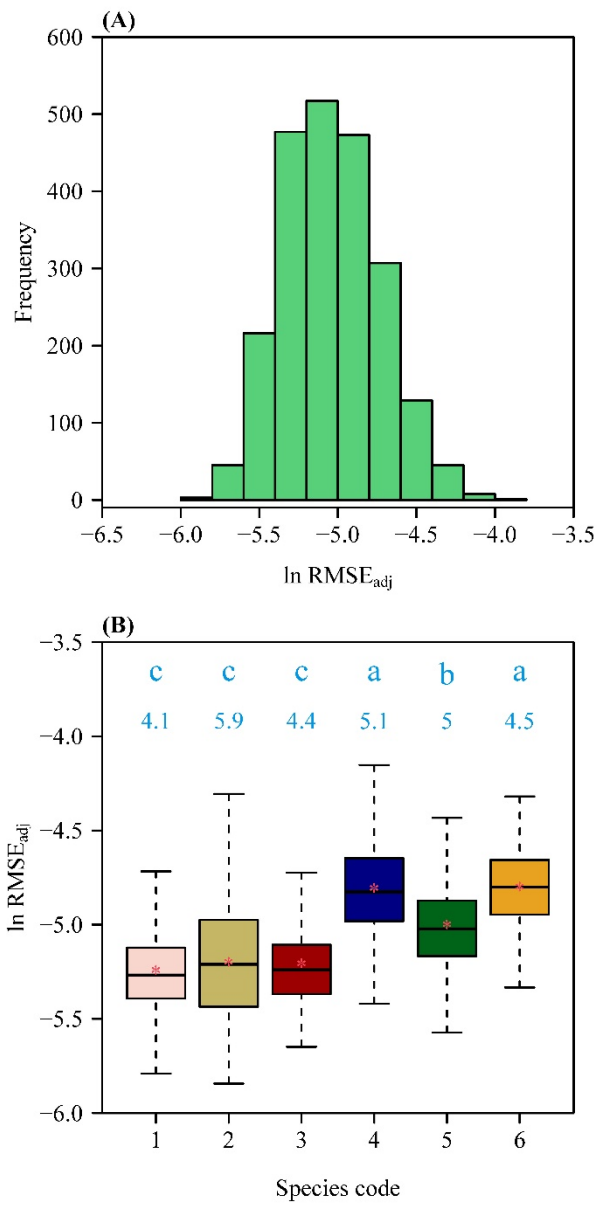


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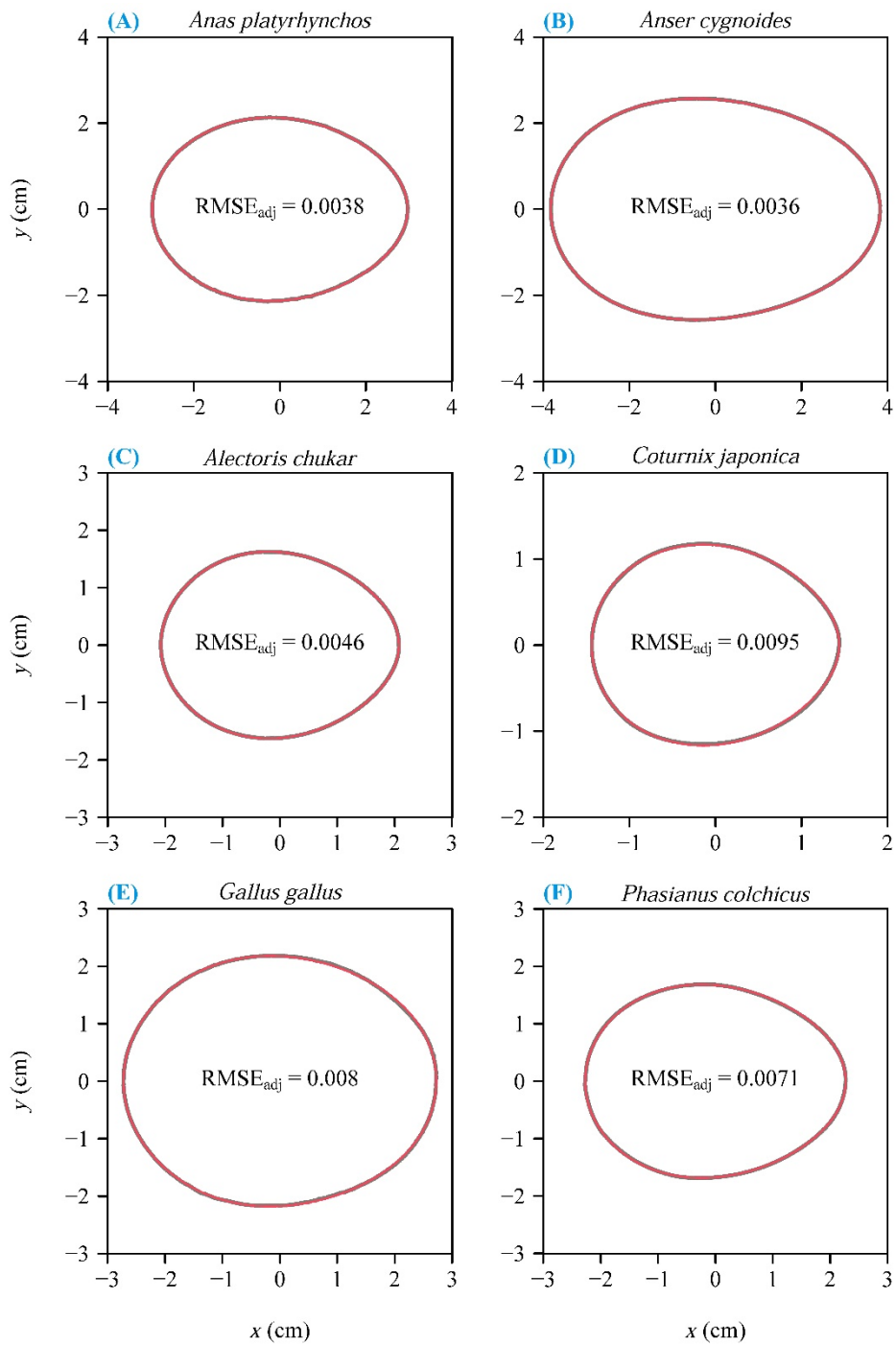


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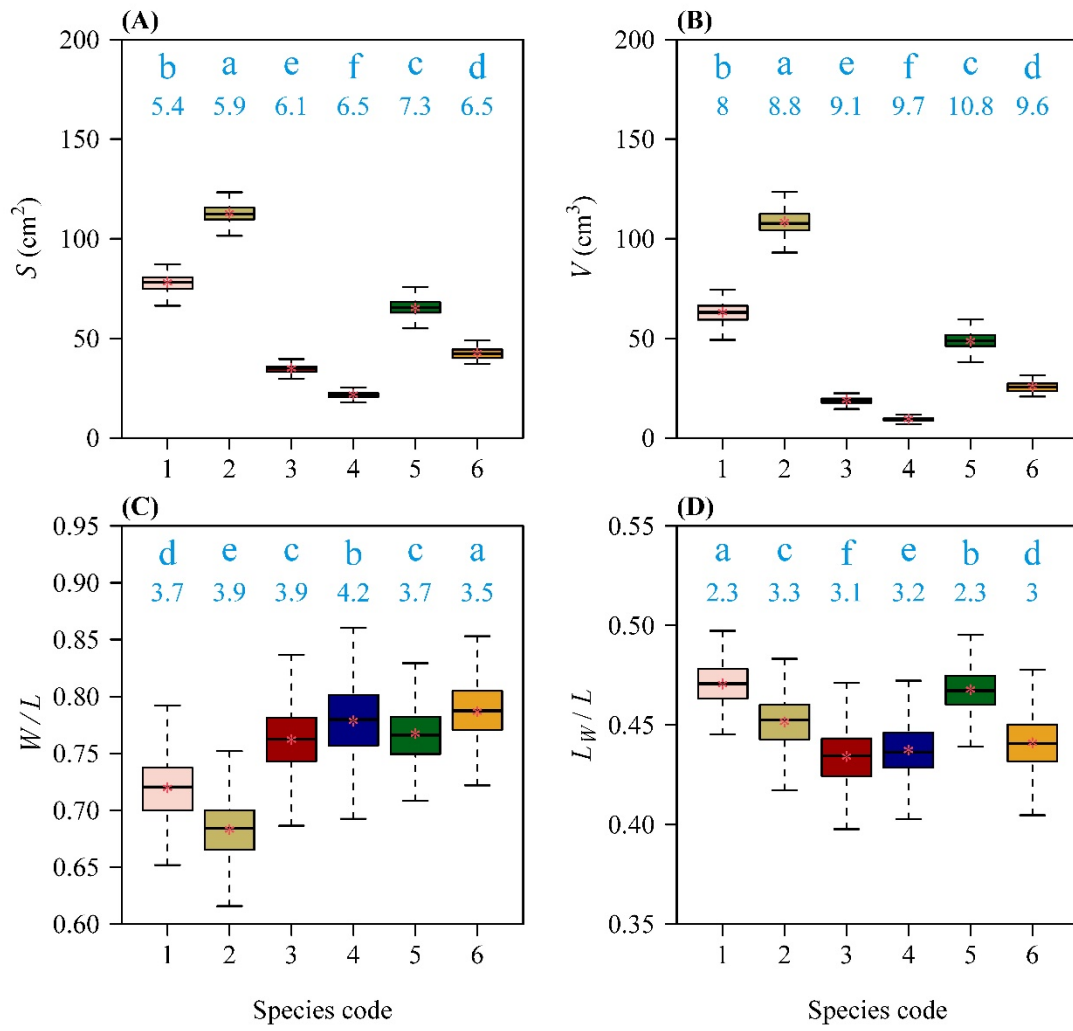


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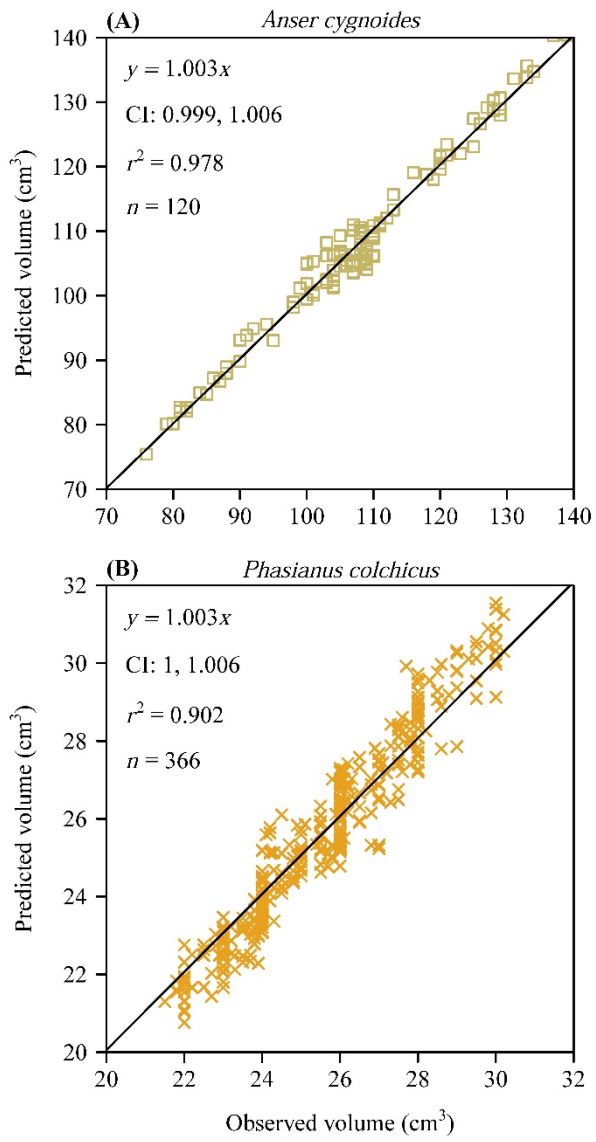


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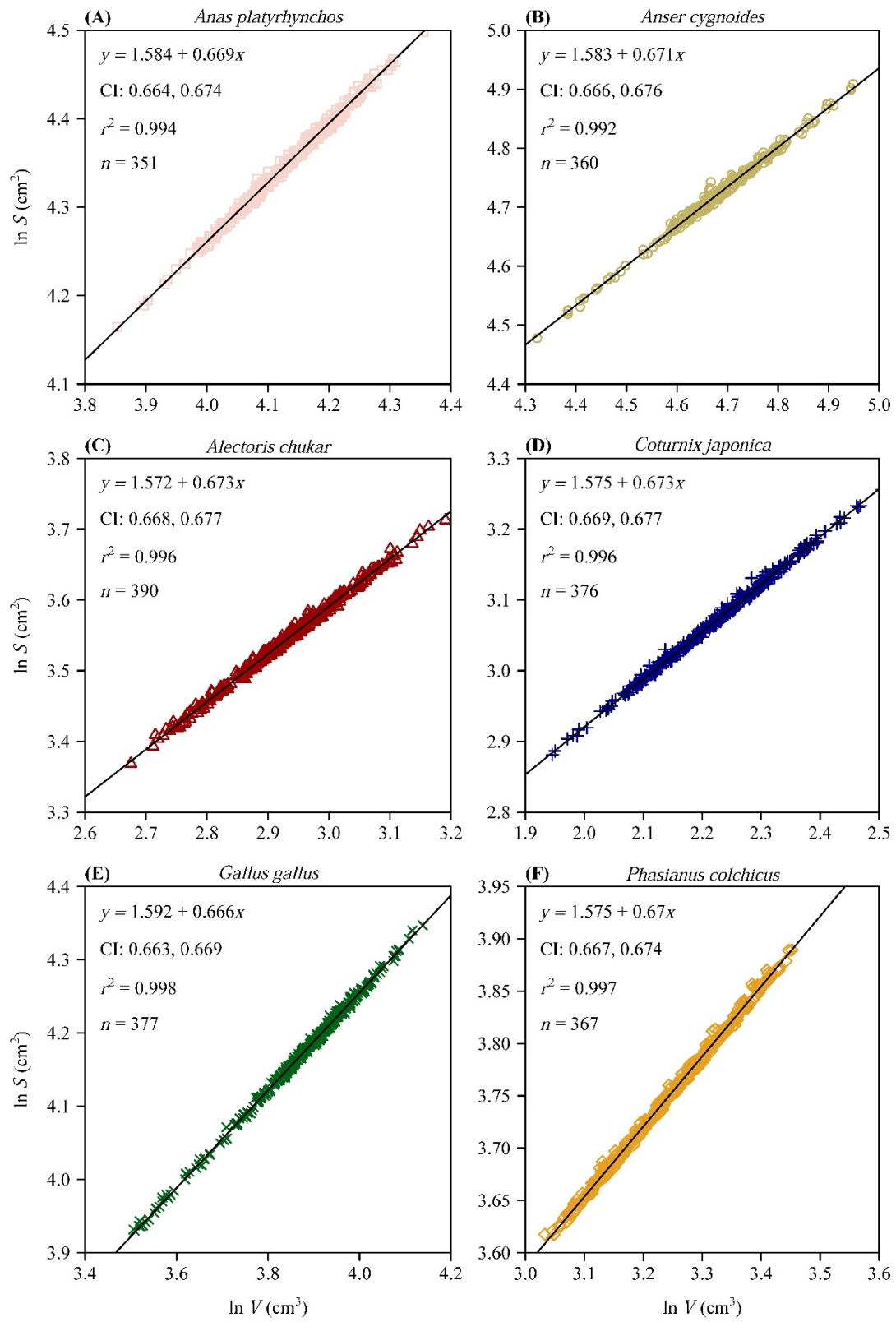


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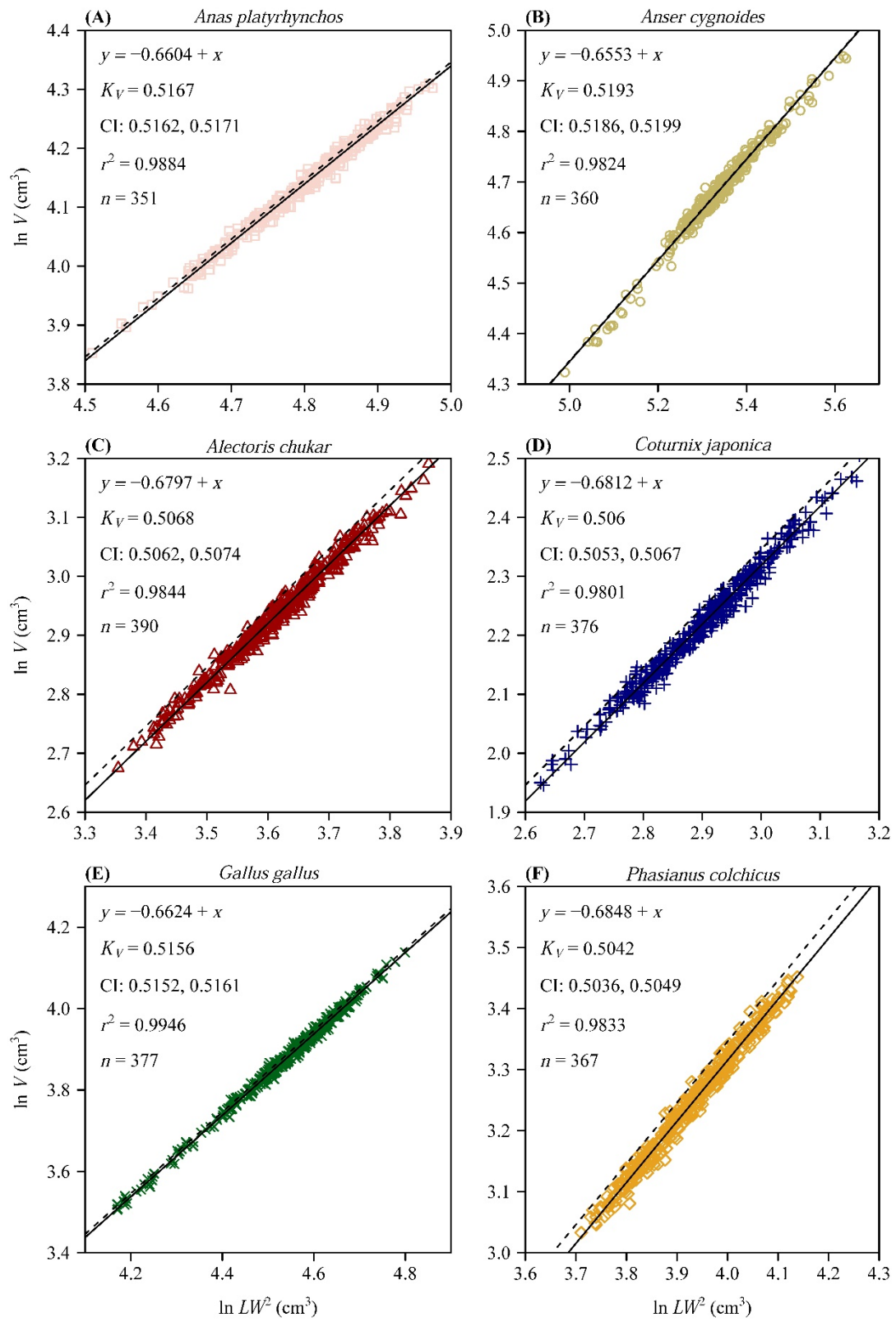


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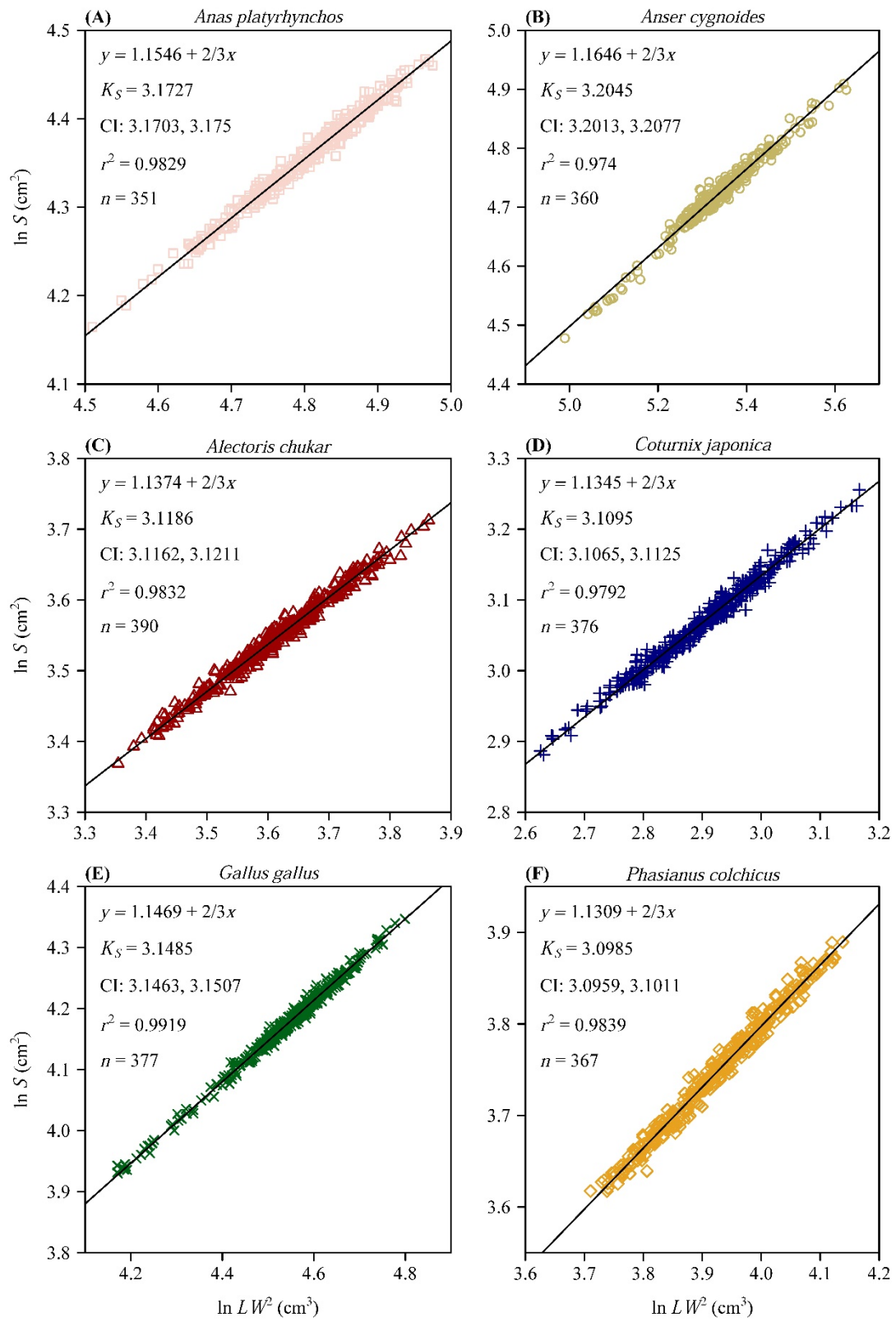


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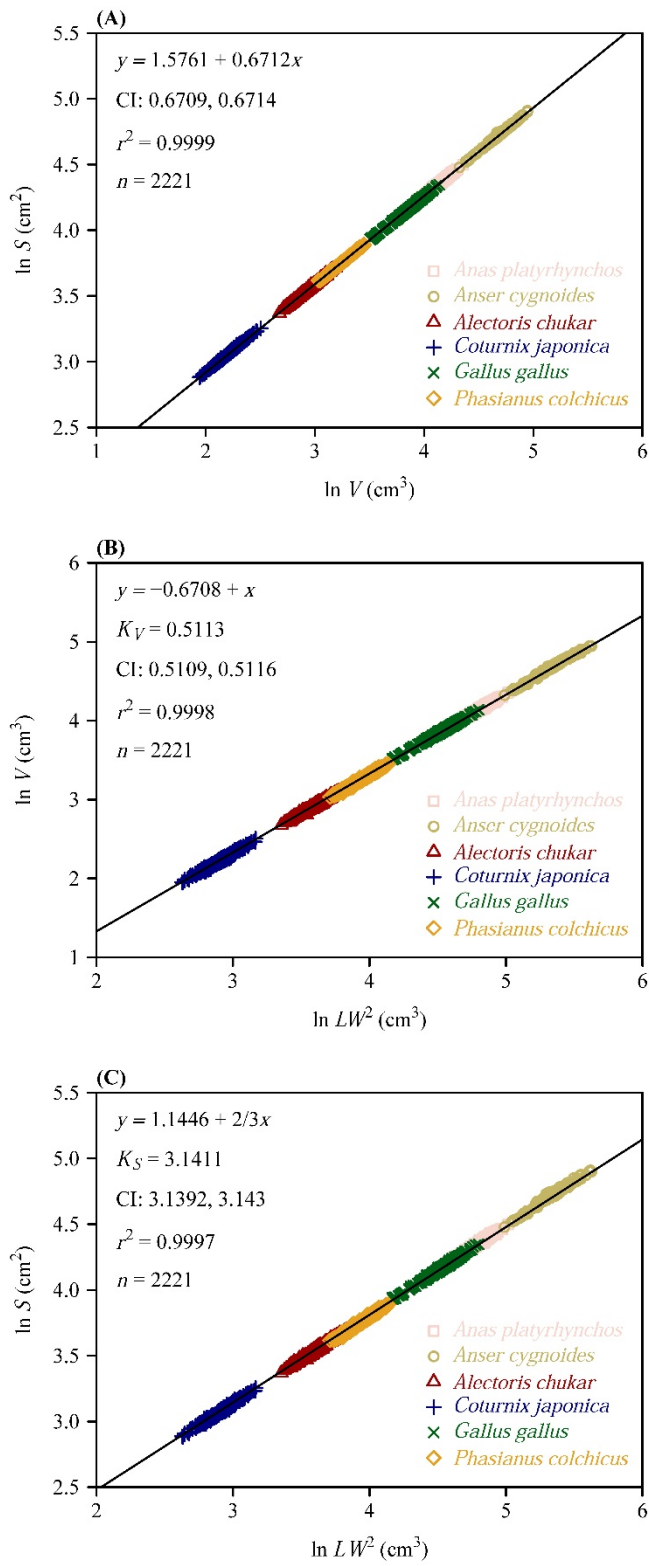


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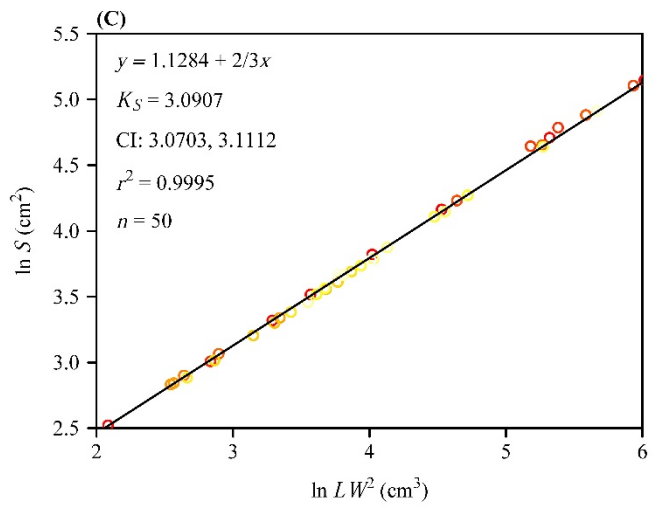
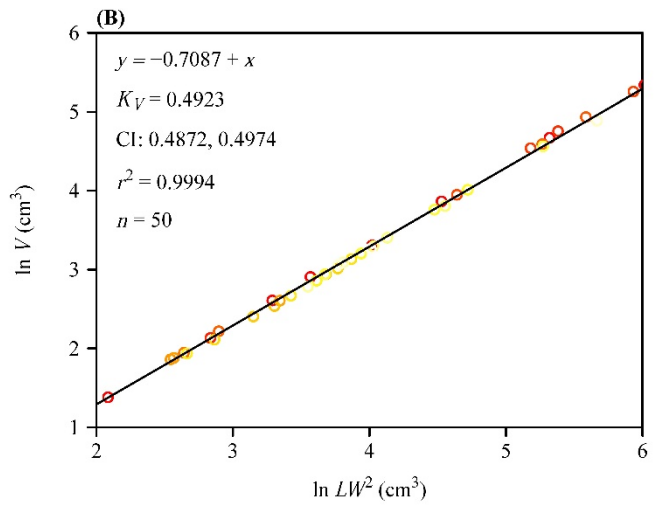
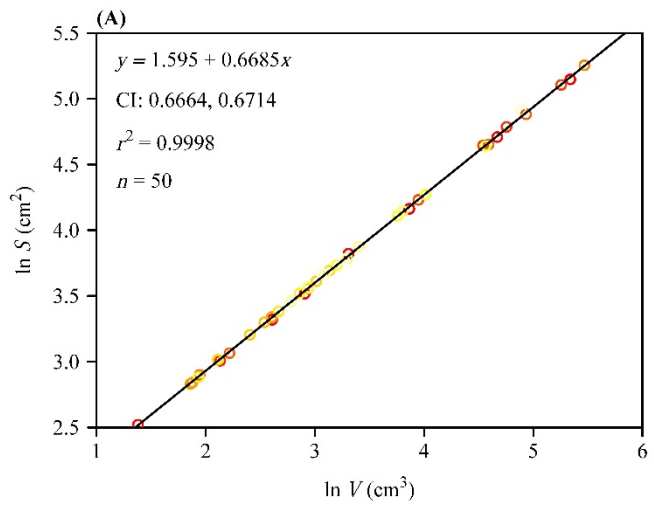


Figure 11