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INVITED PAPER

Scaling Relationships among the Mass of Eggshell, Albumen, and Yolk in Six Precocial Birds

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Synopsis The proportions in the size of the avian egg albumen, yolk, and shell are crucial for understanding bird survival and reproductive success because their relationships with volume and surface area can affect ecological and life history strategies. Prior studies have focused on the relationship between the albumen and the yolk, but little is known about the scaling relationship between eggshell mass and shape and the mass of the albumen and the yolk. Toward this end, 691 eggs of six precocial species were examined, and their 2-D egg profiles were photographed and digitized. The explicit Preston equation, which assumes bilateral symmetrical geometry, was used to fit the 2-D egg profiles and to calculate surface areas and volumes based on the hypothesis that eggs can be treated as solids of profile revolution. The scaling relationships of eggshell mass (M_s), albumen mass (M_a), and yolk mass (M_y), as well as the surface area (S), volume (V), and total mass (M_t) were determined. The explicit Preston equation was validated in describing the 2-D egg profiles. The scaling exponents of M_a vs. M_s, M_y vs. M_s, and M_y vs. M_a were smaller than unity, indicating that increases in M_a and M_y fail to keep pace with increases in M_s, and that increases in M_y fail to keep pace with increases in M_a. Therefore, increases in unit nutrient contents (i.e., the yolk) involve disproportionately larger increases in eggshell mass and disproportionately larger increases in albumen mass. The data also revealed a 2/3-power scaling relationship between S and V for each species, that is, the simple Euclidean geometry is obeyed. These findings help to inform our understanding of avian egg construction and reveal evolutionary interspecific trends in the scaling of egg shape, volume, mass, and mass allocation.

Introduction

The avian egg is a highly integrated biological microecosystem, and egg size is one of the key factors influencing resource investment and the survival rate of birds (Finkler et al. 1998). However, egg size can be measured using different metrics, that is, mass, volume, and surface area (Narushin and Romanov 2002; Biesek et al. 2023). Among these, mass is generally regarded as a reliable predictor because it can reflect the quantity of nutrients stored within an egg (Asmundson and Baker 1943; Collins and Lecory 1972; Ricklefs 1977; Carey et al. 1980; Warham 1983; Troscianko 2014). Typically, egg mass includes the mass of the yolk, albumen, and eggshell (Warham 1983). The yolk is a lipid-rich substance that possesses antibodies. It serves as the primary energy source (Criste et al. 2020). In contrast, albumen is high in water content and provides hydration (Campbell et al. 2003). Finally, the eggshell protects the yolk and albumen and provides extra calcium to the developing bird (Simkiss 1961; Paganelli et al. 1974). In addition, its surface area influences the exchange of atmospheric gases between the embryo and the external environment, which in turn is influenced by the scaling relationship between egg volume and surface area. Collectively, these features affect the developing embryo as it matures within the egg environment and

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draws on its nutritional resources (Dawson and Clark 1996).

Prior studies have primarily focused on the relationship between yolk mass and albumen mass (Asumndson et al. 1943; Collins and LeCory 1972). For example, Warham (1983) examined 23 species of Procellariiformes and found that larger eggs tend to contain less yolk and more albumen than smaller ones. Because the relationship between the yolk and albumen affects the nutritional reserves and body size of newborns, thereby directly altering adaptability and competitiveness (Carey et al. 1980), investigators have proposed theoretical models for explaining the relationship between yolk and albumen mass in the eggs of different species in the context of other factors such as female size and the ambient environment (Birkhead 1985; Badzinsik et al. 2001; Birchard and Deeming 2015). One of the classical developmental models proposes that the allocation of resources should be maximized (Collins and LeCory 1972; Ricklefs 1977).

However, the properties of the eggshell, such as mass and surface area, are rarely mentioned and are usually considered perfunctorily as auxiliary features in the relationship between albumen and yolk (Asmundson and Baker 1943; Warham 1983; Finkler et al. 1998). However, the characters of the eggshell are reported to have a significant influence on the hatching rate of bird eggs (Dyke and Kaiser 2010; Ortiz-Santaliestra et al. 2020). For example, the proportion of eggshell mass to total egg mass is reported to increase with increasing total egg mass, such that eggs with thicker and heavier shells are more likely to hatch successfully than those with thinner and less heavy shells (Asmundson and Baker 1940; Warham 1983; Dawson and Clark 1996; Narushin and Romanov 2002). Based on a broad sample of bird species, the relationship between yolk and albumen content is strongly correlated with the degree of embryo maturation (altricial vs. precocial) and the elongation of the egg, whereas eggshell mass is strongly correlated with the asymmetry of the egg and the body mass of the parent (Birchard and Deeming 2009; Deeming 2018).

It is important to note that most functional egg traits, like many biological features, appear to conform with power-law functions taking the form $Y = \beta X^{\alpha}$, where Y and X are any two interdependent variables of interest (e.g., mass and volume), α is the scaling exponent (i.e., the slope of the ln-ln linear regression of Y against X), and β is the normalization constant (i.e., the Y-intercept of the ln-ln linear regression of Y against X) (Paganelli et al. 1974; Rahn and Ar 1974; Rahn et al. 1975; Birkhead 1985; Dawson and Clark 1996; Badzinsik 2001; for a general review, see Niklas 1994). It is apparent that $dY/dX \propto X^{\alpha-1}$ and $\alpha = \frac{dY/Y}{dX/X}$. When α is greater than unity (i.e., $\alpha - 1 > 0$), the derivative of Y with respect to X is an increasing function of X; when α is smaller than unity (i.e., $\alpha - 1 < 0$), the derivative of Y with respect to X is a decreasing function of X; when α is equal to unity (i.e., $\alpha - 1 = 0$), the derivative of Y with respect to X is a constant. In general, the numerical value of α is seldom equal to unity, that is, allomeric relationships are generally seen in the scaling relationships among animal or plant functional traits (Niklas 1994). This broad generalization provides a hypothesis for the scaling of egg functional traits, particularly regarding the scaling of water and nutrient egg contents with respect to eggshell mass. Specifically, we hypothesized that increases in the albumen and yolk mass do not keep pace with the increases in eggshell mass, that is, the derivative of albumen or yolk mass with respect to eggshell mass is a decreasing function of eggshell mass. This hypothesis is predicated on the supposition that larger eggs require thicker shells to provide mechanical rigidity. This hypothesis also rests on the functional relationships of the albumen and the yolk. Given that the albumen provides an aquatic environment for the yolk and that it serves as a hydrostatic "damping device" that can protect the yolk from excessive mechanical perturbations, it is not unreasonable to suppose that the scaling exponent of yolk mass vs. albumen mass will be less than unity, that is, increases in yolk mass will fail to keep pace with increases in albumen mass.

In addition to variables such as mass and volume, egg shape has received considerable attention (Preston 1953; Bridge et al. 2007; Troscianko 2014; Shi et al. 2023a). For example, Paganelli et al. (1974) report that the surface area (S) versus volume (V) scaling relationship of eggs obeys a 2/3–power rule, a finding that has been explored and verified using an explicit Preston equation (denoted henceforth as EPE) by Shi et al. (2023a) based on the assumption that the egg is a solid of revolution. However, it remains unknown whether the scaling relationships among the masses of the eggshell, yolk, or albumen obey similar rules, although a scaling relationship between egg mass and egg volume (or egg surface area) has been reported (Paganelli 1974). If these scaling relationships hold true across species, it should be possible to non-destructively estimate the proportions of eggshell, albumen, and yolk simply by photographing an egg and quantifying its shape. Indeed, it is feasible to non-destructively measure egg volume and surface area egg using 2-D imaging protocols (Shi et al. 2023a).

To explore the scaling relationships among the foregoing egg functional traits, we examined 691 eggs from six avian species (two species of Anatidae and four species of Phasianidae) and measured the mass of their eggshells (M_s), albumen (M_a), and yolks (M_y) to determine the scaling relationships among these variables

Table 1 Sampling information of avian eggs

Scientific Name	Location	Arrival Date	Number	Family
Anas platyrhynchos	Hanshan, Ma'anshan, Anhui Province	May 22, 2022	111	Anatidae
Anser cygnoides	Shouguang, Weifang, Shandong Province	May 26, 2022	120	Anatidae
Alectoris chukar	Liyang, Changzhou, Jiangsu Province	October 22, 2022	120	Phasianidae
Coturnix japonica	Hanshan, Ma'anshan, Anhui Province	May 22, 2022	112	Phasianidae
Gallus gallus	Hanshan, Ma'anshan, Anhui Province	May 22, 2022	116	Phasianidae
Phasianus colchicus	Shanghe, Jinan, Shandong Province	October 12, 2022	112	Phasianidae

using reduced major axis regression protocols (Niklas 1994). In addition, the scaling relationship between S and V was determined.

Materials and methods

Egg sampling

To engage the variation in the egg size and shape, six avian (commercialized and therefore unprotected) species were used, that is, the two species of Anatidae (*Anas platyrhynchos domesticus* and *Anser cygnoides domesticus*) and four species of Phasianidae (*Alectoris chukar domesticus*, *Coturnix japonica domesticus*, *Gallus gallus domesticus*, and *Phasianus colchicus domesticus*). There were in total 691 eggs, ranging between 111 and 120 eggs per species (Table 1). The geometries of the six species of eggs span a broad spectrum of egg morphospace (Fig. 1).

Data acquisition

To obtain the mass of the three components of each egg, the eggs were placed into a stainless-steel pan (ST24P1; SUPOR Limited by Share Ltd., Zhejiang, China) and boiled for ca. 30 min. After cooling them in cold water, each egg was separated into its components, and the eggshell, yolk, and albumen were weighed separately using an electronic balance (ME204/02, Mettler Toledo Company, Greifensee, Switzerland; measurement accuracy 0.0001 g). The total mass (M_t) of each boiled egg was obtained by summing the masses of the three parts.

Calculation of egg surface area and volume

To determine surface area (S) and volume (V), each fresh egg was photographed by one of two smartphones held by an adjustable tabletop phone mount. Because of their different sizes (see Fig. 1), one smartphone (Huawei P30Pro, Huawei, Dongguan, China) was used to photograph the eggs of *A. platyrhynchos*, *A. cyanides*, *C. japonica*, and *G. gallus*, and another smartphone (Redmi K40S, Xiaomi, Kunshan, China) was used to photograph the eggs of *A. chukar* and *P. colchicus*. Each egg image was saved as a bitmap (i.e., bmp) file at a resolution of 600 dpi by Photoshop (version 13.0; Adobe, San Jose, CA, USA). The Matlab (version $\geq$ 2009a; MathWorks, Natick, MA, USA) procedure was used to extract the planar coordinates of the 2-D profile of each egg (Shi et al. 2018; Su et al. 2019). The "adjdata" function of the "biogeom" package (version 1.3.5; Shi et al. 2022) based on R software (version 4.2.0; R Core Team 2022) was subsequently used to obtain 2000 approximately equidistant data points for each profile.

The S and V of each egg were predicted using the explicit Preston equation (denoted as the EPE hereinafter) (Preston 1953; Shi et al. 2023a).

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

where x and y represent the x- and y-coordinates of a 2-D egg profile in the plane, a is half of the egg length, b is approximately half of the egg's maximum width, and c_1, c_2, and c_3 are parameters to be estimated. The positive and negative signs in the equation represent the upper and lower parts of an egg, with its midline (i.e., the egg length axis) aligned on the x-axis. Based on the hypothesis of the solid of revolution, the S and V were calculated using the formulae (Narushin et al. 2022; Shi et al. 2023a):

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

and

$$V = \pi \int_{-a}^{a} y^2 dx \tag{3}$$

where dy/dx represents the first-order derivative of Equation (1). A prior study has demonstrated that avian egg geometry is a solid of revolution by comparing the predicted V using Equation (3) and the observed V using a graduated cylinder method described by Shi et al. (2023a).

The "fitEPE" function in the "biogeom" package (Shi et al. 2022) based on R (R Core Team 2022) was used to fit the data points to estimate the values of a, b, c_1, c_2, and c_3 based on the Nelder-Mead optimization

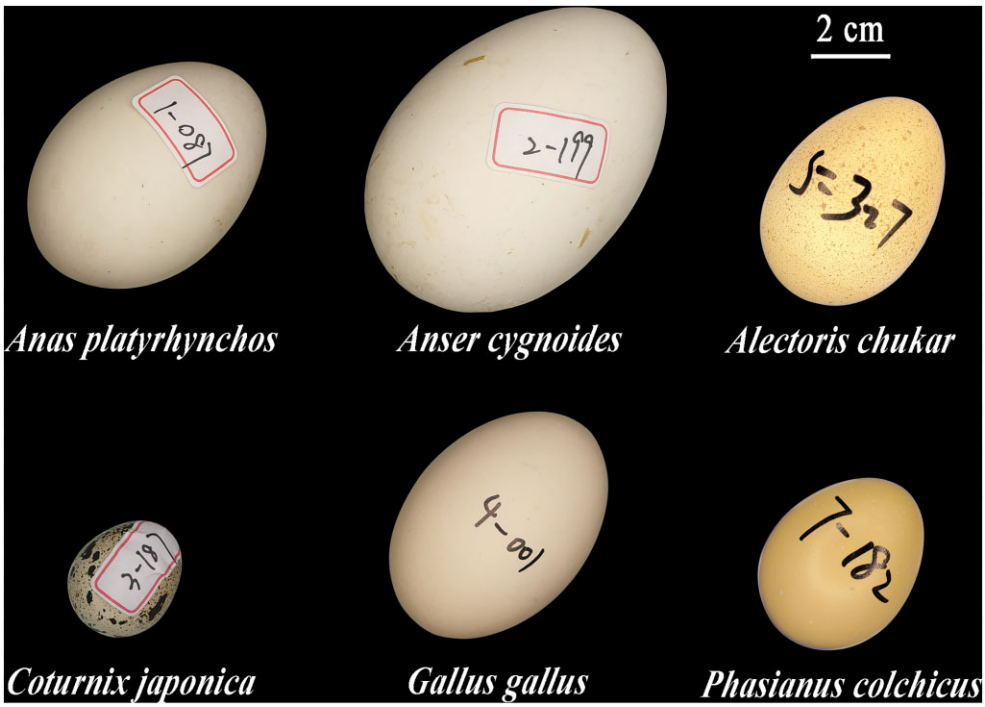

Fig. 1 Representative examples of the eggs of the six studied bird species.

protocols (Nelder and Mead 1965) by minimizing the residual sum of squares (RSS) between the observed and predicted y values. The adjusted root-mean-square error ($RMSE_{adj}$) was used to measure the goodness of fit (Shi et al. 2023a).

$$RMSE_{adj} = \frac{\sqrt{RSS/N}}{W/2} \quad (4)$$

where N represents the number of data points on an egg's profile, and W represents the maximum width of the egg.

Statistical analysis

The power function was used to describe the scaling relationships between any two variables (i.e., M_a vs. M_s, M_y vs. M_s, M_y vs. M_a, M_t vs. V, M_t vs. S, S vs. V):

$$Y = \beta X^{\alpha} \quad (5)$$

where X and Y represent two interdependent variables; β represents a normalization constant; α is the scaling exponent of Y to X. To stabilize the variance of Y, both sides on the power function equation of Y and X were ln-transformed (Niklas 1994):

$$y = \gamma + \alpha x \quad (6)$$

where $y = \ln Y$, $x = \ln X$, and $\gamma = \ln \beta$. The intercept and slope of the regression line were estimated using reduced major axis protocols (Niklas 1994; Quinn and Keough 2002; Smith 2009).

Tukey's honestly significant difference (HSD) test with a 0.05 significance level (Hsu 1996) was used to test whether there were significant differences in the $RMSE_{adj}$ values of the EPE fit across the six species. The bootstrap percentile methods (Efron and Tibshirani 1994; Sandhu et al. 2011) were used to estimate the 95% confidence intervals (CIs) of the slope and intercept of the regression line. All statistical analyses were performed using R (version 4.2.0; R Core Team 2022).

The sample size of eggs varied, albeit slightly, across the six species, ranging between 111 and 120 (Table 1). Because this variation might potentially influence estimates of the numerical values of scaling exponents and Y-intercepts, we randomly sampled 100 eggs from each of the six species and pooled the 600 samples into one data set. We then used reduced major axis protocols to estimate the two statistical parameters using 3000 random samples of 100 eggs drawn from the pooled data set of 600 eggs. The median, lower, and upper bounds of the 95% CI for the scaling exponents and Y-intercepts were calculated to determine whether the 111 and 120 sample size differences across the six species significantly influenced the estimates of the two statistical parameters.

Results

$RMSE_{adj}$ from the EPE for all eggs ranged from 0.0020 to 0.0200, which demonstrated the validity of EPE in

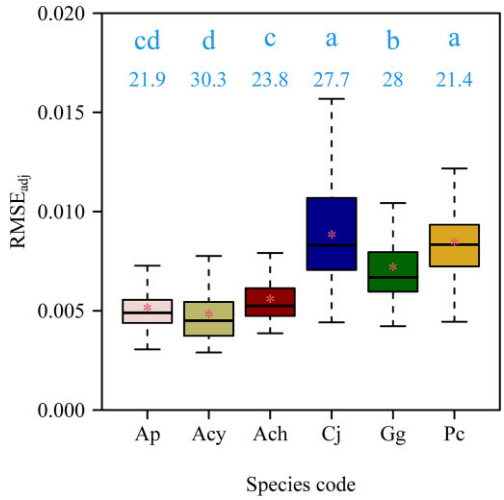

Fig. 2 RMSE$_{adj}$ using the EPE for the profiles of the eggs of the six avian species. The numbers above the whiskers represent the coefficients of variation (%) in the RMSE$_{adj}$ values for the six species of bird eggs; the lowercase letters a–d above the numerical values on the top of each box indicate the significance of the difference in the means between any two species based on the Tukey's HSD test. Means with different letters are significantly different at $P < 0.05$. The horizontal solid lines represent the medians, and the asterisks within boxes represent the means. In the *x*-axis label, "Ap," "Acy," "Ach," "Cj," "Gg," and "Pc" represent *A. platyrhynchos*, *A. cygnoides*, *A. chukar*, *C. japonica*, *G. gallus*, and *P. colchicus*, respectively.

depicting the 2-D profiles of each egg (Fig. 2). Figure 3 shows the fitted results of EPE for the 2-D profiles of six egg samples shown in Fig. 1.

There were statistically significant ln-ln linear scaling relationships between albumen mass (M_a) and eggshell mass (M_s), between yolk mass (M_y) and M_s, between M_y and M_a, between total mass (M_t) and volume (V), between M_t and surface area (S), and S and V (Fig. 4). In each case, the 95% CIs of the scaling exponents did not include zero, and the coefficients of determination exceeded 0.95 (Fig. 4). The numerical values of the scaling exponents of M_a vs. M_s, M_y vs. M_s, M_y vs. M_a, M_t vs. V, and S vs. V were significantly smaller than unity, whereas that of the scaling exponent of M_t vs. S was significantly greater than unity. The data indicated that (1) the increases of M_a did not keep pace with the increases in M_s; (2) the increases of M_y did not keep pace with the increases in M_s; (3) the increases of M_y did not keep pace with the increases in M_a; (4) the increases of M_t did not keep pace with the increases in V; (5) the increases of S did not keep pace with the increases in M_t; and (6) the increases of S did not keep pace with the increases in V. Thus, with increasing egg size, the increases in yolk and albumen mass did not keep pace with the increases in eggshell mass. Finally, the numerical value of the scaling exponent of S vs. V was equal to 0.672, that is, the scaling exponent was numerically approximately equal to 2/3.

The 111 and 120 inequality in egg sample size across the six species did not significantly influence the estimates of the numerical values of Y-intercepts and scaling exponents (Table 2 and Fig. 4). The point estimates of Y-intercepts and scaling exponents of each scaling relationship were approximately equal to the medians of 3000 replicates based on the 600 samples (i.e., 100 eggs for each species), and the medians of 3000 replicates fell within the 95% CIs of the corresponding Y-intercept and slope (Table 2 and Fig. 4).

Discussion

The analyses presented here indicate that (1) statistically strong scaling relationships exist among all of the variables of interest examined in this study; (2) increases in yolk and albumen mass fail to keep pace with increases in total egg mass; (3) eggshell mass increases disproportionately within increasing overall egg size; (4) the surface area to volume scaling relationship of the eggs of each species obeys a 2/3 power rule; and (5) the EPE correctly predicts egg surface area and volume non-destructively. These results are consistent with tradeoffs among the three functionally specialized components of the avian egg, that is, protection (the eggshell), hydration (the albumen), and nutrient reserves for embryo development (the yolk). Overall, a larger yolk requires a disproportionately larger quantity of albumen (presumably to remain hydrated), which in turn requires a disproportionately larger (thicker) egg shell for protection. Compounding these interdependent relationships is the surface area to volume scaling relationship because total egg size (as guaged by volume) has an effect on egg surface area, which exposes the egg to dehydration and is confined to a 2/3 (Euclidian) geometry. These findings are discussed in greater detail in the following sections.

Scaling relationship between yolk mass and albumen mass

There is a large variation in the ratio of yolk mass (M_y) to albumen mass (M_a) across the eggs of avian species (Ricklefs 1977). However, the results presented here indicate that there is a statistically strong scaling relationship between M_y and M_a (Fig. 4C), such that the M_y/M_a ratio depends on egg size. Increases in M_y tend to correlate with disproportionate increases in M_a, which is in accord with the results reported by Warham (1983) based on 23 species of Procellariformes. This phenomenology may be explained by the fact that the albumen contains a large amount of water, which is used for embryo development and is gradually lost

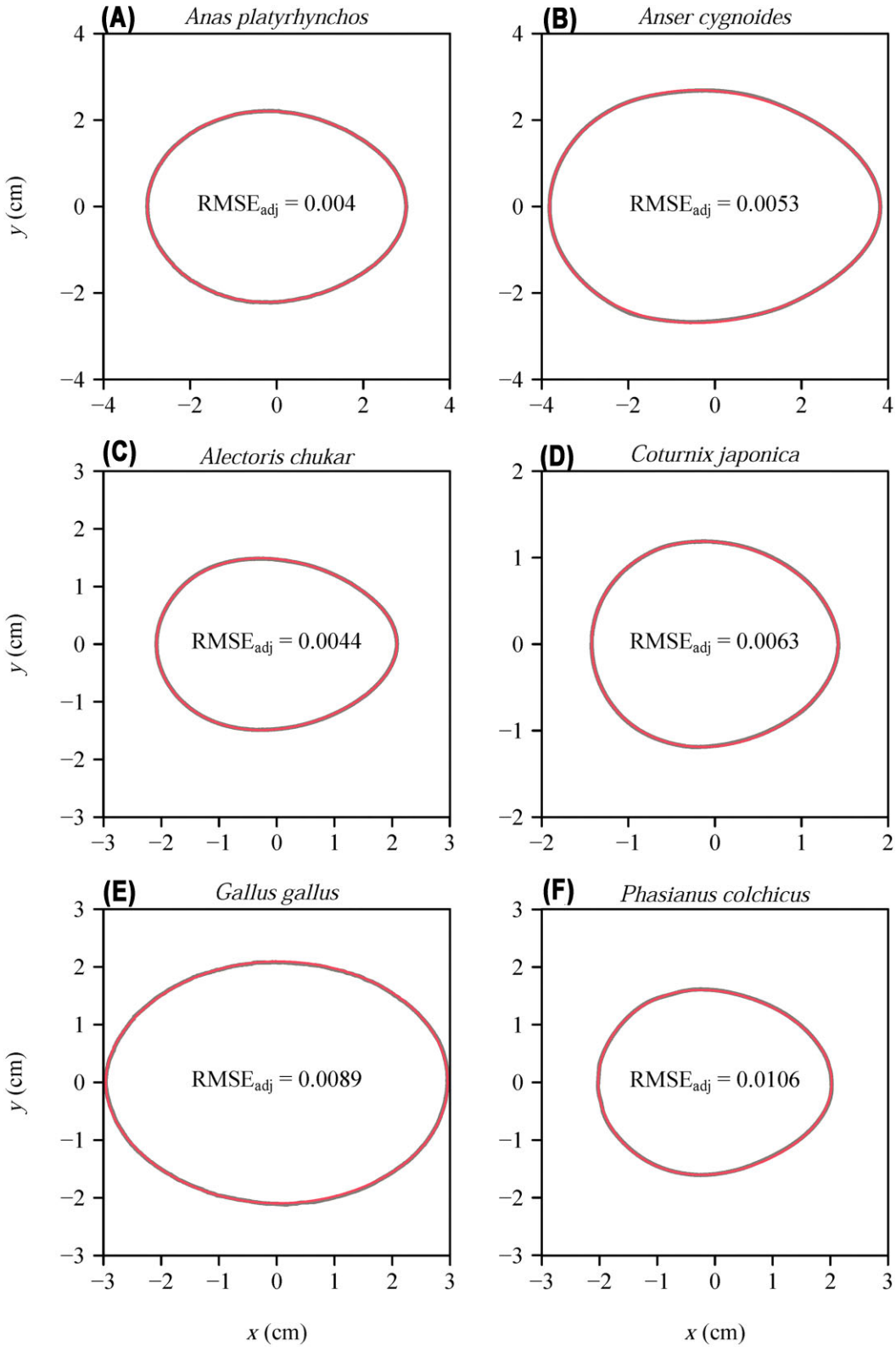

Fig. 3 Observed (gray) and predicted (red) geometries (boundary coordinates) of representative eggs of the six avian species. The red curves were predicted by using the EPE. $RMSE_{adj}$ represents the adjusted RMSE, which equals the ratio of the RMSE between the observed and predicted *y*-values to half the egg's maximum width. Panels (A–F) represent different species.

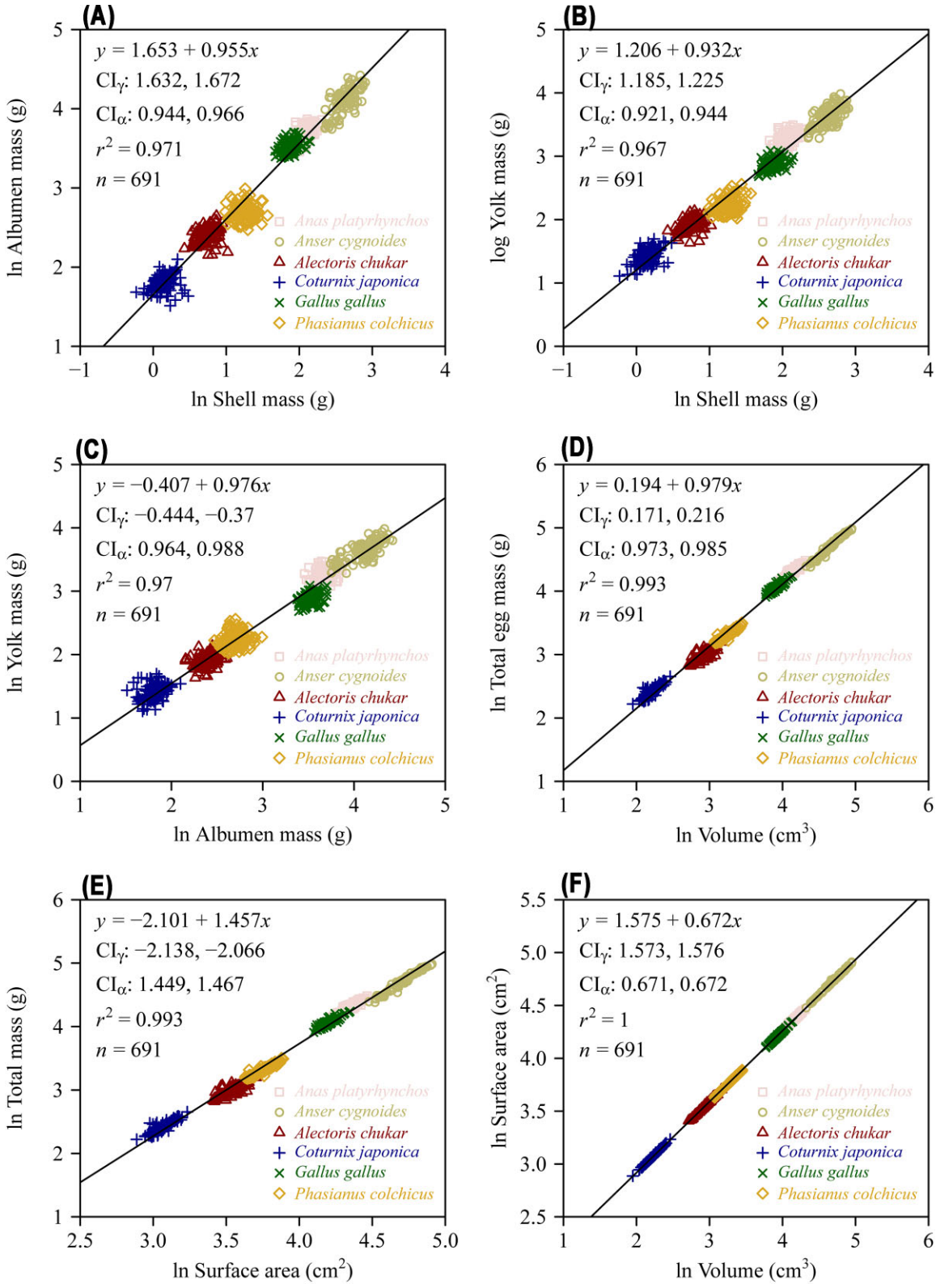

Fig. 4 Bivariate scaling relationships between albumen mass and shell mass (A), yolk mass and shell mass (B), yolk mass and albumen mass (C), total egg mass and egg volume (D), total egg mass and egg surface area (E), and egg surface area and egg volume (F) for pooled data of the eggs of the six avian species. In each panel, the solid line is the regression line; CI_α represents the 95% CIs of the scaling exponent (i.e., the slope); CI_γ represents the 95% CIs of the intercept; r^2 is the coefficient of determination; and n is the sample size

Table 2 Medians and the 95% CIs of the scaling exponents and *Y*-intercepts based on 3000 balanced random samplings

Scaling	γ.Median	γ.LCI	γ.UCI	α.Median	α.LCI	α.UCI
M_a vs. M_s	1.651	1.644	1.658	0.956	0.952	0.960
M_y vs. M_s	1.205	1.199	1.212	0.933	0.929	0.937
M_y vs. M_a	-0.406	−0.419	−0.393	0.976	0.972	0.980
M_t vs. V	0.195	0.190	0.200	0.979	0.978	0.980
M_t vs. S	−2.100	−2.108	−2.093	1.458	1.456	1.460
S vs. V	1.575	1.574	1.575	0.672	0.671	0.672

Here, α and γ represent the scaling exponent and *Y*-intercept, respectively; Median, LCI, and UCI represent the median, lower, and upper bounds of the 95% CIs of the 3000 replicates of the scaling exponent or *Y*-intercept. There are scaling relationships between albumen mass (M_a) and eggshell mass (M_s), between yolk mass (M_y) and M_s, between M_y and M_a, between total mass (M_t) and egg volume (V), between M_t and egg surface area (S), and between S and V. Note: relative to the width of the 95% CI for each parameter based on the 3000 bootstrap replicates (Fig. 4), the width of the 95% CI for each parameter here is smaller, which was caused by not permitting replaceable samplings.

through the eggshell over time. Therefore, the larger the yolk (and therefore the embryo), the more water is required (Carey et al. 1980; Campbell et al. 2003). This scaling relationship has predictive value because M_y/M_a is reported to affect the incubation period, mobility, and the presence of primary plumage in newborn birds (Ricklefs 1977; Finkler et al. 1998; Badzinsik et al. 2001). Among the species examined in our study, the incubation period ranges between 15 days for the small eggs of *C. japonica* and about 32 days for the largest eggs of *A. cygnoides*. Due to the limitation of resources, there is a tradeoff between the mass of the yolk and the mass of the albumen for any given overall egg size (Finkler 1998; Christian 2002; Deeming and Birchard 2007).

To determine whether the scaling relationships among the three components of avian eggs might hold true for other precocial birds, we examined seven eggs of the blue peacock (*Pavo cristatus*) and seven eggs of the African ostrich (*Struthio camelus*) using the same protocols described for the six species examined in detail (Supplementary Table S1). In addition, we used the eggshell, albumen, and yolk data reported for 23 species of petrels published in Table 1 by Warham (1983), which were defined as "precocial birds" based on the proportion of their yolk mass to total egg mass (>24%). Warham (1983) used the mean data based on a very small egg sample for each wild bird species, ranging between 1 and 16 eggs (see Online Supplementary Table S1). Thus, there was no need to use the mean data for the six avian species examined in our study when carrying out linear regression analyses of the two combined data sets because the means reported by Warham (1983) are essentially single data points. The numerical values of the scaling exponents of M_a vs. M_s, M_y vs. M_s, and M_y vs. M_a were observed to change slightly, but did not statistically deviate from those reported for the six species (Fig. 5). Nevertheless, it is clear that larger data sets are required to provide canonical scaling relationships for other precocial birds.

Influence of boiling on the scaling relationship of yolk mass vs. albumen mass

Clearly, direct measurements of fresh non-boiled eggs are desirable. However, in practice, it is very difficult to accurately separate and measure the liquid albumen and yolk, even for an individual egg. For this reason, many prior studies have used the same protocol as adopted in our study (e.g., Curtis 1912; Warham 1983). However, according to one report (Warham 1983), boiling can reduce overall egg weight by as much as 1 — 3%, presumably because of water loss from the albumen, although the basis for this estimate is not made explicitly clear. Fortunately, in the present study, the numerical value of the scaling exponent of yolk mass vs. albumen mass is 0.976 (with a 95% CI of 0.964–0.988), which is significantly smaller than unity. If the albumen lost more water than the yolk, it would have further decreased the scaling exponent of yolk mass vs. albumen mass. Therefore, the conclusion that increases in yolk mass do not keep pace with the increases in albumen mass is not jeopardized (and actually reinforced if albumen water loss due to boiling occurs). Nevertheless, the effects of boiling on estimates of egg scaling relationships merit further investigation.

Eggshell and egg size

Previous studies have examined the correlation between M_s and M_t and have shown that increases in M_t tend to result in disproportionately larger increases in M_s (Paganelli et al. 1974). Here, we focused on the scaling relationships between M_y and M_s, and between M_a and M_s. The pooled data show that increases in M_a and M_y do not keep pace with the increases in M_s (Fig. 4A, B). These results are consistent with the mechanical role of the eggshell, which provides protection in tandem with coping with external and internal pressure, that is, maternal weight at hatching and tubal pressure, respectively (Deeming et al. 2006).

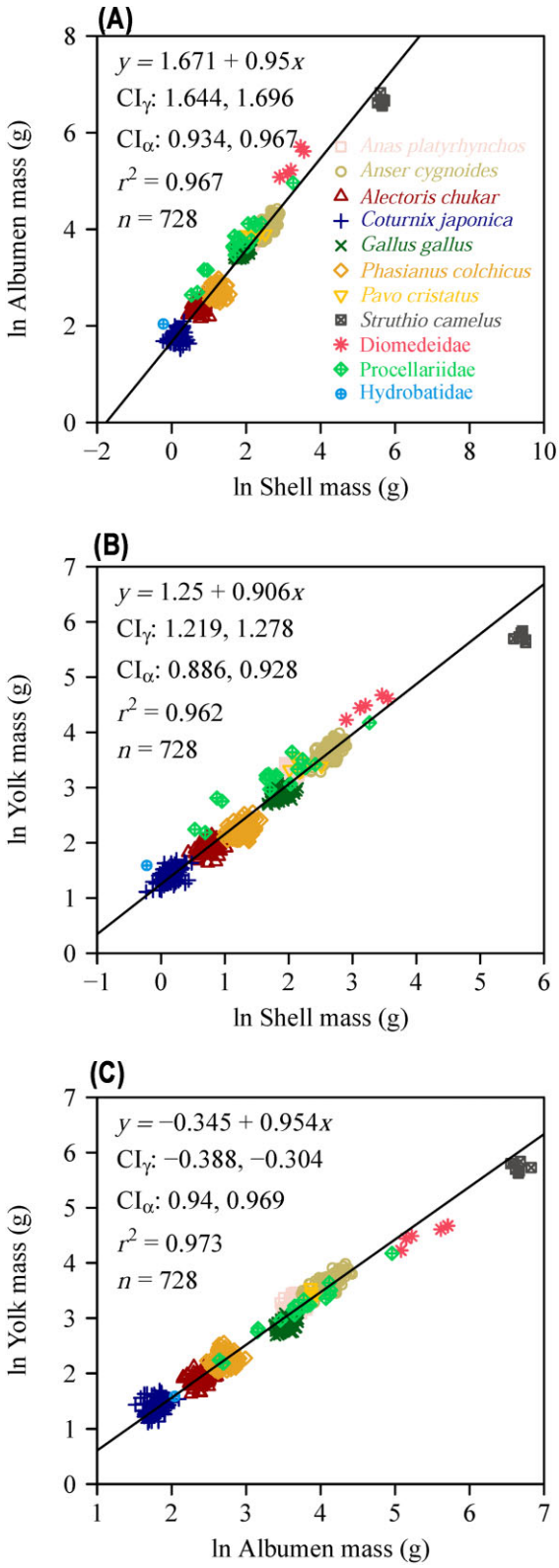

Fig. 5 Bivariate scaling relationships between albumen mass and shell mass (A), yolk mass and shell mass (B), and yolk mass and albumen mass (C) of 31 bird species. In each panel, the solid line is the regression line; CI_α represents the 95% CIs of the scaling exponent (i.e., the slope); CI_γ represents the 95% CIs of the intercept; r^2 is the coefficient of determination; and n is the sample size.

The correlation between egg mass and parental weight is widely confirmed; larger birds produce larger eggs than smaller birds (Paganellt et al. 1974; Deeming and Birchard 2007) because, during incubation, larger female birds sitting on eggs can provide higher accumulative heat for hatching eggs. If the eggshell is mechanically weak, it may break under the weight of the female, resulting in hatching failure. From an evolutionary perspective, eggshell thickness should scale positively with the weight of the hatching parent. In addition, the strong eggshells are necessary for birds to withstand external disturbances, such as wind pressures exerted on the nest or other disruptions (extreme winds causing the nest to move, careless handling by parents, and the behavior of predators), which can cause the eggshell to break (Kemal and Rothstein 1988). In addition, the embryos require calcium to develop their bones (Simkiss 1961), and larger shells can provide extra calcium, which can result in a heavier body in terrestrial animals and a stronger bone density in young birds hatching from larger eggs. In this context, it is worth mentioning that the thinning of bird eggshells due to chemical substances in the environment (such as acid rain and pesticides) poses a great threat to the survival of birds (Ortiz-Santaliestra et al. 2020).

2/3-power relationship between the *S* and *V* of bird eggs

Previous studies have demonstrated a significant correlation between M_t and V, that is, $r^2 = 0.98$ for Canada geese and $r^2 = 0.96$ for Lesser snow geese (Badzinsik et al. 2002), which is consistent with the results for the six species examined in our study ($r^2 = 0.99$). This provides a good basis for using mass to predict egg volume. In this context, it is worth mentioning that S and V are two important parameters for the poultry industry and related biological research, and provide insights for the investigation of population ecology and biomorphology, such as predicting body weight and hatching rate (Nedomova and Buchar 2013). For objects of similar in shape but differing in size, the relationship between S and V is known to follow $S = aV^{2/3}$. For example, Paganelli et al. (1974) obtained $S = 4.951V^{0.666}$ for the eggs of 29 species of wild and domestic birds. Our study also found a significant scaling relationship between S and V. Figure 4E shows that there is a scaling relationship between S and V for the pooled data. This 2/3 power-law relationship has been reported to be related to eggshell porosity (Asmundson and Baker 1940; Narushin and Michael 2002), which has implications for water loss and the exchange of oxygen between the egg (specifically the embryo) and the external atmosphere.

Conclusions

Based on the examination of 691 eggs from six avian species, the adjusted root-mean-square value for each egg was smaller than 0.05 for the EPE fit, which demonstrates the validity of using the EPE to describe egg shape. There were significant scaling relationships between the albumen mass (M_a) and the eggshell mass (M_s), between the yolk mass (M_y) and M_s, and between M_y and M_a, and the numerical values of the exponents were all significantly smaller than unity given that the upper bounds of the 95% CIs of the scaling exponents were all smaller than unity. The data indicate that increases in the nutrient reserve (the yolk) requires a disproportionate increase in the shell (a support cost) and the hydration reserve (the albumen). In addition, the total egg mass (M_t) is not proportional to the egg surface area (S) and volume (V), and increases in S fail to keep pace with the increases in V because of the 2/3-power relationship of spheroids such as eggs. These results likely hold true for other Anatidae and Phasianidae species and can inform our understanding of the evolution and reproduction of precocial birds.

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Supplementary data

Supplementary Data available at *ICB* online.

Conflict of interest

The authors declare that they do not have any conflict of interest.

Data availability

The data underlying this article are available in the Dryad Digital Repository (Shi et al. 2023b), at https://dx.doi.org/10.5061/dryad.f4qrfj719, and in the online supplementary material of this article.

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