Effect of composition on shape of bird eggs

Abstract:
Numerous studies over the past 90 years have described the various bird egg shapes in mathematical terms but few studies have considered the underlying reasons for such interspecific egg shape variability. This study investigated how the size and composition, i.e. proportions of shell, yolk and albumen, were associated with egg shape. Geometric morphometrics were used to generate principal components, which were analysed in relation to taxonomy (i.e. avian order) and degree of neonatal developmental maturity, which correlates with egg composition. The analysis confirmed previous results that most of the variation in shape is associated with degree of elongation (i.e. length divided by breadth) and asymmetry (i.e. position of the broadest part of the egg away from the mid-point of the egg’s length). Egg shape reflected both avian order but not developmental maturity. The degree of elongation of an egg is related to absolute egg mass and the proportion of yolk. By contrast, the degree of asymmetry is related to the proportion of shell and the mass of the egg relative to female body mass. Although significant, the models explained little of the variation in egg shape and so it was concluded that other factors, such as pelvis size and shape, could be more important in determining egg shape in birds.
Effect of composition on shape of bird eggs

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Keywords: birds, egg composition, eggshell outline, egg shape, morphospace

Short Title: Effect of composition in bird egg shape

The size and shape of bird eggs have long held a fascination for ornithologists. The size of an egg, be that measured as mass or as linear measurements, is of interest because it can be used to define the reproductive investment of the female, which may impact on its fitness (Lack 1968). By contrast, the underlying basis for egg shape is poorly understood despite being highly variable, ranging from the spherical barn owl *Tyto alba* egg (Deeming and Ruta 2014) to the highly pointed common guillemot *Uria aalge* egg (Birkhead et al. 2017). To date, most studies have focussed on how egg shape can be mathematically described, with only a couple of studies trying to define the function of various shapes.

The mathematical description of egg shape has a long history of research that continues to this day (e.g. Mallock 1925, Preston 1953, 1968, 1969, Smart 1967, 1969, Todd and Smart 1984, Narushin 1997, Baker 2002, Deeming and Ruta 2014, Troscianko 2014, Mytiai et al. 2017, Stoddard et al. 2017). Other than the challenge of describing a complex shape, the study of egg shape has been
useful in calculating volume or surface area of eggs (Hoyt 1976), and in assessing eggshell strength (e.g. Bain 1991, Anderson et al. 2004, Nedomova et al. 2009). Other studies use shape in comparisons of different populations of the same species or different species (Preston 1969, Johnson et al. 2001), and the relationships between brood parasites and their hosts (Bán et al. 2011). Shape has even been used in study of the evolution of amniote eggs with eggs being defined in terms of their degree of elongation, i.e. length divided by breadth, and their degree of asymmetry, i.e. position of the broadest part of the egg away from the mid-point of the egg’s length (Deeming and Ruta 2014). More recently, the role of the elongated and highly asymmetrical shape of the guillemot egg has been re-evaluated. Birkhead et al. (2017) concluded that, rather than to prevent eggs from rolling off cliff ledges, the pointed shape reflects a way of minimising eggshell surface contamination. In addition, Stoddard et al. (2017) found a correlation between egg shape and flight efficiency in birds, as determined by the hand-wing index, and suggested that flight adaption may have been a critical driver for egg shape variation.

Other studies have studied the role of shape in a reproductive context. For instance, Barta and Székely (1997) explored the reasoning that egg shape reflects the shape of the brood patch and so optimises contact incubation (Andersson 1978). It was concluded that optimal egg shape reflected clutch size although this idea has been challenged (Hutchinson 2000). However, the underlying mechanism that produces an egg of a specific shape has received very little attention. The consensus is that the wall of the oviduct resists deformation whilst peristaltic contractions hold the egg in place within the shell gland as the shell is forming (Romanoff and Romanoff 1949, Aitken 1971, Smart 1991) but the exact mechanism remains unclear. In addition to this idea, Barta and Székely (1997) suggested that egg shape may reflect differences in shell strength (Bain 1991) but offered no suggestion of how such shapes could be produced in the oviduct. Stoddard et al. (2017) correlated egg shape with characteristics of the pectoral limb but suggested that pelvis size may be of more interest. It has been pointed out that variability in egg shape reflects the variability in shape of the pelvic girdle between different bird orders; a round egg is associated with a short pelvis whereas longer pelves can accommodate more elongated eggs (Rensch 1949, Warham 1990). The lack of a description of how egg shape is achieved within the oviduct could be hampering our understanding of the function of egg shape because we are unable to confirm whether there has been selection for shape on the basis of reproductive parameters, e.g. water or energy content. It remains possible that egg shape is a consequence of other morphological features associated with a species’ life history, e.g. terrestrial locomotion (Anten-Houston et al. 2017), that is not directly related to reproduction.

Bird eggs vary in their size and composition across avian orders (Carey et al. 1980, Sotherland and Rahn 1987, Deeming 2007a, 2007b). Mytiai et al. (2017) found that phylogeny was important in determining egg shape, but found minimal effect of developmental maturities, which reflects differences in egg composition, using linear and geometric shape measurements. However, eggs that produce altricial offspring have a greater albumen to yolk ratio than eggs that produce
precocial offspring (Carey et al. 1980, Sotherland and Rahn 1987). It is possible that the differing amounts or proportions of the egg components are important in determining the shape of the laid egg. For instance, perhaps within the physical constraints of the tubular oviduct lying parallel to the long axis of the body, large amounts of albumen may only be accommodated cranially and caudally to the yolk as it moves down the oviduct, therefore forming an elongated egg.

This study investigated the relationships between egg composition and shape. I used geometric morphometrics to quantify egg shape (Deeming and Ruta 2014) in order to test the hypothesis that composition significantly affects both elongation of the egg and its degree of asymmetry. It was predicted that relatively small amounts of yolk, and conversely large amounts of albumen, would be associated with more elongated and asymmetrical eggs. Moreover, it was considered that the strong correlation between egg mass and female body mass (Deeming 2007a) would mean that the absolute and relative size (compared to female body mass) would not affect egg shape.

Methods

Egg shape was quantified using geometric morphometric methods applied to two-dimensional semi-landmarks along the egg outlines as described by Deeming and Ruta (2014). Using a Pentax dSLR digital photographs were taken of one egg from each of 181 species representing 16 orders of birds (see supplementary materials for list of species and data). Many of the images were taken at the Natural History Museum oological collection in Tring, UK, although a few images were taken of ratite eggs from my personal collection. Other images were used from a set of images collected for a previous study (Deeming and Ruta 2014).

Species were chosen on the basis that egg composition was available. Data for mean initial egg mass (IEM) for each species were obtained from literature sources or Schönwetter (1960-1985). The species were also allocated to one of four categories based on the degree of developmental maturity they express at hatching: precocial, semi-precocial, semi-altricial, and altricial (following Deeming 2007a, 2007b). Data for masses (in g) of shell, yolk and albumen, and female body mass (g), collated from the literature were available for each species from a database compiled by Deeming (2007a, 2007b).

Forty equally spaced semi-landmarks were digitized along the right-hand side of each egg outline using tpsDig2 v. 2.17 (Rohlf 2006). The landmark coordinates were transferred to MorphoJ v. 1.05f (Klingenberg 2011) and subjected to a principal component analysis of the variance-covariance matrix of Procrustes-fitted landmark coordinates, i.e. coordinates obtained after removal of scale, translation, and rotation.

The principal component scores (PC1 and PC2) of egg types were normally distributed (as tested in Minitab ver. 17). Pearson’s correlations carried out in Minitab (ver. 17) showed that PC1 and PC2 correlated with Log_{10} transformed values for initial egg mass (IEM). Phylogenetic independent
contrasts were calculated for PC1, PC2 and LogIEM using the ape package in R (R-core team) and correlations were re-run to assess the effect of phylogeny on the relationships between PC scores and LogIEM. Linear models in R (R-core team) were used to do analysis of variance to test for the effect of avian order on PC1 or PC2, and analysis of covariance to test for the effect of avian order on PC2 whilst controlling for PC1 as a covariate.

A phylogenetic tree of the species in the dataset was produced based on a Hackett bonebone using birdtree.org. Phylogenetically controlled general linear modelling (pglm) was performed in R using the packages ape, mvtnorm and MASS (code provided by Dr Carl Soulsbury, personal communication), to test for the effect of developmental maturity, which transcend avian order, on PC2 whilst controlling for PC1 as a covariate, and with interaction terms between developmental maturity and PC1. For further analysis masses of the egg were expressed as a proportion of female body mass, and masses of the individual egg components were expressed as proportions of IEM before being asin-transformed (Fowler et al. 1997) to normalise them prior to analysis. A phylogenetically controlled general linear model was used in R to test for the effects on PC1 or PC2 of egg mass as a proportion of female body mass, shell mass as a proportion of egg mass, and yolk mass as a proportion of egg mass. LogIEM, was only included in the model if there was a significant correlation with the Pc score following phylogenetic independent contrasts analysis. The proportion of albumen (of egg mass) was not included in the model because of the highly significant negative collinearity with the values for yolk.

Results

PC1 explained 82% of the variation and PC2 14% of the variation in egg shape within morphospace. Variation in the PC1 axis was associated with the degree of elongation of the egg with most variation in shape being seen at both ends of the egg and its equator (Fig. 1). More positive values reflected more spherical eggs whereas more negative values represented more elongated eggs (Fig. 2). By contrast, more positive values for PC2 scores were associated with greater asymmetry, with variation in shape at the two poles being opposite in direction and with the upper half of the egg broadening out and the lower half of the egg becoming narrower (Fig. 1) with more symmetrical eggs having more negative values (Fig. 2).

Mean PC scores for each avian order showed that eggs from the various avian orders have different characteristics (Fig. 2). The eggs of the Pelecaniformes were the most elongated with the Strigiformes having the most spherical eggs. The Charadriiformes had the most asymmetrical eggs with the Galliformes, Sphenisciformes and Passeriformes also being relatively asymmetrical. All of the other avian orders had more symmetrical egg shapes (Fig. 2).

There were significant negative correlations between elongation (PC1) and LogIEM (Pearson’s r = -0.335, DF = 179, P < 0.001), and between asymmetry (PC2) and LogIEM (Pearson’s r = -0.218, DF = 179, P = 0.003). Therefore, larger eggs seemed to more elongated and more
symmetrical. Correlation between phylogenetic independent contrasts for LogIEM and PC1 was still significant (Pearson’s r = -0.196, DF = 178, P = 0.008) but the correlation between phylogenetic independent contrasts for LogIEM and PC2 was not significant (Pearson’s r = -0.043, DF = 178, P = 0.565). Therefore, subsequent analysis testing the effects of fixed factors on degree of asymmetry (PC2) did not include LogIEM as a covariate but this covariate was included if the dependent variable was the degree of elongation (PC1).

There was a significant effect of avian order on degree of asymmetry but degree of elongation was not a significant covariate and there was no significant interaction (Table 1). Given this result one-way ANOVA tests were run that showed a significant effect of avian order on the degree of elongation ($F_{15,165} = 7.32, P < 0.0001$) and degree of asymmetry ($F_{15,165} = 14.84, P < 0.0001$). The position of an avian order on Fig. 2 with respect to degree of asymmetry for example is, therefore, not related to degree of elongation.

Mean PC1 and PC2 scores classified under developmental mode are shown in Fig. 3. Precocial and semi-precocial eggs tended to be more elongated (more negative values for PC1) and semi-altricial and altricial eggs were more spherical (more positive PC1 values). Semi-precocial eggs were more asymmetrical, and the semi-altricial eggs were more symmetrical, than the other two groups (Fig. 3). However, phylogenetically controlled general linear modelling showed that there were no significant effects of developmental maturity or degree of elongation (Table 2). The phylogenetic signal was moderately high (0.779). The position of species with a particular developmental maturity on Fig. 3 with respect to the degree of asymmetry is not a function of degree of elongation or developmental maturity.

Phylogenetically controlled general linear modelling showed that degree of elongation was significantly negatively affected by LogIEM and yolk mass as a proportion of IEM (Table 3). Shell mass as a proportion of IEM and IEM as a proportion of female body mass were not significant covariates. By contrast, for degree of asymmetry shell mass as a proportion of IEM and IEM as a proportion of female body mass were both significant positive covariates but Yolk mass as a proportion of the egg contents was not a significant covariate (Table 3). In both cases phylogenetic signal ($\lambda$) was high. Therefore, the most elongated eggs were associated with high initial mass and small amounts of yolk. Greater asymmetry was associated with larger eggs relative to body mass and a greater proportion of eggshell.

**Discussion**

The use of geometric morphometrics to describe egg shape provides a similar set of results for extant birds described by Deeming and Ruta (2014). PC1 values were associated with the degree of elongation and PC2 values were associated with the degree of asymmetry. Each avian order in the data set could be characterised by their PC scores. Whilst controlling for egg mass the composition of the egg also impacted on their shape with yolk-rich (albumen-poor) precocial and semi-precocial eggs
being more elongated, with the latter being the most asymmetrical group. By contrast, the yolk-deficient altricial and semi-altricial eggs were less elongated with the latter group being the closest to a sphere. Rather surprisingly initial egg mass was also a significant factor for elongation scores but for asymmetry it was the size of the egg relative to body mass and the proportion of eggshell that were significant.

The finding that avian order affected egg shape is not surprising. Previous studies have regularly recognised that eggs from different taxa have different shapes (see Mallock 1925, Preston 1953, 1968, 1969, Smart 1967, 1969, Todd and Smart 1984, Narushin 1997, Baker, 2002, Deeming and Ruta, 2014, Mytiai et al. 2017, Stoddard et al. 2017). The difference is that the geometrical morphometrics used here is a methodology that uses principal component analysis to define variation in shape. Most other studies employ a variety of complex geometrical formulae to define egg shape, which use various coefficients that perhaps do not necessarily make interpretation of the results very intuitive for those unfamiliar with the mathematics. Interestingly, egg shape has been suggested as being useful in defining phylogenetic relationships between birds of prey (Mytiai et al. 2016) but whether this approach has a more general application is unclear. Data presented here show that eggs shape in morphospace is order-specific, which would support this idea.

The data suggest that egg shape was not significantly affected by the degree of developmental maturity produced by the species concerned. Mytiai et al. (2017) also examined the effect of developmental maturity on egg shape but defined size as dimensions and three indices of circular zones within the egg. Differences between the developmental maturity groups were often affected by linear measurements and the sequence that different factors were put into the model used for analysis. Mytiai et al. (2017) concluded that phylogenetic relatedness was more influential on egg shape than developmental maturity. The results presented here support this conclusion. Of course a defining characteristic of eggs that produce hatchlings of differing maturities is their differing composition (Carey et al. 1980, Sotherland and Rahn 1987, Deeming, 2007a, 2007b).

This study is the first to demonstrate that, irrespective of taxonomy or degree of developmental maturity, the amounts of the shell, yolk and albumen significantly affected egg shape. The ratio of yolk to albumen was important but in conjunction with egg size. Precocial eggs tend to be larger with large yolks but are more elongated in shape, which suggests that the albumen is found more to the poles of the egg because the central part of the egg is occupied by the yolk. By contrast, altricial eggs tend to be smaller and have smaller yolks so more albumen can surround the yolk on all sides, which may reduce the degree of elongation. With regard to asymmetry shell mass and initial egg mass were important and bigger, more pointed eggs had a greater mass of shell associated with them. Whether this affects the physical properties of the eggshell is unclear and requires further investigation. Most interestingly, asymmetrical eggs form a greater proportion of the body mass of the female. It is possible that such relatively big eggs are harder to accommodate within the oviduct and the surrounding pelvis and so have to adopt a more pointed shape.
Whilst there are significant effects of egg components on elongation and asymmetry the amount of variation explained by the models was very low (<10% in both cases). This implies that there are other key aspects of egg formation that have not been considered in this analysis. Stoddard et al. (2017) showed that skeletal size could be important by linking egg shape with hand-wing index. Only Smart (1991) seems to have fully considered the implications of how differing egg shapes could be produced within the oviduct. It was suggested that differential pressures exerted by various parts of the oviducal wall would produce a variety of shapes. Smart (1991) does suggest that this takes place in the isthmus of the oviduct. Mao et al. (2006) reports that the shell-less eggs adopts an asymmetrical shape at the magnum-isthmus junction but this shape is lost further down the oviduct (Mao et al. 2006). It is possible that the asymmetry observed at the magnum-isthmus junction may reflect the pressures generated by muscles in the oviducal wall to hold the developing egg at this location, which when lost allow the egg to adopt a more symmetrical shape. Perhaps muscular pressures are also applied to hold the egg in place within the shell gland and this shape is fixed irrevocably as the shell is being deposited (see Aitken 1971 for a description of this process).

It has been long been recognised that there is a correlation between egg shape and pelvis shape (Rensch 1949, Warham 1990) although this has not been fully investigated. Elongated eggs are associated with long, shallow pelvis shape whereas more rounded eggs are associated with shorter, deeper pelvis shapes. Whilst particular pelvis shapes are associated with specific taxa there is a better association with locomotor style of the species concerned (Anten-Houston et al. 2017). For instance, foot-propelled divers, e.g. grebes (Podicipediformes) tend to have elongated pelves that are flat with a long post-acetabular region. By contrast, perching songbirds (Passeriformes) have more angled and shorter pelves with a reduced post-acetabular region. Superficially, these differences are also reflected in egg shape with grebes laying long, symmetrical eggs whereas songbirds lay shorter, more asymmetrical eggs. Perhaps the muscular pressures exerted by the oviduct envisaged by Smart (1991) are supplemented by the physical constraint of the pelvis and other associated musculature? These results imply that pelvis shape primarily reflect locomotory style and perhaps egg shape is a secondary characteristic of this relationship? There is certainly a need for more anatomical and physiological research into when and where in the oviduct egg shape is irrevocably fixed.

Anten-Houston et al. (2017) describe a study of the allometry of pelvic dimensions in a sample of birds and this has been complemented by a study of pelvis shape using geometric morphometrics (Anten-Houston et al., submitted). Both studies are largely based on a sample of the same species used in this study of egg shape and so will allow for a combined analysis to determine the extent to which the pelvis shape determines egg shape.

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the two reviewers who helped to improve the final version.

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Table 1. Results of linear modelling to test the effect of avian order on asymmetry (PC2) with degree of elongation (PC1) as a covariate. Significant terms are highlighted in bold.

<table>
<thead>
<tr>
<th></th>
<th>Df</th>
<th>F (P-value)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Avian order</td>
<td>15,149</td>
<td><strong>15.14 (&lt; 0.001)</strong></td>
</tr>
<tr>
<td>Elongation</td>
<td>1,149</td>
<td>0.05 (0.819)</td>
</tr>
<tr>
<td>Avian order*Elongation</td>
<td>15,149</td>
<td>1.29 (0.218)</td>
</tr>
<tr>
<td>R²</td>
<td></td>
<td>0.632</td>
</tr>
</tbody>
</table>

Table 2. Results of phylogenetically controlled general linear modelling to test the effect of developmental maturity on asymmetry (PC2) with elongation (PC1) as a covariate.

<table>
<thead>
<tr>
<th></th>
<th>Coefficient (SE)</th>
<th>t-value (p-value)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Developmental maturity</td>
<td>-0.0022 (0.0018)</td>
<td>-1.22 (0.223)</td>
</tr>
<tr>
<td>Elongation</td>
<td>0.0634 (0.0644)</td>
<td>0.99 (0.326)</td>
</tr>
<tr>
<td>Developmental maturity*Elongation</td>
<td>-0.0344 (0.0264)</td>
<td>-1.30 (0.194)</td>
</tr>
<tr>
<td>F-ratio (p-value)</td>
<td></td>
<td>1.41 (0.240)</td>
</tr>
<tr>
<td>R²</td>
<td></td>
<td>0.024</td>
</tr>
<tr>
<td>Phylogenetic signal (λ)</td>
<td></td>
<td>0.779</td>
</tr>
</tbody>
</table>
Table 3. Results of phylogenetically controlled general linear modelling to test the effect proportions of shell or yolk and the size of the egg relative to female body mass, on PC1 (degree of elongation) and PC2 (degree of asymmetry). Given the significant correlation between elongation and Log initial egg mass (IEM) this term is included in the model. Significant terms are highlighted in bold.

<table>
<thead>
<tr>
<th></th>
<th>PC1 Coefficient (SE)</th>
<th>t-value (p-value)</th>
<th>PC2 Coefficient (SE)</th>
<th>t-value (p-value)</th>
</tr>
</thead>
<tbody>
<tr>
<td>LogIEM</td>
<td>-0.0176 (0.0062)</td>
<td><strong>-2.85 (0.004)</strong></td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Shell as a proportion of initial egg mass</td>
<td>-0.0368 (0.0454)</td>
<td>-0.81 (0.412)</td>
<td>0.0518 (0.0164)</td>
<td><strong>3.16 (0.002)</strong></td>
</tr>
<tr>
<td>Yolk as a proportion of initial egg mass</td>
<td>-0.0917 (0.0353)</td>
<td><strong>-2.60 (0.010)</strong></td>
<td>0.0005 (0.0114)</td>
<td>0.05 (0.959)</td>
</tr>
<tr>
<td>Initial egg mass as a proportion of female body egg mass</td>
<td>0.0165 (0.0354)</td>
<td>0.47 (0.642)</td>
<td>0.0355 (0.0117)</td>
<td><strong>3.03 (0.003)</strong></td>
</tr>
<tr>
<td>F-ratio (p-value)</td>
<td>4.13 (0.003)</td>
<td>4.77 (0.003)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>R²</td>
<td>0.065</td>
<td>0.059</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Phylogenetic signal (λ)</td>
<td>0.851</td>
<td>0.820</td>
<td></td>
<td></td>
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</table>
Figure 1. Lollipop plots produced by MorphJ for PC1 (left) and PC2 (right) of the right-hand side of bird eggs. Dots indicate the position of each semi-landmark whilst the direction and length of the line indicates the pattern in variation in the location of that coordinate within morphospace.
Figure 2. Mean (± SE) values for PC1 and PC2 for sixteen different avian orders as indicated. Samples sizes are shown in parentheses alongside the taxon name in the legend. Interpretation of the PC scores is indicated – along PC1 there is a generally reduction in the degree of elongation from more negative score to more positive scores. For PC2 eggs become asymmetrical as the values go from more negative to more positive. Note that square symbols indicate avian orders with precocial neonates, triangles indicate semi-precocial neonates, diamonds indicate semi-altricial neonates, and circles indicate altricial neonates.
Figure 3. Mean (± SE) values for PC1 and PC2 for four different developmental maturities for neonatal birds. Samples sizes are shown in parentheses alongside the category of developmental maturity in the legend. Interpretation of the PC scores is indicated – along PC1 there is a generally reduction in the degree of elongation from more negative score to more positive scores. For PC2 eggs become for asymmetrical as the values go from more negative to more positive.