

Effect of composition on shape of bird eggs

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Abstract:	<p>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.</p>

1 **Effect of composition on shape of bird eggs**

2 D. Charles Deeming

3

4 School of Life Sciences, Joseph Banks Laboratories, University of Lincoln, Green Lane, Lincoln LN6

5 7DL, UK

6 *Correspondence: Email cdeeming@lincoln.ac.uk

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

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

24 **Short Title:** Effect of composition in bird egg shape

25

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

34 The mathematical description of egg shape has a long history of research that continues to
35 this day (e.g. Mallock 1925, Preston 1953, 1968, 1969, Smart 1967, 1969, Todd and Smart 1984,
36 Narushin 1997, Baker 2002, Deeming and Ruta 2014, Troscianko 2014, Mytiai et al. 2017, Stoddard
37 et al. 2017). Other than the challenge of describing a complex shape, the study of egg shape has been

38 useful in calculating volume or surface area of eggs (Hoyt 1976), and in assessing eggshell strength
39 (e.g. Bain 1991, Anderson et al. 2004, Nedomova et al. 2009). Other studies use shape in comparisons
40 of different populations of the same species or different species (Preston 1969, Johnson et al. 2001),
41 and the relationships between brood parasites and their hosts (Bán et al. 2011). Shape has even been
42 used in study of the evolution of **amniote** eggs with eggs **being** defined in terms of **their** degree of
43 elongation, i.e. length divided by breadth, and **their degree of** asymmetry, i.e. position of the broadest
44 part of the egg away from the mid-point of the egg's length (Deeming and Ruta 2014). More recently,
45 the role of the elongated and highly asymmetrical shape of the guillemot egg has been re-evaluated.
46 Birkhead et al. (2017) concluded that, rather than to prevent eggs from rolling off cliff ledges, the
47 pointed shape reflects a way of minimising eggshell surface contamination. In addition, Stoddard et
48 al. (2017) found a correlation between egg shape and flight efficiency in birds, as determined by the
49 hand-wing index, and suggested that flight adaptation may have been a critical driver for egg shape
50 variation.

51 Other studies have studied the role of shape in a reproductive context. For instance, Barta and
52 Székely (1997) explored the reasoning that egg shape reflects the shape of the brood patch and **so**
53 **optimises** contact incubation (Andersson 1978). It was concluded that optimal egg shape reflected
54 clutch size although this idea has been challenged (Hutchinson 2000). However, the underlying
55 mechanism that produces an egg of a specific shape has received very little attention. The consensus
56 is that the wall of the oviduct resists deformation whilst peristaltic contractions hold the egg in place
57 within the shell gland as the shell is forming (Romanoff and Romanoff 1949, Aitken 1971, Smart
58 1991) but the exact mechanism remains unclear. In addition to this idea, Barta and Székely (1997)
59 suggested that egg shape may reflect differences in shell strength (Bain 1991) but offered no
60 suggestion of how such shapes could be produced in the oviduct. Stoddard et al. (2017) correlated egg
61 shape with characteristics of the pectoral limb but suggested that pelvis size may be of more interest.
62 It has been pointed out that variability **in** egg shape reflects the variability in shape of the pelvic girdle
63 between different bird orders; a round egg is associated with a short pelvis whereas longer pelvises can
64 accommodate more elongated eggs (Rensch 1949, Warham 1990). The lack of a description of how
65 egg shape is achieved within the oviduct could be hampering our understanding of the function of egg
66 shape because we are unable to confirm whether there has been selection for shape on the basis of
67 reproductive parameters, e.g. water or energy content. It remains possible that egg shape is a
68 consequence of other morphological features associated **with a species' life history**, e.g. terrestrial
69 locomotion (Anten-Houston et al. 2017), **that is** not directly related to reproduction.

70 Bird eggs vary in their size and composition across avian orders (Carey et al. 1980,
71 Sotherland and Rahn 1987, Deeming 2007a, 2007b). Mytiai et al. (2017) found that phylogeny was
72 important in determining egg shape, but found minimal effect of developmental maturities, which
73 reflects differences in egg composition, using linear and geometric shape measurements. However,
74 eggs that produce altricial offspring have a greater albumen to yolk ratio than eggs that produce

75 precocial offspring (Carey et al. 1980, Sotherland and Rahn 1987). It is possible that the differing
76 amounts or proportions of the egg components are important in determining the shape of the laid egg.
77 For instance, perhaps within the physical constraints of the tubular oviduct lying parallel to the long
78 axis of the body, large amounts of albumen may only be accommodated cranially and caudally to the
79 yolk as it moves down the oviduct, therefore forming an elongated egg.

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

88

89 **Methods**

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

97 Species were chosen on the basis that egg composition was available. Data for mean initial
98 egg mass (IEM) for each species were obtained from literature sources or Schönwetter (1960-1985).
99 The species were also allocated to one of four categories based on the degree of developmental
100 maturity they express at hatching: precocial, semi-precocial, semi-altricial, and altricial (following
101 Deeming 2007a, 2007b). Data for masses (in g) of shell, yolk and albumen, and female body mass (g),
102 collated from the literature were available for each species from a database compiled by Deeming
103 (2007a, 2007b).

104 Forty equally spaced semi-landmarks were digitized along the right-hand side of each egg
105 outline using tpsDig2 v. 2.17 (Rohlf 2006). The landmark coordinates were transferred to MorphoJ v.
106 1.05f (Klingenberg 2011) and subjected to a principal component analysis of the variance-covariance
107 matrix of Procrustes-fitted landmark coordinates, i.e. coordinates obtained after removal of scale,
108 translation, and rotation.

109 The principal component scores (PC1 and PC2) of egg types were normally distributed (as
110 tested in Minitab ver. 17). Pearson's correlations carried out in Minitab (ver. 17) showed that PC1 and
111 PC2 correlated with Log₁₀ transformed values for initial egg mass (IEM). **Phylogenetic independent**

112 contrasts were calculated for PC1, PC2 and LogIEM using the ape package in R (R-core team) and
113 correlations were re-run to assess the effect of phylogeny on the relationships between PC scores and
114 LogIEM. Linear models in R (R-core team) were used to do analysis of variance to test for the effect
115 of avian order on PC1 or PC2, and analysis of covariance to test for the effect of avian order on PC2
116 whilst controlling for PC1 as a covariate.

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

131

132 Results

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

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

146 There were significant negative correlations between elongation (PC1) and LogIEM
147 (Pearson's $r = -0.335$, $DF = 179$, $P < 0.001$), and between asymmetry (PC2) and LogIEM (Pearson's r
148 $= -0.218$, $DF = 179$, $P = 0.003$). Therefore, larger eggs seemed to more elongated and more

149 symmetrical. Correlation between phylogenetic independent contrasts for LogIEM and PC1 was still
150 significant (Pearson's $r = -0.196$, $DF = 178$, $P = 0.008$) but the correlation between phylogenetic
151 independent contrasts for LogIEM and PC2 was not significant (Pearson's $r = -0.043$, $DF = 178$, $P =$
152 0.565). Therefore, subsequent analysis testing the effects of fixed factors on degree of asymmetry
153 (PC2) did not include LogIEM as a covariate but this covariate was included if the dependent variable
154 was the degree of elongation (PC1).

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

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

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

179

180 Discussion

181 The use of geometric morphometrics to describe egg shape provides a similar set of results for extant
182 birds described by Deeming and Ruta (2014). PC1 values were associated with the degree of
183 elongation and PC2 values were associated with the degree of asymmetry. Each avian order in the
184 data set could be characterised by their PC scores. Whilst controlling for egg mass the composition of
185 the egg also impacted on their shape with yolk-rich (albumen-poor) precocial and semi-precocial eggs

186 being more elongated, with the latter being the most asymmetrical group. By contrast, the yolk-
187 deficient altricial and semi-altricial eggs were less elongated with the latter group being the closest to
188 a sphere. Rather surprisingly initial egg mass was also a significant factor for elongation scores but for
189 asymmetry it was the size of the egg relative to body mass and the proportion of eggshell that were
190 significant.

191 The finding that avian order affected egg shape is not surprising. Previous studies have
192 regularly recognised that eggs from different taxa have different shapes (see Mallock 1925, Preston
193 1953, 1968, 1969, Smart 1967, 1969, Todd and Smart 1984, Narushin 1997, Baker, 2002, Deeming
194 and Ruta, 2014, Mytiai et al. 2017, Stoddard et al. 2017). The difference is that the geometrical
195 morphometrics used here is a methodology that uses principal component analysis to define variation
196 in shape. Most other studies employ a variety of complex geometrical formulae to define egg shape,
197 which use various coefficients that perhaps do not necessarily make interpretation of the results very
198 intuitive for those unfamiliar with the mathematics. Interestingly, egg shape has been suggested as
199 being useful in defining phylogenetic relationships between birds of prey (Mytiai et al. 2016) but
200 whether this approach has a more general application is unclear. Data presented here show that eggs
201 shape in morphospace is order-specific, which would support this idea.

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

211 This study is the first to demonstrate that, irrespective of taxonomy or degree of developmental
212 maturity, the amounts of the shell, yolk and albumen significantly affected egg shape. The ratio of
213 yolk to albumen was important but in conjunction with egg size. Precocial eggs tend to be larger with
214 large yolks but are more elongated in shape, which suggests that the albumen is found more to the
215 poles of the egg because the central part of the egg is occupied by the yolk. By contrast, altricial eggs
216 tend to be smaller and have smaller yolks so more albumen can surround the yolk on all sides, which
217 may reduce the degree of elongation. With regard to asymmetry shell mass and initial egg mass were
218 important and bigger, more pointed eggs had a greater mass of shell associated with them. Whether
219 this affects the physical properties of the eggshell is unclear and requires further investigation. Most
220 interestingly, asymmetrical eggs form a greater proportion of the body mass of the female. It is
221 possible that such relatively big eggs are harder to accommodate within the oviduct and the
222 surrounding pelvis and so have to adopt a more pointed shape.

223 Whilst there are significant effects of egg components on elongation and asymmetry the
224 amount of variation explained by the models was very low (<10% in both cases). This implies that
225 there are other key aspects of egg formation that have not been considered in this analysis. Stoddard et
226 al. (2017) showed that skeletal size could be important by linking egg shape with hand-wing index.
227 Only Smart (1991) seems to have fully considered the implications of how differing egg shapes could
228 be produced within the oviduct. It was suggested that differential pressures exerted by various parts of
229 the oviducal wall would produce a variety of shapes. Smart (1991) does suggest that this takes place
230 in the isthmus of the oviduct. Mao et al. (2006) reports that the shell-less eggs adopts an asymmetrical
231 shape at the magnum-isthmus junction but this shape is lost further down the oviduct (Mao et al.
232 2006). It is possible that the asymmetry observed at the magnum-isthmus junction may reflect the
233 pressures generated by muscles in the oviducal wall to hold the developing egg at this location, which
234 when lost allow the egg to adopt a more symmetrical shape. Perhaps muscular pressures are also
235 applied to hold the egg in place within the shell gland and this shape is fixed irrevocably as the shell is
236 being deposited (see Aitken 1971 for a description of this process).

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

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

256

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261

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For Review Only

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

	Df	F (P-value)
Avian order	15,149	15.14 (< 0.001)
Elongation	1,149	0.05 (0.819)
Avian order*Elongation	15,149	1.29 (0.218)
R ²		0.632

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.

	Coefficient (SE)	t-value (p-value)
Developmental maturity	-0.0022 (0.0018)	-1.22 (0.223)
Elongation	0.0634 (0.0644)	0.99 (0.326)
Developmental maturity*Elongation	-0.0344 (0.0264)	-1.30 (0.194)
F-ratio (p-value)		1.41 (0.240)
R ²		0.024
Phylogenetic signal (λ)		0.779

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.

	PC1		PC2	
	Coefficient (SE)	t-value (p-value)	Coefficient (SE)	t-value (p-value)
LogIEM	-0.0176 (0.0062)	-2.85 (0.004)	-	-
Shell as a proportion of initial egg mass	-0.0368 (0.0454)	-0.81 (0.412)	0.0518 (0.0164)	3.16 (0.002)
Yolk as a proportion of initial egg mass	-0.0917 (0.0353)	-2.60 (0.010)	0.0005 (0.0114)	0.05 (0.959)
Initial egg mass as a proportion of female body egg mass	0.0165 (0.0354)	0.47 (0.642)	0.0355 (0.0117)	3.03 (0.003)
F-ratio (p-value)	4.13 (0.003)		4.77 (0.003)	
R ²	0.065		0.059	
Phylogenetic signal (λ)	0.851		0.820	

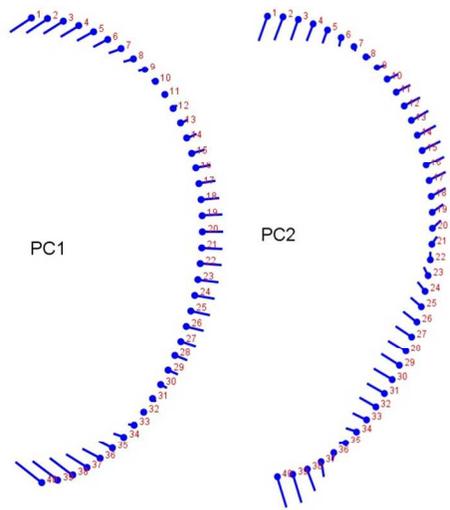


Figure 1. Lollipop plots produced by MorphJ for PC1 (left) and PC2 (right) of the right-hand side of bird eggs. Dots indicate the position of each semi-landmark whilst the direction and length of the line indicates the pattern in variation in the location of that coordinate within morphospace.

338x190mm (96 x 96 DPI)

new Only

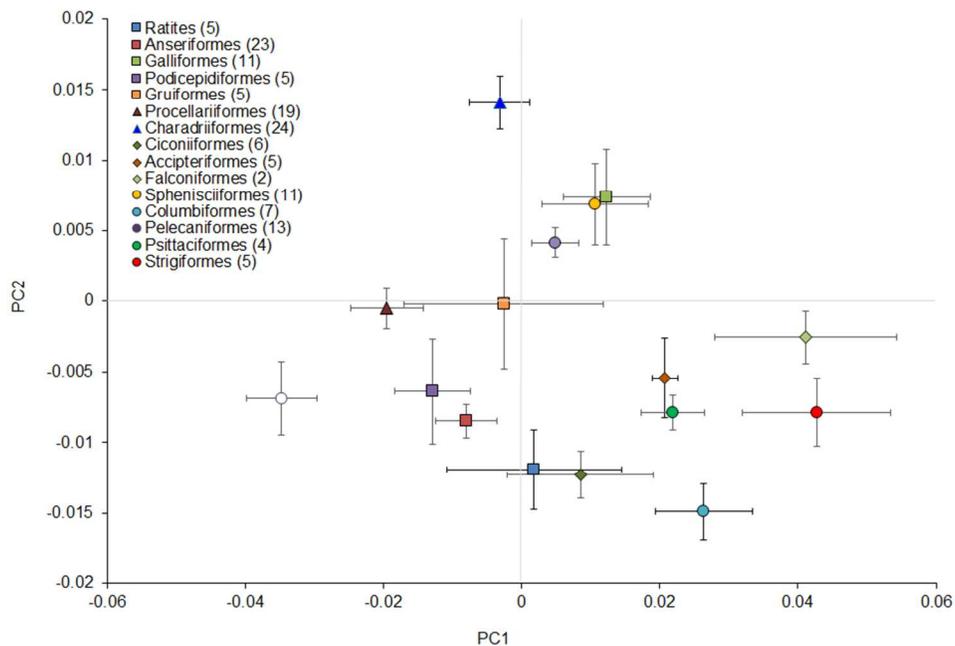


Figure 2. Mean (\pm SE) values for PC1 and PC2 for sixteen different avian orders as indicated. Samples sizes are shown in parentheses alongside the taxon name in the legend. Interpretation of the PC scores is indicated – along PC1 there is a generally reduction in the degree of elongation from more negative score to more positive scores. For PC2 eggs become for 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.

257x169mm (96 x 96 DPI)

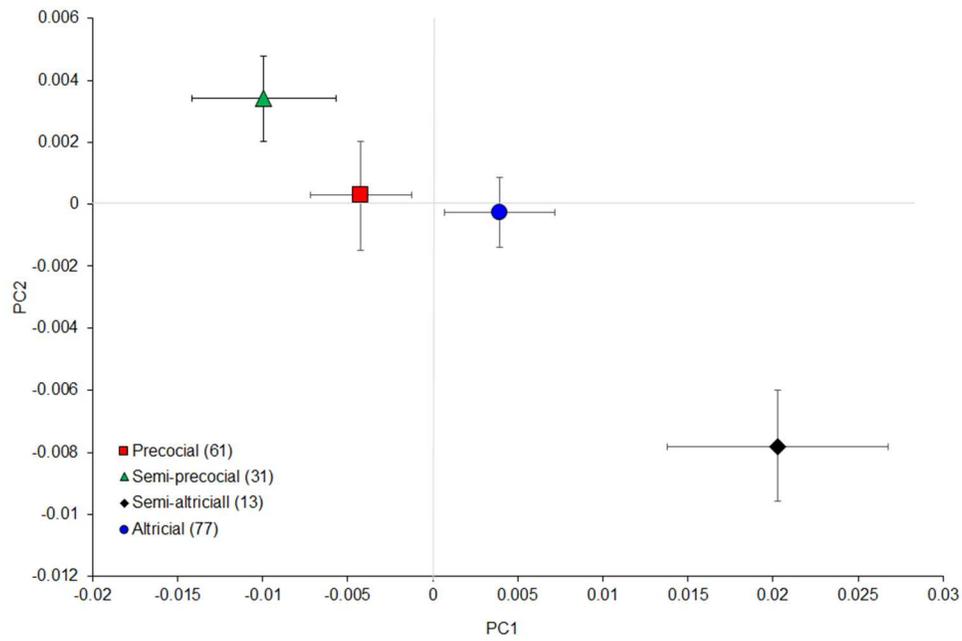


Figure 3. Mean (\pm SE) values for PC1 and PC2 for four different developmental maturities for neonatal birds. Samples sizes are shown in parentheses alongside the category of developmental maturity in the legend.

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.

257x169mm (96 x 96 DPI)

Only