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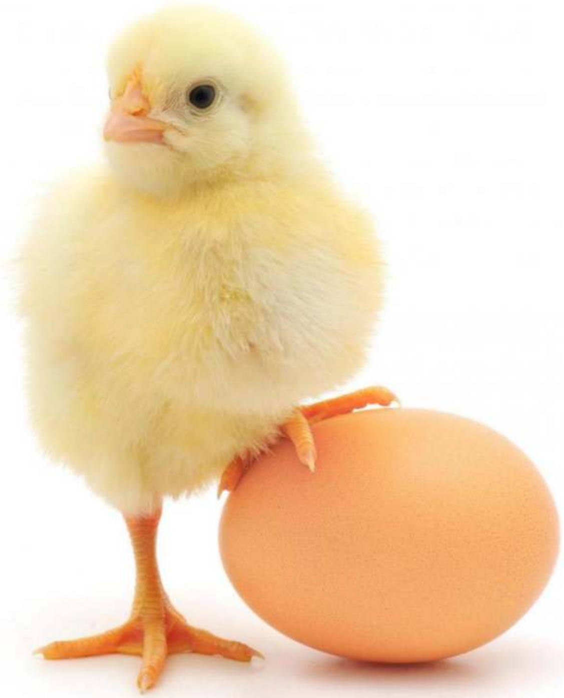

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Research Article
Egg Shape is Constrained More by Width than Length, Evidence from Double-yolked Duck Eggs

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Abstract

Background and Objective: While avian egg shape is species specific there is evidence for intraspecific variation and this variation may be especially great in domestic ducks where selection for egg production was not as intense as in the domestic fowl. Egg shape (visually assessed) and shape index (calculated from egg dimensions) were compared in single-yolked (SY) and double-yolked (DY) duck (*Anas platyrhynchos domesticus*) eggs. **Methodology:** The SY and DY eggs were collected from a flock of Aylesbury ducks and their dimensions were measured. Shape index was calculated (length divided by width) and egg shape was visually assessed. **Results:** There was a significant positive relationship between egg shape and shape index both in SY and DY duck eggs (both $p<0.001$) with the more elongated egg, having a higher shape index. The DY eggs were more elongated than SY eggs in all egg shapes (all $p<0.001$). When compared to SY eggs, the significantly greater length, which is disproportionately more than the significantly greater width, is associated with presence of a second yolk in DY eggs. Further, length had greater variance than width in both SY and DY eggs. The shape index of SY and DY eggs differed significantly between the various egg shapes (all $p<0.05$) validating the use of egg shape as an egg categorization tool. However the ranges of shape indexes of different egg shapes overlapped considerably. **Conclusion:** The shape index is of limited value and thus the visually assessed egg shape should also be used when describing an egg. Further, the egg shape may have important functions during incubation and hatching and the elongated nature of the DY eggs may act as handicap to successful hatching and in part explain why the production of twins from DY eggs has not evolved in avian species.

Key words: Double-yolked eggs, duck, length, egg shape, shape index, shape variation, width

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Competing Interest: The authors have declared that no competing interest exists.

Data Availability: All relevant data are within the paper and its supporting information files.

INTRODUCTION

The egg shape is a characteristic of each species and can differ markedly within avian families[1,2]. The egg shape is acquired in the isthmus segment of the oviduct[3] and is imparted by the action of the isthmus wall which is retained by the shell membranes secreted by the cells lining the isthmus lumen where the egg remains stationary for some time[3,4]. Further the egg shape may influence how the egg is laid[4,5].

The length and the width of an egg is used to calculate the shape index (length divided by width) and will also give an indication of the shape of an egg. For example a lower shape index (e.g., 65.7×49.5 mm = 1.33) suggests a rounder shape, while a higher shape index (e.g., 75.8×48.5 mm = 1.56) suggests an elongated shape. Also, when comparing single-yolked (SY) and double-yolked (DY) duck eggs, DY eggs have higher shape index, because such eggs are generally longer compared to SY eggs[6,7]. Thus DY duck eggs are more elongated in shape than SY duck eggs.

From the functional perspective, interspecific egg shape variations have been related to gas and heat exchanges[8,9], efficient use of the brood patch area of the incubating parent[10], pattern of turning during incubation[11] and adaptation to avoid danger of eggs rolling off cliff[12,13]. In the Common guillemot (*Uria aalge*) and in the Brunnich's guillemot (*Uria lomvia*) the function of the elongated egg shape was recently studied and results show that its function is not consistent with the preventing egg rolling from the cliff hypothesis[14] but is more consistent with two alternative hypotheses, (a) Providing additional egg shell strength to protect the egg by increasing the contact area with the substrate material as parent birds can approach suddenly and with force their nests and (b) Protecting the egg from debris contamination and so protecting the chick[15].

In grey partridges (*Perdix perdix*) egg shape variation was related to female health condition (erythrosedimentation rate) and laying order, i.e., the more pointed and less elongated the egg the poorer the condition (higher erythrosedimentation rate) of the female and the higher the position in the laying sequence the more elongated the egg[16]. There is evidence for intraspecific egg shape variation in domestic species too, such as the domestic duck[7,17-20], where shape index varied over the laying season (decreased or not changed[17], increased[18]).

The British Poultry Standard[21] distinguished six egg shapes namely ideal, biconical, conical, elliptical, ideal, oval and spherical, which suggests that these distinct egg shapes do occur in poultry species. However, recently Stoddard *et al.*[2] claimed that egg shape is a continuum with no division between the traditional shape classes. The traditional egg shape classes fail to identify the most common egg shape of avian species[2], which is very similar to the oval shape. Still, Lowman *et al.*[20] found that the SY duck eggs with the optimal shape had higher hatchability rate even though fertility levels did not differ between the different shapes. Salamon and Kent[7] also found that fertility levels did not differ between different egg shapes in duck eggs but hatchability was not examined in that study.

Poultry egg shape (visually assessed) or shape index (calculated from egg dimensions) can be used to describe how an egg looks like, however this study examines the relationship of these two classification systems in both SY and DY duck eggs using data from a larger study[7] and here we examine whether both classification systems should be used to describe egg shape.

MATERIALS AND METHODS

Eggs (n = 48224) were collected from a flock of Aylesbury ducks over a 2 year period at Ballyrichard, Arklow, Ireland (52.83°N, 6.13°W). The duck flock contained birds of various ages (new layers added every 3-4 months) to maintain continuous egg production[7] and eggs were collected from the onset of laying when DY eggs are most frequently produced[7,22-25] due to multiple ovulations[26]. The duck flock was housed in one shed (12.6×7 m) at night, released at 11:00 h (GMT) to an adjacent grass field with water supply and had access to the shed with feed and water during the day. Ducks were maintained on a natural daylight schedule, with additional electric light until 22:00 h (GMT) to maintain a light schedule close to 16 h/day[7].

From the collected eggs 1343 DY eggs were identified by candling[7] and in this study 928 DY and equal number of SY control eggs were used. The length and width of the eggs was measured with a digital calliper (Laser Tools, UK) (±0.01 mm). A shape index was calculated by dividing egg length by width. Egg shape for SY and DY eggs was assessed visually using the scale devised by Roberts[21].

General linear model (GLM) was used to analyze the data in R^2 (version 3.4.1)[27]. Later, SY and DY eggs were analyzed separately with *post-hoc* Tukey-test to compare different egg shapes. T-test was used to compare the length, width and shape indexes of different egg shapes between SY and DY eggs. Further using generalized least squares, it was tested whether there was a difference between the variance of length and width in SY and DY eggs. In each comparison, one model was fit assuming variance was the same, while the other model assumed differing variance. Then these two models were compared with two-way ANOVA to test the above hypothesis.

RESULTS

Overall, both egg shape (F = 383.56, $p<0.001$, df = 5) and egg type (F = 572.71, $p<0.001$, df = 1) had a significant effect on the shape index (n = 1856, adjusted R^2 = 63.47%).

When SY and DY eggs were analyzed separately, there was a significant positive relationship in SY eggs between egg shape and shape index according to the GLM (F = 238.72, $p<0.001$, df = 927, adjusted R^2 = 56.18%). Thus, the more elongated the egg, the higher the shape index. Further, the *post-hoc* Tukey-test showed that the shape indexes of each egg shape differed from each other significantly (all $p<0.01$, Table 1). Yet, there was considerable overlap in the ranges of the shape indexes for ideal, conical, biconical and elliptical shaped SY eggs (Table 1).

The GLM also showed a significant positive relationship between DY egg shape and shape index (F = 173.21, $p<0.001$, df = 927, adjusted R^2 = 48.16%). Thus, as expected the more elongated the egg, the higher the shape index. The *post-hoc* Tukey-test showed a significant difference in the shape indexes of ideal, conical, biconical, elliptical and oval DY eggs (all $p<0.05$) but the shape index of spherical DY eggs did not differ from those of ideal and oval DY eggs (Table 2). Similarly to SY eggs, the ranges of shape indexes were overlapping in ideal, conical, biconical and elliptical shaped DY eggs (Table 2). The shape indexes of DY eggs were significantly higher than those of SY eggs in all egg shapes (all $p<0.001$, Fig. 1) showing that DY eggs are more elongated (Fig. 2). The length of DY eggs in all shapes were significantly larger than those of SY eggs (biconical: 7.82%, conical: 7.12%, elliptical: 10.13%, ideal: 7.85%, oval: 7.71% and spherical: 1.78%, all $p<0.001$). The width of DY eggs in all shapes except spherical were significantly larger than those of SY eggs (biconical: 2.97%, conical: 3.41%, elliptical: 6.3%, ideal: 4.5%, oval: 4.42%, all $p<0.001$). Thus, the presence of a second yolk disproportionately increased the egg dimensions, i.e., the length of DY eggs was increased significantly more than their width.

Further, the model of equal variance (AIC = 8207.83, BIC = 8224.4, logLik = -4100.91, df = 1856) and the model of differing variance (AIC = 7834.26, BIC = 7856.36, logLik = -3919.13, df = 1856) differed significantly when comparing egg length and width of SY eggs (L-ratio = 375.57, $p<0.001$). Thus there was greater variance in length than in width of SY eggs. Also, the model of equal variance (AIC = 10319.83, BIC = 10336.41, logLik = -5156.92, df = 1856) and the model of differing variance (AIC = 10030.65, BIC = 10052.75, logLik = -5011.32, df = 1856) differed significantly when egg length and width of DY eggs was compared (L-ratio = 291.18, $p<0.001$). Thus the variance in length of DY eggs was greater. This supports the finding that the egg shape is constrained more by width in both SY and DY eggs.

Table 1: Number, length, width and shape index of single-yolked (SY) duck eggs in relation to egg shape

	Egg (%)		Length (mm)		Width (mm)		Shape Index		
Egg shapes	No.	%	Mean	±SD	Mean	±SD	Mean	±SD	Shape index range
Biconical	194	20.91	70.49^{a}	2.45	48.11^{a}	1.29	1.47^{a}	0.05	1.35-1.59
Conical	156	16.81	70.27^{a}	2.60	48.59^{b}	1.27	1.44^{b}	0.05	1.32-1.59
Elliptical	44	4.74	68.71^{b}	2.20	48.42^{ab}	1.21	1.42^{c}	0.04	1.35-1.54
Ideal	389	41.92	68.16^{b}	2.21	48.93^{b}	1.34	1.39^{d}	0.04	1.30-1.50
Oval	133	14.33	66.32^{c}	1.98	50.02^{c}	1.36	1.33^{e}	0.03	1.27-1.38
Spherical	12	1.29	63.06^{d}	1.29	49.32^{bc}	1.15	1.28^{f}	0.02	1.24-1.31

Means in each column followed by a different superscript letter differ significantly ($p<0.01$), shape index is length divided by width

Table 2: Number, length, width and shape index of double-yolked (DY) duck eggs in relation to egg shape

	Egg (%)		Length (mm)		Width (mm)		Shape Index		
Egg shapes	No.	%	Mean	±SD	Mean	±SD	Mean	±SD	Shape index range
Biconical	349	37.61	76.33^{a}	4.61	49.54^{a}	2.54	1.54^{a}	0.06	1.41-1.76
Conical	160	17.24	75.27^{a}	4.44	50.25^{b}	2.48	1.50^{b}	0.05	1.38-1.73
Elliptical	101	10.88	75.67^{a}	4.85	51.47^{c}	2.79	1.47^{c}	0.05	1.38-1.60
Ideal	277	29.85	73.51^{b}	4.62	51.13^{c}	2.61	1.44^{d}	0.04	1.34-1.56
Oval	40	4.31	71.43^{b}	4.10	52.23^{c}	2.36	1.37^{e}	0.03	1.29-1.44
spherical	1	0.11	64.18^{ab}		48.60^{abc}		1.32^{de}		-

Means in each column followed by a different superscript letter differ significantly ($p<0.05$), shape index is length divided by width

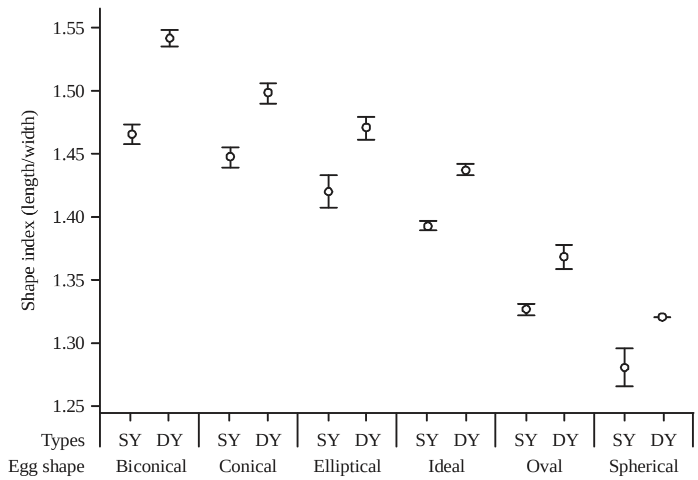

Fig. 1: Shape index of different shapes of single (SY) and double-yolked (DY) duck eggs
Intervals (between and within SY and DY eggs) not overlapping differ from each other significantly (p<0.05, also shown in Table 1 and 2)

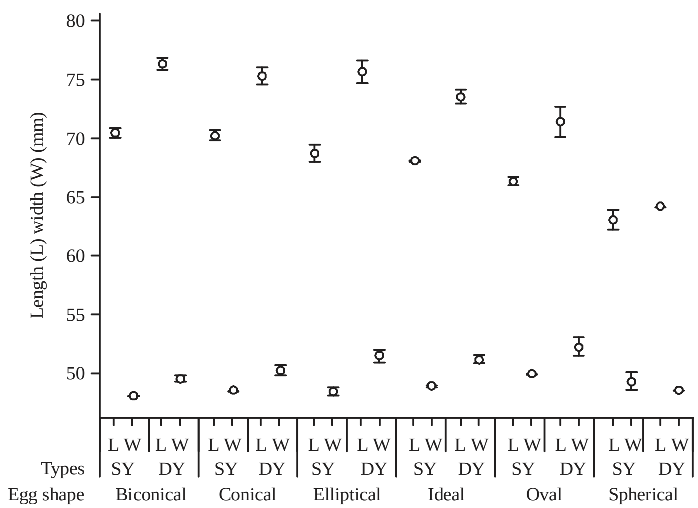

Fig. 2: Length and width of different shapes of single (SY) and double-yolked (DY) duck eggs
Intervals (between and within SY and DY eggs) not overlapping differ from each other significantly (p<0.05, also shown in Table 1 and 2)

DISCUSSION

The findings show that there is a significant relationship between egg shape and shape index in SY and DY duck eggs. However, it has to be noted that the shape index is a value calculated from the length and width of an egg and there may be a constraint in egg width due to the physiological limitation of the female cloaca, which is part of the morphological adaptations for flight[2]. This may be the reason why DY eggs are more elongated than SY eggs[6,7] and why the two yolks are in adjacent position in a DY duck egg when the egg is laid[28]. This is also supported by the findings in this study, where the egg length in DY eggs was 7.12-10.13% greater than in SY eggs, while egg width in DY eggs was 2.97-6.3% greater than in SY eggs. Also, the greater variance in length than width in both SY and DY eggs shows that egg shape is constrained more by width. Further, it was interesting to see that the presence of a second yolk in 52% of DY eggs resulted in an assymetric egg shape (conical, ideal, oval, Table 2). One possible explanation for this may be the difference in size/weight of the two yolks within the DY eggs[6,29-31] due to the difference in developmental days during the rapid growth phase of the follicles[32].

The use of shape index has its limitations. First, it is possible that two different shaped eggs have the same shape index. If a biconical egg and a conical egg have the same length and width, the only difference between these eggs is the location of the widest part of the egg, i.e., in the middle of the biconical egg and on the upper half of a conical egg. Second, a SY and a DY egg can have the same shape index also. If there is a DY egg that is 10% longer and 10% wider than a SY egg, then their shape index is the same. Thus their shape is the same too, only the DY egg is larger. Therefore it is suggested that shape index and egg shape classification should both be used to accurately describe an egg, especially in domestic species. Alternatively, more advanced mathematical models may be used to describe the shape of an egg using different parameters[2,4,33] in an interspecific context. Certain egg shapes may be favored and have positive fitness consequences[10]. In ducks, abnormal eggs (more round eggs, i.e., oval or spherical or more elongated eggs, i.e., biconical or elliptical) had lower fertility and hatchability than normal (ideal or conical) eggs[20]. In Muscovy ducks (*Cairina moschata*) eggs that needed assistance at hatching were more rounded, even though their shape index did not differ from those of normally hatched eggs, which were more pointed[34]. This supports our suggestion to use both egg shape and shape index to describe the shape of an egg. The hatchability of turkey (*Meleagris gallopavo*) and grey partridge eggs with higher or lower shape index was lower compared to those with intermediate shape index[16,35]. In the studies of Cucco *et al.*[16] and Erisir and Ozbey[35] the egg shape was not determined but it is possible that two different egg shapes have similar shape indexes.

CONCLUSION

It was concluded that the shape index is of limited value and thus the visually assessed egg shape should also be used when describing an egg in an intraspecific context. Further, the egg shape may have important functions during incubation and hatching and the elongated nature of the DY eggs may act as handicap to successful hatching and in part explain why the production of twins from DY eggs has not evolved in avian species.

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