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Pelvis morphology suggests that early Mesozoic birds were too heavy to contact incubate their eggs

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Abstract

Numerous new fossils have driven an interest in reproduction of early birds but direct evidence remains elusive. No Mesozoic avian eggs can be unambiguously assigned to a species, which hampers our understanding of the evolution of contact incubation, which is a defining feature of extant birds. Compared to living species eggs of Mesozoic birds are relatively small, but whether the eggs of Mesozoic birds could actually have borne the weight of a breeding adult has not yet been investigated. We estimated maximal egg breadth for a range of Mesozoic avian taxa from the width of the pelvic canal defined by the pubic symphysis. Known elongation ratios of Mesozoic bird eggs allowed us to predict egg mass and hence the load mass an egg could endure before cracking. These values were compared to the predicted body masses of the adult birds based on skeletal remains. Based on 21 fossil species, we show that for non-ornithothoracine birds body mass was 130% of the load mass of the eggs. For Enantiornithes body mass and egg load mass were comparable to extant birds, but some early Cretaceous ornithuromorphs were 110% heavier than their eggs could support. Our indirect approach provides the best evidence yet that early birds could not have sat on their eggs without running the risk of causing damage. We suggest that contact incubation evolved comparatively late in birds.

Keywords: egg size, contact incubation, Mesozoic bird, pelvic canal width, pubis shape

Introduction

The evolution of reproductive behaviour of non-avian theropods and early birds remains poorly understood, with the origin of contact incubation being especially contentious (Deeming, 2002a, 2015; Varricchio & Jackson, 2016). Various eggs of Mesozoic birds have been reported (Varricchio & Jackson, 2016; Lawver et al., 2016), but those that contain embryos remain extremely rare (Deeming, 2015). Although unattributed to adults of any known species, Mesozoic bird eggs are considered to be relatively small compared with extant species (Dyke & Kaiser, 2010; Varricchio & Jackson, 2016; Chiappe & Meng, 2016) and are more elongated than extant and Cenozoic fossil bird eggs (Deeming & Ruta, 2014). Eggs are invariably attributed to birds on the basis of eggshell structure rather than close association between eggs and skeletal remains, as seen for some non-avian theropods and a pterosaur (Clark et al., 1999; Lü et al., 2011; Wang et al., 2017). The hypothesis that non-avian theropods sitting on clutches of eggs are exhibiting contact incubation (Clark et al., 1999; Varricchio, 2011; Varricchio & Jackson, 2016) is not universally accepted (Deeming, 2002a, 2015; Deeming & Unwin, 2004; Bois & Mullin, 2017) and equivalent fossils do not exist for birds. Although an egg clutch from the Upper Cretaceous of Mongolia has been found in close association with fragmentary hind limb bones (Varricchio & Barta, 2015), there are no examples of articulated skeletal remains with associated eggs. The incomplete fossil record of reproduction in Mesozoic birds is therefore restricting our understanding of reproduction in this important group of vertebrates.

In extant birds, egg size is a key element of reproductive performance as it is pivotal in determining clutch size and is related to developmental maturity at hatching (Deeming, 2007), which in turn impacts on the degree of parental care required by the offspring. Egg physiology is attuned to the nesting environment and, in particular, the need for contact incubation by the adults (Deeming, 2002b). Eggshells have to withstand the mass of the adult bird during incubation whilst remaining thin enough to allow the young to hatch (Ar et al., 1979; Juang et al., 2017). Generally, the load masses that bird eggshells can tolerate before breaking are much greater than the parents' mass, but in some extinct large and flightless palaeognathous birds disparity between a very high female body mass and load mass resulted in reverse sexual dimorphism in which the smaller males probably incubated the eggs (Birchard & Deeming, 2009; Huynen et al., 2010).

The size of fossil bird eggs can be measured directly (Varricchio & Jackson, 2016; Lawver *et al.*, 2016) and their elongated symmetrical shape sets them aside from the asymmetrical eggs laid by modern birds (Deeming & Ruta, 2014). Aside from direct fossil evidence, egg size can be predicted from the presumed body mass of the extinct bird using a relationship derived from extant species (Deeming, 2006; Varricchio & Barta, 2015) and generally egg size is relatively small (Varricchio & Jackson, 2016). Unfortunately, the unambiguous association of eggs with identifiable skeletal remains of adult birds inhibits meaningful comparisons across a broader range of taxa.

However, pelvic morphology underwent substantial modifications in the course of avian evolution and it has been suggested that pelvic dimensions of Mesozoic birds could also be used to predict the maximum breadth of eggs (Dyke & Kaiser, 2010; Mayr, 2016). Phylogenetically basal birds outside Ornithothoraces, the clade including the sister taxa Enantiornithes and Ornithuromorpha, are characterised by a closed pubic symphysis. In these birds, the opening formed by the symphysis and the synsacrum effectively delimits the space through which an egg would have to pass (Kaiser, 2007; Dyke & Kaiser, 2010; Chiappe & Meng, 2016). Within Ornithothoraces, the tips of the pubes remain connected in most enantiornithines and in basal ornithuromorphs. A consistently open pubic symphysis, with widely separated pubic bones, characterizes the ornithuromorph subclade Ornithurae, to which modern birds belong (Mayr, 2016, 2017).

Our hypothesis is that egg breadth is physically constrained by the width of the pelvic canal in extinct birds with fused pubic symphysis, which in turn correlates with egg mass. Additionally, the relationship between egg mass and body mass allows contact incubation behaviour in extant birds. Hence, we can use predicted egg mass for extinct species to explore their incubation behaviour. Here we pursue the novel approach of predicting egg dimensions of Mesozoic birds from their skeletal remains. We use measurements of the maximum width of the pelvic canal of a range of bird species from the Late Jurassic and Early Cretaceous to define the breadth of the egg laid by the bird. Using this value in relationships for modern species we calculate egg mass and the maximum load mass the eggs could bear without breaking. We then compare this value with the predicted body mass of the same individual fossil specimens and with equivalent values for extant birds. Finally, we also examine taxonomic differences in pubis shape for Mesozoic birds.

Materials and methods

Data were collected for 21 different species of Mesozoic birds from published reports as listed in Deeming & Mayr (2018). Our taxon sampling includes the Late Jurassic *Archaeopteryx* and Early Cretaceous birds outside Ornithothoraces (e.g., *Confuciusornis*, *Jeholornis* and *Sapeornis*), as well as species of Early Cretaceous Enantiornithes (e.g., *Cathayornis*, *Parapengornis* and *Zhouornis*) and species of Early Cretaceous ornithuromorphs (e.g., *Changzuiornis*, *Gansus* and *Yanornis*).

Species were selected on the basis of published images of a specimen that showed an articulated pair of pubes seen from a dorsal or ventral aspect, and also either had a published measurement for femur and humerus lengths and the length of the pubis, or this value could be derived from the published image. The maximum width of the pelvic canal was measured from the image using ImageJ (https://imagej.nih.gov/ij/). Semilandmarks were digitally imposed on the pubis in TPSDig2 (Rohlf, 2006) to allow for geometric morphometric determination of pubis shape (see Deeming & Mayr [2018] for detailed methodology) (Zelditch *et al*., 2012).

Body mass of the individual specimen was calculated on the basis of femur and humerus lengths based on analysis of data presented by Field *et al*. (2013). Although we appreciate that femur circumference provides a more accurate measure of body mass for most Mesozoic birds such values are not available, or due to crushing of the fossils they are not reliable. Moreover, body mass is going to reflect musculature around both the pectoral and pelvic girdles so calculations that utilise elements of the fore and hind limbs will be more accurate. The original analysis presented by Field *et al*. (2013) was based on measures of skeletal elements of multiple specimens but used a single mean body mass for a species. To correct for this, mean values for femur and humerus lengths were calculated for male and female individuals. Initial analysis showed that sex was not a significant factor affecting body mass predictions from skeletal elements so we averaged any data for a species replicated for both sexes and re-analysed the data. This process reduced the dataset to 315 species (from a sample size of 863 used by Field *et al*., 2013). A phylogenetic tree was generated using the "Hackett All species" option on Birdtree.org, phylogenetically controlled least squares regression (pglm) was used in R (R Core Development Team, 2012) to predict body mass from Log_{10}-transformed data for femur length, humerus length, or femur and humerus lengths together. Akaike Information Criteria were used to determine the best model. Therefore, body mass (g) of Mesozoic birds was calculated on the basis of the equation:

Log Body mass = 1.130·Log Humerus Length +1.356 ·Log Femur Length – 1.690 (Eq-1)

(R^2 = 0.9256; λ= 0.941). Body mass for extant birds were taken from Dunning (2007).

Maximum pelvic canal width was assumed to limit the maximum breadth of the egg. However, published data collected for 17 species of chelonians showed that the maximum egg breadth is on average 0.814 of the maximum pelvic aperture (Deeming, 2018). Therefore, in this study maximum egg breath (B, in mm) was calculated by multiplying the maximum pelvic canal width by 0.814. The length of the egg (L, in mm) was then calculated based on a mean egg elongation ratio of 1.757 (SE = 0.060) derived from published values for Mesozoic bird eggs (Varricchio & Jackson, 2016). These values were used to calculate egg mass (in g) using a modified equation from (Hoyt, 1979; Deeming & Ferguson, 1990):

EM = $0.597 \cdot 1.757 \cdot B^3 \cdot 10^{-3}$ (Eq-2)

where 0.597 is the mean mass constant determined for crocodilian eggs (Deeming & Ferguson, 1990), which better represent the elongated shape of existing Mesozoic bird eggs (mean elongation ratio of 10 crocodilians = 1.64; Deeming & Ferguson, 1990). For extant eggs mass was predicted based on published values for breadth and length from Schönwetter (1960-1985) used in the equation:

EM = $0.548 \cdot L \cdot B^2 \cdot 10^{-3}$ (Eq-3)

where 0.548 is the mean mass constant determined for bird eggs (Hoyt, 1979).

A new relationship was generated for load mass of an eggshell using data for extant species combined from two studies (Ar *et al*., 1979; Juang *et al*., 2017) that took into account phylogeny. Our new relationship excluded the outlying data for the ostrich (*Struthio camelus*) egg, which is two

orders of magnitude greater than the range of egg sizes in this study and so could have biased our natural Log-transformed regression (Packard *et al.*, 2009). Using a phylogenetic tree generated from the "Hackett All species" option on Birdtree.org, a phylogenetically controlled least squares regression (pglm) was used in R (R Core Development Team, 2012) to predict load mass from calculated egg mass. Therefore, load mass (g) of Mesozoic and extant birds was calculated on the basis of the equation:

$$\text{Log Load mass} = 0.835 \cdot \text{Log Egg mass} + 1.861 \ (R^2 = 0.8441; \lambda = 0.734). \quad \text{(Eq-4)}$$

Statistical analysis involved Log_{10}-transformation of the data before doing analysis of covariance to test for the effect of taxonomic grouping (non-ornithothoracine, Enantiornithes and Ornithuromorpha) whilst controlling for femur length as a covariate. General, and general mixed, linear models were analysed using Minitab (ver. 17) to compare the effects of taxonomic group and the body mass and egg load mass as fixed factors. Non-significant interaction terms were observed and removed in all cases reported. Differences in pelvis shape between the bird types were investigated using Kruskal Wallis tests and general MANOVA on PC1 and PC2 generated by principal component analysis of semi-landmarks along the length of the pubis.

Results

Based on femur and humerus lengths, basal non-ornithothoracine birds were heavier than Early Cretaceous members of Ornithothoraces (Table 1). Predicted body masses for Enantiornithes were only about a sixth of the masses predicted for non-ornithothoracine birds and less than half that of the masses predicted for Early Cretaceous Ornithuromorpha (Table 1). Extant species that were similar in the size of the femur to Mesozoic Ornithuromorpha had comparable body masses (Table 1).

The maximum width of the pelvic canal delimited by the pubes was typically in an anterior position close to the ischia and ranged between 10 to 26 mm for all species except for a single large species (*Sapeornis chaoyangensis*), which had a pelvic canal width of 42 mm (see Deeming & Mayr, 2018). The predicted egg masses for the 21 species of Late Jurassic and Early Cretaceous birds averaged 4.7 g (SE of 2.0 with a range of 0.6–10.8 g with an outlier of 41.0 g; Table 1). The largest eggs were laid by non-ornithoracine birds and the smallest were laid by Enantiornithes (Table 1). This estimate for egg mass is significantly smaller than the value of 28 g calculated from the equation describing the relationship between female body mass and precocial eggs mass in extant birds (Deeming, 2007), which at is approximately seven times greater than that predicted from the pelvic canal dimensions (Table 1). Predicted egg masses as a percentage of predicted body mass were 0.80, 1.71 and 1.01 for non-ornithoracine birds, Enantiornithes and Mesozoic Ornithuromorpha, respectively. The extant birds lay eggs that average 8.5% of body mass.

A general linear mixed model, with species as a random factor, was used to compare the calculated maximum load mass (g) that an egg could endure until breaking with the predicted Mesozoic bird mass. The effects of taxonomic group and category of mass were both significant ($F_{2,20}$

= 4.67, $P = 0.023$; $F_{1,20} = 12.61$, $P < 0.001$, respectively; $R^2 = 89.0\%$) but the interaction was not significant and was removed from the model. For non-ornithothoracine birds, body mass was ~87% heavier than load mass, but for the Enantiornithes these values were ~27% lower and for the Ornithuromorpha the predicted body mass was ~79% greater than the load mass (Fig. 1). By contrast, the load mass that extant eggs could support was over three times the body of the birds that laid them (Fig. 1).

Geometric morphometric and principal component analysis (Deeming & Ruta, 2014) revealed that PC1 and PC2 values (29) explained ~75% and 15% of the variation in shape, respectively. General MANOVA showed that PC1 and PC2 were significantly affected by taxonomic group (Fig. 2; Wilk's test: $\lambda = 0.552$, $F_{4,34} = 2.9$, $P = 0.035$). This effect was primarily associated with variation in PC2, which was significantly affected by taxonomic group (Kruskal Wallis test: $H = 8.28$, $DF = 2$, $P = 0.014$) but PC1 was not a significant covariate ($H = 3.45$, $DF = 2$, $P = 0.178$). The length of the pubis was approximately three times longer than pelvic canal for non-ornithothoracine birds and Ornithuromorpha but was only 2.3 times longer in the Enantiornithes (Table 1). Quantitatively, non-ornithothoracine had pubes that were relatively straight and formed a V-shaped pelvic canal. In the Ornithuromorpha the pubes were more recurved anteriorly to the pubic symphysis so forming more of a U-shaped pelvic canal. In the Enantiornithes this pattern was exaggerated further by the relatively shorter pubes having to delimit a relatively wide pelvic canal.

Discussion

Our analyses suggest that the pubic symphysis delimited a pelvic canal that constrained the physical size of eggs to a mass around 25% of that predicted from data for extant species and is such smaller than other estimates for egg size in Mesozoic birds (Varricchio & Jackson, 2016). Evolutionary changes in early birds affected body size but preserved a minimum size for the pelvic canal. However, the calculated lengths of the eggs fit well within the size of the pelvis delimited by the length of the pubis (see Deeming & Mayr, 2018). Hence, the eggs of the Mesozoic birds in this study were relatively very small and this would have had consequences for the pattern of incubation.

The predicted breadth of Early Mesozoic bird eggs is smaller to that of many of the known fossil eggs attributed to birds (Varricchio & Jackson, 2016; Lawver *et al*., 2016), although we appreciate that there are many examples of larger avian eggs in the fossil record. The range of our egg breadths was 8.6–33.9 mm but all but four species had egg breadths predicted to be <15 mm. Of the 14 values reported by Varricchio and Jackson (2016) only 2 were below 20 mm but all of the values were below 41 mm. Likewise, the diameter of enantiornithine eggs from China (Zhou & Zhang, 2004), Mongolia (Balanoff *et al*., 2008) and Argentina (Schweitzer *et al*., 2002; Fernández *et al*., 2013) all lie well within the range of values reported here (20, 22.3 and 27 mm, respectively, from Varricchio & Jackson, 2016).

Some eggs attributed to Mesozoic birds are broader than could be laid by the birds included in this study (Varricchio & Jackson, 2016; Lawver *et al*., 2016). This may reflect the differing temporal and geographical origin of these eggs, which were mainly found in a range of Early and Late Cretaceous locations outside China and not in direct association with comparable articulated skeletal remains. Moreover, assessment of the taxonomic origin of eggs found in isolation can be difficult. For instance, presumed "theropod" eggs from Thailand (Buffetaut *et al*., 2005) were eventually shown to contain remains of a lizard (Fernandez *et al*., 2015). Similarly, an egg originally attributed to a neoceratopsian dinosaur has been shown to contain avian remains (Varricchio et al. 2015). Avian eggs found in Argentina (Fernández *et al*., 2013) have been linked by Varricchio and Jackson (2016) with the enantiornithine *Neuquenornis volans* (Clark & Norell, 2001) and it has been suggested that the eggs were 7.5% of the adult body size. However, such a conclusion if unfounded because, firstly, no skeletal element have been found with the eggs, and, secondly, the same strata contain the remains of both *Neuquenornis* and the much larger ornithurine *Patagopteryx* (Fernández *et al*., 2013), which makes assigning the eggs problematical.

Load mass of eggs of extant species is very high compared to body mass, especially in smaller birds (Ar *et al*., 2017; Juang *et al*., 2017). Whilst load mass correlates with shell thickness (Ar *et al*., 2017; Juang *et al*., 2017), it is unclear why bird eggs need to withstand masses much greater than the incubating adult. We acknowledge that eggs of early Mesozoic birds have a different shape and eggshell structure than those of extant birds (see Deeming & Ruta, 2014; Varricchio & Jackson, 2016) and this could impact on our interpretation of the data. However, limited data for the load mass to break a crocodilian egg show that this is equivalent to that of avian eggs of the same mass, despite the different eggshell structure and more elongated shape (Figure S5; Manolis & Webb, personal communication, 2017). We, therefore, consider that our approach of applying load mass data of extant birds to the eggs of fossil birds is justified.

Predicting egg size from pelvic dimensions is not unrealistic but data from extant species indicates that egg breadth is smaller than the maximal pelvic opening because the bones are surrounded by layers of soft tissue and the gastro-intestinal tract also passes through the pelvic canal. Breadth of turtle eggs averages only 81.4% of the maximal pelvic width and there is a very good relationship between egg breadth and maximal pelvic width (Deeming, 2018). Moreover, the only extant bird species with a closed pubic symphysis, the Ostrich (*Struthio camelus*), has an average egg breadth of 12.5 cm and the maximum pelvic aperture is 15 cm (Deeming, personal observations), which is a ratio of 0.833. In female American alligators (*Alligator mississippiensis*) the average egg is only 42 mm (Deeming & Ferguson, 1990), which is 65% of the 65 mm average width of the pelvic aperture (Prieto-Marquez *et al*., 2007). There is, however, one report of pelvic kinesis in the smallest tortoise *Homopus signatus* that lays eggs that are larger than its pelvic aperture (Hofmeyr *et al*., 2005)

but this may be unusual. It is possible that the small Mesozoic birds described in this study exhibited pelvic kinesis allowing laying of a larger egg. However, egg formation takes place in the pelvic girdle and this would limit egg breadth. Whether the pelvic limb musculature would allow for much movement of the pelvic bones is also unclear.

The degree of preservation of the birds used in this study is remarkable but whilst many skeletons are articulated all exhibit considerable crushing. This could suggest that our measurements of the articulated pubes may be unrealistic. However, the width of the synsacrum is usually very similar to that of the pelvic canal and in life the articulation of the ilium, ischium and pubis would have delimited the space below the synsacrum. Three-dimensional reconstruction of the pelvis is, therefore, likely to limit the width of the pelvic canal further. This means that our measurements are most likely overestimates, which reduces egg breadth and egg size futher.

Using the dimensions of the pelvic canal to calculate egg size in Mesozoic birds provides insight into their reproduction despite there being a lack of fossil eggs attributed to these species. Hence, for the species in our study the fact that pubic length scales with body size, whilst pelvic canal width was conserved suggests that there was a maximum egg width for Mesozoic birds that was physically delimited by the pelvic canal. This limitation means, for example, that in Early Cretaceous Enantiornithes the overall reduction in body size (compared to non-ornithothoracine birds) was reflected in a reduction in the length of the pubis but this bone seems to have changed shape to accommodate the maintenance of a minimum pelvic canal width (> 10 mm in these Chinese Mesozoic birds). The length of the pubes has only exhibited a significant reduction for the Enantiornithes, which means that the shapes of the pubes have changed from relatively straight, long bones forming a V-shaped pelvic canal to relatively short bones delimiting a U-shaped pelvic canal.

A pelvic canal delimited by a pubic symphysis is a feature of non-avian theropods in general. Whilst a comprehensive review of the dimensions of the pelvic canal in theropods is beyond the scope of our study, Hutchinson (2001) provides scale drawings that show that the pelvic aperature of *Allosaurus* measured ~ 7cm in breadth for an animal estimated to weigh 1500 kg (Bates *et al*., 2009). This has profound implications for egg sizes that could be laid by theropods – with an elongation ratio of 2.1 found in some theropods (Deeming & Ruta, 2014) an *Allosaurus* egg is estimated to be ~430 g – only 0.02% of body mass. Data for estimates of body mass and egg mass for four species of theropods (Werner & Griebeler, 2013) suggest that egg mass was very small relative to body mass (0.5-1%) and calculated load masses for eggs were only 20-50% of the predicted. Such values serve to support the view that contact incubation in theropods was very unlikely (Deeming, 2002a; Bois & Mullin, 2017). Clearly, there is a need for further investigation into the size of the pelvic canals of theropods and its implications for egg mass and reproduction in these animals. The concept that non-avian theropods were able to sit on and contact incubate their eggs (Varricchio *et al*., 2008), which is not universally accepted (Birchard *et al*., 2013), is not supported by the present study.

The disparity between body mass and presumed load mass that could be safely endured by the eggs of the Mesozoic birds as indicated here suggests that these species would find it hard to sit on their eggs in a manner similar to extant breeding birds without causing damage. Analyses of body mass, egg size, and shell thickness in extinct ratites suggests that the relatively small size of the eggs combined with thin eggshells meant that there was a low safety margin for contact incubation leading to reversed sexual dimorphism in some species, e.g., moas (Dinornithiformes) (Birchard & Deeming, 2009; Huynen *et al.*, 2010). Egg sizes are relatively small (< 1.5%) in all of the Mesozoic species here and so are comparable to the relatively small eggs of ratites. Differences in the body mass and the load mass of the eggs would have meant that contact incubation, as exhibited by extant birds (see Deeming, 2002c), was most likely precluded in non-ornithothoracines and Early Cretaceous Ornithuromorpha. The difference between eggshell load and bird size in the Enantiornithes is smaller but the scope for egg breakage would still be very high. Only when the pubic symphysis is opened up in the Ornithurae was the restriction on egg size removed allowing birds to lay larger eggs, which can support the body mass and allow evolution of true contact incubation.

It is possible that in the Mesozoic the first birds to sit on their eggs were able to achieve this without applying all of their weight. However, extant birds rely on contact incubation between the ventral skin of the body and the top of the eggs and often develop a brood patch to facilitate heat transfer (Lea & Klandorf, 2002). Such a need to intimate bodily contact and the relative smallness of the eggs does make this scenario difficult to envisage. In addition, the limited data for eggs of enantiornithine birds show that these were at least partially deposited in sediment (Deeming, 2006; Fernández *et al.*, 2013; Varricchio & Jackson, 2016), which contrasts with a modern-type avian contact incubation, in which the eggs also need to be regularly turned for normal development (Deeming, 2002d).

Another possibility is that the shells of the eggs laid by these Mesozoic birds were thicker and so better able to withstand the body mass. We know of no eggs attributed to the species studied here but there are eggs attributed to enantiornithine birds (Lawver *et al.*, 2016). Where available dimensions of these eggs can be used to calculate egg mass and hence predict eggshell thickness from the relationship for extant bird species (Birchard & Deeming, 2009). Comparison of mean (±SD) actual and predicted eggshell thicknesses for these fossil eggs showed that actual thickness is ~10% greater than predicted but this difference was not significant (actual eggshell thickness: 223.3 ± 100.7; predicted eggshell thickness = 200. 8 ± 49.6; paired t-test t_5 = -0.69, p = 0.523). This suggests that enantiornithine eggshells would be able to withstand loads masses to comparable extant eggs but future fossil specimens may allow us to test whether this is generally true.

This study primarily focusses on Mesozoic birds from China, which exhibit remarkable levels of preservation of articulated skeletons. Avian eggs that contain embryos are rare and they tend to be larger than the apparently small size of the eggs predicted here. This size disparity may reflect the chances of fossilisation or discovery. This study does predict that any avian eggs found from the

Mesozoic of China are likely to be very small.

Our study has indirectly demonstrated the limitations imposed upon reproduction in Mesozoic birds. As noted above, our values can only over-estimate egg mass based on the maximum pelvic canal, which suggests that differences between bird mass and egg size can only increase. That Mesozoic birds were much heavier than their eggshells could accommodate strongly suggests that contact incubation, as observed in extant birds, probably evolved only after there was an increase in egg width associated with an opening of the pubic symphysis.

References

Ar, A, Rahn, H., & Paganelli, C.V. 1979. The avian egg: mass and strength. *Condor* **81:** 331-337.

Balanoff, A.M., Norell, M.A., Grellet-Tinner, G. & Lewin, M.R. 2008. Digital preparation of a probable neoceratopsian preserved within an egg, with comments on microstructural anatomy of ornithischian eggshells. *Naturwissenschaften* **95:** 493–500.

Bates, K.T., Falkingham, P.L., Breithaupt, B.H., Hodgetts, D., Sellers, W.I. & Manning, P.L. 2009. How big as 'Big Al'? Quantifying the effect of soft tissue and osteological unknowns on mass predictions for *Allosaurus* (Dinosauria:Theropoda). *Palaeont. Electron.* **12(3):** 14A.

Birchard, G.F. & Deeming, D.C. 2009. Scaling of avian eggshell thickness: implications for maximum body mass in birds. *J. Zool.* **279:** 95-101.

Birchard, G.F., Deeming, D.C. & Ruta, M. 2013. Evolution of parental incubation behaviour in dinosaurs cannot be inferred from clutch mass in birds. *Biol. Lett.* **9:** 20130036.

Bois, J. & Mullin, S.J. 2017. Dinosaur nest ecology and predation during the Late Cretaceous: was there a relationship between upper Cretaceous extinction and nesting behavior? *Hist. Biol.* doi: 10.1080/08912963.2016.1277423.

Buffetaut, E., Grellet-Tinner, G., Suteethorn, V., Cuny, G., Tong, H., Košir, A., Cavin, L., Chitsing, S., Griffiths, P.J., Tabouelle, J. & Le Loeuff, J. 2005. Minute theropod eggs and embryo from the Lower Cretaceous of Thailand and the dinosaur-bird transition. *Naturwissenschaften* **92:** 477–482

Chiappe, L.M. & Meng, Q. 2016. *Birds of Stone. Chinese Avian Fossils from the Age of Dinosaurs.* John Hopkins University Press, Baltimore.

Clark, J.A. & Norell, M.A. 2001. The morphology and phylogenetic position of *Apsaravis ukhaana* from the Late Cretaceous of Mongolia. *Am. Mus. Nov.* **3387:** 1-24.

Clark, J.M., Norell, M.A. & Chiappe, L.M. 1999. An oviraptorid skeleton from the Late Cretaceous of Ukhaa Tolgod, Mongolia, preserved in an avianlike brooding position over and Oviraptorid nest. *Am. Mus. Nov.* **3265:** 1-36.

Clark, P.J., Ewert, M.A. & Nelson, C.E. 2001. Physical apertures as constraints on egg size and shape in the common musk turtle, *Sternotherus odoratus. Funct. Ecol.* **15:** 70-77.

Congdon, J.D. & Gibbons, J.W. 1987. Morphological constraint on egg size: A challenge to optimal size theory? *Proc. Natl. Acad. Sci.* **84:** 4145-4147.

Deeming, D.C. 2002a. Importance and evolution of incubation in avian reproduction. In: *Avian Incubation: Behaviour, Environment and Evolution* (D.C. Deeming, ed.), pp. 1-7. Oxford University Press, Oxford.

Deeming, D.C. 2002b. Functional characteristics of eggs. In: *Avian Incubation: Behaviour, Environment and Evolution* (D.C. Deeming, ed.), pp. 28-42. Oxford University Press, Oxford.

Deeming, D.C. 2002b. Behaviour patterns during incubation. In: *Avian Incubation: Behaviour, Environment and Evolution* (D.C. Deeming, ed.), pp. 63-87. Oxford University Press, Oxford.

Deeming, D.C. 2002d. Patterns and significance of egg turning. In: *Avian Incubation: Behaviour, Environment and Evolution* (D.C. Deeming, ed.), pp. 161–178. Oxford University Press, Oxford.

Deeming, D.C. 2006. Ultrastructural and functional morphology of eggshells supports idea that dinosaur eggs were incubated buried in a substrate. *Paleontology* **49:** 171-185.

Deeming, D.C. 2007. Effects of phylogeny and hatchling maturity on allometric relationships between female body mass and the mass and composition of bird eggs. *Avian Poult. Biol. Rev.* **18:** 21-37.

Deeming, D.C. 2015. The fossil record and evolution of avian egg nesting and incubation. In: *Nests, Eggs and Incubation: New Ideas About Avian Reproduction* (D.C. Deeming & S.J. Reynolds, eds.), pp. 8-15. Oxford University Press, Oxford.

Deeming, D.C. 2018. Role of eggshell structure in chelonian developmental plasticity. *Journal of Experimental Zoology Part A*, in press.

Deeming, D.C. & Ferguson, M.W.J. 1990.Methods for the determination of the physical characteristics of eggs of *Alligator mississippiensis*: A comparison with other crocodilian and avian eggs. *Herp. J.* **1:** 456-462.

Deeming, D.C. & Mayr, G. 2018. Data from:

Deeming, D.C. & Ruta, M. 2014. Egg shape changes at the theropod-bird transition, and a morphometric study of amniote eggs. *R. Soc. Open Sci.* 1: 140311.

Deeming, D.C. & Unwin, D.M. 2004. Reptilian incubation: evolution and the fossil record. In *Reptilian Incubation: Environment, Evolution and Behaviour* (D.C. Deeming ed.), pp. 1-14. Nottingham University Press, Nottingham.

Dunning, J.B. 2007. *CRC Handbook of Avian Body Masses*, Second Edition. CRC Press, Baton

Rouge, Florida.

Dyke, G.J. & Kaiser, G.W. 2010. Cracking a developmental constraint: egg size and bird evolution. *Rec. Aust. Mus*. **62:** 207-216.

Fernández, M.S., García, R.A., Fiorelli, L., Scolaro, A., Salvador, R.B., Cotaro, C.N., Kaiser, G.W. & Dyke, G.J. 2013. A large accumulation of avian eggs from the Late Cretaceous of Patagonia (Argentina) reveals a novel nesting strategy in Mesozoic birds. *PLoS ONE* **8(4):** e61030.

Fernandez, V., Buffetaut, E., Suteethorn, V., Rage, J.-C., Tafforeau, P. & Kundrát, M. 2015. Evidence of egg diversity in squamate evolution from Cretaceous anguimorph embryos. *PLoS ONE* **10(7):** e0128610.

Field, D.J., Lynner, C., Brown, C. & Darroch, S.A.F. 2013. Skeletal correlates for body mass estimation in modern and fossil flying birds. *PLoS ONE* **8(11):** e82000.

Hofmeyr, M.D., Henen, B.T. & Loehr, V.J.T. 2005. Overcoming environmental and morphological constraints: egg size and pelvic kinesis in the smallest tortoise, *Homopus signatus. Can. J. Zool*. **83**: 1343–1352.

Hoyt, D.F. 1979. Practical methods of estimating volume and fresh weight of bird eggs. *Auk* **96:** 73-77.

Hutchinson, J.R. 2001. The evolution of pelvic osteology and soft tissues on the line to extant birds (Neornithes). *Zool. J. Linn. Soc.* **131**: 123-168.

Huynen, L., Gill, B.J., Millar, C.D. & Lambert, DM. 2010. Ancient DNA reveals extreme egg morphology and nesting behavior in New Zealand's extinct moa. *Proc. Natl. Acad. Sci*. **107:** 16201-16206.

Juang, J.-Y., Chen, P.-Y., Yang, D.-C., Wu, S.-P., Yen, A. & Hsieh, H.-I. 2017. The avian egg exhibits general allometric invariances in mechanical design. *Sci. Rep.* **7:** 14205.

Kaiser, G.W. 2007. *The Inner Bird. Anatomy and Evolution*. UBC Press, Vancouver.

Lawver, D.R., Jin, X., Jackson, F.D. & Wang, Q. 2016. An avian egg from the Lower Cretaceous (Albian) Liangtoutang Formation of Zhejiang Province, China, *J. Vert. Paleontol.* **36:** e1100631.

Lea, R.W. & Klandorf, H. 2002. The brood patch. In: *Avian Incubation: Behaviour, Environment and Evolution* (D.C. Deeming, ed.), pp. 100-118. Oxford University Press, Oxford.

Lü, J.C., Unwin, D.M., Deeming, D.C., Jin, X., Liu, Y. & Ji, Q. 2011. An egg-adult association and its implications for pterosaur reproductive biology. *Science* **331:** 321-324.

Mayr, G. 2016. Evolution of avian breeding strategies and its relation to the habitat preferences of Mesozoic birds. *Evol. Ecol*. doi:10.1007/s10682-016-9872-1

Mayr, G. 2017 *Avian Evolution: The Fossil Record of Birds and its Paleobiological Significance*. Wiley-Blackwell, Chichester.

Packard, G.C. & Birchard, G.F. 2008. Allometric equations for predicting body mass of dinosaurs. *J. Zool*. **279:** 102-110.

Prieto-Marquez, A., Gignac, P.M. & Joshi, S. 2007. Neontological evaluation of pelvic skeletal attributes purported to reflect sex in extinct non-avian archosaurs. *J. Vert. Paleontol.* **27:** 603-609.

R Core Development Team 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Rohlf, F.J. 2006. TPSDig, v. 2.05. Stony Brook, NY: Department of Ecology and Evolution, State University of New York.

Schönwetter, M. 1960-1985. *Handbuch der oologie* (ed. W. Meise). Akademie-Verlag, Berlin

Schweitzer, M.H., Jackson, F.D., Chiappe, L.M., Schmitt, J.G., Calvo, J.O. & Rubilar, D.E. 2002. Late Cretaceous avian eggs with embryos from Argentina. *J. Vert. Paleont.* **22:** 191–195.

Varricchio, D.J. 2011 A distinct dinosaur life history? *Hist. Biol.* **23:** 91-107.

Varricchio, D.J., Balanoff, A.M. & Norell, M.A. 2015. Reidentification of Avian Embryonic Remains from the Cretaceous of Mongolia. *PLoS ONE* **10**(6): e0128458.

Varricchio, D.J. & Barta, D.E. 2015. Revisiting Sabath's "Larger Avian Eggs" from the Gobi Cretaceous. *Acta Palaeontol. Polon.* **60:** 11–25.

Varricchio, D.J. & Jackson, F.D. 2016. Reproduction in Mesozoic birds and evolution of the modern avian reproductive mode. *Auk* **133:** 654-684.

Varricchio, D.J., Moore, J.R., Erickson, G.M., Norell, M.A., Jackson, F.D. & Borkowski, J.J. 2008. Avian paternal care had dinosaur origin. *Science* **322:** 1826-1828.

Wang, X., Kellner, A.W.A., Jiang, S., Cheng, X., Wang, Q., Ma, Y., Paidoula, Y., Rodrigues, T., Chen, H., Sayão, J.M., Li, N., Zhang, J., Bantim, R.A.M., Meng, X., Zhang, X., Qiu, R. & Zhou, Z. 2017. Egg accumulation with 3D embryos provides insight into the life history of a pterosaur. *Science*, **358:** 1197-1201.

Werner, J. & Griebeler, E.M. 2013. New insights into non-avian dinosaur reproduction and their evolutionary and ecological implications: linking fossil evidence to allometries of extant close relatives. *PLoS ONE* **8(8):** e72862.

Zelditch, M.L., Swiderski, D.L. & Sheets, H.D. 2012. *Geometric Morphometrics for Biologists: A Primer*. Academic Press, New York.

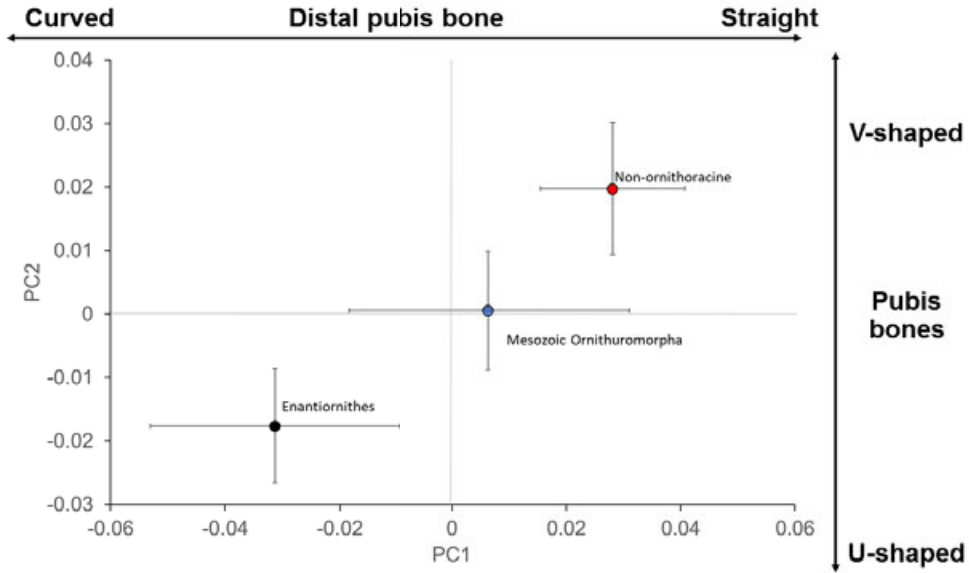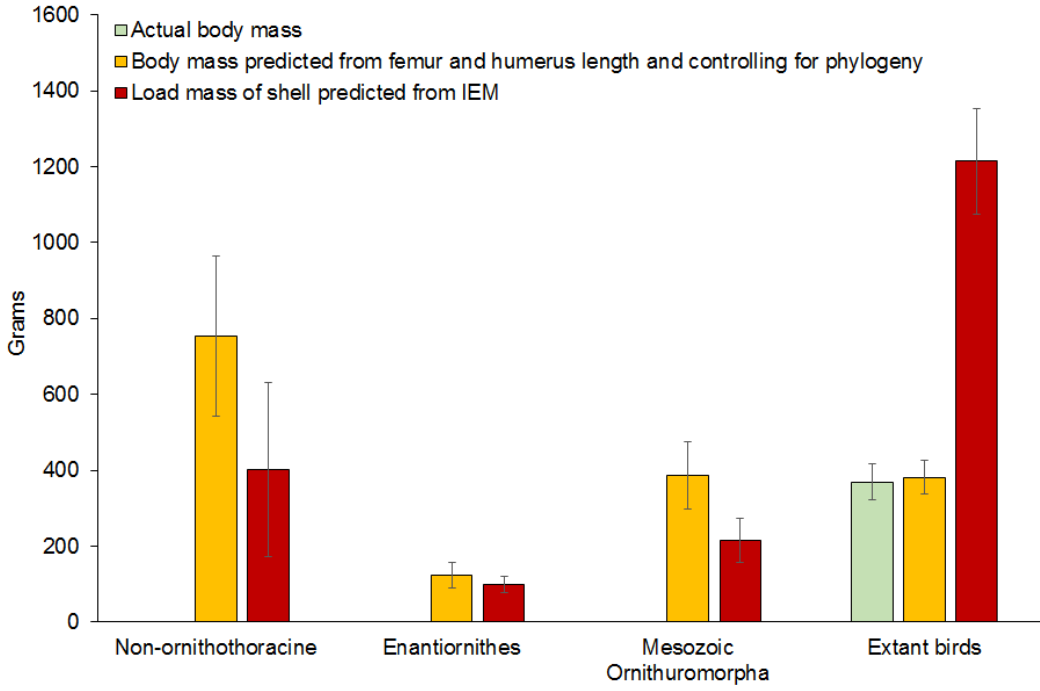Zhou, Z. & Zhang, F. 2004. A precocial avian embryo from the Lower Cretaceous of China. *Science* **306:** 653.

Fig. 1. Mean (± SD) values for bird mass predicted from femur and humerus length, and the load mass required to break an eggshell as calculated from calculated egg mass, for three taxa of Mesozoic birds, and extant species of a similar size. Mean body mass recorded from adult birds is also included as a comparison for extant birds.

Fig. 2. Mean (± SE) values for the first two principal components (PC1 and PC2) derived from a semi-landmark geometric morphometric analysis of pubis shape for the three taxonomic groups of Mesozoic birds in the dataset.

Table 1. Summary statistics (mean ± SD) for femur and pelvic dimensions and various predictions for body mass and egg mass for three groups of Mesozoic birds and extant birds.

	Non-ornithothoracine birds (N = 6)	Enantiornithes (N = 7)	Mesozoic Ornithuromorpha (N = 8)	Extant birds (N = 20)
Humerus length (mm)	76.1 ± 10.6	36.5 ± 4.9	60.0 ± 6.5	59.3 ± 3.2
Femur length (mm)	56.5 ± 5.7	28.2 ± 2.9	42.2 ± 5.1	43.2 ± 2.5
Pubis length (mm)	52.1 ± 6.9	28.5 ± 3.0	48.0 ± 4.8	41.6 ± 2.4
Pelvic canal, width (mm)	19.8 ± 3.8	13.2 ± 1.1	17.3 ± 2.0	-
Pubes length / Pelvic canal width	2.8 ± 0.2	2.2 ± 0.1	2.9 ± 0.3	-
Bird mass (g) predicted from femur and humerus lengths	753.5 ± 210.9	124.7 ± 33.5	386.6 ± 89.4	381.0[*] ± 44.1
Egg mass (g) predicted from bird mass	45.1 ± 8.8	13.0 ± 2.5	28.5 ± 5.1	27.8[#] ± 3.8
Egg mass (g) predicted from pelvic canal width*0.814	8.6 ± 5.6	1.5 ± 0.4	3.5 ± 1.2	-

*Actual mean mass derived from Dunning (2007); [#]Calculated from actual egg dimensions derived from Schönwetter (1960-1985)