Higher level taxonomy affects body mass and femur length as predictors for egg size in birds

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Abstract Interpretation of fossil material using comparative anatomy often relies on relationships predicted from data collected from extant species. Some years ago, it was suggested that femur length of birds could be predicted from egg mass but this relationship was counter-intuitive because egg mass is usually related to a measure of body size. The original analysis was also not phylogenetically controlled. This study used the same data to determine phylogenetically controlled relationships for body mass versus egg mass, and egg mass versus femur length. Further analysis showed that order was important in the prediction of egg mass from either body mass or femur length. For some orders, the single regression estimate through all data significantly over-, or under-estimated egg mass. This problem was more pronounced for femur length compared with body mass. Extrapolation of the relationship between femur length and egg mass for large extinct birds seemed to be provide useful data for the Gastornithidae but under-estimated egg mass for other large bird species of a variety of families. Use of equations derived from extant birds to gain insight into the reproductive biology of extinct species needs to be undertaken with great care.

Keywords: bird order, body mass, egg mass, femur length, giant birds, phylogeny

Összefoglalás A fosszilis anyagok összehasonlító anatómiával történő értelmezése gyakran a ma élő fajokról gyűjtött adatokból becsült kapcsolatokra támaszkodik. Néhány évvel ezelőtt azt javasolták, hogy a madarak combcsonthosszát a tojástömeg alapján meg lehet jósolni, de ez az összefüggés ellentétes volt az intuitív hatásokkal, mivel a tojás tömege általában a testmérethez szorosabban kapcsolódik. Az eredeti elemzés szintén nem vette számításba a fajok filogenetikai viszonyait. Ez a tanulmány ugyanazokat az adatokat használta a testtömeg és a tojástömeg, valamint a tojástömeg és a combcsont hosszának filogenetikailag ellenőrzött összefüggéseinek meghatározására. További elemzések kimutatták, hogy a rend (taxonómia) fontos a tojástömeg előrejelzésében akár a testtömeg, akár a combcsont hossza alapján. Egyes rendeknél az összes adaton alapuló egyetlen regressziós becslés jelentősen túl-, vagy alulbecsülte a tojás tömegét. Ez a probléma hangsúlyosabb volt a combcsont hosszára, mint a testtömegre. A combcsont hossza és a tojástömeg közötti összefüggés extrapolálása a kihalt nagytestű madarak esetében hasznos adatnak tűnt, például a Gastornithidae esetében, de alulbecsülte a tojástömeget a különböző családokba tartozó más nagy madárfajok esetében. A kihalt fajok szaporodásbiológiájába való betekintés érdekében a meglévő madarak adataiból származtatható egyenleteket nagy körültekintéssel kell alkalmazni.

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Introduction

Comparative anatomy relies on an understanding of the scaling of morphological features of animals in order to understand evolutionary patterns among taxa. Such relationships can also be useful in the interpretation of fossil specimens of species that are deemed comparable to extant species. For instance, body mass of extinct birds can be predicted from skeletal elements, although whether estimates are perceived as accurate depends on the method employed (Angst & Buffetaut 2017, Deeming & Mayr 2018). Egg mass of extant birds can be estimated with high accuracy from measurements of maximum length and breadth (Hoyt 1979) thereby allowing a reasonable estimate of size to be calculated for fossil eggs of known linear dimensions (Deeming 2006, Deeming & Mayr 2018). An alternative method for calculating egg mass, proposed by Dyke and Kaiser (2010), used a linear relationship between femur length and egg mass in extant birds to predict egg size in the Jurassic Enantiornithine bird *Confuciusornis*. This method has been used subsequently to estimate egg size in a range of extinct giant birds where eggs are unknown (Angst *et al.* 2014, Angst & Buffetaut 2017).

The relationship reported by Dyke and Kaiser (2010) used egg mass as the independent variable to predict femur length, which was seen as a proxy for body size. This was unusual because egg mass would normally be seen as a function of bird size and would be the dependent variable (Deeming 2007), rather than the other way around. Moreover, the relationship reported by Dyke and Kaiser (2010) did not consider different phylogenetic relationships between various species of birds. Higher level taxonomy has little effect on some allometric relations in birds, for instance, hatchling mass and egg mass (Deeming & Birchard 2007). However, for other relationships, e.g. between egg mass and female body mass (Deeming 2007), or between incubation period and egg mass (Deeming *et al.* 2006), there is a significant effect of order. Therefore, the possibility exists that the relationship reported by Dyke and Kaiser (2010), and subsequently used by Angst *et al.* (2014) and Angst and Buffetaut (2017), could be confounded by phylogenetic relationships.

This report details a study where the relationship between femur length (as the independent variable) and egg mass was explored using the data reported by Dyke and Kaiser (2010). In addition, the relationship between egg mass and body was also explored. In these analyses, the effect of order was examined whilst controlling for phylogenetic relationships within each order. It is predicted that whilst female body mass, or femur length, may serve as a good predictor of egg mass, the order of bird will prove very important in determining the value of any relationship that could be used to predict egg size.

Methods

Data for body mass (g), femur length (mm), and initial egg mass (g) reported by Dyke and Kaiser (2010) were available for 137 species (*Table 1*, which also provides order means) from 20 different orders as classified according to del Hoyo (2020). All data were Log_{10} transformed prior to analysis.

Table 1. Sample sizes and descriptive statistics (mean ± SE) for the 20 orders represented in the dataset provided by Dyke and Kaiser (2010) and used in the analysis. SE values are only calculated for orders where there were three or more species represented

1. táblázat Mintaméretek és átlagolt adatok (átlag ± SE) a Dyke és Kaiser (2010) által használt adatkészletben szereplő 20 madárrendre. A hibaértékeket (SE) csak azokra a rendekre számítottuk ki, ahol három vagy több fajra volt adat

	Species	Female body mass (g)	Egg mass (g)	Femur length (mm)
Accipitriformes	5	2199.8 ± 1338.3	85.7 ± 39.9	80.4 ± 13.3
Anseriformes	7	944.2 ± 179.7	57.1 ± 12.7	46.7 ± 4.4
Caprimulgiformes	6	40.3 ± 8.9	4.5 ± 1.2	18.0 ± 2.2
Charadriiformes	19	349.7 ± 68.2	38.4 ± 6.9	35.1 ± 2.3
Columbiformes	2	228.0	10.6	33.2
Coraciiformes	2	84.5	9.9	21.1
Cuculiformes	4	129.5 ± 53.7	9.8 ± 3.6	34.5 ± 6.8
Falconiformes	4	967.5 ±342.7	40.0 ± 10.1	67.8 ± 11.0
Galliformes	9	1242.3 ± 439.1	50.6 ± 18.7	71.0 ± 7.8
Gaviiformes	4	2856.0 ± 821.7	120.6 ± 19.1	50.6 ± 6.4
Gruiformes	7	2139.0 ± 817.2	78.1 ± 21.4	70.5 ± 17.1
Passeriformes	8	114.3 ± 90.4	10.8 ± 8.6	22.7 ± 6.5
Pelecaniformes	10	2948.1 ± 817.0	84.6 ± 14.4	93.6 ± 6.7
Piciformes	6	56.0 ± 8.1	3.9 ± 0.5	23.4 ± 2.2
Podicipediformes	3	587.7 ± 233.1	27.4 ± 5.5	36.9 ± 5.0
Procellariiformes	10	1753.5 ± 710.3	151.1 ± 48.9	49.3 ± 10.0
Sphenisciformes	3	4020.0 ± 567.2	110.7 ± 5.0	76.4 ± 1.4
Strigiformes	6	579.3 ± 189.7	37.4 ± 6.3	63.4 ± 8.1
Struthioniformes	7	23309.0 ± 9001.0	566.7 ± 170.4	166.7 ± 33.2
Suliformes	15	1514.4 ± 168.4	57.5 ± 3.9	52.4 ± 2.7
Total	**137**	**2323 ± 612**	**82.0 ± 13.7**	**56.8 ± 3.6**

Phylogenetically controlled general linear modelling (pglm) was performed in R version 4.1.0 (R Core Development Team 2020) using the packages ape (Paradis & Schliep 2019), mvtnorm (Genz *et al.* 2021), and MASS (Venables & Ripley 2002) using code provided by Carl Soulsbury (pers. comm.). A phylogenetic tree of the species in the dataset was produced based on a Hackett backbone using birdtree.org (Jetz *et al.* 2014). The first model provided a phylogenetically controlled linear regression estimate for all eggs, the slope of which was then tested against an appropriate isometric slope using a one-sample t-test (Bailey 1981). Residuals for each species were calculated for egg mass predicted from the regression equation and standardised by expressing them as a percentage of the reported egg mass. Order means for these standardised residuals were tested against a mean of zero using a one-sample t-test. A second phylogenetically controlled analysis of covariance (ANCOVA) model tested for the effect of order on egg mass whilst controlling for the covariate (either female body mass, or femur length, respectively), and included an interaction term between order and the covariate.

Results

Female body mass and egg mass

The phylogenetically controlled relationship between female body mass (FBM) and egg mass (EM) was:

$$LogEM = 0.642*LogFBM - 0.176.$$

This was highly significant ($F_{1,135} = 552.2$, $P < 0.0001$) *(Figure 1)*, had an R^2 value of 0.804 and the phylogenetic signal was very high ($\lambda = 0.997$). The slope exhibited significant negative allometry (tested against an isometric slope of 1.0, $t_{136} = -13.1$, $P < 0.001$). Although there were positive relationships between female body mass and egg mass in all orders, the calculated regression line did not fit the values very well, especially for birds of a body mass of 50 g or less *(Figure 1)*. The different relationships for orders meant that, for instance, eggs of a 500 g bird could exhibit a four-fold difference in mass.
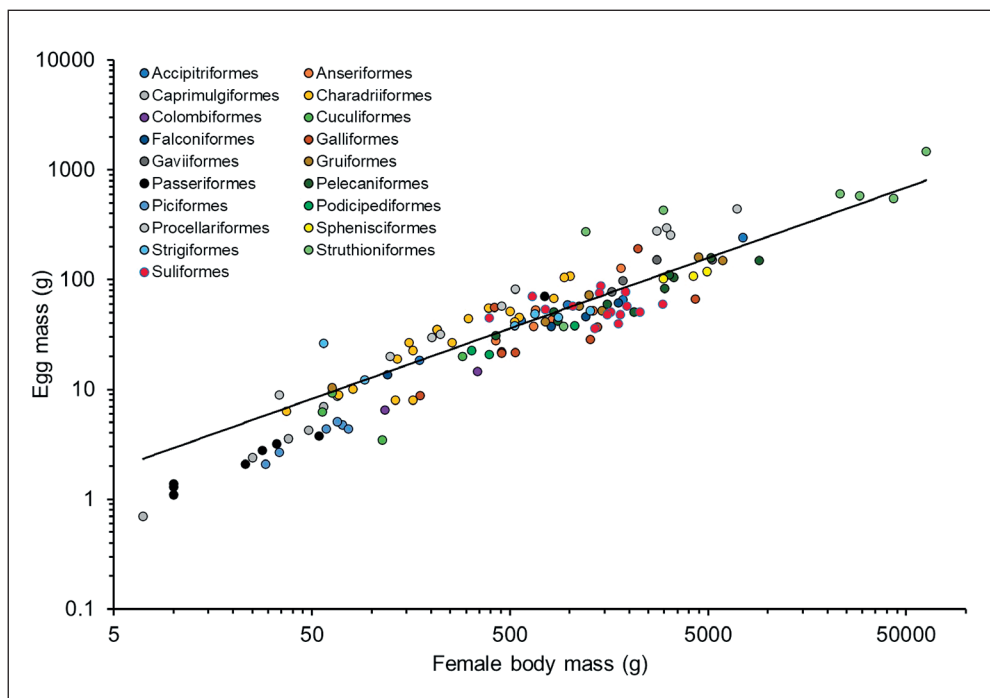

Figure 1. Relationship between female body mass and egg mass for 20 different avian orders. Trendline is generated by a phylogenetically controlled regression in R for all species irrespective of order. The colours correspond to the colour of the symbols indicating each type of bird

1. ábra A tojó testtömege és a tojástömeg kapcsolata 20 különböző madárrend esetében. A trendvonal egy filogenetikailag kontrollált regresszió illeszkedését mutatja a felhasznált madárfajok adataira. A színek megfelelnek az egyes madárfajokat jelző szimbólumok színének
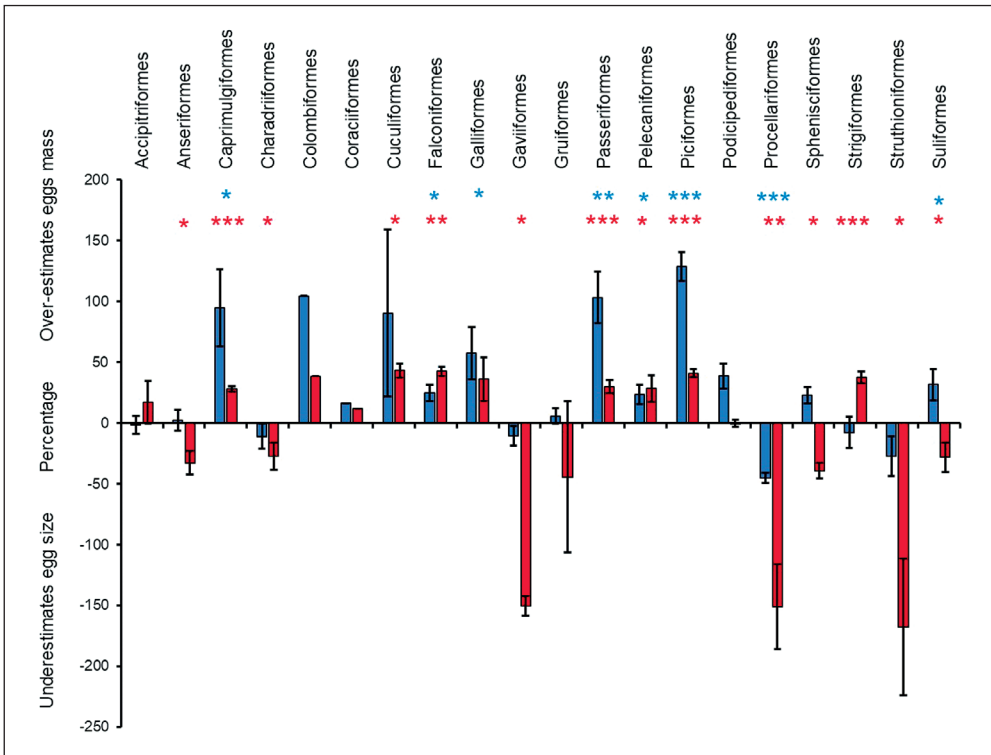
Figure 2. Mean (±SE) for standardised residuals for egg mass. Using phylogenetically controlled regression equations for the relationship with female body mass (blue bars) or femur length (red bars), egg mass was predicted for each species and expressed as a percentage of the actual egg mass for that species. Data were from Dyke and Kaiser (2010). Asterisks represent significant departures from a mean of zero for each order as determined by one-way t-tests; blue symbols indicate significance for egg mass predicted from female body mass and red asterisks indicate significance for egg mass predicted from femur length

2. ábra A tojástömeg standardizált reziduálisainak átlaga (±SE). A tojástömeget minden fajra megbecsültük, és az adott fajra vonatkozó tényleges tojástömeg százalékában fejeztük ki filogenetikailag kontrollált regressziós egyenletek segítségével: kék oszlopok – a tojó testtömegének, piros oszlopok – a combcsont hosszának felhasználásával. Az adatok Dyke és Kaiser (2010) tanulmányából származnak. A csillagok a nulla átlagtól való szignifikáns eltéréseket jelölik, az egyoldalú t-próbák alapján; kékkel a tojó testtömeg alapján előrejelzett tojástömeg jelentőségét, pirossal pedig a combcsont hosszából előrejelzett tojástömeg jelentőségét jelöltük

Representatives of individual orders were not uniformly distributed relative to the regression line. For instance, birds of the Charadriiformes and Procellariiformes were routinely above the line and those of the Piciformes below the line. Mean standardised residuals showed that using the single regression relationship generally over-estimated egg mass, which for several orders was a significant departure from zero *(Figure 2)*. By contrast, for the Procellariiformes the regression line significantly under-estimated egg mass *(Figure 2)*.

A phylogenetically corrected ANCOVA produced a significant interaction between LogFBM and the order ($F_{19,97} = 2.53$, $P = 0.0016$). Therefore, the relationship between

female body mass and egg mass was different for at least some orders, e.g. Suliformes. Within the same model there was a significant relationship between LogFBM and LogEM ($F_{1,97}$ = 2107.81, P < 0.0001) and a significant effect of order ($F_{19,97}$ = 6.85, P < 0.00001). This model explained over 95% of the variance in egg mass (R^2 value = 0.959) but the phylogenetic signal was very low (λ-value < 0.0001).

Femur length and egg mass

For femur length (FL), the phylogenetically controlled relationship with egg mass was:

$$LogEM = 1.505*LogFL - 0.928,$$

which was highly significant ($F_{1,135}$ = 303.4, P < 0.00001) *(Figure 3)*, had an R^2 value of 0.692 and a very high phylogenetic signal (λ > 0.999). This relationship exhibited significant negative allometry (test against an isometric slope of 3.0, t_{136} = -17.3, P < 0.001). However, the calculated regression line did not fit the values very well especially for birds with a femur length below 20 mm and for a femur length of 50 mm there was a 5-6-fold range in egg sizes *(Figure 3)*.
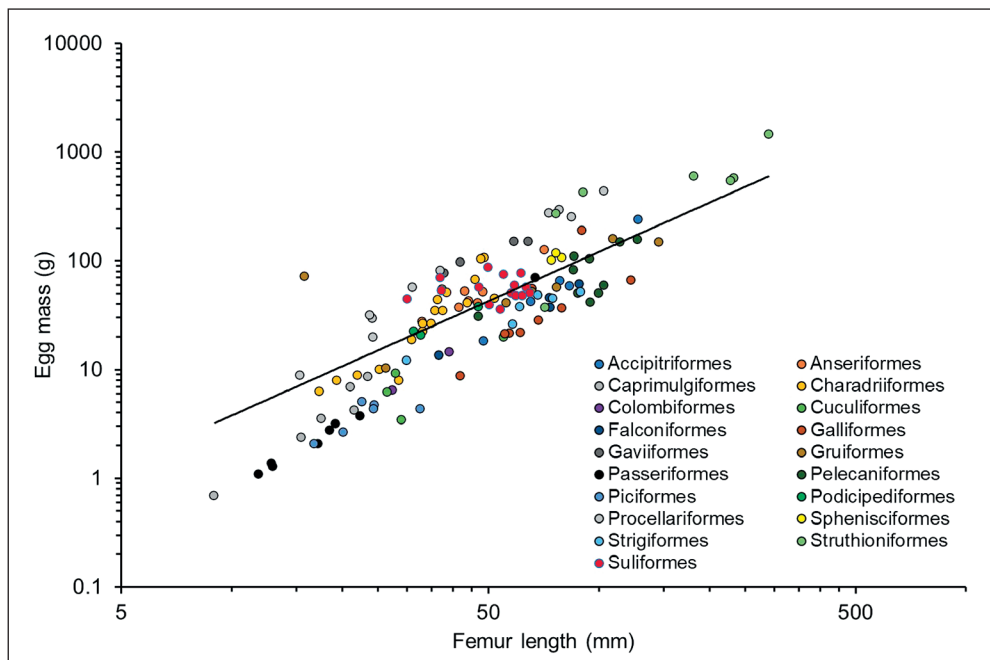

Figure 3. Relationship between femur length and egg mass for 20 different avian orders. Trendline is generated by a phylogenetically controlled regression in R for all species irrespective of order. The colours correspond to the colour of the symbols indicating each type of bird

3. ábra Összefüggés a combcsont hossza és a tojástömeg között 20 különböző madárrendnél. A trendvonal egy filogenetikailag kontrollált regresszió illeszkedését mutatja a felhasznált madárfajok adataira. A színek megfelelnek az egyes madárfajokat jelző szimbólumok színének

Representatives of individual orders were not uniformly distributed relative to the phylogenetically controlled regression line with birds of the Procellariiformes were routinely above the line and those of the Passeriformes below the line *(Figure 3)*. Mean standardised residuals showed that using the single regression relationship did not provide a good prediction of egg mass *(Figure 2)*. For seven of the orders the mean standardised residuals showed that predicted egg mass was significantly over-estimated and for six of the orders it was significantly under-estimated *(Figure 2)*.

The phylogenetically corrected ANCOVA revealed a significant interaction between LogFL and order ($F_{19,97}$ = 3.41, P < 0.0001) because there were significantly different relationships between femur length and egg mass for the Gruiformes and Suliformes. Within the same model there was a significant relationship between LogFL and LogEM ($F_{1,97}$ = 1344.06, P < 0.00001) and a significant effect of order ($F_{19,97}$ = 16.44, P < 0.00001). This model had an R^2 value of 0.947 and the λ-value was very low (< 0.0001).

Discussion

The results of the analysis showed that although egg mass could be predicted from body mass or femur length with a seemingly good level of accuracy, higher level taxonomy, i.e. order, significantly affected these relationships. Female body mass was a better predictor of egg mass than femur length. Therefore, as expected using a single regression relationship to predict egg mass in birds from either body mass, or femur length, introduces a considerable degree of uncertainty because it will depend on the order of bird involved.

It is unclear why Dyke and Kaiser (2010) decided that an analysis to predict body size from egg size was appropriate. The variation in egg size in extant species of different orders means that it is rather unreliable as a method for predicting egg size. Dyke and Kaiser (2010) were interested in understanding the reproductive biology of the Mesozoic enantiornithine bird *Confuciusornis* and were predicting egg size on the basis of the breadth of an egg that could fit through a pelvic canal defined by the fused pubic symphysis. The egg breadth was 17 mm, the eggs were considered as being round and the reported egg mass was 8.2 g. However, using the methodology of Hoyt (1979), i.e., egg mass = 0.548*LB² (L = egg length, B = egg breadth), which Dyke and Kaiser (2010) supposedly used, suggests that such an egg would be 2.7 g. By contrast, Deeming and Mayr (2018) used Hoyt's methodology and for a specimen of *Confuciusornis*, with a pelvic canal width of 14.9 mm, assuming an elongated egg (Deeming & Ruta 2014), the calculated egg mass was 3.5 g. It is unclear why Dyke and Kaiser (2010) had such a high estimate for egg mass. For any of these estimates, egg size in *Confuciusornis*, which has a femur length of 47 mm, it would seem that Dyke and Kaiser (2010) were correct in concluding that egg size would be very small. Deeming and Mayr (2018) concluded that a range of twenty species of Mesozoic birds laid small eggs for their body mass.

Angst *et al.* (2014) used the data published by Dyke and Kaiser (2010) to determine femur length for an egg attributed to the extinct giant bird *Ornitholithus arcuatus* (Gastornithidae), which was calculated to have a mass of 1400 g based on eggshell characteristics. The predicted femur length was 282 mm, which was comparable to other femurs attributed to

Gastornis (Gastornithidae). However, using the phylogenetically controlled relationship reported here for all eggs, a femur attributed to *Gastornis geiselensis* measuring 333 mm (Mayr & Smith 2019) would have a predicted egg mass of 738 g and the range of egg mass of 630–760 g is predicted for other *Gastornis* femurs measuring between 300–340 mm (Angst *et al.* 2014). These estimates are around half the predicted egg mass of 1400 g based on estimated dimensions (Angst *et al.* 2014), which rather undermines the use of egg mass to calculate femur length.

This disparity in egg size estimates is also observed when egg mass is predicted from the femurs of other giant flightless birds. For the Aepyornithiformes of Madagascar, femurs of *Aepyornis* species range from 320 to 430 mm, and for *Mullerornis* species they range from 221 to 246 mm (Angst & Buffetaut 2017). Using the phylogenetically controlled equation reported here, egg masses were estimated as 695–1084 g, and 398–468 g, for *Aepyornis* and *Mullerornis*, respectively. Such estimates are a fraction of the egg mass of 8,000 g predicted from egg dimensions (Angst & Buffetaut 2017). Using the Dyke and Kaiser (2010) relationship the predicted femur length from this egg mass is 618 mm, some 50–100% bigger than fossil bones. For moas (Dinornithiformes) of New Zealand, femur lengths range from 200 to 352 mm (Angst & Buffetaut 2017), which gives predicted egg masses of 342–802 g. By contrast, estimates of egg size from their linear dimensions range from 594 to 4167 g. The largest egg mass would overestimate femur length at 460 mm. Similarly, for *Dromornis stirtoni* (Dromornithidae, Anseriformes) of Australia, has a femur length of 428 mm (Angst & Buffetaut 2017), which predicts an egg mass of 1077 g but thickness of the eggshell predicts that egg mass is over 12,000 g (Murray & Vickers-Rich 2004). Using this egg mass, femur size is predicted at over 740 mm.

These comparisons suggest that for most extinct species the Dyke and Kaiser (2010 relationship does not provide realistic estimates of femur size. Moreover, extrapolation of the phylogenetically controlled relationship between egg mass and femur length does not provide reasonable estimates for egg size. Similar issues are to be expected when attempting to predict egg mass from body mass because Deeming (2007) showed that this relationship varies between orders, a conclusion supported by the analysis reported here. A further problem in predicted egg size in extinct species of giant bird is the estimation of their body mass. For example, estimates for body mass for *Dromornis stirtoni* vary from 440 to 786 kg, and for *Aepyornis maximus* they vary from 243 to 747 kg, depending on the study concerned (Angst & Buffetaut 2017). Whichever equation is used to predict egg mass will be affected by this variation in body mass.

These problems are confounded when the effect of order is taken into account. A single regression estimate would potentially over-estimate or under-estimate egg mass for extant bird species. Extrapolation of the equation to cover the size of larger extinct species could exacerbate the problem. It is possible that a more targeted approach may yield more realistic results. Most extinct giant birds are not closely assigned to extant orders (Angst & Buffetaut 2017), and extreme large size in modern birds is only associated with the Struthioniformes. Therefore, it is difficult to select a subset of extant bird species for which the relationship between body mass or a skeletal measure would be used to predict egg mass in extant species. One exception could be the Dromornithidae, which are attributed to the Anseriformes. It

would be interesting to explore how well phylogenetically controlled relationships for a measure of body size in waterfowl would be able to predict egg size to match those values suggested for the Dromornithidae.

This study has demonstrated that use of single relationships for anatomical features, even if they are phylogenetically controlled, can affect the calculated estimates of egg size of extinct species. Different higher level taxonomic classification is important in attempting to predict egg mass from body mass or femur length. Although superficially attractive, the relationship provided by Dyke and Kaiser (2010) is not particularly useful in predicting the size of birds or eggs. Extrapolation of relationships derived from extant bird species should always be undertaken with great care and interpretation should always be conservative.

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