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Estimating the mass of the Great Auk (*Pinguinus impennis*) and its egg

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The body mass and egg mass of the Great Auk *Pinguinus impennis* were never measured before the bird was driven to extinction in 1844. Previous studies conducted before 1990 used data from related species to estimate the mass of an adult bird at 4500–5000 g, and the fresh mass of its egg as 327–372 g. In the present study, we use a larger dataset of measurements from extant alcids, and statistical methods that control for the effects of phylogeny, to provide new estimates for those traits. The presumed body mass of the Great Auk was initially derived from a hearsay report from the 19th century, and then supported by subsequent comparative analyses based on skeletal measurements. Our new best estimates from currently available data show that the Great Auk's body mass was probably closer to 3560 g and its fresh egg mass was about 350 g. This new body mass estimate is the average of predictions from independent regressions of body mass on (1) tibiotarsus and femur lengths (3441 g) and (2) egg volume (3681 g). We calculated the Great Auk's fresh egg mass from a regression of fresh egg mass on egg volume in the extant alcids. Providing more accurate estimates of the body and egg mass of Great Auk can inform speculation about the developmental mode, ecology and life history of this iconic, extinct species.

Keywords: Alcidae, body mass, comparative methods, egg, extinction, flightless, skeleton.

After more than three centuries of human exploitation, the Great Auk *Pinguinus impennis* was finally driven to extinction in 1844. Despite the tens, or even hundreds, of thousands of adult birds taken for food, oil, feathers and specimens, there is no scientific record of the weight of a single bird. Indeed, none of the 78 skins and mounts now in museums and private collections (Hahn 1963, Fuller 1999) are accompanied by information about the fresh mass of the bird when it was killed. Likewise, there are no records of the weight of a Great Auk's egg even though thousands were taken and the shells of more than 75 eggs have been preserved (Fuller 1999).

All published statements about the mass of the Great Auk seem to lead back to the naturalist Colonel Henry Wemyss Feilden (1838–1921) who visited the Faroe Islands in May–June 1872 (Feilden 1872). During his trip to the island of Skuoe (now Skúvoy), Feilden visited an 80-year-old man, Jan Hansen, who was at the time believed to be the last person on the Faroes to have seen a Great Auk alive. Feilden says that '*This old man, who is now blind, told me that on the 1st of July, 1808, he went with a crew to the Great Dimon [now the island Stóra Dimun] for the purpose of catching rock-birds [seabirds]: upon a ledge at the base of the cliffs of that island they came across a single garfuglir [Great Auk], which was captured: this bird weighed nine Danish pounds, and on the division of the birds, at the conclusion of the fowling, was deemed equivalent to six guillemots*.' In those days a Danish pound ('pond') weighed 499.4 g (Jackson 1882). Thus 9 Danish pounds would have been 4495 g, or somewhere between 4245 and 4744 g, assuming the usual rounding conventions where numbers between 8.5 and 9.4 are rounded to 9. We do not know how the old man obtained that body mass so we cannot be certain that it was not a guess.

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Feilden (1872) also says '*As Clusius and Worm relate, the Dutch first called it Pingvin from its fatness, "pinguedo", it weighing sometimes sixteen pounds*.' Feilden is referring here to Ole Worm (1588–1654) and Carolus Clusius (1526–1609). Clusius was an eminent Dutch botanist who published a compendium of animals and plants (Clusius 1605). As Mullens (1922) points out, that reference to a bird weighing 16 pounds is actually describing a penguin and not a Great Auk. Hence, the claim by Feilden (1872) that the Great Auk was said to have weighed 16 pounds (or 7094 g, based on the Danish pound) is incorrect.

While Clusius (1605) presents a crude illustration of the Great Auk (which he called 'Goirfugel' and 'Mergus Americanus') and a brief description, he says nothing about its body mass. Worm was a Danish physician and natural historian who had three Great Auks, one of which he kept alive in captivity (Feilden 1872) implying that the other two were skins or mounted specimens (Mullens 1922). He obtained that live bird from the Faroes and says that it was a young bird that he kept alive for several months (Worm 1655). Worm also makes no mention of the body mass of this individual or of the species in his account of the Great Auk under the title *Anser Magellanicus seu Penguinis*.

Bédard (1969: Table 1) listed the body mass of the Great Auk as 'c. 5000 g', a rough estimate based on the relationship between body mass and body length of other alcids (see Supplementary Material: Background). Most recently, Livezey (1988) used six external morphological measurements (all variables log-transformed) of 20 extant alcid species to derive an equation to predict the Great Auk's body mass as 4999 g. As Livezey (1988) acknowledged, that method assumes that the Great Auk is structurally the same externally as the other alcids, even though his analyses showed that that assumption is incorrect (see Supplementary Material: Background). Livezey's estimate was presented without any measure of uncertainty and cannot be replicated as the raw data used for that analysis are not available.

To the best of our knowledge, the only estimates of the fresh mass of the Great Auk's egg are in Schönwetter (1967: 462 and 470) and Harris and Birkhead (1985: 179). Schönwetter (1967) calculated egg mass as 372 g using the dimensions of 46 Great Auk eggs to estimate their volume based on the volume of an ellipsoid, the density of fresh yolk and white, and an estimate of shell mass (see Supplementary Material: Background). Harris and Birkhead (1985) calculated the fresh mass of the Great Auk's egg as 327.1 g from the intraspecific relationship between fresh egg mass and a volume index (length × breadth^2) for the eggs of Common Guillemot *Uria aalge*. To support their estimate, they showed that the same method closely predicted the mass of the Razorbill's *Alca torda* egg, the Great Auk's closest extant relative.

We sought to either confirm or revise those previous estimates of egg and body mass using new data on skeletal measurements (e.g. Smith 2016) as well as improved statistical methodologies, including those that control for phylogeny using the latest phylogenetic hypotheses for the Alcidae (e.g. Hackett *et al.* 2008, Smith 2011, Smith & Clarke 2015). In addition, recent evidence that the average body mass of bird species is strongly correlated with their mean egg mass (Rotenberry & Balasubramaniam 2020) suggested to us that the body mass of the Great Auk also could be re-evaluated using the known size and shape of its egg (Birkhead *et al.* 2020). Great Auks laid and incubated a single egg for each breeding episode and about 75 eggshells have been preserved, again without fresh masses.

The present study was designed to provide best estimates of the mass of both the adult Great Auk and its egg to help inform research on chick development (Houston *et al.* 2010), diving performance (Smith & Clarke 2015) and foraging ecology of this iconic extinct bird. There is evidence, for example, (1) of a correlation between relative egg size and chick developmental mode (e.g. Ydenberg 1989, Starck & Ricklefs 1998, Dyke & Kaiser 2010), (2) that wing-loading, calculated from body mass and wing area, influences diving performance in birds (Elliott *et al.* 2013, Lapsansky *et al.* 2022) and (3) that foraging mode and prey size are related to body size in diving birds (e.g. Cook *et al.* 2013).

METHODS

We used regression analyses to estimate the body and egg mass of the Great Auk. To estimate body mass, we used two independent datasets of measurements from the extant species of Alcidae: (1) measurements of hindlimb bones (femur and tibiotarsus; Smith 2016, Livezey 1988) and (2) egg shapes (Pointedness, Polar Asymmetry, Elongation), volumes and linear dimensions using previously published data (Birkhead *et al.* 2020, Montgomerie *et al.* 2021) and some new measurements (Supplementary Material: Datasets). The known specimens of the Great Auk's egg are illustrated in standardized photographs in Tomkinson and Tomkinson (1966) where the 51 unbroken and well-photographed eggs can now be measured, and their shape, volume and fresh mass can be determined accurately (Biggins *et al.* 2018, Birkhead *et al.* 2020).

For each regression analysis, we tried to match the values for response variables (body mass or egg mass) with predictors (egg or skeletal traits) from the same populations, to minimize error due to the between-population variation that has been documented in many alcids (e.g. Barrett *et al.* 2008). Hence, to predict body mass from skeletal traits, we used all available adult body mass data because skeletal data were taken from various populations that were not documented (Supplementary Material: Datasets, Table S2). To predict body mass from egg traits, we used female body masses during the breeding season (preferably during the pre-laying period) from the same or closest populations for which we had egg traits (Supplementary Material: Datasets, Table S3). In each case, we classified the mode of chick development as precocial or semiprecocial; only the four species in the genus *Synthliboramphus* are precocial (Gaston & Jones 1998). To predict fresh egg mass, we used data on egg size, shape and fresh mass from the same populations when possible (Supplementary Material: Datasets, Table S4).

When data were available from different sources, we used the average of mean values per sample rather than weighted means, to provide a general population mean and avoid biasing the calculations toward colonies having larger sample sizes. In at least some species, there appear to be differences between colonies within the same population (e.g. Barrett *et al.* 2008), so we used grand means to minimize that bias. As the grand means and weighted means are highly correlated ($r > 0.999$, $n = 23$ species), both means gave almost the same predicted values from our models.

For body masses and fresh egg masses, we used data from Birds of the World (2023) and primary sources (see Supplementary Material: Datasets for details). For the remaining egg traits, we used data from a study on the evolution of egg shape in birds (Montgomerie *et al.* 2021), to which we added data on 38 eggs of seven species whose eggs were not included in that previous study (Supplementary Material: Datasets, Table S1). For measurements of the hindlimb bones of extinct and extant alcids, we used the available data in Livezey (1988: table 4) and Smith (2016: appendix 1) (see Supplementary Material: Datasets).

Our regression models that use the lengths of tibiotarsus and femur as predictors assume that the relationship between body mass and those leg bones is the same for flying (extant) and flightless (extinct) alcids. This assumption is supported by data from other flightless birds. In the family Rallidae, for example, there is no evidence for a difference between the femur lengths of the nine flightless and 41 flying species, adjusting for body mass (Gaspar *et al.* 2020). We further checked this assumption by looking at the relationship between body mass and femur length in the (flightless) penguins. The range of mean body mass for penguin species is large (0.9–40 kg) and both penguins and alcids forage by wing-propelled diving in the ocean, resulting in some structural convergence (Watanabe *et al.* 2021). Penguins of comparable size to the longer-legged alcids (see Results) – including the Great Auk – have the same relationship between body mass and femur length as those alcids (Supplementary Material: Background, Fig. S2).

All analyses were performed in R 4.4.0 (R Core Team 2024); we provide the code and data for analyses at Borealis (Montgomerie & Birkhead 2024). We report both Ordinary Least Squares (OLS) and Phylogenetic Generalized Least Squares (PGLS) regressions, the latter to show the effects of adjusting for the influence of phylogeny on our best estimates. Adjusting for phylogeny in our analyses had little effect on predicted estimates for the Great Auk because the best-fitting models without adjusting for phylogeny explained almost all the variation in fresh egg mass and adult body mass ($R^2 > 0.94$; Table 1a). As there are only 23 extant species of Alcidae in our dataset, we restricted regression analyses to one or two predictors to minimize the effects of overfitting. When comparing models based on different datasets, we consider the best-fitting models to be those with the lowest RMSE (Root Mean Squared Error; Rotenberry & Balasubramaniam 2020).

To perform PGLS analyses, we downloaded 1000 trees for the Alcidae from version 2 of the Hackett backbone (Stage2 Hackett) at vertlife.org and calculated a maximum credibility clade tree (Supplementary Material: Statistical Analyses, Fig. S3) using the *phangorn* (v. 2.11.1) package (Schliep 2011) in R. We also reconstructed the phylogeny in Smith and Clarke (2015: fig. 2; see Supplementary Material: Analyses, Fig. S4) and a similar one in DiGiacomo (2018: fig. 5) but PGLS analyses using those phylogenies yielded almost identical results (see Supplementary Material: Statistical Analyses, Tables S9 & S10).

PGLS models were analysed using the *phylolm* function in the *phylolm* (v. 2.6.2) package (Ho & Ane 2014) in R. From those models, we calculated predicted values for the Great Auk and prediction limits using the *gls.pi* function in the *evomap* (v. 0.0.0.9) package (Smaers & Mongle 2024). Note, however, that that method for calculating prediction limits is applicable only to models with single predictors. As the Great Auk was much larger than extant alcids, predicted values of egg and body mass for that species are extrapolations well beyond the data used to calculate each regression model. As in all regression analyses, the 95% prediction limits are large when predicted values are extrapolations well outside the range of available data.

Especially in allometric analyses, it is important to test for and exclude data that have a large influence on the slopes and intercepts of regressions (Nunn & Barton 2000). Because of their effect on slopes and intercepts, such influential data will necessarily affect predictions made from such analyses. We cannot be certain why some of our data (i.e. species) are influential, but there are at least four possibilities: (1) species means are based on small sample sizes, (2) mean values for predictors and response variables were calculated from different populations, (3) measurement error, especially with respect to fresh egg mass and adult body mass, and (4) adaptations to life history, locomotion, behaviour or ecology that cause species to depart from the allometric regression.

For OLS regressions, we considered data to be influential – and thus biasing the regression slope or intercept – if the calculated Cook's D was greater than $4/(n–k–1)$ for that sample of n species in a model with k predictors (Fox 2019; see Supplementary Material: Statistical Analyses). For PGLS models, we used the *influ_phylm* function in the *sensiPhy* (v. 0.8.5) package (Paterno *et al.* 2018) in R to identify influential data.

RESULTS

Egg size and shape

To assess variation in the size (linear measurements and volume) and shape of the Great Auk's egg we analysed data from a previous study (Birkhead *et al.* 2020). The egg of the Great Auk was among the largest and most pointed eggs of the 955 species studied by Montgomerie *et al.* (2021), falling within the largest 2% of species across the avian phylogeny with respect to egg volume and pointedness. As for all bird species, there is considerable individual variation in all egg size and shape parameters in the Great Auk, with the coefficients of variation ranging from 2.3% to 12.4% (Fig. 1). Egg volume, for example, varied from 245 to 386 mL. For the 51 Great Auk eggs that we measured, volume was correlated with polar asymmetry ($r = 0.28$, $P = 0.05$), egg length ($r = 0.76$, $P < 0.001$) and egg width ($r = 0.90$, $P < 0.001$). Among the egg shape parameters, pointedness was correlated with elongation ($r = 0.83$, $P < 0.001$) but not with polar asymmetry ($r = –0.10$, $P = 0.48$). We include this information to show that several shape parameters co-vary with egg volume and are correlated with one another, as well as to document the extent of variation in these traits.

Estimating fresh egg mass

Across the extant species of Alcidae, fresh egg mass is a function of egg volume (Fig. 2), with the largest residuals from the regression undoubtedly due to (1) small samples of eggs (fewer than five) used to estimate egg volume for most species, and (2) the volumes and fresh masses of eggs not being measured from the same populations, let alone the same individual specimens.

From the mean volume of the Great Auk's eggs in our sample, its mass is predicted to be 351 g in models that account for 97% of the variation in egg mass in the Alcidae, whether or not controlling for phylogeny (Table 1). As the average volume of Great Auk eggs is 339.1 mL (95% confidence level 330–348; range 245–386 mL, $n = 51$ eggs; Fig. 1), their 351-g egg would have a density (contents and shell) of 1.035 g/mL, similar

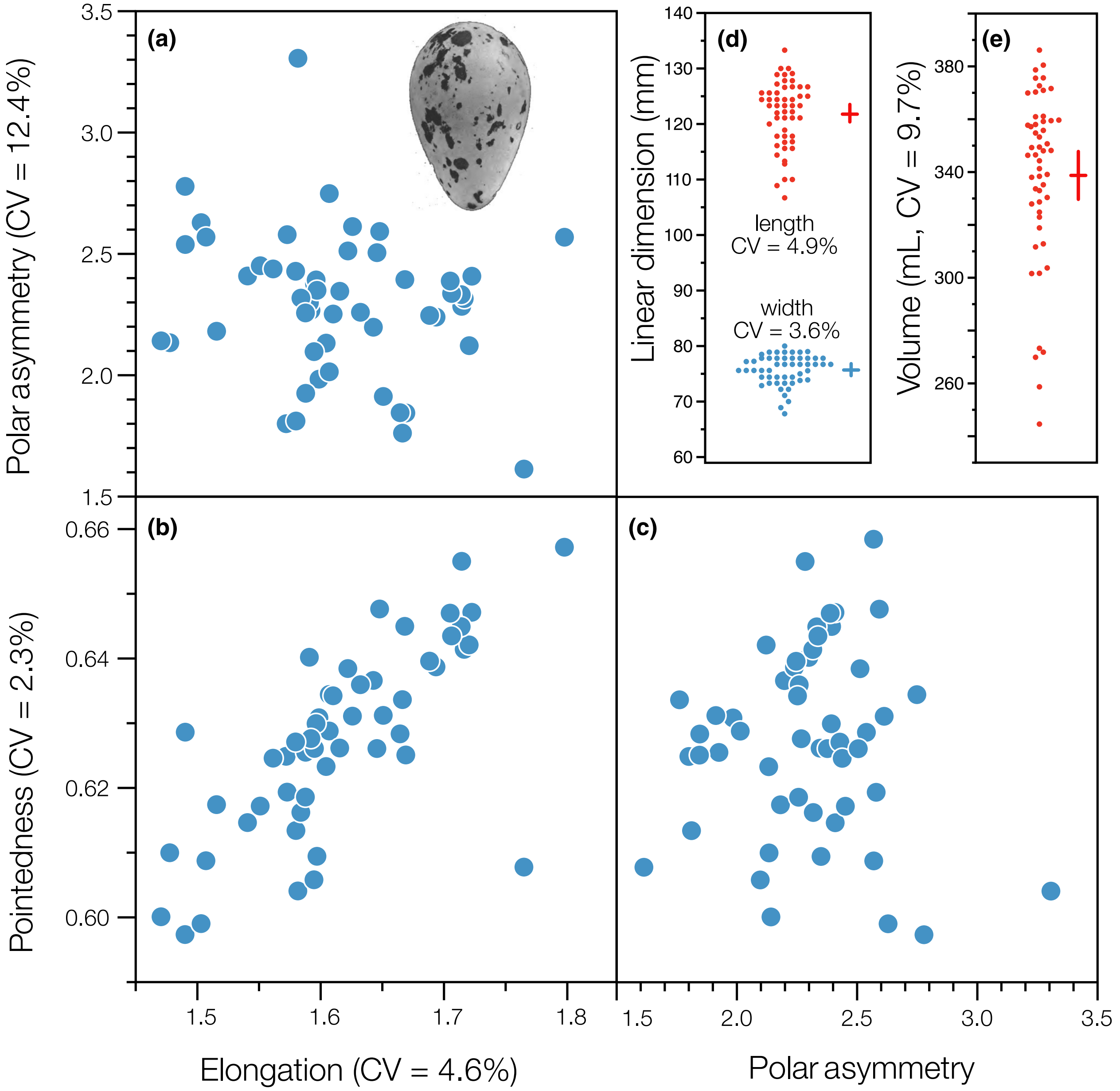

Figure 1. Size and shape of 51 Great Auk eggs (data from Montgomerie *et al.* 2021). In (d) and (e) lines show means ±95% CL. Inset in (a) is Great Auk egg #45 in Tomkinson and Tomkinson (1966). (a, b, c) Elongation = *L*/*W*, polar asymmetry = d*L*/d*S*, and pointedness = LP/*L*, where *L* and *W* are the maximum length and width of the egg, respectively; d*L* and d*S* are the diameters of the largest circles that fit within the large and small ends of the egg, respectively, and LP is the distance from the maximum width of the egg to the small end (Biggins *et al.* 2018).

to the average density of birds' eggs (1.03 g/mL; Paganelli *et al.* 1974, Rahn & Paganelli 1989a, 1989b). Using 1.035 g/mL as the density of the Great Auk's egg and the range of egg volumes in our sample, the 51 Great Auk eggs that we measured (Fig. 1) would have weighed 254–400 g.

Estimating body mass from skeletal traits

We analysed the relationships between alcid body masses and the lengths of their hindlimb bones (femurs, tibiotarsi and tarsometatarsi) as those

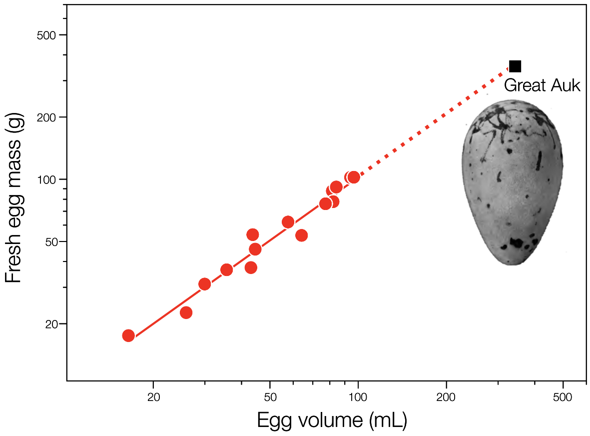

Figure 2. Egg volume predicts fresh egg mass in the Alcidae. The OLS regression shown here is extrapolated (dotted line) to the volume of the Great Auk's egg. The predicted mass of the Great Auk's egg (351 g; black square) is from both OLS and PGLS regressions that include all species (Table 1b). The inset is Great Auk egg #19 in Tomkinson and Tomkinson (1966).

skeletal traits are unlikely to be influenced by flightlessness (see Methods). The lengths of the femurs, tibiotarsi and tarsometatarsi in the seven species in the closely related alcid genera *Brachyramphus* and *Synthliboramphus* are relatively short for their body mass (Fig. 3), possibly related to their modes of terrestrial or aquatic locomotion. Hence, we restricted our analyses to the skeletal traits of 16 species of Alcidae with relatively long legs for their body mass.

Testing all three bone lengths as predictors of body mass for the long-legged alcids revealed that the best-fitting model included only femur and tibiotarsus length as predictors (Supplementary Material: Statistical Analyses, Table S15). Based on those two measurements, the body mass of the Great Auk is predicted to be 3441 g, in a model that accounts for the effects of phylogeny and excludes one influential species (*Alle alle*; Table 1b). That model accounts for 99% of the variation in the body mass of extant, long-legged alcids, and predicts almost the same body mass as a model that does not account for the effects of phylogeny (3303 g) but does include *A. alle* (Table 1a).

Estimating body mass from egg traits

To predict the body mass of the Great Auk from its egg measurements, we restricted our analyses to species with semi-precocial chick development, as a previous study (Houston *et al.* 2010) had shown that that was most likely the Great Auk's mode of development (see Discussion). The best-fitting models (lowest RMSE) to predict the body mass of extant alcids have egg volume as the sole predictor (Fig. 4, Table 1, Supplementary Material: Statistical Analyses, Tables S16–S19). Those models predict the body mass of the Great Auk to be 3681 g, whether (PGLS) or not (OLS) they adjust for the effects of phylogeny (Table 1). Both models account for 94% of the variation in the body masses of the 13 extant species with semi-precocial chicks.

DISCUSSION

Given the available data, the best estimate for the Great Auk's egg mass is 351 g, from the best-fitting models, whether or not adjusting for the effects of phylogeny (Table 1). This estimate could potentially be improved, or corroborated, by obtaining more data on the volume of eggs of various species of Alcidae as well as the fresh mass of those same eggs. Even though none of the data that we analysed were from large samples of fresh eggs that were weighed – nor from any of the same fresh eggs that were both weighed and measured – the statistical models account for most of the variation in egg mass (Table 1).

Our best estimate of the body mass of the Great Auk is 3561 g, the average of two independent predictions from (1) tibiotarsus and femur length (3441 g) and (2) egg volume (3681 g) in analyses that accounted for the effects of phylogeny (Table 1b). Uncertainties in these predicted values are due to the small samples from diverse populations that we used for the values of body mass, egg volume and hindlimb bone lengths. For example, the samples for all variables were rarely from the same population in any species, and some intrapopulation variation is to be expected (Barrett *et al.* 2008). For example, Burness and Montevecchi (1992) reported variation in the Great Auk's body size related to oceanographic conditions, with populations in the Low Arctic Region averaging slightly larger than those in the Boreal Region of the North Atlantic. Nonetheless, as for the analyses of egg mass, regressions to predict body masses in the alcids accounted for most of the variation in the available data (Table 1).

Table 1. Models to predict adult body mass and fresh egg mass in the Alcidae. Analyses to predict body mass from tibiotarsus length include only long-legged species, thus excluding three *Brachyramphus* spp. and four *Synthliboramphus* spp. (Fig. 3).

(a) OLS models

Response	Predictor(s)	Effect (*n*) R^2, RMSE	Predicted (95% PL)
Fresh egg mass (g)	Egg volume (mL): all species	1.02 (15) 0.97, 0.043	351 (258–494)
Adult body mass (g)	Tibiotarsus length (mm), femur length (mm): long-legged species	1.60, 1.47 (16) 0.98, 0.041	3304 (2461–4435)
	Egg volume (mL): all species	1.26 (15) 0.89, 0.103	3746 (1745–8039)
	Egg volume (mL): semi-precocial species	1.22 (13) 0.94, 0.075	3681 (2064–6566)

(b) PGLS models; lambda is Pagel's lambda estimated by bootstrapping

Response	Predictor(s)	Effect (*n*) R^2, RMSE	Predicted (95% PL)	Lambda (95% CL)
Fresh egg mass (g)	Egg volume (mL): all species	1.01 (15) 0.97, 0.041	351 (268–493)	0.11 (0.01–1)
Adult body mass (g)	Tibiotarsus length (mm), femur length (mm): long-legged species	1.27, 1.65 (16) 0.98, 0.045	3009[a]	0.29 (0.01–1)
	Tibiotarsus length (mm), femur length (mm): long-legged species, excluding influential data[b]	1.59, 1.55 (15) 0.99, 0.037	3441[a]	0.06 (0.01–1)
	Egg volume (mL): all species	1.31 (15) 0.89, 0.103	4067 (2353–7311)	0.68 (0.01–1)
	Egg volume (mL): semi-precocial spp.	1.22 (13) 0.94, 0.075	3681 (2037–4751)	0.12 (0.01–1)

CL, confidence limits; PL, prediction limits; RMSE, root mean squared error. All variables were $\log_{10}$-transformed. [a]Prediction limits not available for models with more than one predictor. [b]*Alle alle*.

Hence, our statistical models (Table 1) suggest that the body mass of the Great Auk has previously been overestimated by 25–40%. Our new estimate of egg mass is close to the mean (349.5 g) of the previous two estimates (327 g in Harris & Birkhead 1985, 372 g in Schönwetter 1967). Our analyses differ from previous studies of the body and egg mass of the Great Auk in that we (1) used both skeletal traits and egg volume to provide independent predictions of body mass in the Alcidae, (2) restricted that analysis of skeletal traits to long-legged species, (3) used measured egg volume to predict egg mass rather than body mass (Harris & Birkhead 1985) or linear measurements and estimated volume (Schönwetter 1967) to predict egg mass, (4) restricted that analysis to fresh egg mass and species with semi-precocial chick development, (5) tried to match the relevant populations for each analysis (Supplementary Material: Datasets, Tables S2–S4) and (6) analysed both OLS and PGLS regressions with and without influential data (Table 1). As noted in the Methods, influential data are species that have a large effect on the slope and/or intercept of regressions and so have an undue influence on predicted values. The PGLS regression that included the single influential species, for example, predicted the body mass of the Great Auk to be 3009 g, well below our two estimates (3441 and 3681 g) and all previous estimates (4500–5000 g).

Given that the standard deviation (sd) of body mass in close relatives to the Great Auk (Razorbill, Common Guillemot and Brünnich's Guillemot *Uria lomvia*) is about 6% of mean values, we used that value to estimate the sd for the Great Auk's body mass: sd = ±214 g (for a mean of 3561 g). Assuming that body mass is normally distributed in a population of Great Auks, 95% of a population of this species would have had body mass between 3133 and 3989 g, and 99.7% of the population would have had body mass between 2919 and 4203 g.

The prediction limits for each of our best estimates are wide, in each case encompassing previous estimates of the Great Auk's egg and body masses. However, prediction limits are always large when predicted values are well outside the range of available data, even though the statistical models for our best estimates for the Great Auk accounted for ≥94% of the variation in the extant

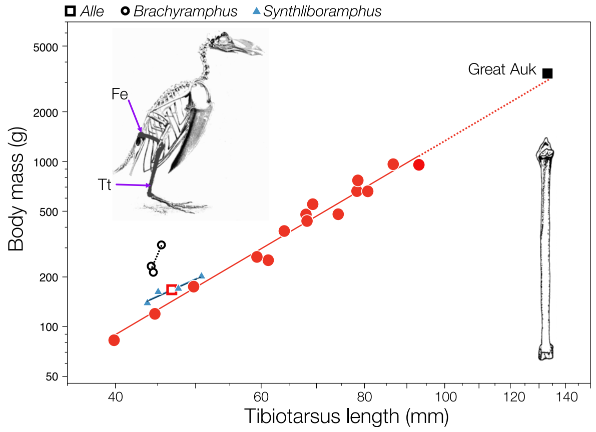

Figure 3. Tibiotarsus length predicts adult body mass in the extant alcids. Red line is the OLS regression for 16 long-legged species (red dots and black square; Table 1a). Dotted black line is the OLS regression for the three *Brachyramphus* species; blue line is the OLS regression for the four *Synthliboramphus* species. Great Auk body mass (black square) is estimated to be 3441 g from a PLGS regression with both femur length and tibiotarsus length as predictors (Table 1), excluding *Alle alle* (open red square). Inset of Great Auk skeleton (upper left) is modified from Wikimedia Commons (File: PSM V62 D515 Smithsonian great auk skeleton.png) and shows the location of the femur (Fe) and tibiotarsus (Tt) bones; inset of tibiotarsus (lower right) is modified from Burness and Montevecchi (1992).

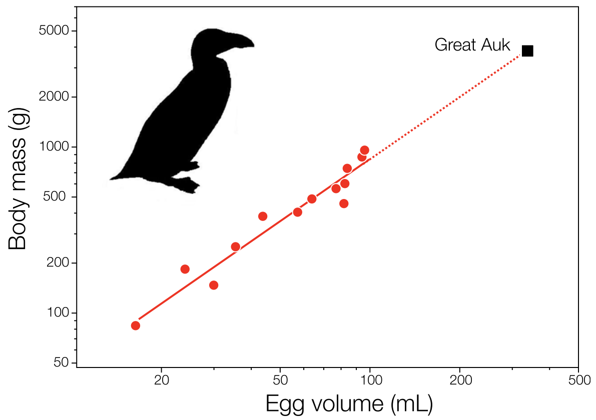

Figure 4. Egg volume predicts adult body mass in 13 extant species of Alcidae that have semi-precocial chicks (Table 1). The OLS regression (red line) is extrapolated (dashed line) to the body mass of the Great Auk (3681 g; black square) predicted from both OLS and PGLS models. Silhouette is from phylopic.org.

species in each model. Crucially, however, our two independent estimates of Great Auk body mass differ by less than 7%. Given that the model to predict body mass from tibiotarsus and femur lengths accounts for 99% of the variation and is a better fit (lower RMSE) than the model to predict body mass from egg volume, that prediction for the Great Auk's body mass (3441 g; Table 1b) might be considered to be more accurate.

Implications

In addition to correcting past estimates for the mass of the Great Auk and its egg, our results potentially have implications for the conclusions of some previous studies of this species. First, the wing-loading of the Great Auk had previously been estimated at 22 g/cm^2 based on an estimate of 230 cm^2 for the total area of the wings and a body mass of 5000 g (Livezey 1988). Birkhead (1993: fig. 7) independently estimated the Great Auk's total wing area to be similar at 225 cm^2. Our new best estimate for the Great Auk's body mass (3561 g) results in a wing-loading of about 16 g/cm^2.

Livezey (1988) assumed that the Great Auk propelled itself underwater with half-folded wings like the other alcids (see Spring 1971), and not with outstretched wings like penguins. Based on his estimate of their half-folded wing area (154 g/cm^2) and our best estimate of Great Auk body mass at 3561 g, its wing-loading would have been 23 g/cm^2. This is close to the wing-loading 24.4 g/cm^2 calculated from data in Sato *et al.* (2010) for the Chinstrap Penguin *Pygoscelis antarcticus*, which is similar in size (3800 g) to the Great Auk as well as being a flightless, wing-propelled diver. However, given the Great Auk's disproportionately small wings compared with the other alcids (Supplementary Material: Statistical Analyses, Fig. S6) and its unusual pattern of feather replacement (see Birkhead 1993), it seems unlikely that it propelled itself underwater with wings folded to the same extent as in the extant alcids. Indeed, as Watanabe *et al.* (2021) have documented, the wing skeletons and musculatures of the flightless (extinct) alcids have converged toward that of the penguins and away from that of the extant and flying alcids, but that convergence is only partial, probably due to the differences in their volant ancestors. This partial convergence is reflected in the relationship between humerus length and body mass in the Great Auk compared with both the flying alcids and the flightless penguins (Supplementary Material: Statistical Analyses, Fig. S7).

Second, our revised estimates of the Great Auk's egg mass (351 g) and body mass (3561 g) can be used to make inferences about the development of their chicks. Alcids show a wide range of chick developmental patterns (Harris & Birkhead 1985, Ydenberg 1989), from precocial (leaving the nest-site 2 days after hatching and weighing 10–15% of adult mass; e.g. Ancient Murrelet *Synthliboramphus antiquus*) to semi-precocial (leaving the nest after 27–55 days and weighing 62–96% of adult mass; e.g. Atlantic Puffin *Fratercula arctica*). In a third group (genera *Alca* and *Uria*), sometimes referred to as 'intermediate', the chicks are semi-precocial but leave the nest site after 17–21 days at 21–25% of adult mass (e.g. Common Guillemot).

The alcids with precocial chick development have relatively large eggs (mean 0.218 g/g body mass; $n = 4$ species) compared with those with semi-precocial (including 'intermediate') chick development (mean 0.146 g/g body mass; $n = 17$ species). Even though the mass of the Great Auk's egg relative to body mass (0.099 g egg/g body mass) is about 50% higher than previously thought (0.065, based on 5-kg body mass and 327-g egg mass), they still had a relatively small egg compared with the fresh egg mass of other alcids relative to their adult body mass (0.11–0.23 g egg/g body mass; Supplementary Material: Statistical Analyses, Table S20). Relative egg size in the Great Auk was, therefore, similar to that of the two largest extant alcids (Common and Brünnich's Guillemots) whose relative egg sizes are both 0.11 g/g body mass.

Assuming that a freshly hatched Great Auk chick would weigh 68% of the mass of a freshly laid egg, like the Razorbill and other closely related alcids (Birkhead & Nettleship 1984), its chick would have weighed about 239 g at hatch (68% of 351 g), or about 6.7% of adult body mass. The chicks of the two largest extant alcids (*U. aalge* and *U. lomvia*) hatch at about 8% of adult body mass and are 'intermediate', whereas the chicks of the four alcids with precocial development hatch at an average of about 19% of adult body mass. Hence, although our findings cannot be used to determine when the Great Auk's chick would have left the colony and gone to sea, they corroborate recent studies showing that their chicks were very likely to have been the 'intermediate' type of semi-precocial development (Houston *et al.* 2010, Birkhead 2022).

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AUTHOR CONTRIBUTIONS

Robert D. Montgomerie: Conceptualization; investigation; funding acquisition; writing – original draft; methodology; validation; visualization; writing – review and editing; formal analysis; project administration; data curation; resources. **Tim R. Birkhead:** Investigation; funding acquisition; writing – review and editing; methodology; resources; conceptualization.

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CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

ETHICAL NOTE

None.

Data Availability Statement

All data and R code scripts are available in a public data repository at Borealis: doi:10.5683/SP3/TIMQAP (Montgomerie & Birkhead 2024).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Relationships between both body mass (left) and tibiotarsus length (right) and femur length in the extant species of Alcidae.

Figure S2. Maximum clade credibility tree from Hackett phylogeny.

Figure S3. Phylogeny of the Alcidae reconstructed from figure 3 in Smith and Clarke (2015), but with equal branch lengths.

Figure S4. Virtually identical OLS relationship between body mass and femur length in the longer-legged extant alcids.

Figure S5. Relationship between egg volume and body mass in the Alcidae.

Figure S6. Wing area increases with body mass in the auks and penguins.

Figure S7. The Great Auk has a shorter humerus for its body mass than the other auks, but still much longer than that of penguins of comparable size.

Table S1. Newly analysed eggs added to a published dataset (Montgomerie *et al.* 2021).

Table S2. Sources of mean adult body masses used to determine the relationship between body mass and skeletal traits.

Table S3. Sources of data used to determine the relationship between female body mass and egg volume.

Table S4. Sources of data used to determine the relationship between egg mass and egg volume.

Table S5. Linear models to compare the three groups shown in Figure 2 and Figure S1(left) to predict tibiotarsus length (left) or femur length (right) from body mass.

Table S6. Schönwetter's (1967: 461–462) table of the measurements of 14 Great Auk eggs.

Table S7. Part of Schönwetter's (1967: 470) summary table of the measurements of eggs of several alcids.

Table S8. Harris and Birkhead's (1985: 179) estimate of the mass of the Great Auk's egg.

Table S9. PGLS models to predict Great Auk body mass (g) from skeletal traits and egg volume using different phylogenies.

Table S10. PGLS models to predict Great Auk egg mass (g) from egg volume using different phylogenies.

Table S11. Model selection to predict egg mass from egg traits in the Alcidae.

Table S12. Model to predict fresh egg mass in 15 alcids, with both volume and polar asymmetry as predictors.

Table S13. PGLS model to predict fresh egg mass in 15 alcids, with both volume and polar asymmetry as predictors.

Table S14. Model selection to predict body mass from skeletal measurements in 23 extant Alcidae.

Table S15. Model selection to predict body mass from skeletal measurements in the 16 species of long-legged, extant Alcidae.

Table S16. Models to predict body mass from egg volume and shape parameters, clutch size and the mode of chick development in the alcids.

Table S17. Best-fitting OLS model to predict body mass from egg volume and chick development in the alcids.

Table S18. Models to predict body mass from egg traits in the 13 extant alcids that have semi-precocial chick development.

Table S19. Best-fitting model to predict body mass from egg volume in the 13 extant alcids that have semi-precocial chick development.

Table S20. Relative egg mass in the extant alcids.

Datasets. Sources of data for this study.

Background. Relevant background information and research.

Statistical analyses. Details of model structure and model selection.