Article:

eprints@whiterose.ac.uk
https://eprints.whiterose.ac.uk/

The Shapes of Birds' Eggs: Evolutionary Constraints and Adaptations

Robert Montgomerie,[1],* Nicola Hemmings,[2] Jamie E. Thompson,[2] and Tim R. Birkhead[2]

1. Department of Biology, Queen's University, Kingston, Ontario K7L 3N6, Canada;   2. School of Biosciences, University of Sheffield, Sheffield S10 2TN, United Kingdom

ABSTRACT: We studied the shapes of eggs from 955 extant bird species across the avian phylogeny, including 39 of 40 orders and 78% of 249 families. We show that the elongation component of egg shape (length relative to width) is largely the result of constraints imposed by the female's anatomy during egg formation, whereas asymmetry (pointedness) is mainly an adaptation to conditions during the incubation period. Thus, egg elongation is associated with the size of the egg in relation to both the size of the female's oviduct and her general body conformation and mode of locomotion correlated with pelvis shape. Egg asymmetry is related mainly to clutch size and the structure of the incubation site, factors that influence thermal efficiency during incubation and the risk of breakage. Importantly, general patterns across the avian phylogeny do not always reflect the trends within lower taxonomic levels. We argue that the analysis of avian egg shape is most profitably conducted within taxa where all species share similar life histories and ecologies, as there is no single factor that influences egg shape in the same way in all bird species.

Keywords: birds, egg shape, oviduct, pelvis shape, clutch size, relative egg size.

Introduction

For centuries, naturalists have marveled at the diversity of sizes, colors, and shapes of what Thomas Wentworth Higginson, in 1862, called the most perfect things in the universe (Birkhead 2016)—the eggs of birds. The diversity of egg size—spanning five orders of magnitude from the eggs of *Mellisuga helenae* (bee hummingbird, at 0.5 g) to those of *Aepyornis maximus* (elephant bird, at 8 kg)—is largely explained by life histories and body size allometries (Lack 1968). The colors and shapes of birds' eggs also vary among orders, families, genera, species, populations, and even in-

dividuals, but the causes of variation in these traits remain somewhat elusive.

The study of egg shape has progressed along two fronts: (i) quantification and (ii) attempts to explain variation. Since D'Arcy Wentworth Thompson (1908, 1917) first tackled the quantification problem in 1908, more than 20 studies have attempted both mathematical and practical descriptions of avian egg shape with mixed success, especially for the most asymmetric eggs (Biggins et al. 2018). Preston's (1953, 1968, 1969) mathematical formulations provided an accurate descriptor of all avian egg shapes using four parameters but have rarely been used to assess interspecific variation in shape. Simpler measures have not been as accurate as Preston's for all species, but a new software tool (Biggins et al. 2018) uses Preston's parameters to derive three accurate indexes of egg shape—elongation, pointedness, and polar asymmetry—that are readily obtained from digital images (Birkhead et al. 2018).

The first studies on the adaptive significance of egg shape focused on species that laid the most asymmetric (pointed) eggs: *Uria* murres (*Uria* guillemots in Europe; Tschanz et al. 1969) and waders (Andersson 1978), both in the order Charadriiformes. The earliest studies of murre eggs suggested that their pear-like shape was an adaptation that made their eggs spin or roll in a tight circle when knocked, thus reducing the chance of rolling off the bare cliff ledges where those birds incubate their eggs (Tschanz et al. 1969). More recent work has shown instead that this shape makes the murres' eggs more stable and less likely to move during incubation changeovers (Birkhead et al. 2018). The pointed shape of wader eggs, on the other hand, allows eggs in their typical four-egg clutches to pack more closely together, presumably enhancing incubation efficiency (Andersson 1978).

We embarked on this study with the primary goal of identifying the evolutionary pressures and anatomical/

* Corresponding author; email: mont@queensu.ca.

ORCIDs: Montgomerie, https://orcid.org/0000-0003-4701-4525; Hemmings, https://orcid.org/0000-0003-2418-3625; Thompson, https://orcid.org/0000-0003-0048-7886; Birkhead, https://orcid.org/0000-0003-2916-4976.

physiological constraints that influence avian egg shape across the entire range of variation in extant species. We had four objectives.

First, we sought to replicate a recent comprehensive study of egg shape across the avian phylogeny (Stoddard et al. 2017) by (i) using more accurate measures of egg shape based on standardized photographs and a new method for quantifying the shapes of all birds' eggs (Biggins et al. 2018), (ii) achieving a slightly broader taxonomic coverage by targeting species from diverse sources, (iii) analyzing independent measures of the elongation and asymmetry components of egg shape so that we could evaluate the factors affecting each of these traits separately, and (iv) categorizing incubation sites according to structural features that might be expected to influence egg shape by optimizing thermal efficiency—maximizing heat gain during incubation and minimizing heat loss when parents are absent. We feel that such replication is useful as we used a different data set with many different species, a different method of quantifying egg shape, and some different predictors in our models (table S1; tables S1–S22 are available online) but also because we have raised questions about the generality of previous conclusions (Birkhead et al. 2019b; but see Stoddard et al. 2019).

Second, to identify and quantify potential constraints on egg shape, we examined oviductal anatomy in a large and diverse family of birds (Galliformes) as well as the available data on pelvis anatomy from a taxonomically broad range of species (Shatkovska et al. 2018). The diameter of the oviduct could plausibly limit egg diameter, and we present new data here to assess how the oviduct influences egg shape. Pelvis anatomy has been previously implicated as influencing egg shape (Rensch 1959; Warham 1990; Deeming and Mayr 2018; Shatkovska et al. 2018), although the underlying mechanisms are unknown.

Third, we explored variation in the factors influencing egg shape within avian families and orders. Our previous work on the evolution of egg shape in the families Alcidae (auks, guillemots, murres) and Spheniscidae (penguins) revealed interesting within-family variation in egg shape that was correlated with incubation site (Birkhead et al. 2018; see also table S3-C in Stoddard et al. 2017). Our exploratory analyses also revealed that the trends within many avian families and orders did not match the general trends across all birds, suggesting that a more comprehensive understanding of the evolution of egg shape required a focus on different clades within the class Aves (see also Stoddard et al. 2019).

We focus most of our analyses at the level of avian families because this is the lowest taxonomic level at which we were able to measure the eggs of enough species to make statistically useful analyses for comparison among and within taxa. These family-level patterns will not always be consistent with patterns at lower taxonomic ranks (subfamily, genus, subgenus) within those families. Thus, without further analysis, we cannot be sure that all of the potential drivers of variation in egg shape are to be found at the level of family. Families in the class Aves also differ in functional morphologies and ecologies, forming clades that are well supported by comprehensive molecular phylogenies (Hackett et al. 2008; Jetz et al. 2012; Jarvis et al. 2014; Prum et al. 2015; Kimball et al. 2019). There is ample evidence that families of birds differ markedly in ecologies and life histories (Lack 1968; Bennett and Owens 2002), with considerably more variation in those traits among than within families. Thus, analyses at the family level control for variation in traits that are not expected to influence egg shape (e.g., foraging ecology, diet, age at first breeding, longevity).

Fourth, we provide—and test predictions from—a conceptual framework for the study of egg shape that focuses on the underlying mechanisms that might either constrain egg shape or select for different shapes that maximize thermal efficiency and minimize breakage. In this context, we define a constraint as a factor that limits optimal shape because of an adaptation to some other aspect of a bird's lifestyle. For example, the optimization of underwater locomotion for foraging favors a streamlined, elongated body shape to reduce drag (Nesteruk et al. 2014), resulting in a relatively narrow pelvis that might constrain egg width (Shatkovska et al. 2018).

Conceptual Framework

Constraints

We looked specifically at two possible constraints on egg shape, one imposed by the size of the female's oviduct and the other imposed by the shape of the female's pelvis. First, as Thompson (1917) suggested more than a century ago, oviduct diameter might influence egg elongation as the unshelled egg is squeezed by the walls of the oviduct.

To assess the possibility of such a constraint on egg shape, we measured several oviduct dimensions in 28 species of Galliformes (land fowl) and found that all were positively related to female mass with negative allometry (slope < 1.0; table S10). The maximum diameter of the isthmus—where an egg expands to its final shape before the shell is added in the uterus—scales with female body size with an exponent of 0.38 (see "Constraints: Oviduct Anatomy") such that larger birds have a much narrower isthmus for their body size than do smaller birds. Thus, if the diameter of the isthmus limits egg width, we expected a positive effect of both female size and relative egg size (controlling for female size) on the elongation of eggs.

Second, almost two centuries ago, Thienemann (1825) suggested that the shapes of birds' eggs might be influenced

by the shape of the female's body, with species having more elongated bodies laying more elongated eggs. Pelvis anatomy has since been implicated as the causal mechanism (Rensch 1959; Warham 1990) but only recently has this relationship been analyzed quantitatively (Shatkovska et al. 2018). Thus, in 173 species, pelvis shape was correlated with an index of egg elongation but not with an index of egg asymmetry (Shatkovska et al. 2018).

Because almost all extant bird species have an unfused pelvis—unlike their Jurassic and Cretaceous ancestors (and the ostriches and possibly other ratites; Deeming and Mayr 2018)—the pelvis is unlikely to be a hard constraint that prevents the passage of a too-wide egg (Kaiser 2010). Birds with relatively narrow pelvises do have relatively narrow bodies streamlined to enhance locomotion (Shatkovska et al. 2018). Thus, narrow pelvises might simply be correlated with some aspect of abdominal anatomy that moderates egg width. These effects should be pronounced in species with particularly large eggs for their body size.

An index of wing shape—the hand-wing index (HWI)—that is related to flight efficiency (Claramunt et al. 2017) was recently found to be correlated with egg shape (Stoddard et al. 2017) but accounted for only 5% of the interspecific variation in indexes of elongation and asymmetry. In that study, the indexes of elongation and asymmetry were moderately correlated (with family as random effect, $r = 0.53$ [95% confidence limits (CLs): 0.49, 0.56], $n = 1,400$ species means), preventing the independent assessment of the factors affecting those two aspects of shape. Species with high HWI are more dispersive and migratory (Sheard et al. 2020), presumably requiring more efficient flight that might in turn be associated with a more streamlined body shape (Stoddard et al. 2017).

Adaptations

The evidence for egg shape being adaptive has so far been restricted to selection acting during the incubation period, with shape influencing egg strength (Bain 1991), egg stability during incubation on different substrates (Birkhead et al. 2019b), and incubation efficiency (Andersson 1978), as well as being related to nest microclimate (Duursma et al. 2018). For example, perfect spheres offer the strongest shell structure (Bain 1991) and lowest surface-to-volume ratio (Paganelli et al. 1974), everything else being equal. Thus, eggs are expected to be more spherical in species with larger clutch sizes (>4 eggs), both to take advantage of closer packing to increase incubation efficiency and reduce heat loss (Andersson 1978) and to reduce the chance of breakage (Bain 1991). Conversely, eggs that are prolate spheroids (elongated spheres) have a relatively larger surface area than perfect spheres and thus allow for a larger region of contact incubation on their long axis such that they heat up more efficiently during incubation, even though they cool down more quickly when no parent is incubating.

Two components of egg shape that represent asymmetry (polar asymmetry and pointedness; fig. 1A, 1B) are likely determined during egg formation by (i) some as yet unidentified structural characteristic of the magnum-isthmus junction (Mao et al. 2006) or (ii) variation in the thickness and structure of the shell membrane (Mallock 1925; Stoddard et al. 2017; Birkhead et al. 2019a) as the albumen takes up water and expands before the ovum moves to the uterus where the shell is applied. Either way, the question remains whether these mechanisms represent anatomical constraints or evolved mechanisms to produce asymmetrical eggs for some adaptive purpose.

Finally, incubation efficiency is thought to be an important selective force on egg shape because any increase in efficiency that enhances heat transfer from the incubating adult—or decreases heat loss when the eggs are not being incubated—reduces the time that eggs and chicks are confined to the incubation site (Martin et al. 2015). For example, asymmetric eggs allow closer packing than prolate spheroids in clutches of three and four in open nests (Andersson 1978), thereby increasing incubation efficiency and reducing heat loss. Such close packing seems to be the clearest explanation for the extremely asymmetric eggs of waders (families Charadriidae, Jacanidae, Pedionomidae, Recurvirostridae, Rostratulidae, Scolopacidae, Thinocoridae), where the clutch size is almost always four and eggs are incubated in open scrapes and platforms. This incubation advantage is predicted to decline as clutch size increases above four (Andersson 1978), so less asymmetric eggs are expected in species with larger clutches, everything else being equal.

Methods

Measuring Oviduct Size

To study oviductal anatomy, we obtained 70 specimens of 28 species of Galliformes euthanized during their egg-laying period. The oviduct (including cloaca and ovary) was removed intact, unraveled, stripped of connective tissue, and cleaned in phosphate buffered saline.

These freshly dissected oviducts were pinned out, photographed, and measured. The entire length of the oviduct was measured (±1 mm) from the infundibulum to the cloaca, as well as the individual lengths of the magnum, isthmus, uterus (shell gland), and vagina. The oviduct was then transferred to a tray, where each section was pinned straight and submerged in 10% formalin to fix the tissue for histological examination. After >48 h in fixative, segments were cut from the vagina, uterus, isthmus, and magnum, then sectioned and stained with hematoxylin and eosin before
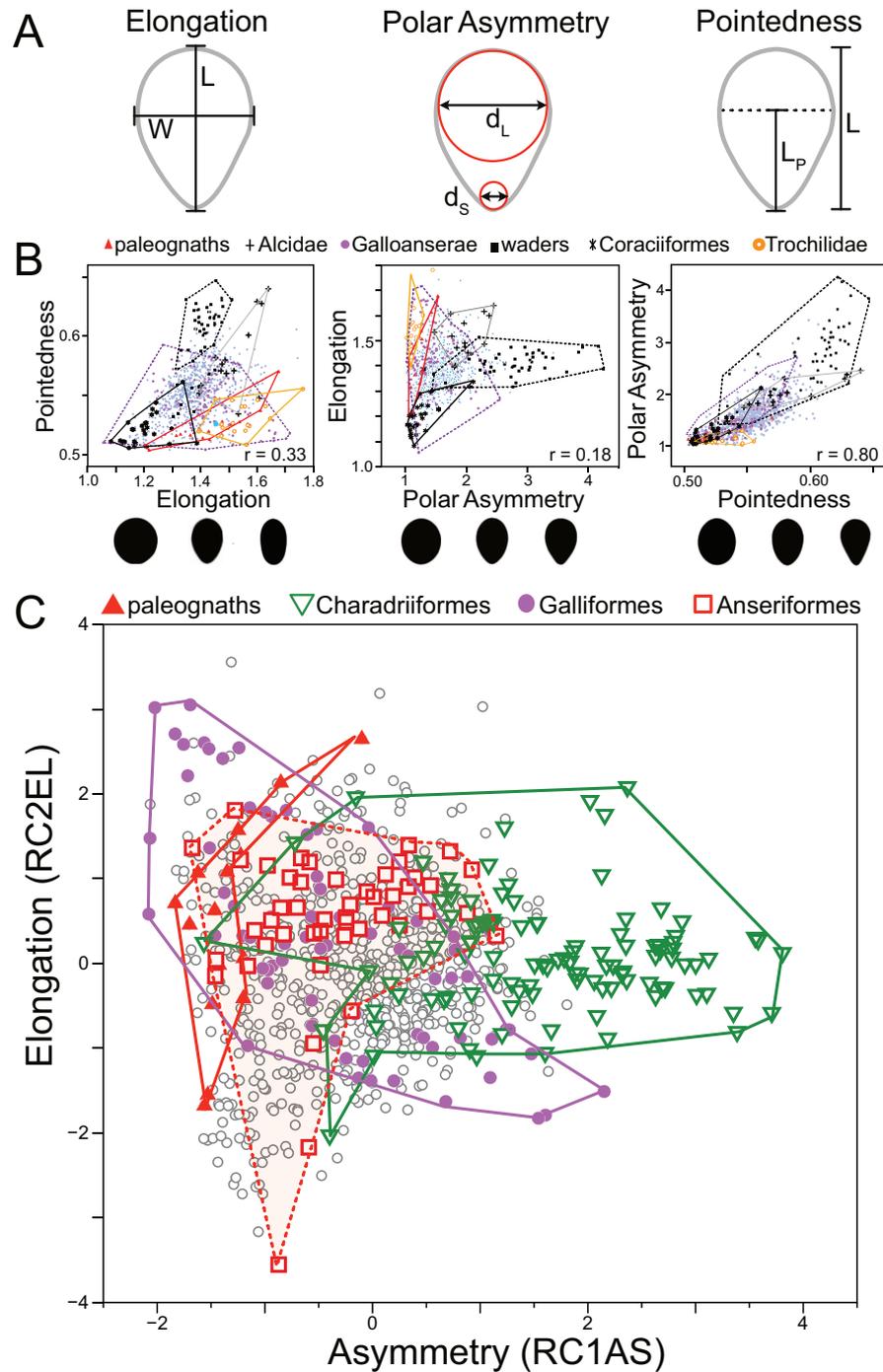
Figure 1: Egg shape parameters and morphospaces. *A*, Three parameters that describe the shapes of all birds' eggs (Biggins et al. 2018): elongation = length (L)/width (W), polar asymmetry = d_L/d_S, and pointedness = L_P/L, where d_L and d_S are the diameters of the largest circles that fit within the large and small ends of the egg, respectively; L is the maximum length of the egg; and L_P is the distance from the maximum width of the egg to the small end. *B*, Morphospaces defined by the three parameters in *A*. As shown by the correlation coefficients, these parameters are not independent. Silhouettes, all shown to the same length, illustrate the range of shapes represented by each parameter. From left to right: pink-headed duck, Australian golden whistler, rufous-breasted hermit, striped kingfisher, Bell's vireo, European golden plover, ostrich, twelve-wired bird of paradise, and plains wanderer. *C*, Egg shape morphospace based on variables calculated as the varimax-rotated principal components of the parameters in *B* with asymmetry (RC1AS) representing the variation in pointedness and polar asymmetry independent of variation in elongation (RC2EL). Symbols show the mean values for each of the 955 species studied, with some representative taxa identified.

being mounted on slides and imaged using a ×100 optical microscope with integrated camera.

To estimate the maximum diameter of the isthmus, we measured the invaginated inner wall of its lumen on composite digital photomicrographs of histological cross sections using the segmented line tool in ImageJ software (Schindelin et al. 2015). We used that measurement as an index of the maximum perimeter of the fully stretched isthmus, from which we calculated the maximum diameter. We recognize that this index probably underestimates the actual diameter of the fully stretched isthmus.

Sources of Anatomical and Life History Data

We used published data sets for body mass (Dunning 2007), pelvis anatomy (Shatkovska et al. 2018), clutch size (Myhrvold et al. 2015), structure of the incubation site (usually a nest; Fang et al. 2018), and HWI (Sheard et al. 2020), corrected and enhanced as needed using Billerman et al. (2020). We also used a standard reference for the developmental mode of chicks (Nice 1962), classifying each species simply as either altricial or precocial, and we categorized the dominant mode of locomotion during foraging for each species as aerial, cursorial, perching, or swimming according to descriptions in Billerman et al. (2020).

Measuring Egg Shape

We analyzed the images of 5,378 eggs of 955 species made from digital photographs taken in the field (408 eggs of 20 species) or museum collections (2,546 eggs of 306 species) as well as from images in books (2,425 eggs of 725 species) when we could be certain that the eggs were photographed or painted to scale with the long axis of the egg parallel to the plane of the image. To ensure the integrity of photographs in books, we contacted the photographers (Harry Taylor for Walters 1994; Douglas Elford for Johnstone and Storr 1998). We also examined correlations between measurements from real eggs and illustrations in books (all $r > 0.95$) to ensure that published illustrations were oriented correctly.

Following established protocols (Birkhead et al. 2019*b*), we used an R script (Biggins et al. 2018) to analyze a silhouette image of each egg (e.g., figs. 1*B*, 6*B*) and calculate elongation, polar asymmetry, and pointedness (as defined in Biggins et al. 2018; fig. 1*A*, 1*B*). The values calculated from each image were checked for accuracy by comparing measures of the actual egg to the output from the script. Errors were always due to anomalies on the silhouettes, which were then corrected and reanalyzed to ensure that any measurement errors were within 4% of the actual egg measurements.

We used principal components analysis (PCA; table S2) with varimax rotation to reduce the three mean egg shape measures for each species (fig. 1*A*, 1*B*) to two rotated variables (fig. 1*C*) that are independent: RC1AS representing asymmetry (accounting for 60% of the total variation and correlated with both polar asymmetry, $r = 0.96$, and pointedness, $r = 0.92$), and RC2EL representing elongation (accounting for 35% of the total variation and correlated with elongation, $r = 0.99$). We used these two indexes in all analyses of egg shape to minimize spurious correlations between egg shape indexes.

Bird and Egg Size

Where possible, we used female mass as a measure of bird size when that was available but otherwise used average mass for either both sexes or males (in that order of preference). The density of birds' eggs is close to the density of water (Paganelli et al. 1974), so egg volume is a reasonable index of egg mass and has the same dimensionality.

We also used PCA to create variables for adult mass (PC1mass) and relative egg size (PC2relegg) that would be independent of one another ($r = 0.004$, $P = .999$) for use in all analyses (table S3; fig. S2; figs. S1–S9 are available online). PC1mass is highly correlated with log(adult mass) ($r = 0.99$). PC2relegg is highly correlated with the residuals of the regression of log(egg volume) on log(adult mass) ($r = 0.99$, $n = $ mean values from 944 species; see also fig. S3) and avoids the statistical issues associated with analyses that use residuals as predictors (Freckleton 2002).

To analyze pelvis anatomy, we used varimax-rotated PCA to reduce the available data (from Shatkovska et al. 2018) to two orthogonal variables (table S4), one representing pelvis size (RC1meas) and the other representing pelvis shape (RC2ratios). RC1meas is positively correlated ($r > 0.92$) with three pelvis measurements such that larger values indicate a larger pelvis. RC2ratios is positively correlated ($r = 0.67$–0.89) with two ratios from different measurements than those described by RC1meas such that larger values indicate a more elongated pelvis.

Allometries

For the analyses of oviduct size and egg size in relation to female body size, we used standardized major axis (SMA) regressions (smatr package in R) on log10-transformed variables. The slopes of these regressions were compared with one another and with slopes of 0 and 1.0 (Warton et al. 2012).

Statistical Models

All data were analyzed using R version 4.0.4 (R Development Core Team 2021). To assess and control for the influence

of phylogeny in general analyses across all species, we constructed phylogenetic general least squares (PGLS) regressions using the phylolm package and a phylogeny based on the Ericsson backbone downloaded from BirdTree (https://birdtree.org/; fig. S1).

We also generated linear models (using the lm function in the base package) for each family with >5 species in our data set, excluding models that did not converge or had singularities. To reduce the effect of overfitting, we included only a few predictors of interest in each of these models.

All continuous variables used as predictors in statistical models were standardized (z-scores) using the scale function in R so that effect sizes (β) could be compared on the same scale. We report this effect size and 95% CLs for each predictor to illustrate the magnitude and variability of the effects across all species.

Results

General Patterns

To evaluate the generality of previous models to explain egg shape (Stoddard et al. 2017), we constructed PGLS models (details in the supplemental PDF, available online). We did not include diet, latitude, developmental mode, temperature, or precipitation in these general models, as none of these factors were previously identified as having an appreciable effect on egg shape (Stoddard et al. 2017) and there is not a plausible mechanism relating those factors to the shapes of birds' eggs.

Stoddard et al. (2017, p. 1249) suggested that "adaptations for flight may have been critical drivers of egg-shape variation in birds," so we sought to evaluate that prediction in birds that use their wings for locomotion. To that end, we focused these general analyses on the large clade of neognaths (921 species in 188 families and 34 orders in our data set) to reduce bias from species that are flightless (orders Struthioniformes, Rheiformes, Casuariiformes, and Apterygiformes) or largely cursorial (Tinamiformes). Inclusion of the paleognaths does not affect our conclusions (table S6).

Elongation (RC2EL). Egg elongation is significantly associated with female mass (PC1mass; positive), HWI (positive), clutch size (negative), and incubation site across all species of neognaths (fig. 2*A*; table S5). The full model explains about 14% of the variation in elongation, with female mass (PC1mass) having the largest effect, about twice that of either HWI or clutch size. Eggs in domed nests or mounds are the most elongated, while those laid in cavities, burrows, and scrapes are the most spherical. These results are consistent with those of Stoddard et al. (2017) with respect to female mass and HWI, but that study found a significant effect of a measure of relative egg size and no

significant effects of incubation site or clutch size across all species.

Asymmetry (RC1AS). Across species of neognaths, egg asymmetry is positively related to female mass (PC1mass), clutch size, HWI, and incubation site (fig. 2*B*; table S5). The full model, however, explains only 8% of the variation in asymmetry. HWI had the largest effect on asymmetry, approximately double the effects of either clutch size or female mass. Eggs laid in scrapes are the most asymmetrical, whereas those laid in mounds have the lowest asymmetry values. These results are also consistent with those of Stoddard et al. (2017) with respect to female mass and HWI, but that study found no significant effects of incubation site or clutch size across all species.

Complications. These general across-species analyses of egg elongation and asymmetry are complicated by model complexity and some multicollinearity among predictors that sometimes obscures the patterns within families. Thus, even predictors with small and nonsignificant effects in these general models across all species are important predictors of egg shape in some families of birds (table S9), with some within-family relationships positive and some negative, often opposite to the sign or magnitude of the effect in the global model (fig. 2*C*–2*J*).

Among the 55 families with ≥5 species in our data set, for example, 24%–64% of the linear model relationships predicting elongation had signs that differed from that in the global model (fig. 2*A*) with respect to female mass (PC1mass, 13/55; fig. 2*C*), relative egg volume (PC2relegg, 35/55; fig. 2*D*), clutch size (20/51; fig. 2*E*), and HWI (27/55; fig. 2*F*; for details, see table S9a). Similarly, linear models to predict asymmetry within families had different signs from that in the global model (fig. 2*B*) with respect to female mass (23/55; fig. 2*G*), relative egg volume (21/55; fig. 2*H*), clutch size (20/51; fig. 2*I*), and HWI (27/55; fig. 2*J*; for details, see table S9b).

Most of these within-family effects are based on small numbers of species and thus have low statistical power and wide CLs (table S9). Nonetheless, closer inspection at the family level reveals some interesting patterns and suggests avenues for further research. A complete family-by-family assessment of the factors influencing egg shape is beyond the scope of this article, but we provide a few illustrative examples of different within-family patterns (figs. S4–S6), providing mixed support for each predictor influencing elongation in the manner suggested by the global model.

Constraints: Oviduct Anatomy

In the 18 species of Galliformes for which we have measurements of both eggs and oviducts from the same females,
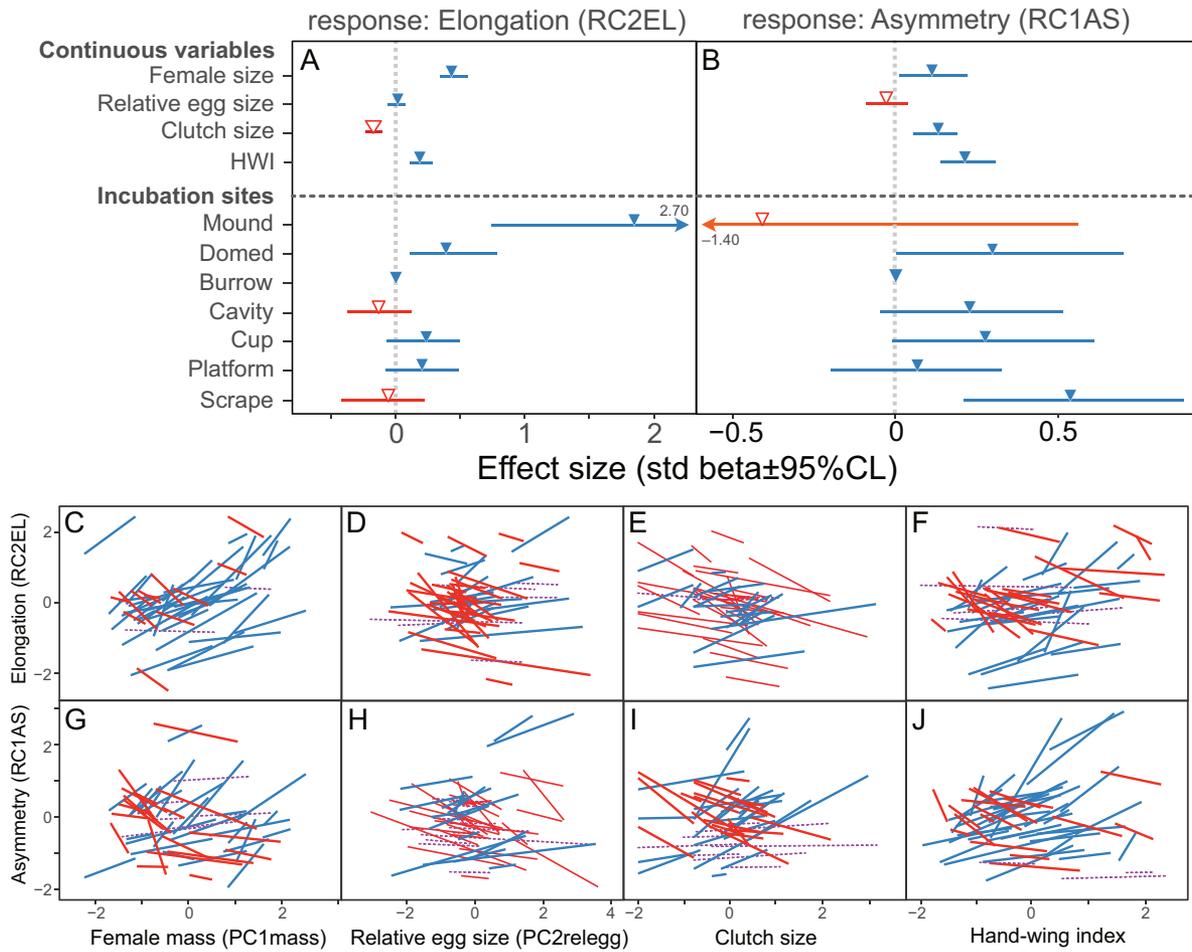
Figure 2: Models to predict egg elongation and asymmetry across the avian phylogeny. *A, B,* Effect sizes (*β* with 95% confidence limits [CLs]) from phylogenetic linear regressions with the same set of predictors, controlling for the effects of phylogeny (for statistical details, see table S5). *C–J,* Relationships between either elongation (*C–F*) or asymmetry (*G–J*) and continuous predictors in each of 55 families with ≥5 species based on linear models with family × focal predictor interactions, controlling for the other three predictors (all predictors are standardized so that slopes can be compared on the same scale). On all graphs, red lines and open triangles indicate negative slopes, and blue lines and filled triangles indicate positive slopes. In *C–J,* dotted purple lines show slopes close to zero.

there is a clear allometric relationship between the diameter of the maximally stretched isthmus and the width of the shelled egg (SMA slope = 0.61 [95% CLs: 0.49, 0.77], $R^2 = 0.81$). The negative allometry here suggests that the isthmus (and the oviduct in general; table S10) constrains egg width, resulting in more elongated eggs in species with larger females.

Data for the family Phasianidae support the prediction that egg elongation increases with female size (fig. 3*B*), controlling for relative egg size (PC2relegg). In the Megapodiidae and Cracidae (both Galliformes), however, elongation increases with relative egg size (PC2relegg; fig. 3*C*, 3*D*) but not with female mass (PC1mass; table S11). These three families differ in that the Phasianidae have relatively small

eggs (mean relative egg size [PC2relegg] = −1.14 [95% CLs: −1.39, −0.89], $n = 34$ species), whereas the Cracidae (0.68 [95% CLs: 0.43, 0.93], $n = 20$ species) and Megapodiidae (2.25 [95% CLs: 1.92, 2.59], $n = 14$ species) have relatively large eggs for their body size (fig. S2). These differences between the families of Galliformes suggest that when species have relatively large eggs, then egg size has the largest influence on elongation, whereas in species with relatively small eggs, the size of the female (and her oviduct) has the largest influence on elongation.

The Megapodiidae provide the clearest example of an effect of relative egg size on elongation (fig. 3*C*), as their eggs are particularly large relative to female size and they are the only birds whose eggs are incubated in mounds of rotting
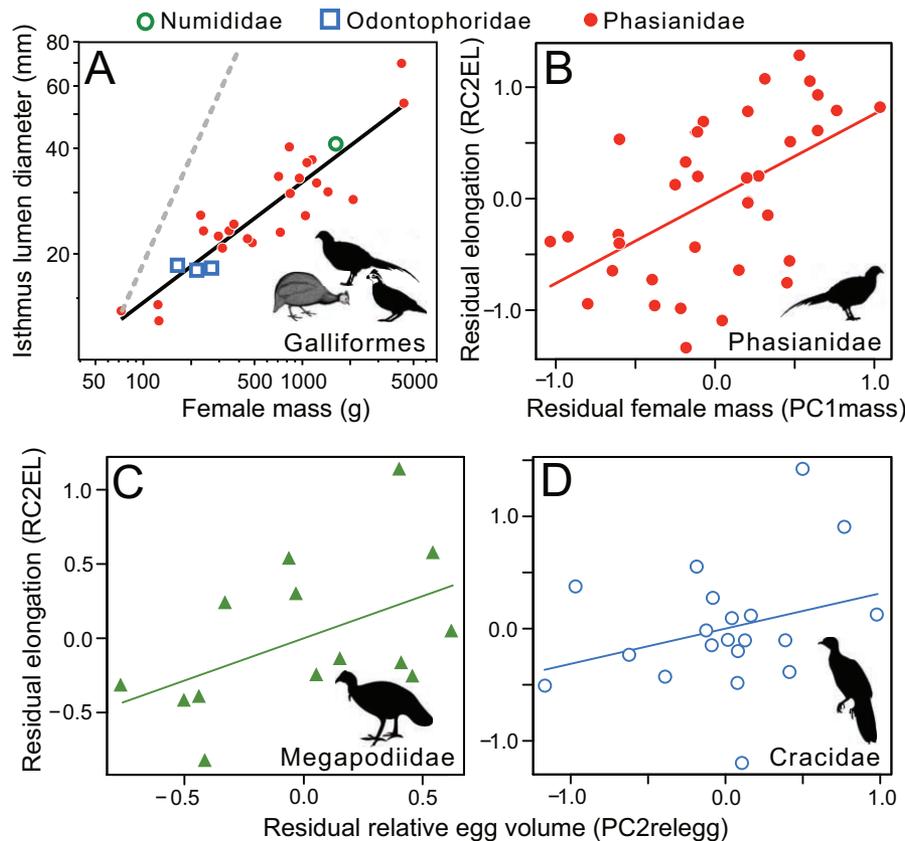
Figure 3: Constraints on egg shape due to oviduct anatomy in the Galliformes. *A*, Allometric relationship between the diameter of the isthmus lumen and female body mass in 28 species of Galliformes in three families (allometric slope $= 0.38$ [95% confidence limits: 0.31, 0.46]). Dashed gray line has slope $= 1$ (isometry). *B–D*, Partial regression (add-variable) plots of the relationship between residual elongation (RC2EL), residual female mass (PC1mass; *B*), and residual relative egg volume (PC2relegg; *C*, *D*) in three families based on linear models (for details and models controlling for phylogeny, see tables S10–S11).

vegetation or warm volcanic soil without contact with either the parent or other eggs. Thus, the shape of their eggs is unlikely to be influenced by selection for increased shell strength or parental contact during incubation, as the eggs are warmed from all sides and are rarely exposed to heat loss.

This oviductal constraints hypothesis is supported by two additional lines of evidence. First, within two orders of birds that lay relatively large eggs, elongation is significantly predicted by both female mass (PC1mass) and relative egg size (PC2relegg), whereas in two orders of birds that lay relatively small eggs, elongation is not related to relative egg size (fig. 4*A*; table S18). Both patterns are expected as a result of the negative allometry of oviduct width constraining egg diameter when birds lay relatively large eggs.

Second, within the paleognaths (ostriches, rheas, cassowaries, kiwis, tinamous), relative egg size is the only variable that predicts elongation (fig. 4*B*; table S19). All paleognaths

are cursorial, but the pattern is the same for both flightless and flying species in this clade.

Constraints: Pelvis Anatomy

The relationships between egg elongation (RC2EL) and pelvis shape (RC2ratios) are positive in species using cursorial, perching, and swimming modes of locomotion (fig. 5*B*; tables S12, S13). The slopes of these relationships (0.20–0.29) are remarkably consistent across modes of locomotion (fig. 5*B*; table S13). Thus, elongation increases with the relative narrowness of the pelvis (RC2ratios), as expected from a previous study (Shatkovska et al. 2018), although the mechanism underlying this relationship is not known.

The relationships between egg elongation (RC2EL) and relative pelvis size (RC1meas) for those three modes of locomotion are negative and also remarkably similar (−0.40
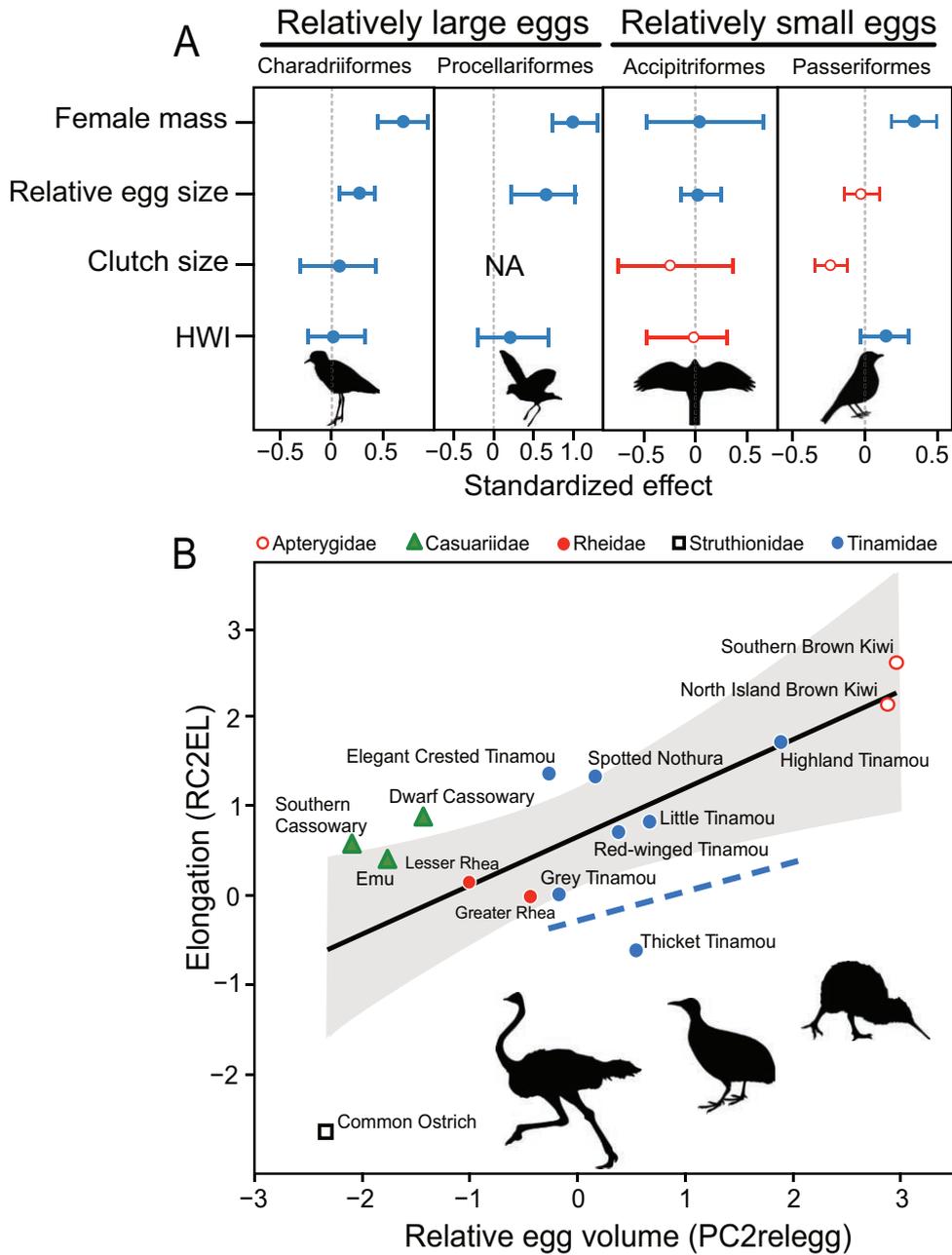
Figure 4: Further evidence for oviductal constraints on elongation. *A*, Elongation is influenced by female size (and its relationship to oviduct diameter) and relative egg size (PC2relegg) within two orders in which species lay relatively large eggs but not within two orders in which species lay relatively small eggs. Standardized effects (95% confidence limits) are shown, controlling for phylogeny, with red indicating negative and blue indicating positive. *B*, In 15 paleognaths, elongation increases with relative egg size (PC2relegg) across all species (black line) and within the Tinamiformes, all of which can fly (dashed blue line, adjusted data not shown for that regression). Regression lines and data are predicted from linear models controlling for female mass and phylogeny (table S19).

to −0.47; fig. 5*A*; table S13). Thus, elongation decreases as relative pelvis size increases, as expected if pelvis size—or something correlated with it—constrains egg width, since those negative relationships control for both female size

and relative egg size. In aerial birds, the signs of the relationships between elongation and both pelvis size and shape are in the opposite directions (fig. 5*A*, 5*B*; table S13), but the reasons for this are not known.
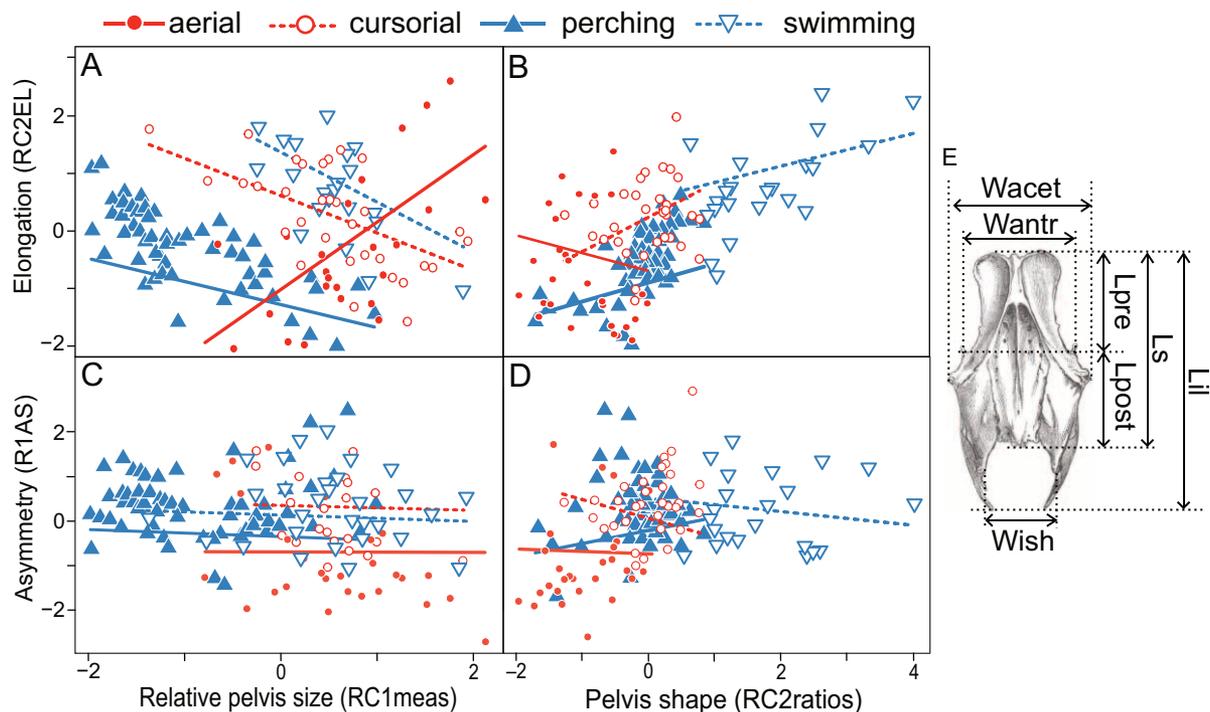
Figure 5: Predicted regression plots for the relationships between components of egg shape (elongation [RC2EL] and asymmetry [RC1AS]) and both relative pelvis size (RC1meas) and pelvis shape (RC2ratios) for species with different modes of locomotion. Models control for female size (log transformed) and phylogeny. Number of species: 37 aerial, 28 cursorial, 72 perching, and 24 swimming. *A*, *B*, Each regression line shown is from a separate model because the interaction terms were significant. *C*, *D*, Predicted regressions are from models with mode of locomotion as a nonsignificant interaction with pelvis size or shape. *E*, Avian pelvis, modified from Shatkovska et al. (2018), showing the dimensions used in our analyses.

The asymmetry component of egg shape is not clearly related to relative pelvis size or shape across species (fig. 5*C*, 5*D*; table S12). Moreover, the statistical models to predict asymmetry explain only 6%–9% of the variation, whereas the models to predict elongation from pelvis size and shape explain 27%–30% of the variation.

Pelvis shape may also explain the relationship that Stoddard et al. (2017) found between egg shape and HWI, if HWI is related to pelvis anatomy. To assess this, we looked at the relationships between HWI and measures of pelvis size and shape available for 173 species (Shatkovska et al. 2018). Both the maximum distance between ischial bones (Wish in fig. 5*E*) and the size of the pelvis (RC1meas) are significantly and positively correlated with HWI (table S14). Among species with the different modes of locomotion, HWI is not consistently related to relative pelvis size (RC1meas) or shape (RC1ratios; tables S15, S16; fig. S7). Thus, HWI is not significantly related to pelvis size or shape in cursorial or swimming birds, but the relationship between HWI and pelvis size is significantly positive for perching birds and significantly negative for aerial birds (table S16; fig. S7). The nonsignificant relationships between HWI and pelvis

shape are positive for aerial birds and negative for perching and swimming birds (table S16; fig. S7).

Revisiting General Patterns

Our analysis of the relationship between HWI and pelvis shape (table S16; fig. S7) suggests that mode of locomotion should be included in general models for egg elongation and asymmetry when HWI is also a predictor (fig. 2*A*, 2*B*). In the revised models, the relationship between HWI (as an index of pelvis shape) and elongation is significant and consistent across modes of locomotion (table 1). In the model to predict asymmetry, however, HWI is not significant (table 1), but the significant interactions with mode of locomotion renders that main effect uninterpretable. Within locomotion modes, HWI remains a significant predictor of asymmetry in both cursorial and perching birds but not for aerial and swimming species (table S17).

Adaptations: Clutch Size

Across species, the effect of clutch size on elongation is negative (table 1; fig. 2*A*) as expected if more spherical

Table 1: Models to predict egg elongation (RC2EL) and asymmetry (RC1AS) from factors thought to influence egg shape in 921 species of neognath birds, controlling for phylogeny, mode of locomotion (LOCO), and the interaction between LOCO and hand-wing index (HWI)

Predictors[a]	Elongation[b]	Asymmetry[b]
Intercept	**−.74 (−1.44, .13) [.05]**	−.65 (−1.32, −.12) [.09]
Female mass (PC1mass)	**.40 (.28, .49) [<.0001]**	.10 (−.01, .21) [.08]
Relative egg size (PC2relegg)	.003 (−.06, .06) [.94]	−.03 (−.11, .05) [.42]
Clutch size	**−.18 (−.24, −.11) [<.0001]**	**.13 (.05, .18) [.0007]**
HWI	**.25 (.02, .48), [.03]**	.01 (−.26, .20) [.91]
Incubation site (cup)[c]	**.41 (.13, .72) [.02]**	**.33 (.04, .60) [.05]**
Incubation site (cavity)[c]	.02 (−.28, .30) [.89]	.27 (.006, .51) [.08]
Incubation site (dome)[c]	**.53 (.25, .86) [.006]**	.33 (−.01, .67) [.08]
Incubation site (mound)[c]	**2.22 (1.34, 3.17) [<.0001]**	−.42 (−1.35, .68) [.44]
Incubation site (platform)[c]	**.44 (.14, .67) [.009]**	.10 (−.21, .35) [.53]
Incubation site (scrape)[c]	.17 (−.17, .56) [.36]	**.48 (.07, .84) [.01]**
LOCO (cursorial)	.14 (−.39, .59) [.55]	−.17 (−.61, .24) [.47]
LOCO (flightless)	−1.02 (−5.88, 5.84) [.75]	−1.64 (−7.80, 3.78) [.59]
LOCO (perching)	.005 (−.52, .51) [.98]	−.26 (−.72, .24) [.29]
LOCO (swimming)	**1.28 (.74, 1.79) [<.0001]**	−.17 (−.68, .33) [.57]
LOCO (cursorial) × HWI	.03 (−.23, .28) [.84]	**.40 (.17, .70) [.005]**
LOCO (flightless) × HWI	−.08 (−3.68, 3.44) [.96]	−1.35 (−4.85, 1.50) [.46]
LOCO (perching) × HWI	−.13 (−.38, .11) [.32]	.20 (−.07, .49) [.14]
LOCO (swimming) × HWI	−.28 (−.56, .03) [.16]	.21 (−.15, .48) [.27]
λ (bootstrapped)[d]	**.75 (.69, .82)**	**.80 (.71, .84)**
R^{2e}	.18	.09

[a] Continuous predictors were all standardized to facilitate comparison of effects on the same scale.

[b] Effects are β, with 95% confidence limits in parentheses and *P* values in brackets. Significant effects are in bold.

[c] Effects are compared with eggs laid in burrows (effect = 0).

[d] Measure of the phylogenetic signal.

[e] Proportion of variance explained controlling for phylogeny specified by λ.

eggs are favored in larger clutches because of their thermal properties (lower rate of heat loss due to lower surface-to-volume ratio) and resistance to breakage. In simple linear models for each of 51 families with >5 species in our data set (table S9a), there are both positive (20) and negative (31) effects of clutch size on elongation.

While the linear effect of clutch size on asymmetry across all neognaths is negligible (table 1), clutch size is positively associated with asymmetry for mean clutch sizes of one to four eggs laid in scrapes (fig. 6A; table S21), as predicted (Andersson 1978). There is also a positive trend across neognaths that do not lay eggs in scrapes, with asymmetry increasing across the full range of clutch sizes. Even within the Passeriformes, where most species do not have particularly asymmetric eggs, asymmetry increases weakly with clutch size across all species up to clutches of six eggs (fig. 6B; table S20), although there are many exceptions with some of the within-family slopes being negative (fig. 6B; table S9b).

Adaptations: Incubation Site

The most elongated eggs are laid singly in mounds of vegetation or soil, with elongation decreasing from domed nests to cups, platforms, and scrapes (fig. 2A; table 1). These incubation sites are progressively less well insulated. Species laying eggs in cavities and burrows do not fit this pattern, as those sites are not exposed, yet their eggs are the least elongated, possibly to reduce the chance of breakage in dark, cramped quarters with little or no nesting material or to increase thermal efficiency when clutch size is large. We used general categories for incubation site for this analysis such that there was no within-family variation, potentially limiting the statistical power, especially as the insulating properties of nests and the potential for egg breakage must vary within these broad categories of incubation site.

Eggs that are closer to being perfect prolate spheroids—from perfect spheres to symmetrical ovoids, with polar asymmetry close to 1 and pointedness close to 0.5—are relatively uncommon in birds (fig. 1A, 1B), confined to a few families with small clutches and well-insulated incubation sites (Trochilidae [hummingbirds], Megapodiidae [mound builders]). Eggs that are near-perfect spheres are found in species with larger clutches laid in cavities without lined nests, where the eggs might be more susceptible to breakage (Coraciiformes [kingfishers and their allies] and some species of Strigidae [owls] and Anatidae [waterfowl]).
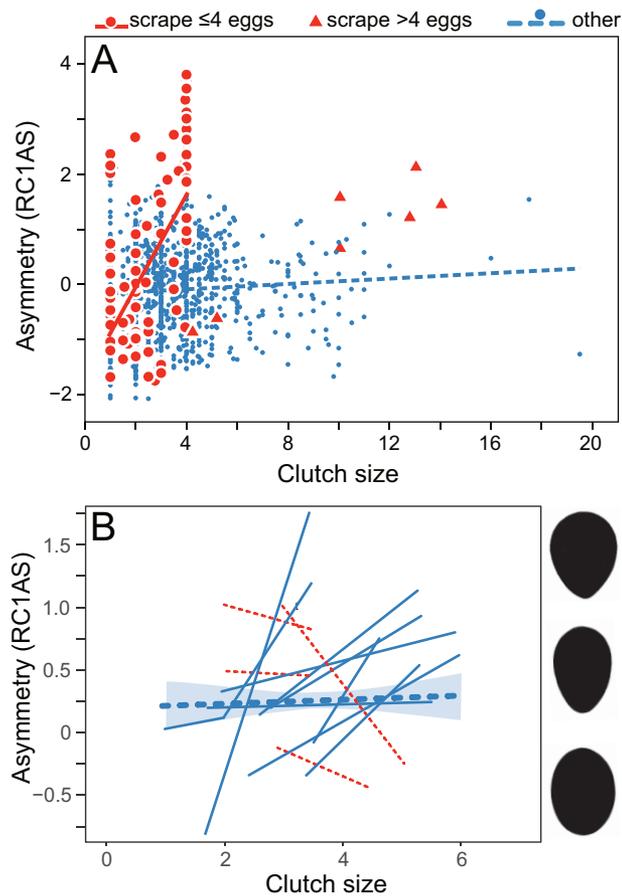
Figure 6: *A*, Relationships between egg asymmetry (RC1AS) and clutch sizes of neognath species that lay their eggs in scrapes with clutch sizes ≤4 (solid red line and circles; 108 species) or >4 (red triangles; 8 species) and for species laying eggs in all other incubation sites (dashed blue line and dots; 811 species). Each regression is predicted from a phylogenetic general least squares (PGLS) model controlling for female mass (PC1mass), relative egg size (PC2relegg), mode of locomotion, hand-wing index (HWI), and incubation site, as well as controlling for phylogeny (table S21). *B*, Relationship between egg asymmetry and clutch size in 16 families of Passeriformes that lay average clutches of ≤6 eggs in cup nests. Shown here are predicted relationships from linear models for each family, controlling for female size (PC1mass), relative egg size (PC2relegg), and HWI. Silhouettes show the full range of asymmetries scaled to the same length in order from top to bottom: common chaffinch, horned lark, and yellowhammer. Solid blue lines have positive slopes, and dotted red lines have negative slopes. The dashed blue line is predicted with 95% confidence limits from a PGLS model on all Passeriformes in our data set that laid eggs in cup nests with clutch size ≤6 (235 species), using the same model structure as for the separate family-level linear models (table S20).

Egg asymmetry is also related to incubation site in that species having the least asymmetric eggs incubate them in sites most protected from heat loss (mounds and burrows). Asymmetry increases as eggs become generally more ex-

posed in incubation sites ranging from mounds and burrows to cavities, cups, and domed nests to scrapes (fig. 2*B*; table 1) in general, as well as within neognath orders that include species with more than one type of incubation site (fig. 7; table S22). While several of these comparisons among the asymmetry of eggs laid in different incubation sites are not statistically significant, the patterns are remarkably consistent within some orders of birds.

Discussion

Across a broad panoply of birds of the world, we found that egg shape is largely determined by (i) anatomical constraints imposed by the oviduct and pelvis and (ii) adaptations that are likely to reduce breakage and increase thermal efficiency of eggs at the incubation site. It is also possible that some of the anatomical constraints that we have identified evolve in response to selection on egg size. For example, when selection favors larger eggs in precocial species (e.g., Boersma 1982) or in species where managing cooling rates is critical (e.g., Martin 2008), we might expect a coevolutionary response in the oviduct and pelvis. In addition to this general conceptual framework, we have documented four key advances over previous work on this topic.

First, while our analyses also provide some support for the conclusion of Stoddard et al. (2017, p. 1253) that "adaptations for high-powered flight . . . may have considerable effects on egg shape," our study suggests that adaptations of the pelvis (or general body conformation) to different forms of locomotion may be more relevant than simply adaptations to high-powered flight. Thus, while HWI is positively related to elongation (table 1) across all bird species, egg shape is not positively correlated with HWI within many avian families and orders (figs. 2*F*, 2*J*, S4–S6; tables S9, S18–S20, S22). One source of this variability is likely the different relationships between HWI and pelvis anatomy in species that use different modes of locomotion (table S16; fig. S7).

Second, the structure of both the oviduct and the pelvis appears to constrain egg shape in a predictable manner (figs. 3–5). Thus, we argue that egg elongation, in particular, is the result of constraints on shape imposed by adaptive responses to selection on body size or mode of locomotion. The occasional occurrence of runt and double-yolked eggs in the clutches of many species (Koenig 1980; Birkhead et al., forthcoming) provides additional support for this idea. Runt eggs are abnormally small eggs, often lacking a yolk, and are invariably more spherical (less elongated) than is typical for the species, just as expected if oviduct or pelvis anatomy limits the diameter of eggs. Similarly, double-yolked eggs are larger than is typical for the species, and those eggs
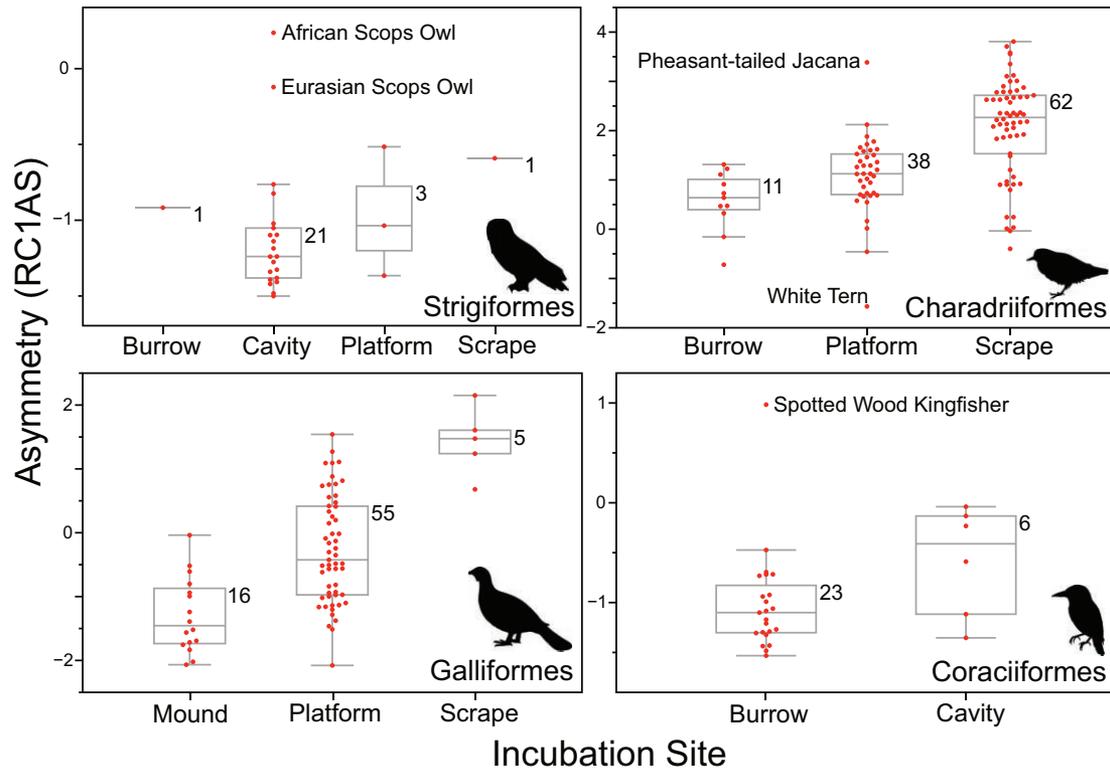
Figure 7: Asymmetry increases with openness of the incubation site within four orders that display a range of incubation sites. Data shown are species means as well as Tukey boxplots summarizing medians, interquartile ranges (IQRs; boxes), and 1.5 times the IQR (whiskers). Sample sizes are shown at the top of each box. For an exception to this pattern, see figure S9.

are, on average, more elongated in the common murre (*Uria aalge*; Birkhead et al., forthcoming).

This study is the first to measure oviductal anatomy in birds, and the data were hard-won because of the need for specimens that were laying eggs. Thus, we quantified oviduct allometry only in the Galliformes and have assumed that the relationships between oviduct size and female size would be similar for all birds, as has been found for other aspects of avian anatomy and physiology (Calder 1984; Burton 2008; Field et al. 2013). Our results support this assumption as elongation increases (i) with female mass (PC1mass; due to negative allometry with oviduct diameter; fig. 3*A*) across all species (fig. 2*A*; tables 1, S5, S6) and within some families and orders (fig. 3*B*; tables S9, S18–S20) and (ii) with relative egg size (PC2relegg) within families and orders in which species lay particularly large eggs (figs. 3*C*, 3*D*, 4*A*, 4*B*; table S18a).

Two recent studies have also looked at the relationship between nest design and egg shape in large avifaunas. Duursma et al. (2018) identified both climate and nest structure as influencing egg elongation in 308 Australian passerine species. Their finding that a warmer within-nest

microclimate selects for more elongated eggs is consistent with our results (table 1). Nagy et al. (2019) looked at correlations between nest and egg characteristics in 855 European birds, simply categorizing nest design as open, semi-open, or closed and quantifying egg shape only in terms of elongation (width/length). Their analyses suggest that eggs evolved to be more spherical in closed nests but more elliptical in open nests. This is supported by our finding that eggs laid in cup nests are more elongated than those laid in cavities (table 1) but is not consistent with our results for other incubation sites. Unlike our study and Duursma et al. (2018), Nagy et al. (2019) did not classify nest design in functional terms (with respect to stability, breakage, thermal efficiency, clutch sizes), and this may account for the differences in our findings. Neither Duursma et al. (2018) nor Nagy et al. (2019) looked at asymmetry or any other measure of egg shape.

Our analysis of pelvic anatomy suggests that pelvis shape also constrains egg diameter, although the underlying mechanism is unclear. Thus, the relationship between elongation and pelvis shape is supported by both a direct relationship between these two variables in a sample of 141 species

(fig. 5*B*; table S12) and an indirect relationship using HWI as a proxy for pelvis shape for all species in our sample (table 1), as well as in within some orders and families (fig. S6*A*, S6*B*).

Shatkovska et al. (2018) looked at the relationship between various measures of pelvis shape and egg shape in 173 species in 25 avian orders and 49 families. They found that pelvis shape was related to both habitat and the mode of chick development, concluding that those factors in turn influenced egg shape. The mode of chick development, however, has no effect on either elongation or asymmetry when controlling for relative egg size (table S8), and mode of locomotion is probably the underlying mechanism—rather than habitat—related to both pelvis shape and egg elongation (table 1). While Shatkovska et al. (2018, p. 10) focused on pelvis size and shape, they concluded that "the shape of pelvis mainly determines body shape, and thus the shape of abdominal cavity and interposition of viscera in it," suggesting that the pelvis itself may not be the underlying cause of egg shape. Further work is needed to determine how pelvis shape or general body conformation influences elongation independent of relative oviduct size.

Third, egg asymmetry increases with both clutch size and the openness of incubation sites across species (figs. 2*B*, 6, 7; tables 1, S5–S7, S21, S22), as expected from both theory (Andersson 1978; Barta and Szekely 1997) and an empirical study (Birkhead et al. 2019*b*), respectively. However, asymmetry is also related to pelvis shape (fig. 5*D*) and HWI (as an index of pelvis shape) in perching species (table S17b), but the underlying mechanism is unknown and needs further study.

Finally, the broad patterns across all bird species conceal an underlying complexity wherein the sign and magnitudes of those patterns vary among the ~50 families that we analyzed separately. Thus, within each family of birds, egg shape is influenced by a variety of anatomical and environmental factors, with often little consistency among even closely related taxa (figs. 2*C*–2*J*, 4, 6, 7). Such taxon-specific patterns have been uncovered in a variety of life history and behavioral traits (Bennett and Owens 2002).

As we have shown, global cross-species patterns of egg shape in relation to anatomical and environmental variables sometimes mask other biologically interesting within-taxon patterns (but see Stoddard et al. 2017, 2019). Thus, we found well-supported trends within families and orders (figs. 3*B*–3*D*, 4*A*, 6, S4–S6; tables S9, S19, S20) that are not consistent with general trends across all species (table 1). General statistical models based on data across a wide diversity of species often tacitly assume that there is no variation in slopes among constituent groups. As a result, small effect sizes in broadscale comparative studies can mask useful insights into the underlying mechanisms, whether these be adaptations or constraints. Such global analyses may often be subject to Simpson's paradox (Samuel et al. 2000) wherein within-taxon trends sometimes have the opposite sign to global trends (figs. 2*C*–2*J*, 4*A*, 6*B*).

The only other study of egg shape across a large taxon looked at the shapes of eggs in 6,706 insect species from 526 families and all extant orders (Church et al. 2019). As in the present study, they concluded that egg shape in the insects cannot be explained by a single factor across such a diverse array of species and that "where eggs are laid . . . underlies the evolution of insect egg size and shape" (p. 58).

Unexplained Variation

Our exploration of the factors influencing egg shape within avian families and orders explained considerably more of the variation in egg asymmetry and elongation than statistical models based on species across the avian phylogeny (e.g., tables 1, S5–S8). Such an increase in explanatory power of models is not unexpected when dealing with traits that vary among taxa in their influence on egg shape (see also Stoddard et al. 2019). Within orders and families, for example, the variables that we studied explained as much as 85% of the variation in elongation and 77% of the variation in asymmetry (tables S18, S22).

While our statistical models are sometimes able to explain much of the interspecific variation in egg shape, there remains considerable unexplained variation that is likely due to measurement error. For example, our measure of female size (body mass) may often be inaccurate because it was based on few samples, on combined values for the two sexes, or on unknown sexes and was rarely restricted to the breeding season. Despite an excellent compilation of avian body masses for almost 85% of extant bird species (Dunning 2007) that is widely used in comparative studies, 10% of those species are represented by a single measurement, and 25% are represented by ≤5 samples, with data explicitly on females for only 400 species. For the analysis of allometric patterns of egg shape and anatomy related to body size, accurate measurements of female size and shape are crucial.

Unanswered Questions

The approach we have taken for understanding the variation in avian egg shapes requires a logical link to the underlying mechanisms. Even though birds' eggs have been intensively studied for more than a century, relatively little is known about the anatomical and physiological mechanisms that we have focused on in this study. How does the isthmus of the oviduct constrain elongation, and how does that constraint vary among families? How does the shape of the pelvis influence egg shape (Shatkovska et al.

2018)? How does the incubation environment (Deeming and Reynolds 2015), the behavior and morphology of the parents (Boulton and Cassey 2012; Deeming 2016), and the composition and shape of the egg itself (Sotherland and Rahn 1987; Deeming 2018) influence how an egg gains heat when a parent is incubating and loses heat when that parent is absent? And how does the thermal efficiency of an egg in a normal clutch size influence chick development and survival (Boulton and Cassey 2012) and thus select for particular egg shapes? In this article, we provide a broad framework in which to address those questions, recognizing that the answers are likely to be complex and often taxon specific. We have also made a fair start at quantifying the shapes of birds' eggs in an accurate, repeatable fashion, but a more complete database from both museum and field studies is essential to understand why birds' eggs are so variable in shape both within and between species.

Statement of Authorship

R.M. and T.R.B. conceptualized the research; R.M., T.R.B., and J.E.T. photographed eggs; R.M. and J.E.T. analyzed egg shapes; N.H. and T.R.B. collected and measured oviducts; R.M. performed all statistical analyses; R.M. and T.R.B. wrote the first draft of the manuscript; all authors contributed to and approved the final version of the manuscript.

Data and Code Availability

All code and data sets required to replicate these analyses are available in the Dryad Digital Repository (https://doi.org/10.5061/dryad.sj3tx9648; Montgomerie et al. 2021).

Literature Cited

Andersson, M. 1978. Optimal egg shape in waders. Ornis Fennica 55:105–109.

Bain, M. M. 1991. A reinterpretation of eggshell strength. Pages 131–145 *in* S. E. Solomon, ed. Egg and eggshell quality. Wolfe, London.

Barta, Z., and T. Szekely. 1997. The optimal shape of avian eggs. Functional Ecology 11:656–662.

Bennett, P. M., and I. P. F. Owens. 2002. Evolutionary ecology of birds: life histories, mating systems and extinction. Oxford University Press, New York.

Biggins, J. D., J. E. Thompson, and T. R. Birkhead. 2018. Accurately quantifying the shape of birds' eggs. Ecology and Evolution 8:9728–9738.

Billerman, S. A., B. K. Keeney, P. G. Rodewald, and S. T. Editors. 2020. Birds of the world. Cornell Laboratory of Ornithology, Ithaca, NY.

Birkhead, T. 2016. The most perfect thing: inside (and outside) a bird's egg. Bloomsbury, London.

Birkhead, T. R., M. Attard, and A. Pilastro. 2019*a*. Subtle egg-shell membrane structures in birds' eggs. Molecular Reproduction and Development 86:353.

Birkhead, T. R., D. R. Russell, and J. E. Thompson. Forthcoming. Abnormal eggs of the common guillemot *Uria aalge*: the role of stress. Seabird.

Birkhead, T. R., J. E. Thompson, and R. Montgomerie. 2018. The pyriform egg of the common murre (*Uria aalge*) is more stable on sloping surfaces. Auk 135:1020–1032.

———. 2019*b*. The evolution of egg shape in birds: selection during the incubation period. Ibis 161:605–618.

Boersma, P. D. 1982. Why some birds take so long to hatch. American Naturalist 120:733–750.

Boulton, R. L., and P. Cassey. 2012. How avian incubation behaviour influences egg surface temperatures: relationships with egg position, development and clutch size. Journal of Avian Biology 43:289–296.

Burton, R. F. 2008. The scaling of eye size in adult birds: relationship to brain, head and body sizes. Vision Research 48:2345–2351.

Calder, W. A. 1984. Size, function, and life history. Harvard University Press, Cambridge, MA.

Church, S. H., S. Donoughe, B. A. S. de Medeiros, and C. G. Extavour. 2019. Insect egg size and shape evolve with ecology but not developmental rate. Nature 571:58–62.

Claramunt, S., N. A. Wright, and M. S. Webster. 2017. Using museum specimens to study flight and dispersal. Pages 127–141 *in* M. S. Webster, ed. The extended specimen: emerging frontiers in collections-based ornithological research. CRC, Boca Raton, FL.

Deeming, D. C. 2016. How does the bird-nest incubation unit work? Avian Biology Research 9:103–113.

———. 2018. Effect of composition on shape of bird eggs. Journal of Avian Biology 49:jav-01528.

Deeming, D. C., and G. Mayr. 2018. Pelvis morphology suggests that early Mesozoic birds were too heavy to contact incubate their eggs. Journal of Evolutionary Biology 31:701–709.

Deeming, D. C., and J. S. Reynolds, eds. 2015. Nests, eggs, and incubation: new ideas about avian reproduction. Oxford University Press, Oxford.

Dunning, J. B., Jr., ed. 2007. CRC handbook of avian body masses. CRC, Boca Raton, FL.

Duursma, D. E., R. V. Gallagher, J. J. Price, and S. C. Griffith. 2018. Variation in avian egg shape and nest structure is explained by climatic conditions. Scientific Reports 8:4141.

Fang, Y.-T., M.-N. Tuanmu, and C.-M. Hung. 2018. Asynchronous evolution of interdependent nest characters across the avian phylogeny. Nature Communications 9:1863.

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

Freckleton, R. 2002. On the misuse of residuals in ecology: regression of residuals vs. multiple regression. Journal of Animal Ecology 71:542-545.

Hackett, S. J., R. T. Kimball, S. Reddy, R. C. K. Bowie, E. L. Braun, M. J. Braun, J. L. Chojnowski, et al. 2008. A phylogenomic study of birds reveals their evolutionary history. Science 320:1763–1768.

Jarvis, E. D., S. Mirarab, A. J. Aberer, B. Li, P. Houde, C. Li, S. Y. W. Ho, et al. 2014. Whole-genome analyses resolve early branches in the tree of life of modern birds. Science 346:1320–1331.

Jetz, W., G. H. Thomas, J. B. Joy, K. Hartmann, and A. O. Mooers. 2012. The global diversity of birds in space and time. Nature 491:444–448.

Johnstone, R. E., and G. M. Storr. 1998. Handbook of Western Australian birds. Vols. 1–2. Western Australian Museum, Perth.

Kaiser, G. W. 2010. The inner bird: anatomy and evolution. University of British Columbia Press, Vancouver.

Kimball, R. T., C. H. Oliveros, N. Wang, N. D. White, F. K. Barker, D. J. Field, D. T. Ksepka, et al. 2019. A phylogenomic supertree of birds. Diversity 11:109.

Koenig, W. D. 1980. The determination of runt eggs in birds. Wilson Bulletin 92:103–107.

Lack, D. 1968. Ecological adaptations for breeding in birds. Chapman & Hall, London.

Mallock, A. 1925. The shapes of birds' eggs. Nature 116:311–312.

Mao, K. M., F. Sultana, M. A. R. Howlider, A. Iwasawa, and N. Yoshizaki. 2006. The magnum-isthmus junction of the fowl oviduct participates in the formation of the avian-type shell membrane. Zoological Science 23:41–47.

Martin, T. E. 2008. Egg size variation among tropical and temperate songbirds: an embryonic temperature hypothesis. Proceedings of the National Academy of Sciences of the USA 105:9268–9271.

Martin, T. E., J. C. Oteyza, A. J. Boyce, P. Lloyd, and R. Ton. 2015. Adult mortality probability and nest predation rates explain parental effort in warming eggs with consequences for embryonic development time. American Naturalist 186:223–236. https://doi.org/10.1086/681986.

Montgomerie, R., N. Hemmings, J. E. Thompson, and T. R. Birkhead. 2021. Data from: The shapes of birds' eggs: evolutionary constraints and adaptations. American Naturalist, Dryad Digital Repository, https://doi.org/10.5061/dryad.sj3tx9648.

Myhrvold, N. P., E. Baldridge, B. Chan, D. Sivam, D. L. Freeman, and S. K. M. Ernest. 2015. An amniote life-history database to perform comparative analyses with birds, mammals, and reptiles. Ecology 96:3109–3109.

Nagy, J., M. E. Hauber, I. R. Hartley, and M. C. Mainwaring. 2019. Correlated evolution of nest and egg characteristics in birds. Animal Behaviour 158:211–225.

Nesteruk, I., G. Passoni, and A. Redaelli. 2014. Shape of aquatic animals and their swimming efficiency. Journal of Marine Biology 2014:470715.

Nice, M. M. 1962. Development of behavior in precocial birds. Linnean Society of New York, New York.

Paganelli, C. V., A. Olszowka, and A. Ar. 1974. The avian egg: surface area, volume, and density. Condor 76:319–325.

Preston, F. W. 1953. The shapes of birds' eggs. Auk 70:160–182.

———. 1968. The shapes of birds' eggs: mathematical aspects. Auk 85:454–463.

———. 1969. Shapes of birds' eggs: extant North American families. Auk 246–264.

Prum, R. O., J. S. Berv, A. Dornburg, D. J. Field, J. P. Townsend, E. M. Lemmon, and A. R. Lemmon. 2015. A comprehensive phylogeny of birds (Aves) using targeted next-generation DNA sequencing. Nature 526:569–573.

R Development Core Team. 2021. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Rensch, B. 1959. Evolution above the species level. Methuen, London.

Samuel, M., S. B. Cox, M. Willig, G. G. Mittelbach, C. Osenberg, and M. Kaspari. 2000. Species richness, species-area curves and Simpson's paradox. Evolutionary Ecology Research 2:791–802.

Schindelin, J., C. T. Rueden, M. C. Hiner, and K. W. Eliceiri. 2015. The ImageJ ecosystem: an open platform for biomedical image analysis. Molecular Reproduction and Development 82:518–529.

Shatkovska, O. V., M. Ghazali, I. S. Mytiai, and N. Druz. 2018. Size and shape correlation of birds' pelvis and egg: impact of developmental mode, habitat, and phylogeny. Journal of Morphology 279:1590–1602.

Sheard, C., M. H. C. Neate-Clegg, N. Alioravainen, S. E. I. Jones, C. Vincent, H. E. A. MacGregor, T. P. Bregman, S. Claramunt, and J. A. Tobias. 2020. Ecological drivers of global gradients in avian dispersal inferred from wing morphology. Nature Communications 11:2463.

Sotherland, P. R., and H. Rahn. 1987. On the composition of bird eggs. Condor 89:48–65.

Stoddard, M. C., C. Sheard, D. Akkaynak, E. H. Yong, L. Mahadevan, and J. A. Tobias. 2019. Evolution of avian egg shape: underlying mechanisms and the importance of taxonomic scale. Ibis 161:922–925.

Stoddard, M. C., E. H. Yong, D. Akkaynak, C. Sheard, J. A. Tobias, and L. Mahadevan. 2017. Avian egg shape: form, function, and evolution. Science 356:1249–1254.

Thienemann, F. A. W. 1825. Systematische Darstellung der Fortpflanzung der Vögel Europa's mit Abbildung der Eier. J. A. Barth, Leipzig.

Thompson, D. W. 1908. On the shapes of eggs, and the causes which determine them. Nature 78:111–113.

———. 1917. On the shapes of eggs, and of certain other hollow structures. Pages 652–669 *in* D. W. Thompson, ed. On growth and form. Cambridge University Press, Cambridge.

Tschanz, B., P. Ingold, and H. Lengacher. 1969. Eiform und Bruterfolg bei Trottellummen. Der Ornithologische Beobachter 66:25–42.

Walters, M. 1994. Birds' eggs. Dorling Kindersley, London.

Warham, J. 1990. The petrels: their ecology and breeding systems. Academic Press, San Diego, CA.

Warton, D. I., R. A. Duursma, D. S. Falster, and S. Taskinen. 2012. smatr 3—an R package for estimation and inference about allometric lines. Ecology and Evolution 3:257–259.

References Cited Only in the Online Enhancements

Björklund, M. 2019. Be careful with your principal components. Evolution 73:2151–2158.

Jetz, W., C. H. Sekercioglu, and K. Böhning-Gaese. 2008. The worldwide variation in avian clutch size across species and space. PLoS Biology 6:2650–2657.

Liker, A., J. D. Reynolds, and T. Szekely. 2001. The evolution of egg size in socially polyandrous shorebirds. Oikos 95:3–14.

Associate Editor: Tony D. Williams
Editor: Russell Bonduriansky

From left to right: band-rumped storm petrel; Bulwer's petrel; Audubon's shearwater; wedge-tailed shearwater; Atlantic yellow-nosed albatross; short-tailed shearwater; white-chinned petrel; southern giant petrel; sooty shearwater; wandering albatross. Credit: Tim Birkhead.