Form, Function and Evolution of Avian Egg Shape

Authors: M. C. Stoddard[1*], E. H. Yong[2], D. Akkaynak[3,4], C. Sheard[5], J. A. Tobias[6†], L. Mahadevan[7*†]

Affiliations:

[1]Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544, USA

[2]Division of Physics and Applied Physics, School of Physical and Mathematical Sciences, Nanyang Technological University, Singapore 637371, Singapore

[3]Leon S. Charney School of Marine Sciences, Department of Marine Technologies, University of Haifa, Israel

[4]Interuniversity Institute of Marine Sciences, Eilat, Israel

[5]Department of Archaeology & Anthropology, University of Bristol, 43 Woodland Rd, Bristol BS8 1UU, UK

[6]Department of Life Sciences, Imperial College London, Silwood Park, Buckhurst Road, Ascot SL5 7PY, UK

[7]Departments of Organismic and Evolutionary Biology, and Physics, and Paulson School of Engineering and Applied Sciences, Kavli Institute for Nanobio Science and Technology, Wyss Institute for Bioinspired Engineering, Harvard University, Cambridge, MA 02138, USA

*Correspondence to: mstoddard@princeton.edu and lmahadev@g.harvard.edu

†These authors contributed equally to this work.

Abstract:

Avian egg shape is generally explained as an adaptation to life history, yet we currently lack a global synthesis of how egg shape differences arise and evolve. Here, we apply morphometric, mechanistic and macroevolutionary analyses to the egg shapes of ~1400 bird species. We characterize egg shape diversity in terms of two biologically relevant variables, asymmetry and ellipticity, allowing us to quantify the observed morphologies in a two-dimensional morphospace. We then propose a simple mechanical model that explains the observed egg shape diversity based on geometric and material properties of the egg membrane. Finally, using phylogenetic models, we show that egg shape correlates with flight ability on broad taxonomic scales, suggesting that adaptations for flight may have been critical drivers of egg shape variation in birds.

One Sentence Summary:

A synthetic approach using morphometrics, mechanics and macroevolution quantifies and explains egg shape diversity in birds – and suggests that flight capability is a driver of egg shape variation.

Main Text:

About 360 million years ago, the ancestors of all terrestrial vertebrates began to colonize habitats out of the water. This transition was facilitated by a critical evolutionary innovation: the development of the amniotic egg, complete with a specialized set of membranes and a shell (*1*). Among the most familiar of these structures are the calcified eggs of birds, which exhibit a variety of sizes and shapes (*2*): spherical in owls, elliptical in hummingbirds, conical in shorebirds and a range of forms in between. However, we still know surprisingly little about the function of egg shape or the physical mechanism by which shape variation arises (*1*, *3*).

Hypotheses proposed for the adaptive function of egg shape typically invoke a decrease in egg loss for cliff-nesting birds laying conical eggs which roll in a tight circle (*4*), an increase in incubation efficiency when egg shape is associated with the number of eggs in a clutch (*5*, *6*), or other advantages related to strength, diet and development. For example, spherical eggs might be advantageous because the sphere is uniformly strong and would be robust to incidental damage in the nest. Spherical eggs, with their minimal surface area to volume ratio, also require the least amount of shell material for a given volume (*7*) and possibly optimize gas exchange by providing a large surface area for pores (*8*). In contrast, conical eggs may be beneficial because they can accommodate an increased concentration of pores at the blunt end, creating a specialized respiratory site for accelerated neural development in precocial birds (*8*). Moreover, conical eggs may protect the blunt end (from which chicks usually hatch) from debris contamination or, in colonial breeders, increase resistance to impacts because a larger proportion of the eggshell is in contact with the substrate (*9*). Finally, it has also been proposed that adaptations for flight influence egg shape indirectly through the morphology of the pelvis, abdomen or oviduct (*10*). Previous studies investigating the diversity of egg shape

have been hampered by small sample size, reflecting the lack of comprehensive data on egg morphometry and life history traits, and therefore most of the above hypotheses remain untested, particularly within a phylogenetic framework (*3*).

Here, we resolve these issues by quantifying egg shape using a morphometric analysis of 49,175 eggs representing ~1400 (~14%) species in 35 extant orders, plus two extinct orders (Database S1). We then use these data to (i) quantify the observed morphologies in a two-dimensional morphospace for egg shape, (ii) provide a mechanistic model of how the egg is shaped in the oviduct, and (iii) test major hypotheses about egg shape variation in the context of key life history and environmental variables at a global scale. As a first step, we plotted egg shape in a two-dimensional morphospace that characterizes the asymmetry A and ellipticity E of axisymmetric eggs (Fig. 1, Figs. S1-S2), in line with earlier proposals that egg shape should be quantified using plane projective geometry (*11*, *12*). This approach showed that the occupied morphospace is triangular (Fig. 1, Fig. S3), with the bounding vertices corresponding to eggs that are symmetric and spherical, symmetric and elliptical, and asymmetric and elliptical. Interestingly, the occupied morphospace lacks spheroidal, asymmetric eggs, somewhat similar in shape to a hot air balloon (Fig. S3), a point to which we will return. A preliminary investigation of morphospace data highlights two key observations.

First, egg shape is a continuum, with no divisions between traditionally defined shape classes. Egg shapes range from $A = 0.001$ (*Streptopelia bitorquata*, Island Collared Dove) to 0.485 (*Calidris minutilla*, Least Sandpiper) and $E = 0.097$ (*Ninox scutulata*, Brown Hawk-owl) to 0.724 (*Macrocephalon maleo*, Maleo) (Fig. 1). A density map (Fig. S4) shows that many species converge on egg shapes with $A \in [0.1, 0.2]$ and $E \in [0.3, 0.4]$, similar in shape to the egg of the Graceful Prinia (*Prinia gracilis*) but not to the familiar "egg shape" of the chicken ancestor, the Red Junglefowl (*Gallus gallus*) (Fig. 1). The most densely occupied region of morphospace includes eggs laid by 26 species in 16 families and 3 orders (Fig. S4). The traditional

egg shape classes often presented in the literature fail to identify this canonical egg form, with no single egg shape class falling near the true most common egg shape (Fig. S5).

Second, avian clades differ widely in their distribution across egg morphospace (Fig. 2, Fig. S6), although substantial within-clade variation generates overlaps between clades (Fig. 2). Clades also differ in the extent of within-clade variation, as quantified by the area of the minimum convex hull containing species within each avian order (Fig. 2, Fig. S7, Table S1). For example, Charadriiformes (shorebirds) (n = 154) occupy a far greater area than do Passeriformes (perching birds, including songbirds) (n = 740) (Fig. 2, Table S1) (*13*) despite the fact that Passeriformes are more speciose than Charadriiformes by more than an order of magnitude. Furthermore, bird eggs span a morphospace that differs from that occupied by theropod dinosaurs, non-avian reptiles and monotreme mammals, particularly in terms of asymmetry (Fig. S8). Elongate, asymmetric eggs evolved prior to the ancestor of extant birds: some theropod dinosaurs laid asymmetric eggs (*14*, *15*) and a survey of Cenozoic fossil bird eggs shows that considerable variation in egg shape arose prior to extant birds (*16*). However, extant birds colonized some new regions of morphospace unoccupied by any other extinct or extant group of vertebrates, including regions of very high (>0.45) asymmetry and very low (<0.2) ellipticity (Fig. S8).

A biophysical model of egg shape

These patterns reveal how egg shape varies across birds and pave the way to a mechanistic theory that can predict shape. Such a theory can generate predictions about physical processes in the oviduct that may facilitate or constrain (Fig. S3) the evolution of egg shape variation. In developing this theory, we assume that egg shape is fixed by the shell membranes rather than by the shell itself, evidence for which comes from x-ray imaging (*17*) and experiments showing that an egg retains its shape even after shell removal (*3*). Egg shape is likely established as the egg moves through the isthmus (*8*), one of the final portions of the oviduct. In the isthmus, the egg is surrounded by its membrane (actually a double membrane), a meshwork of collagenous fibers (*18*). A recent study in chickens suggests that the magnum-isthmus junction, where

membrane deposition is initiated, is the site of shape determination; before reaching this part of the oviduct, eggs are more spherical and less asymmetric (*19*). After leaving the isthmus, the egg enters the shell gland, where the biomineralized calcium carbonate shell is deposited.

Building on these insights, a biomechanical approach based on pressure differences across a closed elastic membrane of varying thickness is a natural starting point (*20-22*). Our proposed model makes the simplest assumption consistent with a non-spherical shape for a pressurized closed elastic membrane: that the membrane properties are inhomogeneous owing to variations in thickness and material properties. When such a membrane is pressurized, it distends and takes up a form determined by two types of variation across the egg's surface: (i) variation in applied pressure difference across the surface; and (ii) variation in the membrane's thickness and material properties across the surface. We extend previous work that has alluded to these ideas qualitatively (*20-22*) by constructing a mathematical model that connects to the available experimental literature and emphasizes the central role played by the membrane. This model accounts for (i) differential forcing on the membrane from external muscular forces and internal pressure and (ii) variations in membrane properties in the axial and azimuthal directions.

We assume that egg growth and morphogenesis proceed as follows: (i) the enclosed membrane is deposited around the sphere of yolk and albumen; (ii) internal pressure is created inside the membrane-enclosed sac, which could arise from fluid being actively pumped into the sac (i.e., water absorption or 'plumping'), differential elasticity of the isthmus wall, muscular contractions, or some combination of these; (iii) the variation in membrane material properties (including collagen fiber composition/direction, elastic modulus and thickness) contributes to differential distortion in response to pressure in the axial and azimuthal directions. Ellipticity results from the fact that the membrane is easier to stretch along the oviduct axis (pole to pole) than perpendicular to it (around the egg's girth). Asymmetry, however, requires a difference in membrane material properties between the two poles. In all cases, the egg is axisymmetric, meaning that variation in shape, pressure and/or membrane properties is symmetric across the egg's major (longitudinal)

axis.

The shape of an axisymmetric egg can be completely described by a planar curve C, with radial and angular coordinates $[r(\sigma),\ \theta(\sigma)]$ as a function of a curvilinear material coordinate σ (Fig. 3). As the membrane distends under pressure, we define the axial extension ratio $\lambda_s = \partial s/\partial\sigma$, where s is the stretched coordinate, and the radial (azimuthal) extension ratio $\lambda_\varphi = r/r_0$, with the associated principal strains $e_{ss} = (\lambda_s^2 - 1)/2; e_{\varphi\varphi} = (\lambda_\varphi^2 - 1)/2$. Assuming a simple linear constitutive relation linking stress and strain (*23*, *24*), we may then write the thickness-integrated axial and azimuthal stresses (Fig. 3) as $t_s = Ae_{ss} + Be_{\varphi\varphi}; t_\varphi = Ae_{\varphi\varphi} + Be_{ss}$, where $A(\sigma), B(\sigma)$ are the thickness-integrated axial and azimuthal stretching stiffnesses of the egg membrane, respectively, and depend on the local elastic moduli as well as the thickness of the membrane. This allows us to write the equations of mechanical equilibrium for the egg membrane in the normal and tangential directions as $P = \kappa_s t_s + \kappa_\varphi t_\varphi$, $\partial(rt_s)/\partial s - t_\varphi \partial r/\partial s = 0$, in terms of the principal curvatures of the membrane $\kappa_s = \frac{\partial\theta}{\partial s};\ \kappa_\phi = \sin\theta/r,$ and the constant pressure difference across the membrane P. Here we have ignored the free boundaries associated with the fact that the egg is not in contact with the walls of the oviduct near the poles, because we assume the shape is preserved even in the absence of the walls. Making the variables in the above equations dimensionless (*13*) allows us to rewrite them in terms of the ratio of the azimuthal to the axial stiffness $\mu(\sigma) = B(\sigma)/A(\sigma)$ and the scaled effective pressure $p(\sigma) = P/A(\sigma)$ (*24*). The solutions of these equations for prescribed forms of these functions give us the shape of the egg; indeed the spatial variation of $\mu(\sigma), p(\sigma)$ (as a function of location across the egg's surface) controls both the asymmetry and ellipticity of the egg (*13*).

To constrain these two functions, we note that early work (*25*) suggests that there is significant variation in the properties of chicken shell membrane along its longitudinal axis, including variation in membrane thickness $h(\sigma)$, membrane density, membrane nitrogen and membrane packing index. This indicates that density of packing of the fibers in the membrane, and thus the membrane's elastic modulus, must vary from

pole to pole due to variations in the type (e.g., collagen), orientation, density and amount of material. Based on these observations, and on the membrane thickness data from (*25*), we use simple power law functions for the scaled pressure, $p(\sigma)$, which depends on $A(\sigma)$. Starting with a spherical egg shape that corresponds to a constant thickness and elastic moduli of the egg membrane, we can generate non-spherical eggs by iteratively changing $p(\sigma)$ and $\mu(\sigma)$ away from a constant value. For example, by making the membrane slightly thicker at one pole, the scaled pressure will be larger at the opposite pole since $A(\sigma)$ will be smaller (thinner) there, so that the egg will become asymmetrical. This serves as a new initial shape on which we can make another incremental change in the membrane thickness, or equivalently in $A(\sigma), B(\sigma)$, and solve the governing equations to get the new shape. In Fig. 3 (B-D), we show how to derive the classic shape of a chicken egg as the number of growth steps N is varied (see also Fig. S9). It is worth noting that our procedure yields egg shape but cannot predict absolute egg size since it uses rescaled variables. For example, if the pressure and membrane material properties are rescaled appropriately, this will result in larger eggs with the same shape.

Changing the functions $p(\sigma)$ and $\mu(\sigma)$ by varying the parameters in the power law form allows us to generate egg shapes that span the full avian egg morphospace (Fig. 3E), as well as counterfactual egg shapes which do not appear in nature (Fig. S10) (*13*). These counterfactual shapes are typically associated with strong and unusual variations in $\mu(\sigma), p(\sigma)$ due to very localized variations in membrane thickness, mechanical properties or both. Therefore, the eggs of living birds are either constrained (because the evolution of extreme variation in membrane properties is challenging) or such shapes have been strongly selected against (because the evolution of bizarre shapes is possible but maladaptive).

Testing functional hypotheses for egg shape variation

Having quantified and mechanistically described egg shape, we investigated the evolution of diverse egg shapes by performing comparative analyses using recent phylogenetic hypotheses for the backbone (*26*) and

tips (*27*) of the avian tree. Focusing on 1209 species in our data set for which molecular sequence data exist, we first assembled a phylogenetic tree onto which we mapped egg size (approximated by the length of the egg's major axis), asymmetry and ellipticity (Fig. 4) (*13*). Egg size and shape vary markedly across this tree (Fig. 4), with increases in asymmetry and/or ellipticity occurring in parallel across different lineages; e.g., highly asymmetric eggs evolved independently in penguins and in shorebirds.

To test functional explanations for the evolution of these diverse egg shapes, we compiled a dataset with biometric, life history and environmental parameters for all species in our sample, including adult body mass, diet, clutch size, nest type, nest location, chick developmental mode (e.g., precocial) and environmental details (latitude, temperature and average precipitation) calculated from geographical range polygons using standard techniques (*13*). We also used biometric measurements from museum specimens to calculate the hand-wing index (HWI), a standard proxy for flight efficiency and dispersal ability in birds (*13*, *28*, *29*). We computed HWI as the ratio of Kipp's distance (the distance between the tip of the longest primary and the tip of the first secondary feather) to total wing chord (distance between the carpal joint to wingtip) (*29*). Although HWI correlates with dispersal distance and migratory behavior in birds (*13*), we note that neither dispersal distance nor migration completely captures the essence of flight ability, since many bird species (e.g., shorebirds, hummingbirds) fly strongly even when they are non-migratory with low dispersal. Using HWI as an index of flight ability sidesteps this issue because even resident species with stronger and more frequent flight tend to have narrower and more pointed wingtips (high HWI), whereas species with weaker and less frequent flight tend to have shorter, more rounded wingtips (low HWI) (*13*). These assorted parameters allowed us to run Bayesian phylogenetic mixed-effect models to explore the extent to which various adaptive hypotheses predict avian egg shape on a global scale (Tables S2-S5) (*13*).

According to these analyses, egg length is predicted by adult body mass, clutch size, diet and developmental mode (Table S2-A). In most cases, these relationships support existing hypotheses given that shorter eggs are associated with larger clutches, and longer eggs are associated with a higher-calcium diet, larger adult body

mass and greater chick precociality. These findings suggest that egg size is regulated, at least in part, by life history characteristics and spatial constraints in the nest. In contrast, we found that egg shape (asymmetry and ellipticity) is not related to clutch size, developmental mode, environmental factors or nest characteristics (Table S2-B, C). These analyses consider variation across the entire avian clade, and at this taxonomic scale we find no support for the hypothesis that asymmetric eggs evolve more often in cliff-nesting birds or that egg shape is related to clutch size, which is consistent with our preliminary morphospace analysis (Figs. S11-S12). While theoretically optimal egg shapes for different-sized clutches have been proposed in the context of incubation efficiency (*5*), these optima fall outside the true occupied morphospace of natural eggs for all but two clutch sizes (n=3, n=9) (Fig. S11).

Instead, egg shape is correlated with egg size (captured by the first principal component of egg length and adult body mass) and HWI, with birds tending to lay eggs that are both more asymmetric and more elliptical if they have a high HWI and/or if the eggs are larger (Table S2-B, C). In addition, ellipticity is significantly predicted by the second principal component of egg length and body mass, such that birds with larger eggs than expected given their body mass (PC2) lay more elliptical eggs (Table S2-C). Given that HWI is positively related to flight efficiency (*13*, *28*, *29*), these results raise the intriguing possibility that adaptations for flight may be key drivers of egg shape variation in birds. This is consistent with a range of observations suggesting that key adaptations for high-powered flight – including reduced body size, a reduced abdominal cavity, and the loss of a functional ovary and oviduct – may have considerable effects on egg shape (*13*). In particular, such adaptations place constraints on the maximum size or wideness of a stretched oviduct, which in turn can be accommodated by increasing ellipticity and/or asymmetry of eggs to increase egg volume while maintaining or reducing girth. In accordance with this idea, we find that for a given girth (the widest part of the egg), species laying eggs that are more asymmetric (Fig. 5A) or more elliptical (Fig. 5B) tend to possess eggs that have higher volumes.

We do not suggest that a female's flight behavior during the egg formation period directly affects egg formation, nor do we suggest that egg shape so strongly influences the flight abilities of female birds during their egg-laying period that selection has produced an aerodynamic egg. Rather, we propose that general adaptations for strong flight select for a constrained, muscular, streamlined body plan in both males and females, giving rise in the latter, directly or indirectly, to asymmetric and/or elliptical eggs. The precise physiological mechanisms by which morphological adaptations for flight might impact egg shape are unknown. However, the answer most likely lies in the two parameters highlighted by our biophysical model: egg membrane thickness and the pressure applied across the membrane, both of which are potentially shaped by selection for a streamlined body plan.

Exploring the effect of flight adaptations on egg shape

Why different avian groups take different evolutionary paths (increased asymmetry, ellipticity, or both) toward maintaining or reducing girth is unclear, but considering the deeper evolutionary history of egg shape may yield some insights. We note that some theropod dinosaurs, particularly the maniraptorans from which birds descended, laid asymmetric eggs (*30*). The loss of a functional ovary and oviduct likely occurred near the maniraptoran-avian transition (*30*, *31*) and may be an innovation unique to birds (*32*). Thus, egg asymmetry and the loss of a functional ovary appeared around the same time as, and are perhaps closely linked to, the emergence of powered flight. Egg ellipticity, by contrast, appears to have originated much earlier in reptiles (crocodilians have elliptical eggs, for example), and may have evolved to accommodate the large egg volumes required for precocial offspring, when egg girth is limited by the oviduct or pelvic opening (*31*).

When it comes to powered flight, does egg asymmetry offer added advantages over ellipticity, or is it a consequence of new and extreme morphological shifts, like oviduct loss? The answer remains unknown. However, if asymmetry is physiologically linked to powered flight, we might expect reduced flight-related selection pressure to be associated with less asymmetric egg shapes. Consistent with this hypothesis, we find

261 that kiwis lay hyper-elliptical eggs with relatively low asymmetry and the other flightless ratites lay eggs that
262 are roughly spherical (ostrich) or elliptical without a high degree of asymmetry (rheas, cassowaries) (Fig.
263 S13). Contrary to this hypothesis, however, we note that not all flightless birds have evolved symmetric
264 eggs. Penguins are a clear exception (Fig. S13), but because they are powerful underwater swimmers it
265 remains plausible that selection for a streamlined body plan has nonetheless influenced the evolution of egg
266 asymmetry in the absence of flight.
267
268 Having found a strong association between HWI and egg shape at a broad taxonomic scale (across all avian
269 orders), we next explored whether these relationships – or others – describe egg shape variation within
270 smaller avian groups with contrasting life histories and ecologies. First, we compared asymmetry (Fig. 5C)
271 and ellipticity (Fig. 5D) of species with high (upper 50%) HWI versus low (lower 50%) HWI within the 12
272 most speciose orders in our dataset. Although we did not control within orders for phylogeny and other
273 factors, these pairwise comparisons are nonetheless broadly matched for phylogeny by comparing within
274 orders. The results reveal considerable variation among orders in the extent to which asymmetry and
275 ellipticity may vary as a function of HWI – but also highlight the generality of the pattern detected in our
276 broad taxonomic analyses (Fig. 5C, D, Fig. S14). Specifically, increased HWI (and hence dispersal ability) is
277 generally associated with an increase in both egg asymmetry and ellipticity within orders.
278
279 Next, we re-ran phylogenetic models restricted to (polyphyletic) seabirds (*13*) (Table S3), (monophyletic)
280 passerines (order Passeriformes) (Table S4), and (monophyletic) shorebirds (order Charadriiformes) (Table
281 S5). The results reveal that some additional explanatory variables can contribute to egg shape variation in
282 particular case studies. For example, in Charadriiformes, variation in egg asymmetry is associated with
283 developmental mode (Table S5-B, Fig. S15) rather than variation in HWI (Fig. S14C), perhaps because
284 highly asymmetric eggs can accommodate a pore-dense respiratory site for rapid neural development in
285 precocial chicks (*8*). In Passeriformes, species are more likely to lay elliptical eggs if they have small
286 clutches, after controlling for other effects (Table S4-C). Thus, life history traits may have a significant

287 secondary influence on egg shape evolution at smaller taxonomic scales, but we still find little evidence for
288 the role of cliff-nesting or clutch size in driving the evolution of egg asymmetry, even in the specific groups
289 that inspired these classical hypotheses (seabirds and shorebirds, respectively). Overall, our results suggest
290 that egg shape is largely influenced by morphological traits associated with flight ability, both in
291 Passeriformes (the most speciose avian radiation; Table S4) and across all birds (Table S2). However, these
292 associations do not apply equally to all smaller clades (Fig. 5C, D, Fig. S14), and further research is required
293 to examine egg shape variation at a range of taxonomic levels.
294
295 **Conclusions**
296 Avian eggs provide a simple but powerful system in which to explore the physical and evolutionary drivers
297 of morphological diversity. We have shown that a two-dimensional morphospace captures the range of egg
298 shapes produced by birds and that a biophysical model can explain this diversity, with testable predictions
299 linking membrane properties to shape. Our macroevolutionary analyses suggest that birds adapted for high-
300 powered flight may maximize egg size by increasing egg asymmetry and/or ellipticity, while maintaining a
301 streamlined body plan. Moving forward, it will be important to determine how the developmental process of
302 egg shaping is coupled, in terms of physiology and genetics, with evolutionary constraints associated with
303 flight strength and efficiency. A starting point may be to demonstrate whether anatomical features, like
304 pelvic width, are correlated with egg size and HWI.
305

306 **References and Notes:**

307 1. P. M. Sander, Reproduction in Early Amniotes. *Science* **337**, 806–808 (2012).
308 2. M. E. Hauber, *The Book of Eggs* (Chicago, IL: University of Chicago Press, 2014).
309 3. T. Birkhead, *The Most Perfect Thing: Inside (and Outside) a Bird's Egg* (Bloomsbury Publishing
310 USA, 2016).
311 4. N. G. Smith, Adaptations to Cliff-Nesting in Some Arctic Gulls (*Larus*). *Ibis* **108**, 68–83 (1966).

5. Z. Barta, T. Szekely, The optimal shape of avian eggs. *Funct. Ecol.* **11**, 656–662 (1997).

6. J. Hutchinson, Three into two doesn't go: two-dimensional models of bird eggs, snail shells and plant roots. *Biol. J. Linn. Soc.* **70**, 161–187 (2000).

7. A. G. Gosler, J. P. Higham, S. J. Reynolds, Why are birds' eggs speckled? *Ecol. Lett.* **8**, 1105–1113 (2005).

8. I. Smart, in *Egg Incubation: Its Effects on Embyonic Development in Birds and Reptiles*, C. Deeming, Ed. (Cambridge University Press, New York 1991), pp. 101–116.

9. T. R. Birkhead, J. E. Thompson, D. Jackson, J. D. Biggins, The point of a Guillemot's egg. *Ibis* **159**, 255–265 (2017).

10. J. B. Iverson, M. A. Ewert, in *Egg Incubation: Its Effects on Embyonic Development in Birds and Reptiles*, C. Deeming, Ed. (Cambridge University Press, New York 1991), pp. 87–100.

11. D. Baker, A geometric method for determining shape of bird eggs. *Auk* **119**, 1179–1186 (2002).

12. F. W. Preston, The shapes of birds' eggs. *Auk* **70**, 160–182 (1953).

13. Materials and methods are available as supplementary materials on *Science* Online.

14. D. K. Zelenitsky, Reproductive traits of non-avian theropods. *J. Paleont. Soc. Korea* **22**, 209–216 (2006).

15. N. López-Martínez, E. Vicens, A new peculiar dinosaur egg, *Sankofa pyrenaica* oogen. nov. oosp. nov. from the Upper Cretaceous coastal deposits of the Aren Formation, south-central Pyrenees, Lleida, Catalonia, Spain. *Palaeontology* **55**, 325–339 (2012).

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

17. J. R. G. Bradfield, Radiographic studies on the formation of the hen's egg shell. *J. Exp. Biol.* **28**, 125–140 (1951).

18. M. T. Hincke *et al.*, The eggshell: structure, composition and mineralization. *Front. Biosci.* **17**, 1266–1280 (2012).

19. K.-M. Mao, F. Sultana, M. A. R. Howlider, A. Iwasawa, N. Yoshizaki, The magnum-isthmus junction of the fowl oviduct participates in the formation of the avian-type shell membrane. *Zool. Sci.* **23**, 41–47 (2006).

20. A. Mallock, The shapes of birds' eggs. *Nature* **116**, 311–312 (1925).

21. D. W. Thompson, *On growth and form.* (Cambridge Univ. Press, 1942).

22. J. Okabe, On the forms of hen's eggs. *Reports of Research Institute for Applied Mechanics* **1**, 7–30 (1952).

23. E. A. Evans, R. Skalak, *Mechanics and Thermodynamics of Biomembranes.* (CRC Press, Boca Raton, FL, 1980).

346 24. A. Goriely, M. Tabor, Biomechanical models of hyphal growth in actinomycetes. *J. Theor. Biol.* **222**,
347 211–218 (2003).

348 25. D. A. Balch, C. Tyler, Variation in some shell membrane characteristics over different parts of the
349 same shell. *Bri. Poult. Sci.* **5**, 201–215 (1964).

350 26. R. O. Prum *et al.*, A comprehensive phylogeny of birds (Aves) using targeted next-generation DNA
351 sequencing. *Nature* **526**, 569-573 (2015), doi:10.1038/nature15697.

352 27. W. Jetz, D. B. Thomas, J. B. Joy, K. Hartmann, A. O. Mooers, The global diversity of birds in space
353 and time. *Nature* **491**, 444–448 (2012).

354 28. R. Lockwood, J. P. Swaddle, J. Rayner, Avian wingtip shape reconsidered: wingtip shape indices and
355 morphological adaptations to migration. *J. Avian Biol.* **29**, 273-292 (1998).

356 29. S. Claramunt, E. P. Derryberry, J. V. Remsen, R. T. Brumfield, High dispersal ability inhibits
357 speciation in a continental radiation of passerine birds. *Proc. R. Soc. London Ser. B* **279**, 1567–1574
358 (2012).

359 30. X. Zheng *et al.*, Preservation of ovarian follicles reveals early evolution of avian reproductive
360 behaviour. *Nature* **495**, 507–511 (2013).

361 31. G. Grellet-Tinner, L. Chiappe, M. Norell, D. Bottjer, Dinosaur eggs and nesting behaviors: A
362 paleobiological investigation. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **232**, 294–321 (2006).

363 32. T. Sato, A Pair of Shelled Eggs Inside A Female Dinosaur. *Science* **308**, 375–375 (2005).

364

365 **Acknowledgements:**

366 MCS was supported by Princeton University, with additional support from the L'Oréal USA For Women in
367 Science Fellowship, the L'Oréal-UNESCO International Rising Talents Fellowship, the Harvard Society of
368 Fellows and the Milton Fund. EHY was supported by a Start-Up Grant No. M4081583 from Nanyang
369 Technological University, Singapore. CS was supported by the Oxford Clarendon Fund and the US-UK
370 Fulbright Commission. Collection of biometric, life-history and environmental data was supported by a
371 Natural Environment Research Council grant (NE/I028068/1) to JAT. LM was supported by fellowships
372 from the MacArthur Foundation and the Radcliffe Institute. We thank Harold Eyster, Daniel Swindlehurst
373 and James Damore for contributing to data collection, Carla Cicero and Rauri Bowie for specimen access,
374 including digitization of the egg collection at the Museum of Vertebrate Zoology, Berkeley (funded by NSF
375 grant #0646475), and the referees for valuable comments. Egg shape data reported in this paper are included
376 in the Supplementary Materials.

This study was conceived by MCS and LM and designed by MCS, JAT and LM. The digital morphometric analyses and coding were conducted by MCS, EHY and DA. MCS, CS and JAT compiled biometric, life history and environmental data for birds. The phylogenetic comparative analyses were led by CS and JAT. LM linked the projective geometry parameters to the asymmetry-ellipticity morphospace, and LM and EHY constructed and solved the mathematical model for egg shape. MCS, JAT and LM coordinated the research, and all authors contributed to writing of the manuscript.

Fig. 1. Morphospace of avian egg shape. Average egg shapes for each of 1400 species (black dots), illustrating variation in asymmetry and ellipticity, as defined in the text. Images of representative eggs are shown alongside their associated points in morphospace (colored red) to highlight variation in shape parameters. Egg images (shown on the same relative scale) are copyright of the Museum of Vertebrate Zoology, Berkeley. Image details and sources are given in Database S2.

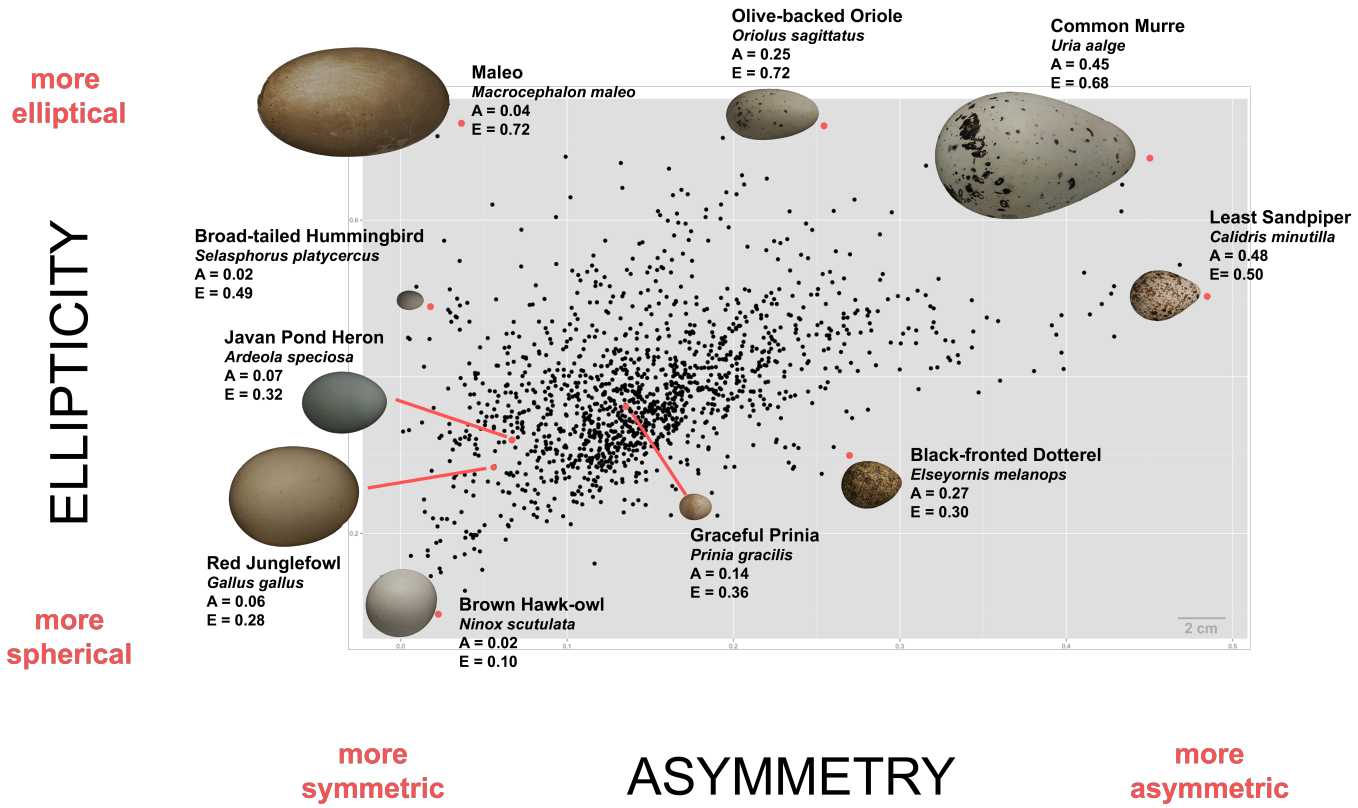


Fig. 2. Partitioning of egg variation among avian orders. Black dots (one per species; n = 1400) show the morphospace of egg shape in two dimensions (asymmetry and ellipticity). Colored polygons show the minimum convex hull plotted for all species within a subset of avian orders (Strigiformes, Apodiformes, Suliformes, Passeriformes, Charadriiformes). Overlap in egg shape is extensive, even among ecologically and phenotypically dissimilar orders. However, some orders (e.g., Charadriiformes) occupy a much larger region of egg morphospace than others.

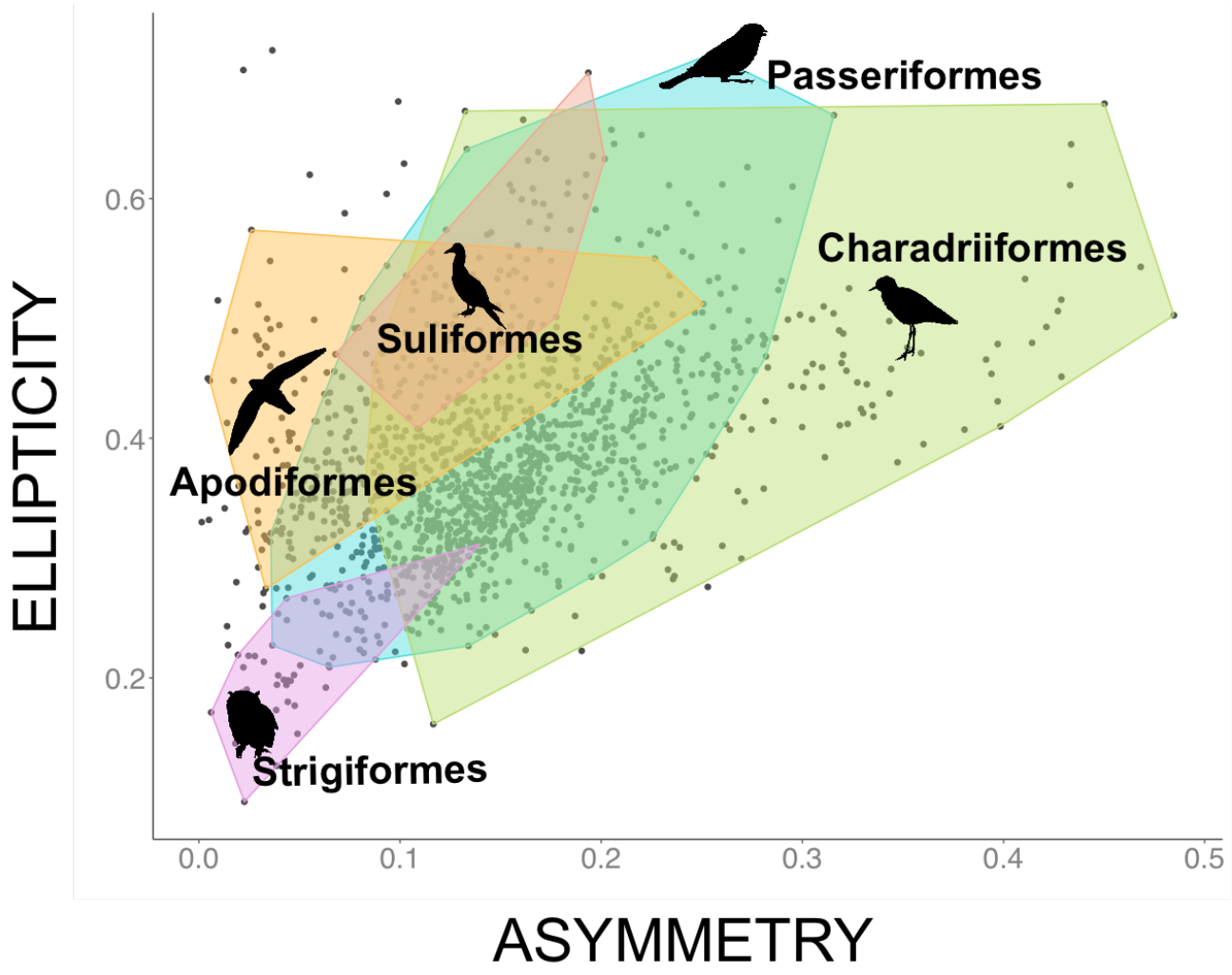


Fig. 3. Biophysical model of egg shape. (A) An axisymmetric egg is described by a planar curve C that, when revolved around the axis of symmetry (z-axis), yields the surface of the egg, with radial and angular coordinates $[r(\sigma), \theta(\sigma)]$ parametrized by a curvilinear material coordinate σ defined relative to one of the poles of the egg. There is a uniform pressure difference P across the membrane, a thickness-integrated axial stress $t_s(\sigma)$ and a thickness-integrated azimuthal stress $t_\phi(\sigma)$ that together characterize the three principal stresses at every location along the axisymmetric egg membrane. Here, e_n is the unit vector in the normal direction and e_s and e_φ are the two orthogonal tangent directions pointing in the axial and azimuthal directions along the membrane surface. The stiffnesses in the axial and azimuthal direction are given by $A(\sigma), B(\sigma)$ and link the stresses to the elastic strains driven by the pressure difference across the membrane (see text and supplementary materials for details). O is the Cartesian origin. (B) Schematic representation of the re-parameterization/growth process. The initial reference shape $r_0(\sigma)$ grows to $r_1(\sigma)$ after one growth step, driven by the scaled pressure $p(\sigma)$ and the ratio of azimuthal to axial stiffness $\mu(\sigma)$ (see text and supplementary materials for details). This new shape is then used as a reference shape in the next growth step, yielding an iterative approach to morphogenesis. (C) Experimentally observed variations in egg membrane thickness taken from Fig. 3 (dotted line) of Balch and Tyler (*25*) allow us to fit a simple power law and parametrize the functions $A(\sigma), B(\sigma)$ (see supplementary materials), and therefore $p(\sigma)$, $\mu(\sigma)$. (D) A spherical egg grows into a classic chicken egg that is both elliptical and asymmetrical in 45 discrete growth steps following the protocol in (B). (E) The full avian morphospace can be generated using different functional forms for the scaled ratio of azimuthal to axial stiffness and the scaled pressure, $\mu(\sigma), p(\sigma)$, respectively (see text and supplementary materials for details).

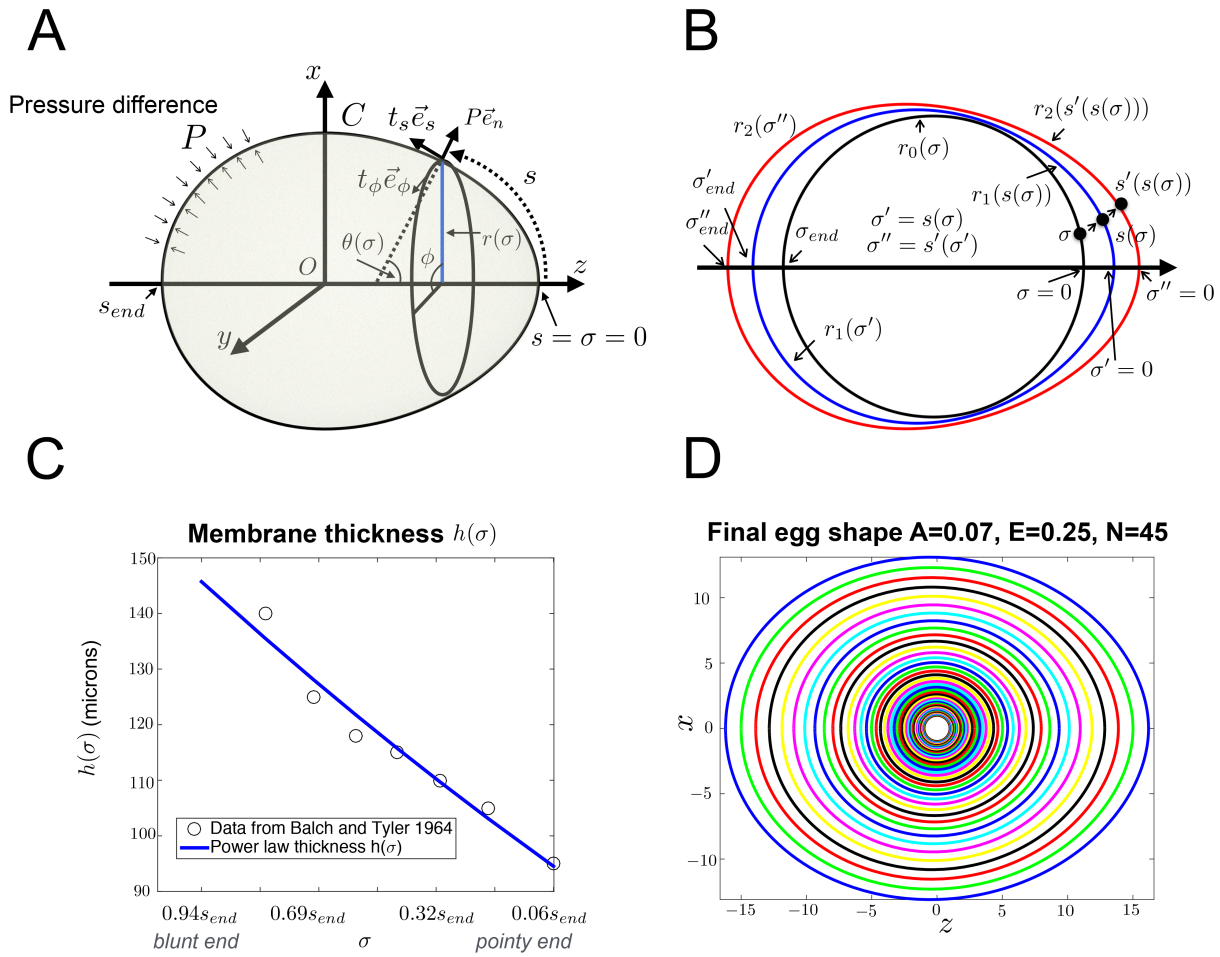

A
Pressure difference
x
C
$t_s\vec{e}_s$
$P\vec{e}_n$
P
s
$t_\phi\vec{e}_\phi$
$\theta(\sigma)$
$r(\sigma)$
ϕ
O
z
s_{end}
y
$s = \sigma = 0$
B
$r_2(\sigma'')$
$r_2(s'(s(\sigma)))$
$r_0(\sigma)$
σ'_{end}
$r_1(s(\sigma))$
$s'(s(\sigma))$
σ''_{end}
σ_{end}
$\sigma' = s(\sigma)$
$\sigma'' = s'(\sigma')$
σ
$s(\sigma)$
$\sigma = 0$
$\sigma'' = 0$
$r_1(\sigma')$
$\sigma' = 0$
C
Membrane thickness $h(\sigma)$
$h(\sigma)$ (microns)
150
140
130
120
110
100
90
Data from Balch and Tyler 1964
Power law thickness h(σ)
$0.94s_{end}$
$0.69s_{end}$
$0.32s_{end}$
$0.06s_{end}$
blunt end
σ
pointy end
D
Final egg shape A=0.07, E=0.25, N=45
10
5
0
−5
−10
x
−15
−10
−5
0
5
10
15
z
E
Ellipticity
Asymmetry
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0.05
0.1
0.15
0.2
0.25
0.3
0.35
0.4
0.45
0.5
Maleo
A =0.04 E= 0.72
Olive-backed Oriole
A =0.25 E= 0.72
Common Murre
A =0.45 E= 0.68
Broad-tailed Hummingbird
A =0.02 E= 0.49
Least Sandpiper
A =0.48 E= 0.50
Javan Pond Heron
A =0.07 E= 0.32
Graceful Prinia
A =0.14 E= 0.36
Black-fronted Dotterel
A =0.27 E= 0.30
Red Junglefowl
A =0.06 E= 0.28
Brown Hawk-owl
A =0.02 E= 0.10

Fig. 4. Evolutionary patterns of egg shape diversity. A phylogeny of 1209 species in our sample for which molecular sequence data exist, based on (*26*) and (*27*). For each species, the average egg length (light blue), asymmetry (medium blue) and ellipticity (dark blue) are represented by line lengths at branch tips. Silhouettes for representative species in each order are shown (details and image sources in Database S2).

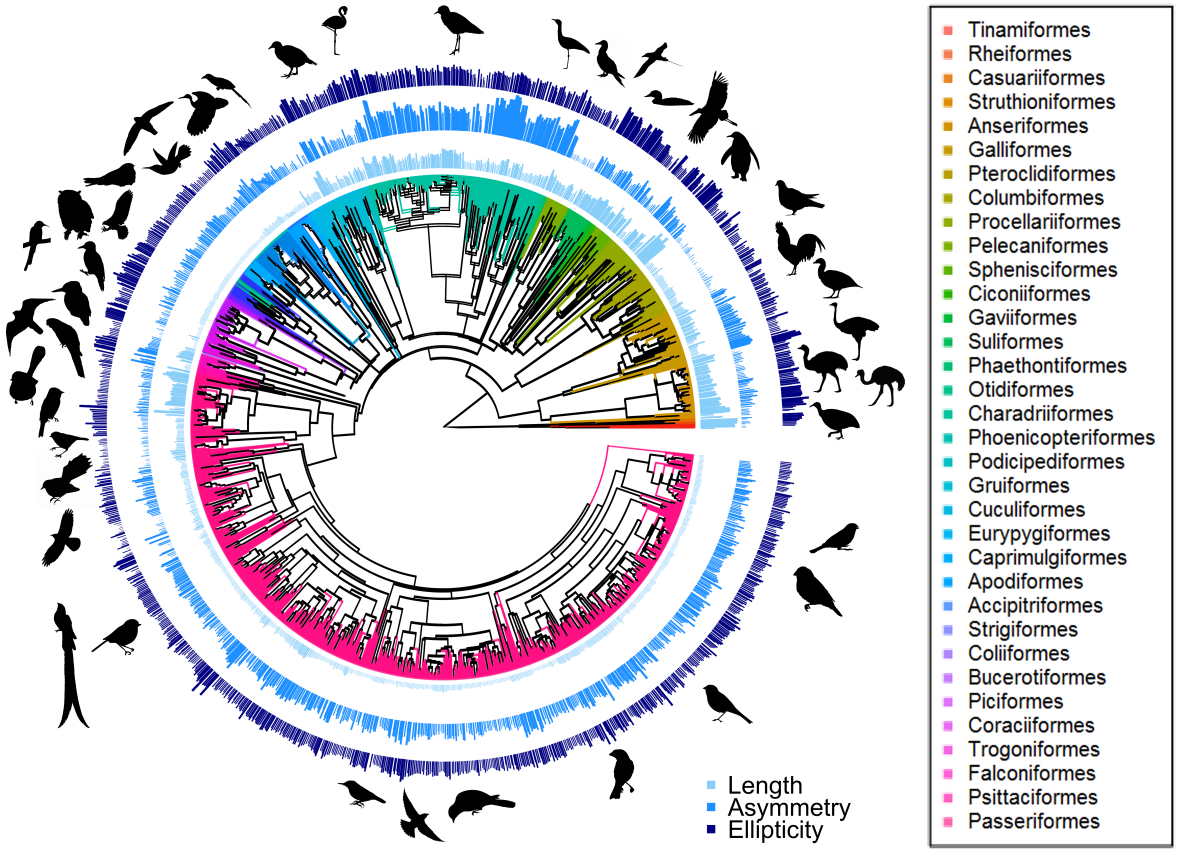
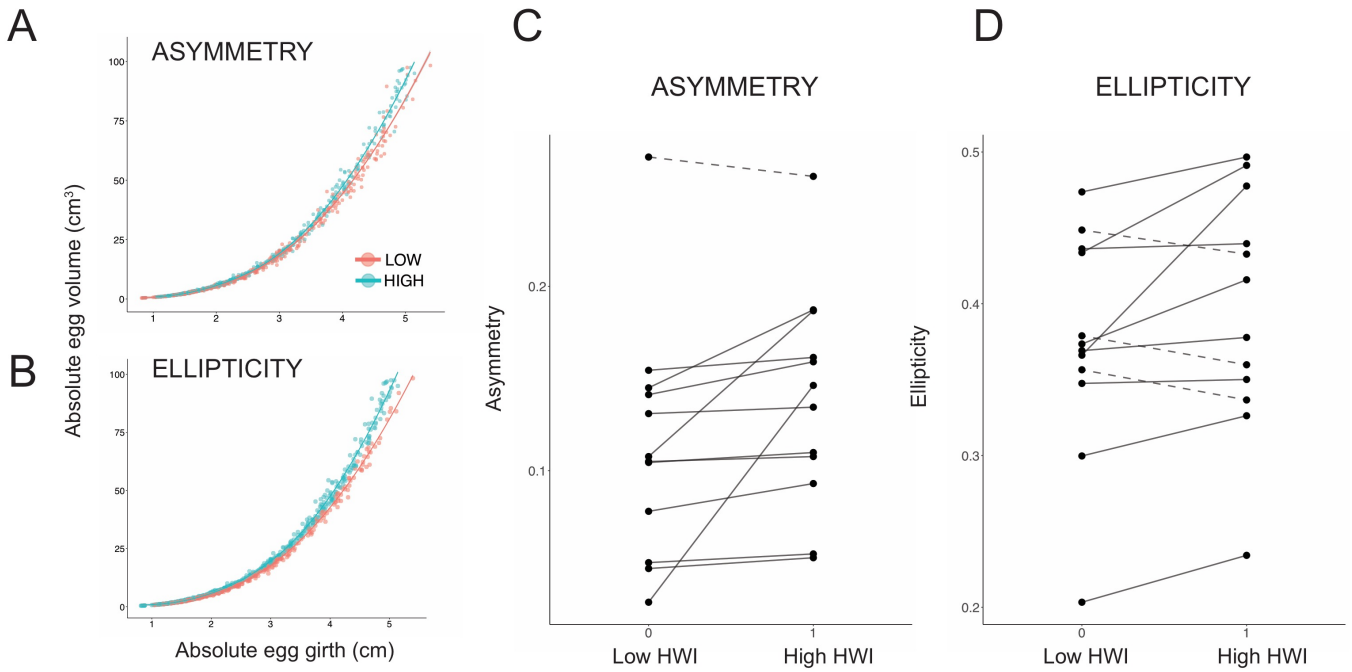


Fig. 5. Egg shape, egg volume and flight ability. (A, B) For a given egg girth, birds increase egg volume by increasing asymmetry and/or ellipticity. In our dataset, eggs that are more (A) asymmetric and (B) elliptical tend to have larger volumes for a given egg girth (wideness). Average egg girth (x-axis) is calculated directly from images; egg volume (y-axis) is derived from Baker (*11*). Eggs with high (upper 50% of all species) asymmetry (A) or ellipticity (B) are shown in turquoise; eggs with low (lower 50% of all species) asymmetry (A) or ellipticity (B) are shown in red. For clarity, we omitted eggs with the highest volumes (top 5% of species). (C, D) Comparison of egg asymmetry (C) and ellipticity (D) between species with high and low flight ability in the 12 most speciose orders in our sample. We divided extant species in each order according to Hand-wing Index (HWI) to directly compare between those with low HWI (lower 50%) and high HWI (upper 50%). Increased HWI (i.e., flight ability) is often associated with increased asymmetry or ellipticity (solid lines) and less often with decreased asymmetry or ellipticity (dashed lines).



Supplementary Materials

The Supplementary Materials file includes:

Materials and Methods
Figs. S1 to S16
Tables S1 to S5
References 33-63

Other Supplementary Materials for this manuscript include the following:

Databases S1 to S2 as zipped archives:
Database S1 Egg shape by species.xlsx
Database S2 Figure details.xlsx