also secondarily evolved in some species, such as honeyeaters, perhaps because enclosing a nest by topping it with a dome enables birds to breed in climatically challenging environments (as might building in trees and other cavities) or can aid in reducing predation. Such nest location choices or structural designs mean that we find small birds living in cooler places than we might expect.

The relative simplicity of many of the phylogenetic patterns to date appear to offer support for the view that nest morphology is innate. But there are some analyses that have shown considerable structural variation within families. For example, while the Neotropical ovenbirds (the Furnariidae), are all cavity nesters, what they build *in* the cavity could be a platform, a cup, or a dome, each of which may be built using different materials, perhaps requiring recognition of appropriate materials and different handling skills, including mud daubing, while yet other species build the clay domes or 'ovens' for which the group is named or take over ovens already built by others. Why this group includes such variety in their nest structure is far from clear yet, although it seems likely that environmental conditions have played a major role. Whether such striking variability in the morphology of a nest might occur over much shorter time periods (such as within a bird's lifetime) is yet to be investigated.

Nests as a cultural tradition?

In humans, architectural styles within societies are a notable form of cultural tradition. However, if nest material choice can be learned, either from a bird's own experience or from watching others, this raises the possibility that nest design could also be a cultural artefact in some birds. Evidence for cultural traditions in non-human animals has been steadily accumulating over the past decade in particular, from songs in whales to tool use in primates. Addressing the role of culture in nest building will involve challenging our assumptions about what birds are and are not capable of. For instance, in humans, if we show that groups diverge in terms of the details of construction or the final product (for example, house size, shape, materials) but that there are also consistencies in the object (for example, a house/castle/igloo/whare) produced, we take the combination of inter-group divergence and intra-group similarity as evidence of culture (i.e. that similarity in object form is due to learning from others). When, however, we see similarity in bird nests, this is taken as evidence of the innateness of nest building, taking it down a cognitive notch or two.

We are only just beginning to understand the role of social learning and perhaps even culture on how nests come to differ across populations and species. What is clear though is that simplistic assumptions of nest-building as innate, as being just 'written in the genes', have not stood up to the growing body of work showing how dynamic and labile nest building can be. Future work that is not just focussed on the end product — the nest — but also on the process of nest building will no doubt further enrich our understanding of not only birds and their constructions, but also how animals manipulate their environments more generally to safely produce the next generation.

DECLARATION OF INTERESTS

The author declares no competing interests.

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Centre for Biological Diversity, School of Biology, University of St Andrews, St Andrews, KY16 9TH, UK.
E-mail: susan.healy@st-andrews.ac.uk

Primer

Bird eggs

Mary Caswell Stoddard

I once spent a summer studying gulls on Appledore Island in the Gulf of Maine, off the east coast of the United States. The rocky island is a breeding colony for herring gulls (*Larus argentatus*) and great black-backed gulls (*Larus marinus*), so I had a front-row seat to the dramas that unfolded as birds paired up, laid and incubated eggs, and raised chicks. I saw chicks hatch from large speckled eggs (Figure 1A), a Herculean feat that took over an hour. Eggs and chicks are extremely vulnerable, and many gull offspring do not survive. Now, when a gull soars past — or pilfers my sandwich at the beach — I appreciate the hurdles it overcame just to reach adulthood.

Bird eggs have a very clear function: to protect and nourish the chick until it hatches. Despite having a precise and short-lived purpose, bird eggs are staggeringly different in their color, pigmentation pattern, size, shape (Figure 1), and fine-scale shell structure. From the emu's (*Dromaius novaehollandiae*) large emerald ellipsoid to the great-tailed grackle's (*Quiscalus mexicanus*) finely squiggled orb, each egg evolved in response to environmental and reproductive conditions suited to its species. When we consider that birds — with over 10,000 species — are the most diverse land vertebrates, the remarkable variety of bird eggs makes sense. Throughout history, bird eggs captured the attention of Aristotle, who wrote about them in *The History of Animals*, as well as many key figures in evolution, ornithology and conservation. These included Charles Darwin, Alfred Russel Wallace, Margaret Morse Nice, Niko Tinbergen, Rachel Carson, and David Lack. Bird eggs also enticed Victorian naturalists, whose avid collection efforts peaked around the turn of the 20th century.

The best-studied bird egg is that ubiquitous kitchen staple: the chicken egg. In the United States, approximately 100 billion chicken eggs are produced each year. Because chicken eggs are commercially valuable, much is known about their formation, development, mechanics and genetics. Less is known about the eggs of most of the planet's other birds: for some species, the eggs have never been described at all. Fortunately, the study of bird eggs is a rapidly growing area of ornithology, with researchers from around the world helping to build a richer picture of egg ecology and evolution. To provide a broad introduction to bird eggs, I first cover how eggs evolved and how they form. I then highlight the diversity of egg appearances in terms of color, pattern, size, shape and shell structure and discuss some of the genes responsible for this variation. I conclude by exploring the influence of nest conditions on eggs and by emphasizing the importance of studying bird eggs in a time of swift environmental change.

Figure 1. Bird eggs are very diverse in appearance.
Shown here are eggs laid by the (A) great black-backed gull (*Larus marinus*), (B) spotted nothura (*Nothura maculosa*), (C) northern jacana (*Jacana spinosa*), (D) American robin (*Turdus migratorius*), (F) crowned woodnymph (*Thalurania colombica*), (G) common pauraque (*Nyctidromus albicollis*), (H) swallow-tailed gull (*Creagrus furcatus*), and (I) common eider (*Somateria mollissima*). Also shown (E) is a nest containing four great reed warbler (*Acrocephalus arundinaceus*) eggs and one parasitic common cuckoo (*Cuculus canorus*) egg, indicated with an arrow. (Image credits: (A,H,I) M.C. Stoddard; (B) C.A. Girotto; (C) E. Buck; (D,F,G) D. Ocampo; and (E) Attila Marton, licensed under CC BY-SA 4.0.)

Evolutionary history

Which came first, the chicken or the egg? Let us settle the debate: the egg came first. Birds evolved from theropod dinosaurs about 150 million years ago, with *Archaeopteryx* typically considered to be the oldest bird. Chickens evolved later. A remarkable fossil nicknamed the 'Wonderchicken' suggests that the ancestors of modern chickens and ducks evolved 66 million years ago. But long before birds, and specifically chickens, arrived on the evolutionary scene, vertebrates were laying eggs.

The vertebrate egg as we know it, complete with an eggshell, a large yolk and a series of membranes (including one called the amnion), is the amniotic egg. It evolved just over 300 million years ago in the amniotes, a group of tetrapod vertebrates. This new kind of egg, which was distinct from the simpler, shell-less eggs of amphibians, kickstarted an evolutionary revolution. In fact, Alfred Romer, an American paleontologist, called the egg "the most marvelous single 'invention' in the whole history of vertebrate life." Because the amniotic egg could develop fully on land without drying out, amniotes were not tied to water for reproduction like their amphibian relatives were. Thus, the egg unlocked new evolutionary potential for amniotes as they colonized novel terrestrial habitats and eventually diversified into two major lineages: one containing mammals, and the other containing reptiles, including birds. Over time, the egg design was tweaked to meet the needs of these different animal groups.

In birds, the egg was refined in several ways. Bird eggs have a rigid shell comprising a pair of shell membranes, several calcified layers and an organic outer covering called the cuticle. Other modern egg-laying reptiles have eggshells, which can be soft or hard, but these shells typically lack the highly structured organization seen in those of bird eggs. In addition, bird eggs tend to have more variable shapes and more diverse colors. Why did birds modify the egg design? Unlike most other reptiles, birds typically lay their eggs above ground, where they are incubated by a biological or foster parent. The sophisticated eggshells of birds likely provided additional mechanical and antimicrobial protection in diverse nest environments, and eggshell pigments provided camouflage against predators.

How eggs form

The next time you crack an egg for breakfast, take a moment to marvel. You are holding one of the fastest-forming biominerals in nature. In chickens, the eggshell forms in under 24 hours, during which time approximately 5 grams of calcium carbonate are deposited. Compare this to nacre — the iridescent mother-of-pearl substance in mollusk shells — in which a few grams of calcium carbonate are added *per year*. As in chickens, many wild bird species require only about a day to create an egg.

Egg formation starts when a mature ovum, surrounded by yolk, is released from the left ovary. Most birds have a single functional ovary; the second one was presumably lost to reduce weight and maximize flight efficiency. The ovum travels down a long stretchy tube called the oviduct, where it can be fertilized if sperm are present. Typically, many sperm enter the ovum. Although only one (or a few) is needed for fertilization, the 'extra' sperm appear to help initiate the embryo's development.

Next, the albumen (or ‘egg white’) is added; it will eventually hydrate the embryo and provide enzymatic protection against microbial invasions. The egg continues down the oviduct and reaches the isthmus. Here, the eggshell membranes — a meshwork of collagen and proteins — are added. The egg then enters the shell gland, located near the end of the oviduct, where the calcified shell forms. Ultimately, the shell consists of 95% calcium carbonate, 3.5% organic proteins and 1.5% water and other elements. Pigments are also added in the shell gland (see next section). As a final step, the cuticle, an organic coating that protects against harmful bacteria and UV radiation, is deposited around the shell in many species.

By the time it is laid, the egg contains almost everything the embryo will need — all of the nutrients, water and minerals — to develop and hatch. Still, some contact with the outside world is required. Thousands of microscopic pores in the shell allow oxygen to be delivered to the embryo and carbon dioxide to be released. One or both parents provide heat to incubate the egg to support embryonic growth. Heat is typically delivered by the brood patch, an area of exposed skin on the adult’s belly, but some birds, like penguins, pelicans and gannets, warm the eggs with their feet. The megapodes, like the Australian brush turkey (*Alectura lathami*), have eschewed body heat altogether. They bury their eggs in mounds of rotting vegetation, to which males add or remove material to adjust the mound’s internal temperature.

Color and pattern

No brief description can do justice to the diversity of colors and patterns found in bird eggs (Figure 1). The underlying background colors of eggs run the gamut from white, beige and brown to blue and green and even yellow, pink and dark purple. Eggs can be immaculate, with no patterns, or covered with speckles, blotches, streaks or squiggles. Until recently, just two pigments were thought to be responsible for egg coloration: blue-green biliverdin and red-brown protoporphyrin. Both pigments are associated with heme, a compound that transports oxygen in the bloodstream. Researchers have now identified two new pigments in the eggs of tinamous, a group of squatty Neotropical birds whose dowdy plumage belies their spectacularly colored, porcelain-like eggs. These two pigments, yellow-brown bilirubin in the green eggs of the elegant-crested tinamou (*Eudromia elegans*) and red-orange uroerythrin in the purplish-brown eggs of the spotted nothura (*Nothura maculosa*; Figure 1B), expand the eggshell color gamut, hinting at future discoveries in diverse taxa.

Eggshell pigments are deposited in the shell gland during the final hours of egg formation. Cells lining the shell gland release pigment, which can be incorporated in the shell as it develops or confined to the outer shell regions and cuticle. The precise mechanism responsible for the elaborate patterns on bird eggs remains mysterious, but a process resembling inkjet printing seems plausible. As the egg is rotated by muscles in the wall of the shell gland, blobs of pigment are added like ink to a blank sheet of paper. Carefully controlled squirts of pigment could produce speckles when the egg is stationary or long squiggles when the egg is in motion, like the calligraphic scrawls on the egg of a northern jacana (*Jacana spinosa*; Figure 1C).

From a functional perspective, what explains the kaleidoscopic variety of colors and patterns in bird eggs? First and foremost, egg color is associated with camouflage. Whereas cavity-nesters like woodpeckers and owls tend to lay white eggs, birds nesting in less protected places — especially on the ground — often lay brown, speckled eggs. But many eggs, at least to human eyes, appear poorly

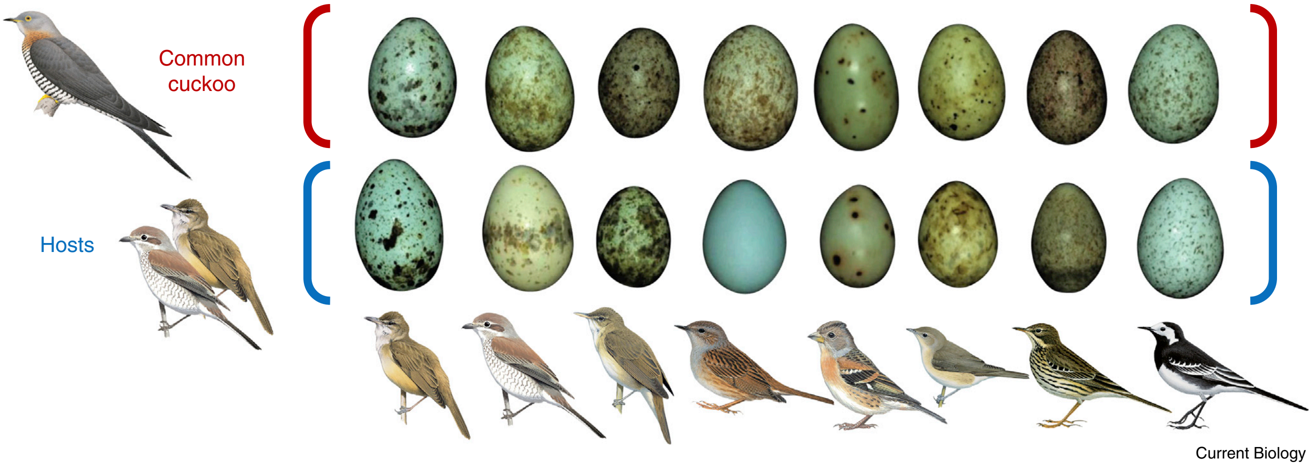


Figure 2. Egg mimicry by the common cuckoo.
Genetically distinct host races of the common cuckoo (*Cuculus canorus*) lay their eggs in the nests of a variety of host species. In instances where hosts have evolved strong egg rejection defenses, cuckoos have evolved eggs that are a close match in color and pattern. Hosts from left to right are great reed warbler (*Acrocephalus arundinaceus*), red-backed shrike (*Lanius collurio*), reed warbler (*Acrocephalus scirpaceus*), dunnock (*Prunella modularis*), brambling (*Fringilla montifringilla*), garden warbler (*Sylvia borin*), meadow pipit (*Anthus pratensis*), and white wagtail (*Motacilla alba*). (Egg images by M.C. Stoddard and © the Natural History Museum, UK. Bird illustrations (not shown to scale) reproduced with permission of Lynx Edicions and drawn by I. Willis, I. Lewington, T. Worfolk, H. Burn, J. Cox and R. Hathway.)

Box 1. Egg mimicry by brood parasites.

Roughly 1% of all bird species are obligate interspecific brood parasites, laying their eggs in the nests of unrelated host species. To succeed in this trickery, some brood parasites have evolved the ability to mimic the egg colors and patterns of their target hosts. Common cuckoo (*Cuculus canorus*) females, but not males, belong to genetically distinct host races, each of which parasitizes a different host species (Figures 1E and 2). Some host species have evolved the ability to identify and remove cuckoo eggs. To deceive these hosts, cuckoos have evolved excellent egg mimicry. Other host species are poor egg rejectors, so cuckoos (for the evolutionary moment) get by without close egg mimicry. Cuckoos and their hosts are locked in a coevolutionary arms race, with each party escalating its adaptations to outwit the other. As evidence of this, some host species have evolved highly recognizable patterns on their own eggs, which act as signatures that are difficult for the cuckoo to forge. The genetics underlying egg mimicry have long been a mystery. A 2022 study of the brood-parasitic cuckoo finch (*Anomalospiza imberbis*) showed that the genes for egg appearance pass from mother to daughter on the female-specific W sex chromosome. In cuckoo finch hosts, however, egg appearance genes are inherited from both the mother and father. This added genetic diversity could help hosts stay one step ahead by creating new egg colors that are tough for the parasite to match.

camouflaged: it is tough to make the case that an American robin's (*Turdus migratorius*) bright blue eggs (Figure 1D) are well disguised. Blue eggs have long baffled biologists. One hypothesis is that blue eggs — gleaming with antioxidant-rich biliverdin — provide a signal to males about the health of his mate and future offspring, allowing him to adjust his investment accordingly. Experimental tests of this idea have received mixed support.

Egg color is also related to thermoregulation. A recent study of 634 species showed that birds tend to lay darker (typically brown) eggs in cold habitats, where dark eggs will heat up quickly and cool down slowly. Egg pigmentation might have mechanical and antimicrobial benefits, too. Beyond their role in camouflage, some eggshell patterns probably help individuals — such as common murres (*Uria aalge*) nesting on jam-packed cliff ledges — to locate their own eggs in a crowd. Finally, cuckoos and other brood parasites use egg color and pattern to mimic and deceive other birds (Figures 1E and 2), in one of nature's best examples of animal subterfuge (Box 1). Overall, colored eggshells serve many functions in modern birds, but they evolved first in non-avian theropod dinosaurs (Box 2).

Size, shape and structure

Bird eggs range dramatically in size. Although the ostrich (*Struthio camelus*) lays the largest egg of any living bird, the largest known egg — of any animal, including non-avian dinosaurs — belonged to the extinct elephant bird (*Aepyornis maximus*) and weighed a whopping 9 kilograms. Hummingbirds lay the tiniest eggs (Figure 1F), clocking in at just half a gram for some species. For the most part, small species lay small eggs and large species lay large eggs. However, an ostrich's egg is a proportionally small amount of the adult female's weight and a hummingbird egg is a proportionally large amount. Kiwis win the prize for laying the largest eggs relative to body size, with the egg weighing up to 25% of the female's body mass in some species. In general, the amount of yolk in an egg provides a clue about what kind of chicks will be born. For altricial species, wherein chicks require a great deal of parental care, the egg is about 15–20% yolk. For precocial species, wherein chicks can quickly feed themselves, the yolk content is much higher (about 35%) to support more development in the egg. In megapodes, the yolk comprises 50% or more of the egg. This is an adaptation to an extreme precocial lifestyle, as the hatchlings receive no parental care.

The shapes of bird eggs vary tremendously, from the generally round eggs of owls to the elliptical eggs of hummingbirds and the pointy eggs of many shorebirds. Many hypotheses have been proposed to explain this variation. One popular theory was that pointy eggs spin in a circle when bumped, making them less likely to topple over a cliff edge. Another was that egg shape was related to clutch size (the number of eggs laid in the nest), so that eggs of certain shapes could fit together like pieces in a puzzle and be efficiently incubated. Another idea was that egg shape was related to the amount of calcium in the diet, with round eggs requiring the least amount of shell for a given volume. To test these ideas, researchers recently examined egg shape variation across hundreds of bird species. One study found that egg shape is related to a bird's adult body size, evolutionary history and flight behavior, with efficient fliers more likely to lay asymmetric or elliptical eggs. The researchers hypothesized that adaptations for efficient flight (for example, in long-distance migrants) led to streamlined body plans (likely influencing the oviduct, abdomen or pelvis), which in turn selected for pointy or elongated eggs that could accommodate large volumes without being too wide.

Box 2. Dinosaur eggs.

Birds are living dinosaurs. Their ancestors are theropod dinosaurs, a bipedal, meat-eating group that first appeared over 200 million years ago. For over a century, scientists thought that only birds laid eggs with colorful shells. However, paleontologists recently discovered biliverdin and protoporphyrin pigments in the eggs of several non-avian theropod dinosaurs, suggesting that colored and patterned eggshells are not uniquely avian. This revelation is consistent with evidence indicating that some non-avian theropods did not bury their eggs. Instead, they laid them in partially exposed nests on the ground and probably actively incubated the clutch. Colorful eggshells would have provided camouflage from visually hunting predators. Another long-held belief was that the earliest dinosaurs laid hard, calcified shells like those of modern birds. However, a new analysis of fossil eggs belonging to *Protoceratops* and *Mussaurus* implies that the first dinosaur egg was probably soft and leathery, like those of many modern turtles. Finally, a stunning discovery in 2021 of an exquisitely preserved embryo inside an egg showed an oviraptor tucking its head in a posture previously seen only in bird embryos preparing to hatch.

Another study found that egg shape is largely related to aspects of female anatomy (such as oviduct size) and incubation conditions (such as clutch size). Overall, there is much still to learn about egg shape, across birds generally and within specific bird lineages.

The fine-scale structure of the eggshell (Figure 3) also varies across birds, although to see this requires a microscope. At the innermost part of the eggshell, there are two shell membranes (Figure 3C,D). Next comes the mammillary cone layer (where calcium carbonate crystals start to grow in conical protrusions), the palisade layer (the thickest part of the shell), the outer vertical crystal layer and finally the cuticle (Figure 3C,D). Embedded throughout the shell is a matrix of organic proteins. Tiny pores traverse the shell, allowing for transport of gases (oxygen, carbon dioxide and water vapor) (Figure 3C,D). The resulting eggshell is a remarkable material — both tough and breakable — that is of great interest to biologists, materials scientists and engineers (Box 3). Although all bird eggshells tend to have the same general architecture, there are key differences. One difference is in the shape of the pores, which appear as straight funnels in some species but are forked or branched in larger species. Branched pores might enhance gas exchange while minimizing water loss across very thick shells.

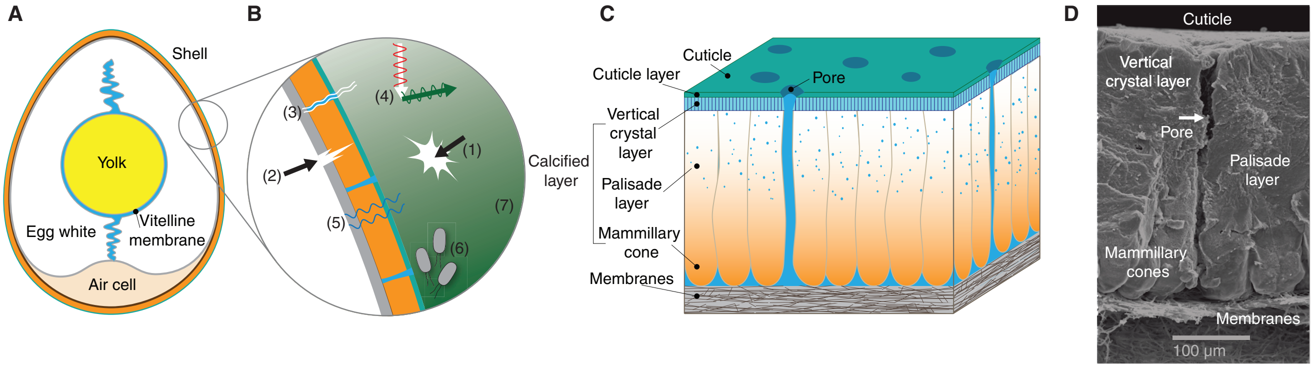
From phenotype to genotype

We have so far discussed the appearance of eggs on the inside (egg yolk, egg white, fine-scale structure of the eggshell) and the outside (color, pattern, size, shape). These are all part of the egg's phenotype — that is, its observable traits. What genes are responsible for these traits? Our knowledge of bird genes and genomes is exploding. In the last decade, the number of bird species with available reference genomes has grown from two to over 500. In addition, transcriptomics and proteomics have revealed the specific genes and their protein products that are expressed in a female bird's oviduct during egg production. Some egg genes, like those related to vitellogenin proteins associated with egg yolk, evolved early in vertebrates. These genes are retained in birds but have been lost in most mammals. Other egg genes are associated only with birds. These include genes associated with ovocalyxin-36 (an eggshell protein involved in immune response), ovocalyxin-32 (an antimicrobial protein found in the outer eggshell and cuticle), ovocleidin-17 (an eggshell matrix protein), and ovocleidin-116 (a protein involved in mineralization), as well as several ovalbumin genes encoding egg white proteins.

Some of the most exciting discoveries linking an egg's phenotype to its genotype involve color. Recent studies have identified dozens of genes, mostly in domesticated species, that are correlated with aspects of eggshell color. In chickens, blue eggshell color is associated with the gene *SLCO1B3*, the expression of which is controlled by a retrovirus inserted nearby in the chicken genome. Ducks appear to make blue eggs in a different way: in mallards, expression of the *ABCG2* gene affects blue color. In chickens, many genes influence brown eggshell color, including *ALAS1*, *CPOX*, and *FECH*, which encode proteins involved in protoporphyrin pigment biosynthesis. What genes are responsible for egg coloration in wild species? Some tantalizing clues are coming from brood parasites (Box 1), the livelihoods of which often depend on mimicking the egg colors and patterns of unrelated hosts.

Eggs in the nest

Once an egg is laid, it must develop and survive in its immediate environment. Many features of this environment, such as nest structure, altitude, clutch size, and parental behavior, have influenced the design and evolution of bird eggs. Like eggs, the nests of birds are extremely diverse. They can be simple scrapes (Figure 1B,G,H) or shallow bowls (Figure 1A,I) on the ground, cup nests in trees or bushes (Figure 1D–F), more elaborate domed or hanging nests, floating aquatic nests (Figure 1C), excavated cavities or mounds



Current Biology

Figure 3. Structure and multifunctionality of the avian eggshell.
(A) Longitudinal cross-section of an egg. (B) Diagram illustrating the many functions of the shell, including: (1) resisting mechanical damage; (2) facilitating crack propagation from the inside during hatching; (3) permitting gas (oxygen and carbon dioxide) exchange; (4) regulating thermal properties; (5) mediating water loss; (6) minimizing microbial invasion; and (7) displaying color for signaling and camouflage. (C) Schematic diagram of chicken eggshell microstructure and (D) corresponding cross-sectional scanning electron micrograph (SEM). (Figure designed by L. Li, with (A) and (C) redrawn from Hincke *et al.* (2012). SEM in (D) provided by Z. Deng.)

of decaying vegetation. One recent study of 1,350 bird species found that eggshell stiffness is correlated with nest type. Birds lay stiffer eggs in unstable nests (for example, domed or hanging nests like those of many weaverbirds and orioles), in which the eggs may be subjected to a higher risk of collision. Altitude can also influence eggshell structure. At higher altitudes, where humidity is reduced, eggshells tend to be thicker or less porous to reduce water loss.

Clutch size ranges dramatically across bird species, from a single egg (as in albatrosses, petrels and some penguins) to as many as 20 (as in some ducks and geese). Why is there such striking variation? Many factors influence clutch size, including habitat, nest type, and whether the chicks are altricial or precocial. One strong trend is that species breeding in more seasonal, northern latitudes tend to lay larger clutches because springtime bursts of food resources make it possible to support more chicks. Finally, parents at the nest exert strong control over how the egg develops. They mediate the nest microclimate (temperature and humidity) and can ward off predators. Remarkably, parents and offspring can sometimes communicate before the egg hatches. In some species, embryonic chicks produce vocalizations that cause parents to adjust their incubating patterns. In other species, offspring may even be able to learn their own species-specific songs and calls before hatching.

Box 3. Eggshell as a model for materials science research.

Materials scientists are increasingly interested in studying natural materials with desirable mechanical properties. Biological composites, which combine brittle mineral and soft organic components, fall into this category: they are stronger than the sum of their parts. Textbook examples of biological composites are nacre (mother-of-pearl), bone and tooth enamel. These materials are designed to be exceptionally tough. Avian eggshell is also a biological composite, with a small amount of organic material embedded throughout the calcium-carbonate-based shell. Unlike other biological composites, eggshell must be strong enough to resist damage from an incubating parent but weak enough to break during hatching. This paradoxical mechanical role makes eggshell a fascinating candidate for materials science research. Many human-made materials, like the glass windows in vehicles, should be resistant to external damage but breakable from the inside in an emergency. In addition, eggshell is a multifunctional, fast-forming, lightweight, breathable and dynamic material (Figure 3). Designed only to last for a short time, the shell thins as the embryo, which siphons off calcium to fuel its own bone growth, develops and prepares to hatch.

Eggs in the Anthropocene

Why should humans care about bird eggs? We are living in a geological era — the Anthropocene — of intense human activity, bringing pesticide use, climate change, and biodiversity loss. Bird eggs reveal a great deal about the health of our ecosystems because they are extremely sensitive to environmental stressors. A hallmark example of this is the devastating effect of the insecticide DDT (dichloro-diphenyl-trichloroethane) on bird eggs, described by Rachel Carson in her 1962 book *Silent Spring*. DDT caused eggshells to thin and break prematurely, leading to substantial declines in many bird populations, especially raptors. *Silent Spring* helped set off the modern environmental movement, leading to a ban on DDT in the United States and the creation of the Environmental Protection Agency. However, pesticides and pollutants are still commonly detected in bird eggs.

Climate change is also impacting bird eggs. A recent study of birds in the midwestern United States showed that some species — in response to early spring weather — are now laying their eggs almost a month earlier than they did in the late 19th century. Climate change is shifting the seasonal rhythms with which birds have evolved, potentially altering the access of birds to mates, food, and nesting sites in unpredictable ways. Habitat loss and degradation pose additional threats to birds, the numbers of which are in sharp decline. A landmark study in 2019 estimated that North American bird populations have plummeted by almost 30% since 1970.

Eggs reflect the state of our environment, but they also inspire innovation. In the 1930s, scientists discovered that vaccines could be produced in chicken eggs. Today, more than 80% of all flu vaccine in the United States is manufactured in eggs. Eggshell also has carbon-capture potential and according to a recent study can be harnessed in the production of clean hydrogen fuel. Finally, eggs affect our diets: in the United States, the average consumer ate almost 280 eggs in 2019.

Outlook

Overall, bird eggs intersect with our lives through our environment, medicine and food, but they also provide a glimpse into the dazzling variety of avian life on the planet. Natural history museums around the world house 5 million bird eggs, most of which were collected between 1890 and 1930. These collections provide valuable historical timelines, enabling the discoveries about DDT and climate change mentioned above. In addition, genetic material can now be extracted from museum eggshells: this could transform the way scientists use museum egg collections, previously thought to be unsuitable for genomic analyses. Despite extensive museum repositories, we still know very little about the eggs and nests of many species. Basic breeding biology information is completely unknown for 30% of all bird species, especially those in the Neotropics. Encouragingly, this paradigm is changing. In 2020, for example, the eggs, nest and chicks of an Andean hummingbird endemic to Peru, the white-tufted sunbeam (*Aglaeactis castelnaudii*), were described for the first time. Today, the study of bird eggs is as vibrant and multidisciplinary as ever. For students, researchers and conservationists joining this field, you have chosen well. There is still so much to discover.

DECLARATION OF INTERESTS

The author declares no competing interests.

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Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544, USA.
E-mail: mstoddard@princeton.edu

Primer

Parental care in birds

Douglas W. Mock[1,2]

Parental care, a usefully imprecise catch-all term for behaviors performed by breeding adults that benefit their offspring, is a popular research area among behavioral ecologists. Across Class Aves, it takes many forms, ranging from warming the eggs during incubation — such that the embryo develops within and eventually escapes from its protective shell — to extensive post-hatching assistance, especially by providing food but also by protecting young from weather and predators (Figure 1). In this primer, I will address the evolutionary forces likely to have shaped the peculiar avian habit of involving both parents in substantial post-fertilization investments, rather than just one. For this, I will focus on the costs, benefits, and complex social dynamics associated with elaborate parental care to show that what we may regard as the simple nuclear family (mom, dad, and a few kids) is anything but simple.

Costs and benefits of parental care

Many of these services are demonstrably costly to parental time and energy budgets, in many cases to their Darwinian fitness. For example, experimentally adding just one extra egg to the two already in common tern nests (and later removing it a day before hatching) leads to reduced food deliveries to the resident chicks. Similarly, removing the first egg in a lesser black-backed gull nest (thereby forcing the female to metabolize a replacement) results in loss of muscle mass and body condition, both of which affect survival and future breeding success.

But on the other hand, for most bird species, the value of parental care is hard to overstate. 'Altricial' young hatch in a relatively helpless state and must depend totally on adult services until they fledge and, often, well beyond departing the nest. Such hatchlings cannot see, regulate internal body temperature, or obtain food on their own. For example, a newly emerged house sparrow, already incubated for 11 days by both parents, weighs approximately one gram, and will increase its mass by 20-fold over the next 11 days. During that period, it will open its eyes, grow a full coat of plumage, and develop endothermy, transformations fueled by a diet of high protein insect prey delivered singly by parents that normally eat seeds. And that labor-intensive food supply is shared with two to four equally hungry siblings in a nesting cycle that parents repeat several times per summer.

The importance of such parental labor is easy to demonstrate. The quantity and quality of food each nestling receives affect its development and subsequent survival. For example, the body mass of chicks just prior to fledging is a powerful predictor of whether they survive to reach breeding age a year or more down the line, a relationship that has been demonstrated for dozens of different bird species.

Unlike mammals, where the task of rearing comparably needy offspring falls overwhelmingly to the parent specialized for gestation and lactation — the female parent — avian parental care is often shared more equally between the sexes and, in a few taxa, is performed exclusively by the male. This expanded male role has many implications for avian mating systems, specifically making social monogamy far more common than in any other vertebrate class.

Brood parasitism

Perhaps the easiest way to appreciate the overall costs and benefits of parental care is demonstrated by the fact that some birds have evolved tricks for stealing it from someone else. Whereas a fertilized mammalian egg implants in the uterus and extracts nutrients from the mother's blood stream throughout embryo development (gestation), the avian egg is shelled and shed less than one day after conception so that early development occurs in a nest. While incubation warmth and protection are provided by one or both of the genetic parents in most species, the trick of laying in somebody else's nest