The Genetic Inheritance of Colored Eggshells in Domestic Mallard-Derived Ducks: A Literature Review of Current Research and Historical Cultural Influences

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> "We have neglected the truth that a good farmer is a craftsman of the highest order, a kind of artist."
>
> - Wendell Berry, *The Gift of Good Land*

Interest in both duck flocks and naturally colored duck eggs has been increasing amongst farmers, homesteaders, and waterfowl enthusiasts. This increasing interest is traceable via statistics. It is estimated that there were 15 million duck eggs sold in America in 2019 (the last year for which statistics were found), with another 30 million eggs consumed from home duck flocks (King, 2020). The industry has seen a steady 5% year-over-year growth, with additional increases during the supply chain insecurities and burgeoning interest in food self-sufficiency occurring throughout the cultural shift wrought by COVID-19 (King, 2020; Mendelsohn, 2022). Niche markets for duck eggs, including on-farm sales, farmer's markets, and specialty food stores have "shown dramatic increases in recent years" (Laatsch, 2023). An informal survey of American small farmers who sell duck eggs finds that colored eggshells increase both salability and price point of duck eggs (Siggins, 2023). Further, it has been noted by producers of eating eggs that "a rainbow effect in the display carton helps spark interest" (Ussery, 2022, p. 319). This means that farms and homesteads producing naturally colored duck eggs have the potential of a higher profit margin as well as a greater volume of sales. Even more important, however, is the aesthetic beauty and genetic diversity represented by naturally colored duck eggs.

In America, 93% of the chicken eggs purchased are white. In Iran and Mexico, that number goes up to 98%.

Historical Background

Producing colored duck eggs requires genetic knowledge and applied strategy on the part of breeders, especially as the trait has been selected against for so long. While the vast majority of modern domestic ducks lay white eggs, wild ducks—including the Mallard which is the ancestor of all but one of the existing domestic duck breeds—lay blue-green eggs. (Domestic Muscovy ducks are not Mallard-derived, and their differing genetics necessitates distinct research.) The blue-green hue is a strategy of cryptic coloration used to ensure that the eggs are better camouflaged in the natural settings in which wild ducks make their nests (see Figures 1 and 2). The question therefore presents itself: why is there such a dramatic difference between the eggshell coloration of wild ducks and that of closely related domestic ducks? John Metzer, owner of Metzer Farms, one of the largest duck hatcheries and duck egg sales businesses in America, believes that domestic ducks were selectively bred for white eggs (qtd. in Ames, 2022). Cultural preference in the 1800s and 1900s is known to have favored white eggs, especially in America. The Water Fowl [*sic*] Club of America's 1913 Yearbook, speaking of Indian Runner ducks, describes the introduction of the colored egg trait as a "drawback" and goes on to explain:

> The American market demands a white egg strain, and the people introducing these crosses [back to the original bloodlines from India], should wait until such times as they could guarantee a pure white egg strain, before offering them. The people buying birds of a green egg strain are very foolish indeed, as they will find they will have very little sale for their stock or eggs. (1913, p. 29)

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Three reasons have been postulated for this historical preference for white duck eggs. First, a strong cultural association existed throughout the 1800s and 1900s in Europe and America, when most duck breeds were being selectively developed, between the color white and traits such as purity, cleanliness, and healthfulness. (*Cf*., "In Europe, traditionally [the color] white was associated more with purity and cleanliness. As an extension of this, white was associated with money and power, particularly when only the wealthy could afford to keep their clothing white. Whiteness was also associated with purity in the context of the marital ceremony, with cleanliness in restaurants, and with religion….These meanings have also long been evident in hospitals. Whiteness was important in European plague hospitals;" Bates, 2023, pp. 4-5). Second, it has been suggested that in the era before refrigeration, white eggs reflected more solar energy, absorbing less heat, and thus had a longer shelf life before spoilage. Third, Metzer theorizes that a large body size and white eggshell color may be genetically linked phenotypes, such that "certain characteristics go hand in hand with blue eggs. In other words, maybe a large body size is on the same gene as white eggs. So, as breeders selected for large body size, such as Pekin, they got white eggs" (qtd. in Ames, 2022). To this day in America, the most commonly consumed chicken egg color is white, with 93% of the market (Guyonnet, 2022). In Iran and Mexico, consumer preference is even more dramatic, as 98% of eggs consumed in those countries are white (Guyonnet, 2022). While not duck egg statistics, these data demonstrate how firmly ingrained cultural preferences can become, without the average consumer having any idea *why* they think of white eggs as the "normal" color. Despite hundreds of years of efforts to the contrary, the colored-eggshell trait has persisted in a small proportion of domestic ducks to this day. Due to the common genetic background of all Mallard-derived domestic ducks, it is possible for the occasional blue-green egg layer to appear in any Mallard-derived duck breed. But certain breeds, such as Anconas, Call Ducks, Cayuga, Indian Runners, Magpie, and Rouen are known for having a higher percentage of colored-egg layers within their gene pool, although even among many of those breeds, the most common egg color remains white. One of the primary attractors for newcomers to these breeds is the beautiful variety of eggshell colors that is possible.

Figure 1. Golf ball in wild duck nest (Otago Daily Times, 2020)

Figure 2. Wild duck eggs (Miller, 2023)

In modern times, we have moved beyond the Victorian-era preference for all things white and "pure." So why do some duck breeders still oppose the development of the colored egg trait? The Ancona breed provides an interesting example. Anconas were at the edge of extinction in the 1980s and were listed as Critically Endangered for years by The Livestock Conservancy, finally graduating down to Watch status in 2016 (Sponenberg, 2016). The professional waterfowl conservationist who saved them from extinction and wrote the current breed description, Dave Holderread, explicitly stated that Anconas were expected to lay multiple colors of eggshells: "white, tinted, blue, green, or spotted" (Holderread, 2011, p. 69). However, some modern Ancona breeders have begun to protest against colored eggs in the breed, vocally advocating for removing all non-white egg layers from the gene pool, and incorrectly implying that blue-green eggs are evidence of crossbreeding. This position is in ignorance of the fact that *all* Mallard-derived domestic ducks have the potential for colored egg genetics in their backgrounds, as descendants of Mallards which lay blue-green eggs. Assuming that some breeders may wish to encourage and increase the colored egg trait in their flock, it is important to review what is currently known about the genetic inheritance of the blue-green egg phenotype in ducks. (The genetic inheritance and physiological process of eggshell color formation is substantially different in chickens and ducks, so the existing research on chickens cannot be assumed to apply to ducks.) Oxford University recently published a comprehensive study of avian color genetics, resulting in a conclusion which seems incomprehensible in the modern era—a time when the entire human genome has been mapped and extensive genetic testing for multiple animal species can be ordered via the postal service, but yet:

> Much of avian color diversity ***remains unstudied or enigmatic*** [emphasis added] from a genetic and developmental standpoint…In spite of the taxonomic breadth and importance of bare part and egg coloration, studies of avian coloration have focused primarily on plumage coloration….The next decade promises to be a pivotal one for eggshell coloration genetics. (Price-Waldman et al., 2021, pp. 397, 406)

In other words: we still do not know all the details of eggshell coloration inheritance with certainty. What is known is that the blue-green color of duck eggshells is caused primarily by biliverdin, which is deposited throughout the eggshell while the egg is being formed in the uterus/shell gland of the duck. Fascinatingly, biliverdin has also been found in dinosaur eggs! It has been isolated from oviraptorid *Macroolithus yaotunensis* eggs, assigned to the Late Cretaceous oviraptor *Heyuannia huangi* (Wiemann et al., 2017). Other pigments at play include biliverdin zinc chelate and protoporphyrin. (The visual appearance of eggshell color and intensity may also be influenced by bloom, which is a coating deposited on top of the eggshell itself, and is able to be washed off. This is a different physiological process which does not influence the structure of the eggshell itself, and thus will not be addressed in depth here.) Liu et al. provided convincing evidence that

biliverdin is likely synthesized in erythrocytes in the uterus/shell gland. Both colored egg laying ducks and white egg laying ducks have been found to have the same concentration of biliverdin in their uterus/shell gland, but much higher concentrations have been found in the uterus fluid of colored-egg-laying ducks when compared to white egg layers (see Figure 3). In fact, when exogenous biliverdin was injected into the uterus of white egg layers, the ducks proceeded to lay blue eggs, leading the research team to conclude that, "All of our evidences pointed out that it is the biliverdin concentration in the uterus fluid that makes the difference in the eggshell color in ducks" (Liu et al., 2010, pp. 166-167). Several genes have been found which are expressed at a higher level in green egg layers as opposed to white egg layers, and they seem to deal with the production, transport, and breakdown of biliverdin (Price-Waldman et al., 2021; Bai et al., 2019). Another Chinese study found that large numbers of genes, as well as epigenetic factors, contribute to egg shell coloration:

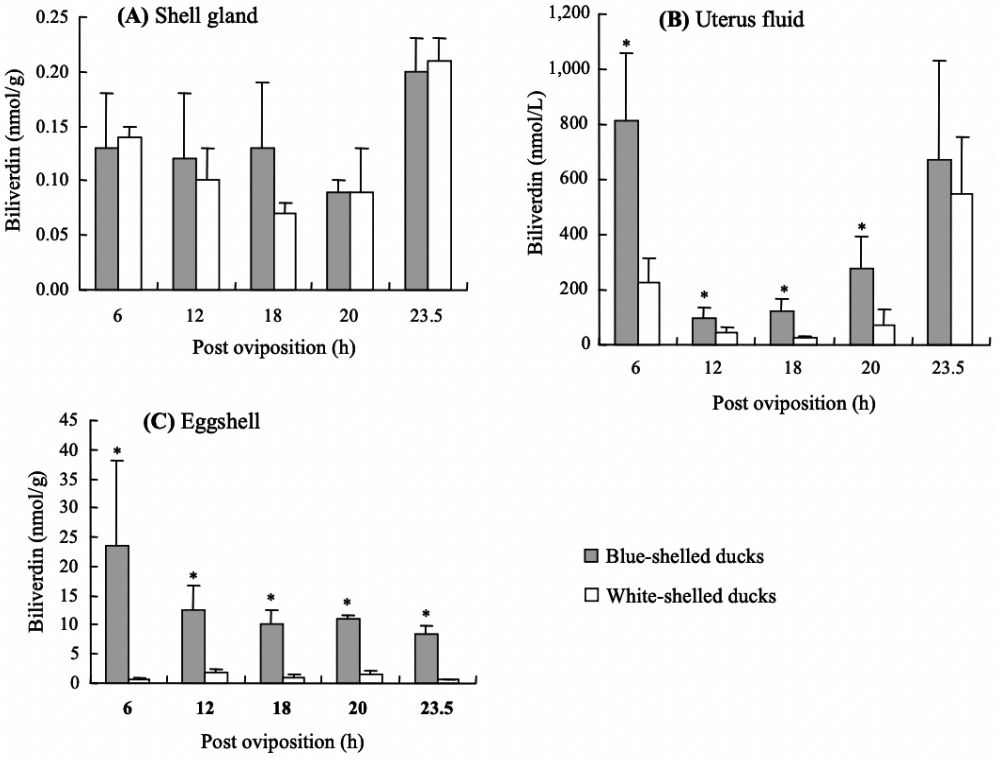
> The green eggshell color produced by ducks is a threshold trait that can be influenced by various factors, such as hereditary, environment and nutrition….A total of 31 differentially expressed miRNAs were found between ducks laying green eggs and white eggs…..Compared to ducks that lay white eggs, ducks that lay green eggs include six up-regulated miRNAs that had regulatory effects on 35 down-regulated genes, and seven down-regulated miRNAs which influenced 46 up-regulated genes. (Xu et al., 2018, p. 1)

The durability of the biliverdin-pigmented eggshell trait across species and over time frames measured in epochs, as well as the large number of genes involved, demonstrate the complexity—and arguably the genetic importance—of the trait.

"Much of avian color diversity remains unstudied or enigmatic"
– Oxford University

Literature Review

While it has been demonstrated that the base color of egg a duck lays will not change throughout her life, the intensity of the eggshell color may be related to diet and health of the duck. Biliverdin pigment is an antioxidant, and as such "possesses important physiological properties. It is a potent in vitro anti-viral and free-radical scavenger, and…mediates immunological responses in mammals" (Morales et al., 2011). Another study postulates that "deposition of biliverdin into eggshells may be costly to mothers due to depletion of their antioxidant reserves" (Butler & McGraw, 2013). The study demonstrated that female ducks supplemented with dietary antioxidants/carotenoids (namely, Kemin's ORO GLO, a marigold flower extract) laid "eggs with more biliverdin-rich eggshells" and that ducks with "higher circulating carotenoid levels at the time of egg laying produced more biliverdin-rich eggshells" (Butler & McGraw, 2013, p. 1). Intriguing suggestions have been made that there is a survival advantage to embryos hatched from biliverdin-infused eggshells, due to the multi-factorial protective properties of biliverdin (Hanley, 2020). This indicates that a mother's body which is replete with nutrients and antioxidants may be able to spare more antioxidants (namely, biliverdin) for the creation of eggshells to protect her offspring and increase the survival rates of her young.



The contents of biliverdin in the shell gland (A), uterus fluid (B) and eggshell (C) at various time points post oviposition for blue-shelled and white-shelled ducks. The bars and whiskers indicate mean±SD. * Significantly different between blue-shelled and white-shelled ducks at same hour post oviposition, $p<0.05$.

Figure 3. Biliverdin concentration in shell gland, uterus fluid, and eggshell for blue-shell-laying ducks and white-shell-laying ducks (Liu et al., 2010, p. 164)

Practical Application

The preceding literature review shows that there is still much that is yet unknown about the genetic details of eggshell color inheritance. But when it comes to practical inheritance, blue-green eggshell coloration (*G+*) in domestic ducks is known to be an autosomal dominant trait, meaning that both males and females inherit and pass on the genes controlling eggshell coloration. However, while it is not sex-linked, it *is* sex-limited, meaning that the phenotype can only be expressed by the females, making breeding selections complex, "awkward," and "difficult to investigate" (F. M. Lancaster qtd. in Ashton, 2023). Test-breeding with homozygous white egg layers (*g/g*) may be used to identify the genotype of a male, but properly collecting the data requires that many of the resultant female offspring must be grown out to maturity, in order to observe the color of eggs laid by each. When the dozens of genes controlling eggshell coloration are simplified, the colored egg gene is the dominant allele. Seeing that the recessive phenotype (in this case, white eggs) is most common in domestic ducks is a fascinating testament to how long and how thoroughly the white eggshell trait has been preferred and selected for. Knowing that colored eggshells are dominant is advantageous for breeders wishing to increase this trait in their flock. However, it also means the recessive white egg phenotype may "pop up" at any time. Even if a female duckling is hatched from a colored egg-laying female duck (*G+/g*) mated to a drake hatched from a colored egg (*G+/g* or *g/g*), that duckling may still grow up to lay white eggs, due to the potential combining of unexpressed recessive genes (see Figure 4). Because of this complexity, developing a flock that lays primarily blue-green eggs may take years of selective breeding. However, with intentional management, every year the percentage of blue-green egg layers will increase. In support of breeders with just this goal, it would be valuable for a research institution

with a robust veterinary genetics department to begin to offer genomic testing for ducks, including testing of eggshell color polymorphisms. Cornell University's Duck Research Lab, U.C. Davis' Veterinary Genetics Laboratory, and Iowa State University's Poultry Research Farm are all well-regarded institutions that could be contacted in pursuit of this goal.

There may be a survival advantage for embryos hatched from biliverdin-infused eggshells.

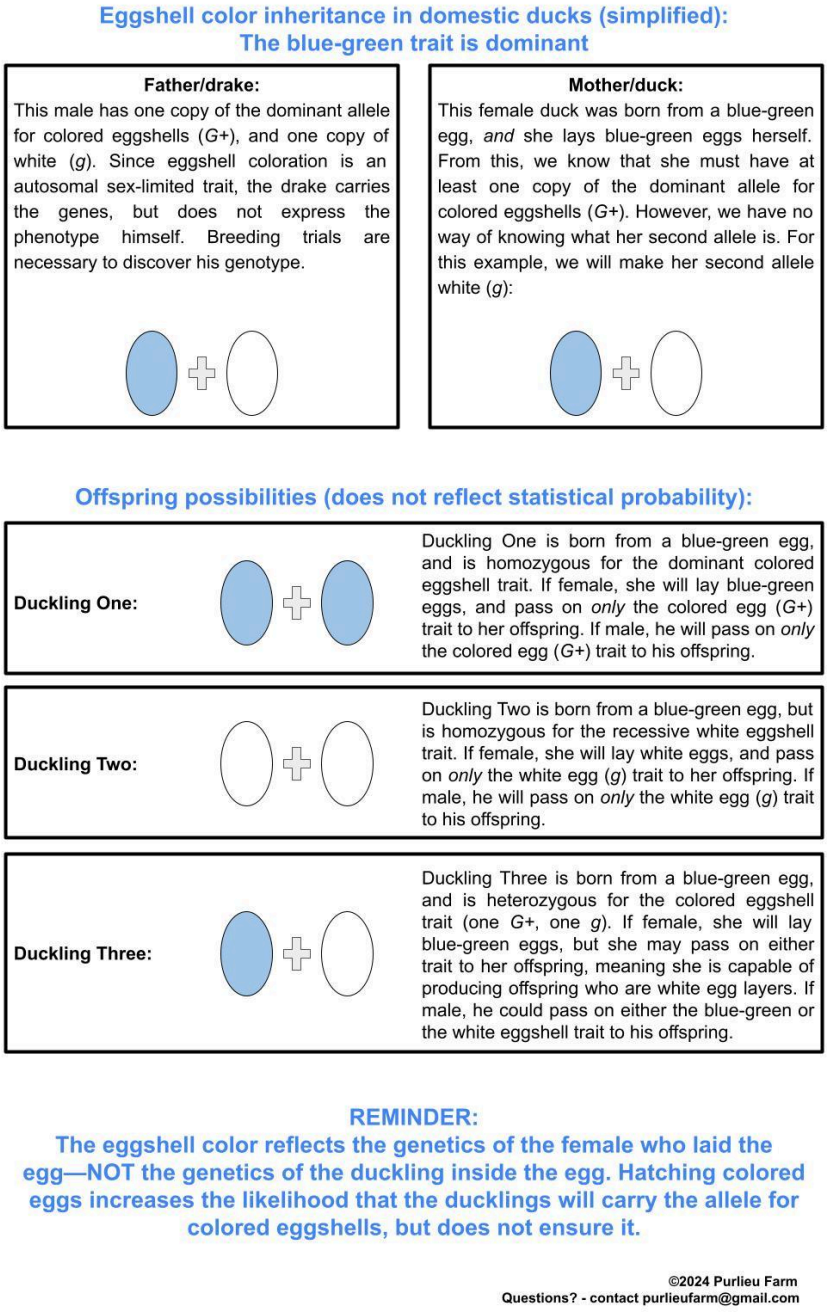


Figure 4. An example of eggshell color inheritance in domestic ducks (Siggins, 2024)

“Green eggs are fun”
- Dr. Carol Deppe

The potential advantages of colored duck eggs to the fancier or breeder, however, vastly outweigh the efforts involved. In addition to the opportunity to foster beauty and preserve diverse genetics, there is the excitement and joy that colored eggs may engender in those who see them. Dr. Carol Deppe, a genius plant breeder with a PhD in Genetics from Harvard University, explains why she selects for colored eggs in her Ancona ducks: “Many of my strain lay green eggs….I've also selected so as to increase the proportion of layers of green eggs. Green eggs are fun, and having at least some of them in each dozen makes the eggs more distinctive when it comes to sales” (Deppe, 2009). The aesthetic appeal speaks for itself, as Figures 5-7 demonstrate.

Figure 5. Multi-colored Ancona duck eggs from Nantahala Farm (Shirley, n.d.)

Figure 6. Blue, pink, white, and cream Ancona duck eggs from Green Herbs Homestead (Rothrock, 2024)

Figure 7. Multi-colored Ancona duck eggs from Nantahala Farm after washing (Shirley, n.d.)

Firmly entrenched consumer preference in many countries shows: as long as consumers believe that chicken eggs can only be white, they don't even think of looking for alternative colors. But as breeders and waterfowl enthusiasts, we can reject the Victorian fallacy that only white eggs are pure and embrace the beauty of colored duck eggs. I concur with Oxford University's prediction that the next decade will be pivotal for new research which will increase our understanding of eggshell coloration genetics. In the meantime, consider embracing the role of citizen-scientists and conservation breeders, and encouraging colored-egg layers—the genetic diversity and health of your flock may benefit, and the beauty of your egg baskets and cartons will assuredly increase.

I welcome questions, feedback, or suggestions from SPPA's readership.

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