REVIEW

Bird Eye Color: A Rainbow of Variation, a Spectrum of Explanations

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Abstract

Birds display a rainbow of eye colors, but this trait has received relatively little study compared to plumage coloration. Avian eye color variation occurs at all phylogenetic scales: it can be conserved throughout whole families or vary within a single species, yet the evolutionary importance of eye color variation within species and across the avian phylogeny is also understudied. Here, we provide an overview of eye color variation in birds, summarizing the state of knowledge about its causes at three primary levels: mechanistic, genetic, and evolutionary. Mechanistically, we show that common avian iris pigments include melanin and carotenoids, which also play major roles in plumage color, as well as purines and pteridines, which are found as pigments primarily in non-avian taxa. Genetically, we examine known associations between genes and eye color, primarily identified from classical breeding studies and recent genomic work in domesticated species. Finally, from an evolutionary standpoint, we present and discuss several hypotheses explaining the adaptive significance of eye color variation. Many of these suggest bird eye color plays an important role in intraspecific signaling, particularly as an indicator of age or mate quality, although the importance of eye color may differ between species and few evolutionary hypotheses have been directly tested. We suggest that future studies of avian eye color should focus on all three levels, including broad-scale iris pigment analyses across bird species, genome sequencing studies to identify loci associated with eye color variation, and behavioral experiments and comparative phylogenetic analyses to test adaptive hypotheses. By examining these proximate and ultimate causes of eye color variation in birds, we hope that our review will spur future research to understand the ecological and evolutionary significance of this striking avian trait.

Keywords: birds, coloration, eye color, genomics, iris, pigments, pteridines, signaling

Lay Summary:

- Birds can have a wide range of different eye colors, and eye color varies between and within species.
- We summarize what is known about the causes of bird eye color variation at different levels, from pigments to genetics to ecology.
- Many distinct pigments and structures in bird irises are responsible for coloration, and in most species these elements have not been studied.
- A small number of genes have been linked to bird eye color, mostly in pigeons and other domestic birds.
- Brightly colored eyes may be commonly used by birds in signaling and courtship.
- Associations between eye color and habitat, vision, foraging, and camouflage have been proposed but have yet to be conclusively demonstrated.
- We suggest avenues for future research on bird eye color: there is much still to be learned.

Introduction

Birds display an incredible variety of colors and patterns, which have given them a central role in the study of evolution during the past two centuries (Wallace 1870, Darwin 1871, Mayr 1942). Unsurprisingly, the primary focus of many studies has been the ecological and evolutionary underpinnings of bird feather colors. However, plumage is not the only facet of bird color variation: birds also display a myriad of eye colors, and avian eye color diversity has been largely overlooked by researchers. As a result, the factors that have generated this rainbow of irises, from chemical to genetic to evolutionary, remain poorly known.

In this paper, we review the current state of knowledge on bird eye color variation, including past advances and future directions. We begin by giving an overview of the eye colors found in birds, describing their relative prevalence, and explaining how they vary at phylogenetic and intraspecific scales. Then, we explore three distinct aspects of the question "why do birds have different eye colors?". From a mechanistic perspective, we discuss the wide array of pigments and structures that give bird irises their coloration. From a genetic perspective, we review the nascent field of avian eye color genomics, and we offer hypotheses about the largely unknown set of genes and regulatory elements that influence those pigments and structures. Finally, from an evolutionary perspective, we summarize ideas regarding how selective pressures, as well as stochastic drift, have shaped patterns of eye color variation across the bird phylogeny. These causes of eye color variation, from proximate to ultimate, are fully interlinked: the array of colors we observe are the result of light interacting with pigments or structures in the iris, the development of these pigments and structures is controlled by genomic loci, and these loci evolve over time due to selection and drift. At all three levels, we summarize existing knowledge, identify unexplored questions, suggest new hypotheses, and offer suggestions regarding future directions of research.

Bird Eye Color Variation

The Colors of Bird Eyes

The variety of hues found in the irises of birds is dazzling – Figure 1 displays a sample. The Birds of the World database (Billerman et al. 2022) includes eye color descriptions that range from the mundane ("dark brown") to the improbably colorful: including "vivid emerald green" (Black-and-red Broadbill, *Cymbirhynchus macrorhynchos*), "sapphire-blue" (Wattled Broadbill, *Sarcophanops steerii*), and "scarlet to crimson" (Bronzed Cowbird, *Molothrus aeneus*) (Ellison and Lowther 2020, Kirwan et al. 2021, Bruce 2021).

Figure 1- A sampling of the diversity of colors and patterns of bird irises. Species pictured are as follows. *First row*: a) Yellow-bellied Tanager, b) Red-throated Loon, c) Bank Cormorant, d) Short-eared Owl, e) Spot-billed Toucanet, f) White Ibis; *Second Row*: g) Three-streaked Tchagra, h) Crested Guan, i) Black-capped Donacobius, j) Sharp-shinned Hawk, k) Red-breasted Toucan, l) Crested Oropendola; *Third row*: m) Red-tailed Hawk, n) Great Antshrike, o) Painted Buttonquail, p) Wire-tailed Manakin, q) Double-crested Cormorant, r) Pink-necked Green-Pigeon; *Fourth row*: s) Greater Roadrunner, t) Black Rail, u) Eurasian Eagle-Owl, v) Acorn Woodpecker, w) Brandt's Cormorant, x) Satin Bowerbird. Photographs used with permission, by Oscar Johnson (a, n), Bryan Calk (b), Peter Ryan (c), Mark Schultz (d), Caio Brito (e, k), Shannon O'Shea (f), Ngulia Ringing Project (g), Marquette Mutchler (h, i, p, v), Mason Maron (j, m), Nathan Rupert (l), Ramit Singal (o), Timothy Krieder (q), J.J. Harrison (r), Nathan Dubrow (s), westshorewalk22 on Flickr (u), Sharif Uddin (w), and Terence Alexander (x).

A small number of authors have attempted to catalog and summarize the diversity of eye colors across birds. One broad pattern that is apparent from these studies is that the majority of bird species have “dark” eyes – brown or black. On the whole, bright irises are less common in birds than in some other vertebrate groups: Worthy (1997) found birds to have darker eyes on average than mammals, reptiles, or amphibians. Worthy (1997) created an index to quantify iris coloration from descriptions in the literature, placing over 5,000 bird species into one of five categories of eye darkness. Using this method on passerines (n=2,587), 64% fell into the darkest two categories, corresponding to brown and black; 19% were placed in an intermediate category that encompassed red, reddish-brown, and light brown; and 17% fell into the lightest two categories, which included yellow, orange, white, pink, blue, and light gray (Worthy 1997). Non-passerines (n=2,724) had lighter eyes on average than passerines (40% dark, 22% intermediate, 38% light), so the overall tallies in the database were 52% dark, 20% intermediate/red, and 28% light (Worthy 1997).

Similar results were reported by Craig and Hulley (2004), who compiled two large datasets of passerine eye colors, one of which included species from five biogeographic regions (n=1,654) and the other of which included species from ten large passerine families (n=1,143). The prevalence of dark-eyed species in these datasets was approximately 82% and 71%, respectively, while the remaining 18-29% of species had light or colorful irises. When Craig and Hulley (2004) further subdivided species in the passerine family dataset between those with red eyes and those with “pale” eyes – the latter group included yellow, white, and blue – approximately 9% of the total were red-eyed and 19% were pale-eyed. These numbers match closely with the data reported by Worthy (1997), especially considering that species in Worthy’s intermediate bins would have been sorted into either ‘red’ or ‘dark’ categories by Craig and

Hulley. A recent study by Davis and Clarke (2022), using data from illustrated plates, found that 16.7% of non-passerines (671 of 4022 species) have yellow, orange, or red eyes, which is broadly consistent with the findings of Worthy (1997) and Craig and Hulley (2004), but because David and Clarke's classification scheme did not group white-eyed species with red- and yellow-eyed species, their results are not directly comparable.

Although the majority of bird irises are shades of brown, black, white, yellow, orange, or red, rarer colors account for some of the most striking bird eyes. For example, the eyes of the Satin Bowerbird (*Ptilonorhynchus violaceus*) are purple-blue, those of the Philippine Green-Pigeon (*Treron axillaris*) are a bright turquoise, and other green-pigeons in the genus *Treron* have bicolored irises of magenta and cobalt (Goodwin 1977, Baptista et al. 2020a, b; Frith and Frith 2020a, del Hoyo et al. 2020a). At the family level, cormorants (Phalacrocoracidae) are particularly notable for their array of colorful eyes, including shades of red, green, and blue (Orta 1992).

Multicolored Irises and Iris Patterns

Multicolored eyes – where color differs between the center of the iris (peripupillary zone) and the periphery – are not uncommon, but they are often relatively subtle. For example, the eyes of Rock Pigeons (*Columba livia*) shift peripherally from yellow to red-orange (Hollander and Owen 1939b, Oehme 1969, Maclary et al. 2021) while Boat-tailed Grackles of the nominate subspecies (*Quiscalus major major*) often have irises that are brown around the pupil and transition into cream-yellow at the outer edge (Pratt 1974). Other species have more dramatically bicolored eyes, including the Greater Roadrunner (*Geococcyx californianus*), with a light ring around the pupil set against an otherwise dark iris (Hughes 2020), and a subspecies of Andean Cock-of-the-Rock (*Rupicola peruvianus sanguinolenta*), which has sharply divided yellow-and-red irises (Ridgely and Tudor 1994, Snow 2020). One unusual iris pattern observed in a few species – notably the Common Myna (*Acridotheres tristis*) and Three-streaked Tchagra (*Tchagra jamesi*) – consists of a ring of light spots or "stars" against a dark background (Feare et al. 2015, Craig 2021). Probably the most striking examples of multicolored eyes in birds are the dramatic blue-and-yellow sharply radially bicolored eyes of some birds-of-paradise in the genus *Parotia* (Bond 1919, Frith and Frith 2020b).

Multicolored eyes that are not radially symmetrical are uncommon in birds, but asymmetrical eyes have been observed in at least ten families (Ryan 2013, Gutiérrez-Expósito 2019, Cardilini et al. 2022). Some examples include several species of toucanets in the genus *Selenidera*, which have chartreuse eyes with darker sections on either side of the pupil (van Perlo 2009, Gutiérrez-Expósito 2019, del Hoyo et al. 2020b, Short 2020, Short and Kirwan 2020, Pearman and Areta 2021), and buttonquails (*Turnix*), which have a "dark crescent" on the lower edge of the pupil (Gutiérrez-Expósito 2019). Similarly, female oystercatchers (*Haematopus*) of multiple species have dark "eye flecks" adjacent to one side of the pupil, giving it a "keyhole-shaped" appearance (Guzzetti et al. 2008, Gutiérrez-Expósito 2019). In these cases, the shape of the pupil itself does not change – the vertical slit pupils of skimmers (*Rynchops*) (Zusi and Bridge 1981) and the square pinhole pupils of some penguins (Martin 1999) are the only non-circular avian pupils (Ryan 2013, Banks et al. 2015). The Bank Cormorant (*Phalacrocorax neglectus*) shows an astonishing "sunset" iris pattern with the eye horizontally bisected into an orange upper portion and a teal lower portion (Cooper 1985, Ryan 2013, Orta et al. 2020).

The Phylogenetic Scale of Eye Color Variation

Interspecific variation in bird eye color occurs at all phylogenetic scales: in some cases eye color is preserved across large clades, while in others it varies between closely-related species. There are several families composed entirely of species with dark eyes, but the reverse is not true: the only large family in which the vast majority of species are light-eyed is the Ardeidae (herons, bitterns, and egrets) (Hancock and Eliot 1978). Worthy's (1997) database of eye colors gives average darkness values for each family surveyed: the darkest-eyed families (minimum 15 species surveyed) are the Apodidae, Trochilidae, Scolopacidae, Hirundinidae, and Caprimulgidae, while the lightest-eyed families are the Ardeidae, Otididae, and Accipitridae. Worthy's (1997) averages for all families can be found in Supplemental Appendix 1a. On the whole, a greater proportion of passerine species have dark eyes than non-passerines, including largely or entirely dark-eyed families such as the Parulidae, Alaudidae, and Rhinocryptidae (Worthy 1997, del Hoyo et al. 2017). The passerine families with the lightest average eye colors include the Sturnidae, Acanthizidae, and Pipridae (Worthy 1997, del Hoyo et al. 2017).

Changes in eye color are often consistent with phylogenetic relationships. For example, the deepest splits within the Hirundinidae and Turnicidae divide them into light- and dark-eyed groups, and the same is largely true, with few exceptions, of the Alcidae and Platysteiridae (Debus 1996, Nettleship 1996, Turner 2004, Sheldon et al. 2005, Pereira and Baker 2008). Similarly, the jay genus *Cyanocorax* is polyphyletic and should be split into two genera, one of which is mostly light-eyed and the other dark-eyed (Bonaccorso et al. 2010). At shallower phylogenetic scales, eye color corresponds to the genetic structuring within the Tawny-crowned Greenlet (*Tunchiornis ochraceiceps*) cryptic species complex (Buainain et al. 2021). And what was thought to be intraspecific variation in eye color of Cream-vented Bulbuls (*Pycnonotus simplex*) on Borneo was found to indicate the presence of a cryptic species, the newly described Cream-eyed Bulbul (*Pycnonotus pseudosimplex*) (Shakya et al. 2019).

Conversely, within certain families and genera, eye colors change rapidly over evolutionary time and appear disconnected from phylogeny. Families that show frequent changes in eye color, even between closely related species, include the Anatidae (Carboneras 1992) Icteridae (Jaramillo and Burke 1999, Powell et al. 2014), Sturnidae (Sweijd and Craig 1991, Craig and Hulley 2004, Craig and Feare 2010) and Pycnonotidae (Fishpool and Tobias 2005). Within these families, genera with a high degree of eye color variability include *Aplonis* (Craig and Feare 2010) and *Aythya* (Carboneras 1992), which each consist of species with white, yellow, red, or brown eyes. Additional genera that show notable variation in eye color are listed in Supplemental Appendix 1b. Studies of clades such as these are likely to yield numerous insights into the factors affecting eye color variation.

Variation in Eye Color Within Species

Thus far, we have focused on variation in eye color between bird species, but eye colors also vary within species. Intraspecific eye color variation is often attributed to differences in age, sex, or geography and is sometimes associated with season, mood, or simply individual variation within a population. Numerous examples of within-species eye color variation are given in Supplemental Appendix 2.

Negro et al. (2017) were among the first researchers to compile a partial database of within-species eye color variation in birds, and in this dataset variation due to age was most common. Specifically, Negro et al. (2017) gave 58 examples of age-related eye color change within bird species, and others have identified a number of additional examples (Trauger 1974, Yunick 1977, Hudon and Muir 1996, Leukering 2000, David et al. 2013, Eitniear 2018, Passarotto et al. 2020, Polakowski et al. 2020). Based on these studies, it seems that age-related eye color variation is ubiquitous in birds. Generally, in species with light eyes, the typical direction of change is from dark to light (Negro et al. 2017); in species with dark eyes the changes are less conspicuous but include shifts from chestnut to rufous or from gray to brown (Yunick 1977, Leukering 2000, Cueva 2018, Polakowski et al. 2020). Outside of these general patterns, some species exhibit different eye color shifts: Osprey (*Pandion haliaetus*) have orange eyes as juveniles that turn yellow as adults, many species of *Accipiter* have yellow eyes that change to red as they age, and Common Goldeneye (*Bucephala clangula*) transition through a brief stage of blue between their dark juvenile and yellow adult eye colors (Snyder and Snyder 1974, Nelson 1983, Rosenfield et al. 2003, Negro et al. 2017, Bierregaard et al. 2020). It has also been noted that females of certain species undergo age-related eye color changes at slower rates than males (Snyder and Snyder 1974, Picozzi 1981, Newton and Marquiss 1982, Scholten 1999). The developmental processes that result in age-related eye color changes are poorly understood because they have been examined only in a small number of species (Bond 1919, Andrews and Naik 1965, Oehme 1969, Sweijd and Craig 1991); we describe the current state of knowledge below.

Sexual dimorphism in eye color also exists, and although sexually dimorphic eyes may be less prevalent than sex-related differences in plumage, the differences can be dramatic. Negro et al. (2017) identified 24 species exhibiting sexual dimorphism in eye color using the database described above; far more presumably have not been formally described or compiled. Given the data that do exist, there does not appear to be a consistent relationship between eye color and sex across birds: for example, both storks of the genus *Ephippiorhynchus* have yellow eyes in females and dark eyes in males (Elliott et al. 2020, Gula 2021), while the reverse is true in the Brewer’s Blackbird (*Euphagus cyanocephalus*) (Hudon and Muir 1996, Jaramillo and Burke 1999) (see Supplemental Appendix 2a for further examples).

In a few species, seasonal changes in eye color also occur, typically resulting in brighter eye colors during the breeding season (see Supplemental Appendix 2b for a partial list). For example, reddening of the iris during peak breeding season has been reported in numerous herons and egrets (Hancock and Eliot 1978, Menkhorst et al. 2017). Similarly, Brown Pelican (*Pelecanus occidentalis*) irises change from brown during the non-breeding season to light blue during the pre-breeding period until incubation (Schreiber et al. 1989). This type of seasonal change in eye color seems to occur primarily in groups, such as pelicans and herons, in which species commonly show seasonal variation in the colors of other bare parts, such as facial skin or legs (Hancock and Eliot 1978, Elliott 1992, Martinez-Vilalta and Motis 1992). In herons, the increased redness of the iris during the breeding season may be caused mechanistically by changes in blood suffusion, while the mechanism underlying eye color changes in pelicans is less clear. In chickens, eye color may change in egg-laying females because the demands of yolk production reduce the carotenoids available for iris coloration (Smyth 1990). With closer study, seasonal variation in eye color may prove to be more widespread in birds, particularly among species where the changes are subtle (Kaufmann 1983, Filchagov 1993, Feare et al. 2015).

Outside of seasonal changes, more rapid temporal changes in bird eye color are possible in some taxa. The eye colors of some species result from the preponderance of blood vessels in the iris, and individuals can change the shade of their iris according to mood or behavior by altering the amount of blood flow to the region, as seen in Inca Doves (*Columbina inca*) (Chiasson and Ferris 1968, Chiasson et al. 1968, Ferris and Bagnara 1972), Black-bellied Starlings (*Lamprotornis corruscus*) (McCulloch 1963, Britton and Britton 1970, Chittenden and Myburgh 1994), and Red-billed Oxpeckers (*Buphagus erythrorynchus*) (Raijmakers and Ellmer 2009). Other species are able to rapidly change the apparent color of their iris by expanding or contracting it to accentuate differently colored regions (McIlhenny 1934, 1937; Craig 2021). This behavior reaches its apex in the parotias, where some species (including Lawes's Parotia, *Parotia lawesii*) can change the appearance of their radially bicolored iris from entirely blue to entirely yellow at a specific moment during their mating display – a remarkable phenomenon that warrants greater study than it has received (Bond 1919, Cordey 2019, Frith and Frith 2020b, c; Frith et al. 2020).

Heterochromia iridis, in which the two irises of a single individual are different colors, has also been reported in several species of birds but seems to be uncommon (Poor 1946, Ryan 2013, David et al. 2013, Ruiz-Esparza et al. 2017, Kinney et al. 2017). However, a study of Common Cuckoos (*Cuculus canorus*) found a consistent tendency for the left eye to have more extensive dark flecking than the right eye (Yoo et al. 2017) – although the mechanism and significance of this tendency is unknown – and few studies have sought to quantify these types of differences.

Not all intraspecific eye color variation can be attributed to differences in age, sex, season, or mood. Just as geographic plumage variation exists between populations and subspecies of a single species, there can also be within-species geographic variation in eye color. In Supplemental Appendix 2c, we give many examples of intraspecific geographic eye color variation, which demonstrates that eye colors can change on short evolutionary timescales. In some cases, closely-related populations that differ in eye color have been elevated to species rank: examples of sister species pairs with different eye colors are listed in Supplemental Appendix 1c.

Less common among birds are eye color polymorphisms that exist within populations. Negro (2017) argued that these types of polymorphisms are essentially absent in wild birds, but several potential examples of population-level iris color variation exist (see Supplemental Appendix 2d). Populations with variable eye color may also exist in contact zones when subspecies or sister species of differing eye color hybridize or intergrade (Megna et al. 2014, Canton 2014, Anderson 2015). However, it is often difficult to verify that eye color variation does not result from differences in age, seasonality, or other extrinsic factors, particularly given that some age-related variation in eye color may be complex and can occur among adults of varying ages (Trauger 1974, Scholten 1999, Rosenfield et al. 2003). For example, age rather than population-level polymorphism has been used to explain the high degree of variation in eye color among adult giant-petrels (*Macronectes*) (Warham 1962, Carboneras et al. 2020). Likewise, it can be difficult to distinguish between discrete morphs and continuous variation when studies are small, so further research on this subject is greatly needed.

Future Work: Characterizing Bird Eye Color Variation

The ease of preserving bird feathers and their colors by preparing study skins has been a tremendous boon to the study of avian coloration. Unfortunately, that advantage does not exist for studying eye color, because irises are not typically preserved during the preparation of traditional study skins. Researchers interested in studying this phenotypic trait are in a situation more like that of museum ichthyologists and herpetologists whose objects of study lose their color on museum shelves. Fortunately, iris color and the colors of other bare parts are now commonly noted on the tags of modern museum specimens, providing a wealth of data. However, these descriptions are usually subjective because there is no standardized system in broad use for describing eye color, rendering tag data difficult to compare. For example, we examined tags of 34 specimens of White-eyed Stipplethroat (*Epinecrophylla leucopthalma dissita*) in the collection of the LSU Museum of Natural Science and found 23 different eye color descriptions, which would complicate any attempt to examine variation associated with age, sex, or geography. Taking color-standardized photographs of irises and other bare parts in-life or immediately post-mortem when collecting specimens would greatly improve our simple descriptive knowledge of avian eye color. These photographs could then be archived and associated with the specimen as part of its database record (Webster 2017).

The wealth of photographs available through eBird, iNaturalist, Wikiaves, and other databases also holds great promise for helping to understand variation in eye color among and within species. Even photos taken in highly heterogeneous light environments can provide usable data to understand geographic variation in eye color, as demonstrated by a recent study on White-browed Scrubwrens (*Sericornis frontalis*) (Cake 2019). However, subtle intraspecific variation in eye color can probably be best identified via standardized photographs of birds in the hand (Cardilini et al. 2022).

There likely remains a significant amount of intra-specific variation that has not yet been characterized. And, careful investigations have revealed new patterns, like consistent heterochromia and seasonal variation, even in common and well-studied species (Feare et al. 2015, Yoo et al. 2017). As demonstrated by the case of the Cream-eyed Bulbul (Shakya et al. 2019), where an eye color difference was a clue to the existence of a cryptic species, this underappreciated variation can be indicative of larger patterns. The question “what color eyes does this species have?” may seem simplistic, but there is value in having a clear answer for all bird species and populations. Simply paying greater attention to this trait will likely reveal new insights.

The Mechanistic Basis of Eye Color Variation

The proximal cause of eye color variation in birds is the presence of different pigments and structures in the avian iris that reflect and absorb light. The mechanistic aspects of bird eye coloration are perhaps better understood than more ultimate causes (the genetic and evolutionary drivers of variation), but even these mechanistic underpinnings are highly complex and poorly known. The mechanisms that affect iris coloration in birds are markedly different from those that affect feather coloration, which have been studied much more extensively. In addition to melanins and carotenoids, which can also affect plumage color, purine and pteridine pigments are major components of iris coloration in birds, and in some species blood vessels, colorless oil droplets, collagen fibers, and other structural features can play a role in determining eye color (Oehme 1969, Oliphant 1987a). Several of these factors, particularly the role of purines and pteridines, are reviewed extensively in Hill and McGraw (2006).

Beyond the distinct chemicals involved, iris color is unique in birds because it is produced by living pigment cells, known as chromatophores, rather than by pigments deposited into non-living keratinous feathers (Oliphant et al. 1992). An array of pigment cells types are found in the integument of fishes, reptiles, and amphibians, but in birds these pigment cells are limited to the iris and the melanocytes of the dermis (Oliphant et al. 1992). The presence of non-melanocyte chromatophores makes the iris a unique and distinctive element of bird coloration.

Chromatophores are often categorized based on their coloration as xanthophores (yellow), erythrophores (red), leucophores (white), and iridophores or guanophores (reflective) (Bagnara 1966, Fujii 2000, Kimura et al. 2014). However, these general classifications do not distinguish between the types of pigments present within each cell (Bagnara 1966, Oliphant and Hudon 1993), and additional terms exist to describe pigment cell types that do not fit neatly into these traditional categories (e.g. "reflecting xanthophore") (Tillotson and Oliphant 1990). Here, we will simply refer to bird irises and their pigment cells by the pigments or structures that they contain and the colors that these pigments and structures produce.

History of Bird Iris Pigmentation Research

During the early 20th century, researchers began to examine avian irises to identify the pigments and structures generating coloration. Most notable among these was Bond (1919), who carefully examined the histology of irises in a variety of domestic fowl and pigeon breeds as well as some wild species. However, Bond did not attempt to separate or identify specific pigments involved in iris coloration. This subsequent work was undertaken by Hollander and Owen (1939a, b), who determined that the yellow coloration of chicken irises is caused by carotenoids, while the orange iris coloration of domestic pigeons results from a different type of non-carotenoid pigment. It was not until the late 1960s that a more complete picture began to form, thanks to the monumental work of Oehme (1969), who examined iris structures and pigments from approximately 150 bird species while working at the Berlin Zoo. Oehme categorized iris coloration into 32 distinct categories based on the types and arrangements of pigments and structures involved. He noted that: dark melanin pigments in the iris are ubiquitous across bird species, carotenoids are present but only in particular taxonomic groups, blood vessels can frequently color or tint eyes red, and structural coloration in the iris can produce blue or white colors without pigments. Most notable was Oehme's recognition – similar to Hollander and Owen's findings in pigeons – that light irises are frequently the result of reflecting or light-colored crystalline substances, which he suggested were pteridines.

During the 1970s-1990s, bird eye color research focused on these light-colored pigments, beginning with Ferris and Bagnara's (1972) work on doves and including many papers by

Oliphant and collaborators in a variety of species (Oliphant 1981, 1987b, a, 1988; Oliphant and Diocee 1982, Tillotson and Oliphant 1990, Oliphant et al. 1992, Hudon and Oliphant 1995, Hudon and Muir 1996). This body of work demonstrated that there are actually two related classes of pigments, pteridines and purines, that are found in an array of bird species and often occur together in light irises to form colored or colorless light-reflecting structures. The use of novel high performance liquid chromatography techniques allowed Hudon and Muir (1996) to identify and quantify the concentrations of four specific purine and pteridine pigments in the irises of New World Blackbirds, demonstrating that variation in the concentrations of these chemicals – of which guanine, a purine, was the most abundant – is associated with differences in observed eye color. However, rather than spurring a wave of HPLC papers identifying the specific iris pigments in a range of bird species, this is the only study to take an HPLC approach, and our knowledge of the pigment composition of bird irises has remained largely unchanged since the mid-1990s.

Types of Bird Iris Pigments and Structures

McGraw et al. (2004) warned about the pitfalls of assuming the pigments involved in bird feather coloration based simply on the colors we observe. This risk is even greater when considering iris coloration, because similar colors are commonly produced by dramatically different mechanisms. For example, the irises of Canvasbacks (*Aythya valisineria*), Red-eyed Vireos (*Vireo olivaceus*), and Bronzed Cowbirds are each vivid red, and a naïve observer might suspect that the same pigments are responsible. However, red irises are produced by red carotenoids in Canvasbacks, by red pteridines in Red-eyed Vireos, and by the red hemoglobin of blood cells present in enlarged vessels on the surface of the iris in Bronzed Cowbirds (Oliphant 1987a, Hudon and Muir 1996). Different mechanisms may also occur in combination as in the iris of the Great-crested Grebe (*Podiceps cristatus*), which appears red but which Oehme (1969) considered to be radially partitioned into four distinctly colored zones, a subtle pattern produced by a complex combination of melanin, carotenoids, pteridines, *and* enlarged blood vessels. Figure 2 gives examples of how different pigments and structures can produce the same eye colors – white, yellow, and red – across species.

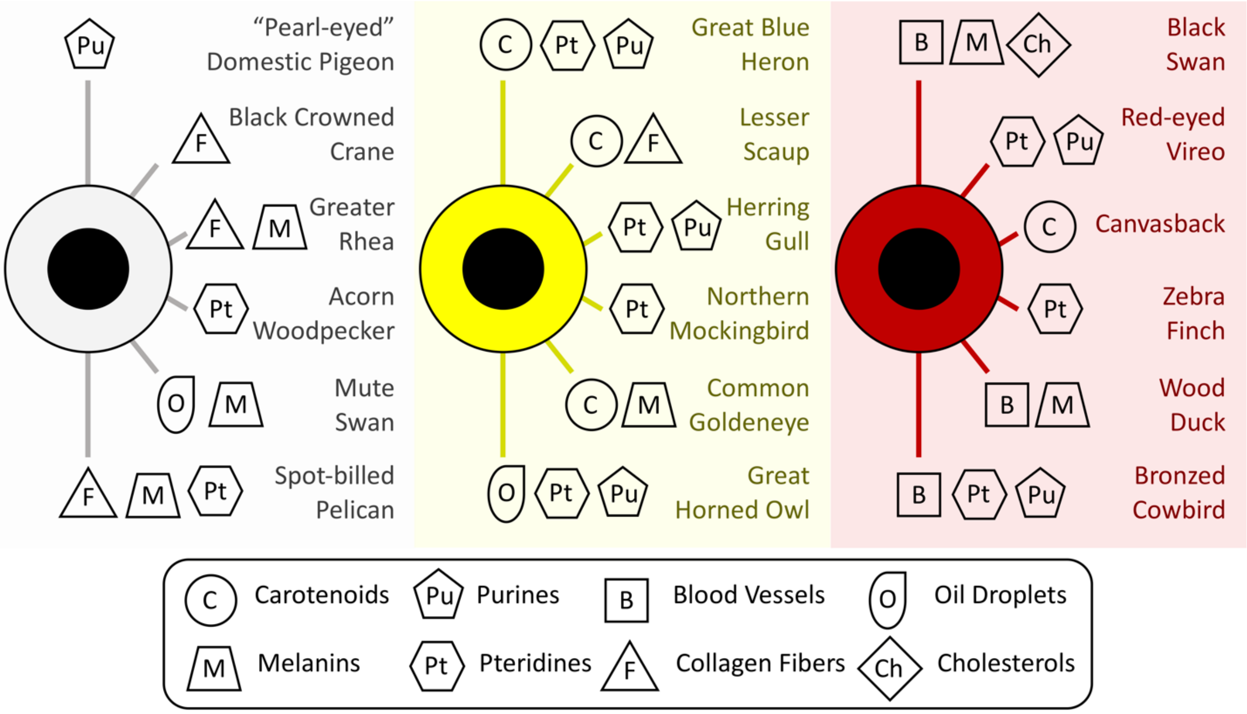


Figure 2- The same eye colors (white/gray, yellow, and red) can be produced by a range of pigments, structures, and combinations thereof. For each eye color, examples of species are listed next to the iris coloration element(s) that have been found to give their eyes that color. For sources, details, and additional examples, see Supplemental Appendix 3.

An additional key principle of bird iris coloration is that it is common for light-colored irises to result from the interaction of colorful pigments with colorless light-reflecting substances, crystals, or structures (Oehme 1969). These reflectors are not technically considered pigments, although they may be informally referred to as such (Oehme 1969, Oliphant 1988, Prum 2006). In these pigment-reflector systems, colored pigments (often non-crystalline pteridines, carotenoids, or hemoglobin) tint the light bouncing off a reflector (such as a crystalline pteridine or purine, a colorless oil droplet, or a collagen bundle) to create a bright color (Oehme 1969, Oliphant 1987a). Among species where only pigments are present, the color is often duller (as in the Northern Flicker, *Colaptes auratus* and Cactus Wren, *Campylorhynchus brunneicapillus* (Oliphant 1987a, 1988)), and in species having only reflecting structures, the iris is white (as in the Acorn Woodpecker, *Melanerpes formicivorus* (Oliphant 1987a, Oliphant and Hudon 1993)).

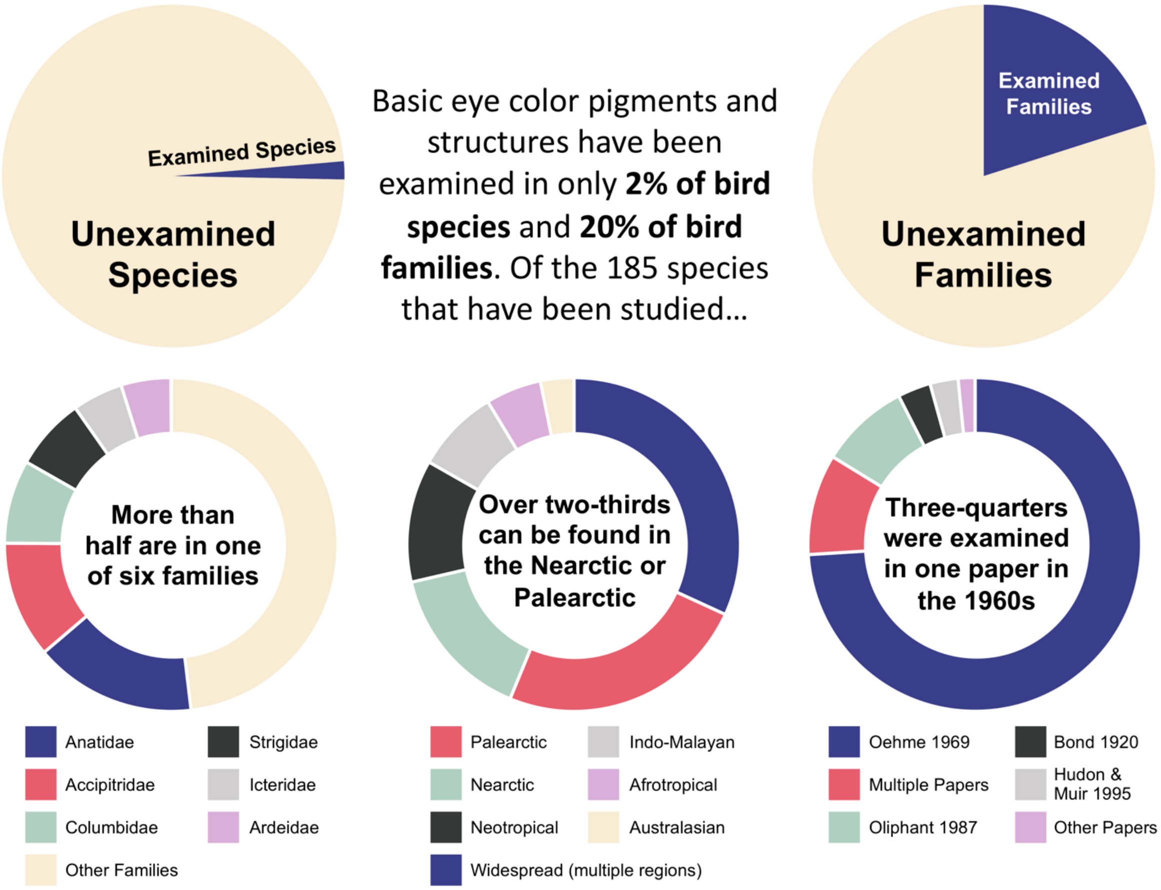


Figure 3- Patterns of study of bird iris pigments and structures. For a complete list of the species examined, see Supplemental Appendix 3.

In Supplemental Appendix 3, we have summarized the known mechanisms of iris coloration for as many bird species as we could find in the literature, drawing in a large part on the groundbreaking work of Oehme (1969) and Oliphant (1987a). We hope this table will serve as an accessible compendium of the available information for the species listed, and we emphasize that the variability recorded among the relatively few bird species included illustrates how little we may know for species that have not been examined. In Figure 3, we explore some characteristics of the species included in Supplemental Appendix 3, and we emphasize how much work still remains to be done to attain a comprehensive view of avian iris coloration mechanisms. Below, we briefly discuss the main groups of pigments or structures involved in bird eye color.

Melanins

Melanin pigments are found in the irises of all bird species that have been examined and often contribute to eye color (Oehme 1969). To understand why melanin is always present in irises but sometimes has no effect on observed color, it is important to distinguish between the layers of bird irises, which are pigmented differently. Avian irises consist of three layers: the posterior (inner) layer of the iris is the highly-melanated pigment epithelium; which is followed by the stroma, a thick middle layer containing muscle, connective tissue, nerves, and often pigment cells; and finally the anterior border layer, which in some species includes pigment cells and/or blood vessels (Oehme 1969, Ferris and Bagnara 1972, Oliphant 1981, 1987b, 1988; Sweijd and Craig 1991; Hudon and Oliphant 1995). The pigment epithelium is always rich in melanin and very dark, but it is generally not involved in visible iris coloration: pigments (melanins or otherwise) present in the anterior two layers often mask the pigment epithelium and are primarily responsible for the observed eye color (Oehme 1969, Hudon and Oliphant 1995). Figure 4 shows a diagram of the layers of the avian iris, and its position within the eye.

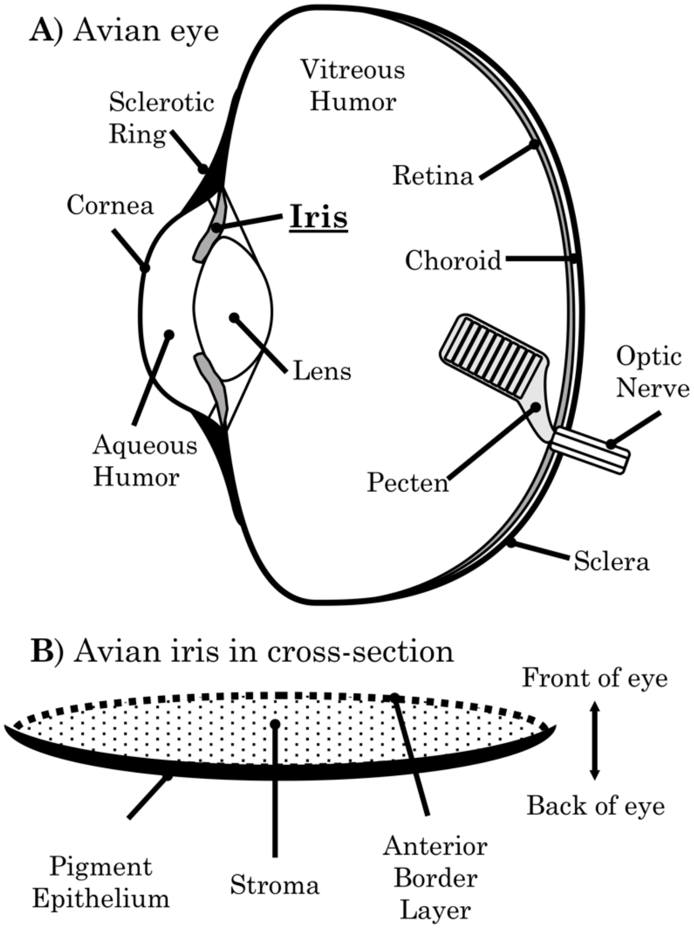


Figure 4- Simplified anatomy of the avian eye and iris. Figure 4A was drawn using information from Mayer (1977), Waldvogel (1990), and Evans (1996), as well as images by Poultry Hub and jimfbleak/Wikipedia. Figure 4B was drawn using information from Oehme (1969), Oliphant (1987b, 1988), Sweijd and Craig (1991), Hudon and Oliphant (1995), and Van den Broeck (2022).

However, there are several exceptions to this general rule. Bond (1919) described the relatively unpigmented irises of some domestic pigeon breeds as being a "simplex" eye, commonly referred to as a "bull" iris by pigeon breeders (Bond 1919, Maclary et al. 2021). In "bull-eyed" pigeons, pigment is not present in the stroma or anterior border layer, and the black eye color observed in these breeds is caused by the melanin in the pigment epithelium. Whether this type of iris coloration occurs in adults of any wild species is unclear: Oehme (1969) specifically noted that he did not identify any species with this type of iris pigmentation, although he found that Eurasian Woodcocks (*Scolopax rusticola*) showed a similar arrangement:

they have relatively little melanin in the stroma and anterior border layer, while the remaining darkness of the iris can be attributed to melanin in the pigment epithelium. The dark eyes of juvenile Jungle Babblers (*Turdoides striata*) are also the result of pigment epithelium viewed through the two unpigmented anterior layers. However, this condition is temporary, and adults are yellow-eyed (Andrews and Naik 1965) (see the "Age-related Development" section below).

For the most part, melanin pigments deposited in the stroma and anterior border layer are responsible for the dark eye colors commonly found in birds. Oehme (1969) described in detail the shape and positioning of the melanin-containing cells, termed melanocytes, in the irises of a variety of species: these can vary from rounded to lumpy to coarsely or finely branched in shape, usually with anterior cells more rounded, posterior cells more ramified, and highly branched melanocytes covering blood vessels. Both eumelanin and pheomelanin can be present in these cells, although eumelanin seems to be more common. Oehme (1969) also observed cells containing both eumelanin and colorless pteridines, which he termed melanopterinocytes. Melanopterinocytes can co-occur with melanocytes and pteridine-containing pterinocytes, and in species having all three cell types, the general pattern is for the more melanin-rich cells to predominate centrally in the iris, near the pupil.

Purines and Pteridines

Purines and pteridines (also more specifically referred to as pterins) are most often the pigments responsible for light eye coloration in birds (Oehme 1969, Oliphant 1987a, 1988). Here, we use the term "pigment" broadly, because pteridines can absorb specific wavelengths of light (Andrade and Carneiro 2021) – functioning as a "true pigment" – but purines and pteridines can also exist in a crystalline form that reflects light: in effect, a form of structural white coloration (Oliphant and Hudon 1993, Prum 1999).

Few overarching conclusions can be drawn regarding the shape and structure of cells containing pteridines and purines. They can range from rounded to branched, and contain pigment granules of varied morphologies, among them “reflecting crystals” and “fibrous pterinosomes” (Oehme 1969, Ferris and Bagnara 1972, Oliphant 1981, 1987b, a, 1988; Oliphant and Diocee 1982, Tillotson and Oliphant 1990, Sweijd and Craig 1991, Oliphant et al. 1992, Hudon and Oliphant 1995, Hudon and Muir 1996). Purines and pteridines often occur in conjunction, with a colored, non-crystalline pteridine and a colorless crystalline purine or pteridine combining to form a “colored reflecting platelet” (Oliphant 1987b, a, 1988). These platelets are good examples of what could be called the “reflector/pigment mechanism” of bright bird iris coloration. In essence, reflecting purine (or, more rarely, pteridine) crystals serve as a backdrop that brightens the coloration of true pigments, including non-crystalline pteridines, carotenoids, or hemoglobin in blood vessels (Oliphant 1987a, 1988).

Oliphant (1987a) identified purines – always including guanine – in the irises of 20 species, all of which also contained pteridines. Conversely, there are cases in which pteridines are present and purines are absent (Oliphant 1987a, Oliphant and Hudon 1993). Due to the close association between pteridines and purines, Oehme (1969) did not recognize that two different classes of pigments were involved and referred only to pteridines in his work. However, pteridines and purines have subsequently been found together in the irises of several species he studied (Ferris and Bagnara 1972, Oliphant 1987b, a; Hudon and Oliphant 1995).

Because they were examined using HPLC techniques, the purines and pteridines of some New World blackbirds (Icteridae) are likely the best-characterized iris pigments of any birds: Hudon and Muir (1996) discovered that the pteridines leucopterin and xanthopterin and the purines hypoxanthine and guanine were present in light-eyed blackbirds at concentrations orders of magnitude higher than in a dark-eyed control species. Guanine was particularly abundant in icterid irises, and it appeared to be the primary reflecting substance responsible for light eye color in the species examined (Oliphant 1987a, Hudon and Muir 1996). In the same study, Hudon and Muir (1996) also looked at one non-icterid species (Red-eyed Vireo) and found evidence for a red pteridine pigment, which may have been pterorhodin. Additionally, the pteridine xanthopterin has been identified in the irises of Great Horned Owls (*Bubo virginianus*) (Oliphant 1981). Outside of this small number of examples focused on particular species, the types of pteridine and purine pigments found in the irises of most birds are unknown, even for those in which the general presence of pteridines and purines has been confirmed.

Carotenoids

Carotenoids were initially assumed to be responsible for the majority of red and yellow irises in birds, but that is not the case (Oehme 1969, Oliphant and Hudon 1993). Rather, carotenoids are responsible for bright eye colors in some avian groups and may be more phylogenetically restricted than other types of iris pigments. Carotenoids are currently known from only eight families: Phasianidae, Anatidae, Ardeidae, Strigidae, and a single species each in Podicipedidae, Phoenicopteridae, Jacanidae, and Accipitridae; see Supplemental Appendix 3 (Oehme 1969, Oliphant 1987a). Carotenoids have not been identified from the irises of any Passeriformes.

The carotenoids xanthophyll and carotene were among the first pigments to be identified in bird eyes (Hollander and Owen 1939a) and give chicken irises their yellow coloration. Similarly, carotenoids are a component of the red, orange, and yellow eyes of some diving ducks, owls, and herons (Oehme 1969, Oliphant 1987a, 1988). Within each clade that possesses carotenoid iris coloration, the structure of the pigment cells is also relatively conserved. For example, owls have characteristic spherical pigment cells containing carotenoids and colorless pteridines or purines, whereas herons have branched pigment cells containing carotenoids and yellow pteridines, overlain by blood vessels (Oehme 1969). The carotenoids themselves are localized within lipid droplets inside these cells.

Blood Vessels

Bright red hemoglobin in the blood has been co-opted as a mechanism of iris coloration in some species. Red color can be produced by the presence of enlarged blood vessels on the anterior surface of the iris, as seen in in male Wood Ducks (*Aix sponsa*) (Oehme 1969), and these red colors can be brightened by a backdrop of purine and pteridine reflectors, as in Bronzed Cowbirds (Hudon and Muir 1996). In some species, hemoglobin present in blood vessels adds a reddish tint to other pigments or structures in the iris, producing a range of oranges and pinks, as in domestic pigeons and Inca Doves (Oehme 1969, Ferris and Bagnara 1972). The orange eyes of Eurasian Long-eared Owls (*Asio otus otus*) may result in part, from the presence of larger iris blood vessels compared to its yellow-eyed conspecifics, but the orange hues could also result from variation in the shade of the carotenoids present (Oehme 1969). As discussed above, in most species which have the ability to change eye color according to mood or season, changes in the degree of redness appear to be controlled by the amount of blood flow in the iris (Ferris and Bagnara 1972, Hancock and Eliot 1978). Immediate post-mortem color change in birds with reddish irises could be one clue to observers in the field that blood vessels play a role in their eye coloration (Gheselin 1975, Oliphant 1988, David et al. 2013).

Structural Blues and Greens

The mechanisms of blue and green coloration in bird irises have not been studied in detail, although it is likely that blue and green eyes have a structural component that determines their color. This general statement is supported by the observations that structural elements produce blue and green colors in bird feathers and bare parts (Prum and Torres 2003, Prum 2006) and in human eyes (Sturm and Larsson 2009). However, the specifics of blue and green coloration in avian eyes are unclear. Oehme (1969) attributed the blue and purple iris coloration of a few species to "Tyndall scattering" – the differential scattering of short wavelengths (Prum and Torres 2003, Prum 2006) – but he did not elaborate on the specific structures responsible. Bond (1919) noted the presence of "very finely fibrillated spindle cells of connective tissue type" that generated blue coloration in the iris of a Lawes's Parotia. Oliphant (1988) examined the velvety turquoise-green iris of a Double-crested Cormorant (*Nannopterum auritum*) and found that the color was produced by the presence of spindle-shaped cells containing membrane-bound granules with ordered arrays of filaments and rods. These studies lend evidence to the idea of a structural component to blue and green bird eye colors, but many of the specifics remain unknown and may differ widely between species.

Miscellaneous Coloration Elements

The pigments and structures described above are responsible for iris coloration in most species, but there are several uncommon elements that can also affect eye color in a smaller number of birds. For example, Oehme (1969) identified interwoven bundles of collagen fibers which generate gray or whitish structural coloration in a handful of species, including Greater Rheas (*Rhea americana*), Black Crowned Cranes (*Balearica pavonina*), Western Jackdaws (*Coloeus monedula*), and Brown Pelicans. These fibers also serve as reflectors in conjunction with colorful pteridine or carotenoid pigments in Great White Pelicans (*Pelecanus onocrotalus*) and Lesser Scaup (*Aythya affinis*) (Oehme 1969, Oliphant 1988).

Oehme (1969) also noted a small number of species – the Mute Swan (*Cygnus olor*), Ferruginous Duck (*Aythya nyroca*), and Velvet Scoter (*Melanitta fusca*) – whose irises contain oil droplets without carotenoids, which may produce a form of structural white coloration. Similarly, colorless lipid droplets can serve as light-reflecting structures to brighten coloration, as in the yellow irises of the Great Horned Owl, which also contain purines and yellow pteridines (Oliphant 1981). This arrangement is the opposite of that observed in most owl species, where yellow iris coloration is produced by carotenoids in lipid droplets and the purines and pteridines serve as colorless reflectors (Oehme 1969, Oliphant 1988)). These colorless lipid droplets have only been identified from the taxonomic families Anatidae and Strigidae, families in which carotenoid-bearing lipid droplets are also frequently present, so it seems possible that these structures are the result of a secondary loss of carotenoids.

Finally, in two species of waterfowl, the Black Swan (*Cygnus atratus*) and the Coscoroba Swan (*Coscoroba coscoroba*), Oehme (1969) identified cells containing a reflecting crystalline structure composed of cholesterols. In both species, these crystals interacted with the red coloration of blood vessels to produce pink irises, thus performing a reflecting function similar to that of pteridine and purine crystals in other species. These structures have not been examined by other authors or identified in other species.

Age-related Development of Coloration Mechanisms

The age-related development of pigments in bird irises is not well understood, except in a couple of species. Generally speaking, juvenile birds tend to have darker irises than adults, although there are exceptions. Depending on the species, darker juvenile irises are often the result of a higher presence of melanin in addition to an absence of light pigments. For example, in African Pied Starlings (*Lamprotornis bicolor*), juveniles have a dark brown iris, which becomes white in adults by the second year. Swejid and Craig (1991) showed that this transformation is the result of two distinct changes in pigmentation: an anterior layer of dark pigment (presumably melanin) is progressively lost, while the stroma fills with pigment cells containing reflecting platelets (presumably purines and/or pteridines) that give adult eyes their white color. Bond (1919) suggested a similar pattern of age-based replacement of dark anterior pigment cells with light-colored or reflective pigment cells in some breeds of domestic chickens and in Herring Gulls (*Larus argentatus*). Oehme (1969) observed a similar process in male Eurasian Marsh-Harriers (*Circus aeruginosus*), wherein melanin and colorless pteridines were present in dark-eyed juveniles, followed by a disappearance of melanin and replacement of colorless pteridines with yellow pteridines during the transition to yellow-eyed adults. In these examples, age-related changes in eye color are not simply a matter of dark pigment disappearing to reveal light pigment or light pigment covering up pre-existing dark pigment; rather these changes are attributable to a simultaneous increase in light and decrease in dark pigments.

On the other hand, Jungle Babblers have been reported to show a simpler mechanism: the dark irises of juveniles are caused by the dark pigment epithelium layer deeper in the eye and the anterior layers are unpigmented (Andrews and Naik 1965). During the transition to adulthood, light pigment cells cover the melanated pigment epithelium, and an increased density of muscle fibers in the iris stroma provides additional opacity (Andrews and Naik 1965). Among Northern Goshawks (*Accipiter gentilis*), Oehme (1969) suggested that more and brighter pteridines were responsible for the age-related yellow-to-orange eye color transition. In the one study that quantified age-related changes in pigmentation, Hudon and Muir (1996) found that a young Brewer's Blackbird with a "pale translucent" iris had between 1% and 3% of the guanine in its iris relative to yellow-eyed adult males and, interestingly, only 25% of the guanine as a browneyed adult female. This suggests that the opaque yellow irises of the adult male are due in part to their high guanine content, but that the effects of increased guanine in the adult female were counteracted by deposition of anterior melanin. As seen from these examples, the specific mechanisms of age-related variation in iris coloration vary between species, and often the color transitions are the result of several co-occurring changes in pigmentation.

Future Work: Mechanistic Basis of Eye Color Variation

While the general structure and pigments involved in iris coloration have been characterized for approximately 185 bird species (see Supplemental Appendix 3), that total represents less than 2% of the currently recognized number of species (Clements et al. 2021); see Figure 3. Irises have been examined from representatives of 50 families and 23 orders, and although some groups, such as hawks, doves, and ducks, are relatively well-represented, there are no data on the mechanistic basis of iris coloration for approximately 80% of bird families and 44% of bird orders. Furthermore, existing data are largely preliminary: rough tests of whether carotenoids or pteridines are present or observations of melanocytes under magnification. Specific pigments have been identified and quantified only for a small number of species (Hudon and Muir 1996), and the relative paucity of data is particularly noteworthy because dramatically different types of pigments or structures can produce similar iris colors (see Figure 2). As a result, we can only speculate on the types of pigments responsible for iris coloration in the vast majority of bird species, and we have no data on the specific chemicals or structures involved. Beyond obscuring the mechanisms that cause different bird eye colors, this lack of data has also masked potentially important phylogenetic patterns. For example, although yellow and red eyes are found across birds, current analyses of pigments (summarized in Supplemental Appendix 3) have suggested that carotenoid iris coloration may be phylogenetically limited to a small number of families, and verifying this preliminary observation will require further research. As it stands, there are many seemingly simple questions for which the answers remain unknown, such as whether or not Passeriformes have carotenoids in their irises, or what causes the bright red eyes of many antbirds (Thamnophilidae).

Therefore, basic research on the pigments and color-producing structures of bird irises is desperately needed. High performance liquid chromatography was used to great effect by Hudon and Muir (1996) in the most comprehensive study of iris pigments in a small number of songbirds. However, in the 25 years since, there have been few studies published that performed similar analyses. These types of pigment analyses and histological studies on a diversity of avian irises have the potential to greatly expand our knowledge of bird iris coloration, more than 50 years after Oehme undertook his pivotal research. To facilitate this work, collectors and collections should preserve eyes or irises when preparing new study specimens, and standard protocols should be developed to help preserve these samples so that they will be most useful.

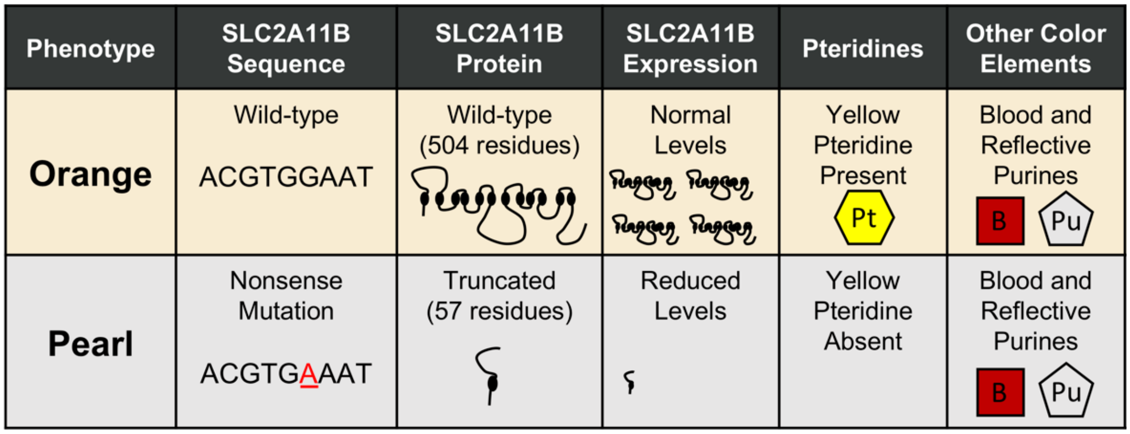
The Genetic Basis of Bird Eye Color Variation

In 1919, Bond wrote "I am unable however to find that much work has been done on eye colour in birds from the genetic standpoint" (Bond 1919), and for the following century that statement held true, with the entirety of our knowledge about the genetics of bird eye color variation originating from breeding studies of domestic pigeons and chickens (Bond 1919, Hollander and Owen 1939a, b). Three recent papers have significantly advanced the field by identifying a specific gene (SLC2A11B) responsible for iris variation caused by pteridine pigmentation in the domesticated Rock Pigeon (Andrade et al. 2021, Maclary et al. 2021, Si et al. 2021).

Eye Color Genetics of Domestic Birds

Probably the most significant historical fact about the genetics of avian iris coloration is that the orange (aka “wild type” or “gravel”) eye color of domestic pigeons is a Mendelian trait, with orange an autosomal dominant to pearl (aka “white” or “fish”) eye color (Staples-Browne 1908, Christie and Wriedt 1924, Bessmertnaja 1928, Hollander and Owen 1939b). Orange irises contain yellow pteridines and reflective purines, while pearl irises lack the yellow pteridines (whether colorless pteridines are present in either is not certain) (Oehme 1969, Oliphant 1987b, a). These color differences have been ascribed to a dominant autosomal locus, referred to in the older breeding literature as *Tr* (Bessmertnaja 1928, Hollander and Owen 1939b)*,* that controls deposition of yellow pteridines.

During the past year, three independent groups have used whole-genome sequencing of orange-eyed and pearl-eyed pigeons to pinpoint the location and identity of this locus, and all came to an identical conclusion (Andrade et al. 2021, Maclary et al. 2021, Si et al. 2021). Each research group found that a small (<10kb) genomic region containing the membrane protein SLC2A11B (solute carrier family 2, facilitated glucose transporter, member 11b) is strongly associated with orange/pearl iris color variation. They further identified a nonsense mutation (W49X) that dramatically truncates the SLC2A11B protein from 504 to 57 amino acids as the likely cause of pearl eyes in domestic pigeons. Figure 5 summarizes the findings of this research.



Phenotype	SLC2A11B Sequence	SLC2A11B Protein	SLC2A11B Expression	Pteridines	Other Color Elements
Orange	Wild-type ACGTGGAAT	Wild-type (504 residues)	Normal Levels	Yellow Pteridine Present Pt	Blood and Reflective Purines B Pu
Pearl	Nonsense Mutation ACGTGAAAT	Truncated (57 residues)	Reduced Levels	Yellow Pteridine Absent	Blood and Reflective Purines B Pu

Figure 5- The pathways to produce orange and pearl irises in domestic pigeons. Data from Si et al. (2021), Andrade et al. (2021), and Maclary et al. (2021).

Si et al. (2021) used a genome-wide association study of 49 orange-eyed and 43 pearl-eyed pigeons to identify a 9kb region of the genome containing SLC2A11B as strongly associated with the pearl iris phenotype. They zeroed in on the nonsense mutation W49X, and genotyped 146 individuals of each eye color, with near-perfect (287/292) correspondence between genotype and expected phenotype. Andrade et al. (2021) took a similar approach, conducting a GWAS and a series of genome scans on 26 orange-eyed and 23 pearl-eyed individuals, as well as genotyping 26 mixed parent-offspring trios, which allowed them to identify the same gene and SNP. Andrade and colleagues genotyped additional birds for confirmation, and all 40 pearl-eyed individuals were homozygous for the nonsense mutation allele, while none of the 52 orange-eyed individuals were. Maclary et al. (2021) took a slightly different approach to identifying the same causative locus, using a whole genome pFst scan of 28 orange-eyed and 33 pearl-eyed individuals. They also conducted a QTL study on the offspring of an experimental cross between orange-eyed and pearl-eyed parents, which once again pinpointed the same locus and causative SNP while also producing a neatly Mendelian ratio of 45 orange-eyed to 14 pearl-eyed offspring.

Gene expression data was used by all three groups to provide additional evidence that SLC2A11B was the causative locus. Si et al. (2021) and Andrade et al. (2021) both found that SLC2A11B was expressed at lower levels in pearl-eyed adults, and Maclary et al. (2021) showed significantly reduced expression of SLC2A11B in embryos homozygous for the pearl allele. Even more convincingly, Andrade et al. (2021) found that in heterozygous individuals, the truncated "pearl" transcript was present at levels four times lower than the "wild type" transcript.

Finally, the effects of SLC2A11B on the the eye color of domestic pigeons are supported by the association between the SLC2A11B gene and leucophore and xanthophore development in medaka fish (*Oryzias latipes*), as well as loss of function experiments in medaka that produced a similar loss of yellow pteridine pigment (Kimura et al. 2014). Considered together, the evidence points to the key role of SLC2A11B, and the W49X mutation specifically, in controlling yellow iris pigmentation in pigeons, making it the first "eye color gene" to be identified in birds.

In addition to the primary *Tr*/SLC2A11B eye color locus, brown or chocolate-colored plumage in domestic pigeons appears to be strongly associated with an alternative pathway to pale eyes, referred to as "false pearl" (Levi 1957, Maclary et al. 2021). Since genetic work has shown that brown plumage results from the tyrosinase gene TYRP1 (Domyan et al. 2014), the same gene likely also has an effect on the pigmentation of the iris.

"Bull" (aka "simplex" or "black") irises of domestic pigeons, which lack all anterior iris pigmentation, are clearly associated with different loci than those involved in orange/pearl coloration. Unlike pearl irises, early crossing experiments involving bull irises did not produce consistent results (Staples-Browne 1908, Bond 1912, Hollander and Owen 1939b). However, the authors of these studies noted an association between the presence of bull irises and the presence of white or piebald plumage (Staples-Browne 1908, Bond 1912, 1919; Hollander and Owen 1939b). This association is interesting, because it suggests that bull eyes are associated with changes in pigment deposition of iris pteridines and purines but also with the deposition of feather melanin. Clearly this iris type, which is not known from wild birds, is the result of significant disruptions of the pigmentation process.

Maclary et al. (2021) examined the bull-eyed phenotype in domestic pigeons, using QTL analyses to study the offspring from two experimental crosses: one between bull-eyed and non-bull-eyed parents and a second between two non-bull-eyed parents that produced some bull-eyed offspring. The QTL data from the two crosses identified overlapping, large (1.5-2Mb) genomic regions associated with the bull-eye phenotype. However, the genetics of the bull-eyed phenotype appear to be complex. The two crosses showed different inheritance patterns, with incomplete penetrance and stochastic factors that affected the observed phenotype, and while both crosses implicated the same genomic region, the resulting bull phenotypes did not seem to be associated with a single genomic variant. Appropriately, given the long-recognized association between bull irises and piebald plumage, Maclary et al. also found a QTL for piebald plumage that overlaps the QTL associated with bull irises. These results suggest that bull irises and piebald plumage seem to be the product of multiple changes, which could be coding or regulatory, at or near a pigmentation gene or a group of linked genes.

Although there are 60 genes in the region identified by the bull iris QTL crosses, one gene within the region stands out as a potential candidate affecting the bull iris phenotype: EDNRB2 (Maclary et al. 2021). EDNRB2 is expressed at substantially lower levels in the embryos of bull-eyed individuals (Maclary et al. 2021), and EDNRB2 and its homologs are associated with depigmentation of feathers, fur, and irises of other birds (Miwa et al. 2007, Kinoshita et al. 2014, Li et al. 2015, Wu et al. 2017, Xi et al. 2020, 2021) and mammals (Hosoda et al. 1994, Ceccherini et al. 1995, Metallinos et al. 1998), including humans (Puffenberger et al. 1994, Attié et al. 1995). EDNRB2 is involved in the migration of neural crest-derived pigment cells (Baynash et al. 1994, Lecoin et al. 1998, Pla et al. 2005, Harris et al. 2008), which may allow it to have far-reaching effects on pigmentation in different tissue types. This is in contrast to the SLC2A11B variant in pigeons, the effects of which seem limited to iris coloration.

Breeding studies involving domestic chickens have produced more equivocal results than those in pigeons. One locus, referred to as *Br*, is known to affect eye color, with dark brown eyes recessive to light eyes (bay, yellow, or orange) (MacArthur 1933, Hutt 1949, Smyth 1990). Linkage mapping has shown that this locus is localized to the Z chromosome (MacArthur 1933, Hutt 1949). Bond (1919) and Davenport (1906) reported results of crosses between a number of chicken breeds of varying eye colors, but their observations do not appear to suggest any consistent patterns. Furthermore, while Bond and Davenport noted an association between dark feathers and dark eyes, MacArthur (1933) suggested that different eye colors can appear in association with any plumage color. These conflicting findings are likely due to the role of multiple loci: although the *Br* locus appears to only affect iris coloration, it is linked to the *Id* locus, which influences eye and shank color, and the plumage melanin locus *E* can also play a role in eye color (Smyth 1990). More recent work has identified the genes GRAMD3 and MC1R as corresponding to the *Id* and *E* loci, respectively (Dávila et al. 2014, Xu et al. 2017).

Eye Color Genetics of Wild Birds

To this point, essentially all research on bird eye color genetics, spanning the breeding studies of the early 1900s to cutting-edge genome sequencing projects, has been conducted using domesticated species. It is not certain that the same mutations – often those with simple inheritance patterns and/or large effects – that have arisen in domestic breeds are responsible for the variation seen in wild populations. Si et al. (2021) traced the origins of the pearl-eye-associated mutation in SLC2A11B to approximately 5,400 years ago during the domestication process, and they provide evidence that it was under strong artificial selection at that time. Additionally, the depigmented "bull" iris of some breeds of domestic pigeon is not homologous to the dark eyes of the Stock Dove (*Columba oenas*) or other wild species, which have melanin in the anterior border layer of their irises (Bond 1919), and so the genes involved (EDNRB2 or others) likely do not reflect the loci that control the evolution of dark eyes in the rest of the Columbidae. Still, the identification of specific loci involved with iris pigmentation in domesticated populations is a significant step forward for the field, and these discoveries have the potential to greatly facilitate similar studies of wild species.

For example, Si et al. (2021) and Maclary et al. (2021) examined the SLC2A11B locus in whole genomes sequenced across the avian phylogeny. Si et al. (2021) identified putatively deleterious mutations in SLC2A11B in the Greater Rhea, Muscovy Duck (*Cairina moschata*), Double-crested Cormorant, House Sparrow (*Passer domesticus*), Anhinga (*Anhinga anhinga*), and African Gray Parrot (*Psittacus erithacus*). While the first four species lack pteridines in their irises, Anhingas and African Gray Parrots have yellow and colorless pteridines, respectively, in their irises (Oehme 1969). Similarly, Maclary et al. (2021) found that a domain of SLC2A11B may be missing from the genomes of the dark-eyed Hooded Crow (*Corvus cornix*) and the white-eyed Wire-tailed Manakin (*Pipra filicauda*), neither of which have yellow pigments in the iris. Any causative links between these potential mutations and the eye colors of these species remain to be investigated.

We can also propose several hypotheses about the genes that may be involved in the iris coloration of wild birds based on the mechanistic basis of that coloration. For example,, a striking difference in the concentration of guanine in the irises of some New World Blackbirds (Hudon and Muir 1996) is strongly associated with light/dark eye color variation, and it is possible that a locus associated with a guanine-deposition pathway could be responsible for this variation. Similarly, the genes underlying melanin (Poelstra et al. 2014, Uy et al. 2016, Toews et al. 2016, Stryjewski and Sorenson 2017, Semenov et al. 2021) and carotenoid (Toomey et al. 2017, Brelsford et al. 2017, Aguillon et al. 2021) coloration in bird feathers and bare parts (Walsh et al. 2012, Mundy et al. 2016, Yu et al. 2017, Enbody et al. 2021) have been the subject of considerable study, and they could be among a suite of candidate loci to examine for effects on iris coloration. In fact, the well-known melanin pathway genes TYRP1 and MC1R have been indirectly shown to affect eye color in domestic pigeons and chickens (Levi 1957, Smyth 1990, Domyan et al. 2014, Dávila et al. 2014). Interestingly, two genes that account for the majority of human eye color variation, HERC2 and OCA2 (Duffy et al. 2007, Kayser et al. 2008), are associated with melanin-based plumage coloration in seedeaters (*Sporophila*) (Campagna et al. 2017, Turbek et al. 2021); these would also be candidates for loci that affect melanin pigmentation of irises. Si et al. (2021) found two pteridine-associated genes, GCH1 and CSF1R, that showed significant expression differences between orange-eyed and pearl-eyed pigeons, and Andrade et al. (2021) identified several genes associated with the same system that showed slight differences in expression; these too would be of interest for future genomic investigations.

Because pteridine and purine coloration has been more extensively studied among reptiles (McLean et al. 2017, Andrade et al. 2019), amphibians (Stuckert et al. 2019, Rodríguez et al. 2020), fish (Henning et al. 2014, Kimura et al. 2014, 2017; Singh and Nüsslein-Volhard

2015, Irion and Nüsslein-Volhard 2019, Luo et al. 2021, Wang et al. 2021), and insects (Ewart and Howells 1998, Meng et al. 2009, Grant et al. 2016, Khan et al. 2017, Pimsler et al. 2017, Vargas-Lowman et al. 2019, Woronik et al. 2019), the literature for these organismal groups may also be a source for identifying candidate genes associated with those types of coloration in bird irises (Andrade and Carneiro 2021, Andrade et al. 2021, Price-Waldman and Stoddard 2021), similar to the situation with SLC2A11B in medaka (Kimura et al. 2014).

Future Work: The Genetic Basis of Eye Color Variation

The stage is set for a dramatic expansion of our knowledge of bird eye color genetics, including the identification of loci associated with eye color differences in natural populations. Compared to the recent explosion in papers examining the genetics of bird plumage color (see Funk and Taylor 2019 for a review), the genetic mechanisms affecting iris coloration have been understudied until recently, and these largely remain a mystery in wild species (Price-Waldman and Stoddard 2021). The same set of tools and analyses that have sparked a revolution in the understanding of bird plumage color genetics, particularly the use of genome resequencing data and genome-wide association studies, would be similarly well-suited to answering questions about the genomic basis of eye color variation. These techniques are most powerful when background genetic variation is low between individuals of varying phenotype, as in hybrid zones or polymorphic populations (Rieseberg and Buerkle 2002, Buerkle and Lexer 2008). As a result, systems of particular interest would be those in which eye color varies within a population or between two closely related populations experiencing gene flow (see Supplemental Appendix 1c, 2c, and 2d). Basic descriptive studies of iris coloration can identify additional examples of promising natural systems for future study. At the same time, captive breeding experiments between closely related species offer a potential avenue of study for particular groups of taxa, and domesticated species such as pigeons, chickens, parrots, and finches will continue to provide ample opportunities for genomic research, as highlighted by the recent impressive work done to identify the SLC2A11B gene.

Evolutionary Drivers of Bird Eye Color

The ultimate causes of bird eye color variation are the selective pressures and stochastic processes that result in the appearance and fixation of new eye colors in lineages over evolutionary time. Evolutionary explanations for eye color variation can be divided into two broad categories: those involving survival and those involving signaling. In the former category would be any potential effects of eye color on vision, UV protection, or camouflage, while the latter category would include the role of eye color as a potential indicator to conspecific individuals of mate quality, age, sex, or presence. Associations between iris color and habitat, light environment, or foraging strategy could point towards a role for survival-based explanations, while associations with social structure or mating system would argue for the importance of intraspecific signaling explanations (Craig and Hulley 2004). Additionally, a set of null hypotheses must be considered, wherein iris coloration may not be under selection and is instead largely influenced by genetic drift or is a byproduct of other processes.

Drift, Pleiotropy, and Relaxed Selection

Before discussing the array of potential selective pressures – affecting survival or signaling – that may drive the evolution of bird iris coloration, we should consider that variation in eye color may not always be the result of selection on eye color. Drift frequently plays a significant role in trait evolution. Conserved eye colors across a clade could be due to constraints on the pigments that can be produced by that group (Craig and Hulley 2004), or simply the effect of phylogenetic history, rather than selection.

Additionally, through pleiotropic effects, selection on plumage coloration or other traits may indirectly shape the evolution of eye color. A recent study on gulls found that dark-feathered heads are correlated with dark irises in the group, which the authors suggest could be the result of melanin pigmentation pathways that are shared between the two traits (Minias and Janiszewski 2020). However, selection on the amount of contrast between the eye and head could also explain the observed pattern, and dark irises in at least some adult gulls result from not just the presence of melanin but also the absence of light pigment (Bond 1919), so a clearer mechanism would need to be identified to give credence to the pleiotropy hypothesis. That said, several studies have noted a connection between plumage and eye color in domestic pigeons, including the association between "bull" irises and piebald plumage (Davenport 1906, Bond 1912, Hollander and Owen 1939b) and between "false pearl" eyes and brown plumage (Levi 1957). The association between "bull" eyes and piebald plumage has been supported by genetic data (Maclary et al. 2021), and it is certainly plausible that selection on other elements of bird coloration could have incidental effects on the evolution of eye color.

These caveats aside, it seems probable that selection must drive at least some of the variation in eye color that we see across birds, either by directly affecting their *survival* or by mediating social interactions (including mate choice) via *signaling*, potentially affecting reproductive success. The non-melanophore pigment cells that give bird eyes their bright color are unique to the iris, which Oliphant et al. (1992) suggested is the result of consistent selective pressure to maintain bright iris coloration, in contrast to relaxed selection on the coloration of the largely feather-covered integument.

Survival

To our knowledge, there are no studies that have directly examined the association between eye color and survival, or the effects of eye color on traits that directly affect survival such as vision, foraging ability, or crypsis. Rather, most studies have addressed these connections indirectly by identifying correlations between eye color and life history characteristics that influence the selective pressures on a bird, such as habitat type, foraging behavior, and nocturnality.

Eye Color and Vision

Given the paramount importance of vision for the survival of birds, it is tempting to speculate about the role that eye color may have on vision, either by directly affecting visual acuity or by protecting the retina against the deleterious effects of UV radiation. However, there are reasons to be skeptical of this category of explanations. Savalli (1995) characterized support for “visual clarity” hypotheses as “anecdotal”. Oehme (1969) was similarly skeptical, noting that the highly melanated pigment epithelium on the posterior side of the iris would have the greatest effect on the light passing through the iris. This layer is similarly pigmented in light- and dark-eyed species, with little or no effect on the visible color of the iris, which is dictated by pigments in the stroma and anterior border layer (Oehme 1969). Non-radially-symmetric dark pigmentation near the pupil in buttonquail, pigeons, and other species has been suggested to play a role in reducing glare and improving vision (Gutiérrez-Expósito 2019), though like other visual hypotheses, this idea has not yet been tested experimentally.

Eye Color and Camouflage

While there is not yet evidence for an effect of eye color on bird vision, there may be an effect of eye color on bird visibility. In one of the few comprehensive, comparative phylogenetic studies of bird eye color, Passarotto et al. (2018) examined a number of owl species and concluded that there is an association between dark irises and nocturnal behavior. They suggested the evolution of dark eyes could be the result of selection for iris colors that make owls less conspicuous to their prey while hunting at night. However, it is not entirely clear that light-eyed nocturnal owls (of which there are many species) would be significantly more visible to their largely mammalian prey than dark-eyed relatives; such a claim would need to be tested to support this hypothesis that dark eyes provide nocturnal camouflage.

Intriguingly, a second comparative phylogeographic study suggests a slightly different camouflage-related hypothesis, and together both studies may point towards a more comprehensive model for the role of camouflage in shaping patterns of avian eye color variation. Davidson et al. (2017) studied the relationships between eye color, parental care, and cavity nesting in passerines and found support for selection against bright eyes in non-cavity nesting birds. They proposed a model in which dark eyes are selectively favored among non-cavity nesters because they make individuals on the nest less conspicuous to predators, while selection may be relaxed in cavity-nesting species where incubating parents are already hidden from predators. Freed from camouflage-based natural selection for dark eyes, cavity-nesting species may then be under selection for bright eyes in a display or signaling context, as discussed below.

A variation of this hypothesis could also be applied to explain Passarotto and colleagues' (2018) results with owls: perhaps dark eyes in nocturnal owls are under selection for camouflage from predators or mobbing songbirds at their daytime roosts. Another relevant point to this hypothesis of selection for dark eyes to enhance crypsis in vulnerable species (e.g., non-cavity nesting songbirds, day-roosting nocturnal owls) is the presence of remarkable keyhole-like notches in the eyelids of potoos (Nyctibiidae), which are extremely well-camouflaged nocturnal insectivores (Borrero H. 1974). These openings are thought to allow day-roosting potoos to see their surroundings without opening their eyelids (Borrero H. 1974) because doing so would expose their large and striking yellow eyes. The presence of this adaptation may suggest that there is selective pressure against exposed bright eyes in these cryptic nocturnal species. A related family of highly camouflaged nocturnal birds, the Caprimuligidae, is entirely dark-eyed.

There are many patterns of bird eye color variation that are not explained by hypotheses related to crypsis. However, the general principle that light eyes are selected against due to camouflage in many species, and that this constraint is stronger in some groups (day-roosting nocturnal species, songbirds with open nests) and weaker in others (diurnal predators, cavity-nesters), warrants further examination.

Eye Color and Foraging Behavior

In a series of papers and books, Worthy (1978, 1991, 1997) put forward a hypothesis that bird eye color can be broadly correlated with foraging behavior, stating that there is a tendency for ambush predators to be light-eyed and "pursuit" predators to be dark-eyed. Under this model, the largely light-eyed herons and the wholly dark-eyed swifts would represent opposite ends of an ecological and eye color continuum. Worthy (1978, 1991, 1997) also proposed multiple possible mechanisms explaining this correlation, including those relating to visual clarity and pleiotropic effects. The data supporting this supposition are interesting, but the hypothesis has not been tested in a comparative framework, and attempts to generalize the principle broadly across animals, including humans, have rightly invited skepticism (Savalli 1995, Elias et al. 2008). Further studies are needed to disentangle whether a genuine relationship exists between eye color and foraging behavior, or whether the putative correlation occurs because of confounding variables including body size (Worthy 1978), light environment, and phylogeny.

Eye Color and Habitat

Associations between eye color and foraging behavior, visual acuity, or camouflage would likely also produce an association between habitat and eye color. In a global survey of bird eye color variation, Craig and Hulley (2004) identified several potential correlations, including a tendency for forest-dwelling species to be lighter-eyed in the Corvidae and South American Icteridae, but they acknowledged that the correlation may be a result of phylogenetic effects rather than habitat. Additionally, they found a higher-than-expected proportion of light-eyed passerines in Australia and South Africa: whether this is a result of habitat, phylogeny, or another factor is unknown. Of course, even genuine correlations between habitat and eye color are not necessarily due to a direct influence of iris coloration on survival: the utility of eye color as an intraspecific signal could also be affected by the light environment, which is associated with habitat type (Endler 1993)

Signaling

While the evidence for a direct effect of eye color on survival varies from speculative to suggestive, there is stronger evidence that eye color plays a role in mediating signaling between individuals. The most obvious examples of these types of interactions involve sexual selection (Darwin 1871), whereby eye color influences mate choice, but bird eye color may also play a role as a signal in a variety of additional social contexts (West-Eberhard 1979).

Sexual Selection

Clearly the brightly-colored irises of some species are involved in courtship and are thus under the influence of sexual selection in the same way that brightly-colored feathers are. For example, both Lawes’s Parotias and Flame Bowerbirds (*Sericulus ardens*) incorporate their flashy irises into their courtship dances (Gunton 2014, Cordey 2019). Male Satin Bowerbirds line their display bowers with blue objects (Borgia 1985), and have glossy purple-to-ultraviolet plumage, both of which are thought to function as sexually-selected ornamentation (Borgia 1985, Doucet and Montgomerie 2003). Their brilliant purple eye – which reflects both short-wavelength visible light as well as ultraviolet light (Endler and Mielke 2005) – presumably evolved under similar selective pressure, although it is not sexually dimorphic (Frith and Frith 2020a). Cormorants, which possess some of the most vividly colored eyes of any bird group, are largely black-plumaged birds which often have patches of bare facial skin that become brightly colored during the breeding season (Orta 1992): colorful eyes could be an extension of this phenomenon. As mentioned above, some species of herons and pelicans have brighter or redder eyes during the breeding season, suggesting a role in courtship. In many species of Icteridae and Thamnophilidae, a vivid red or yellow eye is the only colorful body patch, contrasting with achromatic plumage (del Hoyo et al. 2017): making it plausible that these eye colors would be important for sexual selection, although this idea has not been formally tested. Likewise, the Racket-tailed Treepie (*Crypsirina temia*) has a pale blue eye set against velvety "super black" feathers, which may enhance the apparent brightness of the eye (McCoy and Prum 2019). On the other hand, sexual dichromatism in eye coloration, while not rare, is hardly ubiquitous in birds, and in species where sexually dichromatic eyes occur there is not an obvious trend towards brighter male irises (Negro et al. 2017).

Eye color variation has also been shown to be involved in mate choice, and there is some evidence that it functions as an honest signal of mate quality (Zahavi 1975, Endler 1980, Hamilton and Zuk 1982, Lozano 1994). Thayer's Gulls (*Larus glaucoides thayeri*) have been suggested to mate assortatively by eye color (Smith 1966), but the validity of this finding has been challenged (Pierotti 1987). Eye color has also been suggested to contribute to assortative mating and thus pose a barrier to hybridization in European gulls (Gay et al. 2007). In Yellow-eyed Penguins (*Megadyptes antipodes*), the saturation of their yellow eyes is positively correlated with breeding success in both males and females, even when controlling for age (Massaro et al. 2003). The same study also found evidence of assortative mating by iris hue (but not saturation), while acknowledging the need for explicit mate-choice experiments. A similar correlation between yellowness of irises and nest success (though not mass, clutch size, or egg volume) was observed in female Little Owls (*Athene noctua*), but not in Eurasian Scops-Owls (*Otus scops*) (Passarotto et al. 2020) – observations that warrant additional experimental investigation. Male eye color is associated with nesting success in Eurasian Sparrowhawks (*Accipiter nisus*), though whether eye color results in corresponding changes in female mate choice is uncertain (Newton and Marquiss 1982). Additional associations between eye color and individual health have been found in Northern Saw-whet Owls (*Aegolius acadicus*) (Wails et al. 2018) and American Kestrels (Bortolotti et al. 2003), but not in Cooper's Hawks (*Accipiter cooperii*) (Rosenfield et al. 2003).

Carotenoid-based colors are often cited as honest signals of quality due to the cost of obtaining them and potential immunological and oxidative benefits (Endler 1980, Lozano 1994, von Schantz et al. 1999, McGraw and Ardia 2003). The yellow iris coloration of Little Owls is generated by carotenoids (Oehme 1969), though this is probably not the case for the majority of light-eyed bird species mentioned above, including penguins (Mcgraw et al. 2004), gulls, and raptors (Oehme 1969). The role of pteridine-based colors as signals of mate quality is largely unstudied in birds (Grether et al. 2001, 2005; McGraw 2005, Weiss et al. 2011, 2012; Andrade and Carneiro 2021). Eye coloration in some species could also serve as indirect signals of mate quality by simply indicating the age of individuals, with older birds likely of higher quality (Snyder and Snyder 1974, Picozzi 1981, Newton and Marquiss 1982).

Social Signaling

Behavioral observations and patterns of variation between species suggest a role for eye color in a variety of additional social contexts, including nest defense, intraspecific competition, flock vigilance, and cooperative breeding.

The most significant behavioral experiment on the consequences of bright eyes in birds was conducted in jackdaws, a light-eyed, cavity-nesting corvid. Davidson and colleagues (2014) demonstrated that placing an image of a bright-eyed jackdaw, or even just a pair of bright eyes, in a nest cavity dissuaded other jackdaws from approaching, relative to a dark-eyed control image. They suggested that bright eyes function as a signal that a nest box is defended and are meant to deter potential usurpers.

Birds can dilate and contract their pupils voluntarily, and this ability has been incorporated into social interactions – in species with light irises, the amount of color that is displayed can change dramatically depending on the pupil size (Hardy 1963, Craig 2022). African Pied Starlings have been observed contracting and dilating their pupils during food exchange interactions, with the donor widening their pale irises and the recipient narrowing them (Craig 2022). Similarly, contraction of the pupil to accentuate the iris is common in parrots, where it is called “eye-blazing” or “eye-pinning”, and this behavior is associated with excited states including social dominance interactions and courtship displays (Hardy 1963, Smith 1975, Serpell 1982, 1989; Courtney 1997a, b; Marcuk et al. 2020, Moore et al. 2022). Similar behaviors have been observed in other families and may prove to be widespread across light-eyed birds (McIlhenny 1937, Hardy 1974, Craig and Hulley 2004).

Eye color varies by age in many species of birds and so could function as a social signifier that allows individuals to broadcast their age and social rank and to easily discern the age of conspecifics (Snyder and Snyder 1974, Newton and Marquiss 1982). As discussed above, eye color as an age indicator could also play a role in mate choice and sexual selection. Additionally, the ability to evaluate age via eye color would presumably be advantageous in social species, particularly those with cooperative breeding, where reproductive roles are highly structured by age. Bright-eyed adults and dark-eyed juveniles can be observed in a number of cooperatively breeding starling species (Sweijd and Craig 1991, Craig and Hulley 2004), Jungle Babblers (Andrews and Naik 1965), Gray-crowned Babblers (*Pomatostomus temporalis*) (Matthew and Christie 2020), and Acorn Woodpeckers (Koenig and Walters 2015), although the association does not seem to hold in jays and weavers (Craig and Hulley 2004).

Iris coloration could also relate to “gaze sensitivity”, the awareness of and response to where other individuals are looking (Davidson and Clayton 2016). In humans, white sclerae may have evolved to facilitate gaze perception (Kobayashi and Kohshima 2001, Tomasello et al. 2007, Yorzinski and Miller 2020), though this has been challenged (Caspar et al. 2021). Birds have been shown to be aware of and respond to the direction that humans and other potential predators look (Carter et al. 2008, von Bayern and Emery 2009, Davidson and Clayton 2016); whether there is an association between pale bird irises and gaze sensitivity has not been explicitly studied. However, Guillemain et al. (2012) showed that ducks consistently have different colored eyelids and irises, and they suggested that these differences function as signals of vigilance to other members of their flock by indicating whether the eye is open or closed.

The frequency of brightly-colored, bare eye rings or facial skin in birds may also give insight into the factors affecting the evolution of bright irises, especially since bare part coloration has been implicated in social signaling (Iverson and Karubian 2017). In a few species, notably the Toco Toucan (*Ramphastos toco*) and the “blue-eyed” shags in the genus *Leucocarbo*, a broad colorful eye ring can appear like a large blue or purple iris (Sedgwick 2020, Orta et al. 2021). Similarly, Willis (1969) suggests that the bright skin around the eye of some antbirds may give the illusion of a large eye (akin to an eyespot) to deter predators and/or competitors. Interestingly, in some of these same families, there are also species (such as the Red-breasted Toucan, *Ramphastos dicolorus*, and numerous cormorants) that possess genuine blue or green irises (Short and Sharpe 2020, Frere and Millones 2021, Wallace and Wallace 2021). Whether the occurrence of brightly-colored bare eye rings and irises are correlated is an open question: in some families, such as the Platysteiridae and Thamnophilidae, they appear to be negatively associated, but in others clades like the helmetshrikes (*Prionops*), bright eyes and eye rings occur together (del Hoyo et al. 2017). The interaction between the color of a bare orbital ring and iris has been implicated in mate choice in some gulls (Smith 1966, Gay et al. 2007).

Future Work: Evolutionary Drivers of Eye Color Variation

There are two broad categories of future study which have the potential to greatly increase our knowledge of the evolutionary factors affecting bird eye color variation. The first are phylogenetically-informed comparative analyses of correlations between eye color and ecological factors (Davidson et al. 2017, Passarotto et al. 2018). Moving beyond anecdotal impressions of correlations between eye color and an ecological or life history trait of interest, these studies account for phylogenetic auto-correlation (Felsenstein 1985) to assess whether the trait is genuinely associated with observed eye colors across a phylogeny. These models require a robust and densely-sampled phylogenetic hypothesis of the clade of interest; fortunately, there has been a dramatic increase in the number of large (100s-1000s of species) bird phylogenies inferred with genomic data (Oliveros et al. 2019, McCullough et al. 2019, Harvey et al. 2020), which will provide ample opportunities for applying these methods to test an array of hypothesized correlations between eye color and ecology.

The second critical genre of study that will advance how we study bird eye color variation is behavioral experiments, such as those conducted by Davidson et al. (2014). These will likely be more difficult to perform than correlative analyses, but they are extremely valuable. Only by testing the response of wild conspecifics, predators, or prey to models of varying eye color can we gain insight into how a hypothesized function for eye color variation operates in a natural environment. Similarly, directly testing visual acuity (Caves et al. 2020) and sequencing genes associated with vision (White et al. 2022) in species of varying eye color would allow us to more definitively test hypotheses involving eye color and visual traits.

It would be impractical to experimentally assess the whole array of evolutionary hypotheses suggested to explain elements of avian eye color: a practical path forward would be to first conduct rigorous analyses of correlation in a clade of interest, then validate promising associations with experiments.

Conclusion

Despite their conspicuousness and beauty, bird irises have received relatively little study compared to other aspects of avian coloration. Furthermore, the work that has been done has been scattered across an array of disciplines as diverse as pigment chemistry, game bird breeding, genomics, and behavioral ecology. We hope that bringing together the literature on the patterns of bird eye color variation and its mechanistic, genetic, and evolutionary drivers will spur new advances in our understanding of the rainbow of eye colors in birds. The avenues for future research are myriad. Standardized iris photographs from banding stations and scientific collections, as well as millions of photographs from citizen science databases, will give us a better understanding of the patterns of inter- and intra-specific variation in eye color. Chemical characterization of pigments, including using HPLC, will broaden our knowledge about what mechanisms are involved in iris coloration across the bird phylogeny. Whole-genome sequencing of variable wild populations will identify novel loci that regulate those pigments. And comparative phylogenetic studies and behavioral experiments will provide insights into why such a diversity of eye colors in birds evolved at all. The study of bird coloration has been central to our understanding of speciation and the evolutionary process; greater knowledge of the drivers of bird eye color variation may lead to similar insights and discoveries.

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