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COMPLEMENTARY SESSION PAPER

Hormonal Influences on Sexual Dichromatism Across the Avian Tree of Life: A Primer

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Synopsis Color differences between the sexes (dichromatism) in birds are a hallmark example of a secondary sexual character that is frequently associated with sexual signaling and mate choice. Previous work has shown that the physiological and genetic mechanisms that underlie presence or absence of secondary sexual characters in birds are highly diverse across the avian clade. Hormones such as estrogen and testosterone are known to have important impacts on the development and regulation of plumage coloration across an individual’s lifetime, but the distribution of what we know about hormones and dichromatism, relative to the distribution of dichromatic taxa, is confined to a few well-studied taxa. Here, we review current knowledge of hormonal influences on dichromatism and reconstruct the ancestral states of dichromatism across over 8800 species of birds to highlight where further research is needed. We find that, though two decades have passed since the last major review of hormonal influences on dichromatism, our working knowledge of how hormones influence dichromatism is still functionally and taxonomically limited. Moreover, there is increasing evidence that non-sex hormones such as cortisol and thyroid hormone may have multifarious impacts on dichromatism, including interactive effects on other influential hormones. By combining proximate and ultimate perspectives, we highlight the diversity of hormonal influences on dichromatism in the avian tree of life and put forward ideas for future study.

Introduction

Sexes are complex, multicomponent phenotypes that include traits both directly and indirectly involved in sexual reproduction. In many taxa, the differentiation of sex includes the presence of secondary sexual characters—often defined by divergence in size, ornamentation, or general appearance between the sexes. These traits may be involved in sexual signaling but are not directly involved in gamete production. Birds (class: Aves) have served as a model system for studying the evolution of secondary sexual characters. Sexual dichromatism, defined here as differences in plumage color between the sexes, has been well-studied in many avian species. Since (Darwin 1871), many studies have focused on sexual selection as the force leading to sexual dimorphism (e.g., Andersson 1994; Zuk and Simmons 2018). However, it has also long been recognized that dichromatism may evolve through natural selection (Wallace 1889), and can involve changes in male coloration, female coloration, or both (reviewed in Badyaev and Hill 2003).

In birds, secondary sexual characters are influenced by multiple genetic, hormonal, and developmental pathways. Feathers in particular are diverse in form, function, and development (reviewed in Terrill and Shultz 2023). Recent advances in understanding the cell-

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autonomous processes contributing to sex differences like dichromatism emphasize the need for focused research in understanding the multifaceted, and often interactive, mechanisms that shape phenotype (see Box 2). Though sexual selection and plumage color are both considered well studied, research often overlooks how the mechanisms generating sexual variation within species differ across taxa. The role of endocrine systems in generating differences between the sexes are well-studied in domesticated species like the chicken (*Gallus gallus domesticus*), though can vary across taxa (Kimball 2006). However, there is often a focus on research on males (Smiley et al. 2022), further inhibiting our understanding of mechanisms underlying both male and female coloration. Ignoring interspecific differences in the proximate drivers of within-sex variation can lead to misunderstandings about how sexual phenotypes diverge or overlap across ecological and evolutionary contexts, ultimately oversimplifying descriptions of sexual diversity and the process(es) by which sexual phenotypes evolve.

Kimball and Ligon (1999) and Kimball (2006) reviewed how estrogens, androgens, and luteinizing hormone (LH) regulate coloration patterns in birds, affecting both sexual dichromatism and intrasexual variation. Hormones influence plumage coloration by affecting pigment synthesis, pigment deposition, and feather microstructure; but these influences are not uniform across the avian tree of life. Estrogen-dependent dichromatism, found in orders such as Struthioniformes (ostriches), Galliformes (e.g., chickens, turkey, and quail), and Anseriformes (ducks and geese), is likely ancestral, whereas testosterone, luteinizing hormone, or nonhormonal dependent-coloration are considered to be more derived.

Advances in avian phylogenetics (e.g., Stiller et al. 2024) and hormonal studies since Kimball (2006) necessitate an updated review of hormonal influences on plumage dichromatism and a summary of remaining knowledge gaps. This includes the incorporation of two additional hormones hypothesized to influence sex-specific plumage coloration: glucocorticoids (Kennedy et al. 2013) and thyroid hormones (Emmens and Parkes 1940). Here, we (1) reconstruct the evolution of dichromatism across a modern phylogeny of birds; (2) summarize current knowledge, specifically what has been learned since the previous review, about how four commonly occurring hormone systems are known to impact plumage color (estrogen, testosterone, glucocorticoids, and thyroid) to influence dichromatism; and (3) identify challenges and gaps in the published body of work and suggest directions for future study. We do not specifically discuss luteinizing hormone (LH), since we did not find any new research including this hormone since Kimball (2006). Non-hormonal mechanisms for sexual differentiation, such as sex-specific genes and sex chromosomes, have also been shown to be important in birds (Agate et al. 2003; Zhao et al. 2010). This has been a major scientific development in the last two decades (Bear and Monteiro 2013). However, in this review we focus primarily on hormones, while acknowledging an important role for other factors like genes and gene-hormone interactions on the development of secondary sexual characters like dichromatism.

By bridging proximate and ultimate perspectives, we aim to move toward a comparative understanding of how endocrine regulation repeatedly shapes the evolution of secondary sexual characters. Through this primer, we illustrate the diversity and complexity of hormonal influences on sexual dichromatism within birds, highlight the areas of the avian tree of life that need further exploration, and provide future direction for researchers interested in studying avian sexual dichromatism and/or the impacts of hormonal systems on secondary sexual characters.

Box 1: For the purposes of this review, we define terms that we used in the process of reviewing and summarizing literature. Visible plumage color refers to the structural and pigmented properties of feathers that reflect or absorb light viewable in the visible spectrum. Pigmentation generates color by absorbing specific wavelengths of light (e.g., melanins for browns and blacks, carotenoids for reds and yellows). In contrast, structural coloration produces color through the scattering or interference of light by microscopic feather structures (e.g., many blue or iridescent colors). Many colors are produced by a combination of both pigmented and structural color, such as greens in parrots (Psittacidae) that arise from a blue structural base with a yellow pigment overlay.

We refer to "male" and "female" to describe the different physical and behavioral phenotypes typically associated with sperm or egg production, typically assumed based on the presence of testes or ovaries during dissection of a small number of individuals (sex4, *sensu* Warkentin et al. 2026). Our ability to measure this, however, is limited by descriptions in the literature and field guides. These sources often collapse variation within sexes down to a singular image, ignoring both within-population and between population differences and tending to show maximal dichromatism in order to emphasize the possible range of differences between males and females. We recognize that sexes are more accurately described as a population-level trait hyperspace, and that a single image does not encompass all possibilities.

Monochromatic refers to species in which the sexes have similar plumage colors and patterns. Dichromatic means the opposite, where sexes within the same species have different colors and/or patterns. In many dichromatic species, the male phenotype is labeled as “bright,” “ornamented,” or “conspicuous,” meaning their plumage often possesses more overall pigment than females. However, it is important to note that the males of dichromatic species may also be achromatic (e.g., predominantly white or predominantly black plumage), while still being considered the “bright.” While “brightness” (or value) traditionally measures total light reflectance, biological literature frequently uses “bright” to colloquially describe highly contrasting plumage regardless of its actual achromatic value. As a whole, male birds have a wider range of colors (hues), and greater color intensity (saturation/chroma) than females (Delhey et al. 2023). Conversely, most female phenotypes in dichromatic species are considered to be “dull,” with plumage that better resembles their environment, such as browns, grays, and greens. If a species has “reversed” sexual dimorphism, then the females are considered more bright/ornamented/conspicuous than males. Finally, in some dichromatic species, the degree of difference between male and female plumage color varies seasonally. It is generally greatest when males molt into their “breeding,” “nuptial,” or “alternate” plumage (e.g., bright) and least when males molt into their “nonbreeding,” “eclipse,” or “basic” plumage (e.g., dull). The specific terminology is very taxon-dependent (Pittaway 2000), so for the purposes of this paper we use the more general “breeding” and “nonbreeding” terms.

Literature review

Literature review methods

This review expands upon Kimball’s (2006) review of hormonal influences on plumage coloration by adding an additional 20 years of studies with known associations between hormones and visible plumage dichromatism. We used Google Scholar to identify relevant publications using combinations of search terms that included “estrogen,” “testosterone,” “cortisol,” corticosterone’, “glucocorticoids,” “thyroid,” and “thyroxine.” For each hormone, we used the Boolean operators (AND/OR) combined with “hormone,” “dichromatism,” “dimorphism,” “plumage color,” “ornamentation,” “‘male,” “female,” and “birds” to search for relevant publications. Due to the broad nature of these search terms, we also explored articles citing Kimball and Ligon (1999) and Kimball (2006) and reviewed reference lists of key papers for additional citations. Papers were manually reviewed for information and questions about hormonal impacts on plumage dichromatism.

One of our primary goals was to identify taxonomic gaps in which there is little or no research involving hormones and coloration by mapping the presence or absence of research across the avian tree of life. In a number of cases, hormones were assessed or manipulated for reasons other than understanding their impact on molt or the development of dichromatism and therefore may have been done at times when molt was not occurring. Moreover, there were several studies our search returned that, while focusing more on intrasexual variation within a species than between-sex variation, provided important insights into hormonal mechanisms regulating plumage color and molt. These are included, as they might also be relevant to teasing out whether, or which, hormones are involved in dichromatism. As our understanding of hormonal influences on plumage dichromatism is unique for each taxon, we have included brief supplemental summaries of all of these relevant studies to facilitate future research. In these summaries (Table S1), we included information on hormones considered as well as whether hormones were assessed during molt or during other periods (e.g., the breeding season, when birds are not molting) to allow a quick overview of the existing literature for different species. We also classified methods used in these studies into one of three categories: (1) direct physiological experiments such as administration of hormones, castration, or skin grafts; (2) observations of differences in naturally occurring levels of hormones in wild populations; or (3) associations between plumage phenotype and genes/genomic regions that regulate hormones. Though we did not utilize the qualitative aspects of these studies in our reconstruction or identification of taxonomic gaps, we believe they could provide a “starting point” by highlighting hormone–coloration relationships that may also be important for the development of dichromatic characters during molt. The summaries in Table S1 are organized taxonomically to orient future researchers interested in more deeply pursuing these questions in these various clades.

Similarly, our search also returned some studies addressing hormonal influences on plumage color in predominantly monochromatic species or included color in the ultraviolet spectrum. In some cases, hormonal influences may have impacted plumage color in one sex, but not the other (Fargallo et al. 2014; Cruz-Miralles et al. 2020). Though these papers fall outside of the scope of understanding hormonal influences on visibly dichromatic species and are not included in our summary of literature on dichromatic species, they may provide important context to future studies wanting to investigate gains and losses in sister monochromatic/dichromatic taxa and are summarized in the supplement (Table S2).

Moreover, some studies returned through our search methods addressed the impact of hormones on other color-related secondary sexual characters other than plumage, such as bill, leg, or bare integument (Eens et al. 2000; McGraw 2006; Siitari et al. 2007; Mougeot et al. 2010; Casagrande et al. 2011; Sarasola et al. 2011; Lahaye et al. 2014; Rull et al. 2016; Scheun et al. 2021; Green et al. 2022; Romero-Diaz et al. 2022). However, we considered these studies to be outside of the scope of this review to limit the focus on hormonal impacts on plumage-based dichromatism specifically. We also intentionally excluded manual manipulations or cosmetic applications of pigment, such as daubing behavior in the Crested Ibis (*Nipponia nippon*, Liu et al. 2023) or application of carotenoids on feathers by Greater Flamingos (*Phoenicopterus roseus*, Amat et al. 2018), in our definition of dichromatism.

Literature review results

Including citations from Kimball (2006), we found 50 species, representing 22 avian families, where hormones and sexually dimorphic plumage features were featured (Table 1). Though several of these studies did not directly test the influence of hormones on dichromatism, they may have looked for a correlation of hormones and coloration, typically in the breeding (non-molt) season. We also found one taxon published before 2006 that had not been included previously: the Satin Bowerbird (Ptilonorhynchus violaceus; Collis and Borgia 1993).

Ancestral state reconstruction of dichromatism

Dichromatism dataset

We used a published dataset by Han et al. (2026) which consisted of color measurements taken from standardized reference illustrations (book plates) from Birds of the World (Billerman et al. 2026) for 10,170 bird species to classify visible color dimorphism between sexes. The dataset included both continuous (color measurements) and discrete (monochromatic/dichromatic) representations of dichromatism. For the purposes of reconstructing dichromatism, we used the continuous data to illustrate the diversity of dichromatism across the avian tree of life (Fig. 1A) and the categorical data to denote the number of changes between monochromatic and dichromatic states (Fig. 1B). To avoid uncertainty, we excluded any taxa that had incomplete data (e.g., species that only had illustrations of one sex and were not labeled as monochromatic) in each analysis.

Continuous reconstruction

For the continuous dataset, it is important to note that these illustrations often include non-plumage parts such as legs, bills, and bare integuments. As such, these values aren't precise representations of visible plumage dichromatism. However, plumage color accounts for most of the color space difference, and monochromatic species are represented by only one plate, making the data useful for broader comparisons among taxa. We first converted the color spaces into their RGB values and calculated the weighted mean RGB per species per sex, combining all spaces. We then calculated the overall Euclidean distance between sexes. Monochromatic species were scored as "0." Finally, we reconstructed these Euclidean distances at ancestral nodes using the fastAnc function in phytools (Revell 2024) in R Version (v4.4.3; R Core Team 2025) and plotted the results on an updated tree of all birds (McTavish et al. 2025). As the updated tree did not match the Han et al. (2026) taxonomy, we used the crosswalk in McTavish et al. (2025) to reconcile the taxonomy of our dataset, resulting in a final total of 8882 species (Fig. 1A). To summarize differences in dichromatism across the tree, we also found the average overall Euclidean distance for each family ($n = 231$) and ranked them from highest to lowest (most to least dichromatic, Table S3).

Discrete reconstruction

With the discrete dataset, we separated any taxa with the "monochromatic" descriptor from taxa that had both "male" and "female" descriptions in the Han et al. (2026) dataset. Any taxa that had only one sex listed, and did not have the monochromatic descriptor, were removed to avoid ambiguity, resulting in 8848 species. We summarized the number of monochromatic and dichromatic species in each family (Table S4). We performed 1000 stochastic simulations using the function simmap with equal rates in phytools (Revell 2024) to estimate the evolutionary history of the trait across the phylogeny (Fig. 1B). We found that there were almost twice as many losses of dichromatism (e.g., transitions from dichromatic to monochromatic; $n = 621$) than gains of dichromatism (e.g., transitions from monochromatic to dichromatic; $n = 367$ transitions).

Identifying taxonomic gaps in the literature

We marked families with species found in the literature review on the continuous reconstruction (Fig. 1A), and dichromatic families with over 20 species that did not have studies including the relationship between hormones and coloration on the discrete reconstruction (Fig. 1B). Our review found that the distribution of taxa studied extends across the avian tree of life. However, it also identified several large

Table 1 Avian species where hormonal impacts on sexually dimorphic plumage color have been studied

#	Family	Examples	Citations
1	Struthionidae	Common ostrich (*Struthio camelus*)	(Duerden 1919)
2	Odontophoridae	Gambel's quail (*Callipepla gambelii*)	(Hagelin and Kimball 1997; Hagelin 2001)
3	Phasianidae	Red junglefowl/domestic chicken (*Gallus gallus/Gallus gallus domesticus*)	(Torrey and Horning 1922; Buchanan 1926; George et al. 1981; Widelitz et al. 2019; You et al. 2024; Blivaiss 1947a, 1947b)
		Willow ptarmigan (*Lagopus lagopus*)	Stokkan 1979a, 1979b; Höhn and Braun 1980)
		White-tailed ptarmigan (*Lagopus leucura*)	(Höhn and Braun 1980)
		Common quail (*Coturnix coturnix*)	(Kannankeril and Domm 1968)
		Ring-necked pheasant (*Phasianus colchicus*)	(Danforth 1937a, 1937b; Morejohn and Genelly 1961)
		Lady amherst's pheasant (*Chrysolophus amherstiae*)	(Vevers 1954)
		Reeves pheasant (*Syrmaticus reevesii*)	(Danforth 1937c)
		Wild turkey (*Meleagris gallopavo*)	(Scott and Payne 1934; van Oordt 1936)
4	Anatidae	Mandarin duck (*Aix galericulata*)	(Tang et al. 2025)
		Mallard (*Anas platyrhynchos*)	Goodale 1910, 1918; Walton 1937; Mueller 1970; Endler et al. 1988; Haase and Schmedemann 1992; Haase et al. 1995)
		Blue-winged teal (*Spatula discors*)	(Greij 1973)
5	Scolopacidae	Ruff (*Calidris pugnax*)	(Lank et al. 1999; Loveland, Giraldo-Deck, et al. 2021, et al. 2021)
		Red-necked phalarope (*Phalaropus lobatus*)	(Johns 1964)
		Wilson's phalarope (*Phalaropus tricolor*)	(Johns 1964)
6	Turnicidae	Barred buttonquail (*Turnix suscitator*)	(Muck and Goymann 2011)
7	Falconidae	American kestrel (*Falco sparverius*)	(Quinn et al. 2005; Butler et al. 2010)
		Common kestrel (*Falco tinnunculus*)	(Fargallo et al. 2007)
8	Pipridae	Golden-collared manakin (*Manacus vitellinus*)	(Day et al. 2006)
9	Ptilonorhynchidae	Satin bowerbird (*Ptilonorhynchus violaceus*)	(Collis and Borgia 1993)
10	Maluridae	Red-backed fairy-wren (*Malurus melanocephalus*)	Lindsay et al. 2009, 2011, 2016; Barron et al. 2013; Lantz et al. 2017; Khalil et al. 2020, 2023)
		White-shouldered fairy-wren (*Malurus alboscapulatus*)	Enbody et al. 2018, 2022; Boersma et al. 2020, 2023)
		Superb fairy-wren (*Malurus cyaneus*)	(Peters et al. 2000; Peters 2007)
11	Hirundinidae	Barn swallow (*Hirundo rustica*)	(Eikenaar et al. 2011; Jenkins et al. 2013; Arai et al. 2019)
		Tree swallow (*Tachycineta bicolor*)	(Sarpong et al. 2019)
12	Muscicapidae	European pied flycatcher (*Ficedula hypoleuca*)	(Moreno et al. 2014)
		Black redstart (*Phoenicurus ochruros*)	(Schwarzová et al. 2010)
13	Turdidae	Eastern bluebird (*Sialia sialis*)	Grindstaff et al. 2012; Siefferman et al. 2013)
14	Viduidae	Paradise whydah (*Vidua paradisaea*)	(Ortman 1967; Ralph et al. 1967)
15	Estrildidae	Red avadavat (*Amandava amandava*)	(Thapliyal and Tewary 1961, 1963)
		Chestnut munia (*Lonchura atricapilla*)	(Saxena and Thapliyal 1961)
		Gouldian finch (*Erythrura gouldiae*)	(Crew and Munro 1939)
16	Ploceidae	Southern red bishop (*Euplectes orix*)	(Lindsay et al. 2022)
		Northern red bishop (*Euplectes franciscanus*)	(Witschi 1936; Ortman 1967)
		Yellow-crowned bishop (*Euplectes afer*)	(Ortman 1967; Ralph et al. 1967)
		Baya weaver (*Ploceus philippinus*)	(Saxena and Thapliyal 1961)
		Red-billed quelea (*Quelea quelea*)	(Witschi 1935)
17	Passeridae	House sparrow (*Passer domesticus*)	(Keck 1934; Miller 1935; Mueller 1977; Evans et al. 2000; Lattin and Romero 2013)
18	Fringillidae	European serin (*Serinus serinus*)	(Trigo and Mota 2015)
		Redpoll (*Acanthis flammea*)	(Fairhurst et al. 2014)
		House finch (*Haemorhous mexicanus*)	(Tewary and Farner 1973; Stoehr and Hill 2001; Lendvai et al. 2013)
		American goldfinch (*Spinus tristis*)	(Sughrue et al. 2008)

Table 1 Continued

#	Family	Examples	Citations
19	Passerellidae	Dark-eyed junco (*Junco hyemalis*)	(McGlothlin et al. 2008)
20	Icteridae	Red-winged blackbird (*Agelaius phoeniceus*)	(Kennedy et al. 2013; Merrill et al. 2015)
		Brewer's blackbird (*Euphagus cyanocephalus*)	(Danforth and Price 1935)
21	Parulidae	Common yellowthroat (*Geothlypis trichas*)	(Henschen et al. 2018)
		Yellow warbler (*Setophaga petechia*)	(Grunst et al. 2015)
22	Cardinalidae	Northern cardinal (*Cardinalis cardinalis*)	(Sin et al. 2020)
		Indigo bunting (*Passerina cyanea*)	(Witschi 1935; Hudson and Wilcoxen 2018)

Note: Species are organized taxonomically by family. Table S1 provides further descriptions of findings for all taxa.

families with high levels of dichromatism that have no publications describing any hormonal correlates (i.e., Nectariniidae [sunbirds and spiderhunters], and Thamnophilidae [typical antbirds]). Moreover, families such as Muscicapidae (Old World flycatchers) have multiple gains and losses of dichromatism within the family, making them—and other families with both monochromatic and dichromatic species—ideal systems to study the potential drivers of gains and losses of dichromatism.

Hormones

Estrogens

Estrogen (oestrogen) is one of two primary categories of sex hormones known to contribute to dichromatic plumage in birds. In vertebrates, estrogen hormones such as estradiol (E2) are highly conserved in regulating the female reproductive cycle and secondary sexual characteristics. While estrogen is commonly associated with females, it can be converted from androgens (e.g., testosterone) by the enzyme aromatase in either sex (Schlinger and Arnold 1992; Saldanha and Schlinger 1997; Schlinger 1997). Increased expression of aromatase in domestic chickens have contributed to our understanding of how estrogen induces female-like plumage in males (George et al. 1990; Matsumine et al. 1991; Lambeth et al. 2016) and our overall understanding of sexual development in birds (Jin et al. 2020; Abdulateef et al. 2021). However, modern studies on the impact of estrogens or aromatase on plumage dimorphism in birds, especially wild populations, are largely absent even though the mechanisms to manipulate either estrogens or aromatase in wild birds are available.

Of all hormones related to plumage dichromatism, estrogen's impact is the best studied. Estrogen-dependent dichromatism has been documented in three orders of birds: Struthioniformes (ostriches), Galliformes (e.g., chickens, turkey, and quail), and Anseriformes (ducks and geese), which encompass the earliest divergences among extant birds. All three orders harbor at least one species with dichromatic plumage, include well-studied species, and are globally domesticated for agricultural purposes. Notably, studies on estrogen's effects on plumage have focused on the domestic chicken and mallard, both of which have served as model systems for avian biology, though other species in both orders are commonly maintained in captivity where evidence supports a role for estrogens in plumage dichromatism. While there is suggestion of estrogen's involvement in species from other avian families, such as canaries (see Gazda et al. 2020), this has not been examined in any research studies and so is purely speculative.

In Struthioniformes, Galliformes, and Anseriformes, dichromatism is thought to be solely due to melanin or structural coloration, and estrogen's effects on dichromatism are thought to be limited to melanin production and melanocyte contribution to iridescent coloration (Ma et al. 2021). Genes linked to sex-specific plumage color in these systems are also linked to melanin and melanocyte production, including TYRP1 (Ma et al. 2021) and ASIP in domestic chickens, whose expression is proposed to be moderated by estrogen (Oribe et al. 2012). Mismatches between gonadal sex and secondary sexual characters (Box 2) are frequently reported in both Galliformes and Anseriformes, where female birds gain male-like traits later in life. These gains of "bright" male-like traits in females are associated with the loss of estrogen production that occurs with ovarian senescence (Chiba and Honma 2011).

In birds, it has long been suggested that the evolution of secondary sexual characters such as plumage dichromatism can be attributed to gains of elaborate features on males through female choice (Darwin 1871). However, estrogen's effect on female plumage suggests that, regardless of what affects male coloration, strong selective pressures, such as natural selection to favor crypticity at the nest (Wallace 1889) have also favored mechanisms that suppress bright plumage in females. Estrogens emphasize why understanding the mechanism underlying plumage dichromatism is important: in these groups, the "male" phenotype may arise from the ab-

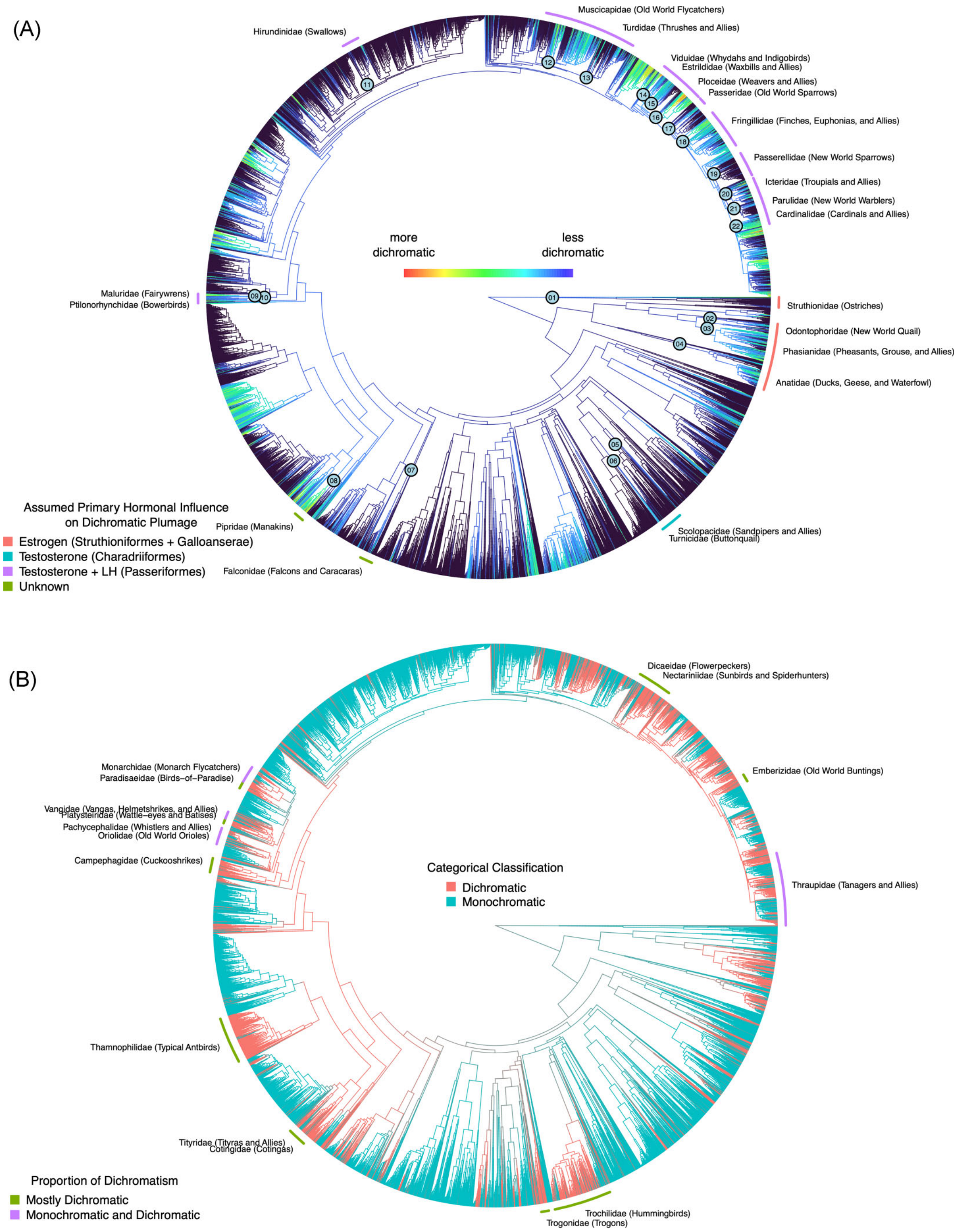

Fig. 1 (A) A phylogenetic tree of 8882 bird species with a continuous reconstruction of dichromatism. More dichromatic means higher degree of difference (higher Euclidean distance) in color between males and females. Less dichromatic means lower degree of difference, or no difference. Euclidean distances were square root transformed for visualization purposes. The families marked on the tree have at least one study where hormonal influences on dichromatism have been investigated. The number of the internal nodes corresponds with studies listed in Table 1. The arc colors represent what the assumed hormonal influences are for each group, if known. (B) A phylogenetic tree of 8848 bird species with a categorical/discrete reconstruction of dichromatism. Families that are labeled have over 20 species that have no known literature on hormonal influences on dichromatism. The colors of the arc labels represent the relative proportion of monochromatic to dichromatic species in that family. Families were labeled as "mostly monochromatic" if less than 40% of their taxa were dichromatic, "mostly dichromatic" if greater than 60% of their taxa were dichromatic, or "mixed" if the proportion of dichromatic taxa fell between 40 and 60% (Table S4). For visualization purposes, families with fewer than 20 species were not labeled on the tree. Alt Text: Phylogenetic trees of 8882 bird species. One tree shows the degree of sexual dichromatism reconstructed as a continuous variable, and highlights clades with the likely hormonal mechanisms underlying sexual dichromatism where known. The second tree reconstructs color as a binary (dichromatic / monochromatic) trait and highlights families that are mostly dichromatic, mixed, or mostly monochromatic.

sence of estrogen rather than from male-biased hormonal signals, challenging a commonly held assumption that sexual selection alone drives plumage dimorphism.

Box 2: Genetic variation and developmental processes can lead to extensive variation in association between sex-related traits, including gametes, gonads, sex chromosomes, anatomy, or morphology. Historically, the discovery and description of individuals that have rare combinations of these traits have often driven deeper inquiry into the proximate mechanisms of sexual dichromatism (Hunter 1780; Brooks 2019). Uncommon combinations of sexual traits are often difficult to detect, but there is evidence that the association between gonads and sex chromosomes may be less aligned than previously thought (Hall et al. 2025). In several of the taxa where hormonal influences have been found, there is also evidence of individuals possessing more than one sexual phenotype in their lifetimes (Forbes 1947).

Bilateral gynandromorphs—individuals that simultaneously possess both male and female phenotypes on either side of their body—have historically challenged our understanding of hormonal influences on plumage dichromatism (Major and Smith 2016). Gynandromorphs have been observed among several avian orders, with a substantial number found within the Passeriformes (see Stępniewski and Surmacki 2023 for review). The clear division of male and female plumage types on a single individual raises an intriguing question: How can an individual whose plumage relies on sex-specific hormonal influence maintain both male and female phenotypes when levels of circulating hormones are equal throughout the body?

The relatively new theory of cell-autonomous sex identity (CASI) proposes a hypothesis. The CASI model states that, in birds, somatic cells possess an inherent, genetic sex ("male" ZZ or "female" ZW) that dictates their sexual phenotype directly, rather than relying primarily on hormones for differentiation (Chue and Smith 2011; Clinton et al. 2012). One of the first studies on CASI investigated gynandromorphic chickens (Zhao et al. 2010) and demonstrated that this model may protect certain cells from hormonal influence, leading to the maintenance of simultaneous male and female secondary sexual characters regardless of the composition of circulating hormones. This has had a significant impact on our understanding of sex expression in birds (Arnold and Itoh 2011), but further research is still needed to fully understand CASI and epigenetic effects on sex development in birds (Lambeth et al. 2016; Zhang et al. 2023) as well as the role of hormones in that development (Lengyel et al. 2024).

While the CASI model is relatively new, the concept that phenotypic expression is based on interactions between cell-specific gene networks and endogenous hormones is a basic concept in developmental biology (West-Eberhard 2003a). In mammals, classic models describe how sex-determining genes dictate gonadal development, while hormones determine the development of sexually dimorphic characteristics. Yet even in mammals, more recent research has shown that this is an oversimplification (Arnold 2020). While gynandromorphic birds have historically questioned how circulating hormones can contribute two distinct phenotypes in the same individual, our growing understanding of how both genes and hormones affect sexual development extends our understanding of the underlying causes of sexually dimorphic phenotypes (Bear and Monteiro 2013). The CASI model in birds demonstrates that hormone-gene interactions may play a more important role in the development of secondary sexual characteristics than previously thought. Yet many questions about the complex interaction between genes, hormones, and the environment remain to be answered before we can fully reconcile how these two models produce these uncommon combinations of sexual characters.

Androgens

Androgens are the other class of sex hormones frequently attributed to sexually dichromatic plumage in birds. Among them, the hormone testosterone is most frequently associated with male-like characteristics and is the most well studied in the context of the regulation of male plumage color in sexually dichromatic species. As with estrogen, testosterone and other androgens can be found in either sex. Ketterson et al. (2005) found a positive correlation between the difference in testosterone levels between males and females and degree of dimorphism (including body size and social behavior, in addition to plumage) across 44 avian families in 9 orders, emphasizing the potential widespread influence of testosterone on the evolution of secondary sexual characters. The relationship between testosterone and plumage dichromatism can also be associated with luteinizing hormone (LH), a peptide hormone that increases the secretion of testosterone and other androgens in both males and females (Kimball 2006). However, though several recently published studies we reviewed in this paper referenced LH, we found no direct tests for its influence on dichromatism in the last 50 years (Table 1).

Studies of testosterone's impact on plumage dichromatism are more phylogenetically widespread than estrogen's—with the largest order of birds, Passeriformes (songbirds), representing the bulk of research. Fairywrens (Maluridae) are a model system for investigating testosterone's effects on plumage color (Peters et al. 2013). The red-backed fairywren (*Malurus melanocephalus*) in particular has been studied at observational, experimental, and genomic levels and this research program has been critical toward our understanding of testosterone's regulation of carotenoid coloration (Lindsay et al. 2016; Khalil et al. 2020, 2023). In Charadriiformes (shorebirds), testosterone is thought to act without the influence of luteinizing hormone, as evidenced by the polymorphic Ruff (*Calidris pugnax*), wherein a male phenotype with a chromosomal inversion has both dull plumage (the female-like "faeder" phenotype) and a decreased output in testosterone production (Loveland, Giraldo-Deck, et al. 2021, Loveland, Lank 2021). Testosterone has also been proposed to play a pleiotropic role in melanin regulation (Béziers et al. 2017) and the induction of breeding/nonbreeding molt in males of dichromatic species with predominantly melanin-based plumage (Tang et al. 2025).

Testosterone has also been documented to impact the onset of bright plumage in the females of some species, though it is suspected that circulating testosterone in females does not regulate secondary sexual characteristics in females the same way as males (Goymann and Wingfield 2014). In white-shouldered fairywrens (*Malurus alboscapulatus*), where ornamentation is considered to be a derived trait in females (Enbody et al. 2022), females with more male-like plumage (*M. a. moretoni*) have been documented with higher circulating testosterone than females with unornamented plumage (*M. a. lorentzi*) (Enbody et al. 2018), though the variation in plumage may be the result of varied regulation of responses to androgens instead of capacity to produce testosterone (see Boersma et al. 2023 for discussion). Female Ruffs treated with testosterone implants exhibited male courtship behavior and molt into male plumage phenotypes, and these effects were reversed when the implants were removed (Lank et al. 1999). In female Barred Buttonquails (*Turnix suscitator*), a sex-reversed species, testosterone exhibited a correlation with melanin levels in females but not in males (Muck and Goymann 2011). While testosterone might seem a logical hormone to regulate dichromatism, and it has been experimentally manipulated to explore its role on behavior in a variety of species, its established impact on plumage dichromatism appears to be limited to a few orders, and, at least among Passeriformes, is only definitively known to affect plumage dichromatism in a handful of families.

Glucocorticoids

Glucocorticoids are a class of steroid hormones that are frequently involved in processes such as stress response, metabolism, and immune function. Most research has focused on two specific glucocorticoids, cortisol and corticosterone (hereafter, referred to collectively as CORT). No studies have identified CORT as affecting dichromatic plumage coloration. However, CORT has been suggested to affect feather microstructure (Kennedy et al. 2013) and is a candidate for modifying feather coloration (e.g., altering brightness) even if it does not alter whether a patch has male or female coloration. Consistent with this, several studies have found a relationship between CORT (or CORT receptors) and aspects of melanin, carotenoid, or structural coloration (Grindstaff et al. 2012; Henderson et al. 2013; Kennedy et al. 2013; Fairhurst et al. 2014; Grunst et al. 2015; Henschen et al. 2018; Cruz-Miralles et al. 2020), though some of these studies were conducted when birds were not molting (see Table S1).

The extent to which CORT has a direct effect on coloration, versus an indirect effect, is not clear. Experimental studies, involving either supplementation of CORT or trimming feathers to stimulate molt found mixed results, with two studies finding no relationship (e.g., Butler et al. 2010; Barron et al. 2013), and only one suggested relationship with UV coloration (Windsor et al. 2019). A challenge in understanding the impact of CORT on melanin-based plumage coloration is due to pleiotropic effects in the melanocortin system (Ducrest et al. 2008; Roulin and Ducrest 2011). Melanocortins are all derived from the prohormone proopiomelanocortin (POMC) gene, and these are capable of binding different melanocortin receptors. For example, the various melanocyte stimulating hormones (α, β, γ-MSH) can bind to melanocortin receptor 1 (MC1R), which affects melanin production. However, the same hormones can also bind to melanocortin receptors 3, 4, and 5, which affect a variety of processes such as metabolism, stress responses, and aggressiveness (Roulin and Ducrest 2011). Thus, a correlation between CORT and coloration may be indirect through pleiotropy rather than causative (e.g., where CORT would directly affect coloration; Jenkins et al. 2013).

Thyroid hormone

Thyroid hormone, a class of amine hormone, plays a number of roles in the life cycle of a bird, including the regulation of metabolic activity, body growth, the timing of seasonal reproductive cycles, and the regulation of annual molts (McNabb 2007). Historic experimental manipulations of thyroid hormone have established their importance in feather development (Hall

1969; Lucas and Stettenheim 1972), including the regulation of melanin (Cole and Hutt 1927). In chickens, thyroid hormone contributes to the development of sexual dichromatism: young male chickens grow female-like feathers under hyperthyroidal conditions (high thyroid hormone levels) but retain male-like behavior and other dimorphic morphologies such as spurs, combs, and wattles (Torrey and Horning 1922; Greenwood and Blyth 1938). Induced hypothyroidism (reduced thyroid hormone levels) can alter female feathers to appear more male-like, but the precise effect is not clear (Greenwood and Blyth 1938).

These studies on domestic chickens underscore the potential pleiotropic effects thyroid hormone may have on sexual dichromatism. Though the previous body of work on sexual dimorphism in Galliformes focused predominantly on the role of estrogen in its regulation, modern research has shown that estrogen-dependent plumage coloration relies on the effects of deiodinases and thyroid hormones in chickens (You et al. 2024). Specifically, estrogen causes a decrease in the expression of DIO3, an enzyme that inactivates thyroid hormones. This increases the conversion of T4 (thyroxine) to the activated T3 form (triiodothyronine), leading to a transcriptomic cascade resulting in female feather coloration. Although gonad–thyroid interactions on plumage dichromatism have been previously proposed (Torrey and Horning 1922), this study has shifted our understanding of estrogen-dependent plumage dichromatism toward a multi-step, interactive, model. Further, the study of thyroid hormone on plumage dichromatism underscores that gonadal hormones such as estrogen only act as they do within the specific developmental ecosystem of each individual at a given stage of development. While we often consider gonadal hormones to be "master regulators" of dimorphism, moving forward it may be more accurate to characterize plumage dichromatism as the result of several interacting genes and hormones.

Discussion and future directions

Here we demonstrate that, while not ubiquitous, studies on hormonal influences on plumage dimorphism can be found across the avian tree of life (Fig. 1A). However, as is clear in Fig. 1B, we still know little about the role of hormones in plumage dichromatism across many notable avian clades. In many groups that have been studied, those studies are limited to a single hormone (e.g., testosterone), making it unclear whether dichromatism might depend on other hormones, or an interaction of several hormones (e.g., You et al. 2024). Thus, there is much work to be done to develop a comprehensive model of the hormonal impacts on plumage coloration throughout the avian tree of life.

As with Kimball (2006), we found further support that estrogen predominantly suppresses bright plumage in females within Struthioniformes, Galliformes, and Anseriformes, which are predominantly characterized by melanin and structural coloration. Studies on testosterone frequently focused on the promotion of carotenoid-based signals in males within Passeriformes, though testosterone may also play a role in the regulation of melanin-based plumage. Research on CORT has not been focused on questions about dichromatism, though its influence on feather microstructure has the potential to modify the strength of sexually dichromatic signals. In contrast, thyroid hormone has a clear influence on sexual dichromatism and a proposed molecular mechanism to its effects on the melanocortin system. However, this has never been studied outside of the domestic chicken, to our knowledge. Furthermore, while LH is known to be important in some species, there have not been recent studies looking at this hormone or further understanding how it interacts with other hormones (such as estrogen; Thapliyal and Tewary 1961, 1963) to affect dichromatism.

While we have some basic knowledge of the role of hormones in affecting plumage dichromatism, recent research has also highlighted some of the complexities in answering questions about the proximate and ultimate drivers of dichromatic plumage. Below we highlight some considerations for future study.

(1) Age and season matter when sampling

Across all birds, age, and time of year can strongly influence interpretations of hormone–plumage relationships. In birds, coloration can also change drastically during different life-stages and seasons. As such, the degree of sexual dichromatism can shift and change depending on the life history of a species. For example, annual cyclical molts between breeding and nonbreeding plumages in some dichromatic species, such as the Mandarin Duck (*Aix galericulata*), can result in dull or "female-like" plumage in males for part of the year. Though dichromatism in ducks (Anseriformes) is considered to be largely controlled by estrogen, recent research shows that male Mandarin Ducks experience a peak in testosterone prior to molting into breeding plumage, and a second peak preceding the molt into eclipse plumage (Tang et al. 2025). Developmental stages may also complicate patterns of dimorphism. In some monochromatic species such as the Mexican Duck (*Anas diazi*), male-like traits present in closely related dichromatic species appear during juvenile stages but disappear in adulthood (Brown et al. 2022). In yellow warblers, lower feather CORT was associated with higher carotenoid hues, but only in young individuals (Grunst et al. 2015). We are just beginning to understand the role that hormones play in annual and developmental molt, but the basic knowledge of these proximate mechanisms can help inform our broader understanding on how dichromatism evolves (Schaedler et al. 2021).

(2) Different pigment classes operate through different proximate mechanisms

When studying hormonal effects on plumage coloration, it is critical to recognize that different pigment classes (e.g., melanins, carotenoids, and structural color) operate through distinct proximate mechanisms and may respond differently to hormonal regulation (Badyaev and Hill 2000). Even within pigment classes, different biochemical pathways can produce contrasting outcomes. For example, eumelanin and pheomelanin have different physiological regulation and ecological correlates (Galván and Solano 2016). In Common Kestrel (*Falco tinnunculus*) fledglings, increased testosterone reduced gray coloration in rump feathers, producing a more “female-like” phenotype. However, this pattern may not reflect suppression of overall melanin production; instead, it may be increases in pheomelanin over eumelanin leading to browner plumage (Fargallo et al. 2007). The regulation of these pigments may also differ between the sexes. For example, superb fairywren (*Malurus cyaneus*) females treated with testosterone begin to molt into male breeding plumage but fail to develop the blue or black structural coloration present in males (Peters 2007).

(3) Divergent genetic pathways lead to dichromatic plumage

As most dichromatic species have a bright male and a dull female, dichromatism may arise either through the loss of bright coloration in females, through gains in brightness in males, or both. There is evidence for multiple hormonal pathways influencing plumage coloration in either sex. Ottenburghs and Harteman (2021) showed that a cross between one monochromatic dull (Philippine Duck, *Anas luzonica*) and one monochromatic bright (Chiloe Wigeon, *Mareca sibilatrix*) species results in a dichromatic hybrid. The (likely) restoration of bright plumage in one sex, but not the other, highlights the importance of studying the genomic influences on plumage coloration in both sexes. In essence, if monochromatic plumage developed due to the same process in both species, it would likely have led to a monochromatic hybrid. In contrast, other waterfowl hybrids between monochromatic dull and dichromatic species [e.g., Mallard (*Anas platyrhynchos*) x American Black Duck (*Anas rubripes*) hybrids], the males possess intermediate plumage phenotypes. These patterns suggest that some plumage traits may be governed by dosage-dependent or additive genetic effects or by pleiotropic loci with sex-limited expression. Understanding the genomic and transcriptomic processes behind “male” and “female” polymorphisms (e.g., Loveland, Giraldo-Deck, et al. 2021, Loveland, Lank 2021) and recognizing the potential for sex-specific evolutionary pathways (Ottenburghs 2024) are important for interpreting patterns of dichromatism and for identifying the selective pressures and physiological mechanisms underlying them.

(4) Multiple selective pressures can drive similar plumage patterns

Our identification of gains and losses of dichromatism across the phylogeny did not test for ecological or behavioral associations with sexually dimorphic plumage. Future studies interested in asking questions about the evolutionary drivers of dichromatism from a comparative perspective would be most effective at a smaller scale with well-resolved phylogenies, comprehensive trait data, and color descriptions that do not rely on simplifications of literature or reliance on binary classification (Johnson et al. 2013; Beltrán et al. 2022; Gao et al. 2025). These more focused studies are also more accurate in determining in which taxa dichromatism is considered ancestral and in which it is derived (Badyaev and Hill 2003), the number of transitions between monochromatic and dichromatic states within a taxonomic group, if sexual dimorphism influences speciation rates within that group (Huang and Rabosky 2014), and whether or not dichromatic features are influenced by hormones. Understanding the mechanisms underlying dichromatism may assist in interpretation of such studies (such as the role of estrogen in suppressing bright plumage in galliform birds suggesting strong selection for female crypticity).

Beyond variation in proximate mechanisms (e.g., pigment-specific pathways or sex-specific hormonal regulation) researchers studying the evolution of sexually dimorphic plumage color should also consider that multiple selective pressures may drive sex differences in plumage, including social signaling, mate choice, and ecological interactions. Research on visual signaling specifically often focuses on interactive effects on hormones, colors, and behavior—such as ties between melanin coloration and aggression (Bókony et al. 2008; Ducrest et al. 2008; Mcglothlin et al. 2008; McGraw 2008) or extra-pair paternity (Valcu et al. 2025). However, there is no single model that explains a link between the proximate mechanisms and evolutionary drivers of dichromatism. For example, in male Song Sparrows (*Melospiza melodia*), higher testosterone levels were associated with increased breast spotting but reduced territorial aggression (Beck et al. 2018); but similar increases in testosterone in male Golden-collared Manakins (*Manacus vitellinus*) increased display behaviors but did not affect plumage coloration (Day et al. 2006). Moreover, in many monochromatic species, hormones may influence non-plumage, sexually dichromatic ornaments such as wattles, combs, legs, and bills (Eens et al. 2000; Siitari et al. 2007; Casagrande et al. 2011; Sarasola et al. 2011; Lahaye et al. 2014; Rull et al. 2016; Scheun et al. 2021; Romero-Diaz et al. 2022) but not plumage color. From a comparative perspective, independent gains of dichromatism, even in closely related taxa, may be the result of different proximate mechanisms compensating for similar evolutionary pressures.

(5) There is no simple definition of dichromatism

In this primer, we attempted to describe dichromatism using both continuous and discrete parameters. However, like sexes themselves, color phenotypes are complex, multidimensional phenotypes. Most sexual color phenotypes are determined through photos and museum specimens which may not represent the entire species and may not represent the full visual spectra of the avian visual system. For example, many species exhibit sexual differences outside the human-visible spectrum, such as cryptic dichromatism in the ultraviolet spectrum of tanagers (Thraupidae; Burns and Shultz 2012) or fluorescent plumage in owls (Strigidae; Griffith et al. 2025) and birds of paradise (Paradisaeidae; Martin et al. 2025). Because data on these traits remain limited, such systems were excluded from our study. However, future research exploring hormonal influences on ultraviolet or fluorescent plumage could reveal additional pathways through which endocrine systems shape sexually dimorphic signals.

Moving forward, in differentiating between "dichromatic" and "monochromatic" species, it is paramount to consider that dichromatism varies on a spectrum of multiple axes. In all species, coloration on different parts of the body can vary independently, and so can the hormonal influences on those patches. For example, in female European pied flycatcher (*Ficedula hypoleuca*), where testosterone is associated with the size of wing, but not forehead, patches (Moreno et al. 2014). Not only is it nearly impossible to find an exemplifying individual of the entire sex—the sum of the secondary sexual characters we use to define "male" and "female" phenotypes often fall within a broader, multivariate, definition of sex (West-Eberhard 2003b; Anderson and Falk 2023; McLaughlin et al. 2023). These "fuzzy edges" (sex4, *sensu* Warkentin et al. 2026) are a natural limitation to these analyses but also a very real aspect of biology. This is especially important to remember when studying hormonal associations with sexual dichromatism because of the substantial variation of hormones both within and between species. Considering the edges of these definitions, such as polymorphisms, and quantifying within-sex variation are critical for studying the underlying mechanisms behind sexual variation and the evolution of differentiation. If we are to move toward a more comprehensive understanding of how dichromatism evolves, we have to first acknowledge that its current definition is incomplete.

Concluding remarks

Much like sex determination, the degree to which the sexes differ in plumage coloration can arise through a variety of underlying mechanisms (Capel 2017). The key difference between the conclusions of the present work and those of Kimball (2006) is that research on hormonal influences on dichromatism is increasingly moving toward a multistep, pleiotropic model—one capable of explaining the substantial variation in dichromatism observed among species. Looking toward the future, advances in genomic sequencing are rapidly expanding our understanding of the genetic architecture underlying these differences, while also clarifying how proximate mechanisms such as hormones interact with the evolutionary processes that shape sexual variation. Integrating genomic, physiological, and comparative perspectives will allow dichromatism to be studied at a greater resolution than any single approach alone. Conclusively, the gaps in our current knowledge indicate that we are just beginning to understand the relationship between hormones and sexual dichromatism in birds.

Author contributions

E.G.: conceptualization, data curation, formal analysis, investigation, methodology, project administration, validation, visualization, writing—original draft, writing—review and editing; J.J.F.: conceptualization, data curation, formal analysis, investigation, writing—original draft, writing—review and editing; R.K.: conceptualization, data curation, formal analysis, investigation, validation, writing—original draft, writing—review and editing

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Supplementary data

Supplementary Data available at *ICB* online.

Data availability

All relevant data are cited within the paper or available within its supplementary files. Scripts are available upon request from the authors.

References

Abdulateef SM, Majid AA, Al-Bayer MA, Shawkat SS, Tatar A, Mohammed TT, Abdulateef FM, Al-Ani MQ. 2021. Effect of aromatase inhibitors on sex differentiation and embryonic development in chicks. Vet Med Sci 7:2362–73. https://doi.org/10.1002/vms3.623.

Agate RJ, Grisham W, Wade J, Mann S, Wingfield J, Schanen C, Palotie A, Arnold AP. 2003. Neural, not gonadal, origin of brain sex differences in a gynandromorphic finch. Proc Natl Acad Sci USA 100:4873–8. https://doi.org/10.1073/pnas.0636925100.

Amat JA, Garrido A, Portavia F, Rendón-Martos M, Pérez-Gálvez A, Garrido-Fernández J, Gómez J, Béchet A, Rendón MA. 2018. Dynamic signalling using cosmetics may explain the reversed sexual dichromatism in the monogamous greater flamingo. Behav Ecol Sociobiol 72:135. https://doi.org/10.1007/s00265-018-2551-1.

Anderson AP, Falk JJ. 2023. Cross-sexual transfer revisited. Integr Comp Biol 63:936–45. https://doi.org/10.1093/icb/icad021.

Andersson MB. 1994. Sexual selection, monographs in behavior and ecology. Princeton, NJ: Princeton University Press.

Arai E, Hasegawa M, Sato M, Sakai H, Ito S, Wakamatsu K. 2019. Eumelanin levels in rufous feathers explain plasma testosterone levels and survival in swallows. Ecology and Evolution 9:2755–64. https://doi.org/10.1002/ece3.4946.

Arnold AP. 2020. Four Core genotypes and XY∗ mouse models: update on impact on SABV research. Neurosci Biobehav Rev 119:1–8. https://doi.org/10.1016/j.neubiorev.2020.09.021.

Arnold AP, Itoh Y. 2011. Factors causing sex differences in birds. Avian Biol Res 4:44–51. https://doi.org/10.3184/175815511×13070045977959.

Badyaev AV, Hill GE. 2000. Evolution of sexual dichromatism: contribution of carotenoid- versus melanin-based coloration. Biol J Linn Soc 69:153–72. https://doi.org/10.1111/j.1095-8312.2000.tb01196.x.

Badyaev AV, Hill GE. 2003. Avian sexual dichromatism in relation to phylogeny and ecology. Annu Rev Ecol Evol Syst 34:27–49. https://doi.org/10.1146/annurev.ecolsys.34.011802.132441.

Barron DG, Webster MS, Schwabl H. 2013. Body condition influences sexual signal expression independent of circulating androgens in male red-backed fairy-wrens. Gen Comp Endocrinol 183:38–43. https://doi.org/10.1016/j.ygcen.2012.12.005.

Bear A, Monteiro A. 2013. Both cell-autonomous mechanisms and hormones contribute to sexual development in vertebrates and insects. Bioessays 35:725–32. https://doi.org/10.1002/bies.201300009.

Beck ML, Davies S, Sewall KB. 2018. Urbanization alters the relationship between coloration and territorial aggression, but not hormones, in song sparrows. Anim Behav 142:119–28. https://doi.org/10.1016/j.anbehav.2018.06.012.

Beltrán DF, Araya-Salas M, Parra JL, Stiles FG, Rico-Guevara A. 2022. The evolution of sexually dimorphic traits in ecological gradients: an interplay between natural and sexual selection in hummingbirds. Proc R Soc B 289:20221783. https://doi.org/10.1098/rspb.2022.1783.

Béziers P, Ducrest A-L, Simon C, Roulin A. 2017. Circulating testosterone and feather-gene expression of receptors and metabolic enzymes in relation to melanin-based colouration in the barn owl. Gen Comp Endocrinol 250:36–45. https://doi.org/10.1016/j.ygcen.2017.04.015.

Billerman SM, Keeney BK, Kirwan GM, Medrano F, Sly ND, Smith MG. 2026. Birds of the World. Ithaca, NY, USA.: Cornell Laboratory of Ornithology. https://doi.org/10.2173/bow

Blivaiss BB. 1947a. Interrelations of thyroid and gonad in the development of plumage and other sex characters in Brown Leghorn Roosters. Physiol Zool 20:67–107. https://doi.org/10.1086/physzool.20.1.30151939.

Blivaiss BB. 1947b. Development of secondary sexual characters in thyroidectomized brown Leghorn hens. J Exp Zool 104:267–309. https://doi.org/10.1002/jez.1401040302.

Boersma J, Enbody ED, Jones JA, Nason D, Lopez-Contreras E, Karubian J, Schwabl H. 2020. Testosterone induces plumage ornamentation followed by enhanced territoriality in a female songbird. Behav Ecol 31:1233–41. https://doi.org/10.1093/beheco/araa077.

Boersma J, Enbody ED, Ketaloya S, Watts HE, Karubian J, Schwabl H. 2023. Does capacity to produce androgens underlie variation in female ornamentation and territoriality in white-shouldered fairywren (*Malurus alboscapulatus*)? Horm Behav 154:105393. https://doi.org/10.1016/j.yhbeh.2023.105393.

Bókony V, Garamszegi LZ, Hirschenhauser K, Liker A. 2008. Testosterone and melanin-based black plumage coloration: a comparative study. Behav Ecol Sociobiol 62:1229–38. https://doi.org/10.1007/s00265-008-0551-2.

Brooks R. 2019. Queer birds: avian sex reversal and the origins of modern sexology. Viewpoint: Magazine of the British Society for the History of Science 119:10–1.

Brown JI, Hernández F, Engilis A, Hernández-Baños BE, Collins D, Lavretsky P. 2022. Genomic and morphological data shed light on the complexities of shared ancestry between closely related duck species. Sci Rep 12:10212. https://doi.org/10.1038/s41598-022-14270-2.

Buchanan G. 1926. The testis and thyroid in a hen-feathered silver-grey dorking cock. J Exp Biol 4:73–80. https://doi.org/10.1242/jeb.4.1.73.

Burns KJ, Shultz AJ. 2012. Widespread cryptic dichromatism and ultraviolet reflectance in the largest radiation of neotropical songbirds: implications of accounting for avian vision in the study of plumage evolution. The Auk 129:211–21. https://doi.org/10.1525/auk.2012.11182.

Butler MW, Leppert LL, Dufty JAM. 2010. Effects of small increases in corticosterone levels on morphology, immune function, and feather development. Physiol Biochem Zool 83:78–86. https://doi.org/10.1086/648483.

Capel B. 2017. Vertebrate sex determination: evolutionary plasticity of a fundamental switch. Nat Rev Genet 18:675–89. https://doi.org/10.1038/nrg.2017.60.

Casagrande S, Dell'Omo G, Costantini D, Tagliavini J, Groothuis T. 2011. Variation of a carotenoid-based trait in relation to oxidative stress and endocrine status during the breeding season in the Eurasian kestrel: a multi-factorial study. Comp Biochem Physiol A: Mol Integr Physiol 160:16–26. https://doi.org/10.1016/j.cbpa.2011.04.011.

Chiba A, Honma R. 2011. A study on the Northern Pintail (*Anas acuta*) females with masculinized plumage: their prevalence, morphological and behavioral traits, and reproductive organs. J Ornithol 152:733–42. https://doi.org/10.1007/s10336-011-0654-9.

Chue J, Smith CA. 2011. Sex determination and sexual differentiation in the avian model. FEBS J 278:1027–34. https://doi.org/10.1111/j.1742-4658.2011.08032.x.

Clinton M, Zhao D, Nandi S, McBride D. 2012. Evidence for avian cell autonomous sex identity (CASI) and implications for the sex-determination process? Chromosome Res 20:177–90. https://doi.org/10.1007/s10577-011-9257-9.

Cole LJ, Hutt FB. 1927. Further experiments in feeding thyroid to fowls. Poult Sci 7:60–6. https://doi.org/10.3382/ps.0070060.

Collis K, Borgia G. 1993. The costs of male display and delayed plumage maturation in the satin bowerbird (*Ptilonorhynchus violaceus*). Ethology 94:59–71. https://doi.org/10.1111/j.1439-0310.1993.tb00547.x.

Crew FAE, Munro SS. 1939. IX.—Gynandromorphism and lateral asymmetry in birds. Proc R Soc Edinb 58:114–34. https://doi.org/10.1017/S037016460001107X.

Cruz-Miralles Á, Avilés JM, Chastel O, Expósito-Granados M, Parejo D. 2020. Phaeomelanin matters: redness associates with inter-individual differences in behaviour and feather corticosterone in male scops owls (*Otus scops*). PLoS One 15:e0241380. https://doi.org/10.1371/journal.pone.0241380.

Danforth CH. 1937a. Responses of feathers of male and female pheasants to Theelin. Exp Biol Med 36:322–4. https://doi.org/10.3181/00379727-36-9216P.

Danforth CH. 1937b. Artificial gynandromorphism and plumage in *Phasianus*. J Genet 34:497–506. https://doi.org/10.1007/BF02982310.

Danforth CH. 1937c. An experimental study of plumage in Reeves pheasants. J Exp Zool 77:1–11. https://doi.org/10.1002/jez.1400770102.

Danforth CH, Price JB. 1935. Failure of theelin and thyroxin to affect plumage and eye-color of the blackbird. Exp Biol Med 32:675–8. https://doi.org/10.3181/00379727-32-7814C.

Darwin C. 1871. The descent of man, and selection in relation to sex. London: John Murray.

Day LB, McBroom JT, Schlinger BA. 2006. Testosterone increases display behaviors but does not stimulate growth of adult plumage in male golden-collared manakins (Manacus vitellinus). Horm Behav 49:223–32. https://doi.org/10.1016/j.yhbeh.2005.07.006.

Delhey K, Valcu M, Dale J, Kempenaers B. 2023. The evolution of carotenoid-based plumage colours in passerine birds. J Anim Ecol 92:66–77. https://doi.org/10.1111/1365-2656.13791.

Ducrest A, Keller L, Roulin A. 2008. Pleiotropy in the melanocortin system, coloration and behavioural syndromes. Trends Ecol Evol 23:502–10. https://doi.org/10.1016/j.tree.2008.06.001.

Duerden J. 1919. Crossing the north African and south African ostrich. J Genet 8:155–98.

Eens M, Van Duyse E, Berghman L 2000. Shield characteristics are testosterone-dependent in both male and female Moorhens. Horm Behav 37:126–34. https://doi.org/10.1006/hbeh.1999.1569.

Eikenaar C, Whitham M, Komdeur J, Van Der Velde M, Moore IT. 2011. Testosterone, Plumage colouration and extra-pair paternity in male North-American barn swallows. PLoS One 6:e23288. https://doi.org/10.1371/journal.pone.0023288.

Emmens CW, Parkes AS. 1940. The endocrine system and plumage types: II. The effects of thyroxin injections to normal, caponized and thyroidectomized caponized birds. J Genet 39:485–92. https://doi.org/10.1007/BF02982886.

Enbody ED, Boersma J, Schwabl H, Karubian J. 2018. Female ornamentation is associated with elevated aggression and testosterone in a tropical songbird. Behav Ecol 29:1056–66. https://doi.org/10.1093/beheco/ary079.

Enbody ED, Sin SYW, Boersma J, Edwards SV, Ketaloya S, Schwabl H, Webster MS, Karubian J. 2022. The evolutionary history and mechanistic basis of female ornamentation in a tropical songbird. Evolution 76:1720–36. https://doi.org/10.1111/evo.14545.

Endler B, Rahmig B, Rutschke E. 1988. On the hormonal regulation of the sexual and seasonal dimorphism of the Mallard (*Anas platyrhynchos*). In: Proceedings of the International Ornithological Congress 24; 1986 Jun 22-29. pp. Ottawa, Canada University of Ottawa Press 2234–9.

Evans MR, Goldsmith AR, Norris SRA. 2000. The effects of testosterone on antibody production and plumage coloration in male house sparrows (*Passer domesticus*). Behav Ecol Sociobiol 47:156–63. https://doi.org/10.1007/s002650050006.

Fairhurst GD, Dawson RD, Van Oort H, Bortolotti GR. 2014. Synchronizing feather-based measures of corticosterone and carotenoid-dependent signals: what relationships do we expect? Oecologia 174:689–98. https://doi.org/10.1007/s00442-013-2830-5.

Fargallo JA, Martínez-Padilla J, Toledano-Díaz A, Santiago-Moreno J, Dávila JA. 2007. Sex and testosterone effects on growth, immunity and melanin coloration of nestling Eurasian kestrels. J Anim Ecol 76:201–9. https://doi.org/10.1111/j.1365-2656.2006.01193.x.

Fargallo JA, Velando A, Lopez-Rull I, Ganan N, Lifshitz N, Wakamatsu K, Torres R. 2014. Sex-specific phenotypic integration: endocrine profiles, coloration, and behavior in fledgling boobies. Behav Ecol 25:76–87. https://doi.org/10.1093/beheco/art088.

Forbes TR. 1947. The crowing hen: early observations on spontaneous sex reversal in birds. Yale J Biol Med 19:955.

Galván I, Solano F. 2016. Bird integumentary melanins: biosynthesis, forms, function and evolution. Int J Mol Sci 17:520. https://doi.org/10.3390/ijms17040520.

Gao L, Wang Y, Li Z, Dong L. 2025. Rapid male plumage evolution drives sexual dichromatism in Ficedula flycatchers. Avian Res 16:100288. https://doi.org/10.1016/j.avrs.2025.100288.

Gazda MA, Araújo PM, Lopes RJ, Toomey MB, Andrade P, Afonso S, Marques C, Nunes L, Pereira P, Trigo S et al. 2020. A genetic mechanism for sexual dichromatism in birds. Science 368:1270–4. https://doi.org/10.1126/science.aba0803.

George FW, Matsumine H, McPhaul MJ, Somes RG, Wilson JD. 1990. Inheritance of the Henny feathering trait in the golden campine chicken: evidence for allelism with the gene that causes Henny feathering in the sebright bantam. J Hered 81:107–10. https://doi.org/10.1093/oxfordjournals.jhered.a110938.

George FW, Noble JF, Wilson JD. 1981. Female feathering in Sebright cocks is due to conversion of testosterone to estradiol in skin. Science 213:557–9. https://doi.org/10.1126/science.213.4507.557.

Goodale HD. 1910. Some results of castration in ducks. Biol Bull 20:35–69.

Goodale HD. 1918. Feminized male birds. Genetics 3:276–99. https://doi.org/10.1093/genetics/3.3.276.

Goymann W, Wingfield JC. 2014. Male-to-female testosterone ratios, dimorphism, and life history—What does it really tell us? Behav Ecol 25:685–99. https://doi.org/10.1093/beheco/aru019.

Green PA, George EM, Rosvall KA, Johnsen S, Nowicki S. 2022. Testosterone, signal coloration, and signal color perception in male zebra finch contests. Ethology 128:131–42. https://doi.org/10.1111/eth.13247.

Greenwood AW, Blyth J. 1938. Sex dimorphism in the plumage of the domestic fowl. J Genet 36:53–72.

Greij ED. 1973. Effects of sex hormones on plumages of the blue-winged Teal. Auk 90:533–51.

Griffith EV, Mackentley N, Neri CM, Canfield BM, Lindsay AR. 2025. Fluorescent pigment concentration correlated with age, sex, and size in Long-eared Owl (*Asio otus*) plumage. Wilson J Ornithol 137:133–43. https://doi.org/10.1080/15594491.2024.2444031.

Grindstaff JL, Lovern MB, Burtka JL, Hallmark-Sharber A. 2012. Structural coloration signals condition, parental investment, and circulating hormone levels in Eastern bluebirds (*Sialia sialis*). J Comp Physiol A 198:625–37. https://doi.org/10.1007/s00359-012-0735-0.

Grunst ML, Grunst AS, Parker CE, Romero LM, Rotenberry JT. 2015. Pigment-specific relationships between feather corticosterone concentrations and sexual coloration. Behav Ecol 26:706–15. https://doi.org/10.1093/beheco/aru210.

Haase E, Ito S, Wakamatsu K. 1995. Influences of sex, castration, and androgens on the eumelanin and pheomelanin contents of different feathers in wild mallards. Pigm Cell Res 8:164–70. https://doi.org/10.1111/j.1600-0749.1995.tb00658.x.

Haase E, Schmedemann R. 1992. Dose-dependent effect of testosterone on the induction of eclipse coloration in castrated wild mallard drakes (*Anas platyrhynchos*). Can J Zool 70:428–31. https://doi.org/10.1139/z92-065.

Hagelin JC. 2001. Castration in Gambel's and scaled quail: ornate plumage and dominance persist, but courtship and threat behaviors do not. Horm Behav 39:1–10. https://doi.org/10.1006/hbeh.2000.1615.

Hagelin JC, Kimball RT. 1997. A female Gambel's Quail with partial male plumage. Wilson Bull 109:544–6.

Hall CA, Conroy G, Jelocnik M, Kasimov V, Gillet A, Portas T, Hill A, Potvin DA. 2025. Prevalence and implications of sex reversal in free-living birds. Biol. Lett. 21:20250182. https://doi.org/10.1098/rsbl.2025.0182.

Hall PF. 1969. Hormonal control of melanin synthesis in birds. Gen Comp Endocrinol 2:451–8.

Han Y, Huang W, Liu Y. 2026. Illustrations of Handbook of the Birds of the World: datasets of RGB values and color classification of birds. Ecology 107:e70320. https://doi.org/10.1002/ecy.70320.

Henderson LJ, Heidinger BJ, Evans NP, Arnold KE. 2013. Ultraviolet crown coloration in female blue tits predicts reproductive success and baseline corticosterone. Behav Ecol 24:1299–305. https://doi.org/10.1093/beheco/art066.

Henschen AE, Whittingham LA, Dunn PO. 2018. Male stress response is related to ornamentation but not resistance to oxidative stress in a warbler. Funct Ecol 32:1810–8. https://doi.org/10.1111/1365-2435.13104.

Höhn EO, Braun CE. 1980. Hormonal induction of feather pigmentation in Ptarmigan. Auk 97:601–7. https://doi.org/10.1093/auk/97.3.601.

Huang H, Rabosky DL, null n, null n. 2014. Sexual selection and diversification: reexamining the correlation between dichromatism and speciation rate in birds. Am Nat 184:E101–14. https://doi.org/10.1086/678054.

Hudson SB, Wilcoxen TE. 2018. Condition dependence of structural plumage coverage in indigo buntings *Passerina cyanea*. Avian Biol Res 11:54–61. https://doi.org/10.3184/175815617×15063340995383.

Hunter J. 1780. XXX. Account of an extraordinary pheasant. Phil Trans R Soc 527–35. https://doi.org/10.1098/rstl.1780.0030.

Jenkins BR, Vitousek MN, Safran RJ. 2013. Signaling stress? An analysis of phaeomelanin-based plumage color and individual corticosterone levels at two temporal scales in North American barn swallows, Hirundo rustica erythrogaster. Horm Behav 64:665–72. https://doi.org/10.1016/j.yhbeh.2013.08.006.

Jin K, Zuo Q, Song J, Zhang Y, Chen G, Li B. 2020. CYP19A1 (aromatase) dominates female gonadal differentiation in chicken (*Gallus gallus*) embryos sexual differentiation. Biosci Rep 40:BSR20201576. https://doi.org/10.1042/BSR20201576.

Johns JE. 1964. Testosterone-induced nuptial feathers in phalaropes. Condor 66:449–55. https://doi.org/10.2307/1365222.

Johnson AE, Jordan Price J, Pruett-Jones S. 2013. Different modes of evolution in males and females generate dichromatism in fairy-wrens (M *aluridae*). Ecol Evol 3:3030–46. https://doi.org/10.1002/ece3.686.

Kannankeril JV, Domm LV. 1968. The influence of gonadectomy on sexual characters in the Japanese quail. J Morphol 126:395–411. https://doi.org/10.1002/jmor.1051260403.

Keck WN. 1934. The control of the secondary sex characters in the English sparrow, *Passer domesticus* (Linnaeus). J Exp Zool 67:315–47. https://doi.org/10.1002/jez.1400670205.

Kennedy EA, Lattin CR, Romero LM, Dearborn DC. 2013. Feather coloration in museum specimens is related to feather corticosterone. Behav Ecol Sociobiol 67:341–8. https://doi.org/10.1007/s00265-012-1454-9.

Ketterson ED, Nolan JV, Sandell M, null n. 2005. Testosterone in females: mediator of adaptive traits, constraint on sexual dimorphism, or both? Am Nat 166:S85–98. https://doi.org/10.1086/444602.

Khalil S, Enbody ED, Frankl-Vilches C, Welklin JF, Koch RE, Toomey MB, Sin SYW, Edwards SV, Gahr M, Schwabl H et al. 2023. Testosterone coordinates gene expression across different tissues to produce carotenoid-based red ornamentation. Mol Biol Evol 40:msad056. https://doi.org/10.1093/molbev/msad056.

Khalil S, Welklin JF, McGraw KJ, Boersma J, Schwabl H, Webster MS, Karubian J. 2020. Testosterone regulates *CYP2J19*-linked carotenoid signal expression in male red-backed fairywrens (*Malurus melanocephalus*). Proc R Soc B 287:20201687. https://doi.org/10.1098/rspb.2020.1687.

Kimball RT. 2006. Hormonal control of coloration. Bird Color 1:431–68.

Kimball RT, Ligon JD. 1999. Evolution of Avian plumage dichromatism from a proximate perspective. Am Nat 154:182–93. https://doi.org/10.1086/303228.

Lahaye SEP, Eens M, Darras VM, Pinxten R. 2014. Bare-part color in female budgerigars changes from brown to structural blue following testosterone treatment but is not strongly masculinized. PLoS One 9:e86849. https://doi.org/10.1371/journal.pone.0086849.

Lambeth LS, Morris KR, Wise TG, Cummins DM, O'Neil TE, Cao Y, Sinclair AH, Doran TJ, Smith CA. 2016. Transgenic chickens overexpressing aromatase have high estrogen levels but maintain a predominantly male phenotype. Endocrinology 157:83–90. https://doi.org/10.1210/en.2015-1697.

Lank DB, Coupe M, Wynne-Edwards KE. 1999. Testosterone-induced male traits in female ruffs (*Philomachus pugnax*): autosomal inheritance and gender differentiation. Proc R Soc Lond B 266:2323–30. https://doi.org/10.1098/rspb.1999.0926.

Lantz SM, Boersma J, Schwabl H, Karubian J. 2017. Early-moulting red-backed fairywren males acquire ornamented plumage in the absence of elevated androgens. Emu—Austral Ornithol 117:170–80. https://doi.org/10.1080/01584197.2017.1297206.

Lattin CR, Romero LM. 2013. The size of a melanin-based plumage ornament correlates with glucocorticoid receptor concentrations in the skin of that ornament. Biol Lett 9:20130440. https://doi.org/10.1098/rsbl.2013.0440.

Lendvai ÁZ, Giraudeau M, Németh J, Bakó V, McGraw KJ. 2013. Carotenoid-based plumage coloration reflects feather corticosterone levels in male house finches (*Haemorhous mexicanus*). Behav Ecol Sociobiol 67:1817–24. https://doi.org/10.1007/s00265-013-1591-9.

Lengyel K, Rudra M, Berghof TVL, Leitão A, Frankl-Vilches C, Dittrich F, Duda D, Klinger R, Schleibinger S, Sid H et al. 2024. Unveiling the critical role of androgen receptor signaling in avian sexual development. Nat Commun 15:8970. https://doi.org/10.1038/s41467-024-52989-w.

Lindsay WR, Barron DG, Webster MS, Schwabl H. 2016. Testosterone activates sexual dimorphism including male-typical carotenoid but not melanin plumage pigmentation in a female bird. J Exp Biol 219:3091–9. https://doi.org/10.1242/jeb.135384.

Lindsay WR, Mendonça R, Slight MW, Prager M, Andersson MX, Mundy NI, Andersson S. 2022. Seasonal but not sex-biased gene expression of the carotenoid ketolase, *CYP2J19*, in the sexually dichromatic southern red bishop (*Euplectes orix*). R Soc Open Sci 9:220434. https://doi.org/10.1098/rsos.220434.

Lindsay WR, Webster MS, Schwabl H. 2011. Sexually selected male plumage color is testosterone dependent in a tropical passerine bird, the red-backed fairy-wren (*Malurus melanocephalus*). PLoS One 6:e26067. https://doi.org/10.1371/journal.pone.0026067.

Lindsay WR, Webster MS, Varian CW, Schwabl H. 2009. Plumage colour acquisition and behaviour are associated with androgens in a phenotypically plastic tropical bird. Anim Behav 77:1525–32. https://doi.org/10.1016/j.anbehav.2009.02.027.

Liu D, Tong Y, Dong R, Ye X, Yu X. 2023. A breeding plumage in the making: the unique process of plumage coloration in the crested Ibis in terms of chemical composition and sex hormones. Animals 13:3820. https://doi.org/10.3390/ani13243820.

Loveland JL, Giraldo-Deck LM, Lank DB, Goymann W, Gahr M, Küpper C. 2021. Functional differences in the hypothalamic-pituitary-gonadal axis are associated with alternative reproductive tactics based on an inversion polymorphism. Horm Behav 127:104877. https://doi.org/10.1016/j.yhbeh.2020.104877.

Loveland JL, Lank DB, Küpper C. 2021. Gene expression modification by an autosomal inversion associated with three male mating morphs. Front Genet 12:641620. https://doi.org/10.3389/fgene.2021.641620.

Lucas AM, Stettenheim PR. 1972. Avian anatomy: Integument. Agriculture Handbook No. 362.Washington, DC: U.S. Department of Agriculture, US Agricultural Research Service.

Ma S, Liu H, Wang J, Wang L, Xi Y, Liu Y, Xu Q, Hu J, Han C, Bai L et al. 2021. Transcriptome analysis reveals genes associated with sexual dichromatism of head feather color in Mallard. Front Genet 12:627974. https://doi.org/10.3389/fgene.2021.627974.

Major AT, Smith CA. 2016. Sex reversal in birds. Sex Dev 10:288–300. https://doi.org/10.1159/000448365.

Martin RP, Carr EM, Sparks JS. 2025. Does biofluorescence enhance visual signals in birds-of-paradise? R Soc Open Sci 12:241905. https://doi.org/10.1098/rsos.241905.

Matsumine H, Herbst MA, Ou S, Wilson JD, McPhaul MJ. 1991. Aromatase mRNA in the extragonadal tissues of chickens with the henny-feathering trait is derived from a distinctive promoter structure that contains a segment of a retroviral long terminal repeat. Functional organization of the Sebright, Leghorn, and Campine aromatase genes. J Biol Chem 266:19900–7.

Mcglothlin JW, Jawor JM, Greives TJ, Casto JM, Phillips JL, Ketterson ED. 2008. Hormones and honest signals: males with larger ornaments elevate testosterone more when challenged. J Evol Biol 21:39–48. https://doi.org/10.1111/j.1420-9101.2007.01471.x.

McGraw KJ. 2006. Sex steroid dependence of carotenoid-based coloration in female zebra finches. Physiol Behav 88:347–52. https://doi.org/10.1016/j.physbeh.2006.04.003.

McGraw KJ. 2008. An update on the honesty of melanin-based color signals in birds. Pigment Cell Melanoma Res 21:133–8. https://doi.org/10.1111/j.1755-148X.2008.00454.x.

McLaughlin JF, Brock KM, Gates I, Pethkar A, Piattoni M, Rossi A, Lipshutz SE. 2023. Multivariate models of animal sex: breaking binaries leads to a better understanding of ecology and evolution. Integr Comp Biol 63:891–906. https://doi.org/10.1093/icb/icad027.

McNabb FMA. 2007. The hypothalamic-pituitary-thyroid (HPT) axis in birds and its role in bird development and reproduction. Crit Rev Toxicol 37:163–93. https://doi.org/10.1080/10408440601123552.

McTavish EJ, Gerbracht JA, Holder MT, Iliff MJ, Lepage D, Rasmussen PC, Redelings BD, Sánchez Reyes LL, Miller ET. 2025. A complete and dynamic tree of birds. Proc Natl Acad Sci USA 122:e2409658122. https://doi.org/10.1073/pnas.2409658122.

Merrill L, Stewart TE, ález-GPL G, O ’Loghlen Adrian L, Wingfield JC, Ellis VA, Rothstein SI. 2015. Epaulet size and current condition in red-winged blackbirds: examining a semistatic signal, testosterone, immune function, and parasites. Physiol Biochem Zool 88:11–21. https://doi.org/10.1086/679475.

Miller DS. 1935. Effects of thyroxin on plumage of the English sparrow, *Passer domesticus* (LINNAEUS). J Exp Zool 71:293–309. https://doi.org/10.1002/jez.1400710206.

Morejohn GV, Genelly RE. 1961. Plumage differentiation of normal and sex-anomalous ring-necked pheasants in response to synthetic hormone implants. Condor 63:101–10. https://doi.org/10.2307/1365524.

Moreno J, Gil D, Cantarero A, López-Arrabé J. 2014. Extent of a white plumage patch covaries with testosterone levels in female Pied Flycatchers Ficedula hypoleuca. J Ornithol 155:639–48. https://doi.org/10.1007/s10336-014-1046-8.

Mougeot F, Martínez-Padilla J, Bortolotti GR, Webster LMI, Piertney SB. 2010. Physiological stress links parasites to carotenoid-based colour signals. J Evol Biol 23:643–50. https://doi.org/10.1111/j.1420-9101.2009.01926.x.

Muck C, Goymann W. 2011. Throat patch size and darkness covaries with testosterone in females of a sex-role reversed species. Behav Ecol 22:1312–9. https://doi.org/10.1093/beheco/arr133.

Mueller NS. 1970. An experimental study of sexual dichromatism in the duck *Anas platyrhynchos*. J Exp Zool 173:263–8. https://doi.org/10.1002/jez.1401730304.

Mueller NS. 1977. Control of sex differences in the plumage of the house sparrow, *Passer domesticus*. J Exp Zool 202:45–8. https://doi.org/10.1002/jez.1402020106.

Oribe E, Fukao A, Yoshihara C, Mendori M, Rosal KG, Takahashi S, Takeuchi S. 2012. Conserved distal promoter of the agouti signaling protein (*ASIP*) gene controls sexual dichromatism in chickens. Gen Comp Endocrinol 177:231–7. https://doi.org/10.1016/j.ygcen.2012.04.016.

Ortman R. 1967. The performance of the Napoleon weaver, the Orange weaver, and the Paradise Whydah in the weaver finch test for luteinizing hormones. Gen Comp Endocrinol 9:368–73. https://doi.org/10.1016/0016-6480(67)90032-9.

Ottenburghs J. 2024. Digest: understanding the evolution of sexual dichromatism also requires a female perspective. Evolution 78:383–4. https://doi.org/10.1093/evolut/qpad221.

Ottenburghs J, Harteman J. 2021. Sexually dichromatic hybrids between two monochromatic duck species, the Chiloé wigeon and the Philippine duck. Ecol Evol 11:16409–12. https://doi.org/10.1002/ece3.8253.

Peters A. 2007. Testosterone treatment of female Superb Fairy-wrens *Malurus cyaneus* induces a male-like prenuptial moult, but no coloured plumage. Ibis 149:121–7. https://doi.org/10.1111/j.1474-919X.2006.00616.x.

Peters A, Astheimer LB, Boland CRJ, Cockburn A. 2000. Testosterone is involved in acquisition and maintenance of sexually selected male plumage in superb fairy-wrens, Malurus cyaneus. Behav Ecol Sociobiol 47:438–45. https://doi.org/10.1007/s002650050688.

Peters A, Kingma SA, Delhey K. 2013. Seasonal male plumage as a multi-component sexual signal: insights and opportunities. Emu—Austral Ornithol 113:232–47. https://doi.org/10.1071/MU12083.

Pittaway R. 2000. Plumage and molt terminology. Ontario Birds 18:4.

Quinn MJJ, French JBJ, McNabb FMA, Ottinger MA. 2005. The role of thyroxine on the production of plumage in the American kestrel. J Raptor Res 39:84–8.

R Core Team. 2025. A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. http://www.R-project.org/

Ralph CL, Grinwich DL, Hall PF. 1967. Studies of the melanogenic response of regenerating feathers in the weaver bird: comparison of two species in response to two gonadotrophins. J Exp Zool 166:283–7. https://doi.org/10.1002/jez.1401660211.

Revell LJ. 2024. phytools 2.0: an updated R ecosystem for phylogenetic comparative methods (and other things). PeerJ 12:e16505. https://doi.org/10.7717/peerj.16505.

Romero-Diaz C, Silva PA, Soares MC, Cardoso GC, Trigo S. 2022. Oestradiol reduces female bill colour in a mutually ornamented bird. Proc R Soc B 289:20221677. https://doi.org/10.1098/rspb.2022.1677.

Roulin A, Ducrest A-L. 2011. Association between melanism, physiology and behaviour: a role for the melanocortin system. Eur J Pharmacol 660:226–33. https://doi.org/10.1016/j.ejphar.2011.01.036.

Rull IL, Nicolás L, Neri-Vera N, Argáez V, Martínez M, Torres R. 2016. Assortative mating by multiple skin color traits in a seabird with cryptic sexual dichromatism. J Ornithol 157:1049–62. https://doi.org/10.1007/s10336-016-1352-4.

Saldanha CJ, Schlinger BA. 1997. Estrogen synthesis and secretion in the brown-headed cowbird (*Molothrus ater*). Gen Comp Endocrinol 105:390–401. https://doi.org/10.1006/gcen.1996.6841.

Sarasola JH, Negro JJ, Bechard MJ, Lanusse A. 2011. Not as similar as thought: sexual dichromatism in *Chimango caracaras* is expressed in the exposed skin but not in the plumage. J Ornithol 152:473–9. https://doi.org/10.1007/s10336-010-0606-9.

Sarpong K, Madliger CL, Harris CM, Love OP, Doucet SM, Bitton P-P. 2019. Baseline corticosterone does not reflect iridescent plumage traits in female tree swallows. Gen Comp Endocrinol 270:123–30. https://doi.org/10.1016/j.ygcen.2018.10.015.

Saxena RN, Thapliyal JP. 1961. Plumage control in black-headed Munia (*Munia atricapila*). Naturwissenschaften 48:652. https://doi.org/10.1007/BF00590615.

Schaedler LM, Taylor LU, Prum RO, Anciães M. 2021. Constraint and function in the predefinitive plumages of Manakins (Aves: pipridae). Integr Comp Biol 61:1363–77. https://doi.org/10.1093/icb/icab063.

Scheun J, Neller S, Bennett NC, Kemp LV, Ganswindt A. 2021. Endocrine correlates of gender and throat coloration in the southern ground-hornbill (*Bucorvus leadbeateri*). Integr Zool 16:189–201. https://doi.org/10.1111/1749-4877.12478.

Schlinger BA. 1997. The activity and expression of aromatase in songbirds. Brain Res Bull 44:359–64.

Schlinger BA, Arnold AP. 1992. Circulating estrogens in a male songbird originate in the brain. Proc Natl Acad Sci USA 89:7650–3. https://doi.org/10.1073/pnas.89.16.7650.

Schwarzová L, Fuchs R, Frynta D. 2010. Delayed plumage maturation correlates with testosterone levels in black redstart *Phoenicurus ochruros* males. Acta Ornithol 45:91–7. https://doi.org/10.3161/000164510×516146.

Scott HM, Payne LF. 1934. The effect of gonadectomy on the secondary sexual characters of the Bronze turkey (*M. gallopavo*). J Exp Zool 69:123–36. https://doi.org/10.1002/jez.1400690107.

Siefferman Lynn. Liu Mark. Navara Kristen J.. Mendonça Mary T.. Hill Geoffrey E. 2013. Effect of Prenatal and Natal Administration of Testosterone on Production of Structurally Based Plumage Coloration. Physiological and Biochemical Zoology, 86:323–332. https://doi.org/10.1086/670383

Siitari H, Alatalo RV, Halme P, Buchanan KL, Kilpimaa J, null n. 2007. Color signals in the black grouse (*Tetrao tetrix*): signal properties and their condition dependency. Am Nat 169:S81–92. https://doi.org/10.1086/510140.

Sin SYW, Lu L, Edwards SV. 2020. *De Novo* Assembly of the Northern Cardinal (*Cardinalis cardinalis*) genome reveals candidate regulatory regions for sexually dichromatic red plumage coloration. G3 10:3541–8. https://doi.org/10.1534/g3.120.401373.

Smiley KO, Lipshutz SE, Kimmitt AA, DeVries MS, Cain KE, George EM, KristenM C. 2022. Beyond a biased binary: a perspective on the misconceptions, challenges, and implications of studying females in avian behavioral endocrinology. Front Physiol 13:970603. https://doi.org/10.3389/fphys.2022.970603.

Stępniewski J, Surmacki A. 2023. The first case of bilateral gynandromorphic plumage type in the bearded reedling *Panurus biarmicus*. Eur Zool J 90:643–7. https://doi.org/10.1080/24750263.2023.2231000.

Stiller J, Feng S, Chowdhury A-A, Rivas-González I, Duchêne DA, Fang Q, Deng Y, Kozlov A, Stamatakis A, Claramunt S et al. 2024. Complexity of avian evolution revealed by family-level genomes. Nature 629:851–60. https://doi.org/10.1038/s41586-024-07323-1.

Stoehr AM, Hill GE. 2001. The effects of elevated testosterone on plumage hue in male House Finches. J Avian Biol 32:153–8. https://doi.org/10.1034/j.1600-048X.2001.320208.x.

Stokkan K-A. 1979a. Testosterone and daylength-dependent development of comb size and breeding plumage of male willow Ptarmigan (*Lagopus lagopus lagopus*). Auk 96:106–15. https://doi.org/10.1093/auk/96.1.106.

Stokkan K-A. 1979b. The effect of permanent short days and castration on plumage and comb growth in male willow ptarmigan (*Lagopus lagopus*). Auk 96:682–7. https://doi.org/10.1093/auk/96.4.682.

Sughrue KM, Brittingham MC, French JB. 2008. Endocrine effects of the herbicide linuron on the American Goldfinch GOLDFINCH (*Carduelis tristis*). Auk 125:411–9. https://doi.org/10.1525/auk.2008.06264.

Tang P-C, Cheng H-C, Lin G-W, Lai Y-C, Liang Y-C, Wu P, Lin T-C, Ng CS, Tsai IJ, Li A et al. 2025. Sexually dimorphic sail feathers in the Mandarin duck as a model for lifelong developmental modulation. Sci Rep 15:36593. https://doi.org/10.1038/s41598-025-20446-3.

Terrill RS, Shultz AJ. 2023. Feather function and the evolution of birds. Biol Rev 98:540–66. https://doi.org/10.1111/brv.12918.

Tewary P, Farner D. 1973. Effect of castration and estrogen administration on the plumage pigment of the male House Finch (*Carpodacus mexicxanus*). Am Zool 13:1278.

Thapliyal JP, Tewary PD. 1961. Plumage in Lal Munia (*Amandava amandava*). Science 134:738–9. https://doi.org/10.1126/science.134.3481.738.

Thapliyal JP, Tewary PD. 1963. Effect of estrogen and gonadotropic hormones on the plumage pigmentation in Lal Munia (*Estrilda amandava*). Naturwissenschaften 50:529–. https://doi.org/10.1007/BF00689250.

Torrey HB, Horning B. 1922. Hen-feathering induced in the male fowl by feeding thyroid. Exp Biol Med 19:275–9. https://doi.org/10.3181/00379727-19-120.

Trigo S, Mota PG. 2015. A test of the effect of testosterone on a sexually selected carotenoid trait in a cardueline finch. Ecol Res 30:25–31. https://doi.org/10.1007/s11284-014-1201-y.

Valcu C-M, Valcu M, Delhey K, Kempenaers B. 2025. Mechanisms of colour-production modulate the link between extra-pair paternity and avian sexual dichromatism. J Evol Biol 38:1359–72. https://doi.org/10.1093/jeb/voaf085.

van Oordt GJ. 1936. The effect of gonadectomy on the secondary sexual characters of the turkey. Arch Port Sci Biol 5:205–11.

Vevers HG. 1954. The experimental analysis of feather pattern in the Amherst Pheasant, *Chrysolophus amherstiae* (Leadbeater). Trans Zool Soc Lond 28:305–48. https://doi.org/10.1111/j.1096-3642.1954.tb00002.x.

Wallace AR. 1889. Darwinism: an Exposition of the Theory of Natural Selection, with Some of the Applications. New York, NY: Macmillan and Company.

Walton A. 1937. On the eclipse plumage of the Mallard (*Anas Platyrhyncha Platyrhyncha*). J Exp Biol 14:440–7. https://doi.org/10.1242/jeb.14.4.440.

Warkentin KM, Casper AMA, Falk JJ. 2026. Evolution, development, and the incoherence of sex: a framework for multiple sex concepts. Presented at the symposium: Sex across origins: Questioning animal-centric assumptions and developing integrative frameworks. Portland, OR: Society for Integrative and Comparative Biology.

West-Eberhard MJ. 2003a. Developmental plasticity and evolution. New York, NY: Oxford University Press.

West-Eberhard MJ. 2003b. Cross-sexual transfer. In: Developmental plasticity and evolution. New York, NY: Oxford University Press.

Widelitz RB, Lin G, Lai Y, Mayer JA, Tang P, Cheng H, Jiang T, Chen C, Chuong C. 2019. Morpho-regulation in diverse chicken feather formation: integrating branching modules and sex hormone-dependent morpho-regulatory modules. Dev Growth Differ 61:124–38. https://doi.org/10.1111/dgd.12584.

Windsor RL, Fox GA, Bowman R. 2019. Consistency of structural color across molts: the effects of environmental conditions and stress on feather ultraviolet reflectance. Auk 136:ukz019. https://doi.org/10.1093/auk/ukz019.

Witschi E. 1935. Seasonal sex characters in birds and their hormonal control. Wilson Bull 47:177–88.

Witschi E. 1936. Effect of gonadotropic and oestrogenic hormones on regenerating feathers of weaver finches (*Pyromelana franciscana*). Exp Biol Med 35:484–9. https://doi.org/10.3181/00379727-35-9025C.

You L, Nishio K, Kowata K, Horikawa M, Fukuchi H, Ogoshi M, Aizawa S, Takeuchi S. 2024. Revisiting the hormonal control of sexual dimorphism in chicken feathers. Gen Comp Endocrinol 357:114601. https://doi.org/10.1016/j.ygcen.2024.114601.

Zhang X, Li J, Chen S, Yang N, Zheng J. 2023. Overview of Avian sex reversal. Int J Mol Sci 24:8284. https://doi.org/10.3390/ijms24098284.

Zhao D, McBride D, Nandi S, McQueen HA, McGrew MJ, Hocking PM, Lewis PD, Sang HM, Clinton M. 2010. Somatic sex identity is cell autonomous in the chicken. Nature 464:237–42. https://doi.org/10.1038/nature08852.

Zuk M, Simmons LW. 2018. Sexual selection: a very short introduction. 1st ed. Oxford: Oxford University Press. https://doi.org/10.1093/actrade/9780198778752.001.0001.