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Hormonal Control of Coloration

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Numerous studies have examined the evolution of avian color patterns, particularly the evolution of sexual dichromatism (Part II, Volume 2). In contrast, fewer studies have examined the physiological mechanisms that determine sexual, seasonal, or age-related dichromatism. Those studies that have examined the mechanisms controlling dichromatism have been restricted to a limited number of taxa (for reviews, see Domm 1939; Witschi 1961; Vevers 1962; Kimball and Ligon 1999). However, understanding the mechanisms that regulate patterns of dichromatism and intrasexual variation in coloration has implications for understanding the function of these traits. Coloration is an important visual signal in birds and can provide such information as an individual's age, sex, or sexual status, as well as information about the individual's potential quality as a mate or rival (Part I, Volume 2). It is these types of information that have helped stimulate much interest in avian coloration. For example, good-genes models of sexual selection predict that females should select males using traits that accurately reflect male condition (e.g., Andersson 1994; Ligon 1999); however, this prediction requires understanding whether certain traits, such as plumage or bare-part coloration, accurately reflect male quality (Zuk 1991). In addition, an understanding of the proximate control of trait expression may result in the establishment of novel hypotheses to explain the evolution of some coloration patterns (e.g., whether bright male plumage is ancestral; Kimball and Ligon 1999).

Because males and females are largely influenced by the same physiological, ecological, and environmental conditions, sexual dichromatism must be controlled by other factors. Hormones, which can vary sexually, seasonally, and ontogenetically, have been targeted as the primary mechanism controlling dichromatism of plumage and bare parts in birds (Ralph 1969). In addition to affecting dichromatism, hormones may also affect variation in coloration in a particular sex or age-class, although this area has received less attention. Here I review the hormonal factors that are known to affect coloration of plumage and nonplumage traits and discuss the functional and evolutionary implications of these patterns.

Hormones and Coloration

Studies examining the mechanisms regulating coloration have primarily included (1) seasonally or permanently sexually dichromatic species, (2) monochromatic species in which both sexes alter plumages seasonally, and (3) monochromatic species in which adults and juveniles exhibit different plumages. These studies have largely focused on adults (but see Strasser and Schwabl 2004), and thus only provide information about the role of hormones and coloration after development has been completed. Whether hormones also have organizational effects on coloration remains to be examined. Experimental methods used to elucidate the mechanisms regulating coloration patterns include castration of males or females (gonadectomy) and supplementation with one or more hormones. For many species, both gonadectomies and hormone supplementation have been used, either in the same study or in different studies on the same species. A smaller number of studies have examined the control of dichromatism by exchanging skin grafts or gonadal tissue between males and females, although these have largely been done in species in which gonadectomy and/or hormone supplementation have also been examined.

In addition to experimental studies, many anecdotal observations exist of individuals that exhibit coloration inconsistent with their sex and age, or exhibit coloration characteristic of both sexes (e.g., bilateral gynandromorphs). Although the specific hormones involved cannot be determined by these kinds of observations, the resulting color patterns frequently support conclusions reached via experimental studies, thus providing additional information regarding color control. There are also studies that have correlated levels of hormones (particularly testosterone) with color expression. However, these

studies do not always indicate that there is a direct relationship between the hormone and plumage coloration, particularly as such studies are often done at times of the year when molt is not occurring. In addition, both testosterone levels and coloration may be dependent on a third variable, such as nutrition, rather than on one another.

Several hormones have been examined with respect to avian coloration, including the steroidal androgens (e.g., testosterone) and estrogens, as well as the peptide hormone, luteinizing hormone (LH). These hormones are involved in reproduction and are part of the same hormonal cascade (Johnson and Everitt 2000; Nussey and Whitehead 2001). The hypothalamus releases gonadotropin-releasing hormone, which stimulates the release of LH and follicle-stimulating hormone from the anterior pituitary. In both sexes, LH stimulates secretion of androgens from the gonads. In females, LH also stimulates the action of aromatase, which converts androgens (particularly androstenedione and testosterone) into estrogens. Negative-feedback loops exist between the secretion of LH from the pituitary and the steroid hormones from the gonads. In addition to secretion of steroid hormones from the gonads, birds are also known to secrete steroid hormones from the brain (Tsutsui and Schlinger 2001) and androgens from the adrenal gland (Boswell et al. 1995; Schlinger et al. 2004). Due to the intertwined and complex nature of these hormonal pathways, the specific hormones that control color may not be readily identifiable in some cases, and published results may need to be interpreted cautiously (Box 10.1). In addition, for some species, the coloration of plumage and nonplumage traits does not appear to be affected by hormones (at least in adults).

Although hormones may frequently affect the presence or absence of color patterns and the intensity of coloration, the specific type of color produced depends on other factors. Black, brown, and gray colors are due to the deposition of melanin pigments (Chapter 6). Carotenoid pigments give rise to red, orange, and yellow colors (Chapter 5). Blue, green, violet, ultraviolet, and white feathers derive their color from the microstructure of the feather (Chapter 7). Many species have color patches that involve a mixture of color types (e.g., both melanin and carotenoid patches). Regardless, environmental factors, such as food access and parasites, can affect all of these color displays (Chapter 12). When hormones affect coloration, they may do so by affecting pigment synthesis, pigment use (deposition or withdrawal), or the formation of specific microstructures.

Box 10.1. Experimental Limitations

Studies examining the hormonal control of avian coloration are necessarily limited in scope, meaning that no one study provides a complete picture of hormonal control of coloration in a species. For example, some studies have examined only a single sex (usually males), used only a single approach (e.g., gonadectomy but not hormone supplementation), or examined only a subset of the possibilities (e.g., supplemental testosterone was given but other hormones were not supplemented or examined). Gonadectomy alone may suggest that steroid hormones (androgens and/or estrogens) are involved in the development of colorful plumage. However, the absence of a change in coloration following gonadectomy does not rule out a role for steroid hormones due to extragonadal steroidogenesis (e.g., Boswell et al. 1995; Tsutsui and Schlinger 2001; Schlinger et al. 2004). Removal of all gonadal tissue, particularly ovarian tissue, is difficult. Although most studies including gonadectomies have performed autopsies to look for residual gonad, this practice is not universal. Many of these studies were done before it was possible to obtain pure and consistently quantified hormones. For example, the hormones administered to birds were often extracted from urine (human or horse), but specific hormones were not further purified, so study subjects may have received a mixture of all hormones present in the original extract. Conclusions from such studies may be affected by impurities, or levels of hormones that are outside normal ranges.

Interactions and interconversions among hormones can also be problematic. Many of these hormones interact in negative-feedback loops, so the release of one hormone, such as androgens or estrogens, can lead to inhibition of other hormones, such as LH (Ball and Bentley 2000). In vertebrates, the enzyme aromatase converts androgens into estrogen, which may lead to a conclusion that testosterone determines coloration, when the agent may actually be estrogen. Careful study can tease apart such complications (e.g., if supplemental estrogens give a similar response as supplemental testosterone, it is likely that the testosterone is being aromatized).

Hormones are also involved in other aspects of molt. For example, depending on the species, androgens can inhibit or delay molt (e.g., Duttman et al. 1999; Stoehr and Hill 2001) and stimulate or accelerate molt (e.g.,

Peters et al. 2000). These interactions, and differing roles for hormones, make it difficult to determine whether a specific hormone is directly affecting coloration or is instead affecting other processes that are regulating color patterns.

Skin grafts have generally yielded mixed results, and authors using this technique have often concluded that dichromatism is affected by a combination of hormonal and nonhormonal factors. However, when both skin grafts and other methods have been employed in the same species, hormones appear to be the primary factor regulating overall color patterns. Why these differences have been obtained is unclear, but it may be due to immune responses or other side effects of transplantation. In some studies, molt was induced by plucking (e.g., Witschi 1961). This practice was implemented when the individual would not have normally molted at that time (e.g., for some species in which females molt once a year whereas males molt twice, investigators have examined what plumage females would molt into if a second molt was induced) or because the manipulations inhibited molt. There is no evidence that plucking influences the induced plumage, but such effects could exist.

The complications discussed here mean that some of the conclusions reached from some of these studies may, at times, be incorrect. However, for many species, multiple methods were used, and when all studies are taken together, the results strongly support a single mechanism controlling coloration. For other species, limited studies can be augmented by more careful research on related species that resulted in similar conclusions, providing some degree of confidence that the correct mechanism was identified.

Hormones and Plumage Coloration

Dichromatism

Experimental data on the hormonal control of plumage coloration exist for only five avian orders. The different mechanisms affecting plumage dichromatism are not randomly distributed among these orders (Table 10.1). Four of the orders appear to have a single mechanism that controls plumage dichromatism; only in order Passeriformes has more than one mechanism

Table 10.1. Experimental Studies Examining Hormonal Effects on Sexual, Seasonal, and Age-Related Plumage Dichromatism

| Species | Type of data ^a | Conclusion ^b | Reference |
|--|---|-------------------------|--|
| Struthioniformes | | | |
| Ostrich (<i>Struthio camelus</i>) | Castrate M, F | Estrogen dependence | Duerden (1919) |
| Galliformes | | | |
| Gambel's Quail (<i>Callipepla gambelii</i>) | Castrate M | Not androgens | Hagelin and Kimball (1997); Hagelin (2001) |
| Scaled Quail (<i>Callipepla squamata</i> ^c) | Castrate M | Not androgens | Hagelin (2001) |
| Lady Amherst Pheasant (<i>Chrysolophus amherstiae</i>) | Hormone supplement; skin grafts | Estrogen dependence | Vévers (1954) |
| Common Quail (<i>Coturnix coturnix</i>) | Castrate M, F; hormone supplement | Estrogen dependence | Kannankeril and Domm (1968); Warner (1970) |
| Domestic Chicken (<i>Gallus gallus</i> / <i>G. domesticus</i>) | Castrate M, F; hormone supplement; gonadal implants; skin grafts | Estrogen dependence | Domm (1939, review); Witschi (1961, review); George et al. (1981) |
| Willow Ptarmigan (<i>Lagopus lagopus</i>) | Castrate M; hormone supplement | Unclear | Stokkan (1979a,b) |
| White-tailed Ptarmigan (<i>Lagopus leucurus</i>) | Hormone supplement | Unclear | Höhn and Braun (1980) |
| Wild Turkey (<i>Meleagris gallopavo</i>) | Castrate M, F | Estrogen dependence | Scott and Payne (1934); van Oortd (1936, review) |
| Ring-necked Pheasant (<i>Phasianus colchicus</i>) | Castrate M, F; hormone supplement; skin grafts ^c | Estrogen dependence? | Danforth (1937a,c); Morejohn and Genelly (1961) |
| Reeves's Pheasant (<i>Syrnaticus reevesi</i>) | Castrate M, F; hormone supplement; skin grafts ^c | Estrogen dependence | Danforth (1937b) |
| Anseriformes | | | |
| Blue-winged Teal (<i>Anas discors</i>) | Castrate M, F; hormone supplement | Estrogen dependence | Greij (1973) |
| Mallard (<i>Anas platyrhynchos</i>) | Castrate M, F; hormone supplement; gonadal implants; skin grafts ^b | Estrogen dependence | Goodale (1910, 1918); Walton (1937); Caridroit (1938); Mueller (1970); Endler et al. (1988); Haase and Schmedemann (1992); Haase (1993); Haase et al. (1995) |

Charadriiformes

| | | | |
|--|-----------------------------------|---------------------|---|
| Herring Gull (<i>Larus argentatus</i>) | Castrate M; hormone supplement | Androgen dependence | Boss (1943) |
| Laughing Gull (<i>Larus atricilla</i>) | Castrate M, F; hormone supplement | Androgen dependence | Noble and Wurm (1940) |
| Common Black-headed Gull (<i>Larus ridibundus</i>) | Castrate M | Androgen dependence | van Oordt and Junge (1933); Groothuis and Meeuwissen (1992) |
| Red-necked Phalarope (<i>Phalaropus lobatus</i>) | Hormone supplement | Androgen dependence | Johns (1964) |
| Wilson's Phalarope (<i>Phalaropus tricolor</i>) | Hormone supplement | Androgen dependence | Johns (1964) |
| Ruff (<i>Philomachus pugnax</i>) | Castrate M; hormone supplement | Androgen dependence | van Oordt and Junge (1934); Lank et al. (1999) |

Passeriformes

| | | | |
|--|--|----------------------------|---|
| Gouldian Finch (<i>Chloebia gouldiae</i>) | Hormone supplement | Not estrogens or androgens | Crew and Munro (1938) |
| Red Avadavat (<i>Amandava amandava</i>) | Castrate M, F; hormone supplement | LH dependence | Thapliyal and Tewary (1961, 1963) |
| Brewer's Blackbird (<i>Euphagus cyanocephalus</i>) | Hormone supplement | Not estrogens | Danforth and Price (1935) |
| Yellow-crowned Bishop (<i>Euplectes afer</i>) | Hormone supplement | LH dependence | Ralph et al. (1967b); Ortman (1967) |
| Orange Bishop (<i>Euplectes franciscanus</i>) | Castrate M, F; hormone supplement | LH dependence | Witschi (1936, 1961); Ortman (1967) |
| Superb Fairywren (<i>Malurus cyaneus</i>) | Hormone supplement | Androgen dependence? | Peters et al. (2000) |
| Chestnut Munia (<i>Lonchura atricapilla</i>) | Castrate M, F | Non-hormonal? | Saxena and Thapliyal (1961) |
| House Sparrow (<i>Passer domesticus</i>) | Castrate M, F; hormone supplement; skin grafts | Non-hormonal | Keck (1934); Mueller (1977) |
| Indigo Bunting (<i>Passerina cyanea</i>) | Castrate M, F; hormone supplement | LH dependence | Witschi (1935); Witschi (1961) |
| Baya Weaver (<i>Ploceus philippinus</i>) | Castrate M, F | LH dependence | Thapliyal and Saxena (1961) |
| Red-billed Quelea (<i>Quelea quelea</i>) | Castrate M, F; hormone supplement | LH dependence | Witschi (1961) |
| Paradise Whydah (<i>Vidua paradisaea</i>) | Castrate M, F; hormone supplement | LH dependence | Witschi (1961); Ortman (1967); Ralph et al. (1967b) |

a. F, female, M, male.

b. Androgen dependence, bright plumage develops in the presence of androgens, dull plumage develops in the absence of androgens; Estrogen dependence, dull plumage develops in the presence of estrogen, bright plumage in the absence of estrogen; LH, luteinizing hormone; LH dependence, bright plumage develops in the presence of LH, dull plumage develops in the absence of LH; Nonhormonal, bright and dull plumages (in adults) develop in the absence of hormones; Not androgens, bright and dull plumages develop in the absence of androgens; Not estrogens, bright and dull plumages develop in the absence of estrogens; Not estrogens or androgens, bright and dull plumages develop in the absence of estrogens or androgens.

c. *Callipepla squamata castanogasteris* exhibits slight plumage dichromatism and was included in Hagelin (2001).

been observed. In the following section, I describe in more detail the different mechanisms that control plumage dichromatism and the orders in which they occur.

*Estrogen-Dependent Dichromatism:
Struthioniformes, Galliformes, and Anseriformes*

The presence or absence of estrogens determines plumage color and pattern in dichromatic species from three avian orders: Struthioniformes, Galliformes, and Anseriformes. Presence of estrogens leads to production of a dull, female-like plumage, whereas its absence results in a bright, malelike plumage. In both sexes, removal of the gonads results in assumption of the bright, cock plumage. Estrogen supplements to either males or females during the molt results in femalelike plumage, regardless of whether the gonads are present. In contrast, treatment with androgens does not affect plumage development in either sex. In these species, therefore, the bright coloration of male feathers does not reflect male hormonal status. Instead, the brightly colored malelike plumage is the “default” condition that results in the absence of ovarian hormone input (Ligon et al. 1990; Ligon and Zwartjes 1995; Owens and Short 1995). In females, the presence of the dull plumage is informative and indicates that the ovaries were functioning normally at the time of molt.

Among paleognathous birds, Ostriches (*Struthio camelus*) have the most sexually dichromatic plumage. The plumage presumably contains melanins and varies from brown and white in females to black and white in males. It is also the only species of paleognath for which information on the control of plumage dichromatism exists. Although this species has not been studied extensively, both experimental (Table 10.1) and observational data (Fitzsimons 1912) suggest that dichromatism in this species is dependent on the presence or absence of estrogen.

Many studies examining hormonal control of plumage dichromatism have been conducted on galliform birds (Table 10.1). In this order, adults of most species undergo a single annual molt following reproduction (but see below for an exception). Males retain their colorful plumage all year. Plumage coloration in galliforms is due to melanins and structural colors, and not carotenoids (Chapters 6 and 7). Extensive studies on the Domestic Chicken (*Gallus gallus*), as well as studies on pheasants, partridges, turkeys, and both Old and New World quail, have generally demonstrated that female plumage develops in the presence of estrogens, whereas the specialized and colorful plumage of males develops in the absence of ovarian hormones (Plate 26). The

extensive work with this group, with multiple independent studies on several species, demonstrates that estrogen dependence (and androgen independence) is characteristic of many species in this order. Studies in Ring-necked Pheasants (*Phasianus colchicus*) are less clear, as fully feminized plumage does not always develop when giving skin grafts to females or with the supplementation of estrogen (Danforth 1937a,c; Morejohn and Genelly 1961), although estrogen clearly has some affect on plumage coloration in Ring-necked Pheasants. Observational data, such as females in malelike or partially malelike plumage (but not males in femalelike plumage), also support the idea that estrogen is the primary hormone involved in plumage dichromatism in galliforms (Harrison 1932; Hagelin and Kimball 1997). Observations also suggest that plumage is estrogen dependent in other galliforms, including the Indian Peafowl (*Pavo cristatus*; Plate 8), Northern Bobwhite (*Colinus virginianus*), and California Quail (*Callipepla californica*; Hunter 1780; Brodkorb and Stevenson 1934; Buchanan and Parkes 1948; Crawford et al. 1987), but experimental studies are still needed for these taxa.

The best evidence for the role of estrogens in determining plumage type comes from extensive experimental studies of hen-feathered roosters in Sebright and Campine chickens. In these breeds, a retrotransposon insertion into the promoter of the autosomal aromatase gene results in constitutive expression of aromatase. The increased aromatase activity converts much of the circulating androgens to estrogens in extragonadal tissues, such as the skin (George et al. 1981; Wilson et al. 1987; Matsumine et al. 1990; Matsumine et al. 1991). Therefore healthy males producing normal levels of androgens will have high levels of estrogens at the feather follicles, which causes males to molt into a femalelike, rather than malelike, plumage.

Two galliform species that do not fit this pattern are the Willow Ptarmigan (*Lagopus lagopus*) and White-tailed Ptarmigan (*L. leucurus*). Among galliforms, male ptarmigan are unique in that they undergo up to four molts per year (some authors only recognize three molts), including into a pure white plumage in winter and into several pigmented plumages during the spring, summer, and fall (Plate 19). Castration and hormone-supplementation experiments have been performed on Willow Ptarmigan (Stokkan 1979a,b; Höhn and Braun 1980; Figure 10.1), whereas only hormone supplements have been examined in White-tailed Ptarmigan (Höhn and Braun 1980). The existing studies, involving gonadectomy and hormone supplementation (with androgens, LH, thyroxine, follicle-stimulating hormone, and α -melanocyte-stimulating hormone), suggest that androgens and LH may be involved in the deposition

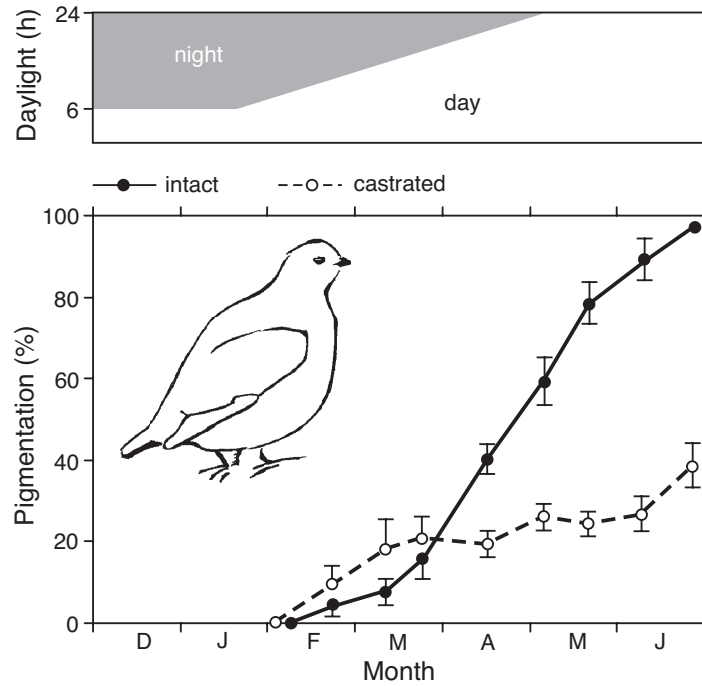


Figure 10.1. Percentage (mean \pm standard error) of the head and back appearing pigmented in intact ($n = 9$) and castrated ($n = 5$) male Willow Ptarmigan experiencing a springlike increase in day length (illustrated in top graph, where night is shaded). Redrawn from Stokkan (1979a).

of pigment in the male breeding plumage (Stokkan 1979a,b; Höhn and Braun 1980), although not all results were consistent. Other pigmented plumages, however, can develop in castrated individuals, suggesting that androgens are not necessary for pigmentation per se (Stokkan 1979a,b; Höhn and Braun 1980). Females, which lack the breeding plumage but otherwise are similar to males, are also hypothesized to require a combination of hormones for the pigmented plumages, including follicle-stimulating hormone, which does not appear to be involved in male plumage coloration (Höhn and Braun 1980). The white plumage assumed by both sexes during the winter is thought to develop in the absence of hormonal stimulation. The possible role of estrogen in the plumage development of either sex has not yet been examined in this species and thus cannot be ruled out (Owens and Short 1995). More work

remains to be done in ptarmigan to determine what hormones are directly involved in determining the color patterns for each plumage and how these hormones interact with genetic and other factors. Due to these complex hormonal patterns, such studies may be difficult and will require the administration of individual hormones and the use of hormone blockers, as well as combinations of these compounds to determine what role hormones have on the development of different plumages in both males and females.

Among the anseriforms, only two species of ducks, both in the genus *Anas*, have been examined experimentally (Table 10.1). In the genus *Anas*, males of species from the northern temperate zones annually undergo two molts, alternating between a bright (alternate) and an eclipse (basic) plumage. As with galliforms, both structural and melanin colors are present. In these species, as in the galliforms, estrogens appear to regulate plumage coloration (Table 10.1). Gonadectomy of both male and female ducks results in maintenance of the bright, alternate plumage all year, whereas supplementation with estrogens during the molt results in assumption of the eclipse plumage. The most detailed studies involve work on the Mallard (*Anas platyrhynchos*; Plate 15, Volume 2). Injection of androgens causes castrated male Mallards to molt into eclipse plumage, although it is suggested that this molt is a result of aromatization of androgens into estrogens (Haase and Schmedemann 1992; Haase 1993). Haase and Schmedemann (1992) examined other possible mechanisms for the control of plumage dichromatism in the Mallard. For example, LH seems unlikely to control color, as males that replace plucked feathers when natural LH levels are high molt into the eclipse plumage, whereas males normally molt into the bright, alternate plumage when natural LH levels are low. Supplemental estrogens (which cannot be converted back into androgens) result in the basic, eclipse plumage in both males and females. Therefore Haase and Schmedemann (1992) concluded that estrogen-dependent plumage dichromatism is the only hypothesis supported by all of the data. The aromatization of androgens into estrogens in male ducks is supported by the high levels of circulating estrogens during the late spring and early summer, when males molt into eclipse plumage (Höhn and Cheng 1967; Humphreys 1973; Donham 1979). Observational data suggest estrogen-dependent plumage in one additional species, the Northern Pintail (*Anas acuta*), in which four females were observed with partially masculinized plumage (Chiba et al. 2004). These females had low levels of estrogen (relative to control females) and showed ovarian degeneration, suggesting that the masculinized plumage was likely due to low levels of estrogen during molt.

Androgen-Dependent Dichromatism: Charadriiformes and Passeriformes

Androgens are important in determining plumage dichromatism in the order Charadriiformes (Table 10.1). In contrast to taxa in which estrogens affect plumage coloration, among the charadriiforms, dull plumage develops in the absence of the gonads, whereas the more brightly colored plumage requires the presence of androgens. For example, in males of the Ruff (*Philomachus pugnax*; Plate 7, Volume 2), androgens are required for development of the ornamental feathers at the neck (van Oordt and Junge 1934), and testosterone supplementation induces females to develop malelike feathers (Lank et al. 1999). Among the sex role-reversed phalaropes, males are dull and females exhibit bright plumage coloration. In the two species that have been studied, the Red-necked Phalarope (*Lobipes lobatus*) and Wilson's Phalarope (*Phalaropus tricolor*), androgens are necessary for females to attain their bright, alternate (breeding) plumage (Johns 1964). This response appears to be mediated in the skin, as the skin of female Wilson's Phalaropes has a greater capacity to convert testosterone to an active metabolite (5 α -dihydrotestosterone) than does the skin of males (Schlinger et al. 1989), at least for one dichromatic and melanin-containing region. In addition, there is little expression of aromatase in the skin of either sex, suggesting that the plumage of females is not due to the conversion of androgens to estrogens by aromatase activity (Schlinger et al. 1989), but rather to the action of androgens themselves.

Gulls are not sexually dichromatic. However, there is seasonal dichromatism, as well as differences in the alternate plumage between juveniles and adults. Experimental studies in three species of gulls, Laughing Gull (*Larus atricilla*), Herring Gull (*L. argentatus*), and the Common Black-headed Gull (*L. ridibundus*) have demonstrated that androgens are necessary for the development of the adult alternate plumage (Table 10.1). In two of these studies, both males and females were experimentally manipulated, and it appears that androgens are necessary for attainment of the alternate plumage in both sexes (Noble and Wurm 1940; Boss 1943; Groothuis and Meeuwissen 1992). A role for androgens has also been suggested for the development of alternate plumage in males and females in the Western Gull (*L. occidentalis*), as high levels of testosterone have been observed in females of this species during the breeding season (Wingfield et al. 1980).

Although androgen-dependent plumage is common in the charadriiforms (six species from four genera), recent data also suggest that androgens may be involved in plumage dichromatism in a passerine as well (Peters et al. 2000).

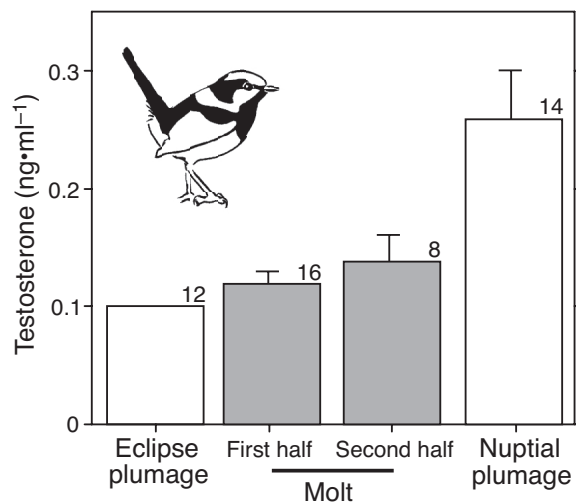


Figure 10.2. Comparison of testosterone levels (mean \pm standard error) in male Superb Fairy-wrens in eclipse plumage, undergoing the prenuptial molt and in completed nuptial plumage. Males were captured in late winter and early spring; numbers above bars are sample sizes. Redrawn from Peters et al. (2000).

In the Superb Fairy-wren (*Malurus cyaneus*), males have both a dull, basic plumage as well as a bright, alternate plumage, and molt into the bright plumage is correlated with elevations in testosterone. In addition, testosterone supplementation to males induces molt into the bright plumage, whereas removal of the testosterone supplement causes cessation of molt (Peters et al. 2000; Figure 10.2). Although the data currently suggest that development of the bright plumage is most likely due to testosterone, more work is needed to definitively conclude that androgens affect plumage coloration in this species. An alternative explanation for the Superb Fairy-wren is that testosterone stimulates molt, but other factors may have determined the coloration of the plumage. In this alternative model, the bright plumage might reflect the conversion of androgens to estrogens due to aromatase activity (however, the development of bright plumage in response to estrogens would be novel) or due to LH or nonhormonal factors.

Luteinizing Hormone–Dependent Dichromatism: Passeriformes

The effects of the pituitary gonadotropin LH on plumage dichromatism have been well studied in several species of passerine birds (e.g., the weavers) in which

males undergo two molts per year (Table 10.1). In these species, males wear a bright (alternate) plumage during the breeding season and a dull (basic) plumage during the nonbreeding season. Females, in contrast, molt only once per year and remain in their dull, basic plumage all year (e.g., Witschi 1961). Gonadectomy of either sex can result in both the brightly colored, alternate plumage, assumed during the prealternate molt (this molt must be induced in females by plucking), and the basic plumage. Because both plumages can be produced in the absence of the gonads, and no effects are seen with supplementation of estrogens or androgens, it is suggested that neither of these hormones directly affects plumage type.

For these passerines, it is the presence of LH that results in assumption of alternate plumage, and the absence of this hormone results in basic plumage (Witschi 1961). Males undergo prealternate molt in the spring, when levels of LH (and androgens) are high in both sexes; females, however, do not molt at this time. Following the breeding season, both sexes undergo the prebasic molt, when LH (and androgen) levels in both sexes are low, and the dull plumage develops. Injection of LH, but not androgens, generally results in the assumption of the bright plumage. The levels of LH necessary to stimulate production of the malelike plumage differ among studies, even in the same species (Ortman 1967). Exactly how LH acts to affect plumage coloration is not known. It appears that local injections of LH result in a systemic response (Hall et al. 1965), although what is involved in that systemic response has been difficult to elucidate (Ralph et al. 1967a).

There is also some observational data on LH control of dichromatism in passerines. A Blackpoll Warbler (*Dendroica striata*) was observed in femalelike plumage, although the bird was behaviorally a male and had been banded in a previous year in male plumage (Rimmer and Tietz 2001). This phenomenon could have occurred if LH levels had been abnormally low during molt, which might result from pituitary problems or inhibition of LH due to excessive levels of estrogens or androgens. While in female plumage, the male sang and tended a nest in which it was the putative father, suggesting that androgen levels were normal at that time (although androgen levels may not have been normal at the time of molt). Female passerines have also been observed in male-like alternate plumage, including a Rufous-sided Towhee (*Pipilo erythrophthalmus*; Bergtold 1916) and a Bay-breasted Warbler (*Dendroica castanea*; Stoddard 1921). Females could grow malelike plumage if they molt at a time when they have naturally high levels of LH (e.g., during the spring in northern temperate areas), or are secreting abnormally high levels of LH. Tumors

that secrete LH have been observed in mammals (Snyder and Sterling 1976), and similar tumors in birds could lead to unusually high LH levels. In species with estrogen-dependent plumage, females in aberrant, malelike plumage are unlikely to breed, because this condition arises when the ovary is producing little or no estrogen. In contrast, there may not be barriers to female reproduction in species in which nongonadal hormones are involved. Supporting this idea, the female passerines that have been observed in male plumage have been found with well-developed ovaries and partially developed ova (Bergtold 1916; Stoddard 1921). Although these observations do not provide unequivocal evidence for the role of LH in plumage dichromatism, they do suggest that, at least for these taxa, steroidal hormones are not involved in plumage coloration.

Gynandromorphs, Mosaics, and Control of Dichromatism

Gynandromorphs—individuals in which half of the body exhibits the plumage of one sex while the other half exhibits the plumage of the opposite sex—have been observed in a variety of avian taxa, including galliforms, anseriforms, and passerines (e.g., see references in Crew and Munro 1938; Patten 1993; Agate et al. 2003; Plate 27). In addition, mosaics, in which there are both malelike and femalelike feather tracts, have been observed in galliforms (Crawford et al. 1987; Hagelin and Kimball 1997), falconiforms (Parrish et al. 1987; Tella et al. 1996), and passerines (Summers and Kostecke 2004). Because hormones circulate throughout the body, the presence of gynandromorphs and mosaics has been used to suggest genetic or other nonhormonal control of plumage dichromatism (e.g., Cock 1960; Witschi 1961; Agate et al. 2003). However, gynandromorphs and mosaics have been observed in species for which hormonal control of plumage coloration has been well established (e.g., galliforms and anseriforms). To explain this phenomenon, Lillie (1931) proposed a hypothesis consistent with estrogen-dependent plumage dichromatism. In many gynandromorphs, one side of the body (usually that with the malelike plumage) is larger than the other (hemihypertrophy). The sensitivity of feathers to the presence of estrogen varies in Domestic Chickens and Mallards (Juhn et al. 1931; Endler et al. 1988), and may be related to feather growth rate (Juhn et al. 1931), such that faster-growing feathers are less sensitive to estrogen. Thus the more rapidly growing feathers on the male side of the body might be less sensitive to estrogen and so develop as though estrogen were not present, whereas the slower-growing feathers on the female side of the body are sensitive to the estrogen and develop into female plumage (Lillie

1931). A similar explanation could be applied to mosaics. However, there are several other possible explanations. For example, there may be differential expression of aromatase or hormone receptors on the different regions of the body that could lead to the observed patterns. Unfortunately, none of these hypotheses has been tested, making it difficult to determine the causes of gynandromorphy or to use this information to better understand the development of plumage dichromatism.

Coloration Type and Hormones Affecting Coloration

From the studies mentioned above, it is not clear whether these hormones differentially affect the type of plumage coloration that results (e.g., melanin versus carotenoid). Of interest is that carotenoids are not known to occur in any of the species for which estrogen-dependent plumage coloration has been observed (but see below for an example of estrogen control of carotenoid-based bare-part coloration), nor are carotenoids present in any of the charadriiforms known to have androgen-dependent plumage coloration. Carotenoids are present in passerines, and thus may occur in some species with androgen-dependent plumage coloration (although the Superb Fairy-wren lacks red or yellow feathers). However, given the many orders for which the hormonal mechanisms are unknown, it is possible that estrogen- or androgen-dependent coloration may occur in species exhibiting carotenoid-based plumages. The passerine species that have been examined include all types of feathers, with most species exhibiting melanins, as well as carotenoids and/or structural colors. It is known that LH and estrogens can upregulate tyrosinase, a critical enzyme in melanin synthesis (Okazaki and Hall 1965; Hall 1966, 1969). However, LH must at least affect deposition of carotenoids as well. Most likely, hormones turn on specific pathways that lead to a suite of plumage characteristics, but they may not be directly related to the type of coloration that develops.

Intrasexual Variation

In addition to their role in shaping gross plumage dichromatism, hormones can also have more subtle (to the human eye) effects on plumage coloration. Although not as easy to detect as those situations in which hormones determine male- or femalelike patterns, hormone profiles may influence the color variation that is seen in a sex or age class in natural populations (e.g., Gonza-

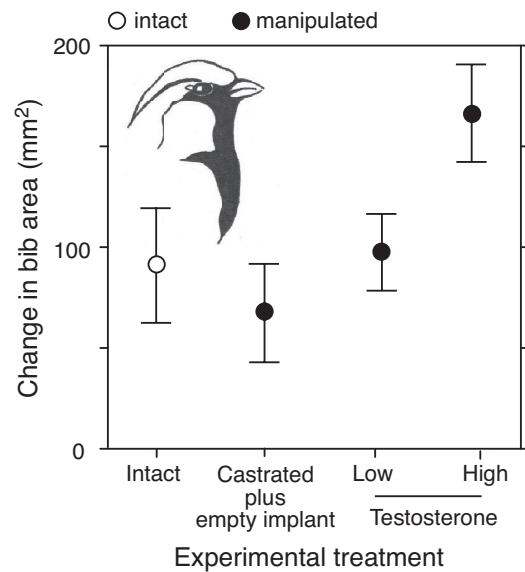


Figure 10.3. Effect of manipulation on the change in bib area during molt (mean \pm standard error) in captive male House Sparrows. Redrawn from Evans et al. (2000).

lez et al. 2001; Stoehr and Hill 2001). Thus understanding how hormones affect variation in color brightness, intensity, and extent is very important in understanding the role of plumage coloration in intra- and intersexual signaling.

Although the presence or absence of male-specific plumage in House Sparrows (*Passer domesticus*; Plate 23) is not affected by hormone supplementation (Table 10.1), hormones may control levels of color expression among males. Several studies have found that supplementation of testosterone may result in larger black badges, whereas supplementation with antiandrogens reduces badge size in adults (Evans et al. 2000; Buchanan et al. 2001; Gonzalez et al. 2001; Figure 10.3). Injections of testosterone into eggs also affects badge size once juveniles attain their adult plumage, although such injections did not affect whether an individual molted into malelike or femalelike plumage (Strasser and Schwabl 2004). A recent study found that males experiencing more aggressive interactions molted into larger badges (McGraw et al. 2003). This study and those indicating testosterone can affect badge size (even months after testosterone supplementation; Strasser and Schwabl 2004) suggest

that the effects of androgens on plumage may be complex, possibly involving a combination of direct and indirect (i.e., social) factors.

Hormones may also affect the degree of carotenoid-based red coloration in House Finches (*Carpodacus mexicanus*; Plate 31), although the mechanisms that determine dichromatism are not well understood in this species. Castration of males results in femalelike plumage, as does supplementation with estrogen (Tewary and Farner 1973). In addition, during the breeding season, redder males have higher testosterone levels than do duller males (Duckworth et al. 2004), although it is not clear whether testosterone during the breeding season correlates with testosterone levels during molt. Even though these studies suggest a possible role for androgens in the development of the red male plumage, an experimental study found that testosterone supplementation results in males that are actually drabber (displaying less red pigmentation) than controls, even among captive males whose diets contained supplemental carotenoids (Stoehr and Hill 2001). At this time, it is not clear why the results of these studies disagree, but it may be that additional hormones are involved, or that the effect of androgens differs seasonally or in response to other hormones.

Other hormones may also influence intrasexual variation in colors. The role of thyroxin has primarily been examined with regard to its effect on molt, but thyroxin may also affect deposition of melanin pigmentation in some species. For example, Miller (1935) found that supplemental thyroxin altered some plumage colors in House Sparrows, although the results varied in different parts of the body. When males were administered thyroxin, feathers that were normally brown or chestnut became gray, the pale belly feathers darkened, and the black badge was replaced with gray feathers. Conflicting results in response to thyroxin (sometimes administered as thyroid rather than purified thyroxin) have been seen across studies, even within a species. For example, in Domestic Chickens, supplementation of thyroid has led to melanism in some cases and albinism in others (reviewed in Miller 1935), although how much this difference is affected by the purity of the extracts or the exact dosing is not known. The thyroid affects gonadal activity, but the activity differs in different species and can depend on other aspects of the individual (Dawson and Thapliyal 2001). These differing responses make it difficult to establish which effects of thyroxin on plumage coloration are consistent across taxa.

Unfortunately, at this time, there is not enough information available to understand the range of modifying effects, either direct or indirect, of hormones on individual variation in plumage coloration.

Hormones and Coloration of Nonplumage Traits

There are many types of nonplumage traits in birds that are dichromatic between the sexes, seasons, or among age classes, or vary in color intensity in these groups. These include the color of the eye, eye rings, bills, legs, or featherless regions of the face and neck (including specialized structures in these regions, e.g., combs, wattles). As with plumage, the effect of hormones on the color of nonplumage traits has only been examined in relatively few species from a small number of orders (Table 10.2).

Dichromatism

In contrast to plumage, in which hormonal pathways may be involved in different orders, the general pattern for nonplumage traits is that coloration (particularly dichromatism) is dependent on androgens (Table 10.2).

However, there are exceptions to the ubiquity of androgen-dependent control of nonplumage traits. For example, seasonal and sexual expression of bill color in the Red-billed Quelea (*Quelea quelea*; Plate 6, Volume 2) is dependent on estrogen, in contrast to other studied species, in which bill color is exclusively dependent on androgens (Table 10.2). Although plumage dichromatism in queleas is typical for passerines and appears to be dependent on LH (Table 10.2), queleas are unusual in that aggression is also thought to be mediated by LH (Lazarus and Crook 1973) rather than by androgens (as for other passerines; e.g., Wingfield et al. 2000). Thus queleas have several endocrinological differences from the majority of passerines that have been studied. LH may also affect bill coloration in the Paradise Whydah, (*Vidua paradisaea*). Castration and LH supplementation indicate that the black bill of the male is dependent on LH (Witschi 1961). LH has also been suggested to affect bill coloration in the Red Avadavat (also called Lal Munia; *Amandava amandava*), although this idea has not been examined thoroughly (Thapliyal and Gupta 1984).

There is some evidence that hormonal control of bill color may also occur in the avian order Anseriformes, but the results in this group are less clear. In wild and domesticated Mallards, castration of females can cause bill color to change, although the bills never become completely masculine (Goodale 1918; Domm 1939), and this response is not universal (Goodale 1910). Castration of males does not affect bill color (Goodale 1916). These studies might suggest that estrogen has some affect on bill color (leading to femalelike bill

Table 10.2. Experimental Studies Examining Hormonal Mechanisms Affecting Coloration of Nonplumage Traits

| Species | Trait | Type of data | Reference |
|---|-----------------------|---|--|
| Struthioniformes | | | |
| Ostrich (<i>Struthio camelus</i>) | Leg color | Castrate M, F | Duerden (1919) |
| Galliformes | | | |
| Domestic Chicken (<i>Gallus gallus</i> / <i>G. domesticus</i>) | Comb and wattle color | Castrate M, F; hormone supplement; gonadal implants | Domn (1939, review); Witschi (1961, review); Zuk et al. (1995) |
| Wild Turkey (<i>Meleagris gallopavo</i>) | Head coloration | Castrate M, F | Scott and Payne (1934); van Oordt (1936, review) |
| Ring-necked Pheasant (<i>Phasianus colchicus</i>) | Wattle color | T supplement | Morejohn and Genelly (1961) |
| Gruiformes | | | |
| Common Moorhen (<i>Gallinula chloropus</i>) | Shield color | T supplement | Eens et al. (2000) |
| Charadriiformes | | | |
| Herring Gull (<i>Larus argentatus</i>) | Bill color | Castrate M; hormone supplement | Boss (1943) |
| Laughing Gull (<i>Larus atricilla</i>) | Bill and leg color | Castrate M, F; hormone supplement | Noble and Wurm (1940) |
| Common Black-headed Gull (<i>Larus ridibundus</i>) | Bill and leg color | Castrate M | van Oordt and Junge (1933) |
| Ruff (<i>Philomachus pugnax</i>) | Eye tubercles | Castrate M; hormone supplement | van Oordt and Junge (1934); Lank et al. (1999) |
| Psitaciformes | | | |
| Budgerigar (<i>Melopsittacus undulatus</i>) | Cere color | T supplement | Nespor et al. (1996) |
| Passeriformes | | | |
| American Goldfinch (<i>Carduelis tristis</i>) | Bill color | Castrate M; hormone supplement | Mundinger (1972) |
| Bobolink (<i>Dolichonyx oryzivorus</i>) | Bill color | T supplement | Engels (1959) |
| Orange Bishop (<i>Euplectes franciscanus</i>) | Bill color | Castrate M, F | Witschi (1935, 1936, 1961) |
| Chestnut-shouldered Petronia (<i>Petronia xanthocollis</i>) | Bill color | Castrate M | Tewary et al. (1985) |
| House Sparrow (<i>Passer domesticus</i>) | Bill color | Castrate M, F; hormone supplement | Keck (1934); Haase (1975) |
| Indigo Bunting (<i>Passerina cyanea</i>) | Bill color | Castrate M, F; hormone supplement | Witschi (1935); Witschi (1961) |
| European Starling (<i>Sturnus vulgaris</i>) | Bill color | Castrate M, F; hormone supplement | Witschi and Miller (1938); De Ridder et al. (2002) |
| Zebra Finch (<i>Taeniopygia guttata</i>) | Bill color | Castrate M; hormone supplement | Cynx and Nottebohm (1992); McGraw (2003) |

Note: Androgens are thought to regulate coloration in all instances.

colors); however, implantation of ovarian tissue in castrated males produced no changes in bill color, even though plumage was affected (Goodale 1918). In Blue-winged Teal (*Anas discors*), the number of spots on the bill was reduced in females that were castrated or supplemented with either estrogen or testosterone (Greij 1973). Thus, at this time, there is insufficient data to be certain of the relationship between bill color and hormones in anseriforms.

Coloration Type and Hormones Affecting Coloration

Similar to plumage coloration, coloration of nonplumage traits, particularly bill color, is often due to melanins and carotenoids. For example, the black coloration in the bills of House Sparrows is due to a deposition of melanins in response to androgens (e.g., Keck 1934; Haase 1975). Other taxa show a different pattern. For example, in European Starlings (*Sturnus vulgaris*; Plate 23) and American Goldfinches (*Carduelis tristis*; Plate 30), androgens cause a withdrawal of melanins (Witschi 1961; Mundinger 1972). The removal of melanins, combined with deposition of carotenoids (the hormonal mechanism regulating this is not well known; Mundinger 1972), results in bills that are yellow/orange during the breeding season. Still other factors can affect coloration in some nonplumage traits. For example, the color of the comb and wattles of the Red Junglefowl (*Gallus gallus*; Plate 26) are due to increased blood flow in these tissues, which occurs in response to androgens (Hardesty 1931; Lucas and Stettenheim 1972). So even though androgens are frequently involved in the coloration of nonplumage traits, it is clear that androgens turn on different biochemical pathways and colors in different tissues and different species.

Intrasexual Variation

Unfortunately, most studies that have examined the relationship between hormones and coloration of nonplumage regions have focused on large-scale color changes (e.g., between a black versus a yellow bill). Much less attention has been paid to the role of hormones in affecting intrasexual variation in the color of those traits, even though such variation may be important in such areas as mate choice (e.g., Johnson et al. 1993). It is known that androgens have an important role in regulating the intensity of red coloration in the combs of junglefowl (e.g., Zuk et al. 1995). In addition, supplementation of testosterone to female Ring-necked Pheasants resulted in redder wattles (Morejohn and

Genelly 1961). Given the potential importance of intrasexual variation in the coloration of these types of traits, further investigation into the role hormones might play in coloration is likely to be fruitful.

Importance of Understanding Hormonal Control of Coloration

A consideration of the hormonal basis of avian coloration can lead to a variety of insights about avian evolution (Box 10.2), as well as to improved understanding of the information content of color signals. One area that has been a focus of attention is the role of coloration in sexual selection. For example, good-genes models predict that females should select males using traits that reflect male condition (Andersson 1994; Ligon 1999). One hypothesis for how hormone-dependent traits might serve as a signal of male quality is the immunocompetence-handicap hypothesis (Folstad and Karter 1992). This hypothesis is based on the idea that androgens can suppress immune function, so that males with high levels of androgens might be more vulnerable to pathogens. Thus only high-quality males with either well-developed immune systems or the energetic resources to tolerate pathogen stress can afford to produce high levels of androgens. Tests of the immunocompetence hypothesis have yielded mixed results (Roberts et al. 2004), although the studies supporting the hypothesis suggest that, at least in some cases, androgen levels may provide information about male immunocompetence.

Consistent with the hypothesis that androgen-dependent traits provide information about individual quality, androgen-dependent nonplumage traits, such as bills or specialized structures like wattles and combs, appear to be important in sexual selection in a number of bird species (Chapter 4, Volume 2). Among those species in which the hormonal control of coloration is known, sexual selection studies have demonstrated a role for androgen-dependent nonplumage traits in a range of different species (Ligon et al. 1990; Zuk et al. 1990, 1995; Johnson et al. 1993; Buchholz 1995). For example, Red Junglefowl females base their mating decisions at least in part on male comb size and color (Zuk et al. 1990, 1995). Coloration of the comb correlates with testosterone levels (Zuk et al. 1995), indicating that combs provide an accurate assessment of male hormonal condition. Female American Goldfinches prefer males with brighter yellow bills (Johnson et al. 1993), the coloration of which is dependent on androgens (Mundinger 1972). In particular, androgen-dependent nonplumage traits can indicate current health status, as androgen

levels and fleshy colors can become depressed in individuals that are ill (e.g., Verhulst et al. 1999).

Androgen-dependent plumage may also be important in sexual selection. In Superb Fairy-wrens, in which androgens appear to stimulate molt and may affect coloration (Peters et al. 2000), females prefer to mate with males that molt earlier (Mulder and Magrath 1994). Female preference for plumage coloration has also been reported in another species of fairy wren, the Red-backed Fairy-wren (*Malurus melanocephalus*; Karubian 2002), and bright male plumage in this species seems likely to respond similarly to androgens. However, the coloration on the red back is probably due to carotenoids, making it difficult to determine whether females might be selecting on the possible androgen-dependent aspects of the plumage or the carotenoid coloration (Chapter 4, Volume 2). Regardless of whether fairy-wrens turn out to be a good test of the role of androgen-dependent plumage in sexual selection, establishing correlations between the mechanisms affecting plumage coloration and sexual selection has the potential to be a fruitful area of research.

Whether other hormones might provide similar levels of information about individual quality or condition is not yet known. However, traits that are not dependent on hormones have the potential to convey less, or at least different, information about individual quality or condition than do androgen-dependent traits (Morgan 1919; Ligon et al. 1990; Ligon and Zwartjes 1995; Owens and Short 1995). Consistent with this idea, females of some galliform and anseriform species appear to pay little attention to male plumage that develops in the absence of hormones (e.g., Buchholz 1995; Ligon and Zwartjes 1995; Omland 1996a,b; Ligon et al. 1998; Hagelin and Ligon 2001).

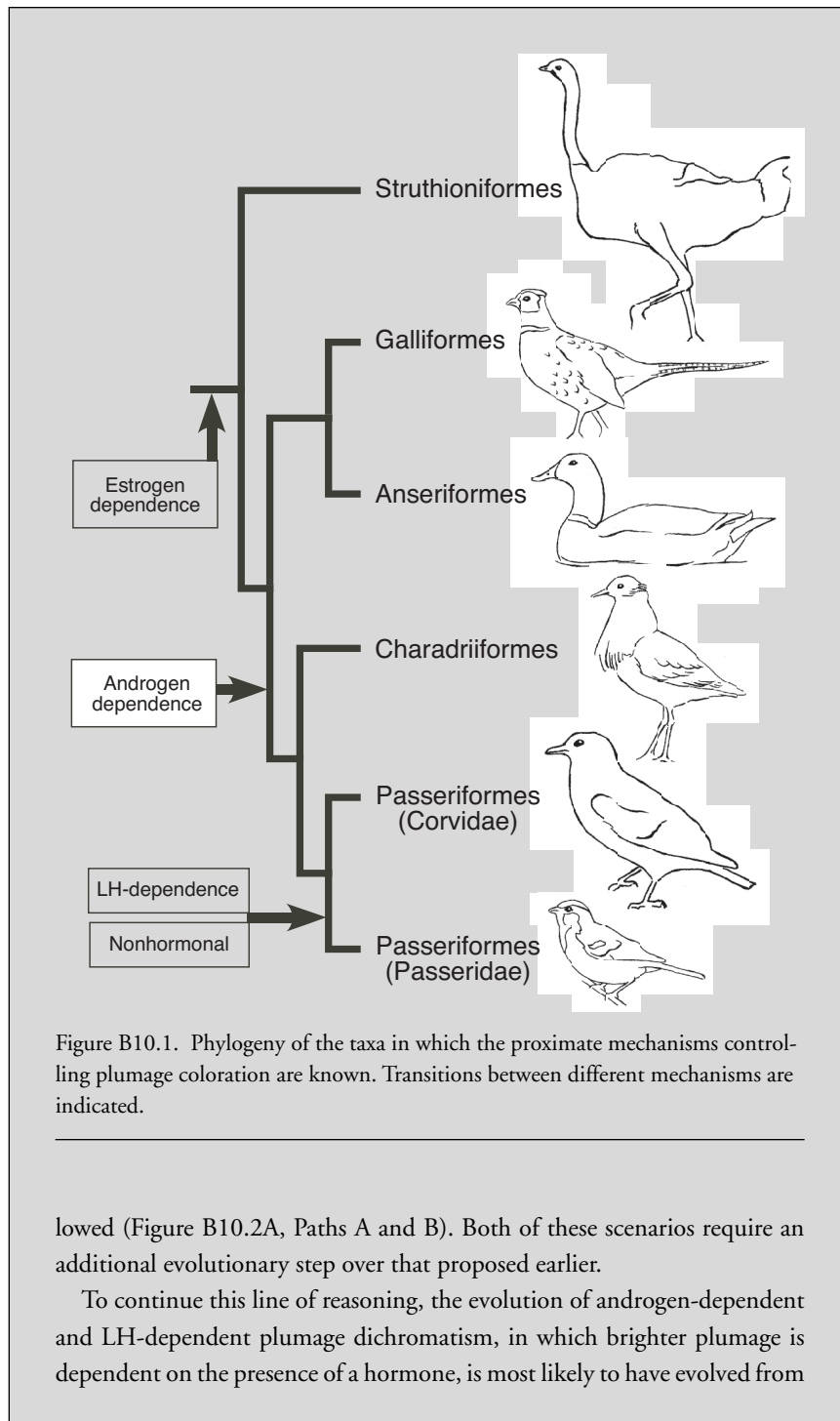
Understanding the hormone dependence of avian coloration can have benefits beyond those conceptually linked to sexual selection. For example, environmental endocrine disruptors, such as estrogen-mimics, could lead to changes in coloration for those taxa with estrogen-dependent traits (Ottinger et al. 2002). Endocrine disruptors are a common form of chemical pollution, and exposure to such disruptors could have negative consequences on fitness by altering some sex-specific signals. Knowledge of the links between hormones and color displays and how endocrine disruptors interfere with such systems also provides an opportunity to assess the degree of environmental contamination. Surveying contamination by assessing coloration of traits could be done easily in species in which individuals can be sexed readily from a distance using other means (e.g., song or other nonplumage traits). In a study on Tree Swallows (*Tachycineta bicolor*; Plate 27, Volume 2), subadult females had more

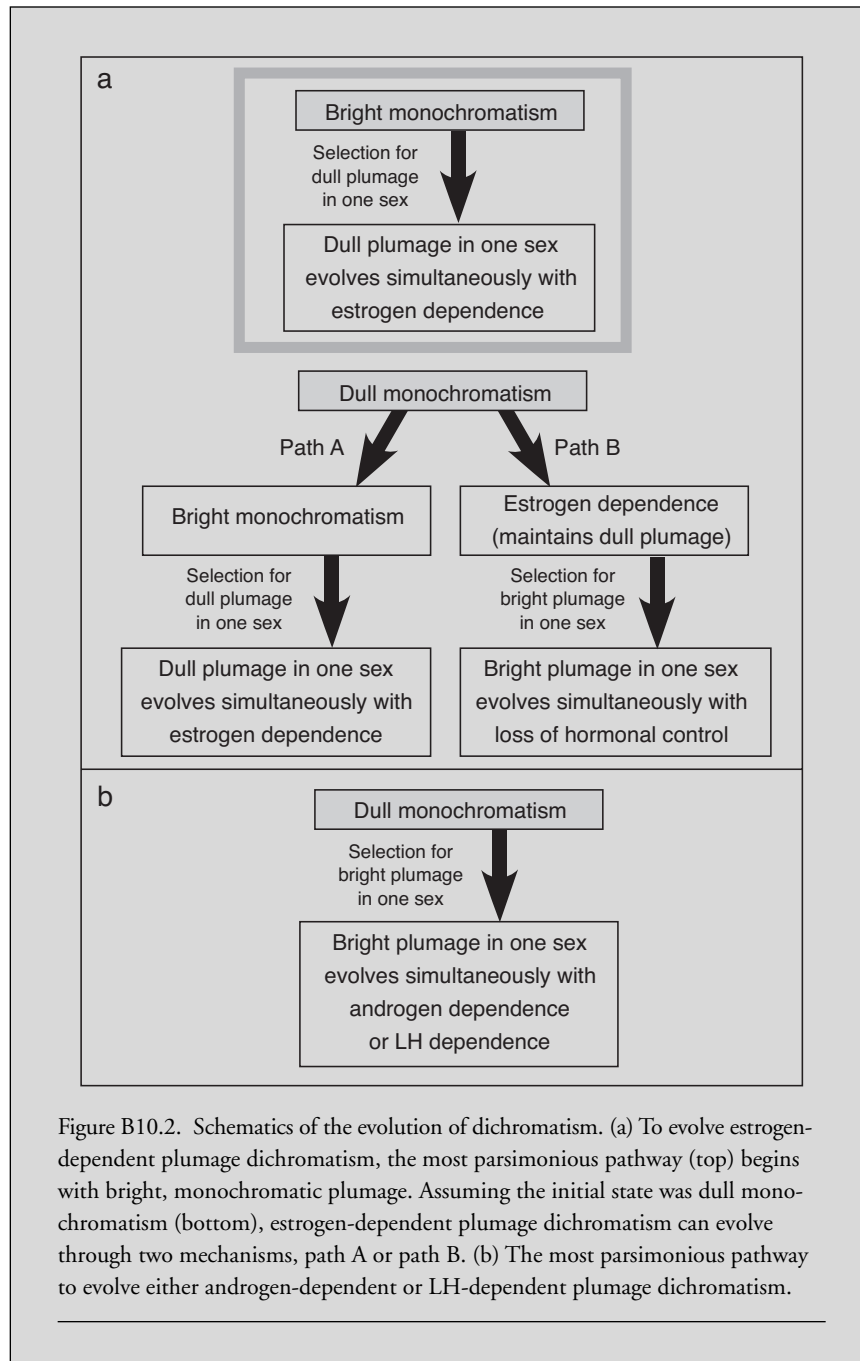
Box 10.2. Evolutionary Pathways of Hormonal Control of Coloration

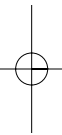
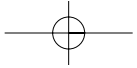
Although the data are limited, it appears that the proximate mechanisms that control plumage dichromatism are largely conserved in broad taxonomic groups, making it possible to examine the evolutionary history of these mechanisms. Most morphological and molecular analyses suggest that paleognathous birds are the most basal lineage of living birds (e.g., Sibley and Ahlquist 1990; Braun and Kimball 2002). Among neognathous birds, the position of the orders Galliformes and Anseriformes are basal and generally thought to form a clade, whereas the orders Charadriiformes and Passeriformes are more derived (e.g., Sibley and Ahlquist 1990; Braun and Kimball 2002). Relationships in the passerines are not fully resolved, although most of the passerines examined in Table 10.1 fall into the Passeroidea; the exception is the Superb Fairy-wren, which belongs to the Corvida (Sibley and Ahlquist 1990; Barker et al. 2001). Using this phylogeny, it appears that estrogen-dependent plumage dichromatism is present in the deepest-branching avian lineages (Figure B10.1). Control of plumage dichromatism by estrogens may have been lost in later lineages, with other mechanisms having subsequently evolved (Figure B10.1).

An examination of the proximate mechanisms of plumage dichromatism among living species can provide clues regarding the evolution of dichromatism, assuming that monochromatism is ancestral to dichromatism among the earliest birds. To evolve estrogen-dependent plumage dichromatism, the most parsimonious pathway begins with bright coloration in both sexes, followed by selection for duller color in one sex (Figure B10.2A, top of figure). This scenario is in contrast to arguments based on sexual selection that assume that dichromatism is a result of selection for brighter coloration in one sex, presumably from a dull, monochromatic ancestor, rather than selection for dull coloration from a brightly colored ancestor, as these data suggest (see also Chapter 10, Volume 2 for further discussion of ancestral color displays in birds).

Alternatively, to evolve estrogen-dependent plumage dichromatism from an ancestral condition in which both sexes were dull would require two steps—the evolution of a bright plumage that develops in the absence of hormones, and the evolution of estrogen-dependence for the existing duller plumage. To achieve these conditions, either of two pathways could be fol-





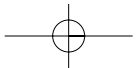


a condition of duller monochromatism (Figure B10.2B). In this way, parallel to the evolution of dull coloration in species with estrogen-dependence, the novel (brighter) plumage evolves in concert with the novel mechanism (hormone dependence), resulting in the observed situation.

These scenarios explain transitions to dichromatism, although there have also been transitions to monochromatism. For species exhibiting estrogen-dependent plumage dichromatism, transitions to bright monochromatism could occur through a mutation that prevented expression of the estrogen receptors at the feather follicle. However, to transition to bright monochromatism in species with either androgen- or LH-dependent plumage coloration, both sexes must molt at times when the appropriate hormone is present. An alternative mechanism would be any mutation that mimics the effect of the hormone, such as changes that constitutively turn on the appropriate biochemical pathway (analogous to the change in the aromatase promoter that results in hen-feathered roosters).

There are several pathways that could lead to dull monochromatic plumage from a dichromatic state. In species with estrogen-dependent dichromatism, any mutation that increased estrogen at the feather follicle in both sexes would result in a dull, femalelike plumage in both sexes. However, estrogens are highly pleiotropic, and such mutations may be deleterious in natural populations. Another pathway to dull monochromatism could be through a shift in the timing of molt, such that it occurs when estrogen levels are high (as in wild-type *Anas*; Humphreys 1973; Donham 1979). For species with androgen- or LH-dependent plumage dichromatism, dull monochromatism could occur if molt occurs at a time when hormone levels are low. For these species (unlike those with estrogen-dependent plumage dichromatism), a mutation causing reduced expression of the appropriate receptor at the feather follicle would also result in dull coloration in both sexes.

The predominance of androgen-dependent nonplumage traits among species and across orders suggests one of two possible scenarios. First, androgen-dependent secondary sexual traits may be primitive among birds, but other mechanisms (e.g., estrogen- or LH-dependence) may have subsequently evolved in the passerines. An alternative is that there has been evolution of multiple hormonal mechanisms in many avian lineages, but selection has favored maintenance of androgen-dependent traits.



adultlike plumage in areas with high polychlorinated biphenyl (PCB) contamination than in PCB-free areas (McCarty and Secord 2000). Unfortunately, the mechanisms affecting plumage coloration in Tree Swallows are not known, so it is not clear why this correlation may exist.

Conclusions

Although understanding the hormonal and nonhormonal regulators of coloration is important for addressing many other evolutionary and ecological issues, there is still much that is not understood about endocrine effects on avian coloration. Unfortunately, the experimental data currently available have been gathered from a very limited sample of avian biodiversity. Even in some of the better-studied groups, such as the passerines, more rigorous sampling is clearly needed. Mechanisms in addition to those discussed in this chapter may occur in taxa not yet examined, and the frequency of shifts among different mechanisms of plumage color may have evolved more frequently than current sampling suggests. Careful experimental studies that distinguish among several alternative hypotheses need to be conducted and placed in an explicit phylogenetic framework (e.g., Badyaev and Hill 2003). Use of carefully quantified and purified hormones, as well as new chemicals that act as hormone antagonists or inhibit specific pathways, will facilitate such studies. For example, there are now aromatase inhibitors (e.g., Vaillant et al. 2003; Moore et al. 2004), antiandrogens (e.g., Gonzalez et al. 2001; Moore et al. 2004), and estrogen-blockers (e.g., Lupu 2000) that have been demonstrated to be effective in birds. Molecular markers, such as mRNAs for aromatase, 5 α -reductase, and hormone receptors, are another set of tools that have the potential to provide information on the hormonal basis of avian coloration. These approaches should stimulate new research on the control of avian coloration, and have the potential to provide a greater understanding of the mechanisms regulating coloration.

Summary

Coloration of plumage and bare parts in birds develops in response to both hormonal and nonhormonal factors. Several different hormones are known to affect coloration, including estrogens, androgens, and LH. To develop sexual plumage dichromatism, the presence of estrogen during molt results in a dull, femalelike plumage among ostriches, waterfowl, and most galliform birds.

Androgens and LH, when present during molt, result in a bright, malelike plumage in charadriiforms (androgens only) and passerines (both androgens and LH). Hormones may also affect the expression of intrasexual variation in plumage coloration (particularly androgens), although this phenomenon has not been well studied. Coloration of nonplumage traits (bills, ceres, leg color, and specialized structures [e.g., combs]) is dependent on androgens in most studied species, although LH and estrogen are known to affect bill color in a few species. As with plumage, little is known about the effects of hormones on intrasexual variation in the color of bare parts. Although understanding the effects of hormones on coloration can provide insights into the information contained in such signals, much work still remains to be done to fully understand the relationship between hormones and coloration of plumage and nonplumage traits.

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