

Evolution of Avian Plumage Dichromatism from a Proximate Perspective

Rebecca T. Kimball* and J. David Ligon†

Department of Biology, University of New Mexico, Albuquerque,
New Mexico 87131

Submitted July 30, 1998; Accepted March 22, 1999

ABSTRACT: Several studies have indicated that sexual plumage dichromatism is a result of four proximate mechanisms: estrogen, testosterone, luteinizing hormone, and nonhormonal factors. In estrogen-dependent dichromatism, dull plumage coloration develops in the presence of estrogen, while bright coloration develops in its absence. In testosterone-dependent and luteinizing hormone-dependent plumage dichromatism, bright plumage develops in the presence of these hormones, while dull plumage develops in their absence. Placing the proximate control of plumage dichromatism in a phylogenetic context suggests that estrogen-dependent plumage dichromatism, found in the avian orders Struthioniformes, Galliformes, and Anseriformes, is likely to be ancestral in extant birds, while plumage dichromatism dependent on testosterone, luteinizing hormone, or nonhormonal factors is a more derived condition. An examination of the possible pathways leading to estrogen-dependent plumage dichromatism suggests that the fewest evolutionary steps are to begin from a condition in which both sexes are more brightly colored, followed by selection for duller coloration in one sex. The fact that estrogen-dependent dichromatism is ancestral in extant birds suggests that more brightly colored monochromatism may have been ancestral in modern lineages of birds.

Keywords: sexual dichromatism, evolution, endocrine, molt, plumage.

Many studies have examined the ultimate selective factors that affect plumage coloration and patterns in extant avian species (for detailed treatments, see Baker and Parker 1979; Butcher and Rohwer 1989; Savalli 1995). Of particular interest are those factors selecting for sexual dichromatism in plumage since both males and females are largely influenced by similar physiological, ecological, and environ-

mental conditions. It has often been assumed that sexual dichromatism can be explained by sexual selection for bright, conspicuous coloration in one sex, usually males (e.g., Witschi 1936; Butcher and Rohwer 1989; Johnson 1991; Andersson 1994; Savalli 1995). Although not always stated explicitly, such a scenario implies that more brightly colored plumage in males evolved from an ancestral condition in which both sexes were duller. Risk of predation also has been suggested to explain the evolution of sexual color dichromatism. Unlike the sexual selection hypothesis, predation hypotheses are not dependent on a particular ancestral condition: predation could have led to the evolution of either more cryptic coloration in females or brighter coloration in males (Baker and Parker 1979; Götmark 1993; Götmark et al. 1997).

Proximate mechanisms controlling sexual or seasonal plumage dichromatism have been examined in a number of taxa (for reviews, see Domm 1939; Witschi 1961; Vevers 1962). Here we propose that a consideration of such proximate mechanisms may provide useful insights regarding the evolution of coloration and dichromatism in birds. After reviewing the proximate controls of plumage dichromatism, we place this information in a phylogenetic context in an effort to obtain a better understanding of the evolution of avian coloration and sexual dichromatism.

Phylogenetic Distribution of Proximate Mechanisms Controlling Plumage Dichromatism

Several experimental studies have examined the proximate mechanisms of plumage dichromatism (table 1). The species examined consist of species with sexual dichromatism that is maintained year long, species with seasonal sexual dichromatism, and monochromatic species that exhibit seasonal differences. Experimental manipulations include castration and/or ovariectomy, hormone supplementation, skin grafts, or a combination of these approaches. For many taxa, both castration and hormone supplementation of estrogen and/or testosterone have revealed whether hormones control plumage dichromatism and, if so, which hormones are involved.

* Present address: Department of Evolution, Ecology, and Organismal Biology, Ohio State University, Columbus, Ohio 43210; e-mail: kimball.23@osu.edu.

† E-mail: jdligon@unm.edu.

Table 1: Experimental studies into proximate causes of plumage dichromatism (sexual and seasonal)

Species	Type of data	Conclusion	Citation
Palaeognathae:			
Struthioniformes:			
<i>Struthio camelus</i>	Castrate M, F	Estrogen dependence	Duerden 1919
Neognathae:			
Galliformes:			
<i>Callipepla gambelii</i>	Castrate M	Not testosterone	Hagelin and Kimball 1997
<i>Chrysolophus amherstiae</i>	Hormone supplement; skin grafts	Estrogen dependence	Vevers 1954
<i>Coturnix coturnix</i>	Castrate M, F; hormone supplement	Estrogen dependence	Kannankeril and Domm 1968; Warner 1970
<i>Gallus domesticus</i>	Castrate M, F; hormone supplement; gonadal implants; skin grafts	Estrogen dependence	Domm 1939 (review); Witschi 1961 (review); George et al. 1981
<i>Lagopus lagopus</i>	Castrate M; hormone supplement	Unclear	Stokkan 1979a, 1979b
<i>Meleagris gallopavo</i>	Castrate M, F	Estrogen dependence	Scott and Payne 1934; van Oordt 1936 (review)
<i>Phasianus colchicus</i>	Castrate M, F; hormone supplement; skin grafts ^a	Estrogen dependence	Danforth 1937a, 1937c
<i>Syrnaticus reevesi</i>	Castrate M, F; hormone supplement; skin grafts ^a	Estrogen dependence	Danforth 1937b
Anseriformes:			
<i>Anas discors</i>	Castrate M, F; hormone supplement	Estrogen dependence	Greij 1973
<i>Anas platyrhynchos</i>	Castrate M, F; hormone supplement; gonadal implants; skin grafts ^a	Estrogen dependence	Goodale 1910, 1918; Walton 1937; Caridroit 1938; Mueller 1970; Haase and Schmedemann 1992; Haase 1993; Haase et al. 1995
Charadriiformes:			
<i>Larus atricilla</i>	Castrate M, F; hormone supplement	Testosterone dependence	Noble and Wurm 1940
<i>Larus argentatus</i>	Castrate M; hormone supplement	Testosterone dependence	Boss 1943
<i>Larus ridibundus</i>	Castrate M	Testosterone dependence	van Oordt and Junge 1933
<i>Lobipes lobatus</i>	Hormone supplement	Testosterone dependence	Johns 1964
<i>Phalaropus tricolor</i>	Hormone supplement	Testosterone dependence	Johns 1964
<i>Philomachus pugnax</i>	Castrate M	Testosterone dependence	van Oordt and Junge 1934
Passeriformes:			
<i>Estrilda amandava</i>	Castrate M, F; hormone supplement	LH dependence	Thapliyal and Tewary 1961, 1963
<i>Euphagus cyanocephalus</i>	Hormone supplement	Not estrogen	Danforth and Price 1935
<i>Euplectes afer</i>	Hormone supplement	LH dependence	Ralph et al. 1967
<i>Euplectes franciscanus</i>	Castrate M, F	LH dependence	Witschi 1961
<i>Passer domesticus</i>	Castrate M, F; hormone supplement; skin grafts	Genetic	Keck 1934; Mueller 1977
<i>Passerina cyanea</i>	Castrate M, F; hormone supplement	LH dependence	Witschi 1935, 1961
<i>Ploceus philippinus</i>	Castrate M, F	LH dependence	Thapliyal and Saxena 1961
<i>Quela quela</i>	Castrate M, F; hormone supplement	LH dependence	Witschi 1961
<i>Steganura paradisea</i>	Castrate M, F; hormone supplement	LH dependence	Witschi 1961; Ralph et al. 1967

Note: M = male, F = female, LH = luteinizing hormone.

^a Some skin graft experiments indicated dichromatism may be controlled partially by genetic factors.

Studies using only skin grafts have been more equivocal, and the authors have often concluded that dichromatism is affected by a combination of hormonal and nonhormonal factors. However, where both skin grafts and either hormone supplementation or gonadectomy have been employed, it appears that hormones actually control plumage dichromatism.

Many anecdotal observations exist of individuals that exhibit plumage coloration inconsistent with their sex and age, and these too contribute to our knowledge of the proximate mechanisms controlling plumage dichromatism (e.g., Hagelin and Kimball 1997). Such observations likewise suggest that hormones are the main factor affecting plumage dichromatism in a variety of birds. Although the specific hormones involved cannot be determined by these kinds of observations, the resulting plumage patterns frequently support conclusions reached via experimental studies, thus providing additional information regarding the proximate control of plumage dichromatism.

To date, several proximate mechanisms have been identified. These include the steroid gonadal hormones estrogen and testosterone and the pituitary peptide hormone, luteinizing hormone (LH). In addition, for some species, plumage dichromatism does not appear to be affected by hormones and may remain invariant throughout an individual's life. Table 1 indicates that the different mechanisms affecting plumage dichromatism are not randomly distributed among birds. Although experimental data exist for only five avian orders, four of these are characterized by only one mechanism controlling plumage dichromatism. In the following section, we describe in more detail the different mechanisms controlling plumage dichromatism and the orders in which they occur.

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

In a number of species in these three orders, the presence or absence of estrogen determines the coloration and pattern of the plumage. Presence of estrogen leads to production of a dull, henny (female-like) plumage, while its absence results in a bright, cock (male-like) 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 assumption of the dull, henny plumage, whether or not the gonads are present. In contrast, testosterone treatment does not affect the resulting plumage in either sex. In these species, therefore, the bright coloration of male feathers does not reflect male hormonal status. Instead, the brightly colored cock plumage is the "default" condition that results from

the absence of gonadal hormones (Ligon et al. 1990; Ligon and Zwartjes 1995; Owens and Short 1995).

Among paleognathous birds, the ostrich (*Struthioniformes: Struthio camelus*) has the most sexually dichromatic plumage. Unfortunately, it is also the only species of paleognath for which information on the control of plumage dichromatism exists. Both experimental (table 1) and observational data (Fitzsimons 1912) suggest that dichromatism in this species is dependent on the presence or absence of estrogen.

Most studies of the proximate control of plumage dichromatism have been conducted on galliform birds (table 1). In this order, adults of most species undergo a single annual molt, following reproduction. Males retain their colorful plumage year round. Extensive studies on the domestic fowl, as well as studies on pheasants, partridges, turkeys, and quail, have demonstrated that female plumage develops in the presence of estrogen, while the specialized and colorful plumage of males develops in the absence of gonadal hormones. Observational data support this conclusion (Harrison 1932; Brodtkorb and Stevenson 1934; Buchanan and Parkes 1948; Crawford et al. 1987; Hagelin and Kimball 1997).

One galliform species that does not follow this pattern is the willow ptarmigan (*Lagopus lagopus*). Among galliforms, male ptarmigan are unique in that they undergo four molts a year, associated with their ability to assume a pure white plumage in winter. Castration and hormone supplementation experiments have been performed on this species (Stokkan 1979a, 1979b; Höhn and Braun 1980); however, these studies were not designed specifically to test the hormonal control of plumage dichromatism and are therefore not comparable to other studies listed. The authors suggest that testosterone and luteinizing hormone (and possibly other hormones; Höhn and Braun 1980) may be involved in the deposition of pigment in the male plumage. However, the possible role of estrogen in the plumage development of males has not yet been examined in this species and thus cannot be ruled out (Owens and Short 1995).

The best evidence for the role of estrogen in determining plumage type comes from extensive experimental studies of hen-feathered roosters in Sebright and Campine chickens. In these breeds, a single-gene mutation on an autosome causes increased aromatase activity that converts androgens to estrogen in extragonadal tissues, such as the skin (George et al. 1981; Wilson et al. 1987; Matsumine et al. 1990, 1991). The presence of estrogen at the feather follicles causes males to molt into a henny plumage rather than the normal cock plumage.

Among the anseriforms, two species of ducks have been examined experimentally (table 1). In the genus *Anas*, males of northern temperate zone species annually un-

dergo two molts, alternating between a bright (cock) and an "eclipse" (henly) plumage. In these species, as in the galliforms, estrogen appears to be the mediating factor (table 1). Gonadectomy of both male and female ducks results in maintenance of the bright cock plumage year round, while supplementation with estrogen during the molt results in assumption of the eclipse plumage. Injection of testosterone and 5α -dihydrotestosterone causes castrated male ducks to molt into eclipse plumage; apparently this is a result of aromatization of androgens into estrogen, as seen in hen-feathered breeds of domestic fowl (Haase and Schmedemann 1992; Haase 1993). The aromatization of testosterone into estrogen in male ducks is supported by the fact that circulating levels of estrogen are high during the late spring and early summer, when males molt into eclipse plumage (Höhn and Cheng 1967; Humphreys 1973; Donham 1979). Haase and Schmedemann (1992) examined other possible mechanisms for the control of plumage dichromatism in the mallard *Anas platyrhynchos* and concluded that estrogen-dependent plumage dichromatism is the only hypothesis supported by all of the data.

*Testosterone-Dependent Plumage Dichromatism:
Charadriiformes*

In at least one order of birds, the Charadriiformes, testosterone is important in determining plumage coloration (table 1). Therefore, unlike the situation in which estrogen affects plumage coloration, in these species, dull plumage develops in the absence of gonadal steroid hormones. For example, in males of the lekking ruff *Philomachus pugnax*, testosterone is required for development of the ornamental feathers at the neck (the ruff; van Oordt and Junge 1934). In the sex role-reversed phalaropes (*Lobipes lobatus* and *Phalaropus tricolor*), in which males are dull and the females exhibit bright plumage coloration, testosterone is necessary for females to attain the bright alternate (breeding) plumage (Johns 1964). This response appears to be mediated in the skin, as the skin of female *P. tricolor* has a greater capacity to convert testosterone to an active metabolite than does the skin of males (Schlinger et al. 1989).

Testosterone also is important in the assumption of adult alternate plumages in both males and females among some monochromatic species in this group. In three species of gulls, *Larus* spp., the presence of testosterone is necessary for the development of the brighter alternate plumage (table 1). In two of these, both males and females were experimentally manipulated, and it appears that, in both sexes, testosterone is necessary for attainment of the alternate plumage (Noble and Wurm 1940; Boss 1943). Testosterone may also be important for development of the alternate plumage in males and females of a fourth

species of gull, *Larus occidentalis*, as high levels of testosterone occur in females during the breeding season (Wingfield et al. 1980).

*Luteinizing Hormone-Dependent
Plumage Dichromatism:
Passeriformes*

The effects of LH on plumage dichromatism have been well studied in several species of passerine birds in which males undergo two molts a year (table 1). In these species, males wear a bright cock plumage during the breeding season (the alternate plumage) and a dull henly plumage during the nonbreeding season (the basic plumage). Females, in contrast, remain in henly plumage year round (see, e.g., Witschi 1961). Gonadectomy of either sex results in alternation between a cock plumage, assumed during the prealternate molt (if this molt is induced in females), and a henly plumage, assumed during the prebasic molt. Since both plumages are produced in the absence of the gonads, and therefore in the absence of estrogen or testosterone, it is clear that neither of these hormones directly affects plumage type. Rather, it is the presence of luteinizing hormone that results in assumption of the cock plumage, while the absence of this hormone results in the henly plumage.

Female passerines have been observed in male plumage (Bergtold 1916; Stoddard 1921), perhaps owing to secretion of abnormally high levels of LH during molt. Thus, passerines contrast with estrogen-dependent ostriches, ducks, and galliforms, in which groups it is the lack of estrogen, rather than the presence of a hormone, that causes molt of females into male-like plumage. In species with estrogen-dependent plumage, females in aberrant, male-like, plumage are unlikely to breed because this condition arises when the ovary is producing little or no estrogen. In contrast, there should be no physiological barriers to female reproduction in species in which non-gonadal hormones are involved. Female passerines in male plumage have been found with well-developed ovaries and partially developed ova (Bergtold 1916; Stoddard 1921), which further suggests that gonadal hormones are not involved in the development of plumage dichromatism in this order.

*Nonhormonal Control of Plumage Dichromatism:
Passeriformes*

In at least one passerine species, the house sparrow (*Passer domesticus*), plumage dichromatism cannot be altered by experimental manipulations (Keck 1934). Skin graft experiments performed on nestling house sparrows demonstrated that when feathers develop, the resulting plum-

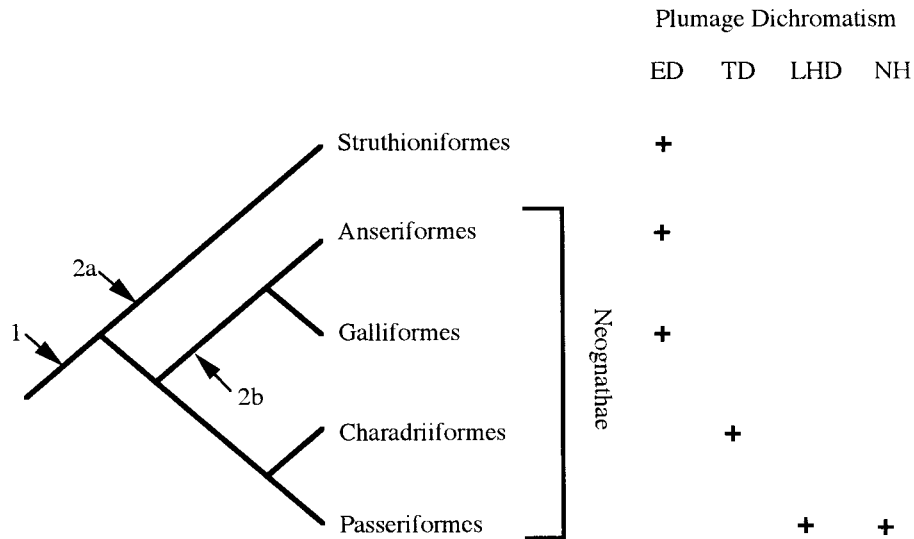


Figure 1: Phylogenetic distribution of the proximate mechanisms controlling sexual plumage dichromatism, using the phylogeny of Sibley and Ahlquist (1990); separating Anseriformes and Galliformes, placing Anseriformes basal to Galliformes, is consistent with Mayr and Amadon (1951) and Wetmore (1960). *1* represents the evolution of estrogen-dependent plumage dichromatism, assuming a single evolutionary event; *2a*, *2b* represent the evolution of estrogen-dependent plumage dichromatism, assuming it evolved twice. *ED* is estrogen-dependent, *TD* is testosterone-dependent, *LHD* is LH-dependent, and *NH* is nonhormonal plumage dichromatism.

age was of the donor sex, not the recipient (Mueller 1977), which suggests no role for hormonal involvement. Although no specific mechanisms have been proposed to explain this pattern, it has been assumed to be determined genetically (Keck 1934; Mueller 1977).

Gynandromorphs and the Control of Plumage 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 (Patten 1993 and references therein). Since hormones circulate throughout the body, the presence of gynandromorphs suggests nonhormonal control of plumage dichromatism, contrary to the cases presented earlier. Several genetic explanations have been proposed to explain gynandromorphs, including loss or nondisjunction of chromosomes early in development and involvement of polar bodies or supernumerary spermatozoa (Cock 1960; Witschi 1961). A hypothesis consistent with estrogen-dependent plumage dichromatism has also been proposed (Lillie 1931). In most gynandromorphs, one side of the body (usually that with the male-like plumage) is larger than the other (hemihypertrophy). The sensitivity of feathers to the presence of estrogen is dependent on 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 are less sensitive to estrogen and so develop as though estrogen were not present, while the slower-growing feathers on the "female" side of the body are sensitive to the estrogen and develop into female plumage (Lillie 1931). It is not known whether a similar hypothesis could explain gynandromorphs in taxa with testosterone- and LH-dependent plumage dichromatism. Unfortunately, none of these hypotheses has been tested; thus, it is difficult either to determine the cause(s) of gynandromorphy or to use this information to better understand the development of plumage dichromatism.

Evolutionary Pathways of Proximate Mechanisms

The fact that, insofar as it is known, the proximate mechanisms that control plumage dichromatism are largely identical within an order suggests that indirect examination of the evolutionary history of the mechanisms controlling sexual plumage dichromatism may be possible. The paleognathous birds, which include the ostrich and other ratites, plus the tinamous, are thought to be the most basal lineage of living birds and thus to represent the outgroup to all other avian lineages, collectively referred to as the neognathous birds (fig. 1). This conclusion is supported by both molecular and morphological anal-

yses (e.g., Stapel et al. 1984; Cracraft and Mindell 1989; Mindell and Honeycutt 1989; Sibley and Ahlquist 1990).

Among neognathous birds, the position of the Galliformes and Anseriformes may be basal (Stapel et al. 1984; Cracraft and Mindell 1989; Mindell and Honeycutt 1989; Sibley and Ahlquist 1990), with some studies placing the two orders together in a clade (Cracraft and Mindell 1989; Sibley and Ahlquist 1990; Caspers et al. 1997; Mindell et al. 1997; but see Ericson 1996). The phylogenetic position of the Charadriiformes, relative to the other orders examined here, is controversial (e.g., Feduccia 1995), but the Passeriformes are generally considered to be the most derived avian order (e.g., Mayr and Amadon 1951; Wetmore 1960; Sibley and Ahlquist 1990). If the Galliformes and Anseriformes are indeed the most basal extant neognaths, estrogen-dependent plumage dichromatism is present in the deepest-branching avian lineages. Control of plumage dichromatism by estrogen may have been lost in later lineages, with other mechanisms, such as testosterone, luteinizing hormone, or nonhormonal control, having subsequently evolved (fig. 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. The arguments are virtually identical whether dichromatism evolved in the avian or the reptilian ancestor of modern birds, since the primary differences involve coloration of plumage versus scales. To arrive at estrogen-dependent plumage dichromatism, the pathway requiring the fewest evolutionary steps begins with brighter coloration in both sexes, followed by selection for duller color in one sex (fig. 2A, *shaded portion*). This is in contrast to arguments based on sexual selection that assume that dichromatism is a result of selection for brighter coloration in one sex. If brighter plumage initially developed in the absence of gonadal hormones (as seen in the ostrich, galliforms, and anseriforms), the evolution of estrogen-dependent plumage dichromatism would require selection for duller plumage in one sex, plus a novel mechanism (estrogen-dependent plumage) for the development of this evolutionarily new plumage (fig. 2A, *shaded portion*).

Alternatively, to evolve estrogen-dependent plumage dichromatism from an ancestral condition in which both sexes were more dully colored and neither sex exhibited hormonal control of plumage, brighter plumage coloration needs to evolve and develop in the absence of hormones, while the existing duller coloration needs to come under the control of estrogen. To achieve this, either of two pathways could be followed. First, brighter coloration could evolve in both sexes, and the pathway described in the preceding paragraph would then occur (fig. 2A, *entire pathway*). This involves an additional evolutionary step

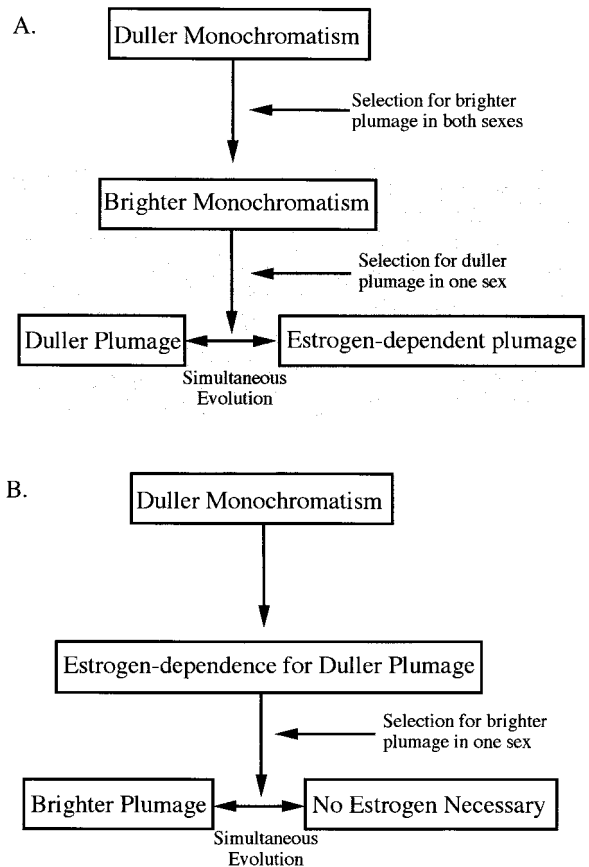


Figure 2: Two alternative pathways leading to estrogen-dependent sexual plumage dichromatism from monochromatism. The shaded portion (A) represents the pathway with the fewest evolutionary steps.

over the situation outlined in the preceding paragraph, in which both sexes initially exhibit more brightly colored plumage. If the evolution of brighter coloration in both sexes was not the first evolutionary step, then a response to estrogen at the feather follicles was the initial evolutionary step (fig. 2B). However, it is difficult to imagine why a novel mechanism (estrogen dependence) would be selected to maintain the original duller phenotype, while, concurrently, a novel (brighter) plumage would evolve that depended on the original, nonhormonal mechanism controlling the development of plumage coloration. These points suggest that duller monochromatism is a derived condition and that the ancestral condition was for both sexes to be brighter than the observed duller coloration that develops in response to estrogen.

To continue this line of reasoning, the evolution of testosterone-dependent (Charadriiformes) and LH-dependent (Passeriformes) plumage dichromatism, in which brighter plumage is dependent on the presence of a hor-

more, is most likely to have evolved from a condition of duller monochromatism (fig. 3). In this way, the novel (brighter) plumage evolves in concert with the novel mechanism (hormone dependence), resulting in the observed situation.

These scenarios suggest that transitions between dichromatic and monochromatic plumages have occurred. This conclusion is also suggested by the presence of both monochromatic and dichromatic species in the avian orders discussed earlier. The transition from estrogen-dependent sexual dichromatism to a monochromatic state can be accomplished in several ways (e.g., table 2). Transitions from testosterone-dependent and luteinizing hormone-dependent plumage dichromatism to monochromatism would likely follow similar pathways.

Patterns of Avian Coloration

Coloration in Primitive Birds

On the basis of the prior considerations, there appear to be two alternative evolutionary scenarios regarding the patterns of plumage coloration among the ancestors of modern avian lineages. Examining the evolution of the proximate control of plumage dichromatism on an avian phylogeny suggests that the earliest mechanism controlling avian dichromatism was estrogen-dependent plumage dichromatism. Assuming this mechanism evolved once, before the separation of paleognathous and neognathous birds (fig. 1), is the simplest explanation in that the complex mechanism (estrogen dependence) evolved only once. This evolutionary scenario suggests that the early ancestors of all living birds, possibly even the reptilian ancestor, may have exhibited relatively brightly colored plumage in both sexes.

In the other scenario, estrogen-dependent plumage dichromatism evolved twice: once in the ancestor of the only strongly dichromatic species of paleognathous bird, the ostrich, and again in the neognathous ancestor of galliforms and anseriforms. In this scenario, the ancestor of ostriches, as well as that of galliforms and anseriforms, was more brightly colored in both sexes. Unfortunately, it may not be possible to determine whether estrogen-dependent plumage dichromatism evolved once or twice.

Independent evolution of estrogen-dependent plumage dichromatism in two lineages, if this occurred, could be a result of the unusual characteristics of ostriches among paleognathous birds. Male ostriches are larger and brighter than females, whereas in other paleognaths the sexes are similar or females are larger and somewhat brighter (Cabot 1992; Folch 1992). Sexual selection appears to be strong in ostriches, with a single male attracting several mates to lay eggs in its nest (Handford and Mares 1985). Except

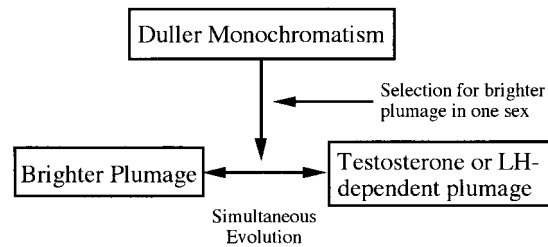


Figure 3: The most likely evolutionary pathway of testosterone-dependent or Leutenizing hormone-dependent sexual plumage dichromatism from monochromatism.

for the ostrich that exhibits biparental care, paleognaths exhibit exclusive male parental care (Handford and Mares 1985). Thus, it appears likely that ancestral as well as most extant paleognaths exhibited male-only parental care (Wesolowski 1994; Ligon 1999); this may have favored dull male coloration in this lineage. Finally, phylogenetic studies suggest that the ostrich is derived among paleognaths (e.g., Lee et al. 1997). This, combined with other unique traits of ostriches, suggests that these birds may differ from other paleognaths in the hormonal control of plumage dichromatism.

Regardless of whether estrogen-dependent dichromatism evolved once or twice, selection for crypticity in one sex may have led to the evolution of the estrogen-dependent plumage dichromatism seen in ostriches, galliforms, and anseriforms. Female ostriches incubate by day on the ground, and in both galliforms and anseriforms, most species nest on the ground where bright and conspicuous coloration may increase the risk of predation (Haskell 1996). As a point supporting a relationship between parental care and plumage coloration, among anseriforms and galliforms the duller sex generally provides more parental care (e.g., Kear 1970; Scott and Clutton-Brock 1989). Thus, in these lineages, visually oriented predators may have provided selection for cryptic females, as the incubating sex, while exerting little or no selection on the already brighter male plumage coloration.

Coloration in Other Avian Taxa

Bright plumage in both sexes also may be ancestral in some more derived lineages. In an analysis of the Fringillidae (Passeriformes), Björklund (1991) concluded that the evolution of dichromatism was not a result of selection for bright males but rather of selection for dull females in bright monochromatic taxa. This contradicts our hypothesis that passerines evolved from a duller, monochromatic ancestor. However, passerines compose the largest avian order, and it is possible that additional mechanisms may

Table 2: Evolutionary pathways from estrogen-dependent dichromatism to monochromatism

Pathway	Description
To bright monochromatism	A single mutation that affected estrogen-dependent plumage dichromatism (e.g., a mutation in the estrogen receptor at the feather follicle).
To dull monochromatism	Increased aromatase activity in males, such as occurs in anseriforms and hen-feathered breeds of chickens. Mutations leading to hen-feathered chickens have been observed in many lineages of chickens (Hutt 1949). Constitutive expression of genes controlling for dull plumage. Selection for dull coloration in males in the absence of hormones. This may lead to reduced selection for estrogen-dependent dull coloration in females, and estrogen dependence could be lost.

affect plumage dichromatism in this order. Irwin (1994) examined the phylogenetic distribution of plumage coloration in the New World blackbirds (Passeriformes: Icteridae) and concluded that in this group there are more evolutionary changes in female coloration and monochromatic species are more likely to be brightly colored.

These studies, combined with the different ancestral conditions we propose (brighter monochromatism in taxa currently exhibiting estrogen-dependent plumage dichromatism, and duller monochromatism in taxa with testosterone- or LH-dependent plumage dichromatism) suggest that transitions between monochromatism, either with both sexes brighter or both sexes duller, and dichromatism have occurred within and between lineages (e.g., Price and Birch 1996; Kimball et al. 1999).

Bright Monochromatism in Extant Species

Many avian taxa, including entire families and even orders, are characterized by relatively bright monochromatic plumage (e.g., Coraciiformes, Musophagiformes, Phoenicopteriformes, Piciformes, Psittaciformes, Trogoniformes). The diversity of taxa in which bright monochromatism occurs suggests several, not mutually exclusive, possibilities. First, selection for cryptic coloration may not be strong in many taxa. For example, some orders characterized by relatively bright monochromatism consist largely of species that nest in holes or burrows (e.g., Coraciiformes). This means that during nesting, visual detection by predators is largely avoided; that is, cavity nesting may reduce selection for cryptic coloration (Ligon 1999). Second, “social selection” (West-Eberhard 1983) favoring bright plumage in both sexes may be common in certain groups of birds. Bright coloration in females has been associated with increased female aggression and territoriality in several species (e.g., Trail 1990; Irwin 1994), which suggests that, in certain cases, there may be selection on females to maintain bright coloration. Third, bright female plumage may be preferred by males. For example, in both house finches (Hill 1993) and least auklets (Jones

and Hunter 1993), mate choice occurs not only by females for males but also by males for females. (This probably will prove to be true in most monogamous species, and the vast majority of birds are monogamous; Ligon 1999.) In these situations, males prefer females exhibiting the same bright plumage traits that females prefer in males. Finally, a genetic correlation between male and female plumage brightness may lead to bright females when strong selection exists for bright male plumage (e.g., Lande 1980; Muma and Weatherhead 1989; but see Bleiweiss 1997).

The widespread distribution of bright coloration also suggests that brightly colored plumage within and between species is, in itself, unlikely to be particularly costly to produce (e.g., Lindström et al. 1993; Bleiweiss 1997). Therefore, bright plumage should not be disfavored by selection on the basis of metabolic cost. Unless there is directional selection for dull, cryptic coloration, such as that necessary to avoid detection by predators, bright plumage may be maintained over long evolutionary time periods.

The Importance of Understanding the Control of Plumage Dichromatism

A consideration of the hormonal basis of plumage dichromatism may be important in gaining a fuller understanding of the types of traits used in sexual selection (Ligon et al. 1990; Ligon and Zwartjes 1995; Owens and Short 1995). Good genes models predict that females should select males using traits that reflect male condition (Andersson 1994; Ligon 1999), such as, for example, traits that reflect testosterone levels (Ligon et al. 1990; Folstad and Karter 1992) or carotenoid uptake (Hill 1991; Gray 1996). For species in which plumage dichromatism is dependent on estrogen, the bright plumage of males provides females with little or no information about male condition (Morgan 1919; Ligon et al. 1990; Ligon and Zwartjes 1995; Owens and Short 1995). Consistent with good genes models of sexual selection, females of some galliform and an-

seriform species appear to pay little attention to male plumage (e.g., Buchholz 1995; Ligon and Zwartjes 1995; Omland 1996a, 1996b; Ligon et al. 1998). A different result would be predicted for mate choice in the testosterone-dependent bright plumage of charadriiforms. Unfortunately, no data are available for this group to test the prediction that females (or males, in sex role-reversed species, such as the phalaropes) use plumage in mate choice decisions.

In this article, we have argued that a knowledge of the proximate mechanisms controlling plumage dichromatism can provide information used to address broader evolutionary questions. Unfortunately, the experimental data currently available represent a very limited sample of avian biodiversity. Additional mechanisms may occur in lineages not yet examined. Clearly, experimental studies involving a broad array of taxa are needed to further understand the evolution of plumage dichromatism and the proximate mechanisms controlling it.

Acknowledgments

E. Braun, J. Hagelin, R. Irwin, and an anonymous reviewer provided helpful comments on earlier versions of the manuscript. P. Zwartjes provided thoughtful discussion on the ideas contained in this article. E. Braun assisted in drawing the figures.

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