Avian Sexual Dichromatism in Relation to Phylogeny and Ecology

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■ **Abstract**   The extent and diversity of sexual dichromatism in birds is thought to
be due to the intensity of current sexual selection on the plumage ornamentation of
males and females. This view leads to an expectation of concordance between eco-
logical conditions and sexual dichromatism. Yet, because expression of dichromatism
is the result of not only current selection, but also historical patterns of development,
function, and selection, the concordance between ecology and current sexual dichro-
matism is not straightforward. Recent studies have revealed a number of trends in
the evolution of avian sexual ornamentation that seem contrary to what is expected
if current sexual selection is the primary force shaping dichromatism. For example,
change in sexual dichromatism is often the result of evolutionary changes in female
rather than male ornamentation. Moreover, sexual dichromatism is often an ancestral
rather than a derived state; current expression of dichromatism is frequently the re-
sult of selection for lesser ornamentation in one sex and not for ornament elaboration.
Loss and gain of sexual ornamentation sometimes precedes changes in preference for
sexual ornamentation, and sexual ornaments can have high evolutionary lability de-
spite their developmental and functional complexity. These findings emphasize that
phylogenetic reconstructions must play a central role in attempts to understand the
function and evolution of sexual dichromatism. With a historical perspective, one can
test the relative importance of direct selection, indirect selection, and drift in relation
to changes of sexual dichromatism. If sexual selection is invoked, the mechanisms of
sexual selection can be explored by examining the concordance between the elabo-
ration of ornamentation and the preferences for ornamentation across species and by
tracing phylogenetic trajectories of sexual ornaments. Finally, placing physiological,
genetic, and developmental mechanisms of sexual ornamentation into such a phylo-
genetic framework will enable greater inference about the past evolution and current
function of sexual dichromatism in birds.

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INTRODUCTION

Sexual dichromatism, defined as differences in the coloration of males and females of the same species, is thought to have evolved in response to selection pressures that differ between the sexes. In turn, the selection pressures on the sexes are influenced by the environment in which breeding occurs. Changes in predation, parasitism, or the distribution and abundance of resources can shift the balance between the benefits of exaggerated ornamental plumage and the cost of maintaining and developing such traits, and these environmental conditions often influence male and female plumage differently. Thus, diversity of ecological conditions commonly leads to substantial intra- and interspecific variability in sexual dichromatism.

Whereas a general relationship between sexual dichromatism and ecological factors has been addressed in many studies (Andersson 1994, Bennett & Owens 2002), major questions remain. First, it is unclear why some families and orders of birds show extensive variation in sexual dichromatism while other taxa, often apparently experiencing a similar range of environments, are remarkably conservative in their sexual ornamentation and degree of dichromatism. Second, it remains poorly understood to what degree the high genetic correlations typically observed between the sexes for plumage traits affect the evolution and diversification of sexual ornamentation. Because most of the physiological and developmental processes that produce sexual ornamentation are shared between the sexes (e.g., Kimball & Ligon 1999), high between-sex genetic correlations themselves might be a product of long-term selection. For example, when selection for sex-biased expression of a trait is not consistent, it may be advantageous for the developmental program of each sex not to respond rapidly to environmental change (Badyaev 2002). This would limit the speed of change in ornamentation in each sex and explain the lack of concordance between current ecology and sexual dichromatism within a species. Third, it is unclear whether sexual dichromatism is generally a derived state, as has been traditionally assumed, or if it can also be an ancestral state. Similarly, in most cases it remains uncertain whether sexual dichromatism is due to selection for greater ornamentation in males, as is commonly assumed, or due to selection for reduced ornamentation in females. Furthermore, it remains poorly understood to what degree ancestral dimorphic traits, such as pigment type and developmental patterns of plumage coloration, bias the evolution of derived ornamental traits and whether such constraints differ between taxa. Finally, the role of sexual selection versus other selective forces in the evolution of dichromatism and, when sexual selection is implicated, the roles of various mechanisms of sexual selection in the production of sexual dichromatism are highly debated issues. As we emphasize in this review, the most fruitful approaches to addressing these questions are comparative analyses of sexual dichromatism in relation to ecological pressures accompanied by reconstruction of phylogenetic pathways of change in dichromatism.

ECOLOGICAL CORRELATES OF SEXUAL DICHROMATISM

Latitudinal Distribution and Migratory Tendencies

A strong association with latitude of breeding and migratory tendencies is one of the most frequently documented ecological patterns of sexual dichromatism. Bird species that are migratory that have a wider geographic distribution, and that breed at higher latitudes are more sexually dimorphic than species that are resident, have restricted geographic ranges, and that breed at lower latitudes (Bailey 1978, Fitzpatrick 1994, Grant 1965, Hamilton 1961, Mayr 1942, Peterson 1996, Price 1998, Scott & Clutton-Brock 1989). Understanding the mechanisms behind these patterns, however, remains elusive.

Three major explanations have been proposed: (*a*) the patterns are driven by geographical variation in the strength of sexual and natural selection (e.g., geographical variation in mate sampling or the importance of mate recognition). (*b*) The patterns are the result of nonselective factors, such as genetic drift. For example, small, resident, and isolated populations might be more prevalent at lower latitudes and more susceptible to the effects of drift. Or, (*c*) the patterns are due to a combination of (*a*) and (*b*). For example, if the intensity of sexual selection (e.g., competition for extra-pair mates) is influenced by the amount of genetic variation in populations, then low genetic diversity in small populations could decrease the intensity of sexual selection and lead, ultimately, to lesser sexual ornamentation (Burke et al. 1998, Petrie & Kempenaers 1998).

To derive testable explanations for latitudinal and migratory patterns of sexual dichromatism, it is essential to know the ancestral state of sexual dichromatism, the sex bias in evolutionary transitions in plumage elaboration, and the relative frequency of sexual dichromatism transformations across lineages. Furthermore, intraspecific studies that examine the development and function of sexual ornamentation in relation to population size, migratory tendencies, and latitude might be informative for understanding the mechanisms behind the interspecific patterns.

Hamilton (1961) documented that, in warblers (Parulidae) and orioles (Icteridae), species at lower latitudes were less sexually dichromatic than their relatives at higher latitudes, and he attributed the pattern to a decrease in female coloration at higher latitudes. Noting that species at low latitudes are often resident and maintain longer pair bonds than species at high latitudes, Hamilton suggested that the duller coloration of females may reduce intrasexual aggression at the time of pair formation and that increased sexual dichromatism could facilitate reliable species and mate recognition. In turn, this would speed up reestablishment of territories and pair bonds favored by the short northern breeding season (Hamilton 1961). Similarly, Bailey (1978) investigated latitudinal variation in coloration across 787 passerine species in North and Central America and found that sexual dichromatism is more pronounced in high-latitude species. Contrary to Hamilton's explanation, however, in species that were dichromatic, females as well as males were more ornamented at higher latitudes.

Several studies have corroborated Hamilton's (1961) idea that greater dichromatism may be associated with a shorter mate-sampling period. For example, resident species and species that mate while in winter flocks may have more opportunities and a longer time to evaluate and compare potential mates based on their actual performance rather than on sexual ornamentation (Slagsvold & Lifjeld 1997). The differences in the time that females have to make mate choices and the costs of mate sampling affect selection on sexual ornamentation (Badyaev & Qvarnström 2002) and might account for the greater dichromatism of migratory birds across geographical regions (Badyaev 1997a, Fitzpatrick 1994).

Alternatively, latitudinal variation in sexual dichromatism could be due to geographical variation in the patterns of natural selection, such as latitudinal differences in predation (Martin 1996; see also below). Bailey (1978) suggested that background matching is a predation-avoidance strategy that favors brighter colors for both sexes at lower latitudes. Alternatively, the reduced coloration of females at higher latitudes could be due to higher predation pressure. Important to understanding the role of predation in shaping latitudinal gradients in sexual dichromatism is the phylogenetic information on whether latitudinal transitions in plumage brightness and predation risk are sex biased.

Several studies documented that sexually dichromatic taxa tend to have wider geographic distributions than monochromatic taxa (e.g., Badyaev & Ghalambor 1998, Price 1998). This pattern is puzzling because other studies found that sexually dimorphic species have higher extinction rates and are less able to colonize novel environments than monomorphic species (McLain 1993, McLain et al. 1995, Sorci et al. 1998), presumably because resources allocated toward elaboration of sexual ornamentation might compromise an organism's ability to track environmental changes (McLain 1993, McLain et al. 1995, Sorci et al. 1998). However, recent study of nonpasserine European birds documented no difference in risk of extinction or in population declines between monomorphic and dimorphic species (Prinzing et al. 2002).

Fitzpatrick (1994) proposed that sexual ornamentation might indicate the ability of individuals to withstand the energetic demands of long migration and to select good quality wintering habitats, and this might be responsible for the interspecific association between migratory tendency and sexual dichromatism. If evolution of sexual dichromatism is related to migratory abilities, then a shift from migratory to resident status, such as in island populations should be followed by a transition from sexual dichromatism to monomorphism. In this case, loss of dichromatism is the result of weaker selection on male sexual ornamentation and thus lesser ornamentation of males. Under this scenario, a gain in sexual dichromatism following the transition from resident to migratory status is as likely as the loss of sexual dichromatism in a resident population (Fitzpatrick 1994).

Crucial to understanding the mechanisms behind latitudinal variation in sexual dichromatism is knowledge of the ancestral state of sexual dimorphism in a lineage. For example, sexual dichromatism in dabbling ducks (Anatidae) is most common in species that have a wide geographic distribution, that breed at higher latitudes, and that occur on continents, whereas monochromatism prevails among nonmigratory,

southern species that have restricted, isolated ranges (Figuerola & Green 2000, Omland 1997, Scott & Clutton-Brock 1989). For these reasons, monochromatism is particularly common among island taxa. Using phylogenetic reconstruction of sexual dichromatism in these birds, Omland (1997) showed that sexual dichromatism is an ancestral stage. Therefore, widely distributed and migratory species, when settling on islands and becoming isolated, might form monochromatic populations because of the effects of genetic drift and inbreeding (Burke et al. 1998, Omland 1997, Peterson 1996). Yet, whereas both genetic drift and natural selection can produce equal gains and losses in sexual dichromatism following shifts in migratory tendencies, given the complexity and sex-bias of many color patterns, genetic drift alone would be more likely to lead to loss of rather than gain in sexual dichromatism (e.g., Omland 1997).

Another proposed reason that island-dwelling species could be less dichromatic than their mainland-dwelling counterparts is that the risk of hybridization is commonly lower and species recognition is less important on islands than on the mainland. Support for this explanation of reduced sexual dichromatism on islands is mixed with some studies finding no association (e.g., Owens & Clegg 1999) while others are finding significant trends (Figuerola & Green 2000).

Mating Systems and Parental Care

Sexual selection arising from difference in the reproductive success and parental investment of males exerts strong selection on sexual ornamentation (Andersson 1994, Kirkpatrick & Ryan 1991, Payne 1984, Owens & Bennett 1997). Thus, the ecological conditions that affect paternal investment should affect sexual dichromatism (Andersson 1994).

Because variance in male reproductive success is expected to be higher in polygynous than in monogamous species, it is commonly assumed that sexual dichromatism should be greater in polygynous mating systems. To the contrary, however, while a close correlation between mating system and ecological conditions is well established in birds (Bennett & Owens 2002), only a few studies have documented a direct association between mating system and sexual dichromatism (Cuervo & Møller 1999, Dunn et al. 2001, Figuerola & Green 2000). The examples in this section address this apparent paradox and illustrate three points. First, the expected association between mating system and sexual dichromatism is often documented only when mating systems are defined at a very detailed scale (Dunn et al. 2001; Møller & Birkhead 1994; Owens & Bennett 1994, 1997; Møller & Cuervo 1998; Scott & Clutton-Brock 1989) and sexual dichromatism is partitioned into developmentally distinct components such as carotenoid-, melanin-, or structurally based coloration (Owens & Hartley 1998). Second, phylogenetic information on sex-biased transitions in ornament elaboration helps to identify what exactly needs to be explained—change in male coloration or change in female coloration—and thus facilitates an understanding of the association between mating systems and sexual dichromatism (Irwin 1994, Burns 1998, Cuervo & Møller 1999, Figuerola & Green 2000). Finally, a hierarchical approach afforded by

phylogenetic studies of mating systems allows examination of temporal concordance in changes of sexual dichromatism and mating systems (Dunn et al. 2001; Owens & Bennett 1995, 1997).

In one of the first studies of the association between mating system and sexual dichromatism, Crook (1964) showed that the monogamous weavers (Ploceidae) were monomorphic, whereas polygynous species were dichromatic. He attributed this pattern to the distribution of food and nesting habitat. Most recent studies, however, have found that the association between mating system and dichromatism is not straightforward. Indeed, most passerines are sexually dimorphic regardless of their social mating system; polygynous European passerines are not more often sexually dimorphic in plumage than monogamous species (Møller 1986). Similarly, despite their polygynous mating system, many species of hummingbirds (Trochilidae) are monomorphic with female coloration showing the most variation (Bleiweiss 1992).

In one of the few studies that documented the association between mating systems and sexual dichromatism, Scott & Clutton-Brock (1989) examined plumage variation in 146 species of Anatidae. They thoroughly delineated mating systems based on frequency of pairing, duration of pair bond, and partitioning of parental care and found that sexual dichromatism was greater in species with shorter pair bonds and with distinct parental roles. Male plumage brightness was most strongly correlated with pair bond duration, paternal care, and nest dispersion (e.g., with mating opportunities), whereas female brightness varied the most with nest placement and features of nesting habitat (e.g., with predation risk) (Scott & Clutton-Brock 1989). These results corroborated Kear's (1970) findings that in the majority of monochromatic species of waterfowl both sexes shared parental duties, while in most dimorphic species females raised the young alone. Figuerola & Green (2000) examined evolutionary changes in sexual dichromatism and concluded that changes in mating system are significantly correlated with changes in dichromatism. Similarly, in passerines, males of monochromatic species were more likely to participate in nest building (Soler et al. 1998) and to share incubation with females (Verner & Willson 1969) than males of dichromatic species.

Extensive paternal care may both reduce mating opportunities for males and increase risk of predation. To distinguish between these two factors it is necessary to know whether variation in sexual dichromatism is due to change in male or female coloration. Owens & Bennett (1994) documented that adult mortality closely covaried with parental care, but not with sexual dichromatism across 37 Palearctic bird species. The association between sexual dichromatism and parental care was mostly due to variation in mating opportunities among species with different paternal care. Similarly, among socially monogamous passerines, male plumage brightness was associated with the frequency of extra-pair paternity; species with higher levels of extra-pair paternity had more ornamented males and greater sexual dichromatism (Møller & Birkhead 1994).

Owens & Hartley (1998) surveyed sexual dimorphism across 73 bird species and found that different types of dimorphism were affected by distinct selection pressures. Sexual dimorphism in size was strongly associated with social mating

system and parental roles (Björklund 1990, 1991; Webster 1992), whereas sexual dichromatism was most closely associated with levels of extra-pair paternity and only weakly with parental roles (e.g., Verner & Willson 1969). Given the apparently distinct patterns of selection on different components of dimorphism, it is interesting to examine the evolutionary lability of these components, which may be greater in environment-dependent traits, such as diet-derived coloration (Badyaev & Hill 2000, Gray 1996, Hill 1996), compared to sexual dimorphism in body size and in complex patterns of coloration that may be more developmentally integrated and thus less labile phylogenetically (Badyaev 2002, Price 2002, Price & Pavelka 1996, Omland & Lanyon 2000).

In a series of comparative studies, Owens and colleagues (Owens & Bennett 1995, 1997; Owens & Hartley 1998) suggested that patterns of diversification in mating systems and life history strategies are historically nested. They argued that phylogenetically distant taxa may have converged on similar mating systems despite different evolutionary histories. Thus, ancestral evolutionary events, such as changes in the partitioning of parental care, nesting, and feeding habits, may determine the response of a lineage to current ecological conditions (Owens & Bennett 1997). Such phylogenetic constraints that limit a taxon to a specific range of mating behaviors could also limit variation in sexual dichromatism and contribute to the lack of contemporary associations between sexual dichromatism and mating systems.

Dichromatism can also vary with ecological factors such as climate or the distribution of nest sites because male parental care, and hence the intensity of sexual selection, changes with such factors. Male parental investment varies with ecological factors such as climate or the distribution of food or nest sites (Badyaev & Ghalambor 2001). For example, colder nest microclimate and spatial separation of nesting and feeding resources, such as is found at high elevations, is associated with greater male care (Badyaev 1997a, Badyaev & Ghalambor 2001). Thus, in monogamous species, the intensity of sexual selection should vary with the breeding elevation. This association was documented across 126 species of Cardueline finches; species occupying lower elevations were more sexually dichromatic than species at higher elevations, and the altitudinal variation was largely due to increased ornamentation of males at lower elevations (Badyaev 1997a).

Irwin (1994) showed that sexual dichromatism varied with mating system (polygynous species were more dimorphic) across family Icteridae and that the association was owing largely to changes in female plumage. She suggested that variation in sexual dichromatism in this group resulted from social selection on females rather than sexual selection on males. More generally, sexual selection on females to display brighter plumage should be greater in monogamous systems (Irwin 1994, Moreau 1960). In turn, mutual mate choice and female-female interactions associated with monogamous breeding may contribute to the association between female plumage brightness, sexual dichromatism, and mating system (Bleiweiss 1992, Irwin 1994, Johnson 1988, Trail 1990, West-Eberhard 1983). In one of the most comprehensive studies to date, Dunn et al. (2001) found strong and consistent associations between sexual dichromatism and social

mating systems across 1,031 species of birds; sexual dichromatism was greater in polygynous and lekking species than in monogamous species.

These studies emphasize the importance of distinguishing between monomorphism when both sexes are ornamented and monomorphism where both sexes have reduced sexual ornamentation. "Dull" monomorphism may arise from monogamous mating systems in which selection pressures associated with breeding are similar between sexes and in which mates have an extended opportunity to evaluate each other based on performance and direct comparisons (references in Badyaev & Qvarnström 2002). "Bright" monomorphism might be more prevalent in monogamous mating systems with short mate-sampling periods (West-Eberhard 1983, Fitzpatrick 1994).

It is commonly expected that sexual dichromatism should be associated with lek breeding, because variance in male reproductive success and hence sexual selection is assumed to be very strong in this mating system (Darwin 1871, Kirkpatrick 1987, Payne 1984). Interestingly, however, lekking species are not more likely to be sexually dichromatic than nonlekking species (Höglund 1989, Payne 1984, Trail 1990; but see Dunn et al. 2001). Studies of the association between lekking and sexual dichromatism illustrate that in addition to examination of the current selection on both males and females it is important to know the historical sequence of transitions such as whether a shift to or from lekking behavior preceded or followed the change in sexual dichromatism. Moreover, one needs phylogenetic information about the ancestral state of the sexual ornamentation of both sexes to generate hypotheses about the patterns of sexual ornamentation in relation to lekking. For example, prior to evolution of sex-biased expression, a transition from monomorphic dull to monomorphic bright states is expected under correlated response of females to selection on male ornamentation (Lande 1980). Increased risk of predation associated with evolutionary transition to lekking may explain changes in plumage coloration from sexually dimorphic or monomorphic bright to monomorphic dull. For example, Bleiweiss (1997) examined covariation of sexual dichromatism and plumage brightness with occurrence of lekking behavior across 415 bird species by analyzing evolutionary transitions of plumage brightness in both sexes. He found that in addition to sexual selection, predation risks and foraging behaviors associated with lekking are likely to constrain ornament elaboration (Bleiweiss 1997). In a recent analysis of phylogenetic transitions of sexual ornamentation, however, Cuervo & Møller (1999) found that acquisition of elaborate plumage ornaments was more closely associated with transition from monogamy to lekking than with change in male parental care, diet, or predation risk.

Ecological Factors Affecting Mortality and Parasitism

One explanation for sexual dichromatism is that it evolved through selection for crypsis in females because of their greater vulnerability to predators around the nest (Baker & Parker 1979, Butcher & Rohwer 1993, Götmark 1999, Wallace 1889). Sexual dichromatism in birds is generally thought to arise from sexual selection favoring conspicuous coloration in males, although natural selection (e.g.,

predation) is thought to ultimately limit conspicuousness (Darwin 1871, Fisher 1930). Alternatively, bright coloration may be favored by predation because it advertises that a prey is unprofitable, and the degree of sexual dichromatism of a species may be owing to the difference between the sexes in their profitability to a predator (Baker & Parker 1979, Butcher & Rohwer 1993, Cott 1947, Götmark 1994). Promislow et al. (1992, 1994) examined variation in sex-specific mortality due to sexual ornamentation in passerines and waterfowl. They suggested that female mortality may constrain the upper limit of sexual dichromatism in a population by limiting the maximum mortality rate of males. In turn, the ornamentation of males could be further constrained by mortality due to elaborated plumage and more intensive sexual competition (Promislow et al. 1992, 1994).

Götmark et al. (1997) showed that predation on adult chaffinches (*Fringilla coelebs*) exerts greater pressure on female than on male coloration, ultimately leading to variation in sexual dichromatism. Similarly, Burns (1998) attributed more frequent evolutionary changes in female versus male sexual ornamentation in tanagers (Thraupidae) to greater predation risk of females associated with nest predation. In cardueline finches, sexual dichromatism and plumage ornamentation in both sexes closely covaried with life history traits, but in opposite directions: fecundity covaried negatively with male sexual ornamentation but positively with female ornamentation (Badyaev 1997b).

Badyaev (1997c) examined variation in the sex-specific costs of plumage elaboration along an elevational gradient in finches and found that the association between fecundity and sexual ornamentation was more similar between the sexes in high-elevation species than in low-elevation species (Badyaev 1997a). Furthermore, Badyaev & Ghalambor (Badyaev 1997b, Badyaev & Ghalambor 2001) suggested that elevational variation in sexual dichromatism was associated with lower juvenile mortality at higher elevations. Such an association between elevation and sexual dichromatism would result when low-elevation environments favor increased and more elaborated sexual ornamentation, but when the development of such traits commonly results in reduced juvenile survival (Owens & Bennett 1994).

While a relationship between sexual dichromatism and mortality is well established, two problems persist: (*a*) identifying the specific factors behind this relationship, and (*b*) determining what is cause and what is effect in the relationship. If nest predation limits ornament elaboration (Wallace 1889, Baker & Parker 1979, Shutler & Weatherhead 1990, Johnson 1991), then male and female ornamentation should vary with the time that each sex spends at the nest vicinity. In particular, because females typically incubate eggs and brood nestlings, we expect reduced female ornamentation when the nest environment exposes females to predators. In contrast, male birds typically do not incubate or brood young, so male ornamentation might not vary as strongly with predation at nests. By separately examining male and female plumage across Parulidae and Carduelinae, Martin & Badyaev (1996) found that female plumage brightness varied with nest placement and was negatively correlated with nest predation. These results suggested that nest predation may place greater constraints on female than male plumage brightness, at least in taxa where only females incubate eggs and brood young. Moreover,

Martin & Badyaev (1996) found that female sexual ornamentation varied at least partly independently of male ornamentation, emphasizing the need to consider variation in both sexes in tests of plumage dimorphism. In warblers and finches, sexual dichromatism differed between ground- and off-ground-nesting species, but the relationship between sexual dichromatism and nest predation was positive rather than negative (Johnson 1991, Shutler & Weatherhead 1990). Specifically, differences in sexual dichromatism between ground- and off-ground-nesting birds resulted only partially from decreased male brightness (Dunn et al. 2001, Johnson 1991, Shutler & Weatherhead 1990). Most of the patterns were the result of an increase in female brightness in ground-nesting birds, which was related to their reduced risk of nest predation compared to off-ground nesters (Martin & Badyaev 1996). Effects of nest predation on sexual dichromatism are most evident when one separately examines sexual dichromatism in different body parts. For example, dichromatism of upper body parts but not lower body parts strongly covaried with nest placement across cardueline finches (Badyaev 1997a). In addition, variation in parasite prevalence across nesting and foraging strata contributed to vertical stratification of sexual dichromatism in birds (Gavrin & Remsen 1997).

The importance of current variation in nesting biology in shaping sexual dichromatism was questioned by Owens & Bennett (1995). Based on comparative analysis of current sexual dichromatism and phylogenetic history of avian groups, the authors concluded that current variation in nesting and feeding habits have little effect on current avian life history strategies, which are almost entirely due to ancient evolutionary events. If ancient and hierarchically nested evolutionary diversifications, such as changes in nest placement, were responsible for changes in sexual dichromatism, we would expect to see concordant and similarly historically nested patterns of divergence in sexual dichromatism. Other studies, however, showed that large-scale diversification in life histories are produced by more recent ecological changes (e.g., Martin & Clobert 1996). These examples illustrate the need to examine historical transitions in sexual dichromatism and plumage ornamentation in relation to changes in nesting strata or parental behavior in order to properly test the association between nesting and foraging habits and sexual dichromatism (e.g., Owens & Bennett 1994, 1997).

Sensory Characteristics, Physical Features of Habitat, and Diet

Exploitation of new habitats by birds is often accompanied by changes in plumage ornamentation. The evolution of novel sexual ornamentation may be favored by both preexisting sensory biases within lineages and characteristics of new environments that make some ornaments more easily perceived (Endler 1992, Endler & Théry 1996, Schluter & Price 1993). Physical characteristics, such as substrate abrasiveness, ultraviolet (UV) radiation, and temperature might affect sexual dichromatism by favoring specific patterns of pigmentation (Burtt 1986). The examples in this section emphasize that comparative studies need to show that color patterns are indeed preceded by habitat shifts (e.g., Marchetti 1993) and that divergence into different habitats promotes divergence in sexually selected traits

(Badyaev & Snell-Rood 2003, Barraclough et al. 1995, Møller & Cuervo 1998, Price 1998, Schluter & Price 1993).

Physical features of habitats may favor certain plumage pigmentation and thereby constrain distribution of other types of pigments or structural colors. For example, melanin pigmentation makes feathers more resistant to mechanical damage and birds living in environments with more abrasive substrates have more melanin-based colors in their plumage (Burtt 1986). Moreover, within the plumage of an individual bird, feathers that are subjected to more wear and abrasion have a higher proportion of melanin pigmentation (Fitzpatrick 1998). The presence of melanin, in turn, might bias the distribution of structural- (reviewed in Prum 1999) and carotenoid-based coloration (references in Savalli 1995). It was also suggested that high absorption qualities of some pigments might protect birds from UV radiation; Brush (1970) attributed more intense pigmentation and sexual dichromatism in tanagers breeding at higher elevations to the greater need for protection from UV.

Price (1996) examined variation in sexual dichromatism across finch species and found that drier and more open habitats had a lower proportion of dichromatic species than did moister, denser habitats (see also Badyaev 1997a). Habitat influences, however, may be confounded by the effects of nest dispersion because greater plumage dichromatism in finches is associated with solitary nesting and most open-habitat species are semicolonial. Price (1996) considered habitat density as a correlate rather than a cause of sexual dichromatism. He suggested that finches in closed habitats may breed at higher densities and thus have increased potential for extra-pair paternity (Møller & Birkhead 1993; but see Westneat & Sherman 1997).

Endler and colleagues (Endler & Théry 1996, Endler & Wescott 1998) reported a high degree of ambient-light specificity in display behaviors of several tropical species. It is unclear, however, whether such behaviors followed existing coloration patterns to maximize their function, or if patterns of coloration evolved as a result of the light environment or display behaviors of a species. McNaught & Owens (2002) found that differentiation in sexual ornamentation among 40 avian species is strongly affected by features of habitat that influence signal transmission. Similarly, differences among habitats and geographical locations in food composition may affect diet-dependent components of sexual dichromatism. For example, geographical variation in intensity of red coloration among populations of the house finch (*Carpodacus mexicanus*) was influenced by local access to carotenoids (Hill et al. 2002).

PHYLOGENETIC STUDIES OF SEXUAL DICHROMATISM

Historical Patterns of Complexity of Sexual Ornamentation

A key starting point in studies of sexual dichromatism is an understanding of the signal content of plumage displays. This requires an examination of the source

of plumage coloration (melanin, carotenoid, or structural) and the factors that might influence their displays. Such studies help researchers understand not just the proximate control of color ornaments but also the roles that developmental and phylogenetic constraints play in evolution of sexual dichromatism.

The examples in this section illustrate three points. First, different types of color display—carotenoid pigmentation, melanin pigmentation, and structural coloration—have different evolutionary lability. Second, knowledge of the phylogeny is essential for an understanding of the sequence of transitions in color patterns and ornament structure. Finally, color traits may differ in their detectability and in the information that they provide in a given environment, and these differences may bias the evolution of sexual dichromatism in such traits.

Hill & Badyaev (Badyaev & Hill 2000, Hill 1996) suggested that because carotenoid-based plumage coloration is more dependent on environment and less constrained developmentally than is melanin-based coloration, variation in sexual dichromatism should be driven more by changes in carotenoid coloration than by changes in melanin coloration. They found that across all cardueline finch species: (*a*) carotenoid-derived coloration has changed more frequently than melanin-based coloration; (*b*) in both sexes an increase in carotenoid-based coloration, but not in melanin-based coloration, was strongly associated with increase in sexual dichromatism; and, (*c*) sexual dichromatism in carotenoid-based coloration contributed more to overall dichromatism than sexual dichromatism in melanin-based plumage (Badyaev & Hill 2000, Hill 1996).

These findings supported the results of Gray's (1996) analyses of male plumage across North American passerines that the extent of carotenoid pigmentation in male plumage was positively associated with overall dichromatism, whereas the extent of melanin and structural coloration in male plumage was not related to overall dichromatism. Gray (1996) noted that carotenoids appear to be used as ornamental signals by granivorous and insectivorous taxa (for which carotenoids are present in the diet but not overly abundant) but rarely used by frugivorous (for which carotenoids are overly abundant in the diet) or carnivorous taxa (for which carotenoids are rare). Subsequently, Johnson & Lanyon (2000) showed that carotenoid-based ornaments are evolutionary labile in New World Icteridae such that transitions to greater carotenoid ornamentation closely followed historical shifts into different environments.

The similarity of coloration patterns and pigment distribution across a wide range of species within taxa suggests common developmental mechanisms and constraints. In their comprehensive study of the evolution of color patterns in *Phylloscopus* warblers, Price & Pavelka (1996) showed that components of melanin-based coloration were repeatedly gained and lost during evolution. They suggested that once a pattern of coloration evolved in a lineage it could persist even if it was not expressed phenotypically and in this way complex patterns of ornamentation could reappear (e.g., under hormonal control) when favored by selection (see below). Moreover, the colors and patterns that are currently expressed necessarily affect the development and evolution of components that are derived from the ornaments such as symmetry (Price & Pavelka 1996; see also Badyaev et al. 2001). In an

analysis of hybrids of domesticated birds, Price (2002) documented a strong historical hierarchy of divergence in sexual ornamentation and high evolutionary lability of plumage color ornamentation. Omland & Lanyon (2000) also reported high evolutionary lability of plumage characteristics within the oriole genus *Icterus*. Among oriole genera, however, the patterns of plumage change provided evidence for developmental constraints. Both examples emphasize that identification of the evolutionary sequences of coloration patterns is essential to the study of sexual dichromatism.

Schluter & Price (1993) noted that sexual selection will favor ornamental traits with more sex-biased genetic and phenotypic variance, greater condition-dependence, and easier detection in a local environment. Under certain conditions, traits like song or behavioral displays will be more likely to invade a sexually dichromatic population and in this way bias the evolution of other sexually dimorphic traits. For example, predation may limit variation in sexual dichromatism in Parulinae warblers, and song complexity may replace plumage characteristics as the target of sexual selection (Shutler & Weatherhead 1990). Badyaev et al. (2002) examined the relationship between song and plumage elaborations in cardueline finches and found that across species song complexity was strongly negatively related to elaboration of plumage ornamentation. Moreover, when plumage coloration was partitioned into carotenoid-based and melanin-based components, song complexity was negatively related to elaboration of male carotenoid-based coloration but unrelated to elaboration of melanin-based coloration. The trade-off between carotenoid plumage and song complexity might be due to their high costs and environmental dependency (Badyaev & Leaf 1997; Snell-Rood & Badyaev, in review). Similarly, Bailey (1978) suggested that structural colors are favored by selection in the tropics because structural colors are easily changed by behavioral displays depending on variable light conditions in dark habitats.

Phylogenetic Inferences About the Origin of Sexual Dichromatism

Sexual dichromatism arises from sex-biased genetic expression or from selection acting on traits with sex-limited or sex-biased genetic and phenotypic variation (Lande 1980). Once sex-specific expression of ornamentation is established, variation in sexual dimorphism can be affected by various forces (Badyaev 2002) that can be revealed by phylogenetic methods. The sources of sex-biased expression of plumage ornamentation could range from mutations on sex chromosomes to sex-limited expression of genes. A majority of expression of sexually dimorphic ornaments, however, is owing to sex-biased expression of developmental programs that are shared between the sexes. Consequently, comparative studies often find little evidence of long-term constraints on the evolution of sexual ornamentation imposed by high between-sex genetic correlations. Phylogenetic studies of the developmental processes that enable sex-biased expression of shared organismal processes hold great potential to further our understanding of the evolution and current function of sexual displays (Badyaev 2003, Kimball & Ligon 1999, Reinhold 1999).

Expression of sex-biased plumage ornamentation often depends on sex-specific hormonal profiles (reviewed in Owens & Short 1995). In some avian groups, dull coloration develops in the presence of estrogen, whereas bright coloration develops in the absence of estrogen. In other groups, expression of sexual ornamentation is regulated by testosterone—bright coloration develops under the influence of testosterone, whereas dull coloration develops when circulating testosterone is absent (Kimball & Ligon 1999). Kimball & Ligon (1999) studied the hormonal control of plumage dimorphism in a phylogenetic context and concluded that estrogen-dependent dichromatism is ancestral and testosterone-dependent dichromatism is a derived state. They suggested that the most parsimonious evolutionary sequence for the evolution of sexual dichromatism was bright monomorphism followed by selection for duller coloration in one sex (Kimball & Ligon 1999). General implication of epigenetic control of sexual ornamentation is that we would predict (*a*) easier and faster loss than gain of male sexual ornamentation, and (*b*) more frequent phylogenetic transition from dichromatism to monochromatism than from monochromatism to dichromatism (e.g., Omland 1997, Price & Birch 1996). If sexual dichromatism results from mutations on sex chromosomes that are magnified by selection favoring dichromatism, no directional bias between loss and gain is expected.

Once sex-limitation is established, genetic drift, selection, and gene interactions could influence the evolution of sexual dichromatism. On a macroevolutionary scale, genetic drift is not expected to produce consistent associations across lineages between sexual dichromatism and factors such as ecological conditions (Leroi et al. 1994, Sheldon & Whittingham 1997). On the contrary, if sexual dichromatism evolved in response to selection, change in sexual dichromatism should follow specific sequences in which shifts to new environments or changes in behaviors are followed by transitions in plumage coloration (Sheldon & Whittingham 1997).

Phylogenetic Reconstructions of Plumage Dichromatism

PHYLOGENETIC RECONSTRUCTION OF TRANSFORMATIONS IN SEXUAL DICHROMATISM   One way to explore biases in the evolution of sexual dichromatism is to examine the relative frequency of changes between monochromatism and dichromatism as well as differences in the rates of evolution of male and female ornamentation (e.g., Price & Birch 1996). Recent phylogenetic studies of avian coloration have revealed that losses of sexual ornaments are more common than gains, but that most of the transitions from dichromatism to monomorphism involve females gaining male-like ornamentation. This is surprising because sexual ornamentation is often assumed to be maintained by current sexual selection on male ornamentation (Wiens 2001).

Price & Birch (1996) estimated the frequency of evolutionary transitions in dichromatism across 5,298 species of passerines and found that sexual dichromatism evolved numerous times independently and that transitions from dimorphism to monomorphism were more likely than transition in the opposite direction. Omland (1997) reached similar conclusions in his study of ducks (Anatidae). He

showed that sexual dichromatism is an ancestral trait and that the evolution of sexual dichromatism was biased toward loss of dichromatism. Similarly, in a phylogenetic study of 47 genera of tanagers (Thraupidae), Burns (1998) found that in males a transition from bright to dull coloration is five times more likely than a transition from dull to bright, and that tanagers descended from an ancestor that was dichromatic with colorful males and dull females. These findings are corroborated in a study by Peterson (1996) in which he examined geographical variation in sexual dichromatism in 158 species of birds representing 43 families. He concluded that sexual monomorphism with bright males and dull females is a likely ancestral stage in birds. Similarly, Kimball et al. (2001), on the basis of thorough molecular analyses, concluded that the two least-ornamented species of pheasants (Phasianidae) are the most derived, implying that the sexual dimorphism and elaborated ornamentation in this clade is an ancestral state.

Whereas several studies suggested that loss of male ornamentation can be favored by adaptive female preference (Badyaev & Qvarnström 2002, Qvarnström et al. 2000, Saetre et al. 1997), comparative studies reveal that loss and gain of sexual ornamentation often precedes changes in preference for sexual ornamentation (reviewed in Wiens 2001) emphasizing the role of genetic drift and developmental processes in the evolution of dichromatism (Lande 1981, see below).

PHYLOGENETIC RECONSTRUCTIONS OF TRANSFORMATIONS IN MALE AND FEMALE PLUMAGE   Several phylogenetic studies have addressed relative changes in male and female ornamentation in relation to evolutionary lability of dichromatism (reviewed in Amundsen 2000). Peterson (1996) examined the relative frequency of "bright" and "dull" monomorphism and concluded that the evolution of female plumage contributed to the evolution of sexual dichromatism as frequently as did the evolution of male plumage. Males were much more likely to lose than to gain bright plumage, whereas in females the trend was the opposite. The fact that loss of sexual dichromatism occurs in both directions (to "dull" and to "bright" monomorphism) makes it unlikely that selection can explain the majority of cases, leading Peterson (1996) to propose genetic drift as the evolutionary force behind variation in sexual dichromatism. Similarly, Björklund (1991) documented that in two lineages of blackbirds, sexual dichromatism resulted from a loss of female coloration rather than a gain in male coloration (see also Burns 1998, Irwin 1994). These recent studies corroborate original observations that an association between plumage brightness and mating systems is mostly due to variation in female plumage (Moreau 1960). A recent study of waterfowl (Anseriformes), however, concluded that evolutionary changes in plumage ornamentation were more frequent in males than females, presumably due to greater sexual selection on male ornamentation (Figuerola & Green 2000).

Sexual Dichromatism in Relation to Mechanism of Sexual Selection

Phylogenetic analyses provide a powerful means of distinguishing between different mechanisms of sexual selection. First, hypotheses of the mechanisms of sexual selection can be tested by experimentally examining the congruence

between current expression of sexual ornamentation and current preference for this ornamentation. Second, different models of selection make distinct predictions of diversification patterns, hierarchical complexity, and convergence among lineages, thus allowing insight into sexual selection mechanisms.

In runaway models of sexual selection, a genetic correlation develops between male ornamentation and female preference and greater expression leads to greater preference until either ornamentation or preference are limited by natural selection (Andersson 1994). Hill (1994a) proposed that the runaway models of sexual selection cannot account for reduction in sexual ornamentation in the absence of changes in female preferences or in viability costs. By examining these predictions in relation to geographic variation in male appearance and female preference across subspecies of the house finch, Hill concluded that the models of runaway mate choice can be rejected in this species. Later modifications of the runaway model showed that a cyclic gain and loss of female preferences could occur without changes in natural selection on female preference (Iwasa & Pomiankowski 1995).

Studies of bowerbirds (Ptilonorhynchidae) by Kusmierski et al. (1997) and manakins (Pipridae) by Prum (1997) showed that patterns of ornament distribution and differential evolutionary lability of ornaments could be used to uncover mechanisms of selection operating within a lineage. In the runaway model, drift along equilibria lines between the male ornamentation and the female preference produces periods of rapid evolution resulting in large-scale diversifications and elaboration of male sexual ornamentation (Lande 1980). Thus, the runaway model predicts rapid differentiation in sexual ornamentation and the evolution of multiple sexual traits among lineages. By this model there should be little convergence between lineages, but one should see a historically nested distribution of traits that are shared among lineages within a clade (Prum 1997). In bowerbirds, sexually dimorphic plumage characters were extremely labile and sexual dichromatism appeared to be largely unconstrained (Kusmierski et al. 1997). Similarly, Prum (1997) found that diversity of manakin displays was explosive, indicating that evolution of these traits is largely unconstrained. Patterns of diversification and hierarchical structure of displays within these lineages is most consistent with the predictions of runaway and sensory bias mechanisms (Endler 1992; see also Irwin 1996) and also may be consistent with phylogenetic predictions of the "chase-away" model of sexual selection (Holland & Rice 1998).

In contrast, evolution of multiple quality indicator traits is constrained because evolution of a new indicator would favor elimination of previous indicators (Hill 1994b, Iwasa & Pomiankowski 1994). Consequently, indicator models predict sequential evolution of increasingly informative and increasingly constrained sets of ornaments within lineages (Badyaev et al. 2002, Hill 1994b, Prum 1997). Johnson (1999) found support for this model in the transitions from more costly to less costly ornamental displays in dabbling ducks, as well as in the gains and loses in some sexual ornaments in relation to presence of other ornaments.

The "chase-away" process of sexual selection also predicts sequential evolution of more exaggerated traits. It also predicts that evolution should be accompanied by

selection for retention of existing sexual ornaments. Sensory bias models predict frequent convergence in ornaments across lineages that have similar preexisting biases (Andersson 1994, Endler 1992, Ryan 1990). In addition, the sensory drive hypothesis predicts convergence of preferences and ornaments across lineages with similar ecological conditions (Hill 1994b, Prum 1997, Boughman 2002). Similarly, if sexual traits evolve to minimize the costs associated with mate sampling and selection, strong convergences in sexual traits among lineages that share similar ecological conditions are expected (Price 1998, Prum 1997, Schluter & Price 1993). Finally, direct selection for species recognition should favor displays that are unique and should select against similar ornaments among lineages, thus resulting in decreased ornament diversity and their reduced hierarchical structure within a lineage (Grant & Grant 1997, Prum 1997).

Virtually all of the studies that we have reviewed used field guides or study skins and assessments by human observers to rank or score the plumage coloration of individuals and to determine the similarities and differences between the sexes. One criticism that could be leveled at these studies of sexual dichromatism is that assessments of dichromatism that are made with human visual systems ignore the UV component of coloration (Bennett et al. 1994). All diurnal birds tested to date perceive UV light and many plumage color displays, particularly color displays that appear violet or blue to human observers, have a substantial UV component (Cuthill et al. 2000). Failure to consider UV coloration could lead to the misclassification of some bird species as monochromatic when in fact they are dichromatic. For example, recent studies in which plumage coloration was measured with a reflectance spectrometer showed that there are substantial differences between the sexes in UV coloration in some species (Andersson et al. 1998, Hunt et al. 1998). The fact that so many interesting patterns related to sexual dichromatism have been revealed in comparative studies that ignore the UV portion of the spectrum suggests that the visible portion of the spectrum must, in many cases, be a reasonable approximation of the overall coloration and dimorphism of a species. At the same time, the revelation that substantial variation in plumage coloration and dimorphism might be missed in studies that ignore the UV component of color displays raises the intriguing possibility that patterns in comparative studies may become clearer and indeed new patterns and explanations might be uncovered if the UV component of color displays is considered in future studies.

We have emphasized in this review that to advance our understanding of sexual dichromatism in birds there is a pressing need to take a historical approach when considering the proximate mechanisms behind sexual dichromatism, life history variation in relation to sexual selection, and patterns of mate choice. Studies that have attempted such syntheses (e.g., Kimball & Ligon 1999, Price 2002, Price & Pavelka 1996) have produced powerful insights into the evolution of sexual ornamentation and sexual dichromatism in birds. Moreover we need more experimental studies of mate choice to be carried in the phylogenetic context with special focus on temporal correspondence between male ornamentation and female preference for such ornamentation (Wiens 2001, Hill 1994a). Phylogenetic reconstructions

will continue to play a central role in uncovering the function and evolution of sexual dichromatism.

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