doi:10.1111/evo.12417

RECONSTRUCTING THE EVOLUTION OF SEXUAL DICHROMATISM: CURRENT COLOR DIVERSITY DOES NOT REFLECT PAST RATES OF MALE AND FEMALE CHANGE

J. Jordan Price[1,2] and Muir D. Eaton[3]

[1]*Department of Biology, St. Mary's College of Maryland, St. Mary's City, Maryland 20686*

[2]*E-mail: jjprice@smcm.edu*

[3]*Department of Biology, Drake University, Des Moines, Iowa 50311*

Received December 8, 2013
Accepted March 20, 2014

Males of sexually dimorphic species often appear more divergent among taxa than do females, so it is often assumed that evolutionary changes have occurred primarily in males. Yet, sexual dimorphisms can result from historical changes in either or both of the sexes, and few previous studies have investigated such patterns using phylogenetic methods. Here, we describe the evolution of male and female plumage colors in the grackles and allies (Icteridae), a songbird clade with a broad range in levels of sexual dichromatism. Using a model of avian perceptual color space, we calculated color distances within and among taxa on a molecular phylogeny. Our results show that female plumage colors have changed more dramatically than male colors in the evolutionary past, yet male colors are significantly more divergent among species today. Historical increases in dichromatism have involved changes in both sexes, whereas decreases in dichromatism have nearly always involved females evolving rapidly to look like males. Dichromatism is also associated with mating system in this group, with monogamous taxa tending to exhibit relatively low levels of sexual dichromatism. Our findings suggest that, despite appearances, female plumage evolution plays a more prominent role in sexual dichromatism than is generally assumed.

KEY WORDS: **Icterid, phylogeny, plumage evolution, sexual dimorphism, sexual selection, vision.**

Sexual dichromatism, or differences in the coloration of males and females, has long intrigued evolutionary biologists (Darwin 1871; Wallace 1889; Cronin 1991). Males typically exhibit more striking color patterns than do females, and thus it is generally assumed that sexual selection plays an important role in the evolution of these sexual differences (Andersson 1994; Badyaev and Hill 2003; Hill and McGraw 2006). Males with more elaborate traits are thought to have advantages over other males in attracting or competing for mates, whereas similar selective mechanisms do not affect females to the same extent (Darwin 1871). This idea is supported by a great deal of research showing mating advantages for relatively elaborate males (Andersson 1994).

This hypothesis is also bolstered by the observation that, in comparisons among sexually dichromatic species, males generally appear more divergent than do females. In birds, for example, species are often identified in field guides primarily by the plumage characteristics of males, in part because females can be more difficult to distinguish (e.g., Sibley 2000). Male plumage colors play an important role in species recognition and reproductive isolation (Price 2008), and studies show that male colors can diverge rapidly (Price and Whalen 2009; Campagna et al. 2012; Seddon et al. 2013). Thus, it is not surprising that sexual dichromatism is generally assumed to be the product of historical changes in males.

Yet, phylogenetic studies show that sexual dimorphism can result from changes in either sex and that dichromatism can be lost as well as gained (Björklund 1991; Irwin 1994; Omland 1997; Burns 1998; Wiens 2001; Omland and Hofmann 2006). For

EVOLUTION
INTERNATIONAL JOURNAL OF ORGANIC EVOLUTION

example, in the New World oriole genus (*Icterus*), sexually dichromatic species have evolved from ancestors in which both sexes were brightly colored (Hofmann et al. 2008; Friedman et al. 2009), indicating that bright colors have been repeatedly lost in females rather than gained in males. Likewise, in Australian fairy-wrens (Maluridae), variation in levels of sexual dichromatism across taxa is largely explained by complex historical changes in the plumage colors of both sexes (Johnson et al. 2013; Karubian 2013).

Furthermore, although numerous comparative studies of birds have shown a strong relationship between size dimorphism and polygynous mating systems (Webster 1992; Andersson 1994; Owens and Hartley 1998), a similar relationship between sexual dichromatism and mating system has received only mixed support (reviewed by Badyaev and Hill 2003). Many socially monogamous bird species are strikingly dichromatic, whereas others exhibit elaborate ornaments in both or neither of the sexes (Amundsen 2000; Amundsen and Pärn 2006; LeBas 2006; Tobias et al. 2012). Even among closely related taxa, sexual dichromatism may show little apparent relationship with estimated levels of sexual selection on male traits. For instance, in the caciques and oropendolas (genera *Cacicus*, *Ocyalus*, *Psarocolius*), plumage colors have evolved more rapidly in polygynous than in monogamous taxa due to sexual selection, yet none of these species are notably dichromatic (Price and Whalen 2009). Moreover, a growing number of studies have noted that levels of dichromatism are positively associated with breeding latitudes or other ecological factors (Hamilton 1961; Scott and Clutton-Brock 1989; Martin and Badyaev 1996; Price and Birch 1996; Friedman et al. 2009; Soler and Moreno 2012; Johnson et al. 2013), indicating the importance of natural selection in the evolution of male–female color differences (Wallace 1889).

Previous evolutionary studies of sexual dichromatism have been limited in several respects. First, most have relied on human perceptions of color rather than more objective measures, although it is now well documented that many species exhibit color dimorphisms that are imperceptible to humans (Eaton and Lanyon 2003; Eaton 2005, 2007; Burns and Schultz 2012). Thus, although human and avian perceptions of dichromatism can be broadly correlated (Armenta et al. 2008; Seddon et al. 2010), many previous studies may have failed to detect color differences that are relevant to the species of interest. Second, colors have often been scored qualitatively as discrete characters (e.g., Irwin 1994; Burns 1998; Price and Whalen 2009; Johnson et al. 2013), despite evidence that colors can vary across a continuous range among taxa (Hofmann et al. 2008). Third, some comparative studies have scored dichromatism as a single character rather than as a composite product of distinct evolutionary mechanisms working in each sex (e.g., Price and Birch 1996; Owens and Hartley 1998; Dunn et al. 2001). Sexual dichromatism may evolve through changes in male coloration, female coloration, or both (Wiens 2001; Omland and Hofmann 2006), so detailed phylogenetic studies of each sex are necessary to understand the evolutionary history behind dichromatism in any particular taxon (Badyaev and Hill 2003).

In this study, we investigate the evolution of dichromatism in the grackles and allies, a diverse clade within the New World blackbird family (Icteridae). We used plumage reflectance data and a model of avian perceptual color space to calculate levels of color divergence within and between species and to reconstruct evolutionary color changes in both sexes across a molecular phylogeny. Phylogenetic relationships in this clade have been well resolved using molecular sequence data (Eaton 2006; Lanyon and Barker 2007; Powell et al. 2014). Our phylogenetic analyses of color distance allowed us to address several long-standing and related assumptions about the evolution of sexual dichromatism: (1) male color patterns tend to be more divergent across extant taxa than female colors, (2) male colors have changed more than female colors in the evolutionary past, and (3) levels of sexual dichromatism are primarily explained by historical changes in males.

The grackles-and-allies clade exhibits a wide range of breeding systems, from social monogamy to extreme polygyny (Björklund 1991; Searcy et al. 1999), and species vary from year-round tropical residents to long-distance temperate migrants (Jaramillo and Burke 1999; Price 2009; del Hoyo et al. 2011). Thus, we were also able to compare levels of dichromatism to various other life-history traits to investigate potential selective influences on historical changes in color.

Methods

PLUMAGE COLOR MEASUREMENT

We sampled 37 species of the grackles-and-allies clade (nomenclature follows Clements et al. 2013). These species were included in a recent molecular phylogeny of 41 members of this group (Lanyon and Barker 2007), which has been used in previous studies of character evolution (Price 2009; Price et al. 2009). We were not able to obtain color measurements for *Curaeus forbesi*, *Hypopyrrhus pyrohypogaster*, *Macroagelaius subularis*, and *Quiscalus palustris*, so these taxa were not included in our analyses. The phylogeny was based on DNA sequence data from four nuclear gene regions (RAG1, beta fibrinogen intron 5, aconitase 1 intron 10, and myoglobin intron 2) and two mitochondrial regions (cytochrome *b* and ND2). A more recent set of phylogenies has been published by Powell et al. (2014), which includes more species and differs from the topology of Lanyon and Barker (2007) in the placement of some taxa. Given that these differences occur among short, weakly supported internodes deep in evolutionary history, we are confident that they would not have altered our general conclusions based on the analyses below.

For each species, we selected high-quality research study skins of three males and three females for capturing reflectance data. Specimens were obtained from the Field Museum of Natural History (Chicago, IL) and the American Museum of Natural History (New York, NY). On each specimen, we measured 22 "feather patches," defined as areas of continuous human-visible coloration greater than 4 mm^2 (Eaton 2006), which was the approximate area of measurement for our equipment. We sampled colors using an S-2000 spectrometer (Ocean Optics, Dunedin, FL) equipped with an R200–7-UV/VIS reflectance probe (fiber diameter = 200 μm) and a PX-2 pulsed xenon light source. Reflectance data were collected using OOIBASE32 software and consisted of the percentage of light reflected at each wavelength from 300 to 700 nm, averaged into 10-nm bins and calibrated against a Spectralon white reflectance standard with the reflectance probe oriented perpendicular to the measured surface. The reflectance probe was housed in a black rubber tube that minimized incident light and kept the distance between the probe and the feather surface constant (~2 mm). We recalibrated the spectrometer between measurements of different specimens. Reflectance data were then averaged across three individuals for each feather patch, separately for each sex within each species, and used in subsequent calculations.

CALCULATING COLOR DISTANCES

We employed the Vorobyev–Osorio color discrimination model (Vorobyev and Osorio 1998) to calculate three sets of color differences (ΔS) for each feather patch: (1) differences between sexes within each species, (2) differences between extant species within each sex, and (3) differences from each ancestral node to the next within each sex on the molecular phylogeny, reflecting relative rates of change, with detailed ΔS calculations described by Eaton (2005). Briefly, this model calculates a linear distance between two colors in avian perceptual color space, defined by the spectral sensitivity functions and signal-to-noise ratios of the four different avian single-cone cell photoreceptors (Vorobyev et al. 1998). Spectral sensitivity and signal-to-noise ratio data were taken from the blue tit (*Parus caeruleus*; provided by N. Hart; Hart et al. 2000) as a representative passerine visual system. Such physiological data do not yet exist for any icterid species; however, DNA sequence data from three members of the grackles-and-allies clade (*Agelaius phoeniceus*, *Molothrus ater*, *Q. quiscula*) indicate that they all possess an ultraviolet-type sensitive photoreceptor like that of the blue tit (Aidala et al. 2012), rather than the violet-type sensitive photoreceptor recently shown in some other passerines (Ödeen et al. 2011).

The Vorobyev–Osorio model was developed to facilitate the comparison of color distances in a perceptual color space, and it allows assessment of discriminability of colors given assumptions of the physiological input parameters (Vorobyev et al. 1998). Although these parameters are likely to vary across species visual systems, thus affecting exact thresholds for color discrimination, these thresholds were not the focus of our study. Rather, for our purposes, the Vorobyev–Osorio model provided an objective and standardized quantification of color across a large number of taxa based on the general physiological properties of avian vision. Although other models have been developed to interpret plumage color diversity mapped into avian perceptual color space (e.g., Stoddard and Prum 2008), we chose to implement the Vorobyev–Osorio model to allow some assessment of levels of dichromatism relative to thresholds for discrimination.

Using average reflectance values for each feather patch, we first calculated quantum catch values using the following equation from Vorobyev et al. (1998): $Q_i = \int_\lambda R_i(\lambda)S(\lambda)d\lambda$, where λ denotes wavelength, $R_i(\lambda)$ is the spectral sensitivity of each cone cell of type i, $S(\lambda)$ is the reflectance spectrum of a given feather patch, and integration is over the entire range of avian visual sensitivity (300–700 nm). Thus, for each feather patch, Q_1 represents the receptor quantum catch of the ultraviolet sensitive cone, Q_2 represents the short-wave sensitive cone, Q_3 represents the middle-wave sensitive cone, and Q_4 represents the long-wave sensitive cone. Together, these four quantum catches represent a quantification of color for each feather patch measured.

We used maximum likelihood reconstructions of continuously valued characters, implemented with the software package ANCML (Schluter et al. 1998), to estimate ancestral values at each node on the grackles-and-allies phylogeny for each of the four quantum catches (Q_1, Q_2, Q_3, Q_4) for each of the 22 feather patches, separately for both males and females. Given these reconstructed quantum catch values, we then calculated the difference in color (ΔS) between the sexes for each feather patch, in both extant and ancestral taxa. Overall color differences between males and females in each taxon (i.e., sexual dichromatism) were calculated by summing the ΔS values for all 22 feather patches (hereafter "all-patch-ΔS"). Dichromatism can occur in a variety of ways, including sexes that differ strikingly in only one feather patch (e.g., *A. assimilis*) or differ less obviously but across all plumage patches (e.g., *Euphagus carolinus*), and combining our patch values into one composite measure of dichromatism potentially ignored such variation. Nonetheless, we felt that these combined values provided a useful estimate of overall plumage distinctiveness.

As defined by the Vorobyev–Osorio model, the threshold value for discrimination of two colors is 1.0 jnd (just noticeable difference), where two colors are barely distinguishable as different by an avian visual system under ideal viewing conditions (Vorobyev et al. 1998; Siddiqi et al. 2004). Using a more conservative value of $\Delta S > 4$ jnd to represent clearly distinguishable colors, nearly all species in the grackles-and-allies clade are dichromatic in that they exhibit detectable differences between

the sexes in at least one feather patch (Eaton 2005, 2007; see below). Thus, for descriptive purposes in this article, we arbitrarily designated species with all-patch-ΔS scores > 100 jnd as "highly dichromatic" and all-patch-ΔS scores < 100 jnd as "less dichromatic." This threshold roughly corresponds to descriptions in the literature based on human-visible colors, which generally describe the males and females of our less-dichromatic taxa as similar in coloration (Jaramillo and Burke 1999; del Hoyo et al. 2011).

In addition to measuring sexual dichromatism, we also calculated all-patch-ΔS differences between extant taxa within each sex, which allowed us to compare relative levels of overall color divergence among males to those among females. We used these comparisons to quantitatively test the widely held assumption that male plumage colors are generally more diverse across species than are female colors.

We further used the reconstructed ancestral quantum catch values to calculate all-patch-ΔS differences between successive nodes on the phylogeny, separately for each sex and including terminal taxon branches (i.e., reflectance data from study skins). This yielded relative internodal plumage color distances in each sex over time, reflecting relative rates of evolutionary color change. Thus, we were able to test the assumption that male plumage colors have evolved more rapidly than female colors. We assessed how often each sex changed more than the other and compared these frequencies to chance levels using *G*-tests. We compared overall mean ancestral color changes in males to those in females, as well as mean color distances among males and among females in extant taxa, using paired *t*-tests.

COMPARATIVE ANALYSES

We compared our sexual dichromatism scores to several other characteristics across species using phylogenetic generalized least squares (PGLS), as implemented in the "APE" package (version 3.0–8; Paradis et al. 2004) in R (R Development Core Team 2013). This method incorporates phylogenetic information into comparisons of variables among taxa to correct for statistical nonindependence due to shared history. PGLS has advantages over other comparative methods in allowing users to specify an underlying model of trait evolution and covariance based on tree structure. Because we could not assume a single model of evolution a priori (see Johnson et al. 2013), we performed these comparisons twice using two different models. We compared traits across taxa assuming a Brownian motion (BM) model of trait evolution and then performed a second analysis assuming an Ornstein–Uhlenbeck (OU) model with a variance-restraining parameter, alpha (Butler and King 2004). BM models assume a random pattern of trait evolution, whereas OU infers selection toward one or more trait optima (Felsenstein 1988). We compared log-likelihood and Akaike information criterion (AIC) scores from these analyses to assess which of these models best fit our data (Burnham and Anderson 2002).

Levels of dichromatism (all-patch-ΔS scores) were compared to social mating system, migratory behavior, and highest breeding latitude of each species, determined from published information (Jaramillo and Burke 1999; Searcy et al. 1999; Price 2009; del Hoyo et al. 2011). We scored social mating systems as either (1) monogamous or (2) nonmonogamous based on the predominant male–female associations as reported in the literature. Nonmonogamous taxa included polygynous species, in which males mate with more than one female concurrently, and species in which mating associations vary depending on habitat or local adult sex ratio. We were not able to consider extra-pair mating in these scores, as this information was not available for most species. Migratory behaviors were scored as either (1) sedentary or (2) migratory based on whether birds are known to be present year-round in their breeding ranges or are seasonally absent. We measured highest breeding latitude as the upper latitudinal limit (ºN in the northern hemisphere and ºS in the southern hemisphere, both as positive values) of each taxon's known breeding range, estimated from published range maps (Jaramillo and Burke 1999; del Hoyo et al. 2011). We measured the highest latitudinal limit of each species, rather than the mean or lowest latitude, based on the assumption that this part of each taxon's range would be most influenced by seasonality and thus would best reflect consequent ecological differences among taxa.

Results

RECONSTRUCTIONS OF COLOR EVOLUTION

Sexual dichromatism, measured as all-patch-ΔS scores, varied widely and continuously across the grackles-and-allies clade (Table 1), from species in which the sexes are nearly indistinguishable (*Dives dives*: all-patch-$\Delta S = 24.3$ jnd; individual patch $\Delta S = 0.3$–3.9 jnd) to species with marked differences between the sexes in every feather patch (*A. phoeniceus*: all-patch-$\Delta S = 222.1$ jnd; individual patch $\Delta S = 4.5$–36.8 jnd). Levels of dichromatism calculated for ancestral nodes on the phylogeny (Fig. 1A) showed that the ancestor of the clade was only moderately sexually dichromatic (all-patch-$\Delta S = 61.4$ jnd; individual patch $\Delta S = 1.3$–4.1 jnd) and that levels of dichromatism have increased and decreased multiple times.

Internodal color distances on the phylogeny indicate that evolutionary changes have generally occurred in the plumages of both sexes (Fig. 1B, color divergences in males/females shown above branches), but that most branches show greater changes in females. Of the 69 branches of the tree showing changes in color, 43 (62.3%) showed greater change in females, whereas only 24 (34.7%) showed greater change in males (*G*-test: $G = 5.47$,

Table 1. Measurements of color distance (ΔS) between the sexes for 22 feather patches from 37 species in the grackles-and-allies clade.

	Feather patch[1]																					
Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	Total
A. phoeniceus	7.0	10.2	36.8	16.0	7.9	10.7	8.1	8.2	6.9	8.3	8.0	8.1	4.8	5.4	7.2	5.3	15.5	11.9	11.3	14.3	5.6	4.5	222.1
A. assimilis	2.0	1.8	30.7	19.1	3.7	4.6	5.9	2.6	3.0	4.7	3.9	2.8	1.8	6.5	3.3	4.1	1.2	4.6	5.0	2.8	1.6	1.8	117.5
A. tricolor	4.5	6.2	38.9	12.2	11.1	8.6	9.0	8.8	5.3	5.3	6.4	8.4	6.5	6.5	4.9	7.3	9.3	15.3	15.7	10.4	3.8	1.8	206.3
A. humeralis	0.8	0.5	2.2	5.8	1.2	1.6	1.5	3.2	0.3	0.3	0.8	0.7	2.3	1.0	0.8	1.2	0.3	1.5	2.0	1.6	0.6	0.5	30.5
A. xanthomus	1.6	1.3	9.8	4.0	2.2	2.7	0.8	2.2	2.1	1.6	2.0	1.4	1.8	2.0	1.4	3.3	3.9	2.3	3.1	1.7	0.6	1.3	53.3
N. nigerrimus	0.9	2.6	4.5	2.2	1.0	1.5	2.2	1.2	2.8	0.7	0.5	1.3	1.5	1.4	2.0	1.9	1.6	1.0	2.0	0.9	0.7	0.9	35.5
Q. mexicanus	3.8	2.7	8.8	6.4	13.5	14.2	9.0	8.0	4.4	20.3	25.7	24.3	20.6	14.1	7.1	8.7	18.0	26.3	18.5	18.6	3.3	3.3	279.6
Q. major	5.1	5.7	8.4	9.1	20.1	23.1	11.1	7.2	4.0	24.3	31.1	34.0	21.4	8.6	3.6	10.0	28.9	28.7	29.2	26.8	4.0	4.1	348.4
Q. niger	1.3	1.9	2.0	3.1	0.5	1.3	2.5	2.8	1.8	2.9	2.4	2.0	3.1	2.9	1.0	2.4	4.8	4.3	1.5	1.6	1.3	0.7	48.0
Q. nicaraguensis	5.3	6.7	9.3	6.2	12.9	13.0	9.2	9.7	7.1	20.6	21.5	21.7	19.2	13.0	8.3	6.4	18.5	21.4	16.1	15.1	3.2	2.4	266.7
Q. lugubris	5.4	6.6	7.9	7.0	11.1	8.6	6.5	7.4	6.3	12.5	18.4	17.5	13.1	6.9	5.6	6.9	14.6	14.9	13.8	13.2	1.7	1.8	207.6
Q. quiscula	2.7	6.7	2.7	3.5	2.4	4.8	2.4	4.1	1.9	6.5	11.5	10.1	3.7	7.4	4.8	6.8	10.2	12.8	11.0	10.9	3.3	3.4	133.8
E. carolinus	2.3	3.4	4.8	3.9	7.1	4.0	4.6	4.9	3.2	5.9	8.6	5.3	5.5	5.5	3.8	4.1	4.1	6.4	6.9	6.2	2.4	1.6	104.4
E. cyanocephalus	3.3	2.5	3.1	4.0	6.2	7.6	4.2	3.9	3.8	5.8	11.8	5.3	3.8	3.9	4.4	4.1	9.9	9.4	11.4	9.2	1.1	0.9	119.6
D. dives	0.5	0.3	0.5	0.5	1.5	1.0	2.0	2.3	1.1	0.5	1.7	1.5	0.5	0.3	3.9	1.7	0.9	1.0	0.7	0.8	0.6	0.7	24.3
D. warszewiczi	3.8	4.0	3.4	3.5	4.2	5.2	5.6	3.6	4.7	5.4	4.9	4.0	6.5	5.0	4.6	4.4	2.7	3.5	5.8	4.9	2.2	2.5	94.4
C. icterocephalus	6.3	11.7	12.0	8.2	14.5	13.3	17.2	6.8	10.7	23.4	11.5	27.0	16.2	8.4	10.6	7.4	9.3	15.9	16.8	22.2	4.2	3.2	276.8
C. ruficapillus	4.6	8.1	7.9	6.5	13.3	6.4	5.4	7.2	6.3	19.5	6.1	13.8	10.1	5.4	6.1	3.1	13.5	4.8	13.2	17.6	2.6	5.0	186.7
P. guirahuro	3.7	1.3	2.4	2.6	5.4	1.9	5.1	2.4	2.5	5.1	4.8	2.8	5.2	2.4	0.7	9.6	2.3	6.1	0.5	1.3	0.5	0.6	69.2
P. virescens	0.6	2.9	7.4	0.6	1.8	2.3	0.4	1.0	1.2	0.6	1.8	4.3	0.9	1.0	0.6	1.8	1.1	4.7	0.9	1.2	1.5	1.8	40.5
X. flavus	3.1	9.7	2.4	23.6	13.3	12.1	7.6	4.7	6.3	10.4	0.4	3.9	9.3	9.6	8.9	6.5	15.7	11.6	18.2	13.1	5.7	3.4	199.5
Ag. thilius	0.2	1.1	1.9	1.7	2.7	0.2	2.1	1.2	1.1	2.2	2.9	1.8	3.2	0.4	0.9	1.8	1.4	2.9	1.6	1.0	0.7	0.7	33.5
C. curaeus	2.3	13.3	15.4	8.2	11.7	3.3	3.4	8.6	8.4	13.6	11.0	11.3	8.9	11.6	7.2	5.3	7.2	11.5	8.5	13.0	5.7	3.9	193.3
Ag. cyanopus	4.2	14.3	5.6	7.5	7.7	6.8	10.9	6.7	8.6	24.9	16.4	22.6	20.7	12.3	10.5	6.8	2.8	16.0	9.3	8.0	1.5	1.4	225.6
Ag. xanthophth.	3.6	3.3	6.4	5.4	8.0	8.5	0.2	4.9	1.0	0.5	4.4	2.0	8.7	6.9	1.5	3.0	1.9	9.3	4.7	10.1	0.7	0.5	95.3
G. chopi	0.9	1.1	0.7	0.5	1.3	0.6	1.0	1.7	1.1	1.9	3.3	2.9	0.9	1.2	1.8	0.5	1.8	1.3	1.1	0.7	0.9	0.8	28.0
Am. holosericeus	0.7	0.6	2.0	1.3	1.3	0.7	1.7	0.7	1.2	1.0	6.2	9.8	0.4	1.1	2.5	3.6	6.0	4.9	5.0	1.1	0.2	0.4	52.5
Agel. badius	1.0	2.0	1.3	2.6	1.9	1.3	2.8	3.0	2.3	1.3	1.0	2.2	1.6	0.7	2.1	0.7	1.1	4.5	1.0	2.2	0.5	0.1	37.3
O. bolivianus	1.0	1.0	0.4	1.0	1.0	0.9	0.5	0.7	1.4	0.6	1.0	1.6	1.3	0.9	1.2	0.8	2.3	3.6	0.8	2.2	0.4	1.1	25.6
L. tanagrinus	0.4	0.6	1.7	0.5	1.8	1.9	3.2	0.7	1.8	0.8	1.7	1.7	3.0	1.0	1.3	0.4	1.0	2.4	1.6	2.0	0.8	0.2	30.4
Gy. mexicanus	0.7	1.3	2.9	2.5	0.4	1.4	0.9	1.6	0.6	3.2	13.6	2.3	1.0	2.1	1.0	5.6	3.5	18.5	1.1	2.4	0.8	0.7	67.8
M. imthurni	0.9	1.2	0.6	2.4	2.1	0.8	0.7	1.1	0.7	2.1	0.8	1.9	2.7	1.2	1.1	0.9	0.6	2.6	1.0	2.0	1.1	0.5	29.0
Mo. bonariensis	5.7	8.6	13.2	11.3	17.1	17.2	14.4	15.1	12.4	22.2	19.8	20.2	23.3	15.1	6.5	14.2	20.1	25.4	22.0	20.5	5.7	4.7	334.7
Mo. ater	5.8	7.7	7.6	8.7	9.4	9.4	7.2	9.9	6.2	9.2	3.6	10.2	6.3	6.9	6.0	3.4	2.7	8.4	0.9	2.4	5.8	2.5	140.3
Mo. aeneus	6.1	7.6	7.3	8.5	6.8	6.9	8.5	4.8	6.8	6.6	1.8	4.8	2.4	0.9	7.0	3.6	1.9	4.5	1.9	5.8	6.1	7.2	118.0
Mo. oryzivora	1.6	2.8	2.6	3.8	5.0	4.5	7.3	1.8	2.5	6.9	8.4	5.3	8.3	7.2	3.2	5.3	4.7	4.5	7.2	3.0	1.6	0.9	98.3
Mo. rufoaxillaris	2.7	3.0	4.1	2.2	3.1	1.6	3.3	2.2	3.5	2.2	5.0	3.4	2.4	1.4	4.4	4.6	2.7	3.0	1.6	1.5	1.6	1.7	61.1

Total dichromatism (all-patch-ΔS) was the sum of all 22 distance scores.

[1]Feather patches were: 1 = tertials; 2 = secondaries; 3 = greater coverts; 4 = greater covert edges; 5 = scapulars; 6 = upper back; 7 = middle back; 8 = lower rump; 9 = upper tail coverts; 10 = anterior flank; 11 = throat; 12 = breast; 13 = belly; 14 = vent; 15 = undertail coverts; 16 = thigh; 17 = posterior auricular; 18 = posterior supercilium; 19 = crown; 20 = nape; 21 = base retrices; 22 = outer retrices.

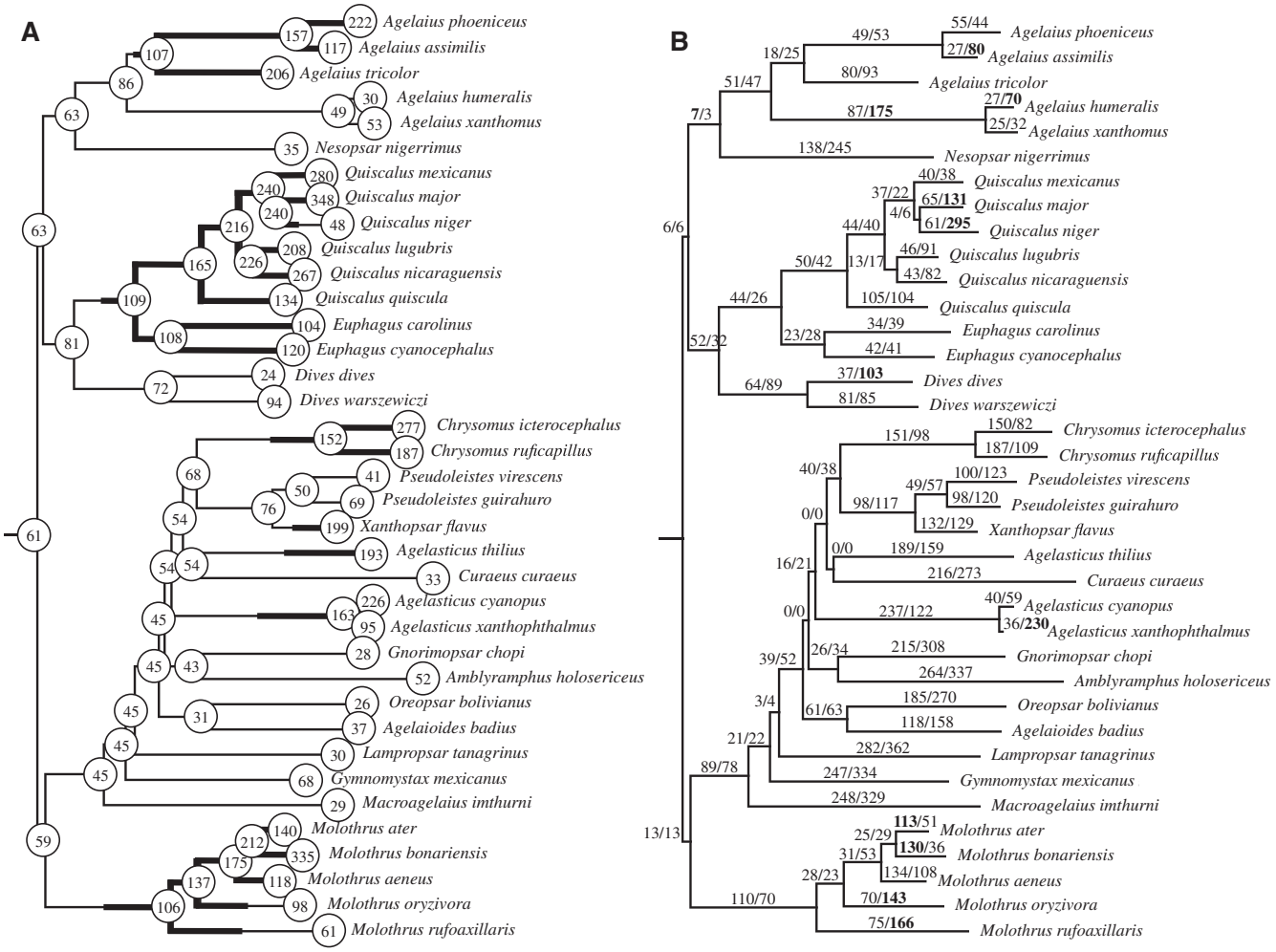

Figure 1. **Evolutionary reconstructions of (A) sexual dichromatism (numbers in circles) and (B) plumage color changes in each sex (indicated for males/females above each branch), measured as color distances (all-patch-ΔS) between the sexes and between nodes on the molecular phylogeny, respectively. (A) Thicker branches on the tree indicate lineages that were relatively dichromatic (all-patch-ΔS > 100 jnd). (B) Numbers in bold indicate branches in which one sex exhibited more than twice as much change as the other.**

df = 1, $P = 0.019$; two branches showed equal change in males and females). Furthermore, on the 43 branches with greater color changes in females, differences in evolutionary rates between the sexes were often relatively dramatic. Female plumage colors diverged more than twice as rapidly as male colors at least nine separate times during the history of the clade (Fig. 1B, numbers in bold), eight of which involved females becoming more similar to males, as indicated by decreased dichromatism scores (Fig. 1A). Only two lineages showed such rapid changes in males (twice that of females), one involving an increase in dichromatism (*M. bonariensis*) and the other a decrease (*M. ater*).

Increases in sexual dichromatism generally involved changes in both sexes in roughly equal measure. Of the 37 increases in dichromatism on the phylogeny (Fig. 1A), 19 (51.4%) showed greater changes in males and 17 (45.9%) showed greater changes in females (Fig. 1B; *G*-test: $G = 0.11$, df = 1, $P = 0.74$). Decreases in dichromatism, in contrast, nearly always involved relatively large changes in female plumage colors. Of the 27 historical decreases in dichromatism, 22 (81.5%) showed greater changes in females and only four (14.8%) showed slightly larger changes in males, a significant difference ($G = 13.72$, $P < 0.001$). Several extant species are relatively monochromatic in comparison to close congeners (e.g., *A. assimilis*, *A. humeralis*, *Q. niger*, *D. dives*, *Agelasticus xanthophthalmus*, *M. oryzivorus*, *M. rufoaxillaris*; Fig. 1A), and these differences are largely explained by historical changes in females.

In pair-wise comparisons among all extant taxa, males were found to be significantly more divergent in their plumage colors than were females (Fig. 2A; paired *t*-test, $t_{594} = 8.35$, $P < 0.001$). However, comparing internodal color distances of males to those of females showed that, on average, past changes in color have been significantly greater in females (Fig. 2B; $t_{71} = -2.67$,

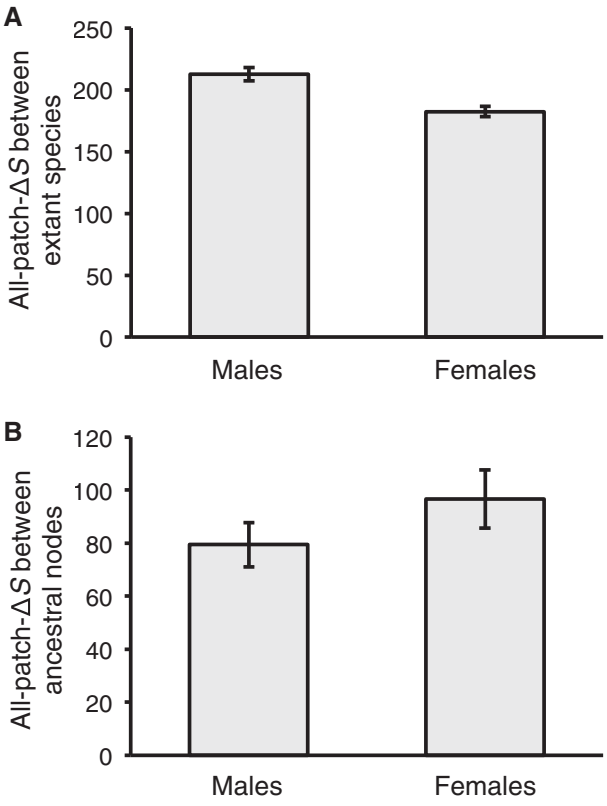

Figure 2. Mean (± SE) measurements in males and females of (A) color distances in pair-wise comparisons between extant taxa and (B) color distances between ancestral nodes on the molecular phylogeny. Males are significantly more divergent than females among extant taxa (paired *t*-test, $t_{594} = 8.35$, $P < 0.001$), but females show significantly greater changes in the evolutionary past ($t_{71} = -2.67$, $P = 0.009$).

$P = 0.009$). Thus, relative to males, greater rates of plumage evolution in females have resulted in lower levels of plumage color divergence among species today.

COMPARISONS TO MATING SYSTEM, MIGRATION, AND LATITUDE

Approximately half the species in our study (19/37) were scored as having relatively low levels of sexual dichromatism (all-patch-ΔS < 100 jnd), and all of these less-dichromatic taxa are reported to be socially monogamous, sedentary, and found only below 23°N latitude (Table 2). In the southern hemisphere, in contrast, several less dichromatic, monogamous, sedentary taxa have ranges that extend to higher latitudes (e.g., 55°S in *C. curaeus*). Polygyny, migratory behavior, and breeding at more northerly latitudes occur only among the more highly dichromatic members of the clade, but each of these traits occurs in only a portion of these taxa, and none occurs in all.

In PGLS analyses, levels of sexual dichromatism were significantly associated with mating system, assuming either a BM or OU model of trait evolution (Table 3, $P < 0.002$), with socially monogamous species being significantly less dichromatic than species with other mating systems. Dichromatism was not significantly associated with migration or with highest breeding latitude in these analyses, assuming either model. Evolutionary patterns in sexual dichromatism best corresponded to an OU model of evolutionary change (OU: log-likelihood = –198.22, AIC = 408.44, alpha = 85.69; BM: log-likelihood = –207.28, AIC = 424.55).

Discussion

EVOLUTIONARY PATTERNS IN MALES AND FEMALES

Calculating color distances within and among grackles-and-allies taxa reveals a surprising pattern. Male plumage colors are significantly more divergent among extant species than are female colors, yet female plumage colors have changed more frequently and dramatically in the evolutionary past. These results seem paradoxical at first glance, but they make sense when considering the past evolutionary trajectories of each sex. Male plumage colors have diverged relatively steadily among species throughout the history of the clade, whereas female colors have frequently evolved either away from or toward the male patterns, resulting in respective increases or decreases in sexual dichromatism (Fig. 1). In multiple cases, females of distantly related taxa have convergently evolved similarly cryptic color patterns (e.g., *A. phoeniceus* and *A. thilius*), which largely explains the lower mean color distances observed among present-day females (Fig. 2A). As a result, many of the rapid, ancestral changes in female colors are not readily apparent today.

These sex-specific patterns of plumage evolution are remarkably similar to those found in a recent phylogenetic study of plumage coloration in the Australian fairy-wrens (Maluridae). Johnson et al. (2013) used a best-fit model selection approach to show that plumage colors in male and female fairy-wrens exhibit different modes of evolutionary change. Variation in male plumage corresponds to a BM model, with males steadily diverging over time, whereas female plumages correspond to an OU model, suggesting natural selection toward one or more adaptive optima (Felsenstein 1988; Johnson et al. 2013). In the grackles and allies, as in the fairy-wrens, these different patterns of change may reflect different mechanisms of selection, with male colors following a pattern of continual divergence through sexual selection (Prum 1997; Price and Whalen 2009) and female colors following an OU-like pattern of punctuated change, presumably influenced by natural selection on female conspicuousness (Hamilton 1961; Scott and Clutton-Brock 1989; Martin and Badyaev 1996; Price and Birch 1996; Soler and Moreno 2012). Levels of sexual dichromatism also correspond to an OU model, shown here and by Johnson et al. (2013), reflecting evolutionary patterns in females. Our results build on those of Johnson et al.

Table 2. Levels of sexual dichromatism, social mating systems, migratory behaviors, and highest breeding latitudes of species included in the study.

Species	Dichromatism[1]	Mating system	Migration	Latitude[2]
Agelaius phoeniceus	High	Nonmonogamous	Migratory	67
Agelaius assimilis	High	Monogamous	Sedentary	23
Agelaius tricolor	High	Nonmonogamous	Migratory	38
Agelaius humeralis	Low	Monogamous	Sedentary	23
Agelaius xanthomus	Low	Monogamous	Sedentary	18
Nesopsar nigerrimus	Low	Monogamous	Sedentary	18
Quiscalus mexicanus	High	Nonmonogamous	Sedentary	43
Quiscalus major	High	Nonmonogamous	Sedentary	40
Quiscalus niger	Low	Monogamous	Sedentary	23
Quiscalus nicaraguensis	High	Monogamous	Sedentary	12
Quiscalus lugubris	High	Monogamous	Sedentary	11
Quiscalus quiscula	High	Monogamous	Migratory	60
Euphagus carolinus	High	Monogamous	Migratory	69
Euphagus cyanocephalus	High	Monogamous	Migratory	58
Dives dives	Low	Monogamous	Sedentary	21
Dives warszewiczi	Low	Monogamous	Sedentary	−15
Chrysomus icterocephalus	High	Nonmonogamous	Sedentary	11
Chrysomus ruficapillus	High	Nonmonogamous	Migratory	−37
Pseudoleistes guirahuro	Low	Monogamous	Sedentary	−34
Pseudoleistes virescens	Low	Monogamous	Sedentary	−40
Xanthopsar flavus	High	Monogamous	Sedentary	−35
Agelasticus thilius	High	Monogamous	Migratory	−50
Curaeus curaeus	Low	Monogamous	Sedentary	−55
Agelasticus cyanopus	High	Monogamous	Sedentary	−35
Agelasticus xanthophthalmus	Low	Monogamous	Sedentary	−12
Gnorimopsar chopi	Low	Monogamous	Sedentary	−35
Amblyramphus holosericeus	Low	Monogamous	Sedentary	−37
Agelaioides badius	Low	Monogamous	Sedentary	−42
Oreopsar bolivianus	Low	Monogamous	Sedentary	−21
Lampropsar tanagrinus	Low	Monogamous	Sedentary	−16
Gymnomystax mexicanus	Low	Monogamous	Sedentary	11
Macroagelaius imthurni	Low	Monogamous	Sedentary	6
Molothrus bonariensis	High	Nonmonogamous	Migratory	−44
Molothrus ater	High	Nonmonogamous	Migratory	60
Molothrus aeneus	High	Nonmonogamous	Migratory	33
Molothrus oryzivora	Low	Unknown	Sedentary	−27
Molothrus rufoaxillaris	Low	Monogamous	Sedentary	−40

[1]High and low dichromatism were defined by all-patch-ΔS scores > or < 100 jnd, respectively. Scores are provided in Table 1.

[2]Positive numbers represent °N and negative numbers °S.

Table 3. Regression coefficients, SEs, and *P*-values for phylogenetic generalized least squares (PGLS) comparisons between dichromatism (all-patch-ΔS) and other species characteristics, employing either a Brownian motion or Ornstein–Uhlenbeck model of trait evolution.

	Brownian motion model			Ornstein–Uhlenbeck model		
Dichromatism versus:	Coefficient	SE	P[1]	Coefficient	SE	P[1]
Mating system	144.79	42.20	**0.0016**	128.57	33.34	**0.0005**
Migration	−46.31	48.50	0.35	5.50	42.39	0.90
Highest latitude	1.54	1.06	0.16	0.48	0.10	0.63

[1]Significant relationships are indicated in bold.

(2013) by showing that these different evolutionary modes can generate female plumages that appear less diverse than those of males, despite having greater evolutionary rates.

These patterns of plumage evolution are also strikingly similar to patterns of song evolution in the family Icteridae, which includes the grackles and allies, in which males show steady rates of evolutionary divergence (Price and Lanyon 2002) whereas females produce either male-like songs or very different vocalizations (Price 2009; Price et al. 2009). Interestingly, of the species in our study known to exhibit frequent female song (Jaramillo and Burke 1999; Price et al. 2009), all exhibit relatively low levels of dichromatism (all-patch-$\Delta S < 120$ jnd), suggesting similar patterns of selection on male–female differences in these traits.

Our results provide clear, quantitative support for previous suggestions that the evolution of sexual dichromatism in birds involves changes in females rather than sexual selection acting on male plumage colors alone (Björklund 1991; Irwin 1994; Burns 1998; Wiens 2001; Badyaev and Hill 2003; Hofmann et al. 2008; Johnson et al. 2013). Although dichromatism is strongly associated with mating system in the grackles and allies, and despite evidence that male plumage colors are significantly more diverse across taxa, sexual dichromatism in this group is largely a product of historical changes in female plumage colors. Approximately half of the reconstructed increases in dichromatism on the phylogeny involved greater changes in females than in males, and the majority (81.5%) of decreases in dichromatism involved greater female changes, including examples in which female coloration evolved several times more rapidly than did male colors (e.g., *A. xanthophthalmus* in Fig. 1B). These complex patterns of change provide strong evidence against the long-standing assumption that sexual selection on male appearance drives sexual dichromatism in birds.

WHAT EXPLAINS RAPID FEMALE COLOR EVOLUTION?

Greater mean rates of female color change in this group (Fig. 2B) are largely explained by the multiple lineages in which female plumages have evolved relatively rapidly to look more like males. Nearly all decreases in sexual dichromatism in our study involved rapid female changes, which corroborates previous observations that transitions from dichromatism to monomorphism in birds typically involve females gaining male-like characteristics rather than the reverse (Irwin 1994; Badyaev and Hill 2003; Johnson et al. 2013). Rapid evolution could indicate strong selection on females for elaborate male-like colors, perhaps through mutual mate choice, intrasexual competition over resources, or other forms of social selection (Amundsen 2000; Amundsen and Pärn 2006; LeBas 2006; Tobias et al. 2012). Such mechanisms could explain the advantage of elaborate female colors, but they do not explain why these colors are shared with males. Thus, we propose an alternative possibility.

Rather than indicating strong selection on females, rapid losses of dichromatism could indicate reduced selection on females for plumage colors different from males (e.g., that are relatively cryptic), resulting in females quickly reverting to male-like appearance. Physiologically, such changes would involve losses of female-specific color mechanisms rather than gains of male-specific patterns (Kimball and Ligon 1999; Wiens 2001), and we should expect such losses to be especially rapid given that the genetic and hormonal architecture for male color patterns are presumably already present (Lande 1980).

Increases in sexual dichromatism, on the other hand, require the evolution of new color patterns in females and/or males, and novel traits may take longer to accumulate, whether through natural or sexual selection. This is evident in the grackles and allies, in which increases in dichromatism have generally involved evolutionary changes in both sexes at similar rates. Moreover, in the few cases in which males have changed dramatically more than females (*M. ater* and *M. bonariensis*), cryptic female plumage appears to be a retained ancestral state shared among closely related taxa (Jaramillo and Burke 1999; del Hoyo et al. 2011), perhaps constrained due to stabilizing selection for female crypsis.

An absence of selection for female-specific colors would explain cases in which similarly colored males and females show large correlated evolutionary changes without appreciable increases in sexual dichromatism, as has occurred throughout the grackles-and-allies clade (Fig. 1). Likewise, in the caciques and oropendolas, a tropical icterid clade closely related to the grackles and allies, no species are discernably dichromatic, yet polygynous taxa show greater rates of color evolution than do monogamous taxa, indicating different levels of sexual selection (Price and Whalen 2009). Rapid female color changes in this group appear to be a genetically correlated response to selection on males (Lande 1980). Polygynous cacique and oropendola species build enclosed nests in colonies that are highly conspicuous (Jaramillo and Burke 1999; del Hoyo et al. 2011), so perhaps females would not gain much benefit by having cryptic plumage patterns different from males (Wallace 1889; Soler and Moreno 2012). Indeed, male-like plumage patterns may benefit females in ecological competition (Tobias et al. 2012).

SELECTIVE INFLUENCES ON DICHROMATISM

Levels of dichromatism in the grackles and allies are strongly associated with mating system (Table 3), with relatively monochromatic taxa tending to be monogamous. Similar relationships have been shown in several previous comparative studies of birds (Scott and Clutton-Brock 1989; Irwin 1994; Dunn et al. 2001), but certainly not in all (reviewed in Badyaev and Hill 2003). Unlike most previous studies, we show that this association is

largely due to variation in female plumages rather than changes in males, presumably due to selection on female conspicuousness (Wallace 1889; Irwin 1994; Martin and Badyaev 1996). Furthermore, although all polygynous taxa in our study were found to be highly dichromatic, a third of monogamous taxa (33%) were highly dichromatic too (Table 2), suggesting that sexual selection alone is not an adequate explanation for the evolution of dichromatism.

Instead, levels of sexual dichromatism in species may reflect levels of selection for female-specific color patterns. In many polygynous icterids, for example, females alone provide parental care at exposed nests (Jaramillo and Burke 1999; Searcy et al. 1999; del Hoyo et al. 2011), which would favor relatively cryptic female plumage patterns and consequently greater levels of dichromatism (Scott and Clutton-Brock 1989; Martin and Badyaev 1996; Soler and Moreno 2012). Similarly, in the brood-parasitic cowbirds (genus *Molothrus*), cryptic female plumage might be favored for avoiding detection by potential hosts. In contrast, in many long-term monogamous taxa, both sexes feed young and collaborate in territorial defense (Jaramillo and Burke 1999; Price 2009), which would not necessarily favor female plumage patterns that differ from males (Amundsen and Pärn 2006; Tobias et al. 2012).

Selection for female crypsis appears to be relatively common among temperate migratory bird species (Hamilton 1961; Martin and Badyaev 1996; Badyaev and Hill 2003; Friedman et al. 2009). Indeed, all species in our study that are migratory and/or breed at high latitudes (at least in the northern hemisphere) were found to be highly sexually dichromatic (Table 2), although neither of these characteristics was significantly associated with dichromatism in PGLS analyses (Table 3). Such a latitudinal gradient is clearly evident in New World orioles, the sister clade to the grackles and allies (Lanyon and Barker 2007; Powell et al. 2014), which are all socially monogamous yet show striking variation in levels of dichromatism (Jaramillo and Burke 1999; del Hoyo et al. 2011). In that group, sexual dichromatism has increased repeatedly due to the evolution of relatively cryptic plumage patterns in females (Hofmann et al. 2008) along with the evolution of long-distance migration to higher breeding latitudes (Friedman et al. 2009). Sexual dichromatism in Australian fairy-wrens is also strongly associated with latitude, although none of these species are migratory, suggesting that relatively cryptic female plumage tends to be favored in more seasonal environments (Johnson et al. 2013). Our findings support this suggestion, given that relatively monochromatic taxa tend to be found at higher latitudes in the southern hemisphere, where seasons are generally more temperate, than in the northern hemisphere. Why female plumage patterns show such latitudinal variation is not well understood (Hamilton 1961; Scott and Clutton-Brock 1989) and clearly warrants further attention.

Sexual dichromatism in plumage may be a product of a variety of factors (Badyaev and Hill 2003), as has been shown for the evolution of male–female differences in song (Price 2009). Future comparative studies focusing on ecological factors, as well as the specific roles of each sex in reproduction and territoriality, may provide clearer insights into the evolutionary mechanisms driving sexual dichromatism in birds.

Conclusions

Our results quantitatively support the widespread perception that male plumage colors are more divergent among taxa than are female colors. Yet, despite these current appearances, our study also provides surprising evidence that female plumage colors have changed more frequently and dramatically in the evolutionary past. Thus, in an avian clade in which levels of dichromatism are strongly associated with mating system, female plumage evolution appears to play a deceptively prominent role in the evolution of sexual dichromatism.

Nearly all species in our study were found to be sexually dichromatic, at least as detected by avian visual perception, and dichromatism varied continuously across the clade from slight (e.g., *D. dives*) to striking (e.g., *A. phoeniceus*). Our results therefore illustrate the importance of treating color as a continuously variable character rather than as a set of discrete character states (Hofmann et al. 2008). Our study also underscores the importance of examining trait evolution in each sex independently to understand the evolution of current dimorphisms (Irwin 1994; Amundsen 2000; Wiens 2001; Omland and Hofmann 2006; Price et al. 2009). Observed patterns of diversity may not necessarily reflect historical patterns of change, as exemplified by the grackles and allies in which male colors are relatively diverse but female colors show greater rates of evolutionary change. This finding in particular highlights the danger of using sexual dichromatism as an indicator of the historic strength of sexual selection: although there is a strong correlation between dichromatism and mating system, variation in levels of dichromatism appears to be driven primarily by selection on females, not males. Selection on female plumage patterns might play an important yet underappreciated role in the evolution of sexual dichromatism in general, and our findings may provide insights into patterns of dimorphism reported in numerous previous studies across a wide range of taxa.

ACKNOWLEDGMENTS

We thank S. Lanyon and K. Barker for generously allowing us to use their molecular phylogeny of the grackles-and-allies clade, and N. Hart for providing spectral sensitivity data. E. Cramer and two anonymous reviewers provided valuable comments to improve the manuscript, and K. Emerson provided valuable statistical advice. We also thank the curators and collection managers at the American Museum of Natural History and the Field Museum of Natural History for access to research collections.

LITERATURE CITED

Aidala, Z., L. Huynen, P. L. R. Brennan, J. Musser, A. Fidler, N. Chong, G. E. Machovsky Capuska, M. G. Anderson, A. Talaba, D. Lambert, et al. 2012. Ultraviolet visual sensitivity in three avian lineages: paleognaths, parrots, and passerines. J. Comp. Physiol. A 198:495–510.

Amundsen, T. 2000. Why are female birds ornamented? Trends Ecol. Evol. 15:149–155.

Amundsen, T., and H. Pärn. 2006. Female coloration: review of functional and nonfunctional hypotheses. Pp. 280–348 *in* G. E. Hill and K. J. McGraw, eds. Bird coloration. Vol. 2. Harvard Univ. Press, Cambridge, MA.

Andersson, M. 1994. Sexual selection. Princeton Univ. Press, Princeton, NJ.

Armenta, J. K., P. O. Dunn, and L. A. Whittingham. 2008. Quantifying avian sexual dichromatism: a comparison of methods. J. Exp. Biol. 211:2423–2430.

Badyaev, A. V., and G. E. Hill. 2003. Avian sexual dichromatism in relation to phylogeny and ecology. Annu. Rev. Ecol. Evol. Syst. 34:27–49.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer-Verlag, New York, NY.

Burns, K. J. 1998. A phylogenetic perspective on the evolution of sexual dichromatism in tanagers (Thraupidae): the role of female versus male plumage. Evolution 52:1219–1224.

Burns, K. J., and A. J. Shultz. 2012. Widespread dichromatism and ultraviolet reflectance in the largest radiation of Neotropical songbirds: implications of accounting for avian vision in the study of plumage evolution. Auk 129:211–221.

Butler, M. A., and A. A. King. 2004. Phylogenetic comparative analysis: a modeling approach for adaptive evolution. Am. Nat. 164:683–695.

Björklund, M. 1991. Evolution, phylogeny, sexual dimorphism and mating systems in the grackles (*Quiscalus* spp.: Icterinae). Evolution 45:608–621.

Campagna, L., P. Benites, S. C. Lougheed, D. A. Liitmaer, A. S. Di Giacomo, M. D. Eaton, and P. L. Tubaro. 2012. Rapid phenotypic evolution during incipient speciation in a continental avian radiation. Proc. R. Soc. Lond. B 279:1847–1856.

Clements, J. F., T. S. Schulenberg, M. J. Iliff, B.L. Sullivan, C. L. Wood, and D. Roberson. 2013. The eBird/Clements checklist of birds of the world. Version 6.8. Available at http://www.birds.cornell.edu/clementschecklist/download/.

Cronin, H. 1991. The ant and the peacock. Cambridge Univ. Press, Cambridge, U.K.

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

del Hoya, J., A. Elliott, and D. A. Christie. 2011. Handbook of the birds of the world. Vol. 16. Lynx Edicions, Barcelona, Spain.

Dunn, P. O., L. A. Whittingham, and T. E. Pitcher. 2001. Mating systems, sperm competition, and the evolution of sexual dimorphism in birds. Evolution 55:161–175.

Eaton, M. D. 2005. Human vision fails to distinguish widespread sexual dichromatism among sexually "monochromatic" birds. Proc. Nat. Acad. Sci. USA 102:10942–10946.

———. 2006. A phylogenetic perspective on the evolution of chromatic ultraviolet plumage coloration in the grackles and allies (Family: Icteridae). Auk 123:211–234.

———. 2007. Avian visual perspective on plumage coloration confirms rarity of sexually monochromatic passerines. Auk 124:155–161.

Eaton, M. D., and S. M. Lanyon. 2003. The ubiquity of avian ultraviolet plumage reflectance. Proc. R. Soc. Lond. B 270:1721–1726.

Felsenstein, J. 1988. Phylogenies and quantitative characters. Ann. Rev. Ecol. Syst. 19:445–471.

Friedman, N. R., C. M. Hofmann, B. Kondo, and K. E. Omland. 2009. Correlated evolution of migration and sexual dichromatism in the New World orioles (*Icterus*). Evolution 63:3269–3274.

Hamilton, T. H. 1961. On the functions and causes of sexual dimorphism in breeding plumage characters of North American species of warblers and orioles. Am. Nat. 95:121–123.

Hart, N. S., I. C. Partridge, I. C. Cuthill, and A. D. T. Bennett. 2000. Visual pigments, oil droplets, ocular media and cone photoreceptor distribution in two species of passerine bird: the blue tit (*Parus caeruleus*) and the blackbird (*Turdus merula*). J. Comp. Physiology A 186:375–387.

Hill, G. E., and K. J. McGraw. 2006. Bird coloration. Vol. 2. Function and evolution. Harvard Univ. Press, Cambridge, MA.

Hofmann, C. M., T. W. Cronin, and K. E. Omland. 2008. Evolution of sexual dichromatism. 1. Convergent losses of elaborate female coloration in New World orioles (*Icterus* spp.). Auk 125:778–789.

Irwin, R. E. 1994. The evolution of plumage dichromatism in the New World blackbirds: social selection on female brightness. Am. Nat. 144:890–907.

Jaramillo, A., and P. Burke. 1999. New World blackbirds: the icterids. Princeton Univ. Press, Princeton, NJ.

Johnson, A. E., J. J. Price, and S. Pruett-Jones. 2013. Different modes of evolution in males and females generate dichromatism in fairy-wrens (Maluridae). Ecol. Evol. 3:3030–3046.

Karubian, J. 2013. Female ornamentation in *Malurus* fairy-wrens: a hidden evolutionary gem for understanding female perspectives on social and sexual selection. Emu 113:248–258.

Kimball, R. T., and J. D. Ligon. 1999. Evolution of avian plumage dichromatism from a proximate perspective. Am. Nat. 154:182–193.

Lanyon, S. M., and F. K. Barker. 2007. Exploring patterns of morphological evolution in the New World blackbirds. 125th Meeting of the American Ornithologists' Union. Laramie, WY.

Lande, R. 1980. Sexual dimorphism, sexual selection, and adaptation in polygenic characters. Evolution 34:292–305.

LeBas, N. R. 2006. Female finery is not for males. Trends Ecol. Evol. 21:170–173.

Martin, T. E., and A. V. Badyaev. 1996. Sexual dichromatism in birds: importance of nest predation and nest location for females versus males. Evolution 50:2454–2460.

Ödeen, A., O. Håstad, and P. Alström. 2011. Evolution of ultraviolet vision in the largest avian radiation—the passerines. BMC Evol. Biol. 11: 313.

Omland, K. E. 1997. Examining two standard assumptions of ancestral reconstructions: repeated loss of dichromatism in dabbling ducks (Anatini). Evolution 51:1636–1646.

Omland, K. E., and C. M. Hofmann. 2006. Adding color to the past: ancestral-state reconstruction of coloration. Pp. 417–454 *in* G. E. Hill and K. J. McGraw, eds. Bird coloration. Vol. 2. Function and evolution. Harvard Univ. Press, Cambridge, MA.

Owens, P. F., and I. R. Hartley. 1998. Sexual dimorphism in birds: why are there so many different forms of dimorphism? Proc. R. Soc. Lond. B 265:397–407.

Paradis, E., J. Claude, and K. Strimmer. 2004. APE: analyses of phylogenetics and evolution in R language. Bioinformatics 20:289–290.

Powell, A. F. L. A., F. K. Barker, S. M. Lanyon, K. J. Burns, J. Klicka, and I. J. Lovette. 2014. A comprehensive species-level molecular phylogeny of the New World blackbirds (Icteridae). Mol. Phyl. Evol. 71:94–112.

Price, J. J. 2009. Evolution and life history correlates of female song in the New World blackbirds. Behav. Ecol. 20:967–977.

Price, J. J., and S. M. Lanyon. 2002. Reconstructing the evolution of complex bird song in the oropendolas. Evolution 56:1514–1529.

Price, J. J., and L. M. Whalen. 2009. Plumage evolution in the oropendolas and caciques: different divergence rates in polygynous and monogamous taxa. Evolution 63:2985–2998.

Price, J. J., S. M. Lanyon, and K. E. Omland. 2009. Losses of female song with changes from tropical to temperate breeding in the New World blackbirds. Proc. R. Soc. Lond. B 276:1971–1980.

Price, T. 2008. Speciation in birds. Roberts and Company, Greenwood Village, CO.

Price, T., and G. L. Birch. 1996. Evolution of sexual color dimorphism in passerine birds. Auk 113:842–848.

Prum, R. O. 1997. Phylogenetic tests of alternative intersexual selection mechanisms: macroevolution of male traits in a polygynous clade (Aves: Pipridae). Am. Nat. 149:668–692.

R Development Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Schluter, D., T. Price, A. Ø. Mooers, and D. Ludwig. 1998. Likelihood of ancestor states in adaptive radiation. Evolution 51:1699–1711.

Scott, D. K., and T. H. Clutton-Brock. 1989. Mating systems, parasites and plumage dimorphism in waterfowl. Behav. Ecol. Sociobiol. 26:261–273.

Searcy, W. A., K. Yasukawa, and S. M. Lanyon. 1999. Evolution of polygyny in the ancestors of red-winged blackbirds. Auk 116:5–19.

Seddon, N., J. A. Tobias, M. D. Eaton, and A. Ödeen. 2010. Human vision can provide a valid proxy for avian perception of sexual dichromatism. Auk 127:283–292.

Seddon, N., C. A. Botero, J. A. Tobias, P. O. Dunn, H. E. A. MacGregor, D. R. Rubenstein, J. A. C. Uy, J. T. Weir, L. A. Whittingham, and R. J. Safran. 2013. Sexual selection accelerates signal evolution during speciation in birds. Proc. R. Soc. Lond. B 280:20131065. doi:10.1098/rspb.2013.0836.

Sibley, D. A. 2000. The Sibley guide to birds. Alfred A. Knopf, Inc., New York, NY.

Siddiqi, A. T., T. W. Cronin, E. R. Loew, M. Vorobyev, and K. Summers. 2004. Interspecific and intraspecific views of color signals in the strawberry poison frog *Dendrobates pumillo*. J. Exp. Biol. 207:2471–2485.

Soler, J. J., and J. Moreno. 2012. Evolution of sexual dichromatism in relation to nesting habits in European passerines: a test of Wallace's hypothesis. J. Evol. Biol. 25:1614–1622.

Stoddard, M. C., and R. O. Prum. 2008. Evolution of avian plumage color in a tetrahedral color space: a phylogenetic analysis of New World buntings. Am. Nat. 171:755–776.

Tobias, J. A., R. Montgomerie, and B. E. Lyon. 2012. The evolution of female ornaments and weaponry: social selection, sexual selection and ecological competition. Philos. Trans. R. Soc. B 367:2274–2293.

Vorobyev, M., and D. Osorio. 1998. Receptor noise as a determinant of color thresholds. Proc. R. Soc. Lond. B 265:351–358.

Vorobyev, M., D. Osorio, A. T. D. Bennett, N. J. Marshall, and I. C. Cuthill. 1998. Tetrachromacy, oil droplets and bird plumage colors. J. Comp. Physiol. A 183:621–633.

Wallace, A. R. 1889. Darwinism. Macmillan and Co., New York, NY.

Webster, M. S. 1992. Sexual dimorphism, mating system and body size in New World blackbirds (Icterinae). Evolution 46:1621–1641.

Wiens, J. J. 2001. Widespread loss of sexually selected traits: how the peacock lost its spots. Trends Ecol. Evol. 16:517–523.

Associate Editor: N. Seddon