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Losses of sexual dichromatism involve rapid changes in female plumage colors to match males in New World blackbirds

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Abstract

Differences in coloration between the sexes (sexual dichromatism) can increase or decrease in a species through evolutionary changes in either or both sexes diverging or converging in their colors. Few previous studies, however, have examined the relative rates of such changes, particularly when dichromatism is lost. Using reflectance data from 37 species of the New World blackbird family (Icteridae), we compared evolutionary rates of plumage color change in males and females when dichromatism was either increasing (colors diverging) or decreasing (colors converging). Increases in dichromatism involved divergent changes in both sexes at approximately equal rates. Decreases in dichromatism, in contrast, involved changes in females to match male plumage colors that were significantly more rapid than any changes in males. Such dramatic changes in females show how selection can differ between the sexes. Moreover, these evolutionary patterns support the idea that losses of dimorphism involve genetic mechanisms that are already largely present in both sexes, whereas increases in dimorphism tend to involve the appearance of novel sex-specific traits, which evolve more slowly. Our results have broad implications for how sexual dimorphisms evolve.

Keywords: color evolution, female plumage, icterid, phylogeny, selection, sexual dimorphism

Introduction

The plumage colors of male songbirds are generally more elaborate and diverse than those of females, reinforcing a long-standing assumption that differences in coloration between the sexes (i.e., sexual dichromatism) evolved primarily through sexual selection on males (Darwin, 1859, 1871). Studies of a wide variety of taxa show that male color patterns have important functions in attracting and competing for mates (Andersson, 1994). Furthermore, male plumage colors are often highly distinctive among species whereas females are relatively drab and more difficult to distinguish (Sibley, 2000), especially in northern temperate species which have been the focus of many previous studies (Hill & McGraw, 2006). Given these patterns of elaboration and diversity, it is perhaps not surprising that sexual dichromatism has often been assumed to be the product of past evolutionary changes in males (Darwin, 1859, 1871).

Yet, phylogenetic studies show that sexual dichromatism can evolve through changes in either or both sexes, and furthermore, it can be either gained or lost (Badyaev & Hill, 2003; Dale et al., 2015; Dunn et al., 2015; Irwin, 1994; Omland, 1997; Omland & Hofmann, 2006; Shultz & Burns, 2017; Wiens, 2001). In the New World blackbird family (Icteridae), for instance, variation in sexual dichromatism among taxa is largely explained by past losses and gains in female colors rather than substantial changes in males (Friedman et al., 2009; Hofmann et al., 2008; Irwin, 1994; Price & Eaton,

2014). Similar evolutionary patterns have been revealed in tanagers (Thraupidae; Burns, 1998), fairy-wrens (Maluridae; Johnson et al., 2013; Karubian, 2013; Medina et al., 2017), and New World warblers (Parulidae; Simpson et al., 2015). Female colors in these groups have changed relatively frequently in comparison to male colors, even though male colors generally appear more elaborate and divergent across species today. These counterintuitive findings may be explained by the evolutionary trajectories of each sex. Male colors have tended to diverge steadily over time, whereas female colors have evolved either away from or towards male patterns, resulting in increases or decreases in sexual dichromatism. In multiple cases, females of distantly related species have converged on similarly cryptic color patterns, which make them appear as if they have hardly changed at all (Price, 2019; Price & Eaton, 2014).

The evolution of sexual dimorphism, whether through changes in females or males, involves sex-specific modifications in mechanisms of genetic expression that are favored in one sex but opposed in the other (Coyne et al., 2008; Gazda et al., 2020; Kimball & Ligon, 1999; Kraaijeveld, 2014, 2019; Kraaijeveld et al., 2007; Weins, 2001). That is, phenotypic divergence between males and females within a species involves genes that may differ in their influences but nevertheless exist in both sexes (Kraaijeveld, 2014), unlike divergences between species in which genes are favored in some lineages but lost in others. Indeed, assuming equal sex ratios, all autosomal genes

should spend roughly half their evolutionary time in males and half in females, regardless of whether they influence male traits, female traits, or both.

Following this reasoning, we should expect evolutionary losses of dichromatism to occur relatively rapidly, given that the genetic and hormonal architecture for the expression of a trait in one sex is largely already present in the other (Gazda et al., 2020; Kimball & Ligon, 1999; Kraaijeveld, 2014; Lande, 1980; Price, 2015). Increases in sexual dichromatism, on the other hand, require the evolution of new color patterns with new developmental mechanisms in females and/or males, and novel traits may take longer to accumulate, regardless of whether they are influenced by natural or sexual selection (Price, 2019). This may help to explain observations in previous phylogenetic studies of New World blackbirds (Barker et al., 2008; Price & Eaton, 2014) and Australasian fairy-wrens (Johnson et al., 2013; Karubian, 2013), in which the evolution of bright male-like plumage colors in females appears to have occurred relatively abruptly.

Male and female plumage colors can be influenced by different combinations of selection pressures, resulting in different patterns of evolutionary change (Badyaev & Hill, 2003; Dale et al., 2015; Dunn et al., 2015; Johnson et al., 2013; Omland & Hofmann, 2006; Shultz & Burns, 2017; Tobias et al., 2012). Male colors often play an important role in attracting and competing for mates, and a great deal of research shows that these traits are influenced by sexual selection (Andersson, 1994). Female colors can have similar functions, at least in some taxa (Amundsen, 2000; LeBas, 2006; Tobias et al., 2012). Both sexes are also subject to natural selection to various degrees, including selection for reduced conspicuousness near the nest (Drury & Burroughs, 2016; Martin & Badyaev, 1996; Medina et al., 2017; Soler & Moreno, 2012; Wallace, 1889). The balance of these competing selective pressures can differ greatly between the sexes, and male and female colors are therefore expected to exhibit different evolutionary modes of change during the evolution of sexual dichromatism (Price, 2019).

In this study, we compare rates of plumage color change in females and males during evolutionary gains and losses of sexual dichromatism in the grackles-and-allies clade within the New World blackbird family (Icteridae). This group exhibits an especially wide range in levels of sexual dichromatism (Jaramillo & Burke, 1999), and these levels are strongly associated with mating system, with polygynous taxa that are more dichromatic than monogamous taxa (Irwin, 1994; Price & Eaton, 2014). A previous phylogenetic analysis by Price and Eaton (2014) showed that past color changes have generally occurred more rapidly in females than in males. A goal of the current study was to determine whether this difference in overall rate has tended to occur when dichromatism was increasing, decreasing, or both. Given previous suggestions that sexual dimorphisms should be lost more easily than gained (Kraaijeveld, 2014; Price, 2015) and that female colors may be subject to a wider range of selection pressures than are male colors (Badyaev & Hill, 2003; Johnson et al., 2013; Price, 2019), we hypothesized that female plumage changes should occur especially rapidly during decreases in sexual dichromatism.

Methods

Data for our analysis were obtained from Price and Eaton (2014), which included reflectance measurements from male and female representatives of 37 New World blackbird species

(Icteridae) in the grackles-and-allies clade. For each species, reflectance data were collected from 22 feather patches on the study skins of three males and three females obtained from the Field Museum of Natural History (Chicago, Illinois) and the American Museum of Natural History (New York, New York). Colors were sampled using an S-2000 spectrometer (Ocean Optics, Dunedin, Florida) with an R200-7-UV/VIS reflectance probe (fiber diameter = 200 µm) and a PX-2 pulsed xenon light source oriented perpendicular to the measured surface. Data consisted of the percentage of light reflected at each wavelength from 300 to 700 nm, calibrated against a Spectralon white reflectance standard and averaged into 10 nm bins, collected using OOIBASE32 software. We averaged the reflectance data across three individuals for each feather patch, separately for each sex within each species.

To calculate color differences (ΔS), we first calculated receptor quantum catch values for each feather patch using the following equation from Vorobyev et al. (1998): $Q_i = \int_\lambda R_i(\lambda)S(\lambda)\mathrm{d}\lambda$, 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). These calculations employed the Vorobyev–Osorio color discrimination model (Vorobyev & Osorio, 1998) to estimate a linear distance between 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 (Eaton, 2005; Vorobyev et al., 1998). Thus, Q_1–Q_4 represented the receptor quantum catch of the ultraviolet sensitive cone, the short-wave-sensitive cone, the middle-wave-sensitive cone, and the long-wave-sensitive cone, respectively. The model defines the threshold value for discriminating two colors as 1.0 jnd (just a noticeable difference), where two colors are just distinguishable by an avian visual system (Eaton, 2005; Vorobyev et al., 1998). In practice, differences between individual color patches ranged from less than 0.5 to nearly 40 jnd (Price & Eaton, 2014), providing a continuous and relatively objective quantification of color differences based on the general physiological properties of avian vision.

For each of the 22 feather patches, we used maximum likelihood reconstructions of continuously valued characters on a molecular phylogeny for the grackles and allies (Eaton, 2006; Lanyon & Barker, 2007). This phylogeny was based on DNA sequence data from two mitochondrial gene regions (cytochrome *b* and ND2) and four nuclear regions (RAG1, beta fibringogen intron 5, aconitase 1 intron 10, and myoglobin intron 2). More recent phylogenies for the Icteridae have been published by Powell et al. (2014) and Barker et al. (2015), which include more taxa but nevertheless are largely consistent with the topology of Lanyon and Barker (2007). We are confident that differences among these trees, which are limited to short, relatively weakly supported internodes at the base of the phylogeny, would not have altered the overall patterns and general conclusions of our analysis. We implemented the software package ANCML (Schluter et al., 1998) to estimate ancestral values at each node on the phylogeny for each of the four quantum catches (Q_1–Q_4), separately for both males and females. These reconstructed quantum catch values, combined with the values of extant species, allowed us to calculate color distances (ΔS) between the sexes (i.e., sexual dichromatism) of both ancestral and extant taxa, as well as color distances (ΔS) within each sex from one ancestral node to the next on the phylogenetic tree, as described by Price and Eaton (2014).

We summed the ΔS values for all 22 feather patches to calculate all-patch-ΔS differences between the sexes, reflecting overall levels of sexual dichromatism, which in turn allowed us to compare past increases and decreases in dichromatism on the phylogeny using independent samples t-tests. We also calculated all-patch-ΔS color changes in males and in females along each phylogenetic branch, which allowed us to compare ancestral rates of change between the sexes when dichromatism was either increasing or decreasing using paired t-tests. We further compared these four categories of change using ANOVA and post hoc Tukey HSD tests. All statistical comparisons were conducted in R (R Development Core Team, 2023).

Results

Sexual dichromatism (all-patch-ΔS between the sexes) has increased and decreased repeatedly in the grackles-and-allies clade (Figure 1). Maximum likelihood reconstructions indicate that the ancestor of the clade was only moderately sexually dichromatic (all-patch-ΔS = 61.4 jnd), whereas extant species vary from slightly dichromatic (*Dives dives*: all-patch-ΔS = 24.3 jnd) to extremely dichromatic (*Quiscalus major*: all-patch-ΔS = 348.4 jnd), including some closely related sister taxa with striking differences in their levels of sexual dichromatism (e.g., *Q. major* versus *Quiscalus niger*: all-patch-ΔS = 48.0 jnd). Sexual dichromatism has increased on the phylogenetic tree more often than it has decreased, increasing on 35 branches and decreasing on 29, and increases in dichromatism have tended to be larger than decreases in dichromatism, on average (Figure 2A; independent samples t-test, t_{62} = −2.010, p = .049), which is not surprising given the relatively low level of dichromatism in the common ancestor of the clade (Figure 1).

Comparing evolutionary changes in males and females along each branch of the phylogeny (all-patch-ΔS between nodes; Figure 2B) shows that increases in dichromatism have involved divergent changes in both sexes at approximately equal rates (paired t-test: t_{28} = 0.593, p = .557). Decreases in dichromatism, in contrast, have involved changes in female colors towards male colors that were significantly more rapid than changes in males (paired t_{34} = −5.155, p < .001). Indeed, changes in female plumage colors to match males were significantly more rapid than all three other categories of change (ANOVA: $F_{3,124}$ = 3.841, p = .011; Tukey's HSD test: female change during decreases in dichromatism versus male change during decreases: p = .049, versus male change during increases: p = .023, and versus female change during increases: p = .023). In multiple, relatively sexually monochromatic taxa across the clade (shaded circles in Figure 1), ancestral female colors changed more than twice as rapidly as male colors as dichromatism decreased.

Discussion

Evolutionary changes in female plumage colors during decreases in dichromatism have been significantly more rapid than any other category of color change (Figure 2B), even despite a general trend across the grackles-and-allies clade of larger increases in sexual dichromatism than decreases (Figure 2A). Increasing dichromatism involves the evolutionary divergence of both sexes at similar rates, whereas decreasing dichromatism primarily involves changes in females to

match the plumage color patterns of males. These repeated, relatively rapid losses of female-specific color patterns appear to explain previous findings that overall rates of color change have been significantly greater in females than in males in this clade (Price & Eaton, 2014). Our results also corroborate previous observations that transitions from dichromatism to monomorphism in birds typically involve females gaining male-like characteristics rather than the reverse (Badyaev & Hill, 2003; Irwin, 1994; Johnson et al., 2013; Kraaijeveld, 2014; Kraaijeveld et al., 2007).

Such rapid changes in females towards male color patterns support previous suggestions that sexual dimorphisms should be lost more rapidly than gained (Kraaijeveld, 2014; Lande, 1980; Price, 2015). Autosomal genes for traits exist in both sexes, regardless of whether they are expressed in males or females or both (Kimball & Ligon, 1999), so male-like color patterns should be easily gained by females because the developmental pathways for those traits are largely already present. In contrast, gains of novel color patterns in either sex tend to involve new mutations and developmental mechanisms and thus should take longer to evolve, regardless of whether they are sexually selected signals in males or cryptic color patterns in females. In fact, our evolutionary reconstructions show that past divergent changes in each sex, including the evolution of bright male colors and dull female colors, occurred at nearly identical rates (Figure 2B).

Female plumage colors may be influenced by different types of selection while either diverging or converging with males. Divergences between the sexes tend to involve the evolution of relatively cryptic color patterns in females (Badyaev & Hill, 2003; Burns, 1998; Friedman et al., 2009; Hofmann et al., 2008; Johnson et al., 2013; Omland, 1997; Price & Eaton, 2014; Simpson et al., 2015; Wiens, 2001), which are thought to reduce conspicuousness near the nest (Drury & Burroughs, 2016; Martin & Badyaev, 1996; Soler & Moreno, 2012; Wallace, 1889). Convergences between the sexes, in contrast, generally involve the evolution of more conspicuous female colors, which may provide benefits during intra-sexual competition over resources or mates (Amundsen, 2000; LeBas, 2006; Tobias et al., 2012). These females are presumably freed from selection to be especially cryptic, perhaps due to reduced nest predation, shared parental care, or the loss of any parental care at all (as in the brood parasitic cowbirds, genus *Molothrus*). In the grackles-and-allies clade, species with low levels of dichromatism tend to be socially monogamous, with males and females that exhibit similar roles in both parental care and joint territorial defense (Jaramillo & Burke, 1999; Price & Eaton, 2014).

Why does the loss of sexual dichromatism tend to involve females rapidly gaining male-like characteristics rather than the reverse? We propose that the rapid evolution of male-like traits in females occurs through a combination of selection and genetic correlation between the sexes. That is, females revert to male-like traits so quickly in part because these traits provide fitness benefits and in part because the underlying developmental mechanisms are largely already present in females, as described above. Males, on the other hand, are rarely selected to gain female-specific color patterns, and thus the genetic architecture for female traits, although present in males, is rarely invoked.

Our results add to previous evidence that male and female plumage patterns in songbirds exhibit different modes of evolutionary change (Badyaev & Hill, 2003; Dale et al., 2015;
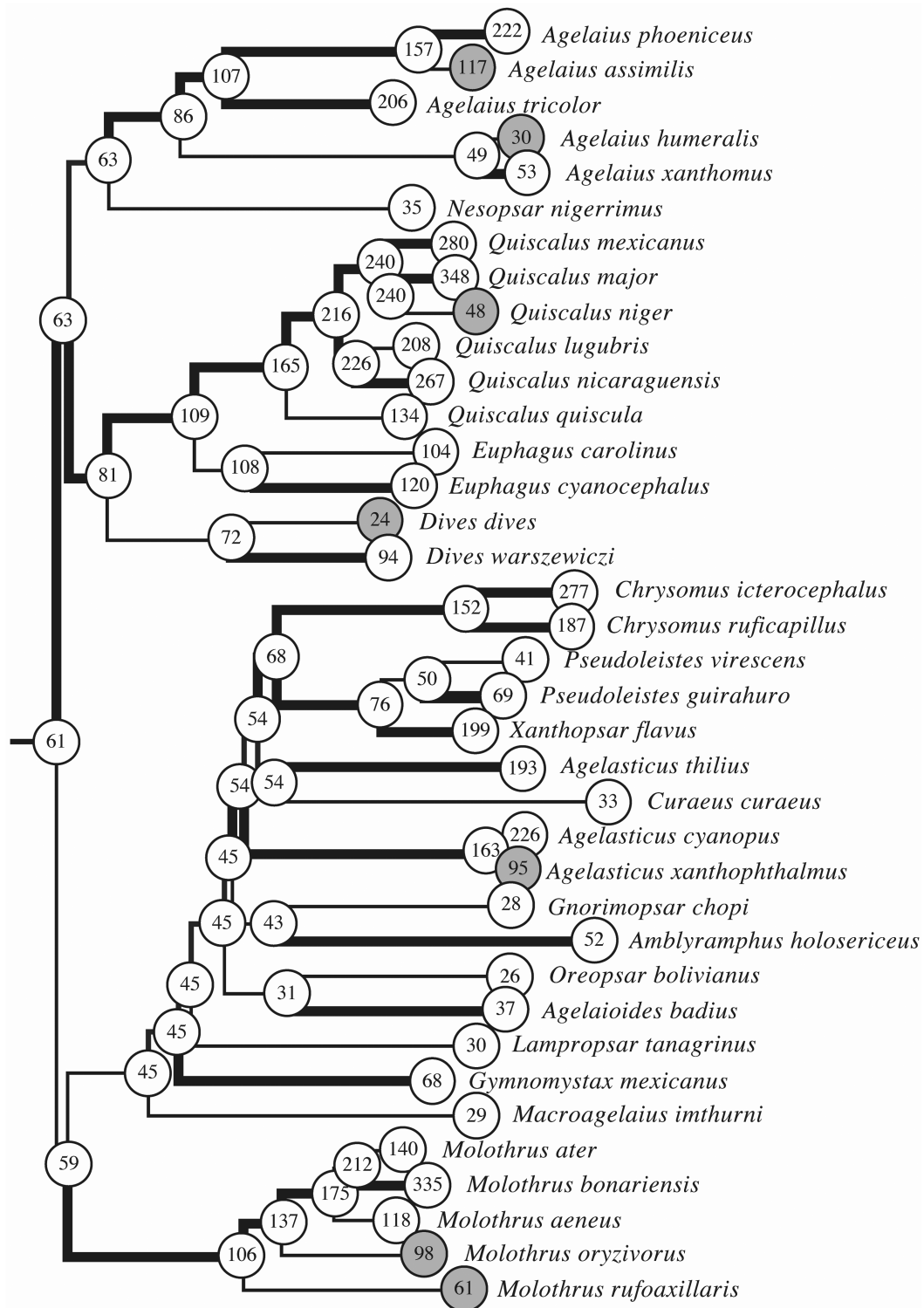
Figure 1. Sexual dichromatism (numbers in circles) reconstructed on the molecular phylogeny as color distances between the sexes (all-patch-ΔS values from Price & Eaton, 2014). Branch thicknesses indicate increases (thick branches), decreases (thin branches), or no change (medium branches) in relative levels of sexual dichromatism. Shaded circles indicate extant, relatively monochromatic taxa in which ancestral female plumage colors changed more than twice as rapidly as male colors as dichromatism decreased.

Johnson et al., 2013; Omland & Hofmann, 2006; Price & Eaton, 2014; Shultz & Burns, 2017). In previous phylogenetic comparative analyses of icterids (Price & Eaton, 2014) and fairy-wrens (Johnson et al., 2013), for example, variation in male plumage was found to correspond best to a model of Brownian motion, with males steadily diverging over

time, whereas female plumages correspond to an Ornstein–Uhlenbeck (OU) model, suggesting natural selection towards one or more adaptive optima. These sex-specific patterns of evolutionary change presumably reflect different mechanisms of selection, with male colors following a pattern of continual divergence through sexual selection and female colors
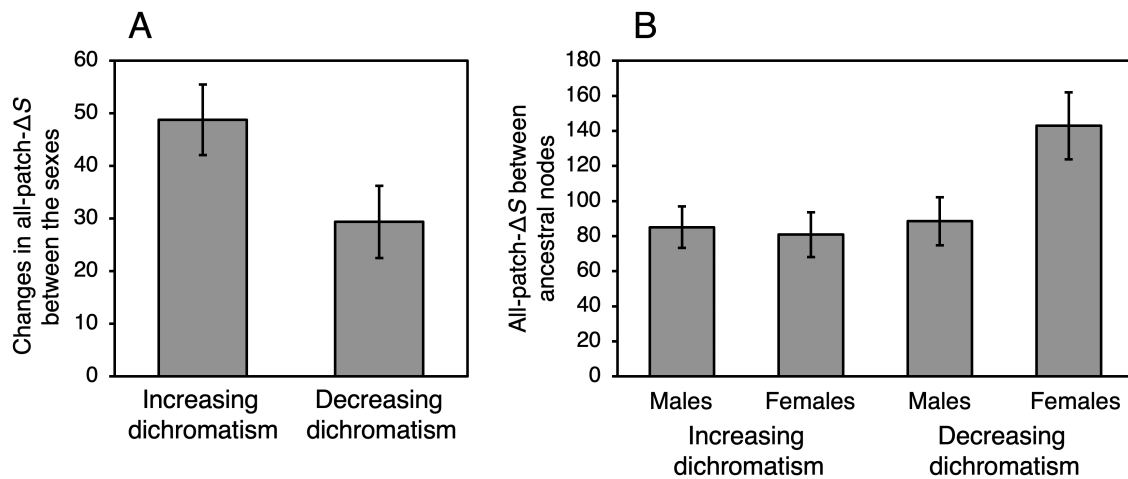
Figure 2. Mean (± SE) changes in (A) sexual dichromatism and (B) male and female colors along each branch of the molecular phylogeny while dichromatism was either increasing ($n = 35$) or decreasing ($n = 29$). Although mean levels of sexual dichromatism have generally increased more than decreased across the clade (t-test: $t_{62} = -2.010$, $p = .049$), the greatest color changes have occurred in females while sexual dichromatism was decreasing (Tukey's HSD test: $p < .05$ in comparisons to the other three types of change).

following an OU-like pattern of punctuated change, periodically influenced by natural selection on female conspicuousness (Drury & Burroughs, 2016; Martin & Badyaev, 1996; Medina et al., 2017; Soler & Moreno, 2012). Our results build on those of Johnson et al. (2013) and Price and Eaton (2014) by showing that changes in females toward male-like colors are significantly more rapid than other types of change in either sex, including changes by females away from male colors.

Color variation within some New World blackbird genera provides clear illustrations of the broader patterns shown in our clade-wide analysis of reflectance data. Among species in the *Agelaius* genus, for instance, males are notably similar in their glossy black plumages and colorful epaulets, whereas females differ substantially among species, with some appearing nearly identical to males (*Agelaius assimilis*, *A. xanthomus*, and *A. humeralis*) and others strikingly different (*A. phoeniceus* and *A. tricolor*), suggesting multiple past increases and/or decreases in dichromatism (Jaramillo & Burke, 1999; Price & Eaton, 2014). Female *A. assimilis* (Red-shouldered Blackbirds) have glossy black plumage that is similar to males but quite unlike the cryptic, brown-striped patterns of females in closely related *A. phoeniceus* (Red-winged Blackbirds) and *A. tricolor* (Tricolored Blackbirds), which are notably similar to each other (Jaramillo & Burke, 1999). The positions of these three taxa on the tree (Figure 1), along with biogeographic evidence (Barker et al., 2008), indicate that the male-like colors of female *A. assimilis* evolved exceedingly rapidly from recent, cryptically colored female ancestors. Similarly dramatic gains of male-like female colors on short phylogenetic branches can be seen in *A. humeralis* (Tawny-shouldered Blackbird), *Quiscalus niger* (Greater Antillean grackle), *Dives dives* (Melodious Blackbird), *Agelasticus xanthophthalmus* (Pale-eyed Blackbird), and in members of the *Molothrus* genus (Figure 1).

The evolution of sexual dichromatism involves a complex interplay between mechanisms of genetic expression and various forms of selection on both sexes, not just sexual selection on males (Dale et al., 2015; Price, 2019). Sexual selection is widely thought to drive rapid phenotypic

divergence of traits (Andersson, 1994), including male plumage (Cooney et al., 2019; Seddon et al., 2013). Yet, in the grackles and allies, a group in which polygynous species are more highly dichromatic than monogamous taxa, the most dramatic evolutionary changes have occurred in females when dichromatism was lost, which at least in some cases occurred during past transitions from polygyny to monogamy (Irwin, 1994; Price & Eaton, 2014). Although rarely reported, such rapid evolutionary losses of dimorphism may be common in animals. Our findings illustrate the importance of examining trait evolution in each sex independently and in different evolutionary contexts, which may provide insights into evolutionary changes in dimorphism across a wide range of taxa.

Data availability

Data are archived in the Dryad Digital Repository: https://doi.org/10.5061/dryad.fbg79cp28.

Author contributions

M.D.E. collected and analyzed reflectance data to calculate color distances, K.G. compared evolutionary rates among lineages and between sexes, and J.J.P. conceived the project and wrote the paper. All authors edited and approved the manuscript.

Conflict of interest: The authors declare no conflict of interest.

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