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Selection, constraint, and the evolution of coloration in African starlings

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Colorful plumage plays a prominent role in the evolution of birds, influencing communication (sexual/social selection), and crypsis (natural selection). Comparative studies have focused primarily on these selective pressures, but the mechanisms underlying color production can also be important by constraining the color gamut upon which selection acts. Iridescence is particularly interesting to study the interaction between selection and color-producing mechanisms because a broad range of colors can be produced with a shared template, and innovations to this template further expand this by increasing the parameters interacting to produce colors. We examine the patterns of ornamentation and dichromatism evolution in African starlings, a group remarkably diverse in color production mechanisms, social systems, and ecologies. We find that the presence of iridescence is ancestral to the group, being predominantly lost in females and cooperative breeders, as well as species with less labile templates. Color-producing mechanisms interact and are the main predictors of plumage ornamentation and elaboration, with little influence of selective pressures in their evolution. Dichromatism, however is influenced by social system and the loss of iridescence. Our results show the importance of considering both selection and constraints, and the different roles that they may have, in the evolution of ornamentation and dimorphism.

KEY WORDS: **Cooperative breeding, iridescence, melanosome, sociality, social selection.**

The diversity of avian colors observed in the nearly 10,000 extant species of birds has been central to the study of how natural and social selection interact to mold phenotypic patterns (Andersson and Iwasa 1996; Bennett and Owens 2002; Badyaev and Hill 2003). In many species of birds, males are brightly colored while females are dull and inconspicuous, suggesting that the balance of natural and sexual selection has tipped in different directions for each sex. However, both sexes may be either dull or ornamented in some species, highlighting the continuous spectrum that conflict between these forces can produce (Badyaev and Hill 2003; Kraaijeveld 2003; Rubenstein and Lovette 2009; Dale et al. 2015).

Traditionally, studies on the evolution of plumage coloration—particularly those of sexual dichromatism—have focused upon how natural and social selective pressures shape the observed patterns of diversity. The evolution of sexual dichromatism has been positively associated with the degree of reproductive skew experienced by males, such that promiscuous mating systems and high rates of extra-pair fertilizations correlate with dichromatism (Møller and Birkhead 1994; Bleiweiss 1997; Owens and Hartley 1998). Increased potential for social selection (defined as selection resulting from social competition, including but not limited to that for mating opportunities, and therefore encompassing sexual selection; Lyon and Montgomerie 2012) may also accelerate the evolution and divergence of plumage color and dichromatism (Price and Whalen 2009; Seddon et al. 2013), potentially exerting a role in speciation (Cardoso and Mota 2008; Seddon et al. 2013), though large-scale patterns are less clear (Kraaijeveld et al. 2011). However, sexual dichromatism reflects not only social selection in males, but the result of the balance between natural and social selection in both sexes, and as

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such, may arise from rapid evolution or increased selection for female dullness (Badyaev and Hill 2003; Johnson et al. 2013; Price and Eaton 2014; Dale et al. 2015), without an increase in social selection.

Although social selection is thought to influence patterns of sexual dimorphism in birds, natural selection can also influence the evolution of plumage coloration. For example, social selection would favor disruptive selection among closely related species whose geographic ranges overlap, a pattern observed in high-latitude birds that have experienced recent dynamic shifts in breeding ranges (Martin et al. 2010). However, other studies suggest that sympatric species are often less divergent than expected, instead showing consistent colors within habitat types, suggesting that the signaling environment plays an important role in the evolution of plumage coloration (McNaught and Owens 2002). Within a community, plumage brightness follows a light intensity gradient, wherein canopy-dwellers are brighter than understory birds, possibly because each group is more cryptic in its respective background (Gomez and Théry 2004). Furthermore, canopy birds also have greater UV reflectance and a broader range of short-wavelength hues. This pattern is also consistent with the importance of signaling environment because the attenuation of these short wavelengths reduces their efficiency towards the understory (Gomez and Théry 2004). In contrast, work in *Phylloscopus* warblers has shown that these birds evolve brighter and more complex color patterns in darker environments, suggesting instead that selection for conspicuousness may play a role in this group (Marchetti 1993). In the large and ecologically diverse radiation of tanagers, light environment also plays an important role in the evolution of plumage coloration, with brighter plumage selected in open habitats and duller plumage in closed habitats (Shultz and Burns 2013). However, in this group, complex and diverse plumage patterns are consistently found in closed habitat species, again supporting the hypothesis that complex and variable patterns are selected to increase conspicuousness when signaling efficacy is reduced (Marchetti 1993; Shultz and Burns 2013).

More recently, the role of color-producing mechanisms themselves on patterns of color evolution and diversification has started to garner attention. For example, Owens and Hartley (1998) found that a significant relationship between plumage dichromatism and extra-pair paternity when considering species that have structural color-based dichromatism, but not for melanin- and carotenoid-based plumage (Owens and Hartley 1998; Bennett and Owens 2002). The evolution of novel color-producing mechanisms can dramatically expand the gamut of colors within a lineage (Stoddard and Prum 2011; Maia et al. 2013), therefore providing differing levels of potential variability on which natural and social selection can act. When color is produced by a limited range of pigments in a lineage, for example, the available gamut is limited and selection will likely often lead to convergence in plumage color (Price et al. 2007; Prager and Andersson 2010; Friedman et al. 2011, 2013). The evolution of novel pigments can then open the colorspace to new phenotypes (Prum et al. 2012). Structural colors, on the other hand, offer a broad range of colors that can be produced under the same template, by altering the size and arrangement of its component structures (Durrer 1977; Stoddard and Prum 2011; Saranathan et al. 2012; Eliason and Shawkey 2012). Adding complexity to this template can further enable color diversification (Maia et al. 2013), and the lability in expressing structural colors themselves can influence the degree and rate of color, pattern, and dichromatism evolution (Shawkey et al. 2006a,b). Furthermore, different color-producing mechanisms can vary in how they influence pattern and dichromatism evolution. For example, in Australian parrots, structural colors are the main source of dichromatism, with melanin- and psittacofulvin-based colors being generally similar between sexes (Taysom et al. 2011), whereas in New World Orioles carotenoids and melanins coevolve in producing dichromatism, without marked differences between these pigments (Hofmann et al. 2008).

To understand how natural and social selection interact with color production mechanisms to influence the evolution of bird plumage, we must jointly test for their effects in a group that is variable in color-producing mechanisms, social systems, and ecologies. African starlings are the only group of birds known to display four different morphologies of melanin-containing organelles called melanosomes that, when nanostructurally organized, produce varying types of iridescent colors (Durrer 1970). We have previously shown that these different melanosomes produce colors that evolve at different rates and that occupy different regions of colorspace, and that lineages with rapidly evolving colors also diversify faster (Maia et al. 2013). However, it remains unclear how natural and social selection may have influenced these patterns of morphological diversification. Additionally, African starlings also vary in the presence and extent of iridescence in their plumage across sexes. Thus, we also consider the relative evolutionary role of gains and losses of iridescence *per se*: its lability across the sexes and influence on overall ornamentation and dichromatism.

African starlings show a diversity of mating and social systems, with nearly half of the 45 species being socially monogamous (i.e., one male and one female attending the nest, with no strict social polygyny reported; Craig and Feare 2009) and more than 40% being cooperative breeders (i.e., more than two individuals care for offspring at the nest; Rubenstein and Lovette 2007, 2009). Cooperative breeding in this group is extremely variable, ranging from species where one or few offspring delay dispersal and help a single breeding pair, to complex societies with multiple breeding pairs and helpers of both sexes (Rubenstein 2016). Because of the high reproductive skew and competition for breeding opportunities within cooperatively

breeding social groups, these complex societies can create intense selective pressures for social competition because (1) many individuals of both sexes will not reproduce (Rubenstein 2012; Tobias et al. 2012; though some opportunities may emerge through extra-pair fertilization both within and among groups, at relatively low levels; Rubenstein 2007a,b), and (2) overall breeding success is low (Craig and Feare 2009). In particular, this reproductive skew can result in selection favoring the evolution of ornamental and competitive traits in females, who also compete for reproduction (Tobias et al. 2012; Young and Bennett 2013). As such, dimorphism and dichromatism (determined visually by human observers) is reduced in cooperative species in this clade, and results from greater female ornamentation and body size relative to their socially monogamous counterparts (Rubenstein and Lovette 2009). Finally, African starlings occupy a broad range of habitats ranging from desert to savanna to forest (Feare and Craig 1998; Rubenstein and Lovette 2007) that vary in their degree of openness, and thus in lighting and signaling conditions. This allows us to test the relative importance of color production mechanisms, social system, and habitat attributes as evolutionary predictors of plumage elaboration, complexity, and dichromatism.

Methods

PHYLOGENY RECONSTRUCTION

We reconstructed phylogenetic relationships for all 113 Starling species and five outgroups (sampling and laboratory methods are detailed in Lovette and Rubenstein 2007; Lovette et al. 2008). The molecular dataset included sequences spanning the NDII, COI, COII, ATPase8, and ATPase6 mitochondrial genes (4118bp), and sequences from rhodopsin intron 1, intron 5 of transforming growth factor β-2, and the closely linked β-fibrinogen introns 5 and 7 (3079 bp total, including indels after alignment) from most samples, while for some only the 1038 bp NDII sequences were available (Lovette and Rubenstein 2007; Lovette et al. 2008). We used these sequences to infer phylogenetic relationships while concurrently estimating branch lengths proportional to time using Bayesian phylogenetic analysis with a relaxed molecular clock approach, as implemented in the software BEAST (Drummond and Rambaut 2007). Following Lovette and Rubenstein (2007) and Lovette et al. (2008), we separately fit a general time-reversible model of nucleotide substitution allowing for gamma-distributed substitution rate variation among sites and invariant sites (GTR+G+I; Yang 1994) to the mtDNA sequences partitioned by codon position and the five nuclear intron partitions. Given the lack of fossil record for Passeriformes in general, and starlings in particular (Cracraft and Barker 2009), we time-calibrated phylogenies by modeling variation among lineages in substitution rates by uncorrelated lognormal distributions (Drummond et al. 2006; Drummond and Rambaut 2007). We used the average substitution rate parameters from mitochondrial molecular clocks estimated for Passeriformes in a normal prior distribution for mtDNA sequences (mean 0.01035, standard deviation 0.003, Weir and Schluter 2008), and we used uninformative priors for the remaining partitions.

Using a Markov Chain Monte Carlo (MCMC) algorithm in BEAST, we sampled the posterior probability distribution of phylogenetic trees and substitution model parameters, given the sequence data. Four MCMC chains were run from independent random starting trees and for 3 x 10^7 generations, sampling every 3000 generations after discarding the first 20% of the chain as burn-in. We verified chain stationarity (stable joint probability distribution across generations) and convergence of independent chains by verifying their split frequency distributions throughout the chains and their correlations between chains using the AWTY software (Nylander et al. 2008), and the effective sample sizes of model parameter estimates were checked to be greater than 200 using the TRACER software (Drummond et al. 2006). We estimated the Maximum Clade Credibility (MCC) Tree from the posterior distribution, and in order to incorporate phylogenetic uncertainty in our comparative analyses, we randomly subsampled 100 trees from the posterior distribution of the combined MCMC run, which we pruned to the African subclade.

PLUMAGE COLOR MEASUREMENTS

We took spectral reflectance measurements of museum specimens from 47 of the 48 species of the African Starling subclade from the American Museum of Natural History in December 2010 (the one species not sampled, Neumann's Starling *Onychognathus neumanni*, has a very similar color to its sister species, and therefore its absence should not influence our analysis). We measured only specimens in full adult plumage and showing no signs of molt. We measured up to 10 males and 10 females from each species according to museum availability (median 8.4 for each sex).

Reflectance spectra were taken from 10 standard plumage patches from all species: crown, nape, mantle, rump, throat, breast, belly, lesser wing coverts, wing, and tail. Additional color patches were measured for certain species when other discrete patches could be distinctly identified (auriculars, mask, wing bar, tail bar, median wing coverts, and lower belly). We took all measurements using an Avantes AvaSpec-2048 spectrometer and an AvaLight-XE pulsed xenon light source connected by a bifurcated fiber optic probe enclosed in a AFH-15 block holder to exclude ambient light (Avantes, Boulder, CO). We took three measurements at coincident normal measurement geometry (Montgomerie 2006) from each color patch of each specimen by completely removing and replacing the probe holder onto the measured area, relative to a WS-2 white reflectance standard (Avantes, Boulder, CO) calibrated before each specimen's measurements. The average for

the three measurements was used to characterize each specimen's color patch. We also classified patches as iridescent or noniridescent, as determined by the angle-dependent appearance of color and the spectral shape of the reflectance curve.

We described plumage in terms of chromatic and achromatic complexity (i.e., how heterogeneous is the overall plumage), conspicuousness (i.e., how much it contrasts with the background), and dichromatism (i.e., the degree of contrast among the sexes in homologous plumage patches), while considering the characteristics of receptor color sensitivity. The avian visual system is defined by three cones sensitive to short-, medium-, and long-wavelength stimuli, and a variable fourth cone type that can be either UV- or violet-sensitive (Hart 2001). Sensitivity of this fourth cone is mostly strongly conserved within families (Hart 2001; Odeen et al. 2011; Odeen and Hastad 2013, but see Odeen et al. 2012), and therefore we used the sensitivity curves and receptor densities of the common starling (*Sturnus vulgaris*) visual system (Hart et al. 1998) in our analyses. To estimate these variables, we represented colors in a perceptual color space by using the Vorobyev–Osorio receptor-noise limited color vision model (Vorobyev et al. 1998, and equations therein). The visual model represents colors based on how much the reflected light from a surface stimulates each photoreceptor, given the illuminant and background conditions. It then considers receptor noise as the main factor dictating if two colors are sufficiently different to be distinguished, imposing a limit to color discrimination (Vorobyev and Osorio 1998; Vorobyev et al. 1998). Therefore, two colors should only be considered different if their difference in receptor stimulation exceeds the threshold determined by receptor noise, which in turn is inversely proportional to the relative density of the different cone types (Vorobyev et al. 1998).

Color distances can thus be represented as distances in receptor stimulation weighted by the receptor noise and measured in Just Noticeable Differences (JND), where a value greater than 1 represents colors that potentially can be reliably discriminated by the observer (Vorobyev et al. 1998). Though these models were designed to interpret detection thresholds, large color differences can still be understood in terms of color space position and divergence based on Fechners assumption of additivity (Renoult et al. 2015). Thus, even though colors many units of JND away from each other cannot be interpreted in terms of being more discriminable than others (i.e., there is no evidence that two colors 20 JND apart are any easier to distinguish than colors 15 JND apart, since both cases represent dramatically different and easily discriminable colors; Endler and Mielke 2005; Kemp et al. 2015), distances in JND can be interpreted in terms of a noise-weighted colorspace, where distances represent the positions of observations in color space given the modeled psychophysical attributes (e.g., Pike 2012; Kemp et al. 2015; Renoult et al. 2015). In essence, this is the sensory equivalent of a morphospace, in which phenotypes are identified as points in a 3-dimensional Cartesian space determined by the four cones and distances are weighted by receptor noise; similar colors will fall in close proximity in the color space and disparate colors will be separated by large distances. This color space is a chromaticity diagram—the chromatic signal (hue and saturation) are represented with the achromatic (brightness) dimension removed, which is adequate because in birds the chromatic and achromatic aspects of the signal are processed independently by specialized receptors (double-cones) and serve different functions in communication (Vorobyev et al. 1998; Osorio et al. 1999; Hart 2001). Differences between colors in achromatic properties can similarly be inferred by how much they stimulate double-cones and the relative density of these double-cones in the avian retina (Siddiqi et al. 2004).

To describe starling plumage coloration, we calculated several measures of the strength and degree of the color signal and color contrasts. First, we calculated the average plumage chromaticity, given by the mean Euclidean distance from the achromatic center (i.e., the region of the colorspace where all four cones are equally stimulated) to measured plumage patch colors. This variable was calculated considering the relative stimulation of the four cones and not considering receptor noise properties, and was intended as an overall measure of the average strength of the color signal of a species' plumage (Endler and Mielke 2005). We also calculated the mean plumage brightness as the average double-cone excitation from the measured patches, where low values represent dark colors and high values represent light colors. We then calculated the chromatic and achromatic interpatch contrasts as the average distance between all pairwise comparisons of the plumage colors for each species for each sex (Doucet et al. 2007). These variables were our measures of plumage complexity, where high values indicate a plumage composed of very distinct and contrasting colors, whereas low values indicate an overall homogeneously colored plumage. Thus, chromaticity and mean brightness can be interpreted as the average strength of the color signal properties, whereas interpatch contrasts represent the degree of heterogeneity and variation in color of the overall plumage.

We also calculated the mean chromatic and achromatic contrasts of the plumage to the background color. Irradiance and background reflectance spectra across the habitats of all measured species are not available, but overall color properties of the vegetation and arid environments inhabited by these species are sufficiently similar (despite their compositional differences; Endler 1993) that they can be approximated using data from similar environments obtained from the literature. We classified each species as inhabiting a habitat that is primarily savannah-like (i.e., mostly open semi-arid habitat with direct sunlight incidence and a mixture of green vegetation and exposed bark as the background), desert-like (i.e., arid habitat with direct sunlight and a rocky, brownish background), and forest-like (i.e., closed habitat

with little direct light and mostly green vegetation as the background), and obtained published measures from similar backgrounds (savannah: Sicsú et al. 2013, arid: Macedonia et al. 2009, forest: Endler 1993) and illumination conditions (Endler 1993) in the models for each species. It is important to note, however, that color-correcting mechanisms result in a proportional shift in the position of colors in perceptual space that preserves their relative distances, and therefore have no effect on the chromaticity and interpatch contrast variables described above (Vorobyev et al. 1998). Similarly, the backgrounds considered are sufficiently similar (i.e., reflectance concentrated in mid-long wavelengths) that considering different backgrounds for different species, or the same background for all species, had negligible effects on contrast calculations. Therefore, we regard these estimates to be robust to the considered approximations.

VARIABLES CONSIDERED

The melanosome morphology of these species has been extensively studied (Durrer 1970; Craig and Hartley 1985; Maia et al. 2013), and we previously confirmed the literature data on melanosome type using Transmission Electron Microscopy to examine one species per genus in the group (Maia et al. 2013). Melanosomes found in the feathers of these species can be of four different types: rod-shaped and filled entirely of melanin (the ancestral morphology, found in most birds; Li et al. 2010; Maia et al. 2013), flattened, hollow, or both flattened and hollow (platelets). Previously, we demonstrated that the three derived melanosome morphologies expand the gamut of colors found in this group by promoting an accelerated disparification and the occupation of different areas of colorspace relative to the ancestral morphology (Maia et al. 2013). However, these effects do not differ between the three derived melanosome types (Maia et al. 2013). Thus, for simplicity and to avoid combinations of factors with few observations, we grouped species based on their melanosome morphology as ancestral (i.e., solid melanin rods) or derived (encompassing the three modified melanosome shapes described above). Finally, we counted how many of the 10 homologous body patches (thus excluding those found only in particular species; see above) were noniridescent in each sex (see below).

For the behavioral and ecological variables, we considered social system (Rubenstein and Lovette 2007, 2009) and habitat lighting characteristics (Feare and Craig 1998; Rubenstein and Lovette 2007; Craig and Feare 2009), obtained from the literature. Social system was classified as "cooperative" or "noncooperative" depending upon the number of adult individuals attending nestlings (Rubenstein and Lovette 2007, 2009). The habitat characteristic considered for the evolution of plumage color is ambient lighting conditions, and specifically if there is mostly direct light incident on a displaying individual or if there is considerable vegetative filtering of incident light (Endler 1993). Therefore, our classification differs from that of Rubenstein and Lovette (2007) in that we grouped savannah and arid ("open") environments and compared them to forest ("closed") habitats (instead of the "savanna" and "nonsavanna" classification used by Rubenstein and Lovette 2007), similar to Shultz and Burns (2013).

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Our classification of colors as iridescent or noniridescent (see above) ignores the melanosome type found in these feathers, as well as the actual color observed, but provides a way of qualitatively identifying the presence of periodically organized photonic structures within these feathers. Therefore this classification scheme can be used to identify the evolutionary origins and losses of this trait.

Dimorphism in the presence of iridescence can result from gains of iridescence in one sex from a noniridescent ancestor, or from the loss of iridescence in one sex from an iridescent ancestor. Therefore, to understand the evolution of iridescence dimorphism in this group, estimating the ancestral morphology and the direction of changes in the group is essential. For each body patch, we thus coded each species as being monomorphic noniridescent, monomorphic iridescent, or dimorphic (iridescent male and noniridescent female, as there are no species with any body patches that are iridescent in females and noniridescent in males). We then used stochastic character mapping (SIMMAP; Huelsenbeck et al. 2003; Ronquist 2004) to reconstruct the evolution of iridescence dimorphism for each of the 10 body patches in the species in this lineage. We reconstructed the evolution of each trait based on the maximum likelihood estimates of the transition rate matrix 1000 times in the Maximum Clade Credibility obtained from the posterior distribution of phylogenies, obtaining the probability of each state at the root of the African starling subclade and the number of transitions between states within this subclade (Wainwright et al. 2012). This allowed us to compare how frequent are gains and losses of iridescence in this clade, as well as if dimorphism in the presence of iridescence occurs due to the loss of iridescence in females from a monomorphic iridescent ancestor, or from gains in male iridescence from a noniridescent ancestor.

EVOLUTIONARY PREDICTORS OF COLORATION

To test for the effect of color-producing mechanisms and putative selective pressures on the evolution of iridescence, plumage color complexity, and dichromatism, while accounting for phylogenetic relationships, we used Bayesian Phylogenetic Mixed-Effects Models (BPMM), implemented in the *MCMCglmm* package (Hadfield 2010; Hadfield and Nakagawa 2010). Given that male and female coloration are not only nonindependent, but can also vary in the degree of relationship depending upon some of the covariates, we used multiresponse models where male and female color attributes were taken as multivariate

response variables (with the exception of dichromatism, where a single measure—the distance between male and female colors—was used to describe its value for each species). This approach allows the concomitant estimation of between-sex mean differences and both overall and sex-specific effects of predictor variables, while also estimating the phylogenetically corrected intersexual correlation between the response variables (Hadfield 2010; Hadfield and Nakagawa 2010).

To test the effect of melanosome type, habitat, sex, and social system on the number of noniridescent patches, we used a generalized multiresponse BPMM with a Poisson error and log-link distribution. We also considered the interaction between sex and social system to determine if cooperative breeding had any sex-specific effects on the evolution of iridescence. In the models for plumage average chromaticity, average brightness, interpatch chromatic and achromatic contrast, and background chromatic and achromatic contrast, we used a linear multiresponse BPMM, and considered the overall effects of sex, habitat, social system, melanosome type, and number of non-iridescent patches (by sex). Given that expressing iridescence or not in different body parts can potentially influence these color attributes differently depending on the melanosome type a species has (and therefore the colors it can potentially achieve), we also considered the sex-specific interactions between melanosome type and the number of noniridescent patches that sex for that species displays. Finally, for chromatic and achromatic dichromatism, we used linear BPMM with social system, habitat, melanosome type, the number of male and female noniridescent patches and its interaction with melanosome type as predictors. Dichromatism and brightness variables were log-transformed prior to analyses, and response variables were standardized for linear models.

The BPMM approach assumes that the residuals of the model conform to a Brownian motion model of evolution (though the phylogenetic heritability, calculated as the ratio of the total variance explained by phylogenetic relationships, can essentially be interpreted as the fit of the model to the Brownian motion model similar to the λ parameter; Hadfield and Nakagawa 2010), which might not be adequate particularly for adaptive traits or traits involved in the speciation process. Ideally, more complex models can be incorporated to the framework in the form of parameters describing the fit of the data to the tree, and these parameters should be estimated jointly in the model (Revell 2010). The BPMM approach necessary for this study, particularly for multiresponse models, does not explicitly incorporate other evolutionary models. However, this can be approximated by transforming the phylogenetic tree using the model parameter, and then fitting the Brownian motion model to the transformed tree (Pagel 1999). Therefore we tested the fit of the Ornstein-Uhlenbeck (OU) model (which models traits evolving toward an optimum θ, to which they drawn to by an attraction parameter α, and is commonly interpreted as a trait evolving under strong selection or constraint, Martins 2000) and a speciational model of trait evolution (where branches are transformed by raising their length to a power κ; when κ approaches zero, branch lengths are all equal and the only phylogenetic determinant of trait evolution is the number of speciation events, when κ is greater than one then longer branches have greater influence over trait evolution, and when κ is equal to 1, the model reduces to a Brownian motion model; Pagel 1999), following Tobias et al. (2014). To achieve this, we transformed the MCC tree considering a range of parameters (OU: α between 0 and 10 in 0.1 increments; speciational: κ between 0 and 2.5 in 0.1 increments) and fitting the BPMM, using the Deviation Information Criteria (DIC) to compare the fit of different models and different parameters. We then chose the model with lowest DIC (or the Brownian motion model if the difference in DIC between the it and the best model was lower than 4) for all future analyses across the posterior distribution of trees using that trait. Given that the DIC can be influenced by the starting values and the sampling of the MCMC, we ran each model 10 times for each parameter value, averaging their DICs.

Models used in model testing, as well as final models, were run for $2x10^6$ generations after a 10^5 burn-in, sampling every 1000 generations for a total sample size of 2000 per tree, and were checked for adequate sampling and stationarity visually and through the effective sample size of parameter estimates. To improve mixing, we used parameter expanded priors for the covariance matrices with a scale matrix and degree of belief of 0.002, and a multivariate normal prior specification with a null mean vector and 10^3 covariance for the three redundant working parameters. This specification induces a scaled F-distributed marginal prior on the variances, with one degree of freedom for the numerator and denominator and scaled to the square root of the variance (Gelman 2006). Final models were run on each of the 100 trees and their results combined to generate the point estimates and their 95% credible intervals from the joint posterior probability distribution. Variables were deemed significant when the credible intervals for the estimated effects did not overlap zero.

The literature has largely considered the effects of selective pressures on coloration and dichromatism without considering the potential constraints imposed by color-producing mechanisms. This can potentially affect conclusions because certain effects may only be detectable or become negligible when accounting for confounding variables. We have previously shown that melanosome type and social system are not correlated (Maia et al. 2013), but other variables considered here may still interact (e.g., social system has been shown to be associated with habitat, though categorized differently as explained above; Rubenstein and Lovette 2007). Therefore, we repeated our analyses on color variables and dichromatism, but without considering melanosome type, number of noniridescent patches, and their interactions. To

reduce the computational time required, we used a simplified version of the protocol described above, testing a narrower range of tree transformation parameters sufficient to detect the best fit transformation (κ from 0 to 2.5 and α from 0 to 10, in 0.3 increments) and only on the MCC tree.

Results

THE EVOLUTION OF IRIDESCENCE

Iridescence was found to be considerably phylogenetically labile in starlings, with an average of 15.81 ± 1.76 transitions between states across the ten examined plumage patches (Table 1). Four of these patches (mantle, nape, rump, wing, and wing coverts) had an estimated monomorphic iridescent ancestor at the root (Fig. 1). The root state for the remaining patches was uncertain, but with great confidence on a monomorphic ancestor, either iridescent or noniridescent (the highest probability of a dimorphic ancestor was found for throat feathers, at 0.18, Table 1). Overall, the most commonly observed transitions were the loss of iridescence in both sexes, and the second most common was the female-only loss of iridescence. Transitions that involved either the loss of male iridescence when the female was already noniridescent, or male-only gains of iridescence from a monomorphic, noniridescent ancestor, were rare (Table 1). Therefore, loss of iridescence is more common than its gain, and iridescence is most commonly lost in both sexes concomitantly or in females only, resulting in plumage dimorphism.

Not surprisingly, females were found to have more noniridescent patches than males (Fig. 2A,B). However, cooperative species also have more non-iridescent patches than noncooperative species, though this effect was consistent across sexes (i.e., no sex-by-social system interaction; Fig. 2B). Finally, species with derived melanosomes tend to have more iridescent plumage coverage (i.e., fewer noniridescent patches; Fig. 2B). An OU model with relatively large α (2.8, ESM Fig. S1) was preferred for this trait, further indicating phylogenetic lability of gains and losses of iridescence.

PLUMAGE ELABORATION, COMPLEXITY, AND DICHROMATISM

Mean plumage chromaticity (i.e., a measure of how colorful and saturated the plumage is) followed a speciational model ($\kappa = 0$, ESM Fig. S1). Overall, females have less chromatic plumage than males, with no effect of social system and no interaction between these terms (i.e., females in both cooperative and noncooperative species have similarly less chromatic plumage than males; Fig.3A). The strongest observed effect, however, was of melanosome type, with derived melanosome species displaying considerably higher chromaticity than species with the ancestral melanosome type (Fig. 3A). Mean chromaticity decreased with increasing number of noniridescent patches in both males and females, but there was also an interaction between the number of noniridescent patches and melanosome type in both sexes: the loss of chromaticity resulting from the loss of iridescence patches was greater in species with derived melanosomes (Fig. 3A). Finally, habitat also influenced chromaticity, with forest species being less chromatic than open habitat species (Fig. 3A).

Plumage chromatic complexity (i.e., mean interpatch chromatic contrast) followed an OU model with $\alpha = 2.1$ (ESM Fig. S1). Females in general have slighlty lower plumage complexity (i.e., more homogeneous plumage coloration), with no effect of social system nor habitat, and no interaction between social system and sex (Fig. 3B). Species with derived melanosomes have greater plumage complexity, and melanosome type interacted with number of noniridescent patches: while the number of noniridescent patches does not affect chromatic complexity in species with ancestral melanosomes, an increase in noniridescent patches considerably reduces chromatic complexity in both sexes of species with derived melanosomes (Fig. 3B).

Patterns of chromatic contrast with the background were similar to those of chromaticity: a speciational model ($\kappa = 0$, ESM Fig. S1) was preferred, with females having lower background contrast, and no overall or interactive effects of social system. Species with derived melanosomes had a higher contrast to the background than those with ancestral melanosomes, and this contrast reduced with an increasing number of noniridescent patches in males, this reduction being more pronounced and observed in both sexes in species with derived melansomes (i.e., significant interaction between melanosome type and the number of noniridescent patches for both males and females, Fig. 3C). Habitat had no effect on chromatic contrast to the background, suggesting that after accounting for the above factors, African starling species' plumage is equally contrasting against the background in open and closed habitats.

A speciational model ($\kappa = 0$, ESM Fig. S1) best described the evolution of chromatic dichromatism. In this model, social system significantly affected dichromatism, with cooperative species being less dichromatic than noncooperative species (Fig. 3D). Interestingly, melanosome type did not influence chromatic dichromatism, and the number of noniridescent patches had contrasting effects in males and females: loss of iridescence in males resulted in a loss of dichromatism, whereas the loss of iridescence in females resulted in a gain in dichromatism, with both of these patterns being more pronounced in species with derived melanosomes (Fig. 3D). Habitat had no influence on chromatic dichromatism.

Average plumage brightness (preferred model: OU with $\alpha = 0.5$, ESM Fig. S1) was unaffected by most of the variables considered. Neither sex, social system, habitat, nor melanosome type influenced average plumage brightness (Fig. 4A). Loss of

Table 1. Ancestral state reconstruction of iridescence in African starlings. Transitions represent mean numbers of transitions per tree across the 1000 reconstructions.

Plumage patch	Root $P_{(M_N F_N)}$	$P_{(M_I F_N)}$	$P_{(M_I F_I)}$	Transitions N	$M_N F_N \rightarrow M_I F_N$	$M_N F_N \rightarrow M_I F_I$	$M_I F_N \rightarrow M_N F_N$	$M_I F_N \rightarrow M_I F_I$	$M_I F_I \rightarrow M_N F_N$	$M_I F_I \rightarrow M_I F_N$
Mantle	0.04	0.04	0.93	12.80	0.56	0.86	0.66	0.64	6.70	3.38
Belly	0.66	0.01	0.33	17.72	3.15	4.33	1.85	1.11	4.48	2.80
Breast	0.33	0.14	0.52	22.79	2.40	3.07	2.63	3.60	7.19	3.91
Crown	0.07	0.16	0.77	20.49	1.57	1.78	2.09	3.40	6.66	5.00
Nape	0.06	0.09	0.85	21.01	1.39	1.68	1.74	3.45	6.84	5.90
Rump	0.04	0.04	0.92	11.05	0.50	0.56	0.63	0.46	5.68	3.22
Throat	0.14	0.18	0.69	22.12	2.58	2.56	2.71	3.70	6.12	4.44
Coverts	0.04	0.04	0.92	9.45	0.43	0.40	0.47	0.41	4.63	3.12
Wing	0.04	0.02	0.94	8.86	0.32	1.09	0.43	0.33	5.40	1.29
Tail	0.31	0.03	0.66	11.85	0.77	2.31	0.67	0.55	4.39	3.15

iridescence tended to result in brighter (in essence, more washed out or "whiter") plumage, but this effect was only observed in females (Fig. 4B). Similarly, the achromatic component of plumage complexity also followed an OU model ($\alpha = 1.5$, ESM Fig. S1), with the only detectable effect being that of the interaction between melanosome type and number of noniridescent patches in both sexes—that is, in species with derived melanosome morphology, the loss of iridescence results in more homogeneous plumage brightness patterns (Fig. 4B).

Achromatic contrast to the background (Brownian Motion model, ESM Fig. S1) was not significantly different between males and females, cooperative and noncooperative species, or in species of open or closed habitat (Fig. 4C). However, species with derived melanosomes had a lower achromatic contrast with the background, which is further reduced with the loss of iridescence (i.e., lower achromatic contrast with the background with more of the plumage being noniridescent; Fig. 4C). Finally, the achromatic component of dichromatism was only affected by the loss of iridescence in females, which increased dichromatism, and the loss of iridescence in males, which decreased dichromatism, with this effect only observed in species with derived melanosome morphology (Fig. 4D; best model: OU with $\alpha = 2.3$, ESM Fig. S1).

When considering models that did not include melanosome type and number of noniridescent patches as predictor variables, most of the remaining effects had similar direction and magnitudes, but in some cases the uncertainty associated with parameters changed such that their overlap with zero changed. In these models, the effect of social system became different than zero on chromaticity and background chromatic contrast, but was not different than zero for chromatic dichromatism (ESM Figs. S2 and S3). The effect of habitat on chromaticity also became nonsignificant, whereas sex differences were detected on background achromatic contrast (ESM Figs. S2 and S3).

Discussion

African starlings likely evolved from an ancestor in which both sexes were mostly iridescent, consistent with the ubiquitous iridescence found in both sexes of their European and Asian relatives (Cuthill et al. 1999). Iridescence was subsequently lost in different parts of the body and different lineages from this ancestor in both sexes, but mostly in females. This loss of iridescence resulted in an overall loss of conspicuousness and elaboration, such that species with more noniridescent patches have less colorful, more homogenous, and less conspicuous plumage. Because they have more noniridescent patches, females are generally less colorful and conspicuous than males. As expected, the impact of the loss of iridescence was stronger in species with derived melanosomes that can produce a broader range of iridescent colors (Maia et al. 2013).

Habitat and signaling environment had little influence on the overall patterns of plumage evolution in African starlings. Only chromaticity was slightly reduced in forest habitats relative to open habitats, suggesting that species in forested environments, where light is attenuated by foliage, have less saturated colors. These results are similar to those of Gomez and Théry (2004) but contrary to those of Marchetti (1993) and Shultz and Burns (2013), suggesting that any influence lighting environment has on plumage evolution in this clade is in the direction of increasing crypsis, not conspicuousness. Together with the overall patterns of iridescence and conspicuity loss, especially in females, this pattern suggests a weak but detectable influence of natural selection for crypsis as a selective force driving the macroevolutionary dynamics of plumage color in African starlings.

Rubenstein and Lovette (2009) showed that cooperative species of African starlings are less dimorphic and dichromatic than noncooperative species, because females in cooperative species are larger and more ornamented than in noncooperative species (a pattern also observed broadly accross Passerines,

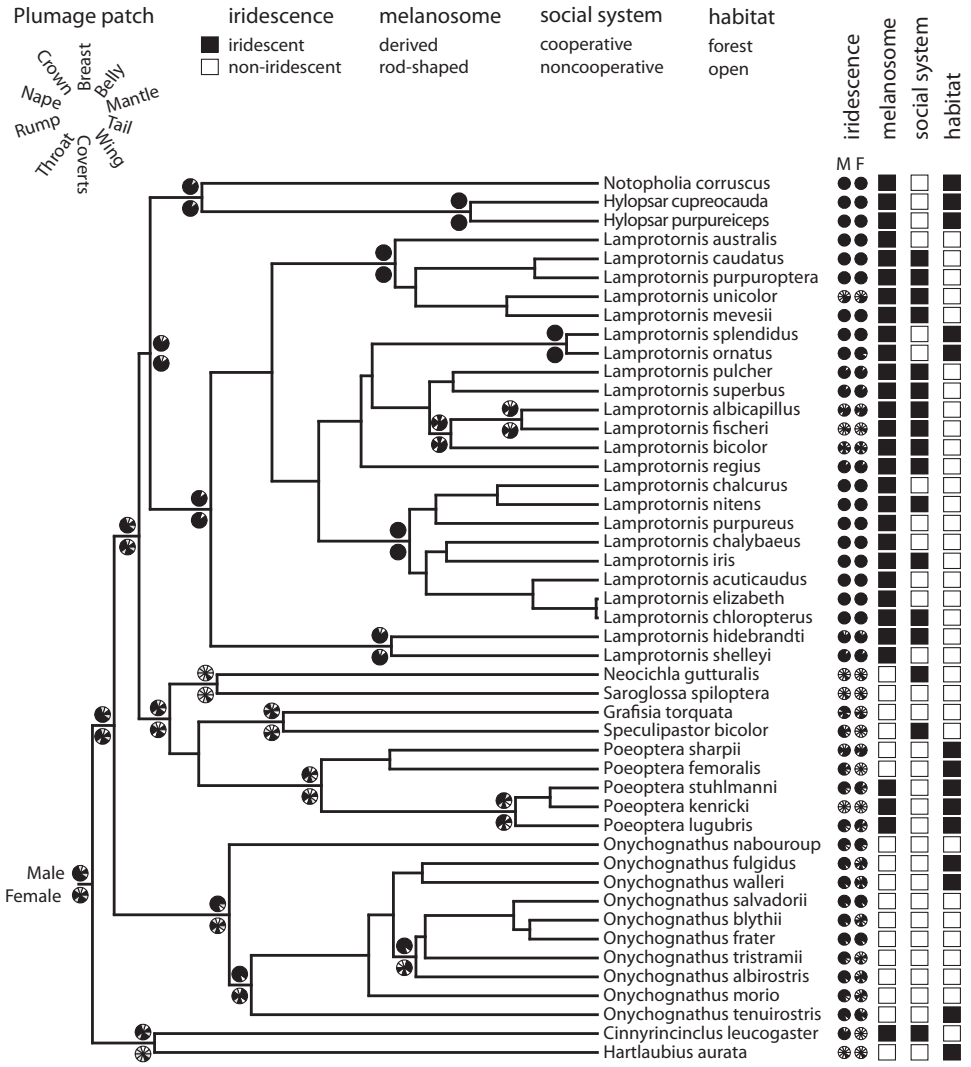

Figure 1. **Phylogeny of African starlings and distribution of traits considered in this study. Ancestral state reconstructions for plumage iridescence are shown at nodes where changes are inferred. Gray color indicates uncertain state (probability for either state at node lower than 0.8).**

Dale et al. 2015). Those results were based on visual assessment of dichromatism, without measuring reflectance or considering the avian visual system, and also included sexual differences in plumage ornaments unrelated to color (e.g., feather crests and tail elongation).

Interestingly, our results suggest that, although both males and females of cooperative species have more noniridescent patches, cooperative species females do not have more iridescent patches nor a more conspicuous and colorful plumage than noncooperative females. In fact, social system was not a good predictor of ornamentation and elaboration of plumage color in African starlings. However, we did still find that social system was indeed an important predictor of dichromatism in these species, with cooperative species being more monochromatic than noncooperative species. These results are consistent with those from Rubenstein and Lovette (2009), but highlight two key considerations when investigating plumage color evolution: (1) the importance of considering overall ornamentation as well as relative male–female ornamentation (dichromatism), as different aspects of this modular phenotype may be subject (and respond) to different selective pressures, and (2) the importance of considering color as a multidimensional trait within a perceptual colorspace. As a case in point, the similarity of plumage complexity in females of cooperative and noncooperative species suggests that the different plumage patches in these females have a similar spread within colorspace. However, the results for dichromatism suggest that, while this spread is similar, its *position in colorspace* is different. In other words, despite females being relatively duller and having a more homogenous plumage than males in both cooperative and noncooperative species, females of cooperative species

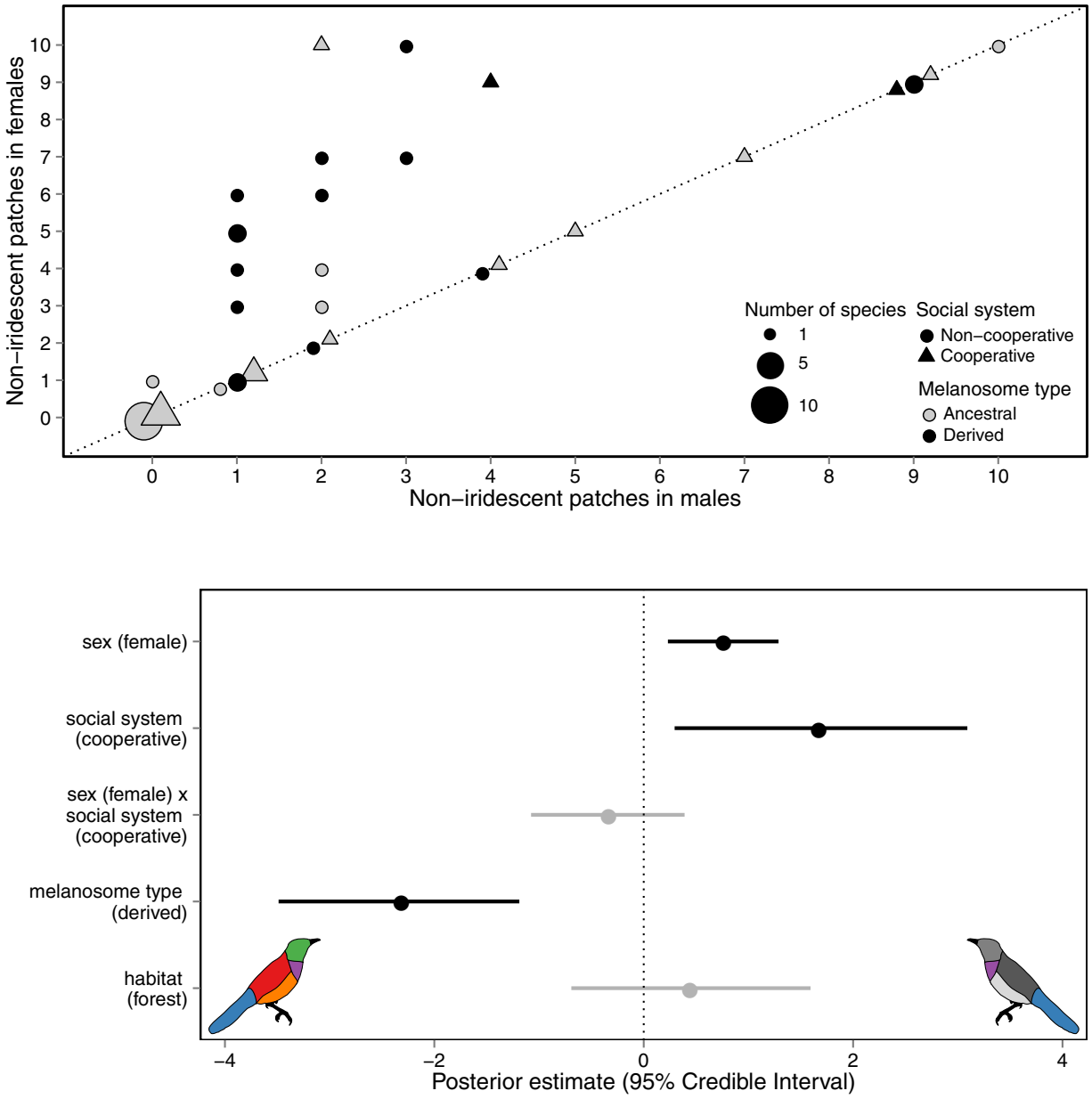

Figure 2. **The evolution of iridescence in African starlings. (A) Number of noniridescent patches in male and female African starling species. Overlapping points are jittered for clarity. (B) Estimates and 95% credible intervals for the effect of the considered predictors on the number of noniridescent patches of African starling species. Gray estimates have a 95% credible interval that overlaps zero. Starling pictographs illustrate the direction of effects on the number of iridescent patches (color online).**

have colors that are more similar to their male counterparts. Thus, despite an overall evolutionary trend leading females to be, in general, less ornamented and to lose iridescence, females from cooperative species retain a more male-like coloration, even if slightly duller than males.

From this perspective, we can begin to consider more critically how selection may act on female plumage evolution. Females from noncooperative species likely experience weaker sexual or social selection, evolving duller colors that are different from males due to natural selection (West-Eberhard 1983; Badyaev and Hill 2003). In cooperative species, however, the same signals used by males in mate choice and competition are likely to be co-opted and used by females, which also experience strong social competition, thus selecting for the maintenance of similar colors and ornaments as those found in males. The fact that females have similar but less ornamented or exaggerated signals than males is commonplace in cooperative mammals and birds (Young and Bennett 2013), and likely results from sexual differences in the balance of natural and social selection pressures. For example, in the African starling clade, only females brood eggs

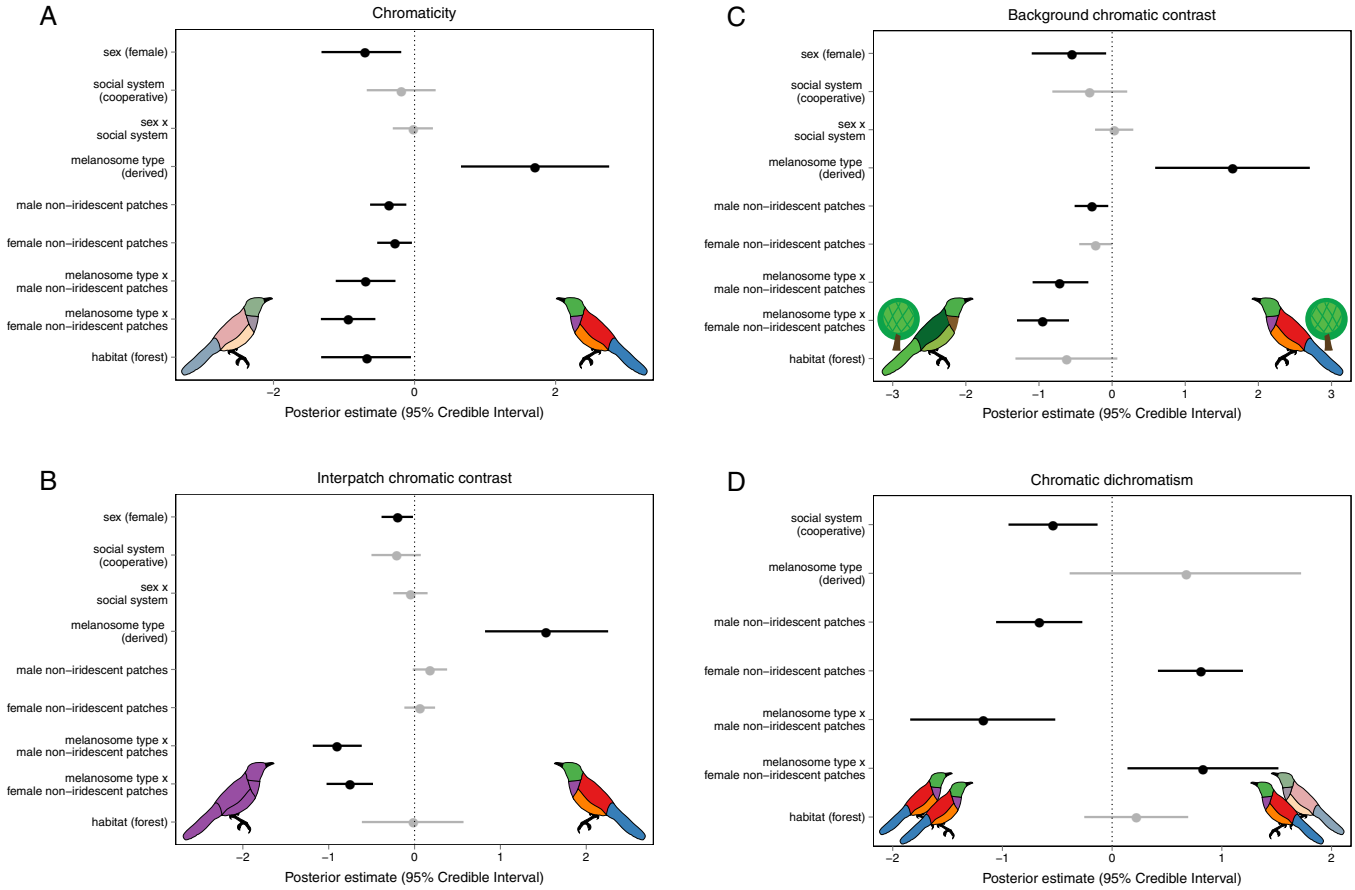

Figure 3. Estimates and 95% credible intervals for the effect of the considered predictors on chromatic components of African starling plumage color. Grey estimates have a 95% credible interval that overlaps zero. Starling pictographs illustrate the direction of effects on the response variables (color online).

and nestlings (Craig and Feare 2009). Therefore, even though cooperative females experience social selective pressures to maintain ornamental colors, there is also selection for reduced conspicuousness, resulting in colors that are similar, but duller, than their male counterparts. Females from noncooperative species, on the other hand, have equally dull but also more different colors than males in the absence of similar social selection pressures. Thus, in a multivariate colorspace, it is clear that similar levels of dullness and inconspicuousness can still produce different levels of dichromatism. Ultimately, these results also likely explain why we do not see complete role reversal in signal intensity in cooperatively breeding species (Young and Bennett 2013).

Many different aspects, from territory and resource competition to access to mates, are likely to influence these patterns and regulate the strength of social competition (and signal evolution) in females (Lyon and Montgomerie 2012). Though patterns are likely variable across species, studies in superb starlings suggest that males and females exhibit similar Bateman gradients, suggesting that both sexes are under strong sexual selection (Apakupakul and Rubenstein 2015). On the other hand, in this species males tend to be territorial and philopatric, whereas females tend to disperse, suggesting competition arising from territoriality is likely to be more pronounced in males than in females. However, another ornament (song) in this species has been shown to be associated with both sexual selection through mate attraction and dominance rank (Keen et al. 2016), suggesting that different factors involved in social selection are likely complex and interact.

Mechanisms of color production most strongly and consistently predicted color evolution trends. Derived melanosomes produced overall plumage that was more chromatic, had more variable and heterogenous patterns, and was more chromatically conspicuous than species with ancestral melanosomes. Gains and losses of iridescence also affected the measured variables, with overall ornamentation and complexity diminishing as the number of non-iridescent plumage patches increased. These effects were also consistently stronger in species with derived melanosomes, which produce colors that evolve faster and are overall brighter and more saturated (Maia et al. 2013). Thus, the loss of iridescence has a stronger effect because the bright and saturated iridescent colors these melanosomes produce are replaced by whites,

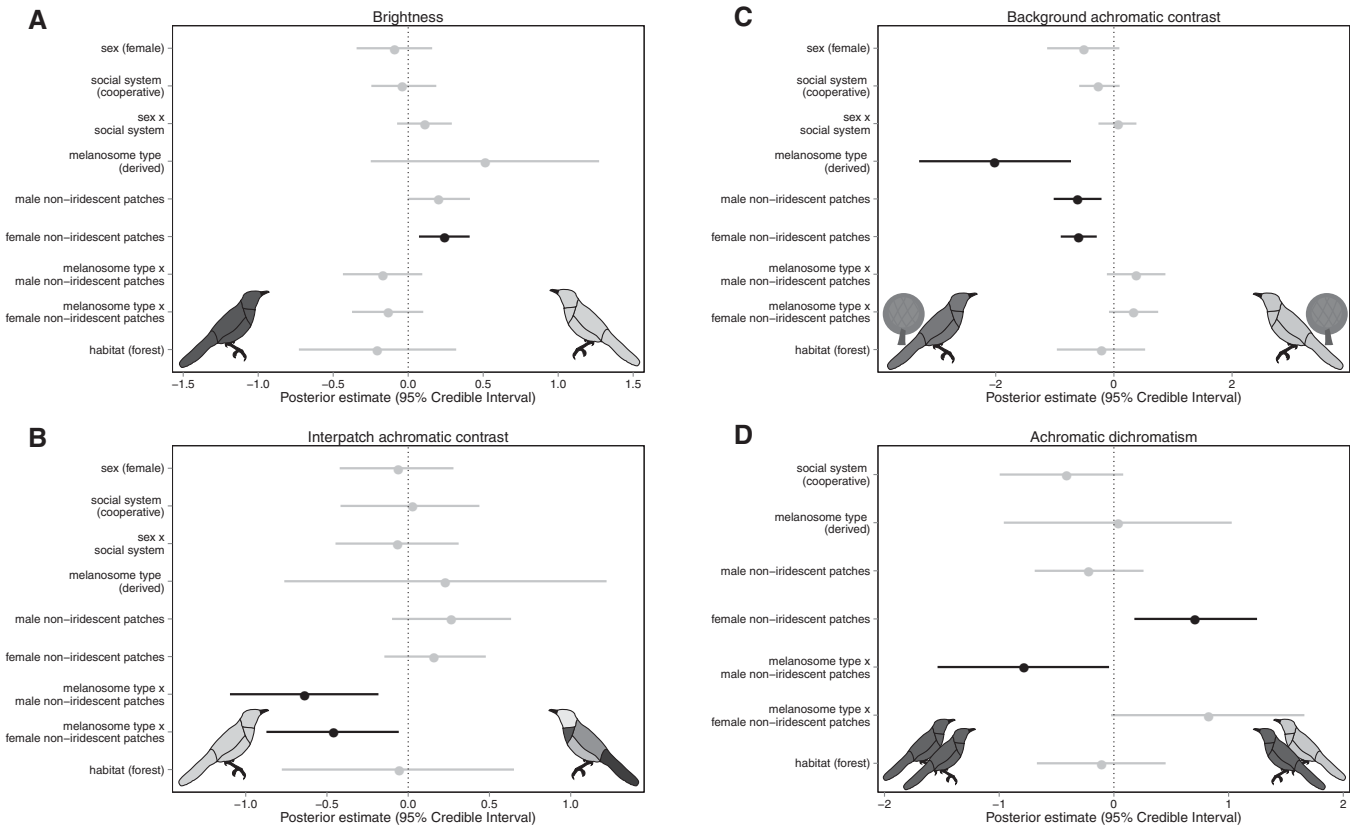

Figure 4. Estimates and 95% credible intervals for the effect of the considered predictors on achromatic components of African starling plumage color. Gray estimates have a 95% credible interval that overlaps zero. Starling pictographs illustrate the direction of effects on the response variables.

browns, and blacks. Having a more labile template to produce a broader range of colors likely allows the evolution of more complex within-plumage color patterns without need for the loss of iridescence or the origin of novel color-producing mechanisms, which would necessitate an evolutionary increase in modularity and independence of patches across a bird's body (Price and Pavelka 1996). This is particularly interesting given that the loss of iridescence is rarer in species with derived melanosomes, suggesting that evolutionary pressures have maintained iridescence precisely in the clades that can more fully optimize the potential signaling role of these colors. This highlights the importance of considering ornamental traits as functional traits, accounting for both the roles that constraints and selective pressures have in shaping their evolution (Irschick et al. 2013).

The higher chromaticity and brilliance of the plumage of species with derived melanosomes also results in chromatically more conspicuous, yet achromatically less conspicuous, colors against the background. Achromatic visual signals usually function as long-distance signals, triggering the visual system's response to movement and outline contrast (Osorio et al. 1999), while chromatic signals commonly function in short-distance communication, allowing a finer examination of variation (Vorobyev and Osorio 1998; Vorobyev 2003). By minimizing the former while maximizing the latter, these derived melanosomes likely produce colors that are more inconspicuous against long-distance detection by predators, while providing a wide gamut of highly contrasting colors that can be closely inspected by a mate or competitor (Doucet et al. 2007).

While melanosome type had no direct influence on the evolution of dichromatism, loss of iridescence had a strong and sex-dependent impact: an increase in the number of noniridescent patches in males led to a reduction in chromatic dichromatism, whereas in females it led to an increase in both chromatic and achromatic dichromatism. Taken together with a female-biased loss of iridescence in this clade, these results suggest that iridescence itself, more than the iridescent colors being expressed, plays a major role in sex-specific coloration. These results further indicate that the sexual linkage in the expression of iridescence might be easier to break, evolutionarily and developmentally, than the iridescent color being produced. Structural colors in feathers seem to be produced by the self-assembly of constituent parts during feather development (Dufresne et al. 2009; Prum et al. 2009; Maia et al. 2012). In the case of iridescent colors, this suggests that controlling the expression of the "parts" (i.e., the amount of

keratin and melanosomes, and their deposition in barbules during development) might be more labile than the more fine-tuned elements of feather development (i.e., the timing and cellular conditions) responsible for the lattice properties of nanostructural organization (Maia et al. 2012). In the case of derived melanosomes, which are modified either within melanocytes before being transferred to developing barbules (Durrer and Villiger 1967) or within developing barbules (Shawkey et al. 2015), this also suggests a strong sexual linkage of the cellular machinery responsible for the properties of these melanosomes. Developmentally, juveniles of many species of African starlings have duller yet still iridescent plumage, and females will show male-like iridescent plumage as juveniles, losing iridescence in specific body parts (e.g., the non-iridescent head plumage in many female *Onychognathus* species) as they become adults (Craig and Feare 2009). This might suggest that oestrogen-specific superimposition of the neutral or default iridescent state of plumage development is responsible for the loss of iridescence in these species (Owens and Short 1995), and the evolutionary loss of iridescence might be linked to the evolution of these sex-specific hormonal profiles.

When variables associated with color production were not considered in our models, the significance of some of the variables were changed. In particular, the effect of social system became significant over several chromatic variables, and lost its effect on dichromatism. Given that melanosome type is not associated with social system (Maia et al. 2013), these differents are likely due to the relationship between social system and the number of non-iridescent patches that species display. These results highlight the importance of considering the effects of both potential selective forces and constraints on the expression and variability of phenotypes, since confounding effects might lead to overlooking important patterns.

To our knowledge, this study represents the first attempt at combining physiological (color-producing), ecological (habitat lighting), and behavioral (social system) attributes in a comparative framework to understand the evolution of plumage elaboration, complexity, and dichromatism. While the patterns we observed are complex and variable, some overall trends emerge: in African starlings, color-producing mechanisms, as well as the female-biased loss of iridescence, strongly and consistently affect plumage elaboration and complexity. By contrast, selective pressures deriving from either social system or habitat openness had little effect on overall ornamentation. This is consistent with, and helps explain, the previously reported effect of these color-producing mechanisms on diversification (Maia et al. 2013). On the other hand, dichromatism is mostly influenced by social system, as has been shown previously in this group (Rubenstein and Lovette 2009). However, the difference in the factors influencing ornamentation and dichromatism contrasts with previous studies (Bleiweiss 1997; Doucet et al. 2007). Our results are also consistent with previous suggestions that losses in female ornamentation, rather than gains of male elaboration, are responsible for the evolution of dichromatism in birds (Burns 1998; Badyaev and Hill 2003; Dale et al. 2015). Thus, the evolution of conflict among females resulting from the social system and the patterns of reproductive skew in both sexes (Rubenstein 2012; Tobias et al. 2012) may play a more important and underappreciated role in the evolution of dichromatism (West-Eberhard 1983; Rubenstein and Lovette 2009) than, for example, levels of extra-pair paternity and the strength of sexual selection in males. This may help explain the inconsistent results from comparative studies using sexual dichromatism as a proxy for the intensity of sexual selection in males (reviewed in Kraaijeveld et al. 2011). Moreover, our work highlights the importance of understanding the factors affecting the evolution of ornamentation and dimorphism separately, and that combining mechanistic and selective attributes is critical to fully elucidate how sexual selection and social competition can shape patterns of ornamental evolution.

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DATA ARCHIVING

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Figure S1. Model selection results for the best fit tree transformation.

Figure S2. Estimates and 95% credible intervals for the e.ect of the considered predictors on chromatic components of African starling plumage color, when colorproducing variables are not considered. Grey estimates have a 95% credible interval that overlaps zero.

Figure S3. Estimates and 95% credible intervals for the e.ect of the considered predictors on chromatic components of African starling plumage color, when colorproducing variables are not considered.

Figure S4. Model selection results for the best fit tree transformation for models, when color-producing variables are not considered.