PNAS RESEARCH ARTICLE | EVOLUTION OPEN ACCESS

Evolutionary predictors of the specific colors of birds

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Edited by Jonathan Losos, Washington University in St. Louis, St. Louis, MO; received October 17, 2022; accepted June 23, 2023

Animal coloration is one of the most conspicuous aspects of human-perceived organismal diversity, yet also one of the least understood. In particular, explaining why species have specific colors (e.g., blue vs. red) has proven elusive. Here, we quantify for nearly all bird species, the proportion of the body covered by each of 12 human-visible color categories, and test whether existing theory can predict the direction of color evolution. The most common colors are black, white, gray and brown, while the rarest are green, blue, purple, and red. Males have more blue, purple, red, or black, whereas females have more yellow, brown, or gray. Sexual dichromatism is partly due to sexual selection favoring ornamental colors in males but not in females. However, sexual selection also correlated positively with brown in both sexes. Strong social selection favors red and black, colors used in agonistic signaling, with the strongest effects in females. Reduced predation risk selects against cryptic colors (e.g., brown) and favors specific ornamental colors (e.g., black). Nocturnality is mainly associated with brown. The effects of habitat use support the sensory drive theory for camouflage and signaling. Darker colors are more common in species living in wet and cold climates, matching ecogeographical rules. Our study unambiguously supports existing theories of color evolution across an entire class of vertebrates, but much variation remains unexplained.

sexual selection | camouflage | sensory drive | social selection | climate

Significance

Why are animals colored the way they are? This basic question is asked by the general public and by biologists alike, but comprehensive tests are lacking. Here, we compute for nearly all species of birds the proportion of the body covered by different color categories and combine this with a large dataset of social selection, life-history, and environmental predictors to establish which of them correlate with the prevalence of each color type. Our results identify multiple drivers associated with the evolution of different colors and provide support for several existing adaptive explanations. However, our study also shows strong phylogenetic dependence and highlights large amounts of unexplained variation.

Why are blue tits blue, robins red, and ravens black? More generally, why is any bird the color that it is? Despite these basic "children's questions" (1) having been asked for a long time, evolutionary biologists still struggle to answer them (1), and comprehensive macroevolutionary tests of existing theories about color evolution (Table 1) are lacking. This deficit stands in strong contrast to the substantial advances in understanding why males and females differ in color (evolution of sexual dichromatism) and why some species display more conspicuous, elaborate, or diverse colors than others (2–5).

The most likely reason for this difference in understanding is that it is easier to compute indices of sexual dichromatism, color elaboration, or color diversity, than it is to quantify the multivariate nature of specific colors themselves. Colors vary along multiple dimensions, such as hue (i.e., the tint), saturation (i.e., the richness), and lightness (i.e., how dark or light a color is). In addition, most species show several colors that cover varying extents of their bodies. Comparative analyses of multidimensional phenotypes are computationally demanding and particularly challenging for large datasets. Indeed, such analyses are typically restricted to smaller clades (6). Alternatively, variation in colors across multiple patches has been summarized by computing the overall average color, effectively reducing the dimensionality of the data (7–11) and converging variation toward the mean. This approach misrepresents species that have many different colors (Fig. 1), and does not allow resolving which results apply to putative conspicuous colors and which ones to putative cryptic colors.

Here, we address this issue using a pragmatic approach. We a priori determine a set of different color categories and quantify, for nearly all of the ~10,000 species of birds of the world, the proportion of the body (as depicted in the book plates) covered by each color category. To do this, we extracted color information [Red, Green, and Blue (RGB) values for each pixel] from the plates (mean ± SD: 5,897 ± 3,123 pixels per image, not scaled by species size) of the Handbook of the Birds of the World (available online at ref. 12). These plates are the most authoritative source of images for all species of birds, and have been used successfully for similar work (2, 8, 9). All pixels were converted into the CIELAB visual space (13), which has two chromatic dimensions (a, b, Fig. 1*A*) and one achromatic dimension (L or lightness, Fig. 1*A*). This visual space is perceptually uniform for humans, but does not include the near ultraviolet range, which birds can perceive (14) (for more details see methods and *SI Appendix, Text S1*). Thus, our study does not provide a complete picture of all the colors perceived by birds. However, it is unlikely that this impacts the overall results. First, our tests (*SI Appendix, Text S2*) and previous work (2, 8, 9, 15, 16) reveal robust correlations

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Author contributions: K.D., M.V., J.D., and B.K. designed research; K.D., M.V., C.M., J.D., and B.K. performed research; M.V., C.M., J.D., and B.K. contributed new reagents/analytic tools; K.D. and M.V. analyzed data; and K.D., J.D., and B.K. wrote the paper.

The authors declare no competing interest.

This article is a PNAS Direct Submission.

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This article contains supporting information online at https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2217692120/-/DCSupplemental.

Published August 14, 2023.

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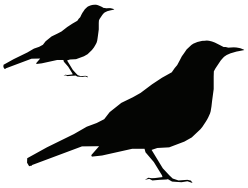
Table 1. Factors that influence colour evolution in birds. We list the main potential factors for which clear predictions or evidence exists regarding either the direction of colour evolution (e.g. red vs blue, dark vs. light) or level of colour elaboration (conspicuous vs. cryptic). When known, we mention the possible process behind the association in parentheses; when not known, we indicate the published empirical data the association is based on. Note that some predictions may be contradictory, and that some have been derived from empirical studies at more limited taxonomic scales. We *a priori* decided to test predictions as previously reported in the literature, independent of whether we consider them likely. A dark purple tick on the right indicates that the prediction was generally supported by our data and a yellow cross indicates lack of support

Category	Predictions	Process/Mechanism	
Sexual Selection	• Sexual selection leads to color exaggeration in different directions, but does not favor the evolution of specific types of colors (17)	• Fisherian sexual selection, arbitrary signals	✓
	• Sexual selection favors the evolution of carotenoid-based colors rich in longer wavelengths (red) (6)	• Honest signalling	✗
	• Sexual selection on males selects for more elaborate male colors and even more strongly for less elaborate female colors (2)	• Balance between signal efficacy and predation risk	✓
	• Intense sexual selection on males selects for lighter male colours rich in short wavelengths (lekking species) or darker male colours (polygynous species) (empirical) (7)	• Maximize conspicuousness (signaling)	✓
	• Males have darker colors than females (18)	• ? (empirical)	✓
	• Gray is more common in males than in females and positively associated with sexual dichromatism (19)	• ? (empirical)	✗
Social Selection	• Year-round territoriality selects for elaborate colors in males and females (2)	• Colors used as agonistic signals to settle competition over access to resources	✓
	• Cooperative breeding selects for elaborate colors, especially in females (2, 20)	• Colors used to signal dominance and status	✓
	• Agonistic signals used to settle territorial disputes and access to other resources are more likely to be red (21, 22)	• Preexisting biases, honest signaling	✓
	• Signals of dominance more likely to be black due to the deposition of melanin pigments (23)	• Pleiotropic effects	✓
Body size 	• Larger species more likely to have elaborate colors (2)	• Differential risk of predation	✓
	• Smaller species are more likely to have elaborate colors (24), mainly carotenoid-based colors (yellow to red) (24)	• Mechanistic, higher levels of carotenoid pigments in smaller species (25)	✗
	• Larger species have shortwave-rich plumage (UV/blue/green) and smaller species have long-wave rich plumage (red)(empirical) (7)	• ? (empirical)	✗
	• Larger species are more likely to be darker and have blue or red plumage colors (8)	• ? (empirical)	✓
Nest safety	• Safer nest locations (higher above the ground or in cavities) select for more conspicuous colors and less safe nest locations select for cryptic colors, especially in the incubating sex (typically the female) (26–28)	• Differential risk of predation/visibility	✓
	• Species nesting in closed nests (dome, cavity) are more conspicuously colored than species nesting in open nests (29)	• Differential risk of predation/visibility	✓
	• Cavity nesters have darker colors (7)	• ? (empirical)	✓
	• Longwave-rich plumage (yellow/brown/red) is more common in species that breed on the ground compared to species that breed in trees (7)	• Camouflage	✓
	• Gray plumage is more common in species with exposed nests (19)	• Camouflage/differential predation risk	✗
Habitat use	• Darker colors and colors rich in longer wavelengths (e.g., red) are more common in more vegetated habitats; and, within forests, more common in understory than canopy (30–32).	• Maximize crypsis (camouflage) and/or conspicuousness (signaling)	✓
	• Within tropical rainforests, violet/blue, green, and yellow plumage colors are more common in canopy, whereas red, pink, and brown are more common in the understory (33)	• Maximize crypsis (camouflage) and/or conspicuousness (signaling)	✓
	• White patches are more common in closed environments (34)	• Maximize conspicuousness (signaling)	✗
	• Elaborate/conspicuous colors are more common in closed than open habitats (24, 35, 36)	• Lower predation risk	✓
	• Gray plumage is more common in open habitats (19)	• Maximize crypsis (camouflage)	✓
	• Less elaborate and chromatic colors are expected in forested/shaded environments (37)	• Lack of light constrains visual signaling	✗

(Continued)

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Table 1. (Continued)

Category	Predictions	Process/Mechanism	
Nocturnality	• Nocturnal species have darker colors (38)	• Maximize crypsis (camouflage)	✓
	• Nocturnal species have white patches (39)	• Maximize conspicuousness (signaling)	✗
	• Nocturnal species have less chromatic colors (39)	• Lack of light constrains color vision	✓
Climate	• Darker colors are more common in wetter, more vegetated regions (Gloger's rule) (10)	• Maximize crypsis (camouflage), parasite resistance	✓
	• Darker colors are more common in colder regions (thermal melanism hypothesis) (10)	• Thermoregulation	✓
	• White is more common in colder regions (40)	• Maximize crypsis (camouflage) against snow	✗
	• More elaborate colors occur in warmer regions (40)	• ? (empirical)	✗
Migration	• Migratory species have lighter plumage (7, 41)	• Thermoregulation	✓
	• Migratory species have long-wave rich plumage (red/orange) (7)	• ? (empirical)	✗
	• Migratory species have more elaborate plumage colors than nonmigratory species (2, 42)	• More intense sexual selection in migratory species	✗
	• Females in migratory species have less elaborate colors than those in nonmigratory species (43)	• Less intense social selection on females	✗
Diet	• Carotenoid-based colors rich in longer wavelengths (red, yellow) are more likely to evolve in species with carotenoid-rich diets (e.g. frugivorous/nectarivorous) (44)	• Mechanistic (pigment availability)	✗
Developmental mode	• Species with altricial young have darker plumage, and long-wave rich plumage (orange/red) (7)	• ? (empirical)	✗

between color data obtained from book plates and color data derived from reflectance spectrometry using models of avian color vision. Second, the nature of our study requires assessing the effects of numerous different types of selective agents that "perceive" colors in different ways (e.g., avian, reptilian, and mammalian predators, vertebrate and invertebrate prey, avian conspecifics, thermoregulation, mechanical abrasion, and parasites), hence no single visual system can provide a one-size-fits-all solution. Third, recent work suggests that despite differences between organisms in visual sensitivities, many colors are perceived as similarly vivid or conspicuous by different types of visual systems (45) and human color classification provides good approximations (15, 16). Hence, we consider it unlikely that differences between human and avian color perception would render the main results of this study invalid. Given the scale of this study, using book plates and human-based visual color space represents an effective compromise that balances taxonomic coverage with detail, and provides a strong basis for future work using more sophisticated approaches.

For each species and sex, we computed the proportion of the body (as depicted in book plates) covered by a set of discrete color categories, defined by splitting CIELAB color space into 12 sections (see *Methods* and *SI Appendix*, Fig. S1). As a result, we obtained—for males and females of each species –12 variables that indicated the proportion of the body covered by each color category (Fig. 1*C*). This classification yielded, in addition to black and white, four color categories representative of putative ornamental colors (blue, red, purple, and yellow) and six color categories representative of putative cryptic colors (green, light brown, dark brown, light gray, dark gray, and rufous). Because the number of color categories and the exact position of the limits defining the color categories in color space are arbitrary, we explored whether alternative limits between categories and different categories change the main conclusions, and they do not (*SI Appendix*, *Text S3* and Figs. S2–S5).

Across all birds, dark gray and black were the most common colors, followed by light gray, white, light brown, and dark brown (Fig. 1*C*). The other colors were much rarer: they generally covered less than 1% of the image and were absent in many species (Fig. 1*C*). Prevalence values for each color category varied between 0 (complete absence) and almost 1 (no species scored 100% for any single color category). We used each color variable as response variable, and modeled it using a zero inflated beta distribution (46). Such models allow to quantify simultaneously the effect of predictors on the extent of the plumage covered by a particular color, and on the presence/absence of the (rarer) colors. Thus, we quantified the effects of a comprehensive set of predictors that cover most adaptive hypotheses of color evolution, as well as previously detected but unexplained empirical patterns (Table 1). After matching color data with predictor variables and phylogenetic information (47), which accounted for phylogenetic relatedness using a phylogenetic covariance matrix as a random effect, our main analyses encompassed 9,186 species (see *Methods* for more details).

Color evolution is thought to be shaped by two largely opposing forces: selection favoring conspicuous colors that function as signals [mainly in the context of social interactions including male–male competition and mate choice, but also signaling to indicate unprofitability to predators (28)], and selection favoring cryptic colors that function as camouflage (mainly to avoid detection by predators or prey). However, which specific color will be selected either for signaling or for camouflage is harder to predict. Theory suggests that the evolution of specific signaling or cryptic colors depends on

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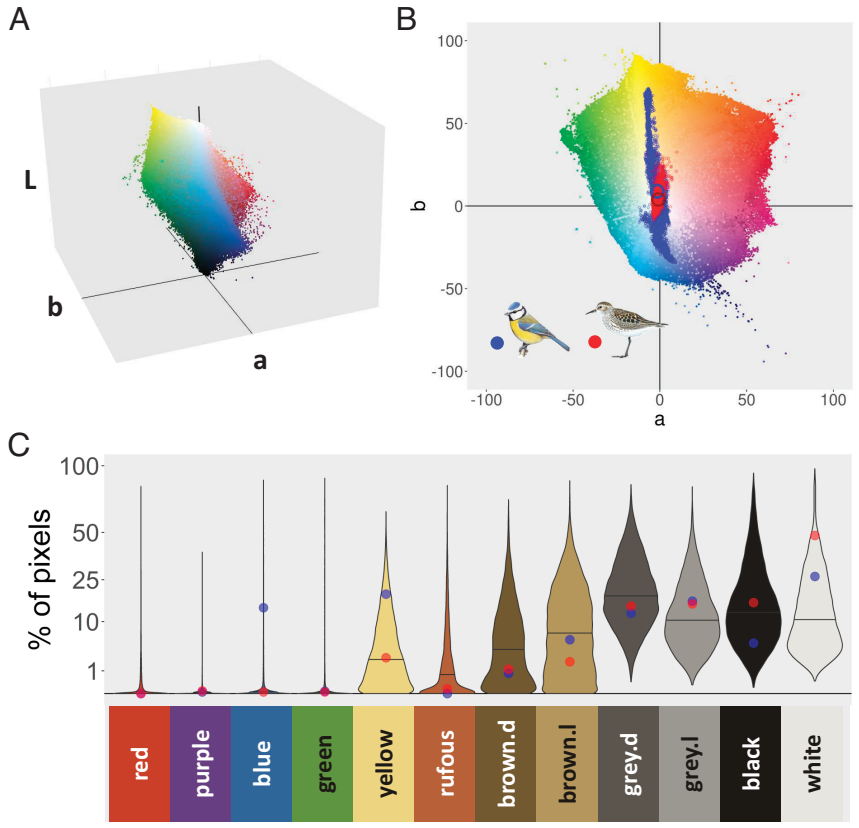

Fig. 1. Computing color variables. (*A*) We used handbook plates to quantify color variation in human-visible CIELAB color space, which has one achromatic axis of variation (L) and two chromatic axes (a, b). In (*B*), we show the same variation in 2-dimensions for ease of visualization (a and b chromatic coordinates, ignoring variation in L, the equivalent of looking at (*A*) from above), and overlay the position of the colors of two species (blue symbols: blue tit, *Cyanistes caeruleus*; red symbols: white-rumped sandpiper, *Calidris fuscicollis*), chosen because their average color coordinates (large blue and red circles in the center) are similar despite having very different colors. Thus, computing the overall L, a, and b averages obscures the important differences in color between these species. Instead, we computed the proportion of the pixels in each image that fall within specific sections of color space (*SI Appendix*, Fig. S1) to obtain 12 color variables per species. These values are depicted in (*C*) for both species (blue and red dots), overlaid on violin plots that represent the distribution of each color variable across all images (horizontal line is the median, and fill color the average color of each category). Thus, despite similar overall average colors, blue tits score higher in blue and yellow, while white-rumped sandpipers score higher for black and white. Bird figures ©Lynx Edicions / Cornell Lab of Ornithology/Birds of the World. Illustrated by Hilary Burn and Francesc Jutglar.

the modulating effects of an animal's surroundings. Indeed, variation in the colors of natural backgrounds and the properties of the light available in the environment strongly influence which colors are conspicuous or cryptic (Table 1). Furthermore, other factors such as thermoregulation, parasites, and the availability of specific pigments in the diet can play a role in the evolution of colors (Table 1). We present and discuss our results within this general framework, after first describing how the sexes differ in color.

How do Females and Males Differ in Color?

To quantify sexual dichromatism and color prevalence across species while accounting for phylogenetic relatedness, we ran for each color category a separate model including only sex as fixed effect. The results indicate that males and females differ in most color variables: Males had higher values of blue, purple, red, and black and to a lesser extent also of green and rufous, whereas females had higher values for light brown, dark brown, light gray, and yellow (Fig. 2 and Dataset S1). Our results quantitatively confirm the observation that black, red, and blue occur more often in males (2), and are consistent with the well-established, general pattern in birds that males show more ornamental colors, and females are more cryptically colored. The main exceptions to this pattern are the higher prevalence of yellow among females and the higher prevalence of green among males. These effects may be due to categorizing yellow and green too broadly, mixing putatively conspicuous and cryptic colors. To evaluate whether this explained the observed patterns of sexual dichromatism, we split yellow and green into high- and low-saturation subcategories and reran the analyses. We expected high-saturation colors to be more common in males and low-saturation colors to be more common in females, but this was not the case. Both high- and low-saturation greens were still more prevalent in males than in females (*SI Appendix, Text S3*), and low-saturation yellows were more prevalent in females, but high-saturation yellows were equally common in both sexes (*SI Appendix, Text S3*). Higher overall prevalence of yellow in females agrees with recent findings showing that yellow carotenoid–based plumage is more common in female than in male passerine birds(48). In general, color prevalence after controlling for phylogenetic relatedness broadly matched the results from the raw data (compare Figs. 1*C* and 2*A*), even though all color variables showed a strong phylogenetic signal (phylogenetic heritability, equivalent to Pagel's lambda, >0.8, Dataset S2). Next, we fit similar models accounting for phylogenetic relatedness, but including all predictor variables to assess their sex-specific effects on each color category.

Sexual and Social Selection Affect Color Evolution in Different Ways

Classically, sexual dichromatism has been attributed to either stronger sexual selection for ornamental colors in males, or stronger natural selection for crypsis in females (2). Our phylogenetically controlled analyses including all predictor variables indicate that the strength of sexual selection on males, estimated by the degree of polygyny, correlates more strongly with variation in female colors. Females in highly polygynous species are less likely to show black and red, and more likely to have putative cryptic colors such as light and dark brown (Fig. 3). In contrast, in polygynous species males are more likely to show the ornamental colors blue, purple, and black, and less likely to be gray, but these effects are weaker (Fig. 3). One possible explanation for a stronger correlation with female colors is that there may be fewer ways to be cryptic than to be conspicuous. We also note that our estimate of sexual selection on males is incomplete, because aspects of the genetic mating system [extra-pair paternity (49)] are not included.

Intriguingly, polygyny is positively associated with dark brown coloration in both males and females (Fig. 3). This is unexpected, but agrees with previous findings (50) showing that polygynous lekking birds can either be sexually dichromatic with colorful

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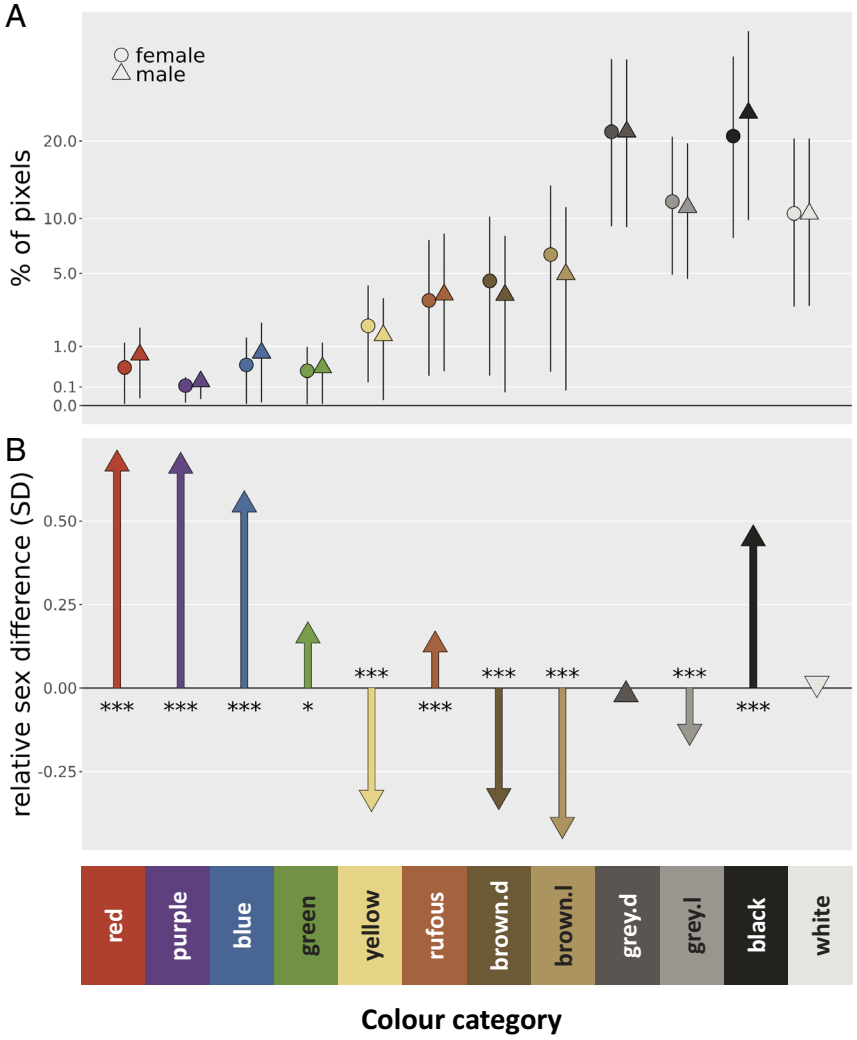

Fig. 2. Sexual dichromatism across different color categories. (*A*) Predicted means from the Bayesian phylogenetic mixed models for males and females and their 95% credible intervals (CI) (Dataset S1). (*B*) Mean standardized sexual dichromatism [males-females/(joint SD)], where positive values indicate higher male and negative values higher female values. $*P < 0.05$, $**P < 0.01$, $***P < 0.001$. Fill colors represent the average color of each category.

males and cryptic females (e.g., manakins or birds of paradise) or sexually monochromatic with cryptically colored males and females (e.g., many shorebird species). It has been suggested that in cryptically colored polygynous species, sexual selection acts on other traits such as body size, displays, and vocalizations (51), which may indicate the existence of trade-offs between visual, behavioral, and acoustic elaboration across species. Alternatively, the positive effect of polygyny on dark brown in males may be driven by the inclusion of some very dark browns, that might better fit in the black category. However, rerunning the model after excluding the darkest browns did not qualitatively change the result (although the *P*-value changed from $P = 0.038$ to $P = 0.059$, Datasets S3 and S4).

The strength of sexual selection on females, as estimated by the degree of social polyandry (results not illustrated, see Datasets S3 and S4), did not show statistically significant effects on color. However, the statistical power to detect such effects is smaller, because comparatively few species are polyandrous.

Social selection is broadly defined as selection driven by social interactions between conspecifics that lead to differential reproductive success (52), and hence includes sexual selection. However, nonsexual social selection also includes selection on signals that are related to dominance within social groups or competition over resources such as food or territories. We note that direct competition and fights over mates are an important component of classic sexual selection. Our estimate of the strength of sexual selection mainly emphasizes variance in reproductive success associated with the mating system and with intersexual selection (as a result of mate choice). It is therefore possible that the effects of intrasexual selection (e.g., male–male interactions) are partly captured by those of nonsexual social selection described below. Previous work showed that social selection can be an important driver of elaborate colors, particularly in females (2, 20). In species with year-round territoriality often both pair members defend the territory against intruders (53), which could select for visual signals in both sexes. Our analyses reveal that year-round territoriality is positively associated with black as well as colors rich in longwave-reflectance (red and rufous), and negatively with light gray. However, all these effects were only significant in females (Fig. 3).

Competition between females is particularly prevalent in cooperatively breeding species (20). Our results suggest that cooperative breeders are more likely to be black or dark gray and less likely to be blue or to have putative cryptic colors (brown through green) (Fig. 3). This supports the hypothesis that cooperative breeding favors the evolution of elaborate colors (particularly black) or selects against cryptic colors in both sexes (Table 1). It is noteworthy that in many species, black and red colors have been linked to agonistic signaling and are often considered badges of status and dominance (23, 54). The reasons for such associations remain unclear but could involve preexisting sensory biases (22) or mechanistic links such as those between steroid hormones and melanin or carotenoid deposition (55, 56). Regardless of the mechanisms,

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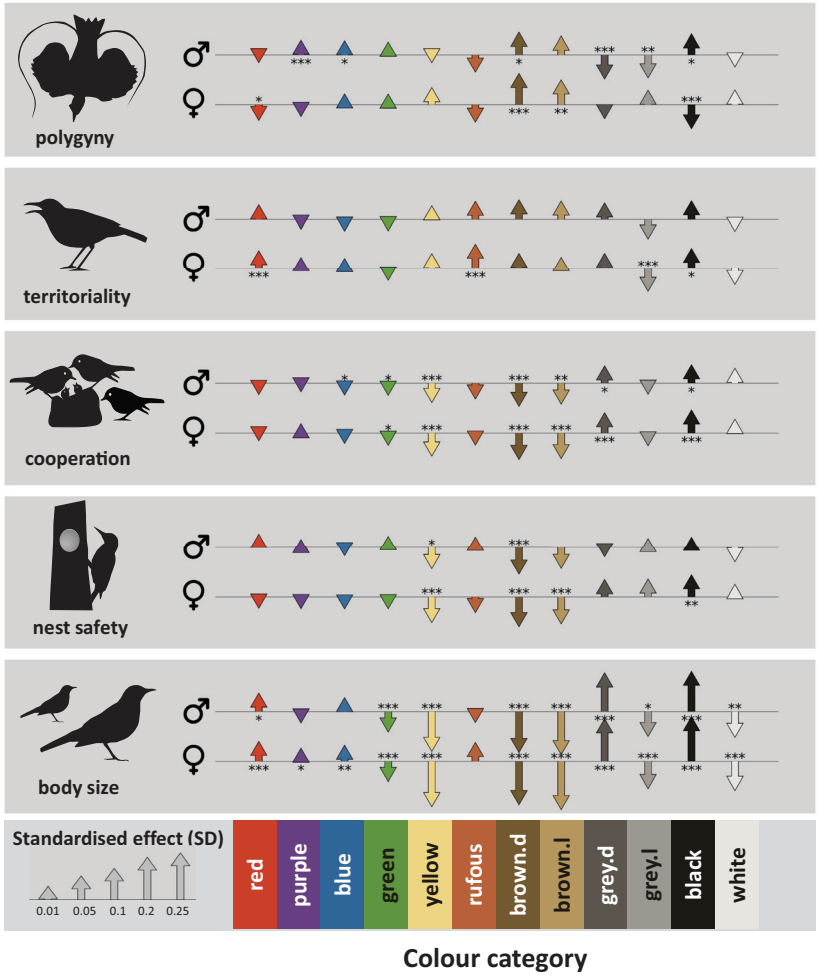

Fig. 3. Effects of sexual and social selection and differential risk of predation (nest safety and body mass) on color categories. Arrows (for males and females separately) depict standardized predicted effects indicating the mean change in color (expressed in SD units) caused by a change in 1 SD of the predictor variable, as derived from Bayesian phylogenetic mixed models (full model results in Dataset S3, standardized predicted effects, PD values, *P*-values, and 95% CIs in Dataset S4). For rarer colors, the predicted effects combine the effects of presence/absence and of the proportion of the body covered by the specific color category (Dataset S3). Arrows pointing up and down indicate positive effects and negative effects, respectively. The length of the arrow is proportional to the strength of the effect as indicated on the legend (note sqrt-scale of arrow lengths for visual purposes). Asterisks denote statistically significant effects where $*P < 0.05$, $**P < 0.01$, and $***P < 0.001$. Fill colors represent the average color of each category.

our results clearly suggest that social selection favors specific signaling colors.

Variation in Predation Risk Shapes the Balance between Cryptic and Signaling Colors

Variation between species in their relative predation risk may constrain the evolution of socially and sexually selected elaborated colors, because they increase vulnerability to predators. On the other hand, safer nesting sites are expected to reduce selection for crypsis, especially in the sex that spends more time in the nest to incubate the eggs [i.e., females (28)]. Our results tend to support this prediction: Birds nesting in safer locations (e.g., cavities) are less likely to be colored light brown, dark brown, or yellow, and these effects are stronger in females (Fig. 3). Safe nesting locations are also positively associated with black in females. The reason behind this pattern remains unclear, but it matches previous empirical results (7), which revealed that cavity nesting species were darker colored. Intense competition for limited nesting cavities (57) may favor dark, melanin-based plumage patches that could function as socially selected signals of dominance (see above).

Predation risk is generally lower in larger species (2, 28, 58). Variation in body mass was by far the most important predictor of color, with pervasive effects across most color categories. Larger species were more likely to be black, dark gray, blue, purple, and red, whereas smaller species were more often yellow, light gray, green, light brown, dark brown, and white (Fig. 3). The only putative signaling color favored in smaller species was yellow, but the yellow category also included many unsaturated colors with a yellow wash, which can be cryptic against a background of green leaves, and even more so against leaf litter (59). Indeed, if we split yellow into high- and low-saturation categories the effect of body mass is much stronger on low-saturation than on high-saturation yellow (although the sign of the effect is the same, Datasets S3 and S4). Previous work concluded that larger species have more elaborate colors across Nearctic/Palearctic birds (28) and in passerines (2). Our results show that this is a general pattern across all birds and that the effects are not restricted to specific colors or bird clades. It is noteworthy that smaller species also tend to be more streaked and barred compared to larger species that are more likely to display blocked or bold color patterns (60).

Environmental Variation Influences Both Cryptic and Conspicuous Color Evolution

Habitat structure has often been hypothesized to play a central role in the evolution of colors, both in relation to camouflage (putatively cryptic colors) or signaling (putatively conspicuous colors; Table 1). The structure of the vegetation strongly influences the spectral composition of ambient light and background coloration, which in turn determines which specific colors will be cryptic or conspicuous in a particular environment (30).

For putative cryptic colors, our results suggest that open, less vegetated habitats select for light colors such as light gray, and against green, dark brown, dark gray, or rufous, which are more

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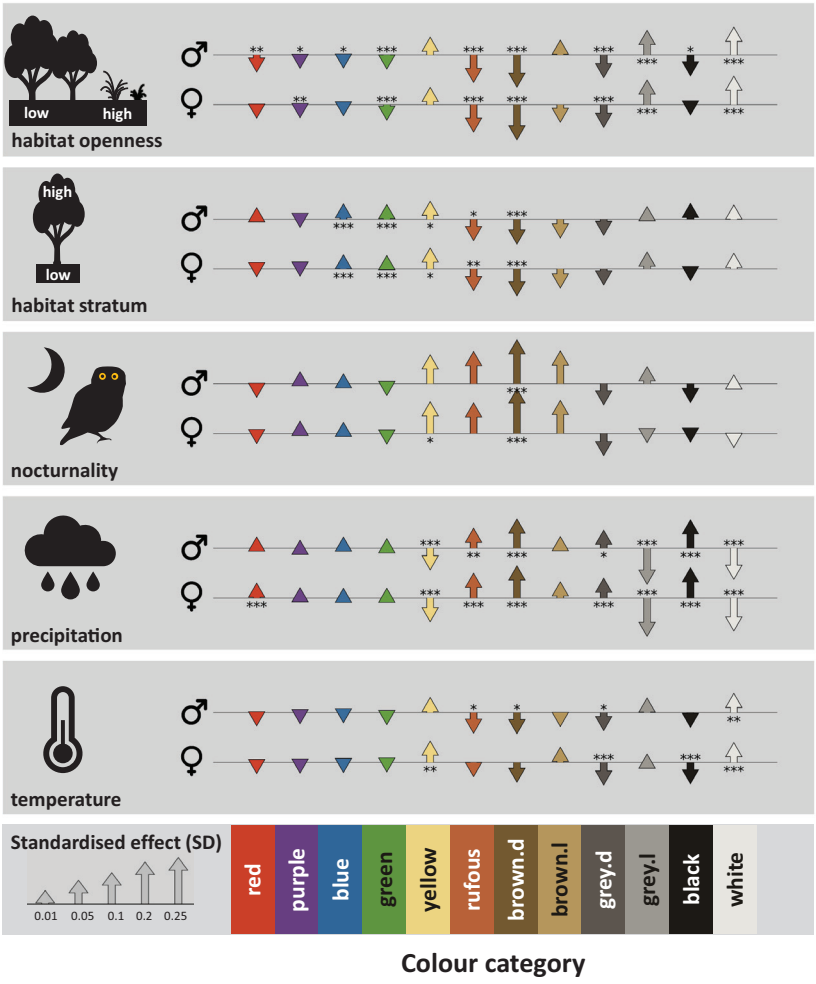

Fig. 4. Effects of habitat use and climatic variables on color categories. See Fig. 3 legend for details.

common in forested environments (Fig. 4). Similarly, living in higher vegetation strata (e.g., forest canopy) selects for green and yellow colors (which would match the color of the leaves) and against rufous or brown colors, which are more common in species living in lower strata (where backgrounds are mainly brown, e.g., leaf litter, soil, trunks). These results confirm that the common colors in each habitat are broadly those that match the prevailing backgrounds (61), and indicate that selection for camouflage is a key driver of bird coloration (Table 1).

For putative signaling colors, we found that open habitats are associated with white (Fig. 4), consistent with previous studies, which suggest that white functions as a long-range signal in such environments (32). White can also be a highly conspicuous signal in dark environments (34), but we found no evidence that selection has favored white in such habitats, possibly because it is too conspicuous to predators. Species that occur in habitats with closed vegetation are more often red, purple, blue, and also black (but only in males) (Fig. 4). Colors rich in long-wave reflectance (such as red) are expected to be more common in forests because they match the dominant wavelengths of the forest light environment, especially in the understory, and this renders them highly conspicuous (31, 33). The fact that red tends to be favored in more vegetated habitats supports this prediction (Fig. 4). However, against expectations, colors rich in short-wavelength reflectance (blue) were also more common in closed vegetation (Fig. 4). This apparent contradiction may be resolved by the fact that these colors are found largely at higher levels in the forest (Fig. 4) where the light environment (which is relatively rich in shorter wavelengths) renders them conspicuous visual signals (31–33, 62). Indeed, a recent study showed that plumage colors rich in even shorter wavelengths (near-UV) are most common in the forest canopy (63). More broadly, our results show that the prediction based on comparative analyses on African Starlings (37), that darker forested environments harbor less chromatic colors because light levels are too low, does not apply across all birds. On the contrary, the complex light environments of forests appear to provide fertile ground for the evolution of multiple different types of colors. In general, chromatic colors may be favored as signals in closed environments where they are viewed at shorter distances, whereas achromatic colors such as white may predominate in open environments where signaling takes place over greater distances.

While variation in habitat structure has a clear impact on the light environment a species experiences, the light quality is even more dramatically different for species that are active mainly during the night (64). Our analyses indicate that nocturnal species are much more likely to be dark brown, and to a lesser extent yellow (in females only; Fig. 5; note that this effect is more marked for low-saturation yellows, Datasets S3 and S4). This coloration likely has a camouflage function because many nocturnal birds rely on immobility and visual crypsis during the day (28). As a result, nocturnal birds may converge toward a mammal-like color palette (1). Our study suggests that nocturnality strongly constrains the evolution of conspicuous signaling colors in birds, and does not support the predicted (Table 1) higher incidence of white in nocturnal species (39), possibly because this would render them too conspicuous to predators. However, it is still possible that small patches [e.g., coverable badges (65)] could be used for signaling in nocturnal species.

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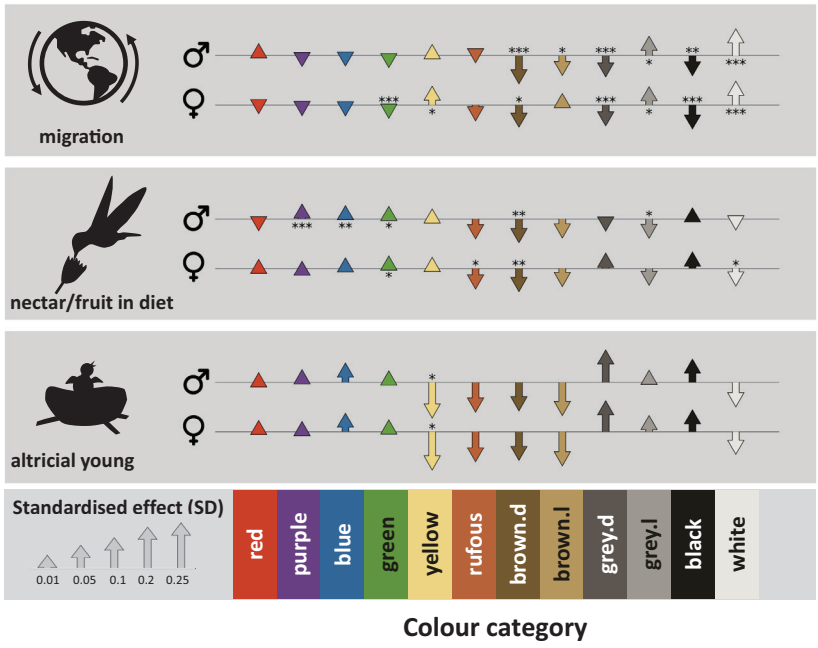

Fig. 5. Effects of other traits on color categories. See Fig. 3 legend for details.

Climate Effects Reflect Ecogeographical Rules of Color Evolution

The modern interpretation of Gloger's rule(10, 66) predicts darker colors in wet regions. Our analysis strongly supports Gloger's rule because we found that darker colors (black, dark gray, dark brown, and rufous) predominate in species living in more humid regions, whereas lighter colors (light gray, yellow, white) are more often found in species inhabiting drier places (Fig. 4). The most likely mechanism behind this effect is improved camouflage of darker colors in wetter regions, complementing the effect of vegetation openness, because higher precipitation leads to more dense and lush vegetation. However, camouflage may not be the only selection factor involved, as darker colors could also evolve in wetter environments because they protect against feather degradation through abrasion and microbial activity (66).

The thermal melanism hypothesis or Bogert's rule (10) contrasts with Gloger's rule in that it predicts lighter colored animals in warmer regions, because lighter coloration absorbs less solar radiation and hence can keep animals cooler. In our analysis, the effects of temperature were generally weaker than those of precipitation, but consistent with the idea that lighter colors (white, yellow) prevail in warmer environments, whereas darker colors (black, dark gray, dark brown, and rufous) are more common in colder regions (Fig. 4). Some dark birds that inhabit warm deserts, however, could avoid overheating by other means (67).

A Link between Migratory Behavior and Color

An association between migratory behavior and color ornamentation has long been hypothesized, in particular suggesting that migration has favored the evolution of ornamental colors in males and constrained their evolution in females (2, 42). The first prediction is based on the "good migrations" hypothesis (42), which posits that ornaments in migratory species are indicative of condition and the ability to withstand the costs of migration. The second prediction is based on the expectation that social selection in females will be less intense in migratory species, because it is predominantly the earlier-arriving sex (typically the male) that acquires and defends the territory (68). Thus, if neither social nor sexual selection favor ornamentation in females, conspicuous colors are often lost, as shown for New-world orioles (43) and passerine birds (2). However, we did not find support for either hypothesis, suggesting that they are not generally valid. Migratory species were more likely to be white or light gray and less likely to be black, dark gray, or brown (Fig. 5). Such a color palette may be a consequence of migratory birds being on average lighter colored than resident species (7, 41). This effect may reflect thermoregulation needs, because migrants are often exposed to strong solar radiation during migration, and being lighter colored could help prevent overheating (41). We found no evidence that migratory birds have colors rich in longer wavelengths, as suggested by previous empirical results (7).

How Does Diet Relate to Color?

The role of diet for the evolution of avian coloration has been intensely researched because diet determines the availability of specific pigments (i.e., red or yellow carotenoids) that are frequently used to color plumage. Hence, species with a carotenoid-rich diet, such as frugivorous or nectarivorous species, are expected to have more of the most common carotenoid-based colors red and yellow (44). Our analyses, however, do not support this prediction: The effects of diet on the occurrence of red and yellow were not statistically significant (Fig. 5). One potential explanation for this lack of an effect is that in many clades red or yellow colors can be produced by other pigments [e.g., psittacofulvins (69)] or through feather microstructure (70). Alternatively, if carotenoids are too abundant in the diet, they may not be limiting. In that case, carotenoid-based colors would not function as indicators of quality and hence may not have been favored by selection associated with honest signaling. On the other hand, we found that frugivorous/nectarivorous species are more likely to be green (in both sexes) or blue and purple (in males only) and less likely to be dark brown rufous or light gray (Fig. 5). The underlying reasons remain unclear, but frugivory/nectarivory has previously been associated with colorful birds (5). We hypothesize that the increased prevalence of green (and reduced brown/rufous) may reflect the color of the most common foraging background in this dietary guild (foliage), enabling foraging birds to blend-in (71).

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Is There a Link between Developmental Mode and Color?

No hypothesis has yet been proposed to explain a link between developmental mode and color. However, previous empirical work showed that species with altricial young have darker colored plumage rich in long wavelengths (7). Our analyses indicate that only yellow was significantly associated with developmental mode (Fig. 5), providing limited support for the previous finding. The increased presence of yellow in precocial birds might be associated with a cryptic (rather than signaling) function, possibly related to ground-nesting. In agreement with this explanation, the effect is more marked for low-saturation yellows (Datasets S3 and S4).

Selective Agents Explain Low Amounts of Color Variation

While our results clearly identify multiple potential drivers determining the directions of color evolution, low marginal r^2 values indicate that the selective agents tested here (fixed effects in the models) explain only a small fraction of color variation, especially in the rarer colors (marginal r^2 values, listed in increasing order: purple: 0.1%, blue: 0.3%, green: 0.4%, red: 0.6%, yellow: 2.7% rufous: 3.3%, light brown: 4.2%, white: 5.0%, light gray: 6.2%, dark gray: 6.5%, dark brown: 7.2%, black: 9.0%). On the other hand, conditional r^2 values, which include the contribution of fixed and random effects, are high (63 to 95%, Dataset S5). These high values are largely due to strong phylogenetic effects (Datasets S2 and S6), suggesting phylogenetic dependence for the evolution of bird colors. A strong phylogenetic effect is expected if certain types of colors are only produced by specific mechanisms or combinations thereof (e.g., deposition and metabolism of carotenoid pigments, or feather microstructure). If these mechanisms are not available in a specific clade, such colors cannot be produced even if there would be an adaptive advantage.

Alternatively, or in addition, there may be other selective factors with a strong phylogenetic signal that were not included in the models. One such candidate would be variation in retinal cone sensitivity functions, which in birds is largely restricted to the ultraviolet (14) and thus not applicable to our data. Although a recent analysis in passerines revealed an association between highly ultraviolet (UV)-sensitive vision and UV reflectance of the plumage, the effect was not statistically significant (63). Another candidate, applicable to the entire gamut of colors beyond UV, would be the proportion of the different photoreceptors present in the retina (cone proportions), which varies substantially between species (72) and affects how colors are perceived (73). In general, between-species differences in the sensory apparatus can cause between-clade variation in sensory biases (22, 74), and hence can potentially explain phylogenetically structured color variation. However, the currently available data are not sufficient to test for such an effect in a large-scale comparative analysis.

Strong phylogenetic dependence of colors could also have resulted from strong and consistent selection that favored specific colors within clades. Whether a strong phylogenetic signal is due to evolutionary constraints or to consistent selection cannot easily be disentangled. Certain types of evolutionary models, such as Ornstein–Uhlenbeck models (OU), allow separating phylogenetic inertia from adaptive processes (75). However, to achieve this, such models require assigning different selective regimes to different parts of the phylogeny [for example species living in the canopy vs. the understory (31)]. Our models aim to test multiple predictors at once and hence include a combination of categorical and continuous predictors, making this type of analysis impractical. Nevertheless, our results can be used to generate a priori hypotheses that can be tested with OU models for specific clades of birds.

Low explanatory power –in particular for putative signaling or ornamental colors– coupled with phylogenetically structured variation would also be expected if colors evolve in an arbitrary fashion, through a Fisherian mechanism of sexual selection (17, 76). This mechanism should not lead to color evolution in a specific direction other than making individuals stand-out from the background (17, 77), which can be achieved in multiple ways (that is, there are presumably more ways to be conspicuously colored than to be cryptic). This would lead to reduced convergence associated with other potential adaptive drivers of color evolution (Table 1), resulting in low explanatory power. Finally, it is likely that color variation, especially in conspicuous signaling colors, is caused by selection to avoid hybridization [species recognition (78, 79)]. This would lead to the divergence of closely related species in potentially arbitrary ways, which cannot be captured by our analyses.

Methodological Limitations

The low marginal r^2 values could also be the result of methodological limitations. First, our results are based on variables obtained from book plates and do not include the near ultraviolet part of the spectrum, which birds can perceive (14). This could introduce noise, especially if the presence or absence of UV in certain colors changes the function or performance of colors. Examples are rare but do exist. For instance, certain carotenoid-based colors have less UV reflectance in frugivorous than in nonfrugivorous species (80), although whether this has any functional implications has not been assessed. Such unaccounted variation may preclude the detection of certain effects, but should not lead to spurious results. However, we note that a recent study analyzing the evolution of UV reflectance in passerine birds using models of avian color vision reported similarly low marginal r^2 values (3 to 7%) and high conditional r^2 values (>85%) (63). This suggests that low explanatory power is unlikely the result of methodological limitations, and fits with the observation that low r^2 values are the norm in evolutionary studies (81).

The second major limitation stems from the heuristic approach to split what is in essence continuous color variation into discrete categories. Although this is necessary to allow analysis, it can be argued that our categories are too broad and that we therefore mix colors that are subjected to different selective regimes, thereby potentially blurring the effects. If this is the case, we would expect that alternative, finer-grained classifications of colors, will yield higher marginal r^2 values. For example, one can split all colors (except black, white and yellow) into light and dark versions. However, doing so does not increase marginal r^2 values (Dataset S5). Similarly, shifting the limits between color categories has only minor effects on the conclusions, and results using alternative color variables are strongly correlated (Datasets S3 and S4 and *SI Appendix*, Fig. S5 and *Text S3*). Hence, while the number of color categories and their exact definition can be a matter of debate, the overall conclusions of this study seem largely robust.

Another limitation of our study is that we considered only the proportion of the body (as depicted in book plates) covered by major coloration types, ignoring the spatial distribution of these colors on the body. Colors can be predictably found in different parts of the body. For example, species are often darker above than below [countershading (82)] and ornamental colors are more often found on the head and the anterior parts of the bird (2, 28, 83). Moreover, bird plumage can show fine-scale patterning such as streaks or bars, which can aid in camouflage or be used in intraspecific signaling (60). If color and patterning are considered

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simultaneously, the links between some colors and potential selection forces may become more obvious [e.g., disruptive coloration (84), within-body contrast (33)]. In addition, some variation may stem from the fact that species are not always depicted in the same position in the book plates, which could introduce noise in the analyses. Finally, our models, while computationally intensive, are simple in the sense that they do not include interactions between predictors (other than with sex). It is plausible that such interactions exist, but clear a priori predictions are needed to minimize type I statistical errors.

In conclusion, while our results validate parts of the existing theoretical framework (Table 1), the large amounts of unexplained color variation clearly indicate that the work is far from being finished. As expertly summarized in one of the first large-scale comparative analyses on bird color conducted over 40 y ago (28): "*… bird coloration is so variable that it is nearly always possible to find both evidence for the rule being presented, and exceptions to it. This indicates that a realistic model of bird coloration must have many parameters and must allow for the existence of many, often conflicting, selective pressures*". Our results are clearly in line with this statement: We identify multiple likely factors behind the evolution of different colors, and yet there are many species that do not conform to expectations. We hope that the results presented here provide a basis to generate theoretical insights and conduct further empirical tests. In the meantime, we can take some comfort in the fact that bird colors seem to broadly follow predictions from existing theories (Table 1), a testament to the progress achieved in understanding color evolution since Darwin and Wallace (85).

Methods

Computing Color Variables. We used bird plates (png files) from the Handbook of the Birds of the World (hereafter HBW) as available on the Birds of the World [(12) hereafter BoW] platform in October 2020 (N = 22,325 images of 10,618 species as identified by BoW). These included plumages but also soft parts such as bill, legs, and eyes and in some cases the perch. After image clean-up and processing (*SI Appendix, Text S1*), each image was reduced to a set of pixels (mean 5,897 pixels per image, SD = 3,123), which were used to compute color variables. RGB values were transformed into CIELAB color space using the function convert_colours in the R package "farver" (86). CIELAB space was chosen because it separates chromatic (a and b, Fig. 1*A*) from achromatic (L, or lightness) components and is largely perceptually uniform for humans.

First, we computed the average L, a, and b CIELAB values across all pixels in each image to assess the match with reflectance measurements (see above and *SI Appendix, Text S2*). This provides an overall color for the image but underestimates color variation in species with different colors (e.g., the blue tit in Fig. 1*A*). Thus, as an alternative approach, we split continuous color variation into a set of meaningful categories and used each category as a response variable. This allows to assess whether specific selection factors have favored the evolution of, for example, red rather than blue colors. Splitting continuous color variation into useful categories has previously been done at smaller scales or focusing on specific color types (63, 44, 74, 87, 88).

To split the continuous multivariate CIELAB color space into discrete categories, we used a three-dimensional grid (Fig. 1 *A* and *B* and *SI Appendix*, Fig. S1), and for each image we extracted the proportion of pixels found in each cell using the function getLabHist from the R package colordistance (89). Using a coarse grid (large cells) would yield a manageable number of color categories to use as response variables. However, as the vast majority of colors are found toward the center of color space, discrete color categories defined by large uniform cells will subsume much of the rarer peripheral colors (*SI Appendix*, Fig. S1) into the most common colors found toward the center. To properly capture color variation, we would then need a finer grid with smaller cells. The downside of this approach is that the number of cells becomes too large to use each one as a separate response variable and most cells only contain a few data points (*SI Appendix*, Fig. S1). The pragmatic solution we adopt here is to merge adjacent cells of the rarer color categories to reduce the number of response variables. However, this brings the associated problem of where to draw the limits between categories, introducing a degree of subjectivity into the process.

We used a grid that split the chromatic axes (a and b) into 12 cells each and the achromatic axis (L) into 4 cells, yielding a total number of 576 cells out of which 216 contained colors. The dimensions of this grid were chosen to balance the need of splitting the space into fine enough categories to find reasonable limits between color categories, while keeping the size of the dataset manageable. Most pixels were found in cells toward the center of the color space (Fig. 1*A* and *SI Appendix*, Fig. S1), while peripheral cells contained much fewer pixels. Thus, we merged adjacent cells into 12 broad color categories (Fig. 1*C*): blue, purple, red, yellow, green, rufous, light brown, dark brown, light gray, dark gray, black, and white. The most common color categories were comprised by few cells (e.g., black, white, and shades of brown and gray, *SI Appendix*, Fig. S1). Rarer colors further away from the center of color space were the result of merging multiple cells, each containing comparatively few data points (*SI Appendix*, Fig. S1). For each image, we then computed the proportion of pixels covered by each color category and used these values as response variables in subsequent analyses. Whenever multiple images were available for males or females of the same species, we averaged color values, yielding one set of color category values per sex and species. The merging of cells into color categories is subjective as color variation is largely continuous, and one may disagree on where to exactly draw the line. To test whether the assignment of color categories affected the conclusions, we computed alternative color scores by varying the position of the limits between adjacent color categories (*SI Appendix, Text S3*), which did not change overall conclusions.

Explanatory Variables. We compiled explanatory variables to test hypotheses in Table 1. We used www.birdtree.org as the source of phylogenetic information for all analyses. Because the taxonomic treatments underlying color data and datasets of explanatory variables differ, we used a synonym database based on https://www.worldbirdnames.org/ to match taxa to the taxonomy in www.birdtree.org. After matching, we obtained data for all variables for 9186 species (out of 9,993 included in www.birdtree.org), and this was the sample size for our analyses (data available in Dataset S7).

Habitat openness. We scored habitat openness between 1 (closed habitat) and 4 (open habitat), based on the habitat types assigned to each species by Birdlife International (http://datazone.birdlife.org), including only categories "major" and "suitable" and excluding artificial habitats. Forests were assigned 1, savanna and shrublands 2, inland wetlands and grasslands 3 and desert and marine environments 4. For species that used multiple types of habitats, we averaged the openness scores of the different habitats used.

Vegetation strata. We used data on foraging strata use from ref. 90 (variables ForStrat.canopy, ForStrat.midhigh, ForStrat.understory, ForStrat.ground) to compute an index reflecting how much each species uses high- vs. low-vegetation strata to forage. The index was computed as a proportion (canopy + mid-high*0.5) – proportion (understory*0.5 + ground).

Nest safety. We used information from the print version of ref. 91 to classify nest type and location. We consulted the online version of Birds of the World (June 2021) to add available information to species with missing data. Nest type and location were combined to obtain a nest safety score (0 to 4, *SI Appendix, Text S4*). Nesting data were available for 7,614 out of the 9,993 species in the phylogeny, for all other species (N = 2,077) we inferred the trait based on the scores of the closest relatives by assigning the same scores as the prevailing score in the genus.

Diet. We classified species as frugivorous/nectarivorous (1) or other (0) based on variable Diet5Cat from ref. 90.

Nocturnality. We classified species as mainly active at night (1) or during the day (0), based on data from ref. 90.

Climate. For each species, we extracted the species' breeding range or the year-round presence range (i.e. excluding wintering and migration ranges for migratory species) from Birdlife International (http://datazone.birdlife.org/) and overlapped these with raster layers of annual mean temperature (BIO1) and annual precipitation (BIO12) [resolution 0.0083 decimal degrees (92)]. We then obtained average annual mean temperature and average annual precipitation for each species, using function "exact_extract" from the package "exactextractr" (93) to average values for raster cells within the distribution of each species.

Body mass. Data from ref. 90. Body mass (in g) was $\log_{10}$-transformed prior to analysis.

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Migratory behavior. Data from ref. 94. Each species was assigned a score: 0 = resident, 1 = partial migrant, 2 = strict migrant.

Sexual selection intensity. We derived an index of sexual selection intensity on males and females based on the social mating system and parental care (data from refs. 12 and 95). This index varied from 0 (monogamy, biparental care) to 5 (polygyny/polyandry, uniparental care). See *SI Appendix, Text S5* for details.

Territoriality. Species were classified as 0 = nonterritorial, 1 = seasonal or weakly territorial and 2 = year-round territorial, using data from ref. 53.

Cooperative breeding. Species were classified as cooperative breeders (yes/no), using data from ref. 95.

Developmental mode. Species were classified as precocial or altricial, based on data from ref. 96.

Statistical Analyses. We ran models using each of the 12 color categories as a separate response variable. These represent the proportion of pixels covered by each color and hence can in theory vary between 0 and 1. In practice, no species had only one color, and so values ranged between 0 and 0.97. Because zeros were common, especially for rarer colors (e.g., red, blue), and because distributions were strongly skewed, with a long tail toward higher values (Fig. 1*C*), we used zero-augmented beta regressions with logit link. These models assume two different data generating processes behind the presence/absence of the trait and its magnitude (46), and correspondingly estimate the effect of each predictor for both processes separately. Common colors (brown to black, Figs. 1 and 2) have no or few zeros (<5%), and therefore we could not estimate the effect of predictors on the presence/absence of these colors.

Models were implemented using a hierarchical Bayesian approach with the R package "brms" (v 2.16.3) (97), an R interface with STAN (98), used to fit the models. For each model, we obtained posterior distributions of all parameters by running four chains in parallel for 1,000 iterations discarding the first 500 as burn-in. We used default priors which included flat, noninformative priors for all fixed-effect slope estimates, Student's *t* distribution for the random effects and a gamma distribution for phi (97). We assessed convergence by ensuring that the R-hat parameter was 1 or close to 1 in all cases (97).

Male and female color values were analyzed in the same model, and hence we fitted species identity as a random intercept to account for pseudoreplication. We accounted for phylogenetic effects by including the phylogenetic covariance matrix as a random effect. The phylogenetic covariance matrix was obtained from a maximum clade credibility (MCC) tree based on 1,000 phylogenetic trees for all species (Ericsson backbone) downloaded from www.birdtree.org (47), and computed using the function maxCladeCred from the R package "phangorn" (99). The use of a MCC tree rather than repeating analyses on a sample of trees was necessary due to computational constraints (each model required a week to run on a Linux computer 5.4, with multicore Intel Xeon processor at 2.20GHz, 1TB RAM). Model fit was assessed visually using posterior predictive check graphs. We ran two different models per variable, one model to estimate the extent of sexual dichromatism in color, which included sex as the only fixed effect, and one model with all predictors, which included the sex-by-predictor interaction to obtain separate effects for males and females.

For most color variables, we obtained two effects per predictor: presence/absence (indicated by the excess of zeros, i.e., the zero-inflation component) and extent (the proportion of the plumage covered by each color). We then combined these into an overall effect by: 1) calculating the posterior distribution of each predicted slope in the original scale of the variable using the function "emtrends" from the R package emmeans (100) and 2) using these posterior distributions to compute a mean effect and its uncertainty (95% credible intervals). Based on these posterior distributions, we computed probability of direction (PD) values with function "p_direction" from the package bayestestR (101). PD ranges from 0.5 to 1, and indicates the proportion of values in the posterior distribution with the same sign as the median. Because PD can easily be transformed into the more commonly used *P*-values (101), we also report these. We present and discuss the overall effect of each predictor on each color category in the main text and provide all statistical results in Dataset S3. We computed marginal and conditional r^2 values using the function "r2_bayes" from the package performance (102).

We estimated the phylogenetic effect from the sex-only and full models as the proportion of the variance accounted for by phylogeny, that is, the intraclass correlation coefficient (ICC) (103, 104), which ranges between 0 and 1 (*SI Appendix, Text S6*). We used the same procedures to estimate ICCs for the random factor "species identity". ICCs for both random effects are reported in Datasets S2 and S6. The dataset to carry out the analyses is available as Dataset S7, and R code is available upon request from the corresponding author.

Data, Materials, and Software Availability. Spreadsheet data have been deposited in Dataset S7. All other data are included in the article and/or supporting information.

ACKNOWLEDGMENTS. We thank the Kempenaers group members for feedback on results, the associate editor, William Gearty, and two anonymous reviewers for comments on the manuscript, Millie Ahlstrom for helping scoring nests and Shinichi Nakagawa for advice on the residual variance of the beta distribution. Finally, we thank countless researchers who have contributed to build the database of ornithological knowledge that underpins this study and Lynx Edicions and the Cornell Lab of Ornithology for making it available. This project was funded by the Max Planck Society (to B.K.). Open access funding provided by the Max Planck Society.

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