Note

Using Human Vision to Detect Variation in Avian Coloration: How Bad Is It?

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Submitted March 12, 2017; Accepted September 12, 2017; Electronically published December 1, 2017

Online enhancements: appendix. *Dryad data:* http://dx.doi.org/10.5061/dryad.nq3fp.

abstract: Assessing variation in animal coloration is difficult, as animals differ in their visual system properties. This has led some to propose that human vision can never be used to evaluate coloration, yet many studies have a long history of relying on human vision. To reconcile these views, we compared the reflectance spectra of preserved avian plumage elements with two measures that are human biased: RGB values from digital photographs and the corresponding reflectance spectra from a field guide. We measured 73 plumage elements across 14 bird species. The field guide reflectance spectra were drastically different from that of the actual birds, particularly for blue elements. However, principal component analyses on all three data sets indicated remarkably similar data structure. We conclude that human vision can detect much of the variation in coloration in the visible range, providing fodder for subsequent studies in ecology, evolution, behavior, and visual ecology.

Keywords: reflectance, birds, ultraviolet, visual systems, digital photography, spectrophotometry.

Introduction

Animal color patterns have long attracted the attention of biologists (Darwin 1859; Thayer and Thayer 1909; Cott 1940; Fox and Vevers 1960). Long before the invention of field-portable spectrophotometers, biologists initiated successful research programs centered around human-detected variation in color patterns; many of these programs continue to this day (mice coloration [Nachman et al. 2003]; mimetic butterflies [Dasmahapatra et al. 2012]; guppies [Gordon et al. 2012]; sticklebacks [Malek et al. 2012; Linnen et al. 2013]). Yet, despite these successes, we still doubt our eyes' ability to accurately detect variation in animal coloration (Endler 1990; Bennett et al. 1994; Eaton 2005; Stoddard and Prum 2011; Kemp et al. 2015). This is for good reason, as human vision often differs from that of other animals (Endler 1990; Partridge and Cummings 1999; Kelber et al. 2003). Species differ in the number and spectral sensitivity of photoreceptors (Hunt et al. 2009); species also differ in the anatomy and neural processing of visual cues (Cronin et al. 2014).

This variation in visual systems raises the question of whether human vision can capture ecologically relevant patterns in animal coloration (Hastad and Odeen 2008; Cronin et al. 2014). Are humans missing the majority of color variation in nature and instead investigating only a narrow subset of variation? Admittedly, humans cannot detect UV, near infrared (NIR), or polarized signals (Land and Nilsson 2012; Cronin et al. 2014). However, the question remains as to whether humans are failing to detect the bulk of color variation in the visible range. We address this question by using a methodology that most visual ecologists would agree is fundamentally flawed by human subjectivity and comparing it to an objective methodology that is free of human perceptual biases. We compared the reflectance spectra of avian museum specimens with reflectance spectra from field guides and RGB values from digital photographs of actual birds.

The reflectance spectra of museum specimens should be free of human visual biases, whereas the reflectance spectra of field guides and RGB values from digital photographs should be highly human biased. The images in the field guide have undergone multiple levels of human-biased filtering (fig. A1, available online). An artist observes a bird with the human visual system. They depict the bird using paints whose spectral properties may not match those of the bird. Finally, the painting is used to create cyan, yellow, magenta, and black subimages for printing. There are multiple steps where animal coloration can be misrepresented. Digital photography can also misrepresent coloration, as it

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Am. Nat. 2018. Vol. 191, pp. 000–000.
DOI: 10.1086/695282

mimics the sensitivity of human vision. Digital cameras overrepresent certain colors, filter out potential UV and NIR signals, and may display nonlinear responses to changes in light intensity (Stevens and Cuthill 2005; Johnsen 2016). Sensitivity also varies between cameras (Stevens et al. 2007).

To quantify the discrepancy between human-biased and nonbiased measures, we compared the reflectance spectra of plumage elements from preserved avian specimens to (*a*) reflectance spectra of corresponding patches from field guide images and (*b*) RGB values of patches from photographs of original museum specimens. We compared reflectance spectra directly and used principal component analyses (PCAs) to determine the extent to which each method captured the patterns of animal coloration. The hypothesis that human vision fails to capture the major components of animal coloration makes three predictions. First, reflectance spectra of actual birds should fail to match those of the field guide. Second, PCAs on the three data sets (actual bird, field guide, RGB values) should reveal different variance structures—meaning (*a*) the proportion of variation accounted for by each principal component (PC) and (*b*) the PC loadings should differ. Third, the PC scores from the different analyses should not be strongly correlated. We test these predictions below.

Methods

We measured the reflectance spectra of avian specimens from the Illinois Natural History Survey (INHS) at the University of Illinois at Urbana-Champaign and from the John Wesley Powell–Dale Birkenholz Natural History Collections at Illinois State University (ISU). Avian museum specimens are convenient subjects (Eaton 2005; Armenta et al. 2008*b*; Seddon et al. 2010) because their coloration is relatively stable over time (Armenta et al. 2008*a*; Doucet and Hill 2009). We sampled multiple species containing blue, red, yellow, brown, black, white, and gray elements (tables A1, A2; tables A1–A3 are available online). Four species were considered to have low sexual dimorphism; we measured five individuals and did not consider sex. For these, the field guide did not distinguish between males and females, except for the pileated woodpecker, for which the only difference was the size (but not color) of certain color patches. The remaining 10 species had appreciable sexual dimorphism. For these, we measured a minimum of three males and three females for each species, with the exception of the female western bluebird, as we had only two females. For four species, we considered only male data, either due to a lack of female specimens or out of concern of oversampling a given color class (e.g., red or blue).

For each species, we measured reflectance spectra for multiple color patches. Table A2 lists the color patches for each species-sex combination and the sample size. We measured the reflectance spectra of the corresponding color elements from field guide images contained in the *National Geographic Field Guide to the Birds of North America* (Dunn and Alderfer 2011). Qualitatively identical results were found using another field guide. We took three measurements for each color element–species–sex combination. We measured reflectance spectra of the actual birds and their corresponding field guide images using a USB4000 spectrophotometer with an R200-7 reflection probe and a PX-2 pulsed xenon light source, which emits light from 220 to 750 nm (Ocean Optics, Dunedin, FL). A Spectralon white standard (WS-1-SL) was used for calibration. We took all readings with the reflectance probe held at 45° relative to the measured surface.

We obtained RGB data from actual birds by taking multiple photographs of both the dorsal and the ventral sides of each bird using a Nikon COOLPIX 8700 digital camera. The camera has been used in previous studies (e.g., Parraga et al. 2002; Bergman and Beehner 2008; Zhou et al. 2014; Johnson and Fuller 2015). The camera was set to underexpose by one f-stop to prevent clipping. Clipping occurs when the R, G, or B value for a pixel reaches its maximum value of 255. Digital photographs were saved as TIFFs. Photographs were taken with an X-rite ColorChecker Classic (Grand Rapids, MI) in the frame. Birds at the INHS were photographed under a mixture of natural and florescent light, while those at ISU were photographed under florescent light. The camera was white balanced at the beginning of each session.

Differences in the lighting can cause deviations in photographic color measurements, which we ameliorated by including color standards in the photographs. The digital photographs were color corrected as outlined by Bergman and Beehner (2008) using the inCamera 4.5 plug-in (version 4.0.1; PictoColor Software) for Adobe Photoshop CS4 Extended with a modified reference file for the X-rite ColorChecker Classic. The program provides the worst and the overall standard deviations for each color channel (R, G, B). For the INHS data, we excluded images in which any channel's worst standard deviation was greater than 3; overall color channel errors fell close to 1 standard deviation and rarely exceeded 1.3. For the ISU data, the blue channel had the worst standard deviation (~3.0–3.9). The overall errors usually fell close to 1.2 standard deviations and never exceeded 1.6. To determine whether the inclusion of the ISU images altered our results, we ran two sets of analyses—one including and one excluding the ISU data. The results were qualitatively identical. Here, we present the combined INHS and ISU data.

Reflectance spectra were averaged every 5 nm from 300 to 750 nm. For the actual birds, there were 901 reflectance spectra from 73 unique species–sex–color element combinations from 14 species across 83 birds. We calculated the average reflectance for each unique combination across replicate birds. Similarly, we calculated the average reflectance

spectra for each of the 73 unique combinations for the field guide images. As the field guide had a single image for each color element, the average was calculated across replicate measurements.

We first asked whether the reflectance spectra differed between the actual birds and the field guide images; we used two-tailed Welch's *t*-tests for each 5-nm interval. Our second analysis asked whether the two data sets captured similar patterns in avian color variation; we performed separate PCAs on the actual birds and field guide images. We also asked whether RGB values from digital photographs corresponded well to actual bird reflectance. We averaged replicate RGB values for each bird's color patches and the RGB values for each unique plumage element (73 total) and then performed a PCA on these 73 RGB values. The PC scores and loadings, as well as proportion of variance accounted for by the PCs for the RGB, were compared with those of the actual bird PCA. We performed a similar analysis on subsets of the data where we considered only red, yellow, blue, or gray color elements (see hue analysis in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.nq3fp [Bergeron and Fuller 2017]). All analyses were performed using prcomp in R (version 3.0.1) using the covariance matrix. Raw data and means for each color element are in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.nq3fp (Bergeron and Fuller 2017).

Results

For all 73 comparisons, reflectance spectra of actual and field guide birds differed in some region of the spectrum (see figures in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.nq3fp [Bergeron and Fuller 2017]), with some color patches contrasting drastically (fig. 1). For instance, in the 600–700-nm range, the field guide was more than twice as reflective for the female Canada warbler's throat patch (fig. 1*C*). Other statistically significant differences existed even when reflectance spectra were similar (differences <2% with P values <.001), due to the field guide's small standard errors. Whether these differences are biologically relevant is unclear.

The reflectance spectra comparisons differed in predictable ways depending on color class (fig. 1). For red elements (fig. 1*A*, 1*B*), the shapes of the reflectance spectra were similar. The field guide often overrepresented red wavelengths and, to a lesser extent, green and yellow wavelengths. In most cases, the field guide was brighter than our data set's brightest bird. The pattern for yellow elements (fig. 1*C*, 1*D*) was similar to that of red but with more overrepresentation of green wavelengths and underrepresentation of the UV wavelengths (<380 nm). The guide poorly represented blue elements; their reflectance spectra (fig. 1*E*, 1*F*) often displayed higher reflectance in green wavelengths (495–570 nm) and lower reflectance in UV (300–380 nm) and violet (380–450 nm) wavelengths. Similar to the other elements, the field guide overrepresents red and orange wavelengths, effectively redshifting the patch's spectra in the field guide.

Despite the dramatic differences in reflectance spectra between the actual birds and the field guide images, PCAs on the two data sets produced nearly identical patterns. For the actual birds and the field guide, the first three PCs accounted for 98.38% and 99.29% of the variation, respectively. The proportion of variation attributable to each PC (table A3) and vector loadings were also very similar (fig. 2*A*–2*C*). PC1 loaded strongly onto the reflectance from ~525 to 750 nm (fig. 2*A*), and there was a small, positive loading in UV wavelengths in both analyses. The PC1 loadings correlated strongly ($r = 0.99$, $n = 91$). There was also a strong correlation between PC1 scores for the 73 species–sex–color element combinations ($r = 0.91$, $n = 73$; fig. 3*A*). PC2 represented blue and green versus red (fig. 2*B*). PC2 loadings were highly correlated ($n = 91$, $r = 0.9393$). There was a small discrepancy between UV loadings (300–380 nm), which were higher for field guides than for the actual birds. The PC2 scores were highly correlated (fig. 3*B*; $n = 73$, $r = 0.78$), even though there was an outlier (mountain bluebird wing). Similarly, PC3 produced very similar patterns for both data sets. PC3 loaded strongly onto the green and yellow wavelengths and negatively onto the blue and red wavelengths (fig. 2*C*). PC3 loadings were highly correlated ($r = 0.98$, $n = 91$), as were the PC3 scores (fig. 3*C*; $r = 0.83$, $n = 73$).

The PCA of RGB values also accounted for the major color variations. The first two PCs accounted for 94% of the variation (table A3). PC loading patterns for RGB data were similar to that of the actual birds. PC1 for RGB loaded similarly to PC1 for the actual birds and field guide, with slightly negative loading of short (blue) wavelengths and high loading values for longer wavelengths (red; fig. 2*D*). PC2 for the RGB data showed a pattern similar to PC2 for the actual bird and field guide by representing a blue and green versus red comparison (fig. 2*E*). PC3 for the RGB PCA loaded for green versus blue and red (fig. 2*F*). There were very strong, positive correlations between PC scores 1–3 for the RGB data and actual birds (fig. 3*D*–3*F*; PC1: $r > 0.91$; PC2: $r > 0.73$; PC3: $r > 0.87$).

Discussion

This study was motivated by the contradictory views that (*a*) human assessments of animal coloration are highly subjective and (*b*) human-assessed coloration studies have provided insight into ecology, evolution, and behavior, particularly in birds (Badyaev and Hill 2003; Price 2007). Our results highlight this dichotomy. Reflectance spectra from field guides did not match the spectra of actual birds on a one-to-one comparison; large discrepancies are likely due

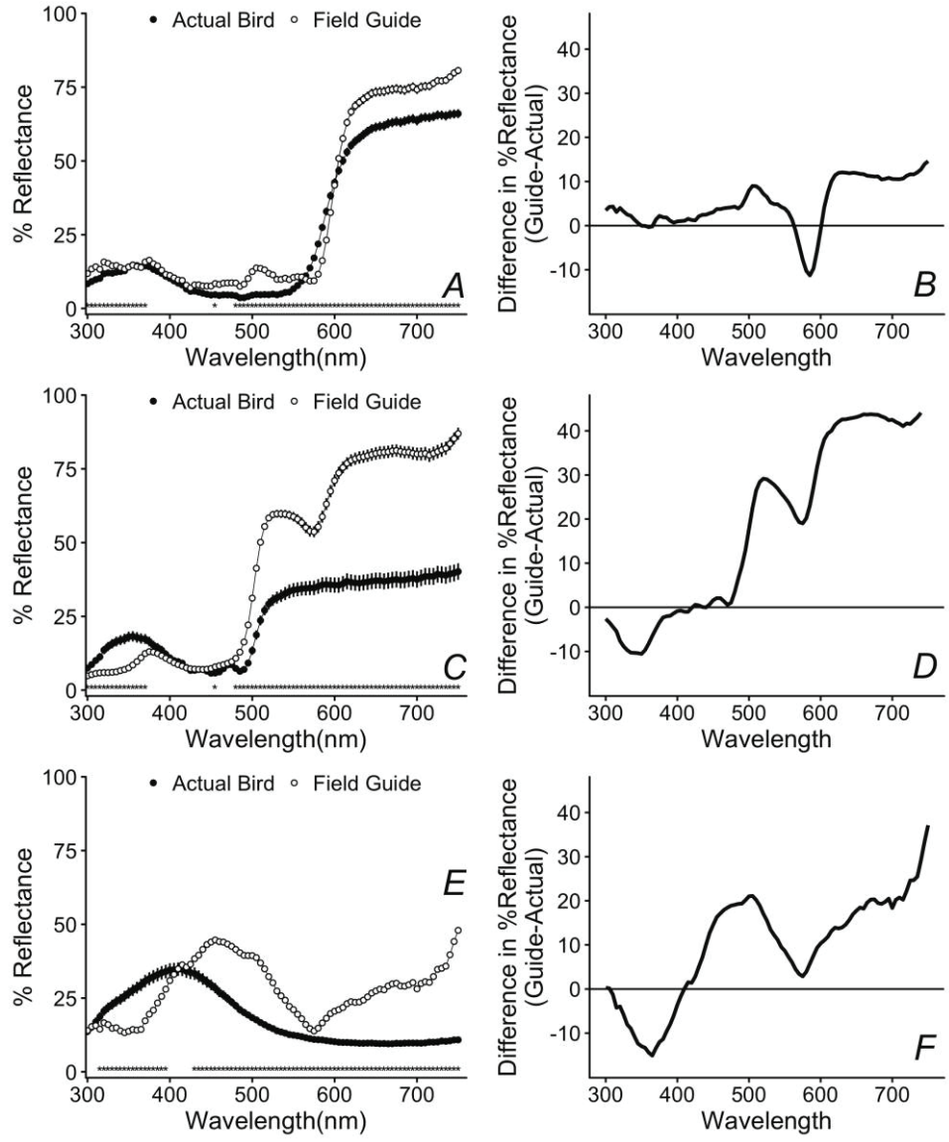

Figure 1: Examples of actual bird and field guide reflectance spectra (*left*) and the difference between them (*right*) for the red back of male scarlet tanagers (*A*, *B*), the yellow throat of female Canada warblers (*C*, *D*), and the blue crown of male blue grosbeaks (*E*, *F*). Field guide spectra are shown as open dots; actual bird spectra are shown as filled dots. Bars show standard errors. Asterisks indicate significant differences between the spectra ($P < .05$).

to filtering from human perception and limited gamuts of paints and inks between the reflectance of the bird and its field guide representation (fig. A1). Despite this, the PCAs produced remarkably similar patterns. All three PCAs produced exceedingly similar variance structure and strong correlations between the PC scores. This result should be tempered by the fact that our 73 unique color elements came from just 14 bird species. Perhaps inclusion of another color element from another species would alter the pattern. Still, the strong correlation between the PC scores across the three separate analyses is striking, considering the poor correspondence in reflectance curves. Below, we discuss the results and attempt to resolve these contradictory findings.

The reflectance spectrum from the field guide images did not perfectly match those of avian plumage, and obviously, attempting to use the former to estimate the latter is highly erroneous and discouraged. The discrepancies between the two were especially noticeable for blue color elements. Despite these discrepancies, the three separate PCAs described exceedingly similar variance structures. The PCAs indicated that the majority of the variation in coloration stemmed from broad patterns across the spectrum (e.g., dark vs. light,

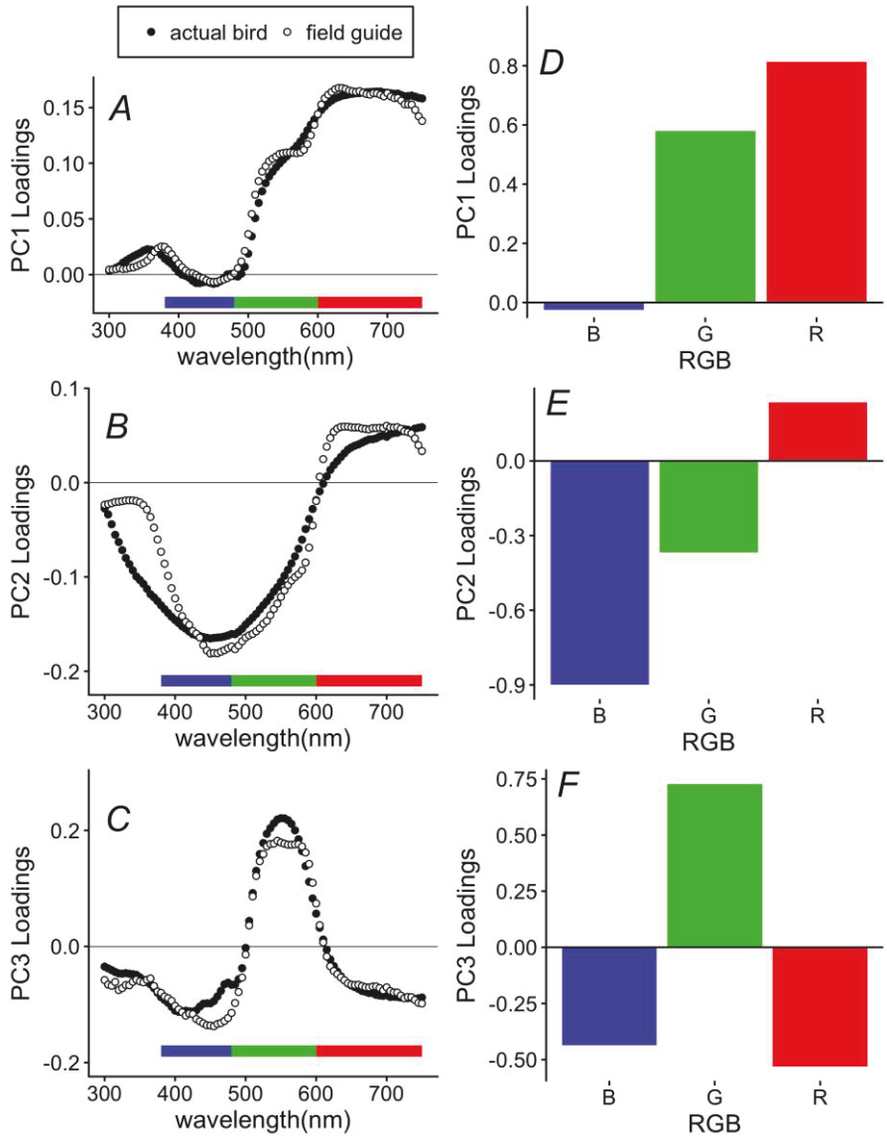

Figure 2: Principal component (PC) loadings for actual bird and field guide principal component analyses (PCAs; *A*–*C*) and the RGB PCA (*D*–*F*) for PC1 (*A*, *D*), PC2 (*B*, *E*), and PC3 (*C*, *F*). Color bars are included in *A*–*C* to indicate the general stretches of the spectrum that are accounted for by the three channels of the RGB data (red, green, and blue).

long vs. short wavelengths, etc.). We suspect that two factors contribute to this pattern. First, most color elements had a broad reflectance spectrum. Second, visual systems do not measure reflectance spectra but instead count photons across broad wavelength regions. Our PCAs similarly condensed variation in broad regions of the spectrum and accounted for >98% of the variation in coloration with three PCs. This result is unsurprising; Maloney (1986) showed that three principal components can account for >98% of the variation in natural reflectance spectra in the human visible range (see also Osorio and Vorobyev 2008). Likewise, past studies indicate that human vision detects much of the variation in animal coloration (Armenta et al. 2008*b*; Hastad and Odeen 2008; Seddon et al. 2010). A study of birds found that RGB values from scanned images of a field guide could account for much of the variation in reflectance spectra from actual bird specimens (Dale et al. 2015). One note of caution is warranted. While our analysis captured most of the variation in coloration in the visible range, it is possible that very subtle variation within species is critical to survival and/or mating success. Hence, the variation that was unaccounted for may potentially be important (Hastad and Odeen 2008).

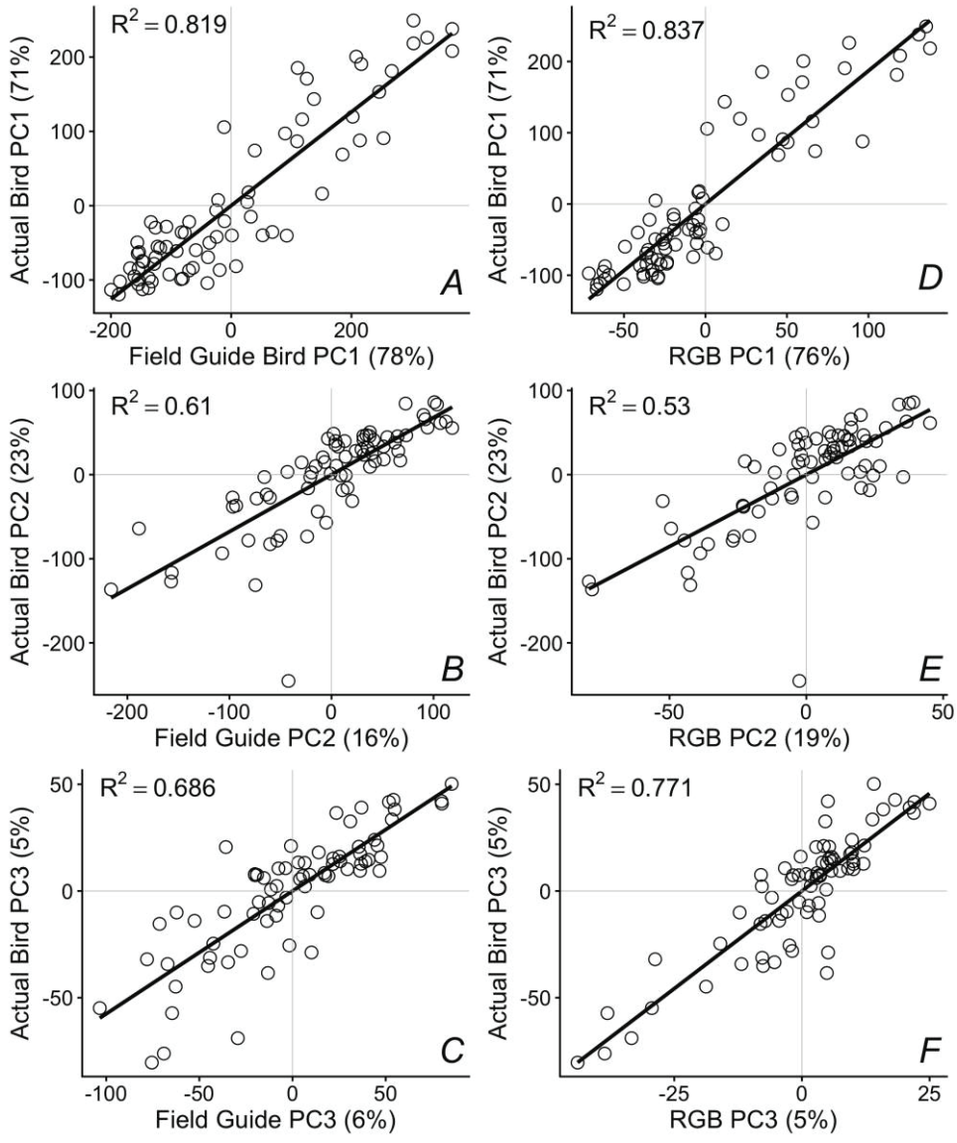

Figure 3: Comparisons of principal component (PC) scores between the actual birds and field guide images (*A*–*C*) and between the actual birds and RGB data (*D*–*F*) for PC1 (*A*, *D*), PC2 (*B*, *E*), and PC3 (*C*, *F*) with linear trend lines. The proportion of variation accounted for by a given PC for its particular analysis (i.e. actual, guide, or RGB) is indicated in parentheses on the axes.

What are we to make of this? Should biologists studying coloration throw away their spectrophotometers and stop thinking about visual detection models? Of course not. Our fear is that readers will take this study as license to ignore the UV, far-red, and polarized light signals and to dismiss the insights that can be gained from considering the visual properties of the receiver. This would be a mistake. Below is a list of important questions that require spectrophotometry and visual detection models: How do females perceive male color patterns? What makes a color pattern conspicuous to a viewer? How do predators perceive their prey? How do alterations in the lighting environment, visual background, or visual properties of the receiver alter the perception of the color pattern? What is the greatest distance at which a color pattern can be seen by a viewer? How different do two items need to be for the viewer to detect the difference? Visual ecology is a fascinating branch of science that is fundamental to studies of coloration (Endler 1992; Johnsen 2012; Land and Nilsson 2012; Cronin et al. 2014).

There are other questions where photography (particularly if it is standardized for differences in lighting conditions; Stevens et al. 2007) will likely do fine. Do different

color variants differ in mating success or survival? Do color variants differ in life-history traits or preferred habitats? Is coloration correlated with parasite levels or other indicators of health? Does variation in genotypes or hormone levels explain variation in color? Are there comparative patterns indicating that species with different hues vary in some interesting manner? In short, provided that one accepts that humans are blind to UV, far-red, and polarized light, one can readily look for interesting correlates of discernible color variation. Many of the questions listed above would benefit from understanding how animals perceive coloration, but it is not always necessary to do so.

We contend that the human visual system and anthropocentric measures of coloration are able to detect much of the meaningful variation in animal coloration within the visible spectrum. Humans can use the variation they perceive to initiate studies and subsequently use more sophisticated methods to gain a deeper understanding of this variation through an objective lens. In reality, sophisticated practitioners of visual ecology already do this (Cuthill et al. 2017). While the human visual system cannot describe the perception of other species, it can point us toward compelling patterns in animal coloration.

Acknowledgments

D. Wylie at the Illinois Natural History Survey and A. Capparello at the John W. Powell–Dale Birkenholz Natural History Collections at Illinois State University kindly provided access to the bird specimens. T. Seerup, S. Feng, N. Karim, and M. Wycoff helped with data collection. A. Uy, Z. Rapti, D. Beck, and the Fuller lab provided valuable comments that improved the manuscript. M. Zhou and R. Moran assisted with color metrics. P. Benham, N. Sly, and J. Birdsley provided helpful input concerning birds. M. Clearwood assisted with the creation of figure A1. Z. Bergeron was supported by the University of Illinois and the National Science Foundation (0953716).

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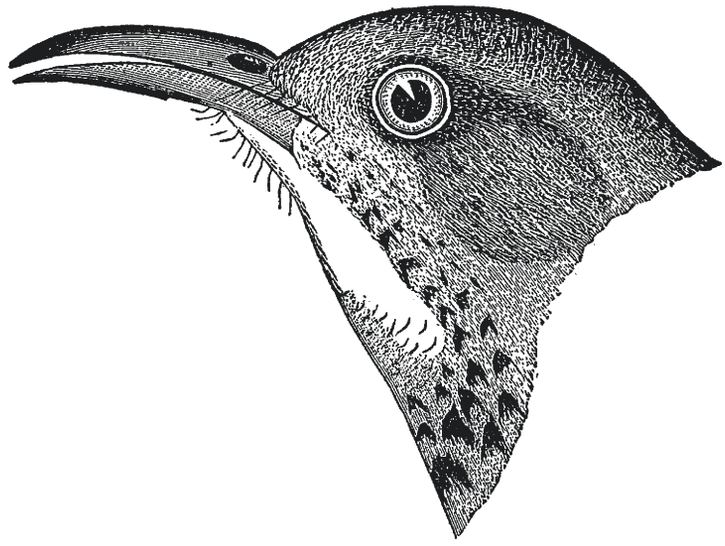

"I will first mention the St. Lucas Thrush (*H*[*arporhynchus*] *cinereus*); it agrees with the thrasher, and differs from all the rest, in being thickly speckled with brownish-black over most of the under parts. It is dull brownish-gray above . . ." From "Some United States Birds, New to Science, and Other Things Ornithological" by Elliott Coues (*The American Naturalist*, 1873, 7:321–331).