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AN EASY, INEXPENSIVE MEANS TO QUANTIFY PLUMAGE COLORATION

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Abstract.—The Colortron (Light Source, San Rafael, California) is an inexpensive, compact, Macintosh-compatible reflectance spectrophotometer that can be used to quantify the coloration of the plumage and soft parts of birds. The Colortron provides a reflectance spectrum (390–700 nm) of the object being measured as well as tristimulus color scores that can be compared to scores from the Methuen or Munsell color references. Because the Colortron fails to measure ultraviolet light (wavelength <390 nm), which is visible to some species of birds, Colortron output must be interpreted cautiously when it is used to describe plumage that may reflect UV, especially if the focus of the study is understanding the function of coloration. The Colortron is especially useful for quantifying carotenoid-based plumage coloration, which reflects primarily in the visible spectrum. I compared visual scores of carotenoid-based ornamental plumage of House Finches (*Carpodacus mexicanus*) made by comparison to *The Methuen Handbook of Colour* to tristimulus color scores generated by the Colortron. Hue and saturation scores from visual assessment were significantly positively correlated with hue and saturation scores from the Colortron. I recommend the use of the Colortron as a means to quantify plumage and soft-part coloration.

UN MÉTODO SENCILLO Y POCO COSTOSO DE CUANTIFICAR LA COLORACIÓN DEL PLUMAJE

Sinopsis.—El Colortron (Light Source, San Rafael, California), es un espectrofotómetro de reflectancia barato, compacto y compatible con procesadores Macintosh que puede utilizarse para cuantificar la coloración del plumaje y partes delicadas de aves. El Colortron provee un espectro de reflectancia (390–700 nm) del objeto medido tanto como medidas de color de tristimulo comparables con las medidas de las referencias de color de Methuen o Munsell. Debido a que el Colortron falta en medir la luz ultravioleta (largo de onda <390 nm), que es visible a ciertas especies de aves, los resultados del Colortron deben interpretarse con cuidado cuando se utilicen para describir plumajes que pueda reflejaren UV, especialmente si el foco del estudio es entender la función de la coloración. El Colortron es particularmente útil para cuantificar el plumaje basado en carotenoides, el cual refleja principalmente en el espectro visible. Comparé los resultados visuales del plumaje ornamental a base de carotenoides de *Carpodacus mexicanus* producidos al compararlos con el "*Methuen Handbook of Colour*" con los resultados tristimulares de color generados por el Colortron. La tonalidad y la saturación de las evaluaciones visuales fueron correlacionadas positivamente con las evaluaciones de tonalidad y saturación del Colortron. Recomiendo el uso del Colortron como un método de cuantificar la coloración del plumaje y de las partes delicadas.

Ornithologists have long needed a dependable, repeatable, and affordable means to quantify the coloration of the feathers and soft parts of birds. Descriptive names for colors, which were used until the twentieth century, failed to capture much of the fine variation in color display. Beginning with Ridgway (1912), ornithologists concerned with recording detailed coloration of birds in a repeatable manner have used sets of color standards. The color chips published by Smithe (1974) in the *Naturalist's Color Guide* are probably the color reference in widest current use by ornithologists (e.g., the *Birds of North America* series recommends the use of the *Naturalist's Color Guide* color chips in describing bird coloration). Unfortunately, the *Naturalist's Color Guide* is a more or less random collection and assemblage of color chips and does not allow ornithologists to describe color in the detail needed for many studies.

The main alternative to the *Naturalist's Color Guide* is the Munsell color system (Munsell 1976) or the similar and much cheaper *Methuen Handbook of Colour* (Kornerup and Wanscher 1984). The Munsell system divides the visible spectrum into 10 equal regions, then within each region (hue), it divides the possible range of blackness (=tone or brightness) from 0 to 10 (very dark to very bright) and the possible range of color saturation (=intensity) from 0 to 6 (very washed out to very intense) (Munsell 1976). This allows one to compare a colored object such as a patch of feathers to a series of chips that change gradually along three color axes. The Munsell system has been used in bird studies that required subtle discrimination among color displays (Burley and Coopersmith 1987, Johnson et al. 1993, Zuk et al. 1990). However, the color codes generated by the Munsell color system do not lend themselves to quantitative analysis. In my studies of plumage coloration in House Finches (*Carpodacus mexicanus*), I generated a numerical score of overall plumage brightness by summing the hue, saturation/intensity, and tone/brightness scores for seven plumage regions that I derived by comparison to the *Methuen Handbook of Colour* (Hill 1990, 1992), which for all practical purposes is equivalent to the *Munsell Book of Color* (Endler 1990). Because of the way I set up my numerical scoring system with higher values corresponding to redder, more saturated, and less black coloration, there was virtually no difference between additive plumage scores and PC1 scores from a principal component analysis that included the same color data (Hill 1990).

Although using standard color references such as Methuen or Munsell provided a more refined means of quantifying coloration than simply naming colors or trying to use *Naturalist's Color Guide,* the technique was still fraught with problems. Endler (1990) gave five fundamental weaknesses of using visual assessment to quantify animal coloration: (1) subjectivity, (2) error introduced by variation in colors surrounding the color patch being scored, (3) error introduced by variation in lighting conditions, (4) individual variation in human visual perception, and (5) differences in the visual perception of the study organism and humans. From my experience in attempting to train dozens of undergraduate and graduate students to use my plumage scoring system, I believe that problems 1 and 4 present the greatest practical difficulty. Under the Munsell or Methuen scoring system, change in color along one axis is often difficult to distinguish from change in coloration along a second axis. For instance, when I score the plumage coloration of an individual House Finch using the *Methuen Handbook of Colour,* I tend to be conservative with respect to changes in hue and to account for variation in coloration across the surface of an individual with changes in saturation. In contrast, many of the students whom I have trained account for the same variation by holding saturation constant and changing hue. In addition to such scoring biases, it is obvious that different observers see the same color differently. Some students score birds consistently redder than me; others score birds consistently less red. Consequently, color scoring is repeatable for any given observer (Hill 1992), but it is not repeatable among observers and one cannot pool visual color scores across observers. My solution has been to score the plumage of all birds personally.

Because of the problems with visual scoring of color, Endler (1990) strongly recommended that coloration be quantified by means independent of the human visual system. Every ornithologist with whom I have spoken over the years realizes that we have long had the technology to measure the color reflectance from the surface of colored objects (e.g., Selander et al. 1964); yet, until very recently almost no ornithologist with a research focus in ecology, evolution, or behavior was using spectrophotometric equipment to quantify bird coloration. The major obstacles to adopting such equipment for myself and most other ornithologists has been the high cost of such equipment and the amount of technical knowhow required to use a machine to make color measurements (e.g., Endler 1990). It was easier and cheaper to make the best of color references such as Methuen and Munsell (or even paint color samples from hardware stores). Add to this the need by many researchers to take color measurements in the field and it seemed impractical to invest time and money into machines for color measurement. However, I believe that a new device for color quantification, the Colortron (Light Source Inc., San Rafael) will make accurate color quantification more widely available to ornithologists.

In this paper I describe how the Colortron can be applied to the study of coloration of the feathers and soft parts of birds. The Colortron is relatively cheap, easy to use, compact, and potentially field-portable. I will describe what information the Colortron provides; I will show how bird plumage scored with the Colortron compares to bird plumage scored by visual comparison to a color reference; and I will suggest the sort of analyses that are now possible with the Colortron that were not possible with visual scoring systems.

DESCRIPTION OF COLORTRON

The Colortron is a hand-held 32-band digital color sensor (Light Source 1994). The Colortron package includes a small (250 g, 9 cm ×

12 cm × 4 cm) color-measuring device that plugs into a Macintosh computer, software to allow the computer to display the output of the color sensor, calibration sheets, and a useful and readable manual. The Colortron retails for about US$1160 (including software and hardware). The Colortron requires a Macintosh computer with a 68020 or better processor running Apple System Software 7.1 or later and with at least 2 MB of available RAM. A color monitor is helpful in interpreting Colortron output, but the function of the Colortron is not affected by a monochrome screen.

To measure the color of opaque surfaces, the Colortron emits light from twin tungsten light bulbs and measures the proportion of light bounced back into the device at 32 intervals between 390 and 700 nm. The measured area is a square 3 mm × 3 mm, small enough for the needs of most ornithologists. No external light source is required, and condition of ambient lighting is irrelevant. Stated more simply, one can point the device at any patch of feathers or area of skin and within 10 s have a reflectance spectrum for the object. It takes less than 10 min of instruction to train an average person (who is familiar with Macintosh computers) to measure plumage coloration with the Colortron.

Most reflectance spectrophotometers are designed to measure coloration of smooth flat surfaces. This hardly describes the surface of a bird. There may be a dominant coloration to a particular patch of feathers, but the coloration is never smooth or uniform. The color will invariably change from the proximal to the distal end of each feather, across the length of the barbs, and from feather to feather within the patch. There are also spaces between the barbs and between the feathers making a patchwork of colored and non-colored surfaces. The Colortron was designed to measure the coloration of objects that are not perfectly smooth and flat, and I have found the Colortron to be good at averaging across this mosaic of color of a patch of feathers and capturing a color like that perceived by the observer.

Occasionally as one attempts to measure the coloration of plumage, one will inadvertently slide the Colortron beneath the contour feathers and measure either skin or down feathers. Such an error gives an obvious false reading: the tristimulus values will be very different than values from the same patch or similarly colored patches of feathers, and the color display will not match the color one is trying to score. It is easy to discard unreasonable output and repeat the measurement. Even within "reasonable" measurements, however, there is variation. For this reason, when I record the coloration of a patch of feathers, I take three Colortron readings (each time lifting and replacing the device on a different spot within the patch being measured) and then average across the three readings. Such averaging requires only the click of a computer mouse. In this way I get a better representation of the overall coloration of the feathered region.

One has several options as to what Colortron output appears on the computer screen. For most ornithological studies, two output boxes will be of most importance: the reflectance spectrum and tristimulus color spaces. The reflectance spectrum is the complete description of the coloration of the surface being measured. From the reflectance spectrum one can look at the wavelength of maximum color reflection, reflection at any particular wavelength interval, and the shape of the reflectance curve. Tristimulus data are the hue/saturation/brightness values under the Munsell Color System, the Red/Green/Blue values used in the publication industry, or any of several alternative systems. All tristimulus systems are interchangeable (See the Colortron manual [Light Source 1994] for a description of the various systems), and the Colortron software allows one to view three such systems simultaneously. Tristimulus data can be derived from a reflectance spectrum, but a reflectance spectrum cannot be derived from tristimulus data (Light Source 1994). Thus, tristimulus data are a less complete description of the color than a reflectance spectrum, but they have great advantages in producing a discrete set of numbers that can be used in analyses.

Once a description of the coloration of a patch of feathers is displayed on the computer screen, the data or part of the data can be downloaded directly into a spreadsheet such as Excel. The data can also be saved as a Colortron file (so that all the information on the screen including the reflectance spectrum is stored). A Colortron file containing all measurements made for one male House Finch, including nine individual color scores, takes up about 12K of disk space. In my study of plumage coloration in House Finches, we find it most useful to record the tristimulus hue/saturation/brightness scores on the banding sheet and save the complete measurements as a separate Colortron file for each bird.

Saturation and brightness scores are given as percentiles from 0 (unsaturated/completely black) to 100 (completely saturated/completely white). Hue is given as a point along a 360° color circle that begins at red (R in the old Munsell terminology) = 0 and ends at purple-red (PR in old Munsell terminology = 360) (see Colortron [Light Source 1994] manual for visual depiction of the "color wheel"). The zero point is an arbitrary break point in the continuous color circle.

The most recent version of the Colortron, the Colortron II, runs directly from an AC power supply; the internal battery is not depleted with use. With the Colortron II, one can make unlimited color measurements without recharging batteries. The Colortron is a rather delicate device that was made for desktop use, but I have been able to use the unit successfully in the field. For field use, I attached the Colortron to a Powerbook 520c that was operated from batteries. I then used an adapter to plug the Colortron into the cigarette lighter of a car and ran the unit from the car's battery. My biggest problem in this operation was dealing with the extremely intense ambient light in south Alabama in the summer. Many of the color measurements that were made in the field were markedly different than color measurements of similar plumage made in indoor condition. I believe that the suspicious measurements resulted from calibrating and operating the Colortron in the intense ambient light. I recommend that if Colortron measurements are made in the field, that they be made in deep shade.

A CAUTIONARY NOTE

I have heard two primary objections to using the Colortron for quantifying the coloration of bird plumage. The first problem is that ultraviolet light is not measured. LightSource Inc. has no plans to produce a unit that would show a reflectance spectrum extending into the ultraviolet (pers. comm.). Lack of measurement in the ultraviolet range is not a problem if one is describing the coloration of plumage for other humans (e.g., for taxonomic studies, species accounts, etc.). It may be a problem, however, when one is studying the function and evolution of plumage coloration. It is well known that many species of birds can see ultraviolet light (reviewed in Bennett and Cuthill 1994, Bennett et al. 1994) and that some plumage has peaks of light reflection below the 390 nm cutoff of the Colortron (Andersson 1996, Bennett and Cuthill 1994). Most carotenoid pigments (exceptions would include violet carotenoids) reflect light primarily in the visible spectrum (Goodwin 1973, Moss and Weeden 1976, Gross 1987), and ignoring reflected light below 390 nm makes little difference in a description of their coloration. For other types of plumage (including white plumage) that obtain their coloration from structural elements of the feather or that are pigmented with melanins, it would be wise to check the reflectance spectrum with a reflectance spectrophotometer that measures light reflection down to about 300 nm. If there are no additional reflectance peaks or significant light reflection in the ultraviolet region, then one could make an argument for focusing an investigation on the visible spectrum and using the Colortron to quantify color variation.

A second criticism of the Colortron is that it generates color vision coordinates (hue/saturation/brightness) that are based on the three-cone system of the human eye. Most birds have at least four types of cones in their retinas (Bowmaker 1977, Chen and Goldsmith 1986). The criticism is that tri-stimulus scores do a poor job of describing color as a bird would see it. My response to this is that, first, the Colortron gives not only tristimulus description but also the reflectance curve of the object being measured. Hence, one has a choice of whether to use the human-based color vision coordinates or some component of the reflectance curve. Second, although human-based color vision coordinates may only approximate the color of an object as seen by a bird, at least for carotenoid-based coloration, it appears to be a very meaningful approximation. Relative to the carotenoid-based plumage coloration of House Finches, tristimulus color scores predict mate choice patterns (Hill 1990, 1991, 1994), mortality patterns (Hill 1991), feather growth rate patterns (Hill and Montgomerie 1994), response to diet (Hill 1992), and parasite load (Thompson et. al. 1997) and they allow scientific investigation to proceed. Until someone works out the equations to convert information from a reflectance spectrum into more appropriate tetra-stimulus values (see

Bennett et al. 1994), there are few alternatives to the tristimulus shorthand. To date, biologists have used reflectance curves to make general, not statistical, comparisons between species or sexes (e.g. Andersson 1996), and nobody has compared among individuals within a population. Making an assessment of bird visual perception even more challenging is the fact that birds not only have a four-cone (or perhaps five-cone) visual system but they also have colored oil droplets in their eyes (Bowmaker 1977, 1989; Goldsmith et al. 1984). Colored oil droplets derive their coloration from carotenoid pigments, and the type and degree of color filtering may prove to vary between sexes and among individuals within a population. Given that no good alternatives exist to using color vision coordinates and that, at least for carotenoid-based pigmentation, human-based vision coordinates are good predictors of how birds respond to colored feathers, I propose that human vision coordinates are an acceptable way to proceed with investigation of the function and evolution of carotenoid-based ornamental coloration.

COMPARISON OF COLORTRON OUTPUT TO VISUAL COLOR ASSESSMENT

I compared the tristimulus color scores generated by the Colortron to the tristimulus scores from visual assessment of plumage using *The Methuen Handbook of Colour.* For this comparison I used males from two sources: (1) AHY male House Finches captured May–July 1995 and April–May 1996 on the campus of Auburn University, Lee County, Alabama, and (2) males that underwent molt on low-carotenoid diet in captivity that were scored in October 1996. Birds in the latter group were used to increase the number of drably plumaged males in the comparison. I scored the plumage of each male by comparing seven plumage regions to chips in the *Methuen Handbook of Colour* (see Hill 1990, 1992 for details). The bird was then taken by one of 12 different undergraduate assistants and its plumage coloration was quantified using the Colortron. For each of three regions (crown, underside, and rump) the students took three Colortron readings and used the Colortron software to calculate a mean Hue/Saturation/Brightness score for the three readings, which was then recorded on the banding sheet. Students did not know my book scores at the time they made color measurements with the Colortron (i.e., the measurements were taken in a blind situation).

Fifty-five male birds had complete tristimulus color scores from both the Colortron and visual assessment. I used a regression analysis to compare the mean (across all plumage regions) values separately for hue, saturation, and brightness for each of the two techniques. I also compared plumage index values (sum of all visual scores including hue, saturation, and brightness; see Hill 1990, 1992) to the PC1 scores from a principal components analysis of all (hue, saturation, and brightness) Colortron scores.

The hue scores from visual assessment and hue scores from the Colortron were highly significantly correlated ($r^2 = 0.92$, $n = 55$, $P = 0.0001$; Fig. 1). The relationship between Colortron scores and scores from *The*

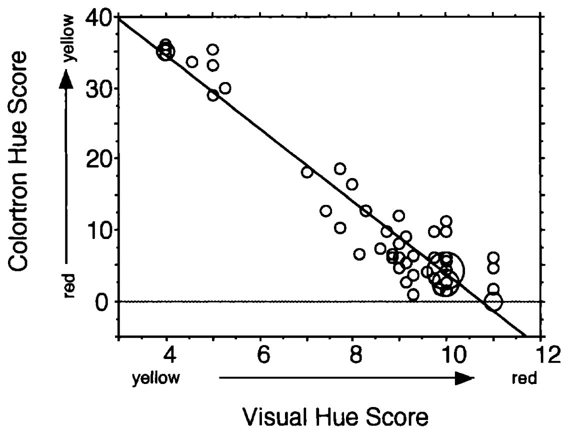

FIGURE 1. Hue scores generated by the Colortron (a hand-held reflectance spectrophotometer) in relation to hue scores of the same pigment region derived from visual comparison to *The Methuen Handbook of Colour* (n = 55). Colortron values represent the mean of color scores from the crown, rump, and ventral surface of each bird. Visual scores represent the mean color scores of the crown, eyestripe, four ventral regions, and the rump (following Hill [1992]). Point size is proportional to the number of overlapping observations.

Methuen Handbook of Colour was negative because book scores increased from 4 to 11 from yellow to red, while Colortron scores decreased from 35 to −1 from yellow to red. The saturation scores from visual assessment and saturation scores from the Colortron were also significantly correlated (r^2 = 0.42, n = 55, P = 0.0001; Fig. 2). There was no hint of relationship between brightness scores from the book and brightness scores from the Colortron (r^2 = 0.01, n = 55, P = 0.97). There was a significant

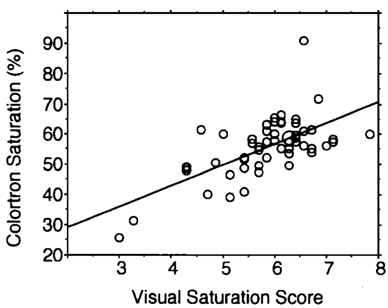

FIGURE 2. Saturation (=intensity) scores generated by the Colortron (a hand-held reflectance spectrophotometer) in relation to saturation scores of the same pigment region derived from visual comparison to *The Methuen Handbook of Colour* (n = 55). See Figure 1 for how machine and visual-scores were derived. Point size is proportional to the number of overlapping observations.

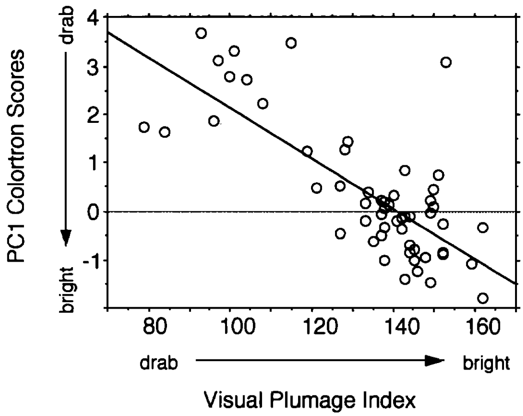

FIGURE 3. Overall plumage color scores generated by the Colortron (a hand-held reflectance spectrophotometer) in relation to overall plumage color scores of the same pigment region derived from visual comparison to *The Methuen Handbook of Colour* (n = 55). Hue, saturation, and brightness scores were derived from Colortron measurements as described in Figure 1, and then an overall Colortron color scores was calculated as the first principal component score from a principal component analysis including all color values. Plumage index from visual assessment was calculated by summing the hue, saturation, and brightness scores from all plumage regions. Point size is proportional to the number of overlapping observations.

positive relationship between the plumage index scores and PC1 score from Colortron data ($r^2 = 0.55$, $n = 55$, $P = 0.0001$; Fig. 3).

There are several interesting conclusions that can be drawn from the results of this comparison. First, the strong correlations between machine-generated color scores and scores generated through my visual assessment, support the assertion that my method of visually scoring color is relatively accurate and hence strengthens the research that I have published based on visual scoring techniques (Hill 1990, 1991, 1992, 1993, 1994; Hill and Montgomerie 1994; Hill et al. 1994). The relative strength of the correlation coefficients from the various comparisons correspond with my general confidence in different aspects of visual assessment. I find it relatively easy to assign a hue score to patches of feathers, more difficult to assign a saturation score, and very tough to assign a tone score. Moreover, in my visual assessment, the range in hue scores (4–11) is larger than the range in saturation scores (3–8), which is larger than the range in tone scores (4–6). With only three tone scores assigned to birds, virtually none of the variation was accurately recorded, and not surprisingly, there was no relationship between machine scores (which presumably are more accurate) and book scores. House Finches are exceptional in the amount of individual variation in the plumage hue of males observed in single populations. For most species of passerine with ornamental plumage, variation in hue is much more subtle and may not be measurable with a visual scoring system. By more accurately and precisely recording variation in coloration, the Colortron may help uncover patterns that have been obscured by poor color measurement in past studies (see also Zuk and Decruyenaere 1994).

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