

TETRACOLORSPACE

Version 1a

MARY CASWELL STODDARD AND RICHARD O. PRUM

USER'S MANUAL

The visual systems of birds, many other reptiles, and many fishes include four color-sensitive retinal cone types. As a consequence, their color vision is more complex than human color vision. We have developed a new computational tool that will allow users to model the visual color stimuli for these tetrahedral visual systems.

TETRACOLORSPACE is a computer program developed for the tetrahedral analysis of colors measured from reflectance spectra or four cone stimulus values, using MATLAB 7 software (MathWorks, Natick, MA). TETRACOLORSPACE can analyze colors based on ultraviolet or violet cone-type avian visual systems, or use any four cone-sensitivity functions input by the user. TETRACOLORSPACE provides an assortment of quantitative analyses and graphical tools for describing color stimulus variation and diversity. Details are available in Stoddard and Prum (2008).

TETRACOLORSPACE is provided for free at <http://www.yale.edu/eeb/prum/>. When using the program, please cite the original publication:

Stoddard, M. C. & Prum, R. O. 2008. Evolution of avian plumage color in a tetrahedral color space: A phylogenetic analysis of new world buntings. *American Naturalist*, 171, 755-776.

GETTING STARTED

TETRACOLORSPACE requires MATLAB 7 software (available for purchase from www.mathworks.com). The Mapping Toolbox add-on is required for the Robinson Projection feature.

Download the **TETRACOLORSPACE** m-file and save it in the MATLAB path. You can set the path by going to **File > Set path** in the MATLAB workspace. Save the Excel files containing the data you wish to import in the same location.

Excel matrices may take one of two forms, depending on the type of data you have.

For reflectance spectra, the matrix should occupy the upper left-hand corner of the Excel file's first worksheet and should have the following general format, with wavelength values (nanometers) in the left-hand column and reflectance values in subsequent columns:

	crown	back	rump	throat	breast	belly	...
300.0500	26.5599	9.4325	15.4560	8.0475	6.1198	7.5456	...
300.4200	26.6650	9.4509	15.4530	8.0358	6.1454	7.4923	...
300.8000	26.9244	9.8091	15.8554	8.5285	6.6647	7.7981	...
301.1700	26.7138	9.5101	15.3388	8.1514	6.1684	7.5190	...
301.5400	26.8933	10.0489	15.8211	8.4540	6.3504	7.7324	...
301.9100	26.8532	10.0740	15.8709	8.3564	6.3689	7.7755	...
302.2800	27.6446	10.4787	16.1085	8.5605	6.6273	8.0674	...
302.6600	27.1638	10.3770	15.9295	8.2208	6.0051	7.7091	...
303.0300	27.995	11.2221	16.7254	8.7492	6.6960	8.4136	...
303.4000	27.9646	11.1451	16.6244	8.7412	6.6489	8.1883	...
303.7700	28.1108	11.3498	16.6868	8.9934	6.8884	8.4025	...
...

For each color stimulus, TETRACOLORSPACE calculates the average reflectance value for each 1-nm window between 300 nm and 700 nm. Data points outside this range may be included in the imported file but will be ignored.

In the above example, the matrix includes the reflectance spectra for all color patches on a bird. However, you may wish to analyze multiple spectra of the same patch (*e.g.*, the “crowns” from multiple individuals). As long as the input matrix is in the format shown above, TETRACOLORSPACE can perform the tetrahedral analyses. Patch names must be included. The first character of the patch name **may not** be a number, but numbers later in the name are acceptable.

For photon catch values already calculated from digital photographs or reflectance spectra, the matrix should occupy the upper left-hand corner of the Excel file’s first worksheet and should have the following general format:

	u/v	s	m	l
crown	0.4867	0.3211	0.1096	0.0826
back	0.1945	0.0646	0.4529	0.2880
rump	0.3577	0.1228	0.1912	0.3283
throat	0.2019	0.1044	0.1806	0.5132
breast	0.1784	0.0735	0.1546	0.5935
belly	0.1967	0.0912	0.1860	0.5261

Note that {*u/v s m l*} values should sum to 1.

To run the **TETRACOLORSPACE** m-file, type “TetraColorSpace” in the MATLAB command window and press Enter. The TETRACOLORSPACE Main Menu should appear with instructions for importing Excel files containing color data and performing a range of analyses.

To stop running the program at any time, press Control + C.



HOW TO USE TETRACOLORSPACE

When you run the **TETRACOLORSPACE_Version_1a** m-file, the **TETRACOLORSPACE Main Menu** prompts you to select the type of data contained in Excel files:

- 1) **Reflectance spectra.**
- 2) **Photon catch data** (already calculated from digital photographs or reflectance spectra).

Selecting 2) **Photon catch data** calls the **Select analysis** menu, the same as in Step 6 for reflectance spectra, described below.

- 3) **Quit.**

Select to exit the program. Press enter in the MATLAB Command Window to close all windows.

Selecting 1) **Reflectance spectra** calls the **Spectra menu**. Click on the first button. Each step should be performed in sequence, although steps 2 and 3 may be omitted. After each step, an output line appears in the MATLAB Command Window.

- 1) **Load spectra file.**

Following the format instructions given above, open the file containing the matrix of reflectance spectra you wish to analyze.

- 2) **Load additional spectra files (OPTIONAL).**

If you wish to analyze spectra contained in multiple Excel files, you may use this option to input additional files. TETRACOLORSPACE combines the data contained in the Excel files and analyzes all colors together. Spectra files should be in the format described above.

- 3) **Load ambient light spectra (OPTIONAL).**

By default, TETRACOLORSPACE estimates the stimulation of each color cone type $\{u/v\ s\ m\ l\}$ by the reflectance spectrum under idealized illumination, following Goldsmith (1990). You may select this option to incorporate ambient light variation, following Endler and Mielke (2005). For details, see “How TetraColorSpace Works.” For ambient light spectra, the matrix should occupy the upper left-hand corner of the Excel file’s first worksheet and should have the following general format, with wavelength values (nanometers) in the left-hand column and the ambient light spectrum in the right-hand column.

300	0.000134
301	0.000142
302	0.000166

303	0.000183
304	0.000183
305	0.000183
...	...

For ambient light spectra, TETRACOLORSPACE calculates the average reflectance value for each 1-nm window between 300 nm and 700 nm. Data points outside this range may be included in the imported file but will be ignored.

4) Choose UVS-type vision or VS-type vision for color analyses.

Colors can be analyzed using the following spectral sensitivity curves:

1. Average avian UVS cone-type retina (Endler and Mielke 2005, supplementary online materials)
2. Blue Tit UVS cone-type retina (from N. Hart, see Hart et al. 2000a; see also Hart et al. 2000b; Hart and Vorobyev 2005)
3. Starling UVS cone-type retina (from N. Hart, see Hart et al. 1998)
4. Average avian VS cone-type retina (Endler and Mielke 2005, supplementary online materials)
5. Peafowl VS cone-type retina (from N. Hart, see Hart 2002)
6. Input your own curves. To use spectral sensitivities for another species, select this option to import a matrix containing spectral sensitivities for each 1-nm window from 300 nm to 700 nm. The matrix should occupy the upper left-hand corner of the Excel file's first worksheet and should have the following format, with wavelength values (in 1-nm windows from 300 to 700) in the left-hand column and spectral sensitivity values in subsequent columns:

300	1.82E-08	0	0	0
301	2.42E-08	0	0	0
302	3.06E-08	0	0	0
303	4.05E-08	0	0	0
304	5.65E-08	0	0	0
...
700	2.40E-06	9.82E-07	2.52E-07	2.24E-05

5) Process spectra.

TETRACOLORSPACE normalizes the reflectance spectrum to have an integral equal to 1. Colors with normalized brilliance <5% are placed at the achromatic center because they are so dark that they yield random hues. The idealized stimulation values $\{u/v\ s\ m\ l\}$ are converted to a point with X, Y, and Z coordinates. For details, see "How TetraColorSpace Works."

6) Analyses

The **Select analysis** menu is called, providing an assortment of quantitative analyses and graphical tools for describing color stimulus variation and diversity. Numeric output is shown in the Command Window, and can be copied and pasted into Excel or another program. Plots and figures are shown in the Figure Window. In the Figure Window, you can zoom in and out, change the size or rotation of the image, and make a number of other modifications using the toolbar at the top of the window. You can save the figure as MATLAB Figure (.fig), which allows you to reopen the figure and modify it without redoing the analysis. Figures may also be copied and pasted or saved directly as an image, with many different formats available.

For details on the analyses listed below, see “How TetraColorSpace Works.”

1. Relative stimulation values of the UVS/VS, SWS, MWS, and LWS cones for color patches.
2. Tetrahedral plot.
3. Robinson projection. (*For use with MATLAB add-on Mapping Toolbox*)
4. Hue functions.
5. Summary of hue and chroma for all colors.
6. Brilliance analysis.
7. Color span analysis and distance matrix.
8. Color volume analysis.
9. Hue disparity analysis.
10. Summary of color measurements.
11. Return to main menu.

7) Return to main menu.

You may begin again by selecting a new Excel file or you may quit.

HOW TETRACOLORSPACE WORKS

TETRACOLORSPACE allows the user to input a matrix of reflectance spectra. For each color in the matrix, TETRACOLORSPACE uses a model based on avian vision to calculate the photon catch for each color cone type, plot the color in tetrahedral color space, and describe its hue and chroma. For each set of colors mapped in color space, a wide range of analyses are performed. This section is adapted from Stoddard and Prum (2008) and accompanying Supplementary Methods and Analyses (online appendix). The equation numbers here refer to the equations provided in the appendix.

I. CALCULATING PHOTON CATCH

To estimate the stimulation of each color cone type $\{u/v\ s\ m\ l\}$, following Goldsmith (1990), TETRACOLORSPACE calculates the idealized stimulus, Q_I , of each color cone type by the reflectance spectrum of a plumage patch:

$$Q_I = \int_{300}^{700} R(\lambda) C_r(\lambda) d\lambda, \quad (\text{A1})$$

where $R(\lambda)$ is the reflectance spectrum of the plumage patch and $C_r(\lambda)$ is the spectral sensitivity function of each cone type r . TETRACOLORSPACE normalizes both the $R(\lambda)$ and $C_r(\lambda)$ functions to have to integrals of 1. Stimulus Q_I is equivalent to Q_r of Endler and Mielke (2005; their eq. [4]) but with the further extension of their simplifying assumption about the transmission spectrum and the veiling light to the ambient light. Following Goldsmith (1990), TETRACOLORSPACE treats the irradiance spectrum $I(\lambda)$ as a constant across all visible wavelengths, with an integral equal to 1. The idealized stimulation values of the four color cones— Q_I —are normalized to sum to 1, yielding relative $\{u/v\ s\ m\ l\}$ values.

TETRACOLORSPACE uses average spectral sensitivity curves for ultraviolet cone- and violet cone-type retina from Endler and Mielke (2005, supplementary online materials) as well as spectral sensitivity curves for Blue Tit (UVS), Starling (UVS), and Peafowl (VS) retina shared with us by N. Hart (see Hart et al. 2000a, Hart et al. 1998, Hart 2002, see also Hart et al. 2000b; Hart and Vorobyev 2005).

TETRACOLORSPACE provides users with the option of inputting an ambient light irradiance spectrum. Following Endler and Mielke (2005), TETRACOLORSPACE calculates:

$$Q_r = \int_{300}^{700} R(\lambda) I(\lambda) C_r(\lambda) d\lambda, \quad (\text{A4})$$

where $R(\lambda)$ is the reflectance spectrum of the plumage patch, $I(\lambda)$ is the ambient irradiance spectrum, and $C_r(\lambda)$ is the spectral sensitivity function of each cone type r , assuming perfect transmission and no veiling light.

TETRACOLORSPACE then calculates the q_r of Endler and Mielke (2005) by performing the von Kries transformation for achieving color constancy:

$$q_r = \frac{\int_{300}^{700} R(\lambda) I(\lambda) C_r(\lambda) d\lambda}{\int_{300}^{700} I(\lambda) C_r(\lambda) d\lambda}. \quad (\text{A5})$$

The von Kries transformation normalizes the quantal catch estimate of each cone channel by dividing it by the quantity of stimulation of a flat, achromatic spectrum under the ambient light. In Endler and Mielke (2005, eq. [10]), following Fechner's Law, the q_r values are log transformed before normalizing to a sum of 1, producing $\{u/v\ s\ m\ l\}$ values of signaler sensory experience to plot in tetrahedral color space. However, we (Stoddard and Prum 2008) found that this produced complex and poorly understood effects on quantal catch values. Therefore, TETRACOLORSPACE does not perform log transformations.

For the avian visual system under natural ambient light spectra, our calculations (Stoddard and Prum 2008) showed that the von Kries transformation is highly effective. The Goldsmith (Q_l) and Endler and Mielke (q_r) estimates of cone stimuli yielded essentially identical color space vectors under natural illumination. Thus, incorporating ambient light spectra and using von Kries color correction produces the same exact result as ignoring ambient light composition entirely (Stoddard and Prum 2008). Consequently, we see no benefit to using ambient light spectral measurements in modeling of avian color stimuli.

II. PLOTTING IN TETRAHEDRAL COLOR SPACE

TETRACOLORSPACE uses the geometry defined by Endler and Mielke (2005), which places the achromatic point of equal cone stimulation (i.e., white, black, or gray) at the origin of a Cartesian coordinate system and the UVS, or u (or VS, v), vertex along the vertical Z -axis. The relative stimulation $\{u/v\ s\ m\ l\}$ data for any color can be converted to a color point in the tetrahedral color space with the Cartesian coordinates X , Y , and Z by the equations (Endler and Mielke 2005) :

$$\begin{aligned}
 X &= \frac{1 - 2s - m - u}{2} \sqrt{\frac{3}{2}}, \\
 Y &= \frac{-1 + 3m + u}{2\sqrt{2}}, \\
 Z &= u - \frac{1}{4}.
 \end{aligned}
 \tag{A2}$$

The Cartesian (X , Y , Z) coordinates of each color point are then converted to its spherical coordinates— θ , ϕ , and r —that define the color vector.

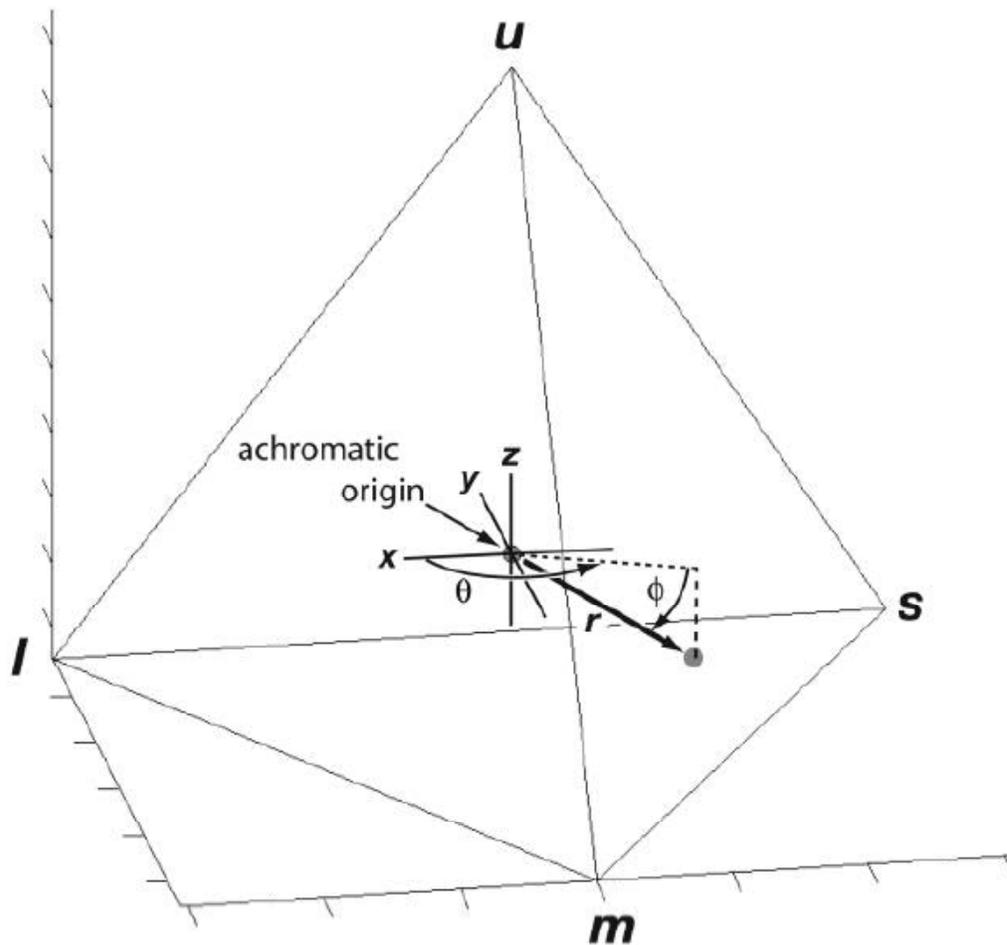


Figure 1: A tetrahedral color space. Each color is a point in the tetrahedron determined by the relative stimulation of the four cone color channels— u (or v), s , m , and l . The achromatic point of equivalent stimulation of all channels is at the origin, and the ultraviolet or violet channel, u or v , is along the Z -axis (Endler and Mielke 2005). Each color can be described by a vector with the spherical coordinates θ , ϕ , and r . Angle θ is the horizontal, azimuth angle from the positive X -axis to the color vector. Angle ϕ is the vertical, elevation angle from the X - Y plane to the color vector. θ and ϕ are analogous to longitude and latitude, respectively. The length of the color vector is given by r . Together, θ and ϕ describe the hue, or the direction, of the color vector, and r is a measure of chroma, or saturation, which describes how different a color is from achromatic white/black.

III. DESCRIBING HUE AND CHROMA

TETRACOLORSPACE computes θ , ϕ , and r for all colors. The advantage of using spherical coordinates is that the position of the color point is described in terms of three meaningful quantities rather than the X , Y , Z coordinates, which are only an arbitrary frame of reference for the tetrahedron. The angles θ and ϕ define the hue, or the direction of the color vector. Angle θ is the angular displacement of the color vector from the positive X -axis, which runs between the m (green) and l (red) vertices. Values of θ range from $-\pi$ to $+\pi$. Angle ϕ is the angular displacement of the color vector from the horizontal X - Y plane. Values of ϕ range from $-\pi/2$ to $+\pi/2$. The chroma, or saturation, of a color is given by the magnitude of r , or its distance from the achromatic origin.

Because the color space is a tetrahedron and not a sphere, different hues vary in their potential maximum chroma, or r_{\max} . The four pure hues at the vertices of the tetrahedron have $r_{\max} = 0.75$. All other hues have $r_{\max} < 0.75$, because a vector of any other hue with $r = 0.75$ would extend beyond the boundaries of the color space. It may be more informative to define the chroma of a color relative to the maximum chroma possible for its hue rather than to its absolute difference from achromatic ($r = 0$) or the maximum chroma of a pure hue ($r = 0.75$). Consequently, TETRACOLORSPACE also calculates the achieved chroma, $r_A = r/r_{\max}$ for each color patch.

To determine the maximum possible chroma r_{\max} for any hue, we identify α_{\max} , the largest of the angles formed between the hue vector and the $\{u/v\ s\ m\ l\}$ vertex vectors. Angle α_{\max} is always the angle between the hue vector and the vertex vector opposite the side of the tetrahedron through which the hue vector points. Using geometry,

$$r_{\max} = \frac{0.25}{\cos(\pi - \alpha_{\max})}. \quad (\text{A11})$$

For a given hue, r_{\max} is the r value at which the cone channel with the most negative slope equals 0. Thus, the functions for relative stimulation versus chroma only apply only over the domain of $r = 0$ to r_{\max} .

IV. COLOR ANALYSES

TETRACOLORSPACE provides a wide range of quantitative analyses and graphical tools for describing color variation and diversity. These include:

- 1. Relative stimulation values of the UVS/VS, SWS, MWS, and LWS cones for color patches.**

The stimulation of each color cone type, or the $\{u/v\ s\ m\ l\}$ photon catches, are calculated as described in Section I above.

- 2. Tetrahedron plot.**

Colors are plotted in the tetrahedral color space as described in Section II above.

3. Robinson projection. *(For use with MATLAB add-on Mapping Toolbox)*

A convenient graphical way to visualize hue variation independently of chroma is to project the hue vectors of each color onto a unit sphere centered at the origin and to view the distribution of hues on the sphere, using the Robinson projection ((Endler et al. 2005), which is commonly used to represent a map of the earth in two dimensions. The Robinson projection is a compromise between the distortions of equal-area and conformal projections.

4. Hue functions.

Hue—the direction of the color vector—is determined by the proportions, or ratios, of the differences in stimulation among the four color channels. A given hue does not have a unique combination of relative stimulation $\{u/v\ s\ m\ l\}$ values. Points along any straight line from the achromatic origin share the same hue; only the chroma, or the magnitude of the color vector, is changing. Thus, there are infinite $\{u/v\ s\ m\ l\}$ combinations that will produce a given hue.

TETRACOLORSPACE calculates the set of four functions that describe how stimulation of the four color channels—ultraviolet or violet (u), short wavelength (s), medium wavelength (m), and long wavelength (l)—varies as a function of chroma r for any given hue, θ and ϕ . These functions are:

$$u(r) = r \cos(\alpha_{h/u}), \quad (\text{A7})$$

$$s(r) = r \cos(\alpha_{h/s}), \quad (\text{A8})$$

$$m(r) = r \cos(\alpha_{h/m}), \quad (\text{A9})$$

$$l(r) = r \cos(\alpha_{h/l}), \quad (\text{A10})$$

where α is the hue disparity angle between the hue vector (h) and each of the vertex vectors u/v , s , m , and l , which extend from the achromatic origin to each vertex of the tetrahedron. The value of α is calculated using

$$\cos \alpha = \cos(\phi_1) \cos(\phi_2) \cos(\theta_1 - \theta_2) + \sin(\phi_1) \sin(\phi_2). \quad (\text{A3})$$

where θ_1 and ϕ_1 are the hue angles of the color vector, and, in this case, θ_2 and ϕ_2 are the hue angles for the specified u/v , s , m , and l vertex vector.

At the achromatic origin ($r = 0$), all vectors have equivalent reflectance, or stimulation, among all four channels. As r increases, the stimulation of each cone changes linearly by the slope of $\cos \alpha$. The slopes of the four functions sum to 0 because the sum of the four channel values remains equal to 1.

5. Summary of hue and chroma for all colors.

TETRACOLORSPACE displays θ and ϕ (hue) and r (chromaticity) for each color, along with maximum chroma, r_{\max} , and achieved chroma, r_A .

6. Brilliance analysis.

Brilliance is processed independently from color and therefore is not analyzed using the color space. For each color patch, TETRACOLORSPACE averages the reflectance values for each 1-nm window between 300 and 700 nm. It determines the peak percent reflectance (intensity), the wavelength λ_{\max} of maximum reflectance, and normalized brilliance $(\text{total reflectance})/(100 \times N)$, where total reflectance is the sum of percent reflectance at all data points between 300 and 700 nm and N is the number of data points between 300 and 700 nm ($N = 401$).

7. Span analysis and distance matrix.

For a set of colors, TETRACOLORSPACE computes the average color span, which is the average of the Euclidean distances between each pair of colors in color space (Δ_T of Endler and Mielke [2005]) and the variance in the color span. Average color span is a measure of overall color contrast among the patches in the plumage, and color span variance measures the uniformity of the color contrast within the plumage.

TETRACOLORSPACE can also display the distance matrix, which shows the distances between all color pairs.

8. Volume analysis.

TETRACOLORSPACE calculates the volume of the color space occupied by a set of colors by computing the volume of the minimum convex polygon that contains all the color points of the plumage. TETRACOLORSPACE uses the CONVHULLN command in MATLAB. Plumage color volume is a measure of diversity in color within a plumage. Unlike span, color volume captures the three-dimensional breadth of color space occupancy. The convex hull is shown in the tetrahedral plot.

9. Hue disparity analysis.

A measure of contrast in hue that is independent of chroma is hue disparity. Hue disparity α is the magnitude of the angle between two color vectors.

TETRACOLORSPACE calculates α by:

$$\cos \alpha = \cos(\phi_1) \cos(\phi_2) \cos(\theta_1 - \theta_2) + \sin(\phi_1) \sin(\phi_2). \quad (\text{A3})$$

where θ_1 and ϕ_1 and θ_2 and ϕ_2 and are the spherical azimuth and elevation angles for any two color vectors, respectively.

Hue disparity can be understood in terms of color complementarity. Complementary colors have maximum hue disparity, $\alpha = \pi$. Alternatively, hue complementarity can be

defined as α/π and reported on a proportional scale of 0 (identical) to 1 (complementary). TETRACOLORSPACE calculates the average hue disparity of all patches in each plumage, which gives a measure of overall hue contrast within a plumage. It also calculates the variance in hue disparity, which is a measure of the uniformity of hue contrast among plumage patches, and can display the hue disparity matrix showing hue disparity between each pair of colors in a set.

10. Summary of color measurements.

TETRACOLORSPACE displays the average color span, span variance, maximum span, volume, average hue disparity, hue disparity variance, maximum hue disparity, average normalized brilliance, and average chroma for a set of colors.

KNOWN BUGS

- There appear to be some MATLAB 7 compatibility problems on Macintosh computers. Plotting colors with labels for the tetrahedral and volume plots does not work. This appears to be related to the “horzcat” command. We are looking into a fix for this problem.
- MATLAB 6 does not recognize the “markeredgecolor” command. We are looking into a fix for this problem.

WHERE TO GO FOR HELP

Questions? Please contact Mary Caswell Stoddard at TetraColorSpace@gmail.com.

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