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QUANTIFYING COLOR VARIATION: IMPROVED FORMULAS FOR CALCULATING HUE WITH SEGMENT CLASSIFICATION¹

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- *Premise of the study:* Differences in color form a major component of biological variation, and quantifying these differences is the first step to understanding their evolutionary and ecological importance. One common method for measuring color variation is segment classification, which uses three variables (chroma, hue, and brightness) to describe the height and shape of reflectance curves. This study provides new formulas for calculating hue (the variable that describes the “type” of color) to give correct values in all regions of color space.
- *Methods and Results:* Reflectance spectra were obtained from the literature, and chroma, hue, and brightness were computed for each spectrum using the original formulas as well as the new formulas. Only the new formulas result in correct values in the blue-green portion of color space.
- *Conclusions:* Use of the new formulas for calculating hue will result in more accurate color quantification for a broad range of biological applications.

Key words: brightness; chroma; flower color; hue; reflectance spectrum; segment classification.

Quantification of color variation is a crucial component of many evolutionary and ecological studies. Color is involved in a wide range of biological phenomena, such as thermoregulation, crypsis, mimicry, and communication (Chittka and Menzel, 1992; Endler, 1993; Forsman et al., 2002; Robertson and Rosenblum, 2009). In plants, color is particularly important for signaling to pollinators, attracting seed dispersers, and mediating interactions with herbivores (Gautier-Hion et al., 1985; Irwin et al., 2003; Fenster et al., 2004; Strauss and Cacho, 2013). Variation in color may appear in different parts of the same individual as well as among individuals of the same species and between individuals of different species. Measuring this color variation is commonly the first step in determining its biological significance.

The way in which color is measured will depend on the objective of any given study, but can be broadly divided into two approaches, one which is independent of any particular visual system and one in which the observer of the object is taken into account (Endler, 1990; Chittka, 1992; Vorobyev and Osorio, 1998). Different observers can perceive the color of a given object differently, even in the same light environment, because of differences in their visual systems. For example, birds have four types of cones in their retinas (ultraviolet, short-, medium-, and long-wavelength) while humans only have the last three types (Bowmaker et al., 1997; Roorda and Williams, 1999). Other differences, such as the relative abundance of cone types and the spectral properties of the visual pigments, can further amplify

differences in the spectral sensitivity and in the perceived color. Thus, when the visual system of the observer is well characterized, the most relevant measure of color is that which accounts for the spectral sensitivities of that observer.

However, a measure of color independent of a particular species' visual system is often more appropriate. Some research questions are not related to a particular observer, e.g., color variation as an adaptation to heat stress or other environmental conditions (Lacey et al., 2010). Also, comparative studies or meta-analyses are often not focused on a single observer and require color measurements that are comparable across species (Hodges et al., 2002; Altshuler, 2003; Smith et al., 2008; Parra, 2010). Finally, even when a certain observer is of interest, its visual system or that of a closely related species may not have been studied. In such cases, one of the most popular approaches for quantifying color is the segment classification method, which uses three variables (chroma, hue, and brightness) to describe the shape and height of reflectance spectra and identify their location in color space (Endler, 1990). These continuous variables are easily calculated, amenable to analysis, and often capture the majority of the variation present in color spectra (Grill and Rush, 2000). However, the original description of one of the variables, hue, is insufficient to calculate its value across the range of spectra in color space. Here I provide improved formulas for computing hue and give examples across the range of colors. Accurate and comparable measurements of hue are a necessity for any future meta-analyses of the growing body of color literature.

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METHODS AND RESULTS

Quantifying and comparing colors with the segment classification method begins with the measurement of reflectance spectra. A reflectance spectrum is a graph depicting the amount of light reflected by an object at different

wavelengths. These spectra are typically obtained using a light source and spectrometer with a fiber optic probe (e.g., from Gröbel UV-Elektronik, Ettlingen, Germany, or Ocean Optics, Dunedin, Florida, USA). The raw reflectance values are standardized by comparison to a white reference standard that evenly reflects all wavelengths of light (e.g., Spectralon, Labsphere, North Sutton, New Hampshire, USA). Examples of standardized reflectance spectra are shown in Fig. 1. Spectra differ by the total amount of light reflected (area under the curve) and the shape of the curve. For example, a red object will reflect more light in the upper “red” end of the spectrum while a white object will reflect all colors of light more or less equally.

The segment classification method aims to capture the variation across reflectance spectra through three variables: chroma, hue, and brightness. Brightness (sensu Endler, 1990) is simply the total area under the curve from 400 to 700 nm, while chroma and hue are calculated by comparing values in different segments of the visible spectrum. First, the spectrum is divided among four equal segments (blue or “B”: 400–475 nm, green or “G”: 475–550 nm, yellow or “Y”: 550–625 nm, and red or “R”: 625–700 nm). The relative brightness of each segment is calculated by summing the area under the curve in that range and dividing by the total brightness. As many animals detect color by opposing input from different receptors (e.g., short-, medium-, and long-wavelength receptors), these relative brightness values are converted to a long vs. medium contrast (*LM*), which equals *R-G*, and a medium-short contrast (*MS*), which is *Y-B*. For any spectrum, the *LM* and *MS* values can be plotted in a two-dimensional graph where *LM* is the value along the y-axis and *MS* is the value along the x-axis (Fig. 2). In this color space, chroma (the saturation of color) is the radius, i.e., the distance of the spectrum from the origin. Following geometric principles, this value can be calculated as $\sqrt{LM^2 + MS^2}$. Spectra with no chroma (white, gray, black) will appear at the center (the origin), and those with high chroma will appear toward the outside. Hue (*H*), the type of color, corresponds to the angle clockwise from the positive y-axis (Endler, 1990). Red colors will have small values (i.e., be close to 0°), while yellow, green, and blue colors will be near 90°, 180°, and 270°, respectively (Fig. 2).

As an angle ranging from 0–360° or 0–2π radians, hue can be calculated from *x* and *y* Cartesian coordinates (*LM* and *MS*) following basic principles of geometry. However, the original description of the metric (Endler, 1990) provided formulas that only result in correct values for a portion of color space. Here, I describe revised formulas that give correct values in all regions of color space and explain their application. I begin by reviewing the formulas originally presented (Endler, 1990), which use either *LM* or *MS* along with chroma (*C*) to calculate the angle *H*:

$$H = \arcsin(MS/C); \quad (1)$$

$$H = \arccos(LM/C); \quad (2)$$

When spectra fall into the upper right quadrant of the color space (Fig. 2), these formulas will provide correct values for *H* (Table 1). However, Eq. 1 will not give correct values in other quadrants, and Eq. 2 similarly gives incorrect values in the left quadrants where *MS* is negative (Table 1). This is because the signs of *LM* and *MS* are needed to specify the quadrant in which the point will fall before the correct angle can be calculated. Using the arcsine and modulus functions, the following equations will specify *H*, the angle clockwise from *R*:

$$\text{If } LM > 0, H = \arcsin(MS/C) \text{ modulus } 2\pi; \quad (3)$$

$$\text{If } LM < 0, H = \pi - \arcsin(MS/C); \quad (4)$$

Similarly, hue can be calculated from the sign of *MS* and the values of *LM* and *C* with the arccosine function (Fig. 2A):

$$H = (\text{sign}(MS) * \arccos(LM/C)) \text{ modulus } 2\pi; \quad (5)$$

It should be noted that measuring the angle clockwise from *R* differs from the convention in geometry, and standard trigonometric equations for converting *x* and *y* values (here, *LM* and *MS*) to polar coordinates will result in a different angle, one that moves counterclockwise from the positive *x*-axis.

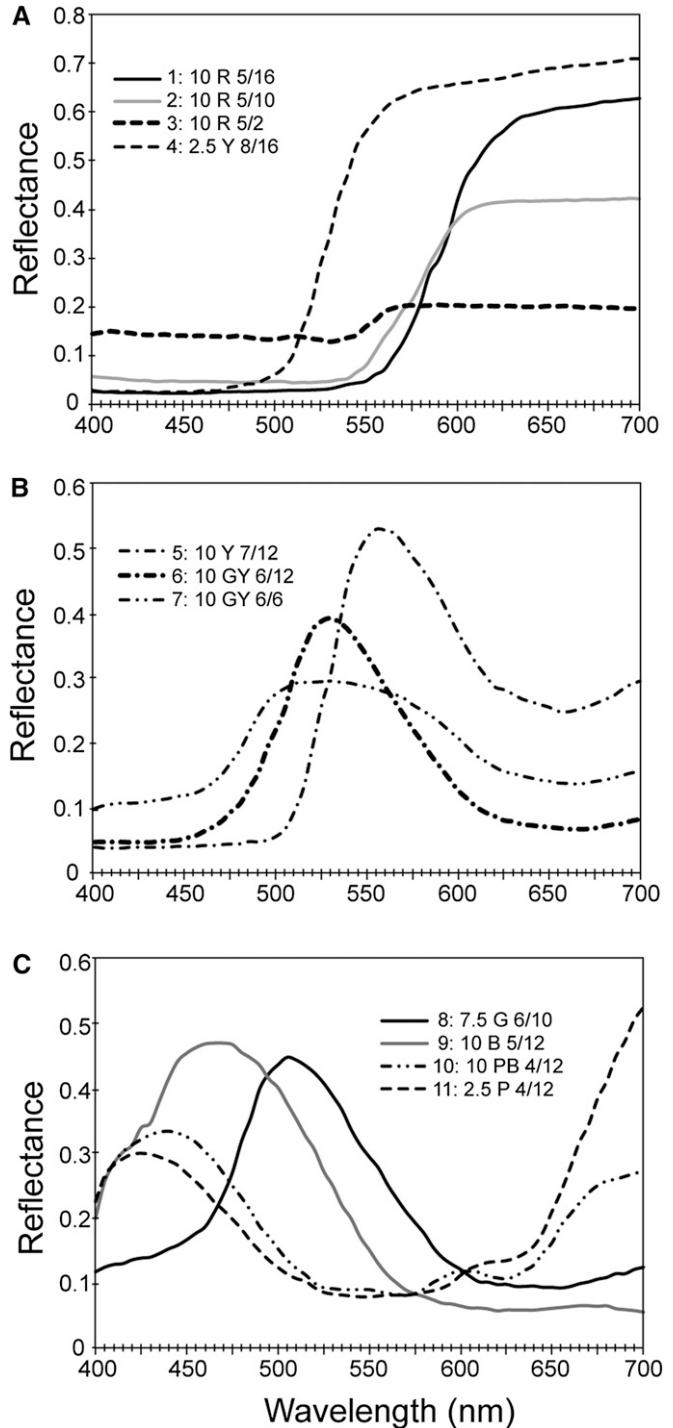


Fig. 1. Example reflectance spectra adapted from Endler (1990). The spectra are named as in the *Munsell Book of Color* (Munsell Color Company, 1976) with the format hue (number and letter) and value/chroma. The hues by letter are R (red), Y (yellow), GY (green-yellow), G (green), B (blue), BP (blue-purple), and P (purple). Red and yellow spectra appear in (A); yellow and green-yellow in (B); and green, blue, and purple in (C).

To demonstrate the application of these formulas to standardized reflectance spectra, we used the same 11 spectra measured from the *Munsell Book of Color* (Munsell Color Company, 1976) that were used in the original paper (Endler, 1990). This edition of the Munsell book is no longer accessible, so the spectra were scanned and digitized using GetData Graph Digitizer 2.24

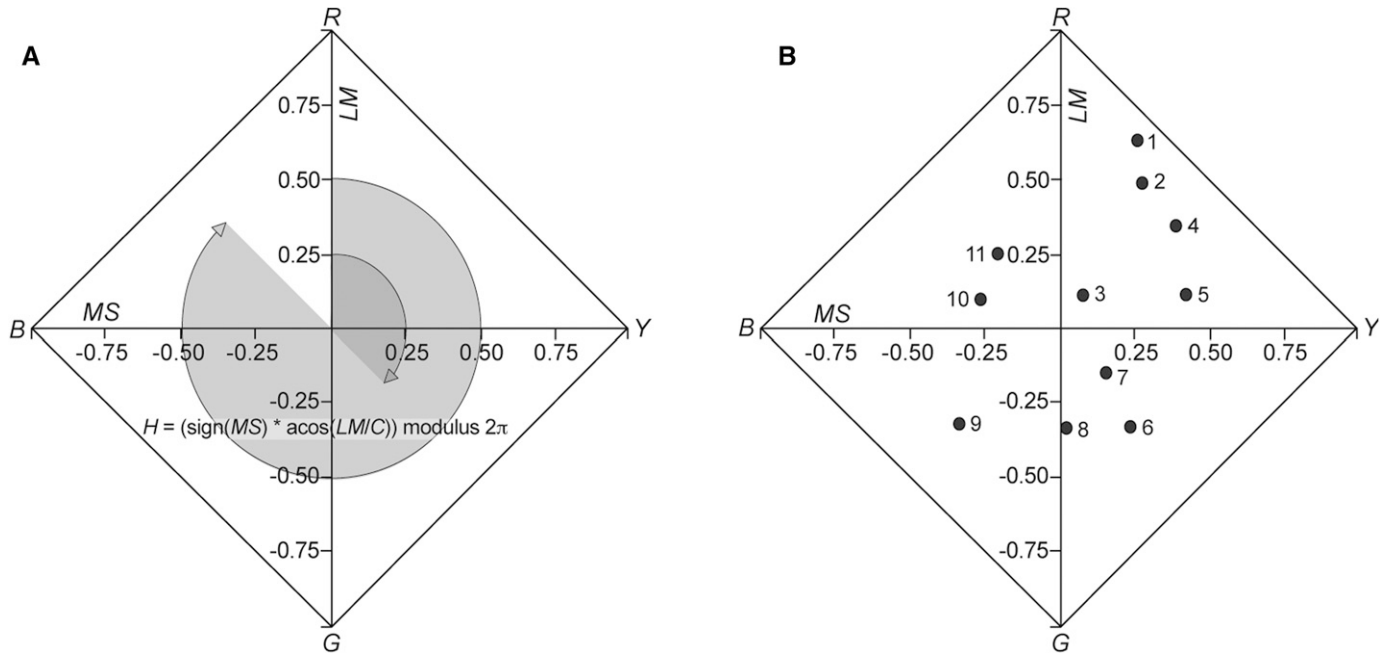


Fig. 2. (A) Color space with the segment classification system adapted from Endler (1990). *R*, *Y*, *G*, and *B* are red, yellow, green, and blue. The difference between long and medium (*R* and *G*) wavelengths (*LM*) is plotted against the difference between medium and short (*Y* and *B*) wavelengths (*MS*). For a given point, chroma (*C*) is the radius, the distance from the origin. Hue is measured as the angle clockwise from *R* (positive *LM* values). (B) Points in color space corresponding to the example reflectance spectra in Fig. 1. Values are given in Table 1.

(<http://getdata-graph-digitizer.com>) from Endler (1990: Fig. 4). The raw spectral data are presented in Appendix 1 and are also available from the author upon request.

Chroma, hue, and brightness were calculated from these spectra (Fig. 1) as described above (see also Appendix 1), and the *LM* and *MS* values were used to plot the spectra in color space (Fig. 2B). These values are presented in Table 1. As expected, spectra that reflect low amounts of light (e.g., spectrum 3) have low brightness scores while those, such as spectrum 4, that reflect highly in part or all of the spectrum show high brightness values. Chroma varied in relation to the contrast in relative brightness in segments of the spectrum; spectra with the strongest differences between reflectance in yellow and blue or red and green (e.g., spectrum 1) gave the highest chroma values. Application of either of the

new equations (Eq. 3 and Eq. 4 or 5) resulted in hue values that correspond to the position of these points in color space (Table 1). Red spectra have low values (occurring in the first quadrant) while yellow, green, blue, and purple spectra have progressively higher values.

CONCLUSIONS

The differences in hue values between the original formulas and those presented here depend on the quadrant in which a spectrum appears. When both *LM* and *MS* are positive (red to

TABLE 1. Calculation of hue values with the original and revised segment classification methods. The proportion of brightness in each segment (*R*, *Y*, *G*, *B*) was measured from the spectra in Fig. 1 as described in the text. *LM* is the difference between *R* and *G*, and *MS* is the difference between *Y* and *B*. Hue (*H*) is given in degrees but could also be given in radians. Formulas for hue presented in the original description (Endler, 1990) and their corresponding values are given in the second and fifth formula lines. Revised formulas and the resulting values are in the remaining lines. Values in bold are the correct values given the sign of *LM* and *MS*; other (incorrect) values are shown unbolded for comparison. Values in italics would be correct if adjusted by modulus 2π .

Variables	Spec1	Spec2	Spec3	Spec4	Spec5	Spec6	Spec7	Spec8	Spec9	Spec10	Spec11
Brightness	14.621	12.249	10.318	23.856	14.011	8.893	11.554	12.306	12.884	11.332	12.142
Red (<i>R</i>)	0.663	0.547	0.309	0.464	0.305	0.130	0.201	0.134	0.076	0.282	0.401
Yellow (<i>Y</i>)	0.282	0.334	0.285	0.400	0.462	0.322	0.304	0.210	0.098	0.132	0.122
Green (<i>G</i>)	0.031	0.058	0.197	0.119	0.192	0.459	0.345	0.466	0.394	0.187	0.146
Blue (<i>B</i>)	0.024	0.060	0.208	0.016	0.042	0.088	0.150	0.190	0.433	0.399	0.331
<i>MS</i>	0.257	0.274	0.077	0.384	0.420	0.234	0.153	0.020	-0.335	-0.267	-0.209
<i>LM</i>	0.632	0.489	0.112	0.345	0.113	-0.329	-0.145	-0.333	-0.318	0.094	0.255
Chroma, $C = \sqrt{(LM^2 + MS^2)}$	0.682	0.560	0.136	0.516	0.435	0.404	0.211	0.333	0.462	0.283	0.329
$H = \arcsin(MS/C)$	22.15	29.27	34.46	48.08	74.92	35.42	46.68	3.38	-46.20	-70.52	-39.34
If $LM > 0$, $H = \arcsin(MS/C)$ modulus 2π	22.15	29.27	34.46	48.08	74.92	35.42	46.68	3.38	313.51	289.48	320.66
If $LM < 0$, $H = \pi - \arcsin(MS/C)$	157.85	150.73	145.54	131.92	105.08	144.58	133.32	176.62	226.50	250.52	219.34
$H = \arccos(LM/C)$	22.15	29.27	34.46	48.08	74.92	144.58	133.32	176.62	133.51	70.52	39.34
$H = \text{sign}(MS) * \arccos(LM/C)$ modulus 2π	22.15	29.27	34.46	48.08	74.92	144.58	133.32	176.62	226.50	289.48	320.66

yellow spectra), both sets of formulas return the same values. The original arccosine formula, but not the arcsine formula, will produce correct values when LM is negative but MS is positive (yellow to green spectra, Fig. 2). However when both LM and MS values are negative (e.g., spectrum 9, Fig. 2B), neither of the original formulas can provide the correct angle. Finally, neither formula gives the correct angle when LM is positive but MS is negative (blue-purple spectra 10 and 11), although value from the original arcsine formula would be correct if adjusted by modulus 2π . By contrast, the new formulas, which incorporate the signs of LM and MS , provide correct values in all sectors of color space.

The application of these corrected formulas may improve the consistency of hue as a metric of color and facilitate its use in comparative studies. In testing methods for quantifying color variation, Grill and Rush (2000) found hue to be the least accurate among the three segment classification variables, particularly for green, blue, and purple spectra. However, this analysis relied on the original formulas, which give incorrect values in that portion of color space. Use of the revised formulas will result in accurate values for hue, a variable that can be directly compared across samples, be they different parts of an individual or different species in a clade. The paper describing the segment classification method (Endler, 1990) has been cited over 700 times, suggesting a potentially vast pool of color studies that would be amenable to broad meta-analyses. Such analyses, however, will be limited by the correct calculation of the color variables. As the correct values for hue can only be confirmed by analyzing the original spectra or, minimally, the LM and MS values, authors should deposit their spectra in publicly accessible repositories (e.g., Dryad [Piwowar and Vision, 2013] or the Floral Reflectance Database [Arnold et al., 2010]) to maximize the potential use of these data in future studies.

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APPENDIX 1. Protocol for calculating segment classification color variables.

Gather standardized reflectance spectra from 400 to 700 nm using a spectrometer and a reference standard (example data are shown in Table A1).

Sum the area under the entire curve for each spectrum (for example, all the values in column 1 for spectrum 1 in Table A1); this value is brightness.

Sum the area in each of four equal segments (blue or “B”: 400–475 nm, green or “G”: 475–550 nm, yellow or “Y”: 550–625 nm, and red or “R”: 625–700 nm) and divide by the total brightness; this is the relative brightness in each segment.

Calculate the chroma as $\sqrt{(LM^2 + MS^2)}$ where LM is $R-G$, and MS is $Y-B$.

Hue can then be calculated in the free R statistical package (www.r-project.org) with the script below. For each reflectance spectrum, simply substitute your values for R , Y , G , B , save the script to your desktop as `calcHue.R`, and run the script by entering at the command prompt: `source('~/Desktop/calcHue.R', chdir = TRUE)`. The script is also available upon request from the author. Values for hue will be output in both degrees and radians as in the example below.

#Substitute your data for the values below

```
R<-0.28
```

```
Y<-0.13
```

```
G<-0.19
```

```
B<-0.40
```

```
calcHue<-function(R=R,Y=Y,G=G,B=B, format="degrees") {  
  MS=Y-B  
  LM=R-G  
  chroma=sqrt(LM^2+MS^2)  
  unmod<-sign(MS)*acos(LM/chroma)  
  hue<-unmod%%(2*pi)  
  if (format=="degrees") {  
    hue<-hue*(180/pi)  
  }  
  else {  
    return(hue)  
  }  
}
```

```
print(calcHue(R,Y,G,B,"radians"))
```

```
#[1] 5.03414
```

```
print(calcHue(R,Y,G,B,"degrees"))
```

```
#[1] 288.4349
```

Alternately, hue (in degrees) can be calculated in Excel with the following formula: `DEGREES(MOD((SIGN(MS)*ACOS(LM/C)),(2*PI())))` where values of MS , LM , and C are calculated as described above.

Regardless of the program used, it is recommended that users test the formula with the example values given in Table A1 to be sure that the correct values are returned before proceeding with their own data.

TABLE A1. Standardized reflectance data for the 11 example spectra digitized from Endler (1990). See also Fig. 1. Values for *R*, *Y*, *G*, *B*, *LM*, *MS*, *C*, and *H* for these spectra are given in the text (Table 1).

Wavelength (nm)	1	2	3	4	5	6	7	8	9	10	11
400	0.027	0.057	0.144	0.028	0.038	0.046	0.098	0.117	0.199	0.227	0.225
405	0.025	0.055	0.147	0.026	0.037	0.046	0.103	0.124	0.255	0.260	0.264
410	0.025	0.054	0.150	0.026	0.037	0.046	0.105	0.128	0.283	0.284	0.281
415	0.024	0.052	0.148	0.026	0.037	0.046	0.107	0.130	0.300	0.301	0.290
420	0.024	0.050	0.146	0.026	0.038	0.046	0.106	0.135	0.311	0.311	0.297
425	0.024	0.049	0.144	0.025	0.038	0.046	0.107	0.138	0.338	0.320	0.299
430	0.023	0.049	0.142	0.025	0.038	0.046	0.109	0.140	0.345	0.327	0.297
435	0.023	0.047	0.142	0.023	0.038	0.047	0.111	0.145	0.379	0.331	0.293
440	0.022	0.047	0.143	0.025	0.038	0.048	0.113	0.152	0.413	0.333	0.287
445	0.022	0.048	0.141	0.025	0.040	0.049	0.117	0.158	0.440	0.330	0.280
450	0.022	0.046	0.141	0.025	0.040	0.052	0.119	0.166	0.452	0.324	0.268
455	0.022	0.047	0.140	0.025	0.040	0.056	0.122	0.176	0.461	0.315	0.255
460	0.023	0.047	0.141	0.027	0.041	0.063	0.129	0.186	0.466	0.301	0.241
465	0.023	0.047	0.139	0.028	0.041	0.070	0.139	0.208	0.468	0.287	0.224
470	0.025	0.046	0.139	0.028	0.042	0.079	0.151	0.235	0.468	0.268	0.212
475	0.025	0.046	0.138	0.034	0.043	0.093	0.170	0.269	0.465	0.249	0.198
480	0.026	0.045	0.140	0.037	0.044	0.106	0.189	0.317	0.453	0.231	0.182
485	0.026	0.045	0.138	0.041	0.047	0.130	0.217	0.353	0.445	0.211	0.164
490	0.027	0.046	0.135	0.043	0.046	0.154	0.242	0.398	0.433	0.186	0.149
495	0.027	0.046	0.133	0.052	0.049	0.193	0.264	0.421	0.413	0.171	0.135
500	0.027	0.047	0.133	0.060	0.055	0.223	0.276	0.434	0.399	0.152	0.124
505	0.028	0.047	0.136	0.075	0.068	0.257	0.285	0.446	0.375	0.135	0.114
510	0.029	0.044	0.139	0.100	0.095	0.311	0.292	0.441	0.351	0.123	0.107
515	0.029	0.045	0.138	0.153	0.132	0.346	0.294	0.433	0.325	0.113	0.103
520	0.029	0.044	0.135	0.202	0.196	0.376	0.294	0.422	0.304	0.100	0.093
525	0.030	0.046	0.132	0.284	0.260	0.389	0.295	0.406	0.271	0.093	0.086
530	0.032	0.047	0.128	0.341	0.309	0.393	0.296	0.386	0.249	0.091	0.083
535	0.036	0.050	0.131	0.421	0.390	0.386	0.294	0.365	0.219	0.090	0.082
540	0.041	0.053	0.136	0.470	0.458	0.373	0.293	0.335	0.199	0.090	0.080
545	0.043	0.066	0.142	0.530	0.495	0.354	0.289	0.311	0.170	0.090	0.079
550	0.047	0.079	0.159	0.559	0.519	0.334	0.287	0.293	0.150	0.090	0.079
555	0.060	0.107	0.172	0.583	0.531	0.311	0.283	0.276	0.129	0.087	0.080
560	0.070	0.137	0.189	0.605	0.529	0.286	0.278	0.251	0.112	0.084	0.082
565	0.097	0.161	0.197	0.621	0.524	0.264	0.275	0.229	0.100	0.083	0.082
570	0.125	0.192	0.201	0.630	0.507	0.243	0.269	0.210	0.089	0.081	0.081
575	0.161	0.212	0.203	0.639	0.487	0.221	0.259	0.193	0.084	0.084	0.083
580	0.207	0.247	0.202	0.646	0.470	0.202	0.251	0.176	0.079	0.091	0.086
585	0.269	0.288	0.203	0.649	0.449	0.180	0.242	0.154	0.074	0.101	0.088
590	0.297	0.320	0.204	0.653	0.425	0.163	0.231	0.139	0.069	0.108	0.093
595	0.345	0.353	0.203	0.654	0.397	0.144	0.219	0.129	0.068	0.115	0.100
600	0.415	0.378	0.203	0.658	0.378	0.126	0.207	0.121	0.065	0.118	0.112
605	0.466	0.395	0.202	0.660	0.345	0.113	0.193	0.111	0.062	0.118	0.122
610	0.493	0.404	0.201	0.662	0.323	0.101	0.180	0.102	0.062	0.116	0.127
615	0.522	0.410	0.202	0.665	0.304	0.092	0.171	0.101	0.060	0.111	0.132
620	0.544	0.413	0.201	0.666	0.287	0.086	0.163	0.098	0.057	0.108	0.133
625	0.559	0.415	0.201	0.669	0.282	0.080	0.156	0.098	0.059	0.106	0.134
630	0.576	0.416	0.201	0.673	0.276	0.078	0.153	0.095	0.059	0.111	0.138
635	0.589	0.417	0.200	0.678	0.268	0.074	0.149	0.095	0.059	0.119	0.145
640	0.594	0.417	0.200	0.682	0.264	0.072	0.146	0.095	0.059	0.128	0.157
645	0.598	0.417	0.200	0.684	0.259	0.071	0.142	0.093	0.060	0.146	0.178
650	0.603	0.418	0.201	0.689	0.255	0.069	0.141	0.093	0.061	0.162	0.210
655	0.607	0.418	0.201	0.690	0.249	0.068	0.138	0.093	0.063	0.188	0.240
660	0.609	0.419	0.202	0.693	0.248	0.066	0.137	0.095	0.064	0.205	0.277
665	0.611	0.418	0.200	0.696	0.251	0.066	0.136	0.099	0.065	0.222	0.316
670	0.613	0.420	0.199	0.696	0.255	0.066	0.137	0.102	0.065	0.238	0.342
675	0.617	0.419	0.200	0.698	0.260	0.068	0.140	0.106	0.064	0.249	0.383
680	0.621	0.420	0.198	0.700	0.266	0.070	0.142	0.109	0.065	0.256	0.409
685	0.621	0.421	0.199	0.702	0.272	0.073	0.145	0.114	0.061	0.259	0.447
690	0.624	0.421	0.197	0.705	0.282	0.075	0.149	0.114	0.059	0.263	0.471
695	0.626	0.422	0.196	0.709	0.291	0.079	0.153	0.121	0.058	0.268	0.503
700	0.628	0.422	0.197	0.709	0.296	0.081	0.155	0.124	0.056	0.272	0.522