

# 1 **Colour vision models: a practical guide, some** 2 **simulations, and *colourvision* R package**

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## 17 **Abstract**

18 • Human colour vision differs from the vision of other animals. The most obvious  
19 differences are the number and type of photoreceptors in the retina. E.g., while humans are  
20 insensitive to ultraviolet (UV) light, most non-mammal vertebrates and insects have a colour  
21 vision that spans into the UV. The development of colour vision models allowed appraisals of  
22 colour vision independent of the human experience. These models are now widespread in  
23 ecology and evolution fields. Here I present a guide to colour vision modelling, run a series of  
24 simulations, and provide a R package – *colourvision* – to facilitate the use of colour vision  
25 models.

26 • I present the mathematical steps for calculation of the most commonly used colour vision  
27 models: Chittka (1992) colour hexagon, Endler & Mielke (2005) model, and Vorobyev & Osorio  
28 (1998) linear and log-linear receptor noise limited models (RNL). These models are then tested  
29 using identical simulated and real data. These comprise of reflectance spectra generated by a  
30 logistic function against an achromatic background, achromatic reflectance against an

31 achromatic background, achromatic reflectance against a chromatic background, and real flower  
32 reflectance data against a natural background reflectance.

33 • When the specific requirements of each model are met, between model results are,  
34 overall, qualitatively and quantitatively similar. However, under many common scenarios of  
35 colour measurements, models may generate spurious values and/or considerably different  
36 predictions. Models that log-transform data and use relative photoreceptor outputs are prone to  
37 generate unrealistic results when the stimulus photon catch is smaller than the background  
38 photon catch. Moreover, models may generate unrealistic results when the background is  
39 chromatic (e.g. leaf reflectance) and the stimulus is an achromatic low reflectance spectrum.

40 • Colour vision models are a valuable tool in several ecology and evolution subfields.  
41 Nonetheless, knowledge of model assumptions, careful analysis of model outputs, and basic  
42 knowledge of calculation behind each model are crucial for appropriate model application, and  
43 generation of meaningful and reproducible results. Other aspects of vision not incorporated into  
44 these models should be considered when drawing conclusion from model results.

45

46

## 47 **Introduction**

48 Animals respond to their surroundings via processing of data acquired by sensory organs (Stevens  
49 2013). The senses can evolve in response to selective pressures from the environment as the  
50 senses can exert selective pressures into other organism morphology and behaviour. E.g. the peak  
51 of sensitivity of marine mammal photoreceptors correlates to the environmental light conditions  
52 (Fasick & Robinson 2000), and flower colours parameters may have evolved in response to the  
53 visual abilities of pollinators (Chittka & Menzel 1992; Dyer *et al.* 2012).

54

55 There are several differences in the vision of animals – between and sometimes within species –  
56 such as density and distribution of receptors in the retina, visual acuity, and presence of oil-  
57 droplets in photoreceptors cells (Cronin *et al.*, 2014). In terms of colour vision, the most obvious  
58 differences are the type of photoreceptors present in the retina (Kelber *et al.* 2003; Osorio &  
59 Vorobyev 2008). Old world primates, including humans, are trichromats (have three cones  
60 types), with sensitivity peaks in blue, green and red regions of the light spectrum, whereas other  
61 mammals are usually dichromats (Kelber *et al.* 2003; Osorio & Vorobyev 2008; Jacobs 2009).

62 Most non-mammal vertebrates are tetrachromats, most insects are trichromats, and both have a  
63 colour perception that spans into the ultraviolet (Bowmaker 1998; Briscoe & Chittka 2001;  
64 Osorio & Vorobyev 2008). A fascinating illustration of how photoreceptor sensitivity may affect  
65 colour perception comes from human subjects that had gone through cataract treatment. The  
66 sensitivity curve of human blue photoreceptor actually spans into the ultraviolet (UV), but  
67 humans are UV-insensitive because pigments in the eye crystalline filters-out wavelengths below  
68 400nm. Cataract surgery occasionally replaces the crystalline with an UV-transmitting lens, and  
69 those individuals are suddenly able to see the world differently: new patterns appear in flower  
70 petals, some garments originally perceived as black become purple, and black light are turned  
71 into blue light (Stark & Tan 1982; Cornell 2011).

72  
73 Therefore, human colour perception is, in most cases, only a crude approximation of other  
74 species colour vision. Thus, studies of animal colouration can clearly benefit from appraisals of  
75 how colour patches are perceived by non-human observers. Moreover, the same colour patch  
76 may be perceived differently not only depending on the observer, but also on the context that this  
77 colour patch is exposed (e.g. background colour and environmental light conditions; (Endler  
78 1978).

79  
80 Colour vision models were firstly developed in an attempt to understand the proximate causes  
81 of human colour vision, and emulate some of human visual perceptual phenomena (Kemp *et al.*  
82 2015). More recently, with the advent of affordable spectrometers for reflectance measurements,  
83 application of colour vision models became common place in ecology and evolution subfields.  
84 Together, some of the most important colour vision papers have been cited over 2800 times  
85 (Endler 1990 (919); Vorobyev & Osorio 1998 (601), Vorobyev *et al.* 1998 (460); Chittka 1992  
86 (324); Chittka *et al.* 1992 (128); Endler & Mielke 2005 (445); Google Scholar search on October  
87 31th 2016). A few examples of use of colour vision models include studies of plant-pollinator  
88 interactions (Whitney *et al.* 2009), evolution of avian plumage (Stoddard & Prum 2008), sexual  
89 selection (Amy *et al.* 2008), visual prey lures (Heiling *et al.* 2003), speciation (Carleton *et al.* 2005),  
90 mimicry (Stoddard & Stevens 2011), camouflage (Thery & Casas 2002) and aposematism (Siddiqi  
91 2004).

92

93 As any model, colour vision models are based on certain assumptions. Knowledge of model  
94 strength and limitations are crucial to assure reproducible and meaningful results from model  
95 applications. Thus, the motivation of this paper is twofold: first to facilitate the use of colour  
96 vision models by evolutionary biologists and ecologists; secondly, to compare the consistency of  
97 between model results and how they behave in common scenarios of colour measurements. I did  
98 not aim to give an in depth analysis of the physiology of colour vision, but to provide a practical  
99 guide to the use of colour vision models, and demonstrate their limitations and strengths.  
100 Guidance on other aspects of colour vision models can be found elsewhere (Kelber *et al.* 2003;  
101 Endler & Mielke 2005; Osorio & Vorobyev 2008; Kemp *et al.* 2015; Renoult *et al.* 2017). I begin  
102 with a mathematical description of the steps for calculation of the most common colour vision  
103 models used in ecology and evolution; then I run a series of simulations using colour vision  
104 models. Both the description and the simulations serve as presentation of the accompanying R  
105 package `colourvision`.

106

#### 107 *Colour vision models*

108 In general, colour vision is achieved by neural opponency mechanisms (Kelber *et al.* 2003; Kemp  
109 *et al.* 2015), although exceptions to this rule do exist (Thoen *et al.* 2014). In humans, two colour  
110 opponency mechanisms appear to dominate: yellow-blue and red-green opponency channels  
111 (Kelber *et al.* 2003). Although colour vision in most other animals studied so far also seem to be  
112 based on opponency mechanisms, the exact opponency channels are usually not known (Kelber  
113 *et al.* 2003; Kemp *et al.* 2015). Nonetheless, empirical studies suggest that the exact opponency  
114 channels do not need to be known for a good prediction of behavioural responses by colour  
115 vision models (Chittka *et al.* 1992; Vorobyev & Osorio 1998; Spaethe *et al.* 2001; Cazetta *et al.*  
116 2009).

117

118 Here I present and test four generalist colour vision models used in ecology and evolution:  
119 Chittka (1992) colour hexagon, Endler & Mielke (2005) model, and linear and log-linear versions  
120 of the Receptor Noise Limited model (Vorobyev & Osorio 1998, Vorobyev *et al.* 1998). Human  
121 colour perception can be divided into two components: chromatic (hue and saturation) and  
122 achromatic (brightness) dimensions. These models are representations of the chromatic  
123 component of colour vision only (Renoult *et al.* 201).

124  
125 Colour vision models require a minimum of four parameters for calculations: (1) photoreceptor  
126 sensitivity curves, (2) background reflectance spectrum, (3) illuminant spectrum, and (4) the  
127 observed object reflectance spectrum (stimulus). In addition, receptor noise limited models  
128 require photoreceptor noise for each photoreceptor type. Photoreceptor sensitivity curves are  
129 available for several animal taxa. If not available, the sensitivity curves can be estimated using  
130 formula based on wavelength at photoreceptor maximum sensitivity ( $\lambda_{max}$ ; Govardovskii *et al.*  
131 2000). Background reflectance can be calculated by measuring the reflectance of materials found  
132 in the environment, such as leaves, twigs and tree bark. Alternatively, the background reflectance  
133 can be an achromatic spectrum of low reflectance value. The illuminant can be a reference  
134 spectrum (e.g. CIE standards), or, ideally, measured directly in the field using an irradiance  
135 measurement procedure (Endler 1990; 1993). Reflectance spectra are usually measured using a  
136 spectrometer (see Anderson & Prager 2006 for measurement procedures), but it can also be  
137 collected using photographic and hyperspectral cameras (Stevens *et al.* 2007; Chiao *et al.* 2011).  
138 All data must cover the same wavelength range as the photoreceptor sensitivity curves (300-700  
139 nm for most cases).

140  
141 I begin with Equations 1-5, which are common to all colour vision models presented here. Then  
142 calculation for each model is presented in a subtopic. I show formulae used to model  
143 trichromatic vision only. Formulae for tetrachromatic vision are available in the supplementary  
144 material. Photoreceptors are grouped by their maximum sensitivity value ( $\lambda_{max}$ ), from shortest to  
145 longest  $\lambda_{max}$ . Honeybees workers (*Apis mellifera*), for instance, have three photoreceptor types  
146 with  $\lambda_{max}$  at ca. 344nm, 436nm and 544nm (Figure 1a; Peitsch *et al.* 1992).

147  
148 The first step is to calculate the total photon capture ( $Q_i$ ) of each photoreceptor type ( $i$ ):

$$Q_i(\lambda) = \int_{300}^{700} I(\lambda)R(\lambda)C_i(\lambda) d\lambda \quad (\text{Eq. 1})$$

149 where  $I$  is the illuminant spectrum reaching the observed object,  $R$  is the reflectance of the  
150 observed object,  $C_i$  is the photoreceptor sensitivity curve of photoreceptor  $i$ . The integration is  
151 usually done from 300 to 700nm, but this range can be changed depending on the animal of  
152 interest. Most mammals, for instance, do not capture photons below 400 nm. The second step is

153 to calculate the photon catch by each photoreceptor ( $i$ ) arising from the background reflectance:

$$Q_{Bi}(\lambda) = \int_{300}^{700} I(\lambda)R_B(\lambda)C_i(\lambda) d\lambda \quad (\text{Eq. 2})$$

154 where  $I$  and  $C_i$  are the same values in equation (1), and  $R_B$  is the background reflectance. In  
155 practice photon catches are done by summation  $Q_i(\lambda) = k \sum_{300}^{700} I(\lambda) \times R_B(\lambda) \times C_i(\lambda)$ , where  $k$  is  
156 the constant representing the interval between measurements, usually 1 nm. The relative  
157 photoreceptor photon catch ( $q_i$ ) is then calculated by:

$$q_i = \frac{Q_i}{Q_{Bi}} \quad (\text{Eq. 3})$$

158 The rationale behind equation (3), referred as the von Kries transformation, is that  
159 photoreceptors are physiologically adapted to the light coming from the background, and that  
160 animals exhibit colour constancy (Chittka *et al.* 2014). So that if the environment is rich in  
161 wavelengths at the green region of the light spectrum, photoreceptors sensitive to this wavelength  
162 region will be less responsive.

163

#### 164 *Colour hexagon model*

165 The colour hexagon model (Chittka 1992) was formulated for hymenopteran vision. However,  
166 due its general form it can, and has been, applied for other taxa. Photoreceptor output ( $E$ ) is  
167 given by:

$$E_i = \frac{q_i}{q_i + 1} \quad (\text{Eq. 4})$$

168 This means that photoreceptors output ( $E$ ) will vary from 0 to 1, and its value will increase  
169 asymptotically to the limit of 1. This is done because the relationship between photoreceptor  
170 input-output is non-linear. E-values are then depicted into three vectors evenly distributed (120°  
171 between them). The resultant of receptor outputs is projected into a plan (chromaticity diagram)  
172 using the following formula:

$$x = \sin 60^\circ (E_3 - E_1) \quad (\text{Eq. 5})$$

173

$$y = E_2 - \frac{1}{2}(E_1 + E_3) \quad (\text{Eq. 6})$$

174

#### 175 *Endler & Mielke (2005) model*

176 The model is originally the first step for a statistical approach to study bird colouration as whole,  
177 not as individual colour patches (Endler & Mielke 2005). The model was adapted from  
178 tetrachromatic to trichromatic vision by Gomez (2006). The first step is to log-transform relative  
179 photon catches:

$$f_i = \ln(q_i) \quad (\text{Eq. 7})$$

180 Then,  $S_i$  is transformed so that photoreceptor outputs  $u + s + m = 1$ :

$$u = \frac{f_1}{f_1 + f_2 + f_3} \quad (\text{Eq. 8})$$

181

$$s = \frac{f_2}{f_1 + f_2 + f_3} \quad (\text{Eq. 9})$$

182

$$m = \frac{f_3}{f_1 + f_2 + f_3} \quad (\text{Eq. 10})$$

183

184 Rationale between equations 8-10 is that only the relative differences in photoreceptor outputs  
185 are used in a colour opponency mechanism. Photoreceptor outputs are projected into a  
186 triangular chromaticity diagram by the following formula (Gomez 2006):

$$x = \frac{2}{3} \times \frac{\sqrt{3}}{2} (m - u) \quad (\text{Eq. 11})$$

187

$$y = \frac{2}{3} \left[ s - \frac{1}{2} (u + m) \right] \quad (\text{Eq. 12})$$

188

189 *Receptor noise limited models: linear and log-linear versions*

190 The receptor noise limited model was developed to predict thresholds of colour vision. One of  
191 the assumption is that thresholds are given by noise arising at the receptor channels (Vorobyev &  
192 Osorio 1998). The first receptor noise limited model uses a linear relationship between  
193 photoreceptor input ( $q_i$ ) and output ( $f_i$ ) so that (linear version of the receptor noise limited  
194 model; Vorobyev & Osorio 1998):

$$f_i = q_i \quad (\text{Eq. 13})$$

195 The log-linear version of receptor noise limited model assumes a log-linear relationship between

196 photoreceptor input and output (log-linear version of the receptor noise limited model;  
197 (Vorobyev *et al.* 1998):

$$f_i = \log(q_i) \quad (\text{Eq. 14})$$

198 Equation (13) can be used when comparing colours that are very similar, otherwise equation (14)  
199 should be used. Then  $f_i$  values are used to find the colour locus  $(x, y)$  in a chromaticity diagram  
200 (Hempel de Ibarra *et al.* 2014):

$$A = \sqrt{\frac{1}{e_2^2 + e_3^2}} \quad (\text{Eq. 15})$$

$$B = \sqrt{\frac{e_2^2 + e_3^2}{(e_1 e_2)^2 + (e_1 e_3)^2 + (e_2 e_3)^2}} \quad (\text{Eq. 16})$$

$$a = \frac{e_2^2}{e_2^2 + e_3^2} \quad (\text{Eq. 17})$$

$$b = \frac{e_3^2}{e_2^2 + e_3^2} \quad (\text{Eq. 18})$$

$$x = A(f_3 - f_2) \quad (\text{Eq. 19})$$

$$y = B[f_1 - (af_3 + bf_2)] \quad (\text{Eq. 20})$$

207  
208 where  $e_i$  is the receptor noise of each photoreceptor, from shortest to longest wavelength. To  
209 date few species had their receptor noise ( $e_i$ ) measured directly (Vorobyev & Osorio 1998). In  
210 lack of a direct measurement,  $e_i$  can be estimated by the relative abundance of photoreceptor  
211 types in the retina and a measurement of a single photoreceptor noise-to-signal ratio:

$$e_i = \frac{\nu}{\sqrt{\eta_i}} \quad (\text{Eq. 21})$$

212 Where  $\nu$  is the noise-to-signal ratio of a single photoreceptor, and  $\eta_i$  is the relative abundance of  
213 photoreceptor  $i$  in the retina. Alternatively,  $e_i$  may be intensity depend (Renoult *et al.* 2017):



$$e_i = \sqrt{\frac{v^2}{\eta_i} + \frac{1}{Q_i}} \quad (\text{Eq. 22})$$

214 where  $Q_i$  is the photon catch given by equation (1). Equation (20) is usually valid in high light  
215 intensities, whereas equation (21) usually holds for dim light conditions (Vorobyev *et al.* 1998;  
216 Vorobyev & Osorio 1998).

217

218 *Distance between colour loci in chromaticity diagrams*

219 Distances in chromaticity diagrams represent chromaticity similarities between two colours. The  
220 assumption is that the longest the distance, the more dissimilar two colours are perceived.

221 Chromaticity distance between pair of reflectance spectra ( $a$  and  $b$ ) are found by calculating the  
222 Euclidian distance between their colour loci ( $x, y$ ) in the colour space:

$$\Delta S = \sqrt{(x_a - x_b)^2 + (y_a - y_b)^2} \quad (\text{Eq. 23})$$

223 By definition, background reflectance lays at the centre of the background ( $x = 0, y = 0$ ).

224 Therefore, the distance of the observed object against the background is given by:

$$\Delta S = \sqrt{x^2 + y^2} \quad (\text{Eq. 24})$$

225 In the receptor noise models,  $\Delta S$  between pair of reflectance spectra ( $a$  and  $b$ ) can be calculated  
226 directly, without finding colour loci in the colour space (Vorobyev & Osorio 1998):

$$\Delta S = \sqrt{\frac{e_1^2(\Delta f_3 - \Delta f_2)^2 + e_2^2(\Delta f_3 - \Delta f_1)^2 + e_3^2(\Delta f_1 - \Delta f_2)^2}{(e_1 e_2)^2 + (e_1 e_3)^2 + (e_2 e_3)^2}} \quad (\text{Eq. 25})$$

227 Where  $\Delta f_i$  is the difference between photoreceptor  $i$  output for the reflectance spectrum  $a$  and  $b$   
228 ( $\Delta f_i = f_{a_i} - f_{b_i}$ ). Using equation (24) will give the same value as calculating  $\Delta S$  using equations  
229 (14-19) and then equation (23). In RNL models,  $\Delta S = 1$  equals one unit of just noticeable  
230 difference (JND). That means that, given the experimental conditions (large static object against a  
231 grey homogenous background), JND = 1 is the threshold for object detection; i.e. the minimum  
232 behaviourally discriminable difference between the object and the background.

233

## 234 **Simulations**

235 I modelled the perception of the honeybee (*Apis mellifera*) using the colour vision models presented  
236 above: Chittka (1992) colour hexagon model (hereafter CH model), Endler & Milke (2005) model  
237 (hereafter EM model), and linear and log-linear versions of the receptor noise model (hereafter

238 linear-RNL and log-RNL models (Vorobyev *et al.* 1998; Vorobyev & Osorio 1998). My aim was  
239 to compare between model results and analyse and illustrate how models behave in different  
240 scenarios. I begin with a basic model setup with simulated data. Then I make a series of changes  
241 to this basic model to investigate how models behave with typical input data used in ecology and  
242 evolution papers. At the end I use real flower reflectance data to compare model results.

243

#### 244 *Simulation 01: Basic model setup*

245 I used honeybee worker (*Apis mellifera*) photoreceptor sensitivity curves (data from Peitsch *et al.*  
246 1992) available in Chittka & Kevan 2005); Figure 1a). As the background reflectance spectrum I  
247 created a theoretical achromatic reflectance with a constant 7% reflectance across 300 to 700nm  
248 (Figure 1b). As illuminant I used the CIE D65, a reference illuminant that correspond to midday  
249 open-air conditions (Figure 1c). For the receptor noise models I used measurements of honeybee  
250 photoreceptor noise (0.13, 0.06 and 0.12 for short, medium and long-wavelength photoreceptors;  
251 data from Peitsch 1992 available in Vorobyev & Brandt 1997). As the stimulus reflectance  
252 spectra I generated reflectance curves using a logistic function:

$$R(\lambda) = \frac{L}{1 + e^{-k(\lambda - \lambda_{mid})}} \quad (\text{Eq. 26})$$

253 Where  $R$  is the reflectance value at wavelength  $\lambda$ ,  $L$  gives the curve maximum reflectance value  
254 (%),  $k$  gives the steepness of the curve, and  $\lambda_{mid}$  is the wavelength (nm) of midpoint. The logistic  
255 curve is a typical reflectance curve of many animal colour patches. I used a maximum value of  
256  $L = 50\%$  reflectance and a steepness of  $k = 0.04$ . I generated curves with midpoints varying  
257 from 300 to 700 nm with 5 nm intervals, in a total of 81 reflectance spectra (Figure 1d). For each  
258 model I calculated photoreceptor outputs, colour loci ( $x$  and  $y$ ), and the chromatic distance to  
259 the background ( $\Delta S$ ) of each reflectance spectra using equations (1-24). In addition, as a  
260 supplementary material, I ran the same simulations with a tetrachromatic vision, and using a  
261 Gaussian function to generate the stimulus reflectance spectra (see Electronic Supplementary  
262 Material).

263

#### 264 *Simulation 02: 10 percent point added to reflectance values.*

265 In the second simulation I added 10 percent point to the stimulus reflectance spectra (Figure 2a).  
266 My aim was to analyse how a relatively small change in reflectance curves affect model results.

267 An increase in overall reflectance value can be an artefact of spectrometric measurement error  
268 (for guidance on spectrometric reflectance measurements see Anderson & Prager 2006).

269

270 *Simulation 03: achromatic reflectance spectra*

271 Colour vision models are designed to deal with chromatic spectra (reflectance spectra that  
272 produces differences in photoreceptor outputs). However, some animal colours have reflectance  
273 spectra with a relatively constant reflectance value from 300 to 700nm, which we perceive as  
274 white, grey and black patches (achromatic variation). These type of spectra are sometimes  
275 modelled into colour vision models. In this simulation I generated a series of achromatic spectra  
276 with constant reflectance values from 300-700nm. I generated 10 reflectance spectra with  
277 reflectance values from 5% to 95%, with 10 percentage point intervals (Figure 2b).

278

279 *Simulation 04: Achromatic reflectance spectra and chromatic background reflectance spectrum.*

280 In the basic model I used an achromatic reflectance spectrum (7% reflectance from 300 to  
281 700nm). In practice, however, most studies that apply colour vision models use chromatic  
282 reflectance backgrounds, such as leaf (e.g. Vorobyev *et al.* 1998), or an average of background  
283 material reflectance spectrum (e.g. Gawryszewski & Motta 2012). Models are constructed so that  
284 the background reflectance spectrum lie at the centre of the colour space. Vorobyev and Osorio  
285 (1998) specifically state that their linear receptor noise model is designed to predict perception of  
286 large targets, in bright light conditions and against an achromatic background. Despite of that,  
287 given that photoreceptors adapt to the light environment condition, usage of chromatic  
288 background is probably reasonable. Therefore, in this simulation I used the same achromatic  
289 reflectance spectra from simulation 03, but instead of having an achromatic background I used a  
290 chromatic background. The background is the average reflectance of leafs, leaf litter, tree bark  
291 and twigs collected in an area of savanna vegetation in Brazil (data from Gawryszewski & Motta  
292 2012).

293

294 *Real reflectance data: comparison between models*

295 In this setup my aim was to compare model results using real reflectance data. I used 858  
296 reflectance spectra from flower parts collected worldwide and deposited in the Flower  
297 Reflectance Database (FReD; Arnold *et al.* 2010). I used only spectrum data that had a

298 wavelength range from 300nm to 700nm. Data were then interpolated to 1nm intervals and  
299 negative values converted to zero. I used the same reflectance background from simulation 04,  
300 and other model parameters identical to the basic model setup. I compared models results  
301 visually, and by testing the pairwise correlation between model's  $\Delta S$  values. I used the Spearman  
302 correlation coefficient because data did not fulfil assumptions for a parametric test.

303

304 *Colourvision: R package for colour vision models and related functions*

305 All calculation and figures presented here were performed using the colourvision R package. The  
306 package has functions for dichromatic, trichromatic and tetrachromatic linear and log-linear  
307 versions of the receptor noise limited model (Vorobyev *et al.* 1998; Vorobyev & Osorio 1998);  
308 and trichromatic and tetrachromatic versions of Chittka (1992) colour hexagon and Endler and  
309 Mielke (2005) models. Results from these models can be easily projected into their chromaticity  
310 diagrams for trichromatic and tetrachromatic vision. The colourvision package complements and  
311 can be used together with pavo R package for colour analyses (Maia *et al.* 2013), although it does  
312 not depend on it.

313

## 314 **Results**

315 *Simulation 01: Basic model*

316 Basic model results projected into chromaticity diagrams show differences between model  
317 predictions of colour perception for the same reflectance spectrum (Figure 3). CH model and the  
318 the linear-RNL model follow a similar path: data points follow a circular path that begins and  
319 ends near the centre of the colour diagram (Figure 3a and 3c). In the EM model, points follow  
320 two lines increasing in opposite directions, with data points reaching values outside colour space  
321 limits (Figure 3b). In the log-RNL model, points begin at the centre of the colour space and  
322 follow a curve increasing in distance from the centre of the colour space (Figure 3d).

323

324 CH model estimates a bell shaped  $\Delta S$  curve against midpoint wavelength, with maximum  $\Delta S$  for  
325 the reflectance curve with midpoint at 535nm (Figure 4a). Individual photoreceptors follow a  
326 sigmoid curve, with maximum values at short midpoint wavelengths and minimum values at long  
327 midpoint wavelengths (Figure 4a). EM model estimates unrealistic  $\Delta S$ -values for reflectance  
328 curves with midpoints between 450-550nm (Figure 4b). A maximum  $\Delta S = 116$  is reached at

329 490nm midpoint wavelength (Figure 4b). Photoreceptor output also reach unrealistic negative  
330 values, and values above 1 (Figure 4b). This is consequence of equations 7-10: when  $q_i$  is below  
331 1, the ln-transformation generates negative values. Consequently, the denominator in equations  
332 8-10 may reach values close to zero, which causes photoreceptor outputs to tend to infinity. Log-  
333 RNL model predicts a sigmoid  $\Delta S$  curve, increasing from short to long midpoint wavelengths,  
334 reaching a maximum  $\Delta S$  at at 700 nm (Figure 4d). Comparably to the EM model, the log-RNL  
335 model generates unrealistic negative photoreceptor excitation values (Figure 4d). Again, this  
336 happens because when  $q_i$  is below 1 the log-transformation generates negative values (eq. 14).  
337 The linear-RNL version estimates a bell shaped  $\Delta S$  curve, with a maximum  $\Delta S$  at 470nm  
338 midpoint wavelength (Figure 4c). Photoreceptors present a sigmoid excitation curve, with  
339 maximum values at short midpoint wavelengths (Figure 4c).

340

341 *Simulation 02: 10 percent point added to reflectance values.*

342 In this setup, models are more congruent in their results. Their chromaticity diagram indicates  
343 similar relative position of reflectance spectra between models (Figure 5). All of them estimate a  
344 bell shaped  $\Delta S$  curve, with maximum values around 500 nm midpoint wavelength (Figure 6). CH  
345 model predicts a bell shaped  $\Delta S$  curve with maximum  $\Delta S$  peaking at 510nm (25 nm difference to  
346 the original model; Figure 6a). However, in comparison to the basic model there is an overall  
347 decrease in  $\Delta S$  (Figure 3a and 6a). This happens because eq. 4 makes E-values non-linear as  $q_i$   
348 increases. Therefore, the relative differences between photoreceptors decreases and, as a  
349 consequence,  $\Delta S$  decreases. Contrary to the basic model, EM model now estimates realistic  $\Delta S$   
350 and photoreceptor excitation values, with a peak at 540nm (Figure 6b). With a 10 percentage  
351 point increase in the reflectance, eq. 3 does not produce values below 1. As a consequence, eqs.  
352 7-10 do not generate negative values and the denominator cannot reach near zero values. The  
353 same pattern occurs in the log-RNL model: no negative values are generated by eq. 14. Model  
354 estimates a bell shaped curve peaking at 505 nm (Figure 6d). The linear RNL model generates  
355 identical  $\Delta S$  and colour loci values to the basic model. The 10 percentage point increase causes  
356 an increases in photoreceptor excitation values (Figure 6c). However, because the relative  
357 differences between photoreceptors remain the same, and the relationship between  $q_i$  and  $f$  is  
358 linear (no transformation of  $q_i$ ) there is no difference in  $\Delta S$  between the original and this model  
359 setup (Figures 4c and 6c).

360

361 *Simulation 03: Achromatic reflectance spectra.*

362 With achromatic reflectance spectra all datapoints are in the centre of the colour diagram.  
363 Consequently,  $\Delta S$  for all models and all reflectance values equals zero. This happens because all  
364 three photoreceptors respond equally to the achromatic reflectance spectra. Nonetheless, the type  
365 of response varies between models. In the CH model, photoreceptor output increases  
366 asymptotically as reflectance increases, which is result of eq. 4. In the EM model, photoreceptor  
367 outputs are not affected by variation in reflectance values. This happens because EM model  
368 considers only the relative differences between photoreceptors response (eqs. 8-10). In the RNL  
369 models, photoreceptor output increases linearly in the linear version, and asymptotically in the  
370 log version.

371

372 *Simulation 04: Achromatic reflectance spectra and chromatic background reflectance spectrum.*

373 Model results of achromatic reflectance spectra against a chromatic background differ to the  
374 model predictions when the background is achromatic (Figure 7 and Figure 8). The chromatic  
375 background causes differences in photoreceptor outputs. Consequently, achromatic reflectance  
376 spectra do not lay at the centre of the colour spaces. The CH model shows a maximum  $\Delta S$   
377 values of 0.31 at 5% reflectance achromatic spectrum (Figure 8a).  $\Delta S$  values then decrease as the  
378 reflectance value of achromatic spectra increases (Figure 8a). Photoreceptor output values  
379 converge to the asymptote as the reflectance value of achromatic spectra increases (Figure 8a).  
380 EM model produce spurious values at 5% reflectance achromatic spectrum because it generates  
381 negative photoreceptor output values (Figure 8b). From 15% beyond,  $\Delta S$  values then decrease as  
382 the reflectance value of achromatic spectra increases (Figure 8b). The linear-RNL model shows a  
383 linear increase in  $\Delta S$  values as the reflectance value of achromatic spectra increases (Figure 8c).  
384 Similarly, photoreceptor outputs also increase linearly as as the reflectance value of achromatic  
385 spectra increases, but with different slopes for each photoreceptor type (Figure 8c). Contrary to  
386 other models,  $\Delta S$ -values in the log-RNL model do not change with varying reflectance value of  
387 achromatic spectra (Figure 8d). Although photoreceptor outputs increase as reflectance value of  
388 achromatic spectra increases (Figure 8d), the difference between photoreceptor outputs remains  
389 the same. Consequently,  $\Delta S$ -values do not change.

390

391 *Simulation 05: Real reflectance data.*

392 When real flower reflectance spectra are used, models also give different relative perception for  
393 the same reflectance spectrum. The results of the CH model and the log-RNL model are similar  
394 both qualitatively and quantitatively: colour loci projected into the colour space (Figure 9) show  
395 similar relative position of reflectance spectra; and there is a high correlation score between  $\Delta S$   
396 values (Figures 9a and 9d;  $\rho=0.884$ ;  $N=858$ ;  $S=12165000$ ;  $p<0.001$ ). Even though many EM  
397 points lay outside the chromaticity, results suggest a high agreement between CH and EM  
398 models (Figure 9a and 9b;  $\rho=0.889$ ;  $N=858$ ;  $S=11718000$ ;  $p<0.001$ ). There was a moderate  
399 agreement between the linear and log version of the RNL model (Figures 9c and 9d;  $\rho=0.434$ ;  
400  $N=858$ ;  $S=59623000$ ;  $p<0.001$ ,  $P<0.001$ ), and between EM and log-RNL models (Figure 9b  
401 and 9d;  $\rho=0.662$ ;  $N=858$ ;  $S=35572000$ ;  $p<0.001$ ). There was a poor agreement between the  
402 linear-RNL and both EM models (Figure 9b and 9c; ( $\rho=-0.264$ ;  $N=858$ ;  $S=133060000$ ;  
403  $p<0.001$ ), and CH models (Figure 9a and 9c;  $\rho=0.037$ ;  $N=858$ ;  $S=101370000$ ;  $p=0.278$ )

404

405

## 406 **Discussion**

407 Application of colour vision models are now widespread in several fields of ecology and  
408 evolutionary biology. However, simulations presented here show that under certain conditions  
409 these models do not agree, and can produce spurious results. As any model, colour vision models  
410 have been developed based on a set of assumptions. Knowledge of model strength and limitation  
411 are crucial to the correct application and interpretation of colour vision model results.

412

413 Colour vision models, in special models that are log-transformed (eqs. 7 and 14) and convert  
414 photoreceptor output to relative values (eqs. 8-10) are prone to produce unrealistic results when  
415 the observed reflectance generates a lower response than the background (i.e.  $Q_i < Q_{Bi}$ ). The  
416 log-transformation (and the transformation in the CH model) is behaviourally justified due to the  
417 Weber–Fechner law of psychophysics (Renoult *et al.* 2017). The law states that the perceived  
418 difference between a pair of stimuli has a non-linear relationship with their absolute difference.  
419 I.e., humans perceive 150g and 100g weights as more dissimilar than 1150g and 1100g weights.  
420 This is illustrated by the photoreceptor outputs in Figure 7. In this simulation the achromatic  
421 reflectance spectrum increases from 10% to 90% by 10 percent point steps. In the linear-RNL



422 model, photoreceptor outputs respond linearly to the 10% increase, so that the difference in  
423 receptor outputs is the same between the 10% vs 20% reflectance spectra as between the 80% vs  
424 90% reflectance spectra. In the log-RNL model, however, the difference between 10% vs. 20% is  
425 greater than the difference between 80% vs 90%.

426  
427 In addition, low reflectance achromatic spectra (i.e. dark colour patches) may also produce  
428 spurious values when the background is chromatic (Figure 8), because at small reflectance values,  
429 small differences between photoreceptor outputs may be large in proportion to photoreceptor  
430 outputs, and consequently generate large  $\Delta S$  values. Interpretation of model results depends on  
431 detailed knowledge of how models are calculated. Inspection of individual photoreceptor outputs  
432 can give insights into colour loci ( $x, y$ ) and chromaticity distance ( $\Delta S$ ) values.

433  
434 Comprehension of the physiology of vision of the animal observing the scene is also imperative.  
435 Honeybees, for instance, use colour vision only when the observed object subtend a visual angle  
436 larger than ca.  $15^\circ$  (Giurfa *et al.* 1996). Moreover, bees appear to completely ignore brightness  
437 when using the chromatic channel (Giurfa *et al.* 1997), so that equation (20) holds even in low  
438 light conditions (Vorobyev & Osorio 1998). In humans, on the other hand, the achromatic  
439 dimension appears to dominate in dim light conditions (King-Smith & Carden 1976; Vorobyev  
440 & Osorio 1998). These models also do not incorporate higher order cognition abilities that may  
441 affect how colour are perceived (Dyer 2012). In bees, for instance, previous experience, learning  
442 and experimental conditions may affect their behavioural discriminability thresholds (Chittka *et*  
443 *al.* 2003; Dyer & Chittka 2004; Giurfa 2004; Dyer *et al.* 2011; Dyer 2012); and in humans the  
444 ability to discriminate between colours is affected by the existence of linguistic differences for  
445 colours (Winawer *et al.* 2007).

446  
447 A common misconception arises from the use of detectability/discriminability thresholds. The  
448 RNL model for instance, predicts well the detectability of monochromatic light against a grey  
449 background. For this model, and given the experimental condition, a  $\Delta S = 1$  equals one unit of  
450 just noticeable difference (JND; Vorobyev & Osorio 1998). Stimuli with values equal or above 1  
451 can be detectable against the background, under the experimental condition. However, this  
452 threshold is not fixed. It can vary depending on the background, on the chromatic difference



453 between the object and the background, and on the subject previous experience. For zebra  
454 finches, for instance, the same pair of similar red object have a discriminability threshold of ca. 1  
455 JND when the background is red, but much higher when the background is green (Lind 2016).  
456 The same study emphasises the difference between detecting one object against the background  
457 and discriminating two similar objects: detection thresholds are usually higher than  
458 discrimination thresholds (as measured by the RNL model; Lind 2016). Given the variation in  
459 thresholds, it is misleading to interpret  $\Delta S$  values as binary variable: i.e. above the threshold,  
460 detectable; below threshold, not detectable. Instead, use of  $\Delta S$  values as they are, a continuum,  
461 makes the interpretation more realistic. E.g., a stimulus with  $JND = 2$  is likely chromatically  
462 similar to the background, and is possibly more often not detected than a stimulus with  $JND = 5$ .

463  
464 In addition, models presented here are pairwise comparison between colour patches, which do  
465 not incorporate the complexity of an animal colour pattern composed by a mosaic of colour  
466 patches of variable sizes. Endler and Mielke (2005) provide a methodological and statistical tool  
467 that can deal with a cloud of points representing an organism colour patches. Use of  
468 hyperspectral cameras or adapted DSLR cameras may facilitate the analysis of animal  
469 colouration as a whole (Stevens *et al.* 2007; Chiao *et al.* 2011). Other aspects that may be  
470 important when detecting a target, such as size, movement, and light polarization (Cronin *et al.*  
471 2014), are also not incorporated into those models.

472  
473 In conclusion, colour vision models are extremely useful and can provide insightful results on  
474 ecological and evolutionary aspects of colour in nature. Nonetheless, they should be regarded as  
475 an approximation of the perceived differences between pairs colours by a particular organism.  
476 Good application of colour vision models depends on the inspection of photoreceptor output  
477 values, knowledge of model assumptions, comprehension of the mathematical formula behind  
478 each model and familiarity with mechanisms of colour vision of the animal being modelled.  
479 Comparison of model results with field and laboratory based behavioural experiments are also  
480 crucial to complement and validate model results.

481

482

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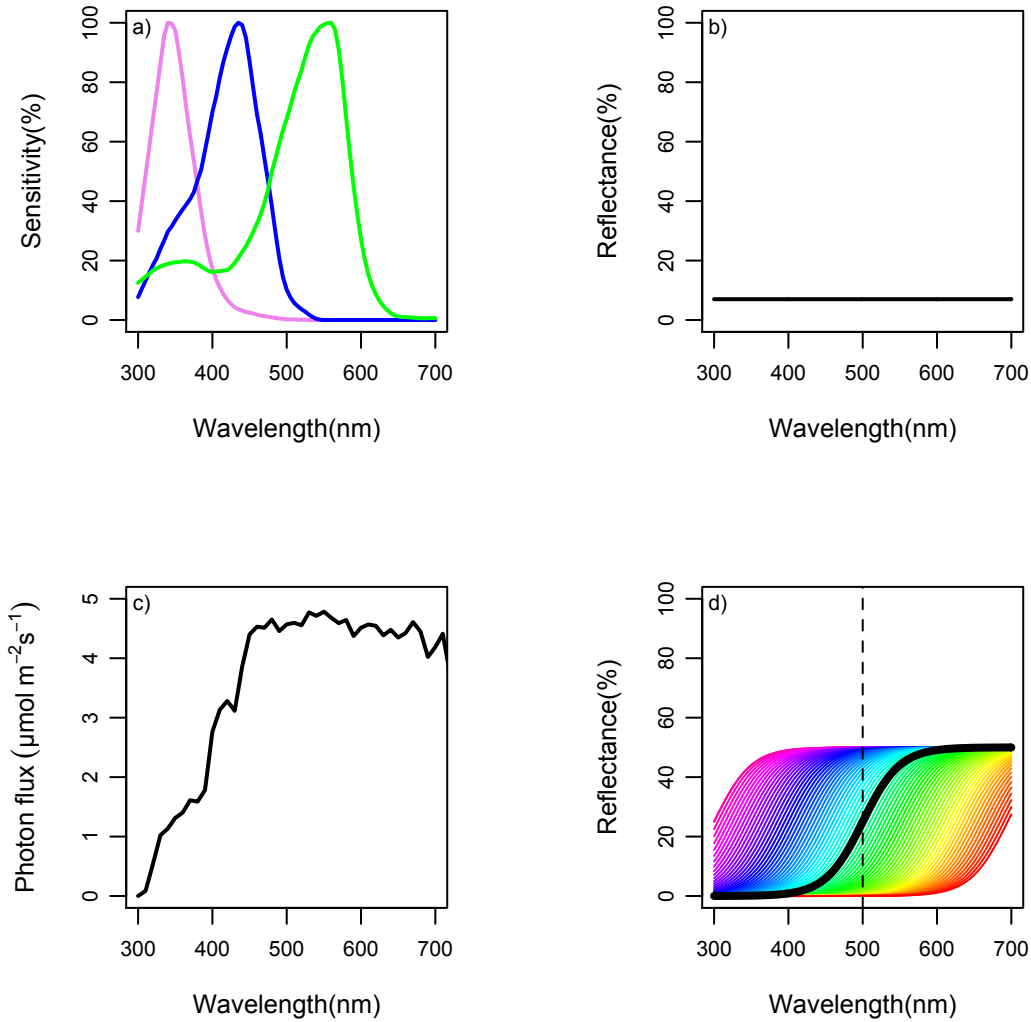
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623 **Figures**



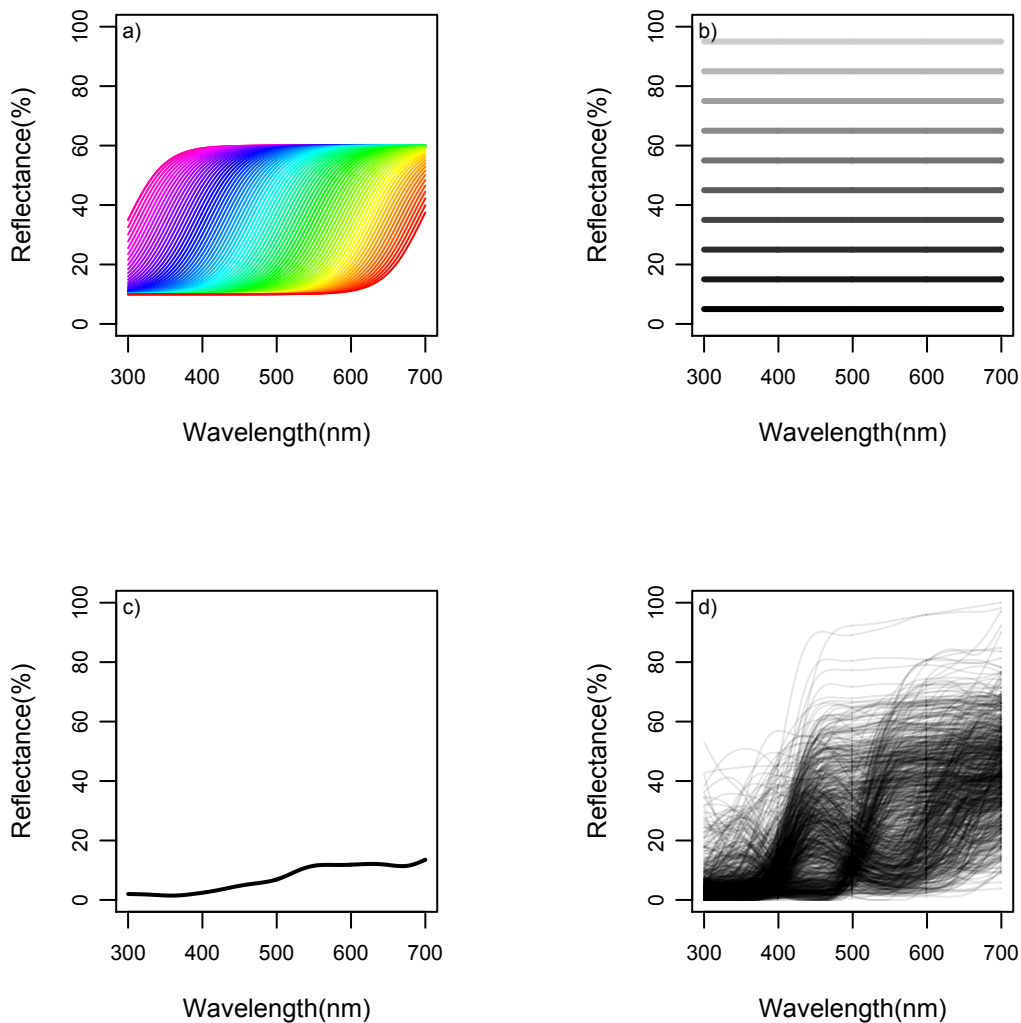
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626 Figure 1. Basic setup used for colour vision model simulations. (a) Honeybee (*Apis mellifera*)  
627 photoreceptor sensitivity curves (data from Peitsch *et al.* 1992 available in Chittka & Kevan  
628 2005); (b) Achromatic background reflectance spectrum; (c) CIE D65 standard daylight  
629 illuminant; and (d) Reflectance spectra generated by a logistic function with midpoints varying  
630 from 300 to 700nm at 5nm intervals. Spectrum colours are arbitrary. In black is shown a  
631 reflectance curve with midpoint at 500nm.

632





633

634 Figure 2. Changes from the basic setup used for colour vision model simulations. (a) Ten percent

635 point added to the original reflectance spectra with midpoints varying from 300 to 700nm at

636 5nm intervals; (b) Achromatic reflectance spectra, with reflectance values from 5% to 95%, at 10

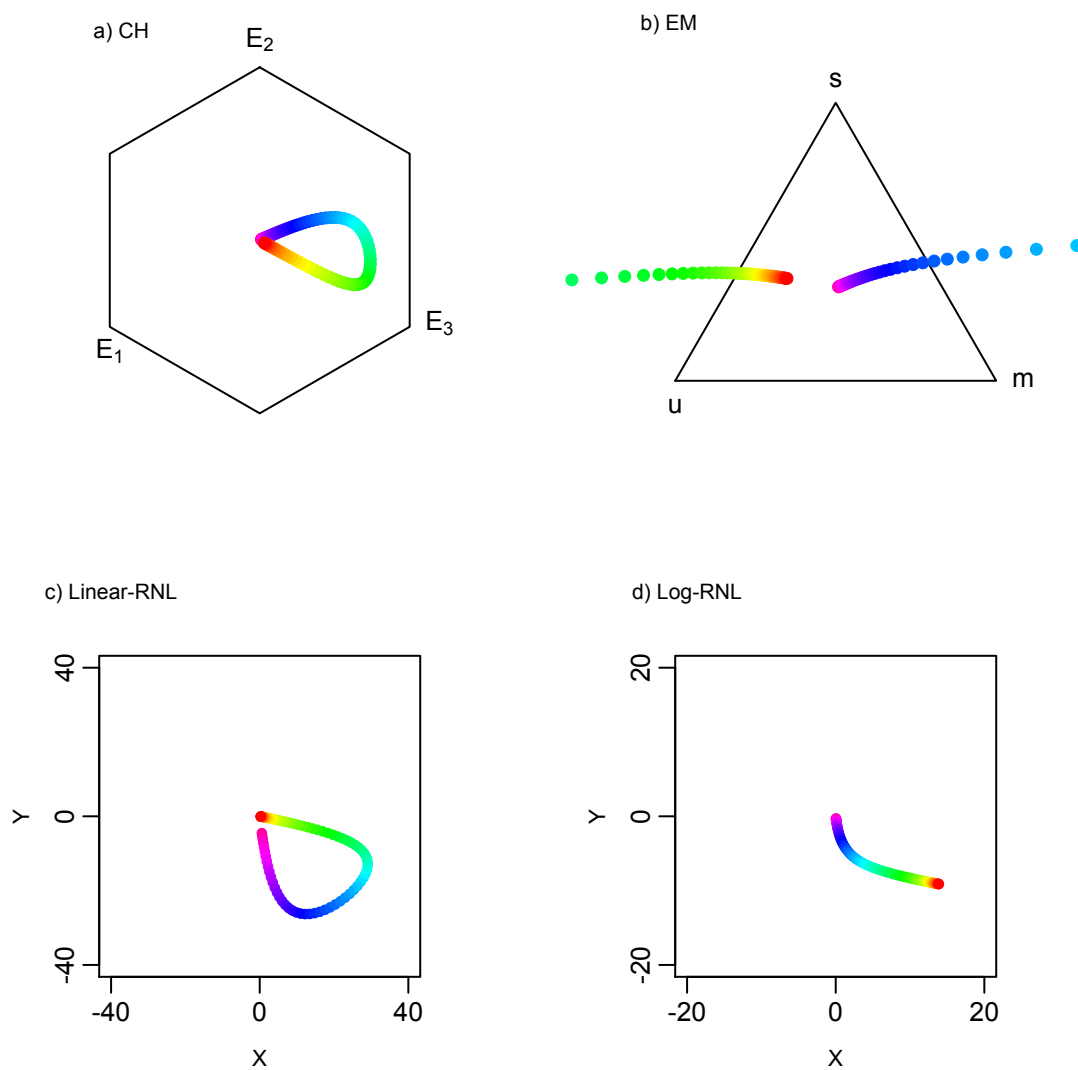
637 percent point intervals; (c) Background reflectance spectra calculated from the average

638 reflectance of leafs, leaf litter, grasses and tree bark collected in the Brazilian savanna (data from

639 Gawryszewski and Motta 2012); (c) Reflectance spectra of 859 flowers collected worldwide (data

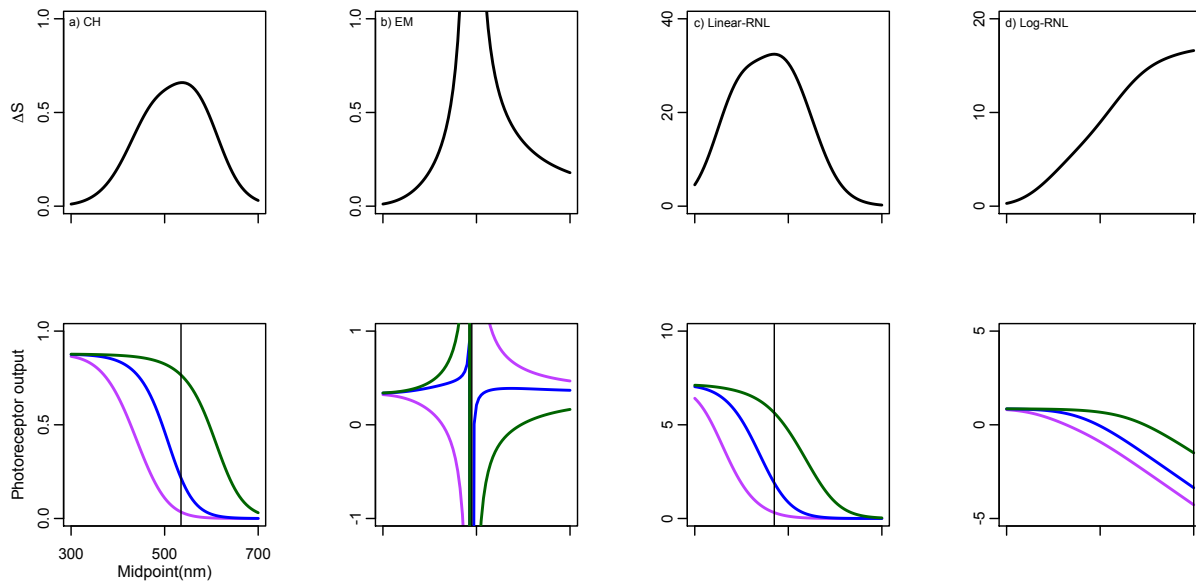
640 from the Flower Reflectance Database; Arnold *et al.* 2010).

641



642  
643 Figure 3. Chromaticity diagrams of the basic setup of colour vision model simulations: Chittka  
644 (1992) colour hexagon (CH), Endler & Mielke (2005) colour triangle (EM), and linear and log-  
645 linear Receptor Noise Limited models (Linear-RNL and Log-RNL; Vorobyev & Osorio 1998;  
646 Vorobyev et al. 1998). Colours correspond to reflectance spectra from Figure 1d.  
647



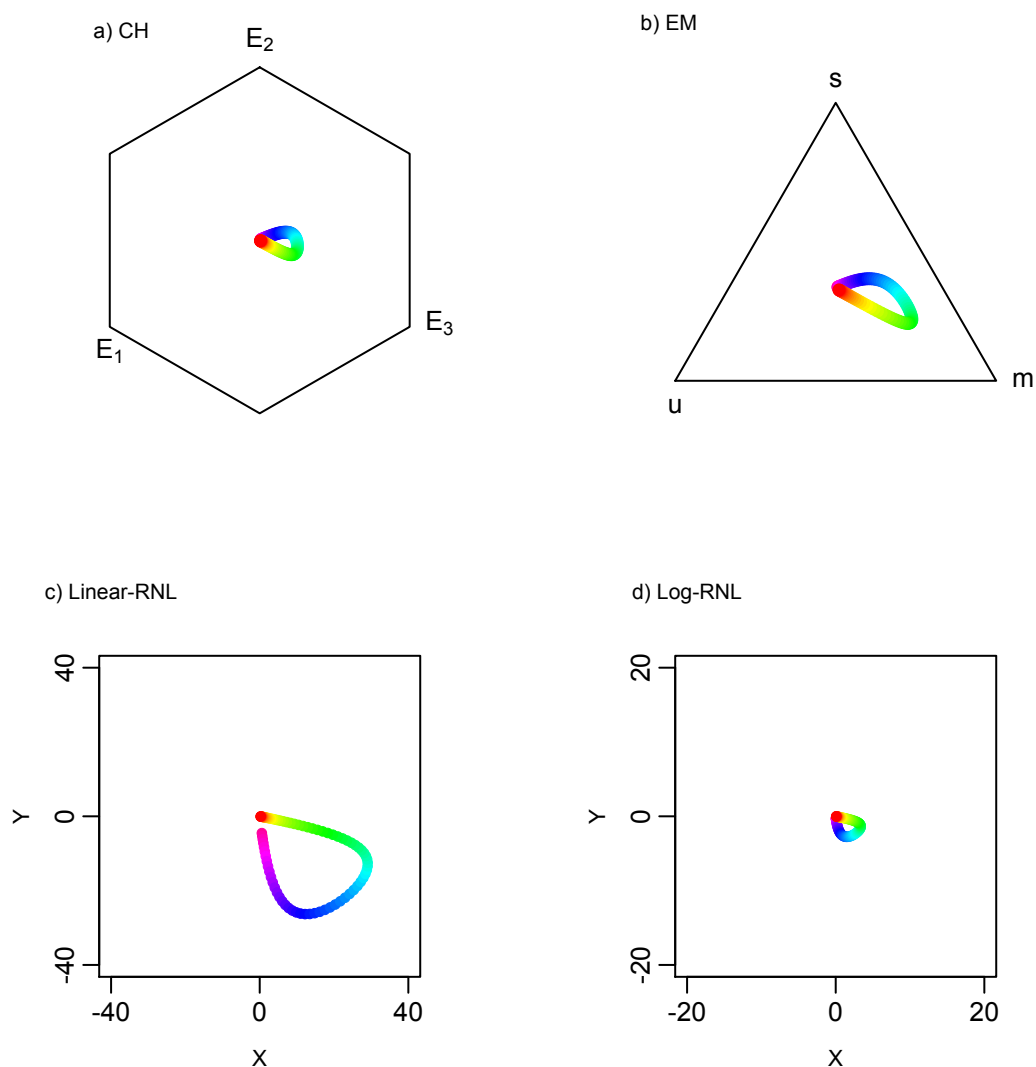


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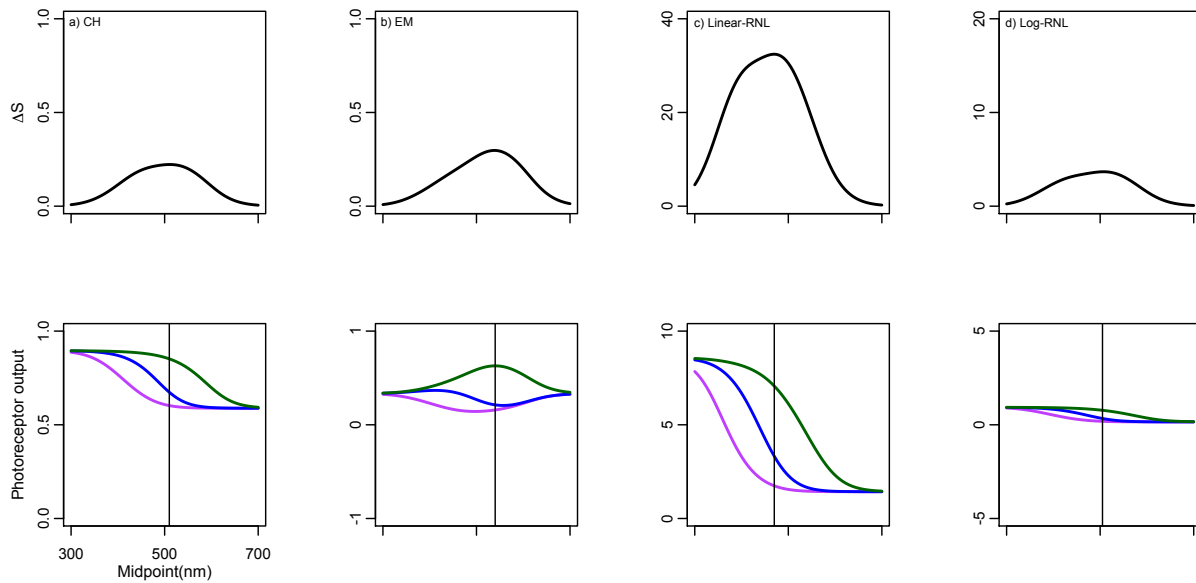
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650 Figure 4.  $\Delta S$  and photoreceptor outputs of the basic setup of colour vision model simulations  
651 (Figure 1): Chittka (1992) colour hexagon (CH), Endler & Mielke (2005) colour triangle (EM),  
652 and linear and log-linear Receptor Noise Limited models (Linear-RNL and Log-RNL; Vorobyev  
653 & Osorio 1998; Vorobyev *et al.* 1998). Variation in  $\Delta S$ -values as a function of reflectance spectra  
654 with midpoints from 300 to 700nm (top row). Photoreceptor output values as a function of the  
655 same reflectance spectra (bottom row). Violet, blue and green colours represent short, middle and  
656 long  $\lambda_{\max}$  photoreceptor types. Vertical lines represent midpoint of maximum  $\Delta S$ -values.

657

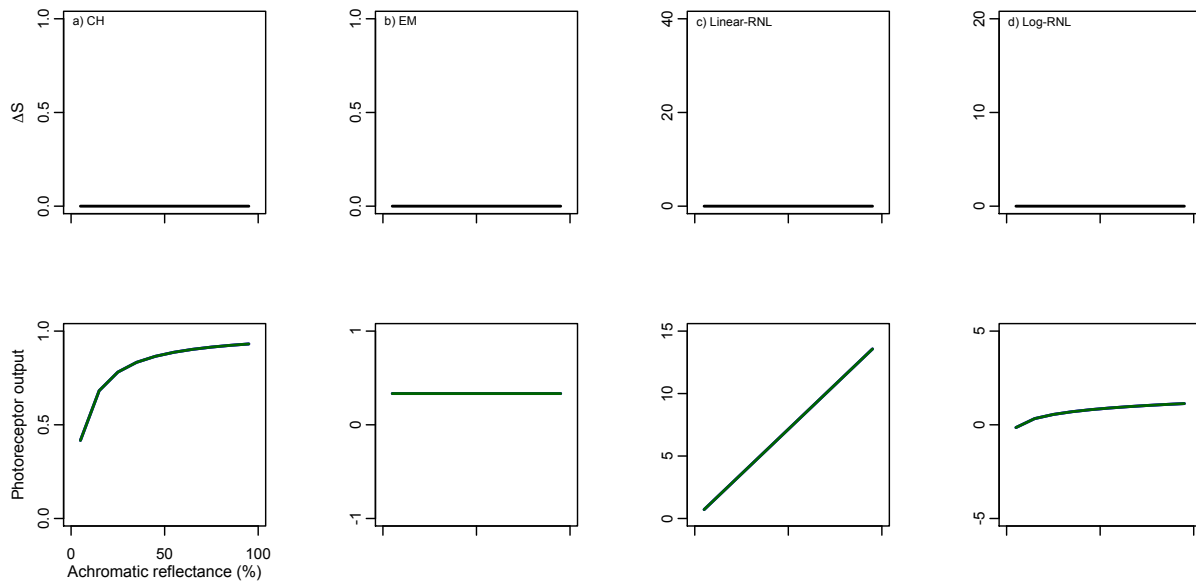


658  
659 Figure 5. Chromaticity diagrams of the second simulation – 10 percent point added to  
660 reflectance values: Chittka (1992) colour hexagon (CH), Endler & Mielke (2005) colour triangle  
661 (EM), and linear and log-linear Receptor Noise Limited models (Linear-RNL and Log-RNL;  
662 Vorobyev & Osorio 1998; Vorobyev *et al.* 1998). Colours correspond to reflectance spectra from  
663 Figure 2a.  
664  
665



666  
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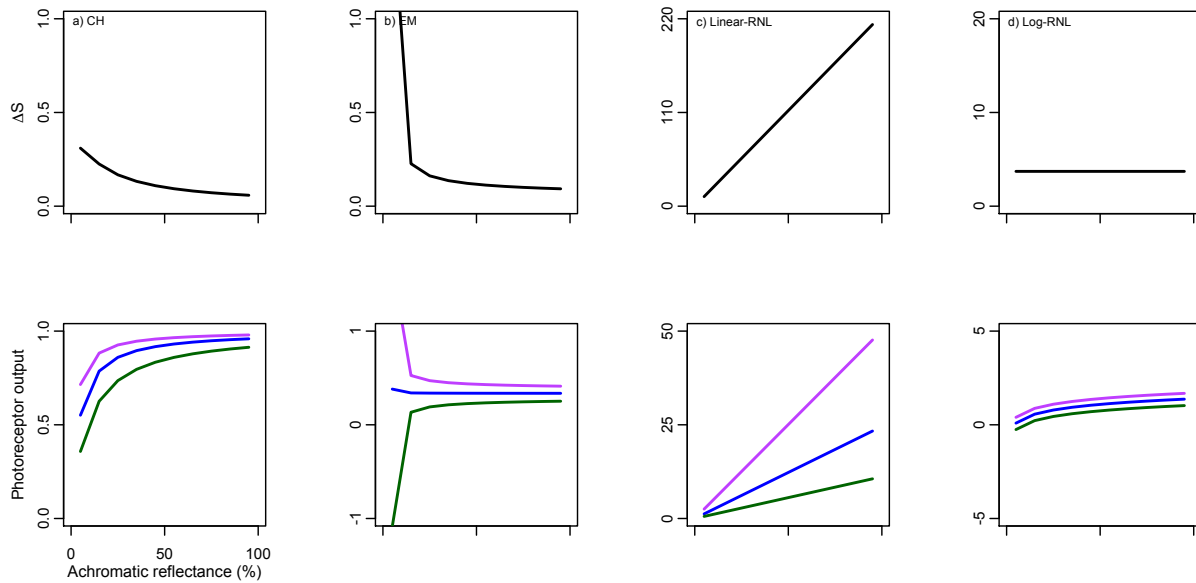
669 Figure 6.  $\Delta S$  and photoreceptor outputs of the second setup of colour vision model simulations -  
670 10 percent point added to stimulus reflectance spectra: Chittka (1992) colour hexagon (CH),  
671 Endler & Mielke (2005) colour triangle (EM), and linear and log-linear Receptor Noise Limited  
672 models (Linear-RNL and Log-RNL; Vorobyev & Osorio 1998; Vorobyev *et al.* 1998). Variation  
673 in  $\Delta S$ -values as a function of reflectance spectra with midpoints from 300 to 700nm (top row).  
674 Photoreceptor output values as a function of the same reflectance spectra (bottom row). Violet,  
675 blue and green colours represent short, middle and long  $\lambda_{\max}$  photoreceptor types. Vertical lines  
676 represent midpoint of maximum  $\Delta S$ -values. For comparison, scales are the same as in Figure 4.  
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680 Figure 7.  $\Delta S$  and photoreceptor outputs of the third setup of colour vision model simulations –  
681 achromatic stimulus against achromatic background: Chittka (1992) colour hexagon (CH),  
682 Endler & Mielke (2005) colour triangle (EM), and linear and log-linear Receptor Noise Limited  
683 models (Linear-RNL and Log-RNL; Vorobyev & Osorio 1998; Vorobyev *et al.* 1998). Variation  
684 in  $\Delta S$ -values as a function of spectra with achromatic reflectance from 5% to 95% (top row).  
685 Photoreceptor output values as a function of the same reflectance spectra (bottom row).  
686 Photoreceptors are colour coded by their  $\lambda_{\max}$  photoreceptor, however they do not appear  
687 because are all superimposed. With the exception of c) Linear-RNL, scales are the same as in  
688 Figure 4.

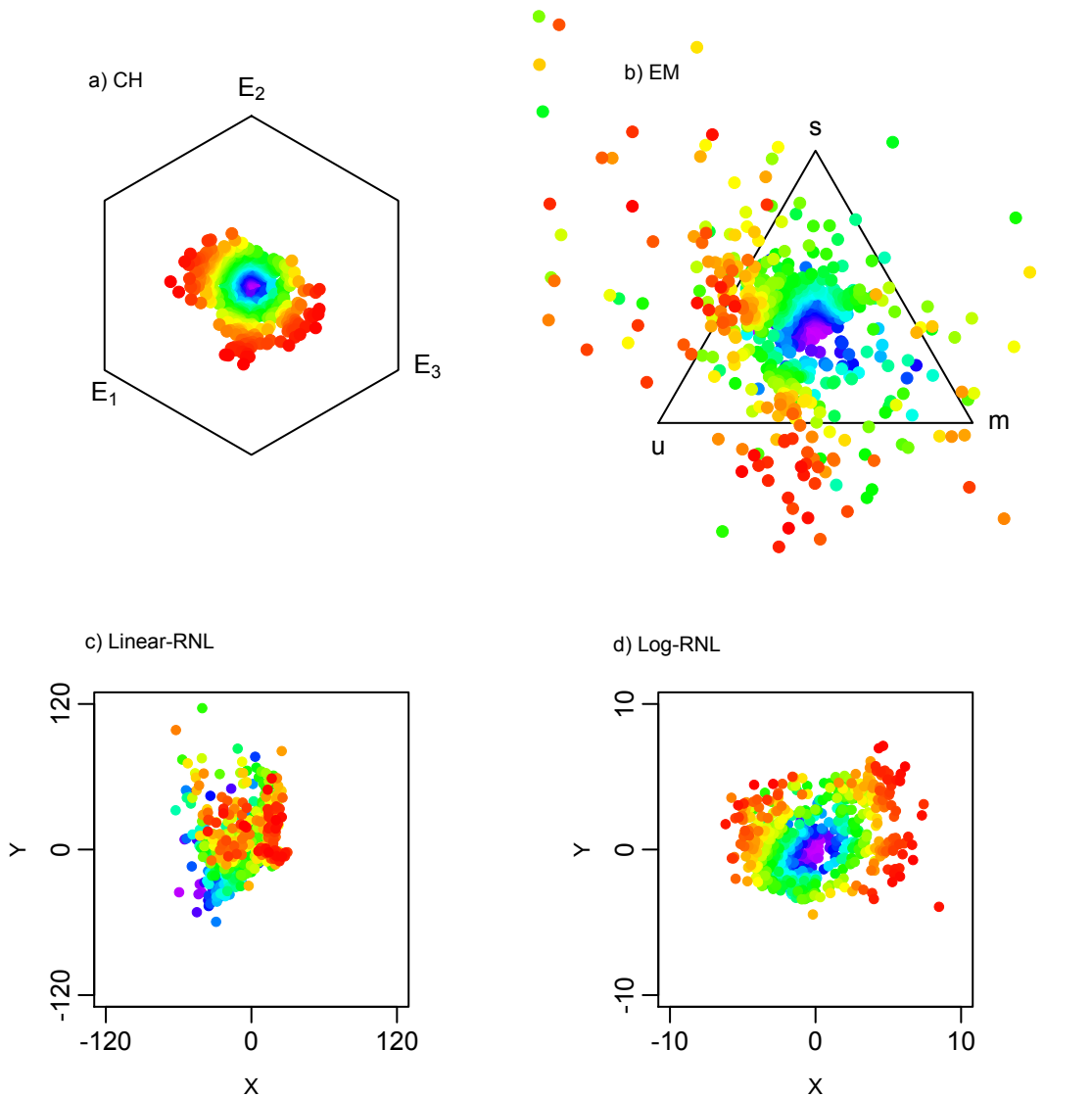


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691 Figure 8.  $\Delta S$  and photoreceptor outputs of the fourth setup of colour vision model simulations –  
692 achromatic stimulus against chromatic background: Chittka (1992) colour hexagon (CH), Endler  
693 & Mielke (2005) colour triangle (EM), and linear and log-linear Receptor Noise Limited models  
694 (Linear-RNL and Log-RNL; Vorobyev & Osorio 1998; Vorobyev *et al.* 1998). Variation in  $\Delta S$ -  
695 values as a function of spectra with achromatic reflectance from 5% to 95% (top row).  
696 Photoreceptor output values as a function of the same reflectance spectra (bottom row). Violet,  
697 blue and green colours represent short, middle and long  $\lambda_{\max}$  photoreceptor types. With the  
698 exception of c) Linear-RNL, scales are the same as in Figure 4.

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701 Figure 9. Flower reflectance spectra (N=858) projected into chromaticity diagrams: Chittka  
702 (1992) colour hexagon (CH), Endler & Mielke (2005) colour triangle (EM), and linear-  
703 linear Receptor Noise Limited models (Linear-RNL and Log-RNL; Vorobyev & Osorio 1998;  
704 Vorobyev *et al.* 1998). To facilitate model comparison, point colours correspond to chromaticity  
705 distances in the CH chromaticity diagram.

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