

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 (λ_{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 (λ_{max}), from shortest to
145 longest λ_{max} . Honeybees workers (*Apis mellifera*), for instance, have three photoreceptor types
146 with λ_{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):

201

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

202

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

203

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

204

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

205

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

206

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

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 ν is the noise-to-signal ratio of a single photoreceptor, and η_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, ΔS 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 Δf_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 ΔS 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 λ , L gives the curve maximum reflectance value
254 (%), k gives the steepness of the curve, and λ_{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 (ΔS) 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 ΔS 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 ΔS curve against midpoint wavelength, with maximum ΔS 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 ΔS -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 ΔS curve, increasing from short to long midpoint wavelengths,
334 reaching a maximum ΔS 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 ΔS curve, with a maximum ΔS 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 ΔS curve, with maximum values around 500 nm midpoint wavelength (Figure 6). CH
345 model predicts a bell shaped ΔS curve with maximum ΔS 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 ΔS (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, ΔS decreases. Contrary to the basic model, EM model now estimates realistic ΔS
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 ΔS 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 ΔS 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, ΔS 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 ΔS
377 values of 0.31 at 5% reflectance achromatic spectrum (Figure 8a). ΔS 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, ΔS values then decrease as
382 the reflectance value of achromatic spectra increases (Figure 8b). The linear-RNL model shows a
383 linear increase in ΔS 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, ΔS -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, ΔS -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 ΔS
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 ΔS 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 (ΔS) 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° (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 ΔS values as binary variable: i.e. above the threshold,
460 detectable; below threshold, not detectable. Instead, use of ΔS 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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484

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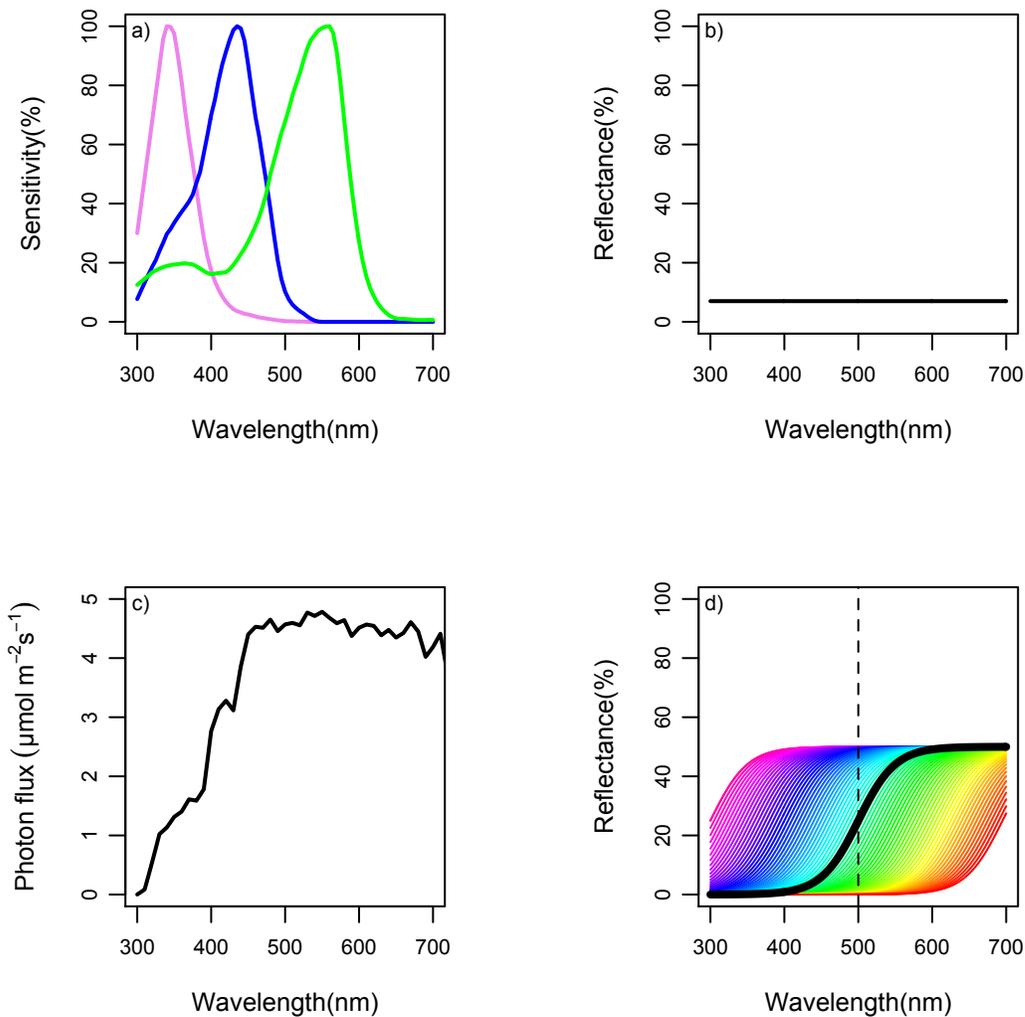
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623 **Figures**

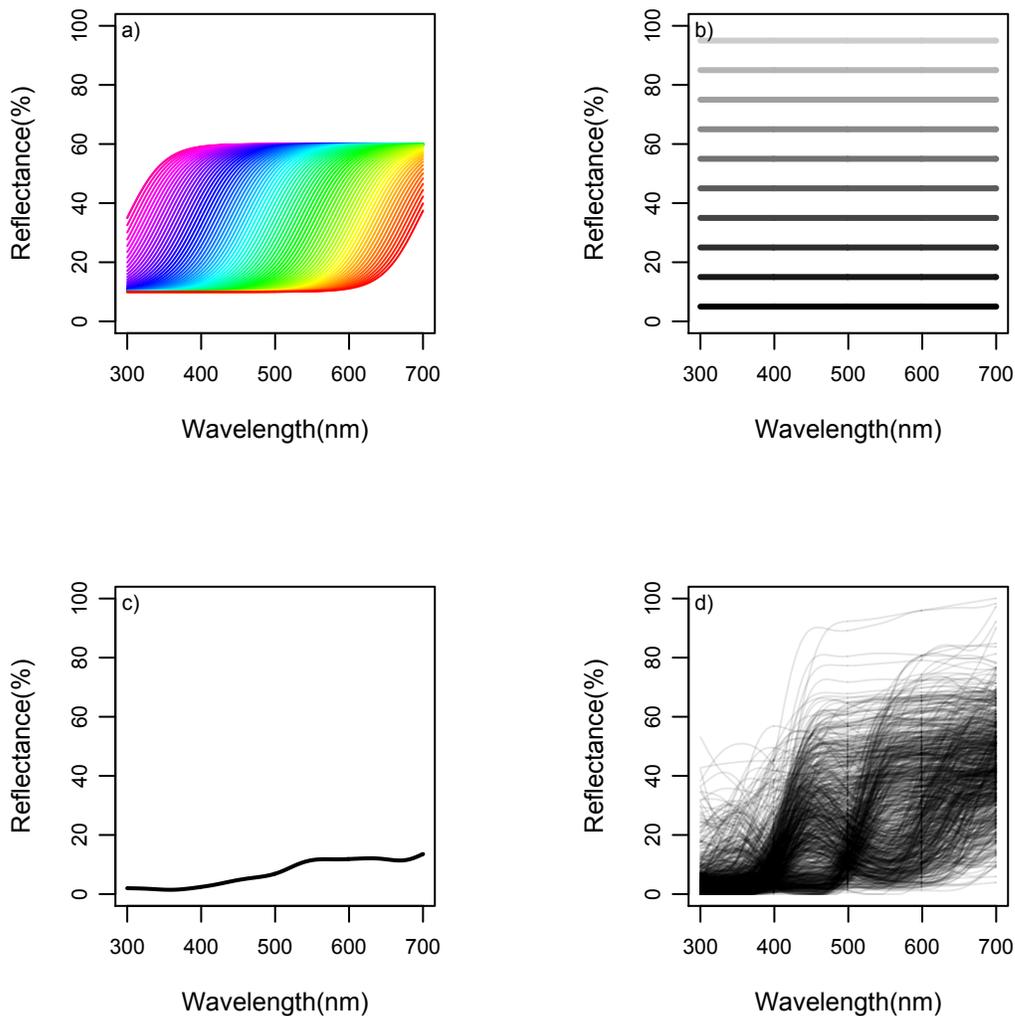


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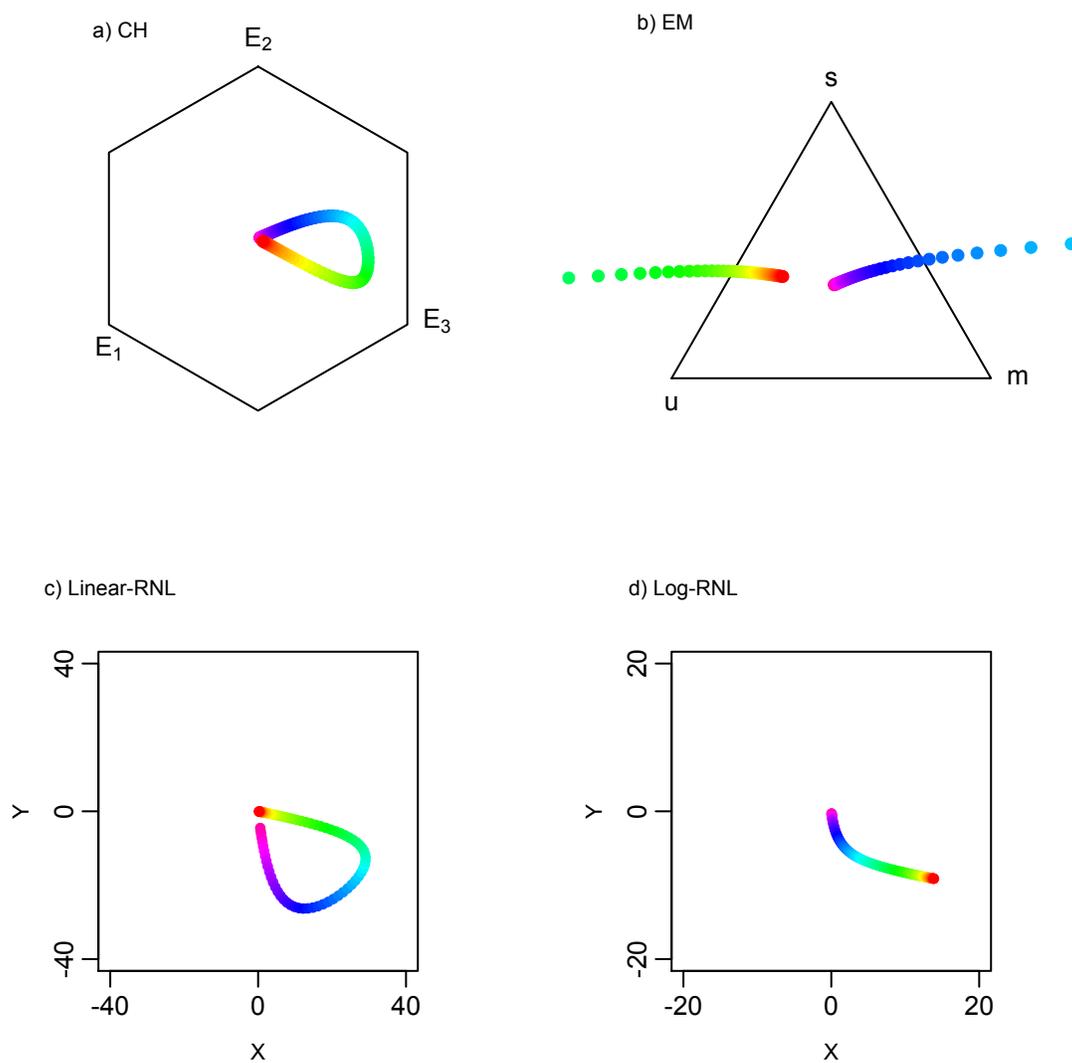
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626 Figure 1. Basic setup used for colour vision model simulations. (a) Honeybee (*Apis mellifera*)
627 photoreceptor sensitivity curves (data from Peitsch *et al.* 1992 available in Chittka & Kevan
628 2005); (b) Achromatic background reflectance 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.

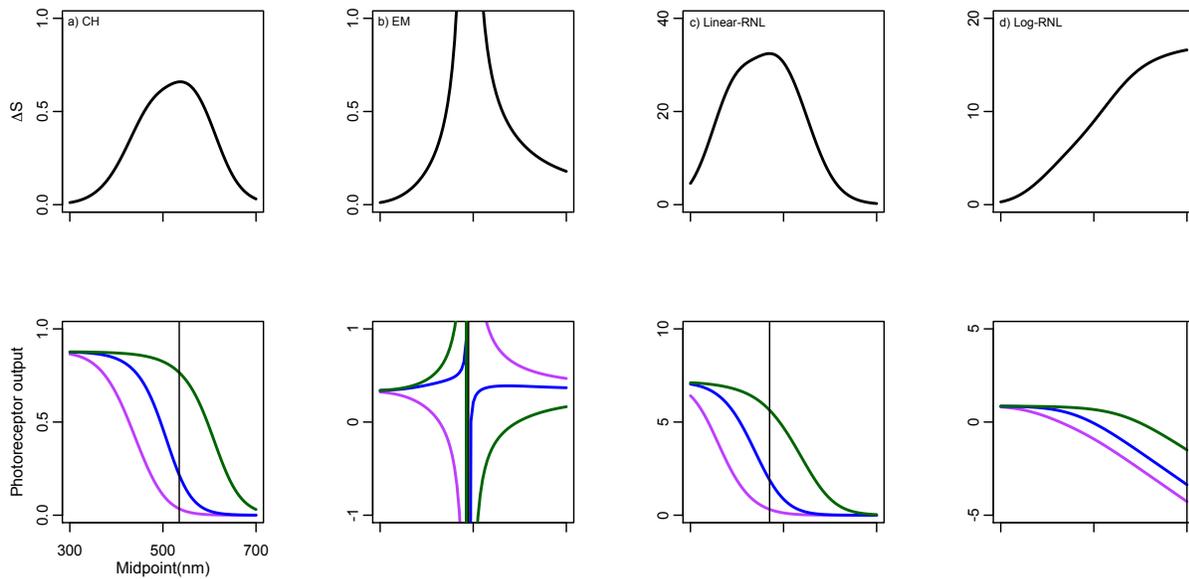
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634 Figure 2. Changes from the basic setup used for colour vision model simulations. (a) Ten percent
635 point added to the original reflectance spectra with midpoints varying from 300 to 700nm at
636 5nm intervals; (b) Achromatic reflectance spectra, 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); (d) 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

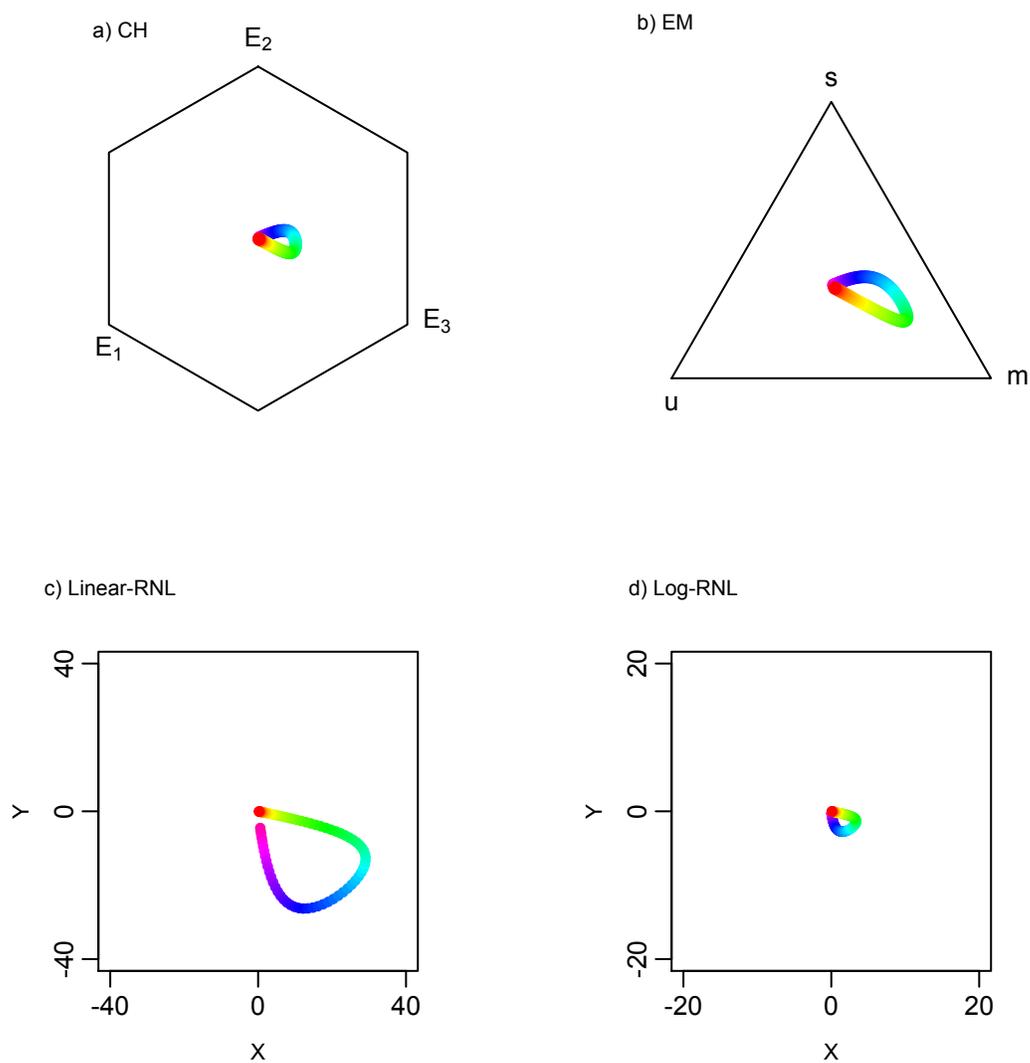


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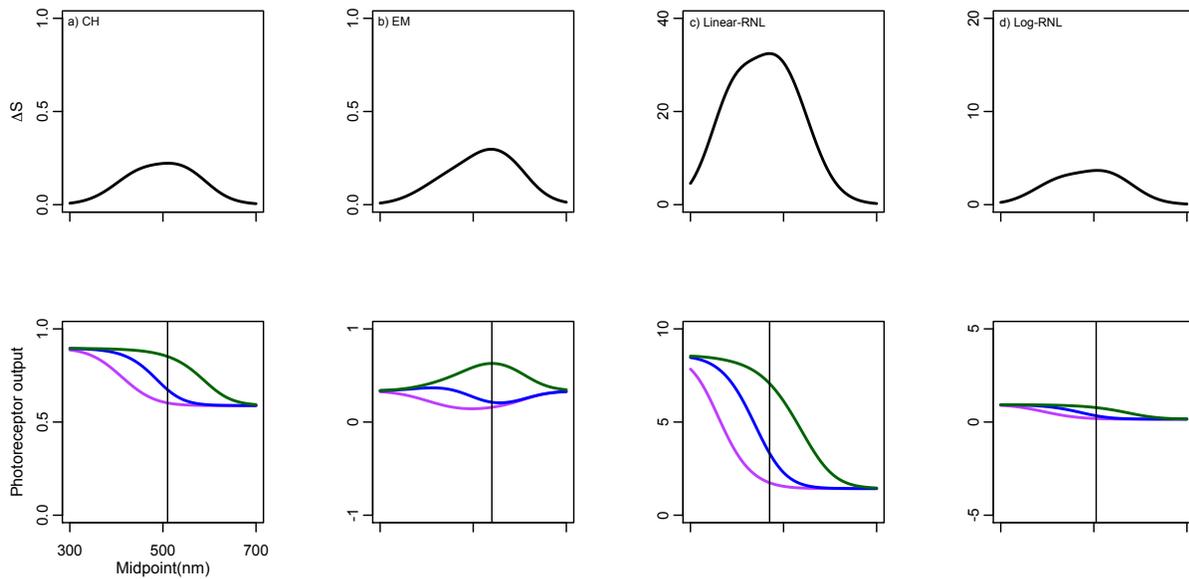
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650 Figure 4. ΔS and photoreceptor outputs of the basic setup of colour vision model simulations
651 (Figure 1): Chittka (1992) colour hexagon (CH), Endler & Mielke (2005) colour triangle (EM),
652 and linear and log-linear Receptor Noise Limited models (Linear-RNL and Log-RNL; Vorobyev
653 & Osorio 1998; Vorobyev *et al.* 1998). Variation in ΔS -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 λ_{\max} photoreceptor types. Vertical lines represent midpoint of maximum ΔS -values.

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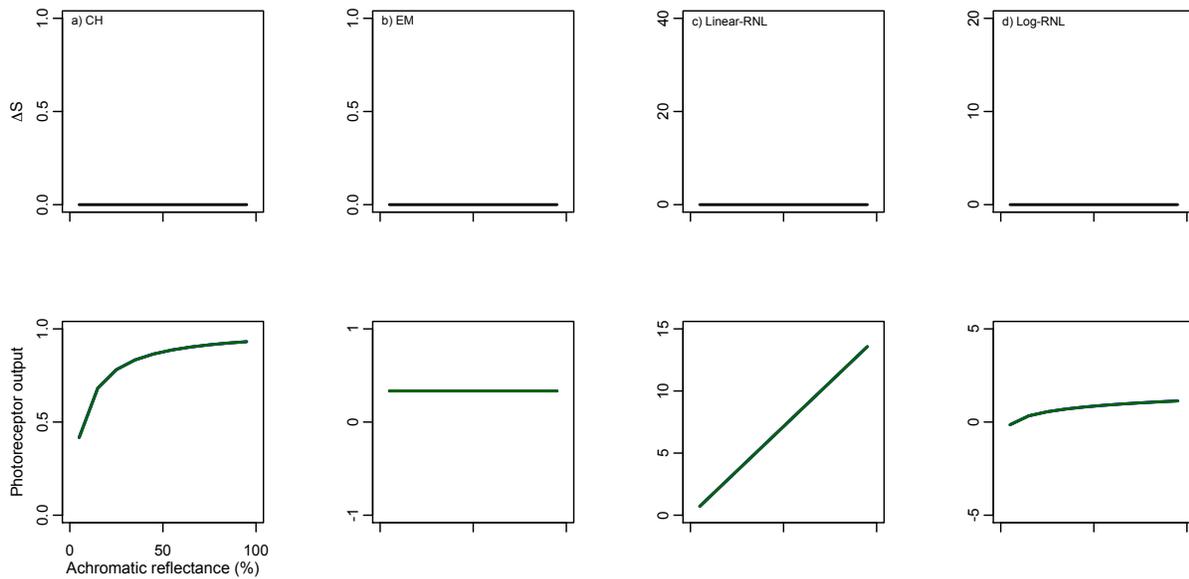


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659 Figure 5. Chromaticity diagrams of the second simulation – 10 percent point added to
660 reflectance values: Chittka (1992) colour hexagon (CH), Endler & Mielke (2005) colour triangle
661 (EM), and linear and log-linear Receptor Noise Limited models (Linear-RNL and Log-RNL;
662 Vorobyev & Osorio 1998; Vorobyev *et al.* 1998). Colours correspond to reflectance spectra from
663 Figure 2a.
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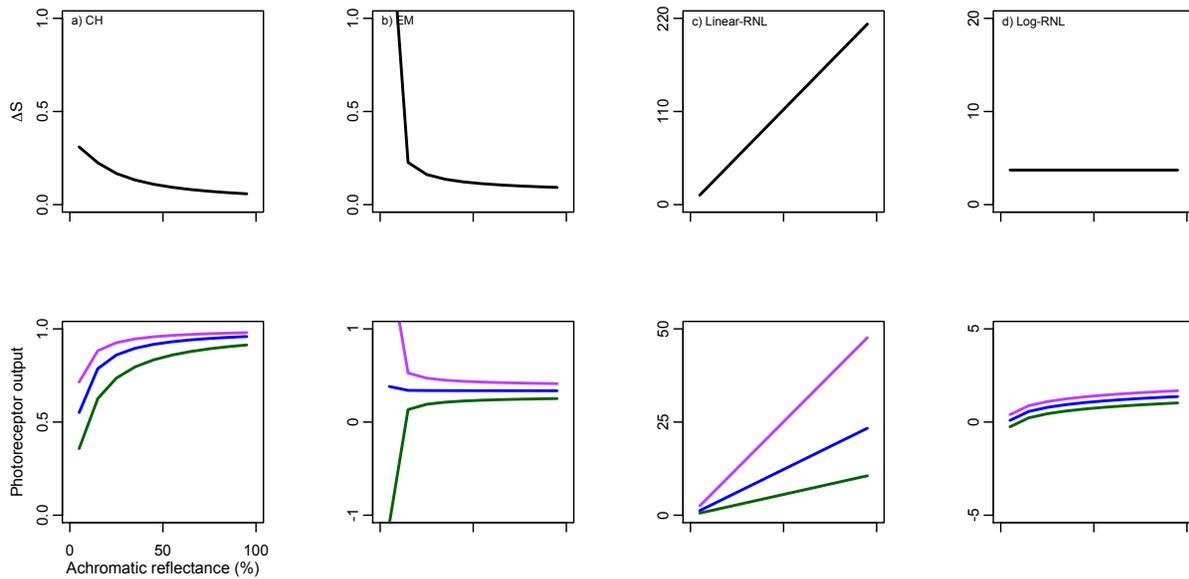
669 Figure 6. ΔS and photoreceptor outputs of the second setup of colour vision model simulations -
670 10 percent point added to stimulus reflectance spectra: Chittka (1992) colour hexagon (CH),
671 Endler & Mielke (2005) colour triangle (EM), and linear and log-linear Receptor Noise Limited
672 models (Linear-RNL and Log-RNL; Vorobyev & Osorio 1998; Vorobyev *et al.* 1998). Variation
673 in ΔS -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 λ_{max} photoreceptor types. Vertical lines
676 represent midpoint of maximum ΔS -values. For comparison, scales are the same as in Figure 4.
677



678

679

680 Figure 7. ΔS 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 ΔS -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 λ_{\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.

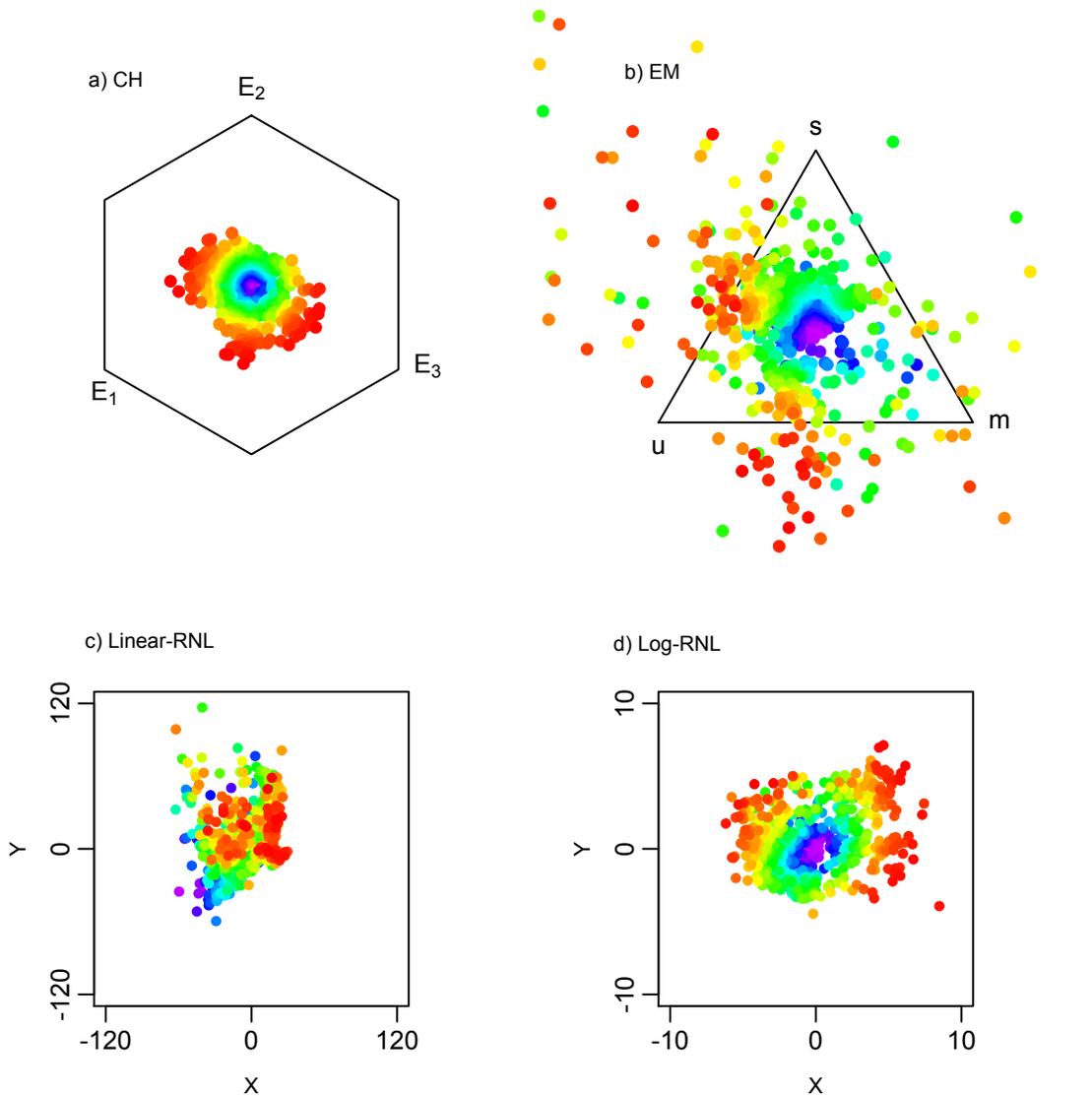


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691 Figure 8. ΔS and photoreceptor outputs of the fourth setup of colour vision model simulations –
692 achromatic stimulus against chromatic background: Chittka (1992) colour hexagon (CH), Endler
693 & Mielke (2005) colour triangle (EM), and linear and log-linear Receptor Noise Limited models
694 (Linear-RNL and Log-RNL; Vorobyev & Osorio 1998; Vorobyev *et al.* 1998). Variation in ΔS -
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 λ_{\max} photoreceptor types. With the
698 exception of c) Linear-RNL, scales are the same as in Figure 4.

699



700

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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