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The colour of flowers in spectrally variable illumination and insect pollinator vision

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Abstract The spectral reflectance of differently coloured Australian native plant flowers and foliage was measured and plotted in a colour triangle to represent the colour space of the honeybee. Spectral variations in illumination are shown to significantly change plant colours for bee vision without colour constancy. A model of chromatic adaptation based upon the von Kries coefficient law shows a reduction in plant colour shift, with the degree of correction depending upon position in colour space. A set of artificial reflectances is used to map relative colour shift caused by spectrally variable illumination for the entire colour space of the honeybee. The rarity of some flower colours in nature shows a correlation to a larger colour shift for these colours when illuminated by spectrally variable radiation. The model of chromatic adaptation is applied to illuminations used in a behavioural study on honeybee colour constancy by Neumeyer 1981. Surface colours used by Neumeyer are plotted in colour space for the various illuminations. The results show that an illumination-dependent colour shift correlates to a decrease in the frequency of bees correctly choosing a colour to which it was trained.

Key words Bees · Bee colour space · Flower constancy · Illumination colour · Chromatic adaptation

Abbreviation CCT correlated colour temperature

Introduction

The spectral composition of most visible radiation reaching the earth's surface is a combination of direct

sunlight and short-wavelength-rich skylight. The skylight results from Rayleigh scatter (Rayleigh 1899), with the ratio of the two sources depending upon the amount of atmosphere the sunlight must traverse. Water droplets, ice crystals and other large particles scatter visible radiation and also vary the ratio of sunlight to skylight (Rayleigh 1899). As the ratio changes the spectral composition of the radiation reaching the ground varies (Judd et al. 1964). The spectral composition of most continuous visible radiation sources can be described by the correlated colour temperature (CCT) of a black body with approximately the same spectral distribution (Judd et al. 1964).

Solar altitude, atmospheric particles, clouds and objects producing shade can all affect the spectral quality of radiation illuminating a flower. Illumination and flower pigmentation determine the spectral quality of radiation reflected by a flower. Australian native plant flowers reflect near-ultraviolet (UV; 320–400 nm) (Inouye and Pyke 1988; Gross 1992; Dyer 1996), blue (B; 400–500 nm), green (G; 500–600) and red (R; 600–700 nm) radiation. Important insect pollinators such as the introduced honeybee (*Apis mellifera*) have colour trichromatic vision based on photoreceptors with maximum radiation absorption at 350, 440 and 540 nm (Autrum and Zwehl 1964; Menzel and Blakers 1976; Menzel et al. 1986).

Individual insect pollinators sometimes exhibit flower constancy and restrict their visits to one flower type even when other rewarding flowers are available (see Waser 1986 for review). Behavioural experiments show that bees can discriminate colours as food signals (Daumer 1956, 1958; Helversen 1972) and it is likely that colour is an important determinant in flower constancy (Waser 1983a,b; Chittka et al. 1997). Flower constancy is of great value to angiosperms because it increases the chance of cross fertilisation within a given species (Darwin 1876; Waser 1983a,b, 1986). Flower constancy may benefit insect pollinators because of the reduced handling time once a flower's characteristics have been learnt (Waser 1983a,b, 1986). Insects are important an-

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glossy pollinators and the variation in the spectral quality of radiation between 300 nm and 650 nm has implications for insect-plant relationships. If changes in spectral illumination resulted in perceived colour change for an insect, then flower constancy would become more difficult.

The problem of spectrally variable illumination for human colour vision is largely solved by approximate colour constancy, which allows an object to appear to have nearly the same colour under different illumination sources (Hurvich 1981; MacAdam 1985). The term approximate is used to distinguish that the correction is not perfect for all colours under all illuminations (Hurvich 1981). Colour constancy for the honeybee has been demonstrated in behavioural experiments by Neumeyer (1981). Neumeyer trained single freely flying bees to land on one of nine coloured fields that were presented on a grey background. The initial training illumination source was then varied with colour filters to see if a bee could still correctly orientate to the training field. The field was preferred under nearly all illumination colours, but the frequency of correct choices fell with increasing filtration strength. It can thus be concluded that the honeybee also has approximate colour constancy. It has also been shown in behavioural experiments that the honeybee demonstrates simultaneous colour contrast (Neumeyer 1980) and successive colour contrast (Neumeyer 1981). The results suggest that chromatic adaptation could be an important mechanism in honeybee colour constancy. Neumeyer (1981) discusses the possibility that relative photoreceptor sensitivities being changed by neuronal interactions between adjacent photoreceptor channels and/or variations in visual pigment concentrations within photoreceptors might be responsible for chromatic adaptation in the honeybee.

Colour constancy has also been demonstrated for the honeybee in a behavioural study by Werner et al. (1988). It was shown that free-flying bees chose a colour to which they had been trained, even when the illumination was changed to make a different colour have the same radiation fluxes as the original training colour. It was thus concluded that colour vision was independent of the spectral content of illumination for the range of colours used. The findings were reported to be consistent with the retinex theory of colour constancy that an algorithm using long-range interactions is required to explain colour constancy (Land 1986; Werner et al. 1988). The results did not exclude the possibility of colour constancy being explained by chromatic adaptation.

Chittka et al. (1994) showed in a study of 1063 flowers from various sites around the world that 85% of the sample could be described by five categories of colour for the honeybee. Each colour category was from a different segment in a hexagonal colour space used in that study. The categories were defined as A1: UV-, B-, G+ and R+ (a yellow flower to humans), A2: UV+, B-, G+ and R+ (a yellow flower to humans), A3: UV-, B+, G+ and R+ (a white flower to humans), A4: (1) UV-, B+, G- and R+ and (2) UV-, B+ and G/R+ (a (1) blue or purple and (2) pink flower to humans), and A5: UV+, B+, G- and R+ (a blue, purple or violet flower to humans).

This work examines the effect of spectrally variable illumination on the colour of Australian native plant flowers from each of the five categories described above. A model of bee colour vision is developed using the spectral data for daylight of Judd et al. (1964), a photopigment spectral absorption model for the photoreceptors (Stavenga et al. 1993) and measured specimen reflectances. Results are plotted in a colour triangle to represent bee colour space. A set of computer-generated reflectances is used to explore the possible effect of spectrally variable radiation on a broad range of colours theoretically visible to bees. A possible solution to spectrally variable illumination is developed using a model of chromatic adaptation based on the von Kries coefficient law (von Kries 1902 in MacAdam 1970; Hurvich 1981; MacAdam 1985). The results are examined in relation to the behavioural work of Neumeyer (1981).

Materials and methods

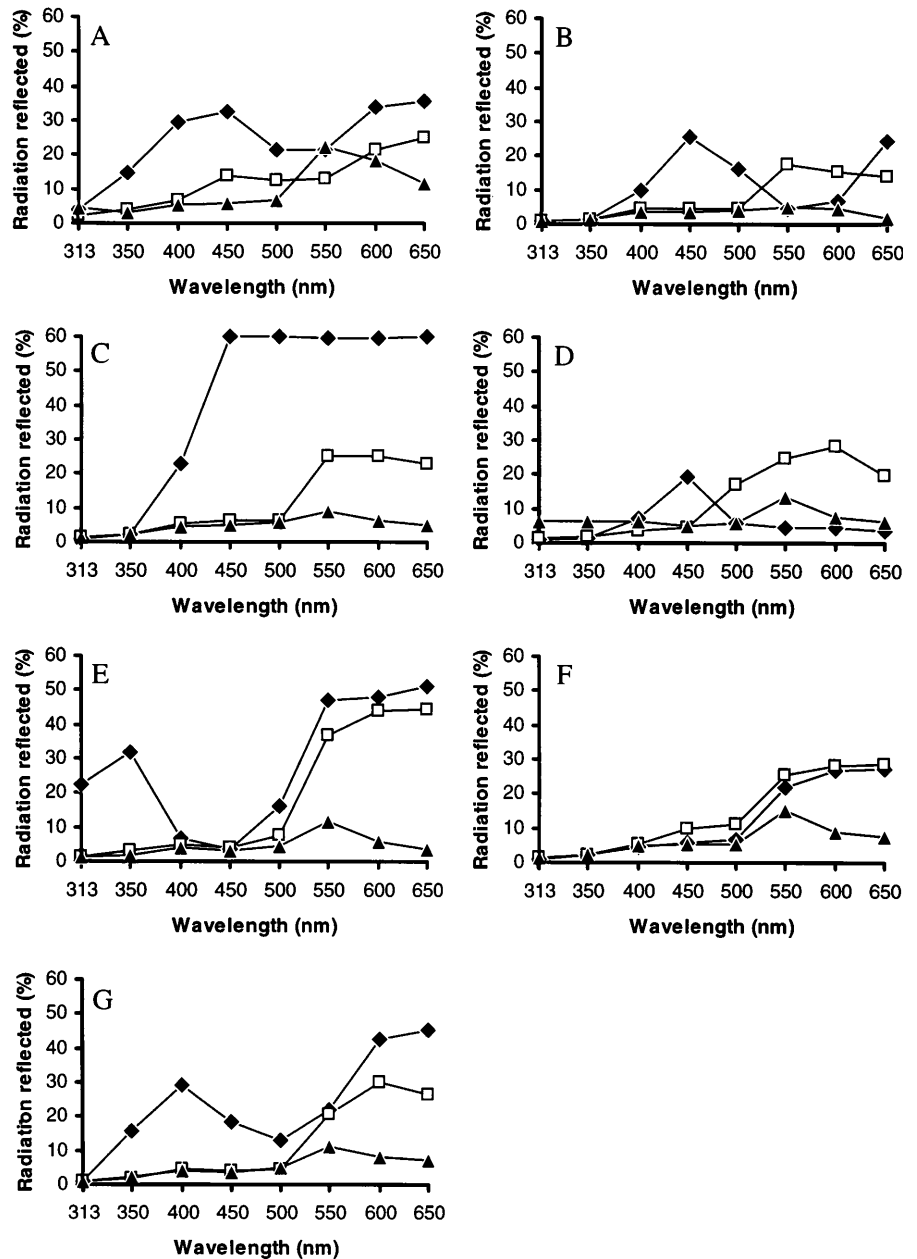
Measurement of floral spectral reflectance

From a previous study on the reflection of UV radiation from flowers of Australian native plants (Dyer 1996) seven flowers (Table 1) were chosen to represent the five main categories of floral colouration described by Chittka et al. (1994). Categories A1–A3 were represented by one flower each, two flowers were chosen for the two colour types in category A4, and two flowers to represent category A5. Spectral reflectance curves were determined by photographing the specimens and a calibrated grey scale (Penny 1983; Dyer 1996) through eight interference filters (Andover, USA) of half band-widths 20 nm or 25 nm and centre wavelengths: 313, 350, 400, 450, 500, 550, 600 and 650 nm. Photographs were taken through a 105-mm Quartz Nikkor lens using a bare Metz 202 ringflash. Kodak 35 mm T-Max 400 film was processed to 3200 ISO (Williams and Williams 1993). Images were digitised and a computer was used to calculate plant reflectance values (Fig. 1) (Dyer 1996).

Table 1 Species of Australian native plant flowers, colour of flower to human viewer and spectral reflectance category of flower according to categories described by Chittka et al. (1994)

Species	Flower colour for humans	Category
<i>Boronia spathulata</i> Lindley	Pink	A5
<i>Brachycome multifida</i> DC.	Pink (yellow centre)	A4
<i>Brachycome multifida</i> DC.	White (yellow centre)	A3
<i>Dampiera linearis</i> R.Br.	Blue (yellow centre)	A4
<i>Hibbertia obtusifolia</i> DC.	Yellow	A2
<i>Isopogon anethifolius</i> (Salisb.) J. Knight	Yellow	A1
<i>Stylidium bulbiferum</i> Benth.	Purple (yellow and white centre)	A5

Fig. 1A–G Percentage radiation reflected versus wavelength from the petal (◆), centre (□) and foliage (▲) of seven Australian native plants: **A** *Boronia spathulata*, **B** *Brachycome multifida* (pink), **C** *Brachycome multifida* (white), **D** *Dampiera linearis*, **E** *Hibbertia obtusifolia*, **F** *Isopogon anethifolius*, **G** *Stylidium bulbiferum*



Measurement of correlated colour temperature

The CCT of radiation reaching the earth's surface in Melbourne, Australia, was measured with a Minolta Color Meter 2 from July to December 1996. Recordings were made with the meter at 90° to the position of the sun and with the meter in shade measuring skylight only.

Colour triangle plots of floral reflections

A template of photopigment spectral absorption developed by Stavenga et al. (1993) was used to model the three photoreceptors of the bee. The absorption peaks of the photoreceptors were taken to be 350, 440 and 540 nm (Autrum and Zwehl 1964; Menzel and Blakers 1976; Menzel et al. 1986), and the pigments assumed to be based on vitamin A1, to give a close match to the three photoreceptors of the honeybee (Stavenga et al. 1993). The radiation source values used were equivalent to CCT = 4800, 5500, 6500 and 10 000 K based on the data of Judd et al. (1964).

The relative amount of radiation absorbed by each photoreceptor (P) was calculated by numerically integrating the product of photoreceptor absorption $S(\lambda)$, spectral reflectance $I(\lambda)$ and the illumination $D(\lambda)$ at 10-nm steps from 310 to 670 nm (Eq. 1). The variable W was used to weight each of the three photoreceptors:

$$P(350, 440, 540) = W \int_{310}^{670} S(\lambda)I(\lambda)D(\lambda)d\lambda \quad (1)$$

The values of $P(350)$, $P(440)$ and $P(540)$ were used to calculate chromaticity coordinates (Eq. 2) (Wyszecki and Stiles 1967) which were plotted in a colour triangle to represent bee colour space. Colour triangles are conventionally used to plot chromaticity coordinates for humans (Rushton 1972; Goldsmith 1990) and insects (Daumier 1956, 1958; Menzel 1979; Neumeyer 1981; Goldsmith 1990). Chromaticity coordinates (uv , b , g) are given by:

$$uv/P(350) = b/P(440) = g/P(540) = 1/(P(350) + P(440) + P(540)),$$

$$\text{and } uv + b + g = 1 \quad (2)$$

The three photoreceptors were weighted by the variable W to simulate chromatic adaptation to various illumination sources. The value of W (Table 3) was determined by the ratio of the three photoreceptors required to plot a stimulus reflecting radiation equally (equal white) in the centre of a colour triangle for a given illumination source (Eq. 3).

For chromatic adaptation to equal white reflecting an illumination source, the ratio of the values of W were varied such that:

$$uv = b = g = 1/3 \quad (3)$$

Frequently occurring flower colours do not cover the whole of bee colour space (Chittka et al. 1994). A set of 99 computer-generated reflectance curves were therefore produced systematically to explore the effect of spectrally variable illumination on a broad range of colours theoretically visible to a bee. The generated curves were the product of nine standard curves (Fig. 2A) and 11 sets of transformation values (Fig. 2B). The basis for the choice of the nine standard reflectance curves is derived from the high frequency of naturally occurring flower colours that have a steep gradient at 375 and 500 nm (Chittka and Menzel 1992). For each standard curve the short (313 and 350 nm), medium (400 and 450 nm) and long (500–650 nm) reflectance values were multiplied by a short, medium and long transformation values. This produces a set of 99 reflectance curves which when plotted for an illumination of CCT = 6500 K gives a good coverage of bee colour space (Fig. 2C). The set includes common plant colours, as well as colours that are rare or unknown in nature. The mapping of colour shift for a broad range of colours allows an evaluation of whether the colours that are common in nature are related to parts of the bees' colour space where chromatic adaptation performance is best.

Calculation of relative colour shift on a colour triangle

The colour shift (cs) of a specimen reflectance $I(\lambda)$ when illuminated by spectrally variable radiation was quantified by the distance between colour loci. Chromaticity coordinates were converted Cartesian coordinates (X , Y) (Eq. 4) which were used in Pythagoras' theorem (Eq. 5) to calculate relative colour shift (Eq. 6).

Representation of chromaticity coordinates as Cartesian coordinates given by:

$$X = \frac{1-uv}{\cos 30^\circ} - b \times \tan 30^\circ \text{ and } Y = b \quad (4)$$

which when substituted into Pythagoras' theorem

$$cs = 100 \times \sqrt{(X_1 - X_2)^2 + (Y_1 - Y_2)^2} \quad (5)$$

gives

$$cs = 100 \times \sqrt{\left[\left(\frac{1-uv_1}{\cos 30^\circ} - b_1 \times \tan 30^\circ \right) - \left(\frac{1-uv_2}{\cos 30^\circ} - b_2 \times \tan 30^\circ \right) \right]^2 + [b_1 - b_2]^2} \quad (6)$$

where uv_1 , uv_2 and b_1 , b_2 are the chromaticity coordinates of $I(\lambda)$ under two spectrally different illuminations.

Relative colour shift values are multiplied by 100 (Eqs. 5, 6) so that distances are relative to the height of a colour triangle (100 units) and are in relative units (u). The values cannot be treated as perceptual colour distance (Backhaus and Menzel 1987) but are used to evaluate relative colour shift in different areas of colour space. An artifact of mapping colour onto a two-dimensional colour triangle is that the relations of the triangle do not account for some colour vision phenomena observed for bees (Backhaus 1991, 1992; Chittka 1992; this is also a problem with some human colour spaces, see MacAdam 1985). These possible discrepancies are that variations in illumination intensity can effect colour hue (the Bezold-Brücke phenomenon), that increases in illumination intensity should shift colours towards an uncoloured white point or decreases towards an uncoloured black point and that the normalisation of values uv , b and g in Eq. 1 may misrepresent the colour position of colours normally outside the bees visible spectrum. The possible effect of these discrepancies on results was minimised by using broad-band reflection spectra that are within the bees visual range, and limiting theoretical variations in illumination to natural daylight conditions.

Results

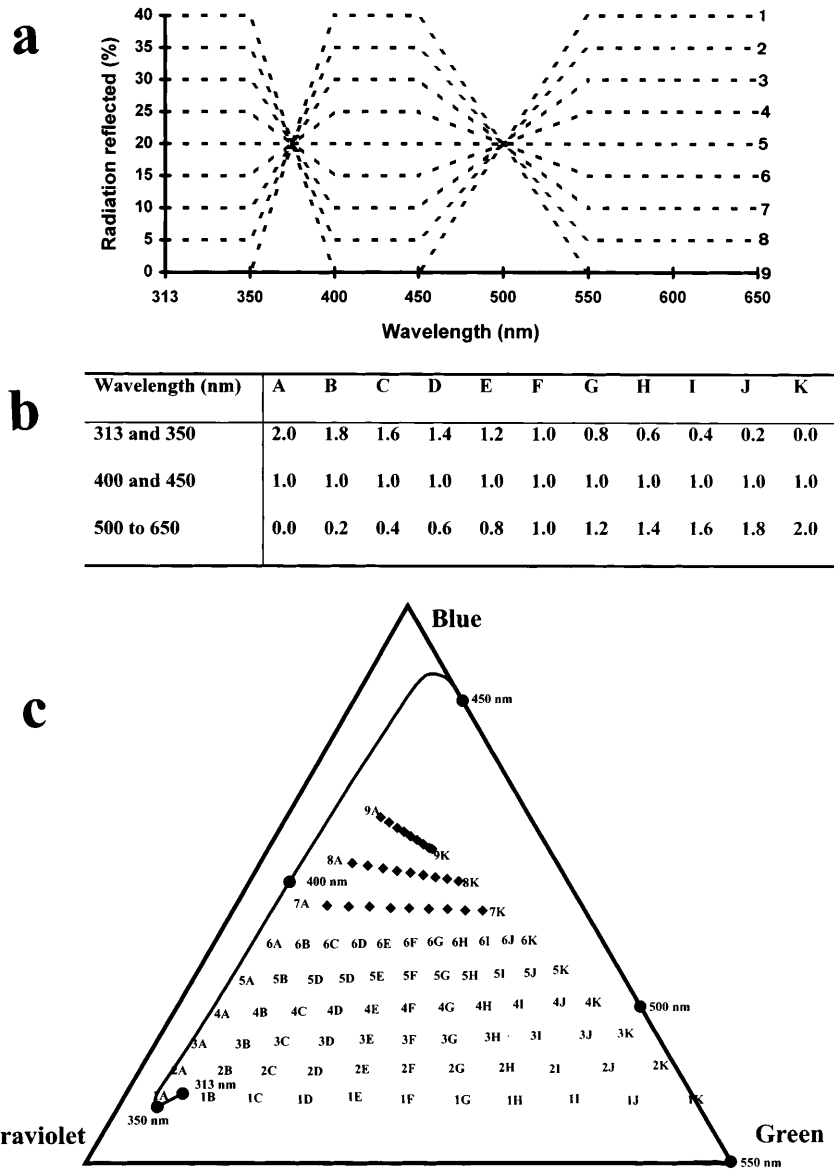
Spectral reflectance of radiation from the seven species of plants (Table 1) is shown in Fig. 1A–G. The distributions of plant petals, centres and foliage colours are plotted in bee colour space (Fig. 3A) for an illumination of a CCT = 6500 K and with the photoreceptors correctly weighted (W) for this source (Table 3). Flower petal colours are well dispersed on the right hand side of the colour triangle and flower centre colours plot towards the lower right hand side of the triangle. Petal colours are labelled with a colour category (A1–A5, see Table 1) as described by Chittka et al. (1994). All the plant foliage had a small peak of reflectance at 550 nm (Fig. 1A–G) and plotted in the centre right-hand side of the colour space of Fig. 3A. None of the measured plant colours plot on the lower left hand side of the triangle which represents colours that are UV rich to insects.

Insect colour vision without colour constancy was simulated by using constant values of W for a CCT = 6500 K (Table 3) and varying the values of $D(\lambda)$

Table 2 The date, time and atmospheric conditions for readings of the correlated colour temperature (CCT) of radiation reaching the ground in Melbourne. Readings were taken with the meter at 90° to the position of the sun and with the meter in the shade measuring skylight only

Date	Time (h)	Atmospheric conditions	CCT (K) with meter at 90° to sun	CCT (K) with meter in shade
9/6/96	1200	Overcast	5300	5500
12/6/96	1200	Sunny	4900	13500
19/7/96	1600	Sunny	4150	7150
20/7/96	1400	Overcast	5850	5850
24/9/96	1500	Sunny	5200	10500
27/9/96	1400	Overcast	5650	5700
9/12/96	1500	Sunny	5500	7800
16/12/96	1400	Overcast	6000	6000

Fig. 2A–C Parameters used to generate a set of colours to cover most of bee colour space: **A** Percentage reflection versus wavelength for nine standard reflectance curves (1–9). **B** Sets of values (*A–K*) used to transform nine standard curves to give 99 different reflectance curves. **C** Plots in bee colour space of the 99 reflectance curves considering an illumination of correlated colour temperature = 6500 K. The spectral locus is a plot of pure spectral radiation



such that CCT = 4800, 5500, 6500, 7500 and 10 000 K. Plots of the consequent colour shift in petal colours under variable illumination are shown in Fig. 3B. Insect colour vision with chromatic adaptation was simulated by assigning a different value of *W* (Table 3) to each photoreceptor depending upon the illumination source. Figure 3C shows the reduced colour shift in petal colours when the photoreceptors were weighted for each of the illumination sources described above.

The effect of spectrally variable illumination on 99 theoretical colours was then determined by the relative colour shift when radiation changed from CCT = 4800–10 000 K. The colour shift was plotted with a constant value of *W* to simulate no colour constancy and with a variable value of *W* to simulate chromatic adaptation. The numeric value of the relative colour shifts (the distance a colour loci would shift with variations in spectral illumination) was calculated and

plotted on colour triangles at the coordinates where theoretical colours would lie for CCT = 6500 K. These numeric values were then converted to contour lines of constant colour shift in separate colour triangles for the cases of no colour constancy (Fig. 4A) and chromatic adaptation (Fig. 4B). A comparison of relative colour shift in the two triangles allows an evaluation of where the correction of chromatic adaptation is best. Measured plant colours were plotted onto the two colour triangles to explore the relationship between plant colour distribution and illumination dependant colour shift (Fig. 4A, B). The chromatic adaptation model has a reduced colour shift ranging from <1 to 11 *u* (Fig. 4B) compared with the system of no colour constancy for which values range from 10 to 36 *u* (Fig. 4A).

Selections of typical illumination conditions in Melbourne for the months of August to December 1996 are shown in Table 2. On some occasions changes in the

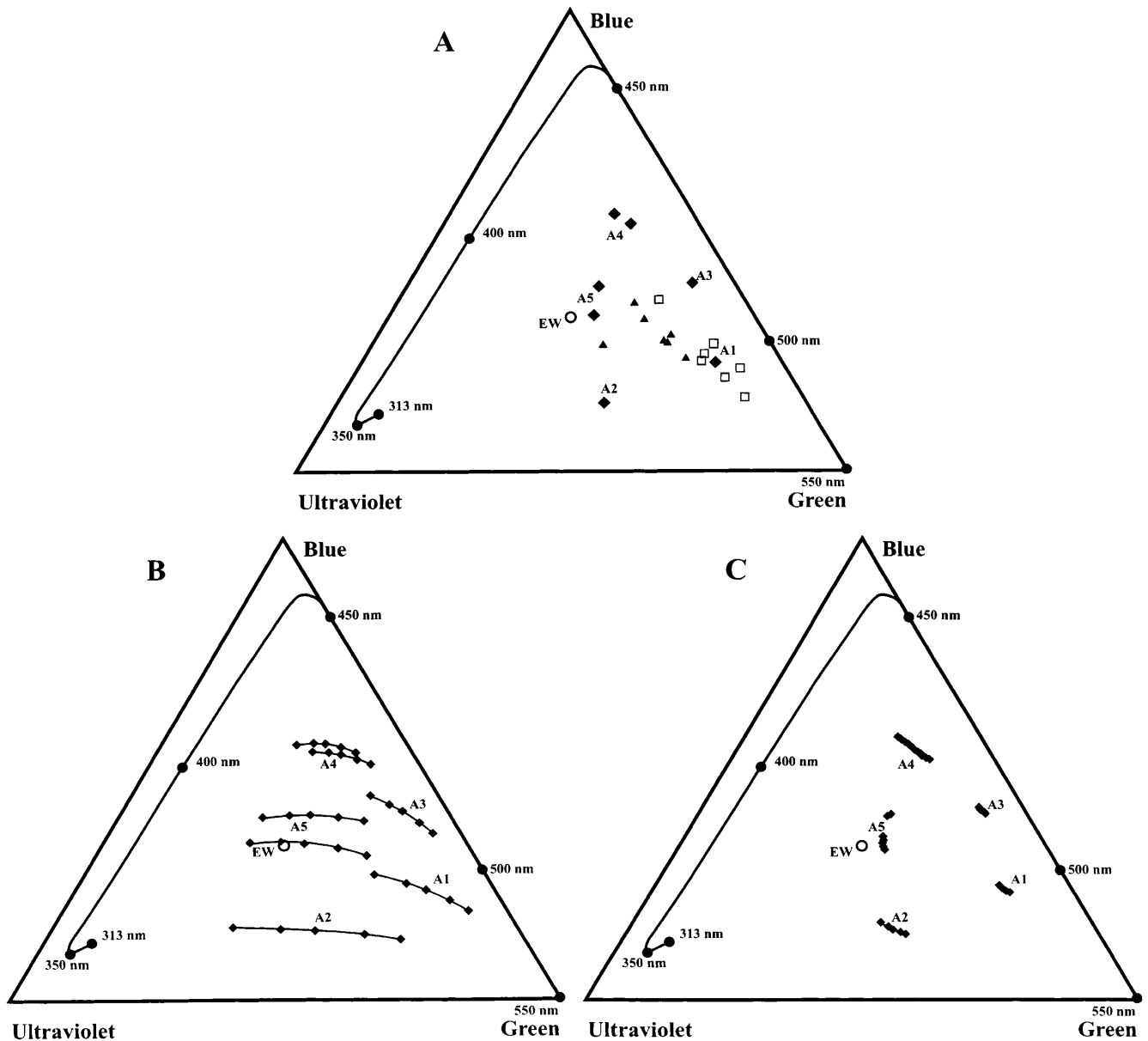


Fig. 3A–C Colour loci of flowers and foliage from seven Australian native plants in the colour triangle of the honeybee: **A** The distribution of the seven plants' petal (◆), centre (□) and foliage colours (▲) considering an illumination source of correlated colour temperature (CCT) = 6500 K; **B** Plots of petal colours under variable illumination sources of CCT equal to 4800, 5500, 6500, 7500 and 10 000 K with the weighting of receptors kept constant for a CCT of 6500 K to simulate no colour constancy; **C** Plots of petal colours under variable illumination sources of CCT equal to 4800, 5500, 6500, 7500 and 10 000 K with the weighting of receptors varied to plot a stimulus reflecting radiation equally at all wavelengths in the centre of the colour triangle (EW) for each illumination source. This simulates chromatic adaptation based on the von Kries coefficient law. Petal colour plots are labelled with categories (A1–A5) from five regions of bee colour as described by Chittka et al. (1994). The spectral locus is a plot of pure spectral radiation

CCT of radiation occurred quickly. For example, measurements of CCT values varied from 4000 to >10 000 K when the radiation source changed from

direct sunlight to blue skylight. These changes were caused by sunlight being blocked by a tree as the sun traversed the sky. Variations in the spectral composition radiation could also occur as solar angle changes over a day and a year.

Discussion

A variation in the spectral quality of radiation illuminating a flower produces a change in the spectral quality of radiation reflected from it. Table 2 shows the wide range of spectral illuminations insects must use whilst foraging for food. An insect without any mechanism for colour constancy would find it very difficult to orientate using colour as a cue because changes in spectral radiation would change the colour of the flower (Fig. 3B).

Table 3 The colour of radiation sources and the required weighting (W) of the short, medium and long photoreceptors to plot a stimulus reflecting radiation equally in the centre of bee colour space according to the von Kries coefficient law

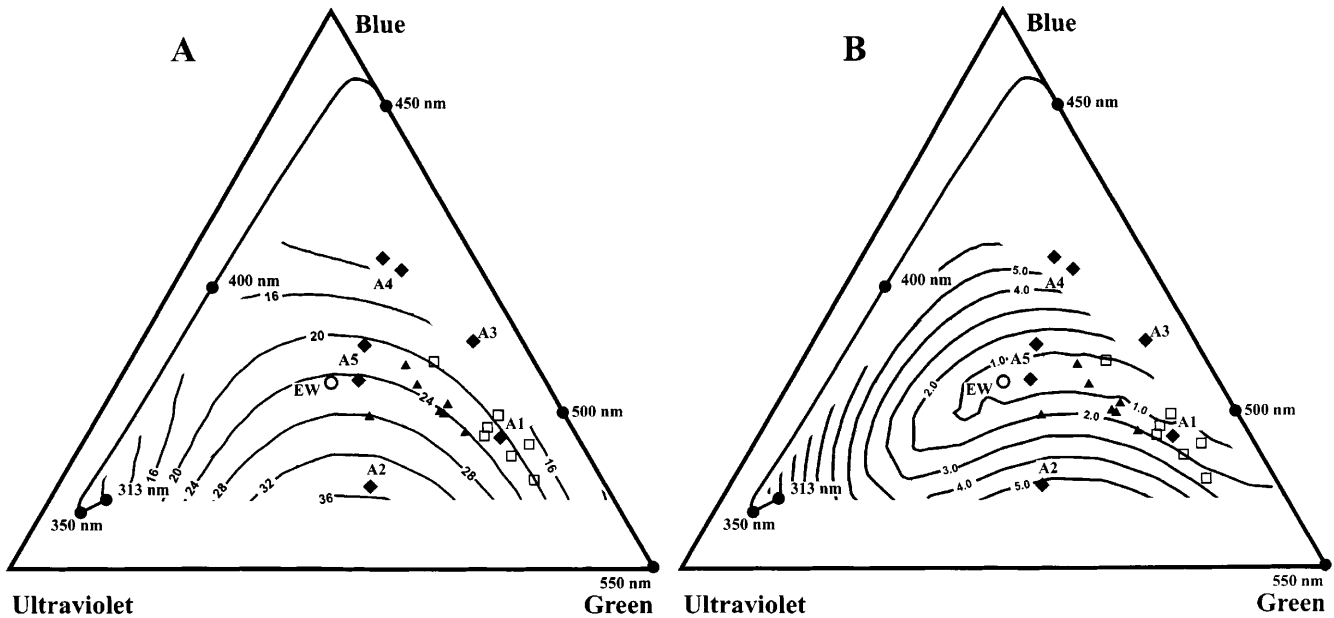
Radiation source colour	Short (W)	Medium (W)	Long (W)
This study. Colour in terms of correlated colour temperature (CCT)			
CCT = 10000 (K)	1.94	1.01	1.00
CCT = 7500 (K)	2.74	1.18	1.00
CCT = 6500 (K)	3.54	1.32	1.00
CCT = 5500 (K)	5.17	1.55	1.00
CCT = 4800 (K)	7.10	1.80	1.00
Neumeyer (1981)			
P (Training source) CCT = 3400 (K)	13.24	3.21	1.00
Yellow 1	13.95	4.16	1.00
Yellow 2	16.86	5.07	1.00
Yellow 3	35.30	8.88	1.00
Yellow 4	136.00	182	1.00
Blue 1	8.72	1.74	1.00
Blue 2	7.57	1.55	1.00
Blue 3	9.56	1.20	1.00

The contour plot of insect vision without colour constancy shows the effect of spectrally variable radiation on different regions of colour space (Fig. 4A). The

contours are symmetrical orientated with similar degrees of colour shift for colours on the left- and right-hand sides of the triangle. Colours that have short- and long-wavelength-reflecting pigments, such as the flower of *Hibbertia obtusifolia* (category A2), have the greatest colour shift as the radiation changes from being long wavelength rich (CCT = 4800 K) to short wavelength rich (CCT = 10 000 K). As increasing quantities of medium-wavelength radiation are reflected by floral specimens the influence of variable radiation upon the short- and long-wavelength-reflecting pigments is reduced. This results in smaller colour shift on the colour space as colours plot towards the apex of the triangle (Fig. 4A). The overall colour shift of all bee colours without any mechanism of colour constancy is large.

Fig. 4A, B Interpolated contour plots of colour shift in bee colour space for spectral illumination varying from a correlated colour temperature (CCT) of 4800 to 10 000 K. The contours represent colour shift for 99 computer-generated surface colours that cover most of bee colour space. The colour-shift distance is relative to the height of the triangle (100 units). Numbers on the contours represent the distance a colour in that region of colour space would shift under the spectral illumination change. **A** Plots made with the weighting of photoreceptors kept constant for a CCT of 6500 K to simulate no colour constancy; **B** Plots made with the weighting of receptors varied based on the von Kries coefficient law to plot a stimulus reflecting radiation equally at all wavelengths in the centre of the triangle (EW) for each illumination source used. Note that the colour shift is much lower for the variably weighted photoreceptors. The distribution of colours from seven Australian native plants is shown on both colour triangles: petals (◆); flower centres (□); and foliage (▲). Petal colour plots are labelled with categories (A1–A5) from five regions of bee colour as described by Chittka et al. (1994). The spectral locus is a plot of pure spectral radiation

The model of chromatic adaptation presented is based on the von Kries coefficient law. Each of the three photoreceptors is weighted (W) so that a surface that reflects radiation equally is plotted in the centre of the colour triangle for any illumination source. If chromatic



adaptation resulted in perfect colour constancy we would expect all colours in the colour triangle to show zero colour shift, but this is not the case. Figure 3C shows that with chromatic adaptation there is a significant decrease in shift of colour loci for petal colours. The correction is not perfect for all colours, however, and appears to vary with position in colour space. The effect of spectrally variable illumination on a wide range of colours was subsequently examined by the colour shift of loci in Fig. 2C.

As contours in Fig. 4A are symmetric in the colour triangle we would expect that if chromatic adaptation treated all colours with a similar (or similar in proportion to distance from EW) level of correction that this contour triangle (Fig. 4B) would be symmetric. The contour plot of insect vision with chromatic adaptation shows a significant reduction in colour shift for all colours (Fig. 4B). The centre right-hand side of the colour space has the highest degree of correction and this is the region where many common plant colours lie. The benefit offered by chromatic adaptation decreases as colours plot towards the UV, B and UV + G regions of bee colour space. The contours are not symmetric in the triangle and chromatic adaptation offers a different level of correction for different bee colours.

Neumeyer (1981) demonstrated that honey bees have colour constancy. Her work showed however that individual bees make more errors in correctly choosing a colour field as the illumination source colour increasingly differs from the training source. The chromatic adaptation model was applied to the data of Neumeyer by plotting the colour of the test field to which bees had been trained in bee colour space for each of the eight illumination sources she used. For each illumination source the photoreceptors were assigned a value of W (Table 3) to simulate chromatic adaptation. The distance the test-field colour shifted for each illumination source was calculated (Eq. 6) and plotted against bee correct choices for the illumination sources (Fig. 5). There were nine colour fields in the behavioural study so when the frequency of correct choices fell to 11.1% the foraging was random. Using a line of best fit for data points the intersect of this line with a Y -axis value of 11.1% occurs at an X -axis value where colour constancy has completely failed. This point is at $30 u$ for linear correlation ($R^2 = 0.7817$). For the model of chromatic adaptation the relative colour shift of all colours theoretically visible to bees is much lower than this figure (Fig. 4B) and it is likely bees would receive some benefit from chromatic adaptation for all colours. The plot of the measured specimen colours shows that 15 of the 21 colours have a colour shift of less than $2 u$ (Fig. 4B) which represents a decrease of 5% in the frequency of correct choices (Fig. 5). As this is the value for a large colour change in spectral illumination of 4800–10 000 K the model of chromatic adaptation appears to be quite efficient for common plant colours. The model of chromatic adaptation might explain the approximate colour constancy reported by Neumeyer. The relative colour

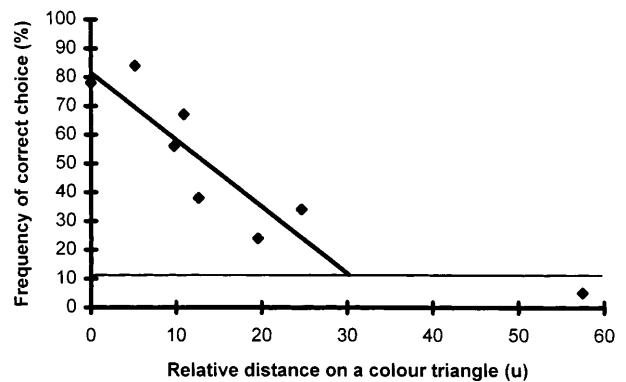


Fig. 5 Frequency of bees correctly choosing a colour test field under spectrally variable illumination versus the relative colour shift of the field when illumination is varied from initial training source. For each illumination source the photoreceptors are weighted to simulate chromatic adaptation according to the von Kries coefficient law. The line $Y = 11.11$ is the value where bee foraging was random. **Bold line** shows line of best fit between data points ($R^2 = 0.7817$). The colour shift is relative to the height of a colour triangle (100 units) and is in relative units (u). Data derived from the method and results of Neumeyer (1981)

shift of the test field loci caused by the imperfect correction of chromatic adaptation could result in a perceived colour shift by bees. As relative colour shift increases with different illumination sources there is a lower frequency of bee correct choices. To substantiate this idea would require behavioural experiments that show that bees perform colour constancy at different levels for differently coloured test fields. For example this idea would suggest that colour constancy would be better performed by bees for colours belonging in the centre right of colour space and poorer for UV-rich colours. The artificial illumination sources used by Neumeyer (1981) were poor in UV output and it is possible that the values reported here are biased. Further behavioural experiments on chromatic adaptation with UV-rich sources would be of great value.

There is evidence to suggest that flower constancy is based on colour (Waser 1983a,b; Chittka et al. 1997). The results of Chittka et al. (1994) recorded that flowers that reflect mainly UV radiation are rare and consisted of 1.6% of the study sample. The relatively poorer solution of chromatic adaptation for colours on the left-hand side of bee colour space (Fig. 4B) could make it difficult for insects to exhibit flower constancy with UV flowers. This may contribute to natural selection (Darwin 1876) not favouring these flowers. Blue and UV + G flowers are common however (Chittka et al. 1994) and are likely to have similar colour shift with spectral illumination changes (Fig. 4B). It is also possible that phylogenetic or biochemical constraints may be responsible for the relative frequency of differently coloured flowers (Chittka 1997). For example there might be physical limits on the way in which pigments can combine to form certain flower colours.

If chromatic adaptation does place selective pressure on flower colouration then colours for which the cor-

rection is poorer may be suited to particular photopic environments. For example it was observed by Stace and Fripp (1977) that differently coloured races of the Australian species *Epacris impressa* were found occupying particular regions. The pink form of the flower was nearly always found in deep shade and was usually winter flowering, whilst the white form populated open fields and was spring flowering. If pink colours (assuming non-UV reflecting; category A4) are at a disadvantage with variable illumination as indicated by Fig. 4B, then continuous shade might offer a more stable photopic environment. White flowers (category A3) are better corrected for by the model of chromatic adaptation (Fig. 4B), and changes in the colour of illumination might pose less of a problem for bee vision. It would be beneficial for future studies of flowers in specific regions to consider the spectral composition of illumination. If colour shift is variable for different colours as predicted by this model of chromatic adaptation, then plants may have evolved to meet this constraint by restricting flower colours or photopic environment.

In conclusion, natural variations in the spectral quality of radiation presents a problem for insects trying to orientate using colour as a cue. Without any mechanism for colour constancy natural radiation changes would produce a large colour shift for flower colours (Fig. 3B). A model of chromatic adaptation shows a reduced colour shift for all bee colours (Fig. 4B). The model predicts a correction that is most efficient in the centre right-hand side of bee colour space and this correlates with the colour loci common plant reflectances (Fig. 4B). The poorer solution of chromatic adaptation for colours on the left-hand side of bee colour space offers a possible or part explanation for the rarity of these colours in nature.

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