

Why background colour matters to bees and flowers

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Abstract Flowers are often viewed by bee pollinators against a variety of different backgrounds. On the Australian continent, backgrounds are very diverse and include surface examples of all major geological stages of the Earth's history, which have been present during the entire evolutionary period of Angiosperms. Flower signals in Australia are also representative of typical worldwide evolutionary spectral adaptations that enable successful pollination. We measured the spectral properties of 581 natural surfaces, including rocks, sand, green leaves, and dry plant materials, sampled from tropical Cairns through to the southern tip of mainland Australia. We modelled in a hexagon colour space, how interactions between background spectra and flower-like colour stimuli affect reliable discrimination and detection in bee pollinators. We calculated the extent to which a given locus would be conflated with the loci of a different flower-colour stimulus using empirically determined colour discrimination regions for bee vision. Our results reveal that whilst colour signals are robust in homogeneous background viewing conditions, there could be significant pressure on plant flowers to evolve saliently-different colours to overcome background spectral noise. We thus show that perceptual noise has a

large influence on how colour information can be used in natural conditions.

Keywords Rocks · Foliage · Spectra · Perceptual-Noise · Colour-Hexagon

Introduction

The biological partnership of flowering plants and bee pollinator colour vision has been widely studied over the past 100 years (Barth 1985; Dyer and Arikawa 2014) and much is known about bee colour photoreceptors and physiology (Peitsch et al. 1992; Hempel de Ibarra et al. 2014), colour learning and perception (Menzel 1967; Dyer and Chittka 2004; Avarguès-Weber and Giurfa 2014), and how colour signals can be modelled in colour space (Backhaus 1991; Chittka 1992; Vorobyev and Osorio 1998; Kemp et al. 2015; Renoult et al. 2015; Telles and Rodríguez-Gironés 2015). Bees are known to restrict their foraging visits to one species for a span of time, a phenomenon known as *flower constancy* (Waser 1986; Chittka et al. 1999). Plants benefit reproductively from this behaviour, and flower colour is important for facilitating flower constancy in bees (Chittka et al. 1999; Dyer and Chittka 2004).

In humans, it is well appreciated that the perception of a particular target colour can be strongly influenced by the background colour on which it is presented (Hurvich 1981). These perceptual effects, termed simultaneous and successive colour contrast, are known to occur in honeybees (*Apis mellifera*) (Neumeyer 1980, Neumeyer 1981), and may influence bee colour choices while foraging. The role of background adaptation on stimulus discrimination is also of interest in other animals, having recently been explored for birds (*Taeniopygia guttata*) (Lind 2016). Despite this,

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few studies have considered the extent to which natural background material may vary in spectral content, and whether this is likely to have an effect on selective pressure for the evolution of flower colour signals (Lunau et al. 1996; Koethe et al. 2016).

Both detection (the capacity of a visual system to reliably find a stimulus against a background), and discrimination (the capacity to reliably identify different stimuli on the basis of spectral differences) have been proposed as important drivers of floral colour evolution (Chittka and Menzel 1992; Shrestha et al. 2013a; Bukovac et al. 2016). For successful pollination, many plant species require that bees can both detect the presence of flowers amongst the array of other visual information the pollinator encounters while foraging (Giurfa et al. 1996; Dyer et al. 2008, 2016; Bukovac et al. 2016), and discriminate the flowers of one species from another (von Helversen 1972; Chittka and Menzel 1992; Dyer and Chittka 2004; Dyer et al. 2012; Shrestha et al. 2013b). Bees have a trichromatic visual system, which is highly conserved among hymenoptera, with photoreceptors maximally sensitive in the UV (~340 nm), blue (~430 nm) and green (~540 nm) regions of the electromagnetic spectrum (Peitsch et al. 1992; Briscoe and Chittka 2001). In honeybees and bumblebees (*Bombus terrestris*), both colour contrast, and in particular, green-receptor contrast, have been shown to be important factors for detecting stimuli (Giurfa et al. 1996; Spaethe et al. 2001; Dyer et al. 2008).

Flower shapes that maximise contrast with the background are better detected by bees (Lehrer and Bischof 1995; Ne'eman and Kevan 2001; Spaethe et al. 2001; Dyer et al. 2007; Morawetz and Spaethe 2012; Ne'eman and Ne'eman 2016). Green contrast and colour contrast are processed separately by both honeybees and bumblebees (Giurfa et al. 1996; Wertlen et al. 2008; Dyer et al. 2008), and apparent target size can affect whether bumblebees use colour contrast or green contrast to detect flowers (Spaethe et al. 2001), suggesting that different background colours could affect detection of identically coloured stimuli. This is certainly the case for honeybees when discriminating between square and diamond shapes, depending upon background contrast (Morawetz et al. 2013). Flower-like stimuli that are composed of colours with different long-wavelength receptor contrasts cause variations in both detectability and discriminability in honeybees (Hempel de Ibarra et al. 2001, 2002).

Bumblebees (*Bombus impatiens*) show stronger colour preferences for stimuli when presented on complex-background photographs than they do for a uniform green background (Forrest and Thomson 2009). In testing whether illumination differences provide direct cues for foraging decisions, Lotto and Chittka (2005) found that rather than

using illumination cues directly, bumblebees (*Bombus terrestris*) were influenced by the background colour's contrast with the target stimuli, regardless of whether the colour contrasts were due to the illumination or manipulation of the scene to appear as if it were under the test illuminant. This complex interaction of illuminant and background has also been shown to be important in human colour perception (Maloney 2002; Maloney and Yang 2003). In the stingless bee (*Melipona mondury*), colour preferences significantly change if the background colour is altered from grey to green (Koethe et al. 2016). These studies collectively indicate that variability in background colour may affect the bee's ability to accurately detect and discriminate between flowers in a natural environment, although currently the magnitude of this effect remains largely unexplored.

Studies of bee colour vision, particularly those relating to floral colour, typically use simple, homogeneous sample backgrounds which are assumed to be achromatic to bees, usually appearing green, grey, or white to human vision (Neumeyer 1980; Giurfa et al. 1995; Dyer 1998; Hempel de Ibarra et al. 2002; Lotto and Chittka 2005; Shrestha et al. 2014; Dyer and Garcia 2014; Bukovac et al. 2016). Natural background colours have previously been assumed to consistently present a strong contrast with floral colours (Lehrer and Bischof 1995), but no study has yet sampled a wide range of background colours present in the natural environment, including the UV part of the spectrum, so we should not conclude that this will always be the case. Indeed, the strong clustering of flower loci in colour space appears to avoid certain spectral colours consistent with some backgrounds (Chittka et al. 1994), and regions of the spectrum where bees seem to have trouble detecting target colours against a particular background (Giurfa et al. 1996; Dyer et al. 2008, 2016; Bukovac et al. 2016). This effect is a potential confound for both colour and green receptor contrast, as the spectral profiles of flower and backgrounds converge in respective signals, as experienced by a pollinator (Giurfa et al. 1996; Dyer et al. 2008).

To determine the variability of real background surface colours we sampled natural surface colours found across Australia (see Figs. 1, 2). We selected three flower-like target reflectance spectra (see Fig. 3a) that are representative of similar and saliently different stimuli for bee perception, and which have been used in a number of prior studies of bee colour discrimination ability (Dyer and Garcia 2014; Dyer et al. 2014; Sommerlandt et al. 2016). Using the hexagon colour model for bee vision (Chittka 1992), we then examined how the loci of these three stimuli varied when presented on these natural adaptation backgrounds, in order to evaluate how background spectral complexity may have contributed to the selective pressure on flowers to evolve salient signals

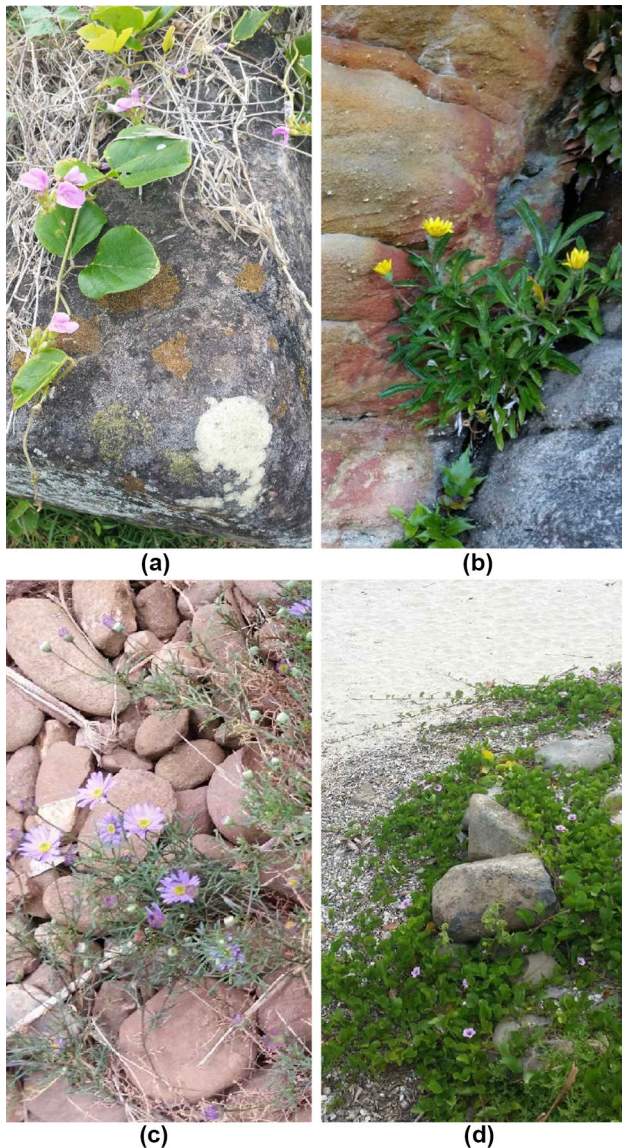


Fig. 1 Examples of the variability of background colours found near flowering species

for reliable colour perception by bee pollinators. We specifically consider how different background spectra may affect the visual problems of (1) correctly identifying a given target stimulus, (2) discriminating between differently coloured stimuli, and (3) detecting the presence of a stimulus against a variety of backgrounds. We conduct this analysis independently of the specific spatial arrangements of flowers and background surfaces, so that our results pertain to the broader evolutionary pressures involved in producing background-contrasting floral colours. We additionally discuss the implications for future studies that could assess related questions for specific plant habitats.



Fig. 2 Examples of the variety of colour seen in natural surfaces, from a human perspective. Images were taken by a linearised (Garcia et al. 2013), digital single lens reflex camera (Canon D40; Canon Inc., Japan)

Materials and methods

Background colour sample collection

We collected a total of 581 natural colour samples (see Fig. 3b). In this study, we consider biologically relevant background spectra, that were categorised as Rocks, Green Leaves, Shells/Sand, and Dry Plant Materials. We determined these to be the object categories most likely to form backgrounds in environments containing flowering plants, based on our observations when collecting samples. We did not include soil samples, as these are primarily composed of elements from our rock and dry plant materials samples, which were both accounted for. Samples were collected from a diverse range of locations in eastern Australia, spanning around 2400 km from tropical Cairns (approx. $-16.90^\circ, 145.75^\circ$) to the southernmost tip of mainland Australia at Wilson’s Promontory National Park (approx. $-39.10^\circ, 146.24^\circ$). The north-eastern region of Australia is home to many native stingless bees (Heard 2016; Michener 2007), whereas the south-eastern region, and other parts of Australia, are dominated by a wide range of other native bee species,

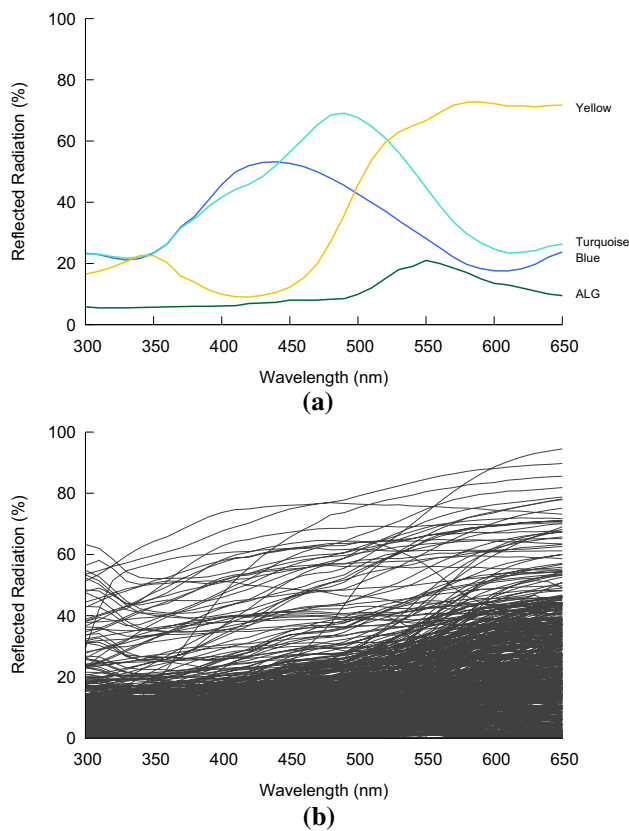


Fig. 3 **a** Spectral reflectance curves of the three sample stimuli; Tonpapier No. 12 (*yellow line*), 32 (*turquoise line*), and 37 (*blue line*) (Baehr, Germany). All three have similar spectral profiles to real floral reflectance spectra. The average reflectance of ten, fresh green leaf samples (the ALG background) is also shown (*green line*). **b** The spectral reflectance of the 581 natural backgrounds

including the blue banded bee (*Amegilla cingulata*) (Dollin et al. 2000; Dollin 2010). Samples were typically in close proximity to where there were flowering plants (see Fig. 1). Because Australian geological history covers all the historical landscapes of evolutionary history on earth, from Precambrian through Quaternary (Taylor 1994), our sampled rocks are diverse in geological origin, and are representative of the types of rock surfaces present during the entire evolutionary history of angiosperms.

We also use an average green leaf spectrum as a reference background (see Fig. 3a), since as we observed earlier, similar backgrounds are typical in studies of flower colour for bee pollinators (Neumeyer 1980; Giurfa et al. 1995; Dyer 1998; Hempel de Ibarra et al. 2002; Lotto and Chittka 2005; Shrestha et al. 2014; Dyer and Garcia 2014; Bukovac et al. 2016). This spectrum is the average reflectance of ten, randomly selected, fresh green leaf spectral samples that are not in the set of 581 natural backgrounds. We refer to this as the ALG background (Average Leaf Green), for brevity.

Colour measurement

A colour photograph of a representative section of each colour sample was taken for identification purposes, and to add to our database for future reference. All photographs were taken by a linearised (Garcia et al. 2013), digital single lens reflex camera (Canon D40; Canon Inc., Japan). Reflectance spectra from 300 to 650 nm wavelength were measured using an Ocean Optics spectrophotometer (Dunedin, Florida, USA, 2011) with a PX-2 pulsed xenon light source. A UV-reflecting white standard (freshly pressed pellet of dry BaSO₄) was used to calibrate the spectrophotometer. A minimum of three measurements were made per sample, and the average was used for subsequent analyses.

Flower-like stimuli

Three stimuli that have spectral profiles similar to real floral reflectance spectra were used in our analysis. Figure 3 shows the spectral reflectance curves of the three stimuli (Tonpapier No. 12 (human colour yellow), 32 (human colour turquoise), and 37 (human colour blue), Baehr, Germany; hereafter referred to as the yellow, turquoise, and blue stimuli). These three stimuli have been used as proxies for floral colour in prior studies that also concern colour discrimination (Dyer and Garcia 2014; Dyer et al. 2014; Sommerlandt et al. 2016), which established in behavioural studies with individual free flying bees that blue and turquoise were similar colours for bees, whilst the yellow stimulus was distinctly different from the other two, from which it was easily discriminated. We chose these stimuli specifically because their behaviourally-established discrimination difficulty relative to each other provides a baseline against which we can compare any background-induced changes to colour perception. Additionally, by choosing standardised and widely available stimuli, it is much easier for any researcher to physically obtain the same stimuli to conduct related studies in future, regardless of whether those studies require the physical target stimuli for empirical tests with real bees, the spectral reflectance for colour modelling, or both.

Colour model

The colour hexagon defines a space in which the relative photoreceptor excitation caused by stimuli for trichromatic bees can be quantified (Chittka 1992). The model functions as a general representation of colour opponent processes while making no specific assumptions about the colour opponent channels present in the animal. Importantly for this current study, in recent times it has been possible to collect empirical data from several bee species demonstrating that distance within the hexagon predicts changes in

bee colour perception (Dyer and Chittka 2004; Dyer and Neumeyer 2005; Dyer 2006; Dyer et al. 2008; Spaethe et al. 2014).

Because of the phylogenetically-conserved spectral positioning of photoreceptors in bees, it is possible to model typical bee perception (Chittka 1996; Briscoe and Chittka 2001). Using the conventional method of reconstructing spectral sensitivity described by Stavenga et al. (1993), we modelled trichromatic bee vision with photoreceptors U ($\lambda_{\max} = 340$ nm), B ($\lambda_{\max} = 430$ nm), and G ($\lambda_{\max} = 540$ nm) (Dyer 1999; Kevan et al. 2001; Briscoe and Chittka 2001; Dyer et al. 2012). The quantity λ_{\max} is the wavelength at which peak sensitivity occurs. If R is one of the three receptors U , B , or G , then the light absorbed by each photoreceptor (photon catch) P_R is given by

$$P_R = \frac{1}{N_R} \int_{300}^{650} T(\lambda)S_R(\lambda)D(\lambda) d\lambda \quad (1)$$

using the following quantities: $T(\lambda)$ is the spectral reflection function of the target stimulus; $S_R(\lambda)$ is the spectral sensitivity function of the photoreceptor R ; $D(\lambda)$ is the spectral function for the daylight illumination; N_R is a scaling factor defined by the illumination reflected from the background.

The daylight function $D(\lambda)$ is always taken to be normfunction D65 (Wyszecki and Stiles 1982), whereas the factor $1/N_R$ is taken to be the von Kries adaptation for the receptor R (Laughlin 1989; Chittka 1992). More specifically, this means that

$$N_R = \int_{300}^{650} A(\lambda)S_R(\lambda)D(\lambda) d\lambda \quad (2)$$

where $A(\lambda)$ is the spectral reflection function of the background to which the photoreceptor R is adapted. This adaptation process is an established feature of bee vision (Neumeyer 1981; Dyer and Chittka 2004).

Voltage signals for a receptor R (the relative excitation $E(R)$) can be calculated by following the Naka and Rushton equation (Naka and Rushton 1966; Chittka 1992)

$$E(R) = \frac{P_R}{(P_R + 1)} \quad (3)$$

By calculating these values for bee photoreceptors U , B , and G with $\lambda_{\max} = 340$, 430, and 540 nm respectively, we determined how each was affected by the stimulus reflectance. Finally, we calculated the colour hexagon locus with

$$x = \sin(60^\circ) \cdot (E(G) - E(U)) \quad (4)$$

$$y = E(B) - 0.5(E(U) - E(G)) \quad (5)$$

Taking each of the 581 spectra from our natural background data set as a different adaptation background $A(\lambda)$ in Eq. 2, we calculated the hexagon colour space loci for

each of the three target stimulus spectra (see Fig. 3a). Thus, for each of these three stimuli we obtained a cloud of 581 hexagon colour space loci, one for each adaptation background. For example, Figure 4 shows these three clouds of loci plotted together, along with the loci of each stimulus adapted to the ALG background spectrum seen in Fig. 3a, as a reference point. Loci that fall near to the origin are perceptually similar to their adaptation background, whereas those far from it have stronger colour contrast with their adaptation background.

Colour discrimination difficulty regions

Prior behavioural work has shown that the colour discrimination difficulty of a pair of loci in the colour hexagon model can be conveniently described by three regions of perceptual certainty (Dyer 2006; Dyer et al. 2012). These regions are:

Distance ≥ 0.11 reliably discriminated, even with absolute conditioning (Distinct).

Distance > 0.04 , < 0.11 only discriminated with differential conditioning (Similar).

Distance ≤ 0.04 not reliably discriminated by bees (Indistinguishable).

Quantifying background-induced colour confusion

To determine how adaptation to real background surface colours could affect floral colour perception, we examined how the loci of the three sample stimuli differed when

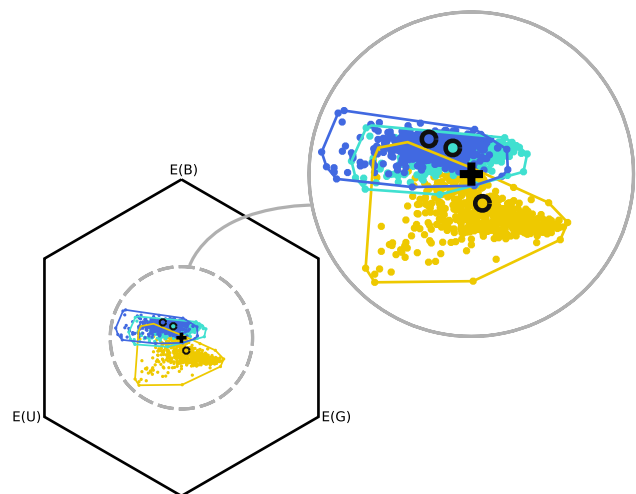


Fig. 4 Coloured points show loci of the three sample stimuli (Tonpapier No. 12 (yellow), 32 (turquoise), and 37 (blue), Baehr, Germany) when adapted to each of the 581 natural surface backgrounds. Circled points indicate loci of each of the three stimuli adapted to the ALG background (see Fig. 3a). Coloured polygons show the convex hull that encloses all loci for the corresponding stimulus. Grey circled region of colour hexagon shown in zoom inset

adapted to the many different natural background colours from our sample set. The distribution of these loci across hexagon colour space indicates the range of variation in colour perception caused by the different viewing backgrounds sampled for this study.

Our goal is to quantify the degree to which our natural background colours may alter colour perception of our three target stimuli. In particular, we are most interested in instances where colour perception is altered to such a degree that identical stimuli are perceived as entirely different colours, or vice versa, where normally different stimuli may be perceived as indistinguishable. In a natural setting, such drastic alterations could reduce reliable flower constancy.

Conveniently, the distances between pairs of loci in the colour hexagon can be classified according to the colour discrimination difficulty regions above. This allows us to classify the distances between loci belonging to the same stimulus, or to different stimuli, and distances between loci and the origin, in order to identify if natural background colours may influence the accuracy of detection and discrimination of target stimuli.

The current accepted position of many studies is that natural backgrounds have little influence on floral colour perception (Lehrer and Bischof 1995; Vorobyev and Menzel 1999; Hempel de Ibarra et al. 2014). Hence, we performed the following experiments to see if the loci of our three stimuli confirmed this as a null hypothesis position. We assessed if natural-background adaptation may affect (1) correctly identifying a given target stimulus, (2) discriminating between differently coloured stimuli, and (3) detecting the presence of a stimulus.

Identifying identical stimuli

Each of the 581 loci in the cloud belonging to a single target stimulus (yellow, turquoise, or blue) is representative of the perceived colour of that stimulus when adapted to one of the 581 backgrounds (see Fig. 4). These loci indicate perceptually different colours, but they originate from an identical stimulus spectrum.

We hypothesise that if adaptation to natural background surface colours has no affect on the ability to identify identical stimuli, then all pairs of loci for that stimulus should fall within the Indistinguishable range of each other. To test this, for each stimulus considered in isolation, we calculated the distances between all locus pairings. Building unordered pairs from a set of 581 loci derived from a single stimulus yields

$$\binom{581}{2} = \frac{581!}{2!(581-2)!} = 168490 \quad (6)$$

individual distances. Each of these distances was classified according to our colour discrimination difficulty regions, given above.

In addition to the above pair-wise comparison of loci, we estimated the overall area of the colour hexagon occupied by the cloud of 581 loci for each stimulus. The area in which the loci of a single stimulus fall can be approximated by determining the bounding convex hull. The smaller the area in hexagon colour space that these loci occupy, the more robust that stimulus is to variation in background adaptation. The convex hull naturally bounds the outlying loci for each stimulus, which is particularly interesting in this instance, by providing a visualisation of how background-induced colour perturbations have shifted colour perception in the most extreme cases for each stimulus (see Fig. 4).

We determined the convex hull for each of the three stimuli using custom software implementing the gift-wrapping algorithm (Jarvis 1973). The total area of the colour hexagon A , which has a side of length 1 (Chittka 1992), was calculated as:

$$A = \frac{3\sqrt{3}}{2} = 2.6 \quad (7)$$

We determined the percentage of this total area occupied by each of the three stimuli's convex hulls.

Discriminating between different stimuli

There are three possible unordered stimulus pairings for our three stimuli: blue–yellow, yellow–turquoise and turquoise–blue. Adapted to the ALG background (see Fig. 3), the discrimination task difficulty for pairs of stimulus colours are Distinct (blue–yellow), Distinct (yellow–turquoise), and Similar (turquoise–blue). Should background colours in any way affect discriminability, we would expect that some pairs of loci drawn from each stimulus pairing may fall further apart, or closer together, than they do when adapted to the ALG background. This would indicate that those stimuli pose either an easier, or harder, discrimination task with those particular two adaptation backgrounds than the same stimuli do when both are adapted to the ALG background.

We hypothesise that if adaptation to natural background surface colours has no affect on the ability to discriminate between different stimuli, then all pairs of loci for the blue–yellow and yellow–turquoise stimulus pairs should fall within the Distinct range of each other. Pairs of loci for the turquoise–blue pair of stimuli should fall within the Distinct or Similar range of each other. The alternative hypothesis would be that some pairs do change colour discrimination difficulty category as described above. To test this, for each of the three stimulus pairs considered in isolation, we calculated the

distances between all locus pairings. Building unordered pairs from two stimuli’s sets of 581 loci yields

$$581 \times 581 = 337561 \tag{8}$$

individual distances. Each of these distances was classified according to our colour discrimination difficulty regions, given above.

Detecting the presence of stimuli

The ALG background-adapted loci of all three stimuli lie outside the Indistinguishable range of the colour hexagon’s origin, with yellow and turquoise both Similar to the origin, and blue Distinct from the origin (see Fig. 4). Close proximity to the origin indicates poor colour contrast with the adaptation background (Chittka 1992). We hypothesise that if adaptation to natural background surface colours has no affect on the ability to detect the presence of stimuli, then no loci for our stimuli should fall within Indistinguishable range of the colour hexagon’s origin, all blue loci should remain Distinct from the origin, and additionally, both yellow and turquoise loci should all be Similar to the origin, just as they are against the ALG background. For each stimulus, there are 581 loci, and hence 581 individual distances from the origin. Each of these distances was classified according to our colour discrimination difficulty regions, given above.

In addition to the above comparison of locus distance from the origin, we assessed whether adaptation to the natural background altered green receptor contrast. Low green contrast has been identified as a potential impediment to detection in honeybees (Giurfa et al. 1996; Spaethe et al. 2001). Green contrast is defined by Spaethe et al. (2001) as the degree to which a stimulus generates an excitation value different from 0.5 in the green receptor. In particular, we use the definition given in Bukovac et al. (2016), and deem low green contrast to be where $E(G) \in [0.4, 0.6]$. Adapted to the ALG background, all three stimuli have high green contrast values $E(G) \geq 0.7$. If the target stimuli instead produce low green contrast values when adapted to any of our natural backgrounds, we can conclude that these backgrounds may impede detection. Consequently, we calculated green receptor contrast values for all stimulus and background combinations to determine if any natural backgrounds could induce low green contrast values, and thus impede detection of the stimuli.

Results

Identifying identical stimuli

Table 1 shows the percentage of locus pairs that falls into each of our discrimination threshold distances for each

stimulus considered in isolation. More than a third of all locus pairs for all three stimuli are perceptually Distinct, demonstrating that many pairs of background samples can dramatically alter perceived stimulus colour, to the point that a bee would perceive identical stimuli as distinctly different colours.

Figure 4 shows the loci for the three colour stimuli adapted to each background, as well as the convex hulls enclosing the loci of each stimulus colour. These polygons occupy respectively 2.7% (turquoise), 3.2% (blue), and 5.8% (yellow) of the total space of the colour hexagon, confirming a dispersal of the perceived colour of all three stimuli. For comparison, a circle with diameter 0.04, the largest area in which all locus pairs would be Indistinguishable, is only ~0.05% of the total space of the colour hexagon.

Discriminating between different stimuli

Table 2 shows the percentage of locus pairs that falls into each of our discrimination threshold distances for each stimulus pair (blue–yellow, yellow–turquoise and turquoise–blue). All three stimulus pairs have some locus pairs that are Indistinguishable. Even the two stimulus pairs that involve the yellow stimulus (blue–yellow and yellow–turquoise), which are both Distinct when adapted to the ALG background, both have a small set of Indistinguishable locus pairs. Additionally, Fig. 4 shows that the convex hulls of all three stimuli overlap, confirming possible background-induced confusion between stimulus colours.

Detecting the presence of stimuli

Table 3 shows the percentage of loci per stimulus that falls into each of our discrimination threshold distances relative to the origin of the colour hexagon. All three stimuli have some loci that fall Indistinguishably close to the origin, indicating very poor colour contrast against some backgrounds. Conversely, some backgrounds have caused the yellow and turquoise stimuli, which are

Table 1 Pair-wise comparison of like-coloured stimuli, with discrimination task difficulty percentages for each of the three stimuli: yellow Y, turquoise T, and blue B. A total of 16,8490 (100%) distances are classified in each row (see “Methods: Identifying identical stimuli”)

Locus pairs	Natural background discrim. difficulty			Total (%)
	Distinct (%)	Similar (%)	Indistinguishable (%)	
Y ↔ Y	63.49	28.58	7.93	100
T ↔ T	36.82	46.14	17.04	100
B ↔ B	39.94	45.44	14.62	100

Table 2 Pair-wise comparison of differently-coloured stimuli, with discrimination task difficulty for each of the three pairings of stimuli: yellow Y, turquoise T, and blue B. ALG Dist. is the distance (in hexa-gon colour space) between the ALG adapted stimulus locus pairs. A total of 33,7561 (100%) distances are classified in each row (see “Methods: [Discriminating between different stimuli](#)”)

Locus pairs	ALG dist.	Natural background discrim. difficulty			Total (%)
		Distinct (%)	Similar (%)	Indistinguishable (%)	
B ↔ Y	0.23 (Distinct)	87.53	10.75	1.72	100
Y ↔ T	0.17 (Distinct)	83.42	13.85	2.73	100
T ↔ B	0.08 (Similar)	44.55	43.14	12.31	100

Table 3 Pair-wise discrimination task difficulty from the origin for each of the three stimuli: yellow Y, turquoise T, and blue B. ALG Dist. is the distance (in hexagon colour space) between the ALGadapted stimulus loci and the origin. A total of 581 (100%) distances are classified in each row (see “Methods: [Detecting the presence of stimuli](#)”)

Locus pairs	ALG dist.	Natural background discrim. difficulty			Total (%)
		Distinct (%)	Similar (%)	Indistinguishable (%)	
Y ↔ Origin	0.09 (Similar)	67.81	23.41	8.78	100
T ↔ Origin	0.09 (Similar)	29.60	58.18	12.22	100
B ↔ Origin	0.16 (Distinct)	55.42	38.38	6.20	100

Table 4 ALG background-adapted green contrast $E(G)$ for each of the three stimuli: yellow Y, turquoise T, and blue B. Also shown is the percentage of the 581 backgrounds which induce a low green contrast with $E(G) \in [0.4, 0.6]$

Stimulus	ALG adapted $E(G)$	% Of backgrounds inducing $E(G) \in [0.4, 0.6]$ (%)
Y	0.79	8.26
T	0.77	9.64
B	0.70	20.18

Similar to the origin when adapted to the ALG background, to be Distinctly different from the origin against some other backgrounds, demonstrating that some natural backgrounds provide better colour contrast than the ALG background.

The percentage of natural backgrounds that induced a low green receptor contrast for each of the three target stimuli are shown in Table 4. While all three stimuli have high green contrast when adapted to the ALG background, between 8 and 20% of backgrounds induce poor green contrast in the three stimuli.

Discussion

Previous studies of bee colour discrimination and detection have often used an assumed bee-achromatic background of green, grey, or white (Neumeyer 1980; Giurfa et al. 1995; Dyer 1998; Hempel de Ibarra et al. 2002;

Lotto and Chittka 2005; Shrestha et al. 2014; Dyer and Garcia 2014; Bukovac et al. 2016). However, our survey of naturally occurring surface colours indicates that bees could encounter a wide range of background colours, and that background colours may have a strong influence on which floral colours are detectable, and discriminable, for foraging bees. Although the full-range of background colours we encountered is unlikely to be experienced by an individual bee, the evolutionary partnership between flowers and bee pollinators constitutes a large span of time, and this suggests that many of our modelled visual-problems may have occurred in the real world. If this is indeed the case, such interactions may have affected flower-signalling evolution.

Identifying identical stimuli

In this study, we show that a floral stimulus can potentially be perceived as a range of different colours, should the adaptation background vary as a bee moves about while foraging. The discrimination difficulty of two loci from the same stimulus spectra can vary from Indistinguishable (≤ 0.04 hexagon colour distance), right up to Distinct (> 0.11 hexagon colour distance). While we know that bees can generalise colours, and that this ability may aid flower constancy (Giurfa 1991; Waser et al. 1996; Gumbert 2000; Dyer et al. 2012), there is ultimately a limit to how much colour generalisation can aid flower constancy if the perceived colour of the target flower changes significantly across successive encounters. Since

discriminability sets an upper bound on the bee's ability to remain constant (Chittka et al. 2001), environmental conditions that may cause identically coloured flowers to appear as saliently different colours are a potential impediment to constancy.

Discriminating between different stimuli

Metamerism occurs when two stimuli appear to match, despite their differing spectral reflectance profiles. This phenomenon, in human vision, is usually considered in the context of varying illumination; while under one light the metameric stimuli are indistinguishably similar, under another they are clearly different (Lee 2005). Our result indicates that background adaptation also has the potential to create a metameric-type effect for bees, albeit only in successive viewing of stimuli against different backgrounds.

In our results, Fig. 4 shows the loci clouds of all three stimuli. It is immediately clear that there is some overlap between all three stimulus groups. There are many combinations of background adaptations among our natural surface data set which can cause the loci of one stimulus to move into regions that are very close to the loci of other, differently-coloured, stimuli (e.g. a yellow locus that lies Indistinguishably near (≤ 0.04) one or more blue or turquoise loci, see Fig. 4). This indicates that it is possible for bees to encounter flowers which, when presented against the same adaptation background are saliently different colours, but if viewed successively against different, naturally-occurring backgrounds, would appear to be the same colour. Similar stimuli (in this case, blue and turquoise) can be mistaken for each other under a wider range of background colour conditions, since a small shift in background colour is sufficient for the two to be conflated. This suggests that perceptual noise, induced by fluctuations in background spectra, has likely had a significant effect on the signals that flowering plants need to generate to be easily recognised by bees foraging in complex natural environments. We define *perceptual noise* as a change in the colour perception of a bee pollinator caused by higher level interactions of colour spatial stimuli, as opposed to a purely physiological constraint as is assumed for the widely used receptor noise model (Vorobyev and Osorio 1998).

Our research is in stark contrast to findings which suggest, based upon theoretical considerations of how the amplitude of noise caused by quantum fluctuations within photoreceptors is the main limit on bee colour choices, that there is little evolutionary pressure for plants to diverge flower colour signals (Vorobyev and Menzel 1999; Hempel de Ibarra et al. 2014). Such a position has been questioned by research showing that bumblebees (Dyer and Chittka 2004), honeybees (Dyer and

Neumeyer 2005) and stingless bees (Spaethe et al. 2014) make probabilistic decisions depending upon the perceptual colour similarity of stimuli. In tests with real flowers, bees do not exhibit flower constancy unless flower colour is saliently different (Chittka et al. 2001). Our new evidence indicates that the spectra of background materials are often highly variable in natural conditions where bees forage on flowers, and that such variation exceeds perceptual thresholds measured in free flying bees (Dyer 2006). However, on a foraging trip, a single bee would likely experience a smaller number of background scenarios than those we model here to represent the magnitude of the problem that might influence flower colour over evolutionary time. This suggests that the use of colour by bees and other animals in natural environments is a far more complex visual problem than predicted by simple physiological constraints mediated by receptor noise.

Detecting the presence of stimuli

Some natural background surfaces result in very poor colour contrast for the floral stimuli (see Table 3). Against the ALG background, the three stimuli are at worst Similar to the origin, but some background adaptations in our experiments cause loci to fall Indistinguishably near to the origin of the colour hexagon (≤ 0.04). These combinations of stimulus and background would render the stimulus colour effectively undetectable to bees, indicating a strong pressure to evolve either favourable contrasting inflorescence/foilage arrangements, or floral colour signals that maximise saliency against local background colours. In many cases, the natural background surfaces can also cause low green receptor contrast (see Table 4), further demonstrating the potential for background-induced detection difficulty. It is possible that olfactory cues are used by some plant species to overcome the problem of colour being a sometimes unreliable signal in natural environments (Giurfa et al. 1995; Leonard et al. 2011; Leonard and Masek 2014), as may other information cues like flower size (Avarguès-Weber et al. 2014; Howard et al. 2017), and shape (Dyer and Chittka 2004). In addition, there may be other mechanisms like differential flowering time to avoid confusion between similar colours (Levin and Anderson 1970; Rathcke 1988), although this has been rarely tested with modern colorimetry principles.

Conclusion

Colour discrimination and detection are some of the drivers identified as contributors to the evolutionary pressures

on floral colour (Bukovac et al. 2016). Our results demonstrate that contrast with a range of natural backgrounds, as well as contrast with other competing floral colours when viewed against a range of backgrounds, could be additional drivers of what is clearly a complex evolutionary process.

The floral colours of many plant species are likely often viewed by bees against a fairly constant background: the foliage colour of the plant. However, this is not the only scenario, especially as plants adapt and spread to new habitats (see Fig. 1). The pressures we describe above may have applied to both the evolution of those species that do present a foliage background, as well as the floral colours of plant species which do not provide such a background. It may be that in providing a consistent background, species that present dense foliage facilitate bee constancy to their floral colour, and our results indicate that such morphological adaptations would be advantageous. There is evidence for adaptations in plants to provide favourable simultaneous colour contrast viewing conditions for easier detection of rewarding flowers by bees (Kudo et al. 2007; Brito et al. 2015), as well as morphological adaptations that may improve colour signal saliency (van der Kooij 2016). Additionally, species that do not present a uniform leaf background may be under more pressure to present floral colours that contrast with a wider range of local background surfaces (Menzel and Shmida 1993). Further studies to elucidate these points would be very valuable.

Our survey of background surface colours captures the extensive range of colours present, not their relative abundance. This is an important distinction to make, because here we are establishing the extent of the colour discrimination difficulties that natural backgrounds may cause. We cannot simultaneously establish the likelihood of encountering any one such task while foraging. That could only be achieved by studies of individual habitats, since the abundance and range of background surface and floral colours vary from one environment to the next. This current study shows that testing the flower-background relationships at a local, community level, may reveal much about flower colour signalling and ecology. The strength of our model is that it gives insights into the many plausible scenarios that may have existed during the long evolutionary partnership of bees and flowers, throughout which different conditions on Earth may have yielded different types of backgrounds.

We have shown that natural background surfaces can induce a wide range of colour shifts in target stimulus colour perception, and hence present an additional flower constancy challenge for bees. Bee constancy to floral colour in natural environments is not only mediated by background colours, but over evolutionary time periods the influences we describe above could have affected

how angiosperms orient their flowers for optimal detection and discrimination, as well as how they use colour to attract and retain pollinators.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no competing interests.

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