Comparing the efficiency of computational colour constancy algorithms in agent-based simulations: Flower colours and pollinators as a model

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Abstract

The perceived colour of an object depends on its spectral reflection and spectral composition of the illuminant. Upon illumination change, the light reflected from the object also varies. This results in a different colour sensation if no colour constancy mechanism is available to form consistent representations of colours across various illuminants. We explore various colour constancy mechanisms in an agent-based model of foraging bees selecting flower colour based on reward. The simulations are based on empirically determined spatial distributions of various flower species in different plant communities, their rewards and spectral reflectance properties. Simulated foraging bees memorise the colours of flowers experienced as being most rewarding, and their task is to discriminate against other flower colours with lower rewards, even in the face of changing illumination conditions.

The experimental setup of the simulation of bees foraging under different photic environments reveals the performance of various colour constancy mechanisms as well as the selective pressures on flower colour as a result of changing light. We compared the performance of von Kries photoreceptor adaptation and various computational colour constancy models based on the retinex theory with (hypothetical) bees with perfect colour constancy, and with modelled bees with colour blindness. While each individual model generated moderate improvements over a colour-blind bee, the most powerful recovery of reflectance in the face of changing illumination was generated by computational mechanisms that increase perceptual distances between co-occurring colours in the scene. We verified the results of our model using various comparisons between modelled bees' performance and that predicted by our models, as well as exploring the implications for flower colour distribution in a variety of representative habitats under realistic illumination conditions.

Acknowledgements

It is my pleasure to thank the tremendous supervision I have received from both Prof. Peter William McOwan and Prof. Lars Chittka. I am very grateful to Peter for stimulating endless inspirational ideas and discussions in my work and providing exceptional support and encouragement throughout my PhD with a lot of patience and belief. The dedication Lars provided as a scientist, an expert and a teacher to supervise me in this PhD has been invaluable. He not only introduced me to the fascinating world of bees, but he pushed me to develop my scientific work, all with an incredible amount of patience. I am very grateful for the knowledge imparted to me by Lars during my time at the bee lab.

I'd like to extend my thanks to all those in the Chittka Lab who provided discussions and shared their knowledge at the lab meetings. Including, Steven Le Comber, Adrian Dyer and especially Sarah EJ Arnold with whom I worked with closely on the Floral Reflectance Database in my first few years of the PhD.

In the Computer Science department, I had the pleasure to be accompanied by various people on my journey (past and present), the people in 'RIM' - Nuzhah Gooda Sahib, Nargis Pauran, people in Theory (with whom I shared my office years with) – Jonathan Heusser, Tom Powell, Tzu-Chun Chen, and also members of the Vision Lab. CS Systems support and their well maintained servers that ran all my experiments and all CS administrative staff, especially Melissa Yeo.

I am very grateful for the support of the scholarship I received from EPSRC that made this research possible. In all, I would like to thank the staff at Queen Mary, University of London. I met many wonderful undergraduate, postgraduate/PhD students along with support staff and academic staff. It is impossible to name all - but in this I would like to thank each and every one of you who supported, encouraged, taught or just took the time to talk to me about research, bees and colours.

I'd like to extend my thanks to family - my brother Zaheer Ahmed and my sisters Mariam and Kashwar for their continuous advice and support. Above all, I am forever grateful for the enormous effort and sacrifice that my mother Kalsum Bibi and father Mohammed Faruq made to ensure that I received an excellent education. To my parents, I dedicate this thesis.

Samia Faruq
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Summary of key contributions

I outline my contribution to the work conducted and presented as a result of the data and result chapters in this thesis:

1. I developed FReD (Floral Reflectance Database) Version 2.0, an open access database for thousands of flower reflectance spectra, a now well established (and heavily used) resource for evolutionary biologists, pollination ecologists and all scientists interested in signal-received interactions. This was based on a preliminary version of a non-web based database by Sarah Arnold and Lars Chittka. Features of the database are described in Chapter 2 and are available to the public. The database in its present form was fully programmed by me to be later used in modelling bee colour vision and the bee simulations (in Chapter 3, 4, 5, and 6); these include:
    a. Modelling of flowers under changes of light in the bee colour space,
    b. Modelling of flowers under assumptions of various receptor spectral sensitivity functions such as the α-band only spectral sensitivity functions and narrowed spectral sensitivity function compared with normal honeybee spectral sensitivity functions – See chapter 3
    c. The calculation of *perceptual colour shift* of flower colours extracted from FReD in the honeybee colour vision model and altered spectral sensitivity of the honeybee described in Appendix I
    d. The calculation of *perceptual colour distances* of flower colours in FReD in the bee colour space and altered spectral sensitivity of the honeybee described in Appendix I leading to understanding the relationship between flower colour occurrences and perceptual colour shift in the entire bee colour visual spectrum.
    e. The development of agent-based modelling with the use of the FReD data to mimic real meadow of flowers leading to understanding the usefulness of colour discrimination under changing illumination compared to perceptual colour shift levels

2. In Chapter 3, I modelled the pattern of perceptual colour shift across the bee colour spectrum under three different illuminations as well as performing analysis of colour shift under altered spectral sensitivity function of the bee. I explored the relationship between perceptual colour shift and colour difference sensitivity in the bee.

3. I modelled an in-silico artificial meadow based on flower distributions of a *natural meadow* (which consists of five co-occurring flowers based on a field study by Chittka et al, (1997))

in the agent-based simulation environment to measure the performance of the bee-agent based on the amount of nectar collected. In Chapter 4, I analysed this performance against another *ideal meadow* consisting of flower species with large colour distances between the flower colours under changes of illumination to the extent to which large colour distances between flower colours in a meadow can improve nectar collection under conditions of varying illumination.

4. I developed an algorithm in Mathematica to assign nectar values based on the distribution of real nectar standing crop values to a given flower species that is occurring in the meadow. Nectar standing crop data was collected by K. Pruefert under the Supervision of Prof. Lars Chittka in Germany near Würzburg in 1999. These raw data shown in Appendix III were arranged in a histogram and a log-normal distribution was formed to assign nectar values to flowers in the simulation meadow based on the probability of the distribution of the nectar standing crop values shown in Appendix III.

5. I analysed the performance of a von Kries adaptation mechanism combined with three computational colour constancy mechanisms related to the retinex theory under the agent-based simulation of the honeybee colour vision under varying illumination. I developed the method of using these algorithms in an agent-based model and to apply it into a two-dimensional scene each time the bee moved in the grid of cells, which was the 'meadow'. The amount of nectar collected in these simulations indicated that performance was best in computational methods of colour constancy when colours in the meadow were distinguishable (i.e. easily discriminable) in the training and testing phase of the simulation.

6. I performed the analysis of the bee-agent model under the natural light changes that affect the performance of the bee, and the affects of a different light condition or flowers in place of the actual conditions found in the Maple forest plant community. Data of the phenology study of the Maple forest plant community were collected by L. Chittka in 1993-4. The reflectance spectra of these flowers come from FReD.

Declaration

I declare that the work in this thesis is all my own, with the exception of the contributions from others mentioned in the "Summary of key contributions" section.

Samia Faruq
August 2012

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1 Introduction

1.1 Introduction

This thesis explores the biological significance and role of colour constancy in performance of a colour-dependent critical task using flower colour and bee colour vision as a model. Colour constancy is the ability of a colour vision system to overcome the changes of illumination that change the colour reflectance of an object (Zeki, 1993). This is challenging since if the illumination spectrum varies, so does the physical reflectance of an object. For example the impression of redness can be generated by a red object under white light, or a white object under red light. In this view, the fundamental challenge of colour constancy can be described as solving $x * y = z$, where z is the perceived colour whilst x (the object reflectance) and y (the illumination) are unknown – theoretically an impossible task (Lotto and Chittka 2005). An ideal colour constancy mechanism would have to recover x, which is the true object colour reflectance independent of the illumination y. This is the basis of all computational colour constancy mechanisms, where the recovery of x is the goal in all algorithms (Ebner, 2007). Since object reflectance and illumination are unknown variables, infinite variations of y (illumination/light) could have achieved a perception of a colour z, and thus the recovery of x (reflectance spectra) remains only approximate through estimation of the illumination y (McCann, 2005). Such estimation may be accomplished through analysing the statistical ensemble of coloured surfaces in a scene (Smithson and Zaidi, 2004, D'Zmura and Iverson, 1994, D'Zmura and Iverson, 1993a, D'Zmura and Iverson, 1993b) or scaling of receptor sensitivities, based on a chromatic adaptation response of the colour receptors (Worthey and Brill, 1986).

Some of the most powerful experiments that demonstrated colour constancy in humans were carried out by Land (Land, 1959c, Land, 1959a, land, 1959b). He underpinned his empirical work with numerous computational colour constancy algorithms (Land and McCann, 1971, Land, 1986a, Land, 1977). Nowadays, such algorithms are used in post-processing of digital images (Ebner, 2007). The critical difference in the real world from that of a static digital image is that the colour vision system is exposed to a change in the scenery content, such as surrounding colours and change in the illuminant over time (Thouless, 1931, Zeki and Marini, 1998). It is thought that memory plays a role in achieving colour constancy especially in the real world where humans encounter colour one after the other in a successive manner and thus the process of colour constancy is mostly successive in the real world (Ling and Hurlbert, 2008, Brainard et al., 1997, Brainard, 1998, Neumeyer, 1981).

There have been numerous experimental methods in human colour constancy with the use of the so called 'Mondrian design' as the experimental presentation (Land and McCann, 1971, Land, 1986a, Land, 1977, Land, 1986b). This is a 'patch-work' of different colours in a pattern that resembles the paintings of Piet Mondrian. At one point on the Mondrian display of colours, a particular patch of colour is exposed whilst the rest of the Mondrian is in darkness (or covered) and the human observer adjusts the illumination to a point that the exposed colour is perceived as 'white'. With such experimentation, it has been demonstrated that perceived colour is not wholly dependent on the light reflected from the object (McCann, 2005). Colour recovery under changing illumination can be quantified by measuring the amount of adjustment a human participant makes in the illumination to flat images (Foster and Nascimento, 1994). It has been found that colour compensation in real-world scenes is better than under simulated scenes such as those using a Mondrian design (Brainard, 1998, Brainard et al., 1997, Yang and Maloney, 2001).

What makes colour constancy biologically relevant is that animals use colour signals as critical cues for identifying valuable food sources (e.g. fruit or flowers), mates or predators. Without colour constancy, changes in illumination might corrupt colour identification, and therefore survival and biological fitness. For correct identification of objects by colour, an animal must associate a colour with a critical stimulus and to recall the colour from memory to make an appropriate behavioural choice (Giurfa, 2007). Colours that look perceptually similar to each other make discrimination more challenging (Chittka et al., 2001) and colours that are discriminated only with difficulty may mean that the animal may not be able to identify colours under changes of illumination (Dyer and Chittka, 2004b). In addition there is the complication of metamerism: a pair of similar colours that are distinguishable under one illuminant might be perceived as identical under another (Wyszecki and Stiles, 1982). It is therefore clear why the change of lighting is only one of the challenges that can hinder identification of colour – it is also important that colours are distinguished from each other. As yet, the interaction between fine colour discrimination and colour constancy under naturally relevant conditions has only rarely been explored in humans and other animals. For this, a real world model of this problem is required. I have used the interaction between flower colour and bee colour vision as a model to discover the biological significance of colour constancy.

Colour is only biologically useful to animals such as bees if the object colours remain at least reasonably constant under different coloured lights, otherwise flower colour would perceptually change every time there is a change in the illumination, thus making the signal unreliable and ambiguous. For flower-visiting bees, inconsistent illumination is common over small temporal and spatial scales caused by the daily change in daylight and shades (Dyer, 1998, Lythgoe, 1979, Endler, 1993). Colour constancy is known to exist in bee colour vision (Mazokhin-Porshnjakov, 1966, Neumeyer, 1981, Neumeyer, 1980, Werner et al., 1988, Lotto and Chittka, 2005, Dyer and Chittka,

2004b) and it is assumed that this helps to achieve foraging success as bees can approximately assess the colour of a flower independently of the illumination. It is reasonable to assume that natural variation in the illuminant would have played an integral part in shaping signal-received relationships in plant-pollinator interactions (Dyer and Chittka, 2004b). Experimental results show that colour constancy in bees and other animals is only approximate, however. It is therefore useful to explore the quality of various colour constancy algorithms under realistic conditions, and to identify strategies by which both bee colour vision and flower colour overcome ambiguity of colour under different lightings. The work in this thesis addresses this through by the use of computerised modelling of bee colour vision, its colour choice behaviour and the environment in which it typically forages for floral rewards.

I examine the role of colour constancy in four chapters. In the first part, I model the perceptual colour shifts under changes of illumination in the general population of flower colour loci in the bee colour space, and I explore differently shaped spectral sensitivity function to identify the extent to which they improve or reduce colour constancy performance. In part two, I develop an agent-based simulation of a foraging bee and examine its von Kries receptor adaptation mechanism as a colour constancy method against a colour-blind and perfect colour vision bee to quantify the performance of its colour vision in collecting nectar. This bee colour vision is tested under two different flower meadows to explore the affects of increased colour distances between flowers in a plant community. In part three, I experiment with various computational colour constancy techniques in an agent-based modelling environment of bees foraging successively on flowers to see how well the different computational colour constancy models perform under changing illumination. Finally in part four, I experiment on a flowering plant community of a Maple forest, using the same agent-based simulation, where the flowers undergo seasonal variation in illumination. Modelled bees forage in each illumination, and across changes in illumination, and their success is quantified depending on their colour constancy performance.

In the remainder of this chapter (Chapter 1 – Introduction), I will review and provide a basic introduction to bee colour vision, colour constancy and studies in pollination ecology that have established the agent-based modelling environment and are used in addressing the experimental design and methods used in the data chapters to understand bee colour vision constancy.

1.2 Introduction: colour constancy in pollinators

From a biological perspective, colour vision serves the purpose of detecting and identifying objects in the environment. For many animals, particular colour signals lead to decision about which food is palatable or if something is dangerous and should be avoided (Allen, 1879, Lythgoe, 1979). Colour vision is critical to bees' survival since colour vision increases the chances of finding flowers of good

reward. It is considered that the colour signal provided by flowers are adapted to bee colour vision to maximise detection and floral identification (Gumbert et al., 1999, Chittka et al., 2001, Chittka, 1997, Dyer, 2006, Tastard et al., 2008), and that bee colour vision is optimal for discriminating flower colours (Chittka, 1997). Plant species benefit from correct identification by pollinators since it facilitates within-species, directed pollen transfer, rather than pollinators switching randomly between plant species. In a plant-pollinator world where colour plays such an important role in decision making and choice, it is also vital to have a receiver that can accommodate the variations that occur in light that affect the perception of a colour. Colour constancy is known to exist in the bee (Mazokhin-Porshnjakov, 1966, Neumeyer, 1981, Neumeyer, 1980, Werner et al., 1988, Lotto and Chittka, 2005, Dyer and Chittka, 2004b), and is thought to play an essential role in natural colour choice.

Colour constancy has been investigated in bee colour vision in a variety of experiments to demonstrate the level of colour constancy that is present in this species. In summary, bee colour constancy is good but it is only approximate. In this chapter I will discuss the findings of bee colour constancy, and the purpose it may be serving in a biologically significant task bees carry out most of their working lives, that is, collecting nectar (Seeley, 1995).

1.3 Bee colour vision

The system of pollination was observed by Darwin, and it was first discussed by Sprengel that the colourful display of flowers was a strategy to attract pollinators for visits and was the main purpose of the variety of colours found in flowers (Darwin, 1859, Sprengel, 1793). Even so, there existed some controversy about whether colour vision existed in pollinators such as bees (Hess, 1913). However, this dispute was settled by von Frisch (Frisch, 1914) and his disciples who showed that bees could choose the correct colour out of a range of shades of grey, and that they could recognise a variety of colours and associate reward to the colour of a food source (Daumer, 1958, Frisch, 1914, Daumer, 1956, Helverson, 1972). This triggered a great interest in bee colour vision, and particularly the question of how flower colour look to bees. Had flower colours been adapted to bee colour vision?

Through intracellular recordings of the spectral sensitivities of the honeybee photoreceptor, it was discovered that the honeybee has a trichromatic colour vision, consisting of Ultraviolet (UV), Blue and Green colour receptors peaking at approximately 344nm, 436m, and 562nm respectively (Autrum and Zwehl, 1964, Menzel and Blakers, 1976, Peitsch et al., 1992). Various species of other hymenoptera (e.g. other bees and wasps) display more or less similar spectral sensitivity peaks near these wavelengths (Briscoe & Chittka 2001). The compound eye of the bee consists of thousands of ommatidia each featuring a set of receptor types; all contain full-length six green receptor cells (Wakakuwa et al., 2005), whilst some ommatidia contain two UV receptors in addition, or two blue receptors, or one blue with one UV receptor (Wakakuwa et al., 2005, Spaethe and Briscoe, 2005).

1.3.1 Trichromaticity theory - Coding of object colour in vision

A comprehensive understanding of colour vision must involve a consideration of all components of the viewed scene. This includes the spectral power of the light, the reflectance spectra of the object and a background that, for bees, typically consists of green vegetation (Chittka, 1997) and is commonly the backdrop of flowering plants in temperate habitats. The photoreceptors measure the amount of light at a particular waveband that the colour receptor is sensitive to, and the quantum catch of a photoreceptor is calculated by integrating over the spectral sensitivity function of the receptor, the reflectance spectrum of the object and the illumination spectrum. The absolute sensitivity of a photoreceptor may also be determined by the reflectance of other objects in the visual scene (Wyszecki and Stiles, 1982).

Human colour vision is also trichromatic consisting of photoreceptors that have sensitivity peaks at approximately 440nm, 545nm and 570nm. However with just three photoreceptors sensitive to a specific band of light does not explain the vast range of hues that are experienced. Each of the human cone photoreceptors that have peak sensitivity to a specific wavelength extend in the spectrum (but with less intensity). In this view the physiological representation of a colour can be thought of as a combination of varying photoreceptor signals. This was proposed in the Young-Helmholtz trichromatic theory by Sir Thomas Young (1802) and Hermann von Helmholtz (1867). It was explained that a physiological representation of a colour is a combination of these three photoreceptor signals. The theory is fundamental for understanding the wide variation of hues that we experience. For example, although there is no photoreceptor that is exclusively sensitive at a ‘yellow’ light, this colour sensation can still be derived if both the Medium (Green) and Long (Red) are stimulated together. When all photoreceptors are stimulated strongly and equally, this produces the colour sensation of pure white.

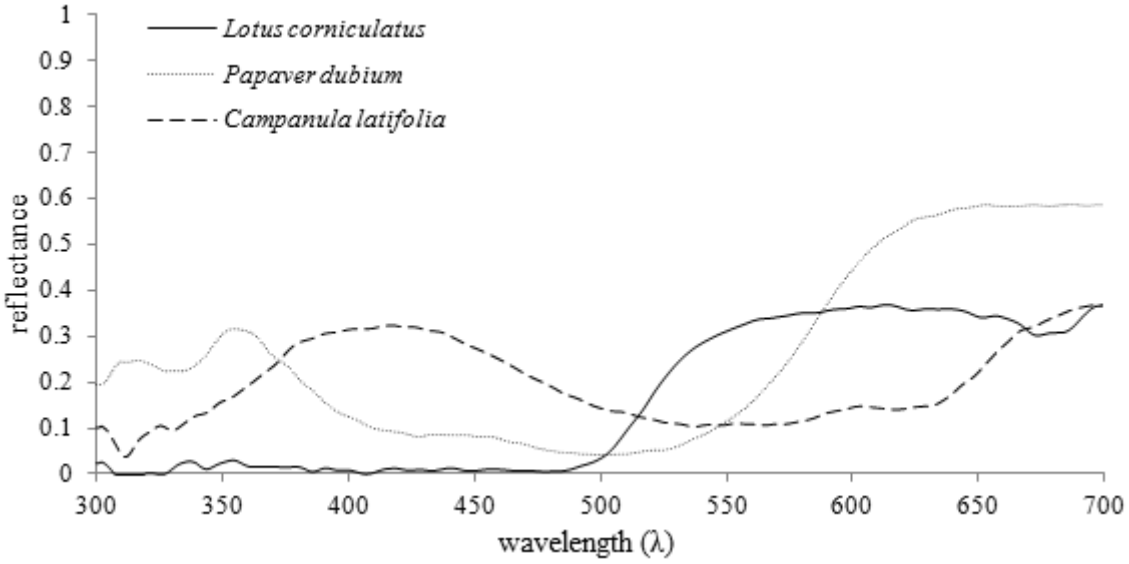


Figure 1-1. Spectral reflectance functions of three different flower species. The reflectance is the proportion of light at each wavelength reflected by the sample. The *Lotus* flower reflects mostly in Green and Red in the human colour vision, and would appear yellow to a human, and bee-green to a honeybee. An interesting example is the poppy flower of *Papaver* – it reflects at both ends of the spectrum, meaning that it appears red to human observers, but UV to a bee pollinator that has a UV receptor, but not a receptor whose sensitivity extends deeply into the red, as humans do. The *Campanula* flower is purple to humans since it reflects both in the blue and red regions of the spectrum, but UV-blue to bees since, while bees cannot see red, the light reflected from this flower will stimulate both the UV and blue receptors of a bee.

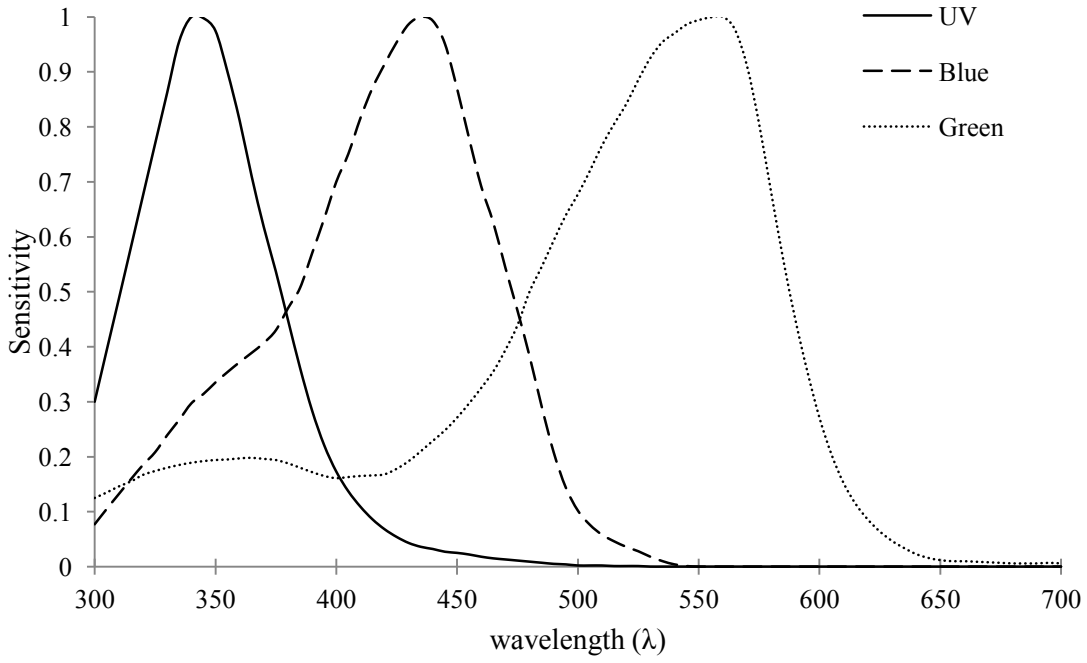


Figure 1-2. Spectral sensitivity of the three colour receptor types of the honeybee (*Apis mellifera*). The honeybee possesses three photoreceptor types whose sensitivities peak at wavelengths in the UV (the short wavelength receptor), Blue (the medium wavelength receptor) and Green (the long wavelength receptor). They are here normalised to equal peak sensitivity (Peitsch et al., 1992). The visual spectrum of the honeybee ranges from 300nm to 700nm, although sensitivity above 650nm is extremely low.

Predicting colour perception through the eyes of the honeybee can be achieved using various colour space models. Considering only the receptor level, a variety of hues can be generated from mixing the primary colours in the honeybee colour vision in the same way that it is thought to have been achieved in the human trichromatic colour vision (Young–Helmholtz theory). For example, the mixture of blue with UV light will generate the perception of an intermediate colour (violet), and it is not possible for the visual system to distinguish this mixture from pure (monochromatic) violet light (Daumer, 1956). For example, Figure 1-1 shows the reflectance spectra of three different flower species where spectra such as the *Lotus* reflect predominantly in the green and red region of the human colour visual spectrum, which would make the human perception of the *Lotus* flower 'yellow', and it would look bee-green in bee colour perception based on the spectral sensitivity of the honeybee (Figure 1-2).

Colour coding in bee vision was first explored using this theory too, using the colour triangle colour space model (Daumer, 1956, Daumer, 1958). This so called trichromaticity theory is useful for understanding the wide variation of hues that we humans experience, since we, like bees, also have three colour receptor types (commonly called blue, green and red receptors).

Photoreceptors do not typically generate action potentials, but only graded potentials. In insects as opposed to vertebrates, photoreceptors depolarise (not hyperpolarise) as a response to light (Skorupski and Chittka, 2010). When normalised to a maximum of unity, the physiological receptor excitation (E) which is the input to the insect brain (Naka and Rushton, 1966) is described as follows:

$$E = P^n/(P^n + 1) \tag{1}$$

P defines the photon flux, or the absorbed photons by a photoreceptor, hence it represents the input to the photoreceptors. In Equation 1, the n exponent is assumed to differ based on the adaptation state or the species in question (Menzel et al., 1986), however for bees exposed to intense light, $n = 1$ (Backhaus and Menzel, 1987).

The adaptation to the light calculated in the photoreceptor to determine relative quantum flux P (Laughlin, 1981, Naka and Rushton, 1966) is as follows:

$$P = R\int_{300}^{700} I_s(\lambda)S(\lambda)D(\lambda)d\lambda \tag{2}$$

$I_s(\lambda)$ is the spectral reflectance of the stimulus such as the functions in Figure 1-1 or Row 1 in Figure 1-3. $D(\lambda)$ is the Illuminant (Row 2 in Figure 1-3); $S(\lambda)$ is the spectral sensitivity (Figure 1-2 or Row 4

in Figure 1-3) of the honeybee photoreceptors where dλ is the wavelength step (i.e. 1nm). The relative sensitivity of the receptors can vary when they are stimulated by shifted or low intensity light, the relative intensity of a receptor will increase when it is poorly stimulated. This is known as the von Kries receptor adaptation response. The sensitivity of the photoreceptors is adjusted by a sensitivity factor *R* as follows:

$$R = 1/\int_{300}^{700} I_b(\lambda)S(\lambda)D(\lambda)d\lambda \tag{3}$$

The adaptation process by the coefficient *R* scales sensitivity whilst adapting to light reflected from the background (Laughlin 1981) and adjusts the sensitivity of the excitation response to half the maximal light reflected from the background denoted as $I_b(\lambda)$. Note that this is probably a simplification – the implication would be that after full adaptation, the background would be achromatic (grey). However, it has been shown at least for strongly chromatic backgrounds that adaptation is not quite that extreme (Dittrich, 1995) and under low intensities there are limits to just how strongly adaptation can compensate (Chittka and Menzel, 1992, Menzel, 1981).

One of the first colour space models to be used for coding bee colour vision was the colour triangle where each point in the triangle represents the relative quantum absorption in the UV, blue and green receptor (Daumer, 1956, Daumer, 1958). The relative quantum absorption in the three photoreceptors based on the colour triangle is as follows:

$$u = P_U/(P_U + P_B + P_G) \tag{4}$$
$$b = P_B/(P_U + P_B + P_G) \tag{5}$$
$$g = P_G/(P_U + P_B + P_G) \tag{6}$$

This means that the colour triangle does not take into account the non-linear transduction process (Equation 1) that determines the graded potentials formed by the receptor cells. This also means that geometrical differences in two stimuli on the colour triangle cannot be predicted as perceptual colour distances (Backhaus and Menzel, 1987) i.e. they are not directly predictive of a bee's ability to distinguish the difference between two stimuli. Figure 1-4 shows an example of the colour loci of several flower colours in the colour triangle for the honeybee, i.e. the same three species whose reflectance is shown in Figure 1-1 above.

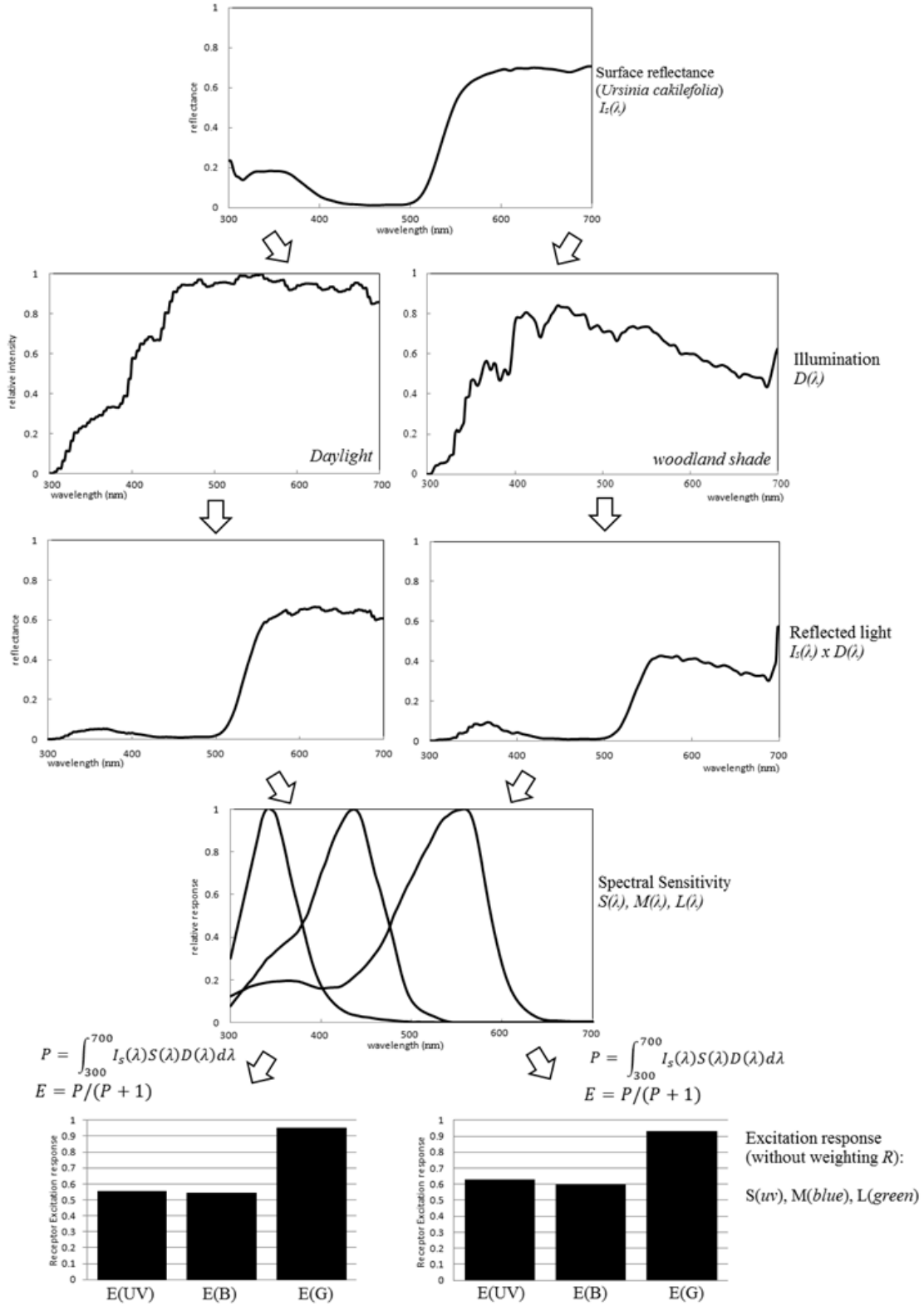


Figure 1-3. The derivation of photoreceptor excitations for one flower reflectance under two illumination spectra. The first row represents the reflectance spectrum of the flower of the South African species *Ursinia cakilefolia* from 300nm to 700nm. The second row represents the light function of two types of natural illumination (Endler, 1993) $I_{daylight}$ and $I_{woodland\ shade}$. The third row shows the spectral light reflected from the flower (i.e. R x I). The fourth row shows the spectral sensitivity functions of the UV, blue and green receptors of the honeybee. The final row shows the UV, B and G receptor excitation signals for the flower under daylight (left) and woodland shade (right).

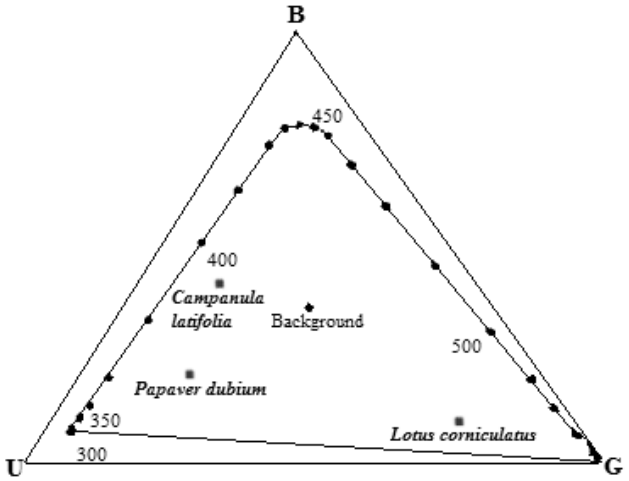


Figure 1-4. The colour triangle for trichromatic bees. The continuous line represents the spectrum locus connecting the loci of monochromatic lights in 10 nm steps. The centre of the colour space represents an achromatic colour, commonly associated to the adaptation background. The loci of three flower species is plotted on the triangle, those reflecting most at a particular spectrum are mostly perceived as the reflected colour. For instance, *Lotus* stimulates mostly the green receptor, and lies in the green corner of the triangle. The poppy *Papaver* (red to us) lies in the UV corner since it stimulates a bee's UV receptors most strongly, whereas the Campanula (purple to human observers) look UV-blue, or violet, to a bee.

1.3.2 Colour opponency in the modelling of bee colour vision

Hering (1892) realised that certain colour experiences and occurrences of colours such as reddish greens or yellowish blues do not exist in human perception. Hering suggested that these may be opponent colours. Later, evidence supporting this opponency theory was found in experiments measuring opponent processes through 'hue cancellation' (Hurvich and Jameson, 1955).

The bee colour opponent mechanisms appear to involve linear transformations of the receptor signal after the phototransduction process. If the weighting of the spectral opponencies are known, as they are thought to have been for bees (Backhaus, 1991) and humans (Hurvich and Jameson, 1955), then one can model the chromaticity in a two-dimensional diagram. For example:

$$A = a_U E_U + a_B E_B + a_G E_G \quad (7)$$

$$B = b_U E_U + b_B E_B + b_G E_G \quad (8)$$

This linear sum is the excitation response of the colour opponent coding. The *E* represents the excitation whilst *a* and *b* are the unknown gain coefficients (i.e. weighting factors) for the spectral opponency mechanism of the colour vision system in question.

The colour opponent coding (COC) by Backhaus (1991) model attempts to address this by calculating an opponency response that can be plotted on a two-dimensional space by two antagonistic response processes, UV versus blue-green and blue versus UV-green calculated by a linear process using receptor potentials (i.e. excitation responses) as the input, and thus determine perceptual colour distances from distances of two stimuli on a colour space. This model is simple and therefore attractive, and predicts many characteristic of bee colour discrimination reasonably well. The neurophysiological underpinnings of the Backhaus (1991) model are debateable, however, because many other types of colour opponent neurons have also been found in the visual system of the bee (Yang et al., 2004). Thus, while behavioural data from several independent labs all confirm the existence of colour opponency in the bee visual system, it is still not clear which precise colour opponent mechanisms mediate behavioural colour discrimination. The COC colour space model for the honeybee is shown in Figure 1-5, with colour loci of our three example flower species.

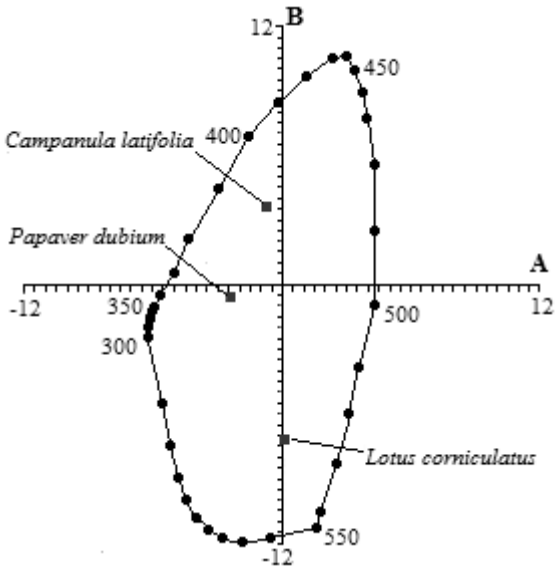


Figure 1-5. The colour opponent coding (COC) space for honeybees. The axes represent the colour opponent mechanism where $A=-9.86\ E_U + 7.70\ E_B + 2.16\ E_G$; $B=-5.17\ E_U + 20.25\ E_B - 15.08\ E_G$. The continuous line represents the spectrum locus connecting the loci of monochromatic lights in 10 nm steps; labels from 300 to 550nm are given in 50nm steps. The line connecting the end points (colour loci for 300nm and 550nm) is the 'bee purple' (UV-green) mixture line, which mixes the lights of 300nm and 550nm in nine ratios, i.e. 9:1, 8:2, 7:3…. 1:9. Colour loci of three flower species are also given.

The complication that the precise nature of the colour opponent dimension in bees is still not known is partially overcome in an alternative model. The colour hexagon (Chittka, 1992) is a general colour opponency diagram widely used due to its simplicity to interpret colour stimuli and to determine perceptual colour distances between two stimuli. Figure 1-6 shows an example of the colour hexagon and three plotted flower colour. It makes no assumption about the specific mechanisms of opponency as Backhaus' (1991) COC model does. Instead weighting factors in opponency associated with the

receptor signals are adjusted so that all possible directions of colour opponency are weighted equally (Figure 1-6).

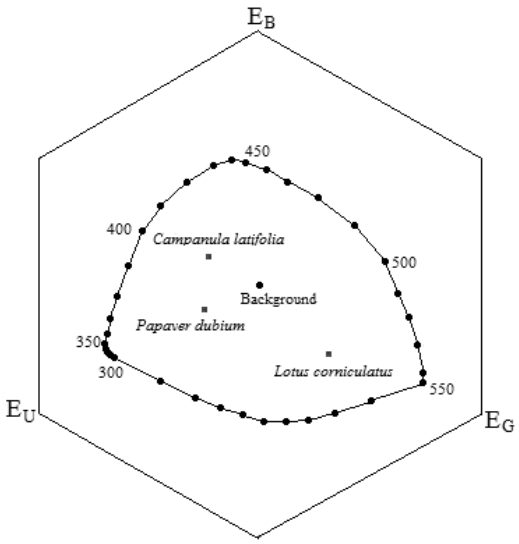


Figure 1-6. The general colour opponent space model for honeybees. The continuous line represents the spectrum locus connecting the loci of monochromatic lights in 10 nm steps. The three labelled corners of the hexagon represent the highest excitation response from the photoreceptors UV, Blue and Green. Colour loci of three flower species are also given.

1.4 Bee colour constancy

Numerous studies on colour vision in bees have shown that colour choice is, to some degree, independent of the spectral content of the illuminant (Mazokhin-Porshnjakov, 1966, Neumeyer, 1981, Neumeyer, 1980, Werner et al., 1988, Lotto and Chittka, 2005, Dyer and Chittka, 2004b), although the compensation is not complete and colour constancy is therefore imperfect. The problem of approximate colour constancy also affects humans (Hurvich, 1981, MacAdam, 1985). The ability to perform approximate colour constancy compensations may be partially due to the bees' ability to directly perceive the changes in the light (Dyer and Chittka, 2004b, Dyer, 2006, Lotto and Chittka, 2005). Spatial cues in colour vision may consist of shadows, brightness and the presence of other coloured object surfaces in a scene and these spatial cues also aid colour constancy in the bee (Werner et al., 1988). The spectral quality of natural illumination holds important information about, for example, weather conditions and time of day. Therefore, animals face the challenge of remaining colour constant and yet to ideally also be able to perceive changes to the light. Perhaps for this reason the compensation provided by colour constancy is not perfect, since this might impair the ability to perceive changes in the light environment (Skorupski and Chittka, 2011, Lotto and Chittka, 2005).

Bees often make successive colour choices when flitting from flower to flower in the field (Chittka et al., 2001, Spaethe et al., 2001), meaning flowers are often encountered alone without the presence of

other flower colours at one given time to make a decision of colour choice. This requires a memory to recall previously visited, learnt colours. The tendency of bees to stay faithful to a flower species that they have experienced as rewarding is called flower constancy (Waser, 1986). Flower constancy is only possible if floral traits are learnt (Waser, 1986, Dyer, 2006, Chittka et al., 1997, Grüter et al., 2011, Raine and Chittka, 2005). The level of flower constancy improves as colour distances between flowers increases – i.e., the more distinguishable the flowers, the more pronounced is flower constancy (Chittka et al., 2001). This behaviour is based on reward levels provided by the flower, since bees associate floral colour signals with rewards, and subsequently tend to revisit those flower types that they have experienced as most rewarding (Menzel and Muller, 1996, Greggers and Menzel, 1993).

Whilst flowers are often encountered by a foraging bee one at a time in nature, the bee must mostly recall from memory if the flower observed at that period in the visual field of the bee matches a colour that was rewarding in the recent past (Neumeyer, 1981, Dyer and Chittka, 2004a, Giurfa, 2004). If, in addition, the bee faces a change in illumination then not only must it recall the correct colour from memory, but the application of a colour constancy function must restore the colour of the flower as it appeared in the illumination that the bee learnt the colour in to associate reward to it. Only a few studies (Dyer and Chittka, 2004b, Dyer, 1998, Dyer, 2006) have focused on both colour discrimination ability in the bee and perceptual colour shift caused by variation of illumination under controlled laboratory conditions, but none have explored this relationship for natural flower colour choice tasks under realistic variation of illumination. The following section describes the features of bee colour vision that are related to achieving colour constancy.

1.4.1 Von Kries receptor adaptation in honeybee colour vision

The von Kries (1905) adaptation theory is based on the assumption that the sensitivity of a photoreceptor is scaled in line with the overall intensity of the light in the receptor's spectral domain. This self-shunting of receptors ensures that receptors can meaningfully code information over intensity ranges of several logarithmic units. Because different spectral receptors can adjust their sensitivity independently of each other, such receptor adaptation can also be considered one of several possible mechanisms in achieving colour constancy. This adaptation mechanism resolves colour inconsistencies arising from changes in the illuminant since intense light-shift can increase the spectral content signal in one receptor more than another, and thus von Kries receptor adaptation can compensate the effects of illuminant changes also. For example, if the photoreceptors are exposed to a light that is blue, the sensitivity of the blue photoreceptor will reduce whilst the spectral shape remains the same, and the sensitivity of the other receptors will stay roughly the same (Hurvich and Jameson, 1955).

As a result of photoreceptor adaptation, and the fact that ambient light conditions are usually depauperate in the UV, the UV receptor in bees has been empirically shown to be 16.5 times more sensitive than a green receptor (Helverson, 1972, Chittka and Menzel, 1992). The model used in Chittka (1992) assumes a von Kries type adaptation response of the photoreceptors, so that a half-maximal response is generated when receptors view the adaptation background (Laughlin, 1981). However, von Kries receptor adaptation is unable to mediate perfect colour constancy, and colour constancy is poorer where there are larger differences in the illuminants (Neumeyer, 1981, Dyer, 1999).

In one study, bee colour vision without colour constancy was simulated by keeping *R* constant to the illumination daylight even under changes of illumination – see Equation 3 (Dyer, 1998), and this was compared to a bee colour vision with von Kries receptor adaptation response (i.e. *R* in Equation 3 varied according to changes in the illumination). If was found that the level of perceptual colour shift was larger when the receptors did not adapt to changes of light than when receptors adapted to the changes of illumination (Dyer, 1998). The conclusion was that von Kries receptor adaptation does achieve a certain level of colour constancy by reducing the level of perceptual colour shift under changing illumination, but it is not perfect in the bee.

1.4.2 The retinex theory

In order to achieve colour constancy, some assumption must be made in which the viewer assesses the illuminant to estimate the surface reflectance. Von Kries adaptation is often applied to keep the appearance of white constant. Achieving scaled receptor response attributed to the von Kries adaptation method is one of the ways of achieving approximate colour constancy, as discussed above in the context to the honeybee colour vision. However, there is considerable evidence that more central nervous processes (i.e. beyond adaptation in the retina) are also involved in colour constancy, and these explored in the retinex theory developed by Edwin Land (Land and McCann, 1971, Land, 1959c, Land, 1977). Retinex here combines elements of ***retin***a and cort***ex***, highlighting the importance of both peripheral as well as cortical mechanisms in human colour constancy. While bees of course do not have a cortex, there is nonetheless evidence that more central nervous processing might also be involved in maintaining colour constancy (Werner et al., 1988). Various algorithms have been spawned from the retinex theory such as *White patch* which assumes that the most intense region of a scene is white, and *Gray world* which assumes that the average colour in the scene is gray (Gonzalez and Wintz, 1977). However, the efficiency of these algorithms might be limited particularly in scenes of non-uniform illuminants (i.e. multiple illuminants in a scene) (Ebner, 2007).

The methods in the retinex theory make estimations of the illuminant from information across the visual field. The fundamental idea of the retinex theories is that colours in the spatial scene are used to recover actual object colour. Also, that equal colour objects are identical to appearance, thus assuming perfect colour constancy. It appears that in bees, the colours in the spatial scene are also used in achieving colour constancy. In experiments by Werner, et al. (1988), bees trained to rewarded flowers on a multicoloured 5 x 5 'Mondrian' checkerboard were able to identify and discriminate colours under changes of illumination. It was considered that various experimental set ups could have different impact on colour constancy ability, for example, if there are enough spatial cues in the form of multiple coloured surfaces such as in a Mondrian, where multiple surfaces are available, then illuminant estimation can be achieved reliably (Land, 1986b). However even achieving a good level of colour constancy is a challenge, particularly because most natural scenes contain a higher level of complexity with non-uniform lighting and three-dimensional objects, both of which affect the performance of retinex constancy algorithms (Lennie and D'Zmura, 1988).

1.4.3 Colour difference sensitivity and colour discrimination ability in bee

Colour discrimination as a function of wavelength has been quantified in the honeybee (Helverson, 1972, Backhaus and Menzel, 1987). This is done by training bees to memorise various monochromatic lights, and determining the wavelength values that can just be distinguished from the training light. The resulting $\Delta\lambda / \lambda$ function shows that level of colour discrimination is better at certain wavelength areas than others. Particularly there are two peaks of especially good discrimination near 390 nm and 480 nm (Chittka and Waser, 1997, Helverson, 1972). A spectral light at which two photoreceptor sensitivity overlap in the honeybee colour vision produces better ability to discriminate resulting in a better ability to distinguish the differences since the signals from two different photoreceptors can be compared. For example at 390nm, both UV and Blue photoreceptor overlap in sensitivity functions, whilst around 480nm both Blue and Green photoreceptor overlap. Moreover, the nature of the overlap means that both receptor types have steep changes in sensitivity in opposite directions in these wavelength ranges. In natural foraging, bees can discriminate flower colours that are spaced 0.1 colour hexagon units (cu) from each other where the maximum colour hexagon unit between two points is a distance of 2cu on the colour hexagon (Chittka et al., 2001).

Colour discrimination has been determined for various pollinating insects including honeybees (Backhaus, 1991, Chittka et al., 1992) and appears to be similar in various species in terms of the wavelength positions of spectral difference sensitivity peaks (Peitsch et al., 1992, Briscoe and Chittka, 2001). Colour discrimination is an important feature of colour vision that may be related to colour constancy (Abrams et al., 2007). It is with the ability to discriminate the differences of change that occurs under changing illumination that one is able to tell if a change has occurred. It is yet to be

examined if the quality of colour discrimination has an impact on bee colour constancy whilst foraging under naturally variable lighting condition. It has been observed that under different classical conditioning methods, differential and absolute conditioning of colour training produces fairly distinct differences in the ability of bees to discriminate colours (Giurfa, 2004, Dyer and Chittka, 2004a). In one, where the bee must retain a memory of the colour with the associated reward and recall if the colour is the same. This is known as absolute conditioning (Dyer and Chittka, 2004a). With the presence of a colour distractor similar to the target during training (differential conditioning), the bee can differentiate the difference better and thus choose the target accurately even if the colour differences between them are small (Giurfa, 2004, Dyer and Chittka, 2004a). These experiments are parallel to findings in humans, as are the effects of successive and simultaneous colour discrimination ability (Romero et al., 1986, Neumeyer, 1981, Neumeyer, 1980, Dyer and Neumeyer, 2005). Although bees can fine-tune their colour discrimination under differential conditioning, colour choice in natural environments in bees seems to be largely governed by absolute conditioning (Dyer and Murphy, 2009) which is the underlying strategy for flower constancy in the bee (Chittka et al., 2001). It is however, uncertain if the observed effect of flower constancy is a cognitive choice/strategy or a lower level mechanism in colour generalisation. Performance of bees for these two conditions (absolute and differential) were tested under patchy light in a 'Battenberg' setup and were found to be insignificantly different (Arnold and Chittka, 2012) so it is uncertain what function the two different discrimination ability in the bee perform in an ecological setting when most flower colour encounters are successive in nature (Chittka et al., 2001). It could be that, the presence of a distractor provides a simultaneous view to discern the spectral difference between the target and distracter, a sort of chromatic contrast (Neumeyer, 1980) to compare difference in colours. However, it is assumed that if colour discrimination is good then colour identification under variations of illumination could be compromised because colours look different. For example, in some animals with colour vision, narrow photoreceptor sensitive to a specific light band may be a strategy to achieve very good colour constancy (Dyer, 1999, Worthey and Brill, 1986), but also to overcome poor colour discrimination by introducing many specific photoreceptors sensitive to many bands of light spectra (Osorio et al., 1997, Cronin and Marshall, 1989) or in oil droplets in certain birds (Vorobyev et al., 1998). It is likely (though speculative), that absolute conditioning serves the purpose of generalisation of flower colour, which may be important to achieve a level of colour constancy as well as flower constancy.

Discrimination ability improves further when penalties are improved for errors, rather than bees just receiving no reward (Dyer and Chittka, 2004a, Giurfa, 2004). In this perspective it is interesting to contemplate colour constancy performance in differential conditioning compared relative to absolute conditioning.

1.4.4 Properties of photoreceptors in the role of colour constancy

Studies on the properties of the bee spectral sensitivity of the photoreceptors such as their broadness, bands and overlapping of the bee colour spectra provide an indication of the bee ability to achieve colour constancy (Chittka, 1996, Chittka, 1997, Dyer, 1999). The broadness of a receptor indicates the amount of the colour visual spectrum that the photoreceptor can intercept; the boarder it is, the more light of the visual spectrum it will intercept. If two photoreceptors overlap, they both are sensitive at the same region of the visual spectrum. It has been thought that overlapping of spectral sensitivity, such that two sensitivity functions have steep sensitivity slopes in opposite directions, improves colour discrimination (Helverson, 1972).

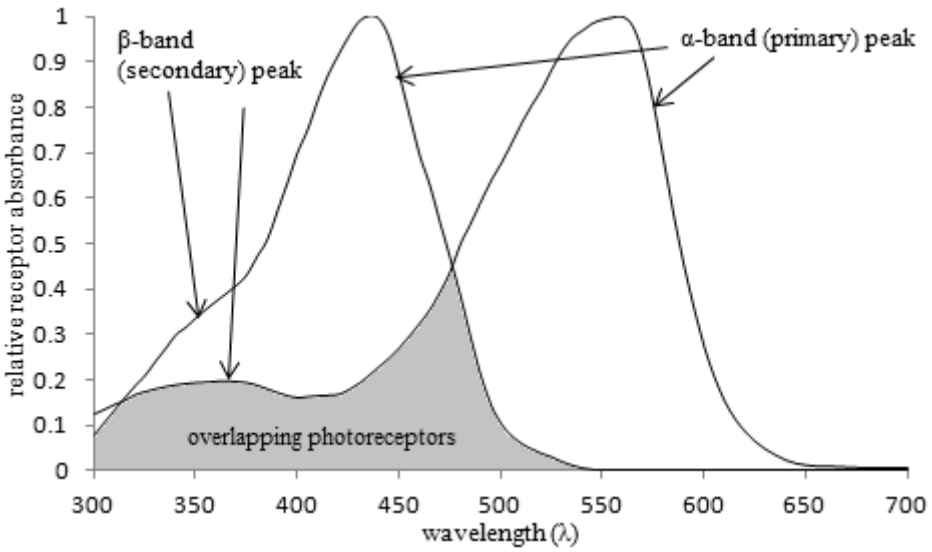


Figure 1-7. Properties of photoreceptors shown in this graph of the medium ('blue') and long ('green') photoreceptor in the honeybee. The main peaks of a photoreceptor with the highest absorbance are α-band and the smaller peaks of the same photoreceptor in the UV are β-band peaks. Such β- peaks are clearly visible in green receptors, whereas for blue receptors they are overshadowed by the nearby α- peak. The gray area represents the area of overlapping sensitivity where colour discrimination is predicted to be better (Helverson, 1972, Chittka and Waser, 1997), but it has been observed that where photoreceptors overlap, colour constancy is poorer (Worthey and Brill, 1986) based on the level of perceptual colour shift of a object colour from one illuminant to another (Dyer, 1999).

It has been theorised that photoreceptors with non-overlapping sensitivity functions, such as where the photoreceptors are sensitive to a specific band of light independent from each other would improve the ability to achieve von Kries receptor adaptation (Worthey and Brill, 1986) and this was confirmed for the bee visual system by Dyer (1999). This means that, reducing overlap of the receptors improves colour constancy, the ability to identify colours under changes of illumination. This could indicate that where colour discrimination is good, such as in the visual spectrum where the photoreceptors

overlap (i.e. bee UV-Blue and bee Blue-green), colour constancy ability deteriorates, and vice versa (Dyer, 1999). Assuming that colour constancy is only mediated by a von Kries adaptation response, colour constancy is predicted to be only approximate. It has been predicted that bee colour constancy performs better in illuminant-induced variation for blue-green colours and poorer for UV colours. This is because of the β-band peak (or secondary peak) in the honeybee photoreceptor sensitivity that results in the asymmetry of bee photoreceptor sensitivity as shown in Figure 1-7 (Dyer, 1999).

1.5 Floral colour and pollination

Like a market attracting shoppers, flowers employ a variety of strategies to 'advertise' themselves and entice visits from a pollinator. One of these strategies, amongst others such as odour, morphology and location, is flower colour. Plant species compete with one another for the services of pollinators, and must therefore present signals that are both detectable (attractive) and memorable to ensure species-specific visits from a pollinator (Gumbert et al., 1999).

The colour of flowers as perceived by humans is different from that perceived by bees, and to understand the interaction between flower colour and bee colour vision, flower colours need to be evaluated based on bee perception of flower colour (Arnold et al., 2010). The aim of the plant is to ensure species-specific pollen transfer under selective pressures of competing flower species in the same community which may be mimicking the same or similar colours (Gumbert et al., 1999, Chittka et al., 1997), and the photic environment that can affect the perception of the flower colour (Dyer, 1998, Dyer and Chittka, 2004b, Richardson and O'Keefe, 2009). In this section, the function of flower colour signal in addressing pollinators is explored.

1.5.1 Flower colour signals and their function in addressing pollinators

A historic view of the interaction between certain flower types and their pollinators is that of "pollination syndromes". This concept held that certain classes of pollinators, e.g. bees, hummingbirds or beetles, were tightly linked to certain flower features, such as their colour. Mutual exclusivity of floral traits to suit specific pollinators or ecological settings was thought to be a dominant feature of pollination ecology. For example, it was thought that red flower colours exclude visits from bees because, so it was thought, they cannot see 'red' (Raven, 1972). Hummingbirds frequently visit red flower colours and possess a colour vision system that includes dedicated 'red' receptors. However, there are complications with such a neat scenario – indeed bees' spectral sensitivity extends far enough into the red to see red flowers. Although they might be might be poorly equipped to discriminate such flowers from other long-wavelength colours, bees can be trained to visit red artificial flowers and do visit red coloured flowers in nature (though detection of and training to red colours takes longer than for other colours (Chittka and Waser, 1997, Spaethe et al., 2001)).

It has recently emerged in many studies that links between floral traits (including their colour) and pollinator classes are less tight than was once thought (Arnold et al., 2009b, Arnold et al., 2009a, Chittka et al., 2001, Ollerton et al., 2009). Even though different pollinator classes predominate at certain times of the year, an extensive statistical analysis of flowers occurring in various plant communities did not find there to be any selective pressure to achieve particular flower colours at different times in the year (Arnold et al., 2009b). Arnold and colleagues also observed there to be a lack of evidence of flower colour composition to differ at different Alpine altitudes (Arnold et al., 2009a), even though low altitudes and high altitudes are dominated by largely different compositions of different pollinator classes. Even where there are weak innate preferences of pollinators for certain flower features (Faegri and Pijl, 1979, Menzel, 1985), these can often easily be overwritten by individual experiences, i.e. learning that certain floral traits are indicative of high reward levels (Raine and Chittka, 2007, Menzel, 1985). Indeed, many if not most pollinator species are generalists, in that they visit a wide range of different flower types on a species level, while individuals might temporarily specialize on flower species that they have experienced as particularly rewarding (Chittka et al 1999).

Thus, to ensure pollinator fidelity to promote species-specific pollen transfer, a plant cannot always rely on just addressing its signals to certain pollinator taxa (such as beetles or bees). Instead they can promote the flower constancy of individual pollinators by advertising their species with highly memorable signals that are clearly divergent from those of other species in the same habitat, for example by presenting a unique colour (Chittka et al., 1997, Gumbert et al., 1999). This will improve colour discrimination between flower species in the same habitat, and potentially facilitate the ability to remain colour constant should the illuminant change. It has indeed been shown empirically that flowers in the same habitat diverge in colour to a larger extent than expected by chance (Gumbert et al., 1999).

If, however, increasing colour distance amongst flower colours of different species of the same habitat happened without any evolutionary constraints, then one might expect that the ideal outcome to be an equal spread of all flower species across all areas on the bee colour space. This is, however, not the case in most natural habitats (Chittka, 1997, Chittka et al., 1994). Flower colours are especially common in the region of bee blue-green (typically white or pink to human observers) whereas flowers in the pure UV sector of bee colour space (often red to human observers) are especially rare (Kevan et al., 2001). The very high frequency of blue-green flower colours appears to be compensated for in part by the fact that bees discriminate very well in the blue-green spectral range. Regions of high spectral difference sensitivity for the honeybee appear to peak at approximately 390nm and 480nm, whilst colour discrimination is poor in the UV range below about 350nm (Helverson, 1972, Chittka and Waser, 1997).

It has also been reported that the blue-green region of bee colour space is also the region of the least colour shift under changing illumination, whilst the largest colour shifts were observed in the UV region. (Dyer and Chittka, 2004b, Dyer, 1998, Dyer, 1999).

Presenting a flower colour that is reliable under conditions of changing illumination is just as important as increasing colour distance from the signals of competing plant species in the same habitat. It is also interesting to note that colours in 400-410nm range are learnt the fastest, whilst colour at 490nm are learnt the slowest (Menzel, 1967, Heinrich et al., 1977), and innate preference of colour in bees appear in the same spectral regions near 400-420nm and 510-520nm (Giurfa et al., 1995, Raine and Chittka, 2007). Figure 1-8 shows the six bee colour categories on the colour space. The correlation of flower diversity, spectral difference sensitivity, level of colour shift under conditions of changing illumination, learning rate of colours and innate preference as observed in bee colour vision are shown in Table 1-1.

In conclusion, these considerations show that, from a plant's perspective, there are different advantages and disadvantages to generating flower colours in different sectors of colour space. In some areas (such as pure UV) there are very few flowers, so that such flowers will enjoy the advantage of uniqueness and memorability, but potentially suffer disadvantages from variable signals under conditions of variable illumination. Blue-green category flowers, on the other hand, are common and it is therefore more challenging to generate a unique signal in this part of colour space; on the other hand, colour discrimination and colour constancy are highly accurate in this spectral domain.

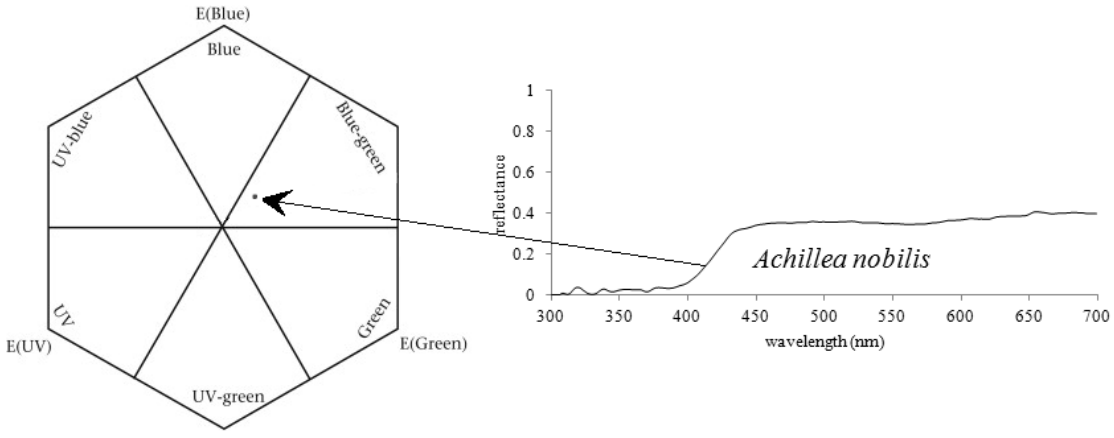


Figure 1-8. Bee colour categories based on the colour hexagon colour space model. One example of a flower colour *Achillea nobilis* plotted on the colour space. This flower colour appears white to humans since it reflects equally across the visual range of human observers. For bees, however, the colour would be categorised as bee blue-green, because the flower absorbs UV light strongly.

Observed phenomenon of flower colour or bee behaviour in colour choice	*Area of colour space region bee colour*	*References*
Highest diversity of flower occurrence	Blue-green, UV-Blue	(Chittka et al., 1994)
Highest spectral difference sensitivity	Blue-green	(Helverson, 1972)
Lowest colour shift caused by spectral variations of illumination	Blue-green	(Dyer, 1998)
Fastest learning of colours	UV-blue	(Heinrich et al., 1977, Menzel, 1967)
Innate preference of colours	Blue-green, UV-blue	(Giurfa et al., 1995, Raine and Chittka, 2007)

Table 1-1. Flower colour or behaviour observed in the bee and the corresponding area in the bee colour space that the phenomenon occurs at.

1.5.2 Flower constancy

Flower constancy is a well-established phenomenon of bees remaining faithful to a flower species that they have experienced as rewarding (Waser, 1986, Chittka et al., 1999). This was observed already by Aristotle who noticed how a bee would move from one flower colour type to another whilst mostly ignoring other flower colours (Christy, 1883). Darwin (1876) suggested that this improved bees' efficiency in handling flowers in the same way as an assembly line worker gains efficiency by learning a certain motor skill and then repeating certain movements over and over (Woodward & Laverty 1992), and this has been confirmed experimentally using artificial flowers (Chittka & Thomson 1997). But even when flowers differ only in sensory signal (such as colour) not in morphology, there might still be advantages to visiting multiple flowers of the same species consecutively. This is because of the limited capacity of working memory; and the signal of a recently visited flower is more swiftly retrievable from the working memory generated by a recent visit to a particular flower than a distant long term memory (Raine and Chittka, 2005, Chittka et al., 1997). To maximise foraging intake with these constraints in mind, remaining flower constant may be a benefit to bees if the flower is rewarding enough and there are many of those flowers available.

Flower constancy is improved when characteristics such as colour, odour, shape and pattern of a particular flower species are distinct from those of other competing species in the vicinity (Goulson and Wright, 1998, Waser, 1986, Waser, 1983a, Gegear and Laverty, 1998, Grant, 1950, Grant, 1954, Pleasants, 1980), and colour is an important component of floral signals to promote flower constancy (Waser, 1983a, Waser, 1983b, Chittka et al., 1997).

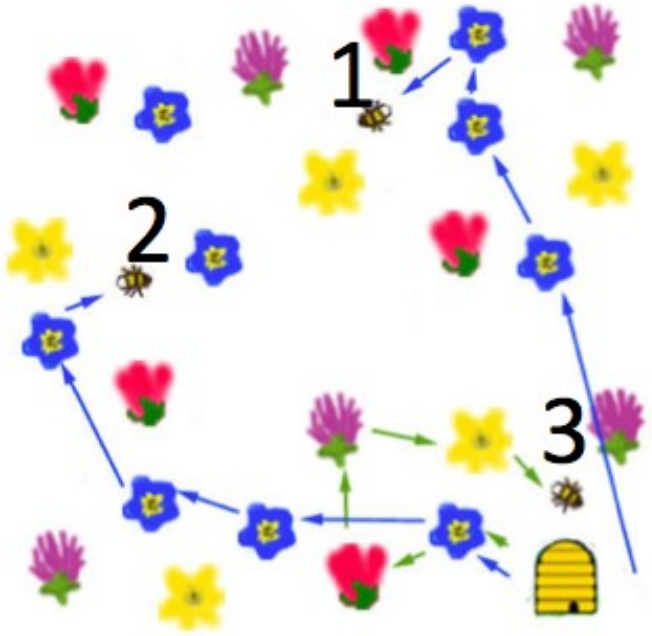


Figure 1-9. Bee flower constancy and flower colour. Four distinctive flower colours are available in this meadow of flowers, and a hive in the bottom right corner. Bees 1, 2 and 3 leave the hive to forage. The arrows indicate the movement of each bees from one flower to the next. Bees 1 and 2 are foraging on the same flower colour (blue) and are *flower constant* since they forage exclusively on one type of flower species, whilst bee 3 exhibits no flower constancy as it switches between flower colours.

Flowers that are distinct in their signal receive the most species-specific pollen transfer (Chittka et al., 1997, Chittka et al., 2001). In other words, the level of flower constancy increases as colour distinctiveness increases. This colour distinctiveness can be quantified as colour distance in a colour space where colour distances are indicative of perceptual colour differences. As an example from one field study, Figure 1-10 shows the level of flower constancy for six species of bees as a function of colour distance between the flowers of several pairs of plant species (Chittka et al., 2001). There is strong evidence that flower colours diverge in a plant community in order to facilitate recognition by pollinators (Chittka et al., 1997, Gumbert et al., 1999).

Flower colours act as a signal in a market of other competitors (other flowers) to attract visits from pollinators. The ‘shopper’ attempts to find the best deal. However, unlike human shoppers or most foraging animals, bee pollinators are unique in continuously looking to find this ‘best deal’ and spend most of their working lives doing so (Tastard et al., 2008). Due to this, bees have adopted strategies to forage efficiently.

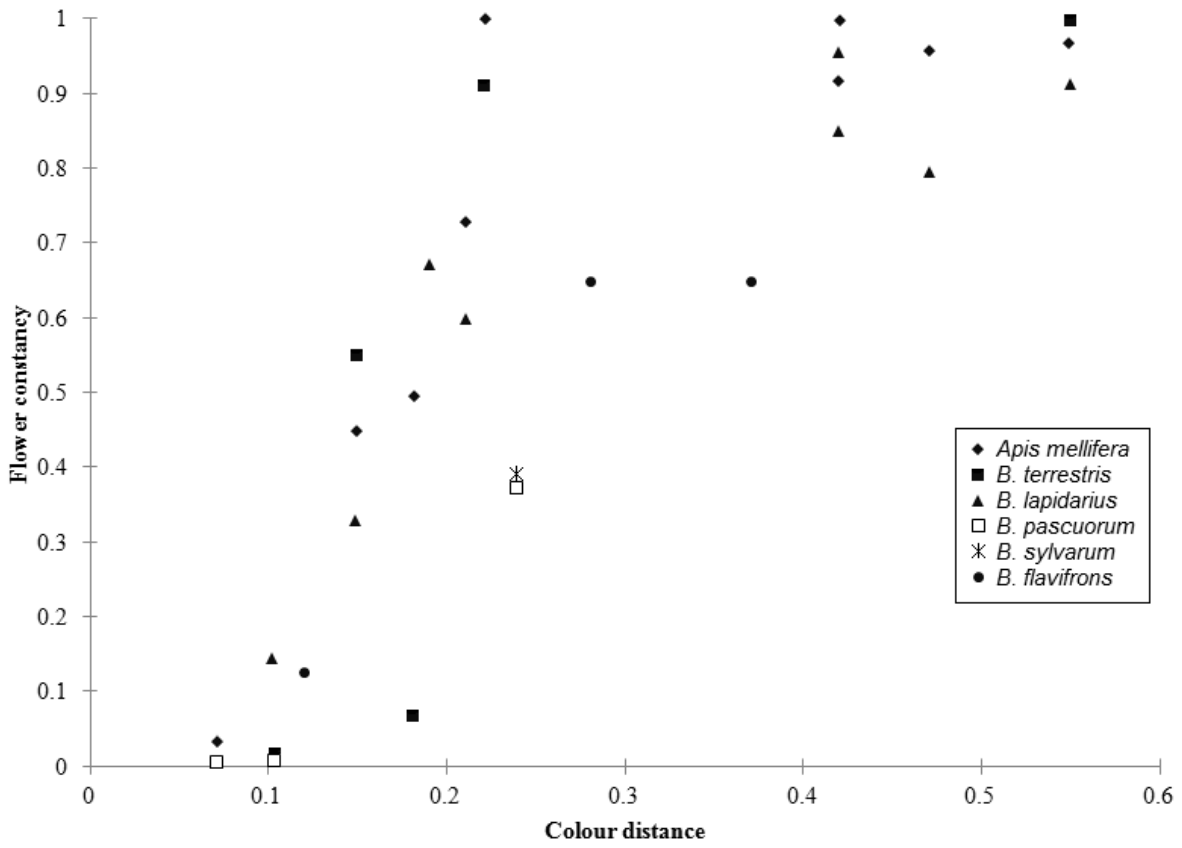


Figure 1-10. Flower constancy in several species of bee as a function of colour distance between pairs of flower types. Based on Chittka et al, (2001), at least 80 choices were recorded for each pair of flower types. Bee flower constancy improves as the colour distance between flowers increases.

Yet in the interest of frequent and conspecific visits from a pollinator, the flowers of particular species in a community may converge or diverge depending on whether it is a rare or common flower in the community (Gumbert et al., 1999, Chittka et al., 1997). However, there has been very little research exploring how these strategies employed by both the plant and the pollinator overcome the ambiguity of varying light (but see (Arnold and Chittka, 2012) and (Dyer and Chittka, 2004b, Dyer, 2006)). In earlier sections of this chapter, it was described that a von Kries receptor adaptation type response can partially compensate the changes of illumination. Yet, it is unknown if flowers are under selective pressure in plant communities that vary in light conditions temporally (such as understory plants in shaded parts of a plant community may be in daylight before the growth of a canopy) to be highly conspicuous.

1.6 Conclusion

The relationship between light environments and the impact that this has had in the development of flower colour diversity and bee colour vision has been examined by Dyer (2006) and Dyer and

Chittka (2004b). There is evidence suggesting that flowers in a plant community diverge in flower colour (McEwen and Vamosi, 2010, Gumbert et al., 1999, Chittka et al., 1997, Chittka et al., 2001). Beyond promoting flower recognition by having unique signals, there can be advantages to presenting particular colours. There exists a clear advantage of flower colours in the blue-green region of the colour space to the bee, because this is the region where bees best discriminate, and this might be the reason why such flowers are especially common (Chittka and Waser, 1997, Helverson, 1972, Dyer and Chittka, 2004b). On the other hand, plant species presenting UV-blue or blue flowers would benefit by addressing directly the innate biases of bees towards such flowers (Raine and Chittka, 2007). Nonetheless, for many pollinator species, the effect of innate preferences is not strong beyond the first few visits, when preferences become increasingly dominated by individual learning. Thus the notion of floral syndromes, where pollinator classes were thought to be tightly linked to certain floral traits, has given way to the view that pollination systems are markets where pollinators choose between flowers based on rewards, and flowers generate signals as to advertise to cleverly choosing pollinators (Arnold et al., 2009b, Arnold et al., 2009a). Flower species diverge in plant communities to increase their chances of within-species pollen transfer, and that increasing perceptual colour distances improves flower constancy (Chittka et al., 2001).

There is potentially an important link between flower constancy, flower recognition and colour constancy. Flowers 'want' to be identified and recognised by pollinators, no matter the lighting conditions, and bees in turn profit from accurate flower identification even when the illumination changes. There have been extensive studies in bee colour constancy, many of which have established that colour constancy is imperfect (Neumeyer, 1981, Dyer and Chittka, 2004b, Dyer, 1998, Werner et al., 1988). Such inaccuracies further emphasise the need for plant species to be maximally distinct in colour signal, so that despite some variation in perceived flower colour, a species is still not confused with another one flowering nearby in the same habitat. In this thesis, I examine the interaction between colour constancy and object recognition under biologically relevant conditions, using the properties of bee colour vision and flower colour as a model. Using agent-based simulations of bees foraging under realistic conditions (including realistic variation of illumination) I will identify optimal computational algorithms for colour constancy in solving real-world foraging problems, as well as strategies used by signallers to promote identification under conditions of naturally variable illumination.

1.7 Motivation

There are, as yet, no thorough studies that examine colour discrimination and perceptual colour shift under change of illumination together to explain the biological significance of colour constancy. A colour shift is a shift in colour perception that is caused by the changes in the illumination and thus a large colour shift would mean that there is a large colour perceptual difference between the colours

that a subject may have been familiar to in association to a reward. Colour discrimination on the other hand, is the ability to tell apart the difference if there is one in the colour of one object from another. The thesis focuses on these two colour visual processes in achieving colour constancy. It also explores the biological significance of various computational colour constancy methods.

1.7.1 The bee as a model for investigation of colour constancy

I use bee colour vision as a model to investigate the performance of various computational colour constancy methods, and the biological significance of colour constancy observed from the bees' perceptive, and the analyses of flower colour to examine the selective pressures arising due to changes of illumination to achieve pollinator visits. The honeybee is an excellent model for the investigation of colour vision, particularly because the worker bee spends a large proportion of its working life looking for flowers (Seeley, 1995) and uses colour as a cue to make accurate choices of rewarding flowers. The task of collecting nectar and pollen must be optimised since successful flower visitation is a key to foraging success and ultimately, colony fitness. Faced with challenges of varying light in the environment, the relationship between flowering plants and bees bound by flower colour and bee colour vision is an exceptionally useful model. This is because of the exclusive nature of the relationship: many flowers depend *entirely* on animals as pollen vectors, and pollinators such as bees are fully dependent on identifying the most rewarding flowers, and spend much of the adult lives doing just that. There has therefore likely been extensive co-evolution between the two sides. The flower foraging environment itself is also an excellent model that can indicate the biological significance of colour constancy. I have described previous studies of flower colour that indicate selective pressures on a local (plant communities) and global (general population of all flowering plant species) scale for flower colours.

I developed a computerised simulation, an agent-based modelling (ABM) environment. The agent-based model is used to generate maps of plant communities, i.e. coordinates of flowers of multiple plant species in a two-dimensional plane (the meadow) based on empirically determined distributions of real flowers. Within this setting, I investigate the colour choices of a bee agent (agent-based model bee) that observes a set of rules and behavioural traits known to exist in real bees whilst foraging. All the modelled forager's traits are based on data from empirical studies, such as flower constancy. I investigate computational colour constancy and its biological significance under changing illumination from the bees' perspective, as well as considering the implication of bee colour choice for the evolution of flower colour. The motivation behind the investigation of colour constancy using various comparisons of hypothetical bees with different colour vision systems has been to establish a measurement of the performance of different degrees of colour constancy. In doing so, I provide a realistic measure of colour constancy performance when assessed against a *colour-blind model* bee

and a hypothetical *perfect colour vision* with computation that restores the colour of the flower completely. The work also relates colour constancy performance to flower constancy, i.e. the tendency of bees to remain faithful to a type of flower species driven by the colour of the flower.

1.8 Aim of thesis

The aim of the thesis is to investigate colour constancy using bees and flower colours as a model. I experiment and analyse colour constancy in natural settings in different ways, by measuring bee performance and colour choice behaviour in the following ways:

- The performance of learning colour under different lights is quantitatively measured by examining colour discrimination in the presence of other colours for foraging bees using a real plant community.
- The biological relevance of colour constancy and the consequences of different colour constancy mechanisms for foraging performance in the bee
- The ability of the bee to identify colours under changes of illumination in a real plant community undergoing changes in photic environment

I first investigate the level of perceptual colour shift across the bee colour spectrum under a normal honeybee spectral sensitivity and altered spectral sensitivity functions. There was an interesting interaction between colour discrimination and colour constancy in different regions of the bee visual spectrum. In spectral regions where discrimination is especially good, the effects of changing illumination are felt especially strongly, because large colour shifts in these regions might compromise colour identification.

Whilst investigating the efficiency of various computational colour constancy methods, it turned out that none of the mechanisms generated perfect colour constancy. However, experimentally determined colour discrimination could be better explained by a mechanism assuming von Kries photoreceptor adaptation combined with white calibration (which would result in better discrimination than what was found empirically).

Finally, I investigate the effectiveness of bee colour vision using a real plant community facing natural variations of illumination over a series of months, a central European forest habitat. From early Spring to late Summer, flowers blooming under a canopy of foliage in this case study plant community undergo variations of illumination from direct sunlight to low intensity light largely determined by reflectance from and transmission through green leaves. The bee model is tested for its ability to learn the colours under a given illumination, and its ability to recognise colours under changes of illumination. This real plant community is tested against randomised flowers to find out if

the flowers that are occurring in this plant community are specifically adapted to cope with the changes in light climate to which they are exposed. The results from this study demonstrate that this is indeed the case. When comparing the distributions of real flower colours in the colour space to random sets of flowers, it turns out that real flower distributions produce significantly larger colour distances, combined with low colour shift under changes of illumination. The results provide an indication of what colour combinations in plant communities would do better in promoting bee colour constancy, and thus more species-specific pollen transfer. Certain flower colours are better recognised under changes of illumination and certain flower colours are better discriminated than others. This may be exploited by flowers to ensure that bees can recognise and discriminate flower colour from each other under challenging photic environments.

1.9 Structure of thesis

Chapter 2 – The floral reflectance database – a web portal for analyses of flower colour

Chapter 2 introduces the Floral Reflectance Database (FReD) that provides free, searchable access to reflectance spectra of a large number of flowers, thus making available extensive information about flower colour that is not inherently human-biased and which can be used when considering the interactions between floral appearance and the visual systems of pollinators (Menzel, 1990, Menzel and Shmida, 1993). The data in FReD are used as one of the experimental tools throughout the remaining chapters.

Chapter 3 – Influences of the shape of pollinator receptor spectral sensitivity functions on perceived colours of flowers under natural variation of illumination

In this chapter, flower colour is analysed under altered spectral sensitivity functions of the honeybee, such as narrower spectral sensitivity and α-band only spectral sensitivity. It has been thought that the shape of the receptor spectral sensitivity function can influence perception under changing illumination. The level of perceptual colour shift under these different spectral sensitivity functions is measured to find colours that achieve better colour constancy than others in relation to the occurrences of flower colour as well as colour difference sensitivity.

Chapter 4 - Development of an Agent-Based Model with bees foraging from flowers under varied illumination

I introduce the development and structure of the computerised agent-based model (ABM) that covers the bee colour choice behaviour, its natural environment and the flowers. In this chapter, I examine the performance of a bee agent based on nectar collection under changing illumination given the

colour vision models from Chapter 2. This is tested both with flower colours chosen from a *natural meadow* and an *ideal meadow* of flowers that are much more distinct in colour than the colours in a real meadow. I analyse if distinct flower colour plays a role in achieving colour constancy under changing illumination.

Chapter 5 – Biological significance of computational colour constancy in an agent based model with bees foraging from flowers under varied illumination

In establishing how light and flower colour in plant communities can affect foraging performance in the bee, this chapter examines the benefits of various computational colour constancy algorithms under biologically realistic conditions. It compares the success of bees equipped with these algorithms with a hypothetical system without colour constancy, or indeed without colour vision (a colour blind bee), as well as with the performance of a modelled bee with perfect colour constancy. The chapter also reports on the performance of bee foraging in the model bee simulation under different retinex theories of colour constancy against the von Kries receptor adaptation mechanism.

Chapter 6 – Seasonal influences of light climate in a temperate forest on bees' foraging performance

In this chapter, I examine performance of bees foraging in variations of illumination over a seasonal scale. This is examined using the Agent Based Model to mimic the inconsistent light environment of a Central European maple forest from early Spring to late Summer. Performance is compared to random sets of flowers to determine if forest flowers are adapted to the light conditions that prevail at the particular time when they are in bloom. I examine the suitability of certain colours to promote better colour constancy in the simulation that result in quantitatively improved nectar collection in the bee agent, using colour occurring in the maple forest plant community as a case study.

Chapter 7 - Discussion and Future Work

This chapter reports the contribution and issues for future work that might arise from the investigations in this thesis.

2 The floral reflectance database – a web portal for analyses of flower colour

Flower colour holds great importance in relation to pollination (Waser, 1983b, Waser, 1986, Waser, 1983a, Dafni, 1984, Chittka and Kevan, 2005). Therefore, it is important that colours of these flowers are interpreted in the way they would be according to the appearance perceived by the pollinator. The way that flower colours look to bees is fundamentally different to that of humans since the photoreceptor colour types that bees possess, as well as post-receptor neuronal wiring, are different between the two visual systems (Peitsch et al., 1992), and thus human judgements of flower colour are inaccurate and irrelevant for an assessment of the biological significance of flower colour.

The Floral Reflectance Database (FReD) contains a collection of floral reflectance spectra made available to the public via a web-based interface, which allows downloading and viewing of spectra and flower colour loci according to widely used models of bee colour space. FReD as a database has undergone extensions beyond a web-portal with spectra of natural light conditions to calculate loci and determine perceptual colour shift or colour distance from one flower spectra and another, which are further described in Appendix II. I later use FReD (in Chapter 3) to model bee colour perception in various photoreceptor shapes of the pollinator spectral sensitivity and later in Chapter 4 in an agent-based simulation of a foraging bee making colour choices between flowers.

In this chapter, I introduce FReD which provides free, searchable access to reflectance spectra of a large number of flowers, thus making available extensive information about flower colour that is not inherently human-biased and which can be used when considering the interactions between floral appearance and the visual systems of pollinators (Menzel, 1990, Menzel and Shmida, 1993). Since the visual ecology of bees is so well understood, and they are also such important pollinators in a variety of habitats (Backhaus and Menzel, 1987), the Floral Reflectance Database has devoted particular attention to modelling and predicting flower colours as they appear to bees, but it would be equally possible to analyse flower colours using another animal's visual system as the base. In addition to the reflectance spectra for all the samples we have reviewed, information is available in the database about their colours as perceived by a bee, including photoreceptor excitations and loci in the colour hexagon, the colour triangle and COC space. Where flowers contain parts with different colours, where possible all the flower parts have been measured and included – this is particularly relevant in

light of multiple studies (Hempel de Ibarra and Vorobyev, 2009, Lunau, 1992, Lunau, 1990, Penny, 1983) emphasising the importance of colour or brightness contrasts between flower parts for detection of flowers by insect pollinators, including from a distance. The database records also contain information about where each sample was collected, as well as other floral parameters and the pollinators of the respective flower species, where known.

2.1 Introduction to FReD

A database for floral reflectance spectra was established over 20 years ago by Lars Chittka, designed to archive reflectance spectra of flowers around the globe. The database was a repository for over 2200 spectra measuring reflected light at wavelengths ranging between 300nm to 700nm. Details included in this database are taxonomic details, plant characteristics of the flower along with location and altitude at which it was collected. The first version of the database became freely available to the public via a website in 2008 (Arnold et al., 2008). Scientists could search the database, download and view details of the spectra as well as information of how bees might perceive and categorise colours based on the colour hexagon (Chittka, 1997). The database also contains the information about the colour category as perceived by human observers.

FReD Version 1 provided keyword searching features to return results from the database (Arnold et al., 2008). With such diverse and extensive floral spectra available with measurements covering the UV range visible for insects and many other animals, it was highly desirable to have these search results modelled into a colour space model as it would be perceived by a pollinator. A well-studied colour visual model applicable to pollination would prove to be useful in building an accurate representation of colour perception of pollinators. FReD 2 (Arnold et al., 2010) is a significant extension and improvement of FReD 1, and in this section I will explain its features. The extensions most notably include the facility to calculate loci plots in various colour spaces for insect pollinators. Figure 2-1 shows the tables and the type of data that are available in FReD 2. FReD 2 is driven by a web-based interface to allow search and retrieval of floral spectra data.

2.2 The database

By providing full reflectance spectra of all the samples, we are making available information that makes no *a priori* assumptions about the colour vision system viewing the flowers. The database provides a selection of natural, ecologically-relevant stimuli that could be used in a variety of colour modelling studies (in the manner of Maloney (1986) and Chittka (1996)). Additionally, as there are species from many plant families of differing ages, the data may, in conjunction with other information about species, have uses in studies of flower colour evolution and investigations of how floral colour relates to other characteristics.

The MySQL database of FReD consists of 16 tables with information on the flower sample and characteristics, location, citation information, colour, collection and taxonomy information, and the wavelength measurements themselves (Figure 2-1).

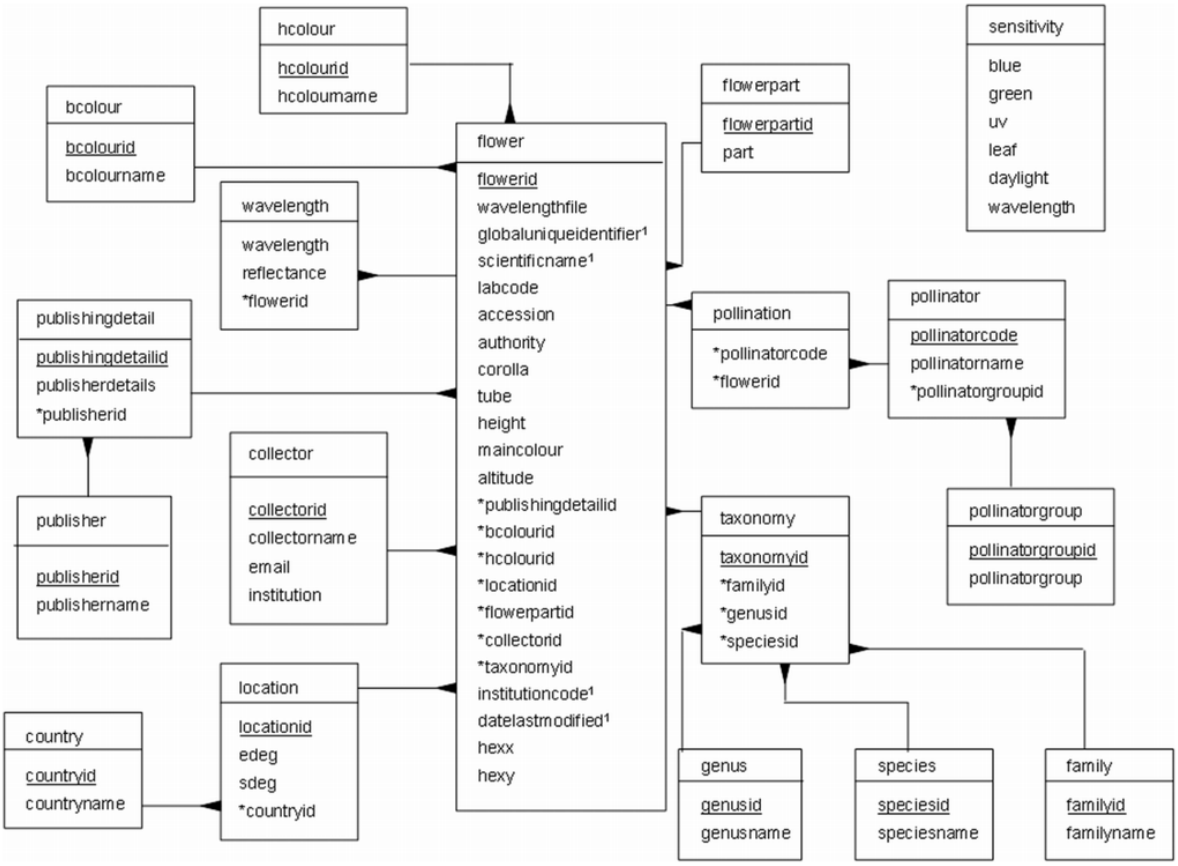


Figure 2-1. Structure of the data in the Floral Reflectance Database. Individual boxes indicate discrete data tables and the fields within each one. Lines linking boxes show data tables that are linked by identification codes (ID numbers); the linked fields are indicated by * in the originating table, mapping to fields that are underlined in subsidiary tables. Superscript "1" indicates those records which correspond to the mandatory Darwin Core (DwC) standard for FReD data to establish with other collections for sharing information on biological diversity.

The *Flower* table is the main table, containing important details of the sample taken, including altitude (m above sea level), plant height (cm), corolla diameter (mm) and tube length (mm) measurements, colour hexagon coordinates, and if the colour information represents the dominant colour of the flower. It also contains information on the herbarium accession number of the sample, if available.

- The *Taxonomy* set of tables provide details about the species and classification of the different flower samples. Where necessary, the colour morph or subspecies of flower can be specified in the "species" field to differentiate it from other samples of the same species.

- The *Location* set of tables provide details on where the flower sample was obtained, including GPS data where available.
- The *Flowerpart* table contains details of what flower section is being measured for each sample, e.g. calyx, tips of petals, upper lip of a zygomorphic flower, etc.
- The *Colour* tables give information on the flower colour, both as seen by a bee and a human.
- The *Pollinator* set of tables contains the information pertaining to the pollinating species, where available.
- The *Collector* table provides information about the researcher who collected the samples.
- The *Publishing* tables give information about the published source and citation information for each sample listed in the database.
- The *Wavelength* table contains the reflectance measurements themselves.
- The *Sensitivity* table is not interlinked with the flower information, but contains information on honeybee photoreceptor sensitivity, spectral components of illumination and other measurements required to calculate coordinates in colour space.

The database often contains multiple reflectance spectra for the same species. Different records may reflect different flower parts being sampled – e.g. the nectar guide versus the keel of the flower – in which case the part measured is specified in the "flowerpart" field. Alternatively, there may be records for different subspecies, cultivars or morphs; many species of plant have more than one floral colour morph (Whibley et al., 2006). In these cases, the "type" of plant sampled is also specified in the species field (e.g. "*Viola lutea* (w)" to indicate the white morph of *Viola lutea* (Huds.)). As the colour of the flower to human eyes is also recorded in the "human colour" field, it is possible to infer the colour morph from this information instead.

The database is also used extensively to create the environments in the agent-based model that will be described in Chapter 4. Parts of the database consist of *table views* (a dynamic table formed based on the query – otherwise known as a function) that calculate the excitation response of a given reflectance spectra and lighting condition dynamically and in real time and are described in Appendix II. This is critical for a simulation that will be dynamically changing in light conditions at a temporal scale.

2.2.1 Colour space facilities

The database also has the function to display the loci of each flower on a colour hexagon diagram, a colour triangle diagram and in COC colour space, as described in Chapter 1. These are three different models of bee colour space (Backhaus, 1991, Chittka, 1992), based on the spectral sensitivities of bee

photoreceptors and the colour-opponent coding mechanisms in bees (Backhaus, 1991). Linear distances between loci within these colour spaces provide an indication of actual colour differences as they would be perceived by a bee. By making the colour loci for all three colour spaces available to users, they are able to obtain instant information about how the flower's colour might appear to a typical insect pollinator with a colour vision system similar to that of *Apis mellifera*.

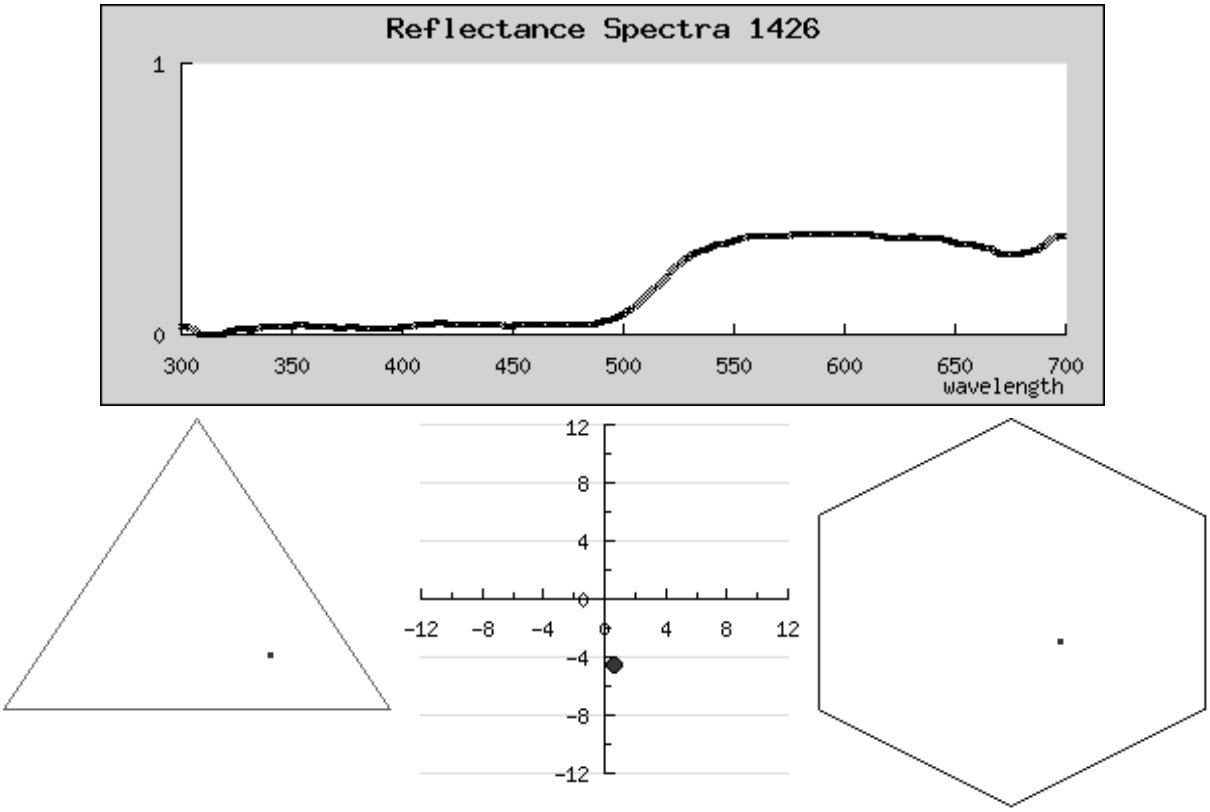


Figure 2-2. View of a reflectance spectrum and the colour space diagrams used in FReD 2 web portal (Arnold et al., 2010). The reflectance spectrum of the flower *Lotus corniculatus* (top). The loci for the flower in various colour space diagrams when viewed under daylight normfunction D65 (bottom row). From left to right: colour triangle (Daumer, 1958, Daumer, 1956), COC model (Backhaus, 1991), colour hexagon (Chittka, 1992). See Chapter 1, Section 1.3 for how the loci are calculated for each reflectance spectra under these colour space models.

The colour space coordinates are calculated taking into account the illuminating light (here, normfunction D65 (Wyszecki and Stiles, 1982)) and the reflectance of the background (assumed in the database to be leaves), as well as honeybee spectral sensitivities over their visible wavelength range (Gumbert et al., 1999). Daylight spectral curves, leaf spectral reflectance data and honeybee spectral sensitivity curves are all taken from published literature (Chittka, 1997, Peitsch et al., 1992, Wyszecki and Stiles, 1982), as are the relevant gain coefficients for the COC model (Backhaus, 1991). Using those data, the relative excitations of the bee's three photoreceptor types can be

calculated, and these three vectors can be converted into coordinates in a two-dimensional colour space diagram (e.g. the colour hexagon).

The flower records present the colour space coordinates for each sample on schematic diagrams, but also give the corresponding coordinates for each space numerically. Additionally, the excitation values for the three bee photoreceptor types are provided. The colour space diagrams for each record are provided as Portable Network Graphics (PNG) image files that can be displayed by most modern imaging software, and can be downloaded by users if desired.

2.2.2 Search facilities

Visitors to the Floral Reflectance Database are able to use the search facilities to run basic or guided searches for flowers with specific characteristics, e.g. flowers from a particular location, of a particular species or colour, or a combination of these. The Advanced Search also allows the user to choose from which data fields he/she wishes to display results (Table 2.1). As the basic search supports Boolean syntax (AND, OR, NOT, and use of quotes) (Frants and Shapiro, 1991), it resembles common search engines and thus is straightforward and intuitive to use.

Field	***Data Type***	***Example***
Family	varchar	Fabaceae
Genus	varchar	Trifolium
Species	varchar	repens
Authority	varchar	L.
ScientificName	varchar	*Trifolium* repens L.
Collector	varchar	Chittka
Bee Colour	varchar	blue-green
Human Colour	varchar	white
Main flower colour	varchar	Y
Flower section	varchar	radially symmetric, whole flower upper side
Country	varchar	Norway
Town/Area	varchar	Oppdal
GPS_East	float	[longitude coordinate, where available]
GPS_South	float	[latitude coordinate, where available]
Pollinator	varchar	bumblebees, large bees
Altitude	float	900
Height	float	15
Tube Length	float	3
Corolla diameter	float	15
Publication	varchar	Chittka, L J. Theor. Biol. 181:179-196
Herbarium accession	varchar	[herbarium accession details, where available]

Table 2-1. Summary of the searchable data fields in FReD and examples of the data format used in each.

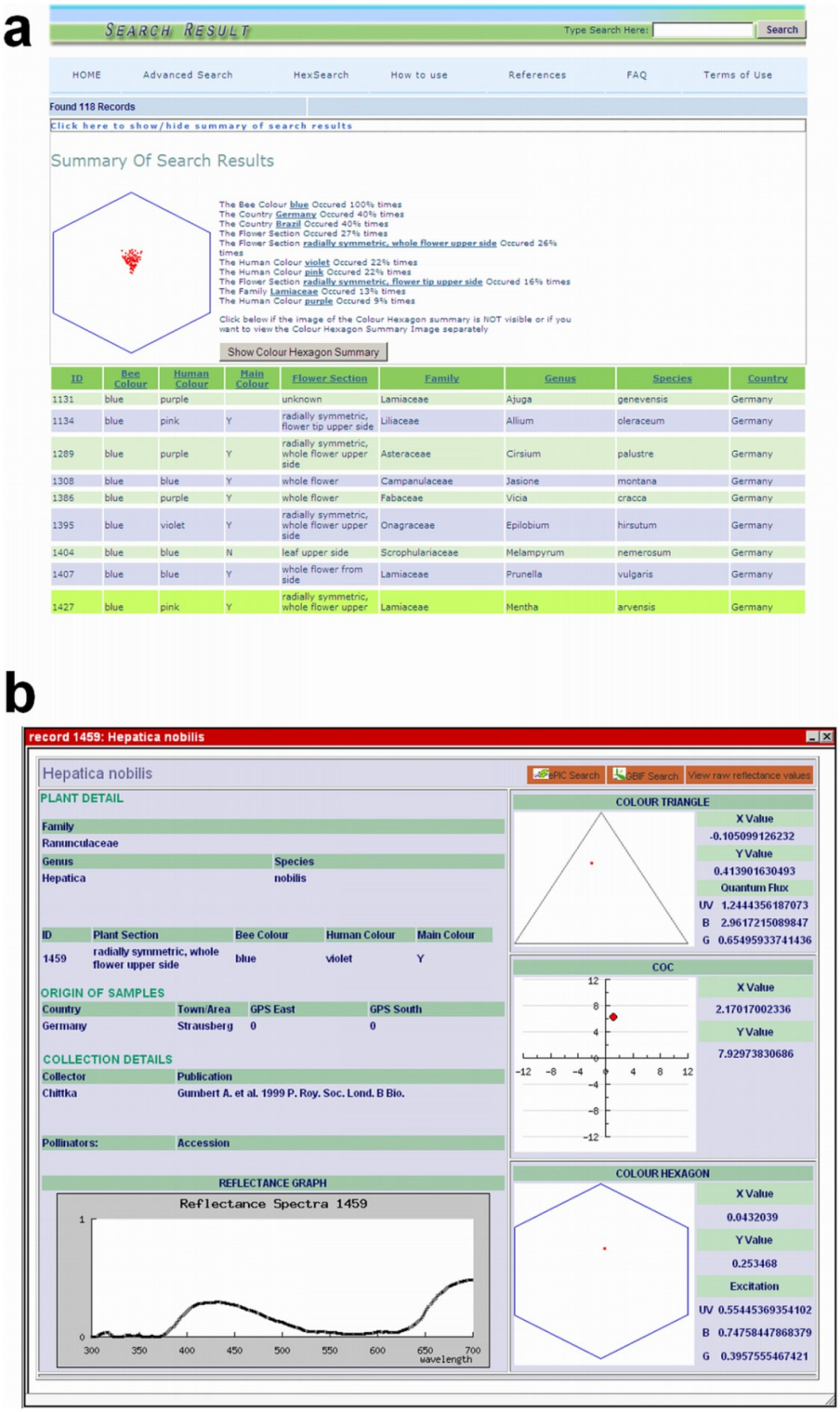


Figure 2-3. Sample search results produced by FReD in response to a search query. (The query is "blue", looking for flowers that are either human- or bee-blue). At the top of the page of search results (a), the user has the option to display the colour hexagon (shown) and some basic descriptive statistics about the composition of the results returned. This is hidden by default to reduce page-loading times. The user can then click on an individual species record to bring up more detailed information (b) about that plant species and its floral reflectance graph, as well as viewing the colour locus for that species in three different bee colour space models.

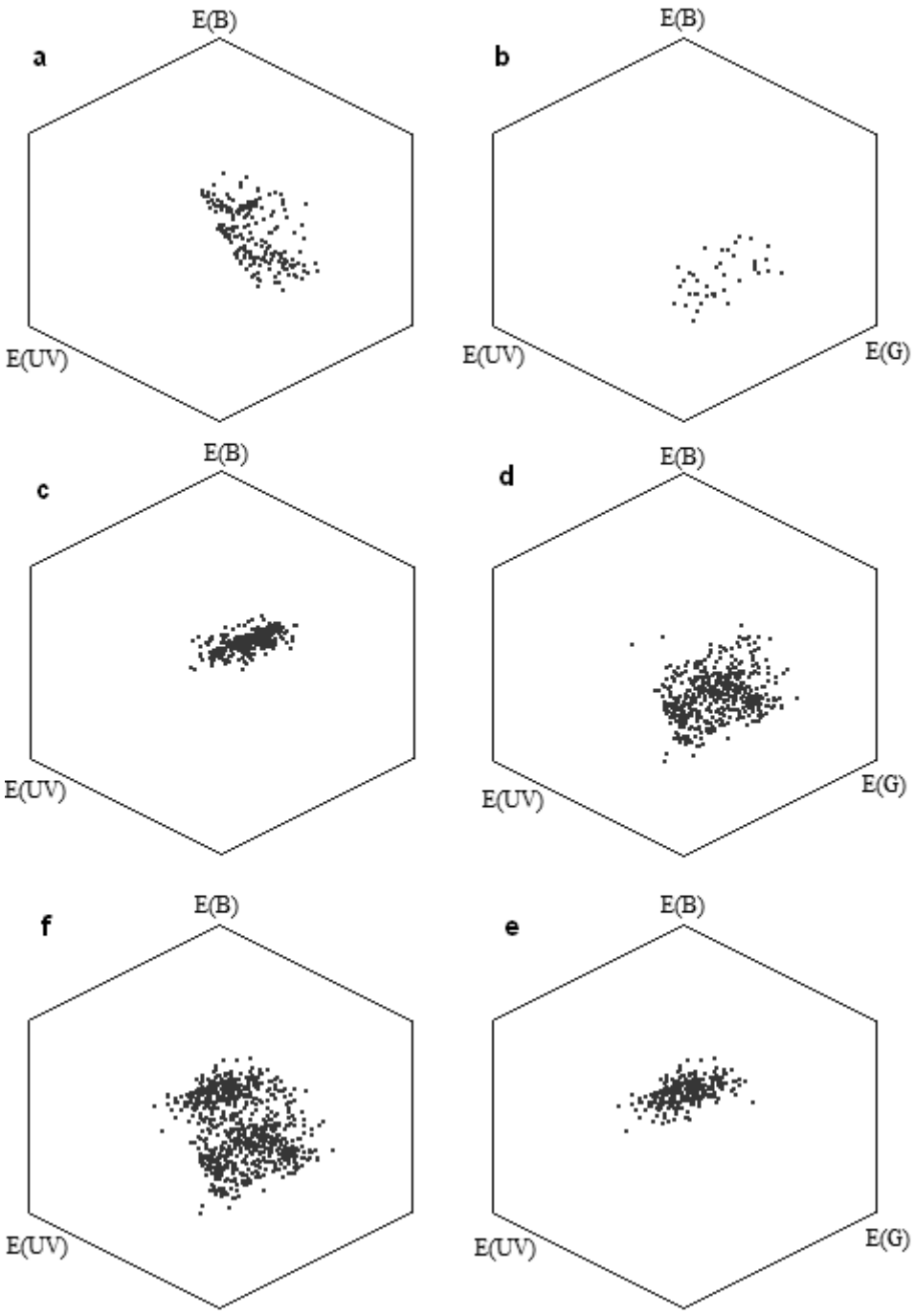


Figure 2-4. Representation of all flower colour loci plotted on the colour hexagon when a user submits a search query in FReD. The three hexagon corners represent maximum excitations of the three photoreceptors of the honeybee, UV (lower left), Blue (top) and Green (lower right), combined with no excitation in the other two receptor types. The patterns of floral loci points occurring on the colour hexagon represent the users' search query. (a) search: 'Asteraceae –UV' (b) search: 'Ranunculaceae Yellow' (c) search: 'white' (d) search: 'yellow' (e) search: 'pink' (f) search: 'pink or yellow' resulting in plots of 787 flowers which is combination of the results in d and e.

Both types of search produce a table of results (Figure 2.3a). The results can be ordered by field, by clicking on one of the column headings. A search summary is available at the top of the page (Figure 2.3a), giving some descriptive statistics on the results returned (most common attributes of results, such as commonest colours, locations, etc.).

A user will then be able to view the reflectance spectra for all the search results. The use of AJAX (Asynchronous JavaScript And XML) technology keeps loading times as fast as possible by minimising the amount of unnecessary information displayed – a user is presented initially with abbreviated records, and can bring up a flower's full record in a pop-up window by clicking on an individual result (Figure 2.3b). Equally, the search summary (Figure 2.3a), containing a colour hexagon showing coordinates of all the results, is not displayed by default; however, it is available from a link at the top of the results page.

From the pop-up window for each flower record, there is a button to display the full reflectance data for the sample as a simple table of numeric values. From the page containing the table, it is possible to either return to the flower record, download the reflectance data in comma-separated values (.csv) format, or close the window and return to the table of search results.

Spectral reflectance functions for each record are displayed as a graph in the flower record (Figure 2-4), for users to assess what pattern of reflectance a flower possess, where the major reflectance peaks occur, etc. These are generated dynamically using the measurements in the Wavelength table, and displayed as a PNG file, so they can be displayed separately from the search results, and saved to a user's local hard drive if required.

2.2.3 Functions for illumination available in FReD

All records of flowers shown in the colour space graphs are under daylight D65 illumination (Wyszecki and Stiles, 1982). However, four different natural sources of illumination are also available in the database to model flower colour perception in the bee colour space (Figure 2-5). The daylight normfunction (D65) (Wyszecki and Stiles, 1982) is the canonical light, and perceptual colour shift is measured from this light source to any three natural illuminants, forest shade, woodland shade or light filtered through small canopy gaps (small gap) (Endler, 1993) in Chapter 3, 4, and 5. The function of these illuminants is used in these result chapters to calculate the level of perceptual colour shift from daylight to another illuminant of a flower reflectance.

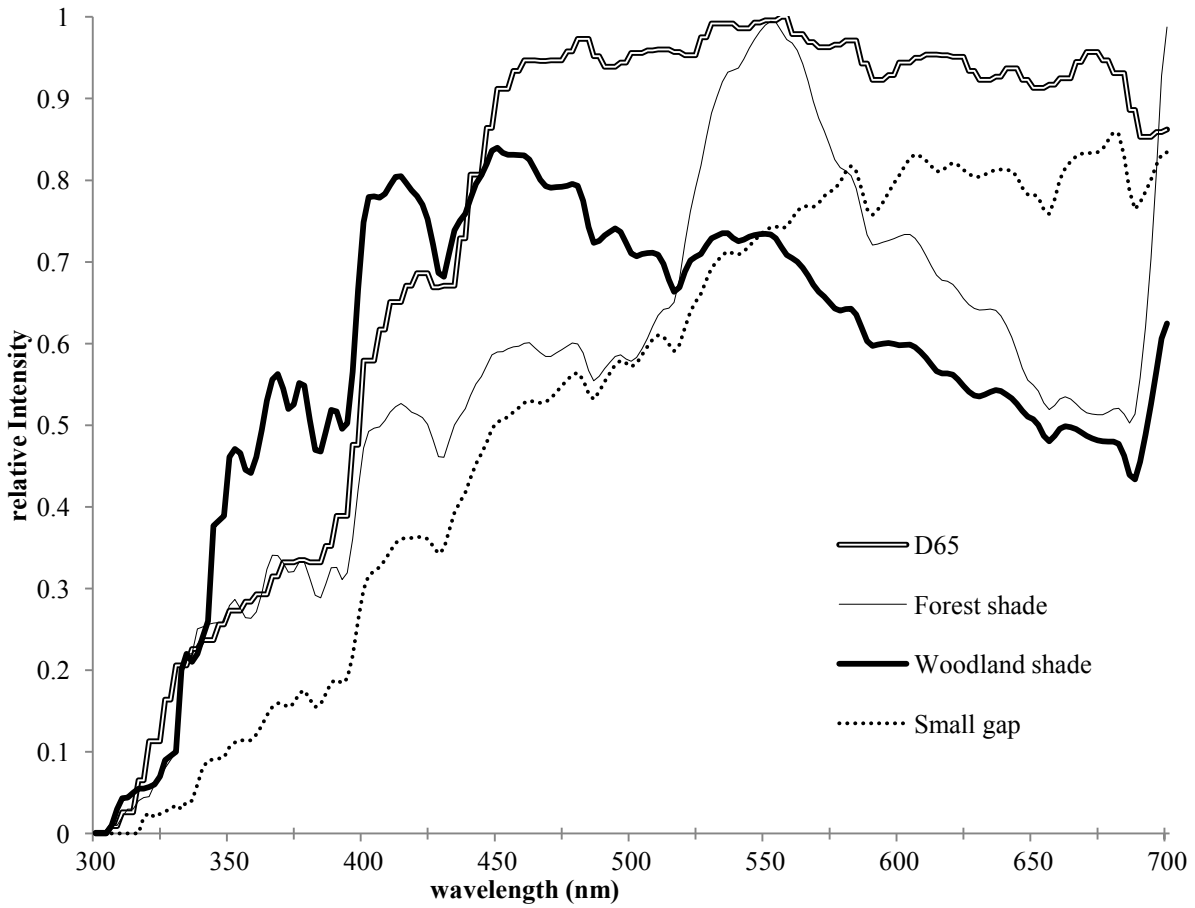


Figure 2-5. Spectral distribution of daylight D65 (Wyszecki and Stiles, 1982), forest shade, woodland shade and light filtered through small canopy gaps (Endler, 1993). The lights are intense at different points, for example, forest shade light is most intense around 550nm, and so the light is 'greener' to a bee because the bee possesses a photoreceptor sensitive to light at 550nm, the Green photoreceptor. Woodland shade is dominantly intense in 400nm to 450nm, and appears 'blue' to the bee. Whilst Small gap is a low intensity light compared to all the other lights in this graph.

2.3 Discussions

The Floral Reflectance Database is a valuable tool to researchers wishing to make between-habitat or global comparisons of floral colour; application of spectral reflectance data in studies of plant communities has already been demonstrated in multiple studies (examples: (Menzel and Shmida, 1993, Arnold et al., 2009b, Arnold et al., 2009a)). With samples from all over the world, collected from a diverse variety of habitats, the database has applications in meta-analyses. We also anticipate its usefulness on a smaller scale, to provide detailed information on the exact colour of flowers of particular species.

As an example of how the Floral Reflectance Database can be used, Figure 2.6 shows the bee-colour composition of different plant communities from various parts of the world, using datasets available in FReD: two sites in Brazil (Ribeirão Preto and São Paulo) (Chittka, 1997) – both tropical locations

in South America, one from a humid meadow near Strausberg (Arnold et al., 2009b, Gumbert et al., 1999) – a temperate location, and one from an altitudinal gradient in the Dovrefjell mountains in Norway (Chittka, 1997, Arnold et al., 2009a) – an alpine location in northern Europe. FReD provides an extensive collection of spectra from all these locations, in which all species present at each site were recorded and measured. From these spectra the bee colours can be calculated as in Chittka (1992). The figure shows that a range of colours are present at all four sites, but also that the exact percentages of different bee colours tend to differ somewhat between locations (χ^2 test, $\chi^2 = 42.3$, $p = 0.0002$), principally in the proportions of blue-green-flowered species (as perceived by bees) and also UV and UV-blue flowers present. This could be due to pollinator-mediated selection with differing pressures in the differing habitats, but as previous studies have indicated that changing pollinator composition does not necessarily result in changing colour composition in a plant community (Arnold et al., 2009b, Arnold et al., 2009a), it is also possible that the differences are due primarily to pleiotropic factors, phylogenetic constraints and/or genetic drift.

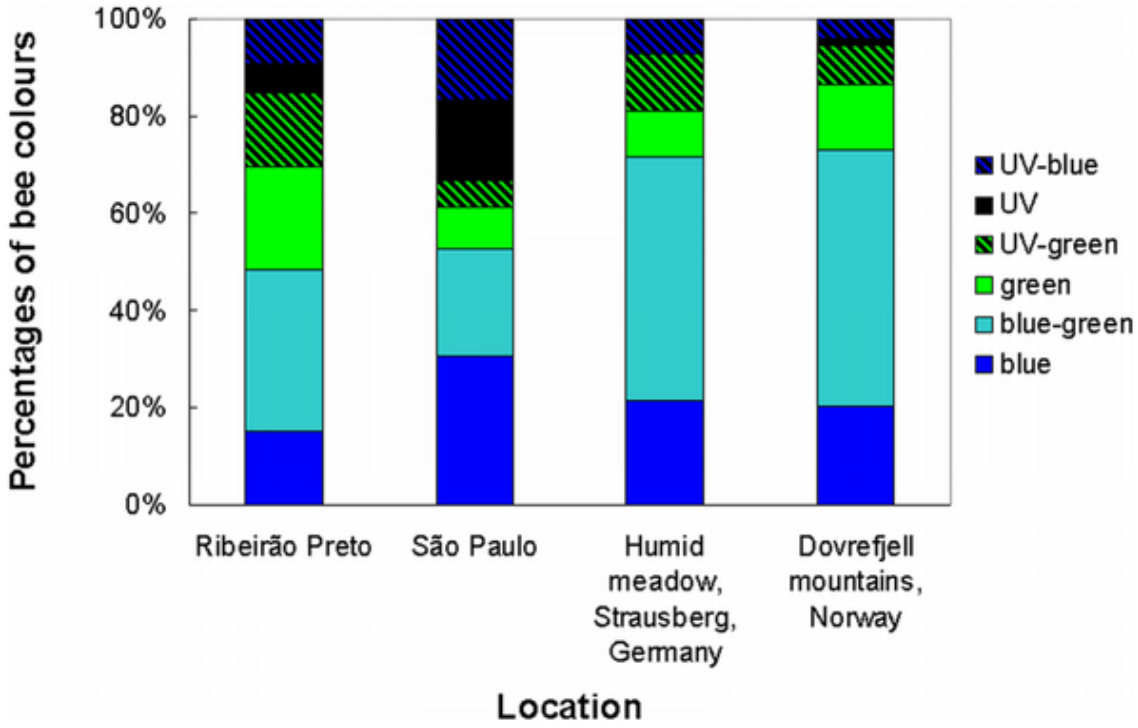


Figure 2-6. Colour compositions of flora from different worldwide locations. The graph shows the relative percentages of plant species with flowers of different bee colours in four different locations: Ribeirão Preto, Brazil; São Paulo, Brazil; Strausberg, Germany and the Dovrefjell mountains, Norway (Chittka, 1997, Gumbert et al., 1999). The differences between the four locations are significant (χ^2 test, $\chi^2 = 42.3$, $p = 0.0002$), but notably, plants with flowers of at least five out of six arbitrary bee colours are present at all locations, suggesting that in all habitats, selection is likely to result in the presence of a range of flower colours.

By providing full reflectance spectra of all the samples, the available information makes no a priori assumptions about the colour vision system viewing the flowers. The database provides a selection of natural, ecologically-relevant stimuli that could be used in a variety of colour modelling studies (c.f. (Maloney, 1986, Chittka, 1996)). Additionally, as there are species from many plant families, the data may, in conjunction with other information about species, have uses in studies of flower colour evolution and investigations of how floral colour relates to other characteristics, such as pollinator species composition, climate, altitude and other ecological factors.

3 Influences of the shape of pollinator receptor spectral sensitivity functions on perceived colours of flowers under natural variation of illumination

3.1 Introduction

Due to variations observed in natural light (Endler, 1993), it is inevitable that bees face inconsistent light that would alter colour perception if it wasn't for (at least partial) compensation by photoreceptor adaptation and colour constancy mechanisms. For most animals, colour constancy may have evolved for the particular variation of illumination in their environment (Neumeyer, 1998, Menzel et al., 1989). It is unclear, however, if floral pigmentation has evolved to help bee colour vision to achieve better colour constancy. It has been observed that at different regions of the bee colour space, the level of perceptual colour shift varies due to asymmetric spectral sensitivity functions for example where there are double peaks in the spectral sensitivity of the honeybee (i.e. see Figure 1-7). The lowest level of perceptual colour shift in the variations of illumination often are found in the blue-green region of the bee colour space (Dyer, 1998). The analysis of different colour vision models in Dyer (1999) described two features that could enhance the result of a chromatic adaptation response like a von Kries receptor adaptation response – narrower photoreceptor spectral sensitivity functions (when plotted over a linear wavelength scale), and reduction of overlap of the spectral sensitivity functions of different classes of photoreceptors (Worthey and Brill, 1986). I will experiment with these manipulated spectral sensitivity functions of the honeybee, for example where the photoreceptor spectral sensitivity functions are narrower than those found empirically. I will be modelling these colour visual systems under changes of illumination and observe this in the presence of flower colour distributions of natural flower colours. The aim is to determine if natural flower colours are under selective pressure to be of a particular floral colour to reduce the phenomenon of perceptual colour shift under changes of illumination, and what distributions of flower colours we might expect if colour constancy was altered in the bee colour vision.

Through the use of FReD (see Chapter 2 for introduction to FReD), I wish to determine regions in bee colour space where perceptual colour shift is minimal and thus colour constancy is best. If colour constancy is found to be better in certain regions of bee colour space, how does it correlate with colour discrimination? Compared to the study by Dyer (1999), I am interested in looking at colour

constancy under pronounced changes in the light environment, for example, where the light changes from daylight to shaded conditions such as a forest shade or woodland shade.

3.2 Material and Methods

The methods to calculate bee photoreceptors signals and loci in colour space are given in Chapter 1, Section 1.3.1 (Equations 1, 2 and 3). I use the data of flower spectra in FReD (Arnold et al., 2010) to be plotted in the bee colour space (1572 floral reflectance spectra, see Appendix I). I will determine the distribution of flower colours in bee colour space, depending on the shapes of receptor spectral sensitivity functions. Starting with the real spectral sensitivity functions of the honeybee, I will then compare the distribution of flower colours using modifications of these functions, and then explore the effects of variations of illumination to analyse the relationship of perceptual colour shift and the ability to discriminate colour in different parts of the bee colour space. This will be observed in relation to the frequency of flowers occurring in different hue sectors of the bee colour space. In colour space, the angular position (as measured from the centre) of particular colour loci (e.g. that of a flower colour) is indicative of bee-subjective hue (Chittka et al. 1994). Distance from the centre of colour space indicates spectral purity, so that with increasing distance from the centre, colours will have increasing spectral purity, while having the same hue (Lunau et al., 1996). For example, colour loci that lie 'straight up' from the centre of the colour hexagon (as shown in Figure 3-3) indicate that that these colours will all be perceived as bee-blue (but with varying spectral purity depending on their distance to the centre of colour space). Colours on a straight line between the centre and the top right corner of the colour hexagon will be perceived as bee blue-green, and so on. To obtain a more fine-grained picture of hue distributions under varied illumination, and using various colour receptor types, I classified the flower colour loci distributions into 10deg sectors in the colour hexagon (Figure 3-2). Each sector thus contains a narrow group of bee-subjective hues.

3.2.1 Hypothetical colour visual systems - α-band and narrow receptor spectral sensitivity functions

Here I compare the influences of modified spectral sensitivity functions to those experimentally determined for the honeybee. Two modifications were explored, in line with those developed by Dyer (1999). One is a receptor set consisting only of α-bands of receptor spectral sensitivity functions. The difference from the honeybee colour photoreceptors is that 'α-band colour vision' lacks a secondary absorption peak. For each main rhodopsin spectral sensitivity peak, there exists a shorter sensitivity peak at around 340nm, known as a β-band, whilst the main peak is the α-band (Stavenga et al., 1993, Dyer, 1999). The narrow receptor spectral sensitivity system consists of the same three-photoreceptor classes as the honeybee, but with narrower spectral sensitivity ranges.

Figure 3-1.B and C show the photoreceptor spectral sensitivity of the honeybee without the β-band peaks and narrow spectral sensitivity functions, respectively. It is thought that these changes to the spectral sensitivity of the photoreceptors can alter colour constancy, such that narrower sensitivity in the photoreceptors achieve better colour constancy. Modelling of such sensitivity functions in the bee has revealed that it may indeed be the case that narrow spectral sensitivity improves colour constancy, but narrower non-overlapping spectral sensitivity are not found in the spectral sensitivity functions in the bee (Peitsch et al., 1992). Instead photoreceptor spectral sensitivity are overlapping which compromises colour constancy but does achieve a good level of colour discrimination. By investigating these hypothetical spectral sensitivity functions compared with real honeybee photoreceptor classes, I can analyse the level of colour constancy measured by perceptual colour shift and colour discrimination ability to explain why the bee does not have narrower spectral sensitivity functions, compared to the photoreceptor sensitivity it actually possesses.

Lighting condition	**Short (R)**	**Medium (R)**	**Long (R)**
The honeybee spectral sensitivity (actual)			
D65 daylight	2.09	0.40	0.13
Forest shade	1.95	0.57	0.16
Small canopy gaps	4.12	0.73	0.18
Woodland shade	1.30	0.40	0.18
α-band honeybee spectral sensitivity			
D65 daylight	2.09	0.42	0.13
Forest shade	1.94	0.61	0.16
Small canopy gaps	4.13	0.76	0.19
Woodland shade	1.29	0.42	0.18
Narrow honeybee spectral sensitivity			
D65 daylight	3.14	0.62	0.23
Forest shade	2.79	0.90	0.25
Small canopy gaps	6.95	1.12	0.30
Woodland shade	1.84	0.62	0.33

Table 3-1. The weighting R of short (λmax = 350nm) medium (λmax = 440nm) and long (λmax = 540nm) colour receptors under actual and altered spectral sensitivity functions of the honeybee different model at different lighting conditions. Weighting is based on a von Kries coefficient law, where spectral sensitivity remains the same and the scalar coefficient vary at the weightings given above.

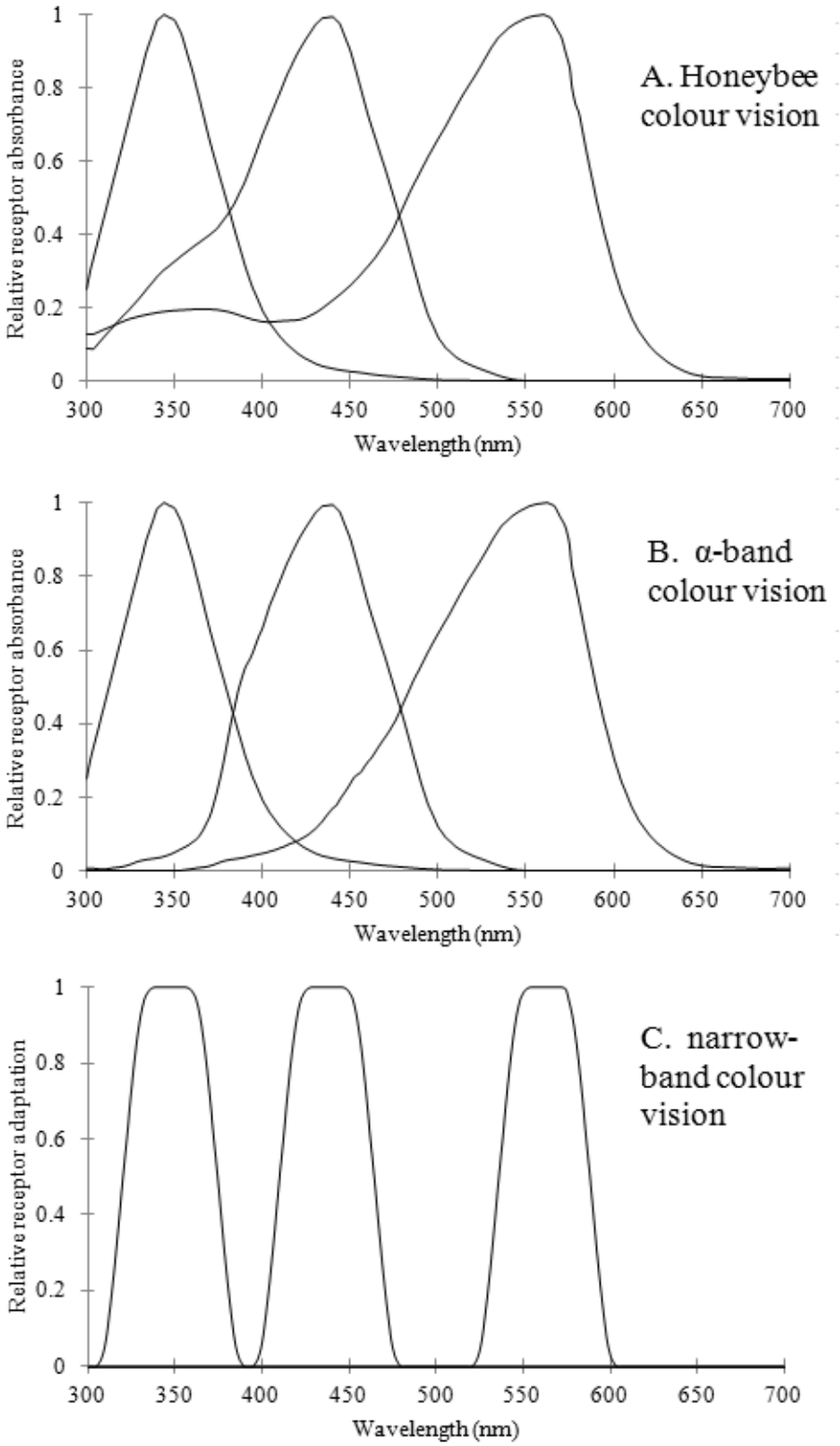


Figure 3-1. Actual and modelled spectral sensitivity functions used in this chapter. The spectral sensitivity functions of the honeybee (*Apis mellifera*) receptors (Peitsch et al., 1992); B. Hypothetical receptor spectral sensitivity function assuming only α-band receptor peaks; C. Hypothetical spectral sensitivity assuming non-overlapping, narrow band spectral sensitivity functions (Dyer, 1999). These three spectral sensitivity function models will be tested in this chapter for their effects on colour constancy based on the level of perceptual colour shift of flower colours under conditions of changing illumination. It is assumed that narrow spectral sensitivity function achieves better colour constancy than broad and overlapping photoreceptor sensitivity.

3.3 Results

In Table 3-2 the contour shade represents the level of colour shift (darker shades represent the shortest colour shift) in angular sectors of the colour hexagon to highlight hues where perceptual colour shift under changing illumination is largest and shortest for that particular colour vision and illumination change. The level of colour shift from daylight D65 to forest shade lighting is shown in Figure 3-3 where the lines represent the amount of perceptual colour shift. The average colour shift from D65 to three other illuminants is shown graphically in the colour hexagon in Figure 3-4. The main feature that is of interest in the contours in Figure 3-4.a, b and c for the three different colour visual models is where colour shift is low (dark shades) and the area of the colour space where this contour lies predominantly. For the purpose of successful pollination under changes of the light environment, one might predict that most flower colour loci might be in areas of dark shade (i.e. least colour shift under changes of illumination).

3.3.1 Flower colour distribution under the assumption of an α-band or narrow photoreceptor set

The overall distributions of flower colour loci under assumption of photoreceptors without β-bands or a colour vision system with narrowed spectral sensitivities show relatively small differences compared to those in a real honeybee colour space (Figure 3-2). The most notable difference is that the loci of flower colours are considerably better spread across colour space under the assumption of narrow photoreceptor sensitivity colour vision system compared to α-band and the normal honeybee colour vision (Figure 3-5c compared to Figure 3-5a or b).

3.3.2 Flower colour under changes of illumination for normal honeybee spectral sensitivity function

Under the assumption of a normal honeybee spectral sensitivity function, the lowest colour shift considering shifts from D65 to any of the three lighting conditions (forest shade, small gap or woodland shade) are found around 110^{O}-150^{O} (corresponding to monochromatic lights of approximately 540-560nm), 220^{O} -230^{O} (approximately 600nm) and 260^{O}-280^{O} (approximately 370-390nm); (Figure 3-3). Regions where the level of perceptual colour shift is low when assuming normal honeybee colour vision correspond to those where colour difference sensitivity in the bee is considerably poorer (Figure 3.4a and Table 3.2); (Helverson, 1972, Chittka and Waser, 1997). Furthermore, the number of flower colours occurring in the bee colour space is larger in areas of lower perceptual colour shift. This phenomenon is most obvious at about 410nm (near 60^{O} on the bee colour hexagon) where the number of flower colour occurrences in the largest, colour difference

sensitivity is the highest, and colour perceptual shift is the largest (i.e. poorest colour constancy relative to all other flower reflectance spectra that were used in this analysis).

Hexagon angle	Honeybee Colour vision				α-band honeybee spectral sensitivity				Narrow honeybee spectral sensitivity			
	Freq	**FS**	**SG**	**WS**	**Freq**	**FS**	**SG**	**WS**	**Freq**	**FS**	**SG**	**WS**
10	38	0.0283	0.0117	0.0368	39	0.031	0.0111	0.0381	43	0.0085	0.0059	0.0046
20	30	0.0275	0.0138	0.0363	35	0.0317	0.0149	0.0403	55	0.0094	0.0051	0.0051
30	38	0.0295	0.0142	0.0391	37	0.0322	0.0139	0.0412	40	0.0081	0.0044	0.0045
40	53	0.035	0.0119	0.0413	54	0.038	0.0121	0.0443	46	0.0068	0.0037	0.0038
50	95	0.0407	0.0105	0.045	102	0.044	0.0105	0.0486	116	0.0075	0.0045	0.0043
60	119	0.0429	0.0113	0.0473	116	0.0438	0.0116	0.0492	131	0.0083	0.0042	0.005
70	49	0.0329	0.0089	0.0355	42	0.0361	0.0092	0.0399	42	0.0078	0.0047	0.0065
80	42	0.0229	0.0053	0.0199	45	0.0228	0.006	0.0206	40	0.0089	0.0037	0.0057
90	29	0.0198	0.0084	0.0151	24	0.0203	0.0082	0.0164	22	0.0094	0.0054	0.0054
100	33	0.0203	0.0077	0.013	35	0.0205	0.0075	0.0149	37	0.0075	0.0046	0.0055
110	51	0.0148	0.0083	0.0093	48	0.0157	0.008	0.0107	39	0.0069	0.0046	0.0046
120	73	0.0144	0.011	0.01	74	0.0148	0.0106	0.0098	56	0.0067	0.0045	0.0045
130	55	0.0138	0.0145	0.013	52	0.0148	0.0139	0.012	51	0.0069	0.0046	0.0044
140	50	0.0126	0.0152	0.0146	49	0.0132	0.0144	0.0121	55	0.0076	0.0047	0.0049
150	31	0.0088	0.014	0.0148	31	0.0093	0.0141	0.012	30	0.0075	0.0052	0.0053
160	18	0.0121	0.0157	0.0219	19	0.0101	0.015	0.0173	28	0.0057	0.0045	0.0042
170	29	0.0153	0.0155	0.0239	30	0.0123	0.016	0.0194	24	0.0072	0.0048	0.0049
180	28	0.0218	0.0143	0.0306	28	0.0124	0.0138	0.0204	38	0.0054	0.004	0.0045
190	27	0.028	0.0158	0.04	32	0.0121	0.0148	0.0235	48	0.0055	0.0033	0.0058
200	23	0.0207	0.0147	0.03	22	0.0118	0.0136	0.0206	33	0.0063	0.0034	0.0065
210	23	0.0153	0.0122	0.0193	27	0.0104	0.0108	0.014	18	0.0037	0.0029	0.0036
220	22	0.0087	0.0068	0.011	16	0.0065	0.0053	0.0075	15	0.0058	0.0031	0.0047
230	14	0.0097	0.0083	0.012	15	0.0133	0.0095	0.0153	14	0.0056	0.0034	0.005
240	20	0.0169	0.0108	0.0172	23	0.0125	0.0109	0.0146	30	0.0067	0.0042	0.0053
250	42	0.0142	0.0108	0.0142	41	0.0133	0.0119	0.0147	36	0.0077	0.0046	0.006
260	52	0.0093	0.0063	0.0089	54	0.0091	0.0068	0.0089	49	0.0058	0.0033	0.0049
270	54	0.0126	0.0055	0.0107	47	0.0115	0.0064	0.01	39	0.0068	0.0033	0.0054
280	47	0.0119	0.0049	0.0104	47	0.0118	0.0056	0.0095	36	0.0073	0.0032	0.0056
290	41	0.0163	0.0068	0.0157	41	0.0176	0.0069	0.0127	31	0.0068	0.0032	0.0051
300	60	0.0175	0.0091	0.0205	61	0.0195	0.0073	0.0151	55	0.0086	0.0041	0.0062
310	65	0.0205	0.0125	0.0263	64	0.0233	0.0108	0.023	32	0.0077	0.0029	0.0047
320	53	0.0212	0.012	0.0287	54	0.0239	0.0107	0.0269	51	0.0105	0.0031	0.0058
330	44	0.0239	0.0116	0.0308	45	0.0268	0.0103	0.0303	53	0.0081	0.0034	0.0052
340	51	0.0256	0.0161	0.0357	50	0.029	0.0154	0.0357	48	0.0096	0.0044	0.0055
350	37	0.0249	0.0142	0.0353	36	0.0276	0.0131	0.035	49	0.0072	0.0038	0.0042
360	36	0.0293	0.0134	0.0392	37	0.0324	0.0127	0.0399	41	0.0084	0.0039	0.0048
	Min:	0.0087	0.0049	0.0089	**Min:**	0.0065	0.0053	0.0075	**Min:**	0.0037	0.0029	0.0036
	Max:	0.0429	0.0161	0.0473	**Max:**	0.044	0.016	0.0492	**Max:**	0.0105	0.0059	0.0065
	Avg:	0.0206	0.0112	0.0243	**Avg:**	0.0204	0.0109	0.0229	**Avg:**	0.0073	0.0041	0.0051

Table 3-2. Colour shift levels measured in colour heaxon units (cu-where largest distance is 2cu, and colours that are typically 0.1cu apart begin to appear distinguishable to a bee (Chittka et al., 2001)) in the colour hexagon for Honeybee, α-band spectral sensitivity function and narrow spectral sensitivity function. Darkest shades for flower frequency occurrence at each 10^{O} sector of the colour hexagon (Freq) represents highest frequency of flower colour occurrences of 1572 flowers in the visual model under FS (Forest Shade), SG (Small Gap) and WS (Woodland Shade). Where flower colours are most common (i.e. around 50^{O}-60^{O} on the colour hexagon - Freq column cell shades darkest) a lower perceptual colour shift would be beneficial (FS, SG and WS column cell shades darkest). For normal Honeybee colour vision, the flower colours predominantly available around 50^{O}-60^{O} show the largest perceptual colour shift under changing illumination from D65 daylight, compared to other regions in the spectrum.

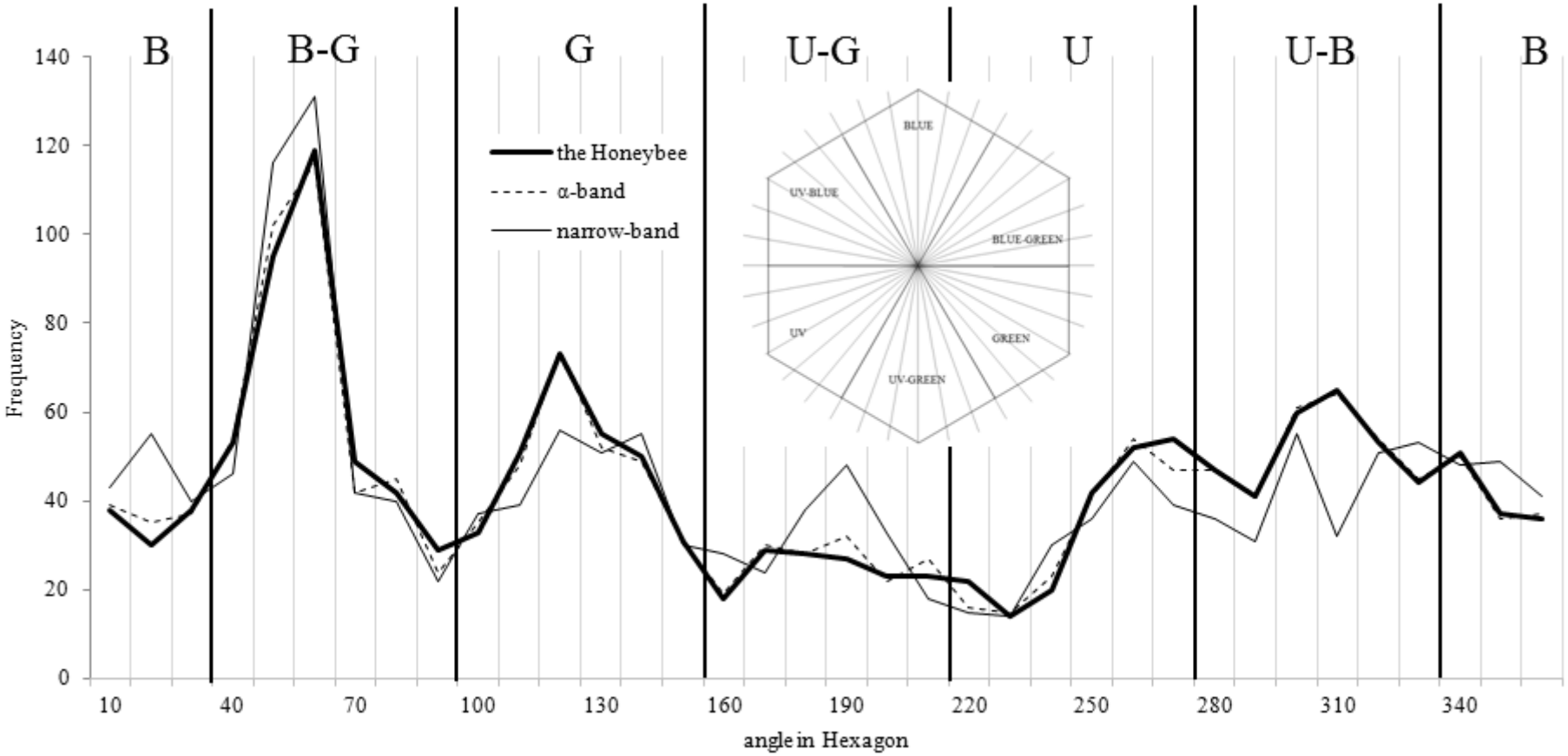


Figure 3-2. Frequency of 1572 flower colour loci within each 10^{O} 'hue sector' of the colour hexagon for a honeybee colour visual model, α-band and narrow honeybee spectral sensitivity functions. The direction 'straight up' in the colour hexagon corresponds to 0^{O}; all other 10^{O} steps are in a clockwise direction. Most flower colours are blue-green, but spectra used are of a variety of flower parts of the same flower, not just main flower colour available in FReD (see Chapter 2). The frequency of flower colour occurrence between α-band honeybee and the normal assumed honeybee colour vision are the same.

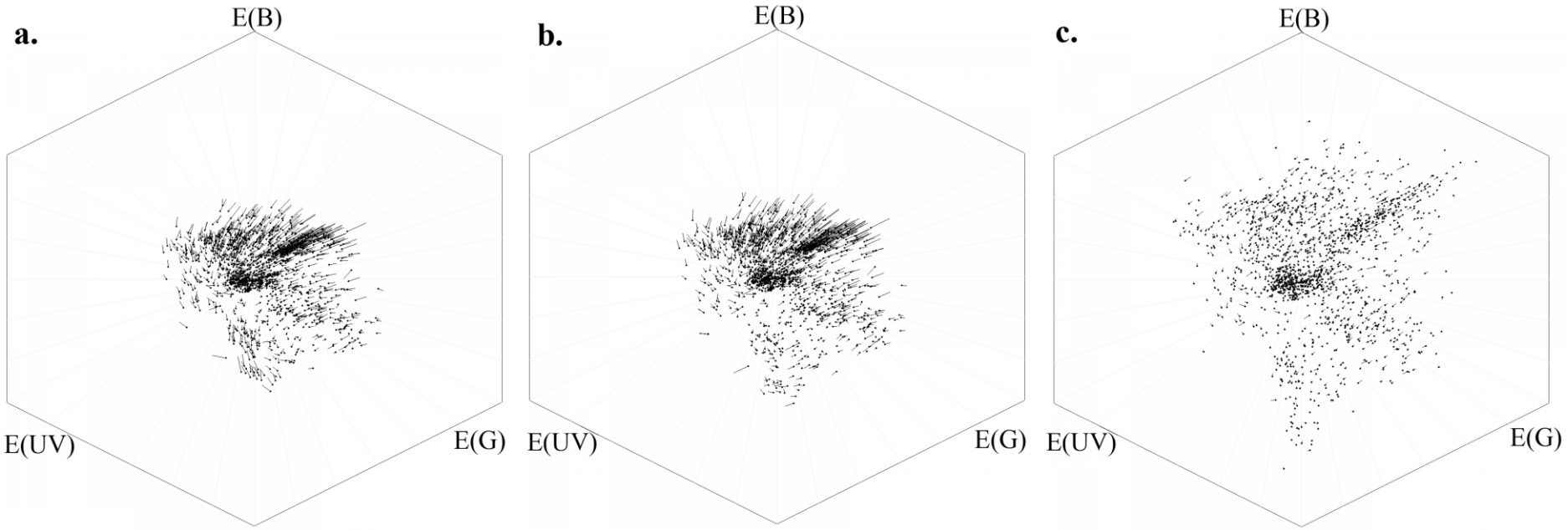


Figure 3-3. 1572 flower loci plot and colour shift in the Honeybee colour space under the assumption of a.) Honeybee spectral sensitivity function, b) α-band spectral sensitivity functions and c.) Narrow spectral sensitivity functions under a Daylight illumination (dot end) to Forest shade (tip end):

Line represent colour shift from daylight D65 (dot end) (Wyszecki and Stiles, 1982) to Forest shade lighting (tip end) (Endler, 1993) for each flower plotted. The line from the dot to tip represents the perceptual colour shift of flowers under D65 daylight to forest shade lighting. The longest lines representing perceptual colour can be observed at 60^{O} from 'straight up' of the diagram on honeybee and α-band spectral sensitivity functions, clockwise, which means that we could expect colour constancy to be poorer where perceptual colour shift is larger.

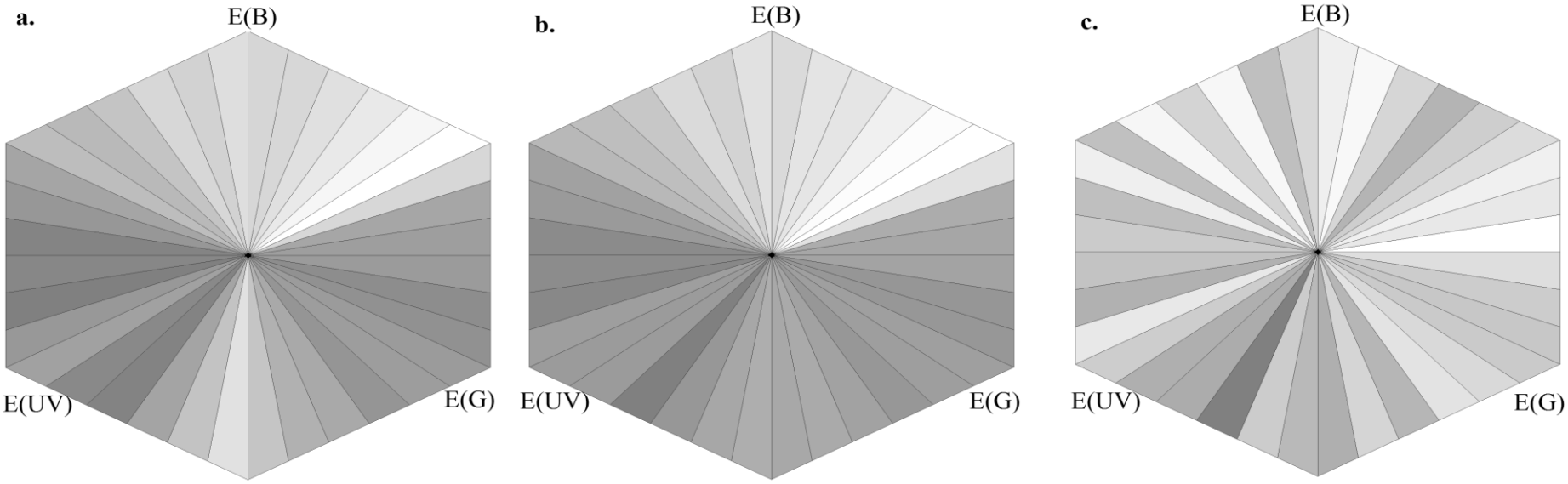


Figure 3-4. Average colour shift level contour across colour space assuming a.) normal honeybee spectral sensitivity function, b.) α-band honeybee spectral sensitivity function and c.) Narrow honeybee spectral sensitivity function. Colour shift levels of 1572 flower colours. Darkest areas on the colour hexagon represent lowest perceptual colour shift from an average of forest shade, woodland shade and small gap light from D65 daylight generated by a honeybee colour vision.

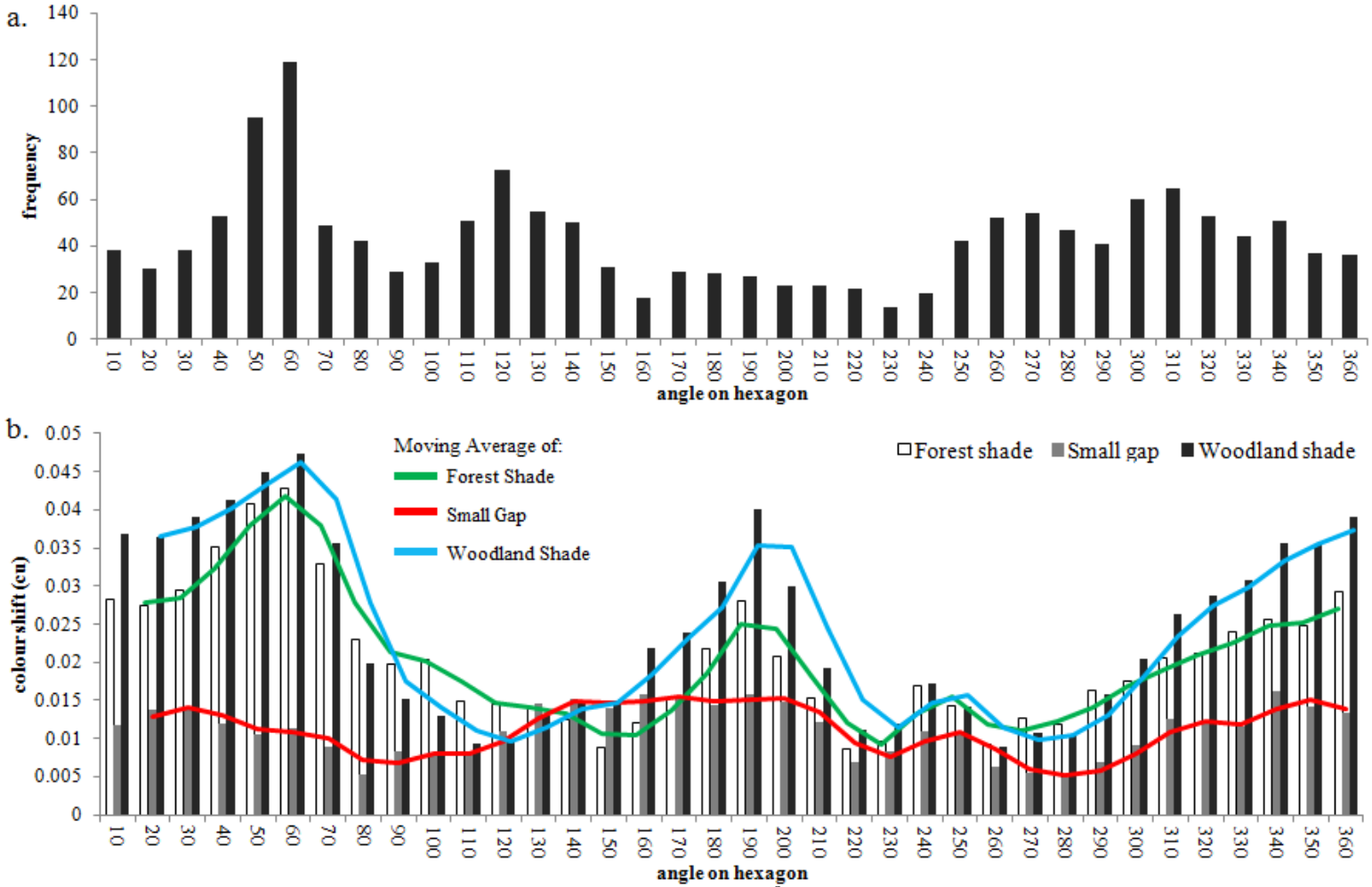


Figure 3-5 – Frequency and average colour shift of 1572 flowers occurring in the colour space at 10^{O} steps in the colour hexagon under the assumption of a honeybee colour vision

a) Frequency of 1572 flowers occurring on the colour space by the angle of the hexagon at 10^{O} steps. b) Level of colour shift in colour hexagon colour units (cu) when illuminants changes from D65 daylight condition to forest shade, small canopy gap light or woodland shade. Lines represent the moving average of colour shift across the entire spectrum of the honeybee colour vision to show areas in the spectrum where perceptual colour shift under changing illumination is large (i.e. 50^{O}-60^{O}, 190^{O} and 340^{O}-360^{O}) or short (i.e. 110^{O}-120^{O}).

3.3.3 Flower colour under changes of illumination for α-band and narrow spectral sensitivity function

The colour shift that occurs with spectral receptor sensitivity functions consisting only of α-bands is very similar to normal honeybee colour vision. On average it produces slightly less perceptual colour shift than under the assumption of real honeybee colour receptors (see Table 3-2 for averages). Narrow spectral sensitivity functions produce the shortest perceptual colour shift under changes of illumination when compared to any of the colour vision models tested. The flower colour loci, assuming narrow spectral sensitivity function, are distributed such that spectral purity of most flowers is high. This is interesting because, if flowers were distributed further apart from each other on the colour space, we could assume that colour discrimination would perform better (Chittka et al., 2001). However, as mentioned before, we have found colour constancy to be good in the honeybee in spectral regions where sensitivity to spectral differences is poor. What can be seen under the assumption of a colour vision system consisting of narrow spectral sensitivity function is that flower colour loci are, on average, further apart from each other.

Although most flowers are bee blue-green, perceptual colour shift is largest in this region of the colour spectrum. None of the models appear to achieve perfect colour constancy. However, a theoretical colour vision system consisting of narrow spectral sensitivity function that have no spectral overlap would indeed produce near-perfect colour constancy; these findings are consistent with the results by Dyer (1999) . However, Dyer' results did not include that the overall distances between natural flower colours increased under narrower spectral sensitivity function. The results in this chapter show that although narrow spectral sensitivity functions reduce the level of perceptual colour shift under changing illumination and thus improve colour constancy, it would also make colour discrimination poorer due to there being a lack of overlapping photoreceptor spectral sensitivity functions. The results show that where colour constancy is good in the honeybee spectrum, these are also likely to be regions of poorer colour discrimination ability and the global distribution of flowers on the bee colour space does not correspond to the discrimination ability of the bee under the assumption of illumination changes from D65 normal daylight to forest shade, small gap or woodland shade.

3.4 Discussion

Flower colours that are different perceptually from each other might benefit from more exclusive visits from a pollinator such as a bee (Chittka et al., 2001). Thus, if flowers could vary their colouration freely without constraints of history or available pigments, we would

expect flower colours within the same habitat to be distributed evenly to achieve maximum perceptual colour distance in the bee colour space between all possible flowers. While such an even distribution is not observed in any habitat so far tested (Chittka et al., 1994), it has been observed that the occurrence of flower colours is linked to the spectral difference sensitivity of bee pollinators. Where sensitivity to spectral differences is good, we find a large proportion of flower species presenting steep changes in reflectance function, maximising discriminability (Chittka and Menzel, 1992).

The results in this chapter show quantitatively the perceptual colour shift under variations of illumination under a von Kries receptor adaptation type response mechanism for colour constancy. Difference sensitivity across the colour visual spectrum is best where photoreceptor responses overlap with steep gradients in opposite directions over the wavelength scale (Helversen, 1972). However this overlap of receptors produces poorer colour constancy as has been demonstrated in the perceptual colour shift from daylight to forest shade, small gap and woodland shade. This appears to be critical because the flower colours under the assumption of a colour vision system with narrow spectral sensitivity functions show flowers distributed such that they produce large colour distances from each other to compensate for poor colour discrimination ability under the assumptions produced by a model based on narrow spectral receptor types. Bees as well as other animals have to cope with the challenge to discriminate colours well but also to achieve good colour constancy. Some animals deal with this challenge by introducing more photoreceptors into the colour vision system, and combine colour receptors with oil droplet filters (Vorobyev et al., 1998) that produce narrow spectral sensitivities (Cronin and Marshall, 1989, Osorio et al., 1997).

However, to find out if bee colour vision might indeed be improved with narrow spectral sensitivities, performance of a modelled bee given this model will need to be tested. A simple model to simulate flower colour choice under an agent-based modelling environment is developed in chapter 4 to test the honeybee colour vision and narrow honeybee spectral sensitivity. This will reveal if better colour constancy (such as a narrow photoreceptor function) is more effective than being able to discriminate colours when bees are faced with changes of light condition.

In the past, the general population of flower colours has been modelled to reveal the relationship of flower colour and bee colour vision (Chittka, 1996, Chittka and Menzel, 1992). It had been demonstrated that the spectral reflectance properties of flowers match the ability of the colour discrimination ability of the bee. For example, the most frequent flower colour is bee blue-green; this coincides with the bee spectral difference sensitivity peak at

500nm (blue-green) (Helverson, 1972) and equally peaks of the spectral discrimination function coincide with the typical spectral reflection functions peaks (Chittka and Menzel, 1992). Although natural flower colour is well suited for the bee difference sensitivity ability, how well would it be suited for recovering colour under changes of illumination? Results in this chapter show that flower colour occurrences are higher in regions of larger perceptual colour shift, or in other words, perceptual colour shift is larger where colour discrimination ability is good. So these flower colours are not suited for recovering colour under changes of illumination. Modelling of various visual systems demonstrated that colour receptors with spectral sensitivity functions that are narrow and minimise spectral overlap achieve better colour constancy (Worthey and Brill, 1986, Dyer, 1999) as well as increased spectral purity. It has been shown that in certain areas of the bee colour space, less perceptual colour shift occurs under variations of illumination, and thus better colour constancy (Dyer, 1998, Dyer and Chittka, 2004b).

Using a normal honeybee colour vision, perceptual colour shift is shortest on the spectrum regions where colour difference sensitivity is highest. This is contrary to the findings of Dyer (1998) that colour shift is lowest around the blue-green region of the bee colour space, which is also the region of highest colour difference sensitivity in the honeybee. It appears that perceptual colour shift is shorter around regions of poor colour discrimination in the honeybee (Helverson, 1972) under larger changes in light conditions from the canonical light (i.e. the light in which the colours of the flowers were first found and learnt. In these models, the canonical light is D65 daylight), and this may possibly also explain why naïve bees avoid unfamiliar lighting (Arnold and Chittka, 2012). This is further supported by the solutions found in some other animal visual systems. For example, numerous overlapping narrow photoreceptors overcome poor colour discrimination and achieve good colour constancy in stomatopod crustaceans (Osorio et al., 1997, Cronin and Marshall, 1989, Vorobyev et al., 1998, Dyer, 1999).

This chapter reveals the relationship between perceptual colour shift levels and colour difference sensitivity, and that colour discrimination is poorer when colour constancy is improved, and vice versa. It appears that colour discrimination has been favoured above the ability to remain colour constant in the bee colour vision. In the next chapter I will use agent-based modelling to simulate bee foraging under varying illuminations. I will be exploring the performance of colour visual models of narrow spectral sensitivity functions and normal honeybee spectral sensitivity functions to find if colour discrimination ability aids colour constancy in a natural foraging scenario.

4 Development of an Agent-Based Model with bees foraging from flowers under varied illumination

Colour memory is crucial in a successive viewing environment where colour and light change the scene statistics and memory is required to retrieve a learnt colour of an object (Dyer and Neumeyer, 2005, Kulikowski and Walsh, 1991). For this reason, colour choice is not easily understood simply by modelling colour perception in colour space diagrams. Colour space diagrams do not necessarily capture changes occurring in colour perception through individual learning and experience, both of which adapt temporally. Moreover, different experimental conditioning methods influence colour choice and the ability to discriminate colours (Dittrich, 1995, Dyer and Neumeyer, 2005, Dyer, 2006, Dyer and Chittka, 2004a, Giurfa, 2004). If we seek to measure performance of colour vision, this can be done through modelling techniques that capture the environment, the colour choice behaviour, learning, cognition and the physiology of colour perception of the animal in question (Abrams et al., 2007).

A model that captures aspects of learning, environment and memory in determining colour choice is developed here to measure performance of the honeybee colour vision. This model is a so-called Agent-Based Model (ABM) that uses pre-generated environments, in our case artificial 'flower meadows', to represent the environment, and an agent that adopts colour choice behaviour similar to that of the honeybee. In this chapter, I provide detail of this Agent-Based Model, the meadows and the behaviours adopted by the agent. I then test this model by developing two types of meadow constructs, one with co-occurring flowers in nature (the *natural meadow*) (Chittka et al., 1997) and another meadow with flower species with colours that have a high level of perceptual colour distance between them (the *ideal meadow*). *Natural meadow* and *ideal meadow* are tested with a bee agent that adopts flower constancy foraging rules based on perceptual colour distances (Chittka et al., 2001). This modelled bee is tested with honeybee and narrow honeybee spectral sensitivity functions that were introduced in Chapter 3. Since perceptual colour shift is shorter under the narrow photoreceptor sensitivity than under the normal honeybee spectral sensitivity, I wish to investigate the performance of this colour receptor model in the agent-based model to determine why it may not be favoured over normal bee spectral sensitivity functions. The

investigation attempts to identify the contribution of foraging fitness of a model with better colour constancy (such as a hypothetical colour vision system with narrow spectral sensitivities) and the biological significance of such colour constancy.

4.1 Introduction to Agent Based Modelling (ABM)

Agent Based Models have the capacity to model individual behaviour of an entity in an environment in which the agents are set to accomplish a task. Such models have previously been used to understand aspects of bee foraging that are not otherwise accessible by experimentation (Dornhaus et al., 2006, Lemmens et al., 2008). The concept behind multi-agent systems is to model a specific behaviour that can be analysed jointly within the environment that the agent operates in. The results of these simulations provide insight into which patterns result in certain behaviour, especially those that can change over a temporal scale. Agent-based modelling simulates behavioural patterns in the agent by modular states adopted by the agent. For example, foraging, moving, and searching and so on are examples of states that a bee can adopt. Each state is programmed to capture behaviour relevant to accomplish the high-level task (e.g. collecting nectar) that is being set to be achieved in the model. A proliferating number of simulations from all areas of biology, from insect behaviour, predator-prey interactions to viruses, and tumours are modelled now using such simulations because they accurately depict such biological processes (Holcombe et al., 2012), and allow crisp predictions of the effects of conditions that are difficult to determine empirically.

One of the key methods of programming real-world scenarios or phenomena in agent-based modelling, is *abstraction* (Lustick and Miodownik, 2009). Natural scenes in which real-world colour tasks are much more complex than artificially constructed scenes like the Mondrian for example (Zeki, 1993). Natural scenes consist of shadows from three-dimensional objects, a variation of light across the scene, a variety of shapes of objects and different colours of surrounding objects (Brainard, 1998, Yang and Maloney, 2001). The more detail there is, the more complex it becomes to define the rules of what can be expected from colour choice in an individual. In lab-based simulated experiments, the form of 'abstraction' to understand colour constancy is in the form of colour matching simultaneously (see discussions by Foster (2003)). In the form of computerised simulations of natural world phenomena, abstraction focuses on the basic concepts of the agents' behaviour and the basic environment to develop the simulation and for the agent to accomplish the high-level task (i.e. collecting nectar).

To model the foraging environment and bee agents, I used NetLogo (Wilensky, 1999) which is a simple programmable Agent-Based Modelling system for simulating natural and social phenomena, especially for modelling the interaction developing over time between the bee agent and its memory dynamics occurring with the changes in the environment – such as changes in the illuminant. NetLogo uses the Logo language, a simple yet fully programmable language dialect. The full program used in NetLogo and the extension developed for the modelled bees visual systems, learning rules and foraging behaviour is shown in Appendix II.

4.2 Agent Based Modelling for simulating colour vision

In this section, I will discuss the bee simulation that compromises the behaviour of the bee agent and its interaction with the colour environment. I provide details of the simulation that are relevant to colour choice in the honeybee and how this fits in to the real world for the purpose of measuring the performance of colour vision.

4.2.1 Colour choice in honey bee agents

A honeybee agent in the Agent Based Model will be in any of six states, *search*, *move*, *forage*, *choice*, *lookup* or *store*. Figure 4-1 illustrates the rules of colour choice in the model by showing the states that the modelled bee can assume. At the beginning, the bee agent starts in the *search* state where the bee agent is actively searching for a flower in a given radius and changes to the *move* state if a suitable flower is not found in the radius the bee agent is currently in. Movement in this model by the bee agent on the two-dimensional cell grid is random. The bee agent will continue to move to and fro from the *search*, *move* and *search* state over and over, initiated by not having found a suitable flower, until the bee agent finds a flower in a given radius from the location of the bee agent. If there is a flower within this radius whilst the bee is in the *search* state, the bee moves into the state of *forage*. The visual scene that includes all the flower colours and background are processed in the *choice* state. Some of these states are programmed as individual procedures in NetLogo; see Appendix II.

In this process, *choice* state may apply a colour constancy function to the scene and move to *lookup* for the known highest rewarding flower colours within this transformed scene where a colour discrimination function will determine if a colour is known or unknown in internal memory (the colour memory). Returning back to *choice* state, the reward and colour (loci) recalled from memory are replaced or added (if it doesn't already exist in the memory) in the *store* state and the model returns the most suitable flower species back to the *choice* state which returns the chosen flower species (i.e. the flower ID of the flower species available in

the FReD database – see chapter 2) to *forage* state so that the bee agent can forage on the content of the flower. From here, the bee agent will return back to *search* state.

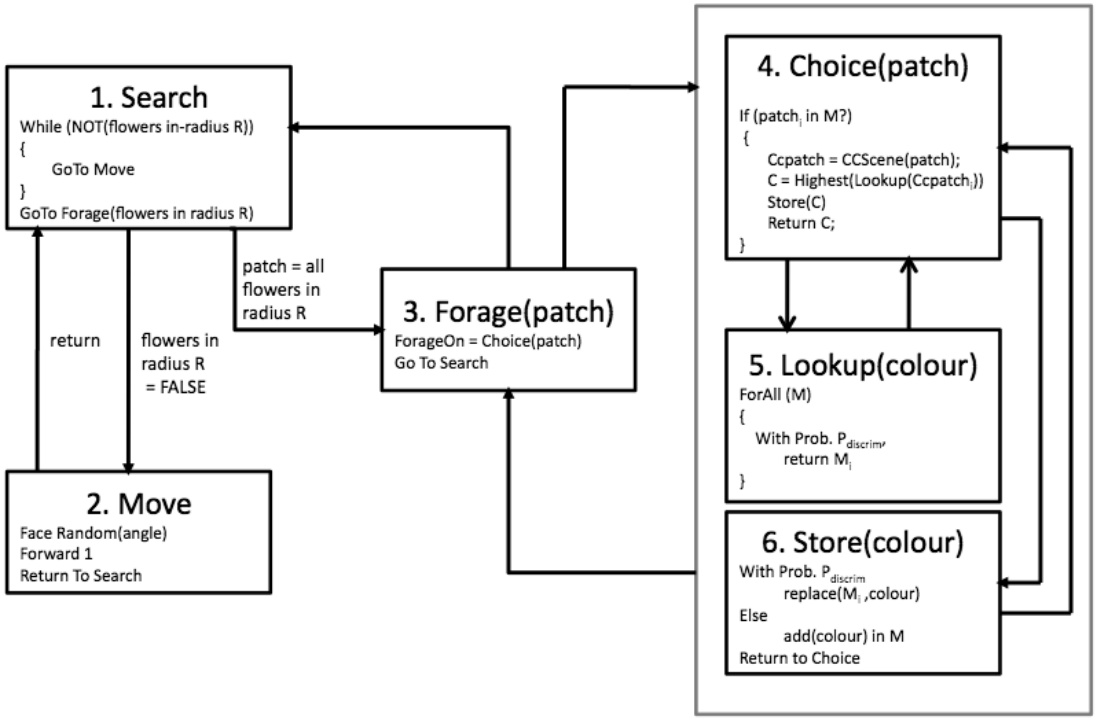


Figure 4-1. Bee colour choice behaviour in an agent-based modelling environment based on flower constancy foraging strategy. The bee agent begins with searching for flowers in a "patch" that is in the vicinity of the bee (flowers in-radius R). Bee agent will switch from move and search state until flowers are found which will result in the bee movements on the grid. The bee makes a decision on if it should or should not forage on the flower based on the other flowers that are available in the 'patch' of flowers. These flowers in the patch are then compared with M based on the most rewarding flower colour, which is a 'memory' with a probability of successful colour discrimination of $P_{discrim}$ otherwise the bee switches to another flower colour.

With this ongoing process of the honeybee moving between different states, a dynamic memory is formed of the flowers visited. Initially, the bee agent will begin by foraging using an innate preference to help build preferences based on learnt floral colour. This 'innate preference' is initially programmed at the beginning to be based on a highest rewarding coloured flower in the simulated meadow - this preference exists because it helps in initial recognition of flower colour (Giurfa et al., 1995) as the bee-agent has no prior experience of flower colour and so the bee agent leaves the hive to search for this colour first. This can be overridden if the flower colour resembles another flower species (over-written using the `replace(`M_i`, colour)` module as illustrated in Figure 4-1). The ability to recall is based on colour discrimination probability $P_{discrim}$ which is used to predict how well foraging bees in nature are able to distinguish between colours of flowers, based on empirical data on flower

constancy in six different species of bee (Chittka et al., 2001). It is well-known that honeybees often remain faithful to a certain type of flower even when there may potentially be more flowers that offer a better reward (Waser, 1986). In the study by Chittka et al., (2001), bee-subjective colour differences occurred frequently with high flower constancy, suggesting colour discrimination between colour pairs to be at colour distances above about 0.1 colour hexagon units and improving as colour distance increases. A curve has been fit to this data set of colour pairs that was used to determine a probability of colour discrimination (i.e. $P_{discrim}$ is determined by the cumulative distribution in Figure 4-2).

Maximising and matching behaviour is used to model foraging behaviour in the honeybee. If a flower colour exceeds 1.0µl of nectar volume then the honeybee agent will visit only this flower species, known as maximising. If a flower colour produces between 0.4 to 1.0µl of nectar, the bee will match its visitation frequencies of more than one species in proportion to the nectar levels in the various species, a strategy known as matching (Greggers and Menzel, 1993). All the while, the bee might fail to distinguish two different flower species whose colours are very similar, or if a change in lighting condition changes colour perception. This is the challenge that the bee faces, and the aim is to measure how well the bee overcomes this challenge by changing the colour constancy function and measuring its performance based on overall nectar collection.

The agent based model accurately captures the interplay of the colour visual system of the foraging bee to make choice between the flower colours in the environment using simple rules of matching and maximising (Greggers and Menzel, 1993). These rules are implemented into the simulation for the bee agent to determine when it should forage on a flower, and are carried out in the *choice* state:

- If overall collection average 0.4 to 1µl, the bee matches its choices against other rewarding flower colours in this range (matching)
- If a particular coloured flower exceeds 1µl in one visit, the bee exclusively visits this flower species if available (maximising) (Greggers and Menzel, 1993, Menzel and Muller, 1996).

The overall nectar collection average is a running average of nectar collected from 3 flowers visited before.

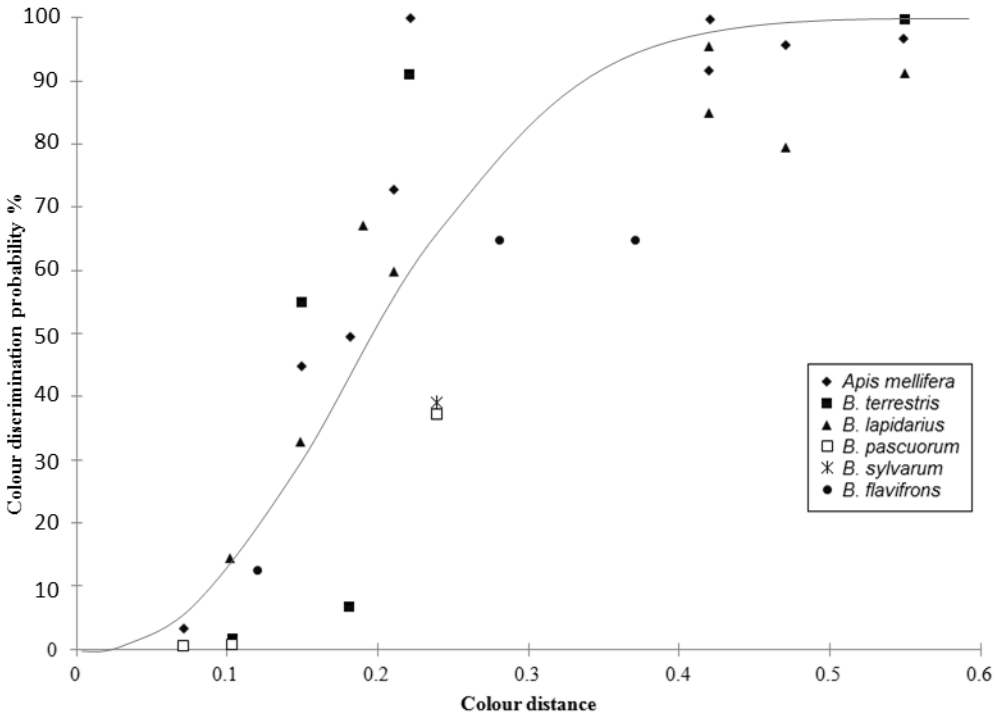


Figure 4-2. Colour discrimination probability in several bee species as a function of colour distance between 15 pairs of natural flower colours, and at least 80 choices were recorded. The curve indicates the flower constancy of bees as a function of how dissimilar the pairs of colours are (Chittka et al., 2001). The curve is a cumulative Weibull distribution (λ=2.2, k=0.23) generated in Mathematica© (a statistical modelling tool) in order to generate random numbers (i.e. colour discrimination level) given this distribution. The probability determines if the bee will switch to another flower colour or continue to remain faithful to it based on the colour distance (i.e. colour units on the colour hexagon) between the two flowers.

4.2.2 Interaction and movement in the meadow environment

Certain foraging strategies have been assumed for various animals, based on the availability and quality of resources in the environment, especially in the honeybee (Pyke, 1984). The basic of all foraging strategies would have the searcher behaving as follows (Viswanathan et al., 2008), and are carried out in the *search* and *move* state in the agent-based model:

- Step 1: If target is in location within *r* (*r*=radius of visual field, see Figure 4-3), move straight to target
- Step 2: If no target in location *r*, choose a direction at random and move in distance *d*, then look for any target in this new location. If none is found, choose another random direction and move distance *d* repeat this step until target found then move to step 1(Viswanathan et al., 2008).

This limited foraging rule is used in the Agent Based Model, and is essentially a 'random walk' spatial movement strategy. The bee agent moves randomly as described in the above steps. This avoids favouring certain flowers that are not influenced by colour preference but by foraging movements instead (Heinrich, 1983, Zimmerman, 1981, Pyke, 1981). Other strategies are also known, such as the near-far search method (Motro and Shmida, 1995) where searching consists of large angular turns and short travel distances in a rewarding flowering patch. The bee agent would move onwards faster, making smaller angular turns when the running average of nectar collection fell under a threshold. This strategy performs well in a spatial distribution of rewards that are clustered, but performs poorly in random resource distribution (Scharf et al., 2009).

In all simulations, flowers were randomly distributed within the meadow at various densities; bee agents encountered these flowers in their random movements in a two-dimensional space. As explained, foraging strategies and type of spatial distributions such as clustering/clumping resources induce bias.

4.2.3 The meadow

The meadow is the environment in which the bee agent moves within. It is a two-dimensional space made up of reflectance spectra belonging to flower species or the background. By default, the background is average of green foliage reflectance spectra (Chittka et al., 1994). The flowers have reflectance spectra that are downloaded from the Floral Reflectance Database (Arnold et al., 2010) in real-time as the modelled bee forages. When a bee makes a choice of visiting a particular flower, flowers that are within the visual field are part of a "scene", alongside the immediate background. In other words, this visual scene encompasses all flower colours and green foliage within a given radius at the location (Figure 4-3) at which the bee decides to make a flower choice. This scene may then undergo the transformation from the original scene to the scene processed through a colour constancy function.

The meadow is constructed before a simulation, and the location of the flowers is random.

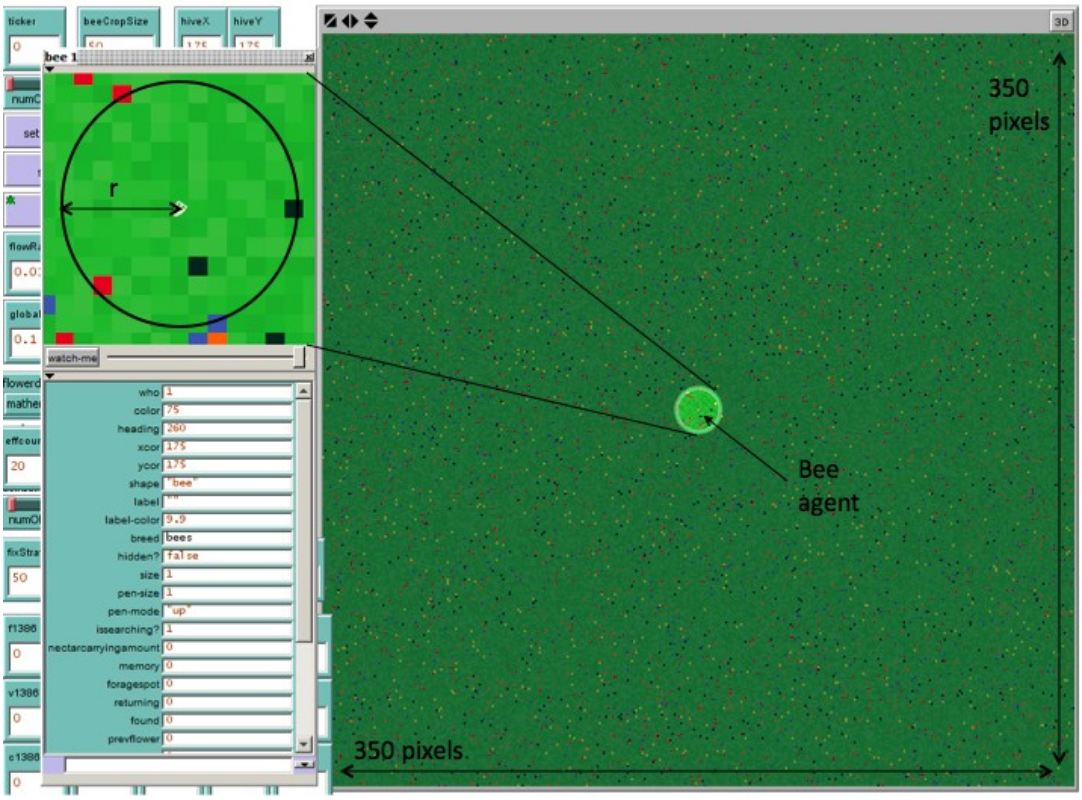


Figure 4-3. Screen shot of the agent-based modelling environment in NetLogo. The coloured dots are flowers (5 floral species) randomly distributed. The circle depicting the visual field of the bee agent has of a radius of 7 cells, where an individual cell can hold one flower; all flowers and background in this visual field are considered as the "scene". On the left side, the state that the bee agent is in is recorded throughout the simulation, for example *isSearching?* Property on the left window is the search state described in Figure 4.1.

In all of the simulation runs, the grid is made up of 350 x 350 cells or "pixels" (Figure 4-3), and each cell is assumed to have either the reflectance spectrum of the background or the reflectance spectrum of a floral species. In all meadow constructions used for the simulation of the foraging bee, all flower species were distributed randomly. This construct is shown in Figure 4-3 on NetLogo with the bee agent and hive located in the middle at the start of each simulation run.

In our experimentation, normfunction D65 is used as the training light. Performance of colour visual variants that were created are then put in testing light of either forest shading, woodland shading or small canopy gap shade (Endler, 1993). The spectral functions of these lighting conditions are shown in Figure 2-5.

4.3 Testing the model: quantitative effects of variations of natural light on bee foraging performance

In the previous chapter, it was discovered that less perceptual colour shift occurred under the assumption of a hypothetical visual model with narrow photoreceptor spectral sensitivity functions, compared to a colour vision with unmanipulated honeybee spectral receptors (Dyer, 1999). In addition, I demonstrated through the modelling of the perceptual colour shift of flower colours viewed under three types of natural light that perceptual colour shift was lower in areas of the bee visual spectrum where colour difference sensitivity was poorer. With an improved colour constancy achieved by the narrowing of the photoreceptor, it is also assumed that colour discrimination of monochromatic light is poorer. However, the model based on narrow spectral sensitivity function produced a better spread of colours on the bee colour space. It is uncertain if low perceptual colour shift achieves colour constancy in a successive task as that which bees face in nature, and what the affect of diverging flower colour has on achieving colour constancy. In this part of the chapter, I use the agent-based model to measure the performance of von Kries receptor adaptation to achieve colour constancy, and I also test the influence of narrower spectral sensitivity functions on colour constancy in two set ups. These simulations are design to test whether the model is sensitive to critical parameters such as the colour vision mechanisms as well as the set of natural flower colours between which the bees must decide.

In the first set up, the bee agent forages on flowers of five plant species known to co-occur in nature (named the '*natural meadow*') from a field study by (Chittka et al., 1997). Here I assume illumination by daylight normfunction D65 for a set period of flower visits, but lighting condition can subsequently change to either forest shade, small gap light or woodland shade in separate simulation runs. In the second set up, the bee agent forages on the same nectar-secreting flowers, except they now exhibit larger perceptual colour distances between each other (named '*ideal meadow*'). The aim is to determine the role that colour discrimination may play in achieving colour constancy (i.e. under a change of illumination).

Performance of narrow spectral sensitivity function and honeybee colour vision by the agent-based model bee are measured against a hypothetical 'colour blind' (no discrimination between any of the flowers) and 'perfect colour constancy' (perfect colour discrimination independent of illumination changes) model.

It is assumed that, in the *ideal meadow*, foragers equipped with all modelled colour vision systems will achieve better nectar collection rates than under the *natural meadow* because

colours are learnt as being different from others and all colours are well discriminable in the former. Narrow spectral sensitivity functions are predicted to perform better than normal honeybee colour vision and may achieve near-perfect colour constancy because a set of narrow spectral sensitivity functions is known to achieve better colour constancy (i.e. less perceptual colour shift under change of lighting) (Dyer, 1999). All these tests are essentially used here to verify that the model is sensitive to critical parameters pertaining to colour constancy, so that the model can subsequently be used to perform tests on the adaptive benefits of various colour constancy algorithms.

The agent-based model will be used to record nectar collection by the bee agent as a measure of performance. In order to achieve this, a relatively small and realistic representation of a plant community is used to model the *meadow*. In one meadow the 5 floral species studied in (Chittka et al., 1997) were *Lotus corniculatus*, *Lathyrus pratensis*, *Vicia cracca*, *Cirsium oleraceum* and *Lythrum salicaria,* which I refer to as the *natural meadow*. Additionally I created another meadow set up of five flowers that observed high colour distances between each other with the same nectar secretion volume as the five flowers in *natural meadow*, they were *Layia platyglossa*, *Ranunculus sceleratus*, *Hepatica nobilis*, *Chelidonium majus* and *Lathyrus cicera* which I refer to as '*ideal meadow*'. The five flowers in both of the meadows are assumed to produce the same nectar overall quantities to ensure any observed differences in nectar collection are based entirely on flower colour (see Appendix III to see the nectar standing crop values that are assigned to the flowers in the *natural meadow* and *ideal meadow*). The honeybee and narrow spectral sensitivity function are tested under the *natural meadow* and *ideal meadow*. The reflectance spectra and colour loci for both of the meadows consisting each of five flowering species are shown in Figure 4-4 and Figure 4-5.

4.3.1.1 Initial set up of the meadow and flower colour

At the start of the simulation, 5000 flowers are placed randomly on a 350 x 350 map of cells. Each cell can hold one flower. In all simulations, each of the floral species from the meadow studied in Chittka et al., (1997) occurred randomly in the map 1000 times. The hive and the single bee are placed in the centre of this map. During the simulation the bee will visit 250 flowers, collecting nectar from the 5 floral species (that generate specific nectar flow rates) before the simulation terminates – nectar standing crop was based on a population of real nectar standing crop secretion that was assigned to each of the 5 floral species that was the same for both *natural meadow* and the *ideal meadow*. Flowers in the meadow are illuminated by lighting conditions daylight D65, forest shade light, small gap or woodland shade lighting (Figure 2-5).

4.3.1.2 Set up for measuring the performance of various colour visual models

Each simulation run contains two phases where the bee visits a total of 250 flowers, a training phase consisting of 50 flower visits and a testing phase consisting of 200 flower visits. In the training phase the bee agent "learns" the flower colours under daylight (D65) (Wyszecki and Stiles, 1982) and retains the colour of the flowers visited in memory (corresponding to a colour locus in colour space). In the testing phase, the environment light changes to any of the three natural illuminants, forest shade, light through small canopy gaps and woodland shade (Endler, 1993) named as the "testing illuminants". Figure 2-5 shows relative spectral power of the training and testing illuminants. Under the testing illuminant the bee agent can only recall the flower colours learnt under the training illuminant (i.e. Daylight D65), and does not store flower colours under testing illuminant in memory. This will ensure that errors in recognising flower colour under changes of illumination are recorded, and that the bee agent does not learn the flower colour during the testing phase.

Results such as the amount of overall nectar collected, number of visits to each floral species are collected at the end of each simulation run. Twenty simulation runs are performed for each colour vision model tested.

4.3.1.3 Colour blind bee and perfect colour vision

To test the computational models against a lower and upper limit of the agent-based model bee, two extreme models of vision were used to evaluate the performance of the colour constancy methods with reference to these extremes– a *colour blind bee* and a *perfect colour vision bee*. A *colour blind bee* forages from all five flower species indiscriminately, as if they were members of the same species – there is no ability to distinguish the differences between the flower species. A *perfect colour vision bee* makes no mistake under a change in illumination or differences in reflectance spectra of objects. It experiences no perceptual colour shift and achieves perfect colour discrimination.

The foraging of a colour-blind bee was modelled by setting flower spectra (i.e. colour of the flowers) the same for all five flowers in the meadow whilst the nectar content reward for all five flower species was the same as that which was assigned to the *natural meadow* and *ideal meadow*. The nectar content assigned to the five flowers in *natural meadow* and *ideal meadow* is also same as to the flowers in the colour-blind model as it is shown in Appendix III. This mimics the flower choice of the model bee where colour is not used as a cue to make an association to a rewarding flower. Conversely, a perfect colour visual model would always discriminate colours, regardless of any level of shift in colour under changing illuminant or between co-occurring flower colours.

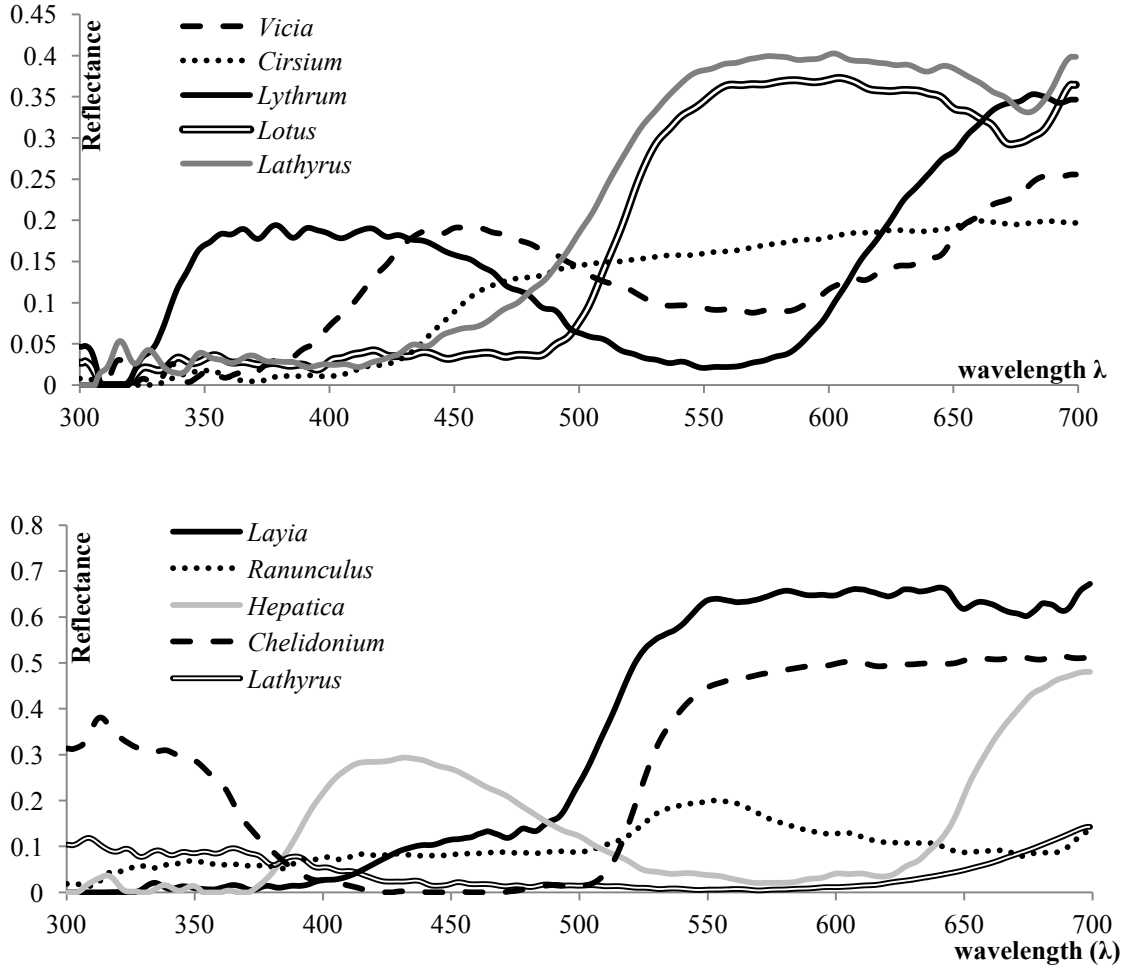


Figure 4-4. reflectance spectra of the five floral species present in *natural meadow* (top) and *ideal meadow* (bottom) (downloaded from Arnold et al., 2010)

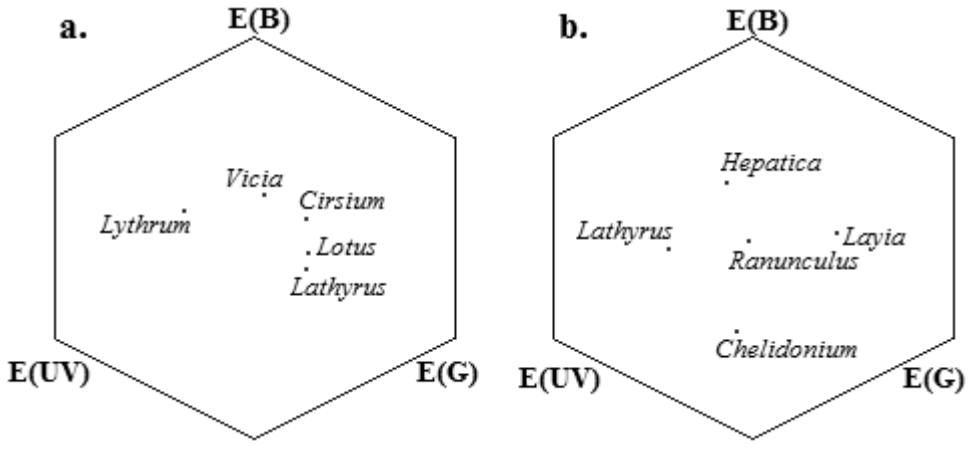


Figure 4-5. Colour loci of the five floral species present in the natural (a) (Chittka et al., 1997) and *ideal meadow* (b). *Ideal meadow* (right),shown in the colour hexagon (Chittka, 1992). Notice the more extensive spacing between the flower colours in the *ideal meadow* compared to the *natural meadow*. The bee agent is likely to collect more nectar under the *ideal meadow* since the colours are more distinct.

4.3.2 Results

4.3.2.1 Performance of agent bee in natural meadow under honeybee colour vision: flower visits and nectar collection

Our modelled bees foraging rules clearly reproduce the adaptive foraging behaviour of real bees. Visits to the highly rewarding flower species are more advantageous than others. For example, to forage on flowers that produce high nectar reward such as the *Cirsium* and *Lathyrus* means that the bee overall collects more nectar than if it were to randomly select flowers in the meadow; an improved visitation to the most rewarding flower species *Cirsium* by approximately 6% (19.43% visits to *Cirsium* under the assumption of a colour blind bee, and 27.09% visits to *Cirsium* under the assumption of a normal honeybee colour vision) significantly improves performance of nectar collection by the bee agent (nectar collected by the colour-blind compared to normal honeybee spectral sensitivity under forest shade; t-test: $t = -6.25$, $df = 38$, $p<0.001$). Figure 4-6 shows the average amount of nectar that is collected by the bee agent from each flower under the assumption honeybee colour vision. After running the simulation under D65 daylight, we find that the most rewarding flower species in the meadow are *Cirsium*, followed by *Lathyrus*, *Lotus*, *Vicia* and finally *Lythrum* being the least rewarding flower since the nectar standing crop varies the most in the *Lythrum* compared to the other available flower species.

The number of visits corresponds to the nectar contents in the flower. The flower species *Lythrum* produces the least nectar or nectar that is unpredictably lower or higher, and is hence visited the least. The amount of nectar collected overall from the *Cirsium* is the highest, and so is the number of visits – yet due to the varying nectar standing crop in *Cirsium* also, visits are not exceptionally higher than *Lathyrus* (see standing crop median labels in Figure 4.6). This would be expected in a real-world scenario of a foraging bee if flower colour is distinguishable with varying nectar rewards between flower species; the bee would favour a particular flower colour over others to collect more nectar (Daumer, 1958, Daumer, 1956). Flowers of the same species producing a stable nectar source in the simulation such as *Lathyrus* are visited more often, and this is evident of flower constancy even though more rewarding flower species may be available in the meadow (Waser, 1986, Chittka et al., 1999).

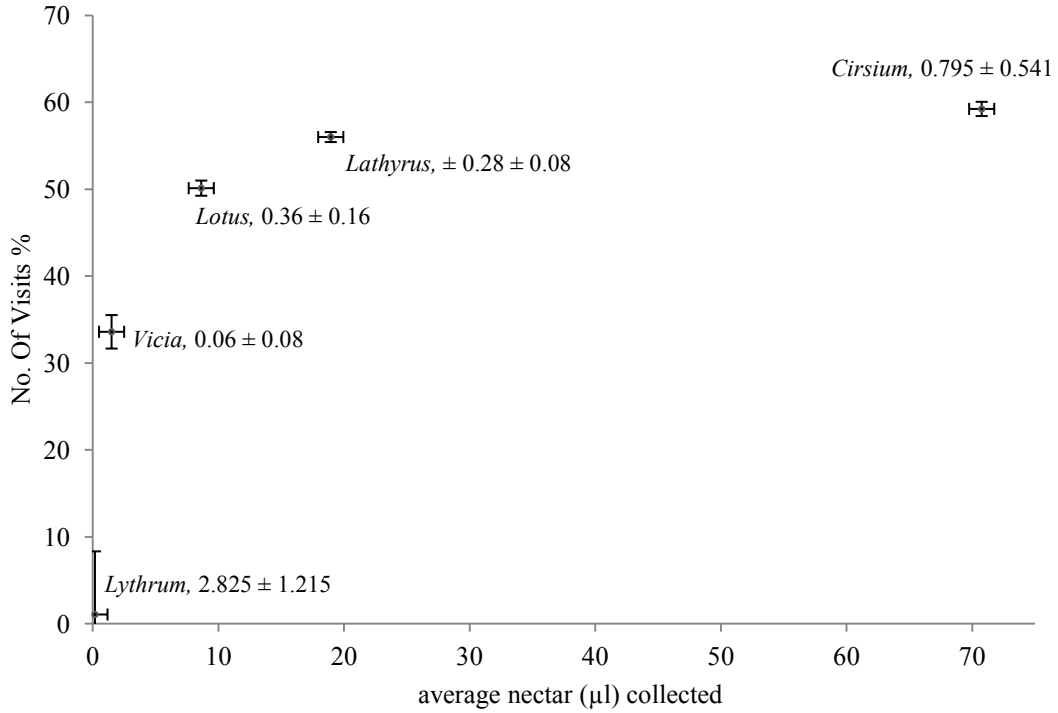


Figure 4-6. Number of visits and nectar collection by agent-based bee model foraging in simulated *natural meadow* on five flowering plant species under D65 daylight under the honeybee spectral sensitivity functions. Points represent the number of visits in % to each of the five plant species and average nectar collected from each plant species in the model. (n=20 ± SD, with 200 flower visits in each simulation run). Nectar standing crop median is shown in labels next to the flower species name (n=10 ± SD). Although *Lythrum* flower has the highest median of nectar standing crop, the amount of nectar available in this flower species varies the most so that a *Lythrum* flower can also be least rewarding which means it has received the least number of visits by the bee agent.

4.3.2.2 Flower visits in natural meadow under the assumption of perfect colour vision and colour blindness

Figure 4-7 shows the percentage of visits to the five flowering species in each colour visual model in the *natural meadow*. What can be observed is that, assuming a perfect colour vision system, all visits are to either *Lathyrus* or *Cirsium*, the most rewarding flower colours in the simulation meadow revealed by the results shown in Figure 4-8.

In Figure 4-8, the number of visits to all of the five flower species in the *natural meadow* by the colour blind bee is equal in frequency even though nectar values for each of the five flower species in the *natural meadow* vary and each species occurs in equal frequency and are randomly placed in the agent-based model. As expected, a colour-blind bee would choose each flower species in equal numbers.

The average numbers of visits to the five flower species are also shown for unmodified honeybee colour vision for comparison. There are fewer visits to the least rewarding flower

Lythrum by the bee agent with the honeybee colour vision compared to the bee agent that is colour blind. It is found that performance measured via nectar collection from the bee agent is better under the assumption of true honeybee colour vision than a colour blind bee, due to the bee agents' selective choice in flower colour compared to random choice in the colour blind bee. Performance in nectar collection will be further improved in the bee agent with perfect colour vision as it exclusively visits the two most rewarding flowers *Cirsium* and *Lathyrus* as shown in Figure 4-7d and Figure 4-8 showing nectar collected by colour blind and perfect colour vision bee.

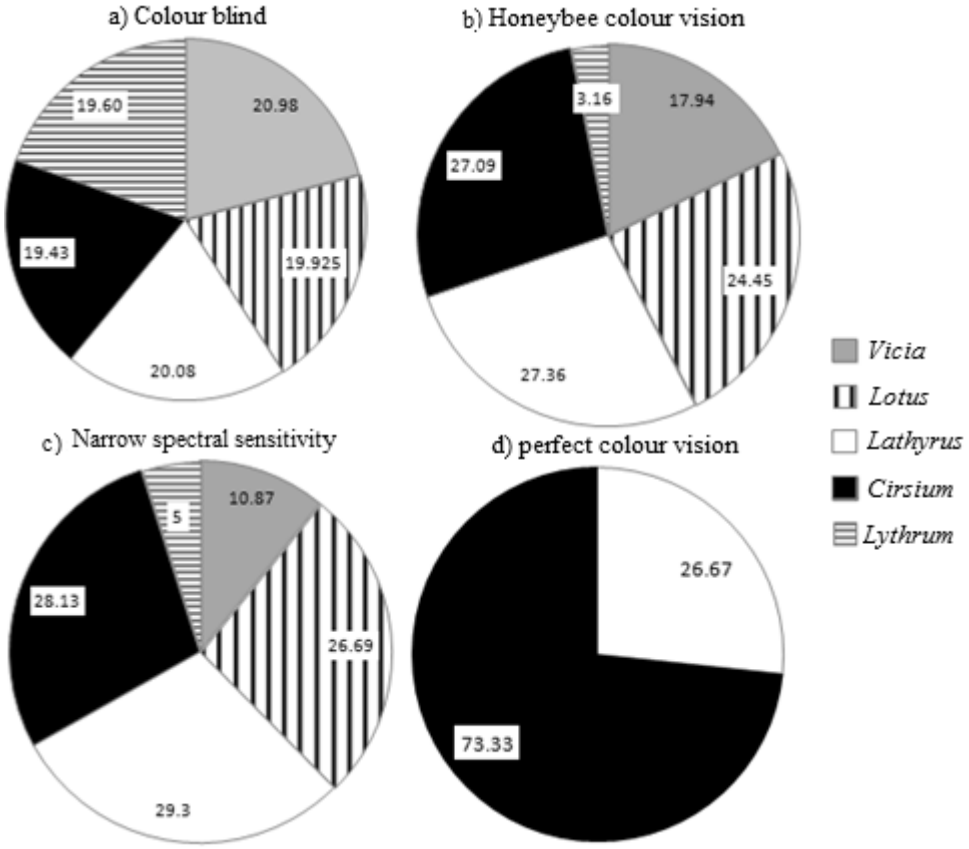


Figure 4-7. Average percentage of visits to five flower species by the bee under the assumption different colour visual models in our bee agents. a.) Colour blind, b) Honeybee colour vision, c) narrow spectral sensitivity function and d) Perfect colour vision in *natural meadow* setting.

4.3.2.3 Effect of changing illumination on foraging performance

Figure 4-8 shows the amount of nectar that is collected in the *natural meadow* by the agent-based model bee. With the short perceptual colour shift under changes of illumination for narrow spectral sensitivity function (see Chapter 3), it was assumed that narrow spectral sensitivity function would achieve near-perfect performance in foraging by bees in the *natural meadow*.

In order to test if diverging flower colour improves colour constancy in the testing phase (i.e. under changes of illumination), the flowers in the *ideal meadow* are perceptually far apart in colour signal (> 0.4cu – see Table 4-1) so each colour is not confused for others (Chittka et al, 2001 and see Figure 4.2). The *ideal meadow* was tested for the two colour visual receptor models, Honeybee and narrow photoreceptor sensitivities. Table 4-1 shows the colour distances from the most rewarding flower in the *natural meadow* and *ideal meadow*. The colour distances are large enough in the *ideal meadow* to achieve nearly perfect colour discrimination based on the agent-based model bee. Figure 4-9 shows the nectar collection in the *ideal meadow* with the narrow spectral sensitivity function model achieving near-perfect colour constancy. This is significantly different from the nectar amount collected under the *natural meadow* (nectar collected by bee agent under the assumption of a narrow spectral sensitivity in *natural meadow* and *ideal meadow*: t-test, $t = -5.51$, $df = 22$, $p < 0.001$) where colour distances between the flowers are shorter than those under *ideal meadow* (see Table 4-1). With the same colour discrimination ability under each colour visual model, colour constancy is better (i.e. shorter perceptual colour shift under changes of illumination that are observed in a narrow spectral sensitivity function as demonstrated in Chapter 3) when the ability to learn colours is improved through increasing colour distances between the flowers as it has been demonstrated in the *ideal meadow*.

	Normal honeybee spectral sensitivity function		Narrow honeybee spectral sensitivity function	
	Distance	**Shift**	**Distance**	**Shift**
Natural Meadow:				
Forest shade	0.329 ± 0.1	0.026 ± 0.005	0.310 ± 0.098	0.011 ± 0.002
Small gap	0.326 ± 0.09	0.014 ± 0.003	0.285 ± 0.076	0.008 ± 0.002
Woodland shade	0.309 ± 0.096	0.023 ± 0.008	0.298 ± 0.101	0.009 ± 0.001
Ideal Meadow:				
Forest shade	0.579 ± 0.111	0.043 ± 0.009	0.457 ± 0.100	0.006 ± 0.0005
Small gap	0.562 ± 0.103	0.018 ± 0.006	0.414 ± 0.091	0.005 ± 0.001
Woodland shade	0.554 ± 0.108	0.048 ± 0.015	0.473 ± 0.089	0.006 ± 0.0007

Table 4-1. Average distance colour unit from most rewarding flower in simulation, *Cirsium* to all other flowers in the *natural meadow* and *Lathyrus* to all other flowers in the *ideal meadow*. Level of colour distance from all flowers is larger under the *ideal meadow* than the *natural meadow*. Average colour shift in all five flowers under three light conditions in the *natural* and *ideal meadow*s show that both Ideal and *Natural meadow* do not elicit very large differences in perceptual colour shift under narrow spectral sensitivity function of the honeybee photoreceptors.

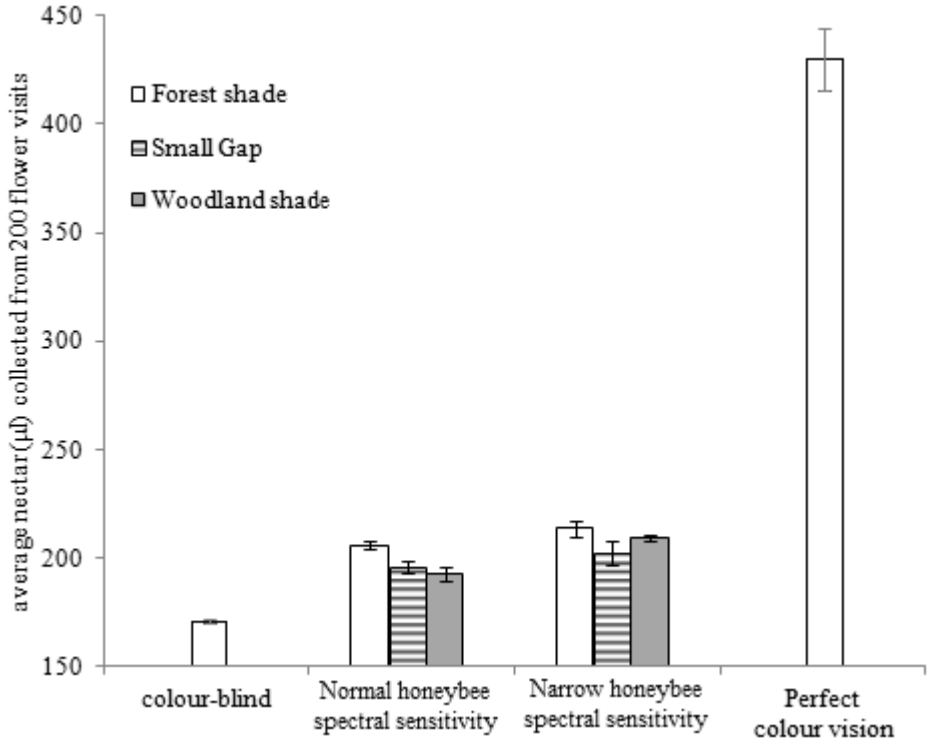


Figure 4-8. Average nectar collection in an Agent-based model of a bee foraging in the simulated *natural meadow* with different colour visual models after bee agent is trained under daylight D65, and nectar collection is recorded under changes of illumination to Forest shade, Small gap or woodland shade. (n=20 ± SD, with 200 flower visits in each simulation run).

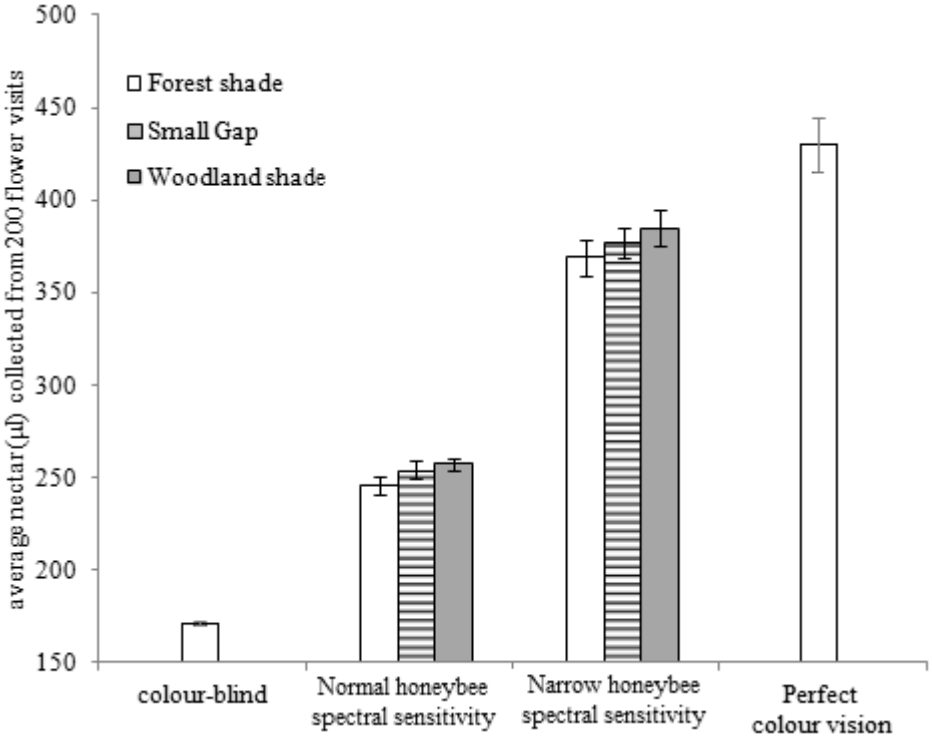


Figure 4-9. Average nectar collection in an Agent-based model of a bee foraging in the simulated *ideal meadow* with different colour visual models after bee agent is trained under daylight D65, and nectar collection is recorded under changes of illumination to Forest shade, Small gap or woodland shade. (n=20 ± SD, with 200 flower visits in each simulation run).

4.3.3 Discussion

This chapter contains the development of an agent-based model of bee foraging in meadows of five flower species of varied colouration. Ultimately this model will be used to test the adaptive benefits of various colour constancy algorithms (see chapter 5). To this end it is first necessary to 'test-drive' the model under various critical conditions, to explore the extent to which the model 'works' – i.e. whether it reproduces natural adaptive foraging behaviour of the bees, whether it is sensitive to the colour vision system implemented in the modelled bees, and whether the colour differences between the flowers makes a difference to foraging performance. Indeed all these parameters critically influence foraging performance, and it can therefore be concluded that the model is sensitive to changes in all critical parameters.

Over time, the bee agent searches for the most rewarding flower colour and increasing visits are then made to a flower colour that it associates with the most reward, which is found in natural foraging behaviour of the bee (Daumer, 1958, Frisch, 1914, Daumer, 1956, Helverson, 1972). The bee may come across the challenges of similar flower colour species in the same meadow, and mistakes in identifying the correct flower species can be made. We assumed that increasing colour distances between flower colour not only improves the ability to discriminate and thus identify different flower species but also achieve better colour constancy because flowers under changes of illumination are not mistaken for others, flowers that are distinguishable improve the level of flower constancy behaviour (Chittka et al., 2001). This was indeed the case when we tested our Agent Based Model in an *ideal meadow* with colour loci widely spaced in bee colour space. Larger colour distances are favourable in reducing the problem of metamerism, where different colours under one illuminant look the same under another (Wyszecki and Stiles, 1982). It also reduces the problem of flower species in the same meadow looking similar. For a foraging bee in the testing phase of the simulation run, colour identification hinges on the extent to which colours perceptually shift. Without adequate compensation, a colour locus might shift to such an extent that the learnt colour appears to be no longer available under the changing illuminant because the learnt colour does not resemble any of the colours under the changed illuminant. Colour constancy should reduce colour shift as much as possible to ensure colours look the same under changing illuminant, which is achieved with narrow spectral sensitivity function of the honeybee – however this is not at all enough to achieve near-perfect colour constancy. By comparing foraging performance in a natural set of flower colours with that in an *ideal meadow* of flowers with high perceptual colour distances between each other, it now is apparent that the ability to discriminate colours aids learning and thus this in turn aids to achieve better colour constancy in a natural setting.

In this chapter, through agent-based modelling, it was shown that learning of flower colour and colour constancy is facilitated by having distinct colours. Under changes of illumination, small perceptual colour shift is not enough to achieve good colour constancy, in a temporal state of foraging, it is important that colours are learnt correctly. Only then can colour constancy be relevant. The results from *natural meadow* and *ideal meadow* also suggest that the better the colours are learnt, the better results of any colour constancy mechanism is achieved. Colours are best learnt if colours are distinct from each other. It is yet to be observed if the challenge of large colour shift of colours where colour difference function is sensitive in the honeybee colour vision is somehow overcome in plant communities where illumination changes dramatically. Illumination changes in a real plant community are explored in Chapter 6.

With a basic model of a foraging bee making flower colour choices as expected, in the next chapter I will explore the performance of computational colour constancy mechanisms under this agent-based model and determine what factors are involved in making a computational colour constancy mechanism in a biologically significant colour choice task successful.

5 Biological significance of computational colour constancy in an agent based model with bees foraging from flowers under varied illumination

In this chapter, I explore the quantitative benefits of various computational colour constancy mechanisms in an agent-based model of foraging bees, where the bee agents select flower colour based on reward under the assumption of the orginal honeybee spectral sensitivity functions introduced in Chapter 3, using different scene statistics algorithms to estimate flower colour in the face of changing illumination. Constancy in chapter 3 has been measured by the level of shift from one illuminant to another. However, the quantitative benefits of this constancy in a real world model have yet to be evaluated. It is known that colour choice in bees improve as perceptual colour shift under varying illuminant reduce (Dyer and Chittka, 2004b), but the co-occurences of flowers can ultimately affect quantitative results in nectar for example where flower species in the plant community are very similar in colour. In this chapter, the amount of nectar collected by the bee in changes of illumination in a typical plant community is used as an indirect evaluation of colour constancy performance.

The experiments in this chapter are designed to test three types of retinex-based computational colour constancy techniques. These are 1) the Gray world assumption which is the assumption that the average colour components of the scene in Red, Green and Blue (or UV, Blue and Green in bee) average to a gray value; 2) the White patch calibration which uses the most intense region of the scene as a reference point and assumes that this point must be white (Kraft and Brainard, 1999), and 3) histogram equalisation which is a technique of chromatic adaptation to enhance colour saturation in digital image processing (Land, 1986b) as well as visual quality in the fly (Laughlin, 1981) which is thought to amplify colour visual input to produce high contrasts. Histogram equalisation is not often considered a colour constancy mechanism, however histogram equalisation produces high chromatic contrast results, and this would be useful in achieving high perceptual colour distances between the flowers in the scene. It would be useful to see if this feature improves the ability to be colour constant as it has been observed in the *ideal meadow* in Chapter 4. I have already established in chapter 4 that larger distinction between colours improves colour constancy, and may

enhance ‘colour memory’. Thus, it is hypothesised that a mechanism for colour divergence in a scene will improve the results of a colour constancy mechanism.

I have performed model calculations under the assumption of the normal honeybee spectral sensitivities. The three computational colour constancy mechanisms will be tested in this colour visual model and I will be using the scene statistics to evaluate colour perception in the bee.

5.1 Introduction

Colour signals are used to identify rewarding flower species under a vast range of variation occurring in natural illuminants of the light environment. If the spectral composition of the illumination changes, then so does the light reflected from flowers, making identification by colour challenging. Without colour constancy, changes in the illuminant would result in significant changes to flower colours (Dyer, 1998). Numerous studies on colour vision in bees have shown that colour choice is under changing illumination is constant (Mazokhin-Porshnjakov, 1966, Neumeyer, 1981, Neumeyer, 1980, Werner et al., 1988, Lotto and Chittka, 2005, Dyer and Chittka, 2004b), although the compensation of the light change is not complete and colour constancy therefore imperfect. While some authors have held that colour constancy needs to be essentially perfect for colour vision to be at all useful (Land, 1977), the penalties paid under natural conditions need to be quantified on a case-by-case basis, depending on the actual variation of the illumination, and colours that need to be distinguished. The fundamental question arising from colour constancy in the real world is what price a foraging bee might pay by misinterpreting flower colours under changing illuminant conditions and in turn how effective various computational colour constancy methods are in their application in the real world. A vast number of models of computational colour constancy make assumptions about the properties of the illuminant and the scene surfaces (Hurlbert, 1998, Land, 1983, Land, 1986b, Brainard and Wandell, 1986, Brainard et al., 2006, Maloney and Wandell, 1986) and have been proposed with different methods of assessing performance. To independently assess the performance of colour constancy under human observation has its challenges particularly because colour constancy is not entirely as straightforward as discounting the light from the scene (Ling and Hurlbert, 2008, Hansen et al., 2006). With a high level of complexity with the colour constancy process, being able to assess the relative advantage attributable to a particular colour constancy method is useful to assess the biological significance of colour constancy algorithms. Empirical studies have identified performances of colour constancy methods under natural viewings (Ling and Hurlbert, 2008, Kraft and Brainard, 1999, Brainard et al., 2003) and colour constancy performance varies under different test methods.

Our modelling attempts to identify the biological significance of one computational colour constancy method over others in solving a real world problem (i.e. choosing the right flower colour and overcoming the ambiguity of flower colour under changing illuminant).

Here we explore quantitatively the biological usefulness of various Retinex computational colour constancy mechanisms using the honeybee spectral sensitivity functions investigated in Chapters 3 and 4 for foraging under conditions of changing illumination.

5.2 Materials and Methods

5.2.1 Simulation model

This setup is similar to that which was used in the modelling of the *natural meadow* in Chapter 4 with the use of five flowers from the study in Chittka et al., (1997), and the model is explained further in the methods section of Chapter 4. The hive and the single bee agent are placed in the centre of a 350 x350 celled map. The set up is in NetLogo, the bee agent in the centre and the area of its visual field defined by a radius *r*. The bee agent is a single bee that forages in each simulation run.

Each simulation run undergoes two phases where the bee visits a total of 250 flowers, a training phase consisting of 50 flower visits under D65 daylight, and a testing phase consisting of 200 flower visits under three other illuminations (forest shade, small gap and woodland shade). 5000 flowers with 5 flowering species studied in Chittka et al., (1997), *Lotus corniculatus*, *Lathyrus pratensis*, *Vicia cracca*, *Cirsium oleraceum* and *Lythrum salicaria,* each occurring 1000 times were used in all simulation runs in this investigation. The reflectance spectra and loci of these are flowers are shown in 4.4 and Figure 4.5, respectively in Chapter 4. Appendix III shows the nectar standing crop values assigned to these flowers in the simulation, labelled the *natural meadow*. Chapter 4 provides details of the results obtained of the nectar collected from these flowers by the agent-based model bee under a honeybee colour vision.

Results such as the amount of overall nectar collected and the number of visits to each floral species are collected at the end of each simulation run. Twenty simulation runs are performed for each computational colour constancy method.

5.2.2 Colour constancy methods

To apply a computational colour constancy method to the scene that the bee has encountered, each time the bee attempts to make a decision between flowers within its visual field, the scene is transformed through a computational colour constancy function. The scene described is a segment of the simulated meadow made up of cells from a location within *r* (*r*=radius – See Figure 4-3) of the bee agent as it forages. Each cell has a reflectance spectrum that is either floral colour or green foliage illuminated by the training or testing illuminants. This two-dimensional scene made up of flower colours and green foliage is processed through one of the computational colour constancy methods each time the bee agent encounters flowers within the location of *r* that it is in.

Performance was measured in three simple computational colour constancy techniques, histogram equalisation (Laughlin, 1981, Gonzalez and Wintz, 1977), White patch – Brightest patch (Land and McCann, 1971, Ebner, 2007), Gray world assumption (Buchsbaum, 1980, Ebner, 2007, Land, 1986b, Helson, 1964) using the honeybee colour receptor signals as inputs. All computational colour constancy methods – histogram equalisation, White patch and Gray world were combined with the original honeybee spectral sensitivity functions described in Chapter 3.

Histogram equalisation, White patch and Gray world methods are commonly used in digital image processing for image correction or image enhancement, and are different techniques of the retinex theory. A visual representation of what happens to the transformation of the bee agents' scene when applying these computational methods is formulated. One example scene of size *r* of a bee agents' location consisting of random distribution of the five floral species is taken and transformed with the respective colour constancy mechanism. The excitation response levels of the UBG (UV, Blue, Green) photoreceptors ranging between 0 and 1 are mapped to RGB (Red, Green Blue) value that ranges from 0-255 in digital images where short wavelength-absorbing receptors of the UBG are mapped to the short wavelength receptors in RGB, medium wavelength of UBG is mapped to the medium wavelength of RGB, and finally the long wavelength of UBG mapped to the long wavelength of RGB. We show the scenes of coloured cells to observe the affect of the colour constancy mechanism to the colours in the scene. Figure 5-1 shows the result of a histogram equalisation, White patch and Gray world correction with a Honeybee colour vision under daylight and forest shade in one visual field scene that a bee agent could typically encounter in the agent based model.

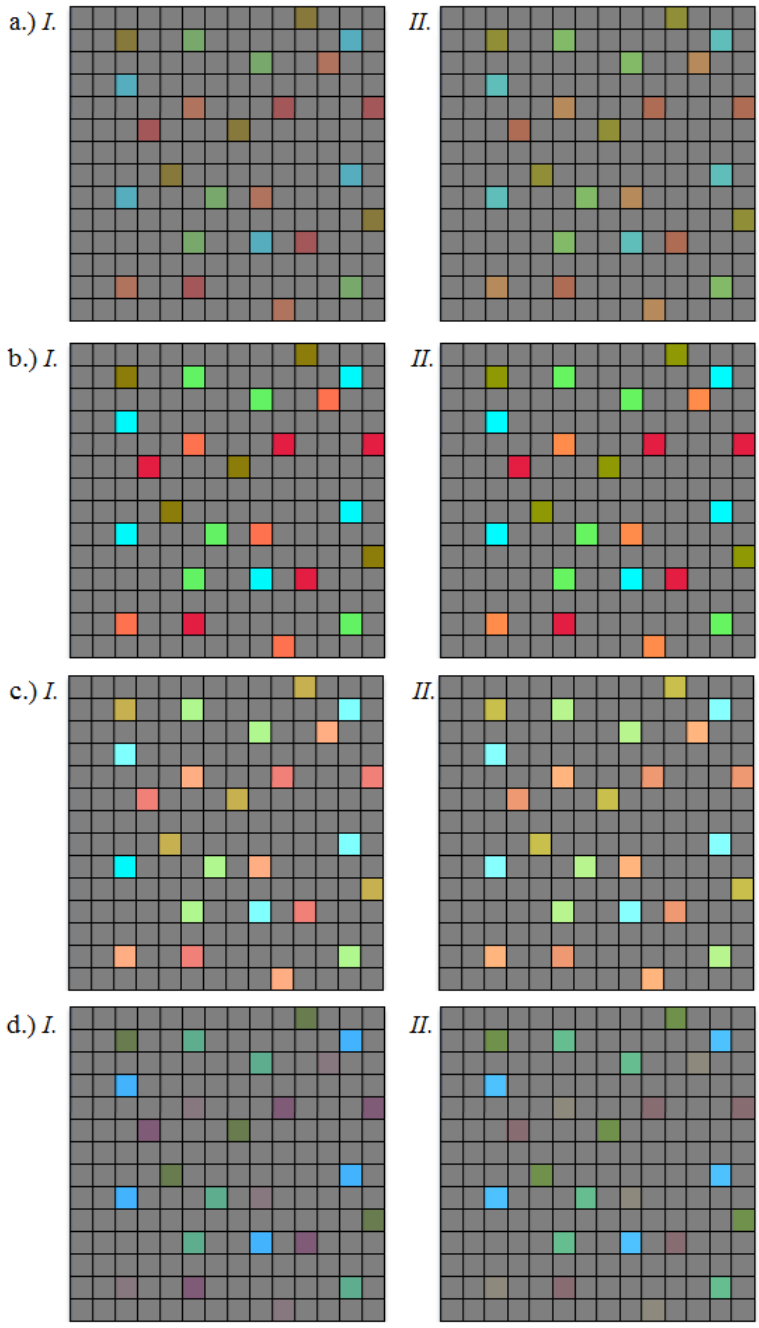


Figure 5-1 - Example of a scene (i.e. visual field, see Figure 4-3) consisting of 5 different flower colours encountered by the agent-based bee model in the simulation, using normal honeybee spectral sensitivity functions as inputs, remapped onto human vision in Red/Blue/Green. The excitation values of UV, Blue and Green range from 0-1, and are mapped to Red, Blue and Green respectively ranging from 0-255. The scene is the visual field in the location the bee is in, and consists of all flowers in *r*, the radius of the visual field. It consists of five flower species under a). i. Honeybee colour vision under D65 daylight, ii. Honeybee colour vision under forest shade. b). i. Honeybee colour vision + Histogram Equalisation under D65 daylight, ii. Honeybee colour vision + Histogram Equalisation under forest shade. c). i. Honeybee colour vision + White patch under D65 daylight, ii. Honeybee colour vision + White patch under forest shade. d.) i. Honeybee colour vision + Gray world under D65 daylight, ii. Honeybee colour vision + Gray world under forest shade.

5.2.2.1 The von Kries receptor adaptation model (Honeybee colour vision)

This adaptation response of the orginal honeybee colour vision based on a von Kries receptor adaptation response is described in Chapter 3, and weightings are given in Table 3.1. Figure 5-1.a. shows an example of the recovery of the five flower colours in an RGB system using the normal Honeybee spectral sensitivity functions under day light and forest shade.

5.2.2.2 Histogram equalisation

This technique involves adjustment of colour contrast in an image. The fly retina uses the same mechanism of histogram equalisation to achieve better visual quality (Laughlin, 1981). By recording the frequency distribution of each colour channel the algorithm stretches the receptor response over the maximal range to provide a maximum receptor response of the scene across the spectrum (Gonzalez and Wintz, 1977).

An 'image histogram' H_i records the distribution of colour intensity in each channel (i = UV, B or G), where $H_{uv}(n)$ holds the number of colours that excite the UV receptor at the n^{th} intensity. The n intensity range is between 0 – 1, where 1 is the highest excitation (or intensity) response of the receptor and the number of possible intensity values are defined as L in Equation 9 (L = 100). With poor brightness or contrast, the intensity of the colours in the image c will be shifted or clustered at one point at the histogram, the transformation of each pixel (the x, y point in the image/scene c) and remapping of intensity is assigned to each channel i, with the histogram of the image as follows:

$$H_i = round\left[(L-1)\ .\ \frac{c_i(x,y) - c_i(x,y)_{(min)}}{c_i(x,y)_{(max)} - c_i(x,y)_{(min)}}\right] \quad (9)$$

The application of this method results in contrasting colours with high receptor excitation response of the UBG receptors under histogram equalisation (i.e. increased spectral purity). When mapped to the RGB system, the colours look consistently the same under both D65 daylight and forest shade (see Figure 5-1.b.).

5.2.2.3 White patch

The retinex theory has been previously been thought to explain colour constancy in the honeybee (Werner et al., 1988). A form of the White patch retinex algorithm is achieved through assuming that the brightest point in a scene is of pure white colour, so that all other colours can be placed in the context of this reference (Land, 1964). In digital image processing it is achieved by finding the brightest (highest excitation response at a given location in the image – i.e. the brightest pixel) level of pixels and to assume this is white

(Ebner, 2007). The mapping of the UBG response to RGB system is shown in Figure 5-1.c for White patch calibration. Computationally, the 'white patch' is the maximum intensity in the UV, B and G bands, and thus that is the estimated illuminant. The scene undergoes a transformation using the estimated illumination as a chromatic adaptation. Initially, the simplest computational version of this is to find the maximal intensity in each receptor response (Ebner, 2007):

$$L_{i,max} = \max_{x,y}\{c_i(x,y)\} \tag{10}$$

In the above scenario, c_i represents the response of the receptors in a given location of x, y coordinates in a given receptor (i.e. Ultra-violet (UV), Blue (B) or Green (G)). The maximum intensity of $L_{i,max}$ is described as the maximum receptor response of c_i given:

$$c_i(x,y) = R_i(x,y)L_i \tag{11}$$

This maximum value in each channel is used to predict the illuminant, which is used to scale all colour points in the scene:

$$\frac{c_i(x,y)}{L_{i,max}} := R_i(x,y) \tag{12}$$

5.2.2.4 Gray world

The Grey world algorithm (Buchsbaum, 1980) assumes that, on average, the colour of the scene is achromatic and so to estimate the illuminant, the average colour in the scene is used (Gonzalez and Wintz, 1977, Ebner, 2007). The average of UV, B and G is found for a scene. In the first step, the average colour in the viewed image/scene is computed:

$$a_i = mean\{c_i(x,y)\} \tag{13}$$

If in all receptor responses a_i (i.e. i = UV, Blue or Green) is equal, then the visual scene already satisfies the gray world assumption. If the average found of one receptor type response is much lower than the other receptor types then the algorithm increases the influence of the lowest receptor type average excitation response (Ebner, 2007). The same process as the transformation in Equation 10 is applied except that the white (maximum intensity) constants will be the average value for the receptor response in UV, B and G. The mapping of the UBG response to RGB system is shown in Figure 5-1.d for the Gray world assumption.

5.2.3 Models

Our method of determining the classification of a colour constancy method is defined by the performance of the overall nectar collected by the agent-based model bee, and ultimately the bee should be able to correctly recognise rewarding colours under changing illumination to achieve successful colour constancy. To test the computational models against a lower and upper limit of the agent-based model bee, two extreme models of colour vision were used to evaluate the performance of the colour constancy methods– a colour-blind bee and a perfect colour constancy vision bee. This is described in Chapter 4.

In summary, the Honeybee colour vision, with histogram equalisation, White patch and Gray world will be simulated for testing the biological significance of computational colour constancy.

5.3 Results

Figure 5.2 shows the results of average nectar collection by an agent bee under the assumption of normal honeybee colour vision, using the three computational colour constancy mechanisms that take the scene statistic to estimate actual reflectance. Nectar collection of both the colour blind and perfect bee is also shown, taken from Chapter 4. The better the reflectance is estimated by the bee-agent under changes of illumination, the more performance in nectar collection improves, and thus we evaluate constancy performance under varying illumination by measuring nectar collection by the bee agent. This is a useful method as it provides a realistic quantitative measurement of performance in colour constancy, unlike perceptual colour shift which does not indicate the quantitative benefits (i.e. nectar reward) of colour constancy in the real world. The results show the computational colour constancy method that best evaluates the actual spectra with just the surrounding scene colour. The bee agent under the assumption of a normal honeybee spectral sensitivity using the histogram equalisation method achieves a nectar collection performance that is 33% better than the colour-blind bee (t-test: $t = -5.84$, $df = 20$, $p < 0.001$) and significantly better than both Gray world (t-test: $t = 4.78.84$, $df = 29$, $p < 0.001$) and White patch (t-test: $t = 2.87$, $df = 31$, $p = 0.003$). None of these computational colour constancy methods achieve perfect colour constancy (i.e. better than the 'perfect colour vision').

The highest nectar collection is found under histogram equalisation given a honeybee colour vision. Interestingly, the honeybee colour visual model under the assumption of a histogram equalisation reveal highest colour distances where overall distances between all the flowers is over 0.9 cu and distances of all flowers from the most rewarding flower *Cirsium* is over 0.7

cu (see Table 5.1) which means these flowers are highly distinguishable from each other under the different lights and would be easily identified as different colour by a bee (Chittka et al., 2001). This is consistent with the results in chapter 4 where bee agents foraging in a meadow of high colour differences in the *ideal meadow* in Chapter 4 collected more nectar.

The overall distance from all five flowering species and from the most rewarding flower species and other flowers is very large under histogram equalisation (see Table 5.1), whilst the level of colour shift between the flowers under White patch, Gray world or histogram equalisation from D65 to forest shade, small gap or woodland shade are not much different from each other. However, the results shown in Figure 5.2 reveal that there are significant differences in nectar collection between the three computational colour constancy methods.

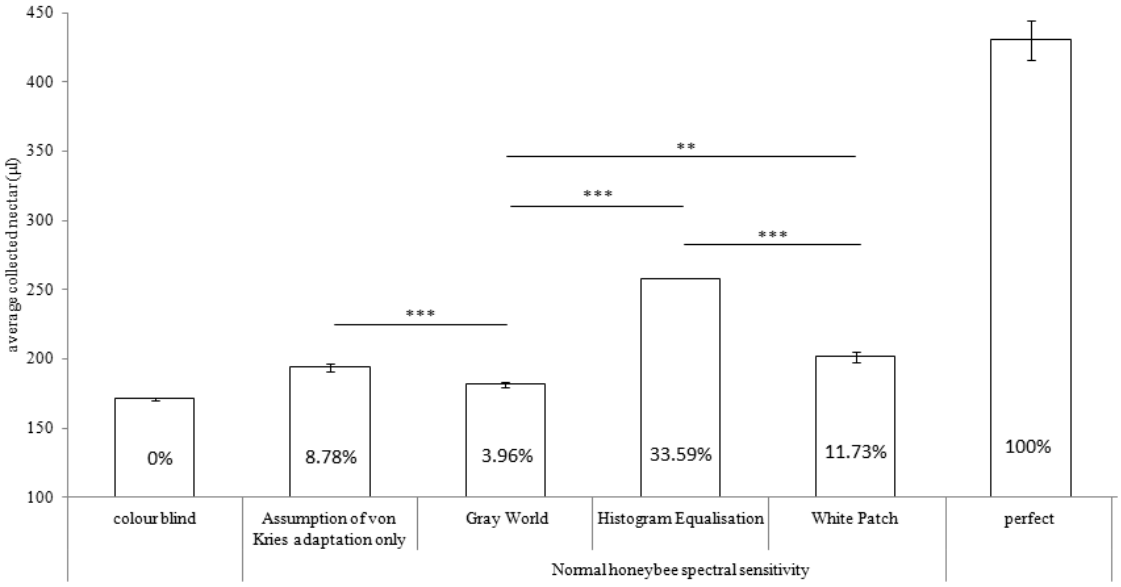


Figure 5-2. Each bar represents average nectar collected from forest shade, small gap lighting and woodland shade under each colour vision model. The colour-blind bee performs the poorest in nectar collection, whilst the perfect colour vision performs the best. Percentages labelled in the bar indicate the improvement in nectar collection compared to a colour blind bee. Histogram equalisation performs the best in nectar collection compared to the other two computational colour constancy mechanisms. (n=60 simulation runs, 20 each in three changing lights from daylight D65, each with 200 flower visits, ± SD). (One star: *p*-value<0.05, two stars: *p*-value<0.01, three stars: -value<0.001)

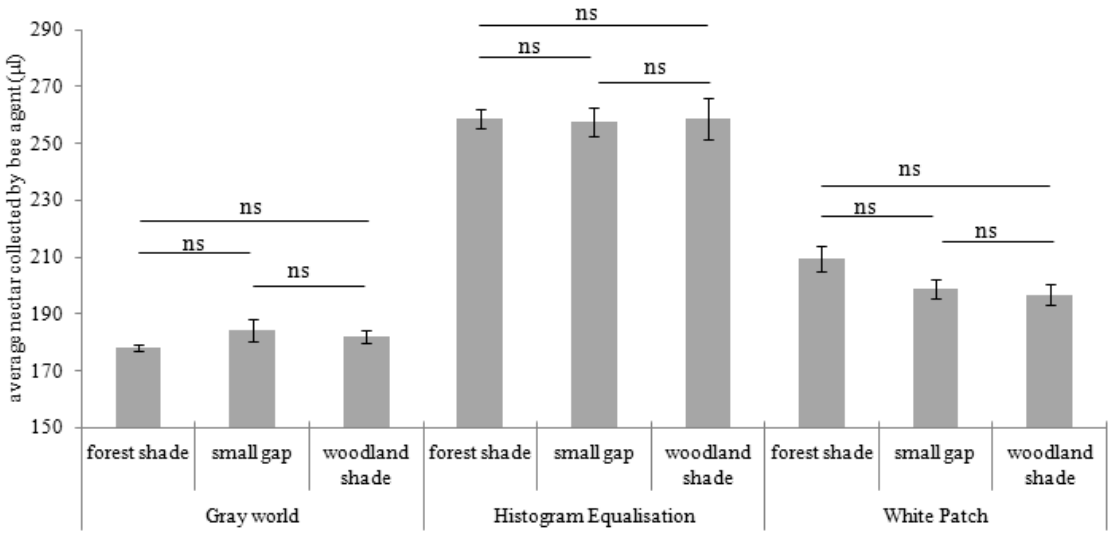


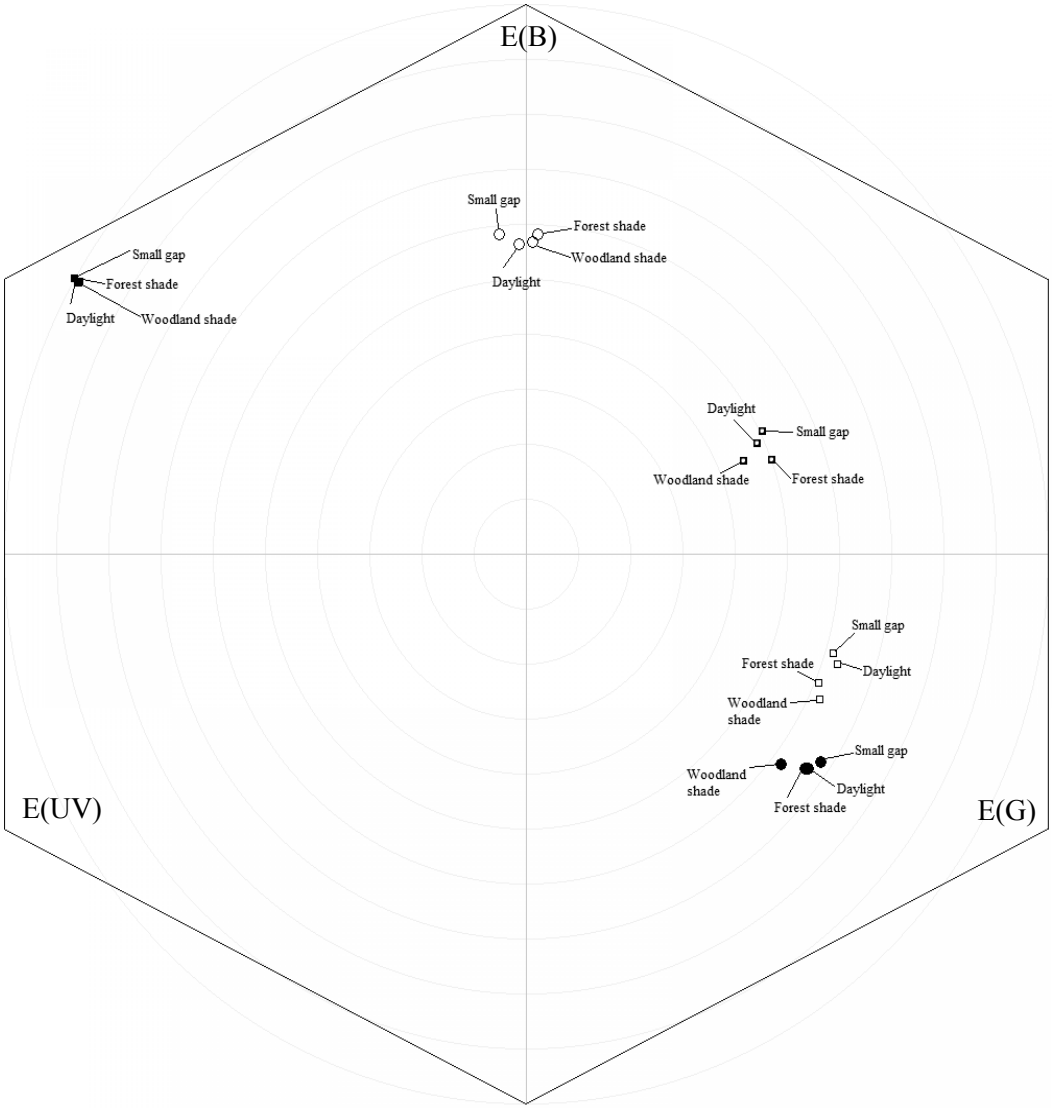
Figure 5-3. Average nectar collection by the agent-based model bee using honeybee colour receptors and Gray world, Histogram equalisation or White patch colour correction under changing illumination From Daylight D65 training to illumination change of Forest shade, Small gap or woodland shade. (ns: p-value > 0.05)

	Overall distances	*Average distance from Cirsium*	*Average shift from D65*
White patch			
Daylight (D65)	0.549 ± 0.092	0.445 ± 0.138	-
Forest shade	0.574 ± 0.099	0.468 ± 0.149	0.027 ± 0.006
Small gap	0.566 ± 0.094	0.464 ± 0.136	0.027 ± 0.007
Woodland shade	0.531 ± 0.089	0.437 ± 0.135	0.038 ± 0.007
Histogram equalisation			
Daylight (D65)	0.935 ± 0.157	0.736 ± 0.203	-
Forest shade	0.933 ± 0.159	0.738 ± 0.213	0.028 ± 0.009
Small gap	0.945 ± 0.158	0.750 ± 0.204	0.025 ± 0.005
Woodland shade	0.919 ± 0.157	0.723 ± 0.198	0.038 ± 0.011
Gray world			
Daylight (D65)	0.417 ± 0.072	0.371 ± 0.125	-
Forest shade	0.431 ± 0.075	0.386 ± 0.129	0.034 ± 0.008
Small gap	0.421 ± 0.072	0.375 ± 0.123	0.014 ± 0.003
Woodland shade	0.412 ± 0.071	0.375 ± 0.124	0.035 ± 0.011

Table 5-1. Average distance colour unit from most rewarding flower in simulation, *Cirsium* to all other flowers in the meadow under the assumption of White patch, Histogram equalisation and Gray world computational colour constancy mechanisms. Level of colour distance from all flowers is larger under Histogram equalisation, followed by White patch and Gray world. Average colour shift under varying illumination from D65 is indifferent under each of the three computational colour constancy models.

It appears that high colour distances between objects in a scene under changing illumination is biologically relevant in the colour vision to achieve colour constancy. Meanwhile, in Figure 5.3 the differences in nectar collection between the different lights under the assumption of Gray world, histogram equalisation or White patch is insignificant (t-test, $p<0.05$, ns = not significant). Figure 5-7 shows the flowers under the assumption of honeybee colour receptor

sets in the bee colour space when a scene of five flowering species is processed through histogram equalisation. The loci are spaced apart much more (see table 5.1 where >0.9 cu overall distances between flowers) compared to the scene processed through White patch (<0.6cu overall distances between flowers and see Figure 5-8) and Gray world (<0.45 cu overall distances between flowers and see Figure 5-9), and thus performance in nectar collection by the bee agent drops as it becomes more difficult to discern the differences between the flower colours under Gray world compared to White patch. It is important to note that, the loci plot of the flowers can change in the same illumination based on the flowers that are actually available in the scene since all three of the algorithms use statistical ensemble of the flower spectral content. Table 5.2 shows the changes in colour distances and average perceptual colour shift under different illuminants.



Lythrum

Lathyrus

Vicia

Lotus

Cirsium

Figure 5-4. Five flowering species *Lotus*, *Lathyrus*, *Vicia*, *Cirsium* and *Lythrum* loci plotted on the colour hexagon under a Honeybee colour vision with the application of histogram equalisation
All five flowering species are plotted under the illumination of Daylight (D65), Forest shade, Woodland shade and Small gap lighting

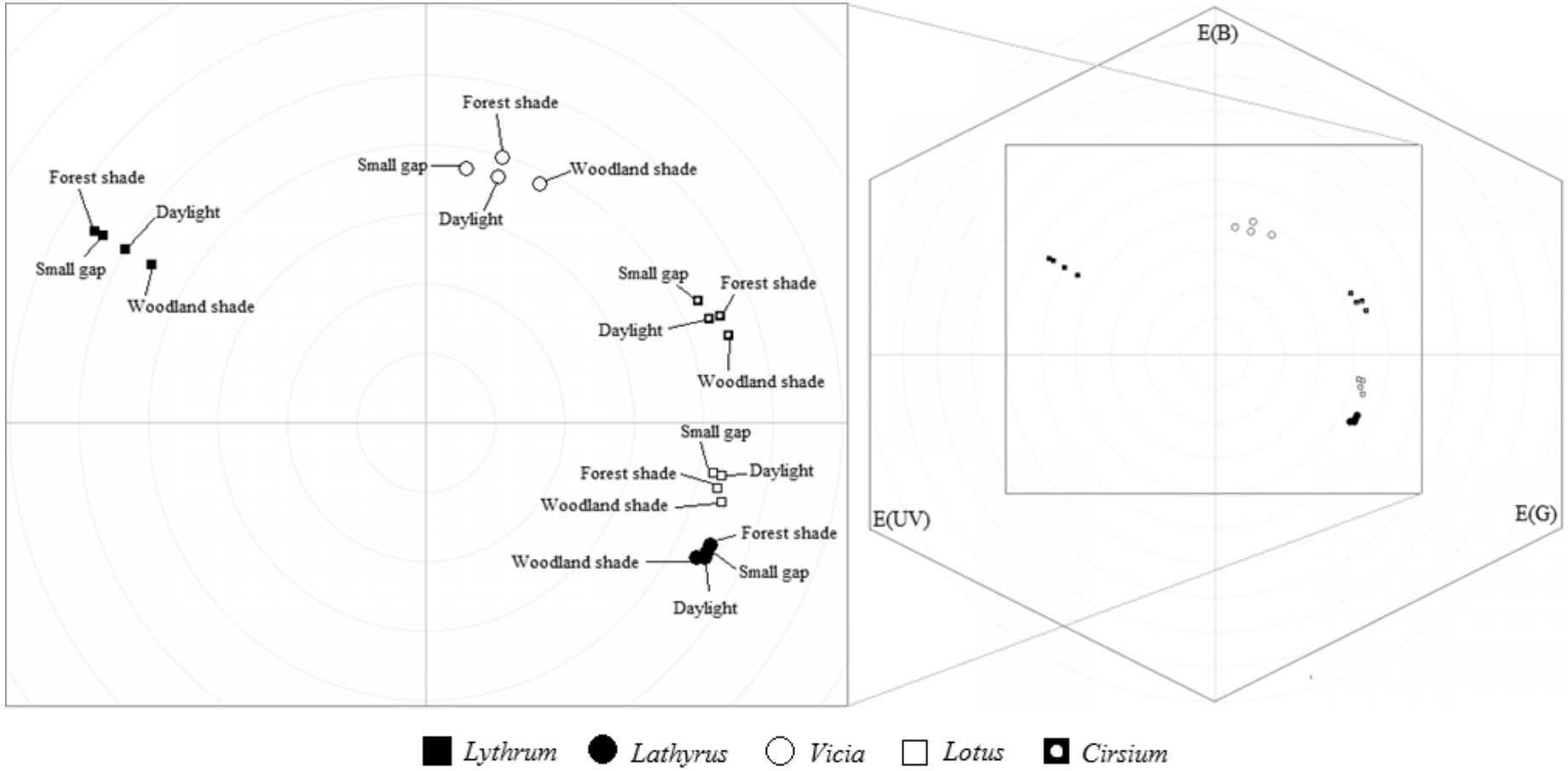


Figure 5-5. Five flowering species Lotus, Lathyrus, Vicia, Cirsium and Lythrum loci plotted on the colour hexagon under a Honeybee colour vision with the application of White patch calibration.

All five flowering species are plotted under the illumination of Daylight (D65), Forest shade, Woodland shade and Small gap lighting

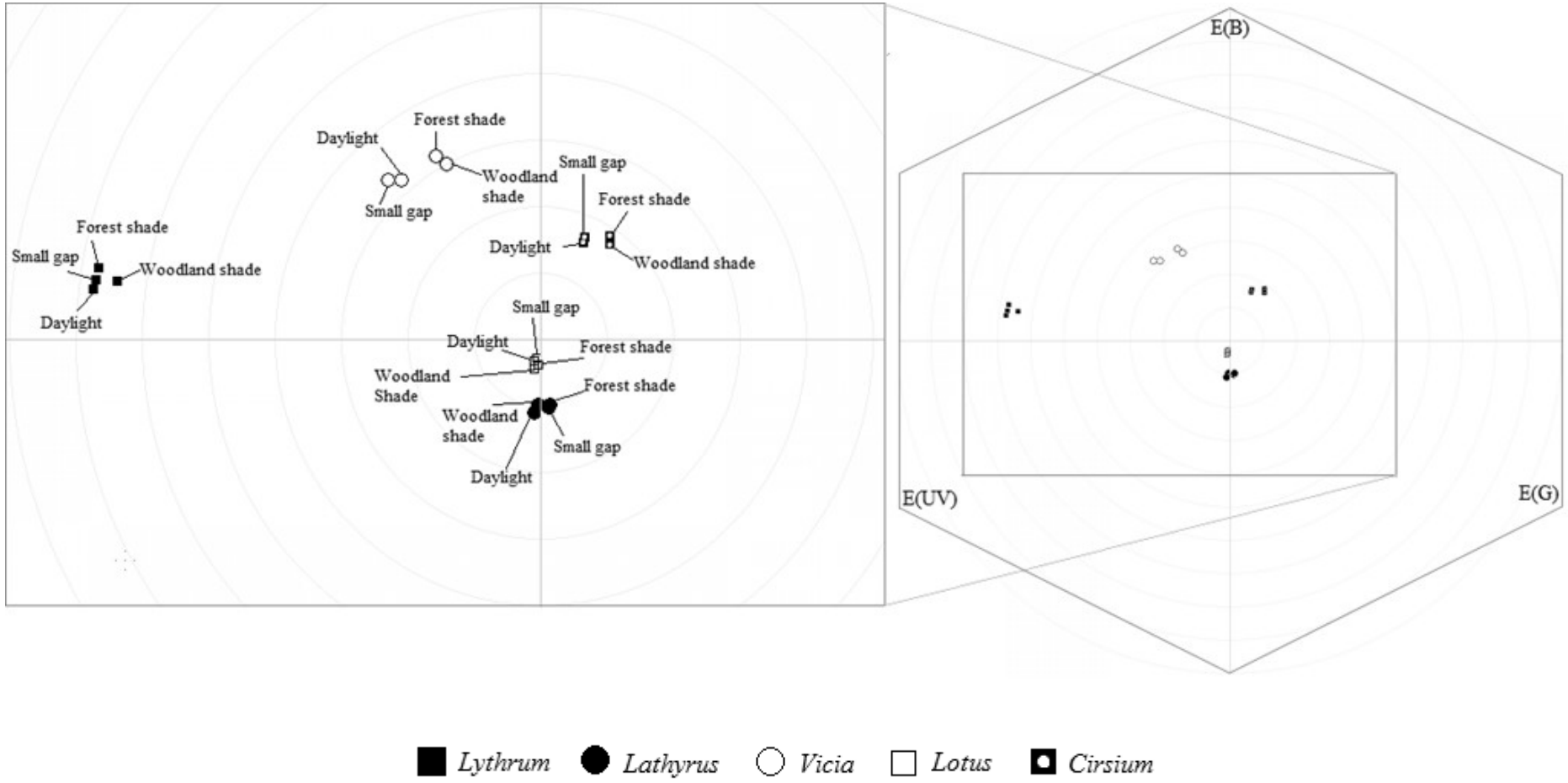


Figure 5-6. Five flowering species *Lotus, Lathyrus, Vicia, Cirsium* and *Lythrum* loci plotted on the colour hexagon with the application of Gray world calibration. All five flowering species are plotted under the illumination of Daylight (D65), Forest shade, Woodland shade and Small gap lighting

5.4 Discussion

It is likely that the strategy of histogram equalisation colour constancy is to make colours perceptually different by increasing the spectral purity of the colour, which would increase the distances between colours that occur in the visual field. It has been discovered that the visual neurons in a fly's compound eye do carry out a similar function as histogram equalisation (Laughlin, 1981) such that neurons exert their resolving capacity to high contrasts. This is considered a common response in any receptor type, since small signals get suppressed and signals become saturated. It has not been explored if bigger contrasts improve the ability to be colour constant. However there have been studies that have suggested that the mechanisms involved in colour contrast account for the sensitivity reduction assumed for bee colour constancy (Neumeyer, 1980) and fish (Neumeyer et al., 2002). The assumption of the White patch algorithm, a form of the retinex theory has also been another explanation for the colour constancy mechanism in the bee (Werner et al., 1988). The two methods which have shown to increase contrast of colours, also achieve better colour constancy performance in the agent-based model.

For the bee, the selection of flower colour is better under histogram equalisation and the White patch algorithm and results in an improved nectar collection rate compared to a hypothetical system that is simply calibrated by a receptor adaptation response. Colour distances between flowers under the assumption of histogram equalisation and the White patch algorithm are large, and both achieve better performance under changing light environment.

Under changes of illumination with a honeybee colour vision, the amount of perceptual colour shift is similar across changes in light and the performance of nectar collection under changing illumination in each computational colour constancy method does not vary significantly (see Figure 5-3). Although speculative, it could be assumed that it would be computationally challenging if the level of perceptual colour shift varied under different lights compared to if the colour visual model produced a specific level of perceptual colour shift under a variety of changes in light conditions. However, using normal honeybee colour receptors, the differences in nectar collection between different lighting conditions are insignificant (see Figure 5.3, t-test, p=ns, not significant ($p > 0.05$) the differences between nectar collected under the three lighting conditions for Gray world, histogram equalisation or White patch are not significant between the lights). To recover actual colour reflectance spectra under changes of any illumination type with a common level of perceptual colour shift might be easier compared to an unknown colour shift level. However, in both cases, colour vision still must determine the 'vector' or the direction of the colour shift since it is not always in the same direction under different coloured lights. For example, under a forest shade light (which is a green coloured light) colour shift is towards the excitation of the green (long) photoreceptor. It is yet to be determined if having a colour vision system where perceptual colour shift levels is constant under all illuminants

(honeybee colour vision) is more advantageous than a colour visual model that produces a variety of perceptual colour shift levels under different lighting conditions in a real world foraging example of the bee. It is likely that it is computationally less expensive for a colour visual model to have a fixed perceptual colour shift for a variety of changing illuminants. However, for certain colour visual models, it may be necessary to be specifically adapted to shorter colour shift levels under a more regularly encountered light condition such as in forest shades for example (Menzel et al., 1989).

Our model demonstrates the biological usefulness of various computational colour constancy methods, where the bee uses its colour vision to perform a colour choice task to resolve a real world problem, that is, the ambiguity of flower colour under changing illumination. The results also highlight the importance of surround and scene content for bees to achieve colour constancy (Werner et al., 1988). Our experiments show quantitatively the amount of nectar collected under changes of illumination under the assumption of different computational models to explore how well the actual colour visual model does in a given meadow. In previous chapters I have demonstrated the significant impact of flower colour discrimination for bee foraging performance under changing illumination, and how it improves the ability to achieve colour constancy in a real world scenario. Under changes of different lighting conditions we can assume that the bee will face a variety of computations to determine the level or amount of perceptual colour shift levels besides the vector or direction of the perceptual colour shift in order to perceive the actual reflectance of an object. However, it is uncertain if having to compute the amount of perceptual colour shift under unknown light change has any affect on foraging performance in the bee in an ecological environment faced with a variety of light changes.

In colour constancy, it has been suggested in many studies that surrounding scene may aid in the evaluation of colour under changes of illumination (Smithson and Zaidi, 2004, Linnell and Foster, 2002). This chapter shows that computational colour constancy mechanisms that make the use of scene surround achieve colour constancy particularly better than just a von Kries receptor adaptation response mechanism alone. Histogram equalisation is an interesting computational image-enhancing algorithm since it is relatively simple to compute and mostly produces high contrasting colours with good effect. This results in good colour contrast and has previously been shown to be a mechanism in the fly retina (Laughlin, 1981) and as demonstrated in this model it also works well as a colour constancy mechanism in a successive colour constancy task, like the task faced by bees in nature (Chittka et al., 2001). The more spaced apart the colours are perceptually, such as under the assumption of histogram equalisation or White patch, the better the performance of nectar collection by the bee-agent under varying illumination. For example, histogram equalisation performs 33% better than a colour blind bee. The White patch calibration performs 11% better than a colour blind bee. A Gray world algorithm performs poorer compared to than just the assumption of a von Kries adaptation (t-test: $t = 2.94$, $df = 32$, $p < 0.003$). As it has been demonstrated that the enhancement of

colour contrast is a mechanism found in a variety of animals such as fly (Laughlin, 1981), fish (Neumeyer et al., 2002) and bees (Neumeyer, 1980), the role of colour contrast in colour vision may not only aid object detection but as demonstrated in this chapter may also help achieve colour constancy.

In the next chapter, a plant community that faces seasonal changes in illumination caused by natural daylight being filtered through a leaf canopy canopy that change the light reaching the understory flowers is used into the agent-based model. I wish to determine how well these flowers are recognised under changes of light by bee pollinators and if the strategies of flower colour to ensure colour constancy explored in this chapter and the previous chapter are applicable to a real world plant community undergoing changes in light environment.

6 Influences of natural light in the role of plant colour occurrences in achieving colour constancy in bees

6.1 Introduction

For flowers, insects act as pollen vectors and play a significant role in the determining the fitness of plants (Darwin, 1876, Kevan, 1978, Feinsinger, 1983). Plants use various strategies of exploiting the learning and sensory capacities of the insect that favour exclusive within-species pollen transfer, for example by promoting flower constancy (see Waser (1986) for review), i.e. pollinators' tendency to restrict visits to a single species, using colour as one of several cues (Chittka et al., 2001, Chittka and Menzel, 1992, Chittka and Waser, 1997, Waser, 1983b). Flowers can exhibit a wide variety of colours that in turn are associated by the insect with reward, usually nectar or pollen (Waser et al., 1996). Thus it is important that flower colour remain unambiguous under variations of light to ensure that the bee can recognise it. The investigation of light environment and perceptual colour shift of plant flower colour have been investigated in Chapter 3 and 4 to determine the factors involved in achieving colour constancy. In Chapter 3, modelling flower colour under different light on the bee colour space revealed that colour constancy in the bee is poorer in regions where colour discrimination (bee colour difference sensitivity) ability is good. Chapter 4 revealed that increasing perceptual colour distances in the learning phase of colours later improves the application of colour constancy under changes of illumination. Colour discrimination has not been demonstrated to achieve colour constancy except in Abrams et al., (2007). However if colour constancy is poor for colours for which colour discrimination is good, then how do flowers exposed to often drastic changes in illumination such as understory plants attempt to overcome this challenge? Are they under selective pressure to either diverge in colour (to achieve high colour distances, in the same way as that which I demonstrated in the *ideal meadow* in Chapter 4) or to adopt floral colours that achieve the least perceptual colour shift (such as flowers with short colour shift from daylight to forest shade in Chapter 3 under honeybee colour vision), or both strategies to achieve colour constancy under changing illumination?

In temperate deciduous forests, the light climate changes substantially over the year. Early in the season, trees are devoid of leaves, and plants blooming at this early time are exposed to direct skylight, much the same as they would if the presented their flowers in open fields. Over the next few months, the canopy gradually closes, generating patchy light conditions in a transition period, and finally generating homogeneous illumination dominated by transmission through, and light reflected

from, green leaves (Arnold et al., 2009b). Late in the season, as leaves in the canopy wilt, the light beneath becomes patchy once more. Plant species in bloom may thus face very different challenges in terms of colour identification depending on their flowering times. I will investigate the phenology of an empirically determined set of flower colours in a temperate Maple forest from March to September undergoing photic changes to explore how flowers might adapt their colouration to the prevailing light climates, using two sets of model calculations.

As a real-world system for this investigation, a Central European Maple forest is used as a case study of an environment that undergoes photic changes through early Spring into late Summer, caused by the gradual obscuration of light to understory flowering plants when Maple trees begin budding and developing leaves (Richardson and O'Keefe, 2009). I investigate if the flowers that bloom under a forest canopy have different colours from those in late Spring or late Summer when the canopy is not closed, and what the nature of that difference is. In the second investigation, the agent-based model bee learns the colour of flowers under lighting when a canopy has not grown to obstruct daylight, to continue foraging on the same flowers from one light (daylight) to when trees begin to grow leaves, obstructing light reaching the flowering plants beneath (forest shade) (Richardson et al., 2006).The performance of the bee-agent in nectar collection from flowers in the Maple forest is compared to a set of 1000 random flower colours that have the same nectar production as the nectar that was assigned to the flowers that bloom in the Maple forest in the agent-based model to find out if the flowers that grow in the Maple forest are better suited for identification or any different by colour than random flowers in place of the actual Maple forest flowers. If so, I will analyse the properties (i.e. colour distance and perceptual colour shift) in colour that promote receiver colour constancy.

Understory plant species may flower at particular times for various reasons. Amongst other factors, the quality of light (Cerdan and Chory, 2003) and temperature (Primack et al., 2004, Fitter and Fitter, 2002) are known to affect flowering times. Many understory flowering species begin budding in early Spring to make the most of unobstructed light before the development of a canopy that would limit the amount of light reaching these understory flowers (Sparling, 1967, Bormann and Mahall, 1978, Muller, 1978). Most of the growing season sees some flowering plant species obstructed by foliage, generating shading (low light intensity) and a green light climate (light filtered through canopy) (Richardson et al., 2006). The implications on the foraging performance of pollinators with approximate colour constancy are as yet unknown.

Arnold and Chittka (2012) experimentally explored the implications of patchy light and found that unfamiliar illuminations are largely avoided by bee pollinators most probably because of high error rate in correct flower colour recognition caused by the change in illumination distorting flower colour. However visits to flowers under light other than normal daylight do improve with experience.

It is not known if flower colours occurring at certain times in a year are a strategy to avoid shaded or shifted light conditions in order to be highly conspicuous to pollinators. This will form a part of the investigation to find out if flowers occurring in challenging photic environments generate colours that are best suited for bee colour vision.

It has been observed that flowers aggregate in certain parts of colour space more than others (Chittka, 1997); for example there are more blue-green bee colour flowers than there are UV bee colour flowers in the general population of flower colours (Kevan et al., 2001). It is uncertain why this is the case since there is sufficient learning capacity in the bee to be trained to such rare colours (Menzel, 1967) so one would assume that flowers would benefit from producing such colour pigments. The aggregation of plant species occurring in certain areas of the colour space rule out that flowers can be freely varied to promote colour discrimination ability by bees, since otherwise we would expect floral colours to be distributed evenly across the colour space to encourage largest colour distances and in turn correct colour discrimination between such flowers, as explained by Chittka, (1997). However, while flower colours are never ideally distributed for colour discrimination, there is at least evidence that in some plant communities they have diverged more than expected by chance, presumably as a strategy to ensure that colours are distinguishable (Feinsinger, 1983, Gumbert et al., 1999, McEwen and Vamosi, 2010). However this is not observed in every flowering plant community (Gumbert et al., 1999). One plausible reason is that certain coloured flowers are best suited to avoid large colour shifts under changing light, and these colours happen to be the ones that predominantly occur in the bee colour space. This was first pointed out by Dyer (1998) and investigated in more detail (Dyer, 1999, Dyer and Chittka, 2004b), however it was not established if there existed an evolutionary benefit in reducing perceptual colour shift rather than increasing colour distance between flowers to improve performance in nectar collection under varying illumination.

6.2 Methods and materials

The investigation specifically focuses on the two transition periods in illumination, which take place from April to May (daylight to forest shade) and July to August (forest shade to small gaps) (Richardson et al., 2006) and to see how well the bee performs given the colour signals that are available in the Maple forest in those months compared to random flowers.

6.2.1 Perceptual colour shift and colour discrimination during annual transition phases in illumination in the maple forest

6.2.1.1 Set up

The Maple forest phenology from March to September is used for modelling sets of flower species among which modelled bee agents will forage. This Maple forest site is located in Germany, near

Strausberg (Brandenburg) and consists of 24 flowering plant species studied by Gumbert et al., (1999). Floral reflectance spectra of these flowering plants are retrieved from the floral reflectance database. Figure 6-1 shows the flowers and the flowering times in the Maple forest. Each flower is assigned a nectar standing crop distribution. Nectar standing crop distributions are reused in each of the months and are assigned to the same flower species where applicable, or if the same flower does not appear in the next month then this same nectar standing crop distribution of the previous month is applied to one of the new flowering plants in the former month to ensure, for our simulation purposes, that nectar availability is comparable between the months.

6.2.1.2 Simulating seasonal light changes in the agent-based

In the Maple forest, the lighting conditions change in two phases – in Spring when the canopy above grows enough to obstruct the light, i.e. in the period from April to May (Richardson et al., 2006, Muller, 1978). In Figure 6-1, the red arrows indicate the flowers that undergo changes in illumination from daylight to forest shade. In late Summer when the colour of the leaves changes from green foliage to yellow and orange, the light is not being filtered through green foliage to produce a 'forest shade' light. In Figure 6-1, the blue arrows show the flowers that undergo changes in illumination from forest shade to small gap light. In this part of the investigation, the model bee forages on flowers that flower in the transition phases between changes of light. The agent-based model measures the amount of nectar collected under the actual flowers occurring in the Maple forest, compared to a set of a 1000 simulations generating random flowers in place of the real Maple forest flowers.

The agent-based model is based on the same set up as in Chapter 4, where the model bee visits 250 flowers in each simulation run. Under changes of illumination the model bee first learns the flower colour under the canonical light (for April to May this is day light, for July to August this is forest shade) during the first 50 flowers it visits. Nectar collection is recorded for after the illumination changes, which is 200 flower visits in each set up. The actual Maple forest flowers simulation runs 20 times. When random flowers replace the actual Maple forest flowers in the simulation, there are 1000 runs of the simulation, where each run selected a random flower to replace the actual Maple forest flower from the Floral Reflectance Database.

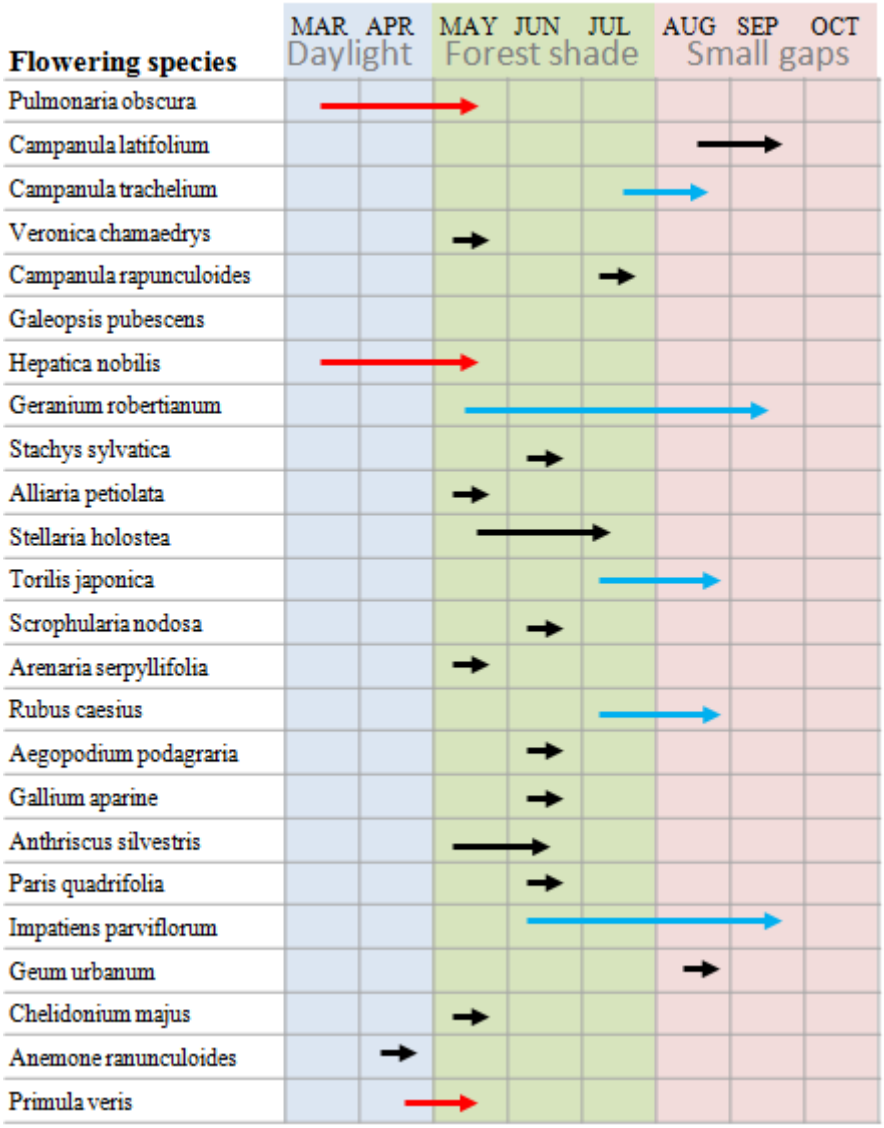


Figure 6-1. 24 Flowering species phenology in a case-study Maple forest plant community (Gumbert et al., 1999) from March to September. Arrows indicate flowering times across months. Red arrows indicate changes of illumination from daylight to forest shade light, blue arrows indicate changes of illumination from forest shade to small gap light whilst the plant is still flowering. Black arrows indicate flowering times within one illumination. March to April flowers are mostly in daylight unobscured daylight (here modelled with normfunction D65) where leaves in the canopy have not yet grown to obscure daylight. In May the leaves on the Maple tree forest have fully grown and obstruct normal daylight, thus the light reaching the understory flowers is forest shade. Later in August, the leaves change colour, and the filtered light is no longer 'green' of forest shade, but of small gap light, obstructed and slightly red-shifted lighting. This transition of light is simulated from forest shade light to small gap lighting.

Simulation of months	*Changing light condition*	*Flowers in the simulation:*
April to May July to August	Daylight (April) to Forest shade (May) Forest shade (July) to Small Gap (August)	3(*obscura*, *nobilis*, *veris*) 5 (*trachelium*, *robertianum*, *japonica*, *caesius*, *parviflorum*)

Table 6-1. Simulation of flowers flowering in the months where changes of illumination occur across different months in the Maple forest plant community. There are two points in the year when this happens, April to May or July to August

6.3 Results

6.3.1 Results I: Colour differences between flowers in early Spring and late Summer

For the flowering plants in April to May plotted, an average perceptual colour shift of the three flowers is less than 0.03 cu perceptual colour shifts from daylight to forest shade (Figure 6-2). The average colour distance between the three flower colour pairs between April to May is 0.58 cu on the colour hexagon, which is different than the distances between colour pairs from a randomly selected data set of flowers, where the average colour distance is 0.25 cu (see Figure 6-3).

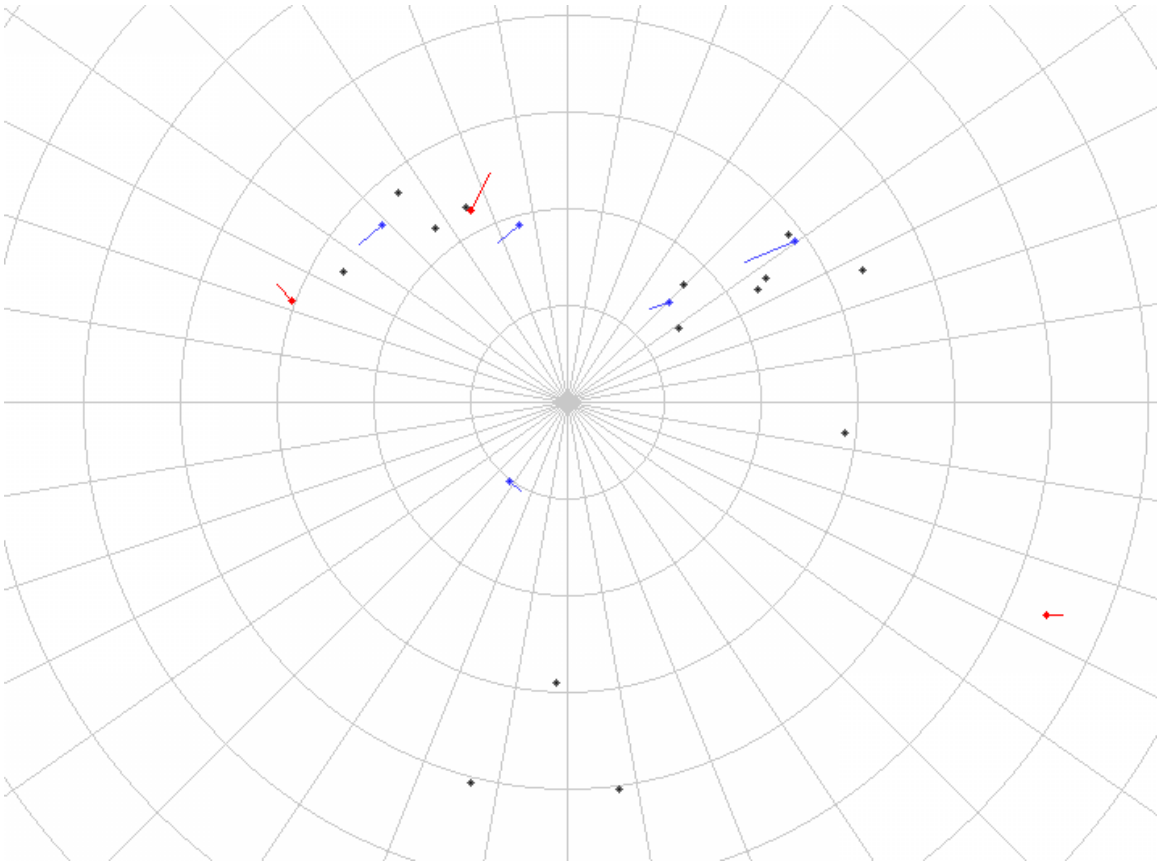


Figure 6-2. Colour loci of the Maple forest plant community flowers (24 flowers) in the bee colour hexagon, and perceptual colour shift under changing illumination. The centre of the diagram represents the centre of the colour hexagon. Each sector separated by the lines is 10^{o} of the colour hexagon. Each radial circle step represents a colour distance of 0.1 cu. Red loci represent flowering plants from April to May with the red line representing perceptual colour shift from daylight to forest shade. Blue loci represent flowering plants in July to August with blue line representing perceptual colour shift from forest shade to small gap light. Black loci plots represent the remaining flowers of the Maple forest that do not flower across changes in the light environment.

When compared to the July to August flowers in forest shade to small gap light, colour distances between the flower pairs are shorter than nearly 0.3 cu than flowers blooming April to May as shown in Figure 6-2 and Figure 6-3.

There is no significant difference in colour distances between flower colour pairs blooming between July to August compared to 1000 randomly selected flowers (t-test, $t = -1.89$, $df = 2$, $p < 0.482$ see Figure 6.3). Maple forest flowers blooming between April to May are suggestive of having higher colour distance between flower colour pairs compared to 1000 randomly selected flowers , though this does not achieve the statistical significance (t-test, $t = -0.04$, $df = 9$, $p = 0.09$, see Figure 6.3). I will next simulate these two transition periods using the agent-based model to investigate if the nature of the suggestive difference between the flower colour pairs blooming in April to May could improve the performance of nectar collection under varying illumination.

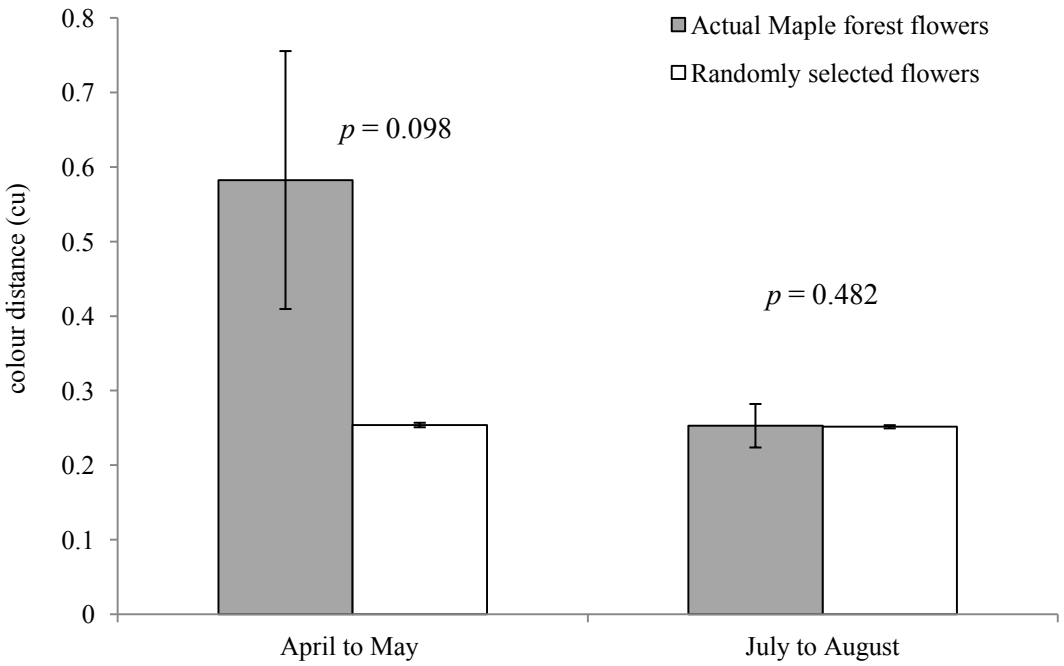


Figure 6-3 - Average colour distance (cu on the colour hexagon) between Maple forest flower colour pairs blooming between April to May (n=3, ± SD) and July to August (n=10, ± SD) (colour distances of actual Maple forest flowers shown as grey bars), and colour distance between same number of colours pairs as actual Maple forest flowers 1000 times between randomly selected flowers from the Floral Reflectance Database (n=1000, ± SD) (colour distance between colour pairs shown as open bars). T-test is used to show the significant difference (p value) in colour distances between flower colour pairs between random or actual flowers. There is no significant difference between colour distances between colour pairs of actual maple forest flowers or random flowers, but colour distances between colour pairs in April to May are suggestive of higher colour distances than random.

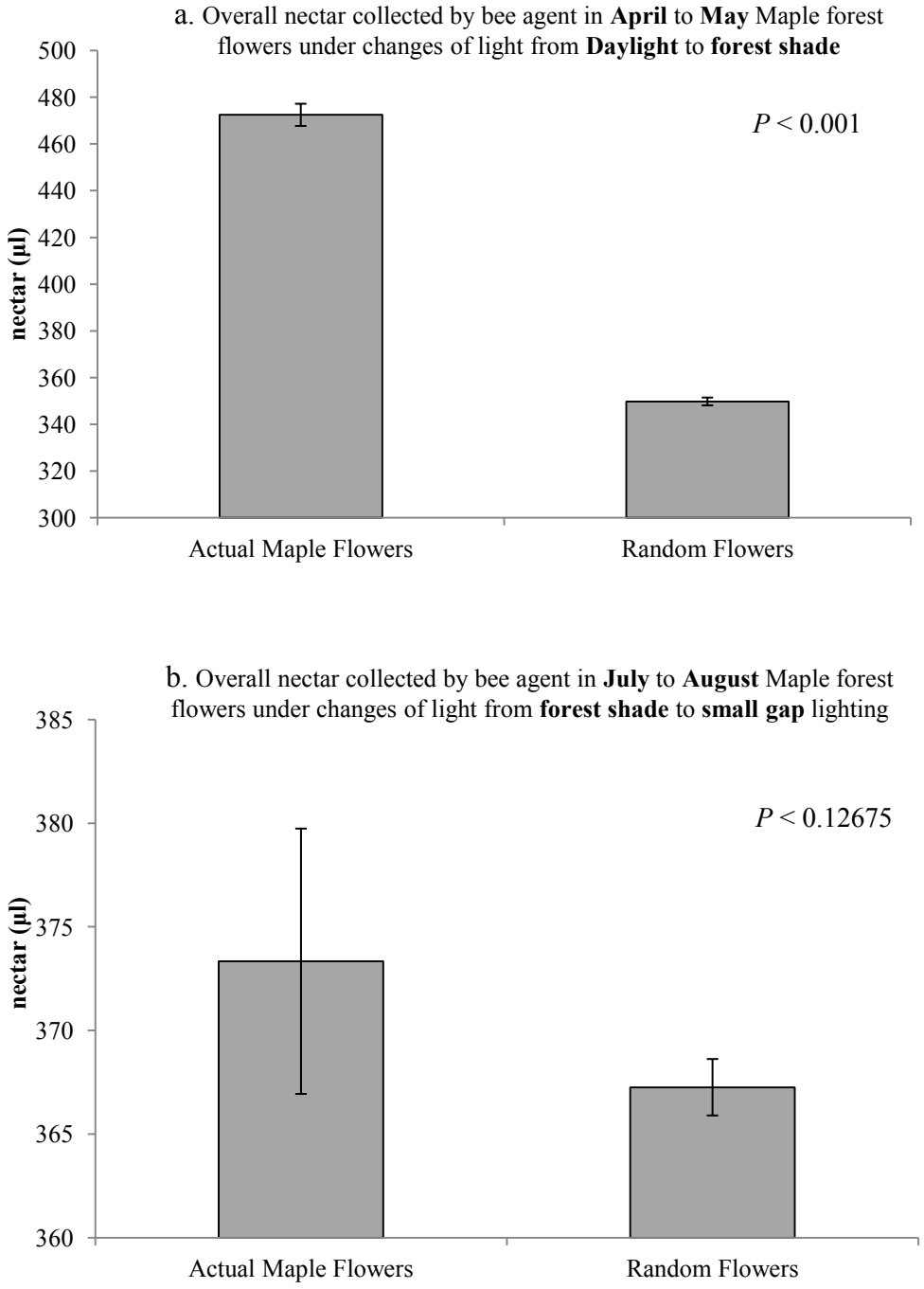


Figure 6-4. Average nectar collection by the agent-based bee foraging model with actual Maple forest plant community flowers flowering under changes of illumination. a.) April to May Maple forest plant community flowers flowering from daylight to forest shade light (n=20 simulation runs, each with 200 flower visits, ± SD) and random flowers (n=1000 simulation runs, each with 200 flower visits, ± SD). b.) June/July to August Maple forest plant community flowers flowering from forest shade to small gap light (n=20 simulation runs, each with 200 flower visits, ± SD) and random flowers (n=1000 simulation runs, each with 200 flower visits, ± SD). T-test is used to show the significant difference (*p* value) between the nectar collected between random or actual flowers. There is a significant difference between nectar collected with actual maple forest flowers than random flowers under the light change in April to May.

6.3.2 Results II: Effects during the illumination transitions in early Spring and late Summer

The amount of nectar collected by the bee agent in the agent-based simulation in the actual Maple forest flowering plant community within April to May under changing illumination from Daylight to Forest shade is significantly more than when it was tested against a same model with random flowers in place of the actual Maple forest flowers, with 1000 random flowers in their place (t-test, $t = 24.32$, $df = 24$, $p < 0.0002$). This means the plants that flower in the period when there is a change in light environment (i.e. Daylight to forest shade between April and May) are suited to be recognised by the honeybee colour vision under the change of light that occurs.

This is however, not the case for July to August flowering plants that are under changing illumination from Forest shade to Small gap lighting. The amount of nectar collected in the control experiment (i.e. randomisation), appeared not to have produced any different results from its corresponding random flower set (t-test, $t = 1.15$, $df = 39$, $p = 0.126$). This means that there is no difference between the flowers in colour recognition by the bee colour vision that occur during the illumination transition from July to August.

6.4 Discussion

Under changes of illumination, it is shown that plants that occur in the Maple forest flowering across months from April to May are best suited in being recognised and identified compared to random flower colours in place of them, possibly due to the high colour distances between the colour pairs. However this was not the case for changes of illumination from July to August, there was no difference between the nectar collected under changing illumination from actual Maple forest flowers in July to August at these flowering times in the month and random flower colours. When the flowering plants available between April and May are compared to July to August, the loci of flower colours shown under April to May plants on the bee colour space show large colour distances compared to flower colours in July to August. Given that nectar collection under changing illumination is better achieved between April and May, the flowers were best suited to promote colour constancy in the bees' receiver system.

Maple forest understory flowers do significantly better than random flowers in Spring under variations of illumination caused by the growth of an overstory canopy, in that the real flower diverge significantly more in colour from random. It was thought that low intensity or shifted light might reduce foraging performance; however this may be overcome in plant communities by adopting flower colour best suited for the challenges of understory photic light throughout the growing season.

From the nectar collection rate from the agent-based model bee obtained from the simulation, this is overcome by diverging in flower colour. This strategy of colour divergence from co-occurring flower colours not only promotes better flower constancy (Chittka et al., 2001) and better visitation for rare flower colours (Gumbert et al., 1999), but from the results obtained in this chapter colour divergence is also a strategy in achieving better colour constancy under changes of illumination.

It is thought that the spectral sensitivity of bee *Melipona quadrifasciata* vary for adaptation to the light in the environment that the bee is mostly exposed to (Menzel et al., 1989). However, it is unknown if this model of spectral sensitivity best suited to that of the *Apis mellifera*, the spectral sensitivity model used in my agent-based model simulation. It would be useful to see if the same experimental model using the spectral sensitivity with blue receptor shifted to shorter wavelengths would improve colour constancy under a green light climate like forest shade. However, considering the flowers occurring in the Maple forest provide a better foraging success than random flower colour, it might not necessarily be useful for some Hymenoptera species to achieve this, since not all are in green light climate throughout their foraging lives.

Considering the flowers in the Maple forest are best suited to be identified under changes of illumination by the bee, flowers may have been under selective pressure to appear in the colours to ensure they are recalled by the bee even when there are changes of light such as from the time when the forest canopy is not closed and daylight reaches the flowers, until the canopy above develops and obstructs daylight and thus produces a green light climate. In this chapter, using the Maple forest flowering times and light, we demonstrated that these flowers were best suited in being recognised compared to any random flower set to substitute them in the same simulation set up. When these flowers were observed on the bee colour space, it appeared that they achieved two fundamental properties that made them suitable for the changing light environment that these flowers were in: 1) low perceptual colour shift, and 2) large perceptual colour distances between the colours that were to be later encountered in the periods where light changes.

7 Discussions and future work

7.1 Discussion

In this thesis, I have explored the biological significance of colour constancy in the bee and investigated this through the use of modelling and simulation of flower colour under natural light as perceived by bees. Throughout the thesis, I have built the investigation of colour constancy in the bee by a) observing flower colour in the bee colour space and quantitatively measuring perceptual colour shift under changes of illumination of particular bee colour hues, b) Measuring the performance of bees through foraging simulation under changes of illumination, c) Testing the biological significance of different retinex colour constancy algorithms in the face of a bee foraging under changing illumination, and finally d) investigating if bloom under forest canopy have different colours from those in early Spring or late Summer when canopy is not closed, and if that nature of difference improves performance in nectar collection in the bee.

Colour cues provided by flowers are used as a signal by pollinators to associate reward provided by the flowering plant (Daumer, 1956, Daumer, 1958). What is known is that a visitation to flowering plants by bee is non-random (Waser, 1983a, Waser, 1983b, Waser, 1986, Chittka et al., 1999), and flower colours are learnt by pollinators. However, bees face foraging conditions where light environment changes, for example different habitats (such as a forest or woodland) or times of the day (early morning or before dusk) and weather (cloudy or sun shine) (Neumeyer, 1998). Without the mechanisms of colour constancy involved, the combination of the illumination change can alter the colour of an object. Colour constancy is thought to be essential for any animal with a colour visual system, and bees and flowers provide an excellent model system to study the biological relevance of colour constancy. Through modelling of perceptual colour shift under changes of natural light environments, it was found that different lights simulated different levels of perceptual colour shift (Neumeyer, 1981) of the same flower colour and that there is no single model to determine a universal perceptual colour shift under change of illumination on the bee colour space for colour hues. Colour discrimination ability affects colour constancy, where if a colour visual system is able to discriminate fine differences in colour it could jeopardise colour constancy which requires the colour visual system to generalise. Studies in the colour vision of stomatopod crustaceans have shown to overcome this through having numerous narrow photoreceptors that overlap (Osorio et al., 1997, Cronin and Marshall, 1989). In bees however, this is overcome by having the ability to discriminate colours and thus being able to learn these colours (Chittka et al., 2001), which has shown to contribute to

successful colour constancy. Through quantitative measurement of perceptual colour shift of flower colour under light change, most large perceptual colour shifts are in the regions of the colour visual spectrum where colour difference sensitivity is good, and vice versa.

Although there is a difference in colour choice and performance caused by changes in perceptual colour shift, this appears to have less impact in performance compared to perceptual colour differences in co-occurring flower species. Flower colours are learnt better by the bee and flower choice is less random when colours are distinct in colour, and diverge in colour from other colours in the plant community. It is thought that due to this, flowers may strategise to diverge from others in the plant community or form a mimicry ring (Dafni, 1984, Gumbert et al., 1999, Chittka et al., 1997). The results in chapter 4, 5 and 6 also demonstrate that under changing illumination, the ability to accurately discriminate against other colours improves colour constancy. In the bee colour space however, flowers are not spaced equally as would be expected to achieve high divergence and differences in colour. Instead, certain flower colours predominate, for example bee blue-green in nature, compared to pure UV flowers that are found to be more rare in nature compared to other flowers (Chittka et al., 1994). However the importance of colour divergence is supported by the bee colour difference sensitivity. Bee colour discrimination is optimal at regions of colour reflecting blue-green colour (Helverson, 1972, Kevan et al., 2001). This may explain that flowers are under some evolutionary pressure to adopt flower colours that are distinct and easily discriminated by the bee from other flowers.

A combination of low perceptual colour shift and high perceptual colour distances can improve the performance of nectar collection, but more importantly in my investigation in Chapter 4, it indicated that the ability to discriminate co-occurring flowers is important to achieve colour constancy in a foraging bee. Low colour shift under changing illumination in a real-world colour choice task is not enough to achieve colour constancy. This is the first study to investigate the impact of both perceptual colour shift and colour distance of co-occurring flowers to achieve colour constancy in pollinators such as bee relying on flower colour to improve performance in nectar collection.

To further investigate flower colour strategies under changing illumination (i.e. low perceptual colour shift or divergence in colour from others in the plant community), the Maple forest plant community phenology was investigated. Flowers flowering across changes of illumination (i.e. daylight into forest shade, from April to May) appear to be advantageous than any random flower colour. Compared to the results from July to August, there was no significant difference in nectar collection performance compared to if random flowers replace the flowers flowering at the time from July to August, though on average, nectar collection was still higher. When comparing the perceptual colour shift levels and overall colour distances, it was found that both low perceptual colour shift and high

colour distance between the flowers is observed for flowers appearing in April to May under light changes from daylight to forest shade, but large colour distance was a prime factor in achieving successive colour constancy. This is the first observation of flower colour attempting to adapt to the changes of illumination in the light environment so that they may be easily recognised by bee pollinators. This is also the first explanation of what strategy was employed to achieve better performance in nectar collection under changes in light environment and that flower colour strategy could aid colour constancy in the bee. A variety of studies have found that larger colour distances between co-occurring plant communities improve bee flower constancy (Chittka et al., 2001), however none have provided a link between bee colour constancy under changing light environments and flower colour occurrences. The colour divergence strategy is improving performance under changes of illumination in two ways. It is enabling the bee to learn the colour due to the distinctiveness of it from other flower colours. Colours that are well learnt can then be recalled (Kulikowski and Walsh, 1991), and this is fundamental in achieving successive colour constancy. In bees, a flower colour that is confused for others in the same plant community may be difficult to learn and may later not be recognised under a change of illumination as it cannot be recalled from memory. Flowers that are more similar to each other risk 'metamerism' under changes of illumination (Wyszecki and Stiles, 1982). Under a change of illumination, the perceptual colour shift of a colour object may be in the direction of another colour that the subject had learnt, say the canonical light (or the training light for the bee). However this is less likely to occur if colours are perceptually distinct from each other. In the Maple forest plant community study in Chapter 6, plotting flower colours flowering across months undergoing changes in light environment, we examined that distinctive flower colours from others in a plant community may be suited to promote colour constancy and that this is observed in the case of the flowers blooming under the transition of light change between April to May in the Maple forest.

Under differential conditioning with a distractor present, bees can fine-tune discrimination of colours (Dyer and Chittka, 2004a, Giurfa, 2004). However given the natural environment (e.g. a patchy distribution of flowers) and the poor bee visual acuity, bees are regularly faced with flowers one by one, in a successive manner which usually results in slightly inferior colour discrimination compared to differential conditioning methods. Under absolute conditioning (the natural condition the bee usually forages in), bees generalise more broadly than after differential conditioning. One of the questions posed by Dyer & Chittka (2004a) was, what purpose do these different discrimination levels serve in bee foraging? It is assumed that if colour discrimination is very good then we can expect the bee to discriminate the differences between a colour in one illumination to another, and the colours look more different under changes of illumination. The tendency of the bee to be flower constant as a foraging strategy may be a cognitive strategy, rather than a lower level generalisation of flower colour as active 'choice', but it would be speculative to suggest that the colour constancy problem is solved

through this same strategy. For example, if flower colour did not change considerably under variations of illumination then a better level of colour constancy is achieved by generalising flower colour, which is possibly achieved through strategies of flower constancy. Thus generalisation would be a better strategy to achieve better colour constancy.

A variety of computational colour constancy mechanisms attempt to use scene analysis, to estimate the illuminant, or to use statistical ensemble to estimate the surface reflectance (Smithson and Zaidi, 2004, Linnell and Foster, 2002). Computational colour constancy mechanisms have not before been assessed based on the biological significance of the subject correctly making colour choices. Assuming certain computational colour constancy mechanisms, performance is improved significantly. These colours observed in the bee colour space are spaced further apart than the flower colours under computational colour constancy mechanisms that performed poorly. Perceptual colour shift was similar between the computational colour constancy methods tested under changing light environments, which means that in a successive colour constancy task the best computational colour constancy mechanisms would be one which makes colours very distinct from each other. This would support the strategy of flowers that diverge in colour to ensure colour constancy under changes of illumination (see Chapter 5).

Through modelling flower colour, and measuring performance of bees making flower colour choices under assumptions of different colour visual models, it has been found that co-occurring flower colours that diverge in colour from each other help in promoting colour constancy in the bee under changes in the light environment. Furthermore, through experimentation of normal plant communities and highly diverse plant communities (in floral colour), successive colour constancy is best achieved by ensuring options and targets of flowers are different in colour from each other, and can be distinguished – this is advantageous for pollinators as it aids learning (Kulikowski and Walsh, 1991). However, this is not necessarily always a strategy employed by flowers, although the Maple forest plant community case study in Chapter 6 is one example of plants that may apply this strategy to overcome the challenges of harsh changes in the light environment which would ambiguate flower colour. This is not applicable to all plant communities that undergo large changes in light environment; in some cases flower colour may converge in colour to others in the plant community (Feinsinger, 1983, Waser, 1986). My study highlights the features of colour that would help promote colour constancy, and such strategies have been observed in one case study of a plant community undergoing harsh changes in the light environment (Chapter 6).

Research area	*Main findings/Contributions*
Resources for modelling colour vision	Development of FReD for modelling colour vision (Arnold et al., 2010)
Flower colour trends across the honeybee colour visual spectrum	Flower colours that are easily discriminated in shorter colour distances are also the colours that often have larger perceptual colour shift under changing illumination Short perceptual colour shift are achieved by non-overlapping photoreceptors
Flower constancy as a cognitive strategy in colour choice in bees	The development of a temporal based model of a bee foraging on coloured flowers using the flower constancy strategy (Faruq et al., 2010)
Successive colour constancy and the role of colour distinctiveness	The more distinct colours are in a scene, the better the results of achieving colour constancy in a successive manner Low perceptual colour shift is important, but without the ability to discriminate the differences between colours, colours are not correctly learnt which is vital in successive colour constancy
Colour constancy in temporal changes in light within habitats	The type of flower colours available can impact the performance of colour vision constancy in habitats where light changes at a temporal scale, and thus flower species may be under selective pressure in challenging light environments
Computational colour constancy in successive colour choice task	The computational algorithm that increased the perceptual colour distances between the available colours resulted in the best performance in nectar collection in the bee agent irrespective of the amount of perceptual colour shift There were insignificant differences in performance under the same computational colour constancy model under changes of different illuminants. It is assumed that if performance varied across different lights it may be more computationally expensive if the amount of perceptual colour shift under an unknown illuminant is not the same for any illuminant

Table 7-1. Main contributions and findings made by this thesis to the field

7.2 Future research directions

The floral reflectance database is a collection of not only raw reflectance spectra, but also makes no *a priori* assumptions about the colour vision system viewing the flowers. This vast amount of spectra data has already been used in multiple studies of animal colour vision. With samples from all over the world, collected from a diverse variety of habitats, the database has applications in meta-analyses. Its usefulness has also been anticipated on a smaller scale, to provide detailed information on the exact

colour of flowers of particular species. There is much potential in the Floral Reflectance Database, since the data can easily be modelled into any colour visual model and colour space, as was done in Chapter 3.

The agent-based modelling environment of foraging bees was developed to overcome the conditions that produced different results of colour constancy and to abstract flower constancy and bee foraging. It also allows colour visual models, and colour processing mechanisms to be replaced, flowers and their arrangement in the model to all be changed. This opens a pool of potentially quantifiable analysis of colour vision and the ecology of colour vision in pollination systems. One can easily test systems of plant communities against a null model as I had done in Chapter 6. However it would also be useful to develop a simple genetic algorithm that could find optimal flower colours for a given light environment, colour visual model, or computational colour constancy mechanism, tested each time in the agent-based model. These evolved optimal models can be compared against actual plant communities or ecological pollination systems that we find matching bee colour vision, where performance is tested based on nectar collection by the bee agent. The agent-based model provides a framework for testing hypotheses about bee foraging, perception and cognition, and there already exist useful ways to develop genetic algorithms that selectively evolve features that could be used to optimise bee foraging. It would be interesting to see resulting models selected by such genetic algorithms, such as if flower colours were distinctively different or same from each other, as being the most optimal solution for foraging bees.

Throughout the analysis of colour constancy in bees in this thesis, a main focus has been in looking at the two main features of colour vision – colour discrimination and colour constancy (i.e. perceptual colour shift) and their interaction in achieving colour vision constancy, measured by the level of nectar collection. In the agent-based modelling environment, there are other measureable properties, such as level of flower constancy, time or consecutive flights from the same flower species. The measurement of these may be of interest when foraging strategies of the bee agent are changed, or if the distribution of resources in the meadow is no longer random (i.e. if the flowers are distributed in clusters). The agent-based simulation can provide, on a temporal-scale the behaviour exhibited by the bee-agent for those interested in studies on resource distribution and foraging strategies in animals.

The Floral Reflectance Database alongside the agent-based modelling environment, provide a complete tool for the analyses of flower colour as perceived by bee pollinators providing an abstraction to the complexity of pollination systems.

Future research topics	*Possible research direction*
Models for colour vision and trends of natural colours as perceived by the animal	FReD can accommodate any colour visual model to calculate the loci plot of the flower colours that are available into the colour hexagon, the colour triangle or the COC model for a trichromatic vision from 300nm to 700nm. For example models for flower colours as perceived by the *Melipona quadrifascata* which are commonly foraging in forest shade (Menzel et al., 1989) could be observed to determine the suitability of flower colour based on colour discrimination ability and colour constancy.
Genetic algorithms for evaluation or generation of colour constancy mechanisms	With the use of agent-based model, an adaptive algorithm such as a genetic algorithm can be used to build/adjust or select the most suitable habitat of co-occurring flower colours for a particular colour visual model or vice versa based on the performance of nectar collection by the agent-based model bee. This can help reveal if flower colours that are co-occurring are most suitable and adapted to be easily recognised by the given colour vision system.
Analyses of flower colour in natural habitats in achieving colour constancy	Detailed spatial distribution of flower species in different habitats can be analysed in the agent-based model to obtain the benefits of different strategies of clustered resources based on the performance of the agent-based model Bee The benefits of convergence or divergence in flower colour in a habitat can also further be analysed (Gumbert et al., 1999, Chittka et al., 1997), and also combined with the use of genetic algorithm to observe if convergence of divergence is preferred given the availability of flower species in a habitat.
Evaluation of cognitive strategies or low level neuronal coding in making colour choice	The agent-based model built is based on the flower constancy type cognitive solution in making colour choices. The agent-based model is capable of accommodating different foraging strategies or colour choice methods (Menzel and Muller, 1996, Greggers and Menzel, 1993). This can further be used to model the differential conditioning and simultaneous colour discrimination and colour constancy in answering if colour generalisation is truly a low level neuronal coding mechanism response in colour choice leading to flower constancy, or a cognitive strategy (Dyer and Neumeyer, 2005, Dyer and Murphy, 2009, Dyer and Chittka, 2004a).

Table 7-2. Possible research direction in the field related to the thesis

7.3 Conclusions

It has long been investigated which computational mechanisms are involved in colour constancy, and what the adaptive benefits of various algorithms might be. It is easier to study colour constancy if the colour identification is crucial to the fitness of individuals of a species, as is this case in pollinating insects. In addition, in this study system, the colours in the environment are themselves under pressure to be of a particular colour to ensure they are recognised, identified and visited. This is why the flower colour and bee colour vision make an exceptionally useful model to study colour constancy. Bee colour constancy is imperfect, and different colour hues will produce different levels of perceptual colour shift and different illuminants will change the spectral content of the reflected colour. For this reason, flower colour in plant communities in light environments that undergo large changes in illumination would be under selective pressure to continue to be different from other flowers, and to be of a colour that does not elicit a large perceptual colour shift under the change of illumination.

Flower colour appearance is non-random, both in small plant communities, and in a global model when the population of all known flower colours is plotted in colour space. In both modes (global and local), there is one very important feature in common - the selective pressure on flower colour to be visited by a pollinator. This is achieved by the receiver pollinator where the bee colour difference sensitivity is good and achieved by the signaller flowers with flowers diverging in flower colour in plant communities. Making colours distinguishable by the bee colour vision not only serves the purpose of successful colour discrimination, but also successful colour constancy.

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Glossary of terms

Absolute conditioning:	Only the reinforced stimulus (S+) is available. This often results in over-generalisation
Agent Based Model (ABM):	Also know as *multi-agent simulation*. A computational modelling method for simulating the interaction between agents (entities) in an environment
Agent:	An agent is an independent or individual entity with behavioural rules that interact with the entire system of the agent-based modelling environment. In the simulations developed, the active individual agent is the bee, interacting with the *patch* agents, the flowers.
Colour constancy:	The ability of a colour vision to recover the true reflectance spectra (colour) of an object, independent of the lighting. Colour constancy is approximate in both humans and bees.
Colour discrimination:	The ability to discern the difference between two different reflectance spectra (colours).
Colour distance:	The distance between two different coloured objects that provides a guide to the perceptual colour differences between the two colours under a given colour vision model. For example, the larger the colour distance is between the two colours then the better the chances are that the colour vision can accurately tell apart the difference between the colours.
Colour hexagon:	A chromaticity colour space diagram typically used for trichromatic insect colour vision based on the photoreceptor excitation as a generalised representation of colour opponency
Colour shift:	The distance between the same coloured object under two different illuminants is the colour shift. For example, the banana under sky light and the same banana under diffused light may produce a large colour difference of the same coloured object – i.e. the perceptual colour shift is large.
Differential Conditioning:	Another stimulus (non-reinforced stimulus S-) is available in the presence of a reinforced stimulus (S+). Once similar stimuli in differential conditioning methods have been reinforced, generalisation is reduced.
Flower constancy:	The tendency of a pollinator (usually bee) to stay faithful to one type of flowering species or morph, sometimes even though a more rewarding flower is available.
Gray world assumption:	A computational colour constancy mechanism based on the retinex theory that assumes on average, the colour of the scene is achromatic and so to estimate the illuminant, the average colour in the scene is used
Histogram Equalisation:	A technique of chromatic adaptation to enhance colour saturation in digital image processing. It is done by recording the frequency distribution of each colour channel and stretching the receptor response over the maximal range to provide a maximum receptor response of the scene across the colour

	visual spectrum.
Java:	Java is a programming language that was used to develop the package for the NetLogo agent-based simulation in order to connect to the FReD database and to carry out complex calculations that could not be done in NetLogo alone
MySQL:	MySQL is a Structured Query language used to retrieve data held in the Floral Reflectance Database
NetLogo:	NetLogo is a programmable agent-based modelling environment
Package/Extension:	A package is a collection of classes (in Java) consisting of modules which can be called (one imported from NetLogo) to carry out calculations or retrieve data in real-time as the simulation runs.
Patch:	A patch, in NetLogo vocabulary is a type of agent that makes up one cell in the grid. In the simulations developed, the patch agent is stationary and holds details of if a flower is available at that particular point in the map
PHP:	A web-based server-side scripting language used to code parts of FReD 2 website
Pollination syndrome:	The result of various flower traits formed to produce as signals that have evolved/adapted to suit the receptors of the pollinator.
Retinex theory:	Theory of colour constancy based on recovery of colour that is combined with both the adaptation response mechanisms at a retinal level and the cognitive recovery based on colour memory at the brain cortex. This theory was first mentioned by Edwin Land.
von Kries adaptation response:	An adaptation response mechanism to scale the response of the photoreceptors. For example if the scene observed produces a low response is one of the receptors due to shifted lighting then the intensity of the response in the receptor is weighted higher.
White patch:	A computational colour constancy mechanism based on the retinex theory (also known as *brightest patch*) to find the brightest point in the scene and assume this is white, by scaling the colours to this white point

Appendix I: flower dataset for chapter 3

1572 Flowers in FReD with the Flower ID and flower name used as the dataset in Chapter 3. The flowers are grouped in 10^{O} angle step in which the flower colour would be plotted in a honeybee spectral sensitivity colour vision on the colour hexagon under D65 daylight. The number in the brackets indicates the number of flowers in that 10^{O} angle out of the 1572 flowers. Each star represents an independent spectral sensitivity function, followed by the flower ID (searchable on FReD online) and then followed by the flower species name in italics.

0-10° (38): *431: *Euphrasia rostkoviana* , *679: *Lupinus polyphyllus* , *681: *Lupinus polyphyllus* , *1009: *Symphoricarpos albus* , *1136: *Erigeron alpinus* , *1173: *Calluna vulgaris* , *1427: *Mentha arvensis* , *1471: *Lathraea squamaria* , *1502: *Allium vineale* , *1540: *Aconitum septentrionale* , *1680: *Achillea millefolium* , *1712: *Epilobium anagallidifolium* , *1804: *Adenostyles alliariae* , *1828: *Dactylorhiza maculata* , *1927: *Traunsteinera globosa* , *1945: *Ranunculus spec.* , *2043: *Valeriana supira* , *2058: *Epilobium montanum* , *2238: *Abutilon spec.* , *2249: *Billbergia spec.* , *2257: *Myosotis alpestris* , *2348: *Canistum cyatiforma* , *2357: *Siphocampylus spec.* , *2423: *Solanum spec.* , *2494: *Galeopsis bifida* , *2518: *Vicia sepium* , *2594: *Epidendrum imatophyllum* , *2629: *Allium trifoliatum* , *2719: *Centaurea pallescens* , *2759: *Cercis siliquastrum* , *2764: *Fumaria densiflora* , *2807: *Fagonia brugueri* , *2818: *Gynandriris sisyrinchium* , *2875: *Launaea angustifolia* , *2920: *Tillandsia cacticola* , *2928: *Onobrychis squarrosa* , *2934: *Orchis tridentata* , *2999: *Satureja thymbra*

10-20° (30): *1093: *Vicia palaestina* , *1166: *Antennaria dioica* , *1170: *Calamintha sylvatica* , *1259: *Viola canina* , *1331: *Pedicularis recutita* , *1386: *Vicia cracca* , *1509: *Coelogyne huettneriana* , *1537: *Restrepia elegans* , *1555: *Viscaria alpina* , *1606: *Trifolium pratense* , *1625: *Geum rivale* , *1650: *Primula stricta* , *1886: *Trifolium montanum* , *1960: *Primula farinosa* , *1972: *Clinopodium vulgare* , *2044: *Valeriana supira* , *2055: *Epilobium collinum* , *2057: *Epilobium montanum* , *2199: *Oxalis spec.* , *2247: *Crocus vernus (p)* , *2288: *gen. spec.* , *2394: *Galinsoga parviflora* , *2477: *Silene acaulis* , *2540: *Centaurea cyanus* , *2541: *Centaurea cyanus* , *2565: *Myosotis sylvatica* , *2737: *Pulicaria incisa* , *2829: *Helianthemum vesicarium* , *2855: *Lamium garganicum* , *2884: *Limodorum abortivum*

20-30° (38): *1134: *Allium oleraceum* , *1135: *Erigeron alpinus* , *1138: *Erigeron uniflorus* , *1164: *Androsace alpina* , *1229: *Tolpis staticifolia* , *1240: *Astragalus alpinus* , *1289: *Cirsium palustre* , *1294: *Epilobium parviflorum* , *1350: *Sedum atratum* , *1416: *Cirsium arvense* , *1561: *Primula scandinavica* , *1633: *Pulsatilla vernalis* , *1654: *Trifolium pratense* , *1674: *Ranunculus asiaticus* , *1788: *Valeriana officinalis* , *1830: *Geranium sylvaticum* , *1865: *Pinguicula vulgaris* , *1900: *Astragalus alpinus* , *2071: *Lilium martagon* , *2189: *Ajuga pyramidalis* , *2211: *Lantana lilacina* , *2214: *Dombeya burgessiae* , *2240: *Lippia lupulina* , *2260: *Polygonatum capitatum* , *2317: *Pterolepis glomerata* , *2339: *Vernonia spec.* , *2412: *Vernonia scorpioides* , *2413: *Euphorbia pulcherrima* , *2421: *Lantana camara* , *2478: *Veronica arvensis* , *2516: *Crocus vernus (p)* , *2564: *Lamium maculatum* , *2567: *Globularia nudicaulis* , *2582: *Dentaria bulbifera* , *2694: *Astragalus amalescitanus* , *2738: *Scabiosa caucasica* , *2885: *Orchis italica* , *2944: *Orchis papilionacea*

30-40° (53): *256: *Carlina acaulis* , *680: *Lupinus polyphyllus* , *1137: *Erigeron uniflorus* , *1186: *Cymbalaria muralis* , *1243: *Dactylorhiza fuchsii* , *1304: *Gypsophila repens* , *1318: *Mentha aquatica* , *1382: *Knautia arvensis* , *1418: *Eupatorium cannabinum* , *1420: *Holosteum umbellatum* , *1531: *Phalaenopsis schilleriana* , *1532: *Phalaenopsis schilleriana* , *1552: *Knautia arvensis* , *1557: *Phyllodoce caerulea* , *1566: *Silene acaulis* , *1578: *Alliaria petiolata* , *1597: *Polygonatum multiflorum* , *1630: *Pulsatilla vernalis* , *1750: *Moehringia muscosa* , *1766: *Rosa pendulina* , *1898: *Astragalus alpinus* , *1926: *Traunsteinera globosa* , *1971: *Capsella bursa-pastoris* , *1973: *Conyza canadensis* , *1976: *Galeopsis tetrahit* , *2102: *Myosotis arvensis* , *2136: *Cardamine pratensis* , *2145: *Stellaria palustris* , *2200: *Rhododendron indicum* , *2256: *Asclepia curassavica* , *2287: *Trifolium alpinum* , *2326: *Siphocampylus convolvulaceus* , *2354: *Camptosema ellipticum* , *2371: *Petasites spec.* , *2372: *Banisteria stellaris* , *2385: *Begonia diadema* , *2409: *Eupatorium pauciflorum* , *2440: *Arctostaphylos uva-ursi* , *2448: *Impatiens sultani* , *2533: *Erigeron spec.* , *2551: *Hibiscus trionum* , *2572: *Lonicera periclymenum* , *2638: *Cephalanthera longifolia* , *2802: *Fagonia mollis* , *2893: *Limonium pruinosum* , *2922: *Orchis galilaea* ,

*2939: *Orchis anatolica* , *2960: *Cyclamen persicum* , *2961: *Lantana hirta* , *2983: *Retama raetam* , *2985: *Retama raetam* , *2986: *Retama raetam* , *2991: *Salvia hierosolymitana*

40-50° (95): *162: *Oophytum oviforme* , *191: *Arenaria biflora* , *1127: *Achillea nobilis* , *1162: *Rosa canina* , *1168: *Arenaria biflora* , *1208: *Matricaria inodora* , *1242: *Cerastium alpinum* , *1244: *Dactylorhiza maculata* , *1265: *Arenaria biflora* , *1279: *Cardamine bellidifolia* , *1283: *Cerastium cerastoides* , *1285: *Cerastium latifolium* , *1310: *Leucanthemopsis alpina* , *1313: *Leucanthemum atratum* , *1337: *Phyteuma hemisphericum* , *1340: *Pulsatilla alpina* , *1341: *Pulsatilla alpina* , *1355: *Silene alpestris* , *1372: *Trifolium thalii* , *1428: *Pimpinella major* , *1431: *Torilis japonica* , *1469: *Lathraea squamaria* , *1479: *Cardamine amara* , *1484: *Syringa vulgaris* , *1490: *Lamium album* , *1512: *Dendrobium kingianum* , *1528: *Miltonea cuneata* , *1530: *Oncidium variegatum* , *1539: *Zygopetalum mackaii* , *1571: *Chamomilla recutita* , *1575: *Matricaria maritima* , *1580: *Cerastium glomeratum* , *1581: *Cerastium holosteoides* , *1586: *Fragaria vesca* , *1592: *Matricaria chamomilla* , *1605: *Stellaria graminea* , *1608: *Vicia hirsuta* , *1609: *Vicia hirsuta* , *1638: *Saxifraga oppositifolia* , *1672: *Gynandriris sisyrinchium* , *1743: *Leucanthemopsis alpina* , *1759: *Potentilla saxifraga* , *1760: *Potentilla saxifraga* , *1770: *Saxifraga rotundifolia* , *1782: *Thesium alpinum* , *1810: *Arabis recta* , *1815: *Astragalus frigidus* , *1855: *Ligusticum mutelloides* , *1867: *Bistorta vivipara* , *1878: *Silene pusilla* , *1889: *Vaccinium vitis-idaea* , *1909: *Leucanthemopsis alpina* , *1913: *Mentha longifolia* , *1953: *Aster bellidiastrum* , *1994: *Viburnum opulus* , *2002: *Arabis pumila* , *2017: *Hieracium sylvaticum* , *2082: *Moehringia ciliata* , *2114: *Coronilla varia* , *2163: *Begonia megaptera* , *2177: *Sorbus aucuparia* , *2222: *Chrysanthemum leucanthemum* , *2248: *Potentilla rupestris* , *2261: *Polygala spec.* , *2280: *Hyptis multibracteata* , *2294: *Zygophyllum dumosum* , *2368: *Cephalanthera longifolia* , *2377: *Begonia acida* , *2397: *Thunbergia grandiflora* , *2444: *Rubus rosaefolius* , *2455: *Begonia heracleifolia* , *2456: *Begonia kellermanii* , *2458: *Begonia kellermanii* , *2464: *Begonia nelumbiifolia* , *2493: *Silene nutans* , *2558: *Lavatera thuringiaca* , *2578: *Lonicera periclymenum* , *2598: *Saxifraga stellaris* , *2622: *Anthemis pseudocotula* , *2635: *Asphodelus tenuifolius* , *2640: *Crataegus azarolus* , *2647: *Allium nigrum* , *2657: *Anthemis cornucopiae* , *2669: *Anthemis maris-mortui* , *2725: *Orchis galilaea* , *2729: *Cistus salviifolius* , *2765: *Erucaria boveana* , *2801: *Fagonia mollis* , *2828: *Helianthemum vesicarium* , *2968: *Prunus ursina* , *2969: *Prunus ursina* , *2982: *Reboudia pinnata* , *2984: *Retama raetam* , *2993: *Salvia hierosolymitana* , *2995: *Salvia hierosolymitana*

50-60° (119): *159: *Selago albida* , *160: *Chlorophytum crassinerve* , *675: *Lupinus polyphyllus* , *1125: *Achillea nana* , *1128: *Aegopodium podagraria* , *1139: *Anthriscus sylvestris* , *1158: *Cornus sanguinea* , *1159: *Galium aparine* , *1160: *Galium mollugo* , *1210: *Minuartia laricifolia* , *1217: *Ranunculus glacialis* , *1233: *Trifolium ochroleucon* , *1236: *Antennaria dioica* , *1252: *Silene vulgaris* , *1261: *Androsace obtusifolia* , *1263: *Anemone narcissiflora* , *1267: *Bunium alpinum* , *1305: *Gypsophila repens* , *1319: *Moehringia trinerva* , *1338: *Pleurospermum austriacum* , *1346: *Scrophularia nodosa* , *1374: *Valeriana sambucifolia* , *1387: *Achillea millefolium* , *1388: *Arabis hirsuta* , *1391: *Berteroa incana* , *1392: *Calystegia sepium* , *1409: *Rubus caesius* , *1413: *Tripleurospermum inodora* , *1430: *Solanum nigrum* , *1462: *Cerastium arvense* , *1465: *Anemona nemorosa* , *1489: *Arenaria serpyllifolia* , *1516: *Dendrobium nobile* , *1533: *Phalaenopsis stuartiana* , *1544: *Cassiope hypnoides* , *1550: *Galium boreale* , *1562: *Prunus padus* , *1563: *Rumex acetosa* , *1579: *Arabidopsis thaliana* , *1583: *Coronilla varia* , *1591: *Maianthemum bifolium* , *1599: *Polygonatum odoratum* , *1603: *Silene alba* , *1613: *Astragalus alpinus* , *1614: *Astragalus alpinus* , *1632: *Pulsatilla vernalis* , *1634: *Ranunculus glacialis* , *1640: *Antennaria dioica* , *1652: *Saxifraga stellaris* , *1653: *Stellaria nemorum* , *1656: *Vaccinium vitis-idaea* , *1666: *Prunus spinosa* , *1671: *Galanthus nivalis* , *1677: *Ranunculus asiaticus* , *1718: *Galium helveticum* , *1721: *Galeopsis tetrahit* , *1753: *Parnassia palustris* , *1797: *Myosoton aquaticum* , *1802: *Achillea macrophylla* , *1872: *Ranunculus aconitifolius* , *1874: *Sedum album* , *1888: *Trifolium repens* , *1915: *Minuartia capillaceae* , *1948: *Achillea atrata* , *1962: *Saxifraga androsacea* , *1970: *Berteroa incana* , *1981: *Potentilla argentea* , *1986: *Arabis glabra* , *2000: *Androsace chamaejasme* , *2003: *Arenaria serpyllifolia* , *2008: *Cerastium uniflorum* , *2009: *Cerastium uniflorum* , *2024: *Moneses uniflora* , *2026: *Orthilia secunda* , *2028: *Pyrola rotundifolia* , *2034: *Saxifraga caesia* , *2036: *Saxifraga hostii* , *2079: *Meum athamanthicum* , *2095: *Sempervivum arachnoideum* , *2130: *Filipendula ulmaria* , *2132: *Symphytum officinale* , *2144: *Moehringia trinerva* , *2149: *Arenaria serpyllifolia* , *2181: *Sambucus nigra* , *2192: *Anemone nemorosa* , *2237: *Lantana hirta* , *2258: *Begonia fulvo-setulosa* , *2259: *Sagittaria spec.* , *2262: *Scandix pecten-veneris* , *2272: *Chrysanthemum leucanthemum* , *2334: *Cochlospermum regium* , *2370: *Anemone nemorosa* , *2376: *Begonia acida* , *2389: *Begonia dietrichiana* , *2391: *Begonia fischeri* , *2422: *Solanum spec.* , *2429: *Aechmea spec.* , *2457: *Begonia imperalis* , *2461: *Begonia ludicra* , *2466: *Begonia violifolia* , *2468: *Penstemon barbatus* , *2485: *Fragaria viridis* , *2519: *Andromeda polifolia* , *2545: *Lamium album* , *2566: *Lavatera thuringiaca* , *2569: *Leucanthemum vulgare* , *2599: *Lamium album* , *2634: *Bellevalia flexuosa* , *2688: *Asperula libanotica* , *2701: *Bellevalia flexuosa* , *2716: *Trifolium repens* , *2730: *Cistus salviifolius* , *2766: *Rhizobotria alpina* , *2777: *Scabiosa caucasica* , *2831: *Orchis galilaea* , *2852: *Kickxia floribunda* , *2869: *Tillandsia vernicosa* , *2903: *Lycium shawii* , *2979: *Crataegus aronia*

60-70° (49): *283: *Cirsium spinosissimum* , *1092: *Vicia hybrida* , *1221: *Saxifraga bryoides* , *1264: *Anemone narcissiflora* , *1281: *Carum carvi* , *1298: *Galium megalospermum* , *1323: *Myrrhis odorata* , *1371: *Trifolium thalii* , *1406: *Peucedanum oreoselinum* , *1410: *Sambucus nigra* , *1518: *Dendrobium pierardii* , *1534: *Phalaenopsis stuartiana* , *1546: *Dryas octopetala* , *1626: *Pedicularis lapponica* , *1637: *Saxifraga cespitosa* , *1641: *Anthriscus sylvestris* , *1642: *Diapensia lapponica* , *1687: *Aconitum vulparia* , *1749: *Mimosa tremula* , *1780: *Teucrium montanum* , *1808: *Angelica sylvestris* , *1823: *Campanula thyrsoides* , *1831: *Heracleum austriacum* , *1845: *Laserpitium latifolium* , *1931: *Cirsium spinosissimum* , *2014: *Heracleum spondylium* , *2064: *Gnaphalium sylvatica* , *2065: *Heracleum minimum* , *2098: *Linaria vulgaris* , *2100: *Linaria vulgaris* , *2118: *Trifolium repens* , *2227: *Aechmea spec.* , *2330: *Serjania lethalis* , *2332: *Gochnatia barrosii* , *2335: *Achyrocline saturejoides* , *2363: *Myrcia uberavensis* , *2433: *Stilpnopappus speciosus* , *2484: *Anthyllis vulneraria* , *2500: *Maxillaria chrysantha* , *2506: *Tibouchina cerastifolia* , *2546: *Lamium album* , *2550: *Hibiscus trionum* , *2560: *Cirsium oleraceum* , *2618: *Acanthus syriacus* , *2679: *Antirrhinum majus* , *2691: *Gymnocarpus decandrum* , *2727: *Arbutus andrachne* , *2901: *Trifolium montanum* , *2916: *Orchis galilaea*

70-80° (42): *190: *Arenaria biflora* , *892: *Rhinanthus minor* , *1090: *Vicia hybrida* , *1156: *Astragalus glycyphyllos* , *1169: *Arenaria biflora* , *1238: *Antirrhinum majus* , *1239: *Antirrhinum majus* , *1262: *Androsace obtusifolia* , *1266: *Arenaria biflora* , *1288: *Cirsium oleraceum* , *1329: *Pedicularis comosa* , *1529: *Miltonea cuneata* , *1610: *Vicia hirsuta* , *1618: *Bartsia alpina* , *1665: *Primula veris* , *1747: *Melampyrum sylvaticum* , *1816: *Astragalus frigidus* , *1912: *Mentha longifolia* , *1949: *Achillea atrata* , *1983: *Sedum maximum* , *1985: *Senecio vulgaris* , *2013: *Gentianella armarella* , *2053: *Cirsium spinosissimum* , *2080: *Meum athamanthicum* , *2091: *Rhinanthus minor* , *2190: *Ajuga pyramidalis* , *2235: *Lavatera thuringiaca* , *2283: *Corylus avellana* , *2331: *Helicteres brevispira* , *2333: *Luehea speciosa* , *2355: *Dietes spec.* , *2434: *Hyptis pauliana* , *2537: *Centaurea pallescens* , *2553: *Hibiscus trionum* , *2677: *Kickxia spartioides* , *2711: *Calendula arvensis* , *2712: *Calendula arvensis* , *2835: *Hyoscyamus aureus* , *2851: *Kickxia floribunda* , *2877: *Lavatera cretica* , *2878: *Leopoldia longipes* , *2981: *Tillandsia incunda*

80-90° (29): *253: *Carlina acaulis* , *891: *Rhinanthus minor* , *1286: *Cerastium latifolium* , *1299: *Galium megalospermum* , *1303: *Gentiana nivalis* , *1317: *Matricaria discoides* , *1347: *Scrophularia nodosa* , *1349: *Sedum atratum* , *1389: *Artemisia vulgaris* , *1527: *Miltonea cuneata* , *1593: *Matricaria chamomilla* , *1648: *Papaver radicatum* , *1688: *Aconitum vulparia* , *2037: *Saxifraga hostii* , *2054: *Cirsium spinosissimum* , *2092: *Rhinanthus minor* , *2201: *Calliandria tweedii* , *2231: *Begonia fischeri* , *2344: *Lonicera japonica* , *2414: *Vriesea incurvata* , *2437: *Cuphea spec.* , *2526: *Veronica chamaedrys* , *2579: *Lonicera periclymenum* , *2685: *Crepis sancta* , *2720: *Centaurea pallescens* , *2778: *Eremostachys laciniata* , *2824: *Lycium shawii* , *2837: *Hyoscyamus aureus* , *2936: *Ononis natrix*

90-100° (33): *1018: *Tanacetum parthenium* , *1091: *Vicia hybrida* , *1188: *Diplotaxis tenuifolium* , *1284: *Cerastium cerastoides* , *1376: *Veronica alpina* , *1492: *Paris quadrifolium* , *1559: *Polemonium caerulum* , *1631: *Pulsatilla vernalis* , *1635: *Ranunculus glacialis* , *1896: *Alchemilla vulgaris* , *1924: *Tofieldia canyculata* , *1925: *Traunsteinera globosa* , *1961: *Primula farinosa* , *2038: *Saxifraga moschata* , *2059: *Epilobium montanum* , *2188: *Aesculus carnea* , *2193: *Biscutella laevigata* , *2205: *Viola tricolor (y)* , *2246: *Convallaria majalis* , *2296: *Salix spec.* , *2375: *Cambessedesia ilicifolia* , *2419: *Desmodium pachyrhiza* , *2462: *Begonia ludicra* , *2520: *Viola lutea* , *2531: *Viola x wittrockiana* , *2552: *Hibiscus trionum* , *2615: *Ononis natrix* , *2705: *Fumana thymifolia* , *2733: *Cistus incanus* , *2744: *Crataegus azarolus* , *2754: *Crepis palaestina* , *2848: *Kickxia spartioides* , *2850: *Kickxia spartioides*

100-110° (51): *158: *Hymenolepis parviflora* , *1133: *Alchemilla glabra* , *1161: *Lathyrus pratensis* , *1165: *Androsace alpina* , *1222: *Saxifraga bryoides* , *1231: *Tolpis staticifolia* , *1268: *Bunium alpinum* , *1302: *Gentiana bavarica* , *1330: *Pedicularis comosa* , *1356: *Silene alpestris* , *1396: *Galium verum* , *1400: *Impatiens parviflora* , *1433: *Trifolium campestre* , *1434: *Trifolium campestre* , *1435: *Trifolium dubium* , *1493: *Paris quadrifolium* , *1565: *Rhodiola rosea* , *1790: *Veratrum album* , *1838: *Hieracium villosum* , *1895: *Alchemilla vulgaris* , *1958: *Primula auricola* , *1963: *Saxifraga androsacea* , *1977: *Galeopsis tetrahit* , *1980: *Potentilla argentea* , *1991: *Medicago lupulina* , *2020: *Melampyrum pratense* , *2099: *Linaria vulgaris* , *2105: *Verbascum densiflorum* , *2157: *Begonia mauricei* , *2195: *Biscutella laevigata* , *2208: *Galeopsis bifida* , *2320: *Asclepia curassavica* , *2327: *Pyrostegia venusta* , *2428: *Pyrostegia venusta* , *2436: *Desmodium pachyrhiza* , *2463: *Begonia nelumbiifolia* , *2495: *Galinsoga parviflora* , *2498: *Maxillaria chrysantha* , *2521: *Byrsonima crassa* , *2571: *Lonicera periclymenum* , *2602: *Acanthostachys strobilacea* , *2621: *Acanthus syriacus* , *2654: *Allium trifoliatum* , *2695: *Anthemis cornucopiae* , *2708: *Sanchezia nobilis* , *2836: *Hyoscyamus aureus* , *2841: *Gynandriris monophylla* , *2843: *Eremostachys laciniata* , *2858: *Lamium amplexicaule* , *2860: *Lathyrus aphaca* , *2972: *Viola lutea*

110-120° (73): *430: *Euphrasia rostkoviana* , *460: *Malva alcea* , *538: *Hieracium alpinum* , *539: *Hieracium alpinum* , *1132: *Alchemilla fissa* , *1152: *Senecio vernalis* , *1207: *Matricaria inodora* , *1214: *Picris hieracioides* , *1227: *Solanum dulcamara* , *1230: *Tolpis staticifolia* , *1237: *Antirrhinum majus* , *1257: *Vicia cracca* , *1282: *Carum carvi* , *1311: *Leucanthemopsis alpina* , *1321: *Mycelis muralis* , *1354: *Senecio viscosus* , *1373: *Trifolium thalii* , *1411: *Sedum sexangulare* , *1414: *Tripleurospermum inodora* , *1473: *Ranunculus ficaria* , *1521: *Eria pannea* , *1525: *Maxillaria variabilis* , *1526: *Maxillaria chrysantha* , *1556: *Melampyrum pratense* , *1572: *Chamomilla recutita* , *1574: *Matricaria maritima* , *1621: *Caltha palustris* , *1622: *Caltha palustris* , *1629: *Potentilla crantzii* , *1661: *Caltha palustris* , *1664: *Primula veris* , *1767: *Saxifraga aizoides* , *1836: *Hieracium lanatum* , *1861: *Orobranche caryophyllacea* , *1897: *Astragalus alpinus* , *1911: *Leucanthemopsis alpina* , *1952: *Aster bellidiastrum* , *1984: *Senecio vulgaris* , *1987: *Asparagus officinalis* , *1989: *Crepis paludosa* , *2169: *Begonia acida* , *2216: *Ouratea nana* , *2279: *Convallaria majalis* , *2289: *Lathyrus aphaca* , *2374: *Vriesea carinata* , *2445: *Asclepia curassavica* , *2460: *Begonia kellermanii* , *2514: *Malva sylvestris* , *2568: *Caltha palustris* , *2591: *Ranunculus acris* , *2616: *Bidens gardineri* , *2673: *Anthemis pseudocotula* , *2675: *Anthemis maris-mortui* , *2713: *Lathyrus aphaca* , *2715: *Calycotome villosa* , *2731: *Cistus salviifolius* , *2734: *Asphodelus tenuifolius* , *2757: *Trifolium repens* , *2788: *Ajuga chia* , *2790: *Erodium cicutarium* , *2820: *Cistanche tubulosa* , *2856: *Lamium garganicum* , *2859: *Lathyrus aphaca* , *2872: *Lathyrus blepharicarpus* , *2909: *Matricaria aurea* , *2910: *Medicago turbinata* , *2912: *Medicago turbinata* , *2929: *Picris longirostris* , *2935: *Ononis natrix* , *2938: *Opophytum forsskalii* , *2947: *Viola x wittrockiana* , *2964: *Picris longirostris* , *2980: *Ranunculus asiaticus*

120-130° (55): *552: *Hypochaeris uniflora* , *890: *Rhinanthus minor* , *1184: *Crepis alpestris* , *1202: *Helianthemum nummularium* , *1205: *Leontodon autumnale* , *1315: *Leucanthemum atratum* , *1316: *Matricaria discoides* , *1359: *Sonchus arvensis* , *1365: *Thalictrum minus* , *1405: *Melampyrum nemerosum* , *1415: *Verbascum lychnitis* , *1421: *Lathyrus pratensis* , *1424: *Lotus corniculatus* , *1426: *Lotus corniculatus* , *1466: *Anemona nemorosa* , *1514: *Dendrobium loddigesii* , *1615: *Astragalus frigidus* , *1646: *Melampyrum sylvaticum* , *1660: *Caltha palustris* , *1662: *Euphorbia cyparissias* , *1722: *Gentiana lutea* , *1851: *Leontodon hispidus* , *1856: *Medicago lupulina* , *1956: *Leontodon montanus* , *1966: *Senecio doronicum* , *2018: *Medicago lupulina* , *2069: *Hypochaeris uniflora* , *2093: *Rhinanthus minor* , *2126: *Tussilago farfara* , *2143: *Lapsana communis* , *2158: *Anthriscus sylvestris* , *2182: *Achillea santolina* , *2187: *Potentilla frigida* , *2220: *Eupatorium pauciflorum* , *2274: *Hippocrepis comosa* , *2291: *Nidularium spec.* , *2310: *Dendrobium aggregatum* , *2360: *Luehea speciosa* , *2481: *Potentilla heptaphylla* , *2522: *Tropaeolum majus* , *2549: *Nemanthus spec.* , *2563: *Lamium galeobdolon* , *2570: *Leucanthemum vulgare* , *2614: *Ononis natrix* , *2627: *Crepis aspera* , *2681: *Euphorbia hierosolymitana* , *2753: *Crepis palaestina* , *2793: *Erodium laciniatum* , *2797: *Euphorbia hierosolymitana* , *2814: *Geropogon hybridus* , *2844: *Hypecoum imberbe* , *2883: *Leontodon laciniata* , *2914: *Mesembryanthemum nodiflorum* , *2942: *Pulicaria incisa* , *2989: *Ruta chalepensis*

130-140° (50): *161: *Lebeckia cf. halenbergensis* , *553: *Hypochaeris uniflora* , *555: *Hypochaeris uniflora* , *556: *Hypochaeris uniflora* , *1204: *Leontodon autumnale* , *1219: *Ranunculus glacialis* , *1254: *Taraxacum officinale* , *1306: *Hypochaeris uniflora* , *1401: *Lysimachia vulgaris* , *1402: *Lysimachia vulgaris* , *1422: *Lathyrus pratensis* , *1423: *Lathyrus pratensis* , *1425: *Lotus corniculatus* , *1468: *Gagea pratensis* , *1536: *Polystachia pubescens* , *1564: *Sedum annuum* , *1616: *Astragalus frigidus* , *1668: *Hieracium spec.* , *1742: *Leucanthemopsis alpina* , *1814: *Arnica montana* , *1835: *Hieracium lanatum* , *1841: *Hieracium villosum* , *1847: *Lathyrus pratensis* , *1848: *Lathyrus pratensis* , *1849: *Lathyrus pratensis* , *1880: *Solidago virgaurea* , *2068: *Hypochaeris uniflora* , *2146: *Trifolium campestre* , *2166: *Hypochaeris uniflora* , *2180: *Aster alpinus* , *2183: *Geum reptans* , *2293: *Lithraea molleoides* , *2323: *Trifolium montanum* , *2435: *Aeschynomene paniculata* , *2452: *Deherainia smaragdina* , *2517: *Eschscholzia californica* , *2555: *Lysimachia vulgaris* , *2624: *Achillea santolina* , *2633: *Anagyris foetida* , *2672: *Anthemis pseudocotula* , *2717: *Cardaria draba* , *2745: *Ruta chalepensis* , *2798: *Anagyris foetida* , *2823: *Haplophyllum tuberculatum* , *2834: *Leontodon laciniata* , *2896: *Linum pubescens* , *2902: *Lotus peregrinus* , *2970: *Rhagadiolus stellatus* , *2977: *Ranunculus marginatus* , *2987: *Tillandsia spec.*

140-150° (31): *1213: *Picris hieracioides* , *1241: *Astragalus alpinus* , *1398: *Hypericum perforatum* , *1690: *Aposeris foetida* , *1740: *Leontodon hispidus* , *1768: *Saxifraga aizoides* , *1806: *Alchemilla alpina* , *1876: *Senecio alpinus* , *2016: *Hieracium sylvaticum* , *2096: *Aster bellidiastrum* , *2223: *Sonchus oleraceus* , *2284: *Anthyllis vulneraria* , *2328: *Pterolepis glomerata* , *2352: *Wedelia paludosa* , *2548: *Eschscholzia californica* , *2581: *Prunus spinosa* , *2587: *Ranunculus acris* , *2632: *Anagyris foetida* , *2664: *Calycotome villosa* , *2668: *Anemone coronaria* , *2721: *Crepis aspera* , *2751: *Crepis aspera* , *2762: *Trigonella kotschyi* , *2795: *Fumaria densiflora* , *2799: *Anagyris foetida* , *2813: *Geranium molle* , *2825: *Hedypnois rhagadioloides* , *2899: *Lotus collinus* , *2907: *Vriesea carinata* , *2931: *Ononis natrix* , *2963: *Picris longirostris*

150-160° (18): *166: *Euphorbia cf. mauritanica* , *1307: *Hypochaeris uniflora* , *1320: *Mycelis muralis* , *1589: *Hieracium murorum* , *1601: *Potentilla reptans* , *1620: *Caltha palustris* , *1723: *Gentiana lutea* , *1769: *Saxifraga aizoides* , *1918: *Ranunculus polyanthemos* , *1919: *Ranunculus polyanthemos* , *2156: *Lonicera periclymenum* , *2276: *Cestrum spec.* , *2527: *Solanum spec.* , *2592: *Ranunculus acris* , *2689: *Asperula libanotica* , *2692: *Hedypnois rhagadioloides* , *2758: *Crepis sancta* , *2897: *Lotus collinus*

160-170° (29): *169: *Arctotis spec.* , *1360: *Sonchus arvensis* , *1408: *Ranunculus acris* , *1412: *Senecio jacobea* , *1417: *Erysimum cheiranthoides* , *1464: *Hieracium sabaudum* , *1647: *Melampyrum sylvaticum* , *1649: *Potentilla erecta* , *1659: *Caltha palustris* , *1881: *Solidago virgaurea* , *1882: *Solidago virgaurea* , *1979: *Potentilla argentea* , *2236: *Justicia spec.* , *2251: *Potentilla heptaphylla* , *2301: *Ludwigia elegans* , *2401: *Siphocampylus convolvulacea* , *2431: *Vriesea incurvata* , *2442: *Ipomoea callida* , *2479: *Lamium galeobdolon* , *2483: *Hieracium sabaudum* , *2663: *Calycotome villosa* , *2746: *Crepis hierosolymitana* , *2760: *Crepis sancta* , *2763: *Launaea angustifolia* , *2791: *Launaea mucronata* , *2796: *Erucaria hispanica* , *2839: *Hypecoum imberbe* , *2870: *Lathyrus gorgonii* , *2898: *Lotus collinus*

170-180° (28): *1201: *Helianthemum nummularium* , *1249: *Ranunculus acris* , *1258: *Viola biflora* , *1339: *Pleurospermum austriacum* , *1344: *Ranunculus sceleratus* , *1467: *Gagea pratensis* , *1504: *Potentilla anserina* , *1588: *Hieracium murorum* , *1658: *Anemone ranunculoides* , *1667: *Hieracium spec.* , *1795: *Berteroa incana* , *1799: *Verbascum lychnitis* , *1812: *Arnica montana* , *1813: *Arnica montana* , *1988: *Crepis paludosa* , *2015: *Hieracium sylvaticum* , *2087: *Potentilla erecta* , *2104: *Verbascum densiflorum* , *2131: *Verbascum lychnitis* , *2142: *Hieracium pilosella* , *2266: *Cochlospermum regium* , *2395: *Lamium galeobdolon* , *2473: *Tussilago farfara* , *2488: *Hieracium laevigatum* , *2523: *Hypericum lobocarpum* , *2544: *Cucurbita maxima* , *2656: *Anagallis arvensis* , *2895: *Linum pubescens*

180-190° (27): *163: *Ursinia spec.* , *164: *Ursinia spec.* , *167: *Ursinia cakilefolia* , *1151: *Senecio vernalis* , *1183: *Crepis alpestris* , *1255: *Taraxacum officinale* , *1353: *Senecio viscosus* , *1397: *Hypericum perforatum* , *1399: *Hypericum perforatum* , *1535: *Polystachia pubescens* , *1570: *Viola biflora* , *1600: *Potentilla reptans* , *1710: *Crepis pyrenaica* , *1877: *Senecio alpinus* , *1978: *Geum urbanum* , *2086: *Potentilla erecta* , *2308: *Chamaecrista spec.* , *2450: *Ludwigia elegans* , *2604: *Solidago virgaurea* , *2652: *Orchis anatolica* , *2722: *Crepis hierosolymitana* , *2756: *Crepis palaestina* , *2809: *Fumana thymifolia* , *2826: *Helianthemum ventosum* , *2847: *Ranunculus ficaria* , *2874: *Launaea mucronata* , *2978: *Ranunculus millefolius*

190-200° (23): *168: *Ursinia cakilefolia* , *1129: *Agrimonia eupatoria* , *1598: *Polygonatum odoratum* , *1604: *Sinapis arvensis* , *1811: *Arabis recta* , *1834: *Hieracium lanatum* , *1840: *Hieracium villosum* , *1906: *Inula salicina* , *1907: *Inula salicina* , *1950: *Achillea atrata* , *1964: *Senecio doronicum* , *1965: *Senecio doronicum* , *2025: *Moneses uniflora* , *2213: *Hieracium spec.* , *2329: *Desmodium pachyrhiza* , *2353: *Byrsonima crassa* , *2530: *Hypericum perforatum* , *2574: *Hypericum perforatum* , *2653: *Allium trifoliatum* , *2736: *Colutea istria* , *2743: *Launaea nudicaulis* , *2930: *Ononis natrix* , *2932: *Ononis natrix*

200-210° (23): *678: *Lupinus polyphyllus* , *1010: *Symphoricarpos albus* , *1130: *Agrimonia eupatoria* , *1429: *Pimpinella major* , *1432: *Torilis japonica* , *1842: *Hypericum maculatum* , *1844: *Hypericum maculatum* , *1866: *Pinguicula vulgaris* , *1957: *Leontodon montanus* , *2027: *Orthilia secunda* , *2029: *Pyrola rotundifolia* , *2122: *Symphoricarpos albus* , *2170: *Hypericum perforatum* , *2194: *Biscutella laevigata* , *2224: *Euphorbia pulcherrima* , *2263: *Tillandsia virescens* , *2345: *Cochlospermum regium* , *2356: *Cambessedesia ilicifolia* , *2358: *Vriesia spec.* , *2490: *Dendrobium aggregatum* , *2703: *Hemerocallis flava* , *2747: *Crepis hierosolymitana* , *2933: *Ononis natrix*

210-220° (22): *693: *Malva nicaeensis* , *1324: *Myrrhis odorata* , *1362: *Taraxacum hopeanum* , *1503: *Impatiens parviflora* , *1596: *Polygonatum multiflorum* , *1689: *Aconitum vulparia* , *1705: *Carduus defloratus* , *1719: *Galium helveticum* , *1923: *Rhododendron hirsutum* , *1990: *Euonymus europaeus* , *2019: *Medicago lupulina* , *2173: *Prunus ursina* , *2217: *Dalbergia ecastaphyllum* , *2573: *Silene dioica* , *2690: *Bellevalia flexuosa* , *2709: *Justicia brandegeana* , *2749: *Crepis hierosolymitana* , *2879: *Leopoldia longipes* , *2905: *Prunus ursina* , *2908: *Lavatera cretica* , *2974: *Ranunculus millefolius* , *2996: *Colcthea crocata*

220-230° (14): *2052: *Campanula persicifolia* , *2072: *Lilium martagon* , *2242: *Potentilla brauniana* , *2367: *Euphorbia pulcherrima* , *2381: *Veronica bellidioides* , *2410: *Chrysanthemum leucanthemum* , *2425: *Canna limbata* , *2446: *Turnera spec.* , *2486: *Stachys recta* , *2651: *Allium trifoliatum* , *2723: *Cephalanthera longifolia* , *2742: *Crataegus aronia* , *2816: *Geranium purpureum* , *2959: *Papaver*

subpiriforme

230-240° (20): *1482: *Syringa vulgaris* , *1691: *Aposeris foetida* , *1744: *Leucanthemopsis alpina* , *1832: *Hieracium auranticum* , *1920: *Ranunculus polyanthemos* , *1959: *Primula auricola* , *2021: *Melampyrum pratense* , *2164: *Petunia spec.* , *2186: *Papaver rhoeas* , *2219: *Papaver rhoeas* , *2250: *Vriesia spec.* , *2325: *Eritrina speciosa* , *2351: *Heliconia velloziana* , *2388: *Geranium sylvaticum* , *2543: *Lythrum salicaria* , *2593: *Ranunculus asiaticus* , *2630: *Sagittaria spec.* , *2714: *Lathyrus aphaca* , *2868: *Lathyrus gorgonii* , *2998: *Glaucium corniculatum*

240-250° (42): *165: *Ursinia spec.* , *254: *Carlina acaulis* , *855: *Platycodon grandiflorum* , *1309: *Jasione montana* , *1345: *Ranunculus sceleratus* , *1523: *Maxillaria chrysantha* , *1594: *Matricaria chamomilla* , *1700: *Campanula cochlearifolia* , *1724: *Gentiana punctata* , *1725: *Gentiana punctata* , *1728: *Gentiana purpurea* , *1731: *Geranium pratense* , *1751: *Moehringia muscosa* , *1758: *Phyteuma orbiculare* , *1765: *Rosa pendulina* , *1796: *Knautia arvensis* , *1803: *Achillea macrophylla* , *1833: *Hieracium auranticum* , *1837: *Hieracium lanatum* , *1839: *Hieracium villosum* , *1883: *Solidago virgaurea* , *2090: *Potentilla grandiflora* , *2101: *Linaria vulgaris* , *2103: *Myosotis arvensis* , *2112: *Papaver dubium* , *2113: *Papaver somniferum* , *2125: *Papaver rhoeas* , *2184: *Papaver rhoeas* , *2230: *Sonchus oleraceus* , *2387: *Malva spec.* , *2417: *Impatiens sultani* , *2497: *Malvaviscus arboreus* , *2525: *Papaver rhoeas* , *2613: *Canna limbata* , *2617: *Crepis aspera* , *2628: *Justicia spec.* , *2666: *Ranunculus asiaticus* , *2671: *Papaver rhoeas* , *2680: *Antirrhinum majus* , *2741: *Ruta chalepensis* , *2817: *Geranium purpureum* , *2845: *Lathyrus gorgonii*

250-260° (52): *1187: *Cymbalaria muralis* , *1280: *Cardamine bellidifolia* , *1322: *Mycelis muralis* , *1361: *Sonchus arvensis* , *1366: *Thalictrum minus* , *1390: *Artemisia vulgaris* , *1584: *Coronilla varia* , *1703: *Campanula stenocodon* , *1711: *Crepis pyrenaica* , *1714: *Epipactis atrorubens* , *1720: *Galeopsis tetrahit* , *1734: *Gymnadenia conopsea* , *1754: *Parnassia palustris* , *1763: *Rhododendron ferrugeum* , *1771: *Saxifraga rotundifolia* , *1781: *Teucrium montanum* , *1783: *Thesium alpinum* , *1791: *Veratrum album* , *1801: *Veronica spicata* , *1807: *Alchemilla alpina* , *1809: *Angelica sylvestris* , *1817: *Astragalus frigidus* , *1843: *Hypericum maculatum* , *1846: *Laserpitium latifolium* , *1857: *Medicago lupulina* , *1863: *Phyteuma betonicifolium* , *1879: *Silene pusilla* , *1887: *Trifolium montanum* , *1908: *Inula salicina* , *1914: *Minuartia capillaceae* , *1951: *Alchemilla fissa* , *2056: *Epilobium collinum* , *2062: *Gnaphalium sylvatica* , *2129: *Trifolium campestre* , *2141: *Lysimachia vulgaris* , *2165: *Centaurea cyanus* , *2172: *Malva sylvestris* , *2176: *Sorbus aucuparia* , *2234: *Sanchezia nobilis* , *2299: *Cirrhopetalum cumingii* , *2341: *Vriesea incurvata* , *2443: *Rubus rosaefolius* , *2535: *Papaver rhoeas* , *2636: *Malva sylvestris* , *2661: *Anagyris foetida* , *2683: *Asphodelus aestivus* , *2811: *Erodium acaule* , *2815: *Salvia indica* , *2821: *Gymnocarpus decandrum* , *2861: *Lathyrus pseudocicera* , *2866: *Lathyrus pseudocicera* , *2867: *Lathyrus pseudocicera*

260-270° (54): *554: *Hypochaeris uniflora* , *859: *Prenanthes purpurea* , *1176: *Campanula rapunculoides* , *1196: *Epilobium fleischeri* , *1203: *Helianthemum nummularium* , *1216: *Prenanthes purpurea* , *1228: *Tanacetum parthenium* , *1235: *Veronica officinalis* , *1271: *Campanula alpestris* , *1314: *Leucanthemum atratum* , *1342: *Pulsatilla alpina* , *1348: *Scrophularia nodosa* , *1363: *Taraxacum hopeanum* , *1619: *Bartsia alpina* , *1624: *Geum rivale* , *1683: *Acinos alpinus* , *1709: *Cicerbita alpina* , *1736: *Lamium maculatum* , *1741: *Leontodon hispidus* , *1789: *Valeriana officinalis* , *1805: *Adenostyles alliariae* , *1822: *Campanula barbata* , *1824: *Campanula thyrsoides* , *1850: *Lathyrus pratensis* , *1871: *Prunella grandiflora* , *1875: *Sedum album* , *1890: *Vaccinium vitis-idaea* , *1917: *Nigritella nigra* , *1996: *Ajuga genevensis* , *2035: *Saxifraga caesia* , *2039: *Saxifraga moschata* , *2061: *Gentianella campestris* , *2066: *Heracleum minimum* , *2084: *Phyteuma hederanthifolium* , *2085: *Potentilla erecta* , *2203: *Vernonia scorpioides* , *2253: *Sanchezia nobilis* , *2322: *Camptosema ellipticum* , *2324: *Euphorbia pulcherrima* , *2342: *Tibouchina granulosa* , *2393: *Justicia brandegeana* , *2403: *Impatiens sultani* , *2418: *Malvaviscus arboreus* , *2420: *Hibiscus rosa-sinensis* , *2454: *Leontodon autumnale* , *2475: *Roemeria hybrida* , *2605: *Glaucium grandiflorum* , *2755: *Alkanna strigosa* , *2838: *Dombeya burgessiae* , *2862: *Lathyrus pseudocicera* , *2941: *Orchis anatolica* , *2946: *Papaver subpiriforme* , *2956: *Papaver hybridum* , *2958: *Papaver hybridum*

270-280° (47): *157: *Gazania heterochaeta* , *1037: *Trifolium ochroleucon* , *1167: *Antennaria dioica* , *1172: *Calamintha sylvatica* , *1193: *Echium vulgare* , *1200: *Geranium pyrenaicum* , *1215: *Picris hieracioides* , *1220: *Ranunculus glacialis* , *1223: *Sempervivum montanum* , *1343: *Ranunculus alpestris* , *1358: *Soldanella alpina* , *1368: *Thlaspi rotundifolia* , *1370: *Thymus oenipontanus* , *1378: *Veronica fruticans* , *1478: *Ajuga genevensis* , *1585: *Cynoglossum officinale* , *1673: *Ranunculus asiaticus* , *1681: *Achillea millefolium* , *1686: *Aconitum napellus* , *1713: *Epilobium anagallidifolium* , *1716: *Erigeron polymorphus* , *1726: *Gentiana purpurea* , *1727: *Gentiana purpurea* , *1748: *Melampyrum sylvaticum* , *1755: *Phyteuma nigrum* , *1756: *Phyteuma nigrum* , *1761: *Potentilla saxifraga* ,

*1854: *Ligusticum mutelloides* , *1860: *Orobranche caryophyllacea* , *1868: *Bistorta vivipara* , *1873: *Ranunculus aconitifolius* , *1916: *Nigritella nigra* , *1967: *Senecio doronicum* , *1999: *Androsace chamaejasme* , *2001: *Arabis pumila* , *2127: *Ajuga genevensis* , *2152: *Pulmonaria obscura* , *2252: *Impatiens sultani* , *2369: *Impatiens sultani* , *2489: *Dombeya wallichii* , *2662: *Echium angustifolium* , *2698: *Astragalus tribuloides* , *2767: *Echium angustifolium* , *2863: *Lathyrus pseudocicera* , *2865: *Lathyrus pseudocicera* , *2882: *Leopoldia comosa* , *2894: *Linum pubescens*

280-290° (41): *804: *Oxytropis pyrenaica* , *1312: *Leucanthemopsis alpina* , *1480: *Cardamine amara* , *1486: *Vinca minor* , *1519: *Dendrobium pierardii* , *1679: *Ranunculus asiaticus* , *1778: *Stachys sylvatica* , *1819: *Bartsia alpina* , *1905: *Hedysarum hedysaroides* , *1998: *Allium schoenoprasum* , *2081: *Moehringia ciliata* , *2151: *Myosotis hispida* , *2162: *Petunia spec.* , *2209: *Impatiens sultani* , *2221: *Impatiens sultani* , *2226: *Cardamine pratensis* , *2254: *Polygonum capitatum* , *2271: *Pulmonaria mollis* , *2282: *Hibiscus rosa-sinensis* , *2302: *Vriesea carinata* , *2309: *Impatiens sultani* , *2312: *Tibouchina granulosa* , *2366: *Impatiens sultani* , *2405: *Impatiens sultani* , *2424: *Camptosema ellipticum* , *2585: *Pulmonaria mollis* , *2625: *Impatiens sultani* , *2655: *Anagallis arvensis* , *2665: *Gypsophila arabica* , *2696: *Astragalus sanctus* , *2697: *Gypsophila arabica* , *2706: *Biscutella didyma* , *2750: *Impatiens sultani* , *2771: *Echium rauwolffii* , *2782: *Erodium crassifolium* , *2783: *Erodium crassifolium* , *2792: *Erodium laciniatum* , *2827: *Helianthemum vesicarium* , *2854: *Ajuga chia* , *2864: *Lathyrus pseudocicera* , *2945: *Orchis papilionacea*

290-300° (60): *1126: *Achillea nana* , *1157: *Campanula patula* , *1189: *Diplotaxis tenuifolium* , *1192: *Echium vulgare* , *1199: *Geranium pyrenaicum* , *1209: *Matricaria inodora* , *1211: *Oxytropis pyrenaica* , *1274: *Campanula rotundifolia* , *1377: *Veronica fruticans* , *1403: *Lythrum salicaria* , *1551: *Geranium sylvaticum* , *1707: *Centaurea nigrescens* , *1715: *Epipactis atrorubens* , *1730: *Geranium pratense* , *1818: *Bartsia alpina* , *2004: *Arenaria serpyllifolia* , *2005: *Campanula capitata* , *2115: *Petunia spec.* , *2119: *Pulmonaria obscura* , *2160: *Petunia spec.* , *2161: *Petunia spec.* , *2215: *Impatiens sultani* , *2277: *Erodium ciconium* , *2281: *Impatiens sultani* , *2290: *Geranium molle* , *2295: *Impatiens sultani* , *2297: *Impatiens sultani* , *2298: *Impatiens sultani* , *2311: *Impatiens sultani* , *2346: *Tibouchina granulosa* , *2359: *Justicia brandegeana* , *2365: *Tibouchina granulosa* , *2379: *Origanum vulgare* , *2390: *Petunia spec.* , *2398: *Tibouchina granulosa* , *2432: *Eremanthus sphaerocephalus* , *2439: *Tibouchina granulosa* , *2447: *Aechmea spec.* , *2451: *Tibouchina granulosa* , *2492: *Impatiens sultani* , *2509: *Lythrum salicaria* , *2510: *Lythrum salicaria* , *2515: *Phacelia viscida* , *2612: *Geropogon hybridus* , *2707: *Moricandia nitens* , *2768: *Echium angustifolium* , *2769: *Echium rauwolffii* , *2770: *Echium rauwolffii* , *2786: *Erodium ciconium* , *2806: *Fagonia glutinosa* , *2808: *Nidularium innocenti* , *2810: *Erodium acaule* , *2853: *Lotus lanuginosus* , *2919: *Moricandia nitens* , *2921: *Moricandia nitens* , *2949: *Orchis papilionacea* , *2951: *Ornithogalum trichophyllum* , *2952: *Ornithogalum neurostegium* , *2997: *Salvia hierosolymitana* , *3000: *Salvia indica*

300-310° (65): *153: *Chlorophytum undulatum* , *154: *Anchusa spec.* , *156: *Cyanella hyacinthoides* , *1174: *Campanula rapunculoides* , *1224: *Sempervivum montanum* , *1226: *Solanum dulcamara* , *1272: *Campanula latifolia* , *1275: *Campanula rotundifolia* , *1276: *Campanula trachelium* , *1277: *Campanula trachelium* , *1327: *Oxytropis jacquinii* , *1477: *Ajuga genevensis* , *1498: *Ornithogalum umbellatum* , *1501: *Symphytum officinale* , *1520: *Dendrobium pierardii* , *1657: *Veronica fruticans* , *1669: *Veronica fruticans* , *1702: *Campanula stenocodon* , *1762: *Rhododendron ferrugeum* , *1777: *Stachys sylvatica* , *1904: *Hedysarum hedysaroides* , *1921: *Rhododendron hirsutum* , *2120: *Ajuga genevensis* , *2148: *Veronica prostrata* , *2155: *Malva sylvestris* , *2159: *Petunia spec.* , *2179: *Platycodon grandiflorum* , *2196: *Campanula scheuchzeri* , *2267: *Hibiscus rosa-sinensis* , *2270: *Urera spec.* , *2292: *Dichorisandra spec.* , *2304: *Camptosema ellipticum* , *2313: *Tibouchina granulosa* , *2319: *Tibouchina granulosa* , *2343: *Tibouchina granulosa* , *2347: *Tibouchina granulosa* , *2362: *Tibouchina granulosa* , *2380: *Cochliostema odoratissimum* , *2396: *Tibouchina granulosa* , *2408: *Impatiens sultani* , *2411: *Impatiens sultani* , *2465: *Anchusa strigosa* , *2508: *Dichorisandra spec.* , *2538: *Centaurea cyanus* , *2547: *Ixiolirion montanum* , *2556: *Campanula trachelium* , *2576: *Veronica chamaedrys* , *2577: *Campanula trachelium* , *2580: *Hyptis suaveolens* , *2583: *Veronica chamaedrys* , *2609: *Campanula rotundifolia* , *2623: *Acanthus syriacus* , *2639: *Convolvulus althaeoides* , *2693: *Centaurea cyanus* , *2702: *Leopoldia comosa* , *2724: *Limodorum abortivum* , *2781: *Erodium laciniatum* , *2784: *Erodium crassifolium* , *2804: *Ixiolirion montanum* , *2881: *Limodorum abortivum* , *2900: *Aechmea miniata* , *2918: *Moricandia nitens* , *2943: *Tillandsia vernicosa* , *2953: *Ornithogalum neurostegium* , *2965: *Moricandia nitens*

310-320° angle (53): *676: *Lupinus polyphyllus* , *806: *Oxytropis pyrenaica* , *1175: *Campanula rapunculoides* , *1190: *Echium vulgare* , *1191: *Echium vulgare* , *1195: *Epilobium fleischeri* , *1212: *Oxytropis pyrenaica* , *1225: *Solanum dulcamara* , *1273: *Campanula rotundifolia* , *1278: *Campanula trachelium* , *1332: *Pedicularis recutita* , *1333: *Pedicularis recutita* , *1393: *Campanula rapunculoides* , *1517: *Dendrobium nobile* , *1602: *Salvia pratensis* , *1611: *Vicia sepium* , *1685: *Aconitum napellus* , *1738: *Lamium maculatum* ,

*1757: *Phyteuma orbiculare* , *1800: *Veronica spicata* , *1820: *Campanula barbata* , *1903: *Hedysarum hedysaroides* , *1922: *Rhododendron hirsutum* , *1974: *Salvia pratensis* , *2050: *Campanula persicifolia* , *2051: *Campanula persicifolia* , *2094: *Sempervivum arachnoideum* , *2138: *Vicia sativa* , *2140: *Vicia sativa* , *2178: *Platycodon grandiflorum* , *2198: *Campanula scheuchzeri* , *2225: *Cardamine pratensis* , *2307: *Fuchsia regia* , *2338: *Tibouchina stenocarpa* , *2402: *Lathyrus montanus* , *2453: *Tillandsia bulbosa* , *2470: *Cirrhopetalum cumingii* , *2491: *Euphorbia milii* , *2512: *Malva sylvestris* , *2524: *Veronica chamaedrys* , *2607: *Campanula rotundifolia* , *2642: *Alcea dissecta* , *2645: *Alkanna strigosa* , *2682: *Centaurea cyanus* , *2739: *Astragalus sanctus* , *2800: *Fagonia arabica* , *2833: *Lotus lanuginosus* , *2880: *Limodorum abortivum* , *2892: *Aechmea miniata* , *2906: *Malva sylvestris* , *2917: *Tillandsia bulbosa* , *2973: *Echium vulgare* , *2988: *Scorzonera papposa*

320-330° angle (44): *255: *Carlina acaulis* , *805: *Oxytropis pyrenaica* , *1218: *Ranunculus glacialis* , *1269: *Campanula alpestris* , *1270: *Campanula alpestris* , *1336: *Phyteuma hemisphericum* , *1357: *Soldanella alpina* , *1419: *Galeopsis pubescens* , *1436: *Veronica spicata* , *1470: *Lathraea squamaria* , *1485: *Vinca minor* , *1573: *Dactylorhiza majalis* , *1590: *Lychnis flos-cuculi* , *1617: *Bartsia alpina* , *1643: *Geranium sylvaticum* , *1675: *Ranunculus asiaticus* , *1676: *Ranunculus asiaticus* , *1684: *Aconitum napellus* , *1698: *Campanula cochlearifolia* , *1704: *Carduus defloratus* , *1821: *Campanula barbata* , *1954: *Gentiana grandiflora* , *1995: *Ajuga genevensis* , *2063: *Gnaphalium sylvatica* , *2083: *Phyteuma hederanthifolium* , *2111: *Papaver rhoeas* , *2167: *Veronica beccabunga* , *2185: *Papaver rhoeas* , *2204: *Thunbergia grandiflora* , *2275: *Veronica spicata* , *2349: *Viola x wittrockiana* , *2392: *Vernonia spec.* , *2430: *Aechmea spec.* , *2588: *Lamium maculatum* , *2643: *Alcea acaulis* , *2684: *Asphodelus aestivus* , *2686: *Asphodelus aestivus* , *2779: *Salvia lanigera* , *2787: *Geranium purpureum* , *2803: *Fagonia mollis* , *2842: *Gynandriris monophylla* , *2857: *Fagonia mollis* , *2966: *Trifolium pratense* , *2971: *Tillandsia cyanea*

330-340° angle (51): *155: *Anchusa spec.* , *267: *Euphrasia rostkoviana* , *692: *Malva nicaeensis* , *1131: *Ajuga genevensis* , *1185: *Cymbalaria muralis* , *1194: *Epilobium fleischeri* , *1247: *Oxytropis lapponica* , *1301: *Gentiana bavarica* , *1407: *Prunella vulgaris* , *1459: *Hepatica nobilis* , *1460: *Hepatica nobilis* , *1636: *Ranunculus glacialis* , *1682: *Acinos alpinus* , *1708: *Cicerbita alpina* , *1717: *Erigeron polymorphus* , *1729: *Geranium pratense* , *1739: *Lamium maculatum* , *1775: *Scabiosa lucida* , *1862: *Phyteuma betonicifolium* , *1864: *Pinguicula vulgaris* , *1869: *Prunella grandiflora* , *1870: *Prunella grandiflora* , *2097: *Cichorium intybus* , *2110: *Ajuga reptans* , *2124: *Hepatica nobilis* , *2154: *Silene dioica* , *2191: *Ajuga pyramidalis* , *2306: *Impatiens sultani* , *2314: *Impatiens sultani* , *2386: *Saintpaulia ionantha* , *2399: *Impatiens sultani* , *2407: *Impatiens sultani* , *2427: *Lathyrus montanus* , *2438: *Ranunculus spec.* , *2441: *Ipomoea callida* , *2474: *Aechmea miniata* , *2596: *Salvia pratensis* , *2619: *Blepharis ciliaris* , *2631: *Orchis anatolica* , *2637: *Centaurea ammonocyanus* , *2659: *Crupina crupinastrum* , *2670: *Asphodelus aestivus* , *2726: *Acanthus syriacus* , *2785: *Erodium crassifolium* , *2805: *Fagonia glutinosa* , *2819: *Glaucium corniculatum* , *2911: *Tillandsia aeranthos* , *2913: *Fagonia glutinosa* , *2940: *Orchis papilionacea* , *2962: *Tillandsia cyanea* , *3001: *Salvia lanigera*

340-350° angle (37): *1171: *Calamintha sylvatica* , *1248: *Pinguicula vulgaris* , *1300: *Gentiana nivalis* , *1308: *Jasione montana* , *1328: *Oxytropis jacquinii* , *1367: *Thlaspi rotundifolia* , *1404: *Melampyrum nemerosum* , *1497: *Ornithogalum umbellatum* , *1587: *Geranium robertianum* , *1670: *Anemone coronaria* , *1678: *Ranunculus asiaticus* , *1701: *Campanula stenocodon* , *1706: *Centaurea nigrescens* , *1733: *Gymnadenia conopsea* , *1737: *Lamium maculatum* , *1764: *Rosa pendulina* , *1774: *Scabiosa lucida* , *1829: *Dactylorhiza maculata* , *1899: *Astragalus alpinus* , *1997: *Allium schoenoprasum* , *2012: *Gentianella armarella* , *2040: *Saxifraga oppositifolia* , *2153: *Myosotis hispida* , *2315: *Cissus spec.* , *2364: *Daphne mezereum* , *2378: *Mimosa spec.* , *2449: *Jacaranda puberula* , *2513: *Malva sylvestris* , *2561: *Lamium maculatum* , *2641: *Limonium pruinosum* , *2646: *Allium neapolitanum* , *2648: *Crupina crupinastrum* , *2650: *Orchis anatolica* , *2676: *Antirrhinum majus* , *2812: *Geranium robertianum* , *2873: *Launaea angustifolia* , *2950: *Orchis tridentata*

350-360° angle (36): *677: *Lupinus polyphyllus* , *1008: *Symphoricarpos albus* , *1163: *Stachys sylvatica* , *1234: *Veronica officinalis* , *1245: *Chamerion angustifolium* , *1251: *Silene dioica* , *1369: *Thymus oenipontanus* , *1381: *Chamerion angustifolium* , *1395: *Epilobium hirsutum* , *1483: *Syringa vulgaris* , *1491: *Lathyrus vernus* , *1513: *Dendrobium loddigesii* , *1515: *Dendrobium nobile* , *1543: *Campanula rotundifolia* , *1558: *Polemonium caerulum* , *1569: *Veronica alpina* , *1607: *Trifolium pratense* , *1663: *Glechoma hederacea* , *1975: *Galeopsis bifida* , *2060: *Gentianella campestris* , *2070: *Lilium martagon* , *2123: *Symphytum officinale* , *2135: *Ranunculus spec.* , *2139: *Vicia sativa* , *2171: *Lychnis coronaria* , *2255: *Polygala alpina* , *2340: *Fuchsia regia* , *2361: *Emilia sonchifolia* , *2404: *Justicia rizzini* , *2416: *Dichorisandra spec.* , *2528: *Chamerion angustifolium* , *2699: *Astragalus tribuloides* , *2832: *Nidularium innocenti* , *2915: *Micromeria nervosa* , *2937: *Fagonia mollis* , *2954: *Scilla hyacinthoides*

PLOTTING AND CALCULATING COLOUR DISTANCES ON THE COLOUR HEXAGON

The following are the portion of code written in PHP to demonstrate how colour shift, colour distances and the location of the flower colour loci on the colour hexagon were calculated. Note, all variables in PHP start with the symbol '$'. All text proceeding the characters '//' are comments. All code in bold are builtin PHP functions:

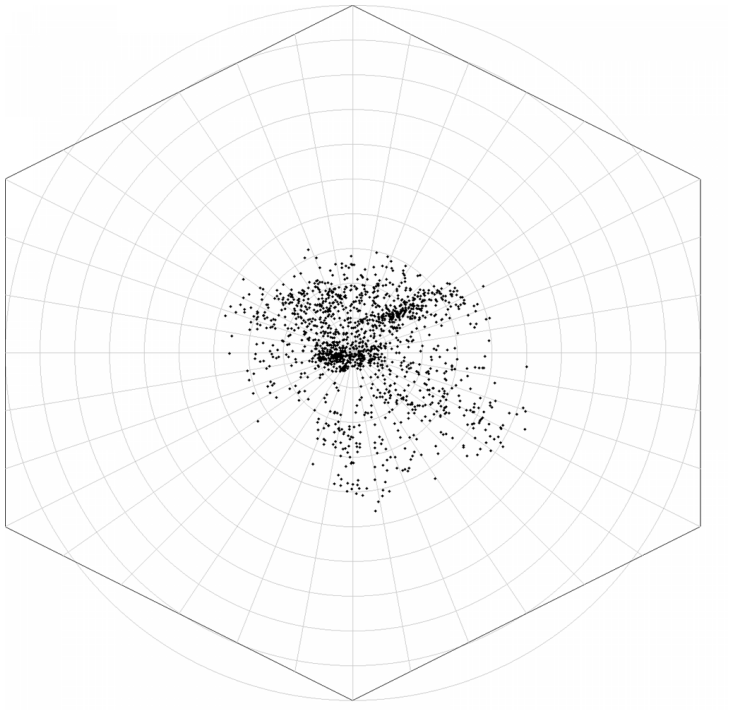
Determining the plot in the colour hexagon from the excitation reponse of the UV, B and G receptors (Chittka, 1992):

```
//$uv, $b and $g hold the excitation response
$x = (cos(30*pi()/180))*($g-$uv);
$y = $b-(0.5*($g+$uv));
```

Finding the angle at which the flower loci is plotted on the colour hexagon:

```
//$startpoint is the middle of the colour hexagon on the computer display
graphic
$plotx = $startpoint + ($x*$startpoint);
$ploty=$startpoint - ($y*$startpoint);
$angleat= atan2(-$x, -$y)/M_PI*180 + 180;
```

`$plotx` and `$ploty` are the coordinates for plotting on a graphic image in PHP. The plot is a dot that is marked into the graphic image. The following is an example of the above code being used to plot the 1572 flowers on the colour hexagon as a dot:



Measuring colour shift or colour distance from two loci points on the colour hexagon (Chittka, 1992):

```
//$x and $y are the first plot, $x2 and $y2 are the second plot
$thisdis = (($x-$x2)*($x-$x2));
$thisdis1 = (($y-$y2)*($y-$y2));
$thisdis = sqrt($thisdis + $thisdis1); //square root
```

The (MySQL) Query for calculating excitation response

MySQL is a language for querying databases. Besides Floral reflectance spectra, the FReD database now also holds spectral sensitivity of α-band and narrow spectral sensitivity function colour visual systems alongside four different spectral light functions. This along with the above PHP code can be used to calculate colour shift under changing illumination of a given colour reflectance function in different colour visual models. The following table shows the data that is held of the colour visual models, the spectral light functions and background spectra in 2nm wavelength (λ) step:

	Spectral sensitivity colour vision														
λ	Normal Honeybee			α-band spectral sensitivity			Narrow spectral sensitivity			Lighting conditions				backgrounds	
	UV	B	G	UV	B	G	UV	B	G	D65	FS	WS	SG	Leaf	Gray
300	0.30	0.08	0.13	0.30	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.20
302	0.30	0.08	0.13	0.30	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.20
304	0.30	0.08	0.13	0.30	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.20
306	0.39	0.11	0.14	0.39	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.05	0.20
308	0.39	0.11	0.14	0.39	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.05	0.20
310	0.49	0.13	0.15	0.49	0.00	0.00	0.05	0.00	0.00	0.03	0.00	0.00	0.00	0.04	0.20
312	0.49	0.13	0.15	0.49	0.01	0.00	0.10	0.00	0.00	0.03	0.01	0.01	0.01	0.04	0.20
314	0.49	0.13	0.15	0.49	0.01	0.00	0.20	0.00	0.00	0.03	0.01	0.01	0.01	0.04	0.20
316	0.58	0.16	0.16	0.58	0.01	0.00	0.35	0.00	0.00	0.07	0.02	0.02	0.02	0.05	0.20
318	0.58	0.16	0.16	0.58	0.01	0.00	0.40	0.00	0.00	0.07	0.02	0.02	0.02	0.05	0.20
320	0.68	0.19	0.17	0.68	0.01	0.00	0.50	0.00	0.00	0.11	0.03	0.03	0.02	0.05	0.20
322	0.68	0.19	0.17	0.68	0.01	0.00	0.60	0.00	0.00	0.11	0.03	0.05	0.02	0.05	0.20
324	0.68	0.19	0.17	0.68	0.02	0.00	0.70	0.00	0.00	0.11	0.04	0.10	0.04	0.05	0.20
326	0.77	0.21	0.17	0.77	0.02	0.00	0.80	0.00	0.00	0.16	0.04	0.12	0.04	0.05	0.20
328	0.77	0.21	0.17	0.77	0.02	0.00	0.90	0.00	0.00	0.16	0.05	0.14	0.04	0.05	0.20
330	0.86	0.24	0.18	0.86	0.03	0.00	0.95	0.00	0.00	0.21	0.05	0.20	0.04	0.05	0.20
332	0.86	0.24	0.18	0.86	0.03	0.00	0.98	0.00	0.00	0.21	0.13	0.20	0.05	0.05	0.20
334	0.86	0.24	0.18	0.86	0.03	0.00	1.00	0.00	0.00	0.21	0.14	0.25	0.05	0.05	0.20
336	0.96	0.27	0.19	0.96	0.03	0.00	1.00	0.00	0.00	0.23	0.15	0.25	0.05	0.05	0.20
338	0.96	0.27	0.19	0.96	0.03	0.00	1.00	0.00	0.00	0.23	0.15	0.30	0.05	0.05	0.20
340	1.00	0.30	0.19	1.00	0.03	0.00	1.00	0.00	0.00	0.24	0.19	0.32	0.06	0.05	0.20
342	1.00	0.30	0.19	1.00	0.04	0.00	1.00	0.00	0.00	0.24	0.20	0.35	0.06	0.05	0.20
344	1.00	0.30	0.19	1.00	0.04	0.00	1.00	0.00	0.00	0.24	0.20	0.35	0.06	0.05	0.20
346	1.00	0.31	0.19	1.00	0.04	0.00	1.00	0.00	0.00	0.26	0.26	0.40	0.09	0.05	0.20
348	1.00	0.31	0.19	1.00	0.05	0.00	1.00	0.00	0.00	0.26	0.26	0.40	0.09	0.05	0.20
350	0.98	0.34	0.19	0.98	0.05	0.00	1.00	0.00	0.00	0.27	0.28	0.46	0.11	0.05	0.20
352	0.98	0.34	0.19	0.98	0.06	0.00	1.00	0.00	0.00	0.27	0.29	0.47	0.11	0.05	0.20
354	0.98	0.34	0.19	0.98	0.06	0.00	1.00	0.00	0.00	0.27	0.28	0.47	0.11	0.05	0.20
356	0.90	0.35	0.20	0.90	0.07	0.00	1.00	0.00	0.00	0.28	0.26	0.45	0.11	0.05	0.20

358	0.90	0.35	0.20	0.90	0.07	0.00	1.00	0.00	0.00	0.28	0.26	0.44	0.11	0.05	0.20
360	0.81	0.37	0.20	0.81	0.08	0.01	1.00	0.00	0.00	0.29	0.27	0.46	0.12	0.05	0.20
362	0.81	0.37	0.20	0.81	0.08	0.01	0.98	0.00	0.00	0.29	0.29	0.49	0.13	0.05	0.20
364	0.81	0.37	0.20	0.81	0.10	0.01	0.95	0.00	0.00	0.29	0.32	0.53	0.14	0.05	0.20
366	0.71	0.39	0.20	0.71	0.10	0.01	0.90	0.00	0.00	0.32	0.34	0.56	0.15	0.05	0.20
368	0.71	0.39	0.20	0.71	0.12	0.01	0.80	0.00	0.00	0.32	0.34	0.56	0.16	0.05	0.20
370	0.62	0.41	0.20	0.62	0.15	0.01	0.70	0.00	0.00	0.33	0.33	0.54	0.16	0.05	0.20
372	0.62	0.41	0.20	0.62	0.17	0.02	0.60	0.00	0.00	0.33	0.32	0.52	0.15	0.05	0.20
374	0.62	0.41	0.20	0.62	0.20	0.02	0.50	0.00	0.00	0.33	0.32	0.53	0.16	0.05	0.20
376	0.54	0.43	0.19	0.54	0.25	0.02	0.40	0.00	0.00	0.34	0.33	0.55	0.17	0.05	0.20
378	0.54	0.43	0.19	0.54	0.30	0.03	0.35	0.00	0.00	0.34	0.33	0.55	0.18	0.05	0.20
380	0.45	0.47	0.19	0.45	0.35	0.03	0.20	0.00	0.00	0.33	0.31	0.51	0.16	0.05	0.20
382	0.45	0.47	0.19	0.45	0.40	0.03	0.10	0.00	0.00	0.33	0.29	0.47	0.16	0.05	0.20
384	0.45	0.47	0.19	0.45	0.45	0.03	0.05	0.00	0.00	0.33	0.29	0.47	0.16	0.05	0.20
386	0.36	0.51	0.18	0.36	0.51	0.03	0.00	0.00	0.00	0.35	0.31	0.49	0.17	0.05	0.20
388	0.36	0.51	0.18	0.36	0.51	0.03	0.00	0.00	0.00	0.35	0.33	0.52	0.19	0.05	0.20
390	0.28	0.57	0.17	0.28	0.57	0.04	0.00	0.00	0.00	0.39	0.33	0.52	0.19	0.05	0.20
392	0.28	0.57	0.17	0.28	0.57	0.04	0.00	0.00	0.00	0.39	0.31	0.50	0.18	0.05	0.20
394	0.28	0.57	0.17	0.28	0.60	0.04	0.00	0.00	0.00	0.39	0.32	0.50	0.19	0.05	0.20
396	0.22	0.63	0.17	0.22	0.60	0.04	0.00	0.00	0.00	0.48	0.36	0.57	0.22	0.06	0.20
398	0.22	0.63	0.17	0.22	0.60	0.05	0.00	0.00	0.00	0.48	0.42	0.67	0.26	0.06	0.20
400	0.17	0.70	0.16	0.17	0.70	0.05	0.00	0.05	0.00	0.58	0.47	0.75	0.30	0.06	0.20
402	0.17	0.70	0.16	0.17	0.70	0.05	0.00	0.10	0.00	0.58	0.49	0.78	0.32	0.06	0.20
404	0.17	0.70	0.16	0.17	0.70	0.05	0.00	0.20	0.00	0.58	0.50	0.78	0.32	0.06	0.20
406	0.14	0.75	0.16	0.14	0.75	0.06	0.00	0.35	0.00	0.62	0.50	0.78	0.33	0.06	0.20
408	0.14	0.75	0.16	0.14	0.75	0.06	0.00	0.40	0.00	0.62	0.51	0.78	0.33	0.06	0.20
410	0.11	0.82	0.17	0.11	0.82	0.06	0.00	0.50	0.00	0.65	0.52	0.79	0.35	0.06	0.20
412	0.11	0.82	0.17	0.11	0.82	0.07	0.00	0.60	0.00	0.65	0.52	0.80	0.36	0.06	0.20
414	0.11	0.82	0.17	0.11	0.82	0.07	0.00	0.70	0.00	0.65	0.53	0.80	0.36	0.06	0.20
416	0.09	0.87	0.17	0.09	0.87	0.07	0.00	0.80	0.00	0.67	0.52	0.80	0.36	0.06	0.20
418	0.09	0.87	0.17	0.09	0.87	0.09	0.00	0.90	0.00	0.67	0.52	0.79	0.36	0.06	0.20
420	0.07	0.91	0.17	0.07	0.91	0.08	0.00	0.95	0.00	0.69	0.51	0.78	0.36	0.07	0.20
422	0.07	0.91	0.17	0.07	0.91	0.08	0.00	0.98	0.00	0.69	0.51	0.77	0.36	0.07	0.20
424	0.07	0.91	0.17	0.07	0.91	0.09	0.00	1.00	0.00	0.69	0.50	0.75	0.36	0.07	0.20
426	0.05	0.95	0.18	0.05	0.95	0.10	0.00	1.00	0.00	0.67	0.48	0.72	0.35	0.07	0.20
428	0.05	0.95	0.18	0.05	0.95	0.11	0.00	1.00	0.00	0.67	0.46	0.69	0.34	0.07	0.20
430	0.04	0.99	0.19	0.04	0.99	0.11	0.00	1.00	0.00	0.67	0.46	0.68	0.35	0.07	0.20
432	0.04	0.99	0.19	0.04	0.99	0.12	0.00	1.00	0.00	0.67	0.48	0.71	0.37	0.07	0.20
434	0.04	0.99	0.19	0.04	0.99	0.13	0.00	1.00	0.00	0.67	0.50	0.74	0.39	0.07	0.20
436	0.04	1.00	0.21	0.04	1.00	0.15	0.00	1.00	0.00	0.73	0.51	0.75	0.41	0.08	0.20
438	0.04	1.00	0.21	0.04	1.00	0.16	0.00	1.00	0.00	0.73	0.52	0.76	0.42	0.08	0.20
440	0.03	0.99	0.23	0.03	0.99	0.18	0.00	1.00	0.00	0.81	0.54	0.78	0.44	0.08	0.20
442	0.03	0.99	0.23	0.03	0.99	0.18	0.00	1.00	0.00	0.81	0.55	0.80	0.45	0.08	0.20
444	0.03	0.99	0.23	0.03	0.99	0.19	0.00	1.00	0.00	0.81	0.56	0.81	0.47	0.08	0.20
446	0.03	0.95	0.25	0.03	0.95	0.19	0.00	1.00	0.00	0.86	0.57	0.82	0.48	0.08	0.20
448	0.03	0.95	0.25	0.03	0.95	0.24	0.00	1.00	0.00	0.86	0.59	0.84	0.50	0.08	0.20
450	0.03	0.87	0.27	0.03	0.87	0.25	0.00	1.00	0.00	0.91	0.59	0.84	0.50	0.09	0.20
452	0.03	0.87	0.27	0.03	0.87	0.25	0.00	0.98	0.00	0.91	0.59	0.83	0.51	0.09	0.20
454	0.03	0.87	0.27	0.03	0.87	0.26	0.00	0.95	0.00	0.91	0.59	0.83	0.51	0.09	0.20
456	0.02	0.78	0.30	0.02	0.78	0.27	0.00	0.90	0.00	0.93	0.60	0.83	0.52	0.09	0.20
458	0.02	0.78	0.30	0.02	0.78	0.28	0.00	0.80	0.00	0.93	0.60	0.83	0.52	0.09	0.20
460	0.02	0.69	0.33	0.02	0.69	0.28	0.00	0.70	0.00	0.95	0.60	0.83	0.53	0.09	0.20
462	0.02	0.69	0.33	0.02	0.69	0.33	0.00	0.60	0.00	0.95	0.60	0.83	0.53	0.09	0.20
464	0.02	0.69	0.33	0.02	0.69	0.33	0.00	0.50	0.00	0.95	0.59	0.81	0.53	0.09	0.20
466	0.02	0.63	0.36	0.02	0.63	0.33	0.00	0.40	0.00	0.95	0.59	0.80	0.53	0.09	0.20
468	0.02	0.63	0.36	0.02	0.63	0.36	0.00	0.35	0.00	0.95	0.58	0.79	0.53	0.09	0.20
470	0.01	0.54	0.39	0.01	0.54	0.36	0.00	0.20	0.00	0.95	0.58	0.79	0.53	0.08	0.20
472	0.01	0.54	0.39	0.01	0.54	0.39	0.00	0.10	0.00	0.95	0.59	0.79	0.54	0.08	0.20

474	0.01	0.54	0.39	0.01	0.54	0.39	0.00	0.05	0.00	0.95	0.59	0.79	0.55	0.08	0.20
476	0.01	0.47	0.44	0.01	0.47	0.39	0.00	0.00	0.00	0.96	0.60	0.79	0.56	0.08	0.20
478	0.01	0.47	0.44	0.01	0.47	0.44	0.00	0.00	0.00	0.96	0.60	0.80	0.56	0.08	0.20
480	0.01	0.38	0.50	0.01	0.38	0.44	0.00	0.00	0.00	0.97	0.60	0.79	0.56	0.09	0.20
482	0.01	0.38	0.50	0.01	0.38	0.50	0.00	0.00	0.00	0.97	0.59	0.77	0.56	0.09	0.20
484	0.01	0.38	0.50	0.01	0.38	0.50	0.00	0.00	0.00	0.97	0.57	0.74	0.54	0.09	0.20
486	0.01	0.29	0.55	0.01	0.29	0.50	0.00	0.00	0.00	0.95	0.55	0.72	0.53	0.09	0.20
488	0.01	0.29	0.55	0.01	0.29	0.55	0.00	0.00	0.00	0.95	0.56	0.73	0.54	0.09	0.20
490	0.01	0.21	0.59	0.01	0.21	0.55	0.00	0.00	0.00	0.94	0.57	0.73	0.55	0.09	0.20
492	0.01	0.21	0.59	0.01	0.21	0.59	0.00	0.00	0.00	0.94	0.58	0.74	0.56	0.09	0.20
494	0.01	0.21	0.59	0.01	0.21	0.59	0.00	0.00	0.00	0.94	0.58	0.74	0.57	0.09	0.20
496	0.00	0.14	0.64	0.00	0.14	0.59	0.00	0.00	0.00	0.94	0.59	0.74	0.58	0.09	0.20
498	0.00	0.14	0.64	0.00	0.14	0.64	0.00	0.00	0.00	0.94	0.58	0.72	0.58	0.09	0.20
500	0.00	0.10	0.68	0.00	0.10	0.64	0.00	0.00	0.00	0.96	0.58	0.71	0.57	0.10	0.20
502	0.00	0.10	0.68	0.00	0.10	0.68	0.00	0.00	0.00	0.96	0.58	0.71	0.58	0.10	0.20
504	0.00	0.10	0.68	0.00	0.10	0.68	0.00	0.00	0.00	0.96	0.59	0.71	0.59	0.10	0.20
506	0.00	0.08	0.72	0.00	0.08	0.68	0.00	0.00	0.00	0.96	0.61	0.71	0.60	0.10	0.20
508	0.00	0.08	0.72	0.00	0.08	0.72	0.00	0.00	0.00	0.96	0.62	0.71	0.60	0.10	0.20
510	0.00	0.06	0.77	0.00	0.06	0.72	0.00	0.00	0.00	0.96	0.63	0.71	0.61	0.11	0.20
512	0.00	0.06	0.77	0.00	0.06	0.77	0.00	0.00	0.00	0.96	0.64	0.70	0.61	0.11	0.20
514	0.00	0.06	0.77	0.00	0.06	0.77	0.00	0.00	0.00	0.96	0.64	0.68	0.60	0.11	0.20
516	0.00	0.05	0.81	0.00	0.05	0.77	0.00	0.00	0.00	0.96	0.65	0.66	0.59	0.12	0.20
518	0.00	0.05	0.81	0.00	0.05	0.81	0.00	0.00	0.00	0.96	0.68	0.67	0.60	0.12	0.20
520	0.00	0.04	0.84	0.00	0.04	0.81	0.00	0.00	0.00	0.95	0.72	0.69	0.62	0.13	0.20
522	0.00	0.04	0.84	0.00	0.04	0.84	0.00	0.00	0.00	0.95	0.76	0.70	0.64	0.13	0.20
524	0.00	0.04	0.84	0.00	0.04	0.84	0.00	0.00	0.00	0.95	0.79	0.71	0.65	0.13	0.20
526	0.00	0.03	0.89	0.00	0.03	0.84	0.00	0.00	0.05	0.98	0.82	0.71	0.66	0.15	0.20
528	0.00	0.03	0.89	0.00	0.03	0.89	0.00	0.00	0.10	0.98	0.85	0.72	0.68	0.15	0.20
530	0.00	0.02	0.93	0.00	0.02	0.89	0.00	0.00	0.20	0.99	0.88	0.73	0.69	0.16	0.20
532	0.00	0.02	0.93	0.00	0.02	0.93	0.00	0.00	0.35	0.99	0.90	0.73	0.70	0.16	0.20
534	0.00	0.02	0.93	0.00	0.02	0.93	0.00	0.00	0.40	0.99	0.92	0.74	0.71	0.16	0.20
536	0.00	0.01	0.95	0.00	0.01	0.93	0.00	0.00	0.50	0.99	0.93	0.74	0.71	0.17	0.20
538	0.00	0.01	0.95	0.00	0.01	0.95	0.00	0.00	0.60	0.99	0.93	0.73	0.71	0.17	0.20
540	0.00	0.00	0.97	0.00	0.00	0.95	0.00	0.00	0.70	0.99	0.94	0.73	0.71	0.17	0.20
542	0.00	0.00	0.97	0.00	0.00	0.97	0.00	0.00	0.80	0.99	0.95	0.73	0.71	0.17	0.20
544	0.00	0.00	0.97	0.00	0.00	0.97	0.00	0.00	0.90	0.99	0.96	0.73	0.72	0.17	0.20
546	0.00	0.00	0.99	0.00	0.00	0.97	0.00	0.00	0.95	0.99	0.97	0.73	0.73	0.17	0.20
548	0.00	0.00	0.99	0.00	0.00	0.99	0.00	0.00	0.98	0.99	0.98	0.73	0.73	0.17	0.20
550	0.00	0.00	0.99	0.00	0.00	0.99	0.00	0.00	1.00	1.00	0.99	0.73	0.74	0.18	0.20
552	0.00	0.00	0.99	0.00	0.00	0.99	0.00	0.00	1.00	1.00	0.99	0.73	0.74	0.18	0.20
554	0.00	0.00	0.99	0.00	0.00	0.99	0.00	0.00	1.00	1.00	0.99	0.73	0.74	0.18	0.20
556	0.00	0.00	1.00	0.00	0.00	0.99	0.00	0.00	1.00	1.00	0.98	0.72	0.74	0.18	0.20
558	0.00	0.00	1.00	0.00	0.00	1.00	0.00	0.00	1.00	1.00	0.97	0.71	0.74	0.18	0.20
560	0.00	0.00	1.00	0.00	0.00	1.00	0.00	0.00	1.00	0.98	0.97	0.70	0.75	0.17	0.20
562	0.00	0.00	1.00	0.00	0.00	1.00	0.00	0.00	1.00	0.98	0.96	0.70	0.76	0.17	0.20
564	0.00	0.00	1.00	0.00	0.00	1.00	0.00	0.00	1.00	0.98	0.94	0.69	0.77	0.17	0.20
566	0.00	0.00	0.98	0.00	0.00	1.00	0.00	0.00	1.00	0.97	0.92	0.68	0.77	0.16	0.20
568	0.00	0.00	0.98	0.00	0.00	0.98	0.00	0.00	1.00	0.97	0.90	0.67	0.77	0.16	0.20
570	0.00	0.00	0.91	0.00	0.00	0.98	0.00	0.00	1.00	0.96	0.88	0.66	0.77	0.16	0.20
572	0.00	0.00	0.91	0.00	0.00	0.91	0.00	0.00	1.00	0.96	0.86	0.66	0.78	0.16	0.20
574	0.00	0.00	0.91	0.00	0.00	0.91	0.00	0.00	1.00	0.96	0.84	0.65	0.79	0.16	0.20
576	0.00	0.00	0.81	0.00	0.00	0.91	0.00	0.00	1.00	0.97	0.83	0.64	0.79	0.15	0.20
578	0.00	0.00	0.81	0.00	0.00	0.81	0.00	0.00	0.98	0.97	0.82	0.64	0.80	0.15	0.20
580	0.00	0.00	0.68	0.00	0.00	0.81	0.00	0.00	0.95	0.97	0.81	0.64	0.81	0.14	0.20
582	0.00	0.00	0.68	0.00	0.00	0.68	0.00	0.00	0.90	0.97	0.81	0.64	0.82	0.14	0.20
584	0.00	0.00	0.68	0.00	0.00	0.68	0.00	0.00	0.80	0.97	0.79	0.64	0.81	0.14	0.20
586	0.00	0.00	0.56	0.00	0.00	0.68	0.00	0.00	0.70	0.94	0.76	0.62	0.79	0.14	0.20
588	0.00	0.00	0.56	0.00	0.00	0.56	0.00	0.00	0.60	0.94	0.73	0.60	0.76	0.14	0.20

590	0.00	0.00	0.45	0.00	0.00	0.56	0.00	0.00	0.50	0.92	0.72	0.60	0.76	0.13	0.20
592	0.00	0.00	0.45	0.00	0.00	0.45	0.00	0.00	0.40	0.92	0.72	0.60	0.76	0.13	0.20
594	0.00	0.00	0.45	0.00	0.00	0.45	0.00	0.00	0.35	0.92	0.72	0.60	0.77	0.13	0.20
596	0.00	0.00	0.36	0.00	0.00	0.45	0.00	0.00	0.20	0.93	0.73	0.60	0.78	0.13	0.20
598	0.00	0.00	0.36	0.00	0.00	0.36	0.00	0.00	0.10	0.93	0.73	0.60	0.80	0.13	0.20
600	0.00	0.00	0.27	0.00	0.00	0.36	0.00	0.00	0.05	0.94	0.73	0.60	0.81	0.13	0.20
602	0.00	0.00	0.27	0.00	0.00	0.27	0.00	0.00	0.00	0.94	0.73	0.60	0.82	0.13	0.20
604	0.00	0.00	0.27	0.00	0.00	0.27	0.00	0.00	0.00	0.94	0.73	0.60	0.83	0.13	0.20
606	0.00	0.00	0.20	0.00	0.00	0.27	0.00	0.00	0.00	0.95	0.73	0.60	0.83	0.13	0.20
608	0.00	0.00	0.20	0.00	0.00	0.20	0.00	0.00	0.00	0.95	0.72	0.59	0.83	0.13	0.20
610	0.00	0.00	0.15	0.00	0.00	0.20	0.00	0.00	0.00	0.95	0.71	0.58	0.82	0.12	0.20
612	0.00	0.00	0.15	0.00	0.00	0.15	0.00	0.00	0.00	0.95	0.69	0.57	0.82	0.12	0.20
614	0.00	0.00	0.15	0.00	0.00	0.15	0.00	0.00	0.00	0.95	0.68	0.57	0.81	0.12	0.20
616	0.00	0.00	0.11	0.00	0.00	0.15	0.00	0.00	0.00	0.95	0.68	0.56	0.81	0.12	0.20
618	0.00	0.00	0.11	0.00	0.00	0.11	0.00	0.00	0.00	0.95	0.68	0.56	0.82	0.12	0.20
620	0.00	0.00	0.09	0.00	0.00	0.11	0.00	0.00	0.00	0.95	0.67	0.56	0.82	0.12	0.20
622	0.00	0.00	0.09	0.00	0.00	0.09	0.00	0.00	0.00	0.95	0.67	0.56	0.82	0.12	0.20
624	0.00	0.00	0.09	0.00	0.00	0.09	0.00	0.00	0.00	0.95	0.66	0.55	0.81	0.12	0.20
626	0.00	0.00	0.06	0.00	0.00	0.09	0.00	0.00	0.00	0.93	0.65	0.54	0.81	0.11	0.20
628	0.00	0.00	0.06	0.00	0.00	0.06	0.00	0.00	0.00	0.93	0.64	0.54	0.80	0.11	0.20
630	0.00	0.00	0.05	0.00	0.00	0.06	0.00	0.00	0.00	0.92	0.64	0.54	0.80	0.12	0.20
632	0.00	0.00	0.05	0.00	0.00	0.05	0.00	0.00	0.00	0.92	0.64	0.54	0.81	0.12	0.20
634	0.00	0.00	0.05	0.00	0.00	0.05	0.00	0.00	0.00	0.92	0.64	0.54	0.81	0.12	0.20
636	0.00	0.00	0.03	0.00	0.00	0.05	0.00	0.00	0.00	0.93	0.64	0.54	0.81	0.11	0.20
638	0.00	0.00	0.03	0.00	0.00	0.03	0.00	0.00	0.00	0.93	0.63	0.54	0.81	0.11	0.20
640	0.00	0.00	0.02	0.00	0.00	0.03	0.00	0.00	0.00	0.94	0.62	0.54	0.81	0.11	0.20
642	0.00	0.00	0.02	0.00	0.00	0.02	0.00	0.00	0.00	0.94	0.61	0.53	0.81	0.11	0.20
644	0.00	0.00	0.02	0.00	0.00	0.02	0.00	0.00	0.00	0.94	0.59	0.53	0.80	0.11	0.20
646	0.00	0.00	0.02	0.00	0.00	0.02	0.00	0.00	0.00	0.92	0.57	0.52	0.79	0.11	0.20
648	0.00	0.00	0.02	0.00	0.00	0.02	0.00	0.00	0.00	0.92	0.56	0.51	0.78	0.11	0.20
650	0.00	0.00	0.01	0.00	0.00	0.02	0.00	0.00	0.00	0.91	0.55	0.51	0.78	0.10	0.20
652	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.91	0.54	0.50	0.78	0.10	0.20
654	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.91	0.53	0.49	0.76	0.10	0.20
656	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.92	0.52	0.48	0.76	0.10	0.20
658	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.92	0.52	0.49	0.78	0.10	0.20
660	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.93	0.53	0.50	0.80	0.10	0.20
662	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.93	0.53	0.50	0.81	0.10	0.20
664	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.93	0.53	0.50	0.82	0.10	0.20
666	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.95	0.53	0.50	0.83	0.10	0.20
668	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.95	0.52	0.49	0.83	0.10	0.20
670	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.96	0.52	0.49	0.83	0.10	0.20
672	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.96	0.51	0.48	0.83	0.10	0.20
674	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.96	0.51	0.48	0.83	0.10	0.20
676	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.95	0.51	0.48	0.84	0.10	0.20
678	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.95	0.52	0.48	0.85	0.10	0.20
680	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.93	0.52	0.48	0.86	0.10	0.20
682	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.93	0.52	0.48	0.86	0.10	0.20
684	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.93	0.51	0.46	0.83	0.10	0.20
686	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.89	0.50	0.44	0.79	0.10	0.20
688	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.89	0.51	0.43	0.76	0.10	0.20
690	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.85	0.56	0.46	0.77	0.11	0.20
692	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.85	0.62	0.49	0.79	0.11	0.20
694	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.85	0.70	0.53	0.80	0.11	0.20
696	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.86	0.81	0.57	0.82	0.13	0.20
698	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.86	0.93	0.61	0.83	0.13	0.20
700	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.86	0.99	0.62	0.83	0.14	0.20

A weighting is determined based on Equation 3 in Chapter 1 (Backhaus and Menzel, 1987). In MySQL, based on the above table (i.e. refered to as 's' in the MySQL query below) an example query for finding the weighting *R*, as determined in Table 3-1 for D65 daylight and honeybee colour vision is as follows:

```
select (
      1 / sum(s.uv * s.daylight) * s.leaf) AS uvfactor,(
      1 / sum(s.blue * s.daylight) * s.leaf) AS bluefactor,(
      1 / sum(s.green * s.daylight) * s.leaf) AS greenfactor
from sensitivity s
```

let's call the above query '`weight`'.

The receptor 'photon flux' or input to receptors based on a given lighting and spectral reflectance is described in Equation 2 in Chapter 1. In MySQL this is determined as follows:

```
select
w.flowerid AS flowerid,
w.wavelength AS wavelength,
w.reflectance AS reflectance,
((w.reflectance * s.uv) * s.daylight) AS uv,
((w.reflectance * s.blue) * s.daylight) AS blue,
((w.reflectance * s.green) * s.daylight) AS green from (
      wavelength w join sensitivity s) where (
            w.wavelength = s.wavelength) and (w.flowerid=flowerID)
```

The above returns a table of the photon flux for the entire spectrum based on the `s.uv, s.blue, s.green` – that is, the spectral sensitivity of the three photoreceptors. At this point, a flower ID must be stated to list the response of the photoreceptors based on the reflectance spectra of the flower in the database. Let's call the above query '`flux`'.

This weighting obtained in the query `weight` is then applied to calculate the excitation response, and is done as follows in MySQL:

```
select (
      sf.uvfactor*sum(hex.uv))/((sf.uvfactor*sum(hex.uv))+1) as
uvexcitation,
(sf.bluefactor*sum(hex.blue))/((sf.bluefactor*sum(hex.blue))+1) as
blueexcitation,
(sf.greenfactor*sum(hex.green))/((sf.greenfactor*sum(hex.green))+1) as
greenexcitation from ".$_GET['h1']." as flux, weight as sf where
hex.flowerid=flowerID
```

Here, the flower ID of the flower in the database that holds the reflectance spectra must be given. The above query returns three values, which is the excitation response at UV, Blue and Green receptor of a given spectral sensitivity that is available in the database.

Appendix II: NetLogo Agent-based bee model Code

NetLogo agent, patch properties and calls to an extension package:

NetLogo is an agent-based modelling tool, The agent-based model consists of the agent (the bee), the 'patch' which is each cell that may consist of a flower. A NetLogo extension was developed to support the simulation of flower colour choice by the bee agent. This extension is a package consisting of various methods that can be called from the NetLogo modelling environment to compute and keep a track of the bee, and the environments' state, and also to change the states temporally.

AGENT STATE/PROPERTY (BEE):

State/property	Description
Issearching?	Boolean – is set true if the bee is in 'search' state. Is set to false, if bee is in 'forage' state (See Figure 4-1 in Chapter 4 for states)
Nectarcarryingamount	Double/Float – keeps a record of the amount of nectar collected by the bee agent in each foraging bout (each foraging bout = 50µl)
memory	String – the flower that the bee agent is currently moving towards to forage on, or is foraging on
Foragespot	Array – array of flowers that are in the radius of the bee, that consist of the scene.
Returning	Boolean – Is set true if the bee is returning to the 'Hive' (centre of map) when it's crop is full (i.e. 50µl)
found	Boolean – is set true if there are flowers available in the scene the bee is currently in

PATCH STATE/PROPERTY (FLOWERS):

State/property	Description
flowerid	String – the Flower ID that is used to connect to the Floral Reflectance Database to download spectra in real time as bee agent encounters the flowers in the meadow
Nectarquantity	Double/Float – A fixed constant value assigned at the beginning of the simulation to each flower (See appendix III), this is the maximum nectar the flower can secrete
Decaypoints	Number – a fixed value that behaves like a counter that replenishes the nectar in this flower up to the Nectarquantity amount if the bee agent has just visited and taken the nectar over a period of time determined by Decaypoints.
amountofnectarholding	Double/Float – varies from 0 to nectarquantity based on the amount of nectar taken by the bee agent

NETLOGO JAVA EXTENSION – REFLECTANCE PACKAGE:

Call	Type	Description
reflectance:start	Command	Creates environment with given pre-generated meadow type and lighting condition. This is the creation of the meadow flowers and the 2D structure internally. NetLogo then later uses setFlowers to plot the flowers into the 2D place.
reflectance:setMemoryBlock	Command	Takes a Boolean (true or false) to set if the bee will continue to learn new flower colour – if false, new flower colour are not registered in memory
reflectance:chooseFlower	Reporter	Takes all flowers in current scene, applies colour constancy function and find high rewarding flower in known memory based on if the colour is similar (using colour discrimination function), returning flower that is best match and highest reward known in memory.
reflectance:setPerfectVision	Command	When set true, perfect vision is achieved by setting probability 1 for colour discrimination
reflectance:createBees	Command	Creates bee internally with memory and colour choice behaviour, NetLogo then later uses setBees to create the bee agent.
reflectance:getAt	Reporter	Returns flower ID of a flower at a given location in meadow - This is the same flower ID used in the FReD database, for downloading spectra and calculating loci plots on the colour hexagon.
reflectance:nectarQuantity	Reporter	Returns amount of nectar available in flower at given location
reflectance:getColour	Reporter	Purely for aesthetic purposes – sets a particular key colour for each flower species in NetLogo, which is first set in the pre-generated meadow files.

NetLogo: Code breakdown

NetLogo is a programmable agent-based simulation environment. More details of the programming in Logo can be found from the developers (Wilensky, 1999). The following provides the code for each procedure (or state, shown in Figure 4-1), The simulation is set up by running the procedure *setup*, and the simulation is run by running the procedure *go*.

Underlined words – these are calls to an extension package, these were developed in Java and the package is imported at the beginning of each simulation run. Each call to the *reflectance* package is explained above.

Italicised words – These are procedure calls in the NetLogo code, for example *SetFlowers* is a procedure call.

Bold – These are keywords preserved in NetLogo

Set-up

Creates an environment object (from the Netlogo reflectance API extension) consisting of various properties. Some do not need to be set if a pre-generated file is being used:

Sensitivityfactor = this the weighting and lighting condition set at the beginning (this can change)

Inputfile = pre-generated meadow set up of flowers in a two-dimentisional celled map

Detectiondistance = this is the radius which consists of the 'scene' that the colour vision will process, for example a detectiondistance of 7 is a visual scene conssiting of 14 x 14 cells.

Max-pxcor & max-pycor = the size of the meadow. By default, all meadows in the simulation were 350 x 350 cells.

Discrimination – this is the type of flower constancy curve that can be set. C1 is the normal curve as presented in Figure 4-2 in Chapter 4. Other curves can be added into the extension.

```
1  To setup
2      Clear-all
3      reflectance:start sensitivityfactor inputfile detectionDistance
   max-pxcor max-pycor discrimination
4      setFlowers
5      setHive
6      setBees
7  End
```

SetFlowers

Sets the flowers into the two dimensional space, by iterating through the entire grid, and checking if a flower should be placed in the location based on the input file that specifies the location of all flowers

```
1   to setFlowers
2    let next 0 ;next plot in the file
3    let i 0
4    let j 0
5    ask patches[
5        set pcolor green + (random-float 0.8) - 0.4 ]
6    ask patches [
7        while [ i < max-pxcor ]   [ ;iteration through grid to set the flowers
8            set j 0
```

```
9           while [ j < max-pycor ] [
10              set next reflectance:getAt i j ;sets flower ID to a cell in the grid
11              if next != "0" [
12                  ask patch-at i j [
13                      set flowerid reflectance:getAt i j
14                      set isFlowering? "1"
15                      ifelse isFlowering? = "1" [;set nectar value if flower
    exists here
16                          set nectarQuantity
    reflectance:nectarQuantity i j
17                          set pcolor blue
18                          set amountOfNectarHolding nectarQuantity
19                          set decaypoints markdecay ]
20                      set nectarQuantity reflectance:nectarQuantity
    i j
21                      set marked 0 ]  ]
22              set j j + 1 ]
23          set i i + 1 ]  ]
24  end
```

SetBees

Sets the number of bees in the simulation. Throughout every simulation, only one bee forages in the meadow at one time, though bee-life is only one simulation. A new bee is created in a new simulation

```
1   to setBees
2     create-bees numOfBees [;sets the properties of the bee
3         setxy hiveX hiveY ;all bees start at the hive location
4         set isSearching? 1 ;bees initially begin to search the moment the simulation runs
5         set nectarCarryingAmount 0
5         set memory 0
6         set returning 0
7         set found 0
8         reflectance:setPerfectVision false
9         reflectance:setMemoryBlock false
10        set prevflower 0
11        set prevflowerx 0
12        set prevflowery 0
13        set avg 0
14        reflectance:createBees who   ]
15  end
```

setHive

Sets the hive location that the bee will return to each time, only one hive in each simulation:

```
1   to setHive
2     create-hives 1 [ ;one hive in each simulation run
3         setxy hiveX hiveY  ]
4   end
```

Forage

These are a set of instructions that the bee follows once it has encountered a flower that is suitable for foraging on. These include instructions of taking the nectar, and recording the number of visits:

```
1   to forage
2       let amounttaken 0
```

```
3       set foragers bees with [isSearching? = 0]
4       ask foragers [;'foragers' are any bees that have found a flower
5           set prevreward nectarQuantity
5           set isSearching? 1
6           set memory 0
7           let emptyamount beeCropSize - nectarCarryingAmount
8           let sipped 0
9           let isMarking? 0
10          set found 0
11
12          ask patch-here [;At this flower, bee takes the nectar content of the flower
13              if occupied? = 0 and isFlowering? = "1" [
14                  set occupied? 1
15                  set decaypoints markDecay
16                  set isMarking? 1
17                  if emptyamount > nectarQuantity [
18                      set sipped 1 ]
19              ]  ]
20          if isMarking? = 1 [
21              ifelse sipped = 1  [
22                  set nectarCarryingAmount nectarCarryingAmount +
    nectarQuantity
23                  set amounttaken nectarQuantity
24                  set nectarQuantity 0  ]
25              [ ; taken a part of nectar
26                  set nectarCarryingAmount nectarCarryingAmount +
    emptyamount
27                  set nectarQuantity nectarQuantity - emptyamount
28                  set amounttaken emptyamount
29                  set returning 1 ]
30          ]
31          set occupied? 0 ]; [;flower no longer occupied by bee
32          set visitnum visitnum + 1 [ ;counter of number of visits to flower + 1
33          ifelse visitnum  = 3 [
34              set avg ((avg + amounttaken) / 2)  ]
35             [set avg ((avg + amounttaken) / 3)  ]
36      ]
37      ;record of nectar and visits to each flower only recorded after 50 visits (the testing phase)
38        let startrecord (v1597 + v1431) > 50
39          if flowerid = "1597" [
40            if startrecord  [
41                set f1597 f1597 + amounttaken ]
42                set v1597 v1597 + 1  ]
43          if flowerid = "1431" [
44            if startrecord  [
45                set f1431 f1431 + amounttaken ]
46                set v1431 v1431 + 1  ]
47  end
```

Search

These are a set of instructions that the bee follows if it is still in search of a flower and has not yet found one:

```
1   to search
2       if v1597 + v1431 + v1592 + v1418 + v1557 = 250 and check = 1 [
3           file-open outputfile2 ;record visits and nectar collection at the end of
    simulation
```

```
4           file-write (word v1597 ", " f1597 ", " c1597 ";")
5           file-write (word v1431 ", " f1431 ", " c1431 ";")
5           file-write (word v1592 ", " f1592 ", " c1592 ";")
6           file-write (word v1418 ", " f1418 ", " c1418 ";")
7           file-write (word v1557 ", " f1557 ", " c1557 "; ;")
8           file-close
9           set check 0 ]
10      if v1597 + v1431 + v1592 + v1418 + v1557 = 50 [;end of test phase
11          set sensitivityfactor "sensitivityfactorwoodlandshade" ]
    ;change the lighting condition in the simulation after 50 flower visits under the lighting set in setup
    procedure
12      ifelse returning = 1 [;If the bee is returning to hive then move towards the hive
    location
13          set prevflower "hive"
14          ifelse pxcor != hiveX and pycor != hiveY [
15              return-to-hive  ]
16          [
17              set returning 0 ; now bee is no longer going to hive
18              set nectaramount nectaramount + nectarCarryingAmount
19              set nectarCarryingAmount 0  ]  ]
20      [
21          let searchers bees with [isSearching? = 1 and memory = 0]
22          let xx xcor;
23          let yy ycor;
24          if any? Searchers [;any bee that is searching for a flower
25              set forageSpot patches with [isFlowering? = "1" and
    marked = 0] in-radius detectionDistance
26              if any? forageSpot with [occupied? = 0 and marked = 0]
    [
27                  let listy [(word flowerid "_" nectarQuantity "_"
    pxcor "_" pycor "_" xx "_" yy)] of forageSpot
28              let f reflectance:chooseFlower who listy 0 0.7 ;choose a
    flower from the location that the bee is in
29              if f != "0" and memory = 0 [
30                  set memory min-one-of patches with [flowerid = f
    and marked = 0] [distance myself] ;if a flower was chosen, then memory is the
    flower that bee will forage on
31                  set found 1  ]
32          ]   ]   ]
33      [
34          set isSearching? 0 ; bee forages on the flower, and stops searching for more
35          forage    ]
36      ifelse found = 1 and memory != 0 [
37          face memory       ;moving towards the flower to chosen
38          fd 1 ]
39      [ makemove ] ;if no suitable flower is found, move randomly,
40  end
```

Go

This is the first procedure that is called continuously until the simulation is stopped. This begins with the bee agent searching:

```
1   to go
2   ask bee 1 [
3     search ]
4   end
```

Makemove

The bee rotates to a random angle, and moves one cell forward:

```
1  to makemove
2    rt -20 + random(20 - -20 + 1)
3    fd 1
4  end
```

Appendix III: Nectar values assigned to flowers in the simulation

Nectar standing crop collected from Germany in 1999 by Kristina Pruefert and Lars Chittka are provided in this appendix, whilst the phenology data of this Maple forest are taken from the study by (Gumbert et al., 1999) used in Chapter 6. The letter in each month indicates the nectar values assigned to each flower in the month.

point	Flowering species	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT
1	*Pulmonaria obscura*	a	a	a					
2	*Campanula latifolium*						c	c	
3	*Campanula trachelium*					i	i		
4	*Veronica chamaedrys*			b					
5	*Campanula rapunculoides*					c			
6	*Galeopsis pubescens*								
7	*Hepatica nobilis*	c	c	c					
8	*Geranium robertianum*			d	d	d	d	d	
9	*Stachys sylvatica*				i				
10	*Alliaria petiolata*			e					
11	*Stellaria holostea*			f	f				
12	*Torilis japonica*					a	a		
13	*Scrophularia nodosa*				a				
14	*Arenaria serpyllifolia*			g					
15	*Rubus caesius*					j	j		
16	*Aegopodium podagraria*				e				
17	*Gallium aparine*				c				
18	*Anthriscus silvestris*			h	h				
19	*Paris quadrifolia*				j				
20	*Impatiens parviflorum*				g	g	g	g	
21	*Geum urbanum*						f		
22	*Chelidonium majus*			i					
23	*Anemone ranunculoides*		h						
24	*Primula veris*		j	j					

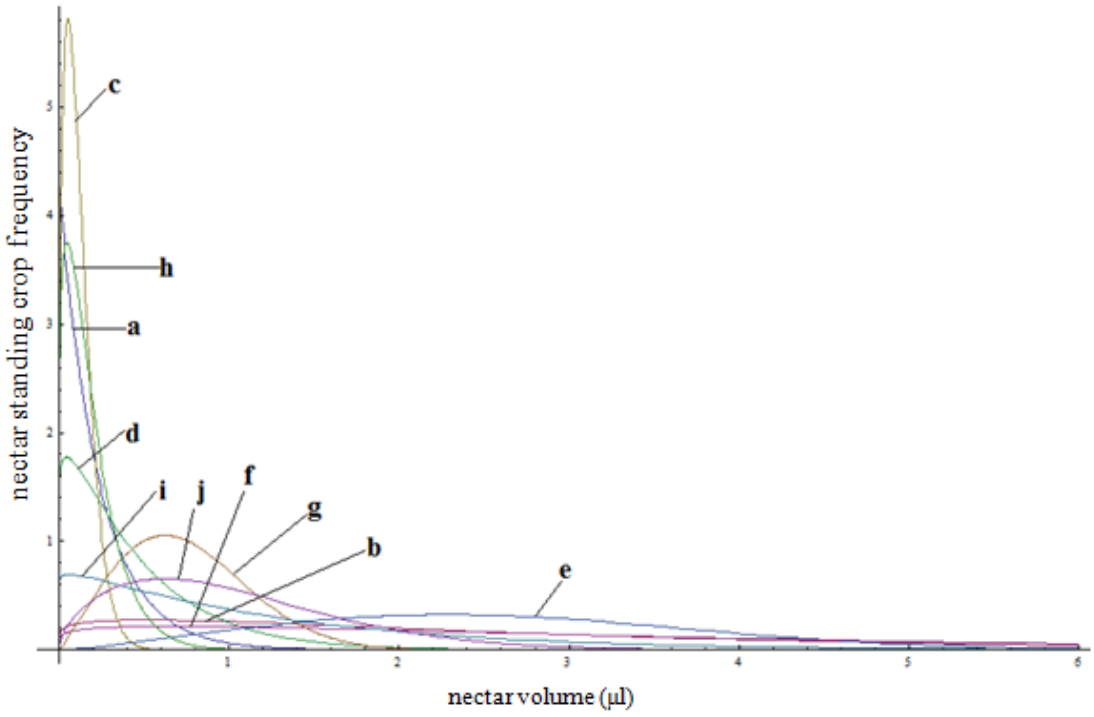
Nectar assignment to the Maple forest plant community meadow simulations in Chapter 6:

Chapter 6 – population of nectar standing crop data used to assign to Maple Forest flowering plant community

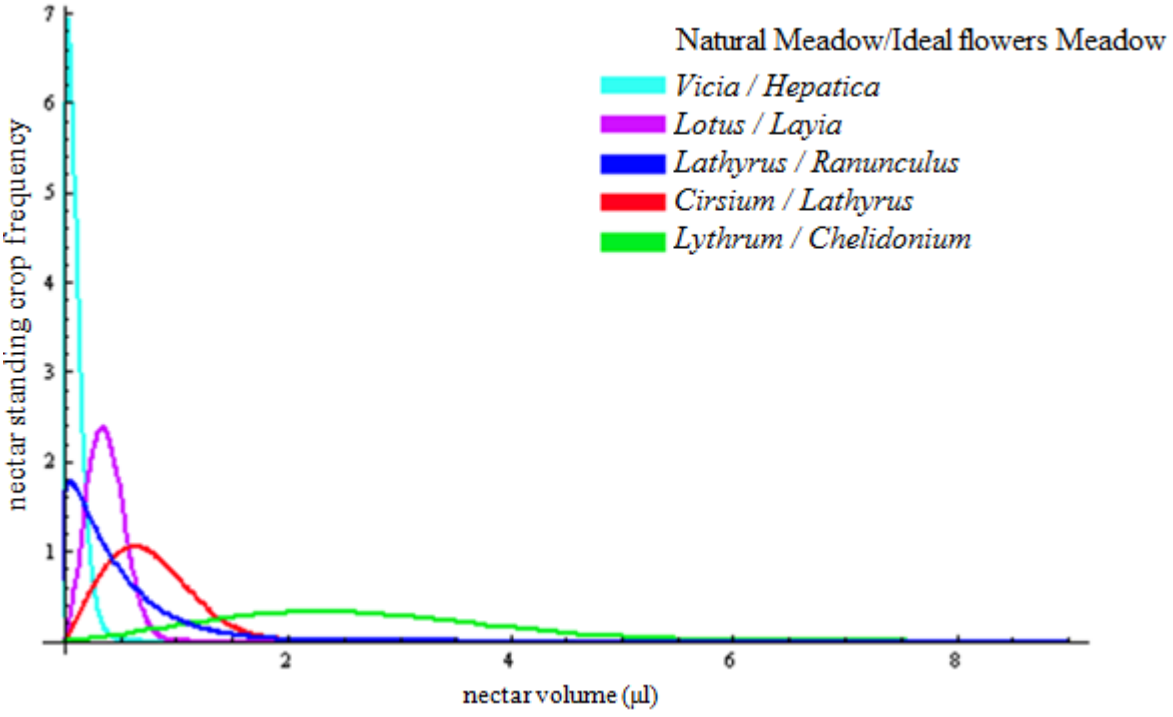
Vinca minor	Lamium album	Silene alba	Alliaria petiolata	Cardamine pratensis	Lamiastrum galeobdolon	Lamium purpureum	Viola canina	Syringa vulgaris	Primula veris

Nectar standing crop data

a	b	c	d	e	f	g	h	i	j
6.62	0.73	1.51	4.1	0.03	2.22	0.09	0.27	0.88	0.31
3.51	0.72	0.03	1.19	0.05	2.94	0.10	0.06	0.95	0.05
2.8	0.48	6.54	4.16	0.05	3.66	0.14	0.05	0.92	0.26
2.58	0.3	0.51	3.86	0.03	2.5	0.14	0.17	0.84	0.18
2.5	0.94	0.81	0.16	0.06	2.9	0.14	0.04	0.89	0.03
7.5	0.66	0.56	3.13	0.02	3.39	0.14	0.03	1.26	0.05
3.95	0.69	0.44	7.09	0.12	3.53	0.15	0.39	0.78	0.02
2.13	1.03	2.25	4.45	0.12	3.45	0.16	0.03	0.81	0.04
0.33	2.69	0.09	6.69	0.03	0.75	0.17	0.07	1	0.43
3.5	1.84	1.31	6.69	0.11	1.44	0.20	0.08	1	0.125
2.32	1.56	0.19	9.84	0.03	3.38	0.21	0.17	1.14	0.2
0.07	0.63	1.81	3.86	0.03	0.88	0.23	0.17	1.31	0.11
9.44	1.31	0.16	1	0.16	3.13	0.24	0.06	1.63	0.3
1.69	0.66	0.64	0.34	0.19	2.43	0.28	0.7	0.75	0.12
3.56	1.25	2.3	0.2	0.34	2.53	0.29	0.08	1.69	0.02
4.75	0.72	0.88	1.95	0.18	1.39	0.29	0.24	0.27	0.2
0.65	0.41	0.79	6.95	0.22	2.94	0.30	1.23	0.45	0.07
3.15	0.69	1.23	2.05	0.11	3.29	0.31	0.38	0.27	0.34
2.09	0.81	1.59	3.94	0.16	6.21	0.31	0.5	0.59	0.07
0.45	2.13	0.28	3.19	0.15	4	0.31	0.06	0.47	0.26
0.52	1.31	4.14	2	0.03	2.75	0.33	0.06	0.36	0.11
0.44	3.16	0.16	0.88	0.04	3.47	0.33	0.79	0.5	0.05
3.22	0.34	1.41	3.61	0.16	1.38	0.33	0.06	0.32	0.11
1.22	0.78	1.83	3	0.09	1.83	0.33	0.07	0.44	0.14
3.07	0.81	1.6	0.06	0.31	3.13	0.35	0.09	0.46	0.3
1.16	0.18	0.44	0.7	0.12	0.72	0.35	0.31	0.35	0.76
0.66		1.25	5.41	0.16	1.41	0.35	0.23	0.41	0.2
0.41		0.88			1	0.38	0.34	0.5	0.16
		0.75			3.69	0.39	0.05	0.47	0.07
					1.34	0.97	0.28	0.63	0.52
						1.00			
						1.00			
						2.43			
						2.44			



Nectar standing crop values and the frequency they occur in assigned to the Maple forest plant community simulation in chapter 6. This is used to assign nectar values to each flower that is added to the simulated meadow in the agent-based bee model.



Nectar standing crop values and the frequency they occur in assigned to the *natural meadow* and *ideal meadow* in Chapter 4 and 5. This is used to assign nectar values to each flower that is added to the simulated meadow in the agent-based bee model. The same nectar standing crop values are assigned to the flowers in *colour blind* and *perfect colour vision* bee agent models