

The evolution of flower signals to attract pollinators

Plants use chemical components to attract potential pollinators to visit flowers and facilitate the efficient transfer of pollen. What is likely to have begun as a simple reproductive solution in the Mesozoic period evolved into a competitive advertising war fuelled by the ability of plants to produce different colours and odours.

Background

Bees receive nutrition by visiting flowers to collect nectar or pollen and are major pollinators of angiosperms (flowering plants). The amount of nutritional reward offered by different flowers is variable and bees use a variety of sensory cues including vision and/or olfaction to facilitate discrimination between rewarding and non-rewarding flowers. Rather than randomly visiting flowers, bees often restrict their visits to a single species of plant, while its flowers offer a sufficient level of rewarding inducement in return. This brand loyalty, termed flower constancy, has been appreciated since the time of Aristotle and is likely to be due to constraints on how the bee's memory stores and retrieves information on multiple food sources.¹ The Darwinian advantage of flower constancy is considerable for plants that can maintain the loyal services of pollinators because these plants receive species-specific delivery of pollen. To help retain the loyal services of pollinating bees, plants have evolved a variety of chemical compounds to produce colours and odours that are distinctive.

The visual system of the bee

There is good evidence that flowers evolved colour signals to suit the visual capabilities of bees. For

example, there is a correlation between the steep gradients of flower reflection curves and the wavelengths of radiation to which the bee's visual system is most sensitive.² However, the bee's visual system is phylogenetically ancient and pre-dates the evolution of angiosperms on Earth, so it appears most likely that flowers have evolved colour pigments to suit the bee's visual capabilities.³

A visual pigment is composed of a retinal-based chromophore to which is attached an opsin protein. The bee's visual system is based on vitamin A₁ chromophore 11-*cis* retinal⁴ and by the attachment of three different opsin proteins to the chromophore the bees have achieved three classes of photoreceptors maximally sensitive to ultraviolet (UV), blue or green light respectively (Fig. 1). Since bees can see UV, many flowers have UV-reflecting pigments.^{5,6} Bees are capable of fine colour discriminations,^{7,8} however, recently it has been demonstrated that, to reduce errors that might be made by bee pollinators, there would have been significant evolutionary pressure on plant species to produce flower colours that are not similar to competing species.⁸

Plants have benefited from evolving colour signals ranging from the UV through to the red regions of the spectrum. The colour of an object can be represented as a geometric projection of loci in a colour space to understand the visual capabilities of a particular visual system.

Bees and humans both have trichromatic visual systems, although the spectral sensitivities of a bee's visual system are shifted to the short wavelength end of the spectrum relative to humans (Fig. 1). A comparative evaluation of flower colours in both bee and human colour space reveals that most flower colours are considerably more conspicuous for bee colour vision.⁹

Evolution of flower colours

Insects most likely began visiting the first flower structures in the Mesozoic period to eat pollen, which is rich in nitrogen and phosphorus.¹⁰ However, nitrogen and phosphorus are elements that are often in growth-limiting short supply in plant habitats and many plants consequently evolved nectar as an alternative reward. Nectar is essentially an aqueous solution of sugars (glucose, fructose or sucrose) and plants can easily produce this carbohydrate reward through photosynthesis of readily abundant water, carbon dioxide and sunlight. Nectar is offered as a reward for insects visiting plant flowers, and the pollen is incidentally transported by insects between plants. To advertise the presence of the nectar, plants use a variety of cues. The first flowers were achlorophyllous and probably whitish-yellow in colour, and then plants may have evolved more distinctive colours through the concentration of pigments.⁹

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Flower colour has long been recognised as an advertisement to attract pollinators^{6,9,11} and variations in the reflectance properties of different plant flowers is determined by the chemistry of flower pigments. For example, flavonoid pigments including anthocyanins are largely responsible for many blue, purple and pink flowers. The colour of anthocyanins can be changed by complexing with metal ions like iron to produce a variety of bluish or purple hues (Fig. 2A). The flavonoid pigments also include flavone, flavonol and anthochlor, which can produce various pigments appearing yellow to the human eye.¹⁰ Flavones strongly absorb near UV and are used by some plants to form dark nectar guide marks, which visually indicate to bees the location of the nectar reward (Fig. 2C, D).¹² Carotenoids comprising tetraterpene hydrocarbons are also commonly responsible for many yellow, orange or red flowers; for example, β -carotene is responsible for the yellow appearance of daffodils to the human eye (Fig. 2B). White flower petals reflect wavelengths of light reasonably equally over the visual spectrum and this is achieved using a variety of pigments and/or white starch grains.¹⁰ Whilst the evolution of flower colours may be partially determined by phylogenetic constraints of chemical pigments in some plant families, most plant families appear to have the ability to produce a wide variety of different flower colours.¹³

Use of odour

The visual signal produced by colour is potentially an unreliable cue in some natural environments because of both changes in illumination conditions¹⁴ and the difficulties posed by judging similar colour signals when viewing conditions are successive.⁸ To reduce the error rate, bees may scent mark non-rewarding flowers in some circumstances.¹⁵

Plants may also use odour to attract bees to flowers. Flower scents are often mixtures of volatile organic substances including aliphatic compounds, benzenoid compounds and terpenoids.¹⁰ For example, the aliphatic compound pentadecane is a paraffin hydrocarbon present in the scent of roses. The ability of honeybees to discriminate between odour mixtures of aliphatic compounds is significantly negatively correlated with the

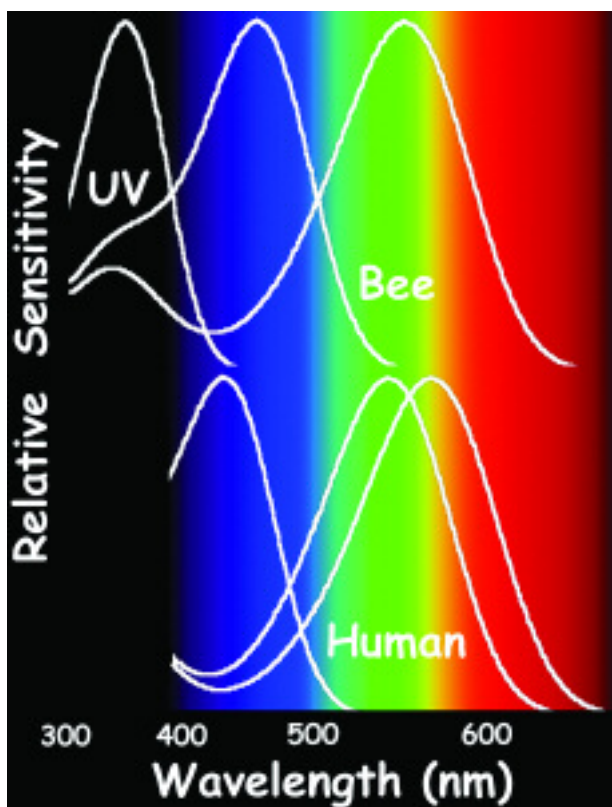


Figure 1. The spectral sensitivity of different visual pigments is determined by the retinal-based chromophore and the attached opsin protein. Bees have colour photoreceptors that are maximally sensitive to UV, blue and green light; and humans have colour photoreceptors (cones) maximally sensitive blue, green and red light.



Figure 2. The chemistry of flower pigments gives rise to a wide variety of colours. (A) In the cornflower (*Centaurea cyanus*) anthocyanins are affected by complexing with metal ions to produce a range of bluish/purple hues. (B) In the daffodil β -carotene produces the distinctive yellowish coloration. (C) The base of petals of the black-eyed susan plant (*Rudbeckia hirta*) contains flavonol glucosides that absorb light strongly in the UV to provide a distinctive nectar guide for bees. (D) Human vision is not sensitive to UV light and the black-eyed susan flower petals appears to reflect all wavelengths of light equally.

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structural similarity of odorants in terms of carbon chain length.¹⁶ There are also similarities in olfactory discrimination abilities of honeybees and humans, suggesting that the structural organisation of olfaction may be determined by similar mechanisms in primates and bees.¹⁶ If this is the case, bees may serve to be an interesting animal model for odour detection.

Other constraints on the evolution of flower colours

The finding that flowers have evolved to suit the visual capabilities of bees and that plant families are reasonably unconstrained to produce a large variety of colours using different chemical pigments suggests that plants should have evolved flowers that are equally represented in a bee colour space. However, this is not the case and indeed some flower colours are poorly represented in bee colour space.⁶ The explanation for the poor representation of some bee flower colours in nature appears to be due to constraints on the bee's visual capabilities for correctly identifying

flowers in conditions where the colour of the illuminating light changes,^{6,8,14} or for detecting colours similar to the background foliage colour.⁸

Conclusion

Since the time of Aristotle the relationship between flowers and bees has fascinated scientists. Bees have well-developed colour vision and odour discrimination, and it appears that the bees' sense of smell is similar to humans. Plants advertise nutritional rewards to potential pollinators using chemical components, and this helps facilitate the Darwinian advantage of flower constancy to plants that can produce distinctive signals.

References

- 1 Chittka L., Thomson J.D., Waser N.M. *Naturwissenschaften* 1999, **86**, 361–77.
- 2 Chittka L., Menzel R.J. *Comp. Physiol. A* 1992, **171**, 171–81.
- 3 Chittka L. *Naturwissenschaften* 1996, **83**, 136–8.
- 4 Briscoe A.D., Chittka L. *Ann. Rev. Entomol.* 2001, **46**, 471–511.
- 5 Dyer A.G. *Aust. J. Bot.* 1996, **44**, 473–88.
- 6 Kevan P.G., Chittka L., Dyer A.G. *J. Exp. Biol.* 2001, **204**, 2571–80.
- 7 Chittka L., Dyer A.G., Bock F., Dornhaus A. *Nature* 2003, **424**, 388.
- 8 Dyer A.G., Chittka L.J. *Comp. Physiol. A*, 2004 (in press).
- 9 Kevan P.G., Backhaus W. In Backhaus W. (ed.) *Color Vision – Perspectives from Different Disciplines*, Walter de Gruyter & Co., Berlin, 1998, pp. 163–83.
- 10 Proctor M., Yeo P., Lack A. *The Natural History of Pollination*, Timber Press, 1996.
- 11 Darwin C. *Cross and Self Fertilization in the Vegetable Kingdom*, Murray, London, 1876.
- 12 Thompson W.R. *Science* 1972, **177**, 528–30.
- 13 Menzel R., Shmida A. *Biol. Rev.* 1993, **68**, 81–120.
- 14 Dyer A.G. *J. Comp. Physiol. A* 1998, **183**, 203–12.
- 15 Giurfa M., Núñez J., Backhaus W.J. *Comp. Physiol. A* 1994, **175**, 773–9.
- 16 Laska M., Galizia C.G., Giurfa M., Menzel R. *Chem. Senses* 1999, **24**, 429–38.

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