

Bumblebee search time without ultraviolet light

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Summary

Bees often facilitate pollination of important greenhouse crops. Individual bumblebees *Bombus terrestris* were therefore tested in an indoor flight arena to evaluate whether or not search time to find flowers was influenced by the inclusion or exclusion of ultraviolet radiation. Plastic model flowers of similar spectral properties to flowers of tomato *Lycopersicon esculentum* Mill. were used to evaluate bee search efficiency. The results show that bumblebees perceive when ultraviolet radiation is either removed or added to an illumination source; however,

the bumblebees rapidly learn to find model flowers with equal efficiency in either illumination environment. The behavioural results are interpreted in relation to a colorimetric analysis showing how bumblebees are capable of using their visual system to forage efficiently in environments that exclude ultraviolet radiation.

Key words: ultraviolet, vision, foraging efficiency, greenhouse, bumblebee, *Bombus terrestris*.

Introduction

Bumblebees *Bombus terrestris* are important pollinators of angiosperms and use their colour vision both to detect flowers (Spaethe et al., 2001) and to choose between flowers (Chittka et al., 1997). Hymenopteran insects including bumblebees perceive ultraviolet radiation (Kevan et al., 2001), whilst human vision is not sensitive to ultraviolet radiation because of the absorption of wavelengths shorter than about 400 nm by ocular filters (Muntz, 1972; Dyer, 2001). The sensitivity of bees to ultraviolet radiation raises the question of whether or not illumination conditions that exclude ultraviolet might affect the efficiency with which bees can use their vision to detect flowers. For example, bumblebees are important pollinators of commercial crops contained within greenhouses (Banda and Paxton, 1991; Kevan et al., 1991), and the ultraviolet transmission characteristics of different materials used to cover greenhouses are highly variable (Morandin et al., 2001c, 2002).

One important example of a greenhouse crop is the tomato *Lycopersicon esculentum* Mill. (Morandin et al., 2001a–c). The pollination of tomato plant flowers requires the agitation of flower anther cones to release pollen (Buchman, 1983) and efficient pollination is achieved either by the use of electronic vibrating systems (Picken, 1984), or more recently by the use of bumblebees (Banda and Paxton 1991; Kevan et al., 1991; van Ravestijn and van der Sande, 1991).

There is evidence that bees perceive changes in the ultraviolet content of illumination. For example, Morandin et al. (2001b) found that in commercial greenhouses fitted with

ultraviolet-transmitting plastic the mean activity of individual bumblebees *Bombus impatiens* was 4.82 ± 0.37 trips per day, whilst in commercial greenhouses that excluded ultraviolet radiation the activity averaged 2.37 ± 0.37 trips per day. Increased activity in greenhouse environments that transmit more ultraviolet radiation has also been reported for several other species of insects (Antignus et al., 1996; Costa and Robb, 1999; Costa et al., 2002). However, in a study using miniature greenhouses in a tightly controlled environment Morandin et al. (2002) did not find that bumblebees were more active under high UV-transmitting coverings.

To estimate the number of bumblebees required to pollinate greenhouse crops efficiently it is important to understand the ability of individual bees to operate visually under conditions where ultraviolet radiation is excluded from the foraging environment. Spaethe et al. (2001) showed that search time is an important parameter for the efficiency with which the bees are able to make visits to flowers. For large flowers, search time correlated well with colour contrast, whilst for small flowers search time was more likely to be explained by green receptor contrast (Spaethe et al., 2001). The spectral signal reflected by a flower to a bee's eye is the product of the spectral properties of the flower's pigments and the spectral quality of the radiation source illuminating the flower (Kevan and Backhaus, 1998). It is thus important that bees are able to discount efficiently any effects of changes in illumination colour, otherwise the value of having colour vision could be compromised (Dyer, 1998). It has been demonstrated that bees

have the ability to make a correction for changes in illumination colour (Neumeyer, 1981; Werner et al., 1988), a phenomena termed colour constancy. However, it is likely that the mechanism(s) of colour constancy is imperfect in bees (Dyer, 1998, 1999; Dyer and Chittka, 2004), and it is important to understand how the bee's visual system might deal with the exclusion of ultraviolet radiation from an illumination source.

This study evaluates bumblebee efficiency at finding model tomato flowers in ultraviolet-rich (UV+) and ultraviolet-poor (UV-) illumination conditions, and the results are interpreted in relation to a colorimetric analysis of the experimental variables. Most commercial crops are planted with a single species in a greenhouse (e.g. Morandin et al., 2001a) and this study considers search efficiency for a single type of flower rather than the ability to choose between flowers of different coloration.

Materials and methods

Foraging environment

Experiments were conducted in a controlled light laboratory in the Bee Research Station at Wuerzburg University (Germany). Bumblebees *Bombus terrestris* L. were housed in a two-chamber wooden nesting box (28 cm×16 cm×11 cm) connected with a Plexiglass tube to a flight arena (120 cm×100 cm×35 cm). Pollen grains were provided directly into the nest. The flight arena had an ultraviolet transparent Plexiglass cover. Shutters in the connecting tube controlled bee movement into the arena. To allow familiarization with the arena the shutters were initially set to an open position and a glass feeder was placed at random coordinates within the arena. Bees were captured at the feeder and marked with a small plastic number on the thorax.

Illumination was provided by six Duro-test 40 W True-Lite tubes and one Osram 36 W Blacklight tube mounted 115 cm above the arena floor (tube frequency converted to 1200 Hz). Illumination was diffused by a Rosco 216 white diffusion (ultraviolet transmitting) screen (Rosco, Germany). For an UV+ environment the illumination was not filtered, and for an UV- environment an Arri 226 (Munich, Germany) ultraviolet-blocking filter covered the illumination. Spectral irradiance of these the sources was measured with an Ocean Optics (Dunedin, FL S2000, Dunedin, FL, USA) spectrometer relative to a calibrated deuterium/halogen radiation source (DH-2000-CAL) (Fig. 1A).

Flower colour for bumblebee vision

Spectral reflectance of a freshly opened tomato flower was measured using the Ocean Optics spectrometer (Fig. 1B). A variety of plastic yellow surfaces were also tested to find a surface that had similar spectral reflectance properties to the tomato flower. A plastic yellow flooring tape (Tape Pacific, NSW, Australia) had similar spectral characteristics to the yellow tomato flower, including ultraviolet reflectance (Fig. 1B), and was used to make model flowers. This was done by attaching the tape to a thin plastic surface and using a punch to make 15 mm diameter model flowers, or hand cutting star-

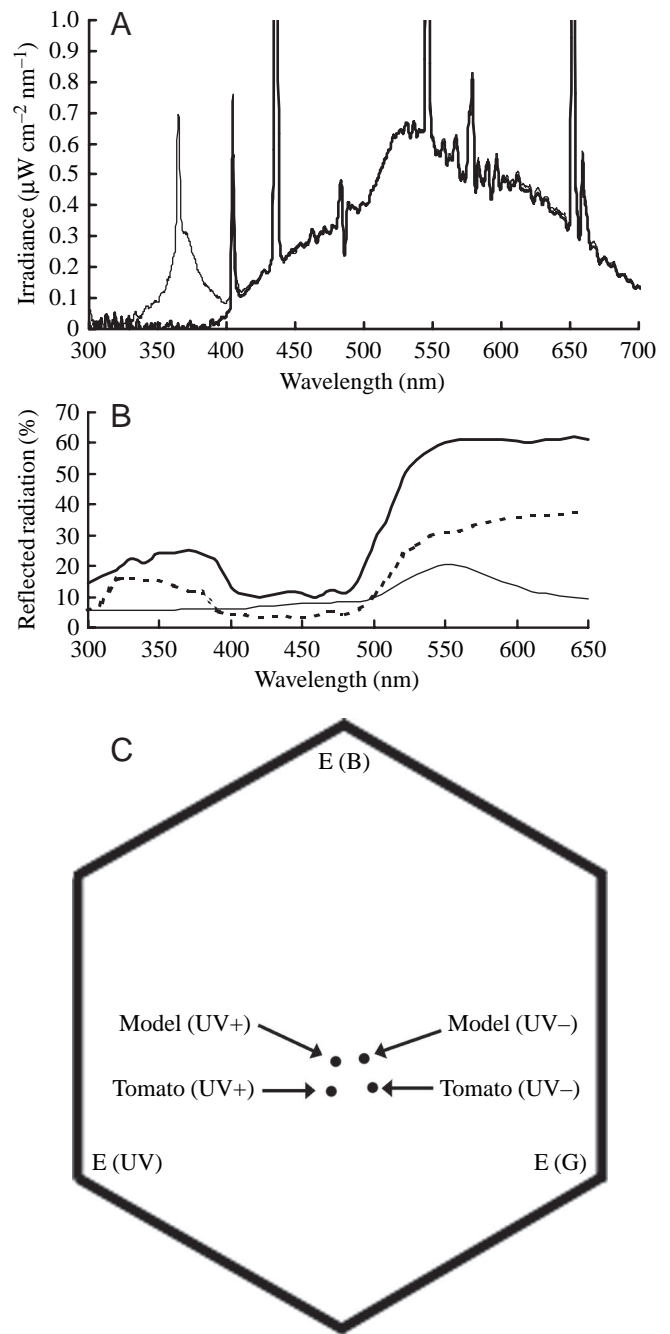


Fig. 1. Colour stimuli and illumination sources. (A) Spectral irradiance of the UV+ (thin line) and UV- (bold line) illumination sources. (B) Spectral reflectance of a tomato plant flower (broken line), an artificial model flower (bold line) and the green foraging background (thin line). (C) Colour loci of stimuli in a colour hexagon assuming adaptation of the visual system to the green background colour in the UV+ and UV- illumination conditions. E, excitation; B, blue; G, green; UV, ultraviolet.

shaped model flowers with a maximum distance of 26 mm between the opposing points.

To represent the colour loci of the tomato and model flower in a colour space for the two illumination conditions a hexagon colour space was used (Chittka, 1992).

The relative amount of light absorbed by each photoreceptor class is given by P :

$$P = R \int_{300}^{650} S_i(\lambda) I(\lambda) D(\lambda) d\lambda, \quad (1)$$

where $S_i(\lambda)$ is the spectral sensitivity of the bumblebees' (ultraviolet, blue or green) receptor class (Peitsch, 1992), $I(\lambda)$ is the spectral reflectance function of the stimulus and $D(\lambda)$ is the spectral distribution of the illuminant when converted to relative photon flux.

The variable R is the adaptation coefficient, which assumes adaptation to the green painted background (I_B),

$$R = 1 / \int_{300}^{650} S(\lambda) I_B(\lambda) D(\lambda) d\lambda, \quad (2)$$

The transduction of photoreceptor absorption (P) into receptor excitations (E) is given by:

$$E = P / (P + 1). \quad (3)$$

Coding is performed by two unspecified colour opponent mechanisms and colour distance can be calculated as the Euclidean distance between stimuli loci in colour space (Chittka, 1992).

Loci were calculated considering that the bees' visual system was adapted to the green background such that E equals 0.5 in each photoreceptor (Equation 3). The excitation of each photoreceptor can vary between 0 and 1.0, and so the maximum contrast in the green photoreceptor is 0.5 (Spaethe et al., 2001). The colour contrast that a flower makes with the background ranges from 0 at the centre of the hexagon to 1.0 at the corners of the hexagon (Chittka, 1992; Spaethe et al., 2001).

Search time

To evaluate search time for model flowers we used a similar methodology to Spaethe et al. (2001), testing one bee at a time. Three model flowers were presented in the arena arranged in the corners of an equilateral triangle shape with a side length of 30 cm. In each foraging bout the triangle position was randomly located on the arena floor, and between each bout the flowers and floor were washed with 30% alcohol to eliminate any use of olfactory cues. A 15 μ l drop of 2 mol l⁻¹ sucrose solution was placed in the center of each model flower. A digital timer was used to measure the flight time from when a bee started foraging until a flower was landed on. Time spent on flowers drinking the sucrose solution was excluded. After a bee had visited all three flowers it was then fed using a micropipette at one of the model flowers until satiated, at which stage it returned to the nest box and the foraging bout concluded.

Each bee was tested for a total of 20 bouts, ten bouts in one illumination condition and ten bouts in the alternative illumination condition. The illumination was changed at the completion of the 10th foraging bout when the bee had returned to the nest box. In each bout the search time for

landing on the first flower, and then the search time to find subsequent flowers was measured. To exclude the distance variability introduced by the random positioning of triangle in the arena, the time it took from leaving the first flower until landing on the second flower was statistically evaluated (Spaethe et al., 2001).

Experiment 1: 26 mm star model flowers

Five bees were individually tested to evaluate efficiency at finding 26 mm star model flowers. Each bee was tested in the UV+ illumination for 10 bouts, and then in the UV- illumination for ten bouts. To measure search efficiency the flight times between the first and second flower within the equilateral triangle were compared for the UV+ and UV- illumination conditions. Data for search efficiency was analyzed for the last five bouts of each illumination condition, so that the bees had an opportunity to familiarize themselves with the condition.

To measure the bees' perception of illumination change, the search time to the first flower within the triangle was also evaluated. Whilst this introduces a variable of distance, search time for the first flower tests whether or not the bees perceive a change in flower colour when illumination conditions change.

Experiment 2: 15 mm model flowers

In this experiment we used 15 mm model flowers to evaluate the bees' search efficiency. Ten bees were evaluated and the sequence order of illumination conditions being tested was reversed for five of the bees. This tested if bees perceive an illumination change when ultraviolet was either added or removed from the lighting environment. The bees' perception of a change in illumination conditions was evaluated with the search time to find the first flower.

To measure search efficiency the flight times between the first and second flower within the equilateral triangle were compared for the UV+ and UV- illumination conditions. Data for search efficiency were analyzed for the last five bouts of each illumination condition, so that the bees had an opportunity to familiarize themselves with the condition.

Results

Colorimetry

Fig. 1B shows the spectral reflectance of a tomato plant flower, the painted green background and a model flower. The spectral characteristics of the model flowers are similar to tomato flowers in that both reflectance curves may be classified as reflecting ultraviolet radiation, absorbing blue radiation and reflecting green radiation. Fig. 1C shows the loci of tomato and model flowers under UV+ and UV- illumination conditions. There is a shift of 0.08 hexagon units in the loci of the model flower, predicting that the bees' visual system is not capable of fully correcting for the illumination change (see Dyer, 1998). Table 1 shows that both the colour contrast and the green contrast remain consistent for the model flower

Table 1. Colour contrast and green contrast of tomato and model flowers under ultraviolet rich (UV+) and ultraviolet poor (UV-) illumination conditions

	Colour contrast		Green contrast	
	Tomato	Model	Tomato	Model
UV+	0.191	0.106	0.113	0.255
UV-	0.198	0.112	0.112	0.254
Ratio (UV-/UV+)	1.036	1.054	0.988	0.996

when ultraviolet radiation is excluded from the foraging environment. A similar result is obtained for the tomato flower, and this indicates that the ability of the bees' visual system to detect model and tomato flowers is predicted to be independent of whether or not the plastic covering material on a greenhouse transmits ultraviolet or not.

Experiment 1: 26 mm star model flowers

Five bees were tested for their ability to find flowers in a UV+ environment, and then in an UV- environment. Fig. 2A shows the search time required to find the first flower in the equilateral triangle over the course of 20 foraging bouts. The bees also made a number of abortive flights (bees approached a model flower but did not land on it) immediately following the illumination change. In the five bouts before the illumination change there were no abortive flights by the five bees, but in the bout following the illumination change bees made several abortive flights (mean \pm S.E.M. = 3.6 ± 0.3 , $N=5$). The reaction of the bees clearly shows that the change in illumination was perceived as there is a sevenfold increase in mean search time for the 11th foraging bout. This increase in search time for the 11th bout was likely to be mainly because of flights where bees approached flowers but did not land. However, the increase in search time does not remain high for subsequent foraging bouts (Fig. 2A) and it appears that the bees quickly learn to find the model flower in the changed illumination conditions.

To exclude the variability introduced by the random positioning of the first flower the search times between the 1st and 2nd flowers were evaluated (Spaethe et al., 2001). The search time in the UV+ environment (mean \pm S.E.M. = 3.3 ± 0.2 s, $N=5$) was not significantly different from the search time in the UV- environment (mean \pm S.E.M. = 3.2 ± 0.2 s, $N=5$) (paired samples t -test $N=5$, $t=0.910$, d.f.=4, $P=0.414$).

Experiment 2: 15 mm model flowers

Five bees were tested first in a UV+ environment and then a UV- environment. Fig. 2B shows the bees' search time for the first flower in the equilateral triangle over the course of 20 foraging bouts. There was a 13-fold increase in the mean search time for the first flower immediately following the switch from the UV+ to UV- environment. However, the search time in subsequent bouts shows that the bees quickly learn to operate in an UV- environment (Fig. 2B).

A separate group of five bees was tested in the reverse order

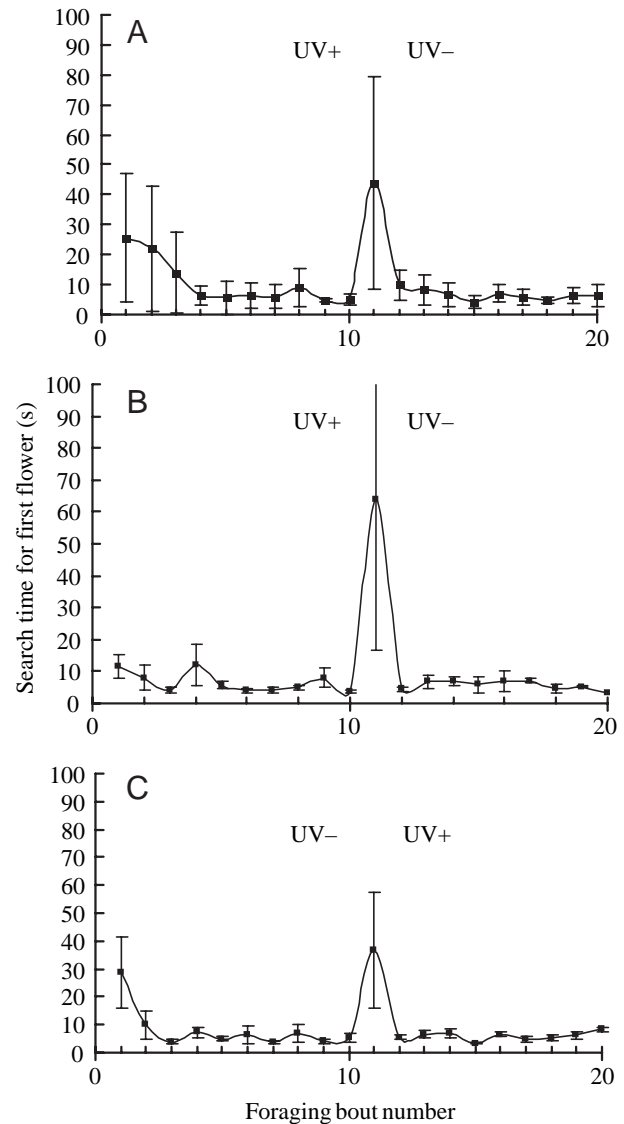


Fig. 2. Search time for bumblebees to find the first flower in the flight arena during a 20-bout evaluation of foraging efficiency. Illumination conditions were changed just prior to the 11th foraging bout. Five different bees are used in each of the three test conditions; values are means \pm S.E.M. (A) Mean data for five bees searching for 26 mm star shaped model flowers initially in UV+ and then UV- conditions. (B) Mean data for five bees searching for 15 mm model flowers initially in UV+ and then UV- conditions. (C) Mean data for five bees searching for 15 mm model flowers initially in UV- and then UV+ conditions.

so that initial testing was in UV- illumination, followed by UV+ illumination. Fig. 2C shows that the bees also perceive this change in illumination conditions as the search time showed a sevenfold increase in search time for the UV+ environment. As with the results for experiments described above, the bees quickly learn to operate in the changed illumination conditions (Fig. 2C).

To compare the efficiency for finding the 15 mm flowers the search times in a UV+ environment were grouped (mean \pm

S.E.M. = 4.3 ± 0.5 s, $N=10$) and compared to the search times for finding flowers in a UV- environment (mean \pm S.E.M. = 4.6 ± 0.6 s, $N=10$). These results were not statistically significantly different (paired samples t -test $N=10$, $t=-0.487$, d.f.=9, $P=0.638$). This is in agreement with the findings of experiment 1 that bumblebee search efficiency is not affected by the presence of a UV+ or UV- illumination environment, at least for the stimuli tested here.

Discussion

Over the past decade the use of bumblebees has become important for facilitating the pollination of crops in greenhouses (Banda and Paxton, 1991; Kevan et al., 1991). Several studies have observed that insects appear to be less active when greenhouses are covered with a material that reduces the transmission of ultraviolet radiation relative to other wavebands of visible light (Antignus et al., 1996; Morandin et al., 2001b; Costa and Robb, 1999; Costa et al., 2002). Fig. 2 shows that bumblebees perceive a change in colour when the ultraviolet content of the illumination source is altered. This finding is consistent with studies on the perception of light environments that are UV+ or UV- for other ultraviolet-sensitive animals such as avians (Bennett et al., 1996, 1997; Church et al., 2001). For example, Church et al. (2001) report that zebra finches *Taeniopygia guttata* exhibit different foraging behaviour when ultraviolet is excluded from the available illumination and argue that this demonstrates that these birds must not have perfect colour constancy. In this current study the bumblebees perceived a change in the colour of the model flower when the ultraviolet content of the illumination was modified (Fig. 2), suggesting that bumblebees have imperfect colour constancy. There is also evidence that bumblebees can directly perceive differences in illumination conditions when UV is present or not, as Morandin et al. (2002) found that bumblebees showed a significant preference for the UV+ arm of a dual choice Y-maze.

The colour hexagon has a built-in assumption of adaptation to the background stimulus that simulates von Kries colour constancy. However, the von Kries model of colour constancy does not predict a perfect colour correction for bee photoreceptors (Dyer, 1999). Indeed the colour hexagon predicts a colour shift of 0.08 units when the illumination changes from UV+ to UV-, and this is qualitatively consistent with the bees' change in behaviour (Fig. 2). When the ultraviolet content of the illumination was modified the bees initially made several abortive flights in which they approached flowers but did not land. This behaviour continued whilst the bees continued to search the arena, but eventually the bees did land on the model flowers. This behaviour might be explained by the bees eventually making a switch flight (Chittka et al., 1997) to a colour that they perceived as being different to the colour they had learnt in the initial stages of foraging.

Experiments 1 and 2 showed that bumblebee efficiency in finding model flowers was not influenced by the inclusion or exclusion of ultraviolet radiation. This result is consistent with the predictions that flower colour contrast and green contrast

are similar in UV+ and UV- conditions (Table 1). A variety of studies have evaluated the merits of using greenhouse coverings that have the ability to transmit ultraviolet radiation. For example, Morandin et al. (2002) found that greenhouses with UV+ coverings were less likely to suffer from the loss of bumblebees through vents than greenhouses with UV- coverings. This is probably because when UV- coverings are used the UV+ vents make a higher colour contrast and the bees may exhibit positive phototactic behavior towards the UV+ (Morandin et al., 2002). There is some evidence to suggest that in UV+ environments bees are more active (Costa and Robb, 1999; Morandin et al., 2001b; Costa et al., 2002), although this was not found in the Morandin et al. (2002) study. The possibility that bees might not forage as efficiently in UV- environments (Morandin et al., 2001b) is likely to be because bees are attracted to any UV+ conditions, so in large greenhouses with UV- coverings bees seek out any UV+ illumination sources (such as vents). However, when UV is totally excluded from the foraging environment the ability of bees to use their visual system to find flowers is not adversely affected.

Conclusion

The results of the current study show that, whilst bumblebees perceive a change when ultraviolet radiation is either included or excluded from an illumination source, the efficiency with which bumblebees use their vision to find important greenhouse crop flowers is not affected by the type of greenhouse covering.

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References

- Antignus, Y., Mor, N., Joseph, R. B., Lapidot, M. and Cohen, S. (1996). Ultraviolet-absorbing plastic sheets protect crops from insect pests and from virus diseases vectored by insects. *Environ. Entomol.* **25**, 919-924.
- Banda, H. J. and Paxton, R. J. (1991). Pollination of greenhouse tomatoes by bees. *Acta Hort.* **288**, 194-198.
- Bennett, A. T. D., Cuthill, I. C., Partridge, J. C. and Maier, E. J. (1996). Ultraviolet vision and mate choice in zebra finches. *Nature* **380**, 433-435.
- Bennett, A. T. D., Cuthill, I. C., Partridge, J. C. and Lunau, K. (1997). Ultraviolet plumage colours predict mate preferences in starlings. *Proc. Natl. Acad. Sci. USA* **94**, 8618-8621.
- Buchmann, S. L. (1983). Buzz pollination in angiosperms. In *Handbook of Experimental Pollination Biology* (ed. C. E. Jones and R. J. Little), pp. 73-113. New York: Van Nostrand-Rheinhold.
- Chittka, L. (1992). The colour hexagon: a chromaticity diagram based on photoreceptor excitations as a generalized representation of colour opponency. *J. Comp. Physiol. A* **170**, 533-543.
- Chittka, L., Gumbert, A. and Kunze, J. (1997). Foraging dynamics of bumble bees: correlates of movements within and between plant species. *Behav. Ecol.* **8**, 239-249.
- Church, S. C., Merrison, A. S. L. and Chamberlain, T. M. (2001). Avian ultraviolet vision and frequency dependant seed preferences. *J. Exp. Biol.* **204**, 2491-2498.
- Costa, H. S. and Robb, K. L. (1999). Effects of ultraviolet-absorbing greenhouse plastic films on flight behavior of *Bemisia argentifolii* (Homoptera: Aleyrodidae) and *Frankliniella occidentalis* (Thysanoptera: Thripidae). *J. Econ. Entomol.* **92**, 557-562.

- Costa, H. S., Robb, K. L. and Wilen, C. A.** (2002). Field trials measuring the effects of ultraviolet-absorbing greenhouse plastic films on insect populations. *J. Econ. Entomol.* **95**, 113-120.
- Dyer, A. G.** (1998). The colour of flowers in spectrally variable illumination and insect pollinator vision. *J. Comp. Physiol. A* **183**, 203-212.
- Dyer, A. G.** (1999). Broad spectral sensitivities in the honeybee's photoreceptors limit colour constancy. *J. Comp. Physiol. A* **185**, 445-453.
- Dyer, A. G.** (2001). Ocular filtering of ultraviolet radiation and the spectral spacing of photoreceptors benefit von Kries colour constancy. *J. Exp. Biol.* **204**, 2391-2399.
- Dyer, A. G. and Chittka, L.** (2004). Biological significance of distinguishing between similar colours in spectrally variable illumination: bumblebees (*Bombus terrestris*) as a case study. *J. Comp. Physiol. A* **190**, 105-114.
- Kevan, P. G., Chittka, L. and Dyer, A. G.** (2001). Limits to the saliency of ultraviolet: lessons from the birds and the bees. *J. Exp. Biol.* **204**, 2571-2580.
- Kevan, P. G., Straver, W. A., Offer, O. and Laverty, T. M.** (1991). Pollination of greenhouse tomatoes by bumblebees in Ontario. *Proc. Entomol. Soc. Ontario*. **122**, 15-19.
- Kevan, P. G. and Backhaus, W. G. K.** (1998). Color vision: Ecology and evolution in making the best of the photic environment. In *Color Vision: Perspectives from Different Disciplines* (ed. W. G. K. Backhaus, R. Kliegl and J. S. Werner), pp. 163-183. Berlin: De Gruyter.
- Morandin, L. A., Laverty, T. M. and Kevan, P. G.** (2001a). Effect of bumble bee (Hymenoptera: Apidea) pollination intensity on the quality of greenhouse tomatoes. *J. Econ. Entomol.* **94**, 172-179.
- Morandin, L. A., Laverty, T. M. and Kevan, P. G.** (2001b). Bumble bee (Hymenoptera: Apidea) activity and pollination levels in commercial tomato greenhouses. *J. Econ. Entomol.* **94**, 462-467.
- Morandin, L. A., Laverty, T. M., Kevan P. G., Khosla, S. and Shipp, L.** (2001c). Bumble bee (Hymenoptera: Apidea) activity and loss in commercial tomato greenhouses. *Can. Entomol.* **133**, 883-893.
- Morandin, L. A., Laverty, T. M., Gagar, R. J. and Kevan, P. G.** (2002). Effect of greenhouse polyethylene covering on activity level and photo-response of bumble bees. *Can. Entomol.* **134**, 539-549.
- Muntz, W. R. A.** (1972). Inert absorbing and reflecting pigments. In *Handbook of Sensory Physiology*, vol. 7 (ed. H. Dartnall), pp. 529-565. Berlin: Springer-Verlag.
- Neumeyer, C.** (1981). Chromatic adaptation in the honey bee: successive color contrast and color constancy. *J. Comp. Physiol. A* **144**, 543-553.
- Peitsch, D., Fietz, A., Hertel, H., de Souza, J., Ventura, D. F. and Menzel, R.** (1992). The spectral input systems of hymenopteran insects and their receptor-based colour vision. *J. Comp. Physiol. A* **170**, 23-40.
- Picken, A. J. F.** (1984). A review of pollination and fruit set in the tomato (*Lycopersicon esculentum* Mill.). *J. Hortic. Sci.* **59**, 1-13.
- Spaethe, J., Tautz, J. and Chittka, L.** (2001). Visual constraints in foraging bumblebees: flower size and color affect search time and flight behaviour. *Proc. Natl. Acad. Sci. USA* **98**, 3898-3903.
- van Ravestijn, W. and van der Sande, J.** (1991). Use of bumblebees for the pollination of glasshouse tomatoes. *Acta Hort.* **288**, 204-121.
- Werner, A., Menzel, R. and Wehrhahn, C.** (1988). Color constancy in the honeybee. *J. Neurosci.* **8**, 156-159.