



Ultraviolet as a Component of Flower Reflections, and the Colour Perception of Hymenoptera

LARS CHITTKA,* AVI SHMIDA,† NIKOLAUS TROJE,‡ RANDOLF MENZEL*

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Based on the measurements of 1063 flower reflection spectra, we show that flower colours fall into distinct clusters in the colour space of a bee. It is demonstrated that this clustering is caused by a limited variability in the floral spectral reflectance curves. There are as few as 10 distinct types of such curves, five of which constitute 85% of all measurements. UV reflections are less frequent and always lower in intensity than reflections in other parts of the spectrum. A further cluster of colour loci is formed in the centre of the colour space. It contains the colour loci of green leaves, several other background materials and only very few flowers. We propose a system to classify the reflection functions of flowers, and a set of colour names for bee colours.

Colour coding Colour vision Flower colours Hymenoptera Signals Spectral reflectance Ultraviolet

INTRODUCTION

Since the discoveries that the reflections of some flowers contain UV signals (Knuth, 1893) and that bees can be trained to associate UV light with a reward (Kühn, 1924), UV patterns on flowers continue to be regarded as spectacular. The mere fact that bees and other insects see something we cannot see has created an aura around UV signals as being something particularly meaningful for their receivers. Many scientists suspected that flowers and bees communicate on a level deliberately hidden from the human observer, and this has given rise to the notion that UV signals are particularly conspicuous and attractive for bees. However, insect eyes exclusively composed of UV-receptors are extremely rare and look into the sky (e.g. *Ascapthalus*, Gogala, 1967), not at objects on the ground such as flowers. Since the most abundant and most efficient pollinators in most natural habitats are hymenopterous, it is most reasonable to interpret floral signals in terms of the colour vision of these insects. Most Hymenoptera have trichromatic colour vision with UV-, blue- and green-receptors (Daumer, 1956; Autrum & von Zwehl, 1964; von Helversen, 1972; Menzel & Backhaus, 1991; Peitsch, Fietz, Hertel, deSouza, Ventura & Menzel, 1992) and thus, any UV-receptor signal must at least be seen in relation to

what is contributed by the other two receptor types (Kevan, 1979).

In order to assess the significance of UV signals in flowers, one first needs a large survey of measurements of floral spectral reflectances, so as to predict what possibilities flowers might have in order to form a colour signal. Analysing the reflectance curves of 1063 different petal colours we will try to answer the following questions:

- (1) Are the properties of floral spectral reflectance functions randomly distributed over the spectrum, or are there distinct types of such functions? If yes, what are these types and how frequent are they? Which types of theoretical reflectance curves do not exist at all? To what extent can UV reflections be generated independently from reflections in other parts of the spectrum? More generally, are reflections and absorptions in given spectral domains obligatorily coupled, or can they be varied freely?
- (2) Are flower colours equally distributed in the colour space of a bee? In other words, can the niches in a bee colour space be addressed with equal probability? Or are certain parts of the colour space covered more densely with floral colour loci than others? Do the colour loci form clusters and leave other areas of the colour space empty?
- (3) What is the relationship between loci in the colour space and the types of floral spectral reflection functions? Is bee colour vision appropriate for

*Institut für Neurobiologie, Königin-Luise-Str. 28-30, 14195 Berlin, Germany.

†The Hebrew University, Department of Evolutionary Ecology, Jerusalem 91904, Israel.

‡Institut für Biologie I, Albertstr. 21a, 79104 Freiburg, Germany.

separating flower colours with different reflectance properties into different areas of the colour space? Or are there cases in which flowers with different reflectance types will generate identical or similar colour loci?

We show that there is a very limited number of basic types of floral reflection spectra. The most frequent types form clusters in the bee colour space which are clearly separated from each other. All of these clusters are in turn separated from a cluster that corresponds to the loci of green leaves.

MATERIALS AND METHODS

A. Measurement and categorization of flower reflectance spectra

The reflectance spectra of the flowers of 573 plant species were measured by means of a photodiode-array-spectrophotometer (SR01, Fa. Gröbel, Ettlingen, Germany). A stabilized circular electronic flash with high UV output illuminated the probe (diameter 1 cm) under an angle of 45 deg to the optical axis of a light guide. The light guide transmitted the light reflected from the object to a holographically recorded concave reflection grating of flat field type (linear dispersion 24 nm/mm). The spectral reflectance data were then recorded by a linear array of 1024 Si-photodiodes (resolution, together with our computer programs: 1 nm). The measurements are given relative to a white-standard (freshly pressed BaSO₄, DIN 5033). If the structures to be measured were smaller than diameter 1 cm, many petals were arranged like fish scales, so that only the identically coloured parts were exposed to the photometer. In case the floral display contained more than one colour, or if age-dependent colour changes or colour polymorphism occurred, a measurement of each colour was taken. Our data comprise 1063 flower colours in total. From 243 species, the reflection functions of the leaves were taken as well. Samples were taken in Israel (Menzel & Shmida, 1993), in Brazil (Chittka, 1993), Norway, the Austrian Alps (Shmida, Chittka & Menzel, in preparation) and in the vicinity of Berlin, Germany (Chittka, Gumbert & Kunze, in preparation). Additionally, we took measurements of several materials that might potentially serve as backgrounds for flowers.

We propose the following system to categorize the flower reflection spectra. The spectrum from 300 to 700 nm is subdivided into four broad domains: 300–400 nm (termed u for UV); 400–500 nm (b for blue), 500–600 nm (g for green) and 600–700 nm (r for red); see also Endler (1990). The spectra are categorized according to whether they absorb in the particular spectral domain (in which case they are labelled “–”) or whether they reflect (label: “+”). The intermediate types are marked “/”. This procedure is appropriate because most changes in the spectral reflection of flowers occur at the boundaries *between* these domains [around 400, 500 and 600 nm (Chittka & Menzel, 1992)]. *Within* these wavelength ranges the reflection curves are usually

characterized by plateaus or only slight changes in spectral reflectance.

B. Determination of colour loci, and how to name bee colours

For the determination of photoreceptor excitations for given spectral stimuli, we use a standard photoreceptor set for trichromatic Hymenoptera. It consists of three Maximov (1988) template functions; the UV-receptor is maximally sensitive at 340 nm, the blue-receptor at 430 nm, and the green-receptor at 540 nm, because these are the most frequent wavelength positions of Hymenopteran photoreceptors (Peitsch *et al.*, 1992). Minor corrections have to be applied to the L- and M-wavelength photopigment templates in the short wavelength part (Chittka & Menzel, 1992).

We assume that the photoreceptors display half their maximal voltage signal when they are illuminated by the light reflected from a given background (Laughlin, 1981; Backhaus & Menzel, 1987). The sensitivity factor R for each spectral photoreceptor type is determined by the equation

$$R = 1 / \int_{300}^{700} I_B(\lambda) S(\lambda) D(\lambda) d\lambda \quad (1)$$

where $I_B(\lambda)$ is the spectral reflection function of the background to which the receptors are assumed to be adapted; $S(\lambda)$ is the spectral sensitivity function of the receptor in question and $D(\lambda)$ is the illuminating daylight spectrum (CIE function D65). Unless otherwise specified, an average function of the reflections of several green leaves is used as the adaptation background (Chittka & Menzel, 1992), because green foliage is the prevalent background for most floral signals.

The effective quantum flux for a given stimulus in the respective photoreceptor is calculated according to

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

$I_S(\lambda)$ is the spectral reflectance function of the stimulus in question. The calculation of physiological receptor voltage signals (relative excitations E) from the quantum catch values P is represented by

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

(Naka & Rushton, 1966; Lipetz, 1971; Backhaus & Menzel, 1987). With these mathematical implements, every coloured stimulus may be represented by three photoreceptor excitation values E in the UV-, blue-, and green-receptors.

Unlike the *receptor space*, the *perceptual colour space* of Hymenoptera is two-dimensional. Its metrics are defined by two colour opponent mechanisms (Backhaus, 1991; Chittka, Beier, Hertel, Steinmann & Menzel, 1992). The perceptual colour space lacks a brightness dimension. Since the specific colour opponent mechanisms differ somewhat between species (Chittka *et al.*, 1992), we use a generalized colour opponent space here, the *colour hexagon*. Any colour opponent mechanism can be defined by a straight line that runs through the

hexagon with a given angle, depending on the weighting factors (Chittka, 1992). The conversion of receptor excitations E into the x/y coordinates of the colour hexagon follows:

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

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

where $E(U)$, $E(B)$ and $E(G)$ are the photoreceptor signals calculated according to equation (3) for the UV-, blue- and green-receptors described above.

In order to communicate how the bee receptors are differentially stimulated by a given spectral stimulus, one needs a code of colour names. We propose the following set of bee colour names: spectral reflection functions that result in a predominant stimulation of only one bee receptor type should be labelled "bee-UV", "bee-blue" and "bee-green", according to which of the respective receptors yields the strongest signal. Spectral stimuli that cause strong signals in two spectral receptor types, but not in the third one, are called "bee-UV-blue", "bee-blue-green" and "bee-UV-green". For this purpose, the hexagon is subdivided into six equally spaced sectors. The colour name is derived from the colour's position in the respective sector (Fig. 1). Colour loci with a distance < 0.1 from the centre of the colour hexagon are termed "uncoloured".

RESULTS

A. The 10 Types of Spectral Reflectance Functions of Flowers

It has been shown previously that the characteristics of floral reflection functions are not randomly distributed over the spectrum (Chittka & Menzel, 1992). We demonstrate here that 96% of the flower spectral reflectance curves can be categorized into 10 basic types. Five of these types are so frequent that they comprise 85% of all measurements. Only 4% of all spectral reflectance functions were so rare that, based on the present amount of data collected, we were not able to categorize them.

Further below, *all* measurements will be shown and it will become clear that they actually *can* be placed into the categories we will now describe. However, it is first necessary to introduce the basic types of floral reflectance curves. The proposed categorization for these curves will be illustrated by applying it to a set of typical examples (Fig. 1).

A1. The $u - b - g + r +$ type (16.6% of all measurements)

Example: *Lotus corniculatus* L., Fabaceae (Germany). This is the typical human yellow flower that absorbs between 300 and 480 nm, has a sharp step at around 520 nm and reflects light over the entire long wavelength part of the spectrum. It is thus a simple step function or cut-off filter (Lythgoe, 1979). It appears yellow to the human eye because it stimulates both our red and green

receptors. In some cases, the long wavelength plateau has a local minimum at approx. 680 nm. Bees will perceive such colours as green, since only the green receptor is strongly excited [Figs 1(a) and 6(a)].

A2. The $u + b - g + r +$ type (13.1%)

Example: the peripheral petals of *Senecio vernalis* W & K, Asteraceae (Germany). This is a human yellow flower that includes an UV reflection. The UV part of the reflection curve is usually somewhat less than half as intense as the long wavelength plateau. The short wave reflection decreases at around 380 nm. The long wave part is similar to the one of type 1. Such flowers appear UV-green to the bee, because both the UV and the green (but not the blue) receptor are strongly stimulated [Figs 1(a) and 6(b)].

A3. The $u - b + g + r +$ type (19.7%)

Example: *Berteroa incana* (L.) Dc., Brassicaceae (Germany). The typical human white flower that reflects equally over the entire human visual spectrum. Since, however, it absorbs UV, it appears strongly chromatic (namely blue-green) to bees (Hertz, 1937; Daumer, 1958) [Figs 1(a) and 6(f)]. The step between short-wave absorption and long-wave reflection occurs at around 410 nm.

A4. The $u - b + g - r +$ and $u - b + g/r +$ type (together 25.2%)

(1) Example: *Polemonium coeruleum* (L.), Polemoniaceae, (Norway), [Figs 1(a) and 6(d)].

(2) Example: *Knautia arvensis* (L.) Coultter, Dipsacaceae (Germany), [Figs 1(a) and 6(f)]. Flowers of this type *always* absorb UV, and reflect blue and red. There is also *always* a minimum between the blue and the red reflection peak. However, there are differences in the degree to which green light is absorbed. In some cases the reflection curve comes close to zero [Fig. 1(a)], in others there is only a "saddle" between the blue and red domains of the spectrum [Fig. 1(a)]. The former type will usually be perceived as blue or purple, the latter as pink by humans.

However, we often had difficulties in deciding whether a flower was actually pink, blue or purple. These difficulties arise because there is actually a continuum in curve shapes between the two extremes [Figs 3 and 6(d, f) see below]. Because there is no clear-cut boundary between the two extreme curve shapes, we propose to place all such flowers into category 4.

Kevan (1978) already pointed out that pink, purple and mauve flowers show considerable overlap in the human colour space. We will later see that there is also no clear separation between them in the colour space of bees.

Many flowers look blue to the human observer at first sight, even though under scrutiny, there is always a red component. This is also apparent in Fig. 6(c, d). Depending on whether "blue" flowers reflect UV or not, they should either be sorted into this or the next category.

Since the bee cannot evaluate the red part of the spectrum, flowers of this category will be perceived as bee-blue if the reflection in the green domain of the spectrum is low enough. If there is only a "saddle" (usually a pink colour to humans), such flowers will appear blue-green to bees (Hertz, 1937; Daumer, 1958).

around 550 nm, and the short wave reflection is extended from 400 nm (last category) down to approx. 370 nm or even shorter wavelengths (this category). This results in a strong stimulation of the UV-receptor. These flowers look blue, purple or violet to the human eye and UV-blue to bees [Figs 1(a) and 6(c)].

A5. The $u + b + g - r +$ type (10%)

Example: *Pulmonaria obscura* Dum., Boraginaceae, Germany. These reflectance functions look similar to the ones described in the last section, with two major differences: there is *always* a conspicuous minimum

A6. The $u + b - g - r +$ type (1.6%)

Example: *Papaver rhoeas* L., Papaveraceae, Germany. This type looks red to the human and UV to the bee eye, since it absorbs light all across the spectral domains of the blue and green receptors. Red *Papaver* species (e.g.

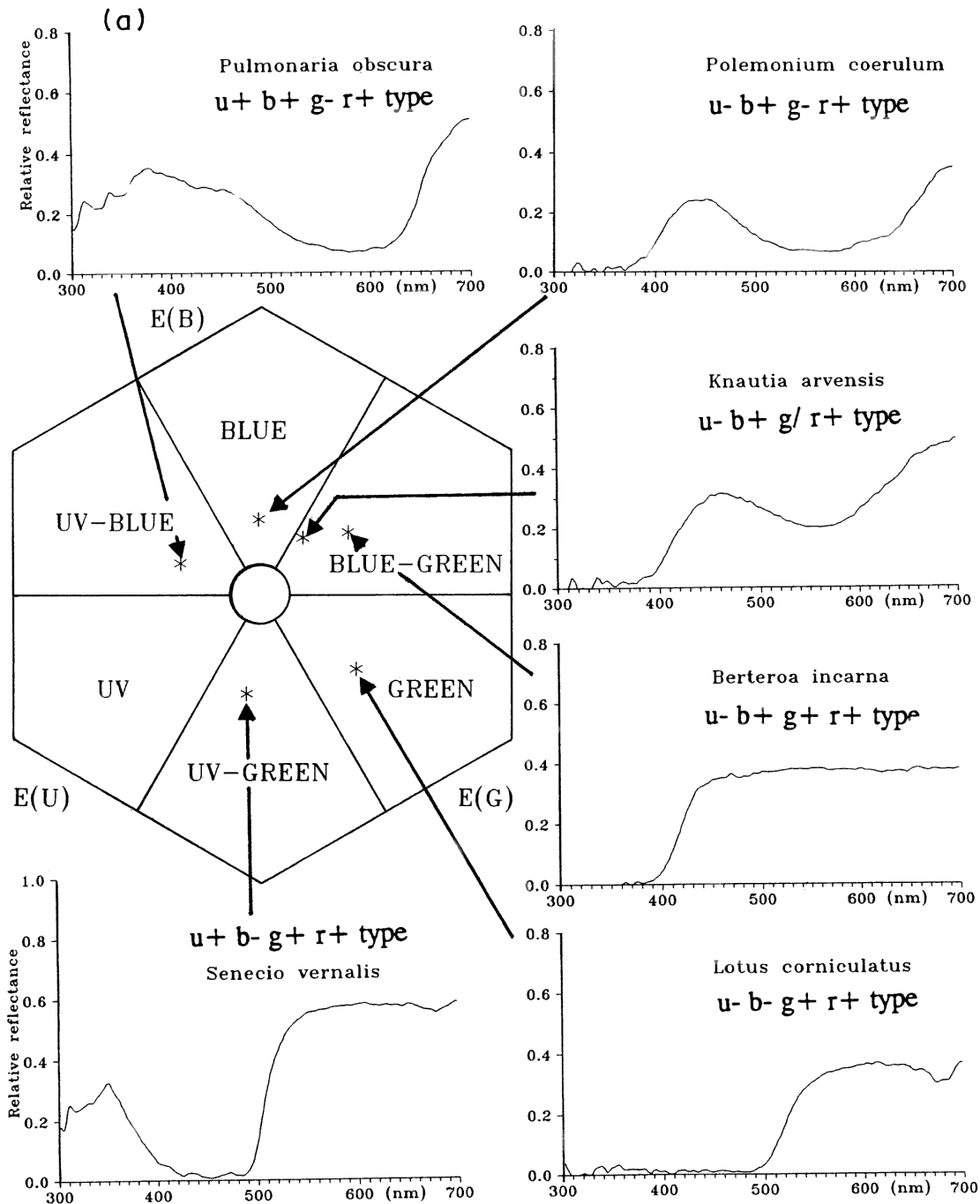


FIGURE 1(a). *Caption on facing page.*

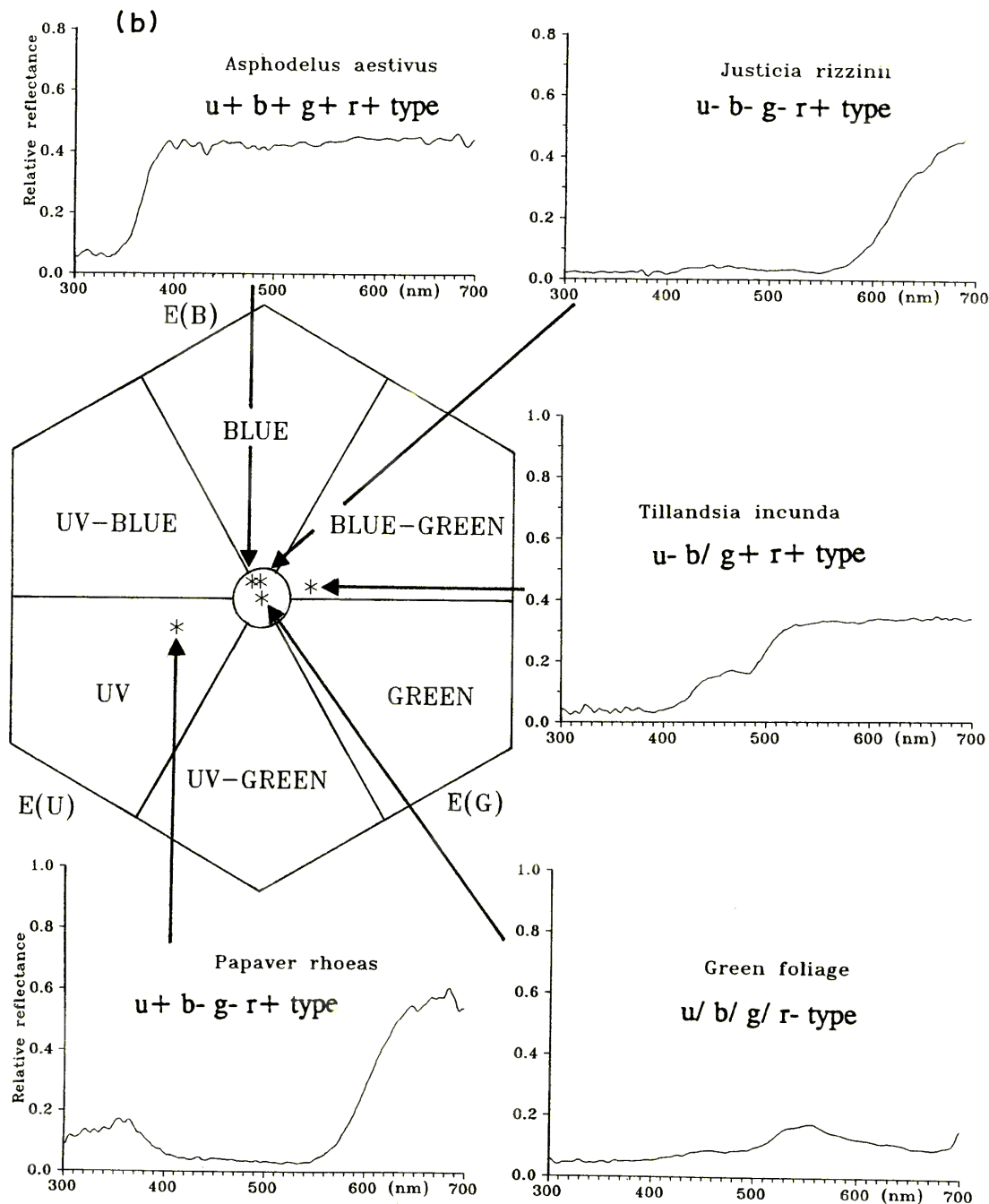


FIGURE 1. A series of the most frequent (a) and the less frequent types (b) of floral spectral reflection functions is shown, together with their loci in the colour hexagon. Arrows point from each spectral reflectance curve to the respective point in the colour hexagon. The central (circular) colour sector is termed "uncoloured". For further explanations of the boundaries between colour sectors and colour names see text.

P. rhoeas) are examples with such a reflection function (Lotmar, 1933), [Figs 1(b) and 6(e)].

A7. The *u - b - g - r +* type (2.8%)

Example: *Justicia rizzinii* Wasshausen, Acanthaceae, Brazil. Such flowers appear red to humans and uncoloured to bees, because they cause minimal excitations in all three bee photoreceptors [Figs 1(b) and 6(g)]. They absorb between 300 and approx. 590 nm. Then, a steep slope rises to a plateau at around 610–20 nm. Such

flowers are frequently hummingbird-pollinated. Flowers with these reflectance properties sometimes have a very small peak in the blue domain of the spectrum.

A8. The *u + b + g + r +* type (0.9%)

Example: *Asphodelus aestivus*, Brot., Liliaceae, Israel. These flowers look white to humans and cannot be discriminated from flowers of type 3 with the naked eye. However, the reflection on the short wavelength side extends down to 350 nm [Figs 1(b) and 6(g)]. Such

reflection functions yield approximately equal stimulation of all three bee colour receptor types. Hence they are of a fundamentally different quality for bees than the type 3 flowers. Lotmar (1933) and Daumer (1958) concluded from their observations that such flowers do not exist. They actually do, but they comprise only 0.9% of all our measurements, or 4% of all flowers categorized as white by the authors. This is not surprising given that green foliage and many other backgrounds such as soil and stones also result in approximately equal excitation of the bees' UV, blue and green receptors (Daumer, 1958; Kevan, 1978). In conjunction with the bees' lack of a brightness coding channel in colour discrimination tasks, this means that such flower colours will mingle with the colour loci of all prevalent background materials and thus are difficult to detect for a bee.

A9. The $u - b/g + r +$ type (3.8%)

Example: *Tillandsia incunda*, Bromeliaceae, Brazil. Flowers with this type of reflection function absorb UV, have a little shoulder in the blue part of the spectrum, and reflect strongly in the green and yellow part of the spectrum [Figs 1(b) and 6(f)]. Such flowers appear as an unsaturated yellow to humans (often termed "cream"-coloured in the botanical literature). To bees, these flowers appear blue-green.

A10. The $u/b/g/r -$ type (0.8% of the flower measurements, 100% of green leaves)

Examples: all green leaves. Green foliage does not selectively absorb or reflect in any part of the spectrum [Figs 1(b) and 6(h)]. It has no rapid transitions over the bee visual spectrum and thus can be predicted to appear comparatively achromatic for bees only on the grounds of its spectral properties (Daumer, 1958; Kevan, 1978; Lythgoe, 1979; Endler, 1990; Chittka & Menzel, 1992). In detail, the curves have the following characteristics: they reflect little (but do not absorb) UV. Reflection in the blue is approx. 1.5 times as high as in the UV. A peak in the green, which is somewhat more than twice as high as the blue shoulder, occurs at 550 nm. Daumer (1958) already related this observation to his findings about the relative sensitivities of the three colour receptor types of the bee (Daumer, 1956; see above) and concluded that leaves should be seen as grey/uncoloured by bees. Leaves appear coloured to humans because they absorb relatively more light in the red domain of the spectrum than in the green. Thus, the red-green colour opponent channel will yield a signal more on the "green side" of its dynamic range. For this reason, this reflection type is marked $r -$, although it might just as well be rated $r/$.

Other types of spectra, which we have not described because of the lack of a sufficient number of measurements, include those that are brown, orange or black to the human eye. The latter occurs in the centre of *Papaver rhoeas* and might be categorized as $u - b - g - r -$.

B. Flower Colours form Distinct Clusters in the Colour Space of a Bee

In Fig. 2, the colour loci of all flowers, leaves and other background materials are depicted in the colour hexagon. First of all, it is obvious that the colour loci of leaves and other backgrounds are clustered in the centre of the colour space, whereas the distribution of flower colour loci leaves this central area more or less free. Secondly, it is also obvious that there is a large empty area between the spectrum locus and the area covered by floral colour loci. Colours of such purity can only be generated by self-luminant monochromatic lights and interference colours, but not by broad-band reflection spectra.

The colour loci are not evenly distributed over the area that contains flower colours. It is clear that there are some areas of higher density and some with less floral colour loci. How can we quantify this observation?

In order to assess whether certain hues are more frequent than others in the bees' colour perception, we proceed as follows: a radial grid of 10 deg sectors (Fig. 3, middle inset) is laid over the distribution of colour loci shown in Fig. 2. The boundaries of each of these sectors are constant hue lines; the area that lies between each two adjacent boundaries represents an area of very limited variability in hue differences. The absolute number of floral colour loci within each sector is counted. The frequencies are depicted in Fig. 3.

There are no 10 deg sectors without any colour loci, and thus, in theory, plants can generate all possible bee hues. However, the floral colour loci are strongly clustered in the colour hexagon. The clusters appear at approximately regular angular intervals of 60 deg. The four most prominent peaks occur at approx. 60, 120, 180 and 310 deg; minima in the distribution are located at around 30, 90, 150, 210, 270 and 330 deg. This distribution of colour loci is the justification for the set of 60 deg-colour-sectors proposed in Fig. 1. We have placed the boundaries between the sectors so that they run through the minima in the distribution of flower colours; maxima of the numbers of floral colour loci are usually formed in the centre of each of the categories. Additional justification for the placement of boundaries comes from the fact that the peaks in the distribution are related to certain ratios in the excitations of the three photoreceptors. The flower reflections are organized in such a way that they predominantly stimulate either one, but not the two other receptors, or they stimulate predominantly two, but not the third receptor of a bee. The distribution of colour loci does not imply that the bee categorizes colours on a perceptual level, in the sense humans do. It simply means that there are groups of similar colours amongst the flowers. Generally, colour distances will be small within each group and larger between two colour loci of different groups.

The only two clusters that are not clearly separated by 10 deg sectors with lower numbers of colour loci are the blue and the blue-green ones. This substantiates what we have pointed out already about the continuum between

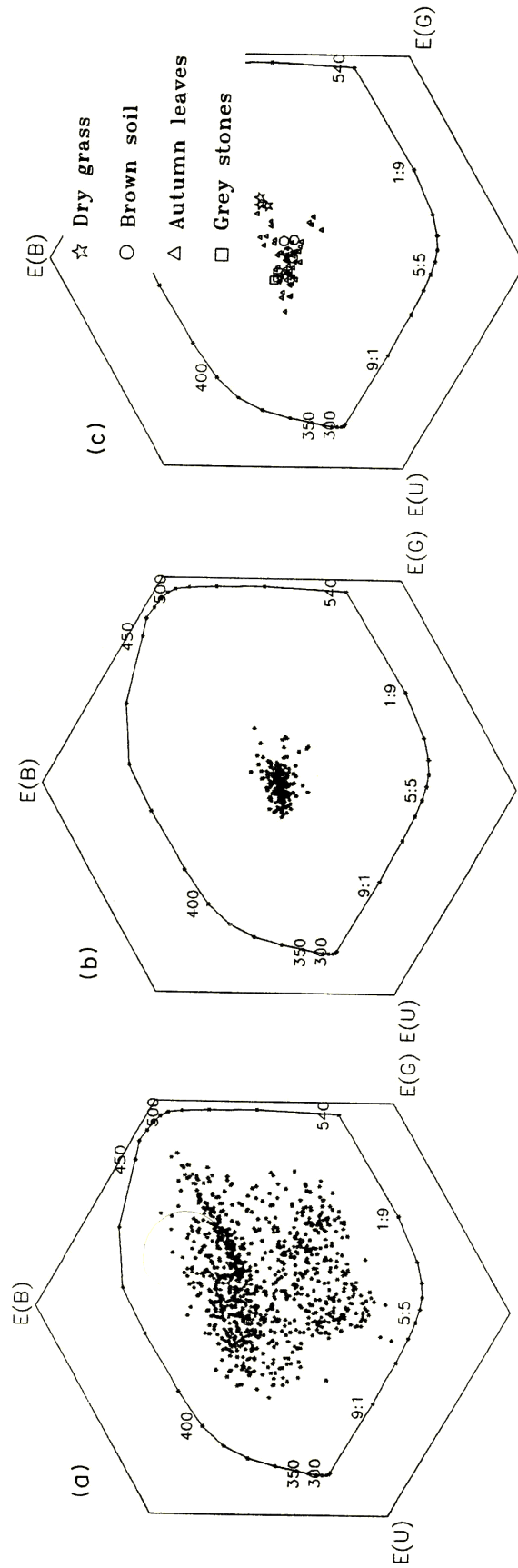


FIGURE 2. The loci of all 1063 measured flower colours are plotted in the colour hexagon (a), as well as the loci of 243 leaves (b) and the loci of several other materials that serve as backgrounds for some flowers (c). The spectrum locus (solid line) connects the loci of monochromatic lights. Together with the UV-green line, it marks the border of the colour space outside which no colour loci can be obtained. Since the locus of a colour changes if the intensity is altered (Backhaus, 1992; Chittka, 1992), the intensity for each monochromatic light is adjusted so that a maximal distance from the centre of the diagram is achieved.

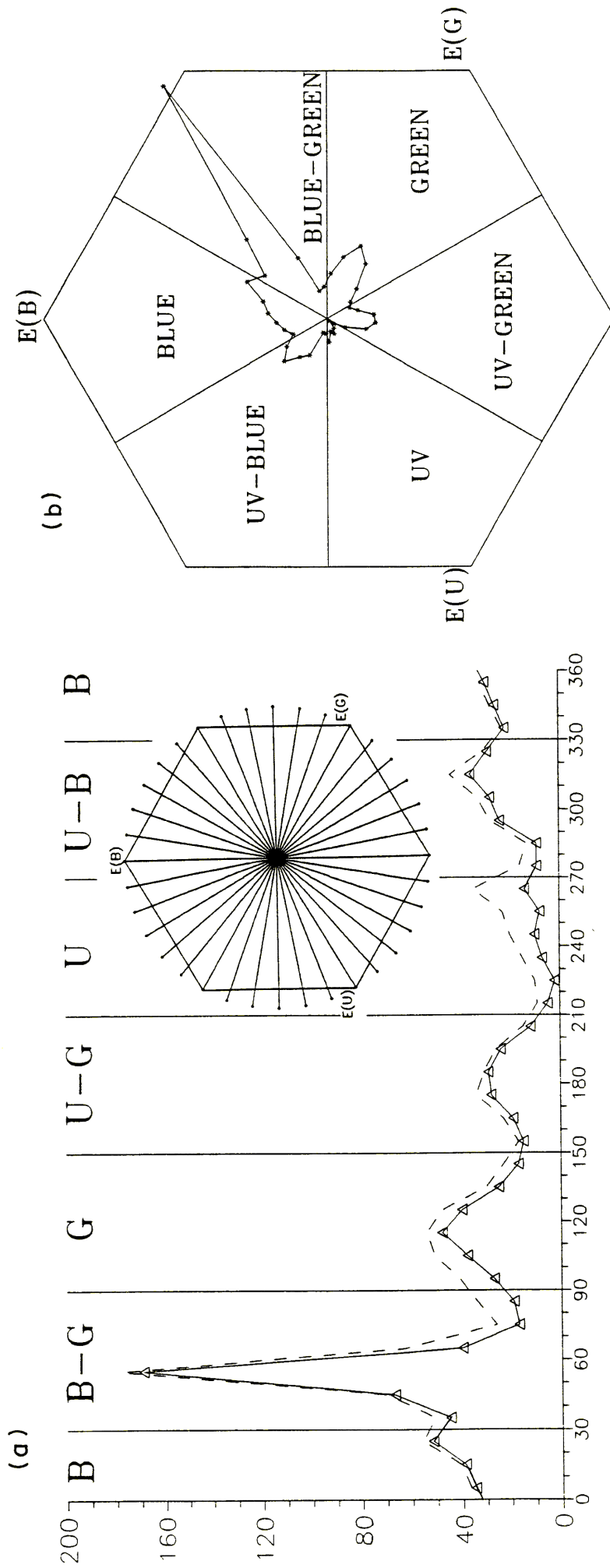


FIGURE 3. In order to assess whether there is any regularity in the way the colour loci are arranged in Fig. 2, i.e. whether there are some more frequent and some less frequent bee hues amongst the flower colours, a radial grid of 10 deg sectors is designed and "laid over" the distribution of floral colour loci in Fig. 2. The number of colour loci within each sector is counted and plotted in (a): 0 deg marks the 12:00 angle in the colour hexagon. All other angles are read clockwise (abscissa). The ordinate value plotted over 5 deg denotes the absolute number of all floral colours between 0 and 10 deg, and so forth. The colours are strongly clustered in certain hue sectors, while there are few in other ones. Most flower colour loci occur between 50 and 60 deg (blue-green flowers); the fewest are between 220 and 230 deg. There is a maximum at approximately every 60 deg throughout the hexagon, i.e. more or less in the middle of the six sectors (categories) designated UV, UV-blue, blue, blue-green, green and UV-green. There are minima at all the boundaries between these categories. The dashed line is calculated for flowers *and* all leaves. The addition of the leaves does not change the distribution significantly. (b) Shows the same result, but the numbers of colours within each sector are plotted *in* the sector in which they were counted. The maximum is normalized to 1, because the distance from the centre of the hexagon to each corner is 1.

human white, pink, and purple flowers, depending on how strongly light is absorbed in the green domain of the spectrum. There is also no clear boundary in the hymenopteran colour space. Obviously the available plant pigments allow this part of the colour space to be more continuously covered than in other areas.

The colours that lie within each of the six categories of the hexagon were counted. Blue-green flowers are the most frequent ones (33%). Blue and green flowers are equally abundant (17% in both cases), and so are UV-green and UV-blue flowers (12 and 11%). Pure UV flowers are by far the rarest (4%).

As follows immediately from equations (1) and (2), the distribution of colour loci will change if the reflection from a different background material is assumed to be the adapting stimulus. Thus, one must test whether the observed clustering of flowers is robust with respect to changing adaptation conditions. For this purpose, we calculated average functions from two background materials from Fig. 1(c), autumn leaves and granite rocks (see inset of Fig. 4 for reflectance functions). With these average functions inserted in equation (1) we recalculated the angular distribution of floral colour loci in the hexagon (Fig. 4, cf. Fig. 3). It is obvious that the clustering of flowers is rather stable. There are changes in the relative heights of maxima and minima, but their differences in angular positions relative to the boundaries established above are minimal.

C. Flower Colours and Leaf Colours are Separated in the Bees' Colour Space

Is there also a clustering in the radial direction of the colour space, i.e. in terms of distance from the un-

coloured point (spectral purity)? In order to tackle this question, we designed a circular grid in combination with the six colour categories defined above (Fig. 5, inset bottom right). The distance between each two circles measures 0.05 (the distance from the centre to one of the corners of the hexagon measures 1).

Each circle denotes a line of equal distance from the uncoloured point, or equal spectral purity. The number of colour loci found within each sector of an area between two adjacent circles is counted (Table 1). Since these areas increase from the centre to the periphery, the obtained values must be normalized by unit area. We define as "unit area" the sector of the area enclosed by the smallest circle, i.e. one-sixth of the circular area with a radius of 0.05.

If the values are pooled for leaves and flowers (total height of the columns) we find a minimum of the density of colour loci between 0.1 and 0.2 in most colour category classes (Fig. 5). The separation of colour loci into two classes of spectral purity becomes much clearer if the objects are subdivided into leaves and flowers. We find a strong separation between the spectral purity of the leaves and that of the flowers. The distributions of spectral purity is significantly different between leaves and flowers in all colour categories ($P < 0.001$, χ^2 goodness-of-fit test). The density of leaf colours is highest at spectral purities of < 0.05 and quickly fades to zero as the distance from the uncoloured point increases. The density of flower colours reaches a peak between 0.1 and 0.25 in most cases. Only in the UV and green categories is the absolute maximum between 0.05 and 0.1. However, there are secondary peaks between 0.2 and 0.25. It must be noted that, if absolute numbers are concerned

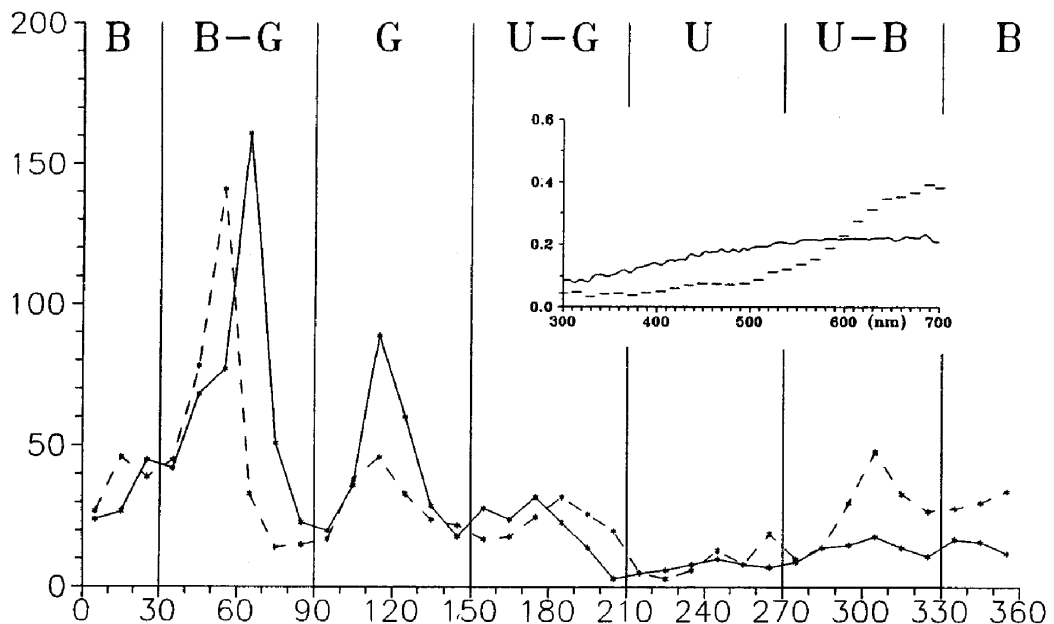


FIGURE 4. See legend of Fig. 3(a). The angular distribution of colour loci is calculated here for two different adaptation states of the photoreceptors. The inset shows the reflectance functions of the two background functions. The photoreceptors are assumed to be adapted to an average function of several measurements of grey stones (continuous curve) and to an average reflectance function of brown autumn leaves (dashed curve). As in Fig. 3, peaks and minima occur approximately at every 60 deg.

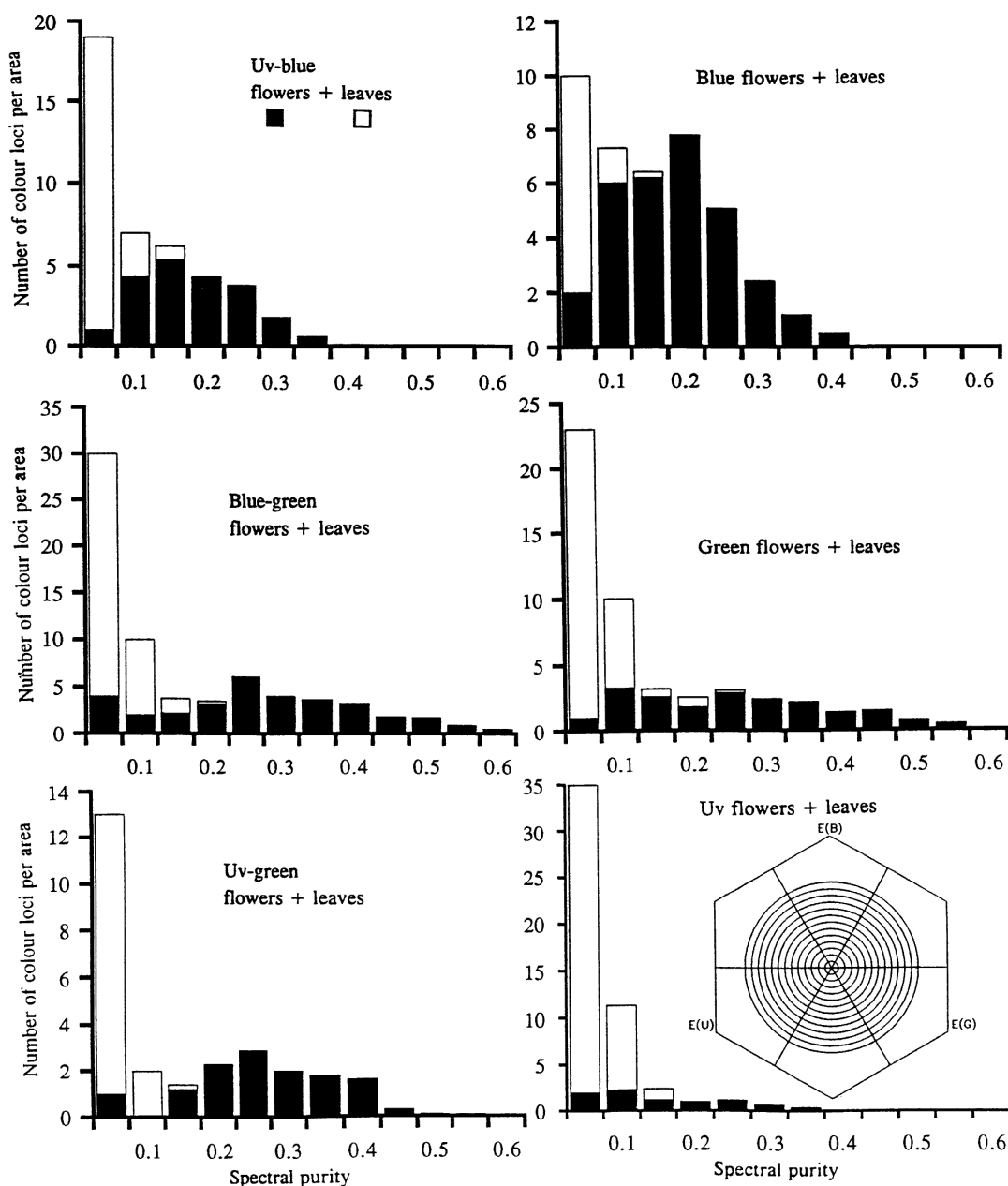


FIGURE 5. The columns denote the numbers of colour loci of leaves (white) and flowers (black) for each colour category as a function of spectral purity (see inset). Only the respective left column (spectral purity < 0.05) may be understood as absolute values. In all the other ones, the values are normalized by unit area (see inset); hence, the ordinate values may be read as density of colour loci. For absolute values within each field see Table 1. The peak for leaf colours is in all cases in the category of lowest spectral purity (< 0.05). The peak for the density of flower colours is in all cases shifted to values of higher spectral purity (mostly between 0.15 and 0.25). Inset bottom right: in order to assess whether there is a clustering in the radial direction within the colour hexagon (i.e. as one moves from the centre to the periphery), a circular grid is designed in combination with the six-category-system shown in Fig. 3(b). The distance between each two circles measures 0.05. The number of colours within each 60 deg sector of a circle is counted. Because the areas of these circle sectors become larger from the centre to the periphery, they must be normalized by a unit area in order to obtain a directly comparable measure of the density of flowers within each circle sector. We define as unit area $\frac{1}{6}$ of the 0.05 circle.

(i.e. not normalized by unit area, see Table 1), the maxima occur at values > 0.15 in all colour categories (Table 1).

In all colour categories, the density of flower colour loci becomes dominant over the density of leaf colour loci at spectral purity values over 0.05 or 0.1. Thus, if we use this circular boundary at $r = 0.1$ for separation of the category “uncoloured” from the other categories,

there is little overlap between the two classes of objects. 87% of all leaves are uncoloured, and 94% of all flowers are outside this category.

D. Spectral Reflectance Functions that Yield Loci in Given Sectors of the Bee Colour Space

We have developed a scheme to categorize flower colours in terms of a bee’s colour vision system. It was

shown that flower colours form clusters in the centre of each of the sectors that correspond to the introduced colour names. We can go a step backwards and ask the question: what types of reflectance spectra generate colour loci that lie in the respective clusters?

We will proceed to plot *all* the spectra that yield loci within each given sector of the colour space, in order to facilitate comparisons of their characteristics (Fig. 6).

D1. Sectors that contain loci generated by only one basic type of spectral reflectance function

D1.1. The spectral reflection functions of bee green flowers [Fig. 6(a)]. The curve shapes that yield colour loci in this sector are very homogeneous. The sector comprises practically exclusively human yellow flowers without a UV reflection. These are the reflectance functions described above as the $u - b - g + r +$ type.

D1.2. Bee UV-green flowers [Fig. 6(b)]. This sector contains human yellow flowers that have also a UV reflection ($u + b - g + r +$ type). The UV component is, on average, 0.3 times as high in reflectance as the long-wave plateau. However, there is considerable variation in the relative height of the two components, and the UV curve parts scatter from 0.1 to 0.6 the intensity of the $g + r +$ components.

D1.3. Bee UV-blue flowers [Fig. 6(c)]. Flowers usually described as violet, blue or purple by humans are found in this sector ($u + b + g - r +$ type). Although the reflectance functions differ somewhat more than the last two types in the wavelength positions of their slopes, the curves in the sector clearly belong to only one basic type. This type of reflectance function is similar to the one described in the next paragraph, and intermediate types exist. However, since there is a clear minimum between the two groups in colour space (330 deg in Fig. 3), they probably represent two different classes.

D1.4. Bee blue flowers [Fig. 6(d)]. Reflectance functions of the $u - b + g - r +$ and $u - b + g / r +$ type generate loci in this category. We have pointed out

before that it is not appropriate to discriminate between the $u - b + g - r +$ and the $u - b + g / r +$ type. Here, it becomes ultimately clear why this is so. There is really a continuum between the two extremes, and there is much more difficulty in separating these curve shapes than any other two types. Depending on the absolute intensity of the reflectance function, as well as the relative intensity of the blue peak and the green minimum, flowers of the $u - b + g / r +$ type of curve will be assorted in either the blue or the blue-green category.

D1.5. Bee UV flowers [Fig. 6(e)]. As has been pointed out, such colours are rather rare. They are mostly of the $u + b - g - r +$ (human red) type. However, the category also contains some human orange and "cream" flowers with a UV reflectance peak.

D2. Categories that contain loci generated by three basic types of spectral reflectance functions

D2.1. Bee blue-green flowers [Fig. 6(f)]. At first sight, this category appears to be rather heterogeneous. At close inspection, however, there are only three basic types of spectral reflectance functions within this category. The first and most frequent type are human white flowers that absorb UV ($u - b + g + r +$ type). Secondly, there are quite a few flowers of the $u - b + g / r +$ type (usually human pink or purple), forming a continuum with flowers of similar curve shapes in the neighbouring blue category (see above). The third type included in this category is what we have described as $u - b / g + r +$ type, which usually appears as an unsaturated yellow to the human eye.

D2.2. Bee uncoloured flowers [Fig. 6(g)], and green foliage [Fig. 6(h)]. This category contains several types of curve shapes that we have not categorized because of their relatively infrequent occurrence. However, there are three more prevalent types; these comprise (a) the human red $u - b - g - r +$ type; (b) the human white $u + b + g + r +$ type; and (c) the type of green foliage spectrum we have described as $u / b / g / r -$, which also exists in some flowers.

TABLE 1. The total number of floral colour loci (normal letters) and leaf colours (italics) within each colour category (lines) and spectral purity category (columns)

Colour category	Spectral purity												
	<0.05	0.1	0.15	0.2	0.25	0.3	0.35	0.4	0.45	0.5	0.55	0.6	
Blue-green	4	6	11	23	55	44	47	49	32	32	20	12	(22)
Green	26	25	8	2	0	3							
	1	10	13	13	26	27	29	21	26	16	10	3	
UV-green	22	20	3	5	2								
	1	0	6	16	26	22	23	24	5	2	2		
UV	12	6	1										
	3	7	6	7	13	7	5	1					
UV-blue	33	27	6										
	1	15	27	30	34	20	8	2					
Blue	18	8	4										
	2	20	31	54	46	27	16	8	1	1			
	8	4	1										

The left column contains the numbers of colour loci with spectral purity values $P \leq 0.05$; the second from left column comprises loci with $0.05 < P \leq 0.1$, and so forth. Only in the blue-green category, spectral purity values > 0.6 occur. The number of these is given in brackets.

The spectral reflectance functions of green leaves, most of which also occur in the uncoloured category, are plotted in a separate graph [Fig. 6(h)]. It is obvious that there is little variability in the wavelength positions of

the curve features. However, the reflections in the blue and UV, as well as the minimum in the red, differ somewhat in relation to the maximal reflection at 550 nm. Generally, the reflection of leaves is low across

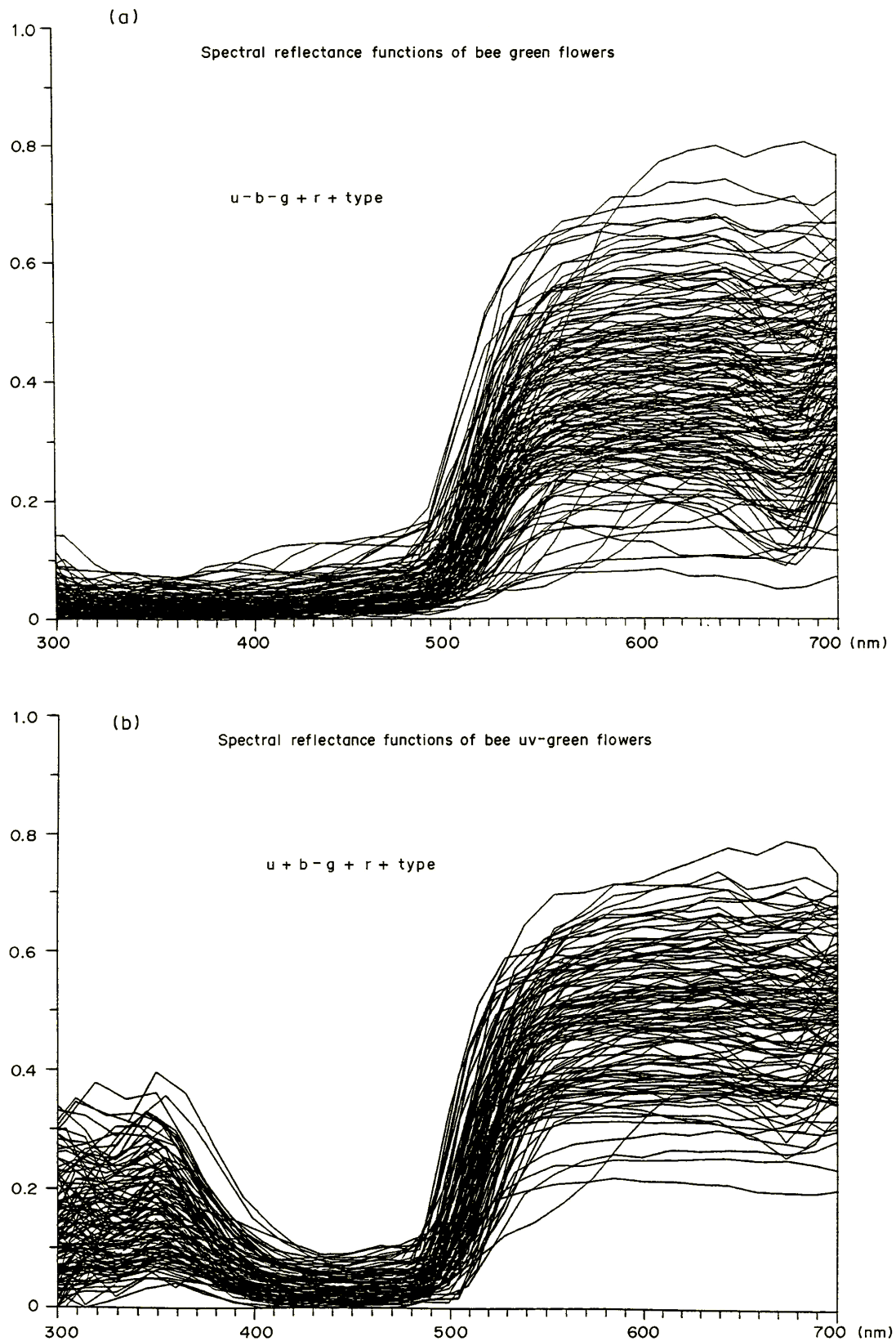


FIGURE 6(a-b). *Caption on p. 1503.*

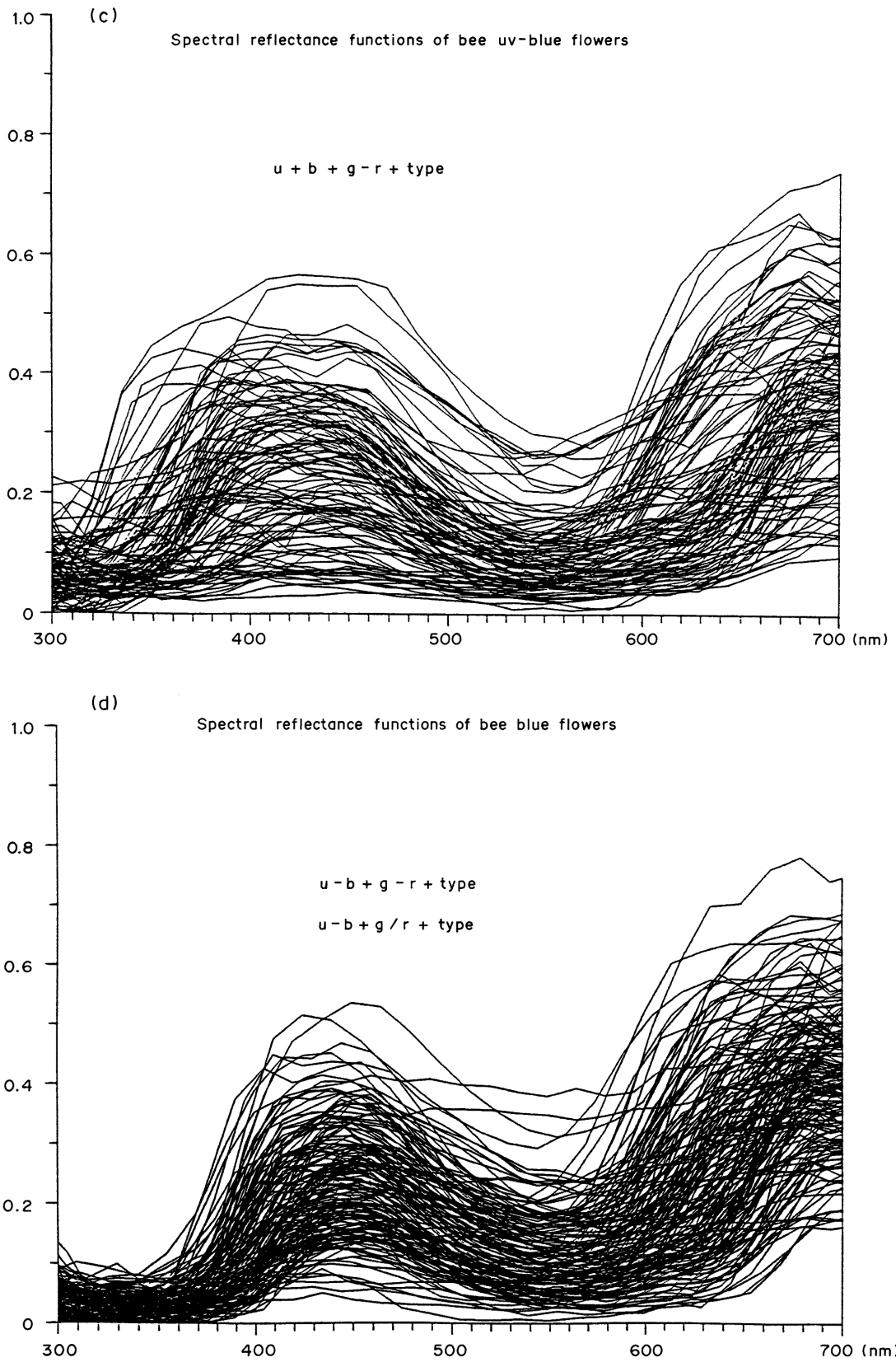
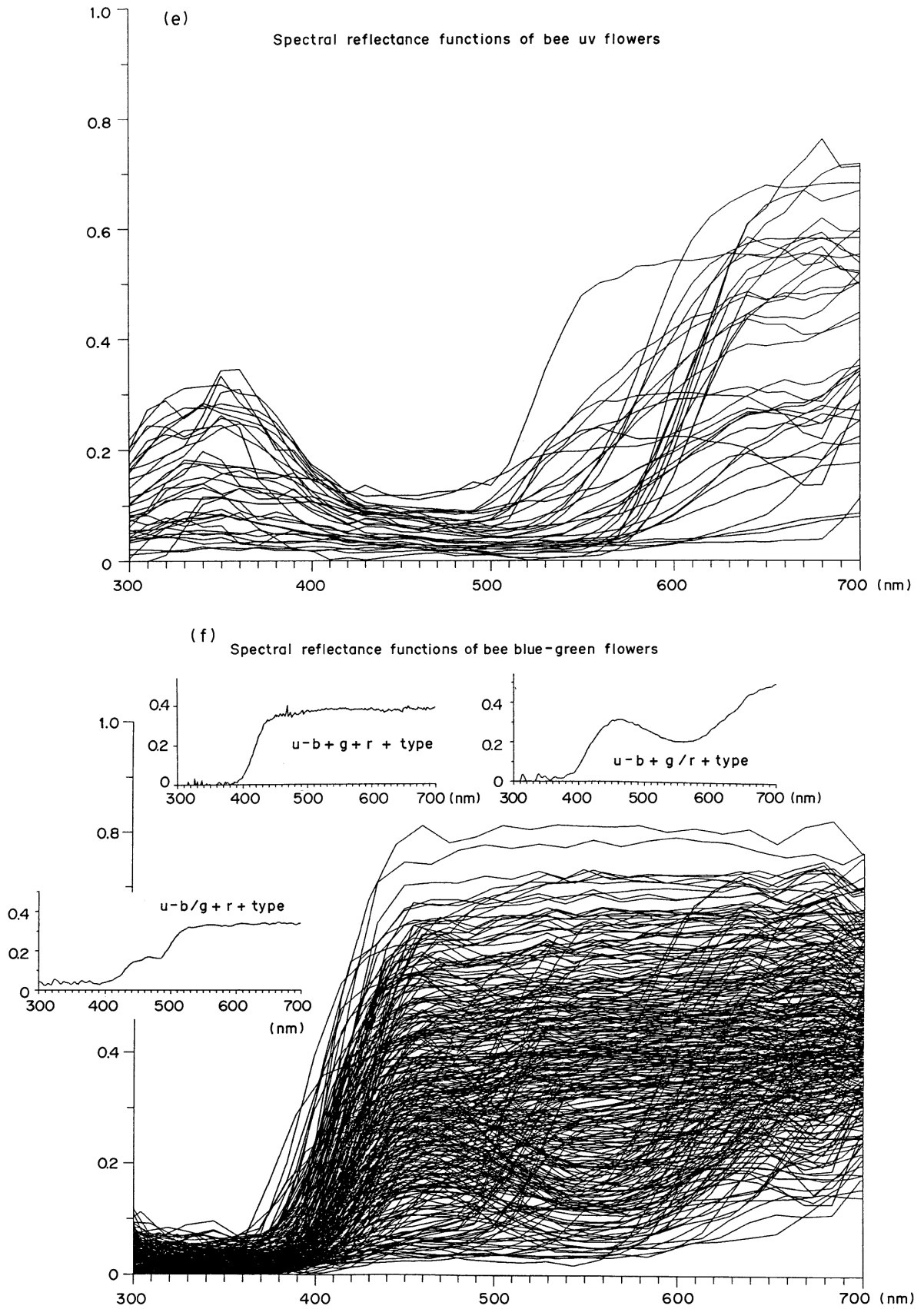


FIGURE 6(c-d). *Caption on p. 1503.*

the whole spectrum. All leaves have an upward slope in the far red at 700 nm.

Another way of looking at the data and to compare the UV-component with reflections in other parts of the

spectrum is the following. We have plotted an averaged curve for all flower and all leaf spectral reflectance functions, together with their standard deviation (Fig. 7, upper left). It is clear from this function that the intensity



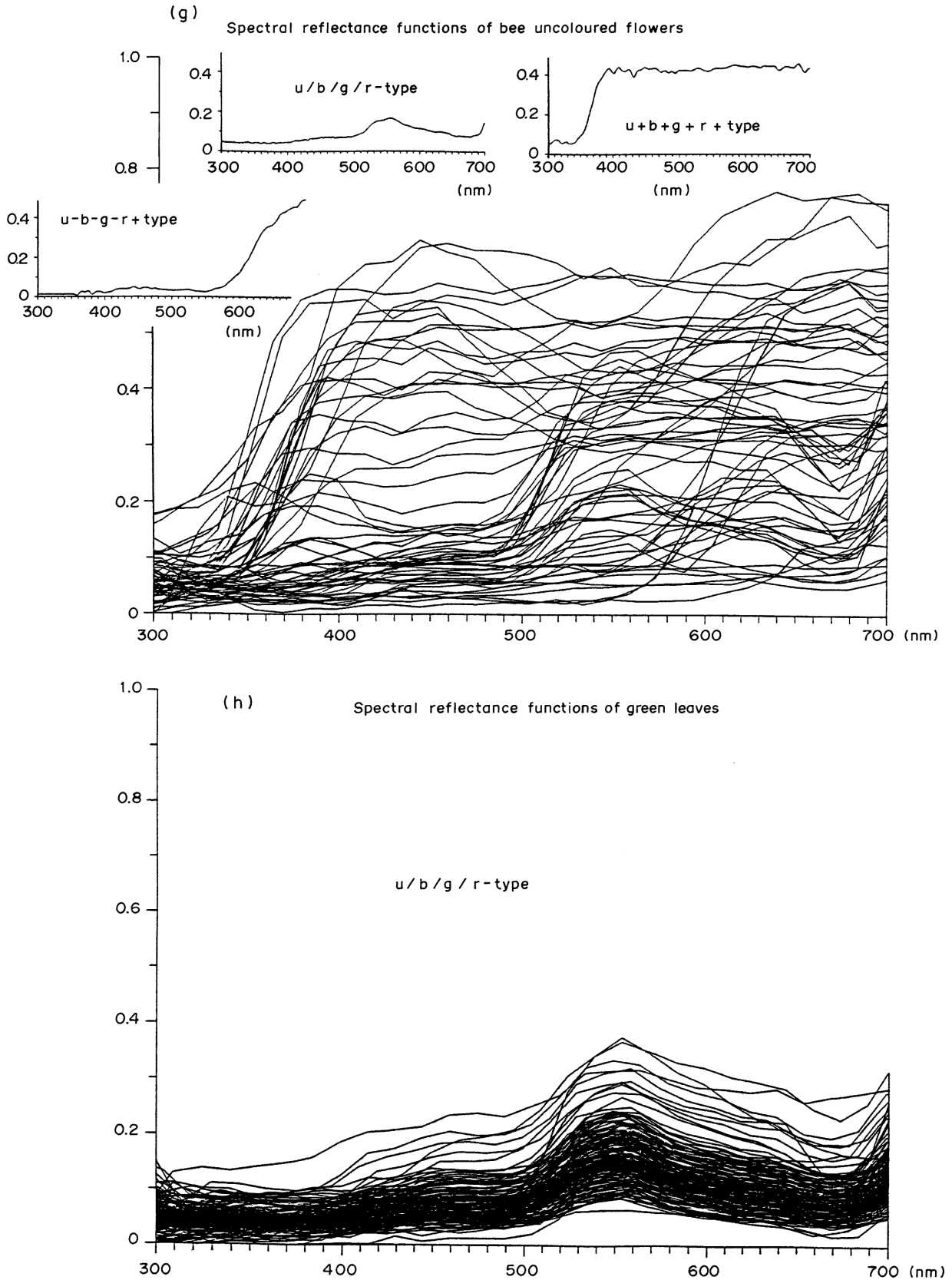


FIGURE 6. (a-h) The spectral reflectance functions of all flowers and leaves. Seven figures (a-g) contain the spectral reflections of flowers that yield loci within the seven bee colour categories UV, UV-blue, blue, blue-green, green, UV-green, and uncoloured. (h) The spectral reflection functions of green leaves. If a graph contains more than one basic curve type, then insets show the curve types included.

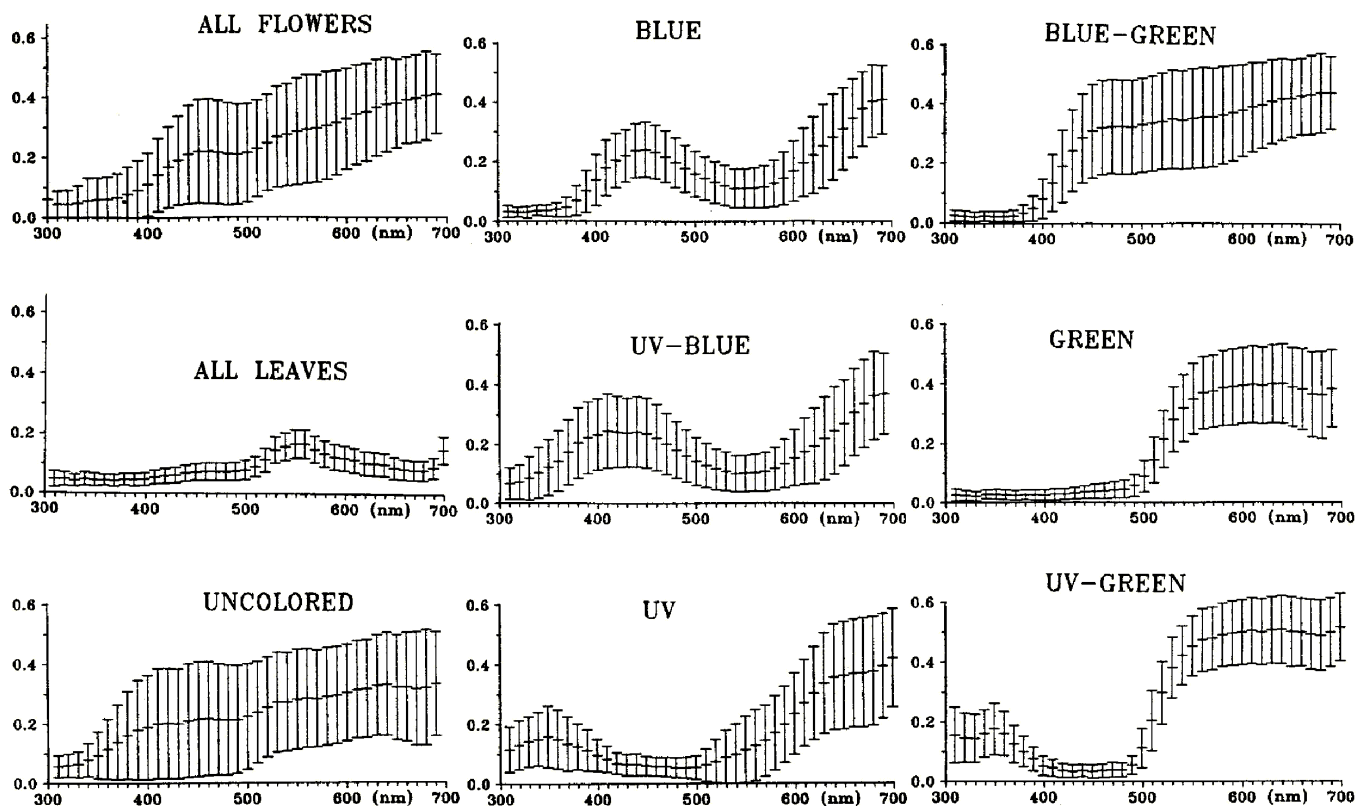


FIGURE 7. The average functions of all flower (upper left) and leaf reflection spectra (middle left), as well as all the functions that yield colour loci within each colour category in the hexagon are given (middle horizontal dashes). Vertical bars denote

of UV-reflectance is always surpassed by the intensity at longer wavelengths. The same is true if one plots the average functions for all floral spectral reflection functions that generate colour loci within each of the colour categories UV, UV-blue, blue, etc. (Fig. 7). The average functions look similar to the exemplary functions we have shown in Fig. 1, indicating that these really were representative examples of spectral reflectance functions for the respective types.

DISCUSSION

A. The reflection functions of flowers and their categorization

We have shown that there is only a limited number of distinct types of floral reflectance functions. 41% are simple step functions or cut-off filters that absorb at short wavelengths and reflect at longer wavelengths. These include the $u + b + g + r +$ type (human white, bee uncoloured, step at 350 nm), the $u - b + g + r +$ type (human white, bee blue-green, step: 410 nm); the $u - b - g + r +$ type (human yellow, bee green, step: 520 nm) and the $u - b - g - r +$ type (human red, bee uncoloured, step: 620 nm). There are no step functions that reflect at short and absorb at longer wavelengths. Generally, no flowers, aside from the green foliage type functions, absorb in the red domain of the spectrum.

Two further types, comprising 15% of all measurements, combine a step at long wavelengths with a roughly Gaussian-shaped reflection peak in the ultraviolet. These include the $u + b - g + r +$ type (human yellow, bee UV-green) and the $u + b - g - r +$ type (human red, bee UV).

All human violet, blue, pink and purple flowers (together 35%; bee-UV-blue, bee-blue or bee-blue-green, $u + b + g - r +$ and $u - b + g - r + / u - b + g / r +$) have a step between 600 and 650 nm and an approximately Gaussian peak between 380 and 450 nm.

In general, there are no reflection functions that change more than three times over the wavelength range from 300 to 700 nm. Sharp changes in spectral reflectance usually have a minimal interval of 100 nm between them. These changes cluster around 400, 500 and 600 nm (Chittka & Menzel, 1992). This observation is the justification for the system we have proposed to categorize the spectral reflectance functions in terms of the four wavelength ranges 300–400, 400–500, 500–600 and 600–700 nm. Such a system can only make sense if the spectra are not randomly distributed, have steps close to the above wavelength boundaries, and usually either absorb or reflect selectively between these boundaries.

We have demonstrated that UV reflections in flowers cannot be generated independently of reflections in other parts of the spectrum. There are no pure UV flowers on the level of the spectral reflection function. Flowers that appear UV to bees are rare and have always a red

reflection. The reflection in the UV is always lower than in other parts of the same reflectance spectrum. Generally, spectral reflectances without UV are more frequent than the ones that include UV.

Obviously, the limited variability in reflection curve shapes is related to the fact that only a limited number of flower pigments are available which can be combined to form the spectral reflections of flowers. However, the relationship between combinations of pigments and surface structures on the one hand and spectral reflections on the other is complicated (see e.g. Asen, Stewart & Norris, 1975) and cannot be treated in this paper.

B. The clustering of flowers in the bee colour space

It was shown that the floral colour loci are clustered in the bee colour space. The question then asked was the following: what is the relationship between these clusters and the physical properties of the colours, i.e. the reflection functions? If each cluster can be traced back to be generated by only one type of spectral reflectance function, this means that bee colour vision is appropriate for separating flower colours according to their physical properties. If, on the other hand, the clusters are composed of flowers with spectral reflectance curves of different classes, the colour vision may be considered sub-optimal from this point of view. For example, the $u + b - g + r +$ and the $u - b - g + r +$ reflectance types would match each other in the human colour space.

In bee colour vision, four of the colour sectors (UV, UV-green, green, UV-blue) contain colour loci generated by only one basic type of reflectance. There is no clear separation between groups of colour loci in the blue and blue-green sectors. This continuum is not a result of an inappropriate colour vision system. It is based on a *physical* continuum that covers all possibilities between two extreme curve shapes ($u - b + g - r +$ and $u - b + g + r +$).

Generally, however, even the rather coarse system of 60 deg sectors in the hexagon is sufficient to separate at least the most frequent types of spectral reflectance functions into their classes.

The only area of the colour space that contains colour loci generated by spectral reflectance functions of entirely different types is the central area which we have labelled "uncoloured". This area is predominantly covered with the loci yielded by green leaves. Additionally, this area contains human-red flowers without UV reflection ($u - b - g - r +$ type) and human-white flowers with UV-reflection ($u + b + g + r +$ type). The former occurs in hummingbird-pollinated flowers that actively exclude bees as visitors. The latter type is extremely rare in nature. Hertz (1937) already suspected a causal relationship between the rarity of UV-reflections amongst human white flowers observed by Lotmar (1933) and the result that bees cannot be trained to UV-reflecting white stimuli presented in front of other achromatic backgrounds of different intensities. Hertz attributed this phenomenon of floral colouration to the selective pressure exerted by the bees (and their psychophysics of

colour vision) on the colours of flowers. The lack of an intensity coding channel in bee colour perception (Backhaus, Menzel & Kreißl, 1987; Chittka *et al.*, 1992) simply means that such flowers will be difficult to detect against green foliage.

Kugler (1963) noted that $u + b + g + r +$ flowers are not predominantly visited by bees, but rather by nocturnal moths. In this case, the UV-reflection seems to be a strategy to enhance detectability by maximizing total reflection for signal receivers to whom the parameter "intensity" is meaningful (unlike bees), and in conditions where the absolute light intensity may set the limits to detectability.

C. Separation of flowers and leaves in the bee colour space

A bee that flies over a green meadow and seeks to detect a flower faces a signal-to-noise problem. For a realistically cluttered background, e.g. dappled foliage, there will be continuous small fluctuations in voltage signals in all three photoreceptors, which the bee must discard as unimportant. The detectability of an object of a given size is dependent on the degree to which this object generates photoreceptor excitations whose differences from the mean background exceed the noisy fluctuations of the background signals significantly. However, the responses from the different receptor colour types may not be considered in an isolated fashion, because the differences in different photoreceptor types may cancel each other in a colour opponent system (Chittka, 1992). In other words, the detectability of a signal is a function of the perceptual colour difference of this signal to the average background. In a first approach, this has been shown by means of behavioural experiments with bumblebees (Chittka & Lunau, 1992).

The quality of a floral colour signal (in terms of its detectability) thus depends on its potential to generate a strong colour difference to its background. We have shown here that (a) leaf colours and other background materials are accumulated in the centre of the colour space; (b) there is a "belt" around this central cluster that is low in the density of floral and leaf colour loci; (c) the clusters of flower colours are arranged outside this belt and thus in the periphery of the colour space. Thus, bee colour vision is appropriate to separate the colours of flowers and leaves. Flowers, in turn, "avoid" the area of the colour space covered by green leaves.

Daumer (1958) and Kevan (1978) already predicted that leaves should appear "grey" to bees because of their spectral properties (i.e. no selective reflection or absorption in any part of the bee visible spectrum). The reason why many other background materials accumulate in the same area as green leaves [see also Menzel and Shmida (1993) for limestones, desert sand etc.] is that the differences in spectral reflectance concern only the intensity of reflectance and the red domain of the spectrum, both of which are not evaluated by Hymenoptera. Hence, a flower that stands out against green foliage can be predicted to be equally conspicuous against brown soil, grey stones and other inorganic backgrounds.

Of course, the discovery that leaf colours cluster symmetrically around the very centre of the colour space is not an immediate consequence of their spectral properties, but rather follows from our assumption that the photoreceptors are adapted to green foliage so that they yield half-maximal response when stimulated by light reflected from these objects (see Methods). Thus, the critical question is whether this assumption about photoreceptor adaptation is correct. The electrophysiological work of Laughlin (1981, 1989) as well as model calculations of Backhaus *et al.* (1987) and Brandt, Backhaus, Dittrich and Menzel (1993) on behavioural results provide hints that this theoretical assumption can explain the experimental data very well.

Thus, even if future research may show that this theory may have to be slightly modified under extreme illumination conditions, the cluster of leaf colour loci will shift only slightly out of the centre of the colour space. In any case, such a small shift would not result in a mixture of the previously separated clusters of colour loci.

D. Ecological and evolutionary implications of the clustered distribution of flower colours

Flower colours compete for niches in the colour memory of pollinators, so as to increase the probability of conspecific flowers being visited (Kevan, 1978; Feinsinger, 1983; Kevan & Baker, 1983; Chittka & Menzel, 1992; Menzel & Shmida, 1993). For pollen transfer to be directed from one flower to another of the same species, flowers must be distinguishable from competitors. Bees learn all detectable colours as food signals (Daumer, 1956, 1963; von Frisch, 1967; Menzel, 1967) and value other signals in terms of their perceived colour difference to the learnt colour (Backhaus *et al.*, 1987; Chittka *et al.*, 1992). In order to favour pollinator discrimination, the colours of flowers of different species in a given habitat should theoretically be maximally and equally different from each other. In order to achieve such a distribution, an important evolutionary prerequisite must be met: there should be an equal probability to generate flower colours in all possible areas of the colour space.

It is obvious that this prerequisite is not fulfilled. There are hardly any pure UV colours, even though these are readily learned by bees (Menzel, 1967). The numbers of colour loci in the other colour sectors also differ fundamentally from each other. Additionally, the loci are not distributed evenly within the sectors, but instead are clustered. This asymmetrical and clustered distribution cannot be explained on the basis of the theory of colour discrimination by flower-visitors.

Colour discrimination is not the only selective pressure exerted on the distribution of flower colours as a whole. The learning experiments of Menzel (1967) predict that different niches in the colour memory of the bee are not equally accessible from the flowers' perspective. UV-blue signals are learned fastest and blue-green signals slowest (Menzel, 1967). UV, UV-green, green and

blue colours were learned with intermediate speeds. Hence the equal distribution of flower colours predicted from colour discrimination may be distorted so that the learning performance is taken into account. One might expect more UV-blue flowers and fewer flowers with blue-green colours if bees are the most important pollinators. However, if the flowers of too many species are UV-blue, then colour discrimination (and thus pollinator constancy, and, consequently plant fitness) will suffer. Therefore there might be an equilibrium in the flower colour distribution that favours both colour discrimination of flowers and anticipates to some degree the learning performance of the pollinators addressed. UV, blue, green and UV-green colours should occur with approximately equal frequencies, because they are learned equally fast.

It is clear that the uneven distribution of flower colours and, particularly, the extremely low frequency of pure UV signals cannot be explained by this assumption. Consequently, neither the theory of colour discrimination nor the learning performance of bees can be used as adaptive explanations for the distribution of flower colours. The observed distribution provides strong hints for evolutionary constraints on the colouration of flowers. Obviously, different colour loci cannot be generated with equal probability. Thus, although bee colour vision is optimal for flower colour discrimination (Chittka & Menzel, 1992; Chittka, Shmida, Vorobyev & Menzel, 1993), flower colours can be predicted not to be optimal in terms of being discriminated by bees. It must be emphasized that these two adaptations do not necessarily go together (see e.g. Enquist & Arak, 1993).

E. Colour names for bees

For communication about bee colours, scientists need a naming code to categorize the colours. All the systems so far proposed (Daumer, 1958; Kevan, 1978) agree in that such systems of colour names are purely operational and do not have any implications for categorial colour perception in bees. The relationship between the previous sets of colour names and the one presented here are summarized in Table 2.

Daumer's (1958) terminology was ingenious in that it was the first attempt to systematize colour names for a colour vision system that differs from humans. However, this concept is somewhat confusing, because some colours are named according to receptor stimulation (UV and blue-green), whereas others are taken directly from human colour perception (violet and yellow), and yet others are transferred from human onto bee colour vision (bee-purple and bee-white).

Kevan (1978) suggested to name bee colours analogously as for humans. This means, for example, that a colour that stimulates predominantly the S (short wave) receptor should be named "blue" both for humans and bees. This terminology is more consistent than Daumer's, because *all* colour names are derived according to the bee S-, M- and L-receptor stimulation and simply transferred to the respective receptors in humans. Additionally, this system has the very convenient

TABLE 2.

Our names	Daumer (1958)	Kevan (1978)
UV	UV	Blue
UV-blue	Violet	Blue-green
Blue	Blue	Green
Blue-green	Blue-green	Yellow
Green	Yellow	Red
UV-green	Purple	Purple
Uncoloured	White	White

advantage that bee colours can be graphically depicted by human colours.

However, we find it most intelligible to classify the colours *exclusively* according to bee receptor stimulation. Thus, we name colours that stimulate predominantly one, but not the other two receptors UV, blue and green, simply according to the spectral positions of the bees' photoreceptors on the common scale of human colour names. Colours that stimulate predominantly two, but not the third receptor are denoted blue-green, UV-green and UV-blue. The term "uncoloured" includes all colours previously labelled "bee-black", "bee-grey" and "bee-white". The use of the latter terms makes little sense if related to a colour perception without a brightness dimension. All colours that yield approximately equal stimulation of all three photoreceptors are assorted into this category.

In addition to a set of colour names, one needs a compulsory regulation for the placement of boundaries between colour naming sectors in the colour space. We have related the number and placement of boundaries to (a) physiological excitation states of the photoreceptors (i.e. only one or two receptors predominantly stimulated, or all three close to equally excited) and (b) to the distribution of flower colours in the colour space (i.e. boundaries are placed at the angular position of the minima in the density of floral colour loci).

F. Conclusion

In the Introduction, we warned against overestimating the significance of UV signals in flowers. We have shown that such signals must be carefully evaluated in terms of a model of colour vision for the receiver. UV signals can be used to make an object cryptic against a background (as in the case of $u+ b+ g+ r+$ flowers and green leaves) or to make it conspicuous in an otherwise cryptic object (e.g. $u+ b- r- g+$ vs $u- b- g- r+$ flowers). In a general sense, we conclude that UV is just one of the components of trichromatic bee colour vision, with no particular salience in comparison to what is contributed by the blue and green receptors. Together, the three colour receptor types comprise the inputs to a colour opponent system. This system forms a colour space on the perceptual level.

In order to address perceptual niches within this space, flowers (and other signallers) may have evolved several strategies for standing out from the background or from competitors, or to be inconspicuous. These strategies involve the contributions of UV, blue and green receptors to equal degrees and with equal importance.

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