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Interspecific diversity and uniformity of flower colour patterns as cues for learned discrimination and innate detection of flowers

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Abstract. The colour patterns of angiosperm flowers visited by bees and hoverflies were shown to provide a dual signalling system, giving the flower-visitors visual orientation cues for the initial detection of flowers, as well as for learned discrimination. Pollinators show an innate response to interspecifically uniform colour signals, which enable them to detect flowers and to orient towards the site of reward. Interspecifically diverse colour signals provide pollinators with cues for learned discrimination between flowers of different species.

Key words. Colour preferences; bumblebees; hoverflies; floral colour pattern; flower signals.

Exactly 200 years ago, C. K. Sprengel[1] suggested in his monograph, 'The Discovered Mystery of Nature in Construction and Fertilization of Blossoms', published in 1793, that floral colours possibly operated as orientation cues for pollinators. It was more than 100 years later that K. von Frisch[2] demonstrated colour vision and colour learning in honeybees. Nowadays, it is known that many flower-visiting insects possess colour vision, can associate colour signals with food, and have efficient foraging strategies[3-10].

Angiosperm plants attract pollinators by means of floral display. In this respect, the flower colouration has two particular functions: firstly, the attraction of potential pollinators which have not yet experienced flowers of a particular species, and secondly, the provision of cues for revisitation, after flower-visitors have experienced a rewarding flower and have learned the floral signals. There are only a few reports on the behaviour of naive, inexperienced flower-visitors, compared with the large number of experiments using trained and rewarded animals.

To describe the properties of colour stimuli as viewed through a flower-visitor's eyes, one may use the parameters intensity, predominant wavelength, and colour purity. These parameters may cause the sensations of brightness, hue, and colour saturation in flower-visitors, (provided that they possess the same perceptual dimensions as humans). In calculating these parameters, one should consider the spectral distribution of daylight, the spectral reflection of floral colours, and the spectral sensitivities of the types of photoreceptor possessed by the flower-visitors.

Most bees and hoverflies visit a variety of unrelated food plants. For initial flower detection, they must use general floral cues. To discriminate between flowers of different species in order to revisit a rewarding flower type, they can use species-specific floral cues. Polyphagous hoverflies and solitary as well as social bees use colour cues for orientation in the innate process of initial detection of flowers[3,4,7,11-15], and in learned discrimination between flowers[4,16-18]. Looking now in more detail at the significance of flower colouration, I suggest two signalling functions. 1) Non-species-specific, uniform colour signals provide inexperienced flower-visitors with cues for innate detection of flowers, such as cues for the distant approach, for the location of the landing site, and for access to the floral reward. 2) Species-specific floral colours and colour patterns provide pollinators with cues for learned discrimination between plants.

The primary objective of this paper is to investigate the colour patterns of genuine flowers, to find out whether they provide a dual signalling system displaying interspecifically diverse as well as interspecifically uniform colour signals. Since the aspects of interspecific diversity of flower colour signals and discrimination learning have recently been analyzed[19], my work focussed on the analysis of the exact key stimuli triggering innate orientation towards flowers in the bumblebee, *Bombus terrestris* (Apidae), and in the hoverfly, *Eristalis tenax* (Syrphidae), as well as on the analysis of interspecifically uniform colour signals.

Materials and methods

Behavioural tests. Larvae of *Eristalis tenax* were collected in manure heaps and reared in the laboratory. Freshly emerged imagos were exposed to white, UV-reflecting artificial flowers, incorporating 4 small screens (each 2 mm in diameter) simulating floral guides, which provided spectral stimuli. Each individual hoverfly was tested 5 times with each spectral stimulus. When the flies walked over the horizontally exposed artificial flowers, the proboscis extension towards the screens was recorded. The spectral test stimuli differed with respect to intensity and wavelength[20].

Queens of *Bombus terrestris* were captured and reared in the laboratory. The flower-naive workers were exposed to coloured artificial flowers against a green background. The artificial flowers consisted of a star-shaped corolla (16 cm^2) and of an anther-shaped guide (14 mm^2). Ten vertically exposed artificial flowers were tested simultaneously with the freely flying workers of one colony at a time[12, 13].

The tests of innate behaviour in response to artificial flowers were carried out with flower-naive and untrained individuals. The animals were not rewarded on reaching the test stimuli.

Measurements of reflection. The flowers were collected in the Botanical Garden in Regensburg and in the field. The spectral reflection was recorded with a diode array spectrometer using a single beam ZEISS MCS 230 photometer unit, a ZEISS CLX 111 Xenon light source, and an MS 20 ceramic white standard (reference of 100% reflection). The flowers were placed on black velvet in a ZEISS GK 111 goniometer. Specimens for testing pollen colour were flattened and placed on black cardboard. The size of the measuring spot was 10 mm^2. Flowers with smaller coloured areas were therefore excluded from the investigation.

Photography of ultraviolet reflection patterns. To check flowers for the presence and spatial arrangement of UV-patterns, UV-photos were taken using a MINOLTA XE5, a UV-transmittant objective ULTRA-ACHROMATIC-TAKUMAR 85 mm with bellows, a filter ULTRA-ACHROMATIC-TAKUMAR 365 nm transmittant only in the ultraviolet, and the UV-sensitive film ILFORD FP4.

Calculation of colour parameters. A standard spectral daylight distribution [Φ (λ)](6500 K correlated colour temperature)[21] (fig. 1b), the spectral reflection of the coloured flower parts [R (λ)], and the spectral sensitivity of the three photoreceptors [$r_{S,M,L}$ (λ)] in the short, middle and long wavelength regions of the honeybee, *Apis mellifera* L.[22] (fig. 1a) are used to calculate the photon absorption in each photoreceptor type. The flower colours are represented by colour loci in a chromaticity diagram. It must be kept in mind that the chromaticity diagram represents the relative absorption of the photoreceptor types, and ignores the non-linear transduction properties of photoreceptors[23]. Consequently, the perceptual colour differences are not related in a linear fashion to the distance between colour loci in the chromaticity diagram[24].

The relative amount of quanta absorbed by each receptor type is calculated by means of the formula

$$X\,[Y,Z] = \int_{300}^{650} k_X[k_Y,k_Z] \times r_S[r_M,r_L](\lambda) \times R(\lambda) \times \Phi(\lambda)\,d\lambda$$

Integrals are approximated by summation of 10 nm intervals. With a scaling convention, (weighting factors calculated as above, k_X, k_Y, k_Z) a bee-white colour with

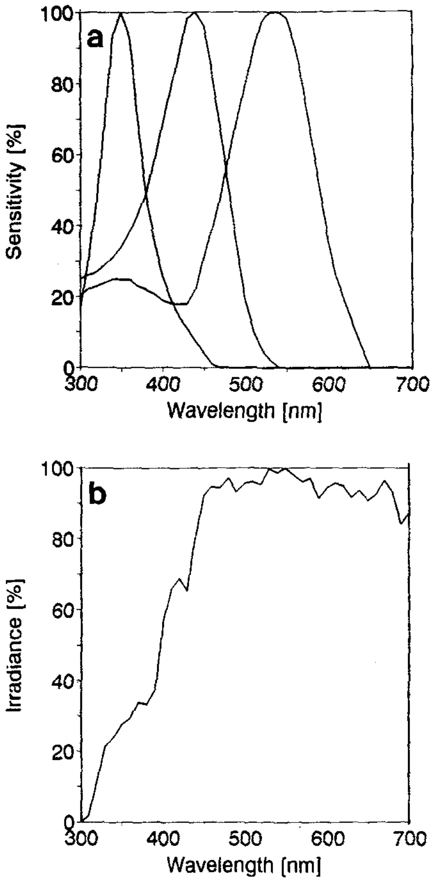

Figure 1. Fundamentals for the calculation of colour parameters as perceived by honeybees.
a) Relative spectral sensitivities of the three types of photoreceptors, as used for all calculations.
b) Spectral distribution of daylight based on 6500 K.

constant reflection in each wavelength interval can be considered to produce the same quantum catch in each receptor type. By means of

$$X'\,[Y',Z'] = \frac{X\,[Y,Z]}{X+Y+Z} \times 100\ (\%);$$

$$(X' + Y' + Z' = 100\%);$$

the coordinates for a two-dimensional plot of the colour triangle are obtained. From the position within the colour triangle the relative absorption of each receptor type can be read off. The three corners of the colour triangle represent colours which would each exclusively stimulate one of the three receptor types. These are the loci of 100% bee-yellow, 100% bee-blue, and 100% bee-ultraviolet. Straight lines from these loci to the neutral point intersect the opposite lines between two corners at loci which represent the complementary colours, bee-violet, bee-purple, and bee-blue-green, respectively[25]. The chromaticity diagram does not provide information about the intensity of flower colours.

The intensity of flower colours is calculated separately as the sum of the tristimulus values, and related to bee-white (100% reflection in the bee-visible spectrum). The dominant wavelength is calculated geometrically. A line from the neutral point to a colour locus is extrapolated to the intersection point with the spectral locus. The wavelength of the intersection point is the corresponding wavelength of the respective colour. The corresponding wavelength of bee-purple colours can be described by the distances of the intersection point to the ends of the bee-purple line. The length of the bee-purple line was defined as 1; the distance of the intersection point to the bee-yellow end of the bee-purple line was registered as the corresponding wavelength.

Colour purity is defined to be minimal (0%) at the neutral point and maximal (100%) at the spectral loci. The colour purity of colours is calculated as the distance from the neutral point to a colour locus, and related to the distance from the neutral point to a reference spectral locus. As a reference spectral colour, the spectral locus of the respective corresponding wavelength is used. The distance between two loci is defined as the euclidian distance measure. The colour purity thus describes the unsymmetrical quantum flux to the three photoreceptor types evoked by a particular light stimulus. The mathematical basis of the calculations has already been described in more detail[26].

The colour patterns of flowers visited by bees and hoverflies were examined and tested to find out whether the spatial arrangement of colours is a gradient of centripetally increasing colour purity fitting the innate orientation of *Bombus terrestris*. The colour parameters have been calculated for the honeybee worker, *Apis mellifera*. Other hymenopteran pollinators, particularly *Bombus terrestris*, have a very similar trichromatic vision system[9]. The reflection in the yellow waveband of floral guides was the parameter which correlated with the innate proboscis extension of *Eristalis tenax*.

Results

Native imagos of *Eristalis tenax* and *Bombus terrestris* respond to coloured artificial flowers, without previous training. Freshly emerged *Eristalis tenax* approached and landed only on yellow artificial flowers[3,4] (not tested in this investigation). After having settled on an artificial flower, they extended their proboscises towards spectral test stimuli (intensity: 10^{13} quanta $cm^{-2} s^{-1}$) in the yellow waveband from 520 nm to 600 nm. At high intensities, up to 80% of the hoverflies showed proboscis extension towards yellow test stimuli, whereas only 5% of the flies extended their proboscises towards spectral stimuli <520 nm, >600 nm, or towards non-illuminated screens (fig. 2).

From some distance away, the approach of *Bombus terrestris* to artificial flowers depended on the colour purity of the corolla colour (fig. 3a). At close range, they approached and antennated artificial guides of superior colour purity. The portion of antennations at the guide instead of at the margin of the artificial flowers depended on the colour purity difference between guide and corolla colour (fig. 3b).

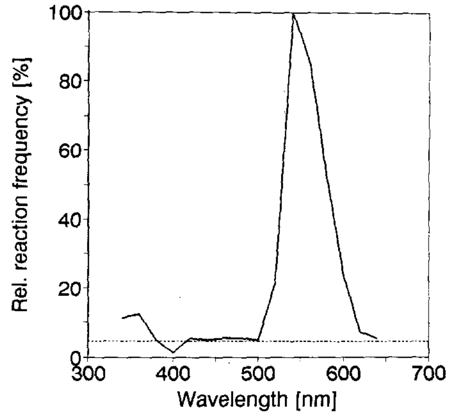

Figure 2. Spectral effeciency function of the innate proboscis extension of *Eristalis tenax* towards monochromatic light stimuli of 10^{13} quanta $cm^{-2} s^{-1}$. Altogether 1594 flies were tested, 5 times each.

The spectral reflection of the floral colour patterns of 76 angiosperm species was measured, and 198 spectral reflection curves were recorded. The pattern usually included three coloured areas: 1) the background (provided by the green leaves), 2) the main area covering the largest and, in the most cases, peripheral area (usually petals and corollas of flowers, bracts and ray florets of inflorescences), and 3) the guide area (usually anthers, pollen, and floral guides, or absent). Some species possess a flower colour pattern consisting of more than three colours. The colours are characterized by the parameters intensity, dominant wavelength, and colour purity as viewed through a honeybee's eyes. The spatial arrangement of colours and the colour parameters were analyzed with regard to the background, the main area, and the guide area.

The intensity of green leaf colours is lower than the intensity of corolla and guide colours (fig. 6). Interspecifically uniform intensity patterns were not found in the spatial arrangement of flower colour patterns.

The predominant wavelength of floral colours can be categorized according to the bee-colours defined by Daumer[28]. These bee-colours reflect the sensitivity ranges of the three photoreceptor types. Three main colours are considered (bee-UV, bee-blue, bee-yellow), and three complementary and mixed ones (bee-bluegreen, bee-purple, bee-violet) (figs 4 and 5). Green leaves are coloured bee-yellow due to the peak of reflection at about 550 nm (fig. 6).

The predominant wavelength of the main areas differed greatly between species. All bee-colours were found: bee-ultraviolet (1%), bee-violet (4%), bee-blue (14%), bee-bluegreen (38%), bee-yellow (29%), and bee-purple

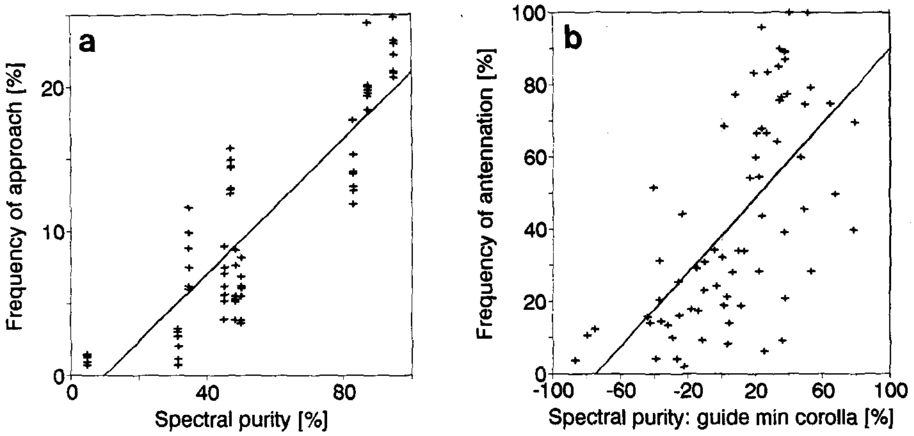

Figure 3. a) Distant approach of inexperienced *Bombus terrestris* towards artificial flowers as a function of the colour purity of the artificial corollas. 10 corolla colours were simultaneously tested in 7 tests. The overall number of approaches towards the 10 artificial flowers in each test is taken as 100%. Single measurements (+) and linear regression line ($r = 0.87$, $df = 68$, $p \ll 0.001$) represented. The corolla hues to humans from left to right are white, brown, light blue, yellow, purple, yellow, white, yellow, yellow, blue. The colours differed in the height of peak reflection and in the UV-reflection. 7262 approaches evaluated.

b) Antennation of guides in inexperienced *Bombus terrestris* as a function of the difference in colour purity between guide and corolla colours. 70 combinations of guide and corolla colours were tested in 7 experiments. For each colour combination, the frequency of antennation was calculated from the number of antennations at the guide per number of approaches towards the artificial flowers. Single measurements (+) and linear regression line ($r = 0.64$, $df = 68$, $p \ll 0.001$) represented. 7262 approaches evaluated.

(14%). Bee-ultraviolet corollas were detected only in *Papaver rhoeas* (Papaveraceae) and *Portulaca grandiflora* (Portulacaceae). Spectral reflection curves of typical corolla colours show that the change from low to high spectral reflection lies at about 400 nm and at about 500 nm, thus covering the wavebands of either one or two photoreceptor types (figs 4 and 6). Bee-black and bee-white main areas reflecting homogeneously throughout the UV and human-visible spectrum were not found among melittophilous flowers.

The colour of guides is more uniform among species than that of corollas. In most cases, the anthers and pollen displayed, as well as the floral guides, are bee-yellow (fig. 6) reflecting only in the yellow and absorbing strongly in the blue as well as in the ultraviolet range of wavelengths. Non-bee-yellow central areas were found in only few species. For example, *Digitalis purpurea* (Scrophulariaceae) has up to 20 bee-bluegreen guide areas of high colour purity, each encircling bee-blue dots of low colour purity (fig. 6). *Papaver rhoeas* has a two-coloured guide consisting of peripheral bee-white and central bee-black areas (fig. 6). *Portulaca grandiflora* has a similar bee-white guide which is also combined with an ultraviolet corolla. The heteromorphic species *Lythrum salicaria* (Lythraceae) displays bee-yellow as well as bee-bluegreen pollen depending on the stamen length.

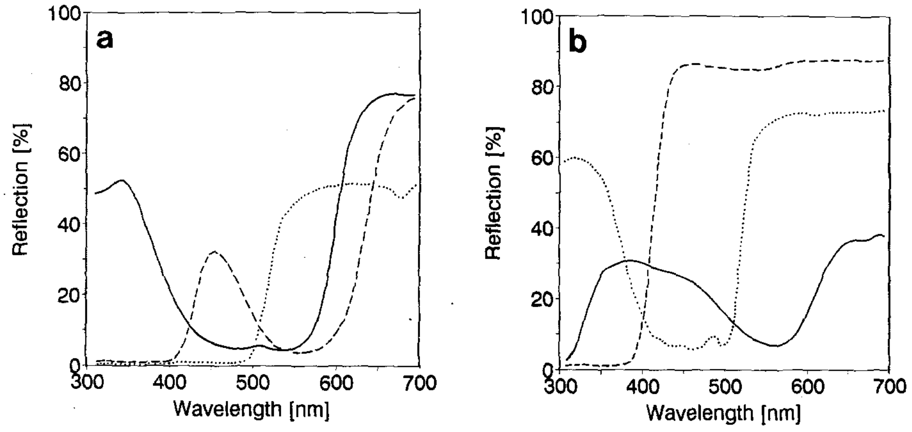

Figure 4. Spectral reflection of typical corolla colours of angiosperm flowers.
a) Main colours stimulating predominantly one photoreceptor type: *Portulaca grandiflora* (solid line), *Agrostemma githago* (broken line), *Lotus corniculatus* (dotted line).

b) Mixed colours stimulating predominantly two photoreceptor types: *Lythrum salicaria* (solid line), *Calystegia sepium* (broken line), *Hypericum perforatum* (dotted line). The same conventions are used in figures 6 and 9.

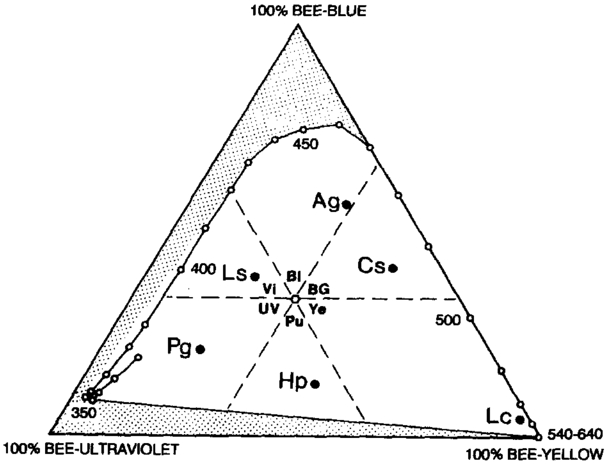

Figure 5. Colour triangle with loci of typical corolla colours of angiosperm flowers (see fig. 4): *Portulaca grandiflora* (Pg), *Agrostemma githago* (Ag), *Lotus corniculatus* (Lc), *Lythrum salicaria* (Ls), *Calystegia sepium* (Cs), *Hypericum perforatum* (Hp). The colour triangle is divided into 6 sections representing the bee-colours Bee-ultraviolet (UV), Bee-blue (Bl), Bee-yellow (Ye), Bee-violet (Vi), Bee-bluegreen (BG), Bee-purple (Pu). The neutral point (hexagon) representing a bee-white or bee-black colour is equidistant from each side of the colour triangle. Spectral loci are marked with open circles. The wavelengths of some spectral loci are indicated. For the representation of bee-purple colours, the spectral loci 350 nm and 540 nm are connected by a line. Only the white area of the colour triangle can theoretically be covered by colour loci. The same conventions ae used in figure 7.

The flower colour pattern of bumblebee-pollinated plants generally provides a gradient of centripetally increasing colour purity which consists of the colours of green leaves, with a mean colour purity amounting to 28.2% (n = 54), corollas (59.8%, n = 70), and anthers and pollen or floral guides (74.0%, n = 56). Among 70 angiosperm species out of 30 families I found only 7 exceptions in which there were inverse gradients.

The illustrations of spectral reflection curves (fig. 6), of the colour loci in the colour triangle (fig. 7), and of the UV-photos (fig. 8), are those of species showing typical or exceptional flower colour patterns. Flowers that are almost entirely yellow to humans exhibit small, but characteristic differences in the spectral reflection of various flower parts. In *Euphorbia polychroma* (Euphorbiaceae), the reflection in the yellow range of wavelengths increases from peripheral to central parts of the inflorescence. The corolla colours of *Narcissus pseudonarcissus* (Amaryllidaceae) and *Colutea arborescens* (Fabacae) show greater reflection in the blue and ultraviolet range than their guide colours. In addition, the wings of *C. arborescens* provide a colour of low colour purity. The spectral reflection of the wings is lower in the ultraviolet (fig. 8) and yellow range of wavelengths than that of the standard. In *Primula veris* (Primulaceae), the change from low to high reflection of the guide is shifted to longer wavelengths, in comparison to the corolla colour, making the guide colour more orange to humans. In many yellow flowers, several of these properties of reflection are combined, e.g. in *Helianthemum hirtum* (Cistaceae). The guide colours exhibit strong reflection in the yellow, and strong absorption in the ultraviolet and blue range of wavelengths. These reflection properties were found in corolla colours only, in cases where a guide is absent, as in *Lotus corniculatus* (Fabaceae) (fig. 4a). In the white flowers of *Nerium oleander*, the change from low to high reflection is shifted to shorter wavelengths in the corolla in comparison to the guide colour, generating a pattern in the UV (fig. 8). Both colours are white to humans and bee-bluegreen to honeybees. The corolla colour exhibits a lower colour purity to the honeybee. *Convolvulus tricolor* (Convolvulaceae) has three different corolla colours, bee-blue, bee-bluegreen, and bee-yellow which, to honeybees, are arranged in a gradient of colour purity. *Eichhornia crassipes* (Pontederiacea), and *Galeopsis speciosa* (Lamiaceae) also display three corolla colours against the green leaves.

Five species with other pollinators were treated for comparison. Two *Ornithogalum* species (Liliaceae) and *Yucca galuca* (Agavaceae), presumably pollinated by nocturnal moths, display white corollas which also reflect in the ultraviolet range of wavelengths (fig. 9a). Two red flowers, *Canna edulis* (Cannaceae) and *Lobelia cardinalis* (Lobeliaceae), which are pollinated by birds, absorb ultraviolet, blue, and yellow light (fig. 9b).

Discussion

The particular arrangement of floral visual colours in a colour purity gradient fits the innate orientation of bumblebees. Since asymmetrical input of the three types of photoreceptors generates colour purity, a colour exhibiting high colour purity has a spectral reflection curve that is not balanced with respect to the three photoreceptor sensitivity ranges of wavelength, the UV (300 nm–400 nm), blue (410 nm–480 nm), and yellow range (490 nm–640 nm), (the limits of these ranges take into consideration the spectral composition of daylight and the weighting factors k_X, k_Y, k_Z). One should keep in mind that the calculation of colour parameters presented in this paper ignores the neural processing of the stimuli. Thus, nothing is suggested about the perceptual dimensions of colour vision in insect pollinators[8,24]. Instead, I try to compare floral colours in terms of differences in the spectral reflection curves and consider the spectral input.

The low colour purity of green leaf colours can be read from the spectral reflection curves (fig. 6). Green leaves homogeneously reflect in the ultraviolet and blue, and peak only weakly in the yellow range of wavelengths. This reflection pattern generates a bee-yellow colour of low colour saturation. The peaks of spectral reflection curves of corolla and guide colours are always higher. In most flowers, the colour purity of the guide area surpasses that of the main area. As can be checked in the chromaticity diagram, the colour loci of guide

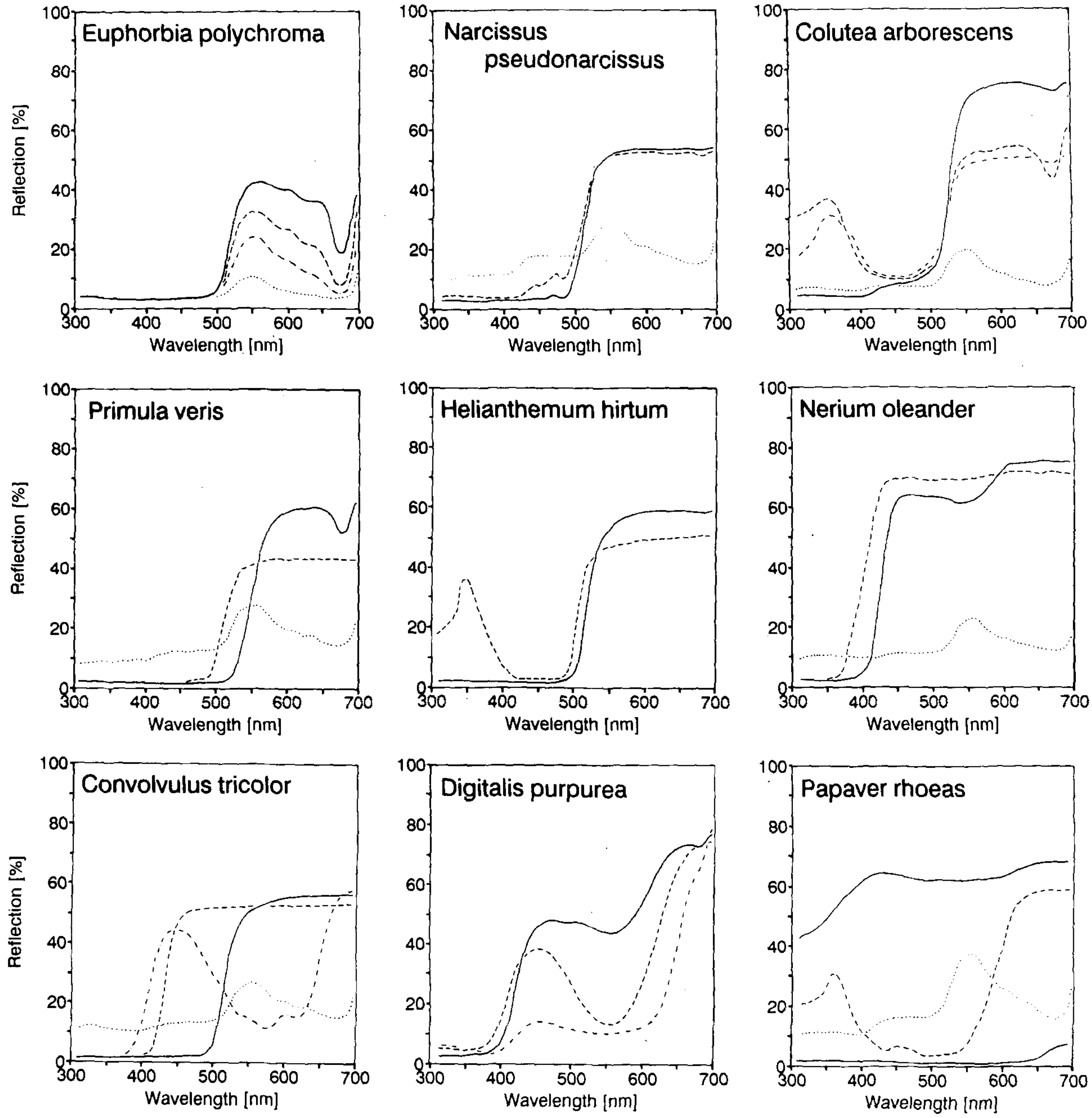

Figure 6. Spectral reflection of floral colour patterns in *Euphorbia polychroma, Narcissus pseudonarcissus, Colutea arborescens, Primula veris, Helianthemum hirtum, Nerium oleander, Convolvulus tricolor, Digitalis purpurea, Papaver rhoeas*. Dotted line: green leaves; broken line: main areas of flowers or inflorescences; broken and dotted line: intermediate areas of flowers or inflorescences; solid line: guide areas of flowers of inflorescences.

area colours are closer to the spectral line than the colour loci of main area colours (fig. 7). If one compares the spectral reflection curves of main area and guide area colours, which differ only in one or a few respects (fig. 6), the mechanisms that contribute to the enhancement of bee-subjective colour saturation of guide colours are revealed. By artificially generating spectral reflection curves, which differ only in one particular respect, it was demonstrated how each of these differences in the spectral reflection affects colour purity in such a way that the colour purity of guide colours surpasses that of corolla colours[26].

Those mulitcoloured flowers which provide three corolla colours against the background of green leaves, i.e. *Convolvulus tricolor*, *Galeopsis speciosa*, and *Eichhornia crassipes*, are most impressive. *Colutea arborescens* also displays different colours in the wings, the standard and the guide area of the standard, with colour purity increasing in this order (fig. 8). In these cases, the colour purity gradient includes 4 colours and

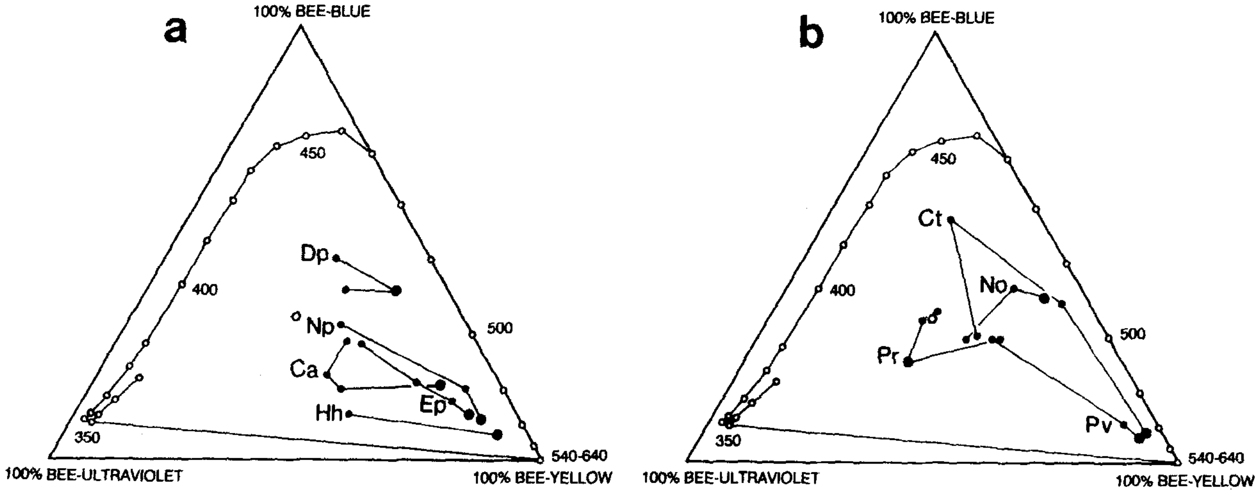

Figure 7. Colour triangle with loci of colour patterns of angiosperm flowers (see fig. 6). The colour loci of each species are connected by a line in the order of spatial arrangement. The colour of highest colour purity in each species is indicated by a larger dot.

a) *Colutea arborescens* (Ca), *Digitalis purpurea* (Dp), *Euphorbia polychroma* (Ep), *Helianthemum hirtum* (Hh), *Narcissus pseudonarcissus* (Np).
b) *Convolvulus tricolor* (Ct), *Nerium oleander* (No), *Papaver rhoeas* (Pr), *Primula veris* (Pv).

represents only one of 24 possible ways of arranging these colours.

When the colours of main and guide areas of flowers and inflorescences are compared, some common characteristics are found: the central parts of colour patterns are mostly bee-yellow and absorb a large amount of ultraviolet and blue light[27]. Main areas reflect less uniformly. Hoverfly-visited plants may benefit from yellow, UV-absorbing pollen and similarly coloured floral guides. Hoverflies of the genus *Eristalis* extend their proboscises only towards yellow areas and cannot even be trained to respond to other colours in this way[4,20].

The suggested phylogeny of flower colour patterns is interesting in this context[28,29]. It has been argued that the primary yellow and UV-absorbing colour of anthers and pollen was due to the presence of flavonoid pigments, whose original function was to absorb mutagenic ultraviolet radiation. This pollen colour initially had no signalling function, as can be demonstrated by the predominance of yellow pollen in wind-pollinated species, but it later acquired one. When, in the course of evolution, anthers began to be concealed in floral tubes, as in many nectar-producing angiosperms, floral guides often replaced the signalling function of pollen. During

Figure 8. UV-photos (right) and black-and-white-photos (left) of a) *Colutea arborescens* and b) *Nerium oleander*.

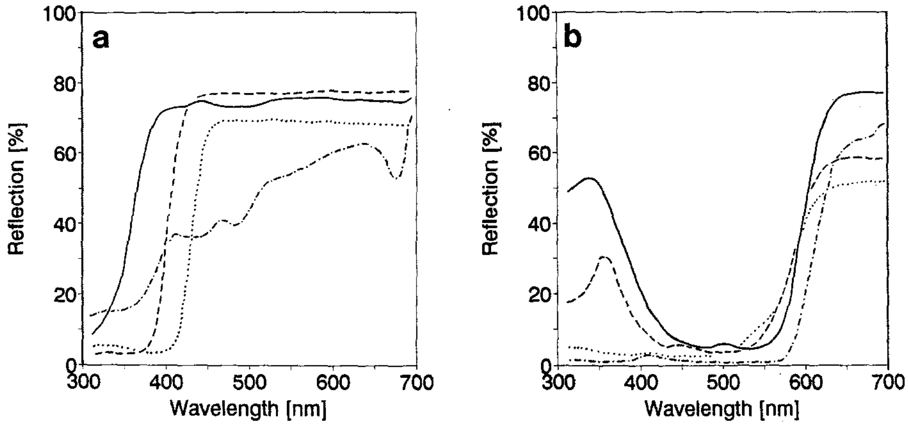

Figure 9. a) Spectral reflection curves of floral colours which would appear white to humans, *Ornithogalum nutans* (solid line), *Galanthus nivalis* (broken line), *Narzissus tazetta* (dotted line), and *Yucca glauca* (broken and dotted line).

b) Spectral reflection curves of floral colours which would appear red to humans, *Portulaca grandiflora* (solid line), *Papaver rhoeas* (broken line), *Canna edulis* (dotted line), *Lobelia cardinalis* (broken and dotted line).

the historical transition stage, when anthers as well as automimetic guides operated simultaneously as signals, there may have been pollinators which responded to the yellow colour. Plants thus evolved guide colours with yellow reflection as a key signal. When some species then switched to pollinators that responded to colour purity as a key stimulus, the yellow guide colour was retained, and its colour purity improved. Furthermore, plant species combining superior colour purity of the guide colour with bee-yellow colouration of the guide can direct non-related pollinating species, such as bees and hoverflies, towards the rewarding site.

The reflection properties of bee-yellow guide colours, characterized by strong reflection in the yellow, and strong absorption in the ultraviolet and blue range of wavelengths, are found in corolla colours only if a guide is absent, as in *Lotus corniculatus*. To a naive bumblebee, this species would be expected to be more attractive from a distance. It cannot, however, guide the flower-visitor at close range by means of colour cues.

Various colour patterns of flowers are associated with uniform UV-patterns: central floral parts, such as anthers, pollen, and guides absorb ultraviolet light, whereas peripheral floral parts reflect it[25, 30–36]. This characteristic UV-pattern has been termed a 'bull's-eye'"[37]. The absorption of large amounts of ultraviolet light by central flower parts is shown to be associated with a common mechanism for enhancing colour purity[26]. Other selective forces may influence the UV-pattern of flowers; for example, flowers often contrast with their natural background (leaves, soil etc.) in the UV range[36, 38].

Walking honeybees show innate proboscidial reactions when they pass from a UV-reflecting to a UV-absorbing flower part[25]. The behaviour is triggered even if no UV-pattern is offered, therefore the stimulus releasing proboscidial reactions cannot be the UV contrast. I suggest that the borderline between two colours exhibiting low and high colour purity is the key stimulus. However, experimental evidence has not yet been gathered.

Some species exhibit exceptional floral colour patterns. A combination of bee-ultraviolet corollas and bee-black or alternatively bee-white floral guides was found in *Papaver rhoeas* and *Portulaca grandiflora*. The guide colours exhibit very low colour purity. The significance of this colour pattern is not known. *Digitalis purpurea* flowers display dark violet and white-bordered dots. The white areas possess a colour purity exceeding that of the violet corolla, whereas the dark violet dots exhibit a low colour purity. Guide areas of highest colour purity are frequently associated with black or reddish dots and lines which would be expected to appear unsaturated to bees. The species investigated, *Colutea arborescens*, *Mimulus guttatus*, *Iris pseudacorus*, and *Catalpa bignonioides*, for example, exhibit dot or line markings of obviously low colour purity in the spatial proximity of guides. I suggest that these dark markings may improve the perception of the colour contrast, but do not have a particular function as a key signal in themselves.

Bee-white flowers will have little attraction for bumblebees due to the low colour purity correlated with the bee-white colour. Human-white flowers absorb great amounts of ultraviolet light[25], and thus would appear saturated bee-bluegreen to a bee. *Nerium oleander* (Apocynaceae) is completely white to humans (figs 6 and 8). Small differences in the amount of reflection in the ultraviolet range result in a lower colour purity of the corolla as compared to the guide colour. While diurnal bees largely ignore brightness cues of flower colours, nocturnal flower-visitors may use brightness as their chief orientation cue. White flowers reflecting ultraviolet light were found in *Ornithogalum* species and in *Yucca glauca*, which may be pollinated by nocturnal flower-visitors.

An analogous phenomenon occurs with flowers which would appear red to humans. However, the bee-pollinated *Portulaca grandiflora* and *Papaver rhoeas* reflect ultraviolet light and thus would appear saturated and bee-ultraviolet to a bee. The bird-pollinated *Canna edulis* and *Lobelia cardinalis* absorb ultraviolet, blue, and yellow light and thus would appear unsaturated, bee-black to honeybees. Flower-visiting birds, e.g. humming-birds, are known to be sensitive to ultraviolet and red light[39–41]. To them, the latter flowers would appear bird-red.

The diversity of floral colours and their great saturation was already noted by Exner and Exner[42], who speculated about their possible significance in the flower-recognition of pollinators.

Daumer[25] analysed flower colours as viewed through a bee's eyes. His results on the bee-subjective colour saturation of green leaves, and of corolla and pollen colours, broadly agree with the findings in the present study. However, Daumer discussed only the great diversity of bee-hues of corollas with respect to learned flower discrimination. The spectral reflection properties of flowers are also well attuned to the honeybees' colour discrimination abilities[8,19]. Brightness patterns of flowers are obviously not used by honeybees and bumblebees. It is known that honeybees largely ignore brightness cues in discriminating between coloured artificial flowers, if differences in chromaticity exist[8,24], and that bumblebees behave likewise in innate flower detection[12].

If the flower colour pattern served only to assist discrimination learning in pollinators, a greater diversity of colour patterns would be expected than is actually found. The uniformity with respect to colour purity gradients, and to some degree guide colours, in all likelihood provides a second, independent signal pattern. The behavioural data suggest that these interspecifically uniform colour signals provide the flower-visitors with keys for the innate detection of flowers and for the location of the site of reward.

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1 Sprengel, C. K., Das entdeckte Geheimnis der Natur im Bau und in der Befruchtung der Blumen. Viehweg, Berlin 1793. Reprint Cramer, Lehre 1972.
2 von Frisch, K., Zool. Jb. Physiol. Tiere *35* (1915) 1.
3 Ilse, D., Nature *163* (1949) 255.
4 Lunau, K., Zool. Jb. Physiol. *92* (1988) 487.
5 Heinrich, B., Ecol. Monogr. *46* (1976) 105.
6 Heinrich, B., Ecology *60* (1979) 245.
7 Haslett, J. R., Oecologia *78* (1989) 433.
8 Chittka, L., and Menzel, R., J. comp. Physiol. A *171* (1992) 171.
9 Peitsch, D., Fietz, A., Hertel, H., de Souza, J., Ventura, D. F., and Menzel, R., J. comp. Physiol. A *170* (1992) 23.
10 Waser, N. M., Am. Nat. *127* (1988) 593.
11 Lunau, K., Eur. J. Neurosci., Suppl. *5* (1992) 103.
12 Lunau, K., J. comp. Physiol. A *166* (1990) 827.
13 Lunau, K., Ethology *88* (1991) 203.
14 Lunau, K., Can. J. Zool. *70* (1992) 2139.
15 Lunau, K., Biol. unserer Zeit *23* (1993) 48.
16 Menzel, R., Z. vergl. Physiol. *56* (1967) 22.
17 von Helversen, O., J. comp. Physiol. *80* (1972) 439.
18 Schnetter, B., Vergleichende Untersuchungen zum Lernverhalten der Bienen und Hummeln unter besonderer Berücksichtigung ihrer Blütenstetigkeit. Diss. Univ. Würzburg, 1979.
19 Menzel, R., and Smida, A., Biol. Rev. *68* (1993) 81.
20 Wacht, S., and Lunau, K., Proc. German zool. Soc. *86* (1993) 275.
21 Henderson, S. T., Daylight and its spectrum. Adam Hilger Ltd., London 1970.
22 Neumeyer, C., J. comp. Physiol. *139* (1980) 165.
23 Backhaus, W., and Menzel, R., Biol. Cybern. *55* (1987) 321.
24 Backhaus, W., Neurosci. biobehav. Rev. *16* (1990) 1.
25 Daumer, K., Z. vergl. Physiol. *41* (1958) 49.
26 Lunau, K., Pl. Syst. Evol. *183* (1992) 51.
27 Kevan, P. G., in: Handbook of Experimental Pollination Biology: Floral colors through the insect eye: what they are and what they mean, p.3. Eds C. E. Jones and R. J. Little. Van Nostrand Reinold, New York 1983.
28 Osche, G., Biol. unserer Zeit *9* (1979) 161.
29 Osche, G., Ber. dt. bot. Ges. *96* (1983) 1.
30 Kugler, H., Planta *59* (1963) 296.
31 Kugler, H., Ber. dt. bot. Ges. *79* (1966) 57.
32 Guldberg, L. D., and Atsatt, P. R., Am. Midl. Nat. *93* (1975) 35.
33 Horovitz, A., and Cohen, Y., Am. J. Bot. *59* (1972) 706.
34 Ornduff, R., and Mosquin, T., Can. J. Bot. *48* (1970) 603.
35 Utech, F. H., and Kawano, S., Bot. Mag., Tokyo *88* (1975) 9.
36 Rosen, D., and Barthlott, W., Decheniana *144* (1991) 72.
37 Silberglied, R. E., A. Rev. ecol. Syst. *10* (1979) 373.
38 Menzel, R., Farbensehen blütenbesuchender Insekten, p. 1. Ed. Internationales Büro der Kernforschungsanlage Jülich GmbH, Jülich 1987.
39 Huth, H. H., and Burkhardt, D., Naturwissenschaffen *59* (1972) 650.
40 Goldsmith, T. H., Science *207*, (1980) 786.
41 Goldsmith, T. H., and Goldsmith, K. M., J. comp. Physiol. *130* (1979) 209.
42 Exner, F., and Exner, S., Sber. Akad. Wiss. Wien, math.-naturw. Kl. *119*, Abt. 1 (1919) 1.