

**BEE COLOR VISION IS OPTIMAL FOR CODING FLOWER COLOR, BUT FLOWER COLORS ARE NOT OPTIMAL FOR BEING CODED—WHY?**

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Model calculations are used to determine an optimal color coding system for identifying flower colors, and to see whether flower colors are well suited for being encoded. It is shown that the trichromatic color vision of bees comprises UV, blue, and green receptors whose wavelength positions are optimal for identifying flower colors. But did flower colors actually drive the evolution of bee color vision? A phylogenetic analysis reveals that UV, blue, and green receptors were probably present in the ancestors of crustaceans and insects 570 million years ago, and thus predate the evolution of flower color by at least 400 million years. In what ways did flower colors adapt to insect color vision? The variability of flower color is subject to constraint. Flowers are clustered in the bee color space (probably because of biochemical constraints), and different plant families differ strongly in their variation of color (which points to phylogenetic constraint). However, flower colors occupy areas of color space that are significantly different from those occupied by common background materials, such as green foliage. Finally, models are developed to test whether the colors of flowers of sympatric and simultaneously blooming species diverge or converge to a higher degree than expected by chance. Such effects are indeed found in some habitats.

**INTRODUCTION**

The question of how biological colors and their receivers, the color vision systems of animals, influence each other's evolution is currently subject to much debate. The evolution of color signals is driven by the sensory and perceptual capacities, learning abilities, and innate biases of the animals that receive them, as well as other signals (and their meaning) present in the same community. The signals may in turn influence the evolution of their receivers. This mutual influence is shaped by the light habitat in which it takes place, as well as by the design principles involved in generating and analyzing signals. The optimization of information transfer throughout evolution is also dependent on genetic variability for the respective traits (Lythgoe, 1979; Lythgoe and Partridge, 1989; Goldsmith, 1990; Chittka and Menzel, 1992; Endler, 1993; Menzel and Shmida, 1993; Shaw, 1995; Chittka, 1996a,b).

Flowers are a class of biological objects whose vari-

ety in color is outstanding. With an estimated 350,000 species, the producers of these signals, the angiosperm plants, are the most successful division of land plants, and the vast majority of them rely on animals as pollen vectors (e.g., 80% in central Europe; Gottsberger, 1989). The large variety of signals used to advertise to pollinators has been implicated in facilitating efficient and directed pollen transfer (Heinrich, 1975; Waser and Price, 1983; Menzel and Shmida, 1993), but also as isolating mechanisms, in speciation processes and maintenance of plant species integrity (Grant, 1949; Jones, 1978; Gottsberger, 1989; but see Chittka and Waser, 1997, this issue). Floral color signals have been assumed to influence the evolution of their receivers, i.e., the color vision systems of flower-visiting animals (Chittka and Menzel, 1992). This supposition is not unlikely, since the economies of many members of several insect orders, such as the Hymenoptera, Diptera, Lepi-

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doptera, and Coleoptera are almost exclusively based on floral resources (Kevan and Baker, 1983; Neff and Simpson, 1993).

Bees are the most diverse and abundant group of insect pollinators (20,000–30,000 species; Neff and Simpson, 1993). They are also the most efficient pollinators for the majority of animal-pollinated plants, and should thus have a fundamental impact on the diversity of flower signals, including their colors (Heinrich, 1975; Kevan and Baker, 1983; Chittka and Menzel, 1992; Menzel and Shmida, 1993). Consequently, this review will focus on floral colors as seen through the bees' eyes.

I review evidence that both flower colors and color receptor wavelength positions are variable traits with the potential to be optimized throughout evolution. Model calculations are used to determine whether bee color vision is optimal for coding flower colors, and whether flower colors are optimal for being encoded. By coding I mean the assignment of a perceptual state (as illustrated by a point in color space) to a floral color stimulus. To be adequate for coding stimuli of a given class, the system must be designed so as to assign different codes to different stimuli; to be optimal, different *physical* signals should be maximally distinguishable by means of their *perceptual* codes. For example, consider two flowers which are equally yellow, but differ in their reflectance of UV. The human color vision system is not optimal for coding these colors, because it assigns the same code (a perception of "yellowness") to two species whose flowers have different physical reflectance properties.

Finally, a phylogenetic analysis is presented to search for the evolutionary origins of bee color receptor sets.

#### HOW VARIABLE IS FLOWER COLOR?

Flower colors result from selective absorption of the ambient light by the tissues of floral petals, and its reflection at cellular particles. The coloration is achieved through pigments of only a few chemical classes, the anthocyanins, flavonoids, carotenoids, betalaines, and chlorophylls; however, all of these classes comprise a large variety of different pigments (Scogin, 1983). Combinations of different pigments are also frequent; e.g., flavonoles, metal ions, and carbohydrates can serve as co-pigments of anthocyanins, thus altering their colors (Gottsberger and Gottlieb, 1981; Scogin, 1983). Different pigments in the same petal can be distributed in separate cells, and these in turn can be located in different arrangements, generating additive or subtractive color mixtures. In purple tulips, red and blue

colored cells are tightly intermixed in the epidermis to form an additive mixture whose components become apparent only under the microscope (Exner and Exner, 1910). The black color at the base of the petals of the red poppy is generated by means of a subtractive mixture of red and blue layers on top of each other (Exner and Exner, 1910). White coloration is not only generated through pigments, but often by means of anatomical structures such as air-filled intracellulars, or starch grains at which total reflection takes place.

This introduction might leave the reader with the impression that floral color is a completely free variable, with literally no constraints for the individual species to generate any color that may be adaptive in a given context. However, as there are different classes of pigments, there are distinct types of floral reflectance (Chittka et al., 1994), and some plant taxa may have a very limited potential to vary color (Gottsberger and Gottlieb, 1981; Menzel and Shmida, 1993). To assess the general limitations of floral coloration, the spectral reflectance functions of 1063 different petal colors were measured (see Chittka and Menzel, 1992; Menzel and Shmida, 1993; Chittka, 1996b for detailed explanations of methods and conversion of spectral reflectance functions into loci in bee color space.)

Are flower colors equally distributed in the color space of a bee? Particularly, can all angular positions (hues) in bee color space be produced with equal probability? Or are certain parts of the color space covered more densely with floral color loci than others? Do the color loci form clusters and leave other areas of the color space empty? Answering these questions is essential to assess the evolutionary potential that plants have in varying their color signals.

In Fig. 1, the loci of 1063 flower colors are depicted in the color hexagon. There is a large empty area between the spectrum locus and the area covered by floral color loci. Colors of such purity can only be generated by self-luminant monochromatic lights and interference colors, but not by broadband reflection spectra. Furthermore, the color loci are not evenly distributed over the area that contains flower colors. To assess whether certain hues are more frequent than others in the bees' color perception, we laid a radial grid of 10° sectors (Fig. 1, inset) over the distribution of color loci shown in Fig. 1 (left). 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 color loci within each sector is counted (Fig. 2).

There are no 10° sectors without any color loci, and thus plants, as a group, can generate all possible bee hues. However, the floral color loci are strongly clus-

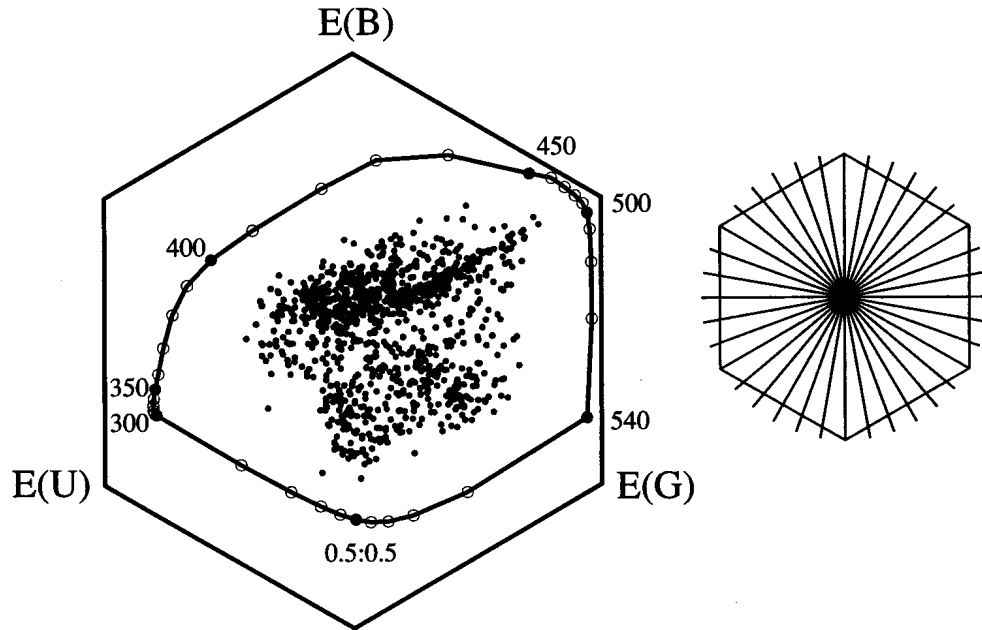


Fig. 1. The loci of all 1063 measured flower colors are plotted in the color hexagon (left). A locus in color space is determined by the photoreceptor signals from the bees' UV, blue, and green receptors produced by a given colored object (for details see Chittka, 1996b). For example, if an object color stimulates the blue receptor strongly, but not the UV and green receptors, its color locus will be in the upper central part of the color hexagon (and thus appear bee-blue). If only the green receptor is strongly stimulated, the color locus will appear in the lower right corner (and thus be perceived as bee-green), and if both the blue and green receptors, but not the UV receptor is stimulated, the locus will be in the upper right corner (bee-blue-green), and so forth. If all three color receptor signals are equal, the color will appear as achromatic (black, white, and gray in human color perception). The hexagonal space is designed so that distances between two color loci can be used to predict how similar the two colors will appear to a bee. If the distance is large (such as between two colors in two opposite corners of the hexagon) the colors will be well distinguishable; if the distance is small, the two colors may be confused. The spectrum locus (solid line) connects the loci of monochromatic lights (lights that contain only a single wavelength). Together with the UV-green mixture line (the curved bottom segment of the spectrum locus), it marks the border of the color space outside which no color loci can be obtained. This is because monochromatic lights have the potential to stimulate one receptor strongly, while minimally stimulating the other two, despite their overlap in spectral sensitivity. Thus, monochromatic lights produce color loci which are maximally distant from the uncolored point (the center of color space). Inset: (right) To see whether there is any regularity in the way the points are arranged in color space, a radial grid of  $10^\circ$  sectors is "laid over" the distribution of floral color loci. The number of color loci within each area of this grid is counted, and plotted in Fig. 2.

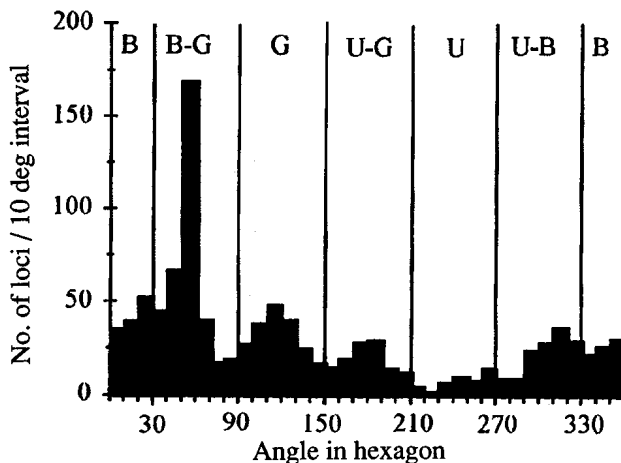


Fig. 2. Floral hues are clustered in the color hexagon. The number of color loci within each  $10^\circ$  sector (Fig. 1) is plotted over the middle angle of each sector.  $0^\circ$  marks the 12:00 angle in the color hexagon. Most flower color loci occur between  $50^\circ$  and  $60^\circ$  (blue-green flowers); the fewest between  $220^\circ$  and  $230^\circ$ .

tered in the color hexagon. The clusters appear at approximately regular angular intervals of  $60^\circ$ . The four most prominent peaks occur at approximately  $60^\circ$ ,  $120^\circ$ ,  $180^\circ$ , and  $310^\circ$ ; minima in the distribution are located at around  $30^\circ$ ,  $90^\circ$ ,  $150^\circ$ ,  $210^\circ$ ,  $270^\circ$ , and  $330^\circ$ , although some of these are not very pronounced.

In a world where the flower color of each species is optimally distinguishable from that of other species in a given environment, flower color would have to be a free evolutionary variable. Each species should have a potential to generate flower colors in all possible areas of color space. In such a world, there should be an equal probability to find flower colors in all possible areas of color space. This is not the case. There are hardly any pure UV colors, even though these are readily learned by bees (Menzel, 1967). The numbers of color loci in the six color categories differ significantly from random ( $\chi^2 = 153$ ,  $df = 5$ ,  $p < 0.0001$ ). Additionally, the loci are not distributed evenly across the sectors, but instead are clustered. These phenomena cannot be explained by means of the selective pressure on discriminability, because this pressure should lead to equal spacing of color loci. Alternatively, aggregations of flower colors in some parts of color space might be explained by better memorability or innate biases of insects towards certain colors. However, empirical studies contradict this hypothesis. For example, honeybees prefer UV-blue and blue colors over blue-green colors, which is reflected in the choices of naive bees (Giurfa et al., 1995) as well as the learning performance of seasoned foragers (Menzel, 1967). On the insects' side, this may be an adaptation to the reliability with which these colors are predictors of a high nectar reward (Giurfa et al., 1995), but flowers, as a whole, do not appear to be adapted to the preferences of these insects: blue-green flowers outnumber blue and UV-blue flowers by far (Chittka et al., 1994), even among the bee-visited flowers (Waser et al., 1996). The observed distribution thus provides strong hints for evolutionary constraints on the coloration of flowers, presumably caused by the ways in which different pigments can be combined to form a floral color. It is likely that the minima in the hue distribution, at least the more prominent ones, correspond to boundaries between pigment classes (Chittka et al., 1994).

#### EVOLUTIONARY CONSTRAINTS ON FLOWER COLOR IN DIFFERENT PLANT FAMILIES

The potential to vary a color signal in the individual species is clearly different in species with different evolutionary histories. A prerequisite of any evolutionary change is the existence of genetic variability within the species. Direct evidence for this variability is often diffi-

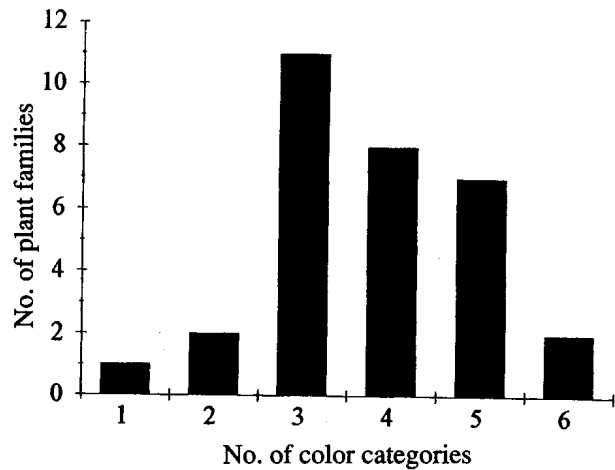


Fig. 3. Variability of flower color in 31 plant families. Families are categorized according to how many of the color categories, UV, UV-blue, blue, blue-green, green, and UV-green, they address. Families within each of these categories are counted.

cult to obtain, but some potential approaches have not been used to date. For example, the flowers of many species undergo ontogenetic color changes during their blooming time (Weiss, 1995), which is clear evidence that a species can vary color. Moreover, many plants produce fruits that differ in coloration from their flowers (Chittka, unpublished measurements), which indicates that a plant species *can* generate different color signals when addressing different visual systems. In these cases, the genetic codes for different colored pigments clearly exist in single species; all that needs to be changed to alter flower color is regulatory machinery to express these genes at the right time during ontogeny. Finally, plant growers have cultivated an amazing variety of color morphs out of many plant species, which indicates that when selective pressures are strong enough, flower color might be subject to rapid evolutionary change in these species.

An approach with limited predictive power to assess the upper limits of variability is to evaluate color variation in a set of closely related species. This approach works only in one direction: if we observe that species of the set have different color signals, this does not imply that each species has the genetic potential to vary color. If, on the other hand, all members of the set have the same color, this is, with some probability, a result of phylogenetic constraint. Even this conclusion is not without complications: limited variability may also reflect stabilizing selection. If, for example, all members of a taxon are most efficiently pollinated by an animal with an innate preference for blue, then "being blue" is adaptive, and not a result of constraint.

I measured color diversity in those 31 plant families

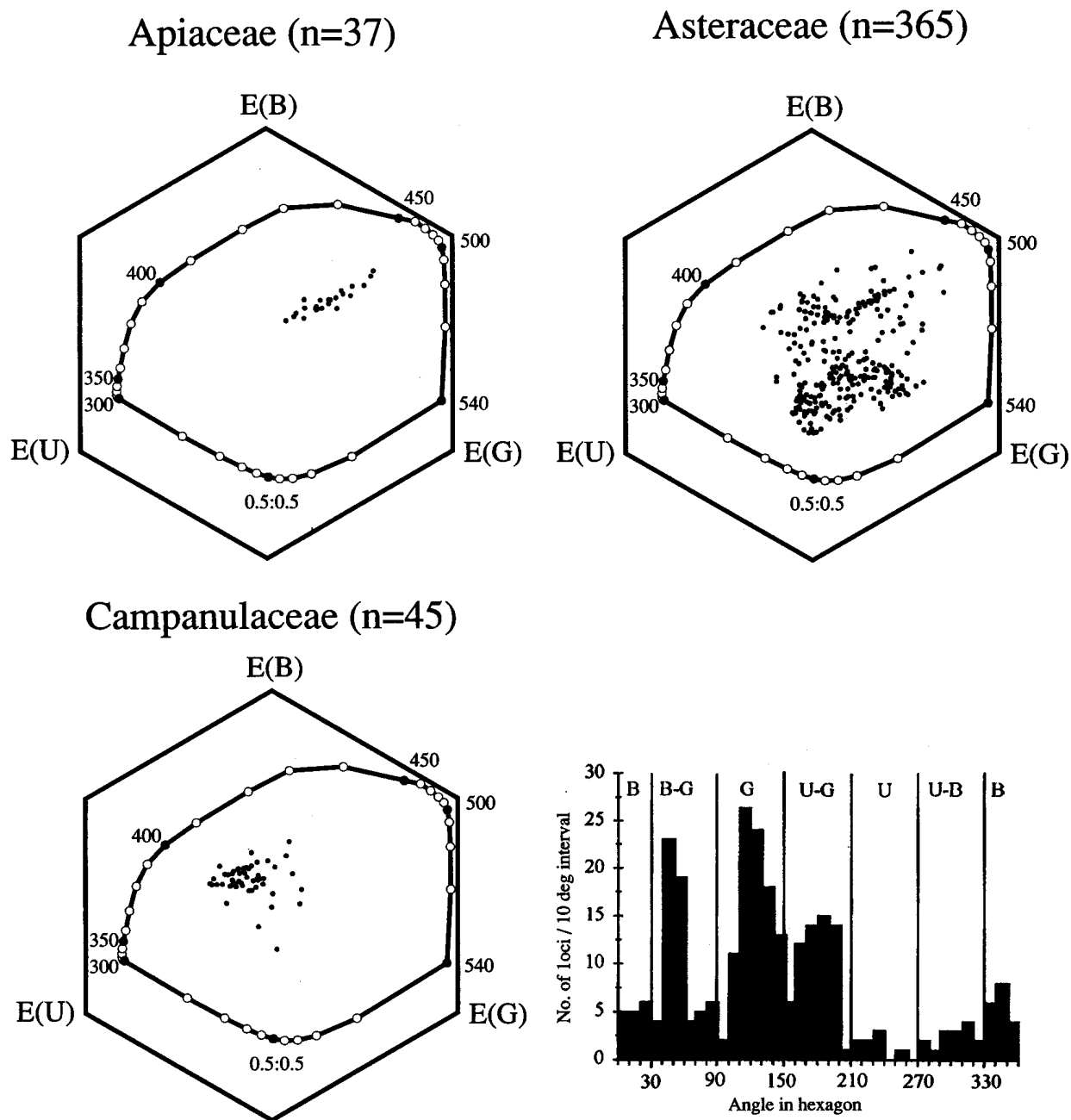


Fig. 4. Variability of flower color for three selected plant families. Distributions of color loci are calculated for 3 families which differ in variability. Values behind family names denote the number of measurements. The lower right figure shows the hue clustering for the Asteraceae; further explanations see Fig. 2.

for which spectral measurements of more than 15 species were available. To assess signal variability in different plant systematic groups, the number of 60° sectors of the color hexagon (operational color categories; Chittka et al., 1994) covered by each family was measured.

Color variability differs strongly among families.

Families whose members produce loci in only a single color category are rare, as are those with color loci in all categories. Most families cover an intermediate range of about half the bee color space (3–4 color categories). Figure 4 shows the color loci generated by three different plant families: one with a large color diversity, the Asteraceae; one with a low diversity, the Apiaceae; and

one which represents the more typical intermediate case, the Campanulaceae.

The Apiaceae are an example of a family with little variation in color. All of the flowers measured were white for humans, and blue-green for bees because they absorb UV. These flowers cover only a very small range of angles in the hexagon; thus they will differ little in hue. The flowers differ only in terms of their distance to the uncolored point, the center of color space. The Campanulaceae are also mostly aggregated in a small area of color space (the UV-blue category), but some loci scatter into adjacent categories. This is a type of distribution one frequently finds in families with limited color variability: most colors accumulate in a small area, with some outliers. The Asteraceae are a family whose members scatter across all 6 color categories. However, even here variability is not without limits. The distribution of color loci is significantly different from the non-Asteraceous data in the *all flower distribution* in Fig. 1 ( $p < 0.001$ , using a chi-squared goodness-of-fit test commonly used to measure associations of plants in space; for details see Krebs, 1978, p. 378). It thus appears that the probability that the Asteraceae generate certain hues throughout evolution is different from random in different parts of color space. Furthermore, as in the *all flower distribution* (Figs. 1,2), the color loci are strongly clustered in color space (Fig. 4, lower right), indicating further constraints on color variability. Again, minima between clusters presumably occur at the boundary between pigment classes. Peaks occur approximately in the center of each of the color categories.

#### FLOWERS AND LEAVES ARE SEPARATED IN BEE COLOR SPACE

An insect that searches a green meadow for flowers 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 significantly exceed the noisy fluctuations of the background signals. However, the responses from the different color receptor types may not be considered in isolation, because the differences in different photoreceptor types may cancel each other in a color opponent system. The detectability of a signal is a function of two parameters: (a) the perceptual color difference of this signal to the background; and (b) the "green contrast", i.e., the difference in signals gener-

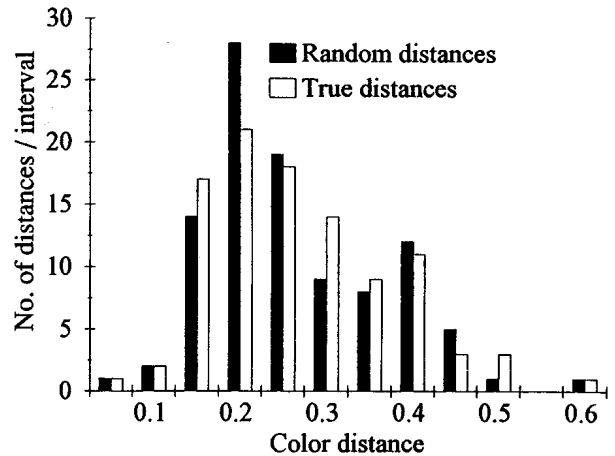


Fig. 5. Color distance distribution of 100 flowers against leaves of their own species (white columns) vs. the color distance distribution of the same 100 flowers against one of the sets of randomly picked leaves (black columns). Distances between colors are calculated in the color hexagon and counted in distance intervals each 0.05 units wide.

ated in the bees' long wave receptor by both background and target (Giurfa et al., 1996). The role of green contrast in a large sample of flower species is currently being analyzed (Menzel et al., 1997, this issue). Here I focus on the role of *color difference* between flowers and backdrops.

For the majority of flowers, green foliage will constitute the prevalent background. The reflection of leaves is low across the whole spectrum. Leaves appear comparatively achromatic for bees (Daumer, 1958; Lythgoe, 1979; Kevan, 1983; Chittka et al., 1994); they look colored to humans because they absorb *relatively* more light in the red domain of the spectrum than in the green. Thus, the human red-green color opponent channel will yield a signal more on the "green side" of its dynamic range.

Are flowers suited to contrast against green foliage, so as to enhance detectability? The difference between the distributions of leaf and flower color loci is significant ( $p < 0.001$ , chi-squared goodness-of-fit test, Krebs, 1978, p. 378). Thus, flower colors as a whole are indeed adapted to be conspicuous on a green foliage backdrop. A flower that stands out against green foliage can be predicted to be equally conspicuous against brown leaves, gray stones, and other inorganic backgrounds in most cases because such backgrounds aggregate in the same area of the bee color space as leaves do (Chittka et al., 1994). Are flowers specifically adapted to contrast against the leaves of their own species? Even though leaves scatter mostly across a small area of color space

(Chittka et al., 1994), there is some variability, and so one might expect that for different leaf hues, different floral hues are favored. I picked a random sample of 100 flower species, and calculated the color distance of each of their flowers against the leaves of the same species. The distribution of color distances obtained is shown in Fig. 5. I then assigned a *random* leaf color to each flower, and calculated the color distances between flowers and leaves. This procedure was repeated with 100 random combinations of the same set of flowers and leaves. The pooled color distance distribution from all random sets was not significantly different from the distribution of color distances of flowers to “their own” leaves (chi-squared goodness-of-fit test;  $\chi^2 = 12.4$ ,  $df = 11$ ,  $p > 0.1$ ).

Thus, flowers appear to use a generalized strategy of conspicuousness that fits all possible backgrounds, not so much the specific background formed by the plants’ own leaves. The question whether flowers are specifically adapted to their specific background promises little reward, precisely *because* most background materials fall into the same area of color space. Menzel and Shmida (1993) found no indication that flowers presented in front of desert sand differ significantly from those presented against green foliage. Chittka et al. (1994) calculated distributions of floral color loci for the assumption that the bee eye is adapted to different natural backgrounds; predictably, few differences in the distribution of color loci were found.

#### DO FLOWERS OF COMPETING SPECIES DIVERGE IN COLOR?

Flower colors may compete for “niches” in the color memory of pollinators so as to increase the probability of conspecific flowers being visited (Kevan, 1983; Feinsinger, 1987; Chittka and Menzel, 1992; Menzel and Shmida, 1993). For pollen transfer to be directed from one flower to another of the same species, flowers must be distinguishable from competitors. Foraging bees move more frequently between flowers of similar color (Chittka et al., 1997). To favor pollinator discrimination, the colors of flowers of different species in a given habitat should, in theory, differ maximally from each other. Several sets of simultaneously and sympatrically flowering species were measured to test this hypothesis. Here I show two distributions of the colors of such sets, one from a German dry grassland in July, 1992 (Naturschutzgebiet Lange Dammwiesen, Brandenburg, Germany) and one Brazilian Atlantic rain forest in June, 1991 (Reserva Biologica de Alta da Serra de Paranapiacaba, São Paulo—canopy flowers were not sampled).

The grassland habitat represents the typical case of a flower color distribution (Menzel and Shmida, 1993); loci are distributed over a wide range of color space (Fig. 6). A color hexagon distance of 0.1 corresponds to 70% discriminability in a dual choice test (Chittka and Menzel, 1992); most color distances in this habitat exceed this value (Fig. 6, histogram). This *may* indicate that selection has favored character displacement so as to enable directed pollen transfer. The differences in color between different species will certainly influence pollinator foraging behavior so as to reduce switches from one species to another. However, if one wants to support an adaptive strategy behind a given distribution of floral traits, the observed distribution must be tested against a statistical null model (Kochmer and Handel, 1986; Feinsinger, 1987). The mere fact that there are flowers of different colors in a given habitat does not mean that there is an underlying strategy: one might arrive at the same distribution by assembling a random sample of flowers from different habitats, or picking flowers blindly from a flower shop.

A *color distance distribution* was generated for each set of flower colors by calculating all hexagon distances between all floral color loci in the hexagon (Fig. 6, histogram). To test whether the flowers in the investigated habitats diverge in color to a higher degree than would be expected by chance, I then produced 100 random sets of flower colors by randomly selecting as many species from the flowers in Fig. 1 as occurred in the respective natural habitats. Each set of real flowers was compared with the overall distance distribution from 100 random samples using the chi-square goodness-of-fit test, using 20 bins of hexagon distances each 0.05 wide. The color distance distribution for the dry grassland set (median distance = 0.32) is not significantly different from the random sets ( $\chi^2 = 24.4$ ,  $df = 19$ ,  $p > 0.1$ ; median for all 100 random samples pooled: 0.336). This is a pattern commonly found when entire sets of sympatric and simultaneously blooming plant species are evaluated (Gumbert, Kunze, and Chittka, in prep.). Does this mean that the wide variety of flower colors we find in many habitats is meaningless? Probably not. The problem is that in each such set, there may be some pairs of plant species which converge in color signal, and others that diverge. Divergence in color signal will promote flower constancy (Chittka et al., 1997), but not all plants have sufficiently dense populations to maintain pollinator interest by themselves. The floral signals of rare plants might have to converge on one another, because members of each species might depend on experience that individual insects have gained on flowers of other species. Rare plants may thus form a “mimicry ring” in order to receive any visits at all

(Thomson, 1981; Rathcke, 1983; Feinsinger, 1987). Yet other plants in a given set may be unable to change their color signal in *any* competitive situation, simply because of phylogenetic constraint (see above). Finally, some flowers may just be transient components of a community, which will add noise to any model calculation as the one described above. In an attempt to eliminate some of this noise, we (Gumbert, Kunze, and

Chittka, in prep.) excluded all rare species from 23 sets of sympatric and simultaneously flowering plants in a nature reserve near Berlin (Naturschutzgebiet Lange Dammwiesen, Brandenburg, Germany). Also, instead of evaluating the distribution of distances between *all* flower colors in a set, we only evaluated the distances between the most similar plants. We found that in 18 of these sets, there were fewer *very similar* pairs of plants

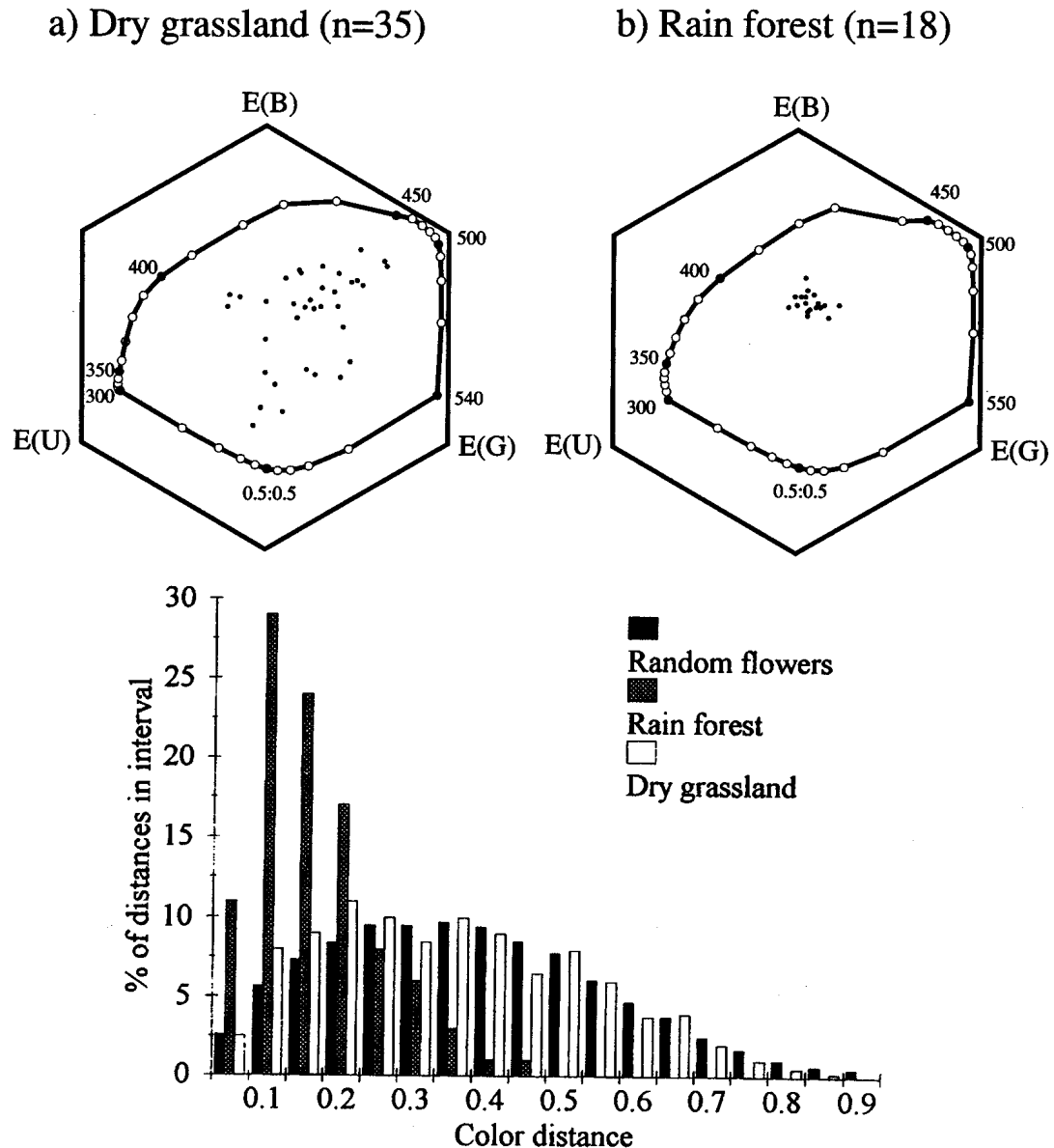


Fig. 6. Distributions of color loci in two habitats. The histogram shows distributions of color distances between all floral color loci in both habitats, and the pooled distribution from 100 random sets of flower colors with  $n = 35$ . The random distribution for  $n = 18$  is indistinguishable from that with  $n = 35$  and is thus not shown. All distances between all flower colors were calculated in the color hexagon, and assorted into categories of 0.05 width each. The color loci for the dry grassland set are calculated for a standard illumination function (D65). The rain forest flower colors and spectrum locus are calculated under the assumption that objects are illuminated by forest light. For this purpose, a forest shade illumination function measured from 350–700 nm (Endler 1993) was extrapolated in a gentle slope down to 300 nm (Chittka 1996b).



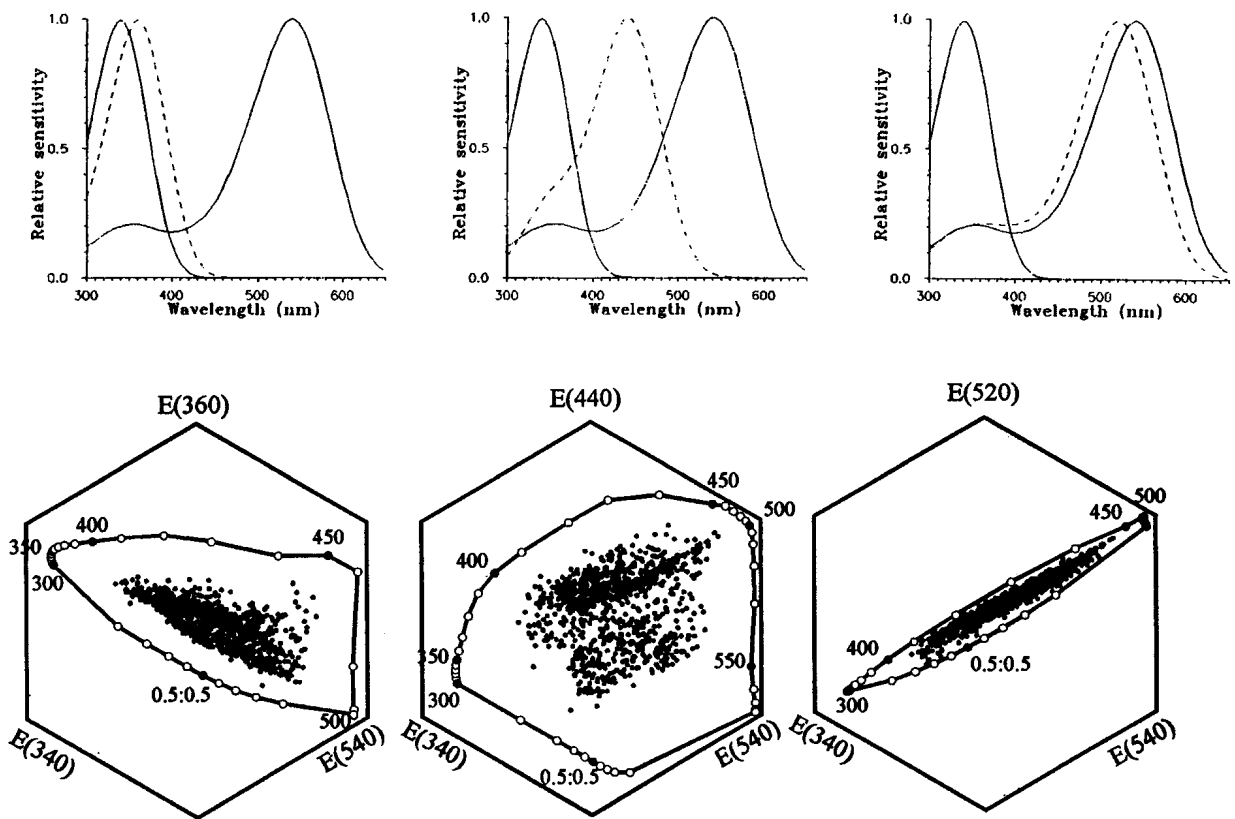


Fig. 7. The loci of 1063 flower colors in the color hexagon (lower row), depending on which set of spectral photoreceptors is employed (upper row). Three examples are given; in all of them, the S (short wave)- and L (long wave)-receptors have  $\lambda_{\max}$  values of 340 and 540 nm. The position of the M (middle wave)-receptor is varied (values see figure).

than expected by chance. Although such divergence has been reported previously (e.g., Heinrich, 1975) this is the first time that it is based on an evaluation of bee-subjective floral traits.

Not all habitats comprise sets of plant species where one might even suspect divergence to have occurred. In the Brazilian rain forest habitat tested, all flowers cluster in a very small region of the color hexagon, mostly the blue part. The peak of the color distance distribution lies below a hexagon distance of 0.1 (this value corresponds to 70% discriminability; see above). Thus, these species are so similar in color signal that foraging bees are likely to switch between species frequently. The color distance distribution (median = 0.176) in this habitat is significantly different from random ( $\chi^2 = 399$ ,  $df = 19$ ,  $p < 0.0001$ ). The relatively high color similarity between all the species in this habitat might be explained when one considers that the populations of all the measured

species were extremely sparse. Thus, distances between individual plants were large, which is common in rain forest plant populations (e.g., Prance, 1985). As pointed out above, this sort of spatial arrangement may favor convergence of flower signals.

#### OPTIMAL SETS OF COLOR RECEPTORS FOR CODING OF FLOWER COLORS

Bees have to make choices within a multitude of different flower species with different colors and rewards. Selection should thus favor flower-visitors that are able to learn the features of any plant species and distinguish it from others in a community. Accumulating confusions of the signals of different flower species may result in a decrease in foraging efficiency, and thus in a reduced fitness of the pollinator. Color is an important cue to guide the learning and choice behavior of the

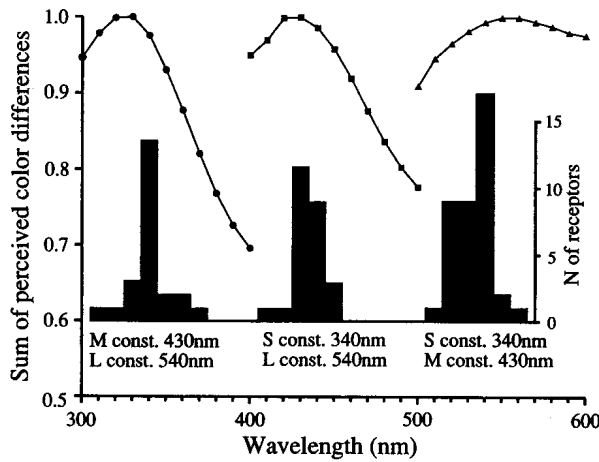


Fig. 8. The determination of an optimal photoreceptor set for discrimination of 1063 flower colors. In each of three variations, two receptors were clamped at the wavelength positions where they most frequently occur in Hymenoptera ( $\lambda_{max} = 340, 430, 540$  nm; see inset), and the third was shifted in 10-nm steps from 300 to 400 nm, from 400 to 500 nm, or from 500 to 600 nm. The spread of color loci was determined depending on which set of spectral photoreceptors was used. For every such set all the hexagon distances between every pair of color signals were determined. All of these distances were summed, and plotted so that the maximum of each curve equals one. The inset shows the absolute number of photoreceptors recorded at every given  $\lambda_{max}$  for 40 different species of Hymenoptera (Peitsch et al., 1992).

insect (Menzel and Shmida, 1993). Is bee color vision optimal for coding flower colors?

To test this possibility, the set of photoreceptor color types that yields an optimal distinction of 1063 flower colors in the color hexagon was determined. For this purpose, spectral sensitivity curves were modeled after Maximov (1988) and shifted systematically along the wavelength scale. If the wavelength position of a photoreceptor is altered, the two-dimensional spread of color loci in the color space changes (Fig. 7). Correspondingly, the perceptual distances between colors change. The photoreceptor set is optimal for discrimination of objects if the perceived differences between all objects to be discriminated are maximal.

In each of three variations, one receptor was varied in 10-nm steps, and the two others were held constant at the wavelength positions where they occur in Hymenoptera. For every such combination of photoreceptors all differences between flower colors in the hexagon are calculated and summed up (Fig. 8). The resulting optima for these sums of perceptual differences at 330, 430, and 550 nm agree well with the photoreceptor wavelength positions as found in the eyes of Hymenoptera (Fig. 8, inset). Similar results are obtained if two or three receptor template curves are varied (Chittka and Menzel, 1992). Thus, the wavelength positions of bee color receptors are indeed close to optimal for the discrimination of

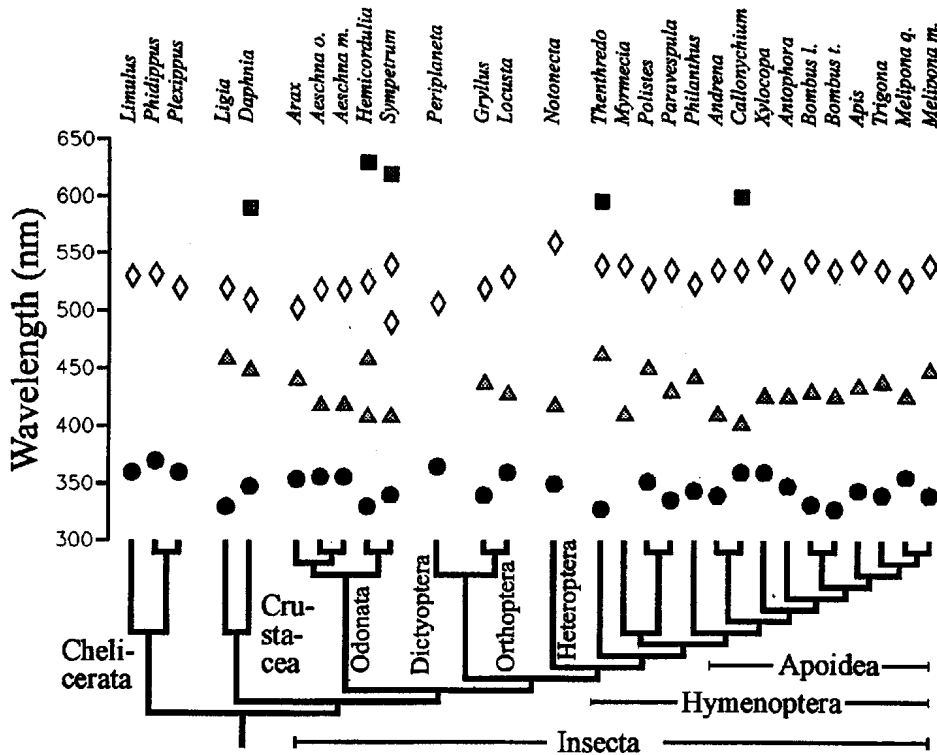


Fig. 9.  $\lambda_{max}$  values of photoreceptors of 29 species of arthropods superimposed on the phylogenetic tree of these species. Only species whose color receptors were investigated electrophysiologically by means of intracellular recordings were taken into account, so as to ensure comparability of wavelength positions. ● — UV receptors (325–370nm); Δ — blue receptors (400–460nm), ◇ — green receptors (490–560nm), ■ — red receptors (590–630). For complete species names and original data refer to the literature cited in Chittka (1996a). Species names are abbreviated where recordings were made for more than a single species of the genus in question.

flower colors. This result has been confirmed with numerous sets of flower colors and different optimality criteria (Chittka, 1996b). Even an ingenious engineer could not design a better receiver for flower colors than the color vision system of bees. Does this mean that bee color vision evolved to discriminate flower colors?

#### HOW ANCIENT IS UV-BLUE-GREEN TRICHRMACY?

To prove that flower signals indeed drove the evolution of bee color vision, it must be shown that the ancestors of bees possessed different sets of color receptors prior to the advent of the angiosperms. But how can we determine in what colors insects saw the world 200 myr (million years) ago? Since time machine projects habitually run into complications (e.g., Wells, 1895), it is now difficult to obtain funding for them, and so evolutionary biologists resort to an alternative strategy called comparative phylogenetic analysis (Harvey and Pagel, 1991). Such an analysis is based on the observation that biological traits are more likely to stay the same than to change; thus, if two sister taxa share a common trait, we assume that it is more likely that this trait evolved once in the ancestor of the two taxa, rather than twice, independently, in both of them. For the present purpose, one has to evaluate members of Arthropod taxa whose evolutionary lineages diverged from those of bees before there were flowers. If the color vision of such animals is indistinguishable from that of bees, this implies that it was present in an ancestor of bees which predated the evolution of flower color.

To test this possibility, I compiled a phylogenetic tree of the Crustacea, Insecta, and Chelicerata (Chittka, 1996a). Only species whose phylogenetic position could be unambiguously determined according to the literature were included. Diptera and Lepidoptera will be treated in a separate study. The reader is referred to the references in Chittka (1996a) for the original literature of phylogenies and photoreceptor wavelength positions.

The  $\lambda_{\max}$  values of the Crustacea and Insecta fall into 3 distinct clusters, around 350, 440, and 520 nm (Fig. 9). Most Chelicerata (represented here by the jumping spiders *Phidippus regius* and *Plexippus validus* and the horseshoe crab *Limulus polyphemus*) lack blue receptors (see Chittka, 1996a for original references), although two Argioid species (*Argiope* spec.) and one Salticid (*Menemerus confusus*) do have them, and the latter even has a fourth receptor whose sensitivity peaks at 580 nm (Yamashita, 1985). Since, however, all other major groups of Chelicerata (including scorpions;

Machan, 1968) have only UV and green receptors (Yamashita, 1985; Chittka, 1996a), it is parsimonious to assume that the ancestor of the Chelicerata had only these two color receptor types. In contrast, almost all Mandibulata possess *at least* the three color receptor types maximally sensitive in the UV, blue, and green (for a more detailed account of spectral sensitivity in the Crustacea see Chittka, 1996a, and references therein). Thus, the blue receptor appears to be an evolutionary novelty in the ancestor of the Mandibulata. The few insect species in which one of the three types is absent (*Periplaneta* and *Myrmecia*) clearly represent cases in which these receptors were lost secondarily. Red receptors show up irregularly both in the Crustacea and Insecta; they have evolved several times independently. The photoreceptor wavelength positions of UV, blue, and green receptors are surprisingly conserved in the Mandibulata.

Thus, we can infer that the Cambrian ancestors of extant insects and crustaceans possessed UV, blue, and green receptors, while the common ancestor of the Mandibulata and Chelicerata lacked blue receptors. Insects were well preadapted for flower color coding more than 500 myr ago, about 400 myr before the extensive radiation of the angiosperm plants which started in the middle Cretaceous (100 myr ago), although their origins might have to be placed in the Triassic (Labandeira and Sepkowski, 1993). The only difference between Hymenoptera and other arthropod trichromats appears to be a shift of the green receptor of about 15 nm towards longer wavelengths, mediated by screening pigments rather than a change of photopigment absorbency (Gribakin, 1988). However, this shift occurs also in the non-apoid Hymenoptera such as wasps and ants, whose members are seldom obligatory flower-visitors. Since the Sphecoidea (containing the Apoidea, the true bees) and the Vespoidea (including the ants and wasps) were already present 220 myr ago in the Triassic (Hasiotis et al., 1995), it is likely that the green receptor had already been shifted to its present wavelength position long before there were flowers.

Why are the wavelength positions of color receptors so conservative in many arthropods? Generating photopigments with  $\lambda_{\max}$  in certain regions of the wavelength range between 320 and 630 nm (the boundaries beyond which no  $\lambda_{\max}$  values have been found so far; Menzel and Backhaus, 1991) does not constitute a technical impossibility, since there are at least a few species in the Crustacea (Cronin et al., 1994) and the Insecta (e.g., Yang and Osorio, 1991) whose retinæ contain 5 or more visual pigments, some of which fill the "empty spaces" on the wavelength scale commonly not occupied by arthropod  $\lambda_{\max}$  values. A more likely explanation

is that genetic variability to modify peak absorbency of pigments has not existed in the species in question (Goldsmith, 1990). However, as few as 3 amino acid substitutions can cause a shift of 30 nm in peak spectral sensitivity (Neitz et al., 1991). In this sense, it is inconceivable how peak sensitivity of the 3 basic arthropod receptors has been maintained for over 500 myr without stabilizing selection.

Thus, the widespread set of UV, blue, and green receptors in arthropods might actually be adaptive, but to an unrecognized set of environmental parameters. The hypothesis that insect color vision was adapted to particular classes of objects, such as flowers in the case of bees, can be rejected on the ground of the present study. It is more likely that UV-blue-green trichromacy constitutes a more general adaptation which provides at least a local optimum for coding all sorts of natural objects under various illumination conditions (Chittka, 1996b).

### CONCLUSION

Finally, what is the answer to the question posed in the title? Bee color vision is indeed optimal for coding flower color, but when we ask why bees possess the color receptors they do, this is equivalent to asking why bees have six legs. The answer, in both cases, is the same: Because their ancestors did. The obvious next question is: Why did their ancestors have this particular set of color receptors? Research is underway to link UV-blue-green trichromacy to the colored environment of the pre-angiosperm world. A preliminary result is that bee color vision is also optimal for discrimination of leaf colors (Chittka, 1996b). The observation that bee color vision is optimally suited to code flower color can probably be explained when one assumes that flower colors adapted to insect vision, and that, as a consequence, they contain the information about the receiver to which they were addressed.

The observation that the receiver system is ideal for the signals directed to this system does not mean that the signals are optimal. Your spouse may be optimal for you, but you may not be optimal for your spouse, and biological signal-receiver systems may be similarly asymmetric. Flower colors are not optimal for discrimination because their production is subject to phylogenetic and biochemical constraint. In addition, while the argument that color divergence of sympatric species will favor a more directed pollen transfer is sound, no one has measured male and female fitness as a function of color difference to flowers of potentially competing species, which is essential to understand the adaptiveness of a floral trait (Wilson and Thomson,

1996). It is conceivable that differences in flower color between two species have no further influence on directness of pollen transfer if they exceed a certain threshold value. In this case, color differences between flowers of potentially competing species need not be maximized; an intermediate color distance may be sufficient.

Preliminary evidence is presented here suggesting that flower colors are adaptive and distributed in the bee color space in a way that is significantly nonrandom. This is not yet a sufficient proof of character displacement (or convergence, respectively); numerous other criteria must be met in order to demonstrate that traits have changed in response to competition (e.g., Robinson and Wilson, 1994). We are currently preparing statistical models, as well as experimental approaches to test these criteria for several sets of plant species (Gumbert, Kunze, and Chittka, in prep.).

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