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WHY RED FLOWERS ARE NOT INVISIBLE TO BEES

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ABSTRACT

A pervasive idea among pollination biologists is that bees cannot see red flowers. This idea has led many workers to assume that red coloration is an adaptation by which flowers exclude bees as visitors. However, recent empirical and theoretical evidence strongly supports the alternative view, that red flowers *are* visible to bees. Our purpose is to marshal this evidence from physiology, behavior, and ecology. First, we define the spectral boundary between orange and red, and show that the visual spectrum of all bee species studied to date extends enough into long wavelengths to provide sensitivity to red light. Such sensitivity differs from the ability to discriminate different monochromatic lights, and we argue that bees will be unable to discriminate such lights above about 550 nm. Second, we point out that flowers do not reflect monochromatic lights. Instead many of them, particularly those that appear red, orange, yellow, and white to humans, have reflectance patterns that are essentially step functions. We predict that bees should be able to discriminate such reflectance patterns over a range of 550–650 nm, since reflectance functions with steps at such wavelengths will occupy different loci in bee color space and thus be distinguishable. In this sense, bees should distinguish between green-, yellow-, orange-, and red-reflecting objects, even if these do not reflect in shorter wavelengths (including UV). A behavioral experiment shows that bumblebees can indeed perform this task. Third, we present information on the spectral reflectance of some typical "red" flowers, combined with field observations of bee visitation to such flowers. We end with a preliminary reassessment of the adaptive significance of red flower coloration, using North American "hummingbird" flowers as an example; we also stress some of the pitfalls facing evolutionary biologists who continue to assume that bees are blind to red objects.

INTRODUCTION

The assertion that bees cannot see red flowers has reached the level of dogma in pollination biology. To take a typical example, the excellent new book on pollination by Proctor et al. (1996, p. 49) states that "most insects are sensitive to ultra-violet radiation but have little or no sensitivity to red . . . ". The authors then proceed to elaborate on the assertion with reference to various insect groups, including bees. And Vogel (1996), in a new edited volume on floral biology, lists "red-blindness" as one of several noteworthy modern discoveries about insect pollinators.

The assumption of red-blindness in bees is perhaps understandable given contradictory and confusing statements in the literature, dating to the earliest days of research on bee color vision. Karl von Frisch (1914, 1914/15) trained honeybees (*Apis mellifera*) to pick blue and yellow targets from different shades of gray, but found that the animals could not perform this task with red targets. Conversely, Molitor (1937, 1939) found that several species of bees and wasps could be trained to red. Kugler (1943) reported that bumblebees (*Bombus lapidarius*) could learn even "far red" targets (wave-

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lengths unspecified), but the bees learned the task more slowly (and forgot it more quickly) under natural light than under artificial illumination. Kühn (1924) determined the long-wavelength (λ) boundary of bee vision as 650 nm, and concluded that bees see red, whereas Daumer (1956) and Frisch (1967) concluded that they see only to orange, based on the same λ boundary. Kevan (1983) specified the boundary as 700 nm, but also concluded that bees only see yellow and orange. Kühn (1924) and Helversen (1972) both found that bees cannot discriminate wavelengths between 530 and 650 nm (i.e., green to red), but Daumer (1956) succeeded in training bees to distinguish between 530, 580, and 616 nm (which he named green, yellow, and orange).

The take-home message that many pollination biologists extracted from this confusion was that bees cannot see red, and red flowers are thus invisible to them (e.g., Raven, 1972; Harborne, 1982; Bradshaw et al., 1995; Proctor et al., 1996). However, the conclusion of red-blindness immediately confronted thoughtful workers with several enigmas. If bees cannot see red flowers, why does one often find bees visiting such flowers (we will return to examples below)? How do bees distinguish yellow flowers from leaves when they cannot discriminate in the entire range from green to red, as claimed by Kühn and Helversen (see above)? How can it be true that bees can neither distinguish red from yellow, nor red from gray, but *can* distinguish yellow from gray?

Our intent here is to resolve such enigmas about bees' color vision. We will show that much of the confusion is generated by failure to differentiate conceptually between monochromatic lights vs. broadband spectral reflection of objects (including flowers); and between the range of colors that bees perceive vs. those they discriminate from one another. In addition, the theoretical and empirical understanding of bee vision has advanced rapidly beyond the level exemplified in the papers cited above. Thus we are able to present recent evidence from physiology, behavior, and ecology that bees see red objects (including red flowers) and discriminate them from other objects. We end by discussing some ecological and evolutionary implications of red flower coloration in light of this evidence, and by pointing out some pitfalls of continuing to ignore the evidence.

THE VISIBLE SPECTRUM OF BEES

Before we ask whether bees can see red, we must agree on what "red" means. In the present context what is meant is how we ourselves perceive color, so we will derive our definition from human psychophysical studies. These studies variously assess the λ boundary between "orange" and "red" as lying between 593 and 625 nm, with a mean of 611 nm (LeGrand, 1968, and references therein). The variation from study to study derives in part from different experimental methods, but also from intrinsic differences among human observers. For example, LeGrand describes one experiment in which a light of 605 nm was judged by 40 subjects as red and by 40 as orange, with 20 undecided. In what follows we will consider the average value of 611 nm as the boundary between red and orange. The question of whether red light is invisible to bees thus boils down to whether they can see $\lambda > 611$ nm.

The ancestor of all insects was likely equipped with UV, blue, and green receptors with maximal sensitivities (λ_{max}) at about 350, 440, and 520 nm, respectively (Chittka, 1996). The ancestral insect long-wave receptor (L-receptor) λ_{max} of about 520 nm contrasts with a human value of about 565 nm (Smith and Pokorny, 1975; Jacobs, 1993; Fig. 1a). However, modern insects in many orders possess L-receptors with greater λ_{max} than this. For example, the values for many Lepidoptera lie in the range of 600 to 630 nm (e.g., Struwe, 1972; Arikawa et al., 1987), and some Coleoptera (Hasselmann, 1962; J. Schorn and R. Menzel, unpublished) and Odonata (e.g., Yang and Osorio, 1991) are similar.

Within the Hymenoptera, such high values of L-receptor λ_{max} are less common. Behavioral studies with the ant *Cataglyphis bicolor* indicate λ_{max} of 570 nm (Kretz, 1979), but electrophysiologists have so far not found this receptor (Paul et al., 1986). Three species of primitive wasp (Symphyta) have λ_{max} between 596 nm and 604 nm (Peitsch et al., 1992). Among more than 50 species of bees (Apoidea), the Andrenid *Callonychium petuniae* is an outlier with an L-receptor λ_{max} of 600 nm (Menzel and Backhaus, 1991; J. Schorn and R. Menzel, unpublished). All other bees examined so far are UV-blue-green trichromats with receptor λ_{max} values most commonly positioned at 340, 430, and 540 nm (Peitsch et al., 1992; Chittka, 1996; Fig. 1b). When we speak of bees in what follows, we mean trichromats with these properties. Can these animals see light which appears red to us, i.e., of $\lambda > 611$ nm?

The answer is yes. The spectral sensitivity curve of the L-receptor of most bees peaks at around 540 nm, but has an extended tail towards longer wavelengths, and reaches zero at about 650 nm (Fig. 1b). Hence, there is a large overlap between wavelengths humans see as red, and those to which bees are sensitive. It is correct to say, however, that bees do not see as far into the red as humans do. This is because the bee L-receptor is positioned at slightly shorter wavelengths (λ_{max} = 516 to 560 nm; Peitsch et al., 1992) than that of humans (λ_{max} =

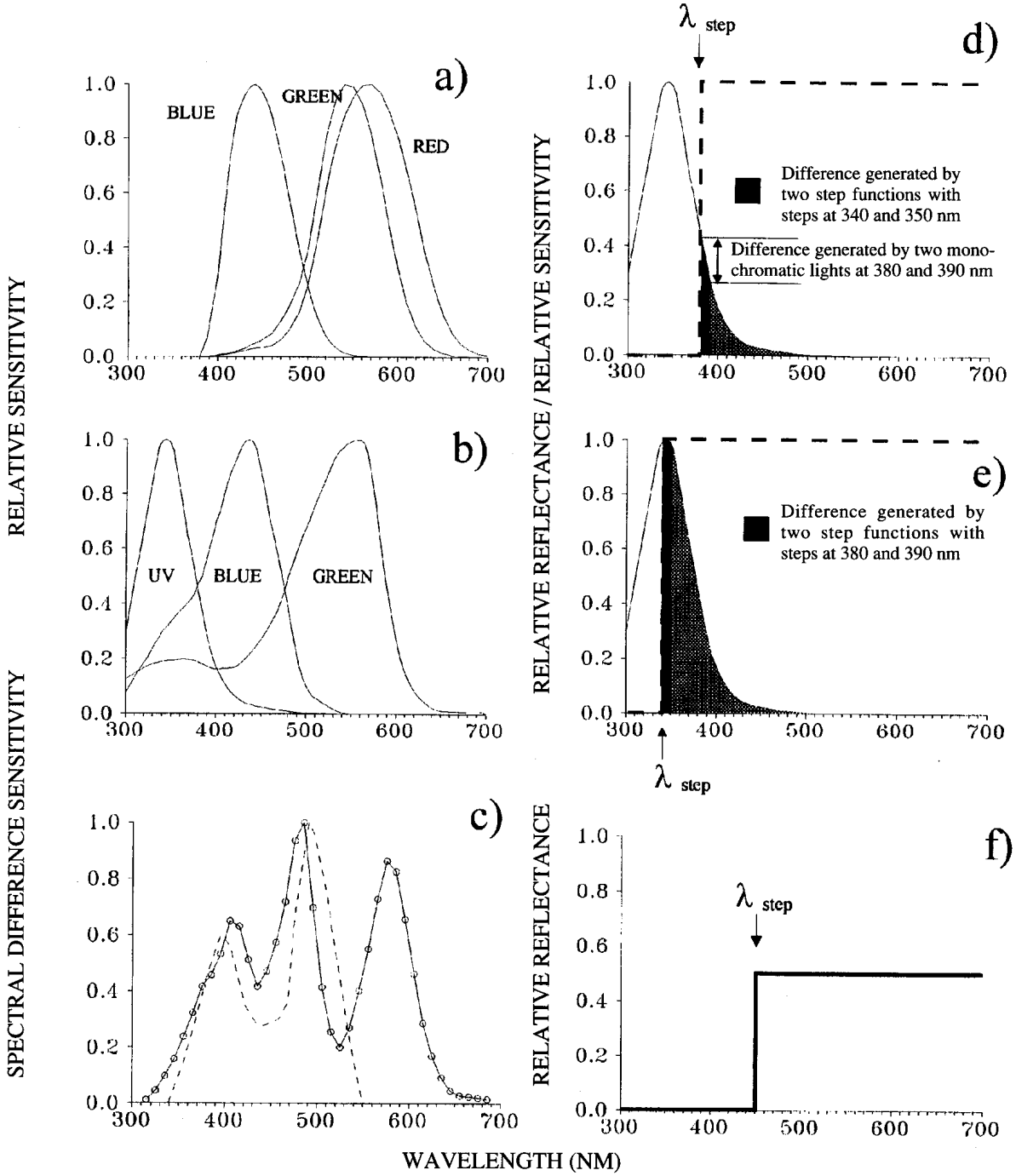

Fig. 1. Spectral sensitivity functions for (a) human color receptors and (b) honeybee (*Apis mellifera*) color receptors. The honeybee functions are representative for a large number of Apoidea (Peitsch et al., 1992). (c) Dashed line: the spectral discrimination function of the honeybee, as determined behaviorally by Helversen (1972); solid line: spectral discrimination functions for step functions. (d,e) Continuous line: spectral sensitivity function of the bee UV receptor. Dashed lines: step functions with λ_{step} at 380 nm (d) and 340 nm (e); these theoretical functions reflect 100% of all light above, and no light below, λ_{step}. Shaded areas (black *and* gray): areas of overlap (convolution) between spectral sensitivity functions of the bee UV receptor and step functions. If λ_{step} is shifted 10 nm to longer wavelengths in both graphs, the convolution is reduced by the area shaded in black. The difference in receptor stimulation by any pair of monochromatic lights can be assessed directly by evaluating the receptor's sensitivity at the two wavelengths in question. (f) An example of the step functions used to calculate the spectral discrimination function in Fig. 1c and in Fig. 2, inner solid line. This particular function has λ_{step} at 450 nm; in contrast to the functions in Fig. 1d and 1e it reflects only 50% of all incident light at wavelengths above λ_{step}.

565 nm; Smith and Pokorny, 1975; Jacobs, 1993), although the difference is marginal in some species, e.g., the Megachilid *Osmia rufa* (λ_{max} = 560 nm). The value of λ_{max} also varies somewhat between studies and measurement techniques, so that, for example, a value of λ_{max} as great as 556 nm has been reported for the honeybee (Menzel and Backhaus, 1991). Hence the statement that the bee visual spectrum is shifted relative to that of humans (e.g., Kevan, 1983) is mostly true in an asymmetrical sense: while the differences on the long wavelength end are relatively small (see above), the differences between the λ_{max} of the bee and human short-wave receptors (S-receptors) are consistently around 100 nm for all species of Apoidea so far tested (Peitsch et al., 1992).

It is also critical to keep in mind that the visual spectrum of an animal does not have absolutely fixed boundaries because the eye adapts to different conditions. Thus it is misleading to evaluate a graph in which sensitivity is plotted on a linear (as opposed to a logarithmic) scale, and to conclude that the visual spectrum ends where spectral sensitivity curves reach zero. The sensitivity of a dark-adapted eye can increase by several log units (Laughlin, 1989), making lights on the far periphery of a receptor's spectral sensitivity curve perceptible. Thus dark-adapted humans can see infrared light with $\lambda > 1000$ nm (Griffin et al., 1947). Mazokhin-Porshniakov (1969) reported that the blowfly *Calliphora* responds to flashes of 710 nm when placed in the dark, even though λ_{max} for its L-receptor is 530 nm and the response of this receptor in a light-adapted eye reaches zero on a linear scale at around 620 nm (Hardie, 1986). The threshold energy to evoke a response at 710 nm is 2000 times higher than at 620 nm, but a response *is* evoked in the fly.

Scientists wishing to experiment with insects in darkness, while being able to observe them, have sometimes used lamps covered with red foil which transmits all wavelengths above 600–620 nm (Chittka, unpublished measurements). Taking into account the above information, this is unlikely to create complete darkness for any insect! Bumblebees (*Bombus impatiens*), for example, exhibit visual orientation, and normal (although somewhat slowed) flight activity, when kept in a room illuminated with a 40-W dark-red light bulb (S82134; Osram Silvania, Inc., L. Chittka, unpublished).

THE RANGE OVER WHICH BEES DISCRIMINATE COLORS

From the evidence above, we conclude that bees are sensitive to red light. However, this does not necessarily mean that they experience red as a unique perceptual quality, as humans do. Mazokhin-Porshniakov (1969) stressed that "there are two different problems that must be clarified: (1) what kind of radiations the insect eye is able to distinguish, and (2) whether it can distinguish one radiation from another." The previous section dealt with Mazokhin-Porshniakov's first point. Here we will discuss his second point.

What is the spectral range over which bees can discriminate between lights of different wavelengths independently of differences in intensity? To answer this question, we must first understand the necessary equipment for wavelength discrimination. By analogy, consider the auditory system, and imagine you were trying to estimate the direction of a sound with only your left ear. Without moving your head, this would not be possible, because you would not be able to tell whether hearing a weak sound meant that there was a soft sound to your left, or a louder sound to your right. To estimate stimulus direction, you must compare the signals from two different sensors. Visual systems face a similar problem. To discriminate colors in a given range of wavelengths, visual systems must possess more than one receptor type sensitive to those wavelengths. If only a single color receptor sends a signal to the brain, the brain cannot decipher if the receptor is moderately stimulated at its wavelength of peak sensitivity, or strongly stimulated at a wavelength far from its λ_{max}. Thus, discrimination of colors independently of intensity is only possible in the wavelength range where the spectral sensitivity functions of two color receptor types overlap.

One way to quantitatively judge color vision abilities of an animal is to measure its spectral discrimination (inverse $\Delta\lambda / \lambda$) function (Menzel and Backhaus, 1991; Jacobs, 1993). A $\Delta\lambda / \lambda$ function depicts the minimal wavelength difference $\Delta\lambda$ needed to produce a just-noticeable difference (or a difference of a fixed behavioral criterion, such as 70% discriminability; Helversen, 1972) relative to a reference wavelength λ. Inversion of this function allows a straightforward judgment of the wavelength discrimination abilities of an animal since peaks of the function denote spectral regions of particularly keen discrimination between closely adjacent wavelengths, whereas minima indicate areas of poor discrimination. Where the function reaches zero, wavelength discrimination is no longer possible.

The honeybee was the first insect in which a spectral discrimination function was measured (Helversen, 1972); other Apoidea have qualitatively similar functions (Chittka, 1992, and references therein). This "bee spectral discrimination function" has peaks around 400 nm and 500 nm (in the bee-UV-blue and blue-green) and a region of poor discrimination in the blue at about 450 nm. The function reaches zero at 350 nm on

the short wavelength end and at 550 nm on the long wavelength end (Fig. 1c). Thus, while the visible spectrum of bees reaches up to the red at about 650 nm, discrimination of single wavelengths is only possible in the range from near UV (350 nm) to green (550 nm). Hence monochromatic lights from green to red are indistinguishable for bees, so long as they are adjusted for equal brightness according to Abney's law (equal sum of voltage signals of the three color receptor types; Backhaus, 1991; Chittka, 1992). The latter point is critical: since the spectral sensitivity of the bees' L-receptor rapidly decreases at $\lambda > 550$ nm, the intensity of the stimulus must be increased as one moves to longer wavelengths for the bee to perceive the same stimulus. If the *physical* intensity of the light is kept constant over the range from 550 nm to longer wavelengths, this will not change the angular position of the stimulus in color space (its hue in terms of human perception); rather, the light will be increasingly dim, until, at >650 nm, it will become imperceptible for the light-adapted eye.

The features of the spectral discrimination function can also be predicted from the locations of monochromatic lights in a *color space*. A color space is a representation of an animal's color perception, designed so that distances between points generated by two colors are related to the animal's predicted ability to distinguish those colors. To create an appropriate color space we need to know not only the physical properties of the colors, but also what signals these colors cause the animal's photoreceptors to send to the brain, and how the brain integrates the signals. In the case of bees, we can calculate the signal generated by the three color receptor types described above (for details see Chittka, 1992). If we normalize the receptor voltage signals so that they range from zero (no signal) to unity (maximum signal), we have defined a cubical vector space that describes how the receptor system responds to any color. This receptor space, however, does not adequately describe color perception because it ignores the processing of receptor signals in the brain. It turns out that the bee's brain integrates the signals via a color-opponent system (Backhaus, 1991; Menzel and Backhaus, 1991; Chittka et al., 1992), as the human brain does also (Jacobs, 1993). A color-opponent system compares inputs from different color receptor types so as to extract information about the spectral properties of an object. Thus, the appropriate color space for a bee is one that represents color-opponency. It can be shown by some simple geometry that a projection of the cubical receptor excitation space onto two dimensions, which yields a hexagon, provides the desired representation of color opponency. Points within this hexagonal color space are defined by constant difference between receptor signals, which is just the sort of algorithm performed by the color-opponent system in the bee's brain (Chittka, 1992).

The hexagonal color space is shown in Fig. 2. The outer solid line within the hexagon is the spectrum locus, a curve which connects the color loci of monochromatic lights in 10-nm steps from 300 to 650 nm. Distances between adjacent points can be used to predict how well the bee will discriminate pairs of wavelengths which differ by 10 nm. In agreement with the spectral discrimination function experimentally determined by Helversen (1972), resolution is good around 400 nm and 500 nm, with a minimum between these values (Backhaus, 1991; Chittka, 1992). Above 500 nm, distances between points become increasingly smaller, and all values >550 essentially fall on a single point in color space.

Do these findings mean that bees cannot distinguish

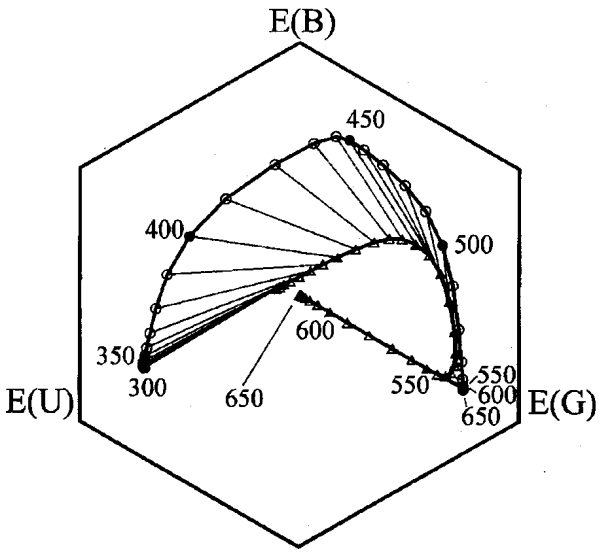

Fig. 2. Color loci of monochromatic lights, adjusted for equal brightness according to Abney's law (sum of relative photoreceptor voltage signals $\Sigma E_i = 1.5$; see Backhaus, 1991 for details), from 300 to 650 nm (outer solid line, circles); and loci of step functions with λ_{step} values for the same range of wavelengths (inner solid line, triangles), both shown within a hexagonal color space for bee vision (Chittka, 1992). The circles and triangles mark loci in 10-nm steps; filled symbols indicate 50-nm steps. Thin lines connect each locus for monochromatic light with the corresponding locus for step functions. For example, the filled circle marked "400" denotes the locus of a monochromatic light of 400 nm; a thin line connects this point to a triangle on the inner solid line, which denotes the locus corresponding to a reflectance function with a λ_{step} positioned at 400 nm.

green from yellow, orange, or red? In one regard the answer is yes: bees cannot distinguish between monochromatic lights in this range in a way that is independent of intensity. Thus, for example, a monochromatic red light of strong intensity will generate the same sensation as a green light of moderate intensity. However, in a more important sense the answer is no. Objects that the bee encounters in its daily life, for example flowers and foliage, *do not reflect monochromatic light.* Such objects instead reflect over large spectral ranges. Quite different rules apply for such broadband reflectance colors than apply for monochromatic lights. In the next section, we address this point in detail.

BEES' ABILITY TO DISCRIMINATE BETWEEN STEP FUNCTIONS

Surprisingly, most flowers have simple broadband reflectance functions. The reflectance curves of many flowers are essentially step functions; this was true for 41% of over 1000 flowers measured by Chittka et al. (1994). The step in these functions is actually sigmoid, but the slope is so steep that the functions can be sufficiently described by saying that all wavelengths above the inflection point of the sigmoid step (λ_{step}) are reflected, whereas all wavelengths below this value are absorbed (Chittka and Menzel, 1992). Objects with such a reflectance function are white for humans if λ_{step} is $\leq$ 400 nm (because in this case all three of our color receptor types are about equally strongly stimulated); they appear yellow if λ_{step} is ~500 nm (since predominantly the green and red receptors are stimulated); and they appear red if λ_{step} is $\geq$ 600 nm, since mostly the red receptor is stimulated (Chittka et al., 1994).

The ability to discriminate between two reflectance functions with similar λ_{step} values is not the same as the ability to discriminate between two monochromatic lights with wavelengths equivalent to these λ_{step} values. The response of a photoreceptor depends on the convolution (area of overlap) between its spectral sensitivity and the reflectance spectrum (Chittka, 1992). Because of this, the difference evoked in a single photoreceptor between two lights with infinitely narrow spectra (monochromatic lights) can be predicted entirely from the receptors' own spectral sensitivity function. Consider the bee's UV receptor and two monochromatic lights at 380 and 390 nm. These lights will differ strongly in the degree to which they stimulate the receptor because the receptor sensitivity function has a steep slope in this wavelength range (Fig.1d). In contrast, two lights with the same difference of 10 nm will yield practically the same receptor signal where the slope of the receptor sensitivity function is close to zero, for example at 340 and 350 nm (Fig. 1e). Now consider two step functions with λ_{step} values of 380 and 390 nm. The convolutions for these two reflectance spectra differ very little (area shaded black in Fig. 1d). In contrast, functions with λ_{step} values at 340 and 350 nm produce a much larger difference in convulutions (area shaded black in Fig. 1e). In summary, the strongest differences in signals from a single receptor type are generated when two step functions are located in the area of peak spectral sensitivity, not in the wavelength ranges of rapidly changing sensitivity as in the case of monochromatic lights. Hence, the spectral discrimination function for monochromatic lights is likely to differ from that for step functions (M. Vorobyev, personal communication).

As explained in the previous section, the ability to discriminate colors independently of intensity relies on signal differences in more than a single color receptor type. Discrimination of monochromatic lights is optimal for bees at around 400 and 500 nm because in these spectral regions two color receptor sensitivity curves overlap with steep slopes in opposite directions. What are the regions of maximal spectral discrimination for *step functions*, considering the contributions from the different color receptor types? Once again, consider two step functions with λ_{step} at 340 and 350 nm. These will generate a strong difference in the UV receptor (Fig. 1e) and a smaller difference in the blue receptor (Fig. 1b). On the other hand, functions with λ_{step} at 380 and 390 nm will produce a smaller difference in the UV receptor but a larger difference in the blue receptor. In addition, as the convolution between receptor spectral sensitivity and step reflectance function changes when the step changes in height, the ability to distinguish between step functions also depends on the percentage of light reflected above λ_{step}. A further complication arises from the nonlinear transduction of receptor stimulation (proportional to the convolutions discussed in the last paragraph) into a voltage signal leaving the receptor (Laughlin, 1989; Backhaus, 1991; Chittka, 1992).

Because of these complications, the regions of maximal spectral discrimination for step functions are more difficult to predict simply by inspection of the spectral sensitivity functions for different receptor types. It is more useful to calculate the loci of different step functions in the hexagonal color space and to examine the separation of these loci to predict the bee's discrimination ability. We have done this at intervals of 10 nm for step functions with λ_{step} between 300 and 650 nm. Our calculations were based on step functions with reflectance of zero below λ_{step}, and of 50% above λ_{step}, which resembles real flowers (Chittka et al., 1994). The result is shown by the inner solid line in Fig. 2. This line connects all the color loci, and starts and ends near the

center of the hexagonal color space, i.e., at the uncolored point (sometimes referred to as the "bee-white" point; Daumer, 1956). The reason is that a function with λ_{step} at 300 nm will stimulate all three bee color receptor types, whereas a function with λ_{step} at 650 nm will stimulate none. What happens in between?

There are three spectral regions in which the distances between loci of adjacent step functions are particularly large. Two regions are centered around 410 and 490 nm, as shown in a corresponding spectral discrimination (inverse $\Delta\lambda / \lambda$) function (Fig. 1c). The discrimination function for monochromatic lights and honeybees measured by Helversen (1972) has these same peaks, and generally resembles the theoretical discrimination function in Fig. 1c for wavelengths < 530 nm. In addition, Fig. 1c predicts a third peak of particularly accurate discrimination in the yellow at 580 nm. These peaks can be predicted only when the nonlinear transduction process in the photoreceptors is taken into account (Chittka, 1992). This is especially apparent for the long wavelength peak because it is caused by signal differences exclusively in the green receptor. While differences in convolutions of receptor spectral sensitivity and step functions are particularly large when differences in λ_{step} are located in the region of peak spectral sensitivity (around 550 nm for the green receptor), this is not so for the receptor voltage signals. These signals are related to the convolutions by a hyperbolic function, so that even large differences in receptor stimulation in the upper dynamic range of that curve will produce only small differences in receptor signal (see Laughlin, 1989, and Chittka, 1992 for details). It turns out that step functions with λ_{step} around 580 nm will generate values of receptor stimulation which are located exactly in that part of the hyperbolic function where it changes rapidly over stimulus intensity. Receptor signal differences will vary greatly between functions with 1 step in that range; hence they are predicted to be well distinguishable.

Note, however, that the differences between step functions that humans would call yellow, orange, and red cannot be hue differences for the bee. In human color perception, hue is specified by angular position in color space measured from the center. As Fig. 2 shows, functions with λ_{step} > 540 nm all lie on a straight line from the periphery to the center; thus, objects with such coloration cannot be distinguishable by means of hue. At the same time, these functions *do* differ in the distance of their loci from the uncolored point (saturation, or the degree to which a given stimulus differs from an uncolored one, in human color perception).

In summary, step reflectance patterns are predicted to provide information to a bees' visual system that is not provided by monochromatic lights. A spectral discrimination function based on step reflectance functions predicts that bees will be able to tell the difference between yellow-, orange- and red-reflecting objects because these occupy distinct points in color space, corresponding to saturation differences in human color perception. Note that, because only a single receptor is stimulated in that spectral range, discrimination of step functions with steps between 550 and 650 nm is not possible entirely independently of stimulus intensity. For example, a step function with λ_{step} = 600 nm which reflects 50% of all incident light above λ_{step} will produce the same signal in the bees' green receptor as a step function with λ_{step} = 610 nm which reflects 100% above λ_{step}, and equally low signals in the UV and blue receptors. Thus, it is possible to adjust the intensity of the one step function so that it will match the other in the bees' color perception. However, the wavelength range over which such adjustments can be made is very limited: no step function with λ_{step} above 610 nm can match the 600 nm step function with 50% reflectance, simply because objects cannot reflect more than 100% of the incident light; in addition, reflectance of flowers rarely exceeds even 70% (Chittka et al., 1994). Monochromatic lights, on the other hand, can be matched over a much wider wavelength range when intensity is varied (see the example above by Mazokhin-Porshniakov, 1969, where two lights 90 nm apart are matched). Intensity-independent identification of step functions with λ_{step} > 550 nm is possible *with limited accuracy* using differences only in the green receptor, whereas this is not the case for monochromatic lights.

We performed a small set of behavioral experiments to see if bumblebees (*Bombus impatiens*) can indeed distinguish between yellow, orange, and red reflecting objects. Three cardboards were chosen (standardized color papers of the HKS N set, K&E Stuttgart-Feuerbach, Germany) with typical step function properties (Fig. 3a); they had the colors red (λ_{step} at 590 nm; HKS 12N), orange (570 nm; HKS 7N), and yellow (510 nm; HKS 3N). A small flight arena (54 cm wide by 65 cm long by 20 cm high) was connected directly to a nest box containing a bee colony. The floor of the arena was covered with green cardboard (HKS 58N) with a broad spectral reflectance similar to that of foliage (Chittka et al., 1994). A 3 × 3 cm colored target was placed on this floor in a location that varied from one learning trial to the next, and a piece of Plexiglas, the same size of the target and bearing a 100-µl droplet of 50% (volume/volume) sucrose solution, was placed over the target. By feeding on this droplet, a bee could entirely fill its crop and would then return to the nest box before the next trial. We trained and tested 15 bees one at a time, 5 to each color. All bees were entirely naive with respect to any foraging tasks outside the colony.

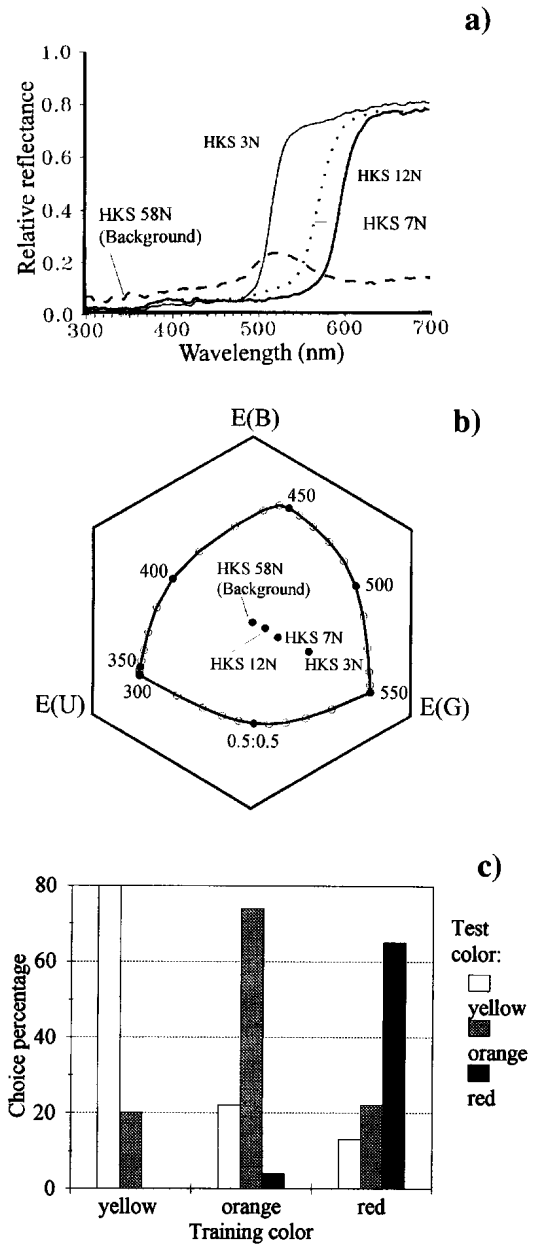

Fig. 3. a) Reflectance functions of the stimuli used in the behavioral trials with bumble bees. Cardboard HKS 12N is red for humans, HKS 7N is orange, and HKS 3N is yellow. The background was made of green HKS 58N. b) color loci of the same materials in the bee color space. c) Choice percentages for bees trained to yellow (N of choices = 50), orange (N = 54), and red (N = 46). Choices of the training color and each test color were tested for significance by means of the chi-squared goodness of fit tests (df = 1). All pairs of choice values were significantly different from random: bees trained to yellow, choices of yellow vs. orange $\chi^2 = 9.8$; $p < 0.01$, yellow vs. red $\chi^2 = 26.6$; $p < 0.001$; bees trained to orange, choices of orange vs. yellow $\chi^2 = 8.13$; $p < 0.01$, orange vs. red $\chi^2 = 21.6$; $p < 0.001$; bees trained to red, choices of red vs. orange $\chi^2 = 5.33$; $p < 0.025$, red vs. yellow $\chi^2 = 9.31$; $p < 0.01$.

Each individual bee received ten rewarded trials, after which we arranged targets of all three colors in the sequence yellow-orange-red from left to right, with spacing of 3 cm. Each target was then covered with a freshly-cleaned Plexiglas square. A single trained bee was let into the arena, and was observed searching for food for 5 min. We counted all instances of the bee landing on or walking across any of the three colored targets.

Bees learned all three colors and distinguished each color well from the other two (Fig. 3c). The choices by all three groups of bees for the training color were significantly different from random (statistics in legend of Fig. 3c). Bees *sometimes* chose the yellow target, which contrasted best against the background (the most saturated of the three colors in terms of human color perception) after training to the least "saturated" target (the red cardboard, whose color locus is closest to the uncolored point), whereas they *never* chose the red target after training to the yellow target. This difference was significant ($\chi^2 = 11.4$; df = 1; $p < 0.001$; see Lunau et al., 1996 for possible explanations). At the same time, the results show that bees can be easily trained to a target that is red for humans, and can distinguish it from orange and yellow targets.

THE SPECTRAL REFLECTANCE PROPERTIES OF RED FLOWERS, AND HOW BEES SEE THEM

Flowers are rarely truly red. Many flowers commonly categorized as red, such as some tulips and roses, have substantial reflectance in the blue (Exner and Exner, 1910); an example is *Dianthus carthusianorum* (Fig. 4). Such flowers will appear blue for bees, since the stimulation of the bees' blue receptor by the flowers' blue reflectance peak is much stronger that the stimulation of the green receptor by the red reflectance. Other red flowers, such as red poppy (*Papaper rhoeas*, Fig. 4), have a reflectance peak below 400 nm, and so will appear UV for bees. Bees certainly visit such flowers (e.g., McNaughton and Harper, 1960), and indeed we would expect these flowers to be clearly distinguishable even for an animal which is truly red-blind. Finally, some "typical" bird flowers, such as scarlet gilia (*Ipomopsis aggregata*) in the western USA, have low reflectance over the range of 300–600 nm (Fig. 4) and reflect all light above ~600 nm. Is such a classical "hummingbird flower" (Grant and Grant, 1968) invisible to bees?

As we have stressed, the visual spectrum of bees extends at least to 650 nm, and so there is little reason to believe that bees will miss such flowers. Thus we are not surprised to see that *I. aggregata*, even though it is

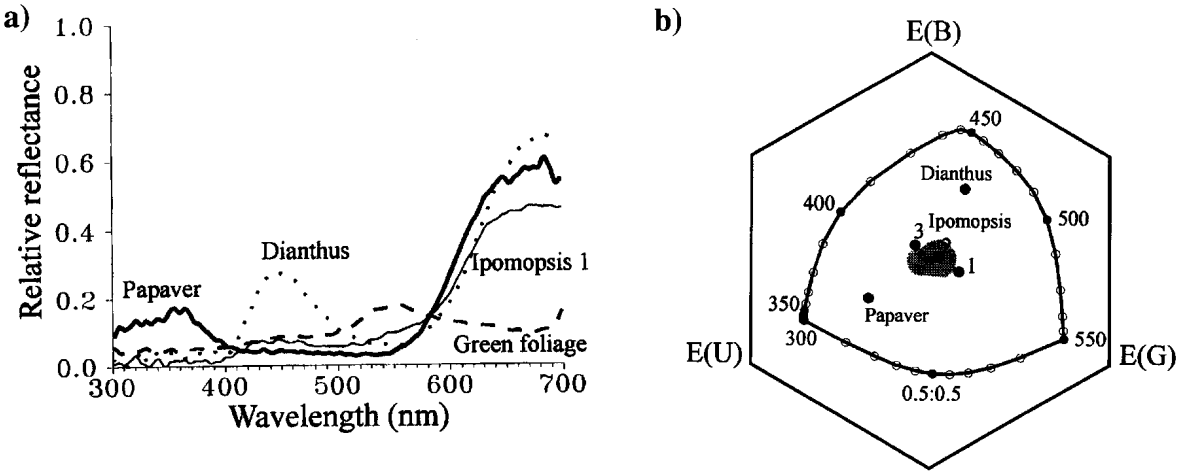

Fig. 4. a) Reflectance functions for three plant species whose flowers appear red to humans, *Papaver rhoeas* (Papaveraceae), *Ipomopsis aggregata* (Polemoniaceae), and *Dianthus carthusianorum* (Caryophyllaceae), and an averaged reflectance function from several green leaves (Chittka et al., 1994). b) Color loci of the same objects in the color hexagon. For *I. aggregata*, three color loci representing three individual flowers are depicted; only one of these is shown in a), belonging to the rightmost color locus. The area shaded light gray is the part of color space occupied by green foliage.

scentless, is visited by bumblebees and solitary bees (Fig. 5), in addition to syrphid flies, hawkmoths, and butterflies—and indeed hummingbirds (Elam and Linhart, 1978; Waser, 1978, 1982; Pleasants and Waser, 1985; N.M. Waser and A.K. Brody, unpublished). Interestingly, some of the bee visitors (and all of the other insect visitors noted above) are "legitimate", that is, they enter the front of the flower to seek pollen or nectar, whereas other bees bite holes in the narrow tubular corolla and rob the flowers of nectar through these holes, without transferring pollen. In some cases nearly 100% of flowers in populations in the Colorado Rocky Mountains are robbed by the bumblebee *Bombus occidentalis*, and such robbing reduces the reproductive success of plants (R. Irwin and A.K. Brody, unpublished). In northern Arizona, *I. aggregata* is robbed in a similarly thorough way by the solitary bee *Xylocopa californica* (L. Chittka, unpublished; Fig. 5). In the presence of such intensive robbing, we might expect natural selection for flowers to become minimally visible to bees. In spite of this, and in spite of the overlap between color loci of some *I. aggregata* flowers and those of green foliage (see below), field observations abundantly show that bees remain able to distinguish the flowers and respond to them.

Other red flowers known to lack UV reflectance are also visited by bees. The red flowers of the tropical forest tree *Sarcotheca celebica* (Oxalidaceae) are exploited by various bee species (Kevan, 1983), as are the red flowers of *Mimulus cardinalis* (Vickery, 1992; Sutherland and Vickery, 1993), which absorb UV strongly (Rosen, 1991). Further examples of flowers shown by Rosen (1991) to be UV absorbing are the red morph of *Zinnia elegans* (Asteraceae) and the red *Salvia splendens* (Lamiaceae), which are visited by bumblebees (Plateau, 1899). The Brazilian Atlantic forest species *Justicia rizzini* (Acanthaceae) and *Siphocampylus convolvulaceae* (Lobeliaceae) fit the "hummingbird flower" stereotype, but are visited by small stingless bees which crawl into the tube (L. Chittka, unpublished; spectral measurements in Chittka et al., 1994). The same strategy is employed by small solitary bees on *Lobelia cardinalis* (Campanulaceae) in northern Arizona (L. Chittka, unpublished; Fig. 5). The bright red, UV-absorbing (Rosen, 1991) flowers of this species are also visited by bumblebees (Stout, 1934). Daumer (1958) described the bee-pollinated, red *Nonea pulla* (Boraginaceae) as UV-absorbing. Dafni et al. (1990) list four species of red, UV-absorbing, primarily beetle-pollinated species (*Anemona coronaria* and *Ranunculus asiaticus* Ranunculaceae, *Tulipa agensis* Liliaceae, and, curiously, *Papaver rhoeas* Papaveraceae, which elsewhere is UV-reflecting; e.g., Fig. 4) which are secondarily pollinated by the bees *Lasioglossum marginatum* (Halictidae) and *Synhalonia plumigera* (Antophoridae).

There are several other examples of bee-visited red flowers whose UV reflectance still needs to be examined. Carpenter bees (*Xylocopa californica*) rob the tubular "hummingbird" flowers of chuparosa, *Justicia californica* (Acanthaceae) in warm deserts of the USA, and honeybees secondarily use the resulting holes to obtain nectar (N. Waser, unpublished). The same spe-

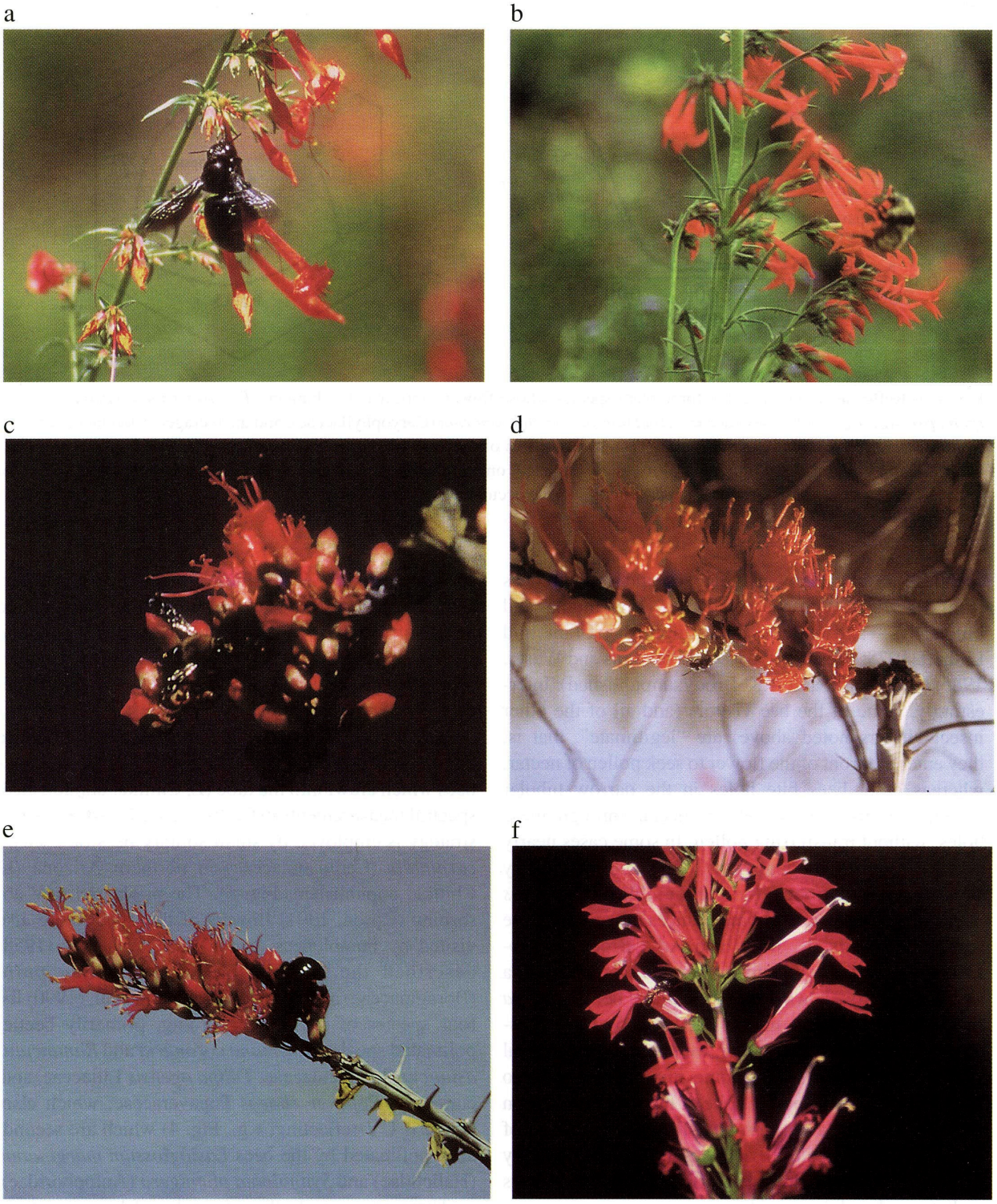

Fig. 5. Examples of bees foraging on red flowers: (a) *Xylocopa californica* punctuates the base of the spur of the scarlet gilia *Ipomopsis aggregata* to "steal" nectar; (b) a *Bombus appositus* queen on *I. aggregata*; (c) *Centris pallida* on ocotillo, or Devil's walking stick, *Fouquieria spendens*; (d) *Lasioglossum* sp on ocotillo; (e) *Xylocopa californica* on ocotillo; and (f) *Ceratina* spec. on the cardinal flower *Lobelia cardinalis*.

cies of carpenter bee robs (but also pollinates) the red tubular flowers of ocotillo, *Fouquieria splendens* (Fouquieriaceae), and these flowers also attract other solitary bees and honeybees along with many other insects and hummingbirds (Waser, 1979; Fig. 5). Macior (1986) describes the flowers of lousewort, *Pedicularis densiflora* (Scrophulariaceae) in California as "scarlet"; they are visited by bumblebees and hummingbirds. Similarly, the red beardtongue *Penstemon centranthifolius* (Scrophulariaceae) in California is visited both by hummingbirds and bees (Straw, 1956; Mitchell, 1989). Olesen and Knudsen (1994) report that bumblebee queens visited both red and white morphs of *Corydalis cava* (Fumariaceae) without apparent preference. The "explosive" red, bird-pollinated flowers of the misletoe *Peraxilla colensoi* (Loranthaceae) are visited by tiny solitary bees *Hylaeus* spec. (Kelly et al., 1996).

How do bees detect red flowers lacking blue or UV reflectance, such as *I. aggregata*, against a backdrop of foliage? This problem differs from the one discussed in the previous section because the reflectance of green leaves is not a step function. Leaves reflect moderately in all parts of the spectrum; they have a smooth reflectance peak in the green (as one might expect), but also reflect some blue and UV (Chittka et al., 1994). In addition, the bee eye adapts to the most common background, which for many flowers is green foliage. This adaptation adjusts the sensitivity of each color receptor type so that decreases in the spectral reflectance of background will be compensated by an increase in sensitivity. As a result most leaves appear achromatic for bees (Chittka et al., 1994), and their color loci fall near the uncolored point. As we have seen, red objects with λ_{step} >650 nm will also produce loci near the center of the color space, and may thus be hard for a bee to detect against green leaves. To be sure, λ_{step} in red flowers occurs at ~600 nm, not >650 nm. Such flowers will stimulate the bee's L-receptor (the green receptor) more strongly than the UV and blue receptors, and thus will appear bee-green (as will yellow flowers) rather than bee-uncolored as green leaves do. At the same time, the color distance between red flowers and green leaves is truly small, so these flowers will be more difficult to detect than flowers of other colors (such as *Papaper* and *Dianthus* in Fig. 4b).

Some flowers of *I. aggregata* have a stronger reflectance peak in the blue than shown in Fig. 4a, and the reflectance extends somewhat into the UV, albeit weakly (e.g., Meléndez-Ackerman et al., 1997). If this secondary peak is substantially larger than shown in Fig. 4a, a flower will appear *bee-UV-blue*, although still with low color contrast against green foliage (Fig. 4b, color locus labeled "3"). If the peak is intermediate in size, the flower may in fact appear as achromatic as green leaves (Fig. 4b, locus "2"). Such flowers will be truly hard to detect by means of color. Note, however, that this is not an effect of the red reflectance being outside the visual spectrum of bees. Instead, the moderate stimulation of the bees' green receptor by a red reflectance near the periphery of its spectral sensitivity is *combined* with a moderate stimulation of the bees' UV and blue receptors; thus all receptor types will contribute roughly equal signals, and an achromatic perception will result.

Even objects, such as a nearly achromatic *I. aggregata* flower, however, are unlikely to be invisible to bees against a backdrop of foliage. As the bee flies, the flower will move across its visual field at a different speed than the background (i.e., at a faster speed if the flower is closer, as is likely). This *motion parallax* helps a bee detect a target, even if both target and background have random patterns (Srinivasan et al., 1990). Furthermore, flowers do *not* have random patterns, and will usually be distinguished from a dappled leaf background by means of their shape. Bees are known to pay particular attention to pattern cues if the color difference between target and background is small (Giurfa et al., 1995).

Thus, while we maintain that red flowers will never be truly invisible for bees, we predict that they often will be harder to detect than flowers of other colors. Target detectability depends both on color contrast with the background (a certain minimal distance between their loci in color space must be exceeded for a target to be detectable), and green contrast (i.e., the signal difference between target and background generated by the bees' green receptor; Giurfa et al., 1996). Thus, for example, objects with poor green contrast must subtend substantially larger visual angles to be detectable (Giurfa et al., 1996); in other words, the bee must be closer to the object to detect it. Red flowers may provide smaller values both in terms of color contrast and green contrast than flowers of other colors. This may matter little in dense populations of plants, or when bees fly between flowers or inflorescences of the same plant. However, where interplant distances are greater, poor detectability may indeed slow the bees down as they locate flowers. Consistent with this expectation, Pleasants and Waser (1985) found that while bumblebee flight speeds between closely adjacent flowers of *I. aggregata* were comparable to those between flowers of "typical" blue-colored flowers also visited by the bees, interplant flights over longer distances were markedly slower. We conjecture that visitation frequencies may be depressed in isolated plants, or when plants with more easily detectable flowers are available at an equal

distance from a given point as those with red flowers.

WHAT IS THE SIGNIFICANCE OF RED FLOWER COLORATION?

The evidence we have marshalled strongly suggests that red coloration cannot be a means of excluding bees as flower visitors, as many pollination biologists have assumed (e.g., Raven, 1972). Red flowers do indeed reflect in a region that is at the periphery of the bee visual spectrum, and this may somewhat decrease their detectability relative, for example, to yellow flowers. But red flowers certainly are not invisible to bees! We hope very much that the weight of evidence from all quarters will finally cause this unfortunate misconception to be laid to rest.

At the same time, we have by no means resolved all enigmas concerning red flowers. For example, red flowers tend to be rare in areas that lack pollinating birds, including central Europe. Conversely, avian pollinators such as hummingbirds have a famous association with red flowers. What is the validity of this association, what is its nature, and how does it bear on the evolutionary significance of red flower coloration?

We first wish to reiterate (as, alas, still seems necessary—yet another tenacious dogma!) that there is no support for the widespread notion that hummingbirds innately prefer red (see Bené, 1941; Collias and Collias, 1968; Miller and Miller, 1971; Goldsmith and Goldsmith, 1979). Hummingbirds visit flowers of all colors essentially in proportion to nectar quality, thus using color as a learned predictor of this reward, not as the primary agent of attraction (e.g., Waser, 1983; Sutherland and Vickery, 1993; Waser et al., 1996). At the same time, there is evidence that red flowers in the Western USA are often pollinated heavily by hummingbirds, and often have a morphology that appears to fit well around hummingbird beaks and heads (e.g., Grant and Grant, 1968). To be sure, this apparent pattern has not been based to date on any rigorous survey of pollination, and quantitative studies of flower shape and of the fit of flower to pollinator are in their infancy (Armbruster, 1990; Wilson, 1995; Campbell et al., 1996; Temeles, 1996). Assuming that the association between hummingbirds and red flowers is real, however, we are left with a new enigma about red coloration. Since it is not an adaptation to match an innate preference of hummingbirds, nor a means to exclude bees, red coloration might perhaps be an adaptation to enhance detectability for birds. As noted above, objects of different coloration will often differ in terms of detectability; for example, to the human eye red berries stand out better against green foliage than blue or black berries (L. Chittka, unpublished). It is possible that hummingbirds detect red flowers more readily than flowers of other colors. At present, it is not possible to test this hypothesis, since a quantitative model of color perception is not available for hummingbirds (T.H. Goldsmith, D.F. Ventura, personal communication). So far, only two of possibly four (or more) color receptor types in hummingbirds have been identified (Chen and Goldsmith, 1986); further complications arise from the fact that light reaching the photopigments in bird receptors is filtered by colored oil droplets, but we do not know which photopigments are combined with which oil droplets (Varela et al., 1993). Thus, not even the receptor basis for these animals' color vision is known, and so a prediction as to whether red flowers contrast well against a leafy backdrop for hummingbirds would be hazardous. In addition, other mechanisms as yet unsupposed might also contribute to the apparent association of birds and red flowers.

CONCLUSIONS

We hope to have slain at least one dragon here, the dragon that tells us that bees cannot see red. Slaying the dragon may actually be important outside of the narrow confines of pollination biology. In some cases, entire scenarios in other biological disciplines have been built on the flawed assumption of red-blindness.

An excellent recent example involves the claim by Bradshaw et al. (1995) to have mapped the chromosomal locations of "speciation genes" in a pair of sympatric monkeyflowers (genus *Mimulus*). Bradshaw et al. imply that constraints of vision restrict bumblebees to pink *M. lewisii* flowers and hummingbirds to red *M. cardinalis* flowers, and that this restriction is a critical part of the complete reproductive isolation of these species (evidenced by an apparent complete lack of hybrids) in areas where they flower together. Under a biological species concept, such reproductive isolation is synonymous with specific status, which led Bradshaw et al. to the claim that the "speciation genes" in this case include genes coding for flower color. But all the evidence we have presented here suggests that flower color differences are unlikely to reproductively isolate plant species via restrictions on pollinator visual perception. Indeed, Vickery (1992) and Sutherland and Vickery (1993) had previously shown that foraging bumblebees and hummingbirds will visit and move between the flowers of different *Mimulus* species (including *M. lewisii* and *M. cardinalis*), in spite of color differences. In short, genes coding for flower color are unlikely to be centrally involved in the erection of strong reproductive isolation, and thereby in the process of

speciation; thus they are unlikely candidates for the long-sought "speciation genes" in angiosperms.

Another interesting example involves red spots on the back of the yellow crab spider *Misumena vatia*, which ambushes pollinating insects on flowers. Hinton (1976) concluded that the spots are warning signals to predators such as birds, but are invisible to insect prey. The spots are so small that they may indeed be hard to detect for insects, whose compound eyes provide relatively poor spatial resolution. But, as we have shown here, it simply is incorrect to assume that red coloration on a yellow background is invisible to insects.

In our opinion these examples of logical scenarios built on shaky foundations may reflect a more pervasive error. The notion persists among many biologists that color signals serve as "private channels" to address particular classes of animals, and that the animals have narrow innate color affinities. But when one looks beyond the context of mate choice, there is growing evidence that many animals, and not just flower visitors (Waser et al., 1996), respond to a broad range of colors, and use these as learned cues for food, danger, and so on. This is just what we would expect in a world that provides rich information in the form of electromagnetic radiation of different wavelengths. We strongly encourage all biologists to reevaluate the use of color signals, and the flexibility of this use, by insects and other animals.

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