Flower Color, Hummingbird Pollination, and Habitat Irradiance in Four Neotropical Forests[1]

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ABSTRACT

Pollinator visual systems differ considerably among broad groupings such as bees, bats, and birds, and it has been proposed that factors shaping the diversity of flower color in tropical plants include differences in pollinator perceptual abilities. Within the pollinators of the Neotropics, one major difference between taxa is that hummingbirds perceive color well across a broad range of wavelengths from 300–660 nm whereas most bees perceive color well over a narrower range spanning 300–550 nm. Thus, hummingbirds can see red and other long-wavelength reflection much better than bees. Another factor that could potentially influence flower color in tropical forests is the difference in light availability among habitats such as gaps, canopy, and forest understory. I conducted a survey of floral color in four Neotropical forests using a portable spectroradiometer to provide an unbiased measure of color reflectance. The primary pollinator agents and light habitats of each plant species were classified using primary literature or accounts of direct observations by experts. Flower color was not influenced by differences in light availability between open and closed habitats but was influenced by pollinator visual systems. Specifically, insect flowers reflected across a broad range of the spectrum but hummingbird flowers reflected mostly long-wavelength light (typically median wavelength >585 nm). Thus, hummingbird-pollinated flowers are not tuned specifically to hummingbird color sensitivity but instead may decrease conspicuousness to bees and other insects that have poor visual sensitivity to long-wavelength color.

RESUMEN

Existen considerables diferencias entre el sistema visual de los diferentes grupos de polinizadores, como las abejas, murciélagos, y aves. La diferencia en la habilidad perceptiva del polinizador ha sido propuesta como uno de los factores determinantes de la diversidad en la coloración de las flores en plantas tropicales. El rango de longitud de onda percibido por los polinizadores es una de las mayores diferencias entre los taxones: los colibríes perciben el color entre un rango de 300 y 660 nm, mientras que las abejas lo hacen en un rango que varía entre 300–550 nm. Por consiguiente los colibríes perciben el rojo y otras longitudes de onda mayores mucho mejor que las abejas. Otro factor potencial que podría estar influyendo en el color de las flores en los bosques tropicales es la diferencia en la disponibilidad de luz entre hábitats como claros de bosque, dosel, y sotobosque. Llevé a cabo un estudio sobre la coloración floral en cuatro bosques neotropicales. La reflectancia del color fue medida utilizando un espectro-radiómetro portátil, obteniendo así mediciones de alta precisión. Los agentes polinizadores primarios y los ambientes de luz para cada especie de planta fueron clasificados usando referencias literarias y expertos locales. El color de las flores no varió entre los hábitats abiertos y los cerrados. Sin embargo se encontraron variaciones relacionadas con el sistema visual de los polinizadores. En particular, las flores polinizadas por insectos reflectaron dentro de un amplio rango del espectro mientras que las de los colibríes lo hicieron dentro de longitudes de luz mayores (longitud de onda media >585 nm). Por lo tanto las flores polinizadas por colibríes no concuerdan específicamente con la sensibilidad al color de los mismos, en cambio son menos conspicuas para las abejas y otros insectos con menor sensibilidad visual a las mayores longitudes de onda.

MEASURING FLOWER COLOR AS IT RELATES TO A VIS-ITING POLLINATOR requires that we consider the visual system of the animals (Gumbert *et al.* 1999, Chittka *et al.* 2001). This presents a problem be-cause humans are trichromatic; *i.e.,* we see three basic colors and all other colors are combinations thereof. In contrast, diurnal birds have a more complex color vision system characterized by four (Chen & Goldsmith 1986, Bennett *et al.* 1994) or possibly five (Varela *et al.* 1993) pigments, as well as oil droplets that can act as filters and refine wavelength perception (Vorobyev *et al.* 1998, Hart *et al.* 2000). Like us, birds have opsin pigments, which are sensitive to wavelengths that are long (red), medium (yellow), and short (blue). It was

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first discovered in hummingbirds that birds also have a pigment sensitive to ultraviolet wavelengths (Huth & Burkhardt 1972), which we are unable to perceive. Considering insect pollinators, the ancestral color vision system is trichromacy with pigments maximally sensitive in the UV, blue, and green (Briscoe & Chittka 2001). A broader spectral range of color vision has evolved in some butterfly and a few bee groups, but many of the butterflies and most of the bees lack sensitivity to red (Bandai *et al.* 1992, Peitsch *et al.* 1992, Briscoe 2000, Briscoe & Chittka 2001). At the other extreme, it appears that New World bats have very poor color vision and rely on other cues for finding and orienting towards flowers (reviewed in Jacobs 1993).

To what extent are the colors of animal attractants tuned to the perceptual sensitivities of animals? This question has been addressed extensively in terms of ultraviolet (UV) color. UV is a common component of fruit color in both temperate and tropical communities (Burkhardt 1982, Willson & Whelan 1989, Altshuler 2001) and experimental removal of UV color decreases fruit attractiveness to birds (Siitari *et al.* 1999, Altshuler 2001). With regard to phylogenetic patterns, UV fruit color has evolved markedly more often in lineages with fruits dispersed by birds and rodents, both of which perceive UV (Altshuler 2001).

Flower color was one of the first natural objects shown to appear differently to some nonhuman animals. Early use of UV photography revealed strong UV color patterns that served as "nectar guides" to pollinating bees (Eisner *et al.* 1969). UV color patterns in flowers have been documented in numerous temperate and tropical species, and UV color appears to be a common feature of insect-pollinated flowers (Chittka *et al.* 1994). Few hummingbird-pollinated plants have been assessed for UV color, but the available data indicate that these species lack nectar guides (Faegri & van der Pijl 1979, Stebbins 1989) or other UV components (Chittka *et al.* 1994).

Human-visual colors have been used to classify flowers into "pollination syndromes" for temperate flowers, but broad surveys, particularly those including tropical flowers, have not revealed clear patterns between pollinators and color as classified by our visual system (reviewed in Feinsinger 1987). The first goal of this study was to measure the true color reflectance of flowers across the wavelengths relevant to pollinators (300–700 nm) and then to determine the relationship between flower color and pollinator visual systems.

Studies concerning habitat structure (*e.g.*, percent canopy cover) and light availability have revealed a strong influence of forest structure on irradiance patterns in forest habitats (Endler 1993). With respect to light, habitats have been classified into one of four types: large gaps, small gaps, woodland shade, and forest shade. In full sunlight, these habitats are typified by white, reddish yellow, blue–gray, and greenish ambient light spectra, respectively (Endler 1993). Because different light habitats are rich in different parts of the color spectrum, it follows that plant and animal colors will vary in their conspicuousness among habitats. This idea was tested among manakins that engage in lek mating and it was found that males display in (and compete for) microhabitats that maximize their color reflectance relative to the background (Endler & Théry 1996).

Contrast against a background of green leaves will be specific to the color vision system of the perceiving animal (Théry & Casas 2002) but can be accomplished most easily by reflecting in a hue very different from green (Chittka 1997). A complementary color for a given reflectance spectrum is $1 - R(\lambda)$, where $R(\lambda)$ is the reflectance at wavelength λ. Within the human visual range, a combination of red and blue (purple) provides the most complementary colors for green. For animals with UV-blue-green and UV-blue-green-red perceptual abilities, the UV portion of the spectrum also complements green. The conspicuousness of UV against a green background may explain why UV-reflecting fruits are common in both open and closed habitats, regardless of overall ambient light intensity (Altshuler 2001). The second goal of this study was to determine if flower color is also habitat-independent or if flowers in different light habitats reflect different colors to enhance contrast with the surrounding vegetation for their pollinators.

Flowers in the forest understory will reflect in two light habitats over the course of a day: forest shade and small gaps (small sun flecks). Because forest shade is rich in green ambient light and small gaps are rich in red light, flowers in the understory were predicted to reflect primarily in long-wavelength color, *e.g.*, yellow, orange, or red, because long-wavelength light is more available than short-wavelength light. Flowers in gaps and edges will be partially in woodland shade habitat and partially in gap habitat. Because woodland shade is rich in blue light and gaps are rich in white light, short-wavelength flowers, *e.g.*, ultraviolet, violet, or blue, should be more abundant in open habitats that will be in woodland shade during part of the day.

The final goal of this study was to assess the role of multiple colors in floral displays. Considerable attention has been given to the role of bicolored versus unicolored displays on rates of fruit removal (Willson & Thompson 1982, Willson & Melampy 1983, Whelan & Willson 1994). Fruits with bicolored displays were removed at higher rates than fruits with unicolored displays, and this difference was stronger in gaps than in the forest understory (Willson & Melampy 1983). If bicolored or tricolored floral displays are better at attracting legitimate pollinators compared to unicolored displays, then it is unclear why most flowers do not reflect multiple colors. I tested for associations among uni-, bi-, and tricolored floral displays with habitat type to determine if multicolored displays were more common in open (woodland shade and gaps) or closed (forest shade) habitats. I also tested for a relationship between the number of colors in a display and the pollinator visual systems (hummingbirds vs. insects).

MATERIALS AND METHODS

I collected data at four sites in the Neotropics between 6 September and 14 November 2001: La Selva Biological Station in Costa Rica (LS), the Barro Colorado Nature Monument in Panama (BCI), the Cocha Cashu Biological Station in Peru (CC), and the Kilometer 41 (KM41) site north of Manuas, Brazil. In Panama, additional fieldwork was conducted on Pipeline Road in Parque Nacional Soberanía. During this period, it was the wet season for sites in the northern hemisphere (LS and BCI) and the end of the dry season for sites at the equator and farther south (CC and KM41). Gentry (1990) provides a complete description of these sites.

HABITAT LIGHT MEASUREMENTS.—Habitat irradiance was measured in three of Endler's (1993) light habitats (large gaps, woodland shade, and forest shade) under both cloudy and direct sun conditions. Small gaps are defined as "sunlit locations in the forest (at any height) in which a canopy hole subtends a solid angle similar to that of the sun" (Endler 1993). This is similar to most definitions of "sun flecks" except that the light from small gaps does not necessarily reach the forest floor. The purpose of my habitat light survey was to test if light habitats of flowers differed among the forests. I added a new category, "medium gaps," to determine if gap size was an additional variable of interest for flower color; medium gaps are sunlight locations

with exposure to at least 1° but not more than 5° solid angle of blue sky. Sites classified as large gaps were created by recent treefalls and irradiance measures (scans) were made at points with direct sunlight and no overhead vegetation across an angle of 10°. A site was classified as forest shade if, during sunny conditions, no sun reached it during the scan and it was not exposed to a large area of open sky such as provided by a gap. Sites of woodland shade were located at the edge of gaps and contained no overhead direct sun exposure but considerable exposure to blue sky. The same sites were measured during cloudy conditions with respect to the estimated position of the sun, but in these cases the clouds obscured the sun.

Irradiance was measured using a portable spectrophotometer (Ocean Optics USB2000) and a cosine-corrected probe (Ocean Optics CC-3). The wavelength calibration was performed using a mercury argon lamp (Ocean Optics HG-1) and the intensity calibration for irradiance was made using a tungsten halogen lamp (Ocean Optics LS-1-CAL), which is only reliable down to 350 nm. Accordingly, the irradiance values below 350 nm are not presented. A minimum of three measurements at each habitat and in each condition was made between 0900 and 1600 h.

FLOWER COLOR.—Flowers were collected along trails, in gaps and clearings, and in the forest understory. Plants were identified to genus or species by local botanists at each site (data available from author upon request). A combination of primary literature, field guides, and personal communication with experts was used to classify plants according to their light habitats, which were classified as either closed (flowering in the forest understory) or open (flowering in gaps, edges, or canopy). Plants that are specialized to edges of gaps and clearings are typically in woodland shade for part of the day and in gap conditions for the rest of the day. Accordingly, their flowers are exposed to direct sunlight for a substantial portion of the day, and edge flowers were placed in the open habitat category.

Plant pollinators were assigned using direct observations, either from published sources or from personal communication with researchers engaged in long-term projects at the sites. This restricted data set was only a fraction of the plants encountered during the study; thus, a second, broader analysis was also conducted using less rigorous requirements by including pollinator assignments from field guides.

Flower color was also measured using the portable spectroradiometer with a reflectance probe (Ocean Optics R400 UV/VIS) and high power xenon strobe light source (Ocean Optics PX2) to attain spectral reflectance values. Specifically, radiance was measured across UV, human visible, and near-infrared (IR) wavelengths (300–700 nm). Reflectance was calculated as the radiance of the color patch divided by the radiance of a certified white standard (Labsphere) made of Spectralon material. Wavelength calibration was performed at each site using the mercury argon lamp. All radiance measures were made at an angle of 45° with the probe shielded from all ambient light, thus allowing only the light source and the sensor to be in the reading chamber. Each color component of each flower was measured three times from which the mean and standard deviation of reflectance across all potentially visible wavelengths were calculated. I also scanned across the color patches to search for UV or other color components invisible to humans. For each species, the median wavelength was calculated as the wavelength that separated the spectrum into two equally intense parts: the integral of the spectrum to the left equaling the integral of the spectrum to the right. After scanning, I classified flowers as being uni-, bi-, or tricolored.

ANALYSIS.—The relationships among flower variables were tested using two methods. I first used analysis of variance (ANOVA) to determine the effects of pollinator class, habitat, and the number of colors in the display on the median wavelength. Associations among the three independent variables were then analyzed using three pairwise chi-square tests of species counts.

My second method consisted of a phylogenetically controlled analysis, which is an important validation for a study involving comparison of multiple taxa. The major requirement for a comparative test is an explicit phylogenetic framework, which was not available for all of the taxa present in my study. Instead I constructed a partially resolved, approximate topology solely for the statistical analysis. The underlying structure of this topology was based on the major family classification for angiosperms (Soltis *et al.* 1999). Phylogenetic studies at the order and family level were used to construct lower-level topology (Brember & Jansen 1991, Scotland *et al.* 1995, Smith *et al.* 1997, Morton *et al.* 1998, Andersson & Rova 1999, McDade & Moody 1999, Spangler & Olmstead 1999, Andersson & Chase 2001, Kajita *et al.* 2001). Correlations between pairs of discrete characters were

then tested using the concentrated changes test (CCT; Maddison 1990). The CCT uses iterative simulations to test for nonrandom association of the evolution of a dependent trait in lineages that contain the independent trait. This analysis was performed using the software MacClade (Maddison & Maddison 1992). All significance values in both types of analysis were adjusted with the sequential Bonferroni correction technique when necessary (Rice 1989).

RESULTS

HABITAT IRRADIANCE.—During cloudy conditions, the irradiance curves converged on the same shape in all of the light habitats, as has been previously noted (Endler 1993). Because light was filtered through clouds, the curves were mostly even across visible wavelengths and thus were rich in white light (Fig. 1). In forest shade, the curve peaked near 560 nm and was thus slightly richer in green light (Fig. 1a). The overall intensity (height of the irradiance curve) decreased with increasing cloud cover such that scans made under thinner clouds had greater intensity and thus overall higher values of irradiance.

Under full sun, the light habitats differed more strongly in the irradiance peaks (Fig. 2). The ambient light in forest shade habitat had peak irradiance near 560 nm and was thus rich in green light (Fig. 2a). The light in woodland shade was strongly influenced by the blue sky as evidenced by the peak irradiance values between 450 and 550 nm (Fig. 2b). In both large gaps and medium gaps (Fig. 2c, d), the irradiance curve was relatively flat and thus rich in white light. In both of these cases, however, slightly more irradiance was available at longer wavelengths. The overall intensity in all of the habitats increased with increasing angle of the sun. The greatest intensity was measured as the sun approached the orthogonal of the plane of the cosine receptor probe.

GENERAL PATTERNS OF FLOWER COLOR.—Reflectance measures were made on all floral components from 115 individual plants comprising 92 species from 28 plant families. These 92 species, however, were not collected randomly because the survey concentrated on flowers that seemed likely to be pollinated by birds (Table 1). Of these plants, 45 species (49%) had unicolored floral displays, 41 species (45%) had bicolored displays, and 5 (5%) had tricolored displays. The ginger *Costus pulverulentus* was unicolored (red) at Barro Colorado Island and
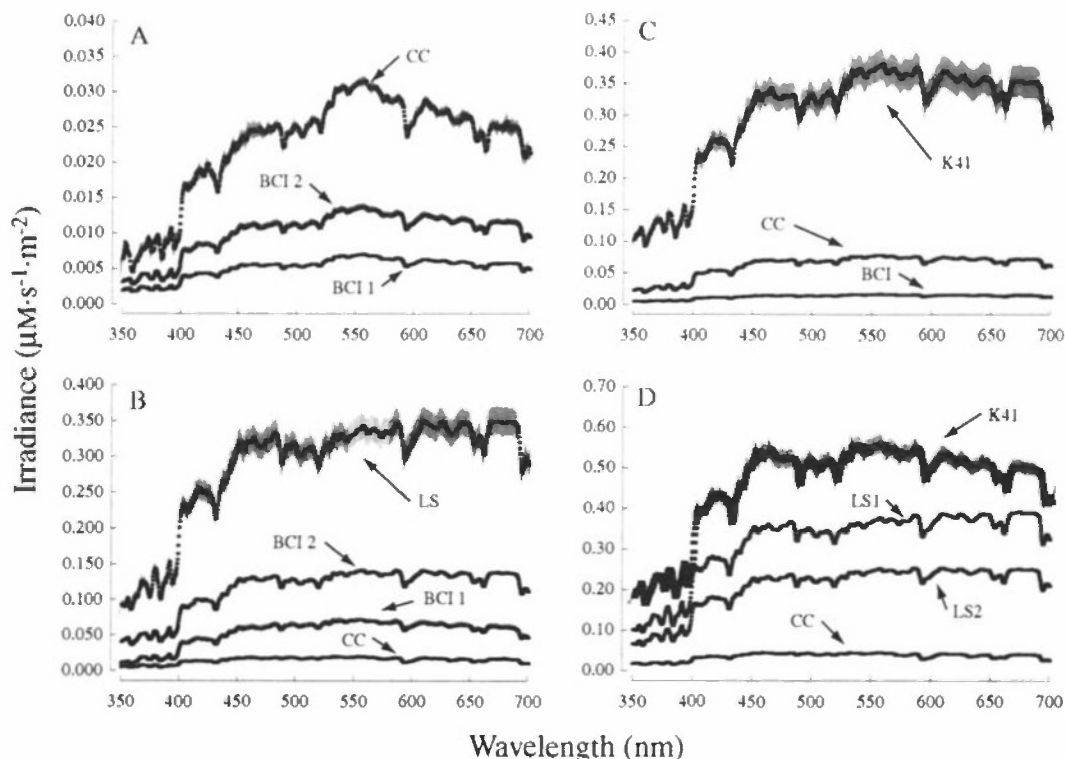
FIGURE 1.   Irradiance in four light habitats during cloudy conditions. Three scans were made for each habitat at each site within three minutes. Mean irradiance (μM/s/m^2/nm) is plotted in black and the standard deviations are plotted as gray lines. The irradiance curves in (A) forest shade were mostly flat but contained a minor peak near 560 nm. The irradiance curves in (B) woodland shade, (C) medium gaps, and (D) large gaps were also close to flat. As cloud cover decreased, the overall intensity increased, producing higher curves. Thus, differences among sites in the height of the curves resulted from scans under varying degrees of cloud cover and do not represent overall site differences.

bicolored (red and yellow) at La Selva without any obvious differences in light habitat or visual background conditions.

Unicolored displays could consist of either "short"-wavelength color (see below) such as purple or pink or a long-wavelength color (*e.g.,* red, yellow). Bicolored displays always contained at least one long wavelength color, but the second color could be a long- or short-wavelength color. Tricolored displays always contained at least one exclusively long-wavelength color, but the second and third colors varied across the spectrum.

Most of the flowers contained a color patch that was exclusively long-wavelength reflection, with 63 (69%) species reflecting red, orange, or yellow as a prominent floral component (Fig. 3). Among the bicolored displays it was extremely common to have two long-wavelength components. Four species had orange/red displays, 4 had orange/yellow displays, and 12 had red/yellow displays (Fig. 3b).

Another common set of colors in flower displays was purple, pink, and maroon. Of the 92 species, 38 (41%) had at least one of these colors in some part of the floral display. All of the purple and pink flowers had reflection curves with two peaks, one in the blue and one in the red portion of the spectrum, effectively color mixing (Fig. 4a, b). These colors were also common in unicolored displays (18 out of 46; 39%) or in bicolored displays with white as the second color (10 out of 43; 23%). An example of the latter pattern in purple and white is given in Fig. 4a. Maroon and deep purple appeared similar to the human eye but relied on different portions of the spectrum. Whereas purple components had a two-peak reflection curve with both long- and short-wavelength components, the maroon colors projected as reflectance curves with only very long-wavelength reflection (Fig. 4c).

Fifteen of the purple and pink flowers also had reflectance in the ultraviolet greater than 10 percent. Nine other plant species had UV reflectance
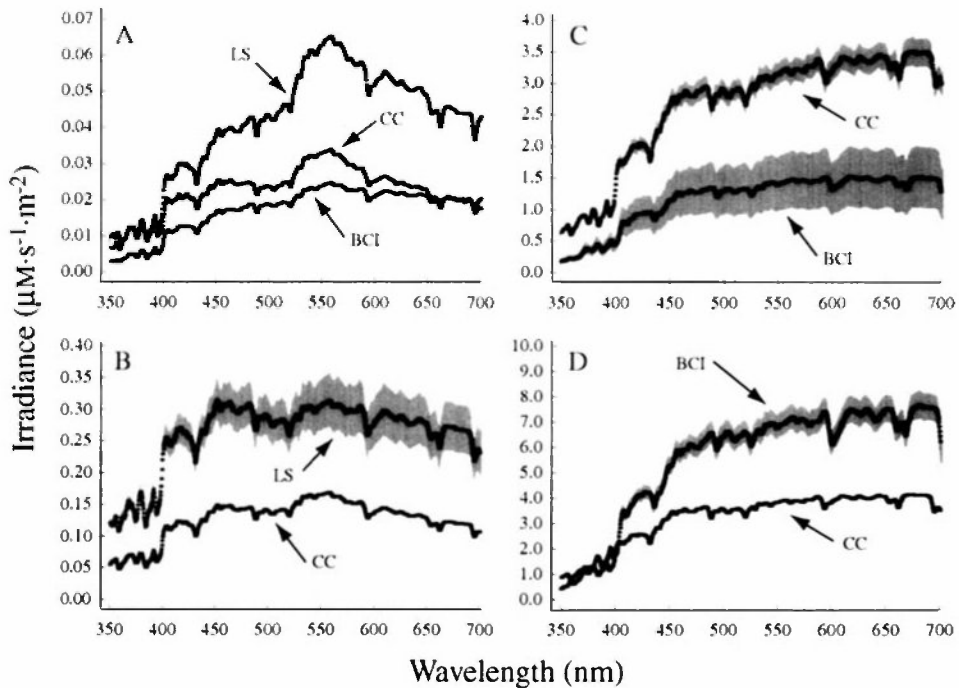
FIGURE 2.   Irradiance in four light habitats during full sun conditions. Mean irradiance ($\mu M/s/m^2/nm$) is plotted in black and the standard deviations are plotted as gray lines. The irradiance curve in (A) forest shade is rich is green light whereas the irradiance of (B) woodland shade is richer in blue light. The irradiance curves in both (C) small gaps and (D) large gaps are rich in white light. As the sun was more directly overhead, the overall intensity increased and the lower curves resulted from scans under sun at lower angles.

but these were colored white or yellow with the spectral curve extending down below 400 nm with greater than 10 percent reflectance. Although ultraviolet reflectance was relatively common in the purple and pink flowers, no flowers had peak reflectance in a color curve below 400 nm. Furthermore, none of the flowers examined in this study contained UV nectar guides.

Although UV was uncommon in the Neotropical flowers surveyed in this study, this color is common in both tropical and temperate fruits

(Burkhardt 1982, Willson & Whelan 1989, Altshuler 2001). Of the 92 species in which the flowers were scanned, 4 species (3 from the genus *Heliconia*) also had ripe fruits at the same time on other or, in some cases, the same individuals in the populations. The reflectance properties of these fruits were measured and compared to flower colors (Fig. 5). Although many species with red and yellow floral displays contained only long-wavelength reflection, their fruits were often strongly reflecting in short wavelengths and appear blue to humans.

TABLE 1.   *The number of plant taxa at each site with measured flowers that could be classified according to the number of colors in the floral displays, the light habitats, and the pollinators. Pollinator numbers represent classifications based on direct observations, with classifications based on all available sources in parentheses. Some taxa were present at multiple sites and are included in multiple lines within a column.*

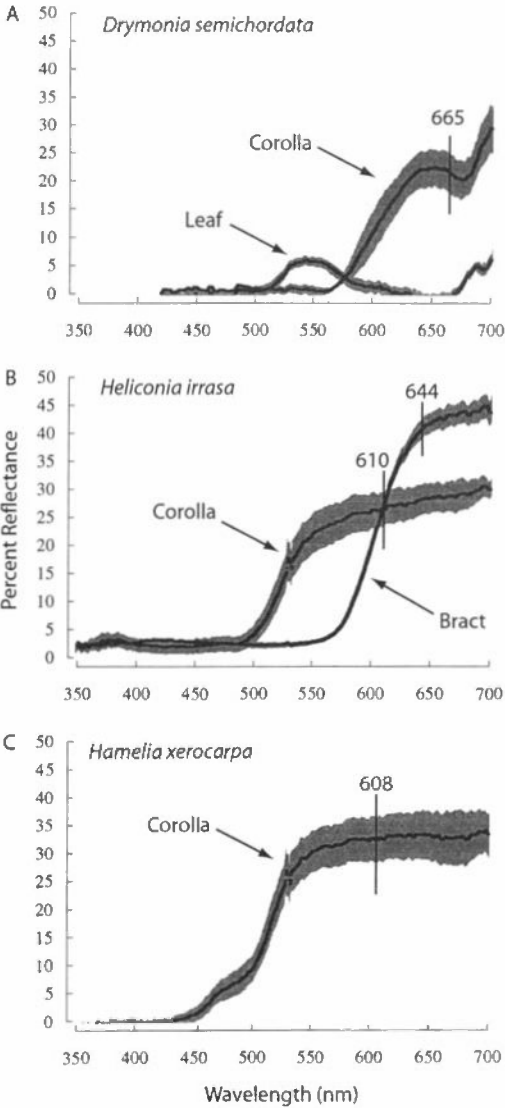| Site	Number of colors		Light habitat		Pollinators	
	One	Multiple	Closed	Open	Insects	Hummingbirds
BCI	11	15	1	3	7 (12)	4 (10)
KM41	9	6	4	11	2 (7)	2 (4)
CC	12	13	6	12	0 (11)	1 (7)
LS	14	17	3	14	5 (6)	15 (17)
Totals	46	51	14	40	14 (37)	22 (38)

FIGURE 3.   Some examples of red and yellow color reflectance in flowers. Floral components reflecting red had curves with median wavelengths that fell between 610 and 665 nm (A,B) and were often located close to leaves, which may have served as an additional color component (A). Flowers reflecting yellow had curves with median wavelengths between 564 and 624 nm (B, C), and were frequently presented in combination with red floral components (B). The median wavelengths are indicated by thick vertical lines with the values written above.
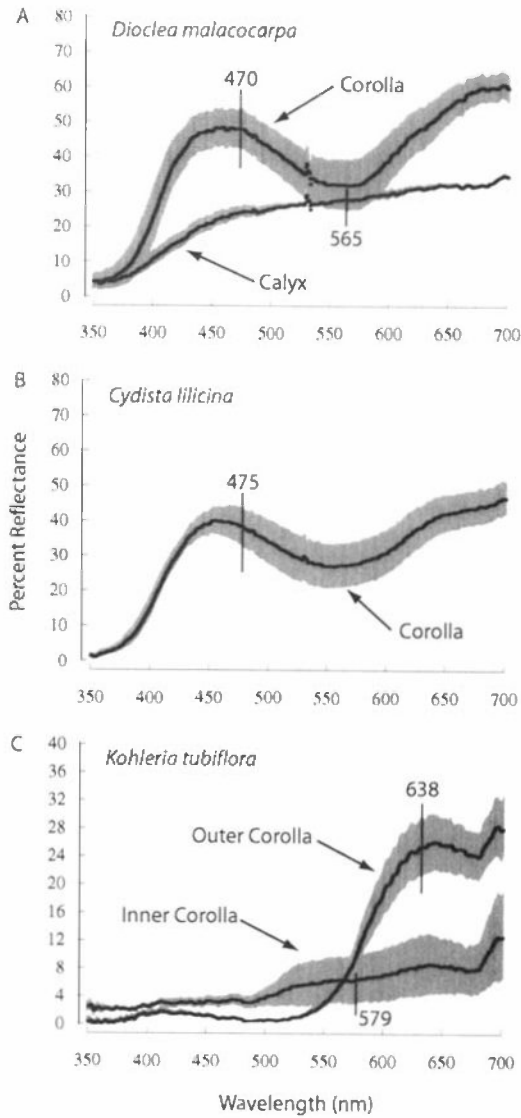
FIGURE 4.   Purple color in flowers. The (A, B) purple flowers had peaks in the reflectance curves at both short and long wavelengths whereas the (C) maroon flowers peaked only in the far-red. For curves with two peaks, the median wavelength was calculated for the lower peak of that portion of the curve from 300 nm to the next lowest trough. The median wavelengths are indicated by thick vertical lines with the values written above or below.

RELATIONSHIPS BETWEEN FLOWER COLOR AND ECOLOGICAL VARIABLES.—All of the flower reflectance curves were high at long wavelengths and varied primarily in the median wavelength. A two-way ANOVA was performed to test for the effects of light habitat (open vs. closed), and pollinator (hummingbirds vs. insects) on the median wavelength for the color components of a given flower with the lowest median wavelength (Table 2). The only significant effect was the pollinator. Specifically, hummingbird-pollinated plants had higher median wavelengths than plants pollinated by insects. Another ANOVA was conducted using the
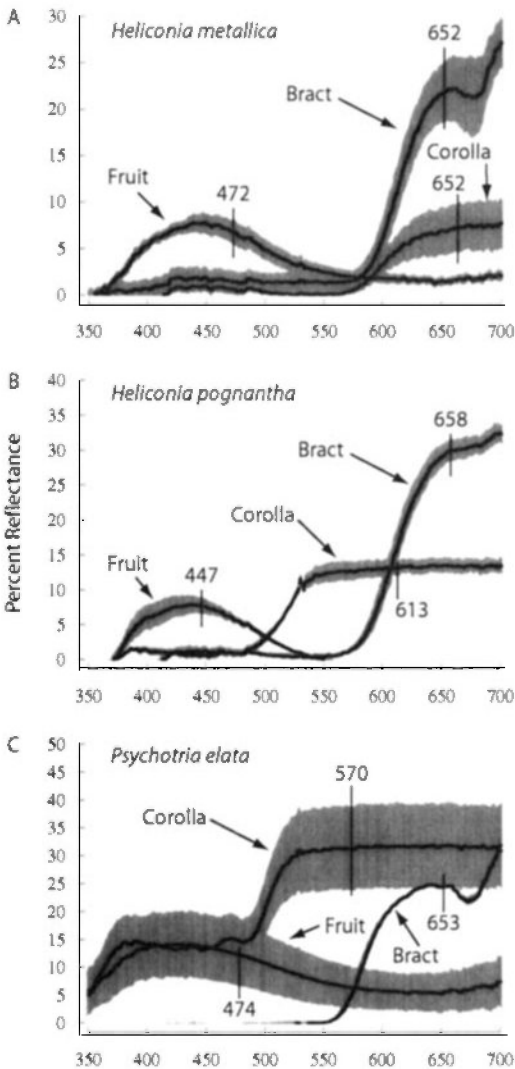
FIGURE 5.   Colors of both fruits and flowers when these occurred together temporally or spatially. The fruits that occurred with flowers reflected primarily in short-wavelength light, with a considerable UV component. The median wavelengths are indicated by thick vertical lines with the values written above or below.

less restricted pollinator assignments so that sufficient sample was available to test three factors: light habitat, pollinator, and color display (unicolored vs. multicolored). As in the first analysis, the only factor related to flower color was the pollinator (Table 3), and this effect was highly significant even after Bonferroni correction across both tables (Rice 1989). Associations among the three discrete, independent variables from the ANOVA were tested using pairwise chi-square tests. No significant associations were detected.

The relationships among flower variables were further tested using the concentrated-changes test to incorporate historical effects of phylogeny. Associations between variables were tested under two assumptions of character state evolution. The DELTRAN model delays trait evolution whereas the ACCTRAN model accelerates trait evolution (Swofford & Maddison 1987). Both results are presented and these two assumptions help to bracket the possibilities for the true character traces. Other features of the tree that can potentially confound the analysis include artifacts of taxon sampling and the accuracy of the topology, which is an error potentially compounded in composite tree assembly

One million simulations per test were used to estimate probabilities that gains and losses in long-wavelength flower color (median reflectance was ≥ 585 nm) were concentrated in clades with an independent character of interest. In the first pair of tests, I hypothesized that gains in long-wavelength flower color were concentrated in lineages with hummingbird-pollinated flowers, whereas losses were concentrated in lineages with insect-pollinated flowers. The null hypothesis of no concentration of changes was strongly rejected with all $P < 0.025$ for both the restricted and the broad data sets under both DELTRAN and ACCTRAN assumptions. I next tested the hypothesis that gains of long-wavelength flower color were concentrated in lineages with plants in closed habitats whereas losses were concentrated in lineages with plants in open habitats. The null hypothesis was not rejected under either assumption (both $P > 0.15$).

TABLE 2.   *Results from a two-way ANOVA for the effects of light habitat and pollinator on the median wavelength of the floral color component with the minimum median wavelength.*

Effect	df	MSE	F	P
Light habitat	1	1480.665	1.17	0.2965
Pollinator	1	36160.876	28.574	<0.0001
Light habitat × pollinator	1	1041.63	0.823	0.3786
Error	15	1265.506		

TABLE 3. *Results from a three-way ANOVA for the effects of light habitat, number of colors in the floral display, and pollinator on the median wavelength of the floral color component with the minimum median wavelength.*

Effect	df	MSE	F	P
Light habitat	1	12.108	0.004	0.9475
Color display	1	2.162	0.001	0.9778
Pollinator	1	37136.516	13.522	0.0009
Light habitat × color display	1	1121.199	0.408	0.5274
Light habitat × pollinator	1	2025.763	0.738	0.3968
Color display × pollinator	1	2923.759	1.065	0.3099
Light habitat × color display × pollinator	1	614.310	0.224	0.6395
Error	32	2746.326		

DISCUSSION

HABITAT IRRADIANCE.—The ambient light characteristics of three of the four habitats I surveyed were first described by Endler (1993). His earlier findings were corroborated here and it was also determined that large gaps and medium gaps are virtually identical in terms of the shape of their irradiance curves. A recent survey focused on the light habitats in the Nouragues National Reserve of Guyana and revealed differences in hue, photosynthetically active photon flux density, and red:far-red ratio in forest shade habitats of different vegetation types and topography (Bongers *et al.* 2001). For example, forest shade habitat was sampled on slopes, in creeks, and in liana understory sites. In contrast, the forest shade habitats sampled among the four sites in the current study were selected to be as similar as possible. Future work on comparative forest ecology would benefit from sampling fine-scale variation among forest shade habitats to determine if the differences detected by Bongers *et al.* (2001) are also similar across sites.

FLOWER COLOR.—The results from the survey of floral color revealed that flowers reflecting longer wavelengths are associated with hummingbird pollination and that the evolution of flowers with the median wavelength greater than 585 nm has been concentrated in lineages pollinated by hummingbirds. Insect-pollinated flowers reflected across the entire visible range of hummingbirds. Furthermore, hummingbirds frequently visit, and may even pollinate, "insect" flowers. Thus, "hummingbird flowers" were unique in being inconspicuous, although not necessary invisible (Chittka & Waser 1997), to bees. Many of the hummingbird-pollinated flowers were further protected from bee visitation by long, tubular corollas as is typical of this syndrome (Feinsinger 1987). This pattern fits the hypothesis recently posed by James D. Thomson, namely, hum-

mingbird flowers are really "not-bee" flowers (Thomson *et al.* 2000). In other words, hummingbirds will visit most flowers, but some flowers are visited only by hummingbirds. This idea has been underscored by numerous behavioral studies (Collias & Collias 1968, Miller & Miller 1971, Stiles 1976, Goldsmith & Goldsmith 1979, McDade 1983) demonstrating that hummingbirds exhibit little or no color preferences (cf. Waser & Price 1981).

The relationships between flower color and hummingbird pollination can vary from highly specialized to generalized depending upon the interactions among the plants, the hummingbirds, and potential nectar robbers (Waser *et al.* 1996). Understanding of the sources of variation in these relationships will benefit from an evolutionary approach to studying color vision (Briscoe & Chittka 2001, Chittka & Briscoe 2001). For example, phylogenetic analyses have revealed that the basic insect trichromacy (UV/blue/green) was probably present in arthropod ancestors 400 million years before the radiation of angiosperms, suggesting that insect-pollinated flowers colors are color-adapted to insect vision, rather than vice versa (Chittka 1997). In contrast, hummingbirds radiated as recently as 15 to 20 million years ago (Bleiweiss 1998b), although red flowers may have existed previously for specialized pollination by insects with red-receptive cone pigments (Briscoe & Chittka 2001). Nonetheless, it would be highly informative to examine the evolution of red flowers in response to the colonization patterns of hummingbirds in the western hemisphere (Bleiweiss 1998a).

The results of this study indicate a tight relationship between flower color and pollinators, and no relationship between the light habitat and either flower color or the numbers of different color components in a display. This raises the question as to how color functions in pollinator attraction. Flower color can function in the initial attraction of a pol-

linator to a new flower patch or color could help returning pollinators relocate flowers. One test designed to distinguish between theses hypotheses was performed using hummingbirds (*Selasphorus rufus*) returning to flowers that they had previously visited. These hummingbirds exhibited a preference for returning to a flower in the same location rather than a flower of the same color (Hurly & Healy 1996). This suggests that hummingbirds use color primarily for the initial search for new floral resources but rely on location for returning to previously visited flowers. Bees, in contrast, utilize color cues for fine-scale orientation such as provided by nectar guides (Jones & Buchmann 1974).

No UV-reflecting flowers were found other than those with blue, yellow, or white flowers, for which the reflectance curves extended below 400 nm. This pattern appears to be a common feature of bee-pollinated flowers in which UV is an important but not exclusive color component (Chittka *et al.* 1994), except for nectar guides. In contrast, flowers that are adapted for exclusive pollination by hummingbirds appear to lack UV in both temperate (Faegri & van der Pijl 1979, Stebbins 1989) and tropical (this study) communities.

Although the bird-pollinated flowers in this study reflected long wavelengths, the bird-dispersed fruits of those same plants frequently reflected short-wavelength color. UV-reflecting fruits are common for tropical plants (Altshuler 2001) but it is also common for tropical fruits to reflect long-wavelength light such as orange and red (Wheelwright & Janson 1985, Willson & Whelan 1990).

Why then this peculiar combination of short-wavelength reflecting fruits with long-wavelength reflecting flowers? The few fruits included in this survey all came from plants that had both flowers and ripe fruits available. In all cases, the plants also displayed both flowers and fruits within or against semipermanent red bracts. These red bracts will thus function well in attracting bird pollinators but the subsequent contrast between UV/blue fruits and the red bract background may facilitate attracting avian fruit dispersers. Strong differences in color between floral and fruit displays may also help distinguish flowers from fruits for pollinators, particularly insect pollinators.

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