Floral color patterns and pollinator attraction in a bog habitat

SHEILA DOUGLAS
Box 297, Port Clements, Queen Charlotte Islands, B.C., Canada V0T 1R0
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Floral color in 14 species of bog plants was examined in relation to intrafloral patterns, flower morphology, background coloration, and pollinators. There were three corolla color groups: UV-absorbing white (eight species), UV-absorbing pink–red (five species), and UV-reflecting yellow (one species). Contrast with vegetational backgrounds in UV light was minimal for species that absorbed UV, but such species exhibited contrast in the visible specrtum which enhanced long-range conspicuousness. Patterns created by contrasting colors within corollas emphasized the reproductive organs and are considered as nectar guides for short-range attraction of pollinators to food rewards. Floral color was not correlated with diameter, height, or density of corollas. Bumblebee pollinators showed preferences for pink–red stereomorphic species, whereas Diptera showed preferences for white actinomorphic inflorescences.

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L'auteur a étudié la couleur de la fleur de 14 espèces de plantes de tourbières, en mettant l'accent sur les patrons à l'intérieur de la fleur, la morphologie florale, la couleur de l'arrière-plan et les pollinisateurs. Il y a trois groupes de couleurs chez les corolles: des corolles blanches absorbant l'UV (huit espèces), des corolles roses ou rouges absorbant l'UV (cinq espèces) et des corolles jaunes réfléchissant l'UV (un espèce). En lumière ultraviolette, le contraste avec la végétation environnante est minimal chez les espèces qui absorbent l'UV, mais ces espèces présentent, dans le spectre visible, un contraste qui rehausse leur visibilié de loin. Les patrons produits par la présence de couleurs contrastées dans une même corolle soulignent les organes reproducteurs; ces patrons sont considérés comme des guides de nectar qui, sur de courtes distances, attirent les pollinisateurs vers une source de nourriture. La couleur de la fleur n'est pas corrélée avec le diamètre, la hauteur ou la densité des corolles. Les bourdons préfèrent les espèces à fleurs stéréomorphes roses ou rouges, tandis que les diptères préfèrent les inflorescences blanches actinomorphes.

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Introduction

Floral coloration is an important long-range visual cue for pollinators, and in some cases, different kinds of pollinators exhibit differing preferences for floral color in their visits to blossoms. Associations between color and specific pollinators have been found in several polymorphic and closely related flowering species. In two species of *Platanthera* which varied in corolla color, the orange species was visited primarily by butterflies and the creamy white one by moths (Smith and Snow 1976). Hinton (1976) found that in *Calyptridium monospermum*, the main pollinator of the rose-petalled race was *Bombus* sp. (Apidae), whereas butterflies, flies, and wasps pollinated the white-petalled race. Among five species of *Chlorogalum*, differences in ultraviolet reflection, as well as in floral scent and time of floral opening, attracted different groups of pollinators (Jernstedt 1980). Mogford (1978) found that in habitats where insect visitation was limited by harsh weather bumblebees preferentially visited the white-flowered morph of *Cirsium palustre* rather than a purple morph of the same species.

On a community or geographical scale, investigations of the relationship between floral color and specific pollinators are limited. In a study of long-range pollinator cues (color, brightness, size, and odor of inflorescences) among 69 nonnative flowering species in Ontario, Mulligan and Kevan (1973) found that none of these cues had special value in attracting any specific insect or group of insects. Among plants in the High Arctic (Kevan 1972), differential attraction was present only in *Stellaria longipes*, a white-flowered species that was visited more frequently by parasitic Hymenoptera than by other insects. In both of these studies, however, there were differences in the frequency of insect visitors to species with different floral colors.

To test whether different pollinators showed color preferences in a habitat with a limited flora, I examined spectral reflectance in 14 species of flowering plants in a *Sphagnum* bog and recorded insect visits to these plants. Other floral characteristics (height, density, and diameter of inflorescences, flower form, and coloration of floral background) which might act in concert with floral color to attract insects were also considered.

Materials and methods

Drizzle Lake Ecological Reserve is located in an expanse of low-lying bog and coniferous forest in the northeast corner of the Queen Charlotte Islands, British Columbia. The 25-ha study area within the Reserve is a raised bog with a perennially wet substrate of *Sphagnum* spp. and a ground cover composed primarily of sedges and low shrubs. Dwarf conifers (*Thuja plicata* Donn and *Pinus contorta* Dougl. ex Loud.) are widely spaced, such that the habitat receives maximum exposure to sunlight. All plant and insect species in the study are indigenous.

Floral hue in the visible spectrum (400–700 nm) and ultraviolet (UV) (340–400 nm) was assessed for 14 species of bog plants. Inflorescences were photographed through a series of Kodak filters that isolated wave bands corresponding to recognized color names (Table 1), similar to a technique used by Kevan (1972). Each species was photographed in its habitat close enough to distinguish details of the inflorescence and its immediate background, and in UV frames, from 1 to 4 m away. General habitat frames were included as well. A Canon macro FD 50-mm lens mounted on a Canon AT-1 body with Tri-X film was used in all cases. The transmittance characteristics of the lens in the UV wave band are 5% at 340 nm, 45% at 360 nm, 67% at 380 nm, and 77% at 400 nm. (T. Takiguchi, personal communication).

A test film was made to select appropriate exposures for the filters. A Kodak Gray Scale (graduated from 0.0 to 1.9 reflectance density in 0.1 density increments) and Kodak test cards (90 and 18% reflectance, approximating densities of 0.1 and 0.6 on the Gray Scale) were photographed at a range of exposure times for each filter combination. Shutter speed was set at 1/250 s for unfiltered meter readings and lens aperture at *f*/11. For each filter combination, the exposure time which showed a gradient in the Gray Scale and maximum difference between 0.0 and 1.9 densities was chosen as a standard. In subsequent photographs, differing light conditions were compensated for by adjusting the aperture to maintain a speed of 1/250 s for unfiltered light. To standardize printing, a four-point graded scale, consisting of chips of the Gray Scale with densities of 0.0, 0.4, 1.0, and 1.9, was included in each frame. As well, species flowering at the same time were photographed against Kodak test cards. Natural daylight illumination was the light source for all photography, and included moderate light levels during cloud cover through to direct sun. Replicates of filtered photographs showed slightly different reflectance values for some species; this may be due to high illuminance creating specular reflections (Kevan 1979). In these cases, luminance factors within the range of values were used.

Measurements were taken of corolla and inflorescence diameter and of height of the corolla above the ground. Species were categorized as to flower form (actinomorphic or stereomorphic). Numbers of open corollas in metre quadrants were recorded for each species at peak flowering. Where the inflorescence appears as a single target rather than separate aggregated corollas, I use the data on inflorescence (rather than corolla) diameter and density. In *Cornus unalaschkensis*, the four white bracts surrounding the inflorescence are treated as the tepals; similarly, in the apetalous *Sanguisorba officinalis* the united sepals are treated as the corolla.

During the flowering seasons of 1979 and 1980, diurnal pollinators and floral visitors on each species were noted; representatives of the most important groups of pollinators (bumblebees, syrphid flies, and butterflies) were collected for identification.

Results

Floral hue in 14 species of bog plants is summarized in Table 2. Half of the species (*Ledum palustre* ssp. *groenlandicum*, *Tofieldia glutinosa*, *Rubus chamaemorus*, *Trientalis europaea*, *Cornus unalaschkensis*, *Coptis trifolia*, and *Gentiana douglasiana*) had corollas which reflected all visible wavelengths, appearing white, and absorbed UV (Figs. 7–13); one visibly white species (*Fauria crista-galli*) showed low (<10%) reflectance of UV light in the outer portion of the corolla (Fig. 2). In five species (*Sanguisorba officianalis* ssp. *microcephala*, *Kalmia polifolia*, *Andromeda polifolia*, *Vaccinium oxycoccus*, and *Loiseleuria procumbens*), corollas reflected most strongly in red, with visible colors of pink, rose, or deep red. *Kalmia*,[1] *Andromeda*, *Vaccinium*, and *Loiseleuria* reflected violet and blue at slightly lower values and reflected green and yellow weakly. *Sanguisorba* reflected only in red with minimal reflectance values. Each of these pink–red species showed low UV reflectance, with the exception of *Loiseleuria*, which absorbed UV (Figs. 3–6 and 14). *Apargidium boreale* had the only inflorescence that appeared yellow. It reflected visible wavelengths of green, yellow, and red and was the only species to show strong UV reflectance, restricted to the distal parts of the florets (Fig. 1).

All species had intrafloral patterns of contrasting hues, in both visible and UV light, that emphasized the reproductive parts, or centres, of the flowers (Table 2 and Figs. 1–14). In most white-flowered species, anthers or pistils reflected combinations of green, yellow, or red (*Fauria*, *Ledum*, *Tofieldia*, *Rubus*, *Trientalis*, *Coptis*) yet in *Tofieldia* and *Coptis*, the anthers also reflected UV. The stigma of *Loiseleuria* reflected strongly in UV in contrast to its UV-absorbing corolla, while in *Fauria*, the stigma was relatively more UV reflectant than surrounding flower parts. In *Coptis* and *Gentiana*, nectaries were green–yellow–red, juxtaposed against white corollas; the nectaries of *Kalmia* were more reflectant in UV than was the corolla. *Gentiana* had spots that appeared deep violet surrounding the mouth of the corolla tube; UV-reflec-

TABLE 1. Kodak filter combinations, their spectrophotometric characteristics (at 0.1% to 100% transmittance), and color name equivalents. Data on filters from Anonymous (1970)

Color name	Wave band transmitted (nm)	Filter Nos.
Ultraviolet	310–400	18A
Violet	400–460	36+98
Blue	460–490	98+4
Green	500–570	65+12
Yellow	550–600	61+22
Red	620–700	92
White	400–700	

[1]After their first mention in the text species will be referred to by their generic name.

TABLE 2. Floral hues of bog plants. Uv, ultraviolet; V, violet; B, blue; G, green; Y, yellow; R, red; W, white; color names refer to wave bands in Table 1 (*N*, part not visible in photographs; —, no apparent hue)

Species	Flower part			
	Tepal	Anther	Pistil	Nectary
Apargidium boreale (Bong.) T. & G.	UvGYR	—	GYR	N
Fauria crista-gallii (Menzies) Makino	W	—	UvGY	Y
Sanguisorba officianalis L. ssp. *microcephala* (Presl) Calder & Taylor	R	—	—	R
Kalmia polifolia L.	VBR	W	GYR	UvVR
Andromeda polifolia L.	VBR	N	N	N
Vaccinium oxycoccus L.	VBR	R	—	N
Ledum palustre L. ssp. *groenlandicum* (Oeder) Hult.	W	YGR	R	W
Tolfieldia glutinosa (Michx.) Pers.	W	UvYR	GY	W
Rubus chamaemorus L.	W	GYR	N	N
Trientalis europaea L.	W	R	YR	W
Cornus unalaschkensis Ledeb.		N	N	N
Coptis trifolia (L.) Salisb.	W	UvW	GYR	GYR
Gentiana douglasiana Bong.	W	UvW	W	GYR
Loiseleuria procumbens (L.) Desv.	VBR	R	UvW	N

tant spots were also evident in the same area. *Andromeda* had exposed sepals which, although visibly similar in color to the corolla, were relatively more reflectant in UV light; *Vaccinium* had a border of UV reflection along the filaments. In *Kalmia* and *Apargidium*, contrast was expressed by UV-absorbing filaments or styles radiating across the more reflectant tepals. In two species (*Apargidium* and *Fauria*), the outer portion of the inflorescence was more reflectant than the centre.

Floral backgrounds

Reflected light in the bog habitat is dominated by green and yellow wave bands; reflectance in UV is low overall. *Sphagnum imbricatum* Russ., the dominant ground cover, is minutely variegated at close range, with UV–violet–blue predominant in buds and green–yellow–red in open leaves. Other important visual components to the bog are *Rhacomitrium lanuginosum* (Hedw.) Brid. (UV–green–yellow), withered *Scirpus cespitosus* L. (UV–white), living sedges (green–yellow), vegetative parts of flowering plants (green–yellow), and *Pinus contorta* (green–yellow). At observational distances of greater than 10 m, many of the color details disappear and vegetation and forest are monotone blocks of low reflectance of green, yellow, and UV. Open sky is rich in UV light.

The height and orientation of a species' inflorescence determined its floral background. Predominant backgrounds included the species' leaves (*Gentiana*, *Cornus*, *Trientalis*, *Loiseleuria*), *Sphagnum* moss (*Rubus*, *Vaccinium*, *Andromeda*), sedges (*Coptis*), and vegetation at distances greater than 2 m (*Fauria*, *Apargidium*, *Kalmia*, *Ledum*, *Tofieldia*, *Sanguisorba*). *Sanguisorba*, with a mean height of 42 cm, often had a background of sky. In visible light, none of the species' inflorescences reflected the identical combination of wavelengths as their backgrounds. As well, even in those wave bands shared by inflorescences and background vegetation (usually green and yellow), inflorescences reflected relatively more light than did vegetation. Among species that absorbed UV light, there was no contrast with the floral backgrounds in the UV wave band, and among those with low UV reflection, contrast was minimal. *Apargidium*, the only species that strongly reflected UV, stood out conspicuously against its background, even at a distance.

Floral characteristics

There was a negative correlation between density and height of inflorescences ($r = 0.56$, $P < 0.05$). Among UV-absorbing species ($N = 13$), there was a positive correlation between white corolla color and actinomorphology and between pink–red corolla color and stereomorphology (Fisher's exact test, $P < 0.05$). No