Insects see the world very differently than humans do. Their eyes are sensitive to energy from sunlight in frequencies somewhat different than ours are (Silberglied, 1979). We can see light in the energy spectrum from red through orange, yellow, green, blue, indigo, and violet, but we cannot normally detect short-wavelength ultraviolet light because our eyes have shielding pigments. Ultraviolet light is electromagnetic energy between 40 and 400 nanometers in wavelength. This so-called “black light” is commonly used to cause visible fluorescent patterns in “psychedelic” posters and other objects containing special pigments. The visual perception of insects generally overlaps with our own, except that insects cannot see red light and can see ultraviolet light. The ability of insects to communicate in ultraviolet light has been investigated by the late Robert Silberglied, of the Museum of Comparative Zoology, Harvard University. This discussion draws on his research.

How do we know that insects can see ultraviolet light? In a simple experiment performed in the late 19th century, Sir John Lubbock exposed an ant colony to different parts of the visual spectrum (a “rainbow”) that had been separated by passing light through a prism. Ants

1 Department of Biological Sciences, Boston University, Boston, Massachusetts 02215.
will normally carry their larvae and pupae away from any light source. Lubbock found that the ants did not leave the area exposed to red light but did leave the other lighted areas, as well as the area beyond the violet that appeared unlighted to a human observer. The presence of ultraviolet light in this apparently unlighted area was demonstrated using fluorescent pigments. This experiment revealed that ants cannot perceive red but can see the other colors including ultraviolet.

Two indirect pieces of evidence also suggest that insects can see ultraviolet light. First, receptors sensitive to ultraviolet light have been found in the eyes of most insects that have been studied. Also, many insects and the flowers that they visit have ultraviolet patterns that are not apparent to the unaided human observer. By means of special photographic techniques, these patterns can be studied to give insights into the world as perceived by an insect. Such techniques generally involve placing a special filter that transmits only ultraviolet light over the lens of the camera. The resulting photographs often reveal hidden bars, spots, and stripes on the bodies and wings of such visually acute flying insects as butterflies and dragonflies. By producing conspicuous patterns in the ultraviolet spectrum, these insects presumably communicate among themselves but are still not conspicuous to birds, which hunt insects by means of the visual spectrum only.

Biologists working with ultraviolet patterns in the flowers of temperate species have shown that the flowers of about 33 percent of all species strongly reflect ultraviolet light (Guldberg and Atsatt, 1975). This ultraviolet reflectance is most often found in large flowers but is not related to whether the flowers show bilateral or radial symmetry. Yellow or violet flowers show a greater tendency to reflect ultraviolet light than do flowers of other visible colors.

About seven percent of all flowers show floral patterns in ultraviolet light that are not evident in visible light. For example, in the black-eyed Susan (Rudbeckia hirta) there is an ultraviolet-absorbing region caused by the presence of flavonols, a class of chemical pigments (Thompson et al., 1972). Flavonol-containing flowers are usually yellow in the visible spectrum, a tendency perhaps due to the fact that many flavonol pigments found in petals both absorb ultraviolet light and reflect yellow light.

The petals of many flowers have spots or streaks of color in the visual spectrum. These markings are called “nectar guides” or “honey guides” by botanists and are considered to be important in aiding pollinating insects to orient themselves on the flowers for feeding and pollen transfer. They are frequently found at the base of the petals or around the nectaries. In many species the flowers appear to be uniformly colored in the visual spectrum but show dramatic patterns of nectar guides in ultraviolet light. For example, in the marsh marigold (Caltha palustris), which is visited in the spring by small bees, the flowers are uniformly bright yellow in the visual spectrum. When the flowers are viewed in ultraviolet light, however, the outer third of each
Above  Caltha palustris. The flowers are uniformly yellow in visible light (left), but the base of the petals and the stamens and pistils are dark in ultraviolet light (right). Below  Geum macrophyllum The flowers are uniformly reflective in visible light (left), but have a dark spot at the base of each petal in ultraviolet light (right). Photographs by R Primack.

petal is highly reflective of ultraviolet light while the inner portion of the petals and the stamens and carpels strongly absorb it. This creates a bull’s-eye effect, which presumably aids the insect to land in the center of the flower. In the mountain avens (Geum macrophyllum), which is visited by flies, the flowers are uniformly yellow except for brown veins at the base of the petals. In ultraviolet light the outer two-thirds of each petal is highly reflective, while the inner third is absorbing. In the cinquefoil (Potentilla norvegica) the base of each petal has a strongly absorbing spot in ultraviolet light that is not present in visible light. These marks presumably help insects to locate the center of the flower, where nectar and pollen are produced.

Also common is a floral pattern in which all or part of one petal absorbs more ultraviolet light than the others. For example, in two species of Rhododendron, R. luteum and R. calendulaceum, which are probably pollinated by butterflies, the petals are more or less uniformly colored, either yellow or orange. In ultraviolet light the
upper petal in both species has a large light-absorbing region that contrasts with the rest of the corolla. These spots probably serve to highlight the location of individual flowers within the inflorescence. Also, in the upper petal of the pink-flowered *R. obtusum*, a large strongly absorbing region is clearly evident in ultraviolet light but is indistinct in visible light. In *R. maximum*, a species with large pink or white flowers, small, dark green pigment spots are present on the upper part of the corolla in visible light. In ultraviolet light, however, these individual spots are not evident, but a large, indistinct area of ultraviolet absorbance is present on the upper petal.

The overall contrast in floral patterns is usually similar in visual and ultraviolet lights. However, in a few species these patterns are dramatically reversed. For example, the yarrow (*Achillea millefolium*) and *Fothergilla major* produce bright, white, terminal inflorescences, which appear almost uniformly dark in ultraviolet light. Another example is the inflorescence of the flowering dogwood,
Achillea millefolium. The flowers are very bright in visible light (left) but dark in ultraviolet light (right). Photographs by R. Primack

*Cornus florida*, which appears to be one large four-petaled flower but is really composed of four bracts surrounding many small flowers. In both this species and the Korean dogwood (*Cornus kousa*) the bracts appear white and the small central flowers are yellowish green in visible light. However, in ultraviolet light the pattern is reversed: the central flowers appear highly reflective and the large bracts dark. Many of the early-blooming ericaceous shrubs that have uniformly white flowers in the visual spectrum have more complicated patterns in the ultraviolet. In ultraviolet light the flowers of mountain andromeda (*Pieris floribunda*) are generally dark except for distinct spots at the base of the corolla and, to a lesser extent, the sepals.

The stamens may strongly contrast with the rest of the flower in ultraviolet light, even when they are not very different in visible light. Stamens that are light colored and not contrasting in visible light may absorb ultraviolet light strongly, thereby contrasting with a reflecting corolla. This is true for Tatarian honeysuckle (*Lonicera tatarica*). Such patterns may be important in plant species in which the pollen is an important food source for pollinators. The opposite effect is shown by the flowers of the toothwort (*Dentaria diphylla*), which have white petals and yellow stamens in visible light. In ultraviolet light, the flower is generally not reflective, but the anthers are highly reflective and can thus be readily located by such pollinators as small bees. In the stamens of *Aesculus arguta*, the filaments are white on the top and dark on the bottom in visible light, but uniformly dark in ultraviolet light.

Many plant species produce hairs at various places in their flowers. Besides serving as useful taxonomic characters for botanists to distin-
Lonicera tatarica. The flowers are uniformly light colored in visible light (left), but the anthers are dark in ultraviolet light (right). Photographs by R. Primack

guish between species, these hairs are usually considered to be important both in preventing small, unwanted insects from entering the flowers to steal nectar and in regulating the temperature and the water loss of the flower. These hairs do not typically show large differences in color from the floral parts on which they occur. In ultraviolet light, however, they are often highly reflective, in contrast to the rest of the flower, in species such as Caragana arborescens, Aesculus arguta, and Rhododendron nudiflorum. Perhaps the hairs serve as beacons, helping the insect to orient on the flower.

Methods of Ultraviolet Photography

There are several ways of examining flowers (or insects) in ultraviolet light. Using a modified camera is relatively inexpensive; this gives high-quality photographs and is probably the best option for most people.

Equipment

The basic piece of equipment is a good-quality camera with a close-up (macro) lens and flash. The ultraviolet pictures shown here were taken with a Canon AE-1 with a 100-mm macro lens, and a Canon 199A Speedlite. Since glass absorbs ultraviolet light, close-up rings and lens filters probably should not be used. Not all flash attachments are suitable for this work since some do not put out sufficient ultraviolet light. In addition, some lenses may not transmit enough ultraviolet light. Testing a combination of equipment is the only way to determine its suitability for ultraviolet work.

One specialized piece of equipment that must be obtained through a camera shop is a Kodak Wrattan 18A filter (about $30). This filter is
a two-inch square of glass that transmits only ultraviolet light. It should be glued onto a threaded ring (such as from a skylight filter or a close-up ring from which the glass has been removed), with black tape used to hold the filter onto the ring and to prevent light from passing between the lens and the ring. The filter can then be easily screwed on or off the front of the camera lens.

Use Kodak Tri-X film, which should be shot at ASA 800 and pushed during developing to ASA 800.

**Calibrating Your Camera**

The following is my simple calibration technique, a combination of practicality and the more theoretical approach of Silberglied (1976). Choose a subject that might have an ultraviolet pattern — a large yellow buttercup flower, a composite head like a dandelion, or a pierid butterfly. Lacking these, use any brightly colored, large, flat flower. Remove the ultraviolet filter from the camera. Using a tripod, compose the picture you want and focus on the subject. Fasten the ultraviolet filter over the lens. Place the flash as close to the subject as possible, using either a tilt flash or an extension cord. Set the shutter speed to the speed used with the flash (1/60 second for most cameras). Now, shoot a sequence of pictures at a complete range of f-stops. When you have developed the film, you will see the best range of aperture sizes for all subsequent shots. For the Canon AE-1 the best apertures are f8 and f5.6. During the calibration procedure and subsequent sessions, you should keep a record of your pictures so that you can continue to refine your technique.

For some cameras, the pictures — particularly the close-ups — may not be in perfect focus, since ultraviolet light has a slightly different focal distance than visible light. In addition, the depth of field is usually so small that even slight movements of the subject can put the picture out of focus. Consequently, the camera might have to be focused somewhat forward or backward from the correct focus in the visual spectrum. Learning the appropriate focus for your camera comes with experience. My technique is to shoot several pictures at slightly differing focal distances.

**Shooting Pictures**

Once the camera has been calibrated for ultraviolet photography, taking the pictures is a straightforward process. It is a good idea to take several shots of each subject, since breezes can easily cause the flowers to come out of focus. Flowers must be perfectly dry for ultraviolet photography, otherwise droplets reflect the flash as points of light.

Black-and-white pictures of the flower in the visible spectrum can be shot at the same time on the same roll of film by removing the filter from the lens. The pictures may need to be underexposed by about one or two f-stops, however, since the film will be developed at ASA 800 rather than ASA 400. For my own work, I carry two cameras. The first camera is loaded with Tri-X film and is used for the ultraviolet
and black-and-white work. My second camera contains color slide film, for obtaining a color record of the flower.

The most common method of taking ultraviolet pictures of flowers — using a powerful flash — is effective for revealing the contrasts in ultraviolet reflection within a flower or inflorescence. However, it has the associated disadvantage of usually making the background appear dark. This is due to the rapid decrease in light intensity with increase in distance from the flash. Since flowers that absorb ultraviolet light do not contrast well with this dark background, the most interesting flowers in ultraviolet photographs are ones that are strongly reflective. Several natural backgrounds, including sand, sky, and hairy or otherwise reflective leaves, do reflect ultraviolet light, and many ultraviolet-absorbing flowers may be conspicuous against these backgrounds (Frohlich, 1976). Consequently, if it is desirable to show the natural background of the flowers, on sunny, windless days pictures can be taken without a flash using longer exposure times. Of course, this technique is more difficult.

Video-Viewing

Another way to view ultraviolet flower patterns is to use a video camera that has a quartz or other lens capable of transmitting ultraviolet light (Eisner et al., 1969). If a Wrattan 18A filter is placed over the lens, the video camera receives only ultraviolet images, which can be viewed directly or displayed on a monitor.

Despite the complexities described here, the basic techniques of ultraviolet photography are easily mastered. The challenge of obtaining well-composed and perfectly focused pictures under field conditions provides continuing enjoyment. Looking at the world of insects and flowers through special ultraviolet eyes opens a new aesthetic dimension to someone who enjoys natural beauty.

References


