

our analysis of personality traits, cognitive performance, and electrophysiological measures to be reported subsequently, the clinical significance of low MAO activity in this young population can only be assessed after longitudinal follow-up.

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13. In probands, information was obtained on traffic violations and on arrests, convictions, and jail for offenses other than traffic. Traffic offenses showed no significant differences between high-MAO and low-MAO probands. In the family history, probands reported relatives with "problems with the law, other than traffic violations."
14. Items were aggregated on the basis of their being both objectively verifiable and serious; the same aggregation is used both for individual and for family data.
15. We thank D. Gastfreund, C. King, A. Nichols, M. Sihvonen, and M. Wigglesworth for technical assistance.

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Fluorescent Nectar

Thorp *et al.* (1) hypothesize that fluorescence of exposed floral nectars acts as an attractant of zoophilous flowers for anthophiles—absorbing ultraviolet light and emitting light of other colors. A critical examination of this hypothesis is needed. Several points suggest that it is unlikely that ultraviolet fluorescence from exposed nectars would contribute to the attractiveness of the flowers, or even be seen by insects. An examination of the spectral sensitivity of insect eyes, their color vision, and the spectral composition of daylight will illuminate the arguments.

The spectral sensitivity of insects ranges from ultraviolet (~ 300 nm) to yellow-orange (~ 650 nm) (2, 3). Ultraviolet (~ 300 to 400 nm) in daylight is relatively impoverished, representing about 12 percent of the energy in the insect visual spectrum (4). To compensate, insects are more sensitive to ultraviolet than to light in other wave bands (2, 3), and the ultraviolet receptors of insects' eyes are narrower in their sensitivity range (2). This explains their greater ability to discriminate colors which contain ultraviolet (3).

It is well known that most fluorescers are poor in terms of quantum efficiency (5); a quantum efficiency of 25 percent produces bright fluorescence. Two nectar constituents, tyrosine and trypto-

phan, fluoresce brightly in neutral water solution, at quantum efficiencies of 21 and 20 percent, respectively (6, 7). The spectrum of fluoresced light is generally as broad or broader than that of the exciting light (5, 7, 8) and the energy efficiency of fluorescence always less than the quantum efficiency, as the photon fluoresced at the longer wavelength has less energy than the photon absorbed.

So, fluorescence of nectar by ultraviolet light takes energy from an impoverished part of the insect visual spectrum to which insects are highly sensitive and transforms it to an already rich part of that spectrum (to which insects are less sensitive) with considerable inefficiency. The contribution of fluoresced light to longer wavelengths reflected from floral parts would probably be obscured by overall diffuse reflection and further minimized by place-to-place variation in diffuse reflectance within the flower, by shading, and by specular reflections (see below).

The nectaries of flowers with exposed nectar are frequently on the hypanthium, which is often greenish to yellowish-green and probably always has a greater spectral reflectance than foliage (9). Such floral parts reflect fairly evenly in all parts of the insect visual spectrum—absorbing red—and so appear as

bee-white to bee-grey with bee-yellowish tints (3, 9). Calculations (using a reflectance of 25 percent from the hypanthium and a quantum efficiency of .20, that is, an energy efficiency of 15 percent, with fluorescence in the wave band 400 to 500 nm) show that equivalent reflectance is only 30 percent (10), or an augmentation of the hypanthium color of only 5 percent in one of the three wave bands in the trichromatic color vision system of bees or other insects (3, 9, 11). Thorp *et al.* (1) also consider depletion of ultraviolet in fluorescent nectar, implying that this could contribute to contrastive insect-color patterns. However, the ultraviolet absorption would have to be very high through the thin film or small droplet to render any color change. Color changes due to a nectar drop would be probably imperceptible to insects. If the color change due to fluorescence were significant, it should impart color to the human eye.

Nectar reflecting ultraviolet alone would be far more effective for two reasons: (i) it would be reflecting, potentially more efficient than fluorescence, in a wave band to which insects are highly sensitive, and (ii) the color, ultraviolet, would contrast with the colors of adjacent floral parts (3, 9). Ultraviolet as an insect color is apparently rare and thus distinctive, being approached most closely by some red flowers (3).

Nectar is often seen as sparkling droplets in flowers, due to specular (mirror-like) reflections from the surface tension film. These would obscure any color imparted through either fluorescence or diffuse reflection, yet would be highly visible to insects. Insects, hovering in front of flowers before foraging or leaving, could be examining for specular reflections or other close-in attractants (such as scent) as clues to the amount of nectar present.

The observation of Thorp *et al.* (1) that there are more plant species with open flowers and easily visible fluorescing nectar than with nonfluorescing hidden nectar bears consideration. The fluorescence is imparted by some constituent or constituents not identified by Thorp *et al.* Mono- and disaccharides are not fluorescers [see also (1)] but other constituents (aromatic amino acids, vitamins, phenolic compounds, and glycerides) are, and may have phylogenetic (12) or anthecological significance (6, 13), but I doubt that fluorescence of nectar per se is important as an attractant for pollinating insects.

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10. The daylight spectrum from 300 to 390 nm has about 350 units of energy, assuming a correlated color temperature of 6500°K (4). At a quantum efficiency of 20 percent, 70 units of energy will fluoresce. Assuming fluorescence at the next wave band to ultraviolet, 400 to 490 nm, the energy efficiency is 15 percent, providing 53 energy units in the fluoresced emitted wave band. The daylight spectrum from 400 to 490 nm has about 1035 units of energy. The reflectance from the hypanthium of the flower at about 25 percent provides 260 units of energy to be augmented by the 53 fluoresced from ultraviolet. The total "equivalent reflectance" is then $313/1035 \times 100$ percent, or 30 percent. The contribution to color from fluorescence of ultraviolet is, therefore, only 5 percent in one wave band.
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14. I thank J. Hostettler, J. Eley, R. Fahrenwald, and D. H. Alman for their interest, constructive discussion, and advice.

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Kevan presents his reasons for doubting our hypothesis (1) that fluorescence or ultraviolet absorption characteristics serve as visual cues by which bees can evaluate the quantities of nectar available in some flowers.

We know of no data from electrophysiological or other spectral sensitivity experiments that support or refute Kevan's calculations relating energy efficiency of fluorescence to that which an insect can perceive. However, the nectars we surveyed (1) fluoresced either yellow or bluish, coinciding with two peaks of sensitivity in the visible spectrum of bees (2).

Kevan, in his contention that ultraviolet absorption would have to be "very high" to render a color change in a thin film, does not appear to consider that such absorption of an additive primary color (ultraviolet for bees) could produce

colorant filters of other additive primaries (for example, the fluorescent blue or yellow) which would act as subtractive primaries in relation to the color of the hypanthium. It is not apparent where qualities of saturation or lightness of the color characteristics of fluorescent nectars might fit into Kevan's calculations, since differences in intensity of the reaction to ultraviolet light are noted by Thorp *et al.* (1).

Specular reflectance of exposed nectars could indeed serve as a visible cue to the presence of nectar in many flowers, including some of those reported as having fluorescent nectar (1) (for example, *Allium*, *Daucus*, *Isomeris*, and some *Fremontodendron*). However, many flowers with fluorescent nectar had their nectaries partly concealed by the filaments (peaches) or dense hairs (some *Fremontodendron*) so the droplets were not reflective, or the nectar was produced in extremely small scattered droplets (almonds) or spread too thinly over the surface of the gland to produce such reflections (plums).

We recognize that other visible changes (1) and odors may also provide cues with which anthophilous insects can associate the presence or absence of food. We were not proposing an exclusive cue, but suggesting that direct perception of nectar by its fluorescence or ultraviolet absorption characteristics may contribute to the foraging efficiency of bees in conjunction with the whole syndrome of cues each flower type may provide. These cues may be ranked in relation to one another and the ranks may change as environmental conditions change, as in orientation learning experiments (3).

We recognized that there are many constituents of nectar which have natural fluorescence and were unwilling to speculate as to which might be responsible for our observations until we had addressed the problem of characterization and identification. While aromatic amino acids might be responsible in some cases, it is interesting to note that bee plants, which appear to be lowest in these compounds (4), have fluorescent nectar (1), but bird, moth, and butterfly flowers, which are higher in amino acids (4), do not have fluorescent nectar (1). In a recent analysis of an almond nectar, after ninhydrin was added the nectar spot continued to fluoresce, which means that something other than amino acids was responsible (5).

Rather than accept Kevan's theoretical arguments, we have initiated tests

of our hypothesis (6). Preliminary results indicate that there is no spontaneous preference involved, but training experiments suggest that honey bees do have the ability to detect the fluorescent or ultraviolet absorption characteristics of nectar. Further refinement of our tests will be necessary before these results can be confirmed.

If experiments support our hypothesis, it becomes important to determine whether bees use the fluorescence, ultraviolet absorption, or both as a cue. Many other important aspects remain to be investigated, including characterization of the excitation and emission wavelengths, identification of the compounds that fluoresce, quantification of lightness or saturation of the fluorescence or intensity of the ultraviolet absorption, relationship of nectar with the substrate and adjacent background color and texture, and whether nectars that absorb in the ultraviolet without fluorescing in the visible or nectars that reflect ultraviolet exist.

Finally, Kevan used the word "attractant," which implies an innate preference, but we used the term "visual cue" to include innate preferences and more likely learned responses to a color characteristic of nectar that may serve as a signal related to the presence of a food reward.

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