men length of $(1.1)^2$ by 8.8 = 10.6 mm. The only sparrow species present on site 1 was the grasshopper sparrow (*Ammodramus savannarum perpallidus*) with a culmen length of 10.8 mm.

The pairwise coexistence matrix for the oak site is shown in Table 2. The only pairs that could coexist consist of hypothetical species 1 with either 3 or 4 but both of these pairs can be invaded by species 2. Hypothetical species 2 has the highest k value of all six species and could coexist with none. Thus, the prediction is that it should be the only sparrow species present. Hypothetical species 2 has a culmen of 9.7 mm. The only resident species in the Oak site was the chipping sparrow (*Spizella passerina arizonae*), with a culmen of 9.6 mm.

Table 2 (riparian site) gives the pairwise coexistence matrix for the riparian site. Hypothetical species 1 or 2 could coexist with 3, 4, 5, or 6; but only the pair consisting of hypothetical species 2 and 3 is resistant to invasion. Actually present were the chipping sparrow with a culmen of 9.6 mm and the brown towhee (*Pipilo fuscus mesoleucus*), with a culmen of 15.2 mm. These correspond most closely to hypothetical species 2 (9.7 mm) and 7 (15.6 mm). Using Eq. 6, one predicts the ratio of abundance for hypothetical species 2 and 7 to be 93 : 7. The observed ratio of chipping sparrows to brown towhees was 94 : 6.

Though not resident, the rufous-crowned sparrow (*Aimophila ruficeps scottii*) was frequently seen in the riparian site. This sparrow is the resident species in the nearby sacaton (*Sporobolus minor*) habitats and apparently occasionally utilizes the riparian habitat.

The theory is upheld well by the observed results. Nevertheless, the discrepancies between predictions and observations are worthy of comment. There were a number of stragglers of other sparrow species and these occasionally showed up in every habitat. The theory, of course, does not predict these. They accounted for less than 2 percent of the total number of individuals seen and are, thus, probably unimportant to the dynamics of the total system. The rufous-crowned sparrow accounted for approximately 4 percent of the individuals in the riparian site. This indicates the importance of neighboring habitats on the diversity within habitats, as previously mentioned. The habitats chosen for this study were large and relatively uniform. In North Carolina and Costa Rica, I have studied sparrows in areas composed of a patchwork of habitats (*3*). In both places, as many as 4 species were seen in a single habitat. Coexistence in these situations is doubtlessly explained by a combination of seed-size allocation within habitats and habitat utilization differences.

For two of the habitats studied the theory correctly predicts which of the seven hypothetical species should be present. For the riparian site, the pairwise coexistence matrix correctly predicts that one small-billed (hypothetical species 1 and 2) and one large-billed (hypothetical species 3 through 7) species could coexist. However, the theory predicts that the species pair actually present is invisible but that another pair, not present, is not invasible. This result indicates that the theory may be useful in predicting when two species may coexist but not precisely which pairs may coexist.

Sparrows in the grasslands were in many ways ideal for testing these predictions. They are easy to observe, their diets are relatively easy to quantify, and the production of grass seeds is easy to measure. The constant ratio of culmen lengths and the normal distribution of seed sizes in sparrow diets made things easier. The models themselves require none of these luxuries and are, conceivably, applicable to a great variety of organisms.

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Nectar Fluorescence under Ultraviolet Irradiation

Abstract. *Nectar, which fluoresces in the visible and absorbs in the ultraviolet spectrum when irradiated by ultraviolet light, occurs in many bee-pollinated plants. It is suggested that these characteristics function as direct visual cues by which bees can evaluate the quantities of nectar available. Thus, they assume an important role in pollination of the flowers and foraging efficiency of bees.*

We observed a brilliant aquamarine fluorescence in the nectar of *Prunus amygdalus* (L.) Batsch., the cultivated almond, and suspected its possible function in pollination ecology and foraging efficiency of bees. Fluorescent nectar had been described previously only by Frey-Wyssling and Agthe (*1*). While studying the mechanism of nectar secretion, they found that both the phloem sap and nectar fluoresce blue. They did not suggest a potential function for the substance.

Cruden (*2*) showed that central areas of *Nemophila* flowers which absorb ultraviolet (UV) light, also fluoresce in the visible spectrum. Indeed many fluorescent compounds are known to absorb UV (*3*). Thus, when we photographed a spot of almond nectar on filter paper using a UV light source with appropriate filters (*2*) (Fig. 1, a to c), we found that it not only fluoresced in the visible, but absorbed in the UV spectrum. Nectar of *Allium cepa* L., cultivated onion, behaved similarly (*4*). None of the nonfluorescent nectar tested (*Aloe, Fuchsia,* and *Mandevilla*) absorbed UV. Sugar solutions (sucrose and glucose) placed on filter paper did not fluoresce or absorb UV.

Patterns of color contrasts in flowers due to differential absorption and reflection of UV wavelengths (300 to 400 nm) were demonstrated about 50 years ago (*5*). Since then many flowers have been shown to exhibit contrasting patterns in the UV spectrum (*6*). Similar guide marks (*7*) in the visible spectrum serve as visual cues directing floral visitors to the nectar reservoir (*8*). The UV patterns, although invisible to man, can be perceived by honeybees and some other insects (*9*) and are important cues to foraging honeybees (*6, 10*).

Some flowers, after pollination or fertilization, undergo changes in visible coloration [for example, *Phyla* (*11*) and *Lupinus*

(*12*)], UV patterns (*13*), or morphology or position [*Trifolium* (*14*) and *Ludwigia* and *Pyrrhopappus* (*15*)]. These alterations generally coincide with pollen or nectar depletion and therefore may serve as visual cues to pollinators that foraging is no longer profitable.

On the basis of these ideas we hypothesized that nectar fluorescence or UV absorption might serve as a visual cue foraging bees could use to determine the quantity of nectar available. Such a visual cue could increase the foraging efficiency of bees, especially on flowers with at least partially visible nectar, and would play an important role in the energetic relationships between bees and the flowers they visit (*16*). It could also explain the rapid flight activity with much hovering before flowers and infrequent landings so commonly exhibited by bees when supplies of nectar and pollen have been severely reduced.

As an initial test of this hypothesis we examined nectar from a total of 102 species in 82 genera and 38 families of flowering plants to determine the extent of this phenomenon (*17, 18*) and the relationship of fluorescent nectar with the pollination syndrome. Nectar was extracted from most flowers with micropipettes (1-μl Drummond microcaps). It was centrifuged from some or was left in situ in excised flowers. We examined nectar in the capillary tubes or flowers for fluorescence in a Chromatovue cabinet with independent long- and short-wavelength UV sources. We observed most of our samples with the long-wavelength source.

Most of the flowers with fluorescent nectar (*17*) are visited by bees, especially honeybees. Many (more than 56 percent) are introduced crop, ornamental, or weedy species which have their origins in the Palearctic and Oriental regions where the honeybee is indigenous. Most have disk- or bowl-shaped flowers with at least partially exposed nectar so that its presence could be detected visually. Even in the sympetalous *Convolvulus arvensis* L., a small drop of brightly fluorescing nectar is usually exposed at the summit of one or two of the five tubes formed by the broad bases of the stamens and the corolla. These characters are not exclusively correlated. Flowers with nonfluorescing nectar (*18*) include several bee-visited types, some of which are disk- or bowl-shaped and have exposed nectar. The two legumes, black locust and soybean, are also unexplained exceptions to our hypothesis. They have typical papilionaceous flowers with hidden nectar.

The pollen of some of the excised flowers (such as almond and carrot) also fluoresced, but much more dimly than the nectar. Thus, pollen may provide a similar visual cue to its availability to pollen-collecting insects.

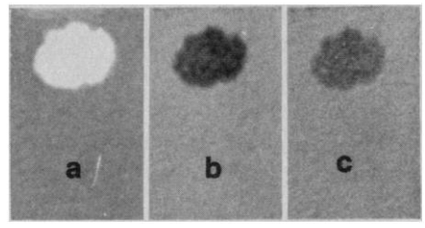

Fig. 1. Spot of *Prunus amygdalus* nectar on filter paper photographed under long- and short-wavelength UV illumination. (a) Wratten 2B filter (yellow) admits only visible light (nectar fluoresces). (b) Wratten 18A filter (deep blue) admits only UV radiation (nectar absorbs). (c) No filter (combined fluorescence and UV absorption of nectar).

The color of fluorescence varied from yellow to blue (*4*) with several nectars appearing a somewhat intermediate aquamarine. We found different colors of fluorescence in nectar from flowers in the same family (for example, blue in *Allium* and yellow in *Muilla*), in the same genus (aquamarine in *Prunus amygdalus* and yellow in *P. ilicifolia*, and in the same species (aquamarine to yellow in *Fagopyrum*).

Intensity of fluorescence also varied. The most intense fluorescence was found in almond, and very intense fluorescence was found in *Allium, Convolvulus, Daucus, Phacelia*, and *Robinia*. The weakest fluorescence occurred in *Crambe, Cucumis*, and *Euphorbia*. We detected intervarietal (genetic) variation in both almond and onion nectar. In *Prunus persica*, the nectar of the peach fluoresced, but not that of the nectarine. Additionally, site, rootstock, and age of the flower in almonds influenced the intensity of fluorescence. Nectar from a limited number of almond trees failed to fluoresce. Flowers on some almond trees lost their petals because of rain and strong winds but still contained fluorescent nectar. This could account for bee visitations to flowers without petals, which we have observed, and indicates a need for caution in emasculating and removing petals as a means of controlling cross-pollinations (*19*).

We conclude that the patterns and range of fluorescence and UV absorption we found are appropriate to serve as guides by which potential pollinators may evaluate the presence and perhaps the abundance of nectar. This mechanism would increase the food-searching efficiency of the anthophilous insects capable of perceiving these stimuli. Pollination efficiency of the plant would be increased through reduction of redundancy of visitation to flowers already pollinated. The fluorescence or UV absorption of floral nectars and the visual capabilities of their principal insect visitors appear to be another example of coevolution of flowers and their pollinators (*16, 20*).

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18. Taxa with nectar that do not fluoresce under ultraviolet irradiation (if more than one species per genus, number is given in parentheses): Aceraceae, *Acer* (3); Apocynaceae, *Mardevilla* and *Trachelospermum*; Asclepiadaceae, *Asclepias* (3); Betu-

laceae, *Betula*; Caprifoliaceae, *Lonicera*; Caryophyllaceae, *Dianthus*; Compositae, *Blennosperma, Cichorium, Stephanomeria, Taraxacum, Tragopogon*, and *Wyethia*; Convolulaceae, *Calystegia*; Crassulaceae, *Sedum*; Cruciferae, *Brassica, Diplotaxis*, and *Nasturtium*; Cucurbitaceae, *Cucurbita*; Ericaceae, *Arctostaphylos* and *Rhododendron*; Euphorbiaceae, *Euphorbia* and *Pedilanthus*; Hippocastanaceae, *Aesculus*; Leguminosae, *Cercis, Medicago, Melilotus, Phaseolus*, and *Trifolium* (3); Liliaceae, *Allium, Aloe, Brodiaea* (2), and *Zygadenus*; Limnanthaceae, *Limnanthes*; Malvaceae, *Gossypium*; Myrtaceae, *Callistemon* and *Eucalyptus* (2); Oleaceae, *Forsythia, Ligustrum*, and *Syringa*; Onagraceae, *Clarkia* and *Fuchsia*; Passifloraceae, *Passiflora*; Polemoniaceae, *Navarretia* and *Phlox* (2); Ranunculaceae, *Aquilegia* and *Delphinium*; Rosaceae, *Amelanchier, Prunus* (4), *Pyracantha, Pyrus, Rubus*, and *Spiraea*; Rutaceae, *Citrus* and *Xanthoxylum*; Salicaceae, *Populus* and *Salix*; Saxifragaceae, *Escallonia* and *Ribes*; Scrophulariaceae, *Anthirrhinum* and *Collinsia*; Solanaceae, *Capsicum, Nicotiana*, and *Petunia*; Tiliaceae, *Tilia* (2); Ulmaceae, *Ulmus*; Violaceae, *Viola*.

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Plant "Primary Perception": Electrophysiological Unresponsiveness to Brine Shrimp Killing

Abstract. *A test of the "primary perception" hypothesis proposed by Backster in 1968 was made by recording electrical activity from the leaves of* Philodendra scandentia *while randomly ejecting the contents of micropipettes filled with brine shrimp or distilled water into boiling water. Test conditions conformed to those published by Backster or communicated in personal exchanges. Data were analysed from five experiments, in each of which recordings were made from four plants in the presence of three brine shrimp killings and two control water ejections. Inspection of the data and analysis by two statistical methods revealed no relationship between brine shrimp killing and electrical "responsiveness" of philodendron.*

With publication of Backster's report (*1*) on a perception capability of plant leaves observed when brine shrimp (*Artemia salina*) were killed, the possibility that communication by unknown physical or chemical means might exist between plant and animal forms was reactivated. Backster's observation has been received enthusiastically by the public but has been disregarded until recently (*2*) by the scientific community. Since neither response is appropriate to an experimentally supported contention, we repeated Backster's basic experiment and designed an additional test (*3*) based on popular accounts of Backster's unpublished work (*4*). Care was taken to duplicate Backster's conditions and in some instances to use more stringent controls. No support for Backster's "primary perception" hypothesis was obtained in either of our experiments.

Philodendron scandens oxycardium were initially grown by the Kenneth Post Laboratories of the Cornell Department of Floriculture and Ornamental Horticulture (*5*). Seven days before use they were transferred to a holding room with a westerly exposure near the experimental laboratory. On the day of the experiments the plants were moved to two light-tight rooms in the laboratory, each of which housed a Faraday cage to electrically shield the plants plus a three-channel polygraph (Grass model 7) for recording simultaneously from two plants and from a 110,000-ohm fixed resistance to simulate an unchanging plant.

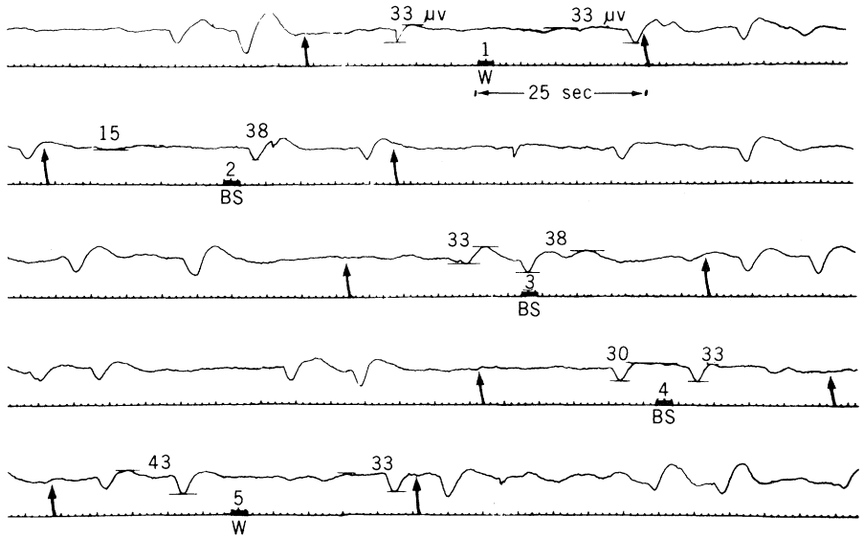

Fig. 1. Representative leaf recordings obtained on curvilinear paper during five ejections (1 through 5) indicated by the signal marker deflection just below the numerals. Two ejections were water (*W*) and three were brine shrimp (*BS*). Vertical arrows mark the beginning of 25-second control periods and the end of 25-second ejection periods. Analysis was made by comparing maximum peak-to-peak voltage deflections regardless of polarity (marked by horizontal lines and recorded in microvolts) for control and ejection periods.

Artemia (*6*) were incubated in a distant room; on the experimental day they were observed microscopically for vigor and then transferred to a laboratory room located between the two recording rooms and containing the shrimp-killing apparatus. These three rooms opened into a monitoring area in which a video tape system recorded the operation of the shrimp-killing apparatus.

The apparatus consisted of five disposable pipettes which were mounted vertically on a modified kymograph drum. An electrical impulse, initiated by a programmable tape reader, activated a solenoid which squeezed a pipette bulb and ejected the contents of the pipette into a beaker of boiling water. Simultaneously, the tape reader marked the recording charts by activating the polygraph signal markers. The solenoid reset and the drum automatically rotated until the next pipette was in position for the next activation. Failure of the ejection apparatus could be detected through the video system or by discoloration of calcium anhydride indicator (Drierite) spread beneath the rotating drum to detect pipette leakage. The tape reader was programmed by means of 16-mm film in which five holes were punched at intervals determined from a random table of digits. When read by the tape reader the film provided five activations of the termination system in 15 minutes. Five different films were made; one was selected by chance before each run.

One-half hour before each recording session four plants were gently washed with distilled water to remove any dust, and the potting soil was saturated with water. Polygraph amplifiers were warmed up one-half hour and then calibrated. The polygraphs operated from a-c mains equipped with radio-frequency filters. Tests were conducted to ensure correct operation of the total system.

Two plants were placed within each Faraday cage, and a pair of gauze-coated electrodes (*7*) for each plant was arranged to contact gently both sides of a leaf having surface area greater than 1.5 times the electrode area. The electrodes were held in place by two arms of a burette clamp pre-