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Critic's Choice Essay

POLLINATION ECOLOGY OF OUR NATIVE PRAIRIE PLANTS

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The Oklahoma prairie in the summer is an ideal place and time to study pollination ecology. With its "cornucopia" pattern of flowering, where many plants flower synchronously, it has many flowers available every day. This past summer at the Oklahoma Department of Wildlife Conservation's Arcadia Conservation Education Area, Dr. Rebecca Pace, an entomologist, and I taught a course in pollination ecology for the University of Central Oklahoma. I was glad to once again slow down and really pay attention to our native plants.

The goals for each student were to choose an insect-pollinated species and determine its flowering phenology, i.e. the timing of the life cycle, its mating system, attractants, and pollinators; to gain an understanding of diverse pollination strategies; and to learn how synchronously-flowering plants within a community compete for and share pollinators.

Students often study members of the sunflower family (Compositae) because they are so common here. Although composites are intimidating because of their tiny flowers that are difficult to manipulate, the students quickly come to appreciate them as they see the diversity of pollinators they attract as well as the intricate details of their phenology. Some students, especially those studying winecup (*Callirhoe involucrata*) and trailing ratany (*Krameria lanceolata*), dealt with high levels of herbivory or florivory. Although it is frustrating to find buds with holes and extensive damage by insect larvae, this is an important phenomenon that affects fruit and seed set in natural populations and that can have long-term effects on the distribution of plant species.

How are such pollination ecology studies conducted? The students first become familiar with their flowers — the numbers and degree of fusion of parts, their symmetry, and whether or not the flowers are aggregated into inflorescences. All these traits influence the orientation and behavior of insect visitors, the placement of pollen on an insect's body, and the subsequent deposition of pollen on stigmas.

Viewing the petals under high magnification allowed students to determine the type(s) of color-producing pigments. If the cells appear to be filled with colored "water balloons", the pigments are water-soluble and are in the cell's large vacuole. If the color is scattered in "dots" within the cells, the pigments are water-insoluble and are located in tiny cellular structures called plastids.

By recording observations each day in the field, students determined their species' phenological events. They described the sequence in which flowers open throughout the life of their plant or inflorescence and described all flower stages from tight buds to withering. The flowers of some species opened early in the morning, but students studying the lazy daisy (*Aphanostephus skirrhobasis)*, sleepy daisy (*Xanthisma texanum)*, and passion flower (*Passiflora incarnata*) had to patiently wait for them to "wake up" by mid-day. By opening at different times of day, flowering species of a community can share pollinators.

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At close inspection, the differences among flowers become apparent, including size and color of the various parts, and position of parts relative to one another. The position of the anthers and stigmas is of crucial importance, as well as how the anthers release their pollen; different species might share pollinators by placing pollen on different parts of a pollinator's body, so that pollen of each species is transferred to a stigma of a flower of the same species. Within a single flower, the anthers sometimes release pollen before the stigma is receptive to it, or vice versa. This difference in timing of the male and female parts of a flower reduces self-pollination.

Nectar production is often associated with the peak activity time of pollinators, but can be highly variable. Tiny capillary tubes can be inserted into nectaries at various stages and times of day to draw out any available nectar. Nectaries are often hidden, located within the flowers, or they may be extra-floral. For example, those of the passion flower (*Passiflora incarnata*) are on the leaf stalk where they attract ants that defend it against herbivores.

Flowers can signal insects that they have pollen and nectar rewards. For example, prairie gaillardia has bright yellow styles and stigmas that contrast with the maroon disk flower petals when rewards for insects are available. As the flowers get older, the styles and stigmas turn maroon. Older flowers might help attract pollinators to the inflorescence, but pollinators will visit younger more-rewarding flowers once they land. The flowers of most composites open from the periphery to the center of the inflorescence, so there are often concentric rings of flowers in various stages.

Students could determine whether their flowers self-pollinated, self-fertilized, or even produced seeds without sex! Pollen-producing stamens were removed from some flowers; then, the flower was bagged and later checked to see if seeds were produced. Some flowers were pollinated by hand with pollen from another flower on the same plant, while others were cross-pollinated with pollen from different plants. Students added pollen to flowers left open to determine whether or not it increased fruit and seed set and to determine if pollinators are sufficient.

From dawn to dusk, students recorded insect visitors to their species. To determine whether insects were just "visitors" or effective pollinators, they gathered pollen from flowers, viewed it under a scanning electron microscope, and compared it with the pollen loads on insect visitors to the same plant. This allowed them to determine whether the visitors were able to carry pollen, and whether they had visited flowers of a single species or several species at the same time. Bees are generally the most efficient insect pollinators; they are able to carry large amounts of pollen, can learn to tell differences among flowers, can learn to "handle" them, and they show floral constancy by revisiting flowers of the same species.

If you would like to delve into and be amazed at what is currently known about pollination biology across the world, I suggest the comprehensive and up-to-date (2011) book *Pollination and Floral Ecology* by Pat Willmer, published by the Princeton University Press.

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Halictid bee visiting passion flower (*Passiflora incarnata*). Note the extra-floral nectaries on the leaf stalk.

Pollinators visit newly-opened flowers of *Gaillardia aestivalis*.

Lanceleaf gaillardia (*Gaillardia aestivalis*). Note ring of styles emerging from newly-opened flowers.

Bumblebee on *Dalea candida*. All photos by Gloria Caddell.

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