Pollination Ecology and Pollinator Behavior

The two most speciose groups of multicellular eukaryotes today are the angiosperm plants and the insects. Angiosperms are distinguished from other kinds of plants by the presence of the reproductive structure known as the flower. Earlier types of seed-bearing plants had cones for seed production; still earlier forms reproduced not with seeds but with spores. Angiosperms may have originated during the early part of the Mesozoic era, but during much of that time period the landscape was dominated by more plesiomorphic plants, including large ferns, horsetails, and various gymnosperms. These plants formed the extensive coal forests during the Mississippian and Pennsylvanian periods of the Paleozoic era, which are thus collectively known as the "Carboniferous" period. The angiosperms first appear in the fossil record early in the Cretaceous period. They blossomed (pun intended!) in a great adaptive radiation during the Cretaceous, soon became more diverse and numerous than the earlier forms, and have remained the dominant plant group since that time.

The insect fossil record is actually quite complete for a group whose members are in general small animals, and for one that is primarily terrestrial, where fossil formation is a rare occurrence. Insects first appear during the Devonian period of the mid-Paleozoic era (about 390 million years ago). Most of the major orders of insects are present in Paleozoic strata, and only a few orders became extinct at the Permian - Mesozoic boundary. The rate of increase in the diversity of insects was exponential during the early part of the Mesozoic, then slowed during the Cretaceous. Some groups, especially the beetles, the lepidopterans, the flies, and the hymenopterans, again proliferated during the Cenozoic. These groups are the most diverse of the Recent insect fauna.

The traditional idea concerning the more or less concomitant adaptive radiations of angiosperms and insects is a coevolutionary one. The argument goes like this: One of the driving selective forces on plants is the ability to transport gametes (pollen) from one individual to another, so as to avoid selfing or inbreeding. Pre-angiosperm plants relied on wind to carry their pollen, and this process necessitated the evolution of sticky female parts to trap the male pollen. This process was inherently inefficient, as there was probably lots of heterospecific (other species) pollen about, and little pollen from your own species. Wind pollination thus probably limited the "seed set" of these primitive plants. Enter the insects. The first true insects, as this story goes, were probably like modern beetles; they were terrestrial and could fly, and probably ate plant parts. Stems and leaves were probably not very good to eat, but pollen and seeds were. Thus the first insects were predators on the reproductive parts of the ancestors of angiosperms. They would fly from plant to plant, eating the pollen and looking for seed-producing tissues. Some of these insects would be trapped in the sticky material intended to trap wind-borne pollen grains; in this case, the insects might also have been carrying pollen, so the pollen would be trapped too. Alternatively, the flying insects might carry pollen from pollen-producing structures of one plant to seed-producing structures of another plant, and deposit pollen on the sticky female structures inadvertently. This scenario sets up the possibility that some plants could preferentially attract insects that were carrying pollen, and thus could increase their seed set (reproductive success). Those plants that were most successful in attracting ancestral pollinators became the angiosperms, and the rapid adaptive radiation of the plants was accompanied by equally rapid diversification of insects.

There are a number of difficulties with this story. First, the diversification of the insects began at least 100 million years before angiosperms appear in the fossil record, and even if we suppose that angiosperms had originated much earlier, they could not have been a major component of the flora or we would have fossils of them. Second, the Mesozoic adaptive radiation of the insects was most intense in the Triassic and Jurassic, and began to slack off during the Cretaceous, just when the angiosperms began to take off. Third, the insect taxa that are the most important pollinators today began their adaptive radiations in the early Mesozoic, well in advance of angiosperm ascendancy. However, these groups (especially the flies, lepidopterans, and hymenopterans) exhibit a marked increase in diversity during the late Mesozoic, and have continued to diversify through the Cenozoic. It is probable that at least during their relatively recent evolutionary history, members of these orders coevolved with angiosperms.

In spite of the debate about the phylogeny and diversification of angiosperms and insects, it is clear that today there are many examples of complex and specialized relationships between plants and their pollinators that could only be the result of prolonged and tight coevolution. Some of the more spectacular examples include orchids and several species of euglossine bees, arum-lilies and flies, figs and fig wasps, and yuccas and yucca-moths. Not all ecological relationships are as striking, but most angiosperms that are pollinated by insects (or vertebrates) show some degree of adaptation to specific pollinators, which in turn have their own specializations. These "flower syndromes" are discussed in more detail below.

Flowers are the genitalia of the angiosperms. The basic function of a flower is to accomplish transfer of gametes from one individual to another, often using an animal for transportation. Flowers consist of four types of structures (sepals, petals, stamens, carpels) borne on a modified stem called the receptacle. There are usually three, four, five, or more of each type of structure in each flower. Two of these structures are sterile and two are fertile reproductive structures. The basal structures are the sepals and the petals, which are sterile. These are the structures that most of us think of when we think of flowers. The main function of sepals and petals (collectively called perianth segments) is to attract pollinators. The apical, fertile structures are the stamens and the carpels. The stamens are the male, pollen-producing structures. These usually consist of a filament which bears an anther, where the pollen is produced. The carpels are the female reproductive structures. A carpel has a distal style with a pollen-receiving structure at the tip (the stigma), and a proximal ovary, where the egg (oocyte) develops. In general, the stamens and the carpels of any particular flower are not mature at the same time to prevent selfing.

Not all flowers have all four of the structures. Some flowers have lost or modified perianth segments. In some cases the perianth segments may be replaced by specialized leaves called bracts, which function to attract pollinators as do the perianth segments. Flowers with both male parts (stamens) and female parts (carpels) are called "perfect" flowers; flowers with either stamens or carpels but not both are "imperfect". Some plant species have separate male flowers and female flowers on the same individual plant; these plant species are called "monoecious". Other plant species have the two types of flowers separated onto different individual plants (there are male plants and female plants); these are called "dioecious".

With the basic flower structure as a starting point, flowers have diversified into a host of morphological types. Some flowers are relatively simple and little different from the basic pattern, with all of the parts, and with more or less radial symmetry (actinomorphic). Many other plants have flowers that have lost some of the parts, or have become bilaterally symmetric (zygomorphic). Still others have developed not individual flowers but clusters of flowers called inflorescences. There are many types and arrangements of inflorescences. In extreme cases (e.g. the composites) inflorescences are so specialized that they resemble individual flowers.

In spite of the almost bewildering array of flower types, there are some patterns in their diversity. Pollination or flower "syndromes" reflect the nature of the most common pollinators of flowers. For instance, flowers with a deep corolla tube (a tube formed by the perianth segments) and radial symmetry are often pollinated by lepidopterans, because these insects have a long proboscis. Daytime foraging butterflies visit colorful flowers, especially yellows and pinks, while nocturnal moths visit pale flowers with strong scents. Beetles are not usually important pollinators, but they visit flowers (or inflorescences) that are wide and flat, that are drab or white, and that have a strong pungent odor. Plants that are pollinated by flies may have flowers that act as traps or that produce noxious odors (because flies are attracted to decay and filth), but other fly-pollinated flowers are colorful and fragrant. Bees usually visit flowers that are relatively shallow, that often are zygomorphic, that are yellow, blue, or white, and that have a strong, sweet aroma. Many flowers that are pollinated by diurnal insects have color patterns that reflect ultraviolet light, which is visible to some insects but not to vertebrates. Finally, hummingbirds pollinate flowers that have a deep corolla and that are bright red or orange (vertebrates see reds better than blues), but that have little if any odor (because birds have a poor sense of smell).

Pollinators are as diverse in their behavior as flowers are in their morphology. The main types of pollinators, the flies, the lepidopterans, and the hymenopterans, are phylogenetically distantly related, are very diverse (with total numbers of species in the hundreds of thousands) and thus have very different ways of foraging and different needs that they fulfill by visiting flowers. Then there are the beetles, which are not very effective pollinators (from the plant's point of view), but are instead predators of plant parts, and thus have a very different effect on the plants than the other insect visitors. Leps and flies do not provision developing offspring, so are interested only in food for themselves. As adult insects (and ones with relatively short lifespans) the leps and flies do not need protein for growth, so visit flowers to collect only nectar. Nectar provides sugars which are the source of energy for flight. Bees, in contrast, collect pollen in addition to nectar, because the pollen is the source of protein for developing larvae (which the worker bees provision). The nectar is processed to make honey, which is the source of sugar (energy) for both larvae and adult workers.

Our purposes for this lab exercise are to a) observe the diversity of pollinators that visit a small set of composite flower species during the fall, b) to compare the foraging behavior of some of these pollinators, and c) to compare pollinators' foraging behavior on different plant types. We will develop hypotheses about pollinator foraging behavior after we have observed some of these species in the field.