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## POLLINATION ECOLOGY IN THE ARID SOUTHWEST<sup>1</sup>

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### ABSTRACT

Comparisons of the pollination biology of members of a number of genera (*Prosopis*, *Helianthus*, *Opuntia*, and *Krameria*) widespread in the arid American Southwest are made between sites in the Sonoran Desert of southern Arizona and the dry oak-juniper grasslands of central Texas. As in the majority of cases studied to date in the dry regions of the Southwest, solitary bees are the dominant pollinators in all of the systems examined. Rich arrays of oligolectic bees are associated with *Prosopis*, *Helianthus*, and *Opuntia*, but none with *Krameria* which offers oils rather than pollen and nectar as the primary floral reward. Nevertheless, *Krameria* appears to have the most restricted pollination system as none of the other taxa are obligately dependent on their specialist bees. Reward production and bee foraging activity were examined in *Opuntia* and *Helianthus*. In *Helianthus*, bimodal pollen presentation, but near constant nectar production, results in different activity patterns of the specialist and generalist bees visiting the flowers. Reward production is unimodal in the *Opuntia* species studied, but diurnal phenological differences can result in apparent partitioning of floral resources by foraging bees.

Key words: pollination, Southwest, oligolecty, *Prosopis*, *Opuntia*, *Helianthus*, *Krameria*.

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### INTRODUCTION

The field of pollination biology was in full flower in Europe and New England in the middle of the nineteenth century, but it was almost 100 years before such studies were seriously undertaken in the arid regions of the American Southwest. The early work, started in the deserts of California by Linsley, Hurd, and co-workers, stressed the abundance and importance of bees, primarily solitary bees, and pointed out the frequent narrow associations of these bees with specific plant groups. Solitary bees can live singly or in aggregations, but they are defined as species in which each female constructs and provisions her own larval cells. Since this early work, there has been an escalation of work on the pollination biology in the Southwest, although much of this has centered in comparatively more mesic montane or shrubland habitats.

In our discussion, we restrict ourselves to arid and semiarid habitats, and focus on solitary bees, the group of flower visitors that is unexcelled in these habitats. Within the arid Southwest, we concentrate on two areas, the desert scrub of the northern Sonoran Desert and the central Texas desert grassland. We restrict the discussion to these two regions to reduce the subject to a manageable size and to highlight the ones in which we have worked most extensively. Before discussing our work, we set the stage by summarizing several of the influential studies of pollination biology in the warm North American deserts and point out the foundation they provided for subsequent work on solitary bees and their flowers. Although early studies of Southwestern pollination biology were taxon oriented, and generally described associations of particular bees with selected plant groups, they provided a great deal of information on the diversity and distribution of

visitors to particular plants as well as on the timings of insect activities. Nevertheless, the narrow focus of these studies made it difficult to put the information they provided into a broad context of pollination biology. In contrast to these studies, much of our work in Arizona and central Texas has tried to consider not only correlations between numbers of captures of particular bees on selected plant species, but also the breeding systems and reward structures of the plants involved, the foraging patterns of the bees, and the diversity of hosts used by the various insect visitors. By looking at the pollination ecology of several species in an area, we have attempted to assess the effects of the environment, both biotic and abiotic, on the pollination systems of many of the important plant species in the two areas.

One of the obvious differences between the northern Sonoran Desert and central Texas is the climate. From west to east across the southern United States there is a change from xerophytic communities dominated by insect-pollinated shrubs and trees to temperate forests in which almost all of the major tree species are wind pollinated (Fig. 1). Central Texas is the natural geographic break between the mesic eastern and xeric western United States, and, as might be expected, the flora is a mixture of eastern and western plant species. Many of the species growing in central Texas which are pollinated by solitary bees are closely related to species in the deserts to the west, with some plant species common to both areas. It is on four such congeneric or conspecific plant groups that we focus here, pointing out similarities and differences in the pollination biology between populations occurring slightly west of Tucson, Arizona, in the northern Sonoran desert and in central Texas west of Austin in the oak-juniper grasslands.

#### MAJOR STUDIES OF SOLITARY BEES AND THEIR PLANTS IN THE SOUTHWESTERN DESERTS

Within the arid and semiarid regions of the Southwest, several studies of solitary bees and their associations with specific plant groups have become "classics" and have served as the stimuli for subsequent investigations. The most important of these centered on the Onagraceae and Cucurbitaceae and their associated bees (Hurd and Linsley 1964, 1966, 1967*a, b*; Hurd, Linsley, and Whitaker 1971; Linsley, MacSwain, Raven, and Thorp 1973; MacSwain, Raven, and Thorp 1973). Taken together, these studies demonstrated the specialized nature of the pollination systems of numerous southwestern plants and the diversity of "specialist" solitary bees associated with them. "Specialist" in this context is used for species of bees with females that "specialize on," or restrict their pollen foraging to, one species or a group of related plant species. Such specialists are often referred to as oligolectic to distinguish them from polylectic ("generalist") bees that forage for pollen on a range of taxonomically unrelated plants. Oligolecty is thus a long-term characteristic of a species or population and is not to be confused with foraging constancy, a short-term property of individuals.

In their work on bees associated with the Onagraceae and the Cucurbitaceae, Hurd, Linsley, and coworkers focused on the phenomenon of oligolecty. The notion of high host specificity among desert bees was in keeping with a popular hypothesis that predicted that specializations between insects and their hosts were most likely where there was a high level of competition for scarce resources (presumed to occur in deserts), but it countered another commonly held hypothesis

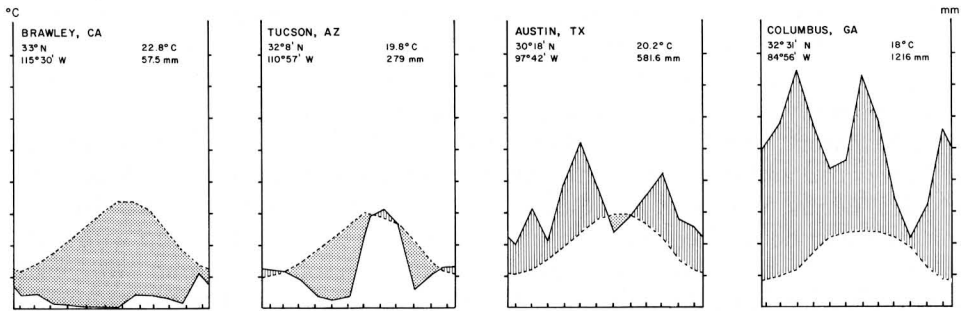


Fig. 1. Climate diagrams of selected sites across the southern United States showing the increased precipitation and reduction in seasonality of moisture from west (left) to east (right). In the upper right hand corner of each diagram are the mean annual precipitation and mean annual temperatures. Latitudes and longitudes are given in the upper left. Each tic mark on the horizontal axis corresponds to a month starting with January. The left vertical axis is temperature in C with each division 20 C. The right vertical axis is precipitation with each division 40 mm of rainfall. Mean temperatures and precipitation are graphed for each month. The dashed line connects monthly temperature means, the solid lines monthly precipitation means. Where the precipitation line exceeds the temperature line (striped areas), there is sufficient moisture for plant growth. Where the temperature line exceeds the precipitation line (stippled areas), there is a deficit of moisture for plant growth. Data from U.S. National Oceanic and Atmospheric Administration. U.S. Dept. of Commerce. 1974. *Climates of the United States. Vol. II. Western States.* Water Information Center, Inc., Port Washington, New York.

that such specializations should be greatest in stable (i.e., wet tropical) habitats. For better or worse, the findings of these entomologists fueled speculation about the coevolution of plants and their pollinators and the possible importance of such evolution in the speciation of various plant groups. However, the actual results and conclusions of their studies were rather restrained and often pointed out the lack of correlation between host specificity of solitary bees and the diversification of the plant groups to which they were restricted.

For example, their survey of the bees of *Camissonia* and *Oenothera* in desert habitats produced a list of over 30 bee taxa that were restricted to members of the Onagraceae as pollen hosts (Linsley, MacSwain, and Raven 1963; Linsley et al. 1964, 1973). A few of these bee species were apparently monolectic (restricted to a single pollen host), but no one-to-one plant/pollinator systems were found. In many cases, the bees harvested pollen from large-flowered *Oenothera* species after the flowers had been visited by hawkmoths. Such bees were, in fact, behaving more like scavengers than primary pollinators. Even in the out-crossing bee-pollinated *Camissonia* species (Linsley et al. 1973), bee pollination apparently had minimal influence on the evolution of the genus. They did note that major shifts in pollination had occurred from bee to moth and vice versa (Linsley et al. 1973), or from outcrossing to autogamy (Raven 1969), and that these shifts may have been important in the evolution of the group, but subtle species-specific interactions were apparently absent.

Another series of investigations, this time with a group that ranged far outside the southwestern United States (Hurd and Linsley 1964, 1966, 1967a, b; Hurd et al. 1971) dealt with the squash and gourd bees (*Peponapis* and *Xenoglossa*, Anthophoridae), robust bees obligately associated with the genus *Cucurbita*. The association of the squash bees with members of *Cucurbita* captured the interest of many people for two reasons. First, several species of *Cucurbita* are commer-

cially important, providing the squashes, zucchinis, and pumpkins of commerce, and, secondly, because the unusual blooming pattern of these plants is closely followed by their specialist bees. All of the species of *Cucurbita* have large flowers that commonly open, and become pollinated, before dawn.

In their work, Hurd and coworkers tried to find associations of species groups of *Xenoglossa* and *Peponapis* with major groupings within *Cucurbita*. Studies by Rhodes, Bemis, Whitaker, and Carmer (1968) had previously indicated that *Cucurbita* could be divided into two major groups, a xerophytic group with eight species subdivided into two subgroups, and a mesophytic group with eight subgroups containing the remaining 21 species of the genus. The five cultivated species of *Cucurbita* are dispersed among five different mesophytic subgroups. The remaining mesophytic species are wild.

Most of the 20 species of the two bee genera showed broad utilization of both the mesophytic *Cucurbita*, including the wild and domesticated taxa, and the xerophytic species. Two exceptions to this pattern were noted: *Peponapis atrata* (Smith) seemed to be restricted to the mesophytic 'Ficifolia' subgroup of *Cucurbita*, and *Peponapis timberlakei* Hurd & Linsley to the xerophytic 'Digitata' subgroup.

In several papers, Hurd and collaborators (Hurd and Linsley 1970; Hurd et al. 1971) proposed a scenario in which evolution of the cucurbits and squash bees involved movement from mesophytic to xerophytic habitats (although the reverse was postulated for *Xenoglossa*) correlated with increasing host specificity. This change in specificity was purported to be accompanied by morphological adaptations of the pollen transporting scopal hairs that supposedly facilitated utilization of the pollens of particular cucurbits. Unfortunately, actual documentation of covariation in pollen size and scopal structure has never been demonstrated. Although some species of squash bees do differ in the cucurbits they utilize, the basis for the differences in utilization patterns remains unclear. Furthermore, while the squash bees are normally the major pollinators of *Cucurbita* under natural conditions, Tepedino (1981) has shown that the introduced honey bee is as effective a pollinator of *Cucurbita pepo* L. on a per visit basis as the specialist, *Peponapis pruinosa* (Say). Such findings undercut arguments about the necessity of specialist bees for the successful pollination of their hosts.

These early studies were all carried out, at least originally, because of an interest in particular bees or plants. In such investigations, work can be very detailed, but the focus on one taxonomic group can often obscure the interrelationships of the pollination systems of the host plants to those of other plants of the communities in which they occur. In our research, first in Arizona and now in Texas, we have taken a broader approach. In Arizona, we specifically carried out a community-level study as part of the International Biological Program (IBP) dealing with the convergence of desert scrub ecosystems. The purpose of the overall project was to determine if evolution in widely disjunct areas with similar climates would produce communities with similar spectra of pollination systems. While our results were useful within the context of the overall IBP project, they, like taxon-oriented studies, had drawbacks because detail was necessarily sacrificed in order to gather information about as wide a range of plants and their pollinators as possible. In the Texas grasslands, we plan eventually to develop an understanding of the pollination ecology of the entire ecosystem, but in doing so we are studying

each plant taxon in depth. As yet, we have adequate data on only a few dozen of the hundreds of insect-pollinated flowers in central Texas, but these allow some interesting comparisons with our findings in Arizona.

Our decision to work in Texas is as much a reflection of our current residence as an interest in the ecosystem itself. Likewise, the choice of plants we include here is dictated by the need for an integrated discussion and does not reflect the extent of our Texas work. In order to provide a comparative link between our work in Arizona and Texas, we have chosen to compare and contrast the pollination biology of species that occur and have been studied in both Arizona and Texas (*Opuntia leptocaulis* DC., Cactaceae; *Helianthus annuus* L., Asteraceae) or with closely related species belonging to genera occurring in both areas (*Prosopis*, Fabaceae; *Krameria*; other *Opuntia* spp.). Studies of the pollination biology of widely separated conspecific or congeneric populations has highlighted the fact that central Texas is a transition zone between the scrub to the west and the moist forests to the east, but one which still contains many western plants with specialized relationships with solitary bees. In a few cases, there are differences in the pollination biology of the related plants in the two areas. Explanations of such differences require an understanding of the presettlement natural vegetation as well as the climatic changes from west to east across the southern United States. We explore these differences by first giving an overview of the work in the Sonoran Desert and then focusing on the cooccurring elements.

#### THE NORTHERN SONORAN DESERT

The area in which we worked in Arizona was 20 miles west of Tucson in the Silver Bell Valley. The area is covered by desert scrub vegetation characteristic of the northern Sonoran Desert. Mean annual rainfall is 279 mm falling in two periods during the year (Fig. 1), but primarily in the winter (Bailey 1977). In terms of physiognomy, the system is a shrub/small tree dominated system. Studies on the phenology showed that almost all of the species are mass bloomers with many of the species having a late spring-early summer peak bloom and, sometimes, a secondary, late summer bloom (Fig. 2). The landscape consists of broad areas of sandy flats, and bajadas that form sloping shoulders jutting out from the mountains that surround arid basins such as the one in which Silver Bell is located. The bajadas are the most diverse parts of the desert scrub system with diversity increasing as one ascends them. The dominant perennial bajada elements (Fig. 2) include *Simmondsia chinensis* (Link) Schneid. (Simmondsiaceae), various *Opuntia* species, *Carnegiea gigantea* (Engelm.) Britt. & Rose (Cactaceae), *Krameria grayi* Rose & Painter (Krameriaceae), *Cercidium microphyllum* (Torr.) Rose & Johnston and *C. floridum* Benth., *Olneya tesota* A. Gray, *Calliandra eriophylla* Benth., *Acacia greggii* A. Gray (all Fabaceae), *Jatropha cardiophylla* (Torr.) Muell. Arg. (Euphorbiaceae), *Fouquieria splendens* Engelm. (Fouquieriaceae), and *Encelia farinosa* A. Gray (Asteraceae). Washes of variable sizes cut through the bajadas and meander across the flats. Along the washes, phreatophytic trees or shrubs such as *Prosopis velutina* Woot., *Acacia greggii*, *Cercidium floridum* (all Fabaceae), and *Celtis tala* Gillies (Ulmaceae) commonly occur. The flats constitute the driest part of the study area and are generally covered by essentially pure stands of *Larrea tridentata* (DC.) Coville (Zygophyllaceae) mixed with *Ambrosia*

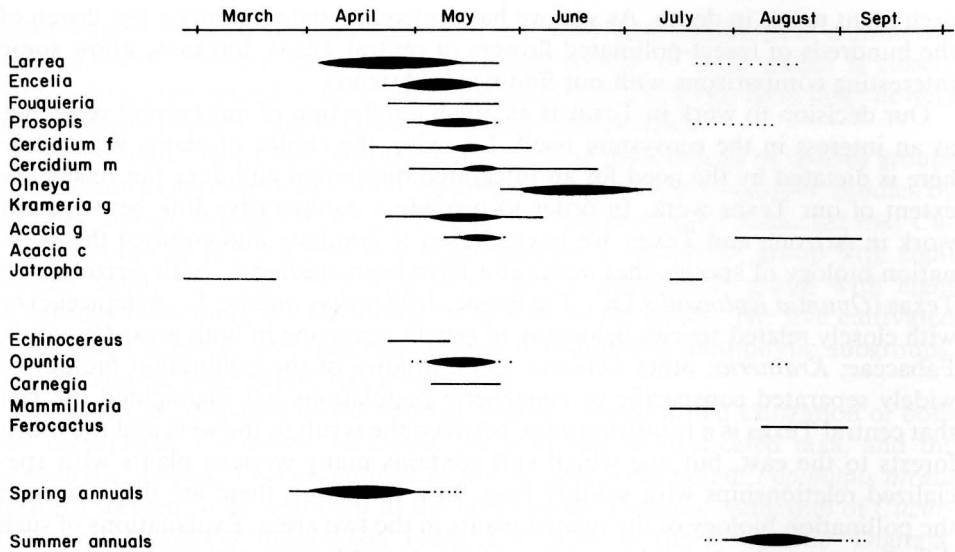


Fig. 2. Blooming times of selected dominant plant groups in the Sonoran Desert west of Tucson, Arizona. The width of the lines gives a qualitative indication of the intensity of the bloom (total numbers of flowers open). Dashed lines indicate variable blooming times.

*dumosa* (A. Gray) Payne and *A. deltoidea* (Torr.) Payne (both Asteraceae). In the spring and later at the end of the summer (following rains), annuals appear. Depending on the quantity of rainfall, annuals can constitute a significant portion of the plant cover for short periods of time.

In our work on the Sonoran Desert scrub ecosystem we made several predictions about the prevalence of various pollination systems (Neff, Simpson, and Moldenke 1977). We hypothesized that selfing would be facultative in many groups of plants but particularly important in the case of annuals. The widespread ability for self-pollination we felt would be of selective advantage in areas such as deserts with unreliable climate (rainfall). It also seemed probable that wind pollination would be of minimal importance compared with other kinds of ecosystems because correlates of wind pollination are relatively low diversity of species, close proximity of conspecifics, and exposed anthers and stigmas (Whitehead 1969, 1983). In desert scrub environments, plants tend to be widely spaced and, because of the probability of rapid drying, delicate sexual parts cannot be exposed for long periods of time. In terms of biotic pollination, it seemed likely that small invertebrates would predominate. Long-term, large supplies of floral rewards are lacking in deserts, and appeared inadequate for maintaining resident populations of flower-feeding birds or mammals that might serve as pollinators.

Some of these predictions (e.g., that annuals should be autogamous) now appear trivial; others were variously borne out by our investigations. We found, as have many workers since, that almost all annuals and herbaceous perennials were facultatively autogamous and depended less than other groups on external pollen vectors. Nevertheless, many annuals including both showy forms such as the Mexican poppy, *Eschscholtzia mexicana* Greene (Papaveraceae) and the bladderpod, *Lesquerella gordonii* (A. Gray) S. Wats. (Brassicaceae), as well as more inconspicuous taxa such as various *Euphorbia* species (Euphorbiaceae) or *Tide-*

*stromia* (Amaranthaceae) support large populations of oligolectic bees. These annuals and herbaceous perennials thus exhibited patterns much like those found in the Onagraceae species investigated in California and adjacent Mexico. We did find that invertebrates, particularly small invertebrates, constituted the largest group of pollinating agents. Of these, bees were the single most important group. During our work in Arizona, we placed particular emphasis on the pollination systems of the dominant woody perennial species. Within this group there proved to be a great diversity of flower morphologies, colors, breeding systems, and pollination syndromes (Simpson 1977). Over half of the dominant perennials in the Silver Bell Bajada were exclusively or predominantly pollinated by bees. Yet, despite the prevalence of insect pollination, there were five notable exceptions to our predictions about pollinating agents. Three of the dominant perennials in the northern Sonoran Desert, *Simmondsia chinensis*, *Ambrosia deltoidea* and *Ambrosia dumosa* are wind pollinated and *Fouquieria splendens* is predominantly pollinated by hummingbirds in this area (Grant and Grant 1968; Waser 1979). In addition, the columnar cactus, *Carnegiea gigantea*, is pollinated in large part by bats (Alcorn, McGregor, and Olin 1961; Cockrum and Hayward 1962).

In examining the possible reason for the unexpected presence of wind and vertebrate pollination, we were forced to reexamine our concept of an unpredictable, low-rainfall regime (Simpson 1977). This reexamination pointed out that, although the area around Tucson falls into a category of a desert scrub ecosystem based on overall moisture availability throughout the year, the pattern of rainfall (Fig. 1) is important in determining times of blooming and, as a result, pollination systems. In particular, the bimodal rainfall pattern with significant amounts of precipitation falling in the cool winter months proved to be important. The presence of available moisture early in the year allows plants to flower soon after temperatures are sufficiently warm for renewed growth. Under such warm, but not hot conditions, exposure of stigmas and anthers is not a liability, and wind pollination becomes feasible for some woody plants, particularly those that tend to grow in dense stands in specific microhabitats (e.g., *Simmondsia* on slopes and the *Ambrosia* spp. on sandy flats). The two species of *Ambrosia* flower and then die back with increasing drought and rising temperatures. *Fouquieria* is a stem succulent and thus is able to bloom in the spring when it can take advantage of hummingbirds, which migrate through this region of the Sonoran Desert in April and May. Nevertheless, carpenter bees (*Xylocopa* spp.) can and do effect a considerable amount of *Fouquieria* pollination around Tucson (Waser 1979; pers. obs.). A similar explanation holds for the saguaro (*Carnegiea gigantea*) for which bats serve as major pollinating agents. There are not, as predicted, any major resident vertebrate pollinators since in both cases the flower-visiting vertebrates are transients in the system.

Wasps are important pollinating agents for *Acacia greggii* and *Jatropha cardiophylla*, both species with generalized pollination syndromes. Butterflies and/or flies are probably the most effective pollinators of *Calliandra* and *Encelia*. The remaining species are pollinated by bees. We discussed the pollination of *Prosopis* (Simpson, Neff, and Moldenke 1977a) and *Larrea* (Simpson, Neff, and Moldenke 1977b) in detail in earlier papers and we have carried out extended studies of *Krameria* and its associated pollinating bees over the last ten years (Simpson, Neff, Seigler, and Martin 1977; Seigler, Simpson, Martin, and Neff 1978; Simpson, Seigler, and Neff 1979; Simpson and Neff 1981, 1983; Simpson, in press). In the



context of our comparison between Arizona and the Texas grasslands we will emphasize several points brought out in these and other studies in Arizona.

#### THE CENTRAL TEXAS GRASSLAND SYSTEM

The Edwards Plateau region west of Austin currently supports an oak-juniper savannah. The region is not a desert, but due to the high variance in rainfall, both within and between years, the normal summer drought (Fig. 1), and the very shallow soils, many of the plants show xerophytic adaptations. Dominant elements include low trees such as the live oak (*Quercus fusiformis* Small, Fagaceae), "cedar" (*Juniperus ashei* Buchh., Cupressaceae), and mesquite, *Prosopis glandulosa* Torr. These are mixed with evergreen shrubs such as agarito (*Berberis trifoliolata* Moric., Berberidaceae), the Texas persimmon (*Diospyros texana* Scheele, Ebenaceae), and various cacti (*Opuntia compressa* [Salisb.] Macbr., *O. leptocaulis*, *O. lindheimeri* Engelm., *O. phaeacantha* Engelm.). Dominant grasses (in our study areas near Austin) are Texas gramma (*Bouteloua rigidiseta* [Steud.] Hitch.), various other gramma species (*Bouteloua* spp.), numerous *Aristida* species such as *A. longiseta* Steud., Texas speargrass (*Stipa leucotricha* Trin. & Rupr.), buffalo grass (*Buchloë dactyloides* [Nutt.] Engelm.), curly mesquite (*Hilaria swallenii* Cory), and on slopes, little bluestem (*Schizachyrium scoparium* [Michx.] Nash). In favorable (wet) years, a rich succession of annual and perennial herbs bloom in the spring with another set flowering in the fall (Fig 3). Common spring flowers include bladderpod (*Lesquerella gracilis* [Hook.] Wats.), winecup (*Callirhoë* spp., Malvaceae), bluebonnet (*Lupinus texensis* Hook., Fabaceae), Indian paintbrush (*Castilleja indivisa* Engelm., Scrophulariaceae), Mexican hat (*Ratibida columnaris* [Sims] D. Don, Asteraceae), and fireweed (*Gaillardia pulchella* Fouq., Asteraceae). Fall flowering is dominated by composites (*Liatris*, *Solidago*, *Viguiera*, *Zexmenia*, *Amphiachyris* and others) with a smaller representation by taxa such as *Euphorbia bicolor* (Euphorbiaceae) and *Agalinis edwardsiana* Penn. (Scrophulariaceae).

Among the dominant species, the most important elements, the grasses, *Quercus*, and *Juniperus*, are all wind pollinated. This prevalence of wind pollination provides a direct contrast to our site in Arizona where the large trees are all insect pollinated and perennial grasses are uncommon. Yet, almost all of the central Texas forbs are insect pollinated and, as in Arizona, bees predominate as the major group of pollinators. However, a significant set of early-flowering forbs (*Phlox*, *Lithospermum*, Polemoniaceae; *Castilleja*) are butterfly and/or bird pollinated. The pollination biology of several of the annuals has been studied and indicates a mixture of facultative selfers and obligately outcrossed taxa. Predominantly self-incompatible taxa include *Phlox*, *Lupinus* (Fabaceae), and many composites.

To date, we have included in our studies *Tinantia anomala* (Torr.) C. B. Clarke (Commelinaceae; Simpson, Neff, and Dieringer 1986), *Ungnadia speciosa* Endl. (Sapindaceae), *Prosopis glandulosa*, *Eysenhardtia texana* Scheele, *Senna lindheimeriana* (Scheele) Irwin & Barneby (Fabaceae), *Krameria secundiflora* DC., *Callirhoë involucrata* (Torr.) A. Gray (Neff, Simpson, and Dorr 1982), *Passiflora lutea* L. (Passifloraceae), *Opuntia compressa*, *O. lindheimeri*, *O. leptocaulis*, *Sabatia campestris* Nutt. (Gentianaceae), *Nemophila phacelioides* Nutt. (Hydrophyllaceae), *Agalinis strictifolia*, *Helianthus annuus* L. (Neff and Simpson 1984), *Viguiera dentata* (Cav.) Spreng., *Rudbeckia hirta* L. (Bear 1985), *Coreopsis basalis*

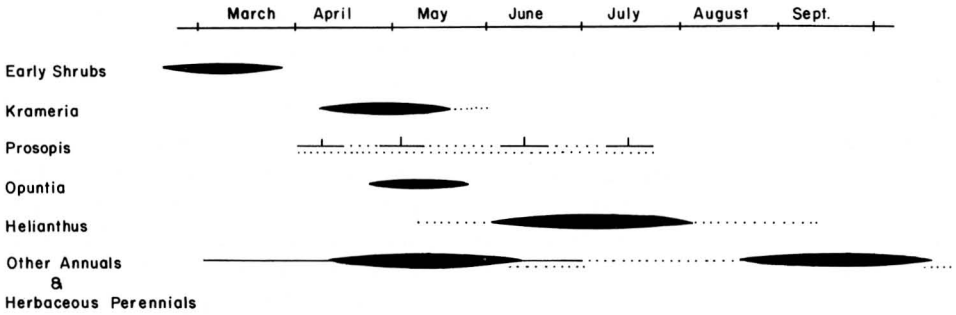


Fig. 3. Blooming schedules of selected plants in the grasslands of the Edwards Plateau west of Austin, Texas. As in Figure 2, the width of the lines reflects the intensity of the bloom and dotted lines represent erratic times of flowering.

(Otto & Dietr.) Blake and *Pyrrhopappus multicaulis* DC. (all Asteraceae). In our discussion we single out the cacti, *Krameria*, *Prosopis*, and *Helianthus*, because of our comparative data from Arizona.

#### THE COMPLEX ARRAY OF CACTUS BEES

The plants that people most often associate with arid habitats are the cacti. Appropriately, our Silver Bell site supports a rich array of cactus species, the most abundant of which are the giant saguaro (*Carnegiea gigantea*), Engelmann's prickly pear (*Opuntia phaeacantha* Engelm.), and the buckhorn cholla (*Opuntia acanthocarpa* Engelm. & Bigel.). Among the less common cacti species are cholla (*Opuntia fulgida* Engelm.), cane cholla (*O. spinosior* [Engelm. & Bigel.] Toumey), desert Christmas cactus (*O. leptocaulis*, named for its bright red, persistent, often viviparous fruits), barrel cactus (*Ferocactus wislizeni* [Engelm.] Rose & Britt.), a hedgehog cactus (*Echinocereus fendleri* [Engelm.] Rümpler), a night-blooming cereus (*Peniocereus greggii*), and a fishhook cactus (*Mammillaria microcarpa* Engelm.).

Most of these cacti flower in the spring (late April and May, Fig. 2). The various chollas and prickly pears of the genus *Opuntia* form the largest group of cacti, and, with the exception of *O. leptocaulis*, which we did not observe in flower at Silver Bell, all share a common suite of visitors dominated by the robust cactus specialist bees of the genus *Diadasia* (*D. rinconis* Cockerell, *D. opuntiae* Cockerell, and *D. australis* [Cresson], all Anthophoridae) and *Lithurge* (*L. gibbosa* [Smith], Megachilidae). Even though the various *Diadasia* are most commonly found on *Opuntia*, they apparently exploit all the large-flowered cacti available to them. To a lesser extent, *Opuntia* flowers are also visited by various generalist bees. Despite the overlapping suite of visitors, the opuntias as a group have flowering times that broadly overlap (Fig. 2). Current data are insufficient to determine if individual constancy or variation in foraging activity separates the plant taxa as might be expected if these cacti were competing among themselves for pollinator service. Alternatively, the nearly simultaneous flowering of the *Opuntia* species may promote the maintenance of large bee populations that provide adequate pollinator service even though it might involve high levels of interspecific pollen transfer. However, such a system would seem wasteful from a viewpoint of male function.

The cacti other than the large-padded *Opuntia* do show some displacements in terms of pollinators and/or blooming times. Flowers of the large-flowered cereoids open at night and may be normally nocturnally pollinated by bats (*Carnegiea*: Alcorn et al. 1961; McGregor and Alcorn 1962; Cockrum and Hayward 1962; Howell 1974) or moths (*Peniocereus*). Saguaro flowers are also heavily exploited by bees, especially *Diadasia*, and birds during the morning before they close. Under restricted experimental conditions, all these classes of floral visitors have been shown to be effective pollinators of saguaro (Alcorn et al. 1961). The small flowers of *Mammillaria microcarpa* appear after the main cactus bloom (Fig. 2) during a period of low general flowering and are visited by small bees.

The most distinctive set of bees, however, is associated with the barrel cactus (*Ferocactus wislizeni*) which flowers primarily in August (Fig. 3) well after most other cacti at our Arizona site had finished. One of the abundant specialist bees of this species is *Lithurge echinocacti* (Cockerell). Another common visitor is *Perdita echinocacti* Timberlake (Andrenidae), sometimes considered a cactus specialist, but this bee obviously does not restrict its visits to the Cactaceae since we find 10–30% noncactaceous pollen in most scopal pollen loads.

Little is known of the breeding systems of Sonoran Desert cacti, but the saguaro, the hedgehog (pers. obs.), and the barrel cactus (McGregor and Alcorn 1959) are all apparently self-incompatible or largely so. All of the *Opuntia* reproduce extensively by rooting of detached joints or vegetative "fruits." Bagging of flowers of *O. phaeacantha* and *O. acanthocarpa* indicated that the prickly pear is autogamous, but that the cholla is not. Reproduction in another cholla, *O. fulgida* Engelm., is apparently entirely vegetative (Grant and Hurd 1979; Neff, pers. obs.).

The Edwards Plateau of Texas is near the eastern limit for many cactus genera, but we still find representatives of most of the major groups except the cereoids. Over the last seven years we have been able to study the floral biology of several cacti and the foraging behavior of their visitors in much greater detail than in Arizona. Most common in our Texas study areas are various species of *Opuntia*. These include the Texas prickly pear (*Opuntia lindheimeri*), Engelmann's prickly pear (*O. phaeacantha*), the plains prickly pear (*O. macrorhiza* Engelm.), and the tesajo (*O. leptocaulis*). The first two of these cacti, and probably also the third, form hybridizing swarms (Benson 1982; Grant and Grant 1979a, b) which makes assignments to species difficult. Other, less frequently encountered cacti include the claret cup (*Echinocereus triglochidiatus* Engelm.), a hedgehog (*Echinocereus reichenbachii* [Terscheck] Haage f.), the horse crippler (*Echinocactus texensis* Höpfer), and *Mammillaria heyderi* Mühlenpfordt.

Our data from Texas indicate that, as in Arizona, many of the cacti share pollinators, in fact, for the most part, the same suite of pollinators as the cacti in Arizona. The central Texas total cactus bloom is comparatively restricted temporally (Fig. 3) but we have still noted only limited diurnal or seasonal staggering of blooming that might suggest an avoidance of competition for the same pollinators. The claret cup, which has a flower that indicates hummingbird pollination, blooms early in the year before the other cacti. However, we have seen few visits of any kind to its flowers. The large-flowered, large-padded *Opuntia* species bloom slightly later in late April or early May (Fig. 3), but within this group, there is extensive overlap in both blooming times and flower visitors. The most common flower feeders are robust specialists such as *Diadasia rinconis*, *Lithurge littoralis*

(Cockerell), *L. gibbosa*, and the smaller but often very abundant *Perdita texana* Cresson. Other specialists such as *Megachiloides casadae* (Cockerell) and *Ashmeadiella* sp. (both Megachilidae) are less common.

*Opuntia macrorhiza* begins blooming slightly later than the larger-padded opuntias but overlap is extensive. Some temporal division can, however, occur during a day. Timed observations at Pedernales Falls State Park (30 miles west of Austin) have shown that one of the *O. phaeacantha*-like forms (possibly *O. edwardsii* of Grant and Grant [1979a]) frequently opens earlier in the day than *O. macrorhiza*. Pollen-collecting bees gradually shift their foraging from one taxon to another as the flowers of the earlier-opening species are depleted (Neff and Simpson, in prep.). Curiously, this pattern is not consistent, and on some days, the opposite occurs (*O. macrorhiza* before *O. aff. edwardsii*).

The similarity of visitors and broadly overlapping diurnal and seasonal phenology means that there are few extrinsic barriers to hybridization between *Opuntia* species. As is the case of cacti everywhere, the inter- and intraspecific compatibilities of few species are known. Grant et al. (1979) indicate that plants of *O. lindheimeri* are self-compatible but not autogamous although, at least in some cases, autogamy may be possible at the end of the season (Grant, Grant, and Hurd 1979). In our studies of *O. macrorhiza*, we have found a complex situation in which both the level of self-compatibility and autogamy varies between individuals, with the degree of autogamy depending on both the level of self-compatibility and the extent of anther-stigma separation (Neff and Simpson, in prep.). Preliminary results suggest that a similar complex system operates in *O. phaeacantha*. Variation in the degree of self-compatibility of cacti species has previously been reported (Lambert 1985).

All of these specialists possess relatively long mouthparts which permit access to the well-hidden cactus nectaries. This adaptation is most pronounced in the relatively small *Perdita texana* which has mouthparts much longer than normally found in "short-tongued" bees. As noted by Grant and Hurd (1979), the flowers may also be visited by generalists including *Bombus*, *Xylocopa*, and various halictines.

Although Grant et al. (1979) reported that *Opuntia lindheimeri* does not produce nectar, we have found at our study sites that all *Opuntia* species (including the ones they studied) produced significant amounts of nectar (over 39  $\mu$ l with 22 mg of sugar equivalents in the maximum case).

Nectar is continuously secreted for up to eight hours in some flowers, although precise estimation is difficult because of the need for destructive sampling and the high variance between flowers. In addition, the numerous glochids on the flowers inhibit one's zeal for accumulating a large number of samples. When foraging for nectar, most of the specialists and large generalists (small generalists cannot collect nectar from these species) exhibit the same behavior. Bees land on or near the stigma and then move downward along the style through the motile anthers, eventually forcing their proboscides through the constriction in the floral tube caused by the basal expansion of the style. Large bees usually trigger the motile anther reaction which forces them to stay close to the style. Smaller forms such as *Perdita texana* usually do not trigger the anther reaction.

If one may judge from their behavior, all the larger bees, both specialists and generalists, are probable cactus pollinators because of the large pollen loads carried

on their bodies and their good stigma contact. Preliminary single-visit studies with *Diadasia rinconis* on *Opuntia compressa* indicate that both male and female bees can produce nearly full seed set with a single visit, even on self-incompatible individuals. Males would appear to be particularly effective as pollinators since they frequently perch on one stigma after another while patrolling many flowers in search of mates.

Smaller cactus specialists such as *Perdita texana* have been downrated as pollinators because of the supposed rarity of stigmatic contact (Barrows, Chabot, Michener, and Snyder 1976; Grant and Hurd 1979). We have found that these bees contact the stigma much more often than other workers suggest, but their having been assessed as playing a minor role as pollinators is probably correct since marked individuals of *P. texana* completed up to seven pollen trips in a row in the same flowers.

While butterflies (particularly *Battus*) and hummingbirds occasionally visit cactus flowers, the only significant nonbee group of visitors is beetles, particularly the large pollen-feeding scarabs (*Euphoria* and *Trichiotinus*) and cerambycids (*Strangalina*). Small beetles of the Nitidulidae and Melyridae are often extremely abundant (scores of individuals per flower) but, as they usually arrive at a flower several hours after the initiation of anthesis and then tend to remain sedentary, their role as pollinators is undoubtedly minimal. The large beetles are much more active and often force their way into unopened buds. Nevertheless, our marking studies indicate that *Euphoria* also tends to be rather sedentary. Individual beetles usually spend the night and sometimes several days in succession in wilted flowers and, when moving, move from flower to flower on the same plant. *Trichiotinus* is a better candidate as a pollinator as it is comparatively active and often makes several long-distance moves on a single day. Nevertheless, neither of these large beetles exhibits a great fidelity to particular cacti species or even cacti in general. Gut contents frequently contain a mixture of pollens from an array of plants with bowl-shaped flowers such as *Argemone* spp. and *Callirhoë involucrata* as well as cacti.

The pollination biology of *Opuntia leptocaulis*, which we have studied in detail, differs in several respects from that of the large showy prickly pears. The inconspicuous, cream-colored flowers of this small, cylindrical-stemmed cactus generally open late in the afternoon, usually about the time that the large yellow flowers of the padded cacti wilt, and close well after dark. Each flower produces a relatively dilute nectar (less than 18% sucrose, wt by vol). At one study site but not at another, the flowers were regularly probed by hummingbirds. Moths initially seemed to be likely candidates as pollinators, but they were very rarely observed. If pollen-collecting individuals of the honey bee were excluded, the most abundant visitors were pollen- and nectar-foraging individuals of the common cactus specialist, *Diadasia rinconis*. Although individuals of other cactus specialists such as *Lithurge* spp. and *Perdita texana* were active on the prickly pears at these sites earlier in the day, we have never discovered any of them at flowers of *O. leptocaulis*. Other less common visitors to the flowers include pollen-collecting halictids and long-tongued nectaring anthophorid bees. Visits by any of these bees except the smallest halictids resulted in deposition of large amounts of pollen on the stigmas. It is likely that much of this is self-pollen which is ineffective in fertilization since preliminary results indicate that *O. leptocaulis* is self-incompatible. In sexually

reproducing individuals of this population, fruit set is high, but natural seed set is low, lower than that of hand-outcrossed flowers. Natural, low seed set is thus apparently due to pollen limitation despite heavy visitation. Unfortunately, much of our first set of study plants was destroyed by an errant bulldozer.

Thus we can see, that except for the night-blooming cereoid cacti which are probably excluded from central Texas by the occasional hard winter freezes, the pollination systems of cacti in Arizona and Texas are very similar. Although data for cactus species remain fragmentary, most southwestern cacti appear to share a common suite of wide-ranging, specialist bees, and a broad array of generalists, many of which are quite capable of pollinating the relatively uniform flowers. Large scarab beetles are generally more abundant in Texas than in Arizona, perhaps because of the greater quantities of rotting wood in which the larvae feed, but, as noted by Grant and Hurd (1979), they are probably of secondary importance as pollinating agents.

The fact that such a similar pollination system persists over an extremely broad geographical area (essentially from the western limit in California to the eastern edge of abundant cacti distribution in Texas) may not seem odd in view of the widespread distribution of genera and even species within the Southwest. However, this pattern contrasts with that of *Prosopis* (see below) with which the cacti cooccur over most of the Southwest. On a broader geographical scale, however, the cacti do exhibit a pattern parallel to that found in *Prosopis*. Both the cacti and *Prosopis* have evolved independent arrays of specialist bees in the disjunct desert scrub ecosystems of North America and South America (Simpson and Neff, 1985).

#### KRAMERIA AND ITS OIL BEES

One of the most interesting pollination systems we discovered in Arizona involved *Krameria* and its pollinators. In the northern Sonoran Desert, two species of *Krameria*, *K. erecta* Willd. ex Schultes (= *K. parvifolia* Benth.) and *K. grayi* Rose & Painter are common in the desert and *K. secundiflora* (= *K. lanceolata* Torr.) is abundant in the desert grassland. At Silver Bell, only *K. grayi* was present. *Krameria* flowers are medium sized (about 2 cm in diam), zygomorphic, and highly modified with two of the petals transformed into oil-secreting structures called elaiophores (Simpson 1982). The flowers produce no nectar. Pollen, presented as a cohesive mass extruded from the poricidal anthers, is only occasionally collected by insects visiting the flowers. The primary floral rewards are fixed oils (free  $\beta$ -acetoxy fatty acids in the case of *Krameria*) that are collected by female bees of the genus *Centris* (Anthophoridae). The oils are used, mixed with pollen and nectar, as a primary larval food. We have explained in detail elsewhere the chemical nature of the oils and the specialized adaptations of female *Centris* for their collection (Simpson et al. 1977; Seigler et al. 1978; Neff and Simpson 1981; Simpson and Neff 1981). Experiments with *K. grayi* and observations of visiting insects suggested that this species was self-incompatible and that essentially all of the pollination was effected by female *Centris* although a few small bee taxa (*Dialictus* spp., Halictidae, *Exomalopsis* spp., Anthophoridae) occasionally visited to glean pollen.

In the beginning of our study, it appeared that the *Krameria-Centris* system

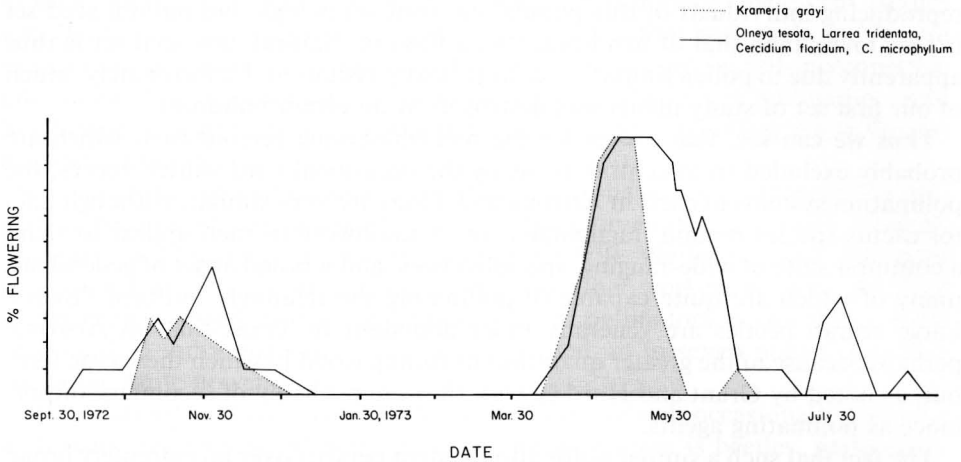


Fig. 4. Blooming times of *Krameria grayi* superimposed on the combined flowering patterns of *Larrea tridentata*, *Cercidium microphyllum*, *C. floridum*, and *Olneya tesota* near Tucson, Arizona. The oil-collecting *Centris* species that pollinate *Krameria* visit these other plants for nectar and pollen.

would illustrate a tight, obligate, coevolved pollination system. Indeed, it is true that *Krameria* does not set significant seed without visits to the flowers by female *Centris*. However, the *Krameria*-visiting *Centris* are not dependent on *Krameria* for oils (unless there are no other oil-secreting plants locally available, and then oil-specificity is externally imposed) because species of *Centris* visit a wide range of oil, pollen, and nectar hosts. At our Silver Bell site, for example, the same female *Centris* that visited *Krameria* could regularly be observed collecting oils from the small-flowered desert vine, *Janusia gracilis* A. Gray (Malpighiaceae). In addition to oil, pollen from a variety of species is collected by females as a protein source for larval provisions and nectar is gathered as an energy source for both the adults and the larval provisions. In our studies, *Krameria* pollen has rarely been more than a trace element in *Centris* scopal loads, but Paloney (1975) in his study of *K. grayi* in California found *Krameria* pollen to be regularly collected by *Centris rhodopus* Cockerell.

The blooming behavior of *Krameria grayi* (and *K. erecta* in other areas of Arizona) appears to be very much affected by the flowering phenology of other plants with which it cooccurs. Such a relationship is expected in view of the fact that the bees which serve as pollinators for *Krameria* must have pollen and nectar sources available at the same time they are visiting *Krameria*. Accordingly, *Krameria* shows a high level of overlap in its blooming (Fig. 4) with several mass-blooming shrubs of the Sonoran Desert (Simpson 1977). Included among these are *Larrea*, both *Cercidium* species, *Olneya*, and *Prosopis*, all of which serve as both nectar and pollen hosts for the oil-collecting *Centris* (*C. rhodopus*, *C. cockerelli* Fox) at our desert site. In contrast to the blooming phenology of *Krameria*, the two species of *Cercidium* and *Olneya* exhibit skewed blooming peaks (Fig. 5). These three legumes are commonly exploited by oil-collecting *Centris*, but their dominant pollinator is typically a large-bodied, extremely abundant, non-oil-collecting *Centris*, *C. pallida* Fox. Unlike *Krameria*, which has a complemen-

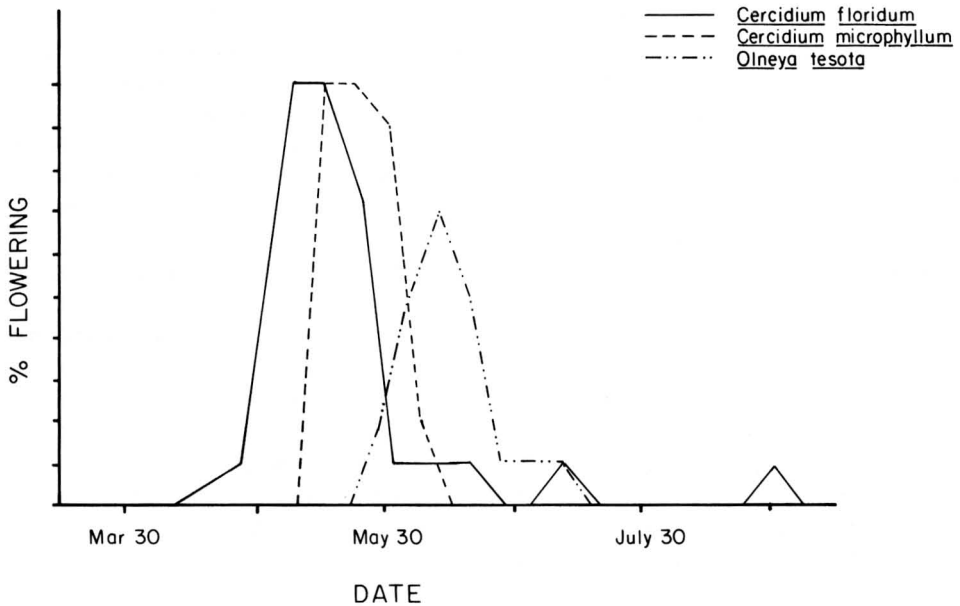


Fig. 5. Blooming patterns (near Tucson, Arizona) of *Cercidium microphyllum*, *C. floridum*, and *Olneya tesota*, all of which depend primarily on *Centris pallida*, a non-oil-collecting *Centris*, for pollination.

tary reward system, the three legumes offer similar rewards, which has fostered divergence of blooming schedules (Fig. 5).

*Krameria grayi* shrubs, like all species of the genus, are hemiparasitic, tapping the xylem of many of the desert plants with which they occur (Cannon 1910). In a sense, *Krameria* species "use" sympatric species of other genera as sources of water and to provide their pollinators with dietary components they do not offer (nectar) or which are rarely used (pollen). In Arizona, root hosts, which in many cases are also the pollen and nectar hosts of *Centris*, are commonly large plants with literally thousands of flowers open at a time. Correspondingly, plants of *K. grayi* are small to medium sized shrubs that mass produce large numbers of flowers. Correspondingly, population sizes of *Centris rhodopus* and *C. cockerelli* are large.

In central Texas, a third species of *Krameria*, *K. secundiflora*, is common in areas of the native grassland. Like *K. grayi* in Arizona, *K. secundiflora* secretes oils from elaiophores as its only floral reward. Its primary pollinators are likewise species of *Centris*, *C. atripes* Mocsary and *C. lanosa* Cresson. *Centris atripes* is a wide-ranging species that reaches west to the grasslands of Arizona and south to Costa Rica. *Centris lanosa* is a strictly southeastern species reaching its western limit in central Texas. Experiments involving artificial self and cross pollinations indicate that this species is self compatible and suggest that other species might be self compatible as well. Compatibility in *Krameria* is extremely difficult to determine because of high levels of fruit abortion coupled with apparent parthenocarpy and frequent fruit predation by gelechiid moth larvae. Even in the absence of fruit predation, literally hundreds of flowers need to be manipulated



before either a cross or self is successful. The indications of self-incompatibility in *K. grayi* (Simpson 1977) might, therefore, have been an artifact of sampling size. In any event, neither *K. grayi* nor *K. secundiflora* is autogamous, and visitation by *Centris* appears necessary in both cases for pollination.

Basically, therefore, the pollination system of *Krameria secundiflora* is the same as that of the *Krameria* species in the Sonoran Desert. The major contrasts lie in the habit and phenology of the different *Krameria* species and the other members of the communities in which they occur. *Krameria secundiflora* differs from the shrubby desert species in that plants are small, often widely scattered, decumbent, herbaceous perennials. With the exception of *Prosopis*, *Eysenhardtia* (both legumes), and *Bumelia* (Sapotaceae) with synchronous but sporadic flowering periods, all of the native spring-blooming shrubs and trees in central Texas flower before the main *Krameria* bloom (Fig. 3). Oil-collecting *Centris* in this region are largely dependent on an array of herbs and other herbaceous perennials (e.g., *Psoralea rhombifolia* Torr. and Gray, Fabaceae; *Monarda* spp., and *Salvia* spp., Lamiaceae) for pollen and nectar. The low resource base in central Texas relative to Arizona apparently leads to comparatively small population sizes of native *Centris* species.

#### THE VELVET AND THE HONEY MESQUITE

In Arizona, the velvet mesquite (*Prosopis velutina*) is a dominant element along washes. Historical accounts indicate that in presettlement times, mesquite woodlands formed extensive stands in areas bordering rivers. These expanses of mature trees offered enormous, comparatively stable, resources for flower-feeding insects. Velvet mesquites in their natural habitats are mass-blooming trees that have a primary flowering season in the spring (April–June). A second bloom can occur later in the summer (August–September) following late rains (Fig. 2). The inflorescences of mesquite are composed of numerous (ca. 263) flowers that offer both nectar and pollen as food for visiting insects. Because of the open, uncomplicated nature of the flowers, and the large numbers of flowers open at a time, mesquite catkins are visited by a wide array of insects. Included among the visitors is an extraordinarily high number of solitary bees. Throughout the Southwest, over 160 species of solitary bees have been collected visiting *Prosopis* flowers (Simpson et al. 1977a). At Silver Bell, we collected in one season 64 species visiting *P. velutina*. Many of these bees visit other pollen hosts in addition to mesquite, but several, notably species of *Perdita*, are oligolectic on *Prosopis*.

Of particular interest at Silver Bell were five species of *Perdita* (*Perdita ashmeadi vierecki* Cockerell, *P. luciae luciae* Cockerell, *P. stathamae stathamae* Timberlake, *P. punctosignata* Cockerell, and *P. obliqua* Timberlake) that confined their pollen foraging activities exclusively, or almost exclusively, to the velvet mesquite. Flight seasons of the first four *Perdita* taxa overlap greatly, with near coincidence patterns of peak abundance and, from timed observations, no difference in foraging activity within a day. The fifth species, *P. obliqua*, shows only minimal overlap with the other four and, unlike its specialist congeners, occasionally collects pollen from shrubs other than mesquite. It is active late in the spring and often has a second flight period associated with the summer mesquite bloom. The other *Perdita* species are not active during the second bloom.

Based on observations of foraging movements, the major pollinators of the

velvet mesquite appear to be medium- to large-sized bees (*Xylocopa*, *Melissodes*, *Centris*, Anthophoridae; *Protoxaea*, Oxaeidae; *Megachile*, Megachilidae) that visit a variety of other plants (Simpson et al. 1977a). Our studies show that the blooming of *P. velutina* follows that of many of the other mass-blooming trees and shrubs, and that the same bees simply move from one species to another as they come into bloom. Some of the larger specialists (*Colletes* spp., Colletidae, and various megachilids) are also likely to be important pollinators, but they are relatively scarce at most sites, and there is nothing to suggest that they have any unique qualities as mesquite pollinators.

The natural distribution of the honey mesquite, *Prosopis glandulosa*, in Texas is somewhat controversial, but there is little doubt that intense overgrazing and the suppression of ground fires have allowed for a dramatic increase in its colonization of the grasslands. In such areas, invasive plants do not behave like the relatively predictable desert phreatophytes in Arizona, but rather have multiple, sporadic periods of flowering (often three or more per season, Fig. 3). During some of these blooms we find a very high proportion of female sterile flowers within an inflorescence (90% or more), but, since there is usually no fruit set at all within populations in these periods, entire plants are functionally sterile.

In our observations over the last seven years, we have found few species of bees associated with mesquite in central Texas. The introduced honeybee (*Apis mellifera* L.) tends to be abundant, while a limited array of generalist bees (*Xylocopa*, Anthophoridae; *Bombus*, Apidae; *Megachile*, Megachilidae; *Agapostemon*, *Augochlora*, *Dialictus*, Halictidae) and small lepidopterans are less commonly seen on the flowers. Bee densities on mesquite in central Texas never approach those commonly seen in Arizona on either a per tree or a per inflorescence basis. Although a few *Prosopis* specialists are known to be associated with *Prosopis glandulosa* in the Rio Grande Valley and the South Texas Plains (both areas likely to have supported significant mesquite populations before the advent of European man), none at all are known from central Texas or the Edwards Plateau. Yet, despite its self-incompatible breeding system, the absence of specialist bees has apparently had minimal impact on the spread of mesquite in central Texas. This is not surprising in view of the generalized pollination system and our finding in Arizona that the specialists were probably not the major pollinators of the velvet mesquite. The absence of specialists in central Texas is expected if the present distribution reflects a very recent expansion of populations into the grasslands. Nevertheless, this situation contrasts with that seen in *Cucurbita* and *Helianthus* (below) which took their specialists with them when man expanded their ranges.

#### WILD SUNFLOWERS AND THEIR BEES

As pointed out above, the dominant perennial members of the Asteraceae at our Arizona site have pollination systems that are comparatively mundane. The two most important Arizona Compositae (the two *Ambrosia* species) are wind pollinated and the third most abundant species, *Encelia farinosa*, is visited by a generalized array of butterflies, moths, flies, and bees.

In central Texas the Asteraceae is one of the most diverse families of plants. Annual and perennial composites are significant components of the spring bloom (e.g., *Pyrropappus*, *Engelmannia*, *Ratibida*, *Coreopsis*, *Rudbeckia*, etc.) and they are, in contrast to the pattern of the dominant Compositae at Silver Bell, pollinated

primarily by bees. Many of these composite-feeding bees native to central Texas, restrict their pollen collection to one, or a group of related, species of the family. There is, of course, a well-developed fauna of specialist bees associated with the annual Asteraceae (e.g., *Malacothrix*, *Pectis*, *Geraea*, and *Verbesina*) in the Arizona deserts, but the overall density and diversity of composites is much greater in central Texas.

Our largest body of data for a member of the Asteraceae has been compiled for the common sunflower, *Helianthus annuus*. The species is a widespread, often weedy, self-incompatible, summer-blooming annual (Fig. 3) that provides an interesting contrast with the mesquites. Our work with *H. annuus* and related species has centered in the Austin area and we have only limited experience with the plant in the southwestern deserts. Fortunately, valuable observations of pollinator associations in the Southwest, although not strictly comparable to our own, are available from the massive survey of P. D. Hurd and coworkers (Hurd, LaBerge, and Linsley 1980).

Our own work with wild sunflowers has focused on intra-head phenology, reward presentation, estimates of pollinator efficiency (and the problems inherent in most direct measures of efficiency), and examinations of the hierarchical foraging decisions of native bees (i.e., when to approach, land, and leave a flower/inflorescence). The heads of wild sunflowers in our area contain 200–250 individual florets which open in the classical pattern of concentric whorls over a 5–6 day period (Fig. 6A). Invariably within a head, the largest number of florets are open on the third day after the capitulum initiates blooming. Individual florets are strongly protandrous with a bimodal pattern of pollen presentation. An initial period of pollen presentation occurs as pollen is pushed out of the anther tube by the elongating style (Fig. 6B–1). Approximately 60% of the total pollen per floret is presented in this initial morning phase of stylar elongation. This first period of pollen availability is followed by 5–6 h during which little or no pollen is presented. In the evening, there is a second period of presentation as the anthers retract. It has not previously been appreciated that this second presentation of pollen is caused by retraction of the anthers (Fig. 6B–3) and not by a second period of style elongation.

In most instances, the style branches diverge and the floret begins its female late in the evening after anther retraction. While this pattern seems straightforward within a floret, it is complicated by the fact that there are differences between plants in the population. The majority (over 80%) of the plants in the populations around Austin follow the pattern as outlined above. However, in some plants (“early females”) the male to female transition within individual florets is exceptionally rapid, so that florets are fully female by mid-afternoon of the first day of floret anthesis. Still other plants (“late females”) seem to have a delayed transition with the final anther retraction (and secondary period of pollen presentation) delayed until the morning after the initial presentation. Within a given plant, however, most of the florets behave in the same fashion. Variation is thus primarily interplant, not interhead.

In our studies, nectar is produced by an individual floret only on the first day of anthesis, and sugar accumulation is constant (0.01 mg/h) from just before the initiation of pollen presentation until dusk (Fig. 6C). Due to the high rate of insect visitation, nectar standing crop is usually less than 0.005  $\mu$ l per floret. Nectar concentration (and accordingly volume) varies widely throughout the day (from

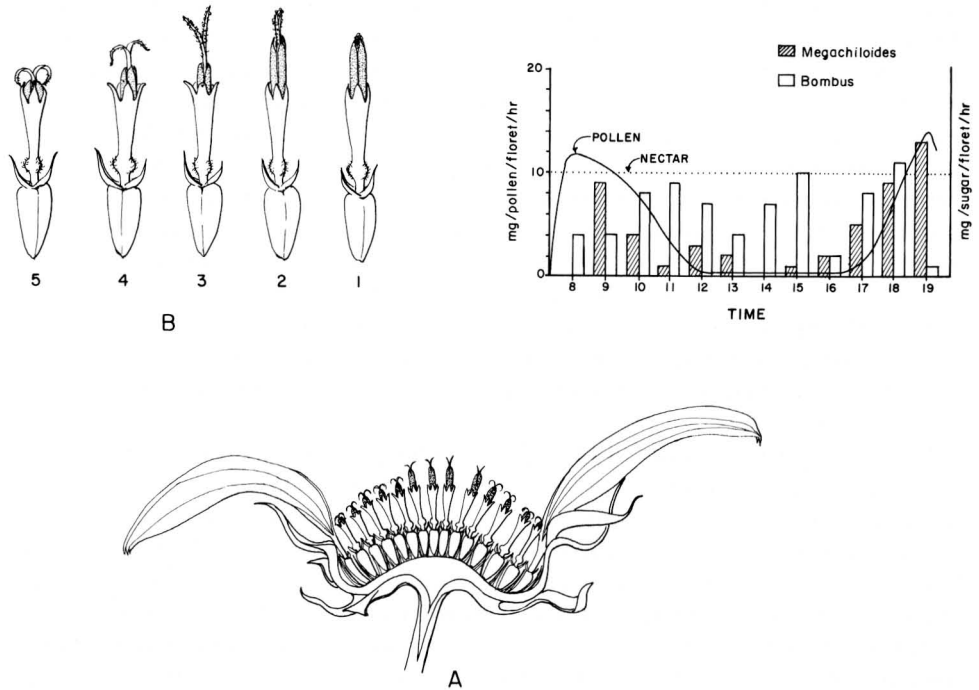


Fig. 6. Intra-head blooming phenology of *Helianthus annuus* and corresponding times of pollen presentation and nectar secretion.—A. A capitulum showing the older flowers near the periphery of the head.—B. The sequence of flowering of an individual floret with the phases numbered 1–5. Florets in phases 1–3 are male and generally appear during the first day of anthesis. Phase 1 usually occurs the first morning of anthesis. Pollen is presented as the style pushes pollen through the top of the anther tube. Phase 2 lacks pollen if there has been insect visitation. During phase 3, there is a second time of pollen presentation as the stamens retract, causing the remaining pollen to be swept from the anther tube. The evening of the first day, or morning of the second, the female phase (4) begins as the style branches spread. Floret 5 is an old floret.—C. The pattern of nectar and pollen availability during the first day (male phase) of anthesis of an individual floret superimposed on patterns of visitation of a *Helianthus annuus* specialist, *Megachiloides fortis*, and a generalist, *Bombus pennsylvanicus*. Note that the visits of the specialist are correlated with times of pollen presentation whereas those of the generalist are not. Time is Central Daylight Time.

under 20% to over 50% sucrose wt/vol). Correlations of nectar concentration from both bagged flowers and bee honey stomachs with environmental variables indicate that the variation is best explained by diurnal changes in temperature and relative humidity if one allows a one-hour lag between the measurement of relative humidity and the nectar concentration. This relationship reflects the fact that the nectar in both the bagged flowers and the honey stomachs are running averages and will not reflect rapid environmental changes. Bagged samples give a much poorer fit than honey stomachs, presumably because the latter is a more “instantaneous” measure. Concentration of nectar in honey stomachs decreases late in the day paralleling evening increases in relative humidity, while concentrations in bagged flowers do not. The contrasting pattern of continuous nectar secretion and bimodal pollen production leads to interesting differences in the foraging patterns of generalist versus specialist bees.

Although *Helianthus* is visited by a range of bee taxa around Austin, we have

focused our studies on three of the most common visitors, *Bombus pennsylvanicus* (Degeer) (Apidae), *Svastra obliqua* (Say) (Anthophoridae), and *Megachiloides fortis* (Cresson) (Megachilidae). Females of all three species and the workers of *Bombus* are about the same size (ca. 100 mg dry wt) and have similar tongue lengths. *Bombus pennsylvanicus* is a common social species which regularly takes nectar from sunflowers but rarely collects its pollen. *Svastra obliqua* is a widespread composite specialist that we often find collecting sunflower pollen, but the species also frequently visits other composites as pollen hosts. Even on a single foraging bout, females of this species can visit sunflowers and one or two other species of Compositae. This species is one of a group of "tummy-tapping" eucerine and nomiine Compositae specialists that collect pollen by tapping the anthers with a brush of specialized hairs on the distal portion of the abdominal venter. Pollen is transferred several times per foraging bout from the abdomen to the scopae on the hind legs.

The last important visitor is *Megachiloides fortis*, a robust ground-nesting leaf-cutter bee which, at least at our site, acts like a true sunflower oligolege since it normally collects only *Helianthus* pollen. Similar to other megachilines, *M. fortis* transports pollen in the scopal hairs of its abdomen although pollen is originally collected passively on various parts of the body. Counts of visits to individual heads indicate that foraging in this species is strongly correlated with the pattern of pollen presentation (Fig. 6C). No such correlation is evident in the foraging behavior of *Bombus* which visits only for nectar (Fig. 6C). The foraging pattern of *Svastra* is more complicated since females of this species use coblooming Compositae taxa such as *Heterotheca* as pollen hosts, and these alternative hosts present pollen during the middle of the day.

Hurd et al. (1980) had previously noted a bimodal pattern of foraging by native bees (primarily pollen-collecting females of the oligolectic *Melissodes agilis* [Cresson]) at some of their sites, but not at others. On the basis of this finding, plus the observed sizes of pollen loads on bees, they suggested a bimodal pattern of pollen presentation for at least some populations of the common sunflower. Since their technique consisted of massive samples without replacement, their results could have been artifactual. Our observations of bimodal activity at both the flowers and the nests confirm that bimodal foraging by specialists is a real phenomenon related to the bimodal pollen presentation we have documented in local *Helianthus* populations.

Single-visit experiments we have conducted (Neff and Simpson, unpubl.) indicate that females of all three common native bees we have studied are highly effective as pollinators (males are less effective, but may be of considerable importance for pollen movement because of the long distances they move between flowers while searching for mates). However, interpretation of single-visit studies is complicated by the unusual manner with which some bees respond to the abnormally high levels of pollen and nectar in bagged flowers which we use for these studies. The different modes of pollen collecting by *Svastra* and *Megachiloides* contribute to the complexity since *Megachiloides* must leave the head for pollen transfer much more frequently than *Svastra*.

In their survey of the bees associated with *Helianthus*, Hurd et al. (1980) listed 131 species of bees as being oligoleges of *Helianthus*, with at least some of these species found in all parts of the range of the sunflower in North America. They

considered 39 species to be 'primary' *Helianthus oligoleges* (bees restricted to the Compositae and primarily associated with *Helianthus*, as pollen hosts) although from our studies in Texas this appears to be a considerable overestimate. Our data, in fact, imply that most of their bees are 'secondary' sunflower oligoleges—bees which specialize on the Compositae, but with only opportunistic associations with *Helianthus*. In any case, even given their liberal interpretation of primary oligolecty, it seems likely that all except their most eastern survey sites are in the adventive range of *Helianthus annuus*. Certainly the lack of any sunflower specialists restricted to their western sites argues for such an interpretation. Highest diversity and endemism of *Helianthus* specialists are found in the broad region that includes much of the Great Plains and Texas east to the Gulf Coast.

While the prehuman range of *Helianthus annuus* is unknown (Heiser 1976a, b), evidence from studies of hybrid zones indicates that it is adventive in California (Heiser 1949). It is also known that the closest relative of the common sunflower, *H. argophyllus* Torr. & A. Gray, is native to Texas (Heiser 1976b). We therefore suggest that *Helianthus* has expanded its range into the far Southwest in relatively recent times with much of the spread actually having occurred in historic times. As the genus spread, it carried with it some of its specialist pollinators. Since the areas into which it moved were already occupied by Helianthieae specialists, sunflowers were simply incorporated into their suite of pollen hosts. This situation provides an interesting comparison with *Prosopis* which has expanded in the northeastern part of its range without any specialists. At the present state of our knowledge of the basis of oligolecty in bees, any explanation for the disparity in the patterns exhibited by mesquite and sunflowers must contain a certain amount of circularity, but factors contributing to the divergent patterns would seem to be the isolation of *Prosopis* in the Mimosoideae, the irregular phenology of shrubs of mesquite in central Texas, and the fact that, unlike the mesquite specialists, most sunflower "specialists" are not completely restricted to *Helianthus*. Consequently, the widespread sunflower specialists had the opportunity to use alternative, related hosts if, or when, populations of *Helianthus* were low, whereas *Prosopis* has no close relatives in North America.

#### SUMMARY AND CONCLUSIONS

Although estimates vary, there are probably more than 14,000 species of solitary, flower-visiting bees. Most of these bees live in warm arid and semiarid habitats. In the American Southwest, they constitute the most diverse group of flower-visiting insects.

The studies of Linsley, Hurd, and coworkers in the American deserts were among the first to emphasize the narrow associations of many of these bees with specific groups of plants. These workers were particularly interested in the phenomenon of oligolecty, or the restriction of pollen collection by solitary bees to one or a few related plant species. In their studies these workers were unable to find any obligate one-to-one association between a plant species and a bee species, and they pointed out that in some cases, specialists even had little to do with the pollination biology of the species to which they were restricted.

Our studies in Arizona and Texas have demonstrated the importance of solitary bees as the primary pollinators for most of the dominant plants in the northern

Sonoran Desert and for the herbaceous flora of central Texas. However, the solitary bees that serve as primary pollinators of a species are not necessarily the ones oligolectic on it, as demonstrated by the sympatric suite of *Perdita* on *Prosopis velutina*.

Our work has repeatedly demonstrated that some plant genera or species tend to have large numbers of specialist bees associated with them. In many cases (e.g., *Prosopis*, *Larrea*, *Opuntia* spp.), the specialists on a single taxon belong to unrelated groups of bees. Other plant groups which would seem to be equally likely as candidates for pollen host specificity support few or no specialists. What determines host specificity still remains a mystery. Likewise, the mechanism that allows radiation of a group of bees on a host without comparable speciation in the host is unclear.

*Krameria*, a genus that occurs all across the southern United States, presents a peculiar situation in that it is pollinated exclusively by female oil-collecting *Centris*. Basically the pollination system of *Krameria* is the same throughout its range in North and South America. However, the *Krameria* species in Arizona and Texas differ in habit. These habit differences, which are related to the climatic and hence the phenological and vegetative differences in the two areas, have effects on the population sizes of their respective *Centris* pollinators. In Arizona, where pollen and nectar hosts are large, mass-blooming shrubs and trees, *Krameria* species are also mass-blooming shrubs, and populations of oil-collecting *Centris* are large. On the Edwards Plateau, the pollen and nectar hosts of the oil-collecting *Centris* are herbaceous. Correspondingly, *Krameria* in this region is a scattered, herbaceous perennial and *Centris* populations are comparatively small.

A comparison of *Prosopis* in Arizona and central Texas underscores the fact that *Prosopis* is invasive on the Edwards Plateau. There is a dramatic contrast between the predictable, mass-flowering, phreatophytic trees of the velvet mesquite in Arizona that support large numbers of solitary bees, both specialists and generalists, and the small, sporadically blooming, branched shrubs of the honey mesquite in central Texas that are visited by few bees and no specialists. When mesquite moved into the oak-juniper grasslands, it failed to carry with it its unique specialist pollinators and once there, it did not find local mimosoid specialists that could adopt *Prosopis* as a pollen host. Pollination of the honey mesquite in central Texas, when it occurs, is thus carried out by generalist bees. This situation contrasts to that of *Helianthus annuus* which was able to carry some of its specialist bees westward as its range expanded and to attract western species of bees that specialized on other members of the Helianthieae. As a result the common sunflower now supports a rich array of solitary bees in both the native and adventive parts of its range.

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## FOOTNOTE

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