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ABSTRACT

At sporadic intervals in the fall the southwestern desert landscape is emblazoned with large, conspicuous, usually orange-colored flowers of the annual *Kallstroemia grandiflora* (Torrey) Gray. These flowers produce an abundance of pollen and nectar, which is exploited in three ways by insects belonging to 12 different families and 46 species, including bees, wasps, flies, and butterflies.

The plant is of special interest from the standpoint of pollination ecology, as both the plant and some of the insects have adaptations in behavior that are not always mutually beneficial. The flowers of *K. grandiflora* are allogamous for most of the daily flowering period and become autogamous as the flowers close. Thus, they can be either cross- or self-pollinated, with the former evidently favored. The flowers have little or no odor, a color range within "bees yellow" (500-650 μ), and a strong ultraviolet reflective pattern on both upper- and under-surfaces. Insects are evidently attracted by color and ultraviolet reflection, with the latter so arranged as to form nonreflective, dark target, "nectar guide" areas on both upper- and under-surfaces.

One group of bees and wasps gather pollen and nectar from the top of the flower, effecting both cross- and self-pollination in the process. A second group of smaller bees and wasps gather nectar from within the flower but avoid contact with the sexual portions and are therefore of no importance in pollination. The third group of honeybees and several other larger bees and wasps, extract nectar from the underside of the flower completely avoiding the sexual parts of the plant and therefore play no role in pollination. Even though the plant gains no direct benefit from this last group of insects it nevertheless supplies them with a sepal nectar guide that directs them to the nectaries. It is proposed that these species may be contributing to the economy of the plant by reducing the quantity of available nectar so that the pollinators have to visit more flowers to get their full nectar supply.

INTRODUCTION

Kallstroemia grandiflora (Torrey) Gray, commonly known in the Southwest as Arizona or Mexican poppy, has large, conspicuous, usually orange-colored (occasionally white or yellow, D. M. Porter, *in litt.*) flowers and, at times, it is one of the most conspicuous annuals on the desert landscape. The flowers produce an abundance of pollen and nectar which are exploited in different ways by various bees and wasps. Opportunities to observe the flower behavior of a number of these insects arose briefly during the summers of 1970, 1971, and 1972. A summary of these observations is presented here.

LOCALITIES

Observations on flower visitors to *Kallstroemia* were primarily made at three sites in the upper San Simon Valley, Arizona-New Mexico as follows: 2 miles east of Portal, Cochise County, Arizona, on the lower slopes of the Chiricahua Mountains below the mouth of Cave Creek Canyon (August 31-September 5, 1970; August 27-September 3, 1971); 2 miles north of Rodeo, Hidalgo County, New Mexico (August 17-23, 1971) and Apache, Cochise County, Arizona (August 15-16, 1972).

Kallstroemia grandiflora Torrey

The genus *Kallstroemia* (Zygophyllaceae), comprising 17 species native to the New World, has been monographed recently by Porter (1969). The following data on the vegetative and floral morphology, reproductive biology, and distribution of *K. grandiflora* have been largely summarized from that publication.

Kallstroemia grandiflora like its congeners and the related species of *Tribulus* (including the South European, naturalized *T. terrestris* Linnaeus commonly referred to in the United States as "puncture vine") is an annual plant with largely prostrate stems radiating from the root. Unlike *T. terrestris* and many species of *Kallstroemia*, the stems in *K. grandiflora* are often ascending. The flowers are borne terminally on the stems but they appear axillary because of the stems' sympodial growth habit (D. M. Porter, *in litt.*). In the Southwest, the plants live in flat sandy areas in the Sonoran and Chihuahuan deserts and develop and blossom following the summer rains. Porter (1969) stated that when plants are growing under extremely favorable conditions, as in ditches where rains collect, they may reach 1 meter in height and several meters in

diameter. He cited Cannon (1911) for an exceptional size of 16 or more square meters. Cannon also reported tap roots reaching 22 cm. into the substrate, a characteristic, Porter elaborated, which enables the plant to resume growth following the normal growing period if an unseasonable rain should occur before the plant succumbs to the dry season.

The species of *Kallstroemia* thus far studied are not pollinated prior to anthesis but the pollen is shed and the stigma is receptive as the flower is fully opened. During anthesis the stamens are appressed to or very near the spreading petals, and the stigma is held erectly above them in the center surrounded by the 10 stamens (Porter, 1969). At this point the flower is virgin but ready for pollination by insects of various types and is openly susceptible to both self- and cross-pollination by these agents. According to Porter (1969), at the end of the blooming period, usually early afternoon, which ends the same day the flower opens, the filaments curve upward and inward moving the anthers into contact with stigma as the petals close and hold them to the stigmatic surface. The petals twist around the style as they are closing, helping to insure self-pollination, which becomes a necessity in the absence of insect visitors.

It appears that the flowers of *Kallstroemia* are designed to be primarily allogamous (cross-pollinated) for most of the flowering period and autogamous (self-pollinated) near or at the end of the period to be safe from no or incomplete fertilization. This plan of pollination, which would insure cross-pollination to some extent, is perhaps negated by the behavior of the female *Protoxaea* and *Campsoscolia* when they hold the stamens against the pistil thereby bringing the anthers, stigma, and their venters into contact. As their body hairs or the scopa undoubtedly contain foreign pollen soon after flight activities begin they would be effecting both cross- and self-pollination, if *Kallstroemia* is self-compatible. It appears that the latter is most probable. According to Porter (1969), *Kallstroemia grandiflora* and three other species in this genus all set seed when grown in the absence of pollinators. *Kallstroemia* like some other plants, probably starts out self-incompatible, becoming more and more self-compatible with time and the decrease of the inhibiting principle until, as the flower closes, it is self-fertilized. It is equally possible that the genetic viability of *Kallstroemia* is maintained even though cross- and self-pollen are introduced onto the stigmatic surface at the same time, because as a rule pollen tubes from different but compatible plants grow much faster than do those from the same plant. Even though *Protoxaea* and *Campsoscolia* females distribute large quantities of both cross- and self-pollen, and negate the effect of keeping the anthers away from the stigma for most of the day, cross-fertilization of at least a large percentage of the ovules in *Kallstroemia* is probably the rule rather than the exception.

There is conflicting information on the floral fragrance of *Kallstroemia maxima* (Linnaeus) Hooker and Arnott (Porter, 1969) and therefore on the function of the nectar as an attractant for insect pollinators. Porter said, "I have not detected any odor in the flowers myself." In *K. grandiflora* we have detected no prominent odor even in concentrated patches of blooming plants or individual flowers but no definitive tests have been made. If, indeed, odor is absent or minimal the flower nevertheless seems adequately endowed with visual stimuli to attract insect pollinators. Its usual deep orange color seems to be well within the visual range known for "bees yellow" (500-650μ), at least in the honey bee.

The ultraviolet reflection pattern of the flower strongly suggests attraction of pollinators by visual stimulation once the insect is near or in the flower. Except for the extreme basal portion and the heavy veins thereon, the large petals are strongly ultraviolet reflective and probably attract from a distance. The pistil, stamens, and pollen grains do not reflect ultraviolet and thus the center of the flower appears as a dark target, "nectar guide," to the insect. On the underside of the flower the petals are strongly ultraviolet reflective, whereas the sepals are not and probably serve as nectar guides for the insect visiting this region. These sepals are narrow and pointed on their outer extremity, gradually widening to the base, directly above which the unreflecting nectary is situated. Although the nectaries appear to be in close contact with the sepals they are actually attached to the receptacle (D. M. Porter, *in litt.*).

According to Porter (1969), the genus *Kallstroemia* is "pollinated promiscuously, being visited by various Diptera and Hymenoptera for pollen, and by these and Lepidoptera for nectar. Very few reports of the types of insects visiting the flowers have been recorded. According to notations accompanying herbarium specimens, *Kallstroemia grandiflora* is visited by bees and wasps in Sonora and Colima, Mexico. The only pollinators of *Kallstroemia* to have been positively identified are bees of the genus *Perdita*. *Perdita pectidis* Cockerell in New Mexico, *Perdita echinocacti* Timberlake in Arizona and Sonora and *Perdita euphorbiae* Timberlake in Sonora." In the present paper the number of insects known to visit *Kallstroemia* is enlarged to 33 species of bees belonging to five families, nine species of wasps belonging to four families, two species of butterflies belonging to one family, and two species of flies belonging to two families. No doubt this total of 46 species belonging to 12 families could be expanded significantly with further sampling.

The change in location from year to year in the present study was dictated by the sporadic appearance of *Kallstroemia* even though no great variance was observed in the physical environment or other features at these localities. An area dominated by *Kallstroemia* one year may have no or very few plants for the next year or two even though conditions conducive to germination appear similar or identical. *Kallstroemia* seeds are viable for at least three years, they germinate at irregular intervals and are difficult to germinate artificially (Porter, 1969). This type of intermittency among plants is known to be influenced by germination inhibitors that must be washed away before germination occurs and by differences in the seed coat, especially in those characteristics effecting permeability. A water soluble inhibitor of germination has been found in the seeds of other Zygophyllaceae including *Larrea tridentata* (DeCandolle) Coville and *Tribulus terrestris*, according to Porter (1969), and may also be present in *Kallstroemia*.

GENERAL OBSERVATIONS

At this site (Portal Road, 2 miles north of Rodeo, New Mexico between the Arizona-New Mexico state line and U.S. Highway 80), *Kallstroemia grandiflora* was present and blooming in large patches on both sides of the road, with scattered small clusters of *Solanum elaeagnifolium* Cavanilles and *Cassia bauhinioides* Gray intermixed. *Calliandra schotti* Torrey was also growing and blooming abundantly along the road shoulder. All of these plant species offered competition for *Kallstroemia* pollinators. Observations of flower visitors were made on August 17, 22, and 23, 1971. The following summary for August 17, 1971, was typical (Mountain Standard Time):

0530. 20°C. *Kallstroemia* flower buds tightly closed.

0554. 19°C. Sunrise. Sky clear. Sun on *Kallstroemia* plants.

0620. 22°C. First bee [*Protoxaea gloriosa* (Fox)] working *Calliandra* for pollen.

0625. 22°C. *Kallstroemia* flowers beginning to open. *Protoxaea* females active nearby taking pollen from *Solanum* and *Cassia* as well as *Calliandra*.

0640. 23°C. Many *Kallstroemia* flowers open ½-1 inch but no visitors. *Centris atripes* Mocsáry now working *Solanum* along with *Protoxaea*.

0700. 23°C. Scattered flowers of *Kallstroemia* now open wide but not reflexed. Female *Protoxaea* approach but do not enter blossoms. Apparently pollen and nectar not yet available.

0715. 23°C. About one-fourth of *Kallstroemia* flowers now open wide. Small bees crawling on stamens but not obtaining pollen.

0728. 23°C. Few small bees (*Exomalopsis*) now showing some pollen on legs. *Protoxaea* still very active on *Calliandra*.

0738. 23°C. *Agapostemon melliventris* Cresson visiting *Kallstroemia* but not obtaining pollen.

0747. 24°C. First *Protoxaea* female in *Kallstroemia* flower. No pollen on body or legs. Many *Protoxaea* working *Calliandra*. *Apis mellifera* Linnaeus extracting nectar from nectaries on top, and at base of, sepals on underside of *Kallstroemia* flowers.

TABLE 1
RELATIVE ABUNDANCE OF BEES AND WASPS TAKING POLLEN AND NECTAR AT FLOWERS OF *Kallstroemia grandiflora*[a]

	Pollen and Nectar	Nectar Only from Above Stamens	Nectar Only from Beneath Stamens	Nectar Only from Underside of Flower
Protoxaea gloriosa	49♀	5♂	–	3♂
Svastra sabinensis sabinensis	2♀	2♂	–	–
Diadasia ochracea	4♀	–	3♂	–
Diadasia megamorpha	2♀	–	–	–
Exomalopsis solani	4♀	–	4♀	–
Psaenythia mexicanorum mexicanorum	9♀	–	–	–
Melissodes montana	1♀	–	–	–
Svastra sila	–	2♂	–	–
Agapostemon tyleri	–	3♀ (2 carrying foreign pollen)	–	–
Agapostemon melliventris	–	2♀ (1 carrying foreign pollen)	–	–
Xylocopa californica arizonensis	–	2♀	–	–
Triepeolus spp.	–	2♀	–	–
Scolia ardens	–	1♀	–	–
Melissodes limbus	–	–	2♀, 1♂	–
Apis mellifera	–	–	–	2♀
Centris atripes	–	–	–	9♀
Bembix u-scripta	–	–	–	2♂, 2♀
Campsoscolia octomaculata texensis	–	–	–	2♀

[a]Two miles north of Rodeo, Hidalgo County, New Mexico, August 17, 1971, 0800-1000 MST.

0753. 25°C. First *Protoxaea* carrying *Kallstroemia* pollen.

0800. 26°C. *Protoxaea* females still working *Calliandra* but few now taking pollen from *Kallstroemia* along with *Psaenythia m. mexicanorum* (Cockerell), *Svastra s. sabinensis* (Cockerell), *Diadasia ochracea* Cockerell and other bees (table 1). *Centris atripes* and *Bembix u-scripta* (Fox) taking nectar from beneath flowers along with *Apis*. Male *Protoxaea* rotating on stamens while extracting nectar; underside of body heavily dusted with pollen.

0900. 28°C. Various bees taking pollen but most seeking nectar only, either from above or below stamens or beneath flower (table 1). Female *Protoxaea* observed resting on stamens rubbing legs together and removing pollen from scopa; after spending about a minute in this activity she flew off without visible pollen.

1000. 29°C. Flowers mostly reflexed and beginning to show signs of wilting. Only visitors were a few nectar seekers. Observations terminated.

Apache, Cochise Co., Arizona. Site an old roadside excavation extending north and south. *Kallstroemia* plants scattered over an area approximately 50 meters wide by 300 meters long. Observations on flower visitors were made on two days in August, 1972. The following sum-

mary is for August 15, 1972 (Mountain Standard Time):

0745. 21°C. Sky clear. Cool breeze. *Kallstroemia* flowers on east-facing bank mostly wide open, those on flat and west-facing bank mostly just beginning to open. No bees evident but substantial number of *Bembix u-scripta* flew rapidly among plants extracting nectar from nectaries on top and at base of sepals on underside of flower.

0802. First bee. (*Agapostemon melliventris*) taking pollen.

0805. Several *Melissodes t. thelypodii* Cockerell collecting pollen.

0815. Various species of bees now taking pollen and nectar (table 2), especially *M. t. thelypodii*. Male bees, primarily *Protoxaea gloriosa*, and scoliid wasp *Campsoscolia o. octomaculata* (Say) becoming heavily coated with pollen while rotating on stamens as they probe nectaries; Tiphiid wasp *Myzinum navajo* Krombein, although as large as *Campsoscolia* avoids contamination with pollen by crawling beneath anthers to get to nectaries.

1000. High proportion of flowers now wilting. Bembicids no longer active. Few nectar seeking bees present, mostly males. Observations terminated.

Two miles east of Portal, Arizona. Observations were made in an open meadow adjacent to and south of the Portal-Rodeo road. The meadow was surrounded primarily by *Acacia constricta* Bentham and *Prosopis juliflora* (Swartz) De Candolle on the north and east and by *Larrea tridentata* on the south and west. These were not in bloom nor were other, less

TABLE 2
RELATIVE ABUNDANCE OF BEES AND WASPS TAKING POLLEN AND NECTAR AT FLOWERS OF *Kallstroemia grandiflora*[a]

	Pollen and Nectar	Nectar Only from Above Stamens	Nectar Only from Beneath Stamens	Nectar Only from Underside of Flower
Melissodes thelypodii thelypodii	25♀	11♂	–	–
Agapostemon tyleri	7♀	–	–	–
Svastra sabinensis sabinensis	6♀	3♂	–	–
Ptilothrix sumichrasti	3♀	–	–	–
Psaenythia mexicanorum mexicanorum	3♀	–	–	–
Diadasia diminuta	2♀	–	9♂	–
Halictus tripartitus	2♀	–	–	–
Protoxaea gloriosa	–	14♂	–	–
Triepeolus sp.	–	3♀, 2♂	–	–
Campsoscolia octomaculata texensis	–	8♀	–	–
Diadasia ochracea	–	–	10♂	–
Pseudopanurgus aethiops	–	–	2♀	–
Andrena accepta	–	–	2♀	–
Coelioxys sp.	–	–	1♀, 1♂	–
Nomada sp.	–	–	1♂	–
Myzinum navajo	–	–	21♀	–
Myzinum frontale	–	–	1♀	–
Centris atripes	–	–	–	1♂, 5♀
Bembix u-scripta	–	–	–	30♂, 16♀

[a]Apache, Cochise County, Arizona, August 15, 1972, 0800-1000 MST.

numerous shrubs. The principal plants competing for pollinators were *Baileya multiradiata* Harvey and Gray, *Gutierrezia microcephala* (De Candolle) Gray, *Eriogonum abertianum* Torrey, *E. fasciculatum* Bentham, *Allionia incarnata* Linnaeus, *Zinnia pumila* Gray, *Lepidium montanum* Nuttall, and *Pectis papposa* Harvey and Gray. Observations were made in connection with another study and centered on *Protoxaea gloriosa*, whose females worked *Kallstroemia* flowers much longer in the day than at any other site encountered. Flower visitors other than female *Protoxaea*, although less diverse than at the Rodeo site, included the following: females of *Melissodes t. thelypodii*, *Svastra s. sabinensis*, *Diadasia ochracea*, *D. megamorpha* Cockerell, *Mellissodes* (E.) *montana* Cresson, *Megabombus* (M.) *pennsylvanicus sonorus* (Say) taking pollen; females of *Xylocopa californica arizonensis* Cresson, *Melissodes limbus* La Berge, *Triepeolus* sp., and *Scolia ardens* Smith and males of *Protoxaea gloriosa*, *Svastra s. sabinensis*, *Svastra sila* (La Berge), and *Diadasia ochracea* taking nectar while on top of the stamens; females of *Exomalopsis solani* Cockerell extracting nectar while beneath the anthers and *Apis mellifera* (hundreds of workers) and females of *Centris atripes*, *Pterocheilus arizonicus* R. Bohart, and *Monobia texana* (Cresson) extracting nectar from nectaries on top of and at the base of the sepals on the underside of the flower. *Protoxaea* pollen collectors in the early afternoon were captured as follows: (September 1 and 2, 1970; Mountain Standard Time): 1304, 1314, 1328, 1334, 1343, 1347, and 1357. No females were evident between 1357 and 1430 when observations were terminated.

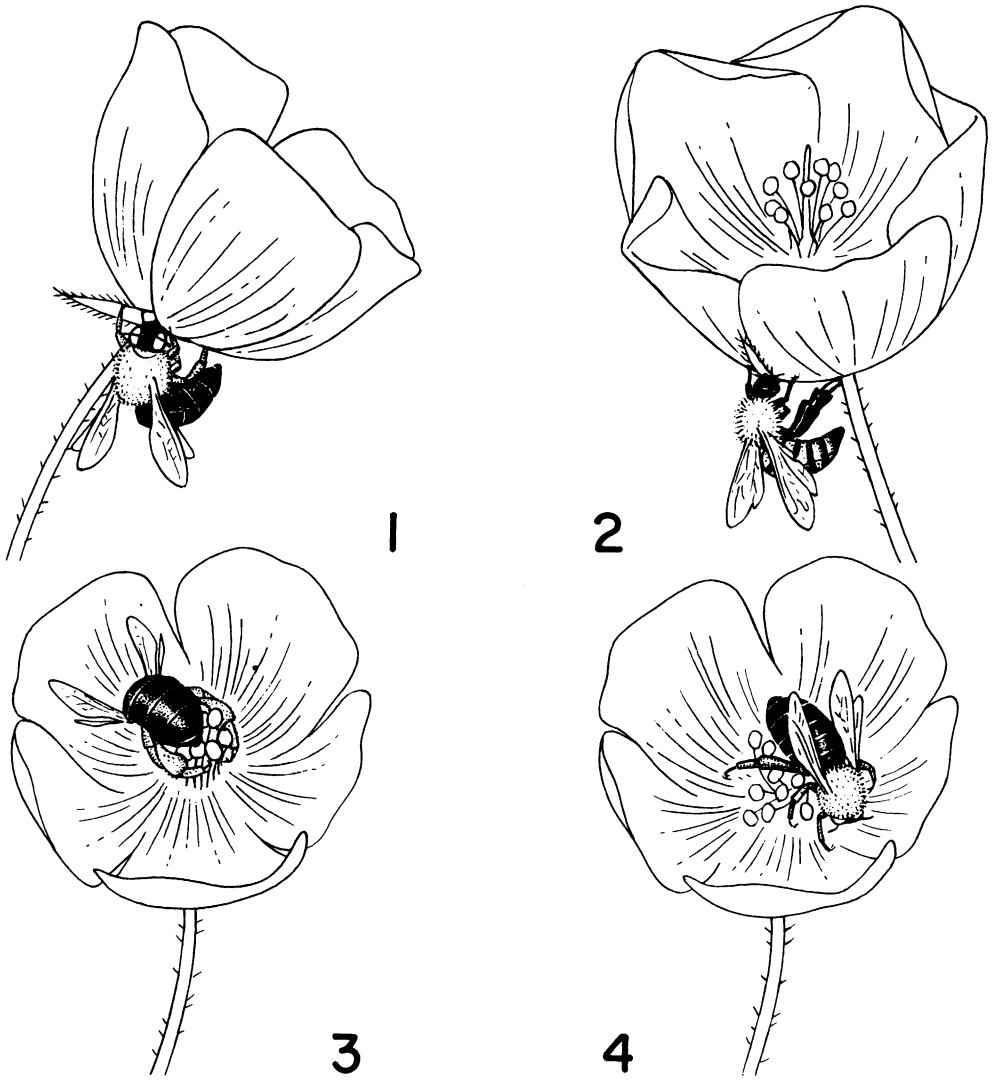
BEE AND WASP BEHAVIOR WHEN COLLECTING FROM FLOWER TOPS

The behavior of bees collecting pollen and nectar in flowers of *Kallstroemia grandiflora* varies according to the size of the insect. Females of *Protoxaea gloriosa* alight in the upturned flowers which droop downward with the bees' weight, sometimes bending 180 degrees so that the bee is working upside down. As they land in the flowers, facing downward, they gather the style and all 10 stamens into the venter, holding them there with all six legs. This places the anthers, which are abundantly covered with large orange pollen grains and the stigma, which is covered with stigmatic fluid, in contact with the abdominal venter and hind legs.

As soon as the bees' hold on the style and stamens is secured, the mouthparts are inserted into the nearest nectary for from a fraction of a second to about one second, presumably depending on the amount of nectar present. From one or two to all five nectaries are visited and on several occasions six mouthpart insertions are made, the first nectary being overlapped. After each nectary is sampled the bee shifts its hold on the style and stamens, shaking them rather violently, as its body moves around to a position from which the mouthparts can contact the next nectary. This shifting and shaking motion of the bee in rotating its position completely around the inside of the flower would account for the large amounts of loose pollen found throughout much of the body of the bee and occasionally in the bottom of the corolla. In *Protoxaea* each stop in the rotary movements is made at the juncture between two petals beneath which is a nectary. These are small, elongate (rectangular), dark green, spongy-looking masses of tissue situated middorsally at the base on the elongate, narrow, hairy sepals issuing from beneath the area where the petals overlap.

By late morning the movements of females on exposed flowers are very rapid because most of these blossoms have already been visited. Very often the bee then samples only one, two, or three of the nectaries before flying to the next flower. When an obscured, previously unvisited flower is found, either inside the plant or beneath another plant in the shade, females slow their flight and make a more complete visitation.

We did not observe honeybees taking pollen from *Kallstroemia grandiflora*, even in areas where they were abundant, as at the Portal locality. However, Porter (1969) made the following observations of honeybee behavior in flowers of a related species: "When a honeybee lands on a flower of *Kallstroemia maxima* it thrusts aside the stamens, while standing over them and the style in order to reach the nectar at the bases of the sepals. In this way pollen is transferred from the anthers to the bee, and from the bee to the stigma. The bee circles clockwise on the flower



FIGS. 1-4. 1. Male of *Protoxaea gloriosa* extracting nectar from underside of *Kallstroemia grandiflora* flower. 2. Worker of *Apis mellifera* extracting nectar from underside of flower. 3. Female of *Protoxaea gloriosa* extracting nectar and collecting pollen while rotating with stamens clasped between legs. 4. Male *Protoxaea gloriosa* extracting nectar while standing on stamers and rotating.

until it has sampled all the nectaries, then moves on to another flower, not uncommonly returning later to the original flower, either to repeat the previous performance or to reject the flower. The bee, therefore, may act not only as an agent in cross-pollination, but also may effect self-pollination by transferring pollen from anthers to stigma in the same flower. This is accomplished in either the initial visit or upon return of the bee to a flower previously visited."

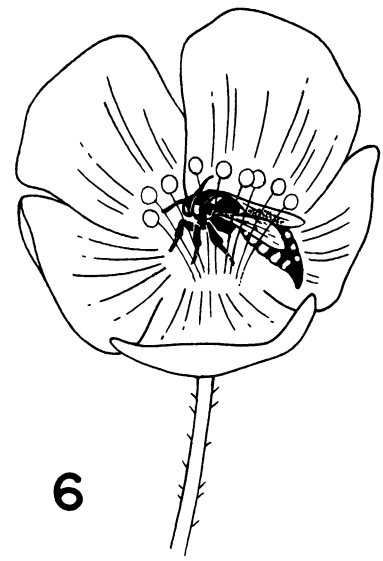
The wasp *Campsoscolia o. octomaculata* actually holds the stamens together under the abdomen, in the manner of larger bees when gathering pollen, and in the process the wasp becomes heavily coated beneath with pollen, even though it has no scopa and is sparsely pilose.

BEE AND WASP BEHAVIOR WHEN EXTRACTING NECTAR FROM WITHIN THE FLOWER

Smaller bees and a few wasps such as the tiphiid *Myzinum navajo* (tables 1, 2) crawl into the flower over the petals and beneath the anthers, among the filaments, and thus reach the nectaries with minimal contamination by pollen, except for that which has been shaken into the corolla by the activities of the larger bees and wasps and through which they have to walk to get to the nectaries. They do not come into contact with the stigmatic surface and therefore are of no importance in pollination. Their small size makes it difficult if not impossible for them to manipulate the sexual portions of the flower, and as their weight does not bend the flower they have no need to hold onto these plant structures. Because the smaller bees avoid the main source of pollen and do not collect "waste" pollen in the corolla, even though pollen is a necessary food for the larvae of at least four of the listed species, it appears that *Kallstroemia* pollen may also have some undesirable characteristic. Also, this partial avoidance of pollen contamination may be a logical step in the evolution of complete avoidance, as discussed later. As *Kallstroemia* evidently produces large amounts of nectar, the "pirating" activities of these species can best be considered as being commensalistic in that the plant is unharmed and the insects are benefited by the nectar. If these insects were using ultraviolet light they would be attracted to the highly reflective surface of the petals or perhaps just to the orange color of the petals or both. Upon landing on the petal the insect may be attracted to the nectaries by olfactory stimuli out of the range of human detection that would guide them down into the corolla and to the nectaries, which are on the edge and beneath the nonreflective central area.

BEE AND WASP BEHAVIOR WHEN EXTRACTING NECTAR FROM THE UNDERSIDE OF THE FLOWER

Honeybees and several of the other larger bees and wasps that seek only nectar from *Kallstroemia*, extract it from a position beneath the flower (tables 1, 2). They approach the flower from beneath, landing on the stem, which they grasp with all six legs. They move quickly up to the flower, pull the sepal down with one or both front legs, and insert the mouthparts into or onto



FIGS. 5, 6. 5. Male of *Diadasia ochracea* extracting nectar from a position underneath the stamens of *Kallstroemia grandiflora*. 6. Female of *Myzinum navajo* extracting nectar from a position underneath the stamens.

the nectary that lies middorsally at the base of the sepal. They move around the stem to get to the other nectaries but are not nearly so quick in completing their visit as species that rotate to the nectaries from a position astride the stamens within the flower. However, this procedure does allow the bees and wasps to avoid contamination with *Kallstroemia* pollen, which clings abundantly and persistently to body hairs.

These species have no role in pollination, being thieves of the nectar supply which they may deplete thereby discouraging those larger bees and wasps that do pollinate while gathering nectar. However, if the nectar supply is merely reduced in volume the pollinators may be forced to visit and pollinate more flowers in order to fulfill their nectar requirements. Thus the robbers could be an asset rather than a liability to the plant which through its ultraviolet reflection of the underside of the petals assisted by the sepal nectar guide, actually seems to encourage these activities.

The pirates of the pollination world, the honeybees, have "learned" this shortcut to the nectaries as they have learned similar shortcuts in other plants to avoid disagreeable features (alfalfa) or to take advantage of more highly concentrated nectar (cotton). In *Kallstroemia* they may have learned by being "rewarded" by the abundance of easily available nectar and by being "penalized," if they go inside the flower, by the large, sticky pollen grains which, for some reason, they do not seem to utilize for larval food. It is well known that some honeybee foragers collect only nectar, some only pollen, and others both pollen and nectar from the same plant. This is the case if both the pollen and nectar are satisfactory to the honeybee but does not seem to apply here as all (hundreds) of our observations indicated complete avoidance of the inside of the *Kallstroemia* flowers and therefore the pollen. Many experiments, especially with economic crops, indicate that the pollen itself can determine the bees' tendency to select it, irrespective of the ease with which it can be collected. Inversely this means a selective avoidance of some pollens, and as it has been shown that bees do not select pollens for their nutritional value, it may be simply a matter of mechanical contamination that makes it undesirable.

It is well known that pollen-collecting honeybees, if offered a choice of pollens, show a preference for some over others. Levin and Bohart (1955) have demonstrated that this is so even when the pollens are separated from the flower structures, color patterns, and perfumes by which they are normally surrounded. They found that pollen color, reflectivity, moisture content, protein, and sugar ingredients all appear to have no influence on attractiveness (they did not unequivocally eliminate odor as a factor). Even inside the hive, bees show a preference among pollens of individual plant species when offered a choice and eat some and reject others (Synge, 1947; Doull, 1966).

In hundreds of observations we failed to see even one honeybee learning by experience. This indicates that there is something more than random foraging activities on *Kallstroemia*. Even the new foragers recruited to *Kallstroemia* appear to have been "instructed" not only that the hive needs nectar and not pollen but also the best way to collect from this source. That the bees have been recruited to *Kallstroemia* indicates that the nectar is good and that at least some preferential recruiting has been accomplished during dancing and Nasanov scent gland exposure. Perhaps information on how to gather the nectar is transmitted by the scouts and foraging bees when they return to the hive. We can, of course, only speculate on how this behavior was originally learned. The most obvious suggestion lies in the fact that the flower advertises its undersurface both in color and ultraviolet reflection in addition to having the sepal nectar guide. Furthermore, the underside of the flower is exposed when the larger insects land on top causing the flower to bend as much as 180 degrees. Wind action may also be responsible for some exposure of the undersurface. Only once did we see a honeybee taking nectar from a flower that was already bent over by a *Protoxaea* bee. However, repeated exposure to the overturned flowers, the reward of easily available nectar, and the lack of sticky pollen may have fixed the visual image pattern in the bee to an extent that it has become communicable. How the other two regular and consistent visitors (solitary) to the underside of the flowers, *Centris atripes* and *Bembix uscripta*, learn and maintain their fixed behavior

pattern in this respect is difficult to understand unless each new generation relearns the pattern suggested for the honeybee or mimics the honeybee in this behavior. That mimicry may occur is suggested by the fact that in all the areas where we have encountered male *Protoxaea* in abundance, they consistently visited the inside of the flower except at the only site where honeybees were abundant near Portal. However, no honeybees were present at Apache, where large numbers of *Bembix u-scripta* were extracting nectar from the underside of the flower.

BEE AND WASP VISITORS TO *KALLSTROEMIA*

FAMILY ANDRENIDAE

Andrena (*Pterandrena*) *accepta* Viereck. Females were found in small numbers at Apache, Arizona, feeding at the nectaries by crawling under the stamens. They were not uncommon in the vicinity of *Kallstroemia* plants taking pollen from *Helianthus annuus* (Linnaeus). As emphasized by La Berge (1967), this species is an oligolege of Compositae. Of 219 females with flower records examined by him, 218 were taken from Compositae and of these, 194 were from *Helianthus*. The species is widespread, ranging from eastern California and Oregon to New Jersey, Georgia, Arizona, and northern Mexico. Their presence at flowers of *Kallstroemia* was undoubtedly opportunistic.

Psaenythia (*Protandrena*) *mexicanorum mexicanorum* (Cockerell). Females of this subspecies have been reported by Timberlake (1955) from flowers of *Kallstroemia grandiflora* at Tucson and Cortaro, Arizona, and from *Solanum rostratum* Dunal near Patagonia, Arizona. We have also recorded it previously taking pollen from *Solanum rostratum* and *S. elaeagnifolium* near Douglas, Arizona (Linsley and Cazier, 1963).

At the Rodeo, New Mexico locality, both sexes were relatively numerous, taking nectar from within the flower working over or between the stamens and as a result usually having some loose pollen on body and legs. Some females, however, had accumulations of pollen on the legs that did not appear to be accidentally acquired and others definitely had *Kallstroemia* pollen packed into the tibial scopa and mixed with nectar. At this site *Solanum elaeagnifolium* was present in scattered patches, and the earliest female nectar visitors to *Kallstroemia* carried pollen from *Solanum*.

A favorite nectar source for both sexes of *Psaenythia* in the surrounding area is *Asclepias subverticillata* (Gray) Vail.

Perdita (*Macroteropsis*) *echinocacti* Timberlake. Recorded by Timberlake (1954) from flowers of *Kallstroemia grandiflora* in the Santa Catalina Mountains, Pinal County, Arizona, and near Nogales, Santa Cruz County.

Perdita (*Perdita*) *pectidis* Cockerell. Three females from *Kallstroemia maxima* at Las Cruces, Dona Ana County, New Mexico, have been reported by Timberlake (1960). According to Porter (*in litt.*), *K. maxima* does not occur in the western United States. The Timberlake record represents either *K. parviflora* Norton (probably) or *K. californica* (S. Watson) Vail.

Perdita (*Epimacrotera*) *euphorbiae* Timberlake. Males and females have been collected at flowers of *Kallstroemia* and *Euphorbia* near Navajoa, Sonora Mexico (Timberlake, 1960). We encountered no *Perdita* at *Kallstroemia* in our study sites.

Pseudopanurgus aethiops (Cresson). Occasionally found taking nectar from beneath the stamens of *Kallstroemia*. In our experience the species is an oligolege of Compositae. We have taken it locally gathering pollen from *Baileya pleniradiata* Harvey and Gray, *Heterotheca psammophila* Wagenknecht (Porter, *in litt.*), *Verbesina encelioides* (Cavanilles) Bentham and Hooker, and *Helianthus* annuus.

FAMILY OXAEIDAE

Protoxaea gloriosa (Fox). This large bee was by far the most abundant and consistent visitor to *Kallstroemia* in the areas sampled. It is a polylectic species, usually active from sunrise to midday, taking pollen from *Solanum*, *Cassia*, *Calliandra*, and *Larrea* during the first two hours of flight (Linsley and Cazier, 1972). However, at flowers of *Kallstroemia*, which do not open and present pollen until an hour or more after sunrise, pollen collecting females may be active in small numbers taking pollen at noon or shortly thereafter, particularly on cool overcast days. Females take

nectar from within the flower, as described earlier. Males were usually found taking nectar from within the flower, in which case they became heavily dusted beneath with pollen. However, at the Portal site, where honeybees were abundant, some but not all males were seen taking nectar from the underside of the flower.

The pollens of several of the plants preferred by this species are fine. Pollen grains of *Kallstroemia* removed from females averaged 66.7μ (range 63.4μ-68.8μ) (Linsley and Michener, 1962) (see also Martin and Drew, 1970), those from *Solanum* 25.6μ (23.5μ - 27.0μ) (Linsley and Cazier, 1963).

FAMILY HALICTIDAE

Halictus (*Seladonia*) *tripartitus* Cockerell. A widespread polylectic species. A few females were observed at the Apache site crawling on the anthers of *Kallstroemia* and gathering pollen.

Agapostemon melliventris Cresson. A widespread polylectic species. Roberts (1972) mapped its range as primarily Great Basin and the desert areas of southwestern United States and northern Mexico, but also extending over most of the Great Plains. We found it in *Kallstroemia* flowers but only taking nectar. When carrying pollen, it proved to be from another plant source.

Agapostemon tyleri Cockerell. This species is more restricted in its distribution than *A. melliventris*. Maps by Roberts (1972) indicate that the two are sympatric primarily in the eastern part of the range of that species. Like *A. melliventris,* females we observed were carrying foreign pollen on the legs, although the body was contaminated with *Kallstroemia* pollen.

Nomia tetrazonata tetrazonata Cockerell. Ribble (1965) recorded three females from *Kallstroemia grandiflora* but did not identify the locality or whether they were taking pollen. We did not encounter the species in our study sites.

FAMILY MEGACHILIDAE

Megachile (*Acentron*) *albitarsis* Cresson. The female of this widespread southern species was recorded by Cockerell (1908) from *Kallstroemia* as *M. kallstroemiae*, new species. The species takes pollen from a variety of plant sources but is not known to do so from *Kallstroemia.*

Megachile (*Pseudocentron*) *sidalceae* Cockerell. *Kallstroemia* is among the wide variety of plant genera reported as flower records for this species by Butler (1965). He did not record the plant species or whether the bee was taking pollen.

Chalcidoma (*Chelostomoides*) *adelphodonta* (Cockerell). Recorded from Arizona by Butler (1965) at *Allionia* and *Kallstroemia* without further data.

Coelioxys sp. Both sexes of this parasitic megachilid were found at the Apache site in *Kallstroemia* flowers taking nectar from beneath the stamens.

FAMILY ANTHOPHORIDAE

Exomalopsis (*Phanomalopsis*) *solani* Cockerell. Females visit *Kallstroemia* flowers primarily for nectar, crawling beneath the stamens to obtain it. The species is polylectic. Timberlake (1947) recorded it from a diverse group of flowering plants but its pollen collecting habits are not well known.

Nomada sp. This parasitic bee was found extracting nectar from a position beneath the stamens of *Kallstroemia* at the Apache site.

Holcopasites caliopsidis carinatus Linsley. A male recorded by Hurd and Linsley (1972) from flowers of *Kallstroemia hirsutissima* Vail at El Salto, San Luis Potosi, Mexico. This parasitic bee probably crawls beneath the stamens to reach the nectaries, avoiding contact with pollen.

Ptilothrix sumichrasti (Cresson). This species was among the bees collecting pollen from *K. grandiflora* at the Apache site. Butler (1967) recorded females taking pollen from cultivated cotton (*Gossypium*) in the Santa Cruz and Gila river valleys, as well as from *Kallstroemia* (precise locality not stated). In these localities both sexes were abundant and mating was observed on the latter flowers. He also recorded visits of *Ptilothrix* to the related *Tribulus terristris* (puncturevine) but did not state whether they were taking pollen. In Mexico the females take pollen from *Ipomoea* spp. (Linsley, MacSwain, and Smith, 1956) and probably also in southern Arizona. They occur in areas of summer rain and require moisture for nest construction. At the site near

Apache the females were nesting in open hard-packed soil in the vicinity of the *Kallstroemia* plants.

Diadasia ochracea (Cockerell). Females of *Diadasia ochracea* were found collecting pollen from *Kallstroemia* at the Rodeo site and males were observed taking nectar from positions beneath the stamens at both the Rodeo and Apache study areas. Habits of the species have been described by Linsley and MacSwain (1957) under the name "*olivacea.*" These authors reported several species of *Sphaeralcea* as pollen hosts in various parts of its range, a genus to which *D. ochracea* has been generally believed to be oligolectic. *Sphaeralcea* is usually evident at both of these sites but relatively few plants were in bloom when *Kallstroemia* was sampled. In a discussion of floral constancy in *Diadasia*, Linsley and MacSwain (1958) described a stress situation in which *D. australis californica* Timberlake, usually restricted to pollen of cactus, turned to *Phacelia* in the absence of its normal host.

Diadasia diminuta (Cresson). *Diadasia diminuta*, like *D. ochracea*, generally regarded as an oligolege of *Sphaeralcea* (Linsley and MacSwain, 1957, 1958), was found taking pollen from *Kallstroemia* at the Apache site under what may have been conditions of stress. Further studies of female behavior in each of these species should be made to clarify the extent of flower specificity.

Diadasia megamorpha Cockerell. Two females of this species were taken from flowers of *Kallstroemia* at the Rodeo site as they were gathering pollen. We did not encounter it on other plants locally and are not familiar with its floral relationships.

Melissodes (*Melissodes*) *thelypoddi thelypoddi* Cockerell. This subspecies occurs from southern California through Arizona and New Mexico to southeastern Texas and northern Durango (La Berge, 1956). As would be expected it takes pollen from wide variety of plants, including cultivated *Gossypium* (cotton) (Butler et al., 1960) and *Carthamus* (safflower) (Butler, Werner, and Levin, 1966). Cockerell (1905) recorded the male from *Kallstroemia* at Mesilla Park, New Mexico, under the name *Melissodes kallstroemiae*, new species, and La Berge listed *Kallstroemia grandiflora* among the flower records but without reference to pollen. Next to *Protoxaea gloriosa* this is one of the most abundant visitors to *Kallstroemia* flowers in the San Simon Valley. Both sexes were present in numbers at all three principal study areas, especially at Apache, taking nectar from within the flower. All but a few of the females were also actively taking pollen.

Melissodes (*Eumelissodes*) *montana* Cresson. *Melissodes* (*E.*) *montana* was regarded by La Berge (1961) as an oligolege of Compositae, and most of our collections confirm a preference for plants of this family. Locally we have found females taking pollen from *Gutierrezia sarothrae* (Pursh) Britton and Rusby and *Heterotheca psammophila.* However, in our study area near Portal females were found taking pollen from *Kallstroemia.*

Melissodes (*Eumelissodes*) *limbus* La Berge. This species ranges from central Arizona through southwestern Arizona and western Texas to south-central Mexico. According to La Berge (1961), it is an oligolege of Compositae, preferring plants of the genera *Verbesina*, *Haplopappus*, and *Baileya*. Females have been observed extracting nectar from *Kallstroemia* at the site near Rodeo inside the flower but beneath the stamens so as to avoid contact with the pollen.

We have found it locally taking pollen from *Haplopappus gracilis* (Nuttall) Gray and *Baileya pleniradiata* Harvey and Gray.

Melissodes (*Tachymelissodes*) *sonorensis* La Berge. Although not encountered by us, La Berge (1963b) recorded males and one female from *Kallstroemia grandiflora* south of Navajoa, Sonora, Mexico.

Svastra (*Epimelissodes*) *sabinensis sabinensis* (Cockerell). This species occurs in south-central Arizona and southwestern New Mexico and has been recorded by La Berge (1956) from plants of several genera of Leguminosae, Compositae, and Malvaceae as well as from *Kallstroemia grandiflora*. We found both sexes at *Kallstroemia* at the Portal, Arizona, Apache, Arizona, and Rodeo, New Mexico, sites. Most females were taking pollen.

Svastra (*Epimelissodes*) *sila* (La Berge). We have found this species locally visiting Compositae for pollen, particularly *Baileya pleniradiata* and *Heterotheca psammophila*, host plants also recorded by La Berge (1963a). This is a southwestern desert species occurring from

southeastern Arizona to Baja California (La Berge, 1958). Males were taken at the Portal study area feeding on nectar from within the *Kallstroemia* flowers, rotating on the stamens.

Centris atripes Mocsáry. This species collects pollen locally from *Solanum* (Linsley and Cazier, 1963) and was active on *Solanum elaeagnifolium* at the Rodeo and Portal sites. However, along with other *Solanum* pollinators it turns to other plants for nectar. Females were abundant at *Kallstroemia* in all three study sites taking nectar from beneath the flower, numerically being second only to honey bees at the Portal and Rodeo sites.

Xylocapa californica arizonensis Cresson. Females collect pollen locally from a variety of plant species but were not observed doing so from *Kallstroemia*. They occasionally visit the flowers for nectar and their weight causes the blossoms to invert, requiring the bee to cling to the stamens for support. In the process they become liberally dusted beneath with pollen which they transport from flower to flower. They were taken at the site near Rodeo.

Megabombus (*M.*) *pennsylvanicus sonorus* (Say). The bumblebee *M. pennsylvanicus sonorus* is one of the most ubiquitous and conspicuous flower visitors in the San Simon Valley area (Linsley, 1960). It is active throughout the day, working early blooming plants such as *Solanum* before sunrise (Linsley, 1962) and late afternoon or early evening flowers such as *Mentzelia* (Linsley and Hurd, 1959). However, we found it taking pollen from *Kallstroemia* only rarely and only at the site near Portal. The status of this species has been recently discussed by Milliron (1973). He showed its range as extending from central California to southern Baja California, south-central Mexico, southern Arizona, New Mexico, and Texas. *Kallstroemia* is not included among the many flower records reported by him.

Apis mellifera Linnaeus. Honeybees were very abundant at the site east of Portal (an apiary was nearby), scarce near Rodeo, and absent at Apache. At no time during the three summers of observations on *Kallstroemia* were individuals seen inside the flower taking either pollen or nectar. All the hundreds of worker bees at the Portal site took nectar from the underside of the flower. However, honeybees do work *Kallstroemia* flowers for pollen, as attested by Porter (1969) and probably would do so at the Portal site under appropriate conditions, such as pollen stress, when foraging for the first time, or when the colony needed it.

Austin (1972) recorded their behavior at flowers of the related *Tribulus cistoides* Linnaeus as follows (text references to illustrations omitted):

"Most of the Honey Bees visiting the flowers approach in the 'normal' bee fashion described by Meeuse (1961) and Faegri & Pijl (1966). Instead of landing on the stamens and stigmas as they should, however, they circle around the flower and land on the outside of the calyx and corolla. After landing they separate two petals[1] with their front legs, insert their tongues, and sip nectar. They continue this procedure around the flower until they have collected nectar between all the petals. Once a flower has been utilized, the bees fly to another and repeat the process. Several flowers are usually visited before the bee disappears.

"Other Honey Bees approach and land within the corolla in the 'normal' manner. In so doing they position their bodies over the stigma and stamens. Normally they insert their tongue between the petals into the nectary, sip nectar and turn around the flower to drink nectar from other nectaries. They dust much of their body with pollen as they turn. After the nectar has been collected, they often brush the stamens with their front legs to gather pollen.

"After nectar has been taken and pollen gathered with the front legs, the bees may fly to another flower to repeat the process. It is common, however, for an individual to brush pollen, fly off and hover in front of the flower, return to brush more pollen, and hover again. This may be done three or four times before the process is repeated at another flower.

"Those individuals which exhibit this hovering behavior usually have their pollen baskets full. The bees with pollen in the pollen baskets have little or no pollen adhering to the hairs of their legs and body. Bees which have no pollen in their baskets rarely hover, and their bodies and legs usually are dusted with pollen."

[1]This is not the case in *Kallstroemia* as observed by us.

HYMENOPTERA SCOLIOIDEA

FAMILY TIPHIIDAE

Myzinum navajo Krombein. *Myzinum navajo* was described from material representing various localities in Arizona and also Sonora, Mexico (Krombein, 1938). No flower records were reported. At the Apache, Arizona, site it was the second most abundant wasp visiting *Kallstroemia* flowers for nectar, *Bembix u-scripta* being the most abundant. Unlike the latter species, which extracts nectar from the underside of the flower, *M. navajo* crawls beneath the stamens to reach the nectaries. It plays no significant role in *Kallstroemia* pollination.

Myzinum frontale Cresson. A single female of this species was taken from a flower of *Kallstroemia* at the Apache site along with females of *M. navajo*. Like individuals of that species, it had crawled beneath the stamens to reach the nectaries and was uncontaminated with pollen.

Krombein (1938) reported the species as occurring from Kansas and Colorado to Texas, New Mexico, Nevada, Arizona, and southern California. Recorded flowers visited include: *Polygonum* and *Eriogonum* (Polygoniaceae), *Melilotus* (Leguminosae), *Chilopsis* (Bignoniaceae), and *Solidago*, *Baccharis*, and *Pluchea* (Compositae).

FAMILY SCOLIIDAE

Scolia (*Trichoscolia*) *ardens* Smith. This large, conspicuous wasp occurs throughout much of southwestern United States and northern Mexico. Females are not uncommon in the San Simon Valley, especially at flowers of *Baccharis*. When taking nectar from *Kallstroemia* they position astride the stamen and the venter becomes dusted with pollen. One female was taken at the site near Rodeo.

Campsomeris (*Campsomeris*) *tolteca* (Saussure). A female was captured while taking nectar from *Kallstroemia* at the site near Rodeo. The venter was heavily dusted with pollen. The species occurs in southern California, Arizona, western New Mexico, and Mexico (Bradley, 1928b). We have taken it locally visiting flowers of *Baccharis*.

Campsoscolia octomaculata texensis (Saussure). This species occurs from western Texas and southern Colorado through Texas, New Mexico, and Arizona to northern Mexico (Bradley, 1928a). When visiting *Kallstroemia* flowers for nectar, the females either enter the flower and hold the stamens together with the legs like a bee and as they rotate from nectary to nectary the venter and legs become heavily coated with pollen (Apache site), or on the site near Rodeo they collected nectar from the underside of the flower.

HYMENOPTERA VESPOIDEA

FAMILY VESPIDAE

Monobia texana (Cresson). This species, ranging from Texas to Arizona (Bequaert, 1940), locally visits a variety of flowers for nectar, including *Baccharis* and *Eriogonum*. At *Kallstroemia* we have observed females taking nectar only from the underside of the flower, in the manner used by *Bembix* and *Pterocheilus* at the site near Portal.

Pterocheilus arizonicus R. Bohart. This southwestern species was found in small numbers at the site near Portal taking nectar from the underside of *Kallstroemia* flowers in 1970 and again in 1971. We have observed a related species, *P. pedicellatus* R. Bohart, chewing its way into the base of the long tubular flowers of *Gilia longiflora* (Torrey) George Don to gain access to the nectaries.

FAMILY SPHECIDAE

Bembix u-scripta (Fox). This was the most abundant wasp observed taking nectar from *Kallstroemia* flowers, particularly at the Apache, Arizona, site. The species differs markedly from other members of the genus both by the possession of functional ocelli and the fact that the females hunt their dipteran prey and provision their nests only in the dusk, around and after sunset (Evans, 1960). It occurs in southwestern United States and Mexico but is generally considered to be rare or localized.

Both sexes take nectar from beneath *Kallstroemia* flowers and the males in particular begin patrolling the plants before the flower buds begin to unfurl, attempting to force their mouthparts into the nectaries. Males were already very active at the Apache site by 0745 when observa-

tions were initiated. Although our observations were made in mid-August and Evans's observations were made in May, it seems likely that *Kallstroemia* nectar may have been providing energy for the morning "sun dance" at a nearby nest site as described by Evans (1960): "Each morning we entered the area about 0800, and at this time the males were already engaged in their 'sun dance.' Each male flew rapidly in loops, figure eights, and irregular patterns only 2-6 cm. above the sand surface, much as in *Bembix cinerea* (Handlirsch) (Evans 1957). By 1030 some reduction of males could be noted, and by 1115 each day the last male had disappeared. By 1500 a few males were once again active, and from 1600-1900 each day there was a second though somewhat less populous 'sun dance.'" If there was an evening "sun dance" near the Apache site, *Kallstroemia* could not have provided nectar for it.

MISCELLANEOUS INSECT VISITORS

LEPIDOPTERA

At the Apache, Arizona site two species of skipper butterflies were present in small numbers taking nectar from the underside of the flowers. These were *Pholisora catullus* (Fabricius) and *Celotes nessus* (Edwards). According to D. M. MacNeil (*in litt.*), the larvae of the former feed principally on various Chenopodiaceae and Amaranthaceae and those of the latter on Malvaceae. Representatives of these families were present at the site. *Pholisora catullus* is a widespread North American skipper; *C. nessus*, a southwestern species.

DIPTERA

Diptera were seen at flowers of *Kallstroemia* at each of the study sites but usually in small numbers. Exceptions were the ubiquitous syrphid *Heliophilus latifrons* Loew and small bombyliids of the genus *Phthiria*. The former brush the stamens as they extract nectar and frequently have small amounts of pollen on the underside. *Phthiria* approach the nectaries below the stamens and avoid contamination with pollen.

SUMMARY AND DISCUSSION

The brightly colored flowers of *Kallstroemia grandiflora*, their conspicuous ultraviolet reflection pattern, their obvious nectar guides, and their copious supplies of both pollen and nectar make the flowers prime targets for insect visitors even though there is no evident floral fragrance. Forty-six species belonging to three orders and 12 families of insects are herein listed as regular visitors to the flowers but not all use the flowers in ways directly beneficial to the plant. Some species gather pollen and nectar from inside the flower and pollinate the flower in the process. Others visit the inside of the flower for nectar only; some visit the inside of the flower but avoid the anthers and stigma and a fourth group avoids the inside of the flower and its reproductive parts and gains access to the nectaries from underneath the flower. The nonpollinators that visit the inside of the flower use the same visual cues as do the pollinators (orange, ultraviolet-reflecting petals and a nonreflecting target area over the nectaries), whereas the ventral visitors are supplied with their own guides (orange, ultraviolet reflecting undersurface of petals and elongate, wedge-shaped, nonreflecting sepals that point to the nectaries) and are therefore encouraged by the flowers to avoid contributing, at least directly, to the primary reproductive function for which the flower was evolved, pollination resulting in fertilization and seed set.

Males among the insect visitors to *Kallstroemia* are interested only in nourishment and are involved in only the three categories of nectar collecting behavior. Females, on the other hand, are not only responsive to the needs of their own energy supply but also to the need for storage of pollen and nectar for the consumption of their larval offspring. All but the honeybee store individual cells in the ground with various mixtures of pollen and nectar and may, depending on the species and the stage in stocking the cell, be gathering pollen and nectar or one or the other. In the social honeybee, the determination on which flowers they forage and what commodity they gather is dictated by the hive, either by the behavior of the sister bees and scouts or by the immediate food requirements of the hive. As in all of our observations of the honeybee at *Kallstroemia*, workers gathered nectar only, it seems reasonable to assume that the primary if not sole activity of the hive or hives was that of honey manufacture and storage at this time of year,

August 17. Also, it may be assumed that the sugar content of *Kallstroemia* nectar was satisfactory, as the flowers were visited frequently even though they were in competition with flowers of other plants.

Why the honeybee and several other species approach the flower from the underside where it takes them longer to reach the nectaries, and how they learn this special technique is more difficult to understand. If indeed *Kallstroemia* pollen is undesirable, as we have already suggested, it may be responsible for the obvious avoidance of the pollen and for the incorporation of such information into honeybee language, including information on the new approach system. However, it is by no means certain that the pollen is in any way repellent. The grains range in size from 63.4μ-68.8μ, average 66.7μ, which is well within the size range of insect transmitted pollens. That it is adhesive may or may not be a disadvantage but this appears to make it more easily carried and to minimize drying. However, there may be a more subtle, undesirable character that may account for the fact that some species shake or brush the pollen off after visiting a flower and others partially or completely avoid it. This type of behavior among the solitary bees and wasps is even less expected unless they mimic the behavior of the honeybee or respond to the ventral nectar guides frequently enough to fix the behavior pattern. Further evidence that the pollen in itself is useful lies in the fact that 11 different species of bees are collecting and utilizing the pollen in their economy.

Although three other species of *Kallstroemia* have been shown to be intermittent in their germination, it is by no means certain that seeds of *Kallstroemia grandiflora* germinate at irregular intervals. Whole areas may be covered with these poppies in the appropriate season of one year and have none for the next several seasons, which strongly suggests an overriding environmental control. Further studies are necessary to determine which factor or factors are responsible for the sporadic appearance of this plant on the desert landscape.

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