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POLLINATION MECHANISMS IN THREE SPECIES OF
SALVIA NATIVE TO SOUTHERN CALIFORNIAFRANK J. VISCO¹ AND BRIAN CAPON*Department of Botany, California State College at Los Angeles*

INTRODUCTION

The genus *Salvia* (Labiatae) is large and diverse, with over 500 species distributed in the warm, temperate regions of the world. Of the 15 recorded species in Southern California, three are the subject of the present study: *Salvia carduacea* Benth., *Salvia columbariae* Benth., and *Salvia dorrii* (Kell.) Abrams ssp. *dorrii*.

Relatively few reports by other workers with the genus in California have considered pollination mechanisms. Grant and Grant (1964), in studying natural hybridization between *Salvia mellifera* and *Salvia apiana*, included data on observed animal visitors to the two species. These included bees of the families Halictidae, Apidae, and Megachilidae as the most effective pollinators of *S. mellifera*. Apidae and Anna's hummingbirds were found to be the most frequent and effective pollinators of *S. apiana*. The only known reference to specific pollination factors for the *Salvia* species described in the present paper are some incidental notes by entomologists. Timberlake (1941), while describing the new species *Anthophora linsleyi* Timberlake, reports that it was collected on plants of *Salvia carduacea* in four different locations. Linsley and MacSwain (1942) found that this bee, in two locations adjacent to the Mojave Desert, collected pollen exclusively from *Salvia carduacea* flowers. They observed that the bees bypassed other plants in flower to obtain *S. carduacea* pollen, even though it was necessary for the bees to fly more than a mile from their nests.

The work described below was directed toward a more thorough study of specific pollination mechanisms of *Salvia carduacea*, *S. dorrii* ssp. *dorrii*, and *S. columbariae*. It involved the examination of floral structures, the examination of animal visitors to the flowers, the determination of relationships between flower structure and visitor's activity, and the consideration of possible abiotic factors in pollination.

METHODS

Salvia plants were observed in the field from early vegetative stages, through flowering, to seed maturation. In addition, 20 plants each of the annuals *S. carduacea* and *S. columbariae* before anthesis were transplanted in some of their native soil to a study site in Burbank, California where they

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were grown separately in cages constructed of a fine mesh nylon screen to eliminate the possibility of animal pollination. Branches of the perennial *S. dorrii* bearing unopened flower buds were covered in the field with fine mesh screen for the same purpose. The development of these isolated plants and branches was observed until they had reached a stage equivalent to uncovered plants which were definitely bearing seeds. Those seeds which were formed in the absence of biotic pollination factors were carefully collected and studied for embryo development compared with randomly collected seeds produced under natural field conditions.

Floral structures of the three *Salvia* species were examined macroscopically and microscopically. Examinations were made of the corolla, nectary, pistil, stamens, and other structures to determine their role in the pollination mechanisms. Microscope slides were made of fresh pollen by the method described below in order to aid in identifying the pollen found on the bodies of the pollinating insects. In addition, anthers and stigmas in various stages of development were permanently mounted in cottonblue-lactophenol on microscope slides to determine the stage and time at which the stigma became receptive to pollen.

Representatives of the insect visitors to the *Salvia* plants were collected on the flowers with an insect collecting net, killed with ethyl acetate, and mounted. Pollen on the insects' bodies was brushed into vials containing 50% ethanol prior to mounting on slides in the following manner: 1 ml of gelatin with 1% phenol was placed on a slide and gently melted; Safranin 0 was then added and mixed until the materials became a homogeneous violet color. A drop of pollen in ethanol was transferred to the gelatin mixture and sealed under a coverslip.

In the field, visual counts were made to determine relative abundance of visitors to the flowers and the number of flowers visited by the animals in a given period of time. Still and motion pictures were made of *Salvia* plants and the behavior of animal pollinators to the flowers. Abiotic environmental factors which were noted during field observations were temperature and wind velocity.

FIELD STUDY AREAS

Three populations of *Salvia carduacea* were studied. One site was located in the Mojave Desert in Los Angeles County near the town of Pearblossom. It is an open, flat desert area supporting creosote bush (*Larrea divaricata* Cav.) as the dominant species and *Phacelia crenulata* Torr., var. *ambigua* (Jones) Macbr. as the most common annual. The population was studied eight times from March 22, 1968, when few plants of *S. carduacea* were in bloom, until May 1, 1968, when flowering had generally ceased. A second Mojave Desert population was located in Los Angeles County near Quartz Hill, a desert foothill community dominated by Joshua Tree (*Yucca brevifolia* Engelm.) and creosote bush. An extensive population of *Salvia columbariae* was also present and served as the sole study site for that species. These two species were studied on frequent visits throughout their flowering cycles from March 2, 1968, to May 28, 1968. The third study area for *S. carduacea* was located in San Diego County in Anza-Borrego Desert State

Park, a section of the Colorado Desert. The flat terrain along Highway S2, 2–3 miles southwest of its junction with Highway 78, was covered with an unusually dense population — 13 plants per square meter, compared with 1–8 plants in the other two study areas. The dominant species in the area is creosote bush and *Opuntia acanthocarpa* Engelm. & Bigel. The area was devoid of other annuals. The population was studied five times from April 20, 1968, until May 27, throughout the peak of the blooming season.

Salvia dorrii ssp. *dorrii* populations were located in three areas in the Mojave Desert and the adjacent foothills of the San Gabriel Mountains, all in Los Angeles County. At a site near Pearblossom, about 2 miles removed from the *S. carduacea* study area, *S. dorrii* was studied on several occasions from April 10, 1968, to the end of May throughout the flowering period. Dominant plants in the area are creosote bush and Joshua Tree. *Phacelia crenulata* var. *ambigua* was the most common annual present at that time. A second area was located near Palmdale, California in a foothill community dominated by *Juniperus californica* Carr. and supporting a large population of *Amsinckia tessallata* Gray. The population of *Salvia dorrii* was studied from March 16 to 22, 1968. The third *S. dorrii* study site was in a hilly area near the borderline of Devil's Punch Bowl State Park in the Angeles National Forest. The area supports *Juniperus californica* and species of *Ceanothus* and *Cercocarpus* as dominant species. The *Salvia* plants were studied several times from May 2, 1968, to June 1 throughout the flowering season.

OBSERVATIONS

1. FLORAL STRUCTURES

a. *SALVIA CARDUACEA* Benth.—The flowers are arranged in from 1 to 4 verticillate inflorescences along a stem. The lavender corolla is zygomorphic, divided into an upper and lower lip (Fig. 1), the lower being tipped with white fringes. The entire corolla forms a narrow tube only 1 mm in diameter, expanded above into the upper and lower lips. The two stamens are composed of two branched filaments. The longer filaments are adnate to the base of the lower lip and exerted from the flower; the shorter filaments are connected to the base of the longer pair. The shorter stamens are arranged with their anthers around the apex of the narrow corolla tube. The anthers of the shorter stamens are smaller than those of the longer stamens. The pollen of both pairs of anthers is red and morphologically indistinguishable from each other. The ovary is four-lobed and has a single style about the length of the longest stamens. A nectary, present below the ovary, produces nectar throughout the day and night.

Salvia carduacea flowers are protandrous. Dissection of unopened flower buds revealed loose pollen adhering to various internal parts. The style was coiled and undivided at its apex. Although pollen was available, none was found adhering to the stigma. With the onset of anthesis, the style and anthers become exerted and the anthers bear large amounts of loose red pollen. The style in this phase remains single and undivided with its apex 1–2 mm short of the anthers (Fig. 4A). In the course of further development of the flower, the style elongates beyond the anthers before splitting

at its apex and becoming receptive to pollen (Fig. 4B-4D). As the stigma develops toward a receptive state there is a progressive decrease in the amount of pollen on the anthers.

b. *SALVIA COLUMBARIÆ* Benth.—The flowers are arranged in from 1 to 3 verticillate inflorescences along a stem. The blue corolla is zygomorphic and divided into an upper and lower lip, with the lower lip tipped with white. The corolla is 10 mm long, with the basal 6-7 mm forming a very narrow tube (Fig. 2). Anthers of the shorter stamens are smaller than those of the longer stamens. Pollen of both pairs of anthers is yellow in color. The ovary is four-lobed and has a single style about the length of the longest stamen.

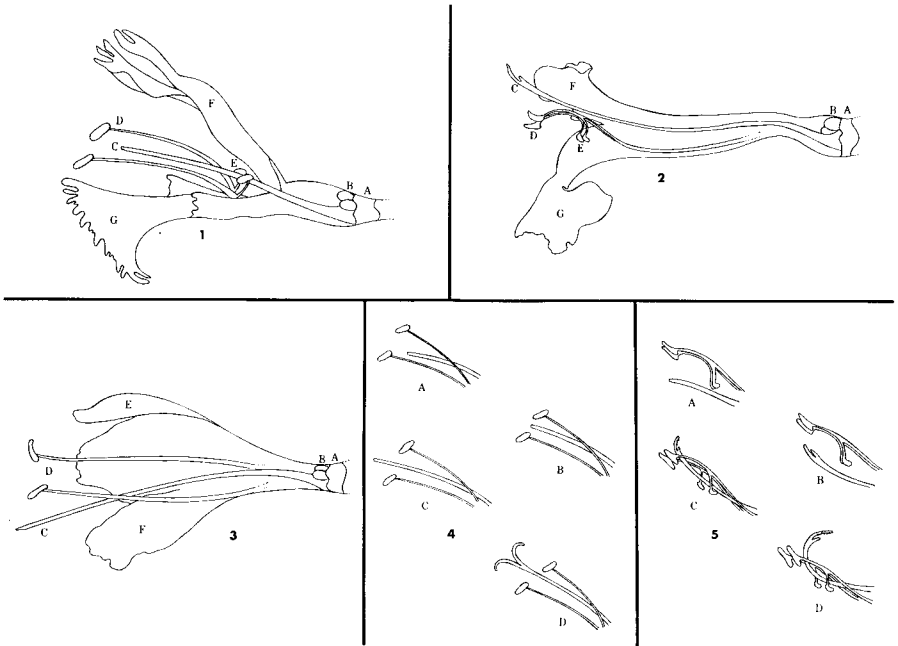


Fig. 1-5.—Fig. 1. Longitudinal view of *Salvia cardiacea* flower. A. Nectary; B. Ovary; C. Stigma; D. Larger stamen; E. Smaller stamen; F. Upper lip; G. Lower lip.—Fig. 2. Longitudinal view of *Salvia columbariae* flower. A. Nectary; B. Ovary; C. Stigma; D. Larger stamen; E. Smaller stamen; F. Upper lip; G. Lower lip.—Fig. 3. Longitudinal view of *Salvia dorrii* flower. A. Nectary; B. Ovary; C. Style; D. Stamens; E. Upper lip; F. Lower lip.—Fig. 4. Stigmatic morphogenesis in *Salvia cardiacea* and *Salvia dorrii*.—Fig. 5. Stigmatic morphogenesis in *Salvia columbariae*.

Salvia columbariae flowers are protandrous. With the onset of anthesis, the style and anthers become exerted, the anthers bearing large amounts of free pollen. The style in this phase remains single and undivided along its length, and is located below the level of the anthers (Fig. 5A). In the

course of further development, the style splits about 1 mm below its apex, leaving a receptive area between the split ends (Fig. 5B). Examination of the stigma reveals some pollen adhering in this condition. As drying of the style tissues occurs during the course of the day, it coils toward then over the upper lip of the corolla and, in the process, passes between the larger anthers (Fig. 5C, 5D). As the style completes this movement, pollen is transferred from anther to receptive stigma.

c. *SALVIA DORRII* (Kell.) Abrams ssp. *DORRII*—The flowers are arranged in from 1 to 4 verticillate inflorescences along a stem. The dark blue corolla is zygomorphic (Fig. 3). The entire corolla is 1 cm long, the basal 4 mm forming a narrow tube approximately 1 mm in diameter, expanding above into the upper and lower lips. The two stamens are of equal size. They are adnate to the base of the lower lip, exerted from the flower, and bear cream-colored pollen. The ovary is four-lobed and has a single style about the length of the stamens. A nectary is present below the ovary and produces nectar at most times of the day and night.

Salvia dorrii flowers are protandrous. The unopened flower bud contains a coiled style and an undivided stigma without pollen adhering to it. At anthesis, the style and anthers are exerted, the anthers bearing large amounts of loose pollen. Similar to *S. carduacea*, the style then elongates beyond the anthers, splits at its apex, and then becomes receptive to pollen.

2. SEED PRODUCTION IN ISOLATED PLANTS

a. *SALVIA CARDUACEA*—Plants grown in screen cages followed the same sequence of floral development as those growing in the field, except for the fate of the pollen and nectar. Pollen on the caged plants dried out, turned white, and remained on the anthers. An accumulation of a highly viscous, sweet-tasting material around the nectary was noted in caged plants. Under field conditions, nectar is removed by animal visitors and has little opportunity to accumulate in this manner.

Out of ten caged plants, 343 flowers were produced from which 21 seeds were set with embryo development similar to that found in seeds set in the field. Under field conditions, this same number of flowers would have produced up to 1,372 seeds.

b. *SALVIA COLUMBARIAE*—In contrast to the flowers of *S. carduacea*, *S. columbariae* produced 274 seeds from 84 flowers. In the field, this same number of flowers would have produced a maximum of 336 seeds. Random selection of seeds from caged plants revealed a normal embryo development.

c. *SALVIA DORRII* ssp. *DORRII*—From branches with approximately 100, 200, 230, 250, and 500 flowers, 1, 3, 0, 2, and 30 seeds, respectively, were produced. Under natural conditions, plants of this species produce up to four seeds per flower. In uncovered flowers, the ovaries swelled to about 2–3 mm in length upon fertilization, remained green for a short time, and then turned a mottled brown in color. In covered flowers, more than 99% of the ovaries remained unchanged in size, turned a dark brown color, and eventually shriveled up. As with *S. carduacea*, the pollen of *S. dorrii* covered flowers dried out and remained on the anthers, and nectar accumulated in the corolla tube.

3. ANIMAL VISITORS

A list of insect flower visitors which were positively identified as pollen-carriers is given in Table 1. All were members of the family Hymenoptera. Other insects found in the flowers were collected but are not considered here. A complete description of all flower visitors is given by Visco (1968). A hummingbird was observed visiting *Salvia carduacea* flowers in the Anza-Borrego population. Since the bird could not be captured, however, its role as a possible pollinator was not ascertained.

4. ACTIVITIES OF PRIMARY POLLINATING INSECTS

a. ANTHOPHORA—Several species of *Anthophora* were frequent visitors to all three *Salvia* species in all but two of the study locations (Table 1). *Anthophora linsleyi* Timberlake was the only one which could be positively identified to species and was found visiting both of the annual *Salvias*. Bees of this species flew very rapidly from flower to flower, beginning their activity shortly after sunrise and continuing in some areas until after sunset. As an individual landed on the lower lip of the corolla of *S. carduacea* or *S. columbariae*, it inserted its 7–10 mm-long tongue into the corolla tube to feed on the nectar. In so doing, it accidentally contacted the anther and stigma with the ventral parts of its body. It should be noted, however, that in *S. columbariae* the receptive stigma was situated in a position favorable to bee pollination for only a short period of time after the stigma matured and before it curled over the upper lip of the corolla. Bees on *S. carduacea* were seen, after feeding, to actively gather pollen from the long stamens by brushing their legs over the anthers. Active collection of pollen from *S. columbariae* was not observed. Examination of collected specimens of *A. linsleyi* showed pollen of only the *Salvia* species from which the bee had been feeding. Pollen was distributed over the heads, thoraces, abdomens, and legs.

Two other, unidentified species of *Anthophora* were found visiting the three *Salvia* species. For the most part, these approached the flowers in a similar manner to *A. linsleyi*, made contact with the anthers, and inadvertently accumulated pollen on various parts of their bodies.

b. APIS MELLIFERA L.—This, the honeybee, was probably the most common visitor to all three *Salvia* species. Its activity extended throughout the daylight hours even during periods of winds up to 40 miles per hour. Two types of flower-visiting activity occurred on *Salvia carduacea*. The first type consisted of the bee's initial landing on the lower lip of the corolla and gathering pollen from the large anthers by brushing them with her legs; she would then fly to another flower on the same or another plant. The second type of honeybee behavior on *S. carduacea* flowers consisted of the bee's landing on the lower lip of the corolla and then inserting her 5–6 mm-long tongue into the corolla tube for a period of 1–10 seconds. During this period the bee would force her head against the apex of the tube by a vigorous leg "digging" motion, using the lower lip as a foothold. This activity caused pollen from the smaller anthers to be transferred to the bee's head. As the bee backed out of the tube it continued to collect pollen by brushing the larger anthers with its legs. The bee would then fly to another

flower on the same or another plant. After an unsuccessful attempt to feed on nectar, worker bees have been observed to switch their activities to strictly gathering pollen.

Commonly, *Apis mellifera* individuals landed on the lower lip of *Salvia dorrii* flowers, rarely contacting the anthers or stigma. On *S. columbariae* contact was generally made. Upon landing, the bee would feed upon the nectar. After this activity, the bee would back out of the corolla tube and actively gather pollen. Examination of pollen on the bodies of honeybees revealed that the pollen present was mostly from the plant species upon which the insect was collected.

TABLE 1. Hymenopteran visitors found bearing pollen.

<i>Salvia carduacea</i> Benth.	
Anza-Borrego population	<i>Anthophora linsleyi</i> Timberlake <i>Anthophora</i> sp. <i>Apis mellifera</i> L. <i>Bombus crotchii</i> Cresson <i>crotchii</i> <i>Emphoropsis</i> sp. <i>Xylocopa californica arizonensis</i> Cresson
Pearblossom population	<i>Bombus crotchii</i> Cresson <i>crotchii</i>
Quartz Hill population	<i>Anthophora linsleyi</i> Timberlake <i>Anthophora</i> sp. <i>Apis mellifera</i> L. <i>Bombus crotchii</i> Cresson <i>crotchii</i>
<i>Salvia columbariae</i> Benth.	
Quartz Hill population	<i>Anthophora linsleyi</i> Timberlake <i>Anthophora</i> sp. <i>Apis mellifera</i> L. <i>Bombus crotchii</i> Cresson <i>crotchii</i> <i>Osmia</i> sp.
<i>Salvia dorrii</i> (Kell.) Abrams ssp. <i>dorrii</i>	
Devil's Punchbowl population	<i>Apis mellifera</i> L. <i>Bombus crotchii</i> Cresson <i>crotchii</i> <i>Bombus edwardsii</i> Cresson <i>Bombus vosnesenskii</i> Radoszkoski <i>Osmia</i> sp. <i>Xylocopa californica arizonensis</i> Cresson
Palmdale population	<i>Anthophora</i> sp. <i>Apis mellifera</i> L.
Pearblossom population	<i>Anthophora</i> sp. <i>Apis mellifera</i> L. <i>Bombus crotchii</i> Cresson <i>crotchii</i> <i>Nomia</i> sp. <i>Osmia</i> sp.

c. *BOMBUS CROTCHII* CRESSON *CROTCHII*—Individuals of this species were frequent daytime visitors to all three species of *Salvia* in all but one study location (Table 1). Both workers and queen bees approached a flower by landing on the lower lip of the corolla and proceeded to feed upon the

nectar with their 8 mm-long tongues. Frequently during the feeding process bees of this species were observed to contact the anthers and stigma with the ventral portion of their bodies. Bees were also observed to actively collect pollen and pack it on their hind legs. Examination of the collected specimens revealed pollen not only from the *Salvia* species upon which the bee had been collected, but in some instances pollen was found from other *Salvia* species. *Bombus crotchii* individuals appeared to visit the majority of flowers on a given *Salvia* plant before moving on to another.

d. *BOMBUS EDWARDSII* Cresson and *B. VOSNESENSKII* Radoszkoski—The flower-visiting activities of these two *Bombus* species were quite similar to that of *B. crotchii* except that they were found only on *Salvia dorrii* in the Devil's Punch Bowl area. Pollen found scattered on the bodies and packed on the legs of these bees was mainly that of *S. dorrii* with only traces of *S. columbariae* pollen found on *B. vosnesenskii*.

e. *EMPHOROPSIS* sp.—The visits of *Emphoropsis* individuals was limited to *Salvia carduacea* flowers in the Anza-Borrego population. Flower-visiting activities of this bee appeared quite similar to that of the unidentified species of *Anthophora* described above. Activity was observed only in the late afternoon, 2–3 hours before sunset. Examination of the bees' bodies revealed *S. carduacea* pollen scattered on the ventral portions of the thorax and abdomen, on the legs and head, and in one individual on the clypeus.

f. *NOMIA* sp.—Visitors of the genus *Nomia* were infrequently found during daylight hours on *Salvia dorii* in the Pearblossom population. Behavior on the flowers could not be determined due to the infrequency of the observed flower visits. *S. dorii* pollen was found scattered on the legs and on the ventral surfaces of the thorax and abdomen of collected individuals.

g. *OSMIA* sp. (Megachilidae)—*Osmia* individuals were observed during the daylight hours visiting *Salvia dorii* flowers at the Pearblossom and Devil's Punch Bowl populations and *Salvia columbariae* at the Quartz Hill area. These visitors were observed to land on the lower lip and insert their 5 mm-long tongue into the corolla tube to feed on the nectar. During feeding, the bee commonly accidentally contacted the anther and stigma with its body and legs. Examination of the individual bees revealed pollen from the *Salvia* species on which they were collected scattered over the bodies with greatest concentration on the ventral surfaces of the abdomen.

h. *XYLOCOPA CALIFORNICA ARIZONENSIS* Cresson—Bees of this species were collected infrequently at Anza-Borrego Desert on *Salvia carduacea* and at Devil's Punch Bowl on *Salvia dorii* during warm daylight hours. Flower approach and feeding activities of these bees were quite similar to those of *Bombus* except that they were more erratic. Individuals were observed to visit one flower, then fly quite a distance before visiting another. Microscopic examination of the bees' bodies collected on *S. carduacea* revealed large amounts of that pollen scattered on the heads, ventral portions of the thoraces and abdomens, legs and wings. Bees collected on *S. dorrii* revealed lesser amounts of that pollen scattered over the bodies.

DISCUSSION

POLLINATION MECHANISMS IN SALVIA CARDUACEA

The flowers of *Salvia carduacea* demonstrate many features favorable to pollination by bees and other specialized flower visitors. The lavender color of the corolla was shown by von Frisch (1914) to be among the colors to which bees respond most readily. Faegri and van der Pijl (1966) have reported that this same color is indicative of specialized insect-visited blossoms. Zygomorphy has been shown to direct insects to enter a flower in a certain direction (Kugler, 1959). The flower depth (as in the 8 mm-long corolla tube of *Salvia carduacea*) has been interpreted by Vogel (1954) as being consistent with the pollination syndrome of *Bombus* and honeybees. The expansion of the corolla tube, forming, in part, the lower lip, provides an adequate landing platform for all hymenopteran and lepidopteran flower visitors. Kugler (1942) and Knoll (1922) have shown that individuals of *Bombus* prefer blossoms that are greatly dissected similar to those found in *Salvia carduacea*. The white tips of the lower lip possibly accentuate the dissected appearance, since Kuhn and Pohl (1924) pointed out that bees see only four contrasting colors: blue, white, yellow, and black.

The two stamens produce a lever mechanism similar to that described for the bumblebee pollinated *Salvia patens* Cav. (Faegri and van der Pijl, 1966). As the lower lip of the corolla in *S. carduacea* is depressed by a flower visitor's weight, the anthers are spread to the lateral portions of the flower, allowing access to the nectar for the bee and bringing the anthers in contact with the bee's body.

Brown (1935) and Eames (1961) have stated that flowers showing a reduced number of anthers in combination with the provision of nectar as an attraction utilize insects as pollinators which are more specialized in their flower-visiting habits. Leppick (1953) states that nectar secreted in a narrow tube becomes limited to only those more specialized long-tongue insects (hymenopterans and lepidopterans). Grant (1950) lent further support to the adaptability of flowers to bee-pollination by pointing out that the flowers pollinated by hymenopterans and lepidopterans, for the most part, have not developed special adaptations for protection of the ovary since these insects do not injure the inner parts of the flower during feeding. *Salvia carduacea* flowers seem to possess the necessary adaptations to visitation by soft-tongue insects. The flowers also have a distinct sweet odor present throughout the day and night. This odor, unlike any in the area, could be easily recognized and reacted to by honeybees and bumblebees. Data of this sort were found for honeybees by von Frisch (1919) and Ribbands (1955), and for bumblebees by Manning (1956).

The protandrous condition found in *Salvia carduacea* flowers, and stated by Grant and Grant (1964) to be common in *Salvia* flowers, indicates an adaptation among such flowers favoring cross-pollination. Meeuse (1961) states that such a structural modification as the difference in time of maturation of anthers and stigma can successfully reduce the amount of self-

pollination. This is accomplished in *Salvia carduacea* flowers; insects remove the majority of pollen before the stigma becomes receptive on any given flower. In addition, cross-pollination is further favored in *S. carduacea* flowers by the receptive stigma always being located above and projecting beyond the anthers. As bees approach such flowers, they initially contact the stigmas. This was observed in the present study and also pointed out by Faegri and van der Pijl (1966) for the *Bombus* pollination of *Salvia patens*.

As the stigmas in the *Salvia* plants studied developed toward a receptive state in the field, there was a progressive decrease in the amount of pollen on the anthers. On the other hand, plants grown in cages retained their pollen on the anthers. In caged plants, exposed only to abiotic environment factors, the significantly reduced formation of seeds could be explained by the apparent absence of biotic factors and the unfavorable morphological relationship between the anthers and stigma for transferring pollen. Possible explanations for the production of the 21 seeds which did form include the transfer of pollen by wind through the screen, contamination of the plants prior to opening of the flowers before transfer to the cages, or the product of apomixis.

The phenomenon of flower constancy was observed in the habits of most of the bees visiting *Salvia carduacea*. In the Pearblossom population, however, although *Bombus crotchii crotchii* was seen to visit only *S. carduacea*, even when confronted with the blue, tubular flowers of *Phacelia crenulata* var. *ambigua*, pollen of both of these plants was found on the bodies of collected specimens. The pollen load analysis agreed with the findings of Betts (1920), Clements and Long (1923), and Brittain and Newton (1933) who found the purity of *Bombus* collected pollen to be between 49% and 59%. It was interesting to note that early in the flowering season these same bees visited plants which had not yet begun to flower, a characteristic noted by Manning (1956) for other species of *Bombus*. This probably illustrates the ability of these bees to associate a certain plant form with its flowers, a theory supported by the findings of von Frisch (1914), Kugler (1942), and Bateman (1951). The flower constancy behavior of most visitors to *S. carduacea* probably functions as a significant reproductive isolating mechanism for this species.

POLLINATION MECHANISMS IN *SALVIA DORRII* SSP. *DORRII*

Similar to *Salvia carduacea*, the flowers of *S. dorrii* display several characteristics favorable to cross-pollination by specialized insect visitors such as bees: the blue color, zygomorphy, depth of the corolla tube, expanded lower lip, unprotected ovary, location of the nectaries, sweet odor, the relationship between receptive stigma and anthers, and the protandrous floral development.

Branches of *Salvia dorrii* which were covered with mesh screen showed evidence of a complete lack of self-pollination. In more than 99% of the 1,300 covered ovaries, no seeds were produced. The small number of seeds

which did mature probably resulted from cross-pollination by wind through the screen or even apomixis. Self-pollination in *S. dorrii* is understandably prevented by the structural relationship between the anthers and the receptive stigma and the form of floral development, as well as possible self-incompatibility factors.

According to Axelrod (1960), the ancestors of our present North American desert plant species and their pollinators probably evolved during the Cretaceous period as a part of the Madro-Tertiary Geoflora. With the formation of the deserts, these plants and their contemporary pollinators could have existed in isolated masses as many of them do in places throughout their present ranges. Baker and Hurd (1968) point out that the massing of plants in almost pure populations, as found in *Salvia carduacea* and to a lesser extent in *S. dorrii*, allows the building up of bee populations that have an assurance of ample food supply for their adults and larvae. Many times, this relationship promotes a condition in which the bees become oligolectic (Hurd and Linsley, 1967; Michener, 1954; Linsley, *et al.*, 1963). Consequently, there is a retention of floral characteristics favoring insect visitation and cross-pollination, and a perpetuation of self-incompatibility factors. *Salvia carduacea* and *S. dorrii* have been seemingly subjected to such an evolutionary history.

POLLINATION MECHANISMS IN SALVIA COLUMBARIAE

In contrast with the other two *Salvia* species described in this study, *S. columbariae* displays a mechanism for self-pollination in addition to a floral structure and color which are favorable to insect visitation. The curling action of the style with its receptive stigma passing between the anthers accounts for the large percentage of seeds formed by the plants grown under mesh screens. Field observations showed that *S. columbariae* was visited most commonly by *Apis mellifera* and *Anthophora linsleyi*. However, the receptive stigma was found to be situated in a position favorable to bee pollination for only a short period of time after the stigma matured and before it curled over the upper lip. Examination of field plants revealed more than 90% having the style curled in this manner.

Being in part self-pollinated, the geographical distribution of this species does not become limited by the distribution of specific animal pollinators. This is consistent with the fact that *Salvia columbariae* has a wider distribution (Munz, 1959) than the other two species of *Salvia* which were nevertheless visited by three of the same insects. The introduction of *S. columbariae* into certain areas, especially at higher altitudes where insects would be less prevalent, is favored by its ability to self-pollinate. The relatively recent introduction and subsequent establishment of the honeybee as part of the *Salvia columbariae* environment, could have a pronounced effect on the future evolution of this species. Since *Apis mellifera* can occupy a wider range of habitats than native bees (Metcalf, *et al.*, 1962), it is conceivable that an increased potential for cross-pollination and subsequent genetic heterozygosity may be accomplished.

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