Acta Botánica Mexicana (1991), 13:75-83

FLORAL VISITORS AND THEIR BEHAVIOR TO SYMPATRIC *SALVIA* SPECIES (LAMIACEAE) IN MEXICO[1]

GREGG DIERINGER
Department of Botany, University of Texas at Austin,
Austin, Texas 78713, USA

T.P. RAMAMOORTHY AND PEDRO TENORIO LEZAMA
Instituto de Biología, Universidad Nacional Autónoma de México
Apartado Postal 70-233, Ciudad Universitaria,
Delegación Coyoacán, 04510 México, D.F. México

ABSTRACT

A field survey in southwestern Mexico was undertaken to locate and identify sympatrically flowering populations of *Salvia* and to characterize their visiting bee faunas. Twenty nine species of *Salvia* were observed and 33 species of bees collected. The most common bee visitors were *Bombus* species comprising 66% of the bee species collected. Of the 36 localities visited, 42% had sympatric, concurrently flowering *Salvia* species. As many as five flowering *Salvia* species may co-occur and share pollinating visits from the same bee species. Potential interactions between *Salvia* species and their pollinating bees are discussed.

RESUMEN

Se realizó un estudio de campo en el suroeste de México con el fin de localizar e identificar poblaciones simpátricas de *Salvia* en floración, y caracterizar a sus abejas visitantes. Se observaron 29 especies de *Salvia* y se colectaron 33 taxa de abejas. Las abejas visitantes más comunes fueron especies del género *Bombus*, comprendiendo 66% de los taxa de abejas colectados. De las 36 localidades visitadas, 42% contenían especies simpátricas de *Salvia* floreciendo al mismo tiempo. Se encontraron coexistiendo hasta 5 especies de *Salvia* y en algunas ocasiones recibiendo visitas de abejas polinizadoras pertenecientes a los mismos taxa. Se discuten las interacciones potenciales entre las especies de *Salvia* y sus abejas polinizadoras.

INTRODUCTION

The genus *Salvia*, although thought to have originated in the Mediterranean, has its greatest diversity in Mexico with approximately 300 species (Epling 1939, Ramamoorthy, unpublished). It is estimated that 88% of *Salvia* species are endemic to Mexico. Personal observations have indicated that there are numerous localities where several *Salvia* species cooccur and flower simultaneously. *Salvia* possesses what may be the most complicated pollination mechanism within the Lamiaceae in that the anthers contact a pollinator's dorsum via a fulcrum attachment of the filaments to the corolla (Fig. 1). Populations of sympatrically

[1] This study received support from a grant awarded by CONACYT of Mexico to T.P.R., project PCCBBNA 021142.

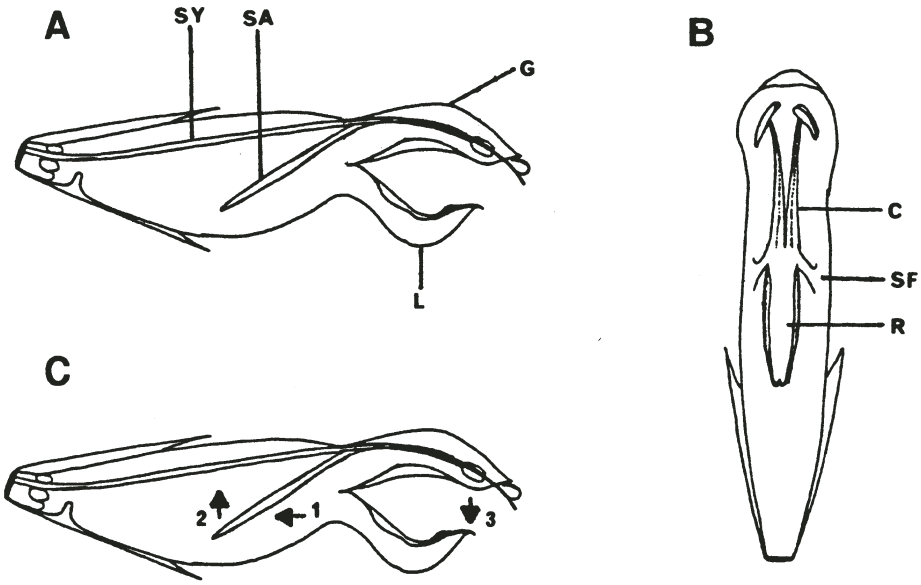

Fig. 1. Flower of *Salvia mexicana*. A. Side view depicting the stamen (SA), style (SY), galea (G), and lower lip (L). B. Longitudinal view illustrating the relative position and attachment of the staminal filament (SF), connective (C), and rudder (R) to one another. C. Pollen deposition onto a pollinating bee occurs when a bee's tongue is inserted into the flower contacting the rudder (1), pushing it upwards (2), and causing a concomitant downward movement of the connectives (3) on which the anther sacs are located. The anther sacs contact the bee's dorsum and deposit pollen.

flowering *Salvia* which share pollinators could provide material for studies of the pollination ecology of closely related, sympatric species. Therefore, our objective in this study was to document specific areas of sympatrically flowering *Salvia* and to identify the major visiting bees and their behavior.

MATERIALS AND METHODS

During the months of November and December 1985, a wide ranging field survey of southwestern Mexico was taken to locate and identify sympatric *Salvia* species and their flower-visiting bees. Thirty six localities in the states of Michoacan, Guerrero, Distrito Federal, Morelos, Puebla, and Oaxaca were visited. At each locality, voucher specimens

of *Salvia* were collected and deposited at MEXU and TEX (Appendix). Between 60-90 minutes were spent at each locality collecting bees which were visiting *Salvia* flowers. When 8-10 specimens of a particular bee species had been obtained, collection of that species was halted. If *Apis mellifera* was observed visiting these flowers, only one specimen per locality was collected. Our primary interest was in native bee species. Individual bee foraging movements were not recorded.

RESULTS

Salvia species were found in habitats ranging from dry scrub to montane forest, frequently at altitudes above 1000 meters. Habitats with greatest species diversity were those of pine-oak montane forest. A total of 29 *Salvia* species and 33 bee species were observed and collected. *Bombus* species were the most common bee visitors comprising 263 (66%) of the 396 bees captured on 24 of the 29 *Salvia* species studied (Tables 1,2). Other common bee genera included *Xylocopa, Deltoptila, Osmia,* and *Anthophora.*

Flowers of *Salvia* species vary in color from blue/purple to white/cream and red/pink (Table 2). Generally, blue-and white-flowered *Salvia* were visited, and presumably pollinated, by bees (based on observations of foraging behavior). All red-flowered *Salvia* were robbed of nectar by their visiting bees through perforations made at the base of the corolla. Red-flowered *Salvia* are probably hummingbird pollinated based on color, shape, and absence of any legitimately visiting bees.

Of the 31 observations of bees robbing flowers of nectar, 11 (36%) were of *Xylocopa* and 12 (39%) of *Bombus* (Table 2). Of 25 *Xylocopa* flower visits and 48 *Bombus* visits, 11 (44%) and 12 (25%) respectively, were visits where nectar was robbed through corolla perforations.

Areas of sympatric, concurrently flowering *Salvia* species were found to be fairly common especially in pine-oak montane forests. Of the 36 localities visited (Appendix), 15 (42%) had more than one species present. As many as five different *Salvia* species were observed flowering within a circle of approximately 100 meters in diameter. It was not uncommon to find the same *Bombus* species pollinating more than one *Salvia* species at a locality. For example, at Rosario, Michoacan, *S. gracilis, S. lavanduloides, S. mexicana, S. iodantha,* and *S. fulgens* co-occur and flower simultaneously. The former three species are blue-flowered while the latter two are red-flowered. Both *S. gracilis* and *S. lavanduloides* were pollinated by *Bombus ephippiatus.* At locality #34 (see Appendix), *B. diligens* was observed pollinating both *S. lavanduloides* and *S. inconspicua,* and at Ajusco, D.F., *B. nigrodorsalis montezumae* pollinated *S. lavanduloides* and *S. polystachya.*

The following data also provide some insight into the floral color preferences and nectar robbing behavior of *Bombus* within *Salvia* communities. Of the 258 worker and male bumblebees recorded -5 queens were also collected-, 12 male bumblebees pollinated 2 white-flowered *Salvia*, no workers were observed on white-flowered *Salvia*. Four red-flowered *Salvia* were robbed by approximately equal proportions of male (14 or 44%) and worker (19 or 56%) bumblebees. Eighteen blue-flowered *Salvia* were pollinated predominately by workers (140 or 65%).

Table 1. Bees visiting *Salvia* species in Mexico.

Name of Species	Number Collected
Colletidae	
1. *Caupolicana (Zikanapis) elegans*	1
2. *Colletes* sp.	2
Halictidae	
3. *Caenaugochlora ctenaugochlora*	1
4. *Pseudaugochloropsis graminea*	5
Megachilidae	
5. *Anthidium (Anthidium)* sp.	2
6. *A. (Melanthidium) carri*	3
7. *Chalicodoma (Chelostomoides)* sp.	2
8. *C. (Cressoniella)* sp.	1
9. *Osmia (Diceratosmia)* sp.	11
Anthophoridae	
10. *Anthophora californica*	1
11. *A. capistrata*	6
12. *A. montana*	1
13. *Deltoptila elefas*	30
14. *D. aurolentocaudata*	2
15. *Exomalopisis (Phanomalopsis) binotata*	1
16. *Melissodes* sp.	1
17. *Thygater (Thygater) rubricata*	1
18. *Xenoglossodes* sp.	4
19. *Xylocopa (Neoxylocopa)* sp.	1
20. *X. (Notoxylocopa) guatemalensis*	9
21. *X. (Xylocopoides) cyanea*	1
22. *X. tabaniformis azteca*	19
23. *X. tabaniformis melanosoma*	11
24. *X. tabaniformis tabaniformis*	7
Apidae	
25. *Apis mellifera*	9
26. *Bombus diligens*	38
27. *B. ephippiatus formosus*	100
28. *B. medius*	15
29. *B. nigrodorsalis montezumae*	87
30. *B. pennsylvanicus pennsylvanicus*	2
31. *B. steindachneri*	15
32. *B. trinominatus*	6
33. *Psithyrus* sp.	1
Total	396

Table 2. *Salvia* species with their visiting bee species corresponding to Table 1.

Blue/Purple-Flowered *Salvia*

S. anastomosans -29* (1)
S. breviflora -7* (1)
S. fluviatilis -5*, 6*, 11* 15*, 31* (1)
S. fruticulosa -7*, 9*, 25*, 29* (1)
S. gracilis -27*, 13* (1)
S. helianthemifolia -27* (1)
S. inconspicua -2*, 4*, 6*, 9*, 19*, 20*, 22*, 24*, 26*, 29*, 31* (4)
S. keerlii -9*, 11*, 18*, 25*, 29* (1)
S. lavanduloides -3*, 22*, 25*, 26*, 27*, 29*, 31*, 32*, 33* (7)
S. longifolia -12*, 23, 25*, 26*, 29* (1)
S. longispicata -27*, 29* (1)
S. mexicana -13*, 20, 27, 29 (5)
S. mocinoi -22* (1)
S. pannosa -13*, 27*, 29* (1)
S. polystachya -1*, 2*, 9*, 11*, 13*, 14*, 22*, 23*, 25*, 26*, 27*, 28*, 29*, 30* (7)
S. rhyacophila -22*, 26*, 27*, 29* (1)
S. rubiginosa -4*, 28* (1)
S. sapinaea -27* (1)
S. semiatrata -4, 10, 20, 22, 23, 26, 27*, 29 (2)
S. thymoides -5*, 22*, 23*, 25*, 27* (1)
S. thyrsiflora -8*, 20*, 21*, 27*, 30* (1)

White/Cream-Flowered *Salvia*

S. albiflora -27* (1)
S. tenoriana -11*, 23*, 29* (1)

Red/Pink-Flowered *Salvia*

S. cinnabarina -20, 25, 26, 27, 29 (3)
S. elegans -17, 22, 27, 29 (1)
S. iodantha -13, 22, 27 (1)
S. lasiantha -16, 25 (1)
S. longistyla -24 (1)
S. purpurea -22, 24, 25, 27, 29 (3)

*signifies the bee species as a potential pollinator; those lacking an asterisk were observed robbing the flower through corolla perforations. Parentheses indicate the number of localities observed.

DISCUSSION

Most blue- and white-flowered *Salvia* species seem to be able to utilize any species of *Bombus* as a pollinator. The requirements for pollination are a strong animal visitor with only a short to moderate tongue length. These conditions are easily met by most bumblebee species, and *Bombus* seems to participate in robbing behavior less frequently than *Xylocopa*..

One case of possible monophily was observed. Populations of *Salvia mexicana* were observed at five different localities in three different states plus the Distrito Federal. In every

case, the only pollinating bee was *Deltoptila elefas,* which has a very long tongue that corresponds to the long corolla tube of this species.

There is some evidence that bumblebees forage indiscriminately between plant species of similar appearance (Macior, 1970; Thomson, 1981). Therefore, areas of sympatric, concurrently flowering *Salvia* species generate questions regarding pollinator fidelity and the possible transfer of pollen between different *Salvia* species. If indiscriminate foraging by bees were to occur between sympatric, concurrently flowering *Salvia* species, excessive pollen waste and/or reduced seed set could be expected (Campbell, 1985; Waser, 1978).

However, since sympatric, concurrently flowering *Salvia* are common, it seems unlikely that significant pollen and/or seed loss is occurring within these assemblages. There are a number of possible explanations to account for this: 1) individual bees do not forage indiscriminately; 2) *Salvia* species are so diverse that they are morphologically different enough, by chance, to avoid the effects of indiscriminate bee foraging; or 3) selection eliminates those species which are morphologically similar and affected by indiscriminate bee foraging.

Male and worker bumblebees robbed the nectar of red-flowered *Salvia* in equal proportion. It was expected that males would be observed in greater proportion than workers on red-flowered species since males forage only for nectar while workers forage for both nectar and pollen. *Bombus* workers were observed in greater proportion than males on blue-flowered *Salvia* which probably is in relation to collecting pollen. The association of white-flowered *Salvia* with only male *Bombus* is most likely a result of small sample size.

The effect of nectar robbing on the reproductive success of co-occurring *Salvia* would also be of interest. Most red-flowered *Salvia* co-occurring with blue-flowered *Salvia* were being robbed of nectar by bumblebees. Red-flowered *Salvia*, therefore, provide and added food resource for bees that were also pollinating blue-flowered *Salvia*. Does the association of red-flowered with blue-flowered *Salvia* detract or augment the visitation by bumblebees to blue-flowered *Salvia*? Clearly, further detailed observations and experiments are needed to understand the complex relationships of sympatric, concurrently flowering *Salvia* presented here.

ACKNOWLEDGEMENTS

We would like to thank Beryl Simpson, John Neff, and Leticia Cabrera R. for reviewing earlier drafts of the manuscript. *Salvia* species were identified by T.P. Ramamoorthy. All bee species except the Anthophorini were identified by Dr. John L. Neff. Anthophorini were identified by Dr. Robert W. Brooks. Katie Bear drew the ilustration of *Salvia mexicana.*

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APPENDIX

Localities and collection numbers of *Salvia* species in this study. Vouchers located at MEXU and TEX

Michoacan:
1.- Mil Cumbres
S. fulgens (Ramamoorthy et al. 4831+); S. inconspicua (Ramamoorthy et al. 4826); S. iodantha (Ramamoorthy et al. 4825); S. mexicana (Ramamoorthy et al. 4823); S. mocinoi (Ramamoorthy et al. 4830); S. purpurea (Ramamoorthy et al. 4827)
2.- 3.7 km SW of Rosario
S. helianthemifolia (Ramamoorthy et al. 4832)
3.- 8 km SW of Rosario
S. fulgens (Ramamoorthy et al. 4841+); S. gracilis (Ramamoorthy et al. 4839); S. iodantha (Ramamoorthy et al. 4837); S. lavanduloides (Ramamoorthy et al. 4838); S. mexicana (Ramamoorthy et al. 4840)

Guerrero:

4.- 15.7 km N of Iguala
S. fluviatilis (Ramamoorthy et al. 4802)
5.- 6 km W of deviation to Chichihualco from Mexico/Acapulco road
S. breviflora (Ramamoorthy et al. 4803)
6.- 5.2 km after turn to Filo de Caballo from road to Chichihualco
S. inconspicua (Ramamoooorthy et al. 4804)
7.- 9.7 km N of Ayotla
Salvia species *(Ramamoorthy et al. 4807)*
8.- 11.4 km of Ayotla
S. polystachya, no voucher
9.- 5 km W of Filo de Caballo
S. cinnabarina (Ramamoorthy et al. 4821); S. mocinoi (Ramamoorthy et al. 4822); S. polystachya (Ramamoorthy et al. 4817)
10.- 1.2 km E of Chilapachaca
S. rhyacophila (Ramamoorthy et al. 4822A)
11.- 16 km E of Chilapa
S. lavanduloides (Ramamoorthy et al. 4822B)
12.- 2 km NW of El Balcon
S. longistyla (Ramamoorthy et al. 4842)
13.- 10.3 km NW of El Balcon
S. lavanduloides (Ramamoorthy et al. 4845); S. thyrsiflora (Ramamoorthy et al. 4846)

14.- 5.5 km NE of Nueva Delhi
S. sapinaea (Ramamoorthy et al. 4849)

Distrito Federal:

15.- Ajusco, entrance to Tlalpuente, off old road to Cuernavaca
S. lavanduloides (Ramamoorthy & Dieringer 4758); S. mexicana (Ramamoorthy & Dieringer 4759, 4760); S. microphylla, no voucher+; *S. polystachya (Ramamoorthy & Dieringer 4761)*

Morelos:

16.- 11 km after the turn to Cuernavaca from Ocuilan
S. iodantha (Ramamoorthy et al. 4763); S. lavanduloides (Ramamoorthy et al. 4764); S. mexicana (Ramamoorthy et al. 4762); S. polystachya (Ramamoorthy et al. 4766)
17.- Cuernavaca, near road exiting to Ocuilan
S. purpurea (Ramamoorthy et al. 4769)
18.- 4 km SW of Tres Marias
S. polystachya (Ramamoorthy & Dieringer s. n.)

Puebla:

19.- 14 km from Teotepec
S. tenoriana, Ramamoorthy ined. *(Tenorio & Dieringer 10648)*
20.- 0.5 km S of San Miguel
S. longispicata (Ramamoorthy et al. 4795)
21.- Tatexea, Sierra Norte de Puebla, 12 km N of San Isidro
S. albiflora (Ramamoorthy et al. 4797)
22.- 5 km W of Zapotitlan
S. rubiginosa (Ramamoorthy et al. 4798)
23.- 6 km W of Ahuacatlan
S. polystachya (Ramamoorthy et al. 4800)

Oaxaca:

24.- 5 km after Tamazulapan on road to Chilapa from Tamazulapan
S. anastomosans (Ramamoorthy et al. 4773); S. lasiantha (Ramamoorthy et al. 4770); S. polystachya (Ramamoorthy et al. 4771); S. semiatrata (Ramamoorthy et al. 4772)
25.- Cerro Pericon, NW of San Pedro de Nopala
S. pannosa (Ramamoorthy et al. 4777); S. purpurea (Ramamoorthy et al. 4779)
26.- Teposcolula
S. fruticulosa (Ramamoorthy et al. 4783); S. keerlii (Ramamoorthy et al. 4782); S. semiatrata (Ramamoorthy et al. 4784); S. thymoides (Ramamoorthy et al. 4785)
27.- 24 km S of Yolomecatl
S. inconspicua (Ramamoorthy et al. 4790); S. cinnabarina (Ramamoorthy et al. 4791); S. longifolia (Ramamoorthy et al. 4792)
28.- 8 km SE of Chocani
S. thymoides (Ramamoorthy et al. 4781)
29.- Huajuapan
S. lasiantha (Tenorio & Dieringer s.n.)

30.- Cerro Verde, near Huautla
S. mexicana (Tenorio & Dieringer 10691); S. polystachya (Tenorio & Dieringer 10680*); S. purpurea (Tenorio & Dieringer 10686*)*
31.- Cerro Adoracion, E of Huautla
S. elegans (Tenorio & Dieringer 10692); S. lavanduloides (Tenorio & Dieringer 10693*)*
32.- 93.8 km S along MEX 175 from Tuxtepec to Oaxaca
S. longispicata (Tenorio & Dieringer 10703)*
33.- 143.3 km S of Tuxtepec on MEX 175
Salvia species (red flowers) *(Tenorio & Dieringer 10704*)*
34.- 157.3 km S of Tuxtepec on MEX 175
S. inconspicua (Tenorio & Dieringer 10706); S. lavanduloides (Tenorio & Dieringer 10711*)*
35.- 12 km S of Tuixtla
S. inconspicua (Tenorio & Dieringer 10712); S. semiatrata (Tenorio & Dieringer 10713*)*
36.- 10 km S of Piedra Larga, towards Puerto Escondido
S. lavanduloides (Tenorio & Dieringer 10730); S. nicolsonii* Ramamoorthy ined. *(Tenorio & Dieringer 10731*+)*

+no bees observed

*located at MEXU only