1966

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Recommended Citation

Grant, Verne and Grant, Karen A. (1966) "Records of Hummingbird Pollination in the Western American Flora: I. Some California Plant Species," *Aliso: A Journal of Systematic and Floristic Botany*: Vol. 6: Iss. 2, Article 5.

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RECORDS OF HUMMINGBIRD POLLINATION IN THE WESTERN AMERICAN FLORA

I. SOME CALIFORNIA PLANT SPECIES¹

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The mutual relationships between various plant species and hummingbirds in western North America, in respect to flower feeding and pollination, pose many interesting problems of evolutionary significance. Some of these problems are currently being investigated by the authors. It is desirable as a first step in such studies to present the factual evidence regarding the role of hummingbirds in pollination in the western American flora.

There is no adequate comprehensive body of evidence in print on the subject of hummingbird pollination in the western American flora. The present paper is the first of a series in which we plan to publish pollination records based on adequate field observations. This first paper lists some California plant species which have been studied by ourselves and/or by other workers.

METHODS

We have made observations in natural populations of various plant species. Each population studied has been observed over long periods of time in order to determine what animals feed on the flowers and how they do so. As the activities of pollinators vary with time of day and with early, peak, or late period of bloom, the observations are best carried out at different times of day and different periods of the blooming season.

The observed visitors to the flowers must next be assessed as to their importance in the role of pollinator. Pollination is effected only when the animal visitor carries pollen on its body and transfers the pollen to the receptive stigmas of the flowers. The visits of an animal to a specific flower may not effect pollination at all, or may do so regularly, or only accidentally. Adaptations of plant species to particular pollinating agents, then, can not be determined by observation of visitors alone, but additional information regarding the correspondence between the body parts of the feeding visitor and the essential organs of the flower is required.

¹This project is supported by research grant GB 3620 from the National Science Foundation.

Hummingbirds may be seen to visit the flowers of a wide array of plant species. In some cases, the hummingbird may merely visit the flowers to catch insects, whereas in others nectar may be sought. Further, such visits may be either incidental or regular. Specialization of a plant species for pollination by hummingbirds can be inferred only from the finding of good structural and behavioral correlations between flower and bird.

The data which we have collected in the field on hummingbird-pollinated species include observations of the behavior and feeding habits of the hummingbirds; measurements of the flowers relevant to the pollinator such as location and depth of nectar, length and diameter of corolla tube or spurs, length and relative positions of stamens and stigma; and notes on flower color and odors. Observation through field glasses and/or photographs of the hummingbirds while feeding usually reveals whether pollen adheres to the birds' bill or to feathers of its head, chin, or breast. In some cases we have found it necessary to insert the bill of a hummingbird specimen into the fresh flower to determine whether a feeding bird contacts the essential organs.

Although the foregoing requirements for the satisfactory determination of mode of pollination are simple and obvious, they have often been ignored in the past. Many references in the botanical and ornithological literature to flowers visited by hummingbirds are inadequate from the standpoint of pollination ecology in one way or another. The plant species involved are frequently identified only vaguely; the observations are rarely tied to any particular natural plant population, and may even have been made in a garden; and information as to whether the feeding visits bring about pollination is often lacking. Particularly worthless are uncritical lists of flowers visited by birds, such as those assembled by Pickens (1931, 1936, 1941, 1955, etc.), and casual notes made during the course of other (i.e., taxonomic) studies have little value.

In compiling a first list of California plant species pollinated by hummingbirds, we have therefore included only selected cases from the older literature. We have utilized observations recorded by several ornithologists (Dawson, 1923; Bent, 1940; Grinnell and Miller, 1944), and by several students of flower pollination (Nobs, 1954; Straw, 1956; Davis, 1956; Sprague, 1962; Beeks, 1962; Raven, 1963). However, we have relied mainly on our own field studies, initiated by one of us (V.G.) in 1949 and continued as a joint project since 1960.

In the list which follows, the pollination records are set off typographically under each plant species. These records are those of the present authors unless stated otherwise. The previously published observations of other workers are included along with our own in the summary statement under each plant species.

The hummingbirds, particularly the females, were often unidentified as to species. Where identified, they are listed by their common names in the following account. Their scientific names are given for reference here. Allen hummingbird (*Selasphorus sasin*); Anna hummingbird (*Calypte anna*); Black-chinned hummingbird (*Archilochus alexandri*); Calliope hummingbird (*Stellula calliope*); Costa hummingbird (*Calypte costae*); Rufous hummingbird (*Selasphorus rufus*).

POLLINATION RECORDS

CARYOPHYLLACEAE

1. *SILENE LACINIATA*

A perennial herb occurring in the foothills of coastal southern California, *Silene laciniata* bears red flowers with a long tube and a broad corolla limb of laciniately dissected lobes. The anthers and stigma are situated above the greenish entrance to the floral tube.

Wooded canyon in the foothills of the San Gabriel Mts., north of Claremont, Los Angeles Co., July 10, 1951, and repeatedly in subsequent summers. Hummingbirds were observed visiting the flowers. Insect visits to the flowers are rare or lacking and it seems likely that this population of the species, at least, is pollinated entirely by hummingbirds.

RANUNCULACEAE

2. *AQUILEGIA FORMOSA*

This widespread columbine occurs in moist woods in the mountains of California. The flowers hang down with the five red nectar-bearing spurs turned up vertically. The spreading yellow petal blades surround the central stamen column. Hummingbirds are the most regular visitors to the flowers and are the normal pollinators, although visits by pollen-collecting bumblebees also lead to pollination (cf. Grant, 1952). Swallowtail butterflies also visit the flowers and possibly bring about some pollination.

Echo Lake, El Dorado Co., July 20, 1949. Hummingbirds were visiting the flowers. The birds probe the spurs for nectar from a hovering position beneath the flowers, contacting stamens and stigma on either the chin and throat or the back of the head, depending on whether the bird is oriented ventrally or dorsally with respect to the stamen column. The birds were observed to fly directly from the *Aquilegia* to nearby clumps of *Delphinium scopulorum* and back to the *Aquilegia*, making pollinating visits on both species.

Harvey Monroe Hall Natural Area, east of Tioga Pass, Mono Co., Aug. 20, 1950. Rufous hummingbirds were observed visiting the flowers of *A. formosa* and its intermediates with *A. pubescens*, slashing off the spurs of the latter species. A pollen collecting bumblebee was also visiting *A. formosa*.

Tahquitz Valley, San Jacinto Mts., Riverside Co., July, 1951. An unidentified hummingbird was probing the flowers of *A. formosa*.

Icehouse Canyon, San Gabriel Mts., Los Angeles Co., Sept. 13, 1958. Hummingbirds were systematically visiting the flowers. Same locality, July 21, 1963. An Anna hummingbird was feeding on the flowers, and a bumblebee was collecting pollen. Same locality, Sept. 9, 1965. Unidentified hummingbirds were seen visiting the flowers regularly.

Glacier Lodge, Big Pine Creek, Inyo Co., July 13, 1964. Calliope hummingbirds and unidentified hummingbirds were regular and frequent flower visitors. Swallowtail butterflies clung to the stamen column while attempting to reach the nectar, and some pollination may be effected in this way. Bumblebees were collecting pollen.

3. *DELPHINIUM CARDINALE*

(Fig. 1)

The red and yellow flowers of *D. cardinale*, a late spring-blooming perennial of coastal southern California, are borne on tall flower stalks 3–6 feet above the ground. The single red nectar-containing spur is 2.0–2.4 cm long and is oriented in a more or less horizontal position. The upper pair of petals are yellow, standing at the entrance to the spur. The stamens and carpels

stand below the entrance to the spur. Dawson (1923) reports that *D. cardinale* is one of the favorite nectar sources of Black-chinned hummingbirds.

San Antonio wash, north of Claremont, Los Angeles Co., July 9, 1951. Hummingbirds were visiting the flowers, probing the spur for nectar from a hovering position in front of the flower. The birds contact the stamens and stigma with their chin. No insects were observed to visit the flowers.

Flat east of Rancho Santa Ana Botanic Garden, Claremont, Los Angeles Co., June 6 to July 5, 1965. A population was observed several hours a day throughout the peak of its blooming season. Many hummingbirds were present in the area of this plant population. The Costa hummingbird was most abundant, although several adult male Allen hummingbirds were also seen. The hummingbirds fed nearly exclusively on the *Delphinium* flowers through the period of observation. *Salvia apiana* and *Penstemon spectabilis* also occurred in the area; their flowers are visited by hummingbirds in other areas where *D. cardinale* is absent, but were not being visited by the birds here. No insects were ever observed to visit the *Delphinium* flowers. It thus appears that hummingbirds are the sole visitors and pollinators of *D. cardinale*.

CRASSULACEAE

4. DUDLEYA CYMOSA MINOR

This species grows in dry rocky places in the mountains of southern California. The petals are bright pinkish-red or yellow, erect, and form a tube about 1 cm long through close pressure. The stamens and styles are included in the narrow false tube.

Cow Canyon, San Gabriel Mts., Los Angeles Co., June 10, 1959. Hummingbirds were feeding on the flowers, the tips of their bills fitting into the floral tube and contacting the essential organs. The pollen adheres to the bills.

5. DUDLEYA LANCEOLATA

San Antonio wash, Claremont, Los Angeles Co., June 6, 26, 1965. Hummingbirds were visiting and apparently transferring pollen, although additional observations are needed to confirm the latter point.

SAXIFRAGACEAE

6. RIBES SPECIOSUM

This tall shrub of coastal southern California produces long arching branches bearing racemes of brilliant red flowers which are pendant on long flexible pedicels. Sepals and petals are appressed to form a tube 1 cm long containing nectar in the upper (basal) part. Stamens and stigma hang 1.5 cm below the distal end of the perianth. That *Ribes speciosum* is abundantly visited by hummingbirds is apparent from the following quotation from Dawson (1923, p. 941): "A catalogue of Anna's favorite flowers would be nearly equivalent to a botany of southern California. But if one had to choose *the* favorite it would probably be *Ribes speciosum*, our handsome red flowering gooseberry, for it is upon the abundance of this flower that Anna relies for her early nesting."

Canyon in Torrey Pines State Park, San Diego Co., Calif., March 31, 1959. An unidentified female hummingbird, probably an Anna, was feeding on the flowers from a hovering position beneath the flowers, probing the perianth for nectar. The pendant anthers and stigma contact the base of the bill or head of the feeding bird.

7. *RIBES SANGUINEUM*

This related species of *Ribes* in the mountains of northern California is similarly visited in great abundance by the Rufous hummingbird according to Bent (1940, p. 397). Further investigation is needed to determine how it is pollinated.

FOUQUIERIACEAE

8. *FOUQUIERIA SPLENDENS*

This species occurring on desert mesas in southern California blooms in the early spring. Abundant flowers are produced in dense one-sided racemes at the tips of the long erect branches. The corollas are red, tubular, and secrete nectar at the base of the 2 cm long corolla tube. Stamens, with abundant yellow pollen, and stigma are exerted 6–12 mm above the orifice. *Fouquieria splendens* is regularly visited and pollinated by hummingbirds.

Desert wash west of Colorado River, south of Needles, San Bernardino Co., April 9, 1953. Unidentified hummingbirds were regularly visiting the flowers; the yellow pollen of *F. splendens* adheres to the feathers of the bird's head and breast.

Borrego Valley, San Diego Co., Calif., March 29, 1957. Unidentified hummingbirds were feeding on the flowers.

Mecca Hills, Riverside Co., March 7, 1959. Unidentified hummingbirds were feeding on the flowers. Same locality, March 25, 1963. A male Costa hummingbird, unidentified females (probably Costas), and a male Rufous hummingbird were feeding on the flowers. A finch was also visiting the flowers and apparently getting nectar.

Little Fargo Canyon, east of Indio, Riverside Co., Calif., April 12, 1965. A male Rufous hummingbird and unidentified females were visiting the flowers. Nearby, in an area with no *F. splendens* plants, a male Costa was feeding on *Hyptis emoryi*.

Joshua Tree National Monument, Riverside Co., Calif., May 7, 1965. An unidentified female hummingbird was seen flying among the plants of *F. splendens*, but was apparently unable to feed in a very strong wind.

ONARGACEAE

9. *ZAUSCHNERIA LATIFOLIA*

This species has a wide distribution in the higher mountains of California. The showy flowers with red calyx and corolla are tubular and contain nectar at the base of the 2.2 cm long tube. The flowers are abundantly visited and pollinated by hummingbirds in the later summer and early autumn.

Icehouse Canyon, San Gabriel Mts., Los Angeles Co., July 13, 1951, and Sept. 13, 1958. Hummingbirds were feeding on and pollinating the flowers. *Xylocopa* visits the flowers illegitimately by piercing the calyx tube and sucking the nectar without effecting pollination.

Upper San Antonio Canyon, San Gabriel Mts., Los Angeles Co., Aug. 21, 26, and Sept. 1, 1964, and Sept. 8–23, 1965. Allen, Anna, and probably Rufous hummingbirds were feeding on the flowers. In late summer and early fall, *Z. latifolia* is the predominant plant species at higher elevations in the San Gabriel Mts. on which hummingbirds feed. At this time, several different species of hummingbirds may be observed in the area. Each hummingbird seems to have one or several perches in or near a small patch of *Z. latifolia*, and each may be seen to chase intruder hummingbirds from its guarded patch of flowers.

Fig. 1. Left: Costa (?) hummingbird feeding on *Delphinium cardinale*, in wash near Claremont, California. Center: Anna (?) hummingbird on *Mimulus cardinalis*, in San Gabriel Mts. Right: Hummingbird on *Trichostema lanatum*, in Rancho Santa Ana Botanic Garden.

10. *ZAUSCHNERIA CALIFORNICA*

This plant of rocky hillsides and cliffs of coastal California bears brilliant red flowers.

Stanford, Santa Clara Co., November, 1949. Hummingbirds were observed visiting and pollinating the flowers; honeybees also visited the flowers.

ERICACEAE

11. *ARCTOSTAPHYLOS PARRYANA PINETORUM*

In the early spring the manzanitas blossom out with clusters of short-tubed pink or white flowers. Being early bloomers, they attract hummingbirds which have few or no other sources of nectar so early in the year. We have seen Anna hummingbirds probing the flowers of *A. parryana pinetorum* in the San Gabriel Mts. when snow covered the ground. Some pollination may be effected by the hummingbirds, as the tip of their bills probably contacts the stamens and stigma as they probe into the floral tube.

Cow Canyon, San Gabriel Mts., Los Angeles Co., spring, 1959 and subsequent years. Anna hummingbirds visited the flowers regularly.

12. *ARCTOSTAPHYLOS GLAUCA EREMICOLA*

In the pinyon zone above Pioneertown, Riverside Co., Feb. 28, 1959. A hummingbird (probably a Black-chin) was seen probing the clustered flowers from a hovering position. Pollen is probably carried on the tip of the bird's bill.

POLEMONIACEAE

13. *GILIA SPLENDENS*

The race of this species which occurs in the higher parts of the San Bernardino Mts. of southern California has brilliant pink flowers with long stout corolla tubes. These flowers are visited and pollinated by hummingbirds (Grant & Grant, 1965, p. 69 ff.).

14. *IPOMOPSIS AGGREGATA*

(Fig. 3)

A summer-blooming species of the mountains, *I. aggregata* has a widespread distribution in western North America. The red long-tubed flowers are borne horizontally in long panicles. Hummingbirds are the normal pollinators, although insects sometimes visit and pollinate the flowers. We have seen Rufous and Calliope hummingbirds pollinating the flowers in five populations in the Sierra Nevada, and Broadtailed hummingbirds (*Selasphorus platycercus*) pollinating them in six populations in the Colorado Rockies. (See Grant & Grant, 1965, pp. 77 ff. for details.)

LABIATAE

15. *SALVIA SPATHACEA*

This spring-blooming perennial herb of coastal southern California produces whorls of dark red, tubular flowers containing much nectar at the base of the

Fig. 2. Top: Male Costa hummingbird feeding on *Beloperone californica*, in Joshua Tree National Monument, California. Bottom: Hummingbird on *Lilium humboldtii*, in Rancho Santa Ana Botanic Garden.

Fig. 3. *Ipomopsis aggregata* and Rufous hummingbird. Life size. (From *Flower Pollination in the Phlox Family*, by V. Grant and K. A. Grant, Columbia University Press, New York, 1965, with the permission of the publisher.)

tube. Two stamens and the style are exerted beyond the orifice. The association of the flowers with hummingbirds is reflected in the common name, Hummingbird sage. Dawson 1923, p. 929) and Bent (1940, p. 415) have recorded that Allen hummingbirds are visitors and pollinators of this species. We also have observed visitations in the following locality.

Casmalia hills, Santa Barbara Co., June 7, 1963. A hummingbird was probing the flowers for nectar and bringing about pollination.

16. *TRICHOSTEMA LANATUM*

(Fig. 1)

This mint, a leafy shrub occurring in the chaparral of the southern California Coast Ranges, bears numerous blue flowers in long spikes covered with dense pink to purple wool. The corollas are typically labiate in conformation; but the extremely long stamens and stigma are much exerted from the corolla tube. In the Rancho Santa Ana Botanic Garden in Claremont, a patch of flowering *T. lanatum* is much fought over by the hummingbirds. Photographs of hummingbirds feeding on the flowers clearly reveal the stamens and stigma brushing the top of the feeding hummingbird's head. The blue pollen of *T. lanatum* can be seen as a bright blue patch on the heads of hummingbirds regularly probing the flowers for nectar. Thus pollination is effected by the visits of hummingbirds. We have not yet observed this species in its natural habitat. However, Grinnell and Miller (1944, p. 220) report that *Trichostema* (presumably *T. lanatum*) is much sought after by the Anna hummingbird in nature. Additional field observations are needed for this very interesting hummingbird-pollinated species.

SCROPHULARIACEAE

CASTILLEJA

The genus *Castilleja* is widespread in California where it is represented by numerous species. These mostly perennial herbs bear spikes of usually inconspicuously-colored tubular corollas and brightly-colored (red, sometimes yellow) calyces and bracts. Hummingbirds probe the long corolla tubes for nectar. Bill or head pollination occurs or is inferred from observed relative position of the bird's head and bill and the essential floral organs. Records of hummingbird pollination have been obtained for the following species.

17. *C. APPLEGATEI*

Near summit of Snow Mountain, Colusa-Lake Co. line, July 25, 1956. Larry Heckard (pers. comm.). An unidentified hummingbird was observed making pollinating visits to many of the *Castilleja* plants.

18. *C. BREWERI*

Mammoth Lakes area, Mono Co., July 17, 1965. Calliope and unidentified hummingbirds were abundantly visiting *C. breweri* as well as *Penstemon newberryi* in an area above Lake George where both species grew intermixed.

19. *C. FOLIOLOSA*

Cow Canyon, San Gabriel Mts., Los Angeles Co., May 12, 1963. An unidentified female hummingbird visited the flowers of *C. foliolosa* every 10-15 minutes, flying to and from its nest in some bushes about 200 feet away.

20. *C. LINARIAEFOLIA*

Mammoth Lakes, Mono Co., July 17–20, 1965. Female hummingbirds, probably Calliope and Rufous, were visiting the flowers in several plant populations.

21. *C. MARTINII*

Barrett Canyon fireroad, San Gabriel Mts., Los Angeles Co., April 2, 1961. Unidentified hummingbirds were feeding on the flowers. In the early season of the year when few flowers which hummingbirds visit are in bloom, the hummingbirds regularly visit the *Castilleja*; but at the height of the blooming period in the general flora these *Castillejas* are visited relatively infrequently by hummingbirds. Thus the pollination of *C. martinii* in this area mostly occurs before other competing flower species begin to bloom.

22. *C. MINIATA*

Echo Lake, El Dorado Co., July 26, 1949. L. H. Day (pers comm.). Unidentified hummingbirds were observed feeding on the flowers.

Munson Meadows, Crater Lake National Park, Oregon, Aug. 7, 1956. Larry Heckard (pers. comm.). An unidentified hummingbird was observed feeding on flower after flower in a population.

Above Glacier Lodge, Big Pine Creek, Inyo Co., July 15, 1964. Many individual plants grow intermixed with *Ipomopsis aggregata*. Although the *Ipomopsis* flowers contained no visible nectar, the *Castilleja* flowers had abundant nectar. During the observation period (2½ hours), hummingbirds (Calliope and Rufous) were regular and frequent visitors to the *Castilleja* flowers, but did not attempt to feed on the *Ipomopsis* flowers.

23. *C. STENANTHA*

San Jacinto Mts., Riverside Co., July 1951. An unidentified hummingbird was observed to visit a columbine flower, *Lilium parryi*, *Castilleja stenantha*, a closed *Oenothera hookeri* flower, and then flew back to the *Castillejas* to feed on them for awhile, intermittently visiting the flowers of a *Dudleya*. In its visits to *C. stenantha*, pollen adheres to the top of the bird's head.

24. *MIMULUS CARDINALIS*

(Fig. 1)

This perennial herb grows along mountain streams and in moist places at middle elevations throughout most of California. The flowers are borne on pedicels on herbaceous stems about 2 feet above the ground. The long tubular, bright orange-red corollas are oriented more or less horizontally. Exserted stamens and stigma stand above the entrance to the corolla tube. Hummingbirds regularly visit the flowers and in probing the corolla tubes for nectar contact the essential organs with the top of their heads, as noted by Nobs (1954) and by ourselves in the following station.

San Antonio Canyon, San Gabriel Mts., Los Angeles Co., July 13, 1951. Hummingbirds were systematically visiting the flowers, the *Mimulus* pollen being visible on the top of their heads. Same locality, Aug. 4–12, 1964. Several hummingbirds (probably the Anna) had perches in trees above the population of *M. cardinalis*, and regularly and exclusively visited these flowers for nectar. Swallowtail butterflies were observed to cling to the corollas in an attempt to get nectar; however, their visits effected pollination only accidentally. Also ineffectual as a pollinator, but a very frequent visitor, was *Xylocopa*. These large bees systematically went from flower to flower, settling down on the corolla tube and piercing it to obtain the nectar. Same locality, summer 1965. The above observations were repeated.

25. *DIPLACUS PUNICEUS*

A spring-blooming perennial of dry hillsides in coastal southern California, this species bears bright red flowers with a narrow tube and expanded throat. Hummingbirds are the normal pollinators of *D. puniceus*, as recorded by Beeks (1962) and by ourselves at the following station.

Ortega Summit, Santa Ana Mts., Riverside Co., June 1, 1955. Hummingbirds were feeding on the flowers and contacting the essential organs with their heads.

26. *DIPLACUS AURANTIACUS*

This species grows on dry hills and canyon sides in the Coast Ranges and Sierra Nevada foothills. The flowers have a shape similar to that of *D. puniceus* but are salmon-colored. Hummingbirds are reported to be the principal pollinators of this species (Beeks, 1962). The long-tongued fly, *Eulonchus smaragdinus*, also visits and pollinates the flowers. Additional field observations are needed to determine the relative importance of these two pollinating agents.

Hillside above Casmalia, Santa Barbara Co., June 6, 1963. A large population of *D. aurantiacus* which covered an entire hillside was observed for pollinators. A hummingbird (probably a female Anna) was seen to feed on the flowers. But the most numerous and frequent visitors of the flowers were cyrtid flies, *Eulonchus smaragdinus*. This fly crawls into the throat of the *Diplacus* flower and probes the corolla tube for nectar with its extremely long proboscis. One specimen captured after visiting a flower had a thick covering of the *Diplacus* pollen on its dorsal thorax and abdomen.

27. *DIPLACUS LONGIFLORUS*

This common species of the chaparral zone in southern California has long-tubed orange flowers. Beeks (1962) and we have observed both hummingbirds and *Eulonchus smaragdinus* visiting and pollinating the flowers. The relative importance of the two agents in pollination remains to be determined.

Cobal Canyon, San Gabriel Mts., Los Angeles Co., March 31, 1954. Costa hummingbirds nesting in nearby brush were visiting the flowers.

Evey Canyon, San Gabriel Mts., Los Angeles Co., June 4-5, 1964. A population in full bloom was observed in the early morning on successive days. On both mornings *Eulonchus smaragdinus* was actively flying about the plants and feeding on the flowers, but neither hummingbirds nor other insects were seen to make floral visits.

28. *GALVEZIA SPECIOSA*

This spring-blooming shrub occurs on Santa Catalina, San Clemente, and Guadalupe Islands. The trumpet-shaped red flowers are borne on slender pedicels in a nearly horizontal position. Nectar is secreted at the base of the long (1.6-1.7 cm) floral tube. Stamens and stigma are included within the corolla tube. Hummingbirds hover before the flowers, probing for nectar and contacting the essential organs with their bill or chin. Raven (1963) has observed hummingbird visits on San Clemente Island and we on Santa Catalina.

Whites Landing, Santa Catalina Island, May 3, 1953. An unidentified hummingbird was feeding on the flowers off and on throughout the day. A large bumblebee also visited the flowers, reaching the nectar with some difficulty, but contacting the essential organs with its head. *Galvezia speciosa* can thus be pollinated by bees, although hummingbirds are probably the principal pollinators.

San Clemente Island, July 11, 1962. Hummingbirds were actively visiting the flowers (Raven, 1963).

29. *PEDICULARIS DENSIFLORA*

A low perennial herb growing on wooded hillsides of the Coast Ranges, the Sierra Nevada, and the San Gabriel and San Bernardino Mts., *P. densiflora* bears racemes of bright red tubular flowers. Pollination of this and related *Pedicularis* species in California has been studied by Sprague (1962), who reports hummingbirds as the normal pollinators of *P. densiflora*. Four species of hummingbirds (the Anna, Allen, Rufous, and Black-chin) visit and pollinate the flowers, carrying pollen on the feathers at the base of the bill or on the crown of the head (Sprague, 1962).

PENSTEMON

Penstemon is a large genus with many species distributed in California. A number of these species bear long tubular flowers of bright red or pinkish-red colors. Hummingbird pollination has been recorded for several of these red-flowered species and is expected for others on the basis of the similar floral form.

30. *P. BRIDGESII*

A widespread species occurring on talus or rock outcrops of the higher mountains of California, *P. bridgesii* produces racemes of bright red flowers in mid-and late-summer. The pendant flowers are tubular-funnelform, bearing nectar at the base of the 3.0–3.5 cm long corolla tube. Stamens and style are situated just under the tip of the upper lip. Hummingbirds are the normal visitors and pollinators of this species.

Above Glacier Lodge, Big Pine Creek, Inyo Co., July 10, 1964. Rufous hummingbirds and unidentified hummingbirds (probably female Calliope) were probing the flowers for nectar at frequent intervals. The yellowish white pollen adheres to the upper part of the bill.

31. *P. CENTRANTHIFOLIUS*

Penstemon centranthifolius occurs at lower elevations in coastal southern California and on the desert borders. This spring-blooming species bears erect racemes of bright red tubular flowers. Hummingbird pollination of *P. centranthifolius* is recorded by Straw (1956 a, b) who reports it especially visited by Costa and Anna hummingbirds. We have made similar observations in the stations listed below.

Cajon Pass, San Bernardino Co., April 16, 1961. Black-chinned hummingbirds were visiting the flowers.

Jacumba, San Diego Co., May 6, 1965. An unidentified female hummingbird was flying from plant to plant, probing the flowers for nectar.

32. *P. CLEVELANDII*

This species, occurring in the chaparral of eastern San Diego Co., bears long tubular-funnelform flowers of a bright magenta color. Straw (1956 a) states,

"There is relatively little information available concerning the pollination of *Penstemon clevelandii* on a quantitative basis, but it is visited and pollinated by both solitary bees (Anthophoridae) and hummingbirds."

33. *P. LABROSUS*

A summer-blooming species occurring in chaparral and forest at moderate elevations in the mountains of southern California, *P. labrosus* bears long tubular red flowers.

Idyllwild, San Jacinto Mts., Riverside Co., July 1951. An unidentified hummingbird was observed visiting and pollinating the flowers.

34. *P. NEWBERRYI*

This montane species grows on rocky ledges and cliffs in the higher mountains of northern California where it blooms in mid and late summer. Hummingbirds are the principal visitors and pollinators of this species, although bees may also be occasionally seen feeding on the flowers and effecting some pollination. The feeding hummingbirds contact the essential floral organs with the upper part of their bills as they probe for nectar.

Echo Lake, El Dorado Co., July, 1946. Hummingbirds were observed feeding on the flowers.

Slate Creek Valley, near Tioga Pass, Mono Co., Aug. 28, Sept. 1, 1956. Hummingbirds and bumblebees were both visiting and pollinating the flowers.

Above Lake George, Mammoth Lakes, Mono Co., July 18-24, 1965. Numerous hummingbirds fed on the flowers throughout the daylight hours. The identified hummingbird species included the Rufous, the Allen, and the Calliope. In this area, *P. newberryi* was the predominant species visited by hummingbirds at elevations above 9000 feet.

Devil's Postpile National Monument, Madera Co., July 26, 1965. Unidentified hummingbirds were observed visiting the flowers.

35. *P. TERNATUS*

This shrubs of the higher mountains of southern California bears long tubular scarlet flowers on long arching branches. Hummingbirds visit and pollinate the flowers.

Idyllwild, San Jacinto Mts., Riverside Co., July, 1951. Unidentified hummingbirds were probing the flowers.

North slope of Sunset Peak above Cow Canyon, San Gabriel Mts., Los Angeles Co., Aug. 3, 1958. Hummingbirds were actively feeding on the flowers.

San Antonio Wash, east of Claremont, Los Angeles Co., June 6, 1965. An unidentified hummingbird probed the flowers of *Delphinium cardinale*, then flew to a bush of *P. ternatus* and probed flower after flower, returning to the *Delphinium* to feed again on it.

ACANTHACEAE

36. *BELOPERONE CALIFORNICA*

(Fig. 2)

Beloperone californica grows along watercourses in the Colorado Desert of California. In the early spring, dark red tubular flowers are borne at the tips of the numerous leafless branches of this desert shrub. The 3 cm long corollas contain much nectar. Hummingbirds pollinate these flowers, contacting the included stamens and stigma with the top of their heads as they probe for

nectar. Jaeger (1940, p. 245) reports that "Linnetts and Gambel sparrows bite off and eat the nectar-filled flower bases. Black-chinned hummingbirds probe the blossoms for both insects and nectar."

Open desert plains between Palm Desert and the San Jacinto Mts., Riverside Co., May 19, 1953. Black-chinned hummingbirds were feeding on and pollinating the *Beloperone* flowers. Honeybees were also observed to visit the flowers, perhaps effecting pollination.

Palm Canyon, near Palm Springs, Riverside Co., March 11, 1963. Costa hummingbirds were visiting the flowers. Same locality, April 24, 1964. Numerous hummingbirds (probably the Black-chin), were observed flying about the population of *B. californica* scattered along a watercourse, feeding on the flowers at midday and again in the mid afternoon. Honeybees were also visiting the flowers.

Mecca Hills, Riverside Co., March 23, 1965. Adult male Rufous hummingbirds and some female birds, presumably also Rufous, were visiting the *Beloperone* flowers.

Joshua Tree National Monument, south of Cottonwood Pass, Riverside Co., March 23, 24, 1965. Eight or ten *Beloperone* plants were in full bloom along the roadside in a very dry year. Four or more hummingbirds maintained perches in the *Beloperone* bushes and regularly probed the flowers for nectar. Other hummingbirds flew in from time to time to feed on the flowers. The identified birds included male Costa hummingbirds (these were most abundant), and a male Rufous. A female bird was probably a Costa. Same locality, May 7, 1965. The same bushes still bore abundant flowers, although they were past their peak of bloom. Only one female hummingbird was feeding on the flowers at this time.

LILIACEAE

37. LILIUM PARVUM

The plants grow in moist places in the high mountains. The flowers are large, solitary, erect, funnellform, and orange with purple dots. Hummingbirds pollinate this species to some extent at least, though further records are desirable.

Slate Creek Valley, near Tioga Pass, Mono Co., Aug. 27-29, 1956. A female hummingbird was visiting the flowers regularly, contacting anthers and stigma with its bill and face. The bird fed on the flowers at frequent intervals through the day and returned daily. Bees also visit the flowers and may effect some pollination. Butterflies in the area were not attracted to the lily flowers.

38. LILIUM HUMBOLDTII

(Fig. 2)

This summer-blooming lily occurs in woods and chaparral of the Sierra Nevada and cismontane southern California. The large, showy, orange-red flowers, spotted with maroon or purple, are pendant, the recurved perianth segments revealing the long stamens and stigma. Both swallowtail butterflies and hummingbirds visit and pollinate the flowers. The similar observations of Davis (1956) and ourselves are combined below.

Cobal Canyon, San Gabriel Mts., Los Angeles Co., July 9-10, 1951, and June 29, 1958. Swallowtail butterflies were visiting the flowers, contacting the drooping stamens and stigma with their wings.

Cobal, Palmer, and Evey Canyons, San Gabriel Mts., Los Angeles Co., summer 1956. Both Swallowtail butterflies and hummingbirds were making regular pollinating visits (Davis, 1956).

Canyon on road to Doane Valley, Palomar Mt., San Diego Co., July 23, 1951. During an afternoon of observation no butterfly visits to the flowers took place,

but the flowers were visited by hummingbirds, and pollination was brought about by the bird's belly brushing against the anthers and stigma as it hovered before the flowers.

SUMMARY

Hummingbird pollination is established by field observations for 38 species belonging to 12 families in the California flora. In the case of some of these plants (i.e., *Diplacus aurantiacus*), hummingbirds share the role of pollinator with an insect agent, and further study is needed to determine the relative importance of the different types of animal visitors in pollination. Other plant species listed (*Delphinium cardinale*, *Fouquieria splendens*, etc.) are pollinated mainly or solely by hummingbirds.

Those plant species in the California flora which are pollinated more or less exclusively by hummingbirds are usually bright red, long-tubed, trumpet-shaped, and borne on long flexible pedicels, as has long been recognized. It is of interest to note in addition that flowers fitted for hummingbird pollination have evolved, not only by elongation of the floral tube, but also through elongation of stamens and stigma, as in the case of *Ribes speciosum* and *Trichostema lanatum*.

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