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HAWKMOTH POLLINATION IN THE GENUS *OENOTHERA*^{1,2}

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POLLINATION OF SPECIES IN OTHER SUBGENERA OF *OENOTHERA*

Species in several other subgenera were studied during the spring of 1959 and 1960. Each species was observed from one to several times, but if several observations were made, they were at different colonies, no one colony studied over a long period as with *O. hookeri*. In this chapter the species involved will be taken up by subgenus and the observations summarized and compared (Fig. 1).

THE SPECIES AND COLONIES

Salpingia.—Two species of this subgenus were studied, *Oenothera greggii* at two localities and *Oenothera bartwegii* at three. These colonies all grew along the road, on rolling mesquite desert at the lower elevations (Fig. 10) and on grassy plains at the higher elevations. The localities and dates were the following:

Oenothera bartwegii

- (1) near Fort Davis, Jeff Davis County, Texas, at 5000 feet, on 9 May, 1959
- (2) in Ector County, Texas, at 2800 feet, on 10 June, 1960
- (3) south of Monahans, Ward County, Texas, at 2600 feet, on 12 May, 1959

Oenothera greggii

- (4) west of the Chiricahua National Monument, Cochise County, Arizona, at 4000 feet, on 2 June, 1960
- (5) east of Sanderson, Terrell County, Texas, at 2800 feet, on 24 May, 1959.

The plants of both species are low, shrubby perennials with few to many stems growing from a woody base (Fig. 10). The colonies studied contained from 25 to over 100 scattered plants, each bearing from 10 to 100 fresh flowers per night. The largest colony was the one near Monahans of which more than half is shown in Fig. 10. At most of the localities, colonies such as the ones studied were growing at intervals of several hundred yards to several miles along the road, so that each colony was usually part of a larger population.

The temperature during the observations was usually warm. The high wind which is so characteristic of western Texas was the most noticeable difference from the conditions prevailing at colonies of *O. hookeri*. On two occasions, at Sanderson, Texas, and in Arizona, the sky was heavily overcast.

¹Part of a doctoral dissertation prepared at the Rancho Santa Ana Botanic Garden and the Claremont Graduate School, Claremont, California.

²See *Aliso* 5(3): 357-384, 1963 for the first section of this paper.

Pachylophis.—One species, *Oenothera caespitosa*, was studied at six localities and another, *Oenothera primiveris*, was observed briefly during study of a colony of *O. deltooides* ssp. *ambigua* in Nevada. All colonies of *O. caespitosa* grew in rocky soil, usually on the road shoulder but sometimes also in canyon bottoms, washes or rocky slopes away from the road. They grew in upper desert communities through the pinyon-juniper zone and into heavy pine forests (the two colonies north of the Grand Canyon). The localities and dates for *O. caespitosa* were the following:

Oenothera caespitosa var. *marginata*

- (1) between Harrisburg Flats and Wild Rose Station in the Panamint Mountains, Inyo County, California, at 5000 feet, on 10 May, 1960
- (2) along the road up Kyle Canyon in the Charleston Mountains, Clark County, Nevada, from 3000 to 8000 feet, on 6 May, 1960
- (3) east of Jacob Lake, Coconino County, Arizona, at 7500 feet, on 22 June, 1960
- (4) at Point Sublime on the north rim of the Grand Canyon, Coconino County, Arizona, at 7400 feet, on 20 June, 1960
- (5) along the road into Mesa Verde National Park, Montezuma County, Colorado, at 7500 feet, on 15 June, 1960

Oenothera caespitosa var. *longiflora*

- (6) west of Westgard Pass, Inyo County, California, at 6000 feet, on 6 May, 1960

Plants of *O. caespitosa* are caespitose perennials which bear from one to several flowers each night (Fig. 11c). A population of this species is usually made up of several small colonies growing at intervals down a canyon or wash. The total number of flowers in such a population is much less than in most other species of *Oenothera*.

Environmental conditions at lower altitudes were similar to those encountered at the colonies of *O. bookeri*. At higher altitudes the temperature at night was somewhat lower. The high winds of the low desert were rarely encountered at the colonies of *O. caespitosa*.

Anogra.—Five species of this subgenus were studied, *O. deltooides*, *O. wigginsii*, *O. californica*, *O. runcinata* and *O. engelmannii*. The colonies of *O. deltooides* were all in open, sandy desert with scattered individuals of *Larrea* and other small shrubs and annuals, except for the colony in the palm grove. Localities and dates of observation for this species were the following:

Oenothera deltooides ssp. *deltooides*

- (1) across the highway from Thousand Palms, Riverside County, California, on 19 March, 1960
- (2) in a date palm grove near Palm Desert, Riverside County, California, at 230 feet, on 6 April, 1960
- (3) near Essex, San Bernardino County, California, at 2000 feet, on 12 April, 1960
- (4) 21 miles east of Twenty-Nine Palms, San Bernardino County, California, at 2000 feet, on 29 April, 1960.

Oenothera deltooides ssp. *ambigua*

- (5) several miles west of the Valley of Fire, Clark County, Nevada, at 1500 feet, on 3 May, 1960

All of the colonies were large with several hundred plants spread over a wide area. Plants of the subspecies studied are erect annuals, usually branching from the base and varying in size depending on conditions, in a good year reaching two feet in height. Depending on number of branches and size, a plant will bear up to 20 flowers per evening. The location and extent of population of this species vary greatly with rainfall. In a good year

there may be many very large populations as well as small ones, while in a bad year there may be very few populations of any size.

The colonies of *O. wigginsii* were all growing in shifting sand with many small shrubs and annuals. Three colonies were studied, one in 1960 and two in 1962.

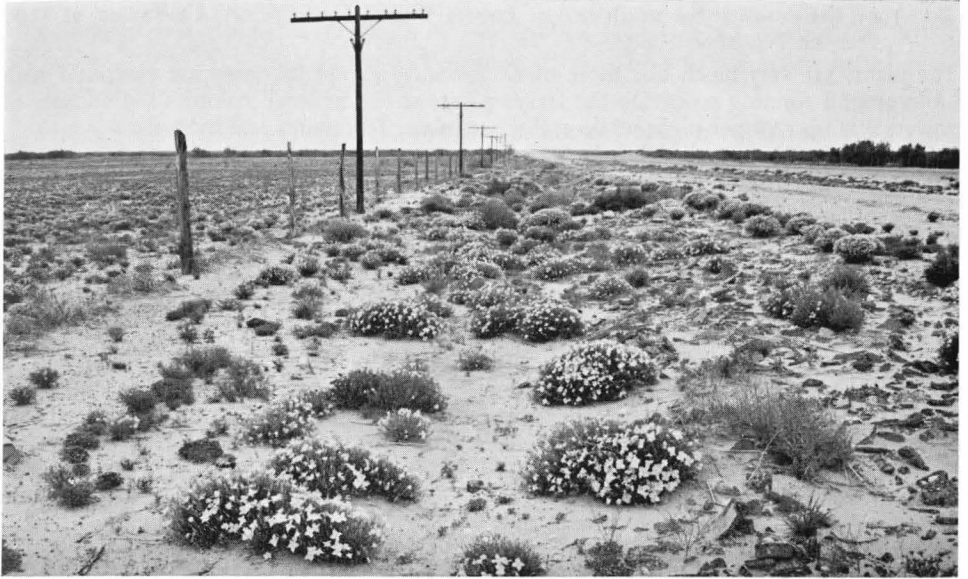


Fig. 10. The habitat of *Oenothera bartwegii* in western Texas, just south of Monahans, Ward County.

Oenothera wigginsii

- (1) on the dunes bordering San Quintín Bay just south of the cannery, Baja California, Mexico, on 7 March, 1960
- (2) on dunes behind Pabellon Beach about 7 miles south of San Quintín and in a sandy area near the road 13 miles south of San Quintín, on 30–31 March, 1962

These colonies were composed of several hundred small scattered plants. In habit the plants were similar to *O. deltooides* var. *typica* but were generally smaller with up to 5 flowers per night.

The three colonies of *O. californica* studied grew in three quite different situations (A few plants of *O. californica* ssp. *arizonica* were watched for a very short period at Bouse, Arizona, on 18 April, 1959 [Fig. 13f]). The one at Cima was in a juniper-pinyon area along the road shoulder and in the nearby wash. The Jean colony was at the roadside in an area very similar to those in which *O. deltooides* was observed. On the dunes in Eureka Valley the plants grow in pure, shifting sand; the dunes are surrounded by sparse *Larrea* desert. The first two colonies were quite large while the third was smaller, numbering about 100 plants in several small groups and one larger group. The localities of the three populations follow:

Oenothera californica ssp. *avita*

- (1) 11 miles southeast of Cima, San Bernardino County, California, at approximately 5000 feet, on 1 May, 1960
- (2) near Jean, Clark County, Nevada, at 2000 feet, on 2 May, 1960

Oenothera californica ssp. *eurekaensis*

- (3) on the dunes at the south end of Eureka Valley, Inyo County, California, at 3100 feet, on 7-8 May, 1960

The plants are very much like those of *O. deltoides* except that they are perennial with underground running roots. On the larger plants at the first two colonies the number of flowers was near 20 per night while at the last colony few plants had more than five.

Two species were studied less intensively, each at one locality.

Oenothera runcinata

A single colony of this species was studied briefly 5 miles west of Las Cruces, Dona Ana County, New Mexico, on 4 May, 1959. The colony was in a wide wash off the highway in *Larrea* desert and covered an area with a diameter of about 100 yards. The plants were freely branching, bushy perennials with from only a few to over 100 flowers per night.

Oenothera engelmannii

One aberrant colony of this species was studied at Big Spring, Howard County, Texas, at 2500 feet, on 9 June, 1961. This colony was growing with *O. laciniata* var. *grandiflora* in red sandy clay along a dirt road and at the edge of a fallow field on rolling hills. There were about 75 plants of *O. engelmannii*, most of the plants bearing many abnormally small and late-opening flowers.

All of the species of the subgenus *Anogra* studied during this work grew in desert or near desert environments, the evening temperatures being generally warm but colder at the high desert localities especially early in the season. The most distinctive environmental factor was the strong wind that was commonly encountered during the evening at these localities.

Raimannia.—Three species of this subgenus were studied, each of them at a single location.

Oenothera albicaulis

A colony of about 100 plants was studied 4 miles west of Alpine, Brewster County, Texas, at 4500 feet, on 21 May, 1959. The plants grew near the highway in this area of rangeland with scattered junipers. The plants were low, branching annuals similar to plants of *O. deltoides* in habit and bearing from 5 to 25 flowers per night.

Oenothera laciniata var. *grandiflora*

This was the same locality near Big Spring, Texas, at which *O. engelmannii* was studied on 9 June, 1960. The plants are erect, branching annuals with up to 25 flowers each night on large plants. Only 15 plants grew in this small colony with the more prevalent *O. engelmannii*.

Oenothera drummondii

The colony was a very large one of several hundred plants half a mile from the ferry to Port Aransas, San Patricio County, Texas; the date of observation was 7 June, 1960. The plants grow with low shrubs on the sandy flats along the bays in back of the barrier beach. The plants are large, usually full shrubs, the larger plants bearing several hundred flowers each night when in full bloom. The night spent at this colony was a balmy one with a slight breeze.

Lavauxia.—One species, *O. taraxacoides*, was observed at one locality near Cloudcroft

in the Sacramento Mountains, Otero County, New Mexico, on 12 June, 1960, at 8000 feet in the pine-fir-poplar forest. There were about 50 scattered plants in the colony which grew in the black loam of grassy openings along the road and on the stoney road cuts. The plants were caespitose perennials bearing from 1 to 3 open flowers each night and were similar in habit to *O. caespitosa*. The nights are quite cold at this elevation.

Gauropsis.—A colony of *O. havardii* was studied by Verne Grant north of Rodeo, Hidalgo County, New Mexico, on 4 September, 1961. The nearly stemless tufted plants grew on alkali flats in the open desert.

Megapterium.—Three plants of *O. brachycarpa* var. *wrightii* were observed near Charleston Park in the Charleston Mountains, Clark County, Nevada, at 7800 feet on 27 June, 1960. This very small colony grew in a rocky clearing in the pine-fir-poplar forest. The plants are caespitose perennials with one or two open flowers per night and like the preceding species are similar in habitat to *O. caespitosa*. *Oenothera longissima* and *O. caespitosa* var. *marginata* were also blooming nearby but were not studied.

Size and structure of *Oenothera* populations in the species listed above fall into three main types. The montane species have very small colonies or groups of plants scattered at intervals, with each canyon in an area supporting such a series of colonies. Examples of this pattern of distribution are found in *O. caespitosa*, *O. taraxacoides* and *O. brachycarpa*. These species are all perennial and have fewer flowers per plant and thus far fewer flowers per population than most of the annual desert species.

A second type of structure is that of populations which fluctuate greatly in size depending on amount of rain and other factors. If the colonies are small they tend to be widely scattered but at maximum size the population would be nearly continuous over large areas. *Oenothera deltooides*, *O. albicaulis* and *O. wigginsii* are representative of this group of species. These species are annuals with a large number of flowers per plant; these are usually plants of deserts or arid plains.

The third type of population structure includes a series of species which fall somewhere between the two extremes just described. They tend to be distributed in fairly large colonies which are often quite isolated but sometimes scattered at intervals over a wide area. *Oenothera greggii*, *O. bartwegii* and *O. drummondii* have this type of population structure and are perennial, the plants usually large with many flowers per season. *Oenothera bookeri* is also of this type but is annual or biennial, again with many flowers per plant.

FLORAL MORPHOLOGY

The seven subgenera of *Oenothera* considered here can be divided into four groups as to floral morphology. The flowers of the species in the subgenera *Anogra* (Fig. 11d) and *Raimannia* are generally similar in size, shape and relation of parts to those in subgenus *Oenothera* (*O. bookeri*). The flowers of the species in *Lavauxia* and *Megapterium* are generally similar to those in *Oenothera* but are larger, usually with a much longer hypanthium with a wider orifice. In *Gauropsis* the flowers resemble those in *Megapterium* but are much smaller. In the species of *Pachylophus* (Fig. 11b) the aspect of the flower is quite different from that of the above species. The flower is nearly actinomorphic and the hypanthium is very variable in length as well as much wider at the top. In *Salpingia* the flowers are regular and smaller than the species of *Pachylophus* but have the same relatively wide hypanthial orifice. The stigma is discoid in *Salpingia* whereas it is four-lobed in all of the other subgenera reported on here. All of the species studied show the general characteristics of crepuscular anthesis, comparatively long hypanthium with nectar at its

base, yellow or white petals, guide-lines formed by ridged corolla lobes, distinctive usually agreeable odor, and exerted stamens and style, the pollen connected by viscin threads.

At nearly all of the colonies studied anthesis occurred from one hour before to one hour after sunset. The flowers of *O. bartwegii* and *O. greggii* started to open at least one hour before sunset except at Fort Davis where anthesis started only 15 minutes before the sun went down. At these colonies, with the one exception, all of the flowers were open while the sun was still above the horizon. In *O. drummondii* anthesis started 30 minutes before sunset, while in *O. albicaulis* it started 15 minutes after sunset. The five colonies of *O. deltooides* showed nearly the same range of variation in time of first opening as *O. bookeri*, discussed previously. The time in these colonies varied from one half hour before sunset to one half hour after sunset. The time in *O. californica* was much closer to sunset at all three colonies. Anthesis in *O. caespitosa* was consistently later, occurring from just after to nearly one hour after sundown. In *O. taraxacoides* the time was soon after the sun had set. In all cases the flowers had at least started to open before full darkness. From 20 to 30 minutes elapsed in all the species between the opening of the first and last flowers.

The mechanics of opening were never very different from those described previously for *Oenothera bookeri*. After the flowers are open, the position of the flower and relative position of its parts are nearly the same in *O. bookeri* and all other species except *O. greggii*, *O. bartwegii* and *O. caespitosa*. One minor exception is important. In *O. drummondii* and *O. wigginsii* the style is not exerted beyond the stamens as far as it is in the other species, and in the latter it is just beyond the anther tips (Fig. 11e).

In *O. caespitosa* the flower is actinomorphic but often appears zygomorphic, for when the flower is not vertical the stamens often curve slightly toward the upper corolla lobe (Fig. 11b). The style is usually oriented just outside the ring of stamens with the stigma below the level of the stamens and at least one centimeter beyond them. In *O. bartwegii* and *O. greggii* (Fig. 11a) the flowers are actinomorphic, the stamens are never oriented toward one side and the stigma is usually only slightly off vertical although it sometimes does hang outside the ring of anthers. In some colonies exertion of the stigma varied from 1 to 2 mm to a cm beyond the anther tips. Comparison of the figures should make the basic differences clear.

The hypanthium is different in the several types in shape, internal pubescence and extremes of length. The basic differences as compared to the situation in *O. bookeri* described earlier are the following. In the flowers similar to *O. bookeri* the hypanthium has the same shape and dimensions and nearly the same variation in length (Table 7), but the internal pubescence varies. In *O. deltooides* and *O. californica* the whole hypanthium is lined with minute hairs, no long hairs like those in *O. bookeri* being present. In both of these species the hypanthium is about 2.5 mm wide at the orifice, narrowing to 1.0 mm wide one centimeter below the orifice and maintaining this width to the base where the nectar occurs. In the flower of *O. californica* there is an angle in the tube of about 20° one centimeter below the top. In the flower of *O. drummondii* hypanthial width is the same but between one centimeter below the orifice and one centimeter above the nectary the tube is lined with fairly long downward-pointing hairs. The base of the tube is lined with

Fig. 11. Flowers of four species of *Oenothera*, d taken shortly after dark, the other four in the morning.—a. *Oenothera bartwegii*, note the position of the stigma in the different flowers.—b. *Oenothera caespitosa* var. *marginata*.—c. *Oenothera caespitosa* var. *longiflora* showing the habit of the plant and the hypanthium.—d. *Oenothera deltooides* ssp. *deltooides*.—e. *Oenothera wigginsii* showing how close the stigma lobes are to the anthers and the strands of pollen between anthers and stigma. The flower has not been visited.

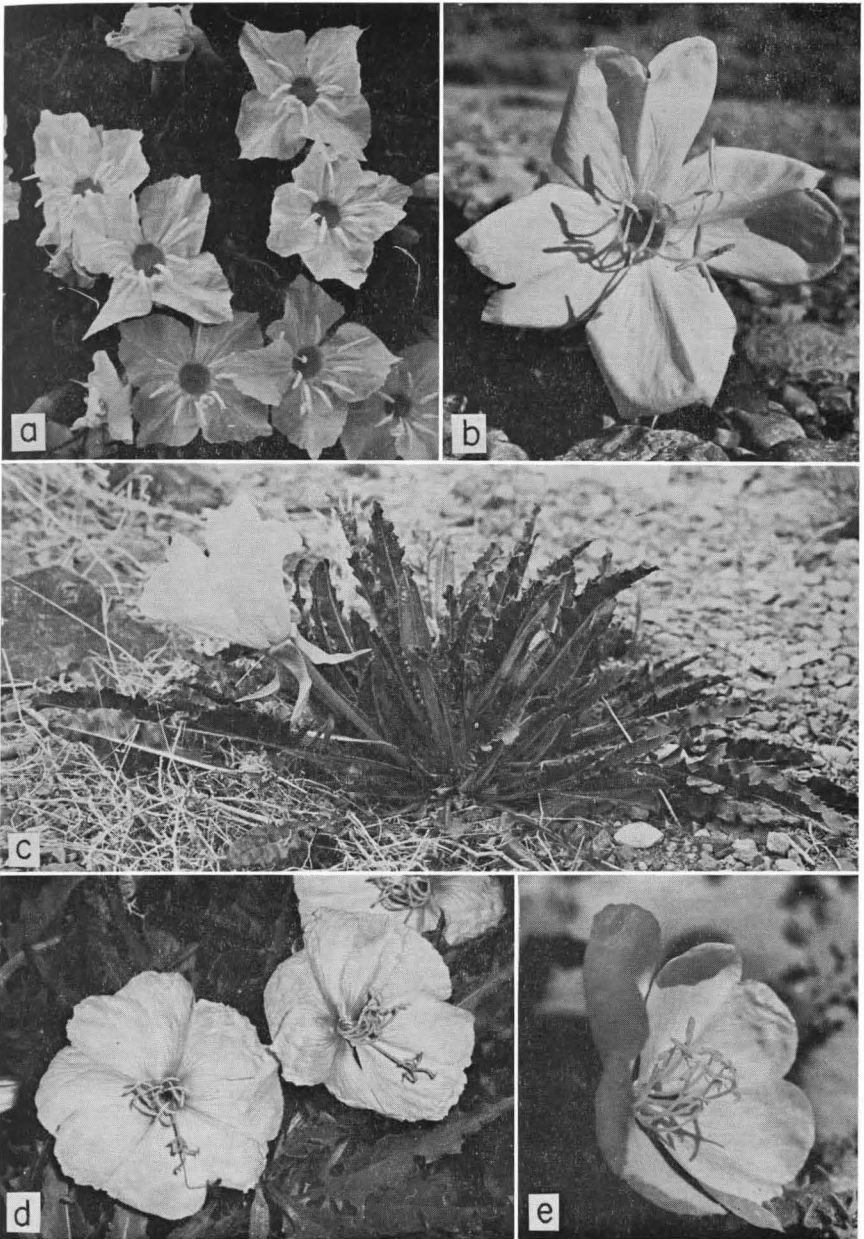


FIGURE 11

very short hairs and the upper portion is glabrous. In these three species the average nectar level is one centimeter above the base at anthesis. The style narrows perceptibly at about the same level, perhaps being a factor in controlling nectar rise. None of the species discussed here have pubescence on the style as in *O. hookeri*.

The hypanthium of *O. caespitosa* is slightly narrower in width than in the above species but starts to widen about 3 cm below the orifice and is usually about 8 mm wide at the top. In *O. taraxacoides* the hypanthium is similar but the tube starts to widen nearer the orifice and never gets quite as wide. The inner wall of the hypanthium is glabrous in both of these species. In them the style also narrows perceptibly near the middle of the hypanthium at nearly the level of nectar at anthesis. Nectar level is often considerably higher in the tubes of these species than in the flowers of the species with shorter tubes. The hypanthia of the flowers in *O. greggii* and *O. hartwegii* increase gradually in width from about 1 mm at the base to 6 mm at the orifice and are glabrous within. The style is uniform in width. Nectar level averages between 1.0 and 1.5 cm from the bottom of the tube.

The odor given off by the flowers varies greatly in intensity and in quality. The odor of *O. deltooides* and *O. californica* is like lemon juice but is far more intense in the first species. In *O. hartwegii* the odor is pleasant but very weak to the human nose. *Oenothera caespitosa* has a very slight, sharp, rubbery odor while *O. taraxacoides* has a sharp, bitter odor of about the same intensity.

The flowers of the species observed are either white or yellow. In the subgenera *Salpingia* and *Lavauxia* the flowers are bright yellow, while in *Megapterium* they are paler yellow. In *Anogra* all of the species have white flowers. In *Pachylophis*, *O. caespitosa* has white flowers and *O. primiveris* has yellow ones, while in *Raimannia*, *O. albicaulis* has white flowers and *O. drummondii* and *O. laciniata* have bright yellow ones. All of the flowers have green or yellow-green areas at the base of the corolla lobes and in the upper hypanthium.

In Table 7 the average and range of length of the hypanthium is given for each colony studied intensively. In *O. caespitosa*, *O. taraxacoides* and *O. brachycarpa* variation in length is extreme both within and between colonies.

THE SPECTRUM OF VISITORS TO THE FLOWERS AND THE POLLINATING AGENTS

As already outlined in the corresponding section under *Oenothera hookeri*, the primary methods used to determine the spectrum of visitors and their relative abundance at a given colony were direct observation of the flowers and captures at the light-trap which was usually run for one hour during the early evening. Many of the insects given in the list of visitors for *O. hookeri* were encountered again at other species, especially some of the hawkmoths.

The animals responsible for pollination, and the relative importance of each species if more than one was involved, were determined using the methods already described for *Oenothera hookeri*. At most of the colonies studied 50 or rarely 25 flowers were emasculated and tagged. This series or a random series of the same number of unemasculated flowers was checked during the evening and more critically the next morning. These data are given for all of the colonies where they were obtained in Table 11. Direct observation of animals visiting the flowers in the evening and the next morning was correlated with the data from these checks in determining pollinating agents and their relative importance.

The colonies of each species studied are discussed by subgenera giving (a) the spectrum of visitors to the flowers and their relative abundance and (b) the pollinating agents.

TABLE 7. Length of hypanthium in centimeters for each colony.

COLONY	NO. OF FLOWERS MEASURED	AVERAGE	EXTREMES
SALPINGIA			
<i>Oenothera bartwegii</i>			
Fort Davis, Jeff Davis Co., Texas	7	3.8	3.6- 4.0
Ector County, Texas	10	4.5	3.8- 4.9
Monahans, Ward Co., Texas	19	3.4	1.5- 3.7
<i>Oenothera greggii</i>			
Chiricahua Nat. Mon., Cochise Co., Arizona	13	4.0	2.7- 4.5
Sanderson, Terrell Co., Texas	5	3.3	2.8- 3.7
PACHYLOPHIS			
<i>Oenothera caespitosa</i> var. <i>marginata</i> and <i>Oenothera caespitosa</i> var. <i>longiflora</i>			
Harrisburg Flats, Inyo Co., California	10	7.9	6.5- 9.3
Kyle Canyon, Clark Co., Nevada	7	7.2	4.5-10.7
Jacob Lake, Coconino Co., Arizona	10	10.2	8.1-15.3
Mesa Verde, Montezuma Co., Colorado	2	8.4	7.3- 9.5
Westgard Pass, Inyo Co., California	2	10.3	10.2-10.5
<i>Oenothera caespitosa</i> var. <i>caespitosa</i>			
Gros Ventre, Teton Co., Wyoming*	12	5.5	3.9- 6.7
<i>Oenothera primiveris</i>			
Valley of Fire, Clark Co., Nevada		5.0	
ANOGRA			
<i>Oenothera deltooides</i>			
Thousand Palms, Riverside Co., California	7	3.4	2.9- 3.7
Palm Desert, Riverside Co., California	10	3.4	2.5- 3.8
Essex, San Bernardino Co., California	4	2.6	2.4- 2.7
29 Palms, San Bernardino Co., California	8	3.1	2.9- 3.3
Valley of Fire, Clark Co., Nevada	9	2.8	2.5- 3.3
<i>Oenothera californica</i>			
Cima, San Bernardino Co., California	13	3.2	2.6- 3.6
Jean, Clark Co., Nevada	8	3.0	2.2- 3.8
Eureka Valley, Inyo Co., California	7	3.1	2.5- 3.7
<i>Oenothera wigginsii</i>			
San Quintin, Baja California	8	3.3	3.1- 3.5
<i>Oenothera runcinata</i>			
Las Cruces, Dona Ana Co., New Mexico	5	2.7	2.5- 2.8
RAIMANNIA			
<i>Oenothera albicaulis</i>			
Alpine, Brewster Co., Texas	4	3.6	3.4- 3.9
<i>Oenothera laciniata</i>			
Big Spring, Howard Co., Texas	6	3.5	3.4- 3.6
<i>Oenothera drummondii</i>			
Port Aransas, San Patricio Co., Texas	25	3.4	2.7- 4.0
LAVAUXIA			
<i>Oenothera taraxacoides</i>			
Cloudcroft, Otero Co., New Mexico	20	13.2	7.2-19.2
GAUROPSIS			
<i>Oenothera havardii</i>			
Rodeo, Hidalgo Co., New Mexico		4.7	
MEGAPTERIUM			
<i>Oenothera brachycarpa</i>			
Charleston Mountains, Clark Co., Nevada	2	9.3	9.0- 9.7
Jeff Davis County, Texas*	2	12.2	11.5-13.0

*These colonies were not studied in detail but are given to show variation.

Salpingia

Spectrum and relative abundance.—The data for *O. hartwegii* and *O. greggii* will be considered together because of their great similarity. A composite list of the insects seen at their flowers is given in Table 8.

TABLE 8. *Visitors to the flowers of O. greggii and O. hartwegii at the five colonies studied.*

HAWKMOTHS

Celerio lineata (Fabr.)
Phlegethontius quinquemaculata (Haw.)
Herse cingulata (Fabr.)
Sphinx dolli Neum.

BEES*

Anthophora affabilis Cresson
Lasioglossum (Evylaeus) galpinsiae Cockerell
L. (Speocodogastra) noctivagum Linsley and MacSwain
Agapostemon angelicus Cockerell
Bombus (Fervidobombus) sonorus Say
Melissodes sp.
Megachile sp.

*I would like to thank Drs. J. W. MacSwain, E. G. Linsley, and P. D. Hurl, Jr., and Mr. Robbin Thorp for the identifications of the bees.

Bees were observed collecting pollen during the evening only at the colony below Monahans, Texas. Four species were working half an hour before sunset; individuals of *Lasioglossum (Evylaeus) galpinsiae* were abundant while individuals of *Anthophora affabilis*, *Lasioglossum (Speocodogastra) noctivagum* and *Agapostemon angelicus* were numerous. These were the earliest visitors seen at any of the colonies.

The earliest time of appearance of hawkmoths was 15 minutes before sunset. At four of the colonies *Celerio lineata* was the first species to arrive but at Sanderson, where *Phlegethontius quinquemaculata* was the most abundant visitor, this species was the first to appear. At Sanderson and Chiricahua *P. quinquemaculata* started visiting just after sunset but at the other three colonies this species was not active until deep dusk or after dark. These two species were present at all five colonies. *Herse cingulata* was taken at Fort Davis after dark and *Sphinx dolli* at Sanderson just before dark. *Celerio* was abundant at Fort Davis and Monahans (Fig. 12a) for about one hour and occasional thereafter. At peak abundance as many as three moths were seen at a time visiting one plant. At the other three colonies *Celerio* was not as abundant but was a regular visitor until after dark. *Phlegethontius quinquemaculata* was abundant only at Sanderson but a regular visitor for at least one hour after dark at the other colonies (Fig. 12b). Thus, the usual situation was a peak of *Celerio* about one half hour after sunset and of *P. quinquemaculata* shortly after dark.

Bees were seen at only one colony, Chiricahua, during the morning, *Megachile*, *Melissodes* and *Bombus (Fervidobombus) sonorus* making occasional visits for pollen and nectar.

Pollinating Agents.—The flowers of *O. hartwegii* and *O. greggii* were usually open nearly an hour before sunset, so that the flowers were available for at least an hour and a half before dark. At two colonies, Monahans and Ector County, over 50% of the flowers had been pollinated, most lightly, before any hawkmoths were seen. At Monahans four species of bees were collecting pollen before sunset and were responsible for most of the

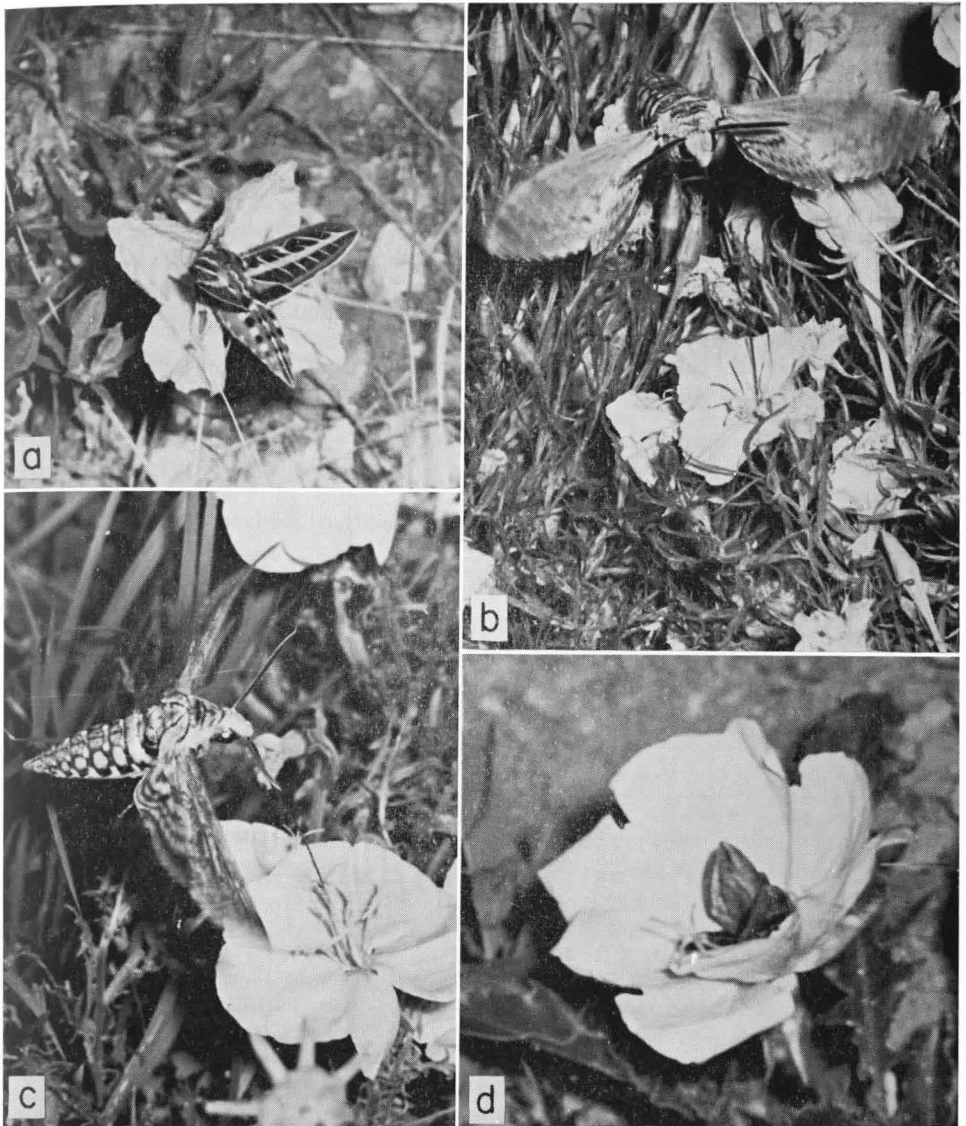


Fig. 12. Hawkmoths feeding at four species of *Oenothera*, all shortly after dark.—a, an individual of *Celerio lineata* visiting *Oenothera greggii*, the moth has stopped its wings and is pushing its head into the wide mouth of the hypanthium.—b, an individual of *Pblegethontius quinquemaculata* visiting *Oenothera bartwegii* with its proboscis fully inserted. Note the distance between the body of the moth and the stamens and stigma.—c, an individual of *P. quinquemaculata* visiting *Oenothera albicaulis*. Again the proboscis is fully inserted, note how close the stigma lobes are to the pollen on the proboscis.—d, an individual of *Sphinx drupiferarum* visiting *Oenothera caespitosa* var. *marginata*. The wings of the moth are at rest and its head is well into the orifice of the hypanthium.

pollen transfer. They also removed enough pollen to influence the effectiveness of hawk-moths later in the evening. Some of the flowers which had pollen at the edges of the peltate stigma showed single flower self-pollination but since all of the colonies of these species which have been tested are self-incompatible, this would not be effective pollination. Such transfer of pollen from the anthers to the stigma of a single flower would be expected even in the absence of insects in the many flowers with stigmas placed just beyond the anthers, especially with the high winds often encountered at these colonies.

Most of the cross pollination at these colonies and at the other three observed was effected by *Celerio lineata* (Fig. 12a). *Pblegethontius quinquemaculata* was responsible for some cross pollination for, as at colonies of other species of *Oenothera*, this moth carried a mass of pollen on the proboscis at the level of the anthers and since the stigma was often within the circle of anthers, some of this pollen undoubtedly was caught by the edge of the stigma as the proboscis was inserted or withdrawn (Fig. 12b).

Bees were observed at only one colony, Chiricahua, during the morning, but at this colony and probably at others they added to the total amount of pollination.

Pachylophis

Spectrum and Relative Abundance.—The six colonies at which *O. caespitosa* was observed were spread from California to Colorado and Arizona, and the spectrum of visitors varied with the location. A list of all the visitors encountered is given in Table 9.

TABLE 9. Visitors to the flowers of *O. caespitosa* at the six colonies studied.

HAWKMOths	
	<i>Celerio lineata</i> (Fabr.)
	<i>Sphinx chersis chersis</i> (Hbn.)
	<i>Sphinx perelegans asellus</i> (R. & J.)
	<i>Sphinx drupiferarum</i> A. & S.
	<i>Sphinx dolli</i> Neum.
	<i>Sphinx vashii</i> Stkr.
	<i>Pblegethontius quinquemaculata</i> (Haw.)
BEES	
	<i>Lasioglossum</i> sp.
	<i>Agapostemon</i> sp.

Celerio lineata was seen at every colony except Point Sublime and the moth undoubtedly occurs there as well. This was the only species visiting the flowers at Harrisburg Flats, Kyle Canyon and Westgard Pass. At the colonies it was an infrequent but regular visitor during the first hour or two after the flowers opened and occasional during the later evening. At the other three colonies in Arizona and Colorado at high elevations species of the genus *Sphinx* were at least as abundant and usually more abundant than *Celerio*. *Sphinx chersis chersis* and *S. dolli* were observed at Jacob Lake, *S. perelegans asellus* at Point Sublime, *S. drupiferarum* (Fig. 12d) and *S. chersis chersis* at Mesa Verde, and *Sphinx dolli* and *S. vashii* in the Wasatch Mountains above Marysvale, Utah (V. Grant, in June, 1955). These species were all first seen just before full darkness and were most abundant during the early hours of darkness. As with *Celerio* in the colonies in California and Nevada, the species of *Sphinx* were never abundant but were infrequent visitors to the flowers at regular intervals during the early part of the night. *Pblegethontius quinquemaculata* was occasional at Mesa Verde.

Several medium sized bees were seen at the flowers of *O. caespitosa* collecting pollen but such observations were rare. It is likely that a number of other bees besides those listed in the table occasionally visit the flowers of this plant.

Pollinating Agents.—At the colonies of *O. caespitosa* studied *Celerio lineata* and the five species of *Sphinx* were responsible for nearly all of the pollination (Fig. 12d). Hawkmoths with longer tongues such as *Pblegethontius quinque maculata* and *Herse cingulata* would usually be just as effective as the short-tongued hawkmoths as pollinators of this species because of the longer hypanthium, but these moths were never common at the colonies studied. Because of the smaller number of flowers at the colonies of *O. caespitosa* a very small number of hawkmoths could pollinate all of the flowers effectively; however, at all of the colonies discussed here, moths were relatively abundant. Very few bees were seen and they are probably never a factor in pollination.

Anogra

Spectrum and Relative Abundance.—By far the most abundant visitor to the flowers of *Oenothera deltoidea* was *Celerio lineata* (Fig. 13c and d). Two other hawkmoths and several bees were also observed at this species; these insects are listed in Table 10.

TABLE 10. *Visitors to the flowers of O. deltoidea at the five colonies studied.*

HAWKMOTHS	
	<i>Celerio lineata</i> (Fabr.)
	<i>Pholus achemon</i> (Dru.)
	<i>Pblegethontius quinque maculata</i> (Haw.)
BEES	
	<i>Andrena (Onagradora) linsleyi</i> Timberlake
	<i>Apis mellifera</i> L.
	<i>Hesperapis wilmattae</i> Cockerell
	<i>Agapostemon melliventris</i> Cresson
	<i>A. angelicus</i> Cockrell
	<i>Dufourea</i> sp.
	<i>Anthophora</i> 2 spp.
	<i>Megachile</i> sp.

At the first colony observed on 19 March, 1960, at Thousand Palms, no hawkmoths at all were seen at the many flowers of the large colony. Just over two weeks later at the nearby colony near Palm Desert *C. lineata* was quite common but not abundant. At Essex on April 12 the moth was again common and on April 29 east of Twenty-Nine Palms it was exceedingly abundant. The number of individuals taken at the light-trap, run for one hour about an hour after dark at the four colonies, illustrates this increase in abundance. At Thousand Palms no moths were taken, at Palm Desert 22 moths, at Essex 31 moths and at Twenty-Nine Palms 121 moths in half an hour. First appearance of the species varied with abundance, at Palm Desert and Essex being about 30 minutes before dark and at Twenty-Nine Palms almost an hour before sunset, before the flowers had begun to open. For *Celerio* the peak of abundance at the flowers was just about sunset at Twenty-Nine Palms and somewhat later at the other colonies but this moth was still quite active two hours after sunset. *Pholus achemon* was observed only occasionally at one colony, Palm Desert. *Pblegethontius quinque maculata* was rare at Essex and occasional at Twenty-Nine Palms where it was first seen about sunset. At the population near the Valley of Fire, *Celerio* was the only insect observed and was abundant from a half hour before sunset until dark.

One small bee, *Hesperapis wilmattae*, was discovered after dark ensconced for the night with its abdomen in the upper hypanthium of the flowers at Thousand Palms. It probably visits before dark and was observed in abundance next morning from 6:30 am until after noon. *Andrena (Onagradora) linsleyi* was rare at Thousand Palms from 6:30 to 7:05

am and more abundant at Essex from 6:15 to 7:00 am, while at Twenty-Nine Palms this bee was fairly abundant at the flowers of *O. deltooides* between 7:30 and 9:15 am, also visiting *O. decorticans* var. *desertorum* as at Essex and in addition *O. clavaeformis* ssp. *aurantiaca*, the last two being small flowered species of *Oenothera*. Honeybees were common at the flowers from sunrise through the morning at Thousand Palms and Palm Desert, while several other bees were occasional visitors during the morning at all colonies (see the papers by Linsley, MacSwain and Raven (1963a, b, c) for many other records and discussion of bees visiting these species).

Celerio was the only insect observed at the three colonies of *O. californica* (Fig. 13a and b) and was abundant at all three. Light-trap figures were 30 individuals at Cima, 40 at Jean and 20 at Eureka Dunes. The moths were first seen before sunset at Jean and Eureka Dunes but not until just after sunset at Cima. Several individuals of *C. lineata* were seen after sunrise at Eureka Dunes.

Only four individuals of *Celerio* were seen at *O. runcinata* near Las Cruces starting just after sunset, but the moth was probably occasional during the evening.

During two evenings and two mornings of observation in colonies of *O. wigginsii* in different years, no hawkmoths and only one individual of *Hesperapis* were seen at the flowers. One individual of *Anthophora* taken while visiting *Lycium* was carrying pollen of both this species and of *O. wigginsii*.

Pollinating Agents.—By far the most important pollinator of both *Oenothera deltooides* and *O. californica* was *Celerio lineata* (Fig. 13a-d). Early in the season when *Celerio* is absent or rare, other insects are responsible for what pollination is effected as illustrated at Thousand Palms, or add to the evening pollination by *Celerio* during the morning as at Palm Desert. But usually populations of *Celerio* are far larger than necessary to bring about complete pollination. At Twenty-Nine Palms and at Jean, the number of celerios was so great and competition for nectar so acute that the moths were feeding at buds that had just begun to open (Fig. 13d), and probably pollinating some in this way. At these colonies pollination was so complete just after sunset that further pollination would have been hard to achieve.

When pollination was not completed by *Celerio* during the evening several species of bees added to the total the next morning. One of the species responsible was *Andrena* (*Onagrarendra*) *linsleyi* which, however, was not very efficient as a pollinator because individuals rarely made good enough contact with the stigma. *Apis mellifera* probably did most of the morning pollinating at Thousand Palms and Palm Desert and is often a factor when previous pollination is incomplete although this bee is also a relatively inefficient pollinator. Two species of *Anthophora* were effective pollinators but were usually not abundant. Other bee species observed were too small to be very effective.

Oenothera wigginsii appears to be almost completely self-pollinated, although still having most of the floral characteristics of *O. deltooides* to which it is closely related. The significant differences are the distance the style is exerted beyond the anthers and self-

Fig. 13. Hawkmoths feeding at the flowers of three species of *Oenothera*, d taken about sunset, a-c, e and f taken shortly after dark.—a-b. *Celerio lineata* visiting *Oenothera californica* ssp. *californica*. In a the moth is approaching the flower and in b the proboscis is fully inserted, the body cradled by the stamens.—c. an individual of *C. lineata* visiting *Oenothera deltooides* ssp. *ambigua*, the fore part of the moth's body is in contact with the stigma.—d. buds of *O. deltooides* ssp. *deltooides* probed by *C. lineata* before opening.—e. an individual of *C. lineata* leaving a flower of *Oenothera albicaulis*, the small clump of pollen on the proboscis is very close to the stigma.—f. *Phegathontius quinque maculata* visiting *Oenothera californica* ssp. *arizonica* near Bouse, Arizona, on 18 April, 1959.

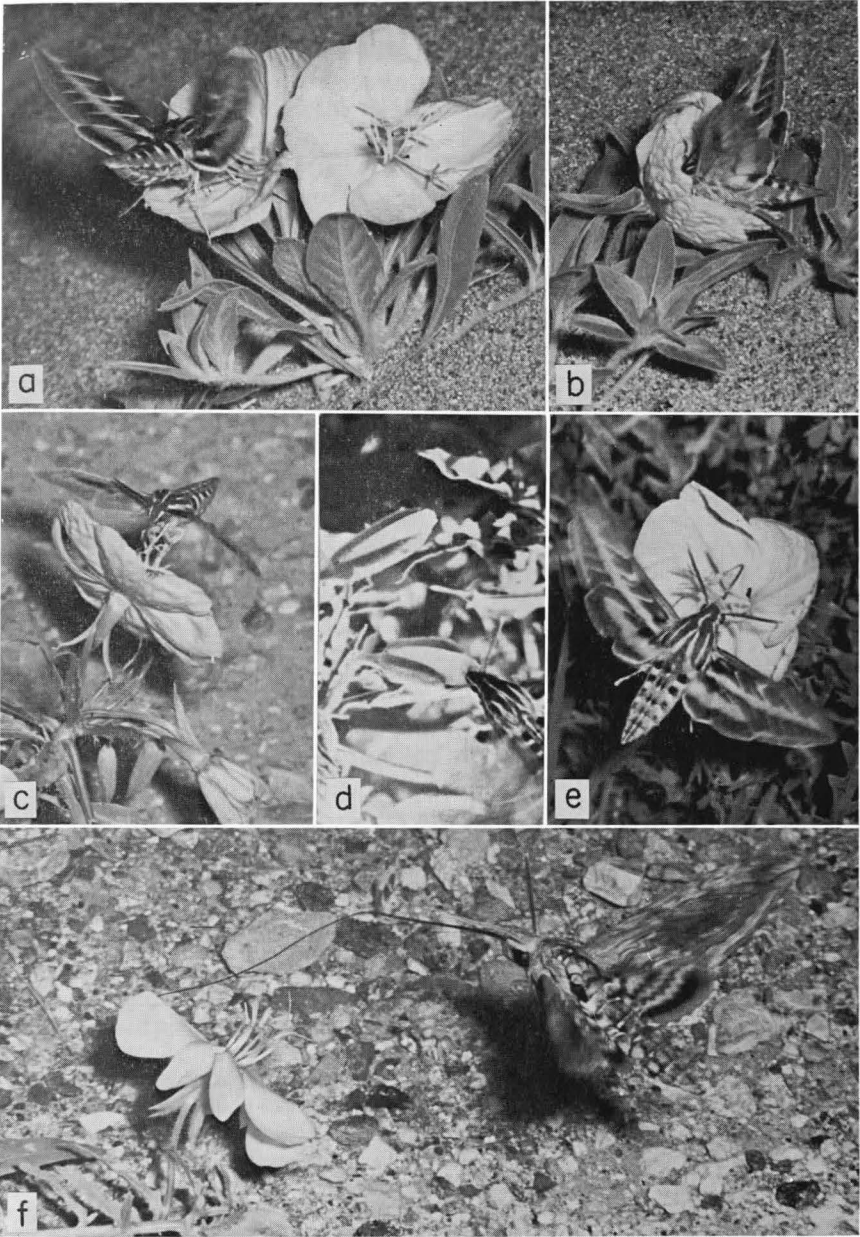


FIGURE 13

compatibility. In *O. wigginsii* the style is usually only two or three millimeters beyond the anthers (Fig. 11e) and most of the flowers at the two colonies observed near San Quintín had strands of pollen from the anthers draped over the stigma lobes. *O. wigginsii* is self-compatible. No hawkmoths were seen at the flowers or even seen in the area at all and no bees were seen although one *Anthophora* was collected carrying pollen of this species. No evidence was seen of cross pollination although bees are undoubtedly responsible for some.

Oenothera runcinata is pollinated extensively by *Celerio lineata* although to exactly what extent was not determined.

Raimannia

Spectrum and Relative Abundance.—In the colony of *Oenothera albicaulis* near Alpine both *Pblegethontius quinquemaculata* (Fig. 12c) and *Celerio lineata* (Fig. 13e) arrived while the flowers were opening just before dark. *Pblegethontius quinquemaculata* was abundant for at least an hour and *Celerio* was a regular visitor during the same period.

At the colony near Big Spring both *O. laciniata* and *O. engelmannii* were abnormal in opening time, the first opening at 9:00 pm and the second after 11:00 pm. Flower size in the second species was also abnormally small. Observation of the typical spectrum and order of visitors was impossible but at the light-trap, run between 9:15 and 10:15 pm, 14 celerios and 1 *P. quinquemaculata* were taken as well as a long series of a nocturnal bee, *Lasioglossum (Sphecodogastra) texanum* (Cresson). *Celerio* was visiting *O. laciniata* at 10:30 and the bee probably visits both species just after the flowers open when anthesis is normal.

The most abundant visitor at the flowers of *Oenothera drummondii* at Aransas Pass was this same bee which started to collect pollen when the flowers opened half an hour before sunset and continued until just after dark. There were individuals working about sunset when all the flowers were open. Hawkmoths were very rare at this colony; only one *Celerio* was seen at the flowers and one *Celerio* and one individual of *Herse cingulata* were taken during one hour at the light-trap.

Pollinating Agents.—The most important pollinator of *Oenothera albicaulis* was *Celerio lineata* (Fig. 13e) with *Pblegethontius quinquemaculata* probably responsible for a few flowers (Fig. 12c). No pollination lines were run at this colony but a high percentage of the flowers were pollinated during the evening. No observations on bees were made in the morning.

Oenothera laciniata at Big Spring was definitely pollinated by *Celerio lineata*, 25 flowers checked at 10:30 pm all being pollinated, about 90% heavily. *Lasioglossum (Sphecodogastra) texanum* (Cresson) undoubtedly pollinates a few flowers when they open at the normal time and may reduce hawkmoth pollination somewhat by removing a large amount of pollen. Presumably *O. drummondii* which grew mixed with *O. laciniata* here had the same pollinators, but the flowers were so abnormal in size and anthesis that little could be determined. The plants were setting very little seed.

Oenothera drummondii is another species which is possibly often self-pollinated. It is self-compatible and the style is nearer the anthers than in most *Oenothera* flowers which are otherwise comparable. There was certainly some pollination by *Celerio* at Aransas Pass but *Lasioglossum (Sphecodogastra) texanum* (Cresson) took so much pollen during the hour or more before dark that pollination by *Celerio* was greatly reduced. As Table 12 shows, pollination was not above 68% at 7:00 am. The table also shows, however, that 50% of the flowers were pollinated by *Celerio* between 10:30 pm and 7:00 am but most of these were lightly pollinated as might be expected. Other bees which were not observed probably raised the percentage of flowers pollinated as might be expected. Other bees which were

not observed probably raised the percentage of flowers pollinated later in the morning. Two or three butterflies were also seen visiting the flowers after 8:00 am, but so little pollen was left by this time that no agent would be very effective.

Lavauxia

Spectrum and Relative Abundance.—*Celerio lineata* was again the most abundant visitor to the flowers in the colony of *O. taraxacoides* at Cloudcroft starting just after the flowers opened, while it was still quite light. This moth was a regular visitor until dark but only occasional thereafter. *Pblegethontius quinque maculata* appeared after dark in small numbers. No bees were seen at this colony.

Pollinating Agents.—*Oenothera taraxacoides* was pollinated almost entirely by *Celerio* but some additional pollinating was effected by *Pblegethontius quinque maculata* which is just as efficient a pollinator of this long-tubed flower. The latter moth arrived at the flowers slightly later and was less abundant, however.

Gauropsis

Spectrum and Relative Abundance.—A number of individuals of *Celerio lineata* were observed by Grant in 1961 visiting the flowers of *O. havardii* at dusk.

Pollinating Agents.—*Oenothera havardii* was pollinated mainly by *Celerio lineata* according to the observations of Grant.

Megapterium

Spectrum and Relative Abundance.—Only two plants of *O. brachycarpa* with three open flowers were observed at Charleston Park for about an hour after dark. Two individuals of *Sphinx chersis gerhardi* B. & B. were seen making several visits to these flowers.

Pollinating Agents.—*Oenothera brachycarpa* was pollinated at Charleston Park by *Sphinx chersis gerhardi* but casual observations in Jeff Davis County, Texas, indicate that it is also pollinated by *P. quinque maculata* and perhaps by *Celerio* as well. It may also be pollinated by *Celerio* at Charleston Park but no celerios were seen on the night of observation. They were responsible for pollination of *O. caespitosa* at lower elevations in the same canyon (Kyle Canyon) earlier in the year.

GENERAL CONSIDERATIONS ON THE BREEDING SYSTEM IN THE LARGE FLOWERED, EVENING OPENING SPECIES OF OENOTHERA

RATIO OF SELF- TO CROSS-POLLINATION IN GENOTHERA HOOKERI

Cleland (1935) found during his cytogenetic study of *O. hookeri* that several populations, representing all of the sub-species now recognized, were made up of self-compatible plants. Based on the assumption that this was true for the populations I studied, I made an attempt to estimate the ratio of self- to cross-pollination in this species. In making such an estimate it is important to consider a number of factors.

Some evidence on this ratio can be obtained by comparison of the emasculation and control lines. Usually the percentage of pollinated flowers was nearly the same for the two lines, and the number of stigmas in each category was often nearly equal. Such data would suggest little single flower self-pollination on the control line. However, one detail in which the two series regularly did not agree was the number of stigmas bearing hawkmoth scales; a far higher number of scales was usually found on the stigmas of the emasculated flowers as can be seen in Table 12. The same pattern of deposition of scales was observed in all of the other colonies of *O. hookeri* where hawkmoths were at all common. The most logical explanation is that when the stamens were not present below the moth's body as it fed, closer contact was possible with the stigma below. Actually, if this explanation is

TABLE 11. Proportion of flowers at each colony that were pollinated at various times after opening.^{1, 2}

	Percentage of emasculated flowers that were pollinated in various degrees.					Percentage of unemasculated flowers that were pollinated in various degrees.				
	HEAVY	GOOD	FAIR	SLIGHT	PERCENT TOTAL	HEAVY	GOOD	FAIR	SLIGHT	PERCENT TOTAL
SALPINGIA										
<i>Oenothera bartwegii</i>										
Fort Davis (sample 40)										
8:00 a.m.	25%	33%	25%	10%	93%					90%
Ector County										
7:30 p.m.						few			many	72%
11:30 a.m.						24%	44%	14%	12%	94%
<i>Oenothera greggii</i>										
Chiricahua										
10:00 p.m.						few			many	88%
8:00 a.m.	6%	26%	18%	36%	86%	16%	54%	8%	22%	100%
9:30 a.m.										
PACHYLOPHIS										
<i>Oenothera caespitosa</i>										
(sample 25)										
9:15 p.m.									20%	80%
8:00 to										
10:30 a.m.						16%	40%	12%	24%	92%
Mesa Verde										
10:15 p.m.						20%			4%	100%
8:30 to	30%	40%	20%	6%	96%	36%	42%	18%	4%	100%
9:45 a.m.										
Jacob Lake										
10:30 p.m.										100%
7:30 to	56%	24%	20%	0%	100%	56%	28%	8%	8%	100%
8:40 a.m.										
ANOGRA										
<i>Oenothera deltoides</i>										
Thousand Palms										
7:15 to	2%	6%	0	6%	14%					
7:45 a.m.										
Palm Desert										
11:35 p.m.									20%	44%
5:30 a.m.									10%	60%
6:50 to	10%	46%	14%	22%	92%	20%	28%	14%	30%	92%
7:30 a.m.										
29 Palms										
8:30 p.m.						20%				100%
Valley of Fire										
8:30 p.m.										100%
7:20 to	72%	28%	0	0	100%	62%	38%	0	0	100%
8:15 a.m.										
<i>Oenothera californica</i>										
Cima										
6:30 to	14%	46%	26%	14%	100%					99%
7:30 a.m.										
Jean										
7:45 p.m.										98%

¹A sample of 50 flowers was observed except where otherwise stated.²Where there are blanks in the table only the categories listed were read.

TABLE 11. *Proportion of flowers at each colony that were pollinated at various times after opening.^{1,2}*
(continued)

	Percentage of emasculated flowers that were pollinated in various degrees.					Percentage of unemasculated flowers that were pollinated in various degrees.				
	HEAVY	GOOD	FAIR	SLIGHT	PERCENT TOTAL	HEAVY	GOOD	FAIR	SLIGHT	PERCENT TOTAL
<i>Oenothera californica</i>										
Jean										
6:15 to 7:20 a.m.	64%	36%	0	0	100%					100%
Eureka Dunes (sample 25)										
8:30 p.m. to 9:00 a.m.	68%	20%	8%	4%	100%	84%	16%	0	0	100%
RAIMANNIA										
<i>Oenothera drummondii</i>										
Port Aransas										
10:30 p.m. to 8:00 a.m.	2%	16%	6%	38%	62%	0	12%	4%	15%	18%
LAVAUXIA										
<i>Oenothera taraxacoides</i>										
Cloudcroft (sample 25)										
10:00 a.m. to 8:30 a.m.	32%	48%	20%	0	100%	few 40%	32%	20%	many 8%	100%

correct, some additional deposition of pollen might make the emasculation series appear to be more nearly equivalent with the control series than is truly the case.

Estimating the amounts of self and foreign pollen on a stigma is very difficult and only general estimates can be made after considering all of the evidence. Even the most effective pollinators of *O. hookeri* do not transfer pollen on every visit to a flower and when they do transfer pollen, the amounts vary from a few grains to one or more large masses. In many instances a stigma is probably pollinated several times. Emerson (1939) in his study of *O. organensis* found that the number of different alleles of the self-incompatibility locus occurring in a series of plants grown from single open pollinated capsules collected in the field indicated that a number of stigmas had been pollinated more than once or that the

TABLE 12. *Number of stigmas bearing hawkmoth scales at East Highland (based on 50 flowers in each case).*

DATE	EMASCULATED FLOWERS	CONTROL
26 July	19	9
5 August	28	9
23 August	39	32
28 September	10	2

pollinating agent had been carrying a mixture of pollen from several plants with different S-locus alleles.

Self-pollination can be brought about either with pollen from the same flower or with pollen from another flower on the same plant. Judging from the observational evidence, self-pollination of the first type is probably rare in *O. hookeri* and when it takes place involves only a few grains. The ways in which such selfing takes place are illustrated in several of the figures. Of the relatively small amount of pollinating done by *Phlegethontius sexta*, some is probably in this category, strands of pollen catching on the proboscis while the moth is feeding and being pulled out and across the lobes of the stigma as the moth backs away (Fig. 8a). Some strands of pollen are undoubtedly pulled back and laid across the stigma by small hawkmoths as well, Fig. 3c showing what is probably the result of such a case. Also *Xylocopa* sometimes pulls out strands of pollen on leaving a flower which could result in much the same situation (Fig. 9c). In colonies of *O. deltooides* on the desert when the wind is high, strands of pollen are often dislodged and while hanging off the anthers are sometimes blown across the stigma. In my experience the wind near an *O. hookeri* colony has never been high enough to bring about this type of pollen transfer.

The second type of self-pollination is much more important, for many of the plants of *O. hookeri* are very large, bearing 50 or more flowers on their several branches (Fig. 1a). After dark the smaller hawkmoths *Celerio* and *Pholus* work steadily from one flower to the next, making it likely that several flowers on one plant would be visited in order. When so many plants are growing together so closely, however, branches of different plants overlap, lessening the above tendency. A conservative estimate would be that *Celerio* and *Pholus* normally visit at least three flowers on one plant before moving to a flower on another plant. This would mean that approximately two out of three flowers would probably be self-pollinated. The situation is not as simple as that, of course, and one important factor might be the composition of the pollen festoons on the legs of the moth. Would this mass of pollen be a somewhat intertwined mixture of pollen from the several most recently visited flowers, or would it be predominantly pollen from the last flower visited? The type of pollen carried would differ depending on the amount of pollen present on the anthers when it was picked up, the amount of pollen already carried by the moth and the distance covered between flowers. Probably one out of two stigmas at least would be predominantly or completely self-pollinated but with many stigmas bearing a mixture of pollen corresponding to the mixture on the underparts of the insect. *Xylocopa* would do nearly the same amount of the second type of self-pollinating except that these insects undoubtedly carry a mixed load any part of which could be responsible for pollination. Where a mixture of self and foreign pollen is placed on a stigma, competition may follow between the two types even though the plant is self-compatible. Temecula was the one colony at which self-pollination was probably well below 50%. Here the plants hardly branched at all and since it was late in the season, usually bore only one flower, so that transfer of pollen between flowers on the same plant could not occur.

The exact ratio of self- to cross-pollination was not determined for any colony during this work but considering the above evidence it seems probable that at least 50% of the pollination at all of the colonies except Temecula was self-pollination, and that the amount of such pollination varied over a wide range above this figure. To determine the exact ratio of self- to cross-pollination at any colony for a certain time of year, exact genetic data would have to be obtained.

COMPARISON OF THE BREEDING SYSTEMS OF SPECIES IN ALL OF THE SUBGENERA INVESTIGATED

Most of the species considered here are predominantly outcrossers but self-pollination

has developed in a few species or particular populations within species. The most important characteristic leading to outcrossing is the morphology of the flower, which is remarkably constant within all of the subgenera. The position of the anthers and stigma in this type of flower favors the transfer of pollen from one flower to another without preventing self-pollination. However, in many of the species an S-allele system of self-incompatibility prevents self-fertilization (Emerson, 1938; Crowe 1956). Presumably, in such species, only outcrossing takes place. All of the species discussed in this chapter (as represented by the particular subspecies studied) except *Oenothera wigginsii*, *O. drummondii* and one colony of *O. deltooides* ssp. *deltooides* near Palm Springs were found to be self-incompatible by William Klein in work done at the Rancho Santa Ana Botanic Garden and by other workers as reported in the literature (Hagen, 1950; Crowe, 1955). The compatibilities of *O. taraxacoides* and *O. havardii* are not known.

Only one of the species observed during this work, namely *O. wigginsii* illustrates the other extreme—predominant selfing. In this species the marginal habitat has favored "fitness" over "flexibility" of the genotype and thus self-pollination. Lack of pollinators is probably also a factor favoring selfing.

There are several other self-pollinating species (not studied here) in the subgenera *Oenothera* and *Raimannia*. *Oenothera strigosa* and the *O. biennis* complex are two of the best examples. The genetic system in these species is, of course, a highly specialized one, the plants being permanent true breeding heterozygotes with a ring of 14 chromosomes maintained by balanced lethals (Cleland, 1949, 1954; Cleland et al., 1950). Self-pollination is an important part of this system and the flowers are much smaller than those of the related *O. hookeri* and have a short style which does not elevate the stigma beyond the anthers. There is evidence that the present permanent heterozygotes were initiated by hybridization between overlapping races with different patterns of translocation. The flowers at this time were probably large with long styles, much like those of *O. hookeri* at present. With the establishment of the permanent heterozygotes the floral morphology favoring self-pollination became selectively superior.

Among the *Raimannias* two species in North America and several in South America show a similar change to self-pollination. In both *O. laciniata* and *O. rhombipetala* there are two types of breeding system within each species (Hecht, 1950). Some populations have large flowers with long styles and are self-incompatible, while other populations have smaller predominantly self-pollinating flowers and are self-compatible. The latter populations are like those of *O. biennis* in having a ring of 14 chromosomes and probably balanced lethals. Both breeding systems seem to be successful in these species.

The third major type of breeding system spans the gap between predominant cross-pollination and predominant self-pollination; it is the combination of self- and cross-pollination in varying proportion. Six closely related species in subgenus *Oenothera*, *O. hookeri*, *O. elata*, *O. jamesii*, *O. longissima*, *O. argillicola* and *O. grandiflora* and several species in *Raimannia*, mostly South America, have such a breeding system. Species or populations in other subgenera have come into this category through loss of self-incompatibility.

Of the species in subgenus *Raimannia*, *O. drummondii* is a good example. The flowers are basically adapted for outcrossing and hawkmoths seem to be the most important pollinators but the plants are self-compatible and the style is shorter than in most outcrossing oenotheras, apparently making possible much self-pollination. This species is a strand plant, probably native to the coast of the Gulf of Mexico from Texas to Vera Cruz, but which has become established on beaches in many parts of the world (Munz, 1935).

Establishment of colonies in new localities would of course be facilitated by self-pollination. (Baker, 1955).

In subgenus *Anogra* many species are self-incompatible but some are self-compatible, whereas others have subspecies some of which are in one category and some in the other. Of the two widespread subspecies of *O. deltooides* in California, ssp. *deltooides* of the Mohave and Colorado deserts is self-incompatible while ssp. *cognata* of the San Joaquin Valley is self-compatible (Klein, pers. comm.), but there is little difference in the flowers. Thus a mixture of self- and cross-pollination is possible in ssp. *cognata*, placing it in the intermediate category as far as breeding system is concerned.

In summary, many species in the subgenera discussed here are complete outcrossers, being self-incompatible. Several such as *O. bookeri* and *O. deltooides* ssp. *cognata* have flowers favoring outcrossing but are self-compatible, so that a mixture of self- and cross-pollination is the norm. A few, especially in the subgenera *Oenothera* and *Raimannia* are predominantly self-pollinated, having flowers which greatly restrict cross-pollination.

THE BEHAVIOR AND MORPHOLOGY OF POLLINATORS OF OENOTHERA

In determining the role of a pollinating animal in the floral biology of a plant species, several aspects of its behavior must be understood. Of these, behavior at the flower, pattern of flight, duration and time of activity and floral constancy are important while the insect is in a colony of the plant in question. The life span and total area covered by a pollinator are also important, particularly when the plant species grows in small, somewhat isolated colonies. Morphology of organs essential in feeding or collecting food and in transferring pollen must be considered as well.

Two groups of animals were by far the most important pollinators of the species of *Oenothera* studied during this work, hawkmoths and bees. The relevant behavior and morphology of the important pollinators in these two groups will be considered in turn in this chapter.

BEHAVIOR OF POLLINATORS IN A COLONY AND THE PROCESS OF POLLINATION

Ten species of hawkmoths were observed visiting flowers at the colonies discussed in the last two chapters. These fall naturally into two groups as pollinators of *Oenothera*. The first group is made up of moths with tongues approximating 4 cm in length, while the second includes those with tongues usually over 8 cm in length. Two of the species of *Sphinx* are intermediate in tongue length but fall more nearly into the first group.

More than one species of each group are often encountered at a single colony and the species can usually be identified by general behavior as well as by size and markings when they have been frequently observed. The commonest moth in the first category is *Celerio lineata* which often starts visiting flowers well before dark and is sometimes seen in full daylight. *Pholus achemon* and the several species of *Sphinx*, the other moths in this category, are seldom seen before deep dusk or full darkness. When it is still light *C. lineata* is quite wary, tending to feed quickly and skip from one flower to another at a distance, sometimes flying in large circles over the colony. This is especially true if an observer is close by in which case the moths will often swing close to the observer's head as if to satisfy whatever curiosity they have.

When feeding during deep dusk or darkness the species with relatively short tongues are steady and direct in flight, with slight characteristic variations, and appear faster than the larger and longer tongued group of moths. They usually visit several flowers in a row which are next to each other or even two or three on a single inflorescence, then skip several and again visit a number of contiguous flowers. Often a flower will be visited twice in a single sequence. The moths seem to visit a flower no matter how many times it has been

tried by other moths or by themselves. At Eureka Dunes several flowers of *O. californica* ssp. *enrekensis* were watched for 30 minutes and each was visited from 20 to 50 times during that period. The moths insert the proboscis for usually 3 or 4 seconds at a flower with nectar in the hypanthium whereas at empty flowers the proboscis is immediately withdrawn. The pattern of flower visits is highly variable for these species, probably depending on the security of the moth and the distribution of the flowers, which of course varies with the species of *Oenothera* as with size and spacing of plants within a colony.

The species with relatively short tongues are effective pollinators of all species of *Oenothera* considered here; however, the process of pollination by them differs slightly for the four basic morphological types of flower found in the nocturnal species of *Oenothera*. The process of pollination by these moths will be compared for the four floral types.

In the first type of flower as represented by *O. hookeri* and *O. deltoides* (Fig. 3a-b and 11d), the flower is approached from directly in front and slightly above the level of the hypanthial orifice. The legs of the moth hang down as it settles into the flower after the proboscis has been introduced. A detailed comparison of tongue lengths and hypanthial lengths will be made later in this chapter but most of the species of *Oenothera* with this floral type have hypanthia that are on the average within 1 cm more or less of the average tongue length of *Celerio*, *Pholus* and three of the species of *Sphinx*. Thus when the proboscis is fully inserted the labial palpi are right at the mouth of the hypanthium (Fig. 9a) or within a centimeter of it. Often the moth will tip the rear end of the body up and, still working the wings, appear to drive the proboscis further into the tube. This is probably done when a moth with a tongue shorter than the hypanthium is trying to reach nectar which is just below the proboscis when the organ is normally inserted. When a moth is fully inserted, its body is right in the cradle of the stamens as can be seen in Fig. 9a and 13b. As the moth settles in, the legs are pulled closer to the body with the front surface down. On the three pairs of legs this surface of the several tarsal segments is covered for its complete length with short spines directed towards the claw. Also present on all the legs are long tibial spurs and on the front first tarsal segment there is a row of spines intermediate in length. These spines probably help the insect hold on when landed, but they are also instrumental in catching viscin threads connecting the pollen grains as the moth backs away from the flower, pulling its legs back over the anthers. Some pollen adheres to the scales of the lower thorax of the animal, and this also appears to be facilitated by the adhesive viscin threads, for loose pollen of other plants visited by hawkmoths seems to have little affinity for the smooth surfaces of scales and legs.

The pollen lies in the open anthers at the time of anthesis in four multi-grained rows, seemingly absolutely free from the anther and just lying on it. Usually each side or sac will come out in one strand or in clumps, the grains being connected, of course, by the viscin threads. If a dead *Celerio* is placed at the anthers of a flower in the position the live moth usually takes, it is easy to demonstrate the catching of pollen strands on the numerous projections, the body scales to some extent, but mostly the spines on the legs. There seems to be no resistance to the departure of the pollen except its own weight which stretches out the viscin threads and at times breaks them. Considering the motion of a living *Celerio* it is easy to see how the legs pull away even larger masses of pollen than would be the case using a dead specimen.

When a moth with festoons of pollen on its legs, as illustrated for *Pholus achemon* in Fig. 9b, approaches the flower, pollen will be dragged across the stigma lobes as the moth settles down in flowers which have a high enough stigma. In the plant shown in Fig. 9b the stigma is exceptionally low and would not necessarily receive pollen. When the dead specimen mentioned before is touched to the stigma of an *Oenothera* flower, the stickiness

of the stigma is such that adhesion of pollen is much greater than the power of attachment to the moth so that the pollen is readily transferred. Scales from the body are also transferred if they touch the stigma lobes. Thus the proportions of both flower and moth are such that a maximum of pollination can be effected by an animal which is able to obtain nectar readily.

In the second type of *Oenothera* flower, exemplified by *O. taraxacoides* and *O. brachycarpa*, the process of pollination is essentially the same but the relatively short-tongued hawkmoths always tip in as far as possible for the nectar often rises only 3 to 4 cm in a hypanthium of up to 15 cm. Moths with relatively short tongues will sometimes tip so far into the mouth of the hypanthium, which is somewhat wider in these species, that they stop their wings and hold onto the organs below with their feet. They must obtain some nectar even when the respective measurements are at different extremes since *Celerio*, for example, will visit *O. taraxacoides* steadily for a long period. The species of *Sphinx* with intermediate tongue-length seem slightly better adapted to these plants.

Oenothera caespitosa is typical of the third floral type (Fig. 11b-c). Moths visiting this species fly in immediately over the long-exserted stigma, land and then force the head into the wide mouth of the hypanthium so far that the wings are forced back nearly into resting position (Fig. 12d). This species usually has an hypanthium far longer than the proboscis of the short-tongued moths. The stamens are not all oriented to one side so that they are under the insect and attachment of pollen to the visitor is not as efficient as in the first and second type of flower, but the style does hang below the stamens. The process of removal and deposition of pollen is similar to that described for the previous species of *Oenothera*.

The last floral type studied is illustrated by the two species of the subgenus *Salpingia*, *O. hartwegii* and *O. greggii* (Fig. 11a). These flowers are approached more from above, the moth settling down into the ring of stamens and onto the style which is usually included within this ring. The head is inserted into the wide opening of the hypanthium and the body flattens out the style and stamens (Fig. 12a). As in *O. caespitosa*, the head is inserted so far into the hypanthium that the wings are stopped as the moth tips in fully. Pollination takes place less by dragging of pollen across the stigma than by pollen-carrying organs pushing down on the stigma as the moth settles in.

The behavior of the second group of hawkmoths, those with probosci from 8 to 12 cm in length, is in many respects similar to that of the first group but the amount of pollination resulting from their visits varies greatly with length of the hypanthium. The three species observed during this work were *Pblegethontius sexta*, *P. quinquemaculata* and *Herse cingulata*. These species generally started to visit the flowers in deep dusk or darkness except in some of the colonies of *O. hookeri* where *P. sexta* was often the first species seen, and in two colonies of *O. hartwegii*.

Pblegethontius is distinctive in its "looping" or undulating flight which might even be described as jerky when a moth is near a flower and the radius of the undulations becomes smaller. The overall pattern of flight is nevertheless direct and in darkness they go steadily from one flower to another. *Pblegethontius sexta* and *P. quinquemaculata* are very wary if flying before dark and when started will fly up and around the colony making circles in their undulating flight, or leave for another part of the colony. After starting to feed, the proboscis is left completely or partially uncoiled while in flight from one flower to another (see Fig. 8b). The moths approach a flower from the front and about 6 in. above because of the dangling proboscis. As the proboscis is inserted they often pump up and down as if trying to work the organ deeper into the hypanthium, this being done with the whole body, a rapid up and down flight. When the proboscis is inserted as far as it will go, presumably to the bottom of the hypanthium, the body of the moth is approximately 2 in. from the

mouth of the hypanthium in shorter tubed flowers and well away from the floral parts (Fig. 8c and 12b-c). In flowers with longer hypanthia (*O. caespitosa*, *O. brachycarpa*, *O. taraxacoides*) the moth is close to or in contact with the stamens and style.

The proboscis is usually inserted from 3 to 5 seconds in the hypanthium if there is any nectar but only about one second if the nectar has already been taken. The moths apparently have to insert the proboscis to tell whether nectar is still present. How long they would continue to visit flowers after the nectar was gone in all the flowers is an interesting question, but they may get enough dregs to stimulate a further visit.

Visits of these moths to the flowers with long hypanthia were similar to visits of the short-tongued species, and the process of pollination was almost identical. In the flowers with short hypanthia the moth is so far from the stamens that neither the body nor the legs make contact with the pollen or the stigma. Sometimes the proboscis contacts the anthers in going in and coming out, for, as can be seen in Fig. 8a-b and 12c, there is often a large clump or clumps of pollen on the proboscis at a level corresponding to length of the hypanthium. The viscin threads stick to the proboscis and pollen is pulled away by it (Fig. 8a). Then as the proboscis is inserted in the next flower, the pollen is tamped up to the level of the orifice of the tube. How often the pollen mass on the proboscis does contact a stigma depends on the floral morphology. In the morphological type including *O. bookeri* and *O. deltoides* this pollen would seldom contact the stigma as the proboscis is inserted from above making at least a 45° angle with the style.

In *O. bartwegii* and *O. greggii*, however, where the stigma is nearer the axis of the flower, contact takes place more often. This would be especially true if the moths were working in a high wind as is often the case in western Texas. The moths have more trouble inserting the proboscis as they are fighting the wind (sometimes so strong they are blown to the ground) and are blown back and forth a bit as it is being inserted, possibly facilitating contact with the stigma. The strands of pollen that are pulled off by the proboscis are also a factor in self-pollination of self-compatible species as mentioned for *O. bookeri*. All considered, pollination of short-tubed flowers by this group of moths is not very frequent or important.

Knoll reported (1922) an isolated case of floral constancy in a European hawkmoth. In colonies of most of the species of *Oenothera* studied during this work there was no question of the floral constancy of the hawkmoth pollinators as the only nectar source present was the single species of *Oenothera*. In a few colonies other species of *Oenothera* in very different subgenera or annuals in other families were possible sources, and *Celerio* did not appear to be constant, visiting some of the other species if near enough to be attracted. At Twenty-Nine Palms *Abronia villosa* and *O. clavaeformis* ssp. *clavaeformis* were visited whereas at Eureka Dunes *O. clavaeformis* ssp. *funerea* was often visited by *Celerio*. *Oenothera clavaeformis* is a small-flowered member of the subgenus *Chylismia* in which the flowers open a short time before sunset. The species has an hypanthium only about 4 mm long and *Celerio* would be about as efficient a pollinator of this species as *P. quinquemaculata* would be of *O. californica*.

In two other cases hawkmoths did appear to be constant to one plant species. In Big Bend National Park, Texas, a mixed colony of *Penstemon havardii* and *Cirsium undulatum* was observed from 10 pm to 12:30 am on 18 May, 1959. Several individuals of *Xylophanes tersa* (L.) were observed visiting the red-flowered *Penstemon* only and several specimens of *Pholus achemon* observed visiting only *Cirsium*. In Sanders County, Montana, on 28 August, 1960, a small mixed population of *Oenothera strigosa* and *Cirsium vulgare* was watched from 7:30 to 9:45 pm. Several celerios made many visits to the flowers of *Cirsium* but did not once visit the *Oenothera* although the flowers were only a foot away at the

nearest point. I suspect that in a mixed colony of two species of the plants studied in this work, the hawkmoths would visit both without discrimination.

Many species of bees were observed during the course of this work visiting the flowers of the several species of *Oenothera* studied. Of these most were insignificant as pollinators either because of small numbers or because of behavior at the flower that seldom resulted in pollen transfer. Four species of bees did some pollinating whenever they were present and, when hawkmoths were scarce or absent, they were sometimes important pollinators. The most important bee was *Xylocopa tabaniformis orpifex* which was present at several of the colonies of *O. hookeri*, usually visiting the flowers for pollen in the evening and for pollen and nectar in the morning.

This bee is a large one, about the size of a large bumble bee. In visiting the flower it usually orients itself directly in front of the anthers and then lands directly on them, often brushing the stigma as it goes by. Pollen is collected rapidly, strands of pollen being left on the anthers or hanging from them and sometimes draped over the stigma on leaving. *Xylocopa* is well adapted to pack and carry the specialized pollen of *Oenothera*. Species of the genera *Anthedonia*, *Diandrena*, *Andrena*, *Diadasia*, *Anthophora*, *Lasioglossum* and others which are oligoleges of species of *Oenothera* have the scopae on their rear legs specialized for collection of *Oenothera* pollen; the scopae are composed of long, simple bristles (Linsley, 1958). The species of *Xylocopa* associated with *O. hookeri* are certainly not oligolectic, visiting many other plants for pollen and nectar, but the scopae are generally not unlike those of *Oenothera* oligoleges, being composed of long, simple bristles which are, however, probably denser in distribution on the rear leg. Several flowers are visited before a full load of pollen is obtained, often flowers on more than one plant as they do not always visit contiguous flowers.

Where this species is abundant as in the colony of *O. hookeri* at Prairie Fork, pollen is collected from the time of anthesis until very near dark when bees were seen to approach the flower from the rear. In the morning the bees start collecting pollen again, usually with the first light. When most of the pollen is gone, they land directly on the stigma and clean off the available grains of pollen there. By this time they carry so little pollen that hardly any pollen transfer takes place.

Before or after the pollen is gone the bees turn to collecting nectar. When gathering nectar *Xylocopa tabaniformis* orients itself briefly in front of the flower as it does when collecting pollen but goes right over the anthers, up and over the corolla and then down the outside of the hypanthial tube head first. Stopping near the base, the bee inserts its galeae, making two small incisions, and obtains what nectar is left in the hypanthial cavity (Fig. 9d). The bee is very skillful in getting to the tube and very little pollen is brushed off in passing the anthers, this small amount being stored quickly on the rear scopae so that if the bee is not loaded with pollen when collecting nectar, little pollen is transferred. Several times at East Highland much pollen was left when most of the bees turned to nectar collecting, and some individuals were collecting both pollen and nectar, pollinating very effectively. This species removes a great deal of pollen when numerous and can lower the pollinating efficiency of hawkmoths that visit the flowers later. A second species, *Xylocopa brazilianorum varipuncta*, was observed at several colonies of *O. hookeri* but was seldom abundant enough to effect total pollination greatly. The behavior of this bee is similar to the first but it is nearly twice as big so that it is individually a more efficient pollinator.

Apis mellifera was often abundant in the morning and rarely abundant in the evening at colonies of several species, particularly *O. hookeri* and *O. deltoides*. These bees approach the flower and fly almost in place in front of it as if orienting themselves. Then they usually approach directly at the level of the stamens, just above the stigma, sometimes landing on

the anthers or a single anther, sometimes going past the anthers to the opening of the hypanthium or rarely landing on the stigma. Although *Apis* is well adapted for handling the pollen of a wide variety of plants, it is very clumsy when handling the pollen of *O. hookeri*, the grains being comparatively large and connected with viscin threads. They gather pollen on the anthers and try to work it into the pollen baskets as usual but it apparently will not go into them, instead dangling down from the rear legs and finally dropping off in irregular masses (Fig. 3c and 9e). Even when a single bee has dropped a great deal of pollen, it continues to attempt to pack the pollen, sometimes landing on the plant while so engaged.

As the bees are often over the flowers while dropping pollen, some lands on the stigma or more often is brushed off on the stigma as the bee goes in toward the anthers. They do, of course, carry some pollen away but probably only a small portion of what they have harvested. When pollen is gone from the anthers, *Apis* will land directly on the stigma and attempt to collect, thus distributing pollen over the stigma and taking off some of the clumped grains.

Although inefficient, *Apis mellifera* is often present in abundance and can be an important pollinator when the normal agents are absent. Of course, it is an introduced species and has not been a factor in the evolutionary history of these species.

Several bees of the genus *Andrena* (*Onagrandra*) have oligolectic relationships with several species of *Oenothera* in the subgenera *Chylismia*, *Eulobus*, *Sphaerostigma* and *Taraxia*. The bees usually arrive shortly after these flowers open and take the pollen before any competitors appear. The small flowers of such plants are regularly pollinated while these bees are collecting pollen. *Andrena* (*Onagrandra*) *linsleyi* is oligolectic on *Oenothera deltoides*. This bee goes into the flower from the front, usually landing directly on the stamens. It is not a very efficient pollinator, my estimate at Twenty-Nine Palms being one flower pollinated for every five visited and pollination was usually light. Therefore these bees must be numerous to do a significant amount of pollinating and will only be effective when hawkmoths are scarce or absent. Much data on the behavior of bees in this subgenus have recently been published (Linsley, MacSwain and Raven, 1963a, b, c).

Other species of bees on several species of *Oenothera* and the bombyliid and syrphid flies that are commonly found on and near the flowers of *O. hookeri* seldom transfer pollen and their behavior will not be described here.

MORPHOLOGY

Species of Sphingidae have tongues which range in length from less than a millimeter (*Smerintbus*, *Pachysphinx*) to 25 cm in *Cocytius cluentius* of tropical America. Proboscis length in the species described here ranges from 2.7 cm in *Celerio lineata* to 13.7 cm in *Phegethontius quinque maculata* and *P. rustica* (Table 13). This extreme variation parallels the variation in length of hypanthium between species that has been discussed for *Oenothera* and which is present in several other plant genera. It is probable that the evolution of longer hypanthia is an adaptation increasing pollination by hawkmoths with longer tongues. This could be a direct relationship between a given moth species and a given plant species or selection could operate through the increased spectrum of pollinators open to a plant with a longer hypanthium in an area where moths of various tongue lengths were present.

If the first hypothesis is true one would expect to find the plant species with longer hypanthia pollinated more by long-tongued hawkmoths than by moths with medium-long tongues. This was not clearly the case with any of the species of *Oenothera* of this type studied during this work, in fact the major pollinator was *Celerio* for both *O. caespitosa* and *O. taraxacoides*. However the number of colonies studied and the brevity of the period of

observation make the data inconclusive. A better-documented tendency was for the long-tongued moths to visit the shorter-tubed species of *Oenothera* and compete for the nectar with the more effective pollinators. The geographic distribution of the moths and plants in western America does support the general hypothesis. The hawkmoths with longer tongues such as *Pblegethontius sexta*, *P. quinquemaculata*, *P. rustica*, *Herse cingulata* and *Cocytius antaeus*, a species not encountered during this study, were much more abundant in the southwest than in the north, and the last three are primarily Mexican. *Celerio* and some of the species with relatively short tongues are more equally abundant north and south. A number of genera of plants in western America have several species with hypanthia that correspond in length to the tongue length of the relatively short tongued hawkmoths and one species, almost always in the southwest, with a much longer hypanthium or spur corresponding in length with the tongues of the longer-tongued moths. Among the genera showing such a pattern are *Oenothera*, *Aquilegia*, *Abronia*, *Mirabilis* and *Acleisanthes*. In *Oenothera caespitosa* such a pattern is shown less dramatically by the several varieties, hypanthia generally being shorter in the northern and longer in the southwestern populations. More work on a species such as *O. caespitosa* is needed at many localities and over a longer part of the season before positive conclusions can be drawn.

Very few tongue measurements of hawkmoths are recorded in the literature. Table 13 gives averages and extremes for the species encountered during this study. Nearly equal numbers of males and females are represented in the samples measured as the sexes were equally abundant both at the flowers and at the light-trap. What variation there was in most species was due to overall size of moths; the tongue varied little independently of body size, as determined by a ratio calculated between wing length and tongue length which was very constant for most species. Variation between subspecies of *Sphinx chersis* in tongue length is independent of size, and might indicate selection for longer tongues in the moth populations of certain areas. The sample of *Pholus achemon* from Big Bend National Park probably also shows significant difference in tongue length from the moths of California.

In the three most abundant species, *Celerio lineata*, *Pblegethontius sexta* and *P. quinquemaculata*, little significant variation was found over large geographical areas. Variation was least in *C. lineata*, while the two species of *Pblegethontius* were slightly more variable and differed overall by about 1 cm although individual specimens of the two overlapped broadly. One small collection of *P. quinquemaculata* taken visiting *Acleisanthes longiflora* in Texas had a definitely longer average tongue-length, but the differences was probably not statistically significant.

HAWKMOTH DISPERSAL IN RELATION TO CROSS-POLLINATION

The species of *Oenothera* studied during this work grow in small or large colonies, several of which make up a population. These larger units are often separated by a distance of several miles or more. To what extent such widely spread populations of *Oenothera* interbreed is of interest to anyone concerned with evolution and speciation in the genus. Hawkmoths are the most important pollinators of these species and these insects seem to be ideal agents of long distance pollen transfer. Little direct evidence has been obtained to prove whether or not such transport takes place but a discussion of some of the indirect evidence, mainly evidence on hawkmoth dispersal, may be in order here.

Several factors of the hawkmoth life-cycle and facets of hawkmoth behavior suggest that these insects often range over a wide area during the life span of the adult. Many of the species have an innate tendency to wander from the place where they emerge. I quote Rothschild and Jordan (1903). "As the greater number of species have a powerful flight,

and are, moreover, often wanderers, covering wide distances, the area inhabited by some of the species is very extensive." The term wandering implies random dispersal and this behavior does seem to occur in some species of Sphingidae. Dispersal can of course be caused by more specific factors. The three most important are (1) the search for a source of nectar required by the very active adults, (2) the search for the larval food plant, sometimes a specific species but more often one of several, and (3) the necessity of water for the adult in addition to nectar. The two types of food plant often do not grow together and even species having great latitude in plant species that can be utilized, such as *Celerio lineata*, often cannot stay in one small area. Competition for larval food plants undoubtedly intensifies dispersal when numbers of hawkmoths are high as is often the case with *C. lineata*, at least in the southwestern United States.

TABLE 13. Length in centimeters of proboscis in various western American species of Sphingidae.

SPECIES AND LOCALITY	MEAN	STANDARD DEVIATION	RANGE	NO. OF MOTHS
<i>Celerio lineata</i>				
Numerous widespread colonies, California to Colorado and Texas	3.8	.4	2.5-4.8	425
<i>Xylophanes tersa</i>				
Big Bend National Park, Texas	3.5		3.2-3.7	5
<i>Pholus achemon</i>				
<i>Oenothera hookeri</i> , several colonies	4.3		3.9-4.5	15
Big Bend National Park, Texas	5.0		4.8-5.3	3
<i>Sphinx libocedrus</i>				
<i>Oenothera greggii</i> , Sanderson, Texas	4.5			1
<i>Sphinx chersis oreodaphne</i>				
<i>Oenothera hookeri</i> , several colonies, California	4.4		3.8-4.6	7
<i>Sphinx chersis gerbardi</i>				
<i>Oenothera brachycarpa</i> , Charleston Park, Nevada	5.9		5.8-6.1	2
<i>Sphinx chersis chersis</i>				
<i>Oenothera caespitosa</i> , Arizona and Colorado	6.1		5.3-6.9	4
<i>Sphinx drupiferarum</i>				
Mesa Verde National Park, Colorado	6.0		5.1-7.0	4
<i>Sphinx perelegans asellus</i>				
<i>Oenothera hookeri</i> , two colonies, California	6.1		5.8-6.5	3
<i>Sphinx istar</i>				
Big Bend National Park, Texas	6.9			1
<i>Herse cingulata</i>				
Two colonies, Texas	9.6		9.3-9.9	2
<i>Phlegethontius sexta</i>				
Several colonies, California	9.0	1.2	5.9-12.1	94
<i>Phlegethontius quinquemaculata</i>				
Several colonies, California to Texas	10.3	1.2	7.7-13.6	42
<i>Phlegethontius quinquemaculata</i>				
<i>Acleisanthes longiflora</i> , Sanderson, Texas	13.0		12.1-13.7	3
<i>Phlegethontius rustica</i>				
<i>Acleisanthes longiflora</i> , Sanderson, Texas	13.7			1

Many species of moths move seasonally in a given direction over long distances in large or small numbers, and this phenomenon is called migration (Williams, 1957; Ford, 1955) although return to the place of origin has been documented for only a few species and may not be a regular characteristic of migration in this sense. I quote Williams (1957) on this phenomenon in the Sphingidae in general and *Celerio lineata* in particular.

"In the moths very extensive migrations occur in many species of the Sphingidae, which are unusually large insects with a powerful flight. Out of 17 species of the family known

to occur in Britain, 8 are complete migrants and seldom or never survive the winter in these latitudes. One of the most interesting species is *Celerio lineata* (Fabricius) which has one subspecies, *C. l. lineata* (Fabricius) in America, and another, *C. l. livornica* (Esper) in Africa and Europe. The latter breeds in North Africa during the winter and invades Europe in small or large numbers in the spring . . . In North America there is a very similar state of affairs. The insects breed during the winter somewhere in Central or South America, almost certainly in the semiarid climate of the western coast. Thence they move north in the spring into the southern states . . .”

I made one collection at the light-trap that may be an illustration of such migration. On 11 June, 1960, 50 miles north of Van Horn, Texas, I ran the light-trap between 9:00 and 10:00 pm in a very dry desert habitat with no evidence of annual plants for several miles. Five individuals of *Celerio lineata* were taken which must have been flying at some distance from adult or larval food plants. What is probably the same phenomenon is illustrated in faunal lists, for example Tietz in his *Lepidoptera of Pennsylvania* mentions a number of species of hawkmoths that are native to the deep south but occasional in Pennsylvania, out of range several hundred miles.

There is much evidence that insects can be carried long distances by wind or taken up by rising air currents and displaced on descent. Wallace (1889) cites several records of moths taken at sea as much as 1000 miles from land and Mani (1962) gives extensive records for insects carried high into the Himalayas by rising air currents.

The morphological uniformity of many species of hawkmoths over a very large geographic area also attests to dispersal and interbreeding over a wide range. Rothschild and Jordan (1903) state that a very high proportion of hawkmoth species, especially in the subfamilies with more powerful flight, are geographically uniform compared with the situation in other families of Lepidoptera, in which species show more subspeciation. For example, *Celerio lineata* is found throughout the world and has only three subspecies. One inhabits continental Asia, Africa and Europe, a second tropical Australia, and a third the Americas from Canada to Argentina. If this species and its subspecies are as uniform as Rothschild and Jordan indicate, then exchange of genes must be geographically very extensive. *Phlegethontius sexta* is another example of wide geographic uniformity and there are many others.

The categories of evidence cited above all indicate movement of individual hawkmoths over a wide area during their adult life. In the summer of 1961 at the colony of *O. bookeri* near East Highland, California, an experiment was attempted to determine the rate of turnover of individuals in the local hawkmoth population. Moths were captured on 14 nights over a period of a month, marked and released, and recaptures on the following nights were recorded. The results were not conclusive enough to warrant giving them in detail and were mainly for *Phlegethontius sexta* which is not an important pollinator at this colony (although it does carry pollen on the proboscis). However a rapid turnover in the local population of *P. sexta* was indicated by the rapid decrease in number of moths recaptured from a given previous night, and by the very different total number of moths taken per night. For example, of the 50 moths marked on August 5, five were recaptured on the 16th, four on the 17th, three on the 19th and 20th, none on the 22nd, one on the 23rd and one again on the 28th. On the dates not mentioned no work was done. No moths marked on the 5th were taken after the 28th. Both of the above phenomena could be explained either by mortality or by dispersal but the data did not make it possible to determine definitely which was the more important in this area. There was little doubt that arrival of new individuals and departure of other individuals, including marked moths, were taking place. Differences in number of captures at the light-trap did not correlate with

the slight changes in temperature from night to night, with amount of moonlight or with any other environmental factor that I could determine. It seems certain that *P. sexta*, and probably the other species also, move into and out of the colony in one or a very few nights.

How long pollen adheres to hawkmoths in flight is not known but large quantities are carried in flight through a colony while visiting the flowers and since the moth has no means of cleaning its underparts, some at least must remain for long periods.

There is some evidence that pollen is distributed between scattered colonies over a wide area. In 1937 Emerson (1939) studied four colonies of the self-incompatible *Oenothera organensis*, which is undoubtedly pollinated by hawkmoths, in the Organ Mountains of southern New Mexico. As described by Emerson the plants grew in gravel-filled pockets in the eroded floor of several steep-walled canyons at elevations above 6000 feet. The plants were scattered in small groups down the canyons. Emerson estimates that "the entire population of this species consists of less than 1000 plants and very likely less than 500." Many plants were grown from seed and cuttings collected in four canyons. Two of the colonies were at Dripping Springs, one in the East Fork and one in the North Fork of the canyon, the two colonies being 600 feet apart and separated by a ridge 300 to 400 feet high. A third colony was a Modoc Waterfall which is just under a mile from the colonies at Dripping Springs with "high land" in between. The fourth colony was in McAllister Canyon, three miles from the first localities and separated from them "by the highest part of the range." Each colony was made up of several small groups of plants spread up the canyon.

Many plants were grown in Pasadena and the number of alleles of the self-sterility (S) locus for each colony was determined by crosses (Emerson, 1938, 1939). These alleles were mutations at a single locus and of separate origin. A total of 37 alleles of this gene was identified and the distribution between canyons (excluding Modoc Waterfall) was as follows: 14 alleles were found in only one of the colonies, 14 were found in two of the colonies and eight were found in all three of the colonies. Modoc Waterfall had alleles which occurred in each of the other colonies. This shows that there was some gene exchange even over a distance of three miles across the highest part of the range. Based on an assumption that the total population effectively falls into 50 inbreeding groups of 10 plants each, and given a mutation rate of about 10^{-5} or 10^{-6} , Sewall Wright (1939) has suggested that inbreeding occurs approximately 98% of the time, intergroup crossing 2% of the time. This seems to me to be a realistic figure considering what is known of hawkmoth behavior.

DISCUSSION

The flowers of species of *Oenothera* in the subgenera *Oenothera*, *Salpingia*, *Pachylophis*, *Anogra*, *Raimannia*, *Lavauxia*, *Gauropsis* and *Megapterium* have flowers with the following characteristics in common. (1) relatively large corolla lobes which are white or yellow and conspicuous, especially in dim light, (2) a long, narrow hypanthium with nectar at the base, (3) exserted style and stamens, the stigma usually well beyond the anthers and of elongate lobes or peltate, (4) abundant pollen which is held in masses by viscin threads, (5) a weak or strong, heady, sweet odor given off at night, (6) anthesis shortly before or after sunset. These characteristics are specializations for attraction of and pollination by large nocturnal moths of the family Sphingidae, although they do not limit the visiting species to members of this family or insure that all of such moths will be effective pollinators. These moths feed on the nectar at the base of the hypanthium.

Almost all of the species of *Oenothera* studied during this work were visited both by hawkmoths with relatively short tongues and by hawkmoths with long tongues. The rela-

tively short tongued moths were probably not able to reach the main nectar reservoir in the flowers with longer hypanthia, yet they continued to visit these flowers. In species such as *O. taraxacoides* and *O. caespitosa* with long hypanthia both types of moth were effective pollinators, but in species such as *O. hookeri*, *O. deltoides* and *O. greggii* with shorter hypanthia only the moths with relatively short tongues were consistent pollinators. In the second case, the flowers are adapted for pollination only by those with shorter tongues, whereas the flowers with longer hypanthia are adapted for pollination by both types of hawkmoths. The species of *Oenothera* with long hypanthia which were studied during this work had a greater range of pollinators, as the shorter tongued hawkmoths, especially *Celerio*, were always as abundant and usually more so than moths with longer tongues at these flowers.

Many colonies of species with short hypanthia, especially *O. hookeri*, *O. greggii* and *O. hartwegii*, were also visited by both long and shorter tongued hawkmoths in abundance. In these cases the long tongued moths, particularly the two species of *Phegathontius*, were competing with short tongued moths for nectar but doing very little pollinating. It is probable that an increase in length of hypanthium would be selected for in such colonies, since it would increase the number of effective pollinators among the moths already visiting the flowers. For example two species of *Oenothera* in which such an adaptation may have taken place are *O. jamesii* of northern Mexico, Texas and Oklahoma, and *O. longissima* of southern Utah and Nevada and northern Arizona. These species are similar to *O. hookeri* both morphologically and chromosomally (Cleland, 1950). Their flowers are larger, however, with a hypanthium up to more than twice the length of the hypanthium of *O. hookeri*, 6-11 cm in *O. jamesii* and 8-12 cm in *O. longissima* (Munz, 1949). This elongation of the hypanthium may well be an adaptive response resulting in increased pollination.

The floral specializations enumerated in the first paragraph do not limit the spectrum of potential visitors to hawkmoths. Pollen is readily available and abundant and is collected by bees both in the short interval between opening and complete darkness and during the following morning if still available. Some of these bees are even specialized to work in near or complete darkness, for example *Lasioglossum (Sphex) dogastra*. On the other hand bees are not able to obtain nectar from these flowers easily; however, some species visit the mouth of the hypanthium, and *Xylocopa* cuts through its base. Some of the bees visiting *Oenothera* for pollen or for nectar bring about pollination, and some, as we have seen, adversely influence potential pollination by competing for nectar or by removing pollen.

Where bees capable of pollination are an important part of the spectrum of visitors the plant species may show a shift from their close adaptation to hawkmoths toward bees. One example of this is shown by colonies of *O. greggii* and *O. hartwegii*. The flowers of these plants are well adapted for pollination by hawkmoths but in some colonies the flowers open earlier than others. This might well be a consequence of bee pollination during the late afternoon, earlier opening make the flowers available to the bees for a longer time before dark. There is not enough data to substantiate this possibility completely but the observation at Monahans, Texas, indicates strongly that earlier opening time may be an adaptation to another group of potential pollinators. The influence of regular late-afternoon bee pollination on time of anthesis has been shown by Raven (1962) in *O. clavaeformis*, one of the few species of *Oenothera* subgenus *Chylismia* having flowers that open in the evening. In the subspecies regularly visited by the oligolectic bee *Andrena (Onagrandrena) rozeni*, the flowers open earlier than in those subspecies visited by other, less closely adapted, bees. These subspecies are also visited by small moths after dark and it is probable that earlier opening has been a consequence of late-afternoon bee pollination in this species.

Another consequence of bees gathering pollen from flowers of *Oenothera* species not adapted for pollination by them was illustrated by the observations on *Oenothera drummondii* in Texas. In this colony the species *Lasioglossum (Sphæcodogastra) texanum* was very abundant collecting pollen but hardly ever pollinating because of its small size. This bee is adapted for collecting *Oenothera* pollen in two ways (Linsley, 1958); it is nocturnal, having enlarged ocelli, and it has scopae which are specialized for collection of the large grains of *Oenothera* pollen which are connected by viscin threads. The bee was so abundant and such an efficient collector that a great deal of pollen was removed from the flowers of this colony before any hawkmoths, which are the effective pollinators, appeared, greatly reducing the effectiveness of the hawkmoths in pollen transfer. In this case the increase of an added species of regular and abundant visitor seriously decreased the amount of pollination rather than supplementing it.

During observations of *Oenothera wigginsii* in Baja California in 1960 and 1962 very few insects of any kind, and no hawkmoths, were observed at the flowers. The only bee taken at the flowers was an individual of *Hesperapis* sp. but two specimens of *Anthophora* sp. were captured carrying pollen. The first bee was not an effective pollinator but the second bee could have been. *Oenothera wigginsii* is very closely related to *O. deltooides* of the Mohave and Colorado deserts (Klein, 1962) but is geographically well separated from it, occurring 75 miles to the west on the other side of a high mountain range. It differs from *O. deltooides* in being self-compatible and in having smaller flowers with a short style that brings the stigma so close to the anthers that self-pollination can easily be effected by a moderate breeze. Although the flowers still have basic characteristics adapted for pollination by hawkmoths, self-pollination is the mode. The species is in a marginal habitat when compared with its close relative *O. deltooides* as far as ecology is concerned. Colonization of such a habitat is favored by duplication of a well adapted genotype which is in turn made possible by self-pollination. In a plant with a basically outcrossing flower colonizing an area where pollinators are scarce self-pollination might also be favored.

SUMMARY

The eight subgenera of *Oenothera* considered here have highly specialized flowers. This complex of specializations is for pollination by hawkmoths but does not limit the spectrum of visiting insects to hawkmoths.

At the eight colonies of *O. bookeri* studied in various habitats in southern California, some of them through a complete flowering season, a wide variety of insect species was observed visiting the flowers (Table 2). Different combinations of these insects were seen at different dates during the summer and abundance of any one insect also varied with the date of observation (Fig. 4, 5, 6 and 7). The most abundant visitors to the flowers were three hawkmoths, *Celerio lineata*, *Pholus achemon* and *Phelegethontius sexta*, and three bees, *Xylocopa tabaniformis orpifex*, *X. brazilianorum varipuncta* and *Apis mellifera*. All of these did some pollinating but on most occasions *Celerio* and *Pholus* were much more important. The colony at Prairie Fork was an exception because of differences in relative abundance of both hawkmoths, which were rare, and carpenter bees, which were very abundant. Here the bees were, at least for part of the season, as important or more important than hawkmoths as pollinators.

At the 27 colonies of species in the other subgenera of *Oenothera*, most of them observed only once, a wide variety of insect visitors was also seen (Tables 8, 9 and 10). *Celerio lineata* and *Phelegethontius quinque maculata* were the most abundant visitors at the flowers of almost all of these species, with different species of *Sphinx* being abundant at certain colonies, especially in montane localities. Bee species were very different depending on the

location of the colony and the species of *Oenothera*, and none of the bees is as widely distributed as the two species of hawkmoths. Total abundance of insect visitors varied greatly from the very high numbers of *C. lineata* visiting *O. deltooides* on the Mojave Desert of California to the one bee seen at the flowers of *O. wigginsii* in Baja California. *Celerio lineata* was the most important or one of the important pollinators at colonies of almost every species, both species with short and those with long hypanthia. *Phlegethontius quinquemaculata* was also an important pollinator at colonies of species with long hypanthia, though rarely as important as *C. lineata*. Bees were important pollinators of *O. greggii* and *O. hartwegii* in certain localities and did some pollinating of other species especially when hawkmoths were rare. At the colony of *Oenothera drummondii* bees had a negative effect on pollination by removing pollen in quantity without pollinating. They undoubtedly played a similar role at colonies of other species but to a lesser extent. *Oenothera wigginsii* in Baja California is apparently largely self-pollinated.

Hawkmoths are probably one of the most wide-ranging of insect groups because of their strong flight and tendency to wander and migrate. Some evidence of these tendencies was obtained during a short capture-recapture experiment and on running the light-trap in open desert away from food plants. The wide-ranging behavior suggests that hawkmoths may be responsible for small amounts of pollen dispersal over long distances. No evidence of such dispersal was obtained during this work but one case in the literature is discussed (Emerson, 1939).

The species of *Oenothera* investigated show several types of breeding system. The flowers in the subgenera included in this study are basically of an outcrossing type. Many of the species are also self-incompatible which assures cross pollination. Others such as *O. hookeri* are self-compatible and since hawkmoths do transfer pollen from flower to flower on a single plant as well as transferring some pollen from stamens to stigma of a single flower, a certain percentage of self-pollination does take place in self-compatible species even if the flower is of an outcrossing type. This percentage is usually over 50% in *O. hookeri* but varies over a wide range depending on many factors. *O. wigginsii* is self-compatible and the floral morphology has changed enough so that self-pollination seems to be predominant.

The hawkmoth species visiting the flowers of the species of *Oenothera* observed fall into two groups, those with relatively short tongues (*Celerio lineata*, *Pholus achemon*) and those with long tongues (*Phlegethontius sexta*, *P. quinquemaculata*). If a moth of either group is visiting an *Oenothera* flower with a hypanthium of a length equal to or greater than that of its proboscis, so that its body comes in contact with stigma and stamens, pollination is effected by pollen carried on the legs and to a lesser extent on the body of the moth. The pollen is carried in large masses because the grains are held together by viscin threads. If a long tongued moth is visiting a flower with a much shorter hypanthium little pollination takes place. Since species of both groups of hawkmoths were abundant at most of the colonies of *Oenothera*s, both those with short and those with long hypanthia, it is probable that the long hypanthium is an adaptation making possible pollination by all of the hawkmoths visiting the flowers instead of only those with relatively short tongues.

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