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HAWKMOTH POLLINATION IN THE GENUS *OENOTHERA*¹

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INTRODUCTION

The genus *Oenothera* is large and heterogeneous, comprising approximately 125 species in 15 subgenera. Nearly all of the species in nine of the subgenera have large, white or yellow flowers which open just before or after sunset. In the other six subgenera the species have much smaller, usually yellow flowers, the majority opening in the early morning, and pollinated primarily by bees. The study presented here deals with 15 species scattered in eight of the evening flowering subgenera of *Oenothera*.

The first student of floral biology, Joseph Kölreuter, who published his observations on insect pollination in 1761-66, considered *Oenothera* among other examples. The first worker to describe the floral biology of this genus in some detail was Christian Sprengel, who described and figured the floral morphology of *Oenothera biennis* in 1793 and suggested that this species must be pollinated by nocturnal insects. The general characteristics of the nocturnal hawkmoth flower were later developed by Federico Delpino (1868-74), Hermann Muller (1873) and P. Knuth (1898), the characteristics given including nocturnal anthesis, pale color, strong agreeable odor, and nectar secreted at the bottom of a long corolla-tube or spur.

Several other European workers have added to the concept of the hawkmoth flower during the twentieth century, both by field observation in Europe and in the tropics and by assumption from floral morphology. One, Fritz Knoll, did basic work on sensory perception in both day and night flying hawkmoths (Sphingidae) published in papers from 1922 on.

The first worker to seriously consider the concept of the nocturnal moth flower in terms of a portion of the North American flora was Verne Grant who made field observations of four species of *Oenothera*, *O. californica*, *O. deltoides*, *O. hookeri* and *O. caespitosa* in southern California from 1950 onwards. These species all show the characteristics that in the 200 years since Kölreuter's work have come to be recognized as adaptive in attracting nocturnal moths. Grant's observations confirmed the supposition that these species of *Oenothera* were visited by hawkmoths and were often pollinated by them.

With the foregoing as a point of departure, I began in 1958 an intensive study of hawkmoth behavior in relation to the floral biology of several species of the genus *Oenothera*.

The species studied in greatest detail was *Oenothera hookeri* (subgenus *Oenothera*), picked for concentrated observation because it is common in southern California and the several colonies picked for study were readily accessible to Claremont.

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

Species in several other subgenera were studied as follows: In the subgenus *Anogra* five species were included: *O. deltooides* in the Colorado and Mohave deserts of California, *O. wigginsii* in Baja California, *O. californica* in the Mohave desert of California, *O. engelmannii* in Texas, and *O. runcinata* in New Mexico. In the subgenus *Raimannia* three species were studied: *O. albicaulis* in Texas, *O. drummondii* along the Gulf coast of Texas, and *O. laciniata* in central Texas. In the subgenus *Pachlophs* two subspecies of *O. caespitosa* were examined at several stations from California to Arizona and western Colorado. Two species of subgenus *Galpinsia* were studied: *O. greggii* and *O. hartwegii*, both in western Texas. Of the subgenus *Lavauxia* one species, *O. taraxacoides*, was studied in the Sacramento Mountains of New Mexico. A single species in subgenus *Megapterium*, *O. brachycarpa*, was studied in the Charleston Mountains near Las Vegas, Nevada. These species were studied in from one to five localities but for only a single night and morning at each, so that the data are not as complete as for *O. hookeri*. These subgenera show marked variation in floral morphology, although definitely on a common theme and always exhibiting the complex of characteristics listed above. Represented among them are species with quite different breeding systems.

This study has yielded evidence on the following problems. (1) The relative importance of hawkmoths as pollinators of the species of *Oenothera* studied and the exact description of such pollination. (2) The question of whether morphological differences in the flowers adapt them to specific pollinators and, if so, if pollination is restricted to these particular animals. (3) The change in spectrum of pollinators for a single species or morphological type of *Oenothera* flower with changes in geographical area or in habitat. (4) The occurrence of differences in breeding system between species of *Oenothera* and the significance of such differences. (5) The abundance and behavior of the pollinating insects.

METHODS

The main method used during this research was direct field observation. This was supplemented in several ways. Photographs of the flowers and of the visiting animals were taken with a 35 mm camera. A strobe light was used for photography after dark. Moths and other insects were captured for identification, to measure morphological characteristics having to do with pollination, and for a capture-recapture experiment. They were taken either at the flowers with a net or at a light-trap composed of a 15-watt ultraviolet lamp set up in front of an ordinary sheet. This trap was usually set up within 10 yards of the plants.

At most of the colonies studied, a series of 50 flowers was emasculated about dusk and checked during the night and following morning with a series of 50 unemasculated flowers. This technique is described in more detail later. Vouchers of the plants studied were collected and have been deposited in the herbarium of the Rancho Santa Ana Botanic Garden. Flowers were often collected in FAA for study in the laboratory as well.

Specimens of a number of species were grown at the Rancho Santa Ana Botanic Garden for determination of self-compatibility relationships. This work was done in cooperation with Mr. William Klein.

ACKNOWLEDGEMENTS

I would like to thank the many people among the staff and students of the Rancho Santa Ana Botanic Garden who have helped in various ways during this study. I am greatly indebted to all of the professors at the garden, especially the following: Dr. Verne Grant suggested the general outlines of the problem and advised the study from beginning to end. Dr. Peter H. Raven read the manuscript critically and made many valuable suggestions concerning both interpretation and presentation. Dr. Philip A. Munz made suggestions on

the manuscript and Dr. Richard K. Benjamin supervised the preparation of the figures. Many of the former students at the garden have given both material aid and encouragement, particularly the following. I am very much indebted to William Klein for his help with the photography and for his ideas on methods of field observation. He also made many suggestions on interpretation while the work was in progress and supplied information on the compatibility relationships of many species. Charles Quibell, John Olmstead and Clifford Anastasiou all took an interest in the work and aided in various ways.

I wish to thank Lloyd Martin of the Los Angeles County Museum for many identifications of insects and for his critical reading of the manuscript. Dr. Jack Hall of Riverside identified the flies.

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POLLINATION OF *OENOTHERA HOOKERI*

Starting in June, 1961, seven populations of *O. hookeri* were studied from one to nine times, several from June through August or September or from the beginning of full flowering until flowering ceased. An eighth colony had been studied in 1959 at the mouth of San Antonio Canyon. The eight colonies, all in southern California, were the following (Fig. 1):

- (1) just east of East Highland in the foothills of the San Bernardino Mountains, San Bernardino County
- (2) Rancho Santa Ana Botanic Garden, Claremont, in the San Gabriel foothills, Los Angeles County
- (3) Coldwater Canyon in the San Gabriel Mountains, Los Angeles County
- (4) Grass Valley just west of Lake Arrowhead in the San Bernardino Mountains, San Bernardino County
- (5) San Antonio Canyon in the San Gabriel Mountains, Los Angeles County
- (6) near Temecula in southern Riverside County
- (7) Prairie Fork in the San Gabriel Mountains, Los Angeles County
- (8) just below Crestline in the San Bernardino Mountains, San Bernardino County.

Some of the eight colonies grew in disturbed areas but most were in relatively natural habitats, between them representing all of the ecological situations in which the plant grows in and near the San Gabriel and San Bernardino mountains. The observations at each of them are summarized and compared in this chapter.

THE COLONIES

East Highland.—The population at which the greatest number of observations were made grows outside of the small town of East Highland, about nine miles east of San Bernardino, at an elevation of 1100 feet. The land in this area slopes gently up from the Santa Ana River bottom in the valley to the foothills of the San Bernardino Mountains immediately above, this particular spot being in the valley rather than in the foothills. The plants grow in a long ditch about 15 feet wide situated between a branch line of the railroad on one side and a quiet country road on the other. Spreading for several miles on each side (Fig. 2a), it is an area of extensive orange groves which border both the road and railroad. These groves are watered regularly and some of this water undoubtedly reaches the ditch either directly or through seepage, for the plants flourished the whole summer. This is

certainly a "weedy" spot, very much influenced by the architectural and agricultural changes of man, but still not unlike those in which *O. hookeri* might grow naturally in a good year along the edge of the Santa Ana River.

The plants of *O. hookeri* grew in large numbers very close together as can be seen in the photograph (Fig. 2a) and when in flower presented a dense mosaic of many hundred

Fig. 1. The locations of the colonies of *Oenothera* studied.

flowers. They were not continuous down the whole 150 yards of the ditch but grew in clumps spaced several yards apart, of which the one in the picture was probably the largest.

The population at East Highland was discovered on June 23 and at this time there were only from 50 to 100 flowers open. The number of flowers open each night increased steadily, 200 to 300 flowers opening on July 1, as many as 500 opening on July 9, and an estimated 700 or 800 on July 15. On July 26 my estimate was that over 1000 flowers opened in the area which flowered first, and other patches were now coming into full flower, so that the total must have been at least 1500, possibly 2000 flowers opening per night. On August 23 the number of flowers was probably near the highest of these figures and this was probably

the maximum. The plants in the original area were through flowering on September 28 and the total number of flowers was down below 1000 again and dropping rapidly. The period of maximum flowering probably lasted 6 or 7 weeks at this colony, from around July 20 to

Fig. 2. Two habitats of *Oenothera bookeri* in southern California.—a. At East Highland, looking north toward the San Bernardino Mountains.—b. The habitat along the stream at Prairie Fork in the San Gabriel Mountains. The logs are probably nesting sites of *Xylocopa tabaniformis orpifex*.

September 10; however, the whole colony did not start at the same time so that the period of maximum flowering was somewhat prolonged.

This population was visited first on June 23 and 20 times thereafter, making a total of 21 visits. Of these eight were for general observations on floral biology and 14 for a short series of capture-recapture observations to attempt an estimate of hawkmoth population size and movement. On one night both types of observation were carried out. The work covered a period of slightly more than 3 months from June 23 to September 28 with the majority of visits for general observation falling in the first month and a half.

Maximum and minimum temperatures were recorded from the table in the *Los Angeles Times* for San Bernardino, the nearest station to the colony at East Highland. The average minimum temperature for San Bernardino was 66°F. Temperatures during the early hours of darkness were probably well within 10° of the listed minimum temperature. Most of the evenings at East Highland were clear and warm with at most a slight breeze.

Rancho Santa Ana Botanic Garden.—The population of *O. hookeri* growing in the Rancho Santa Ana Botanic Garden is cultivated along with the other native California plants that are grown there. The whole ecological situation is an artificial one, yet given the situation, *O. hookeri* is not out of place. The many plants growing in association with *O. hookeri* here that would not ordinarily be present constitute the greatest anomaly of the situation. The colony grows under small alder and sycamore trees near the intermittent stream at the west side of the garden. Actually there are four small sub-colonies separated by from 10 to 100 yards with shrubs and trees between.

The garden is just below the foothills of the San Gabriel Mountains at 1100 feet elevation, surrounded by a golf course to the west, orange groves to the north, and coastal sage scrub to the east and south with scattered houses on all sides. Just below the garden is the small town of Claremont proper. Therefore the surrounding area is nearly as disturbed as at East Highland, but is composed of various changes, with orange groves at a greater distance. The position of this colony relative to the mountains is similar to that of the colony at East Highland.

The plants at the garden grew in dense stands at each one of the four sub-colonies. The four groups of plants started blooming at different times because of differences in irrigation, so that except for the middle of the blooming period around July 21, when all four were blooming at once, there was not as large a number of flowers as at East Highland. Flowering started around June 1 and was completely finished except for a few odd plants by the end of August. A series of nine observations was carried out at this colony, from June 11 to August 21. Atmospheric conditions at the garden were similar to those at East Highland except that several evenings were damper. The average minimum temperature as recorded from the table in the *Los Angeles Times* for Ontario, the nearest station, was 63.5°F.

Coldwater Canyon.—On August 8 and 9, 1961, observations were made in a medium-sized colony of *O. hookeri* in Coldwater Canyon just southwest of Mount San Antonio in the San Gabriel Mountains. This colony was growing in and near an apple orchard at an elevation of 3900 feet. This area just above the floor of the canyon is watered by three springs, the surrounding plants including grasses, sedges, *Monardella* and *Stachys*. Large coniferous and broad-leaved trees grow along the stream below, while above trees grow on one slope and chaparral on the other. Some of the *O. hookeri* plants were scattered among the apple trees but most of them were on the open grassy slope just below the springs. Twenty or more plants grew in close proximity in one spot while the others, approximately 40 in number, were distributed singly or in small groups over an area about 100 yards in diameter. The plants were tall and strict as at Prairie Fork, but branched more, some of them bearing as many as 15 open flowers. The colony was nearly at the height of the flowering

period; the total number of flowers was approximately 450.

Grass Valley.—A small population of *O. hookeri* was studied in the dry bed of Grass Valley Creek, 2 miles west of Lake Arrowhead in the San Bernardino Mountains. The altitude of Grass Valley in this locality is approximately 5000 feet. The area is in a rather flat, grassy valley surrounded by low hills bearing a predominantly coniferous forest. The small creek, dry during the summer, has cut a wide bed some 15 to 20 feet deep into the valley floor, and this bed is filled with shrubs, many of them dead. Some of the plants of *O. hookeri* were scattered among the branches of these dead plants, some were in the small clearings between them. The plants grew singly or in small groups and were of strict habit, usually with a single inflorescence bearing from one to three open flowers each night. On July 19, early in the season for *O. hookeri* here, 27 flowers were found, at least twice as many were found on July 30, and on August 30, when the season was nearly over, only three plants still were blooming and they bore a total of six flowers.

Temperatures at Grass Valley were lower than at any other colony studied, falling to a low of between 35° and 45°F on the three nights of observation.

San Antonio Canyon.—The first colony of *O. hookeri* observed during this work was in San Antonio Canyon about 2 miles above the check dam, at an elevation of 3000 feet. It was situated immediately beside the old road in the bottom of the canyon near one of the few springs. The colony grew under sycamores and alders with sedges, *Mimulus cardinalis* and other herbaceous plants characteristic of such a wet spot. At the height of flowering, there were about 35 strict plants bearing a total of under 200 flowers.

Temecula.—A large population of *O. hookeri* near Temecula (elevation 1000 feet) in San Diego County was studied for one night on July 16, 1961. This was a very large population growing in a fallow field, a colony which unfortunately was in its last few days of flowering. The scattered plants were taller with less branching than at any other colony studied, and even though it was late in the flowering season, 200 or 300 flowers must have been open, rarely more than one or two on a plant.

Prairie Fork.—One of the most interesting colonies studied during the summer of 1961 was along Prairie Fork, a small tributary of the East Fork of the San Gabriel River lying to the northeast of Mount San Antonio in the San Gabriel Mountains. The elevation of the area is about 4500 feet. The stream flows through the canyon bottom which is 100 yards wide and is heavily wooded near the stream (Fig. 2b). Elsewhere the canyon has large areas of perennial herbs and shrubs as well as open areas of gravel with scattered plants. In all of these areas there are many large logs in varying stages of decomposition, probably washed down by flooding; these are undoubtedly the nesting sites of the very large population of *Xylocopa tabaniformis orpifex* found here (Fig. 2b).

Plants of *O. hookeri* were scattered intermittantly over the whole canyon bottom both in the wooded and more open habitats. An area about 400 yards long was studied during these observations, but the plants grew continuously for at least a mile down the canyon and probably a good distance up stream also. There were a great many plants in the whole population. In certain spots a number of plants grew together but never in dense stands as at East Highland and the Rancho Santa Ana Botanic Garden. Most of them were scattered singly or in twos or threes. The habit of the plants at Prairie Fork was stricter. The total number of flowers in the whole population would be hard to estimate; in the area of these observations there were approximately 1250 flowers on August 1 when all plants were in full bloom. On July 12, the first night of observation, when the plants were just beginning to bloom, there were less than 500 flowers open. Many plants had finished blooming on September 6 so that the number of flowers was probably lower than on either of the previous dates.

At Prairie Fork the early evenings were nearly as warm as at East Highland. The temperature dropped lower during the night so that the early mornings, especially on September 6, were somewhat colder.

Crestline.—Three brief observations were made of a small colony of 20 plants growing on a steep bank above the road to Lake Arrowhead just before the place where the road goes under the overpass to Crestline, at an elevation of 4300 feet. The population is an isolated one, watered by a spring from above, and the area in general is very dry. On July 5, 20 flowers were open. The colony was watched until 10:45 p.m. During this time hundreds of cars went by about 25 feet from the flowers—an almost uninterrupted stream of cars which probably lasted well into the night. On two later mornings, the amount of pollination was checked.

FLORAL MORPHOLOGY

The flowers of *O. hookeri* (Fig. 3b and 9a) are relatively large, with corolla lobes 2.0–4.5 cm long and nearly as wide near the apex, and a narrow hypanthium 2–5 cm long with nectar at its base. The stamens and style are exserted, with the stigma a centimeter or more beyond the anthers. The predominant color of the corolla lobes is light yellow. Flowers of this species have a very slight sweet odor to the human nose. The flowers open in the evening shortly before or after sunset.

Arnold (1959; also, Hillman, 1962) found that in *O. berteriana* and *O. campylocalyx* the time of day at which the flowers open is set by the day length that the buds have been subjected to previously and is nearly independent of other environmental factors. That this may not be strictly true for *O. hookeri* is suggested by the abnormally early opening of the flowers at the Rancho Santa Ana Botanic Garden on the overcast evening of July 2. Time of anthesis relative to sunset varied with the colony over a narrow range. At the populations in San Antonio Canyon and Coldwater Canyon, anthesis started from 20 to 30 minutes after sunset. In the colony at East Highland the flowers started opening 15 minutes after sunset. In the population at Crestline, anthesis started a few minutes before sunset, at Prairie Fork and the Rancho Santa Ana Botanic Garden about 15 minutes before sunset and at Grass Valley 20 minutes before sunset. There was a range of 50 minutes for the colonies studied. Each flower opened in approximately 5 minutes, but 20 to 30 minutes elapsed before all of the flowers in a colony were open. All of the flowers at all of the colonies were open before full darkness.

The opening flowers first crack along one seam of the calyx. The stigma is either just within the calyx or already outside the calyx, and sometimes the stigma lobes are spread before the flower starts to open. After the first crack appears, the petals start to unroll and as they exert pressure on the calyx the other three calyx seams open at the base, then begin to bulge. Next the whole calyx starts to slip down the corolla as the whorl of petals unrolls further and this, of course, allows for more and faster unrolling. As the slipping continues, the corolla finally becomes free from the clasping calyx and, pushing it aside, expands fully in another minute or two. The pressure that has been present at the base of the petals is made evident in the pushing of these organs beyond the plane that they usually assume later, as if the flower were starting to turn inside out. The stamens spread, disposed in an arc of usually 200° in front of the lower petals (Fig. 3b). The filaments are curved so that the pollen is presented upwards, the versatile anthers sometimes nearly parallel with the ground and sometimes tilted slightly toward the front. The plane of the corolla is tilted ca. 20° back from the vertical which brings the anthers towards the horizontal (Fig. 3a). The style is often in the same plane as the anthers but there is much variation. Often the style hangs down at as much as a 30° angle to the plane of the anthers.

Fig. 3. Flowers of *Oenothera bookeri*, a, b and d taken shortly after dark, c taken in the morning.—a. An emasculated flower from the front showing the mouth of the hypanthium and a flower in side view, flower unvisited. Note the loops of loose pollen hanging from the anthers.—b. The flower from directly in front.—c. Heavily pollinated flower. Notice the pollen looped over the stigma from the anthers and the clump of pollen on the lower petal, probably dropped by *Apis mellifera*. This flower is both cross- and self-pollinated.—d. A flower at Prairie Fork just after an evening visit by a pollen collecting individual of *Xylocopa tabaniformis orpifex*, showing slight self-pollination. Note the strings of pollen.

Looking at the flower from the front, each petal is nearly obcordate in shape with a ridge running down the center (Fig. 3b). To the human eye the four ridges radiate more clearly from the center than do the edges of the petals. Yellow is the predominant color of the petals but they are greenish just at the base around the opening of the hypanthium.

The hypanthium is about 3 mm in inner diameter at the orifice, narrowing to 1.5 mm

approximately 1 cm below and maintaining this diameter to the base (assuming in this example that the hypanthium is 4 cm long). The walls of this tube are covered with hairs of two kinds. Starting approximately 1 cm below the orifice, or where the tube narrows, the walls are covered for a length of 1 cm with long lanate hairs which point downward generally. Below this area there is a dense mat of very short hairs coming straight out from the wall, and these continue down to the nectary which is a ring of tissue protruding into the hypanthium just above its base. From the base of the style to the segment at the level of the hypanthial hairs the style becomes gradually thicker, so that for the lower 1.5 cm there is an open chamber around the style. Above this the short hairs begin to abut on the style leaving no space at all and where the longer hairs begin there is a corresponding segment of the style with lanate hair; however, this hair in general points toward the orifice and so opposes that of the hypanthial wall. The style narrows slightly again at the level of the widening tube and then is constant to the four lobed stigma.

There is, then, a natural chamber at the base of the hypanthium where the nectar collects and its length (1.5 cm) correlates with the depth of nectar observed in almost all *O. hookeri* tubes at the time of opening. The lanate hairs probably serve the function of preventing small bees, flies, ants or beetles from reaching the nectar chamber below, as species of all of these groups have been observed at the mouth of the hypanthium. The brush of short hairs in the lower tube might serve in conducting excess nectar up the lower tube, but if this is the case, the amount of nectar so carried is very small. It must be enough to stimulate a moth with a tongue too short to reach the nectar chamber proper to keep visiting other flowers. This will be discussed later. To the human nose the odor of the flowers of *O. hookeri* is very slight as compared with the strong and characteristic odors of other species—odors that are powerful many yards away.

When the flower opens, the anthers have already dehiscent longitudinally, the pollen lying in four rows, free from the anther. The pollen grains are, however, held together in long chains by the viscin threads, several of these fine strands attaching any two grains. The threads can be stretched to many times their original length before they break, thus holding large numbers of grains together even when they are pulled suddenly off of the anthers. The threads are very sticky so that they readily adhere to an insect.

The average length of the hypanthium (Fig. 9a) differed from one population to another, the extremes being 3.7 cm and 4.8 cm. The flowers of three colonies were measured early and late in the season and hypanthial lengths showed no significant change. Table 1 gives the extremes in length of hypanthium and the average for each colony. As can be seen from Table 1, the length of the hypanthium varies within a population as much as 2.1 centimeters.

TABLE 1. *Length of hypanthium in centimeters for each colony of O. hookeri.*

COLONY	NO. OF FLOWERS MEASURED	AVERAGE	EXTREMES
East Highland	35	4.0	3.1–5.1
Rancho Santa Ana Botanic Garden	41	3.7	2.8–4.6
Coldwater Canyon	11	4.8	3.5–5.6
Grass Valley	24	4.6	3.5–5.7
San Antonio Canyon	7	4.7	3.8–5.5
Temecula	11	4.0	3.5–4.9
Prairie Fork	54	4.6	3.2–5.7
Crestline	11	4.4	3.3–5.0

THE SPECTRUM OF VISITORS TO THE FLOWERS AND THE POLLINATING AGENTS

The spectrum of animals which visited the flowers of *O. hookeri* at the eight colonies

studied includes insects in three orders and hummingbirds. In table 2 all of the species are given with their higher classification. Almost all of the pollinating was done by four species of hawkmoths and three species of bees. These species are marked with an asterisk in table 2. The other species listed were observed visiting the flowers at one or more colonies, a few regularly but most sporadically. None of them was responsible for much pollination, either because of size, small numbers, behavior or a combination of these.

The ratio of any one species to the others visiting the flowers varied considerably on the different dates during the summer. Also the ratio varied during any one night or morning, although not to as great an extent. The primary method of estimating relative abundance of each species was direct observation. In addition, the black light was run for one hour (or one-half hour) usually about 9:00 p.m. (times given in this section are all Pacific Daylight Saving except for September 28 which is Pacific Standard) to obtain an estimate of the abundance of the different hawkmoths. Running the light-trap for only one hour at an arbitrary time was a limitation since the ratio of one species to another may not have been constant during the whole evening. Also, the different species of hawkmoths may have been attracted more or less strongly by the light, but by putting together this data with that obtained from the flowers, a better estimate of relative abundance of hawkmoths was possible.

Transfer of pollen starts soon after the flowers open and continues during the night and usually into the next morning. During this time several very different types of animals visit the flowers as outlined in the following sections, at least two types being capable of pollination. The observations made on pollination fall into two main categories. Several times during the period when the flowers were open a typical series of flowers was checked to determine the extent and degree of pollination; this also allowed a rough estimate of the time that pollination occurred. Such checks, when correlated with the abundance of any pollinators present during corresponding periods, allowed estimation of the amount of pollen transfer carried out by each animal species. Close observation of the various animal species visiting the flowers made it possible to determine their efficiency in transferring pollen. This was especially important when two or more species were visiting during a period of heavy pollination for one was often much more important than the other. The behavior of the several pollinating agents will be discussed in a later chapter.

On most of the observation dates a series of 50 flowers was emasculated and marked with numbered tags. Emasculating was started just before the normal opening time and continued into the time that the flowers were opening. These flowers did not seem to show any abnormal reaction to the removal of the stamens just above the base, and the moths did not appear to be selective in their visits, although bees gathering pollen probably found the situation unique. Fifty unemasculated flowers were always checked with the emasculated ones so that comparisons could be made. A typical flower of each series is shown in Fig. 3a taken shortly after emasculation was finished. The two lines were checked once or twice during the evening, usually once in the early morning and then a final reading was taken when pollination was virtually complete. On the early checks the number of stigmas which were heavily pollinated and the number which showed only slight pollination were recorded along with the total number pollinated. In recording the final reading a more precise estimate of the degree of pollination was attempted and the categories used were: slight (fewer than 100 pollen grains), fair (100 to 400 grains), good (400 to 700 grains), and heavy (700 to over 1000 grains). The average number of ovules per capsule of *O. hookeri* was 300 (100-500), so that a stigma in the fair category would in most cases bear enough pollen grains to fertilize every ovule present in the capsule below. Therefore the recording of amount of pollen on the stigma through use of these categories was not an attempt at estimating the amount of functional pollen but was simply an estimate of amount of pollen placed on the stigma.

TABLE 2. *Classification of all of the visitors to the flowers of O. hookeri observed during this study.*

INSECTS

LEPIDOPTERA

Sphingidae

Acherontiinae

Phegeothontius sexta* (Joh.)*Phegeothontius quinquemaculata* (Haw.)Sphinx chersis oreodaphne* (Hy. Edw.)*Sphinx perelegans asellus* (R. & J.)

Philampelinae

**Pholus achemon* (Dru.)

Choerocampinae

**Celerio lineata* (Fabr.)

Arctiidae

several species

Phalaenidae

several species

DIPTERA

Bombyliidae

Villa sinuosa jaennickeana (Coq.)*Villa lateralis lateralis* (Say.)*Phthyria* sp.

Syrphidae

Syrphus sp.*Eristalis* sp.

Lonchaeidae

Lonchaea sp.

Muscidae

Hylemya sp.

Tachinidae

one species

HYMENOPTERA

Apoidea

Colletidae

Hylaeinae

Hylaeus sp.

Halictidae

Halictus (Seladonia) sp.*Lasioglossum (Chloralictus)* sp.*Agapostemon* sp.

Apidae

Anthophorinae

Emphorini

Diadasia sp.

Xylocopinae

Ceratini

Ceratina 2 spp.

Xylocopini

Xylocopa tabaniformis orpifex* SmithXylocopa brazilianorum varipuncta* Patton

Apinae

Apini

**Apis mellifera* L.

BIRDS

Trochilidae

Calypte anna (Less.)*Selasphorus rufus* (Gmel.)

Discussion of each of the eight colonies studied follows taking up (a) the spectrum of visitors to the flowers and their relative abundance and (b) the pollinating agents. The data on first appearance, period of maximum abundance and relative abundance of the several important visitors to the flowers have been summarized in bar graphs, and the results of the checks and final reading of the emasculation and control lines are given in tables for the colonies at East Highland, Coldwater Canyon and Prairie Fork. These colonies represent the three typical situations encountered in the eight colonies; the others are compared with them.

EAST HIGHLAND

Spectrum and Relative Abundance.—Observations on relative abundance were made on eight dates from June 23 to September 28. Modified bar graphs for each of the six important flower-visiting insects are given in fig. 4 and 6.

As fig. 4 shows, the first visitor after the flowers opened was *Xylocopa tabaniformis orpifex*, this insect being present only until deep dusk, and not seen at all on the last two dates of observation. Next to appear were *Phlegethontius sexta* (Fig. 8a-c) and *Celerio lineata* (Fig. 9a). The pattern for *P. sexta* was sudden appearance of a large number of individuals followed by a period of maximum abundance and then a gradual decrease to an occasional individual through the rest of the night. This pattern held generally throughout the summer. For *C. lineata* a similar pattern was observed during mid-summer but during early and late summer relative abundance of the species was less. *Pholus achemon* (Fig. 9b) appeared later in the evening than the other hawkmoths and in smaller numbers, again the pattern changing during the summer as indicated on the graph. In the morning *Apis mellifera* (Fig. 9c) appeared first, becoming gradually abundant and then dropping off in numbers, while *Xylocopa brazilianorum varipuncta* (Fig. 9c and d) was relatively less abundant for 2½ hours.

Table 3 gives the numbers of hawkmoths taken at the light-trap on the several dates of observation.

TABLE 3. Numbers of hawkmoths taken at the light trap at East Highland in 1961.

DATE	TIME	<i>Celerio lineata</i>	<i>Pholus achemon</i>	<i>Phlegethontius sexta</i>	<i>Sphinx chersis</i>
23 June	9:15–10:00	1		7	1
1 July	9:35–10:05		2	5	
9 July	9:30–10:00	1		10	1
15 July	9:30–10:00		2	10	
26 July	9:00–10:00	5		1	
5 August	12:00–1:00	4		11 ^a	
23 August	at intervals	3	1	9	
	8:30–11:30				
28 Sept.	6:30–7:30			9	

^a10 *P. sexta* and 1 *P. quinque-maculata*

Pollinating Agents.—By comparing table 4, which gives the data for checks and reading of the emasculation and control series, with the previous description of relative densities of various visitors to the flowers at different times, some definite conclusions on pollination can be drawn and some tendencies suggested.

On the dates of observation from July 9 through August 23 at East Highland, 80 to 90% of the flowers of both lines had been pollinated by 9:00 p.m. By this time a few xylocopas had visited the colony for a short period while the hawkmoths had been present for close to one hour. On September 28 only about 40% of the stigmas had been pollinated by this time and no small hawkmoths or xylocopas had been seen at all. Usually a high percentage

of pollination in the heavy category occurred during the first hour of activity, again with the exception of the final date of observation. *Celerio* (Fig. 9a) and *Pholus* (Fig. 9b) together were the most prevalent hawkmoths on July 15 and 26 and on August 5 and 23, while *Phlegethontius* (Fig. 8a-c) was prevalent on July 9, and on September 28 was the only species seen.

These observations show that a large part of the total pollination was being accomplished by the common smaller hawkmoths *Celerio* and *Pholus*. Also that this was accomplished within an hour after the flowers opened. That as much as 40% pollination should occur during the first hour on September 28 when no small hawkmoths were seen, seems contradictory except that almost all of the stigmas were very lightly pollinated. Such light pollination probably occurred on all of the evenings listed, the animal responsible being *Phlegethontius sexta*; when *Celerio* and *Pholus* were common, such light pollination would be quickly obscured by the heavy pollination characteristic of these animals. It is very probable that one or two small hawkmoths were present also as several flowers did show pollination of the type attributable to them. The observations also suggest that very few of the small hawkmoths need to be feeding to bring pollination to a high level, as illustrated particularly on July 9 when numbers of *Celerio* and *Pholus* were comparatively low yet pollination was high for the first hour. There is a correlation between the number of stigmas in the highly pollinated categories and the number of small hawkmoths present during the evening, as especially illustrated on August 23 when numbers of *Celerio* and *Pholus* were at a maximum.

Table 4 also shows that enough additional pollination usually took place in the morning to bring the number of pollinated stigmas very close to 100%, and also to increase pollen deposition on many of the previously pollinated stigmas. *Xylocopa* (Fig. 9c-d) and *Apis* (Fig. 9e) were responsible for this, the latter being the more important because of greater numbers and activity, even though the less efficient pollinator of the two. The discrepancy which was found in several cases between number of stigmas in the heavy category during the last line check and the final line reading, may be partly due to interpretation but is mostly due to pollen knocked off by further visits or to pollen collected by bees investigating the stigma.

The importance of *Xylocopa* and *Apis* as pollinators in the morning depended on the number of flowers left unpollinated by the small hawkmoths during the preceding evenings.

Also shown on table 4 is the small number of stigmas that fall in the categories below that of fair pollination. The category fair is the lowest one in which number of pollen grains would at least equal the number of ovules available for fertilization (an average capsule bears 300 ovules, the extremes being about 100 and 500). It is likely that even those few flowers still in the lowest categories at the time of the line readings would subsequently receive enough pollen to set a full complement of seed. That almost every capsule on the plants at East Highland did set all of its seeds is the strongest argument for this. Also on two occasions 25 tags were left on flowers whose degree of pollination had been recorded. These capsules were collected after ripening and there was little correlation between capsules with unfertilized ovules and those that had been recorded in the lowest pollination categories. Seed set was nearly 100% for the capsules checked at any rate, except for one or two that had obviously aborted for other reasons.

Fig. 4. The relative abundance during the evening and night of the major insect pollinators of *Oenothera hookeri* at East Highland. The relative abundance of each insect species during the hours before or after sunset is shown on the separate graphs. The height of the bars represent averages for observation periods throughout the summer. The time of anthesis is indicated by an arrow. Relative abundance is expressed on the ordinate in terms of six arbitrary grades as follows: (1) none (2) rare (3) a few individuals (4) numerous (5) abundant (6) extremely abundant.

FIGURE 4

TABLE 4. *Proportion of flowers of O. hookeri at East Highland that were pollinated at various times after opening on six observation dates.*^{1, 2}

DATE AND TIME	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
9 July, 1961										
9:00 p.m.	34%			several	82%	many			several	90%
10:00 p.m.	42%			several	88%	many			several	92%
15 July										
8:45 p.m.	42%			few	90%	44%				80%
10:15 p.m.	62%			few	94%	48%			few	94%
26 July										
10:05 p.m.	42%			10%	82%	38%			8%	82%
5:30 to 6:30 a.m.	48%	18%	20%	12%	98%	32%	20%	20%	24%	96%
5 August										
9:00 p.m.	30%			4%	80%	12%			10%	68%
10:30 p.m.	32%			4%	88%	24%			10%	80%
1:10 a.m.	32%			10%	92%	24%			10%	86%
6:00 a.m.	42%			10%	94%	30%			10%	94%
8:30 to 9:30 a.m.	24%	26%	26%	20%	96%	36%	24%	32%	8%	100%
23 August										
9:00 p.m.	22%				78%	18%			20%	88%
10:30 p.m.	42%				98%	22%			14%	100%
7:30 to 8:50 a.m.	58%	21%	16%	6%	100%	56%	36%	6%	2%	100%
28 September										
8:45 p.m.	4%				42%	2%				46%
11:20 p.m.	4%				46%	2%				36%
8:15 a.m.	4%				46%	2%				48%
9:30 to 10:40 a.m.	0%	4%	32%	34%	70%	4%	10%	20%	28%	62%

¹A sample of 50 flowers was observed in each case.
²Where there are blanks in the table only the categories listed were read.

RANCHO SANTA ANA BOTANIC GARDEN

Spectrum and Relative Abundance.—Observations were made on nine dates, from June 11 to August 21. The important visitors to the flowers were the same and patterns of abundance for a given date, as well as for the summer, were quite similar to those recorded for East Highland with the following qualifications and exceptions. The main general difference between the garden and East Highland was in the absolute numbers of several visiting species, particularly hawkmoth species. Although relative abundance was usually similar, fewer individuals of each animal appeared in the garden, and the time of first appearance for the hawkmoths was generally later at the garden colony. *Xylocopa tabaniformis orpifex* was not seen at all on three of the evenings, one in the middle and two toward the end of the summer. *Apis mellifera* also started visiting during the evening on July 21 and was numerous until nearly dark on three dates of observation. *Phlegethontius sexta* was the predominant species during the first half of the summer but was not nearly as common after the middle of July, being rare on the last date of observation in August. *Celerio* and *Pholus* followed the pattern shown for early and late summer at East Highland on all of the observa-

tion dates at the garden, never reaching the greater abundance shown during mid-summer at the former colony. The light-trap data for the garden reflected both the similar relative abundance and lesser absolute abundance of hawkmoths compared to East Highland. In the morning *Apis mellifera* was the most abundant species showing a pattern similar to that at East Highland, while both *X. tabaniformis orpifex* and *X. brazilianorum varipuncta* were often present, especially the former early in the summer.

Pollinating Agents.—Lines were set and checked at the garden on seven dates from June 25 to August 21. The data were similar to those from East Highland except that pollination was a more gradual process in the garden. Early in the summer, only 20–40% of the flowers were pollinated during the first hour after opening, most of these lightly. This would be expected from the lesser number of smaller hawkmoths present and their later appearance, as well as the insignificant numbers of bees during the early evening. Again illustrated was the inefficiency of *P. sexta* as a pollinator, for the relative abundance of this hawkmoth during the first hour was not accompanied by the pollen transfer one would have to expect if the moth were efficient. As at East Highland, some of the light pollination of the first hour was undoubtedly due to this insect.

The rate of pollination was influenced by the number of flowers available in the population on a given night. The numbers of *Celerio* and *Pholus* were not significantly greater on the last two nights of observation, but the number of flowers was far smaller, accounting for the faster pollination. The nearly 100% pollination seen early in the morning was probably a result of steady visits by a few small hawkmoths during most of the rest of the night, a situation similar to that at East Highland. On the mornings when total pollination was only 80 or 90% at dawn, *Apis* and to a very small extent *Xylocopa* did pollinate 10 or 20% of the flowers as well as increasing the increment of pollen on some previously pollinated stigmas.

COLDWATER CANYON

Spectrum and Relative Abundance.—The patterns of relative abundance at this population of *O. hookeri* were typical of the second general situation observed. Here there were no bees visiting the flowers in the evening. Between 8:00 and 8:30 p.m. four species of hawkmoths were seen in relatively low numbers as shown on the modified bar graphs (Fig. 5 and 6). After this first short period, three species became rare while one, *P. quinque-maculata*, stayed at the same level of abundance. All of the species probably continued to visit at intervals during the night as indicated. Two specimens of *Sphinx chersis oreodaphne* (Fig. 8e) were seen visiting the flowers just before dawn on August 10. No moths at all were taken at the light-trap run from 11:00 to 11:30 p.m. on August 9. The only important species visiting the flowers in the morning was *Apis mellifera*. A good sized colony of *Xylocopa tabaniformis orpifex* was nearby but these bees were observed to visit the flowers of *O. hookeri* only occasionally.

Pollinating Agents.—Table 5 gives the data obtained from line checks. On August 8 the three short-tongued hawkmoths were responsible for a high percentage of pollination. The early morning check was made after *Apis* had started collecting pollen so it was impossible to determine exactly how important bee pollination was the first morning. Essentially all of the remaining pollen had been collected by 6:15 a.m. on both mornings. The line reading at 9:15 p.m. on August 9 showed that about 60% of the flowers had been pollinated by the early concentration of hawkmoths. This figure was raised to 80 or 90% at dawn by the further occasional visits of the smaller hawkmoths during the night. In the morning, pollination was nearly completed by *Apis mellifera*, although never raised to 100%. After the pollen was mostly gone, at 6:15 a.m., many honeybees landed directly on the stigma, attempting to take free pollen and thus slightly reducing the amount of pollen on many

stigmas. *Xylocopa tabaniformis orpifex* had almost no part in pollinating here, unlike some other colonies, and the other small bees were also ineffectual in this regard.

TABLE 5. Proportion of flowers of *O. hookeri* at Coldwater Canyon that were pollinated at various times after opening on two observation dates.^{1, 2}

DATE AND TIME	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
8 August, 1961										
10:15 p.m.	12%			12%	64%	28%			16%	96%
6:15 a.m.	32%			0%	96%	40%			4%	96%
12:00 to 12:35 p.m.	48%	24%	8%	20%	100%	40%	28%	12%	20%	100%
9 August										
9:15 p.m.	18%			0%	58%	12%			22%	54%
5:20 a.m.	30%			few	88%	36%			4%	82%
11:45 to 12:45 p.m.	30%	30%	18%	16%	94%	32%	40%	16%	10%	98%

¹A sample of 25 flowers was observed on the first date and one of 50 flowers on the second date.
²Where there are blanks in the table only the categories listed were read.

GRASS VALLEY

Spectrum and Relative Abundance.—The pattern of activity in the Grass Valley population was generally similar to that at Coldwater Canyon. *Celerio lineata* and *Sphinx perelegans asellus* were the only visitors seen at the flowers of *O. hookeri* in Grass Valley during evening. On July 19 *Celerio* was the first moth seen, coming in at 8:15 p.m. about 10 minutes after the flowers were all open. *Sphinx perelegans asellus* was first seen at 8:25 p.m., near deep dusk. Between 8:15 and 8:45 p.m. three individuals of *S. perelegans asellus* and five celerios visited the particular flowers under observation, at least one individual appearing every five minutes. No moths were seen after 8:45 p.m., but the flowers showed evidence of slight moth activity subsequently. However, the period of most concentrated activity was just before dark. Only one hawkmoth was seen on July 30, an individual of *S. perelegans asellus* at 8:30 p.m. (Fig. 8d) ; on August 30 no evening visitors of any kind were seen. The light trap was run from 10:10 to 10:40 on the 19th and from 9:45 to 10:45 on the 30th of July with no results. In the morning *Apis mellifera* was fairly numerous at the flowers after 8:00 a.m. No *Xylocopas* at all were seen at this colony.

Pollinating Agents.—The pollination of the flowers of *O. hookeri* in this colony was accomplished mainly by the short-tongued hawkmoths *Sphinx perelegans asellus* (Fig. 8d) and *Celerio lineata*. On nights when these moths pollinate only 80 or 90% of the flowers, the rest are mostly pollinated by *Apis*, the small species of *Halictus* being responsible for a few. Pollination on July 19 was as complete as this observer has ever seen it in *O. hookeri* and the hawkmoths were responsible for all of it. On July 30 when only one hawkmoth was seen, these insects were responsible for only 80 to 90% of the pollination ; the two species of bees present were undoubtedly responsible for the rest. On August 30 when only six flowers

Fig. 5. The relative abundance during the evening and night of the major insect pollinators of *Oenothera hookeri* at Coldwater Canyon. The relative abundance of each insect species during the hours before or after sunset is shown on the separate graphs. The height of the bars represent averages for two observation periods during the summer (see text). The time of anthesis is indicated by an arrow. Relative abundance is expressed on the ordinate in terms of six arbitrary grades as follows: (1) none (2) rare (3) a few individuals (4) numerous (5) abundant (6) extremely abundant.

FIGURE 5

remained, these had not been visited by 7 a.m. Between this time and 9:30 a.m., four were pollinated, probably by *Apis mellifera*, and the other two were undoubtedly pollinated by this bee later. Seed set was nearly 100% at this colony as determined by spot checks of capsules. The situation at Grass Valley was very similar to that at Coldwater Canyon, the main difference being the replacement of *Sphinx chersis oreodaphne* by *Sphinx perelegans asellus* at this colony.

SAN ANTONIO CANYON

Spectrum and Relative Abundance.—One or two individuals of *Xylocopa tabaniformis orpifex* visited the flowers in the evening, but anthesis took place so late that there was little time for visits by these bees. On July 19 the flowers were watched from 8:00 p.m. to midnight, on July 21 from midnight to 2:00 a.m., and on July 25 from 2:00 a.m. to 6:00 a.m.—the three nights covering the time from 8:00 p.m. to 6:00 a.m. Probably every moth visiting the colony during this period was seen, though a few were not identified. Of the four species seen, *Sphinx chersis oreodaphne* was the commonest (11) followed by *Pholus achemon* (7), *Celerio lineata* (4) and *Pblegethontius quinquemaculata* (1). A list follows giving the time at which individuals were seen:

19 July, 1959	
8:30 p.m.	<i>Celerio lineata</i>
8:35	<i>Sphinx chersis oreodaphne</i>
8:50	<i>Sphinx chersis oreodaphne</i>
8:55	<i>Sphinx chersis oreodaphne</i>
9:05	<i>Pholus achemon</i>
9:25	<i>Pholus achemon</i>
9:25	unidentified
10:05	<i>Celerio lineata</i>
10:10	<i>Celerio lineata</i>
10:30	<i>Pholus achemon</i>
10:40	<i>Sphinx chersis oreodaphne</i>
10:45	<i>Pholus achemon</i>
10:48	<i>Pholus achemon</i>
10:50	unidentified
10:55	<i>Pholus achemon</i>
11:20	<i>Pholus achemon</i>
11:25	<i>Pholus achemon</i>
11:28	<i>Pholus achemon</i>
11:40	<i>Pholus achemon</i>
21 July, 1959	
12:00 p.m.	unidentified
12:30 a.m.	<i>Sphinx chersis oreodaphne</i>
1:40	<i>Celerio lineata</i>
1:50	unidentified
25 July, 1959	
2:25 a.m.	<i>Sphinx chersis oreodaphne</i>
2:35	<i>Sphinx chersis oreodaphne</i>
2:55	<i>Pblegethontius quinquemaculata</i>
3:20	<i>Sphinx chersis oreodaphne</i>
4:05	<i>Sphinx chersis oreodaphne</i>
4:45	<i>Sphinx chersis oreodaphne</i>

Fig. 6. The relative abundance during the morning of the major insect pollinators of *Oenothera hookeri* at East Highland (above) and Coldwater Canyon (below). The relative abundance of each insect species during the hours before or after sunrise is shown on the separate graphs. The height of the bars represent averages for several observation periods at East Highland and for two observation periods at Coldwater Canyon. Relative abundance is expressed on the ordinate in terms of six grades as follows: (1) none (2) rare (3) a few individuals (4) numerous (5) abundant (6) extremely abundant.

East Highland

Coldwater Canyon

FIGURE 6

The pattern of relative abundance at this colony most resembles that at Coldwater Canyon except that at least *Sphinx chersis oreodaphne* was more numerous and the early concentration of moths lasted longer. It also illustrates the occasional visits of all of the species from the end of the early concentration until dawn. It started to get light at 5:00 a.m. At 5:25 a.m. the first individual of *Xylocopa tabaniformis orpifex* was seen, numerous individuals continuing until 6:00 a.m.

Pollinating Agents.—The three hawkmoths, *Sphinx chersis oreodaphne* (Fig. 8e), *Pholus achemon* (Fig. 9b) and *Celerio lineata*, did most of the pollinating at this population. No formal line was prepared or checked, but the extent of pollination was recorded on two nights. The 128 flowers open on July 21 were all pollinated at midnight, most of them heavily, and the 174 flowers open on July 25 were all pollinated except two, most of them heavily, by 2:00 a.m. *Xylocopa tabaniformis orpifex* undoubtedly pollinated any flowers that were not pollinated by the small hawkmoths. Again the situation was similar to that at Coldwater Canyon with *Xylocopa* doing the early-morning pollinating instead of *Apis mellifera*.

TEMECULA

Spectrum and Relative Abundance.—Very few hawkmoths were observed at the flowers of this colony, but it is so large and scattered that the moths present were widely dispersed. Four small hawkmoths, probably *Celerio lineata*, were seen between 8:30 p.m. (near dark) and 9:00 p.m. After 9:00 p.m. several individuals of *Pblegethontius quinquemaculata* were seen but no more small hawkmoths, although a rare individual was no doubt present through the night. The pattern at this colony, then, was quite similar to that at Coldwater Canyon with an early concentration of a short-tongued hawkmoth which was rare thereafter and a long-tongued species which was more abundant for a longer time. No hawkmoths were taken at the light-trap which was run from 9:45 to 10:45 p.m.

Apis mellifera arrived at 5:30 a.m. in the morning, shortly after dawn, increasing in numbers until 9:00 a.m. when the species was extremely abundant. *Xylocopa tabaniformis orpifex* was first seen at 6:00 a.m. but was never abundant, while one individual of *X. brazilianorum varipuncta* was seen at 7:45 a.m.

Pollinating Agents.—By 9:30 p.m. 70% of the flowers had been pollinated, many of them heavily, the short-tongued hawkmoths being the pollinators. A check of 50 flowers at 11:30 p.m. showed no increase in pollinated flowers while another check at 5:30 a.m. showed total pollination to be about 85%. These data confirmed the observation that the smaller hawkmoths were less abundant after 9:30 p.m. but there must have been a few which were responsible for the 15% rise in pollination before dawn. The last flowers were pollinated by *Apis mellifera* with a slight assist from *X. tabaniformis orpifex*.

PRAIRIE FORK

Spectrum and Relative Abundance.—At this colony a third general pattern was observed (Fig. 7) although there was some variation in it on the last date of observation. The commonest visitor to the flowers was *Xylocopa tabaniformis orpifex* which was abundant from anthesis until dark, except on the last date of observation when none were seen in the

Fig. 7. Relative abundance during the evening and morning of the major insect pollinators of *Oenothera bookeri* at Prairie Fork. The relative abundance of each insect species during the hours before or after sunset or sunrise is shown on the separate graphs. Height of the bars represent averages for three observation periods during the summer (see text). The time of anthesis is indicated by an arrow. Relative abundance is expressed on the ordinate in six arbitrary grades as follows: (1) none (2) rare (3) a few individuals (4) numerous (5) abundant (6) extremely abundant.

FIGURE 7

evening. Occasional hawkmoths were observed on all three dates but they were rarer here than at any other colony except the one at Crestline. The light-trap was run from 9:30 to 10:30 p.m. on July 12, from 11:00 to 11:30 p.m. on August 1, and from 8:35 to 9:35 p.m. on September 6, no hawkmoths being attracted at all.

In the morning *Xylocopa* became abundant between 7:00 and 8:00 a.m. and *Apis mellifera* was observed from 7:00 a.m. on, though this species was never abundant.

Pollinating Agents.—At the Prairie population of *O. hookeri* two very different insects were the important pollinators: the small hawkmoths, principally *Celerio lineata*, and the carpenter bee, *Xylocopa tabaniformis orpifex*. Their relative importance was different on each of the three dates of observation as it probably is during portions of the flowering season.

Both the hawkmoths and xylocopas start visiting shortly after the first flowers open and both are likely to pollinate any flower visited at this hour; so it is largely a question of which animal visits the most flowers first. *Xylocopa tabaniformis orpifex* has only a limited time between anthesis and dark. This species, in addition to effecting pollination, also removes a large quantity of pollen. Consequently, although its time of flight is limited, it can remove enough pollen so that there will be significantly less for transferral by hawkmoths.

On July 12 no lines were set up so that the estimates of relative importance of pollinators were made by combining observations on insect abundance and a check of the flowers to determine type of pollination. During the time the flowers were opening, *Celerio lineata* was rare and the xylocopas were common. Several groups of flowers were observed closely for a few minutes or checked quickly before dark. In one such group, most of the flowers were pollinated but had very little pollen left on the anthers (Fig. 3d). In another group some flowers were pollinated but had nearly empty anthers, some were pollinated while the pollen on the anthers had been disturbed but was still mostly present, some were unpollinated but had empty anthers and some had not been visited. In a third group all of the flowers were pollinated but much of the disturbed pollen remained on the anthers; shortly after, almost all of the pollen was taken by xylocopas. The first group of flowers had almost certainly been pollinated by xylocopas, in the second, about half had been pollinated by hawkmoths and half by xylocopas, while in the third all had been definitely pollinated by a hawkmoth but the xylocopas added pollen to some stigmas afterwards. In some groups of flowers the situation was not as easy to diagnose. These were areas in which most of the flowers had probably been visited by both insects. A final rough estimate of most of the flowers in the population showed that of the 80% of the flowers pollinated, 50% had been pollinated mainly by xylocopas and 30% mainly by hawkmoths, while the other 20% could not be classified. Most of the unpollinated flowers still had a full complement of pollen; however, much of the pollen of the other flowers had been collected by xylocopas or pulled off on hawkmoths. Approximately half of the remaining unpollinated flowers were pollinated by hawkmoths during the night, leaving 10% which were mostly pollinated by the first xylocopas to arrive the next morning. Of course any hawkmoth that visited during the

Fig. 8. Three of the hawkmoth species that visit *Oenothera hookeri*, pictures taken shortly after dark.—a. *Phlegethontius sexta* backing away from a flower. Note the pollen clumps and single strands of pollen being pulled off the anthers by the proboscis.—b. *Phlegethontius sexta* in flight between flowers. The proboscis is carried unrolled and there is a large accumulation of pollen on it.—c. *Phlegethontius sexta* with the proboscis fully inserted in the hypanthium. Note the distance of the body from stigma and stamens.—d. *Sphinx perelegans asellus* probably fully inserted.—e. *Sphinx chersis oreodaphne* only partially inserted in an emasculated flower.

FIGURE 8

night would transfer more pollen to some of the flowers that had been pollianted during the early evening as well as increasing the total number of flowers pollinated. At 5:30 next morning almost all of the pollen was gone from the anthers making it impossible for much further pollen transfer to take place no matter how many xylocopas were working.

The data for line checks and reading on August 1 is given in table 6. The data for the line of emasculated flowers is not a true reflection of pollination because the last few flowers were emasculated after the bees had stopped visiting. No hawkmoths were seen at the flowers during the evening but the xylocopas were numerous. Nearly 60% of the flowers of the unemasculated line had been pollinated by 9:46 p.m., approximately 80% of these by xylocopas and 20% by small hawkmoths. Some had been visited and undoubtedly pollinated by both. Total pollination of both lines was brought to 90% during the night, presumably by small hawkmoths. There was enough pollen left on the flowers so that pollen was still transferred during the night by hawkmoths, but it was not transferred to the extent that would have been possible if the xylocopas had not removed so much pollen.

TABLE 6. *Proportion of flowers of O. hookeri at Prairie Fork that were pollinated at various times after opening on two observation dates.^{1, 2}*

DATE AND TIME	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	HEAVY	GOOD	FAIR	SLIGHT	PERCENT
					TOTAL					TOTAL
1 August, 1961										
9:45 p.m.	14%			14%	46%	24%			10%	58%
5:35 a.m.	32%			12%	76%	36%			12%	90%
7:00 to 8:45 a.m.	8%	40%	20%	26%	94%	18%	34%	26%	8%	86%
6 September										
10:05 p.m.	0%			6%	6% (see text)	22%			10%	62%
5:50 a.m.	2%			2%	28%	26%			few	78%
10:15 to 11:15 a.m.	0%	20%	38%	36%	94%	8%	30%	46%	16%	100%

¹A sample of 50 flowers was observed in each case.
²Where there are blanks in the table only the categories listed were read.

At 5:50 a.m., just after the xylocopas started collecting, all pollen was gone in the open areas although some still remained in the wooded areas. Most of the unpollinated flowers of both lines were on plants in the woods when the line was checked at 5:35 a.m. It seems probable that the xylocopas visit a higher percentage of flowers earlier in the open areas and this may also be true of the hawkmoths. The morning visits of xylocopas account for pollination of the last flowers if available pollen lasts long enough, which it probably did on this date, although the last pollinations were probably very light. As the line data show, the stigma cleaning by xylocopas, and to some extent by *Apix* later, reduce the number of heavily pollinated stigmas, possibly also increasing pollination of a few lightly pollinated ones. This is an increasingly self-limiting situation.

On September 6 many of the emasculated flowers were tagged after dark (virgin flowers were picked for emasculation of course) so that this line was under-pollinated. During the last half hour before dark no xylocopas were seen at the flowers, yet many of the flowers in the open areas were pollinated just before dark. Judging from the large amount of pollen remaining on the anthers of most of the pollinated flowers, pollination by small hawkmoths

Fig. 9. Three of the insect species that visit *Oenothera bookeri*, a and b taken shortly after dark and c, d and e taken in the early morning.—a. *Celerio lineata* tipping its body to penetrate the hypanthium as far as possible, the body is cradled in the stamens. Note the clumped pollen on one fore and one rear leg and the hypanthium in profile.—b. *Pholus achemon* fully inserted, note the pollen hanging from the legs. This flower has an exceptionally low stigma.—c. An individual of *Xylocopa brazilianorum varipuncta* leaving a flower pulling a strand of pollen behind, note the pollen load.—d. The same species puncturing the base of the hypanthium to obtain nectar.—e. A pollen collecting individual of *Apis mellifera* hovering in front of a flower, note the unpacked pollen hanging from the rear legs.

seemed highly likely although only one small hawkmoth was seen at the flowers. Most of the 62% total pollination recorded for the unemasculated line at 10:05 p.m. probably occurred just before dark and may have been carried out by two or three moths working steadily. The small increment of pollination between 10:05 p.m. and 5:50 a.m. shows that the small hawkmoths undoubtedly responsible were rare, pollen being still quite plentiful. The bees were late in starting on this date but the line readings at 10:15 a.m. show how effective they can be as pollinators. The last 22% of the flowers on the unemasculated line were pollinated, probably well before 10:00 a.m.; the unnaturally negative emasculated line was brought from 28% to 94% pollinated flowers, although as the data show, there were many stigmas in the scant category. On this date the xylocopas started to rob nectar before all the pollen was gone, so a few of these flowers were probably pollinated by *Apis mellifera*. The population of *Xylocopa tabaniformis orpifex* was definitely smaller on September 6 than it had been on the previous dates. The reason that the bees turned to nectar collecting so early may well have been the almost complete lack of flowering in the other nectar plants at this time.

The relative importance of these two most important pollinators was, in summary, the following: on July 12—*Xylocopa* 58% and the small hawkmoths 42%, on August 1—*Xylocopa* 58% and the small hawkmoths 42%, and on September 6—*Xylocopa* 22% and the small hawkmoths 78%; no other animals visiting *O. hookeri* were at all significant as pollinators. Whether these three nights indicate a pattern that persisted over a period of the flowering season or whether changes in relative importance were constantly taking place is not known. It is certain, however, that in a colony of *O. hookeri* such as the one Prairie Fork where *Xylocopa* is present in sufficient numbers, this insect can at times be the most important pollinator regardless of floral adaptation.

CRESTLINE

Spectrum and Relative Abundance.—No animals were seen at this population during one 3-hour evening check and two brief morning checks. No moths were taken at the light-trap from 10:00 to 10:30 p.m. on July 5.

Pollinating Agents.—At 10:45 p.m. on July 5 no flowers had been visited and none were pollinated. At 10:00 a.m. on July 20 no flowers had been visited and none were pollinated. Again on July 31 there was no evidence of visitors and no pollination at 11:00 a.m. On the 5th several wilted flowers from previous nights were checked and many had been pollinated, some by hawkmoths as evidenced by scales on the stigma lobes. Approximately one-third of the capsules checked had not developed and contained few or no good seeds. All of the data strongly suggest that this colony may go completely unvisited by effective pollinators for whole 24-hour periods. The reasons are undoubtedly its isolation and unnatural situation. Also the data indicates that when the flowers are pollinated, the agents are probably hawkmoths that are moving from one spot to another or possibly bees foraging at some distance from their nests.

(To be continued)