TECHNICAL BULLETIN NO. 55 JUNE 1963

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ACKNOWLEDGMENT

This study was made possible because of the kind assistance of many people. The observations were made largely on the farms of commercial growers and much of the field work was conducted with the assistance of Mr. Akira Kubota and Mr. Asher Ota, former Assistants in Entomology. The illustrations were prepared by Mr. Barton Matsumoto, student Assistant in Entomology. The insects collected on passion fruit flowers were identified by Dr. D. Elmo Hardy, Mrs. Marian Adachi Kohn, and Mr. Kay Sakimura. The honey bees were supplied and transferred to Waimanalo from the University of Hawaii by Dr. R. Namba. Some of the observations were made on the field plots of Mr. Francis A. I. Bowers at the Hawaii Agricultural Experiment Station experimental farm at Waimanalo, Oahu. It is with great pleasure that I extend my thanks to all these people for their generous cooperation and assistance which made this study possible.

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A carpenter bee about to gather nectar from a passion fruit flower.
(Approximately 1.5× life size.)

ECOLOGY of the POLLINATORS of PASSION FRUIT

TOSHIYUKI NISHIDA

Preliminary studies on the entomological problems of the yellow passion fruit, or lilikoi, *Passiflora edulis* f. *flavicarpa* Degener, were initiated in 1954 (Nishida, 1954). These studies showed that one of the important problems of this crop was lack of pollination and that insects were the major pollinating agents. The importance of pollination in the production of passion fruit has been subsequently pointed out by various authors (Akamine *et al.*, 1956; Nishida, 1958; Akamine and Girolami, 1959). The present paper summarizes studies on the ecology of the insect pollinators conducted during 1954–1961.

METHOD OF STUDY

The studies reported herein were conducted in commercially-grown passion fruit orchards on Oahu and Hawaii. A limited amount of work was also carried out in the noncommercial orchards of the Hawaii Agricultural Experiment Station experimental farm at Waimanalo, Oahu. In general, the orchards concerned in these studies were located in areas considered to be most suitable for passion fruit culture. In these areas, various selections or strains of the yellow passion fruit, evidently the same as those described by Seale and Sherman (1960), were planted. However, the selections involved in these studies are not indicated in this paper because at the time these studies were initiated growers had no information on the selections that they were growing in their fields. During these studies commercial growers applied only little or no insecticides; thus, it was possible to study the flower-visiting insects undisturbed by man.

The insect species that visited the passion fruit flowers were determined by field surveys made in every passion fruit field that could be found. The insects observed were collected by the use of an insect net, except for small insects which were collected directly off the flower by the use of an aspirator.

The relative abundance of the insects visiting passion fruit flowers was determined by direct counts in the field at the time of full bloom, usually about 2:00 to 3:00 P.M. Before making the counts, plots 3 feet wide and varying in length from 100 to 200 feet were staked out at various locations in the field. The observer then walked along the plots, quickly examining each flower in bloom and tallying each insect present by use of a multiple laboratory counter. This procedure precluded the recording of minute insects such as flower thrips and midges. The exclusion of these small insects in the counts did not alter the final results because it was subsequently found that they were too small to be effective transfer agents of the relatively large pollen grains.

The efficiency of the pollinators was determined by the tagging method. Fully developed buds were selected at random from various parts of the field and were tagged, hand-pollinated, and bagged according to the following procedures: A, flowers tagged and bagged; B, flowers tagged, hand-pollinated, and bagged; C, flowers tagged and left without bagging; and D, flowers hand-pollinated and left without bagging. The reasons for the use of this technique were: (1) to determine whether or not self-pollination was possible (procedure A); (2) to determine the maximum fruit set possible when pollination was adequate (procedure B); (3) to determine the extent of pollination by natural agencies (procedure C); and (4) to determine whether bagging had any adverse effect on fruit set (procedure D). In table 1 are shown examples of the results obtained from preliminary trials conducted at Waimanalo and Kunia, Oahu. These data as well as others will be discussed later; however, at this point it appears pertinent to point out that covering had no adverse effect on fruit set.

In hand-pollination the following procedures were used. The anthers were obtained from a plant other than the one bearing the flowers which were to be pollinated. Although not always possible because of insufficient numbers of flowers, the anthers were obtained in each test from a single plant. These procedures were necessary because previous observations had indicated that the passion fruit was self-sterile and also cross-noncompatible among certain strains (Akamine *et al.*, 1956; Akamine and Girolami, 1959). In pollinating, a liberal amount of pollen was applied to each of the stigmatic lobes of the unemasculated flower by gently rubbing the anthers against the stigma. The flowers were examined 3 to 7 days later during which time unfertilized ovaries turned yellow and dropped off while those fertilized remained on the plant.

Preliminary tests were conducted on the use of various bags for covering the flowers. Polyethylene bags were not satisfactory because of the excessive accumulation of moisture within them. Fruit set was very poor when flowers were covered with polyethylene bags even when small holes were made to take care of the excessive moisture. Otter Kraft paper bags, which were easily sealed with a hand stapler, were found to be satisfactory.

An evaluation of the efficiency of pollination by natural agency was made by comparing the percentage of pollination obtained by hand-pollination (procedure B) and that obtained by natural agency (procedure C). If the natural pollinators are efficient there should be only a small discrepancy between the values obtained by these two procedures and, conversely, a wide discrepancy when the pollinators are not efficient.

FLOWERING CYCLE AND POLLINATION

The problem of unsatisfactory fruiting of the passion fruit, a plant with perfect flowers, has long been recognized. Pope (1935) ascribed the unsatisfactory fruiting

TABLE 1. Sample data showing the results obtained in a preliminary study on the technique of determining the efficiency of pollination

TREATMENT	WAIMANALO		KUNIA A		KUNIA B		KUNIA C		KUNIA D	
	Total Flowers	No. of Fruits Set	Total Flowers	No. of Fruits Set	Total Flowers	No. of Fruits Set	Total Flowers	No. of Fruits Set	Total Flowers	No. of Fruits Set
A. Flowers tagged and bagged	15	0	15	0	15	0	15	0	15	0
B. Flowers hand-pollinated and bagged	15	0	15	12	15	14	15	15	15	15
C. Flowers tagged and left unbagged	15	7	15	8	15	2	15	1	15	10
D. Flowers hand-pollinated and left unbagged	15	0	15	13	15	15	15	15	15	15

behavior to lack of pollination caused by (1) unsatisfactory environment and (2) protandrous habit; i.e., the pollen ripening before the stigma is receptive to the pollen. With respect to unfavorable environment, Pope observed that, when this crop was grown at elevations of 100 to 1,200 feet, the plant grew vigorously but rarely produced high fruit yields. The heaviest yields were obtained near sea level. It is not known whether the poor yields obtained were due to lack of pollination or to other factors. The protandrous habit of this plant has not been investigated; thus, its importance as a factor contributing to unfruitfulness is not known.

Although recognized in the past, the problem of passion fruit pollination by insects has not been investigated to any great extent. Pope (*op. cit.*) reported that certain kinds of pollen carriers, viz., the carpenter bee (*Xylocopa varipuncta* Patton), large moths, and humming birds, were of such size that they were capable of transferring pollen from the stamens to the stigma by carrying pollen adhering to their bodies. It was stated, however, that although the carpenter bee was frequently seen visiting the passion fruit flower, moths were rarely seen, and humming birds do not occur in Hawaii. In addition to the carpenter bee, Pope believed that under dry, sunny conditions, winds aided in the transfer of pollen from the stamen to the stigma of the same flower. However, this type of pollen transfer is of no importance in view of the recent finding that the passion fruit is self-sterile to a very high degree (Akamine *et al.*, 1956; Akamine and Girolami, 1959). Furthermore, wind-pollination does not appear to be of importance in cross pollination because the large, heavy, and sticky pollen grains are not readily disseminated by wind. By use of pollen traps it was shown by Akamine and Girolami (1959) that the number of pollen grains carried by air currents was very small, and hence pollination by wind was not important. On the other hand, there are features which suggest strongly that pollination is accomplished by insects. These are: (1) large attractive flowers—a characteristic of many insect-pollinated flowers, (2) a strong odor which permeates throughout the field during the blooming period, (3) an abundance of nectar, and (4) large sticky pollen grains. The fairly large number of insects associated with the flowers also suggests the importance of insects as pollinators.

Flowering Cycle of the Passion Fruit

The flowering cycle of the passion fruit was studied because it was felt, *a priori,* that the population and activity of the pollinators would be influenced by the quantity as well as the seasonal distribution of the blooms. During 1957, six plots, each approximately 200 feet in length, were marked off in various locations within two commercial orchards. The fields were visited once a month, and at each visit the number of open flowers was recorded. These records were taken only on clear days, for there appeared to be evidence indicating that unfavorable meteorological factors such as heavy overcast could delay the opening of the buds.

The results obtained indicate that there is a definite seasonal blooming cycle of the passion fruit (fig. 1). The blooming period extended from April to November in field A, and from May to November in field B. These data indicate that, in general, the passion fruit was in bloom 8 to 9 months of the year. The data presented also indicate that there were two major flowering peaks. These peaks, however, did

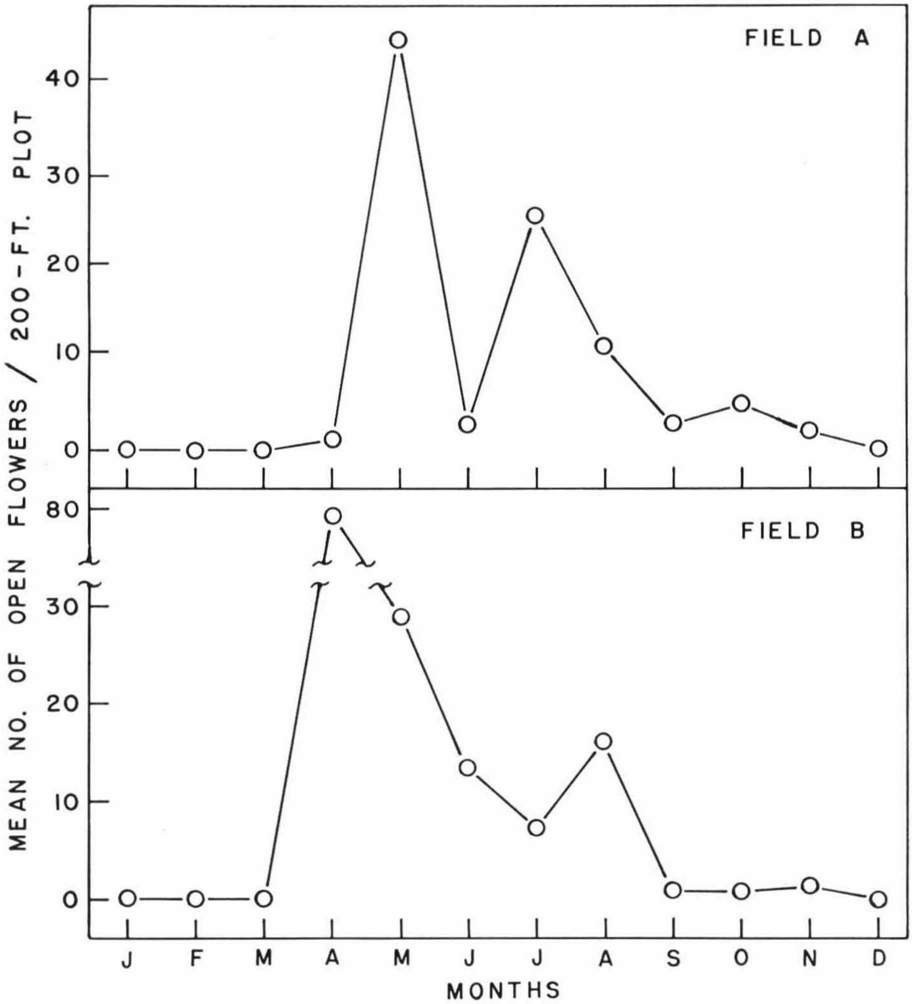

FIGURE 1. Seasonal trends in the blooming cycle of the passion fruit in two fields at Waimanalo, Oahu, 1957.

not occur at the same time even though the fields were less than half a mile apart. Varietal differences as well as differences in cultural practices no doubt played important roles on the flowering habits observed in this study.

In addition to observations on the seasonal flowering cycle, observations were also made on the diurnal variation in the opening and closing of the flowers. At Waimanalo, three 100-foot-long plots were selected for observation. Within these

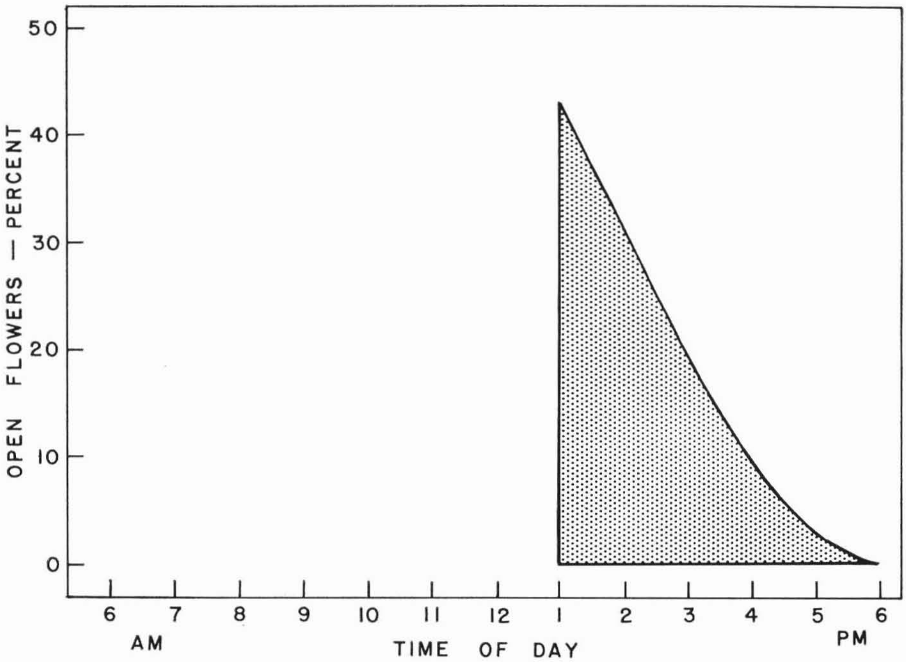

FIGURE 2. The percentage of flowers that opened at various times of the day.

plots the number of flowers in bloom was recorded at various hours of the day. At every recording, each open flower was marked with a tag of different color, thus making it possible to identify flowers that opened at various times. Furthermore, by this procedure it was possible to determine the number of hours each flower was exposed to pollinating insects.

The results of these observations showed that the flowers began to open at about 1:00 P.M. and continued to open until about 6:00 P.M. (fig. 2). It is also evident from the data that the percentage of flowers that opened varied from hour to hour; viz., 43.7 percent at 1:00 P.M., 20 percent at 3:00 P.M., and zero at 6:00 P.M. From figure 2 it is possible to estimate the number of hours the open flowers were exposed to pollination. For example, taking sunset time as 6:00 P.M., it is evident that 43.7 percent were exposed for 5 hours and 20 percent for 3 hours. It was observed that the flowers that opened on a particular day did not close during the daylight hours of the same day. The precise closing time of the flowers was not determined. However, observations showed that at 8:00 P.M. there were no closed flowers. On the following morning, however, there were open flowers as well as closed flowers. The closing of the flowers appears to be a gradual process occurring during the night and early morning hours.

Insect Visitors of the Flowers

One of the first studies conducted was concerned with determining the insects that visited the flowers. An attempt was made to collect and identify all insects that were found in passion fruit flowers in commercial plantings on Oahu, Maui, and Hawaii. The relative abundance of each species collected was arbitrarily rated as rare, occasional, and frequent, on the basis of general field observations.

The insects observed on passion fruit flowers, listed in table 2, indicate that there were 17 flower-visiting insects: 1 in each of the orders Orthoptera, Thysanoptera, and Coleoptera; 4 in Hymenoptera; and 10 in Diptera. Among these, the species found most frequently associated with the passion fruit flowers were: the carpenter bee, *Xylocopa sonorina;* the honey bee, *Apis mellifera;* and the flies, *Chrysomya megacephala*, *Eristalis arvorum*, *Euxesta quadrivittata*, and *Volucella obesa*.

TABLE 2. The insects associated with passion fruit flowers and their relative abundance

INSECT	RELATIVE ABUNDANCE		
	Rare	Occasional	Frequent
Orthoptera			
Conocephalus saltator (Sauss.)	x		
Thysanoptera			
Thrips hawaiiensis f. *imitator* Pr.		x	
Coleoptera			
Conotelus mexicanus Murray	x		
Hymenoptera			
Apis mellifera L.			x
Iridomyrmex humilis Mayr	x		
Pheidole megacephala (Fab.)	x		
Xylocopa sonorina Smith			x
Diptera			
Chyromya sp.	x		
Chrysomya megacephala (Fab.)			x
Dacus cucurbitae Coq.		x	
D. dorsalis Hendel		x	
Desmometopa sp.	x		
Eristalis arvorum (Fab.)			x
Euxesta quadrivittata (Macq.)			x
Ophyra nigra (Wied.)	x		
Milichiella lacteipennis Loew.	x		
Volucella obesa (Fab.)			x

A further study was undertaken to obtain data on the abundance of some of the species that were consistently associated with the flowers. In this study 100-foot-long

TABLE 3. The relative abundance of the carpenter bee (*Xylocopa sonorina*), honey bee (*Apis mellifera*), hover fly (*Volucella obesa*), and the oriental blow fly (*Chrysomya megacephala*) in passion fruit fields

DATE (1956)	LOCATIONS	MEAN NUMBER PER 100-FOOT-LONG ROW				RELATIVE ABUNDANCE OF FLOWERS IN BLOOM
		Carpenter Bee	Honey Bee	Hover Fly	Oriental Blow Fly	
	Hilo, Hawaii					
Nov. 14	A	0.0	3.8	1.9	1.9	Few
Nov. 15	B	0.5	5.1	2.0	0.0	Few
Nov. 15	C	0.4	2.3	0.0	0.0	Few
Nov. 17	D	0.0	4.5	1.9	0.0	Few
Nov. 19	E	0.2	4.7	1.1	0.2	Few
	Kunia, Oahu					
June 20	A	0.0	53.4	0.0	0.0	Abundant
June 20	B	0.0	70.0	0.0	0.0	Abundant
	Waimanalo, Oahu					
July 12	A	12.0	0.0	3.0	0.0	Abundant
July 12	B	5.0	15.0	1.7	0.0	Abundant
July 12	C	2.5	7.5	0.0	0.0	Abundant
June 13	Upper Manoa, Oahu	1.0	11.5	3.5	0.0	Abundant
June 21	Lower Manoa, Oahu	11.5	0.9	3.6	0.0	Abundant

plots were staked out and the number of insects on the flowers was recorded. The data presented in table 3 show that the relative abundance of each species varied with locality. However, it is evident that the carpenter bee and the honey bee were the most abundant insects. The carpenter bee was abundant in the Waimanalo and Manoa areas of Oahu, but the honey bee was more abundant than the carpenter bee in the Kunia area of Oahu and in the Hilo area of Hawaii.

During the course of these studies, information was also obtained on the general distribution of the carpenter bee and the honey bee in Hawaii. These two important pollinators of the passion fruit were found in many areas of Hawaii. However, the carpenter bee was usually present in the lowland areas under dry to moderately dry situations. The honey bee was also found in similar situations; however, in addition, it was also present in the wet native forests where the carpenter bee was not present. Swezey and Williams (1932) observed that the honey bee was common up to elevations of 8,000 feet on the island of Hawaii, where it was observed gathering food from the flowers of the native mamani, *Sophora chrysophylla* (Salisb.) Seem. Other specific aspects pertaining to the ecology of the honey bee and the carpenter bee will be presented in detail in a later section of this bulletin.

In other countries where various varieties of passion fruit are grown, the passion fruit flowers are visited by a number of insects. Berry (*in litt.*, 1957) stated that in El Salvador the species commonly associated with passion fruit flowers are: *Bombus ephippiatus* Say, *B. mexicanus* Cr., *B. niger* Fr., *Trigona amalthea* (Oliv.), *T. clavipes dorsalis* Sm., *T. fulviventrus* Guer., *T. corvina* Ckll., *T. ruficrus corvina* Ckll., *Xylocopa* *brasilianorum* (L.), *X. fabricii* Ckll., *X. fimbriata* (F.), and *X. lateralis* Sm. Cox (1957) reported that in Australia the honey bee is an efficient pollinator. Evidently, it is highly attracted to the variety of passion fruit grown there, for he observed the honey bee forcing open the anthers to obtain pollen early in the morning before anthesis had occurred. Hurd (*in litt.*, 1960) made observations on bees visiting the flowers of the passion fruit in Sao Paulo, Brazil. He found two genera of bees collecting pollen, *Xylocopa* and *Epicharis*. These observations by Berry and Hurd indicate that there are a number of passion fruit flower-visiting insect species that do not occur in Hawaii.

Pollination Efficiency

Studies were conducted on the efficiency of pollination in various localities to obtain data on the extent of fruit loss due to lack of pollination. In addition, studies of preliminary nature were made to determine whether pollination efficiency could be improved through artificial means.

The data presented in figure 3 indicate the variation in pollination efficiency with locality. The lowest values were obtained at Waimanalo, Oahu, and the highest at Kunia, Oahu (November 2, 1956), and at Hilo, Hawaii. Furthermore, the data presented show other features concerning passion fruit pollination. Where flowers were bagged without emasculation so that self-pollination could take place, there was no fruit set. This failure to set fruit indicates that passion fruit flowers are not self-pollinating, a corroboration of the results reported by Akamine *et al.* (1956) and Gilmartin (1958). The data obtained also indicate that the maximum fruit set potentially possible varied with locality. For example, at Waimanalo this maximum was 100 percent, but for unknown reasons it was lowest at Kunia (November 2, 1956). The failure to obtain the maximum potential fruit set among hand-pollinated flowers indicates that the failure to set fruit is in part due to causes other than lack of pollination.

A further study was conducted at Waimanalo during the flowering season of 1957 because previous observations indicated that there were seasonal variations in pollination efficiency. This study, conducted during May to October, was made to determine whether there were changes in pollination efficiency with season.

The data obtained indicate that the efficiency of the pollinators varied among the three fields studied (fig. 4). In field A the efficiency was consistently low throughout the 6-month period. In field B the efficiency was low during May to August; however, there was a marked increase during September and a drop again during October. The best efficiency was observed in field C, but for unknown reasons the percentage pollination among hand-pollinated flowers was lower than that obtained by natural pollinators in 4 out of the 6 months. A similar observation was made by Gilmartin (1958), who found that fruit set by hand-pollination was 33 percent as compared to 70 percent by natural pollinators. The cause of this high rate of abscission among hand-pollinated flowers in certain fields is not known.

An experiment was conducted to determine whether pollination can be increased by artificially increasing the population of pollinators. During the blooming season, a honey bee hive containing several hundred individuals was placed in a passion

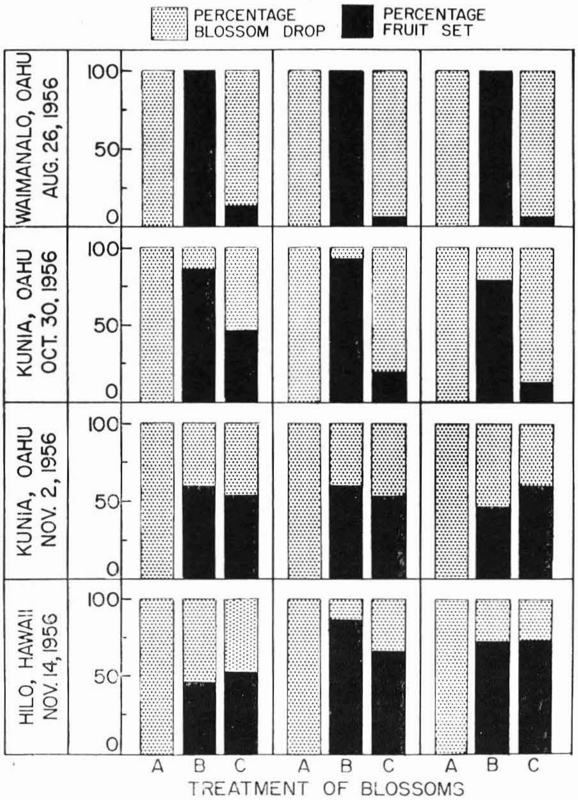

FIGURE 3. The variation in pollination of the passion fruit in some of the major fruit-growing areas in Hawaii as determined by the tagging and bagging technique. *A*, blossoms bagged; *B*, blossoms hand-pollinated and bagged; and *C*, blossoms tagged and left unbagged.

fruit field at Waimanalo, Oahu (fig. 5). To prevent ants from invading the colony, the hive was placed on a redwood post treated with a 5% DDT oil solution and the weeds around the post were removed periodically. Data on the percentage of pollination were taken 2 weeks before and 4 weeks after placing the hive in the field. The results obtained showed only a slight increase in pollination following the placing of the hive in the field. A marked increase was not obtained, possibly because the bees went on to other flowers besides passion fruit to collect nectar and pollen, for field counts indicated no increase in the honey bee population in the passion fruit field.

Studies on increasing pollination by placing suitable logs, such as sisal logs with holes bored into them, in the field to increase the population of the carpenter

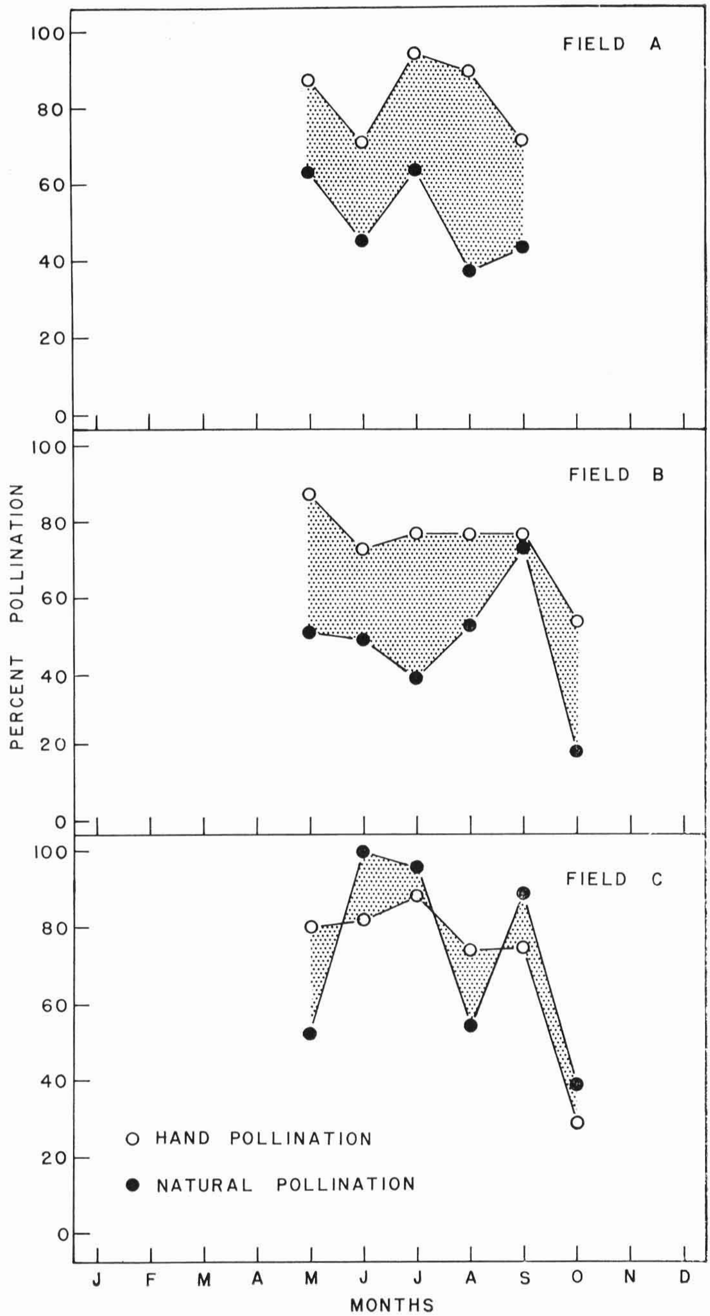

FIGURE 4. Seasonal trends in the efficiency of pollination in three fields at Waimanalo, Oahu, 1957.

FIGURE 5. An experimental honey bee hive placed in a passion fruit field at Waimanalo, Oahu. Hive placed on redwood posts treated with a 5 percent oil solution of DDT to keep ants out of hive.

bee are being continued. To date it has been found that this procedure resulted in an increase in the carpenter bee population in certain fields, but in others the bee failed to nest in the sisal logs provided.

STUDIES ON HONEY BEES

One of the common flower-visiting insects of the passion fruit flower is the honey bee, *Apis mellifera* L., an insect well known since ancient times for its honey. Honey bees were first introduced into Hawaii in about 1857, but it was not until about 1894 that commercial apiaries were established. Most of the apiaries were operated by cattlemen because of their interest in the pollination of the kiawe (*Prosopis chilensis* Mol. Stuntz), which produced the bean pods used for cattle feed (Eckert and Bess, 1952). Many of the honey bees escaped from the apiaries and may be found today as feral bees. The present study is concerned largely with these feral bees.

General Biology

Because the honey bee is one of the most beneficial insects to man, its biology has been studied in great detail by many investigators. A brief résumé of the biology will be given here, but those interested in further details should refer to the recent book by Eckert and Shaw (1960).

The honey bee is one of the insects with a highly developed caste system in which the colony is composed of the queen, the workers, and the drones. The function of the queen in this caste system is to lay eggs. The workers, which are actually underdeveloped females, do most of the work, such as cleaning the hive, feeding the young, the queen, and the drones, ventilating the hives, guarding the colony, and collecting pollen and nectar. The drones perform no work other than to fertilize the queen.

The life cycle of the honey bee is less complicated than its social organization. The queen lays the eggs in combs built of wax by the workers. When the egg hatches the workers feed the larva, and when fully grown, the larva in the comb is sealed in by the workers. Pupation occurs within the enclosed cell. Upon developing into the adult, the young bee breaks open the cap and emerges from the cell. Among the many individuals that emerge, some are queens; others, workers; and still others, drones. At various times the old queen and some of the workers leave the hive in swarms to start a new colony. The feral bees in Hawaii nest in such places as crevices in rocks, trees, and buildings.

In the present study on passion fruit pollination our concern was not with the bee colony as a whole, but only with the worker bees that come into the field to gather nectar and pollen. Besides passion fruit flowers, it is known that the worker bees gather nectar and pollen from a large number of plants. The principal sources of pollen and nectar in Hawaii are kiawe, *Prosopis chilensis* Mol. Stuntz; Java plum, *Eugenia cumini* L. Druce; ohia lehua, *Metrosideros collina* Forst.; and *Eucalyptus* spp. In addition to these there are more than 24 other species of plants from the flowers of which the honey bee collects nectar and pollen (Eckert and Bess, 1952).

Population Composition and Seasonal Trends

The composition of the foraging honey bee population was determined in passion fruit fields during the flowering season. This study was undertaken because field observations indicated the presence of nectar- and pollen-gathering bees. Although indistinguishable morphologically, the nectar- and pollen-gathering individuals were relatively easy to recognize on the basis of their foraging behavior. The nectar gatherers crawl into the base of the style where the nectar is present; the pollen gatherers, on the other hand, are present on the anthers. Usually the

TABLE 4. The mean number of nectar- and pollen-collecting bees per 200-foot-long plot in passion fruit field in bloom at Kunia, Oahu, during October and November

TIME OF DAY (PM)	OCTOBER 2, 1956			NOVEMBER 2, 1956		
	No. of plots	Nectar gatherers	Pollen gatherers	No. of plots	Nectar gatherers	Pollen gatherers
12:30	5	2.0	0.0	4	3.0	0.7
1:00	5	6.2	0.0	4	5.2	7.2
1:30	5	9.0	0.0	4	5.2	5.2
2:00	5	4.8	0.0	4	5.2	5.5
3:00	–	–	–	4	6.0	6.7
4:00	–	–	–	4	7.0	7.0

corbiculae of the pollen gatherers are filled with yellow pollen grains. Occasionally, it was not possible to differentiate between nectar and pollen gatherers when the bees were on the leaves. Although these bees were most likely nectar gatherers seeking out secretions from the glands on the leaves, they were not included in the data.

The data obtained indicate that the population of nectar and pollen gatherers was different during October and November (table 4). During October, the honey bees in the passion fruit field were all nectar gatherers. However, during November, there was a change in the composition of the population; during this month, the numbers of nectar and pollen gatherers were approximately equal. Field observations also showed that the relative abundance of nectar and pollen gatherers varied with locality. For example, during April to June, 1957, although there was a high proportion of nectar gatherers at Waimanalo, most of the honey bees at Kunia were pollen gatherers.

In addition to these, data were also taken on the seasonal trends in abundance of the honey bee from three commercial fields at Waimanalo (fig. 6). These data, which include pollen and nectar gatherers, do not represent the actual honey bee population in the area. They merely indicate the number of bees that came into the field to collect pollen and nectar. However, it is believed that such field counts do give a useful index of pollinator abundance.

The data presented in figure 6 indicate that, in the three fields studied, honey bees were usually abundant during the months in which the passion fruit was in bloom. A few honey bees were observed in the field during the off-season months. These bees were observed collecting exudations from the glands of the plant. One of the distinctive features of the data is the variation in the peaks of abundance among the fields studied. In field A there were three major peaks of abundance; but in fields B and C, there was only one major peak. Furthermore, the data show that the peaks did not occur simultaneously in the three fields.

The seasonal variation in the abundance of the honey bees in passion fruit fields may be attributed to their foraging habits. It is known that honey bees prefer the nectar and pollen of certain plants more than others. The seasonal variation of the

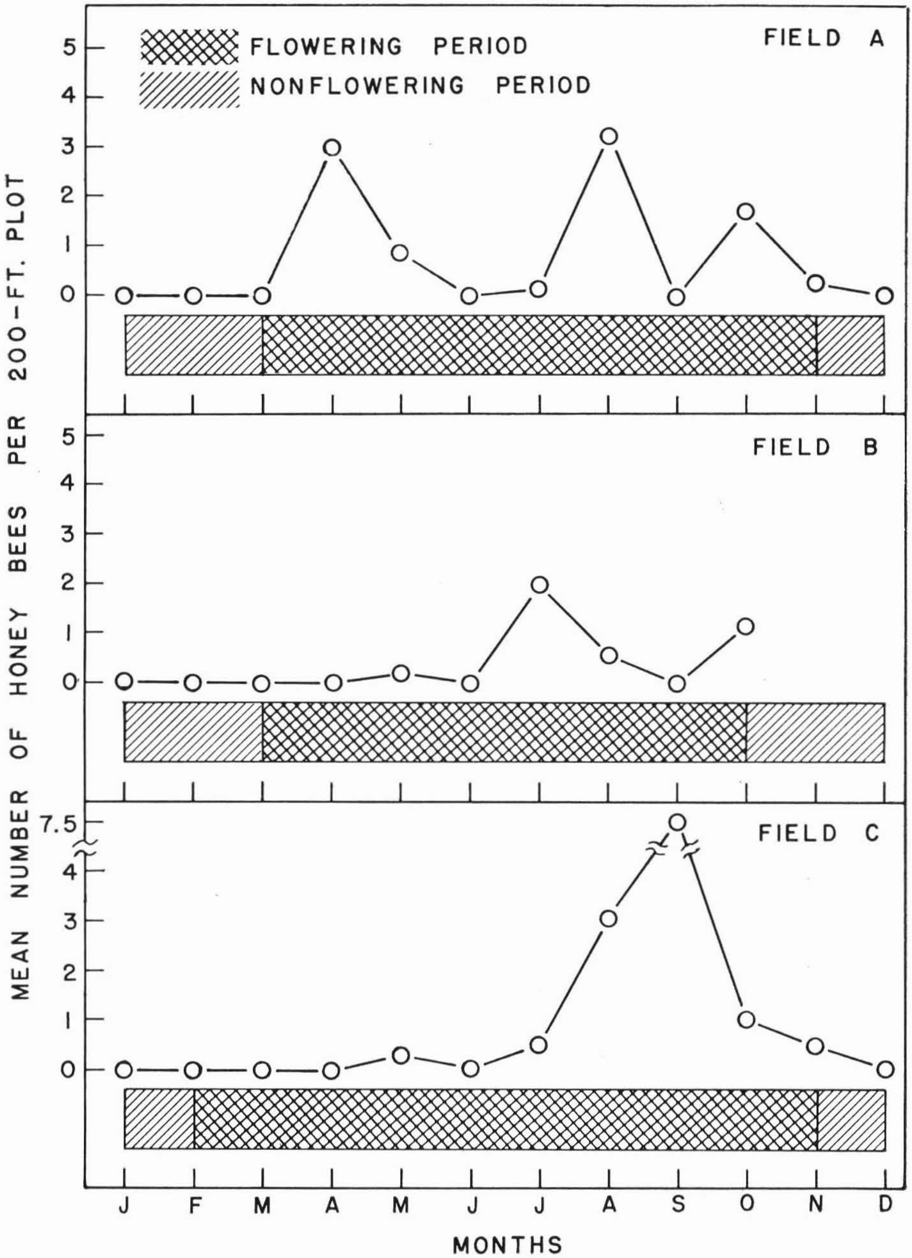

FIGURE 6. Population trends of the honey bee in three passion fruit fields at Waimanalo, Oahu, 1957.

honey bee population in passion fruit fields may be due to their movement to the more preferred sources of food when they are available. However, during times of food shortage, honey bees may enter the passion fruit fields in large numbers. For example, during August, 1957, honey bees were so numerous in passion fruit fields at Waimanalo that there was nearly complete removal of pollen from the anthers shortly after the flower opened. During the same period, several dairies complained that large numbers of honey bees were entering the feed troughs and were carrying away particles of cattle food. These observations indicate that there are periods of food shortage and that honey bee behavior is markedly influenced by the availability of food.

Incidentally, some of the growers feared that the complete removal of pollen from the anthers by the honey bee might be detrimental to pollination. Several determinations were made on pollination efficiency during the period when there was complete removal of pollen by the honey bee. The results showed that the complete removal of pollen did not result in decreased pollination, possibly because the honey bees pollinated the flowers before the complete removal of pollen.

Diurnal Activity

Preliminary field surveys conducted in Hilo, Hawaii, indicated that honey bees were most numerous in passion fruit fields during the afternoon hours. Further

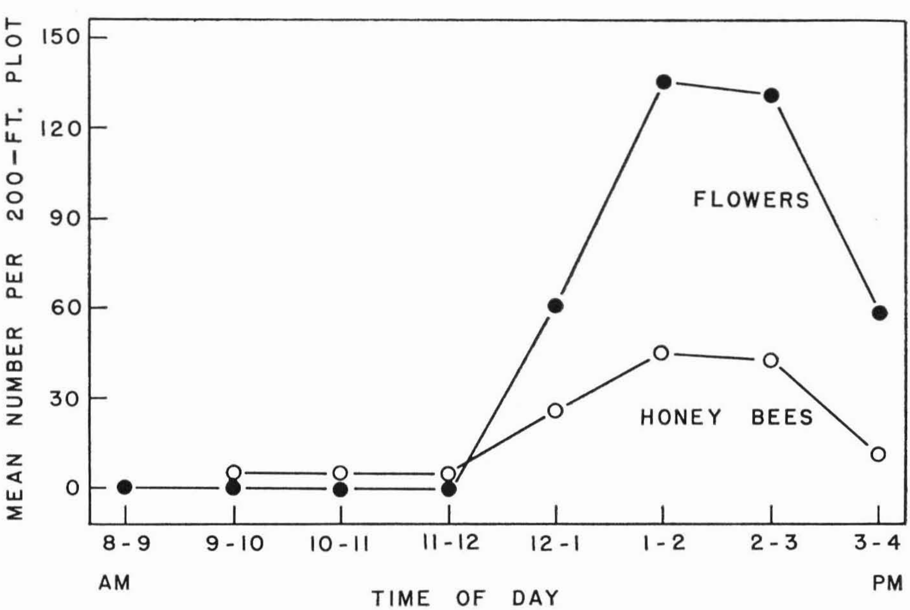

FIGURE 7. The diurnal movement of honey bees into passion fruit fields in relation to the number of open flowers.

observations on the diurnal activity of this pollinator were made at Kunia, Oahu, during the summer of 1957, at which time quantitative records were obtained. This locality, situated at the base of the eastern foothills of the Waianae Range, was selected for study because of the predominance of honey bees in passion fruit fields. The data on diurnal activity were taken by making field counts on 200-foot-long plots. Although many sets of records were taken throughout the flowering season, only a few are presented.

The data presented in figure 7 indicate the scarcity of bees in the field during the morning hours and the increase of bees during the afternoon hours. The few bees observed during the morning hours were probably nectar gatherers seeking exudations from extra-floral glands on the petioles of passion fruit plants. The increase of bees during the afternoon hours coincided with the opening of the flowers.

STUDIES ON CARPENTER BEES

The carpenter bee, *Xylocopa brasilianorum sonorina* Smith, has been in Hawaii since as early as 1879. This bee, known as *X. varipuncta* Patton in Hawaiian literature, is also present in southwestern United States (Timberlake, 1922; Hurd, 1955). Although present in Hawaii for many years, its value as a pollinator was not recognized until in recent years when the passion fruit began to be grown as a commercial crop in Hawaii. Probably for this reason, information on this bee as a pollinator is very scant. Many consider this wood-boring insect a pest because it builds nests in fence posts, water tanks, houses, and other structures made of redwood. It is also considered a pest because of its stinging habit when disturbed. On the other hand, Hurd (1955) states that its value as a pollinator of many plants more than offsets the damage it causes to structures.

General Biology

The biology of the carpenter bee is inadequately known. This insect is difficult to study because, as a wood borer, the immature stages occur deep in the wood. Although these studies were not primarily concerned with its biology, an attempt was made to obtain information on this subject by use of sisal logs, *Agave sisalana* (Engelm). These logs were used because the bees nested in the soft pith, making it easy to dissect and examine the immature stages. Sisal logs 18 inches long with holes bored into them, approximately the same size as those made by the bee, were exposed to carpenter bees at their nesting sites. Each month, six pieces were exposed, and, after 1 month, they were cut open and the immature bee stages dissected out.

From these studies, information on some aspects of the biology of the carpenter bee was obtained. It was observed that the female selected the artificial holes bored into the sisal wood for nest building. From the artificially-made hole she first bored into the wood perpendicular to the log, and then, parallel to the longitudinal axis of the log. The eggs, laid in the terminal portion of the tunnels, were attached singly to a ball of pollen and nectar about 8 mm in diameter. After the eggs were laid, the female sealed off the terminal end of the tunnel with small wood particles

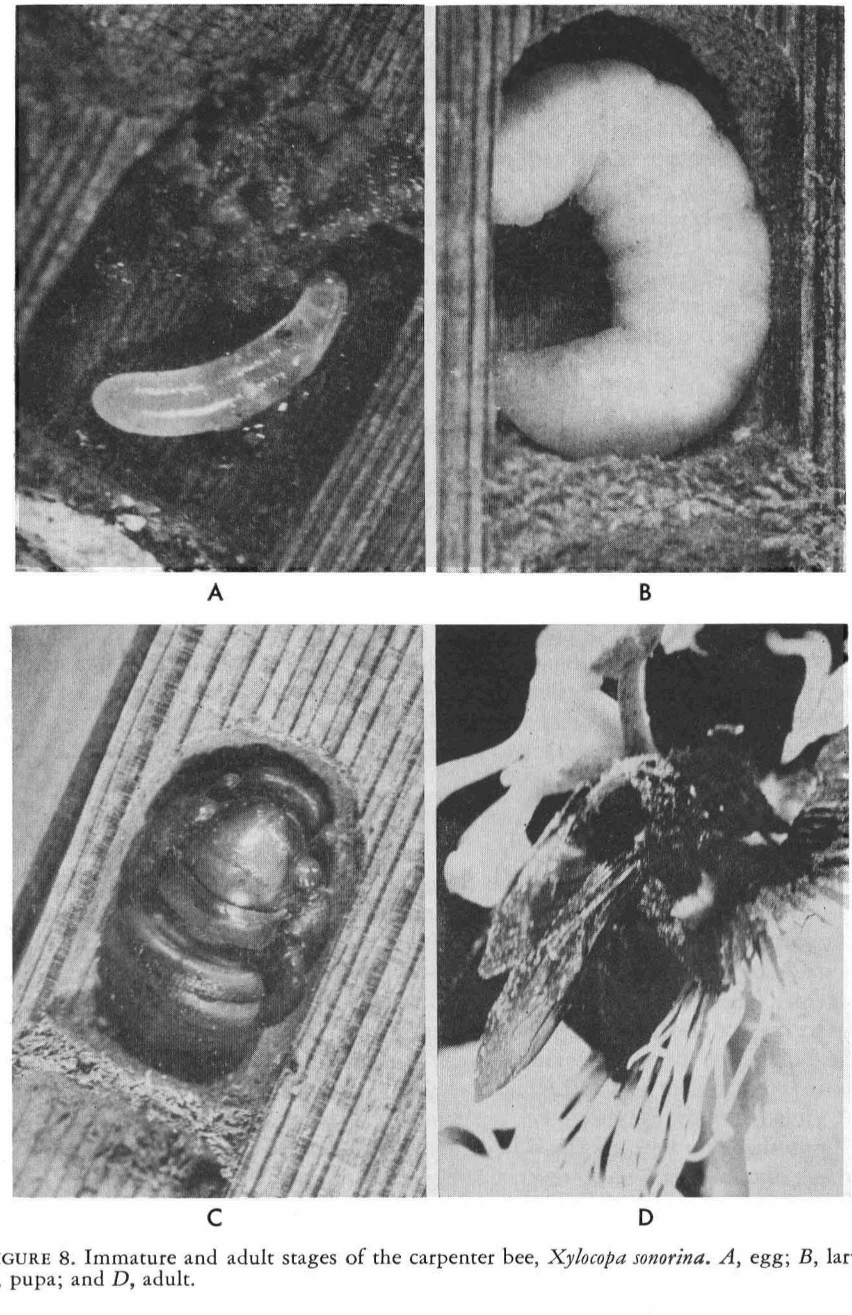

FIGURE 8. Immature and adult stages of the carpenter bee, *Xylocopa sonorina*. *A*, egg; *B*, larva; *C*, pupa; and *D*, adult.

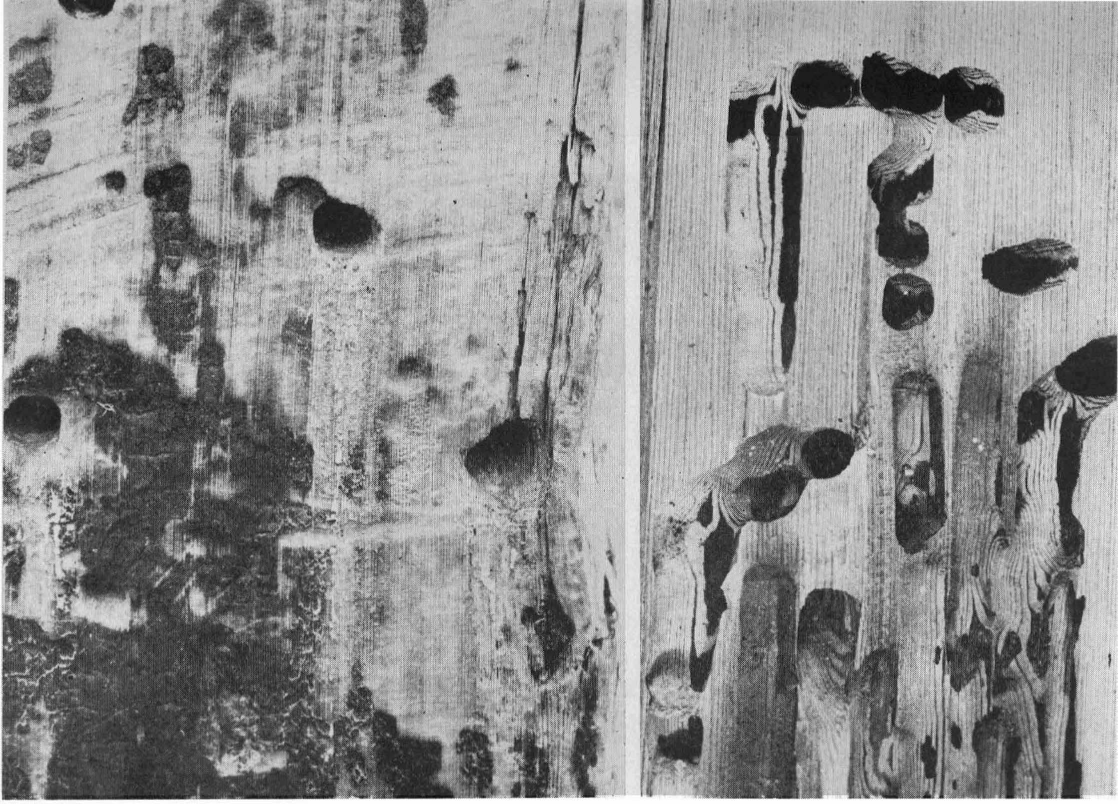

FIGURE 9. Tunnels in redwood made by the nesting carpenter bee, *Xylocopa sonorina*. *Left*, entry holes; *right*, wood split open to show tunnels.

cemented together. Upon hatching, the larva fed on the ball of provisioned food. When fully grown, the larva pupated within the chamber. Upon reaching the adult stage, the young individual chewed through the temporary partition made by the female and entered the main channels. The various stages of the carpenter bee are shown in figure 8, and the maze of tunnels in an infested redwood log, in figure 9.

The adult bee collects nectar and pollen from the flowers of many species of plants. Besides passion fruit, some of the important plant sources of food are: allamanda (*Allamanda oenotheraefolia* Pohl.); morning glory (*Ipomoea* spp.); shell ginger (*Alpinia nutans* (Andr.) Roscoe); *Cassia* spp.; golden shower (*Cassia fistula* L.); rattlebox (*Crotolaria mucronata* Desv.); thunbergia (*Thunbergia grandiflora* Roxb.; *T. erecta* T. Anders.); hibiscus (*Hibiscus* spp.); royal poinciana (*Delonix regia* (Bojer) Raf.); plumbago (*Plumbago capensis* Thunb.); beans *Phaseolus* spp.); and watermelon (*Citrulus vulgaris* Schrad.). In addition to these, the flowers of the leguminous tree, *Gliricidia sepium* (Jacquin) Steudel, are very attractive to the carpenter bee. When in full bloom the flowers of this tree were often observed to be visited by large numbers

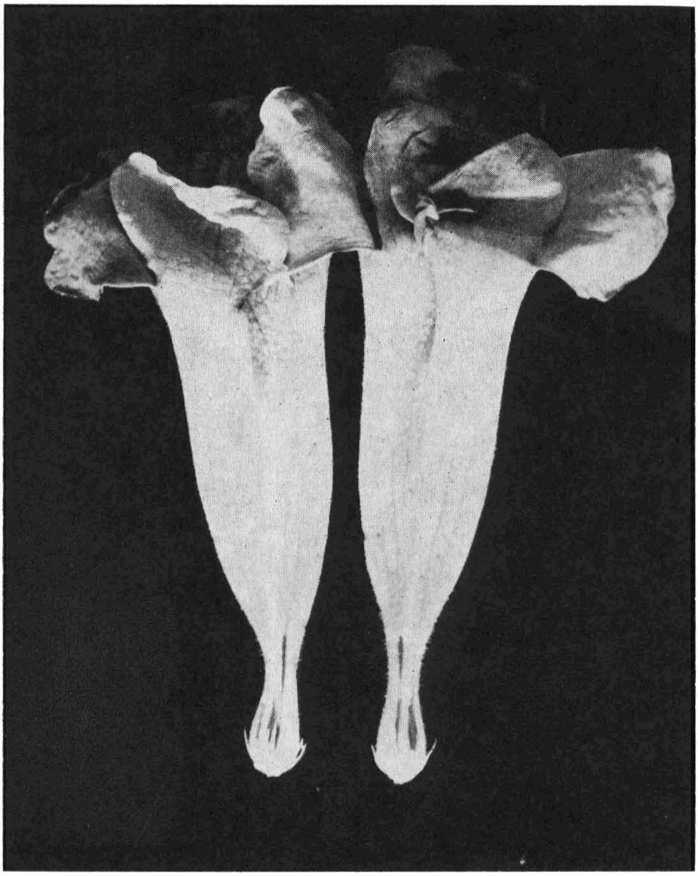

FIGURE 10. Longitudinal slits made by the carpenter bee at the base of the corolla of *Thunbergia erecta.*

of bees in the Honolulu area. The carpenter bee usually enters the flower to collect nectar. However, when collecting nectar from campanulate flowers too small for entry, the bee cuts a longitudinal slit at the base of the flower and collects nectar through the slit (fig. 10). The common flowers in which these lateral slits were observed were *Allamanda oenotheraefolia* Pohl., *Ipomoea* spp., and *Thunbergia erecta.*

The incidence of lateral slits in the morning glory flower was determined at various localities on Oahu during May, 1956. It was thought that the incidence of slits might be used as an index of the abundance of bees in a particular area. The data obtained from sampling flowers from various areas on Oahu, presented in table 5, show that the highest incidence of slit flowers was found at Waimanalo,

TABLE 5. The incidence of flower slits made by the carpenter bee in *Ipomoea* sp. at various localities on Oahu

LOCALITY	DATE (1956)	NO. OF FLOWERS EXAMINED	NO. OF FLOWERS WITH SLITS	PERCENT OF FLOWERS WITH SLITS	NO. OF SLITS (RANGE)	MEAN NO. OF SLITS PER FLOWER
Koko Head	May 7	25	6	24	0–2	0.2
Makapuu	" "	25	0	0	–	–
Waimanalo (A)	" "	25	16	64	0–2	0.7
" (B)	" "	25	22	88	0–3	0.9
Mikiloa (A)	May 9	25	6	24	0–2	0.2
" (B)	" "	25	16	64	0–2	0.6
" (C)	" "	25	11	44	0–3	0.4
Lualualei (A)	" "	25	12	48	0–2	0.5
" (B)	" "	25	7	28	0–2	0.3
Waianae (A)	" "	25	2	8	0–1	0.1
" (B)	" "	25	20	80	0–3	0.8
Halawa	May 16	25	0	0	–	–
Kaaawa	" "	25	24	96	0–2	1.0
Hauula (A)	May 14	25	24	96	0–2	1.0
" (B)	" "	25	21	84	0–3	0.8
" (C)	" "	25	18	72	0–2	0.7
Paumalu	" "	25	17	68	0–2	0.7
Pupukea	" "	25	23	92	0–2	0.9

Waianae (B), Kaaawa, Hauula, and Pupukea. There appears to be a variation in slitting even within the same localities. This variation might result from the proximity of the sampling sites to nesting sites. In spite of this variation, it seems that the incidence of slitting might be used as an index of carpenter bee abundance. Such an index might be useful in selecting areas for passion fruit culture.

Population Composition and Seasonal Trends

The carpenter bee is not a social insect even though it often lives in large numbers within a single log. It has no social organization comparable to that of the true social insects, such as honey bees, termites, and ants. The adult population of the carpenter bee consists of the males and females. The sexes of this bee can be easily determined even at a distance because of the striking difference in color. The females are jet black and the males are yellow. At times individuals with black and yellow colors, which are gynandromorphs possessing male and female characteristics, were observed.

During 1956, records were taken at monthly intervals on the number of males and females at six nesting sites at Waimanalo to determine the male and female population of the carpenter bee. From the data presented in figure 11, it is evident

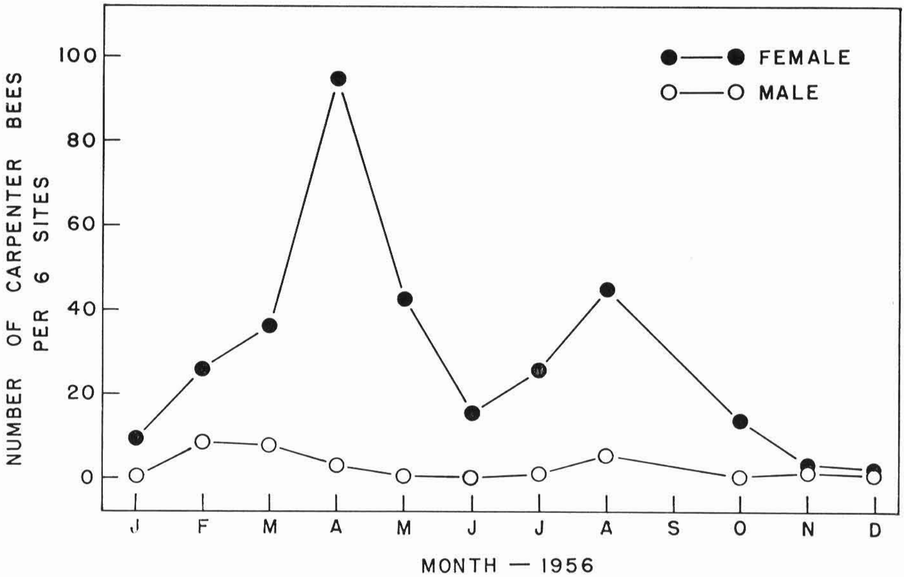

FIGURE 11. Seasonal trends in the abundance of the male and female carpenter bees at nesting sites.

that the female population was much higher than that of the male and that the population of the male followed the same general trend as that of the female. The cause of the scarcity of males in the population is not known. Some writers have speculated that the scarcity of males is due to the shorter male life expectancy than that of the female. However, our observations showed that the scarcity of males was not due to differences in life expectancy, because even in the pupal stage the males were few in comparison to the females. For example, during August, 1956, a total of 21 females and 5 males was obtained from six sisal logs placed near nesting sites. This observation suggests that this abnormal sex ratio is due to genetic factors rather than to differential life expectancy.

During 1957, the seasonal trends in the abundance of the carpenter bee in passion fruit fields were followed in three fields at Waimanalo. The data presented in figure 12 show that carpenter bees were abundant in the field during the flowering period. It may also be noted that there appear to be no marked seasonal peaks of abundance. In field A, the population was highest during October; whereas, in field C, the population was highest during November. In field C there was no definite peak. The results also show considerable field-to-field variation in abundance. For example, the carpenter bee population was higher in field C than in either field A or field B.

In addition to studies on the population trends in passion fruit fields, studies at the nesting sites were also conducted during the same year. The data presented in

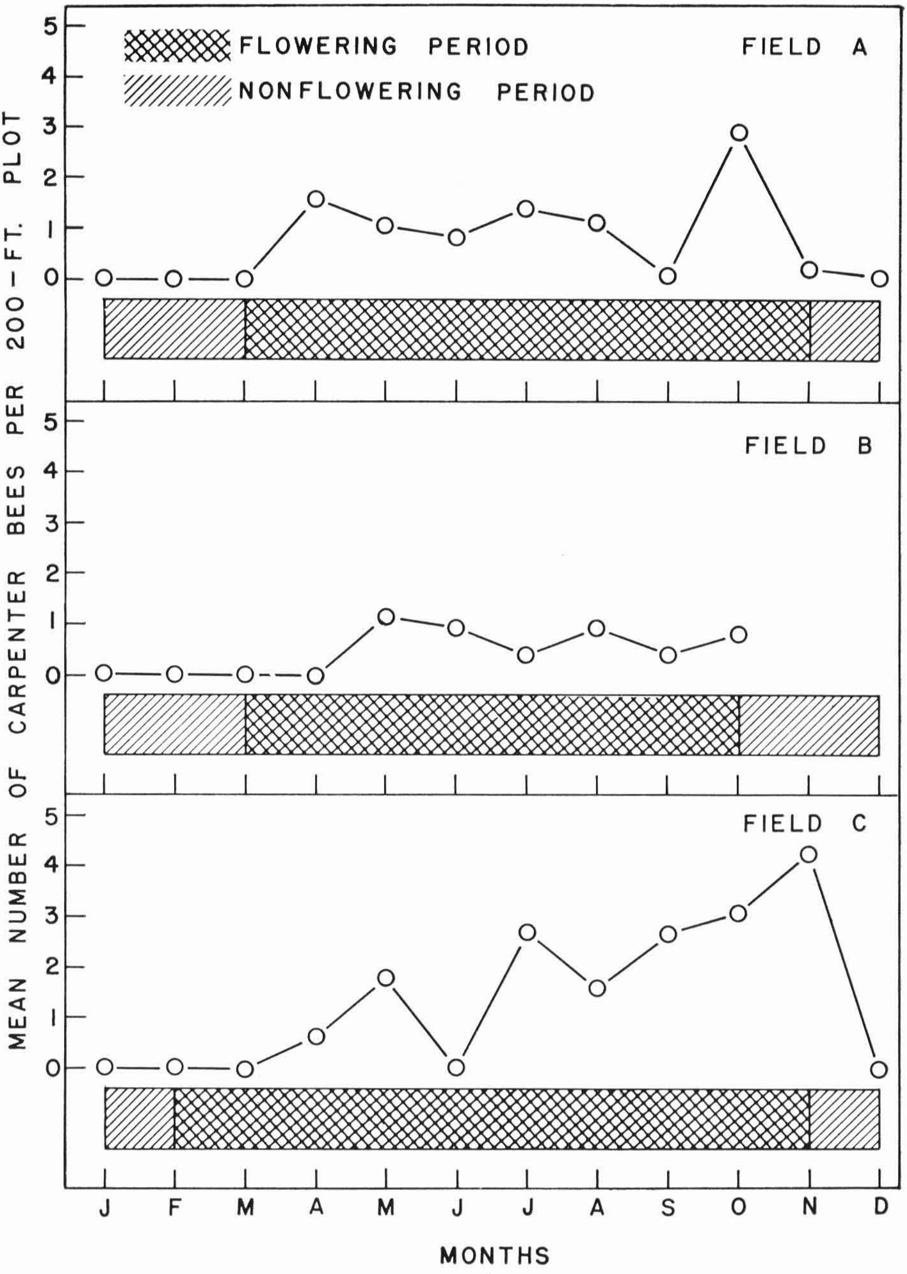

FIGURE 12. Population trends of the carpenter bee in three passion fruit fields at Waimanalo, Oahu, 1957.

figure 11 show that there were two distinct peaks of abundance, one during April and the other during August.

In comparing the seasonal population trends in the field with those at the nest, it becomes evident that the major difference is the absence of distinct seasonal peaks of abundance in the field. These data indicate that at the nest the peaks represent a brood effect, the peaks representing emergence of young bees from the pupal stage. At the nesting site, both young nonforaging and mature foraging individuals were being measured; but in the field, only the populations of the foraging bees were being measured.

Throughout these studies males were not observed in passion fruit flowers. Their feeding habits are not known. Since the females do all the nectar and pollen gathering, they are the effective pollinators. The females were often seen perched on twigs or at the entrance of the nest with a clear droplet of liquid on the tip of the mouth parts. They appeared to manipulate the droplet so that it went in and out of the mouth. One individual was observed doing this for over 30 minutes. The significance of this behavior is not known.

Diurnal Activity

The diurnal foraging activity of the carpenter bee in passion fruit fields was studied at Waimanalo and Kunia, Oahu. The records obtained from counts of bees visiting the flowers at various hours of the day, presented in figure 13, indicate that the carpenter bees were not present in the field during the morning hours; however, during the afternoon hours they were very active in the field. The activity of the bees coincided with the opening of the flowers.

TABLE 6. The number of female carpenter bees with or without pollen observed at six nesting sites adjacent to a passion fruit field at Waimanalo, Oahu, November, 1955

TIME OF DAY	NO. WITH POLLEN	NO. WITHOUT POLLEN	TOTAL	NO. OF OPEN FLOWERS[1]
9:30 A.M.	0	4	4	0
10:00	0	1	1	0
10:30	0	1	1	0
11:00	0	0	0	0
11:30	0	0	0	0
12:00 P.M.	0	0	0	0
1:00	0	2	2	1
1:30	0	1	1	5
2:00	2	2	4	16
2:30	5	2	7	37
3:00	2	3	5	52
3:30	14	0	14	52
4:00	1	1	2	52

[1]Number per six 100-foot-long plots.

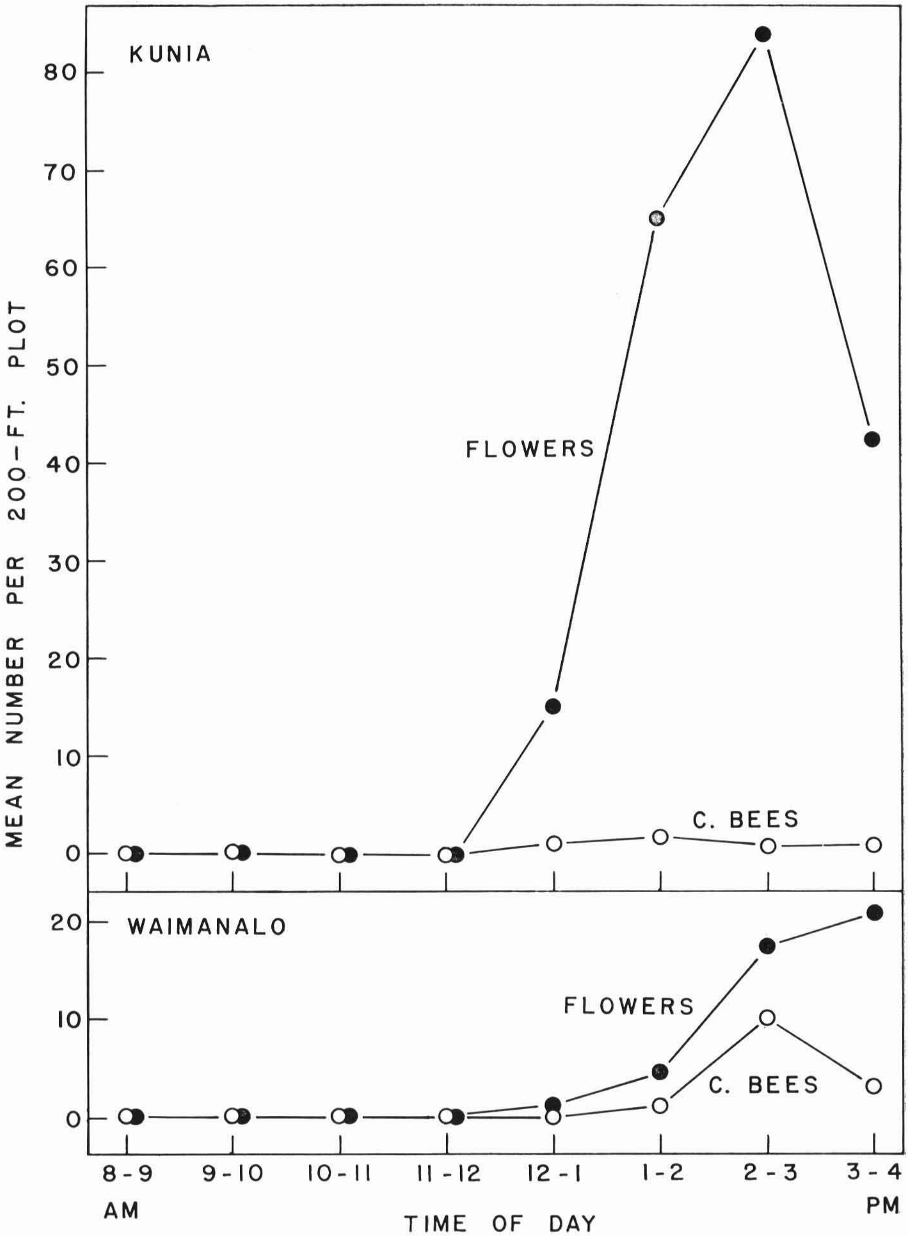

FIGURE 13. The diurnal movement of carpenter bees into passion fruit fields in relation to the number of open flowers.

TABLE 7. Comparison of the diurnal carpenter bee activity at nest and in passion fruit field during nonflowering and flowering periods

TIME OF DAY	NONFLOWERING PERIOD								FLOWERING PERIOD							
	Nest				Field				Nest				Field			
	Jan.	Feb.	Mar.	Av.	Jan.	Feb.	Mar.	Av.	May	June	July	Av.	May	June	July	Av.
9:00 A.M.	0	3	3	2.0	0	1	0	0.3	1	0	2	1.0	0	1	0	0.3
9:30	1	8	4	4.3	0	0	0	0.0	3	0	3	2.0	2	0	0	0.7
10:00	0	2	2	1.3	0	0	0	0.0	0	2	0	0.7	0	2	0	0.7
10:30	3	9	2	4.7	0	0	0	0.0	1	1	3	1.7	1	0	0	0.3
11:00	1	1	3	1.7	0	0	0	0.0	0	2	3	1.7	0	0	0	0.0
11:30	2	5	2	3.0	0	0	0	0.0	3	0	0	1.0	2	0	0	0.7
12:00 P.M.	0	0	0	0.0	0	0	0	0.0	0	0	0	0.0	0	3	0	1.0
1:00	1	1	3	1.7	0	0	1	0.3	4	1	0	1.7	11	23	4	12.7
1:30	1	2	3	2.0	0	0	0	0.0	8	4	6	6.0	12	31	10	17.7
2:00	0	2	3	1.7	0	0	0	0.0	7	3	3	4.3	12	44	11	22.3
2:30	0	0	1	0.3	0	1	0	0.3	8	2	0	3.3	13	51	12	25.3
3:00	0	1	9	3.3	0	0	0	0.0	5	0	4	3.0	8	25	17	16.7
3:30	0	1	8	3.0	0	0	0	0.0	2	1	3	2.0	10	25	10	15.0
4:00	0	0	1	0.3	1	0	0	0.3	1	0	0	0.3	6	25	7	12.7

The number of bees returning to nesting sites with pollen was also recorded at various hours of the day. The individuals that had visited passion fruit flowers were easy to identify because of the orange pollen on the dorsum. It was observed that there were few active carpenter bees during the morning hours, and none of them had pollen on the dorsum. The number of bees with pollen increased after 1:30 P.M., almost simultaneously with the opening of the flowers (table 6).

Further studies were carried out to compare the activity of the carpenter bee at the nesting sites and in the field during the nonflowering and flowering seasons of the year. As in the previous studies, counts were made of the bees in the field and at the adjacent nesting sites. The data presented in table 7 indicate that during the nonflowering period there were hardly any carpenter bees in the field; however, larger numbers were encountered at the nesting sites. During the flowering season, the number of bees recorded at the nesting sites and in the field was generally higher than that recorded during the nonflowering season. These observations point out that the reproductive activity, which includes the gathering of food, is greater during the flowering season than during the nonflowering period. It seems then that the continuous growing of the passion fruit in a given area should provide food for the bee, which in turn could result in an increase in the population, provided other factors, such as nesting sites and climate, are conducive to reproduction.

RELATIONSHIP BETWEEN POLLINATOR ACTIVITY AND FLOWERING

Some aspects pertaining to the relationship between the pollinating insects and the opening of the flowers have been discussed. An attempt is made in this section to examine this relationship in greater detail.

Field observations, as well as some of the data already presented, showed that there was a definite relationship between the blooming of the passion fruit flowers and the movement of honey bees into passion fruit fields. The passion fruit flowers usually burst into bloom almost exactly at 1:00 P.M. on every clear day. At this time the air in the vicinity of the field is filled with fragrance from the flowers.

To obtain a quantitative expression depicting the relationship of honey bee activity and blooming, counts were made of the number of bees in the field and also the number of open flowers on 200-foot-long plots selected at random. The data, subjected to correlation analyses, indicated a highly significant correlation ($r = +0.815$, significant at the 1 percent level) between the two variables which suggests the presence of a stimulus that causes the influx of honey bees into the field. This stimulus might be the aroma of the passion fruit flowers.

The relationship between the number of honey bees observed in the field and the percentage of fruit set was also investigated. The number of honey bees were counted per 200-foot-long plot. Within these same plots, 45 flowers were tagged and after 3 days the number of fruits that had set were counted. The data obtained, presented in figure 14, show that at low population densities the fruit set was relatively high. However, at high densities there was a tendency of the fruit set to decrease. This anomalous situation resulted because, apparently, as the number of honey bees increased the number of nectar gatherers, which are not effective pollinators, also increased.

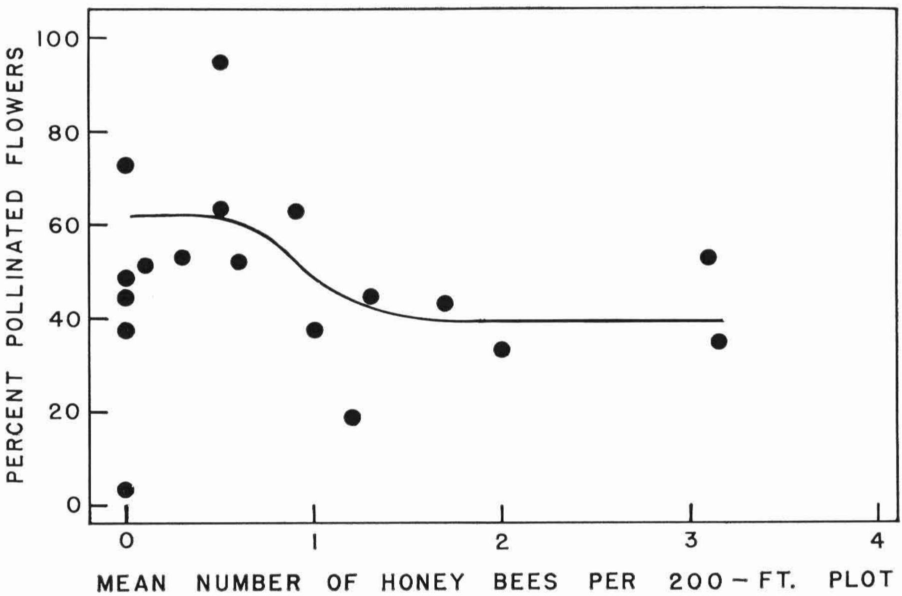

FIGURE 14. Relationship between the number of honey bees in passion fruit fields and percent pollinated flowers.

TABLE 8. The correlation coefficients (r) between carpenter bee activity and blooming of the passion fruit flower

CORRELATED VARIABLES		VALUE OF r
X	Y	
Bee count at nest	Bee count in field	+0.627*
Bee count at nest	Number of open flowers	+0.656*
Bee count in field	Number of open flowers	+0.690**

*Significant at 5 percent level.
**Significant at 1 percent level.

As in the case of the honey bee, the carpenter bee was also found to be active during the time when the flowers were open. Similar analyses were made on data pertaining to this insect. It was fortunate that in several fields there were nesting sites nearby which made it possible to obtain data on activity at the nest in addition

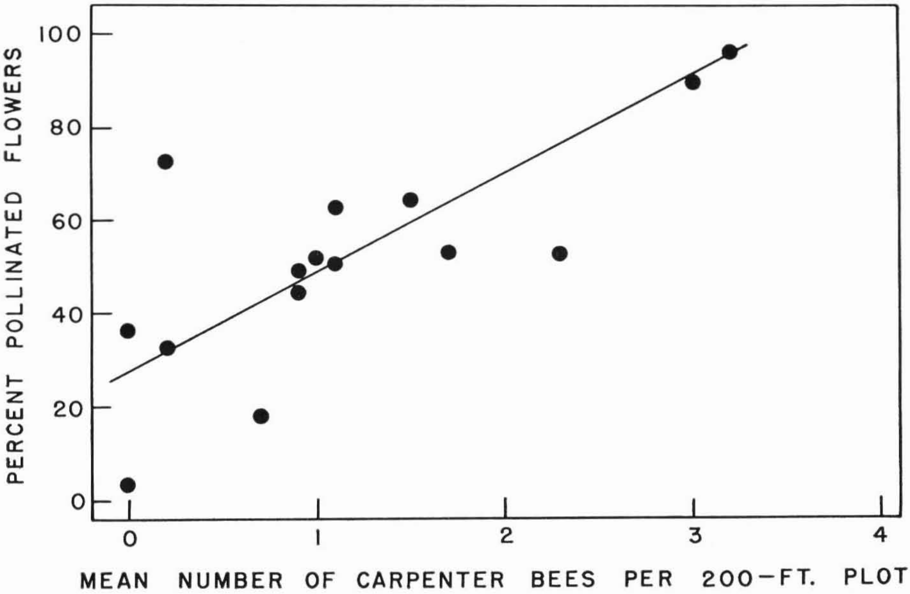

FIGURE 15. Relationship between the number of carpenter bees in passion fruit fields and percent pollinated flowers.

to that in the field. The calculated r values among the variables, presented in table 8, indicate that the r value between the bee count at the nest and the bee count in the field, and the r value between the count at the nest and open flowers, were significant at the 5 percent level. However, the value of r between the number of bees in the field and the number of open flowers was significant at the 1 percent level. The relatively low value of r between the number of bees at the nest and the number in the field indicates that not all of the bees counted at the nest were visiting the passion fruit flowers. Actually, counts at the nest showed that 58 percent of the bees had yellow pollen, presumably having visited passion fruit flowers, and 42 percent did not have yellow pollen. It is assumed that the bees with the deep-yellow pollen grains were those that had visited the passion fruit flowers, for observations indicated that it was only during the passion fruit flowering time that bees with this type of pollen were noted. The relatively low value of r between the bee count at the nest and the number of open flowers probably means that the number of bees visiting passion fruit flowers remained stable and further increases in the number of flowers did not affect the number of bees in the field.

The relationship between the number of carpenter bees and the percentage of fruit set was studied in the same way as in that of the honey bee. This relationship, depicted graphically in figure 15, shows that with an increased number of carpenter bees there was an increase in pollination.

BIOLOGICAL ATTRIBUTES AND INCREASING POLLINATOR ACTIVITY

The present study has shown that certain insects are effective pollinators while others are not. Among the 17 species found to visit the flowers only 2, the carpenter bee and the honey bee, were found to be the most effective pollinators. The biologies of these 17 species that visit the passion fruit flowers vary considerably; however, they may be classified into two categories on the basis of their habits: (1) those that gather and provide food for the young, and (2) those that do not gather food. Insects in the first category are the most effective pollinators because they forage over large areas to gather food for their young and in so doing visit many flowers. Insects in the second category are not effective because of their sluggish habits. In general, these insects remain inactive on or under the leaves after feeding.

Insects in five orders were found to visit the passion fruit flowers: Orthoptera, Thysanoptera, Coleoptera, Hymenoptera, and Diptera. Insects in the order Hymenoptera, superfamily Apoidea, would be the most desirable pollinators because many insects in this large group are nectar and pollen feeders and in addition they provide food for the young.

The ability to survive in areas suitable for passion fruit culture is also important. In the present study, it was noted that the carpenter bee and the honey bee differed in respect to their adaption to different ecological conditions. The carpenter bee was adapted to the relatively dry lowland areas. However, the honey bee, which apparently possesses the ability to survive under a wide range of ecological conditions, was found in the lowland areas as well as in the high native forest areas under humid conditions. In the lowland areas, both species were frequently found within the same passion fruit field, but in general the carpenter bee was the predominant pollinator.

The size of the pollinator appears to be important only to a certain extent. In general, very small insects were not good pollen-transfer agents because of their inability to carry the large sticky pollen grains. However, with larger insects, size is not important, for other factors such as actual numbers and rapidity of movements could easily offset this factor. It has often been stated that a large insect, such as the carpenter bee, is necessary for the pollination of the large passion fruit flower because it was believed that the body of the insect with the pollen must come in contact with the stigma while the insect was walking on the corolla. The observations made during this study indicate that size is not as important as it was once believed.

The absence of the stinging habit is something that is to be desired. However, there appear to be few effective pollinators that do not sting. The importance of this habit in relation to importation of pollinators will be discussed later.

There are several approaches to the problem of increasing pollination, but basically it involves methods of increasing the population of insect pollinators. The honey bee population in the fields can be increased by placing hives of domesticated bees in suitable sites. The carpenter bee can be encouraged by placing heaps of old redwood tiles, sisal logs, hau logs, or other soft woods in the field. The planting of the sisal plant, which produces annually a long flowering stalk in which the carpenter bee nests, in the vicinity of passion fruit fields, is worthy of consideration.

Another approach to this problem is the introduction of new insects that pollinate the passion fruit from areas such as Brazil, the native home of this plant. On the basis of observations made during this study, it seems logical to consider species with nesting and food-provisioning habits, for they would be the most effective pollinators. The species in the superfamily Apoidea would be most desirable, for many of them have desirable characteristics as pollinators. However, all of the food-provisioning Hymenoptera have stinging habits, with the exception of the so-called stingless bees in the genera *Melipona* and *Trigona* (Eckert and Shaw, 1960). The pollination of the passion fruit flowers in El Salvador by several species of *Trigona* has been reported by Berry (*in litt.*, 1957).

On the other hand, the stinging habit is not as serious as it looks superficially, in view of the observations of Dr. Paul Hurd in Brazil (*in litt.*, 1960). He found two genera of bees, *Xylocopa* and *Epicharis*, pollinating the passion fruit. Concerning the behavior of these bees, he states:

"Although the period of observations was not a protracted one, it is clear that at least at that locality and at that time of the season that two genera of bees; viz., *Xylocopa* and *Epicharis*, were collecting pollen in some numbers from the flowers. However, the contrast in efficiency and numbers of pollen collecting bees of the genus *Epicharis* to that of *Xylocopa* was so great that *Xylocopa* rated a very poor second indeed. I was very impressed not only with the rapidity with which *Epicharis* collected pollen from each flower, but by the greater number of flowers visited for this purpose by a single individual bee of the genus *Epicharis* in contrast to that of *Xylocopa*. The *Epicharis* were very rapid and quite 'shy' bees, moving rapidly over the flowers, and leaving for other flowers at the seemingly slight intrusion either by ourselves or other bees. The *Xylocopa*, represented by two species of the same sub-genus (*Neoxylocopa*) as your Hawaiian species, were in contrast sluggish and quite lumbering. It is true that *Epicharis* possesses a sting approximately as effective as *Xylocopa*, however, since it is a 'shy' bee, ready to fly off at the slightest provocation, I think, on the basis of these observations, there is little possibility, if any, that a person could be stung by this bee while it was visiting the flowers. I must confess that the only time I have been stung by *Epicharis* during the past year in Brazil was when I mistook a female in the net for a male. On the contrary, I have lost track of the number of times that I have been stung by *Xylocopa* when trying to coax her from a flower into a cyanide jar, a feat I have never been able to do with *Epicharis* because of their 'shy nature'."

These observations point to the need of re-evaluating our ideas on the stinging habit. Temperament of the bees in question should be considered. It seems that the introduction of effective pollinators such as *Epicharis* that are "shy" and *Trigona* that do not sting is worthy of consideration.

DISCUSSION

The question as to which is the most efficient pollinator has arisen quite frequently throughout the course of these studies. The bagging technique that was employed measures the total efficiency of all pollinators. Thus, it was not possible to segregate the contribution of each of the 17 species that visited the flowers. There is no doubt that each species pollinated the flowers to varying extent; however, the honey bee and the carpenter bee are considered to be the important pollinators. These two bees are more effective than the other flower-visiting insects because of their general level of abundance and their wide distribution. They also possess biological attributes necessary for effective pollinators; viz., (1) they are nectar and pollen gatherers exclusively, and (2) they provision food for their young. Because of the food-provisioning habit, these bees often move long distances and gather considerable amounts of pollen. The ability of the honey bee to collect pollen is shown by the work of Keck (1942), who reported that 6½ pounds of pollen per 5 days were collected in pollen traps from 10 hives. He stated that in other areas, as in California, 40 pounds of pollen could be collected per season from a single hive.

The question has also been raised as to the relative values of the carpenter bee and the honey bee as pollinators of the passion fruit. It is difficult to answer this question because each has its own biological attributes that are valuable as pollinators. The honey bee is valuable because it nests in hives that can be easily manipulated by man. It is valuable also because of its adaptability to the lowland areas as well as to the humid upland areas. The carpenter bee, on the other hand, is valuable because it can survive under very arid conditions. As individuals, carpenter bees are more efficient than honey bees because of their rapid movements and their ability to carry large loads of pollen and nectar per trip. Eckert and Shaw (1960) state that according to some reports the *Xylocopa* tripped 23 alfalfa flowers per minute as compared to 7 by *Apis*. These figures show that *Xylocopa* is three times as efficient as *Apis*. Furthermore, the data obtained in this study (figs. 14 and 15) point to the superiority of the carpenter bee as indicated by the slopes of the curves.

The over-all efficiency of the pollinators was found to vary within the areas where these observations were made. Such variations may result from differences in the general level of abundance of the pollinators. Passion fruit fields located in areas unfavorable to either the carpenter bee or the honey bee are likely to suffer from lack of pollination. Furthermore, the proximity of the field to nesting sites is also an important factor. Unfortunately, the nesting sites of both of these bees were unknown in most fields that were studied. The simultaneous flowering of wild plants with the passion fruit might also cause poor fruit set, for the pollinators might be attracted to the wild plants. This type of situation was observed when honey bee hives were placed in passion fruit fields. The honey bees evidently did not remain in the passion fruit field, for the population counts revealed no increase of the bees. The presence of these wild plants is an important and uncontrollable factor in Hawaii, for open flowers of various species may be found almost every month of the year.

The present study showed locality differences in the pollination activity between the honey bee and carpenter bee which may be due to differences in the ecology of these insects. The honey bee appeared to be adapted to a wide range of ecological conditions. It was active in both the dry lowland areas as well as in the humid native forest areas extending into the high elevations. Such a wide range of activity of the honey bee might be due to the existence of several races of the honey bee (Eckert and Bess, 1952), each adapted to different ecological conditions. The carpenter bee, however, appeared to be restricted in its distribution. Its activity was greatest along the dry to moderately wet coastal areas. In encouraging pollinators in passion fruit fields, these biological differences should be considered.

The maximum fruit set possible as determined by hand pollination and bagging was found to vary considerably. Such variations were evidently observed as early as 1935 by Pope, for he stated that in certain areas the fruits failed to set even with hand pollination. To be sure, some of these failures may be attributed to self- and cross-incompatibility, two types of sterility reported by Akamine *et al.* (1956), Gilmartin (1958), and Akamine and Girolami (1959).

The need for increased pollination was indicated by these studies as well as by those of Akamine *et al.* (1956), Gilmartin (1958), and Akamine and Girolami (1959). This need becomes greater if we consider the reproductive peculiarities of the plant. Self-sterility and cross-incompatibility factors make it necessary to have highly effective pollen transfer agents. Furthermore, since the juice yield has been found to be influenced by the amount of pollen that goes on the stigma (Akamine and Girolami, 1959), it is evident that the pollinators must not merely pollinate; they must place a liberal amount of pollen on the stigmatic surface. To accomplish this, large numbers of pollinators would be necessary.

SUMMARY

Preliminary studies on the entomological problems of the passion fruit in Hawaii indicated that pollination was one of the major entomological problems of this crop. These studies, as well as those conducted subsequently, showed that insects were the major pollinators. The present study summarizes the results of studies on the ecology of the major insect pollinators in particular reference to passion fruit pollination.

Studies on the flowering cycle showed that the passion fruit plant blooms during February to November. During this period at least 17 species of insects were found to visit the flowers. Among these the honey bee, *Apis mellifera*, and the carpenter bee, *Xylocopa sonorina*, were the important pollinators. The most effective pollinators were those species that gathered nectar and pollen in large quantities to provide food for the young. Those that did not possess these habits were usually not effective pollinators.

Population studies showed that the honey bee and the carpenter bee were abundant in passion fruit fields only during the flowering season. There appeared to be no general trend in the peaks of abundance. Studies on the diurnal opening of the passion fruit flowers indicated that the highest percentage of flowers opened at noon and that the percentage decreased rapidly thereafter until about 6:00 P.M. The foraging activity of the honey bee and the carpenter bee was correlated with the opening of the flowers.

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