Ecology of the Squash and Gourd Bee, *Peponapis pruinosa*, on Cultivated Cucurbits in California (Hymenoptera: Apoidea)

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and A. E. MICHELBACHER

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ABSTRACT

Hurd, Paul D., Jr., E. Gorton Linsley, and A. E. Michelbacher. Ecology of the Squash and Gourd Bee, *Peponapis pruinosa*, on Cultivated Cucurbits in California (Hymenoptera: Apoidea). *Smithsonian Contributions to Zoology*, number 168, 17 pages, 4 figures, 8 tables, 1974.—This investigation focuses primarily on those ecological aspects involved in the natural history of the squash and gourd bee, *Peponapis pruinosa*, as it occurs in commercial squash and pumpkin plantings of the Sacramento Valley of California. Information is presented on this species' nesting habits, nest site selection, burrow construction, distribution and density of nest cells, diurnal and seasonal nesting activities, competition at the nesting site, diurnal and seasonal field activity, number of annual generations, and the results of transporting and introducing the adult bees into squash and pumpkin plantings in geographical settings well removed from their natal area.

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Contents

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Introduction

The principal pollinators of plants of the genus *Cucurbita* (gourds, squashes, and pumpkins) are bees. Of these, the native squash and gourd bees belonging to the genera *Peponapis* and *Xenoglossa* are by far the most important, and their evolutionary history has been closely interrelated with that of their cucurbit hosts (Hurd, Linsley and Whitaker, 1971). These bees are solely dependent upon *Cucurbita* for pollen and in the process of gathering pollen and nectar from the flowers, pollination is accomplished. The bees are well adapted for the collection of the large pollen grains of *Cucurbita* and their diurnal flight period is synchronized with the opening cycle of the flowers.

Eleven species of squash and gourd bees occur in the United States, six of *Peponapis* and five of *Xenoglossa* (Hurd and Linsley, 1964). Two members of each genus occur in southern California. One is typically a desert inhabitant (*Peponapis timberlakei* Hurd and Linsley), one primarily a desert species extending to the coast (*Xenoglossa angustior* Cockerell), and two largely cismontane and coastal (*Peponapis pruinosa* (Say) and *Xenoglossa strenua* (Cresson). The first two species range from New Mexico and Arizona into Mexico and southern California and are attached primarily to the gourds *Cucurbita digitata* and *C. palmata*. However, *Xenoglossa angustior* also takes pollen from the gourd *Cucurbita foetidissima* and the cultivated squashes and pumpkins and has apparently extended its range into the San Joaquin Valley (Kern, Fresno, Tulare, Madera, Merced, and Stanislaus counties), as these plants became available through farming and other activities of man.

Peponapis pruinosa and *Xenoglossa strenua* are widely distributed species ranging transcontinentally from the Atlantic Coast to southwestern United States and Mexico, taking pollen from the widespread gourd *Cucurbita foetidissima* and all of the cultivated species of squash and pumpkin. Both species apparently spread eastward from the Great Plains region with the development of agriculture, but only *P. pruinosa* has extended its range significantly from southern California north of the Tehachapi Mountains, the northern limit of the presumed range of its wild host in California before the advent of man. As presently known, its California distribution includes coastal southern California and the western desert margins and the

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San Joaquin and Sacramento valleys of central and northern California to at least as far north centrally as Anderson, Shasta County, as far west as Willits, Mendocino County, and east as far as Susanville, Lassen County. It occurs most abundantly in valleys, not only where squashes and pumpkins are grown, but virtually everywhere that its native host, *C. foetidissima,* occurs. Although *Peponapis pruinosa* is a relatively recent invader in the northern part of California, it is well established and adapted in this region. Except in the central and southern San Joaquin Valley, where *Xenoglossa angustior* is present, the females have no squash or gourd bee competitors for *Cucurbita* pollen.

Although squash and gourd bees are the principal pollinators of cultivated *Cucurbita,* other bees often play an important role. The most important of these is the introduced honeybee, not only in areas where squash and gourd bees do not occur, but also during the early- and late-season periods when adult squash bees are not active. When both squash bees and honeybees are present in numbers, however, the former have a competitive advantage because of their somewhat larger size, more rapid flight, and earlier period of diurnal pollen-collecting activity.

ACKNOWLEDGMENTS.—We wish to express our appreciation to Rea and Hal Gardner, Tim Tokuno, and Robert Starkey, all of Gridley, California, for their cooperation in making available to us their fields and gardens for the conduct of these investigations. The studies would not have been possible without free access to their properties.

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Methods of Study

NEST SITE OBSERVATIONS.—The seasonal pattern of burrow construction was determined by periodic counts of burrow entrances and tumuli in specified areas of the nesting sites. The general level of activity over the nest area was judged subjectively at various times during the day throughout the season. Time intervals for activity spent away from and within the burrow were recorded for individual females, and the return of foraging females noted for the presence or absence of pollen loads. Such observations were made at various times of day and during different portions of the season. An indication of the distribution and density of cells in the nest site was obtained during the winter by excavating square-foot columns of soil, dissecting out the cells, and recording their number at various levels below the surface. This also provided data on survival as well as loss from mold or disease.

FLOWER SITE OBSERVATIONS.—Population trends and abundance of bees at the flowers of *Cucurbita* were determined at various times of day throughout the season by two methods. The first involved recording the number of bees by sex in each of 100 flowers selected at random. The second involved recording by sex the number of bees observed in randomly selected flowers during a 15-minute interval. Experience revealed that early in the season, data obtained by the two methods were virtually identical since approximately 15 minutes was required to count the bees in 100 flowers, although at times a survey of 100 flowers took somewhat longer. As the season progressed and the density of the flowers increased, less time was required to examine 100 flowers and 15-minute counts yielded more individuals and more consistent data. The contrast became even greater toward the end of the season, with a decline in the bee population and the resultant reduction in the time required to count the bees in 100 flowers.

Study Sites

Two prinicpal areas were utilized in the studies reported here. A number of sites were selected in the vicinity of Gridley, Butte County, California, in the center of the Sacramento Valley. This is a region having a deep rich soil, is largely under

irrigation, and is devoted to the growing of orchard, field, and truck crops. It is an ideal area for the study of *Peponapis pruinosa* because of the dense concentration of host plants. The Gridley area is not only a center for the growing of pumpkins for the canning industry, but contains numerous commercial plantings of both summer and fall type squashes richly supplemented by many home plantings. The large populations of squash bees have been under observation since 1962 and give every evidence of having been in existence for many years previously.

The second study area is located at Berkeley, Alameda County, on the Oxford Tract Agricultural Experiment Station plot adjacent to the campus of the University of California. This site was selected because continuous observations and experiments could be conducted on planned *Cucurbita* plantings. Further, the climate of Berkeley is modified by coastal influences and the cooler summer and warmer winter provide a useful contrast with the continental climate at Gridley.

Results of Study

GENERAL NESTING HABITS.—*Peponapis pruinosa* is a gregarious, ground-nesting bee. The burrows are constructed in flat ground. The main shaft is vertical or nearly so with single cells at the end of downward-slanting laterals. At our nest sites the burrows were constructed similarly to those described and figured by Mathewson (1968), but were generally deeper.

SELECTION OF THE NESTING SITE.—Nesting sites of *Peponapis* were discovered at Gridley in 1969 on lawns near homes in a rural area. At the first site the burrows were located in a lawn which had been maintained for 32 years and in recent times has been watered for four hours once a week. Certain areas in the lawn appeared to be more attractive for nesting than others. These were areas of deep, relatively undisturbed soil with a sustained supply of moisture. Lawn grass also attracts the bees which avoid old dense stands of Bermuda grass with nearly impenetrable mats of underground stolons or rhizomes.

In the first nesting site, the lawn covered 1600 square feet, but the burrows were mostly concentrated in one section. On 10 July 1969, 10 square-foot areas were selected at random throughout the lawn, the grass clipped, and the number of burrows in each sample was counted. They ranged from 0 to 11 per square foot with an average of 5.3. The variation primarily reflected variations in the density of old stands of Bermuda grass.

At the second nesting site, burrows extended well beyond the lawn area. Here the owner watered the lawn each evening. As with the first site, nesting was uneven and in the lawn there was an area where the concentration of nests was much greater than elsewhere. In this respect the two nesting sites closely paralleled each other. Unlike the first location where the burrows were confined to areas of dense grass, the bees were nesting in bare ground in considerable numbers. However, there may be a tendency for the females to seek some protection as burrows were found more concentrated under shrubs, boards (see also Mathewson, 1968), and at the base of clumps of grass. On 11 July 1969, under the dead branches of a small juniper shrub 10 burrows were found in a square-foot area (Figure 1). In the bare open ground 10 square-foot random samples were taken. In an arbitrarily selected site under a 12-inch plank, 10 burrows were observed in a square-foot sample (Figure 2). Here the number of burrows ranged from 0 to 7 with an average of 1.8 per square foot. Thus, the evi-

FIGURE 1.—Burrow entrances to nests of *Peponapis pruinosa* (Say) located under dead branches of a small juniper shrub.

dence strongly indicates that objects that offer some protection influence females seeking burrow sites.

According to homeowners, the same nesting sites had been used by the bees over an extended period of years. Further, over an extended period of years the areas of highest burrow concentration have remained essentially the same. Both nesting sites occur in a region of host abundance, consisting mostly of pumpkin fields. These plantings were either adjacent or close to the nesting sites.

BURROW CONSTRUCTION.—During late fall of 1970 a two-foot-wide cement walk was laid at the second nesting site, separating the lawn from the bare-ground nesting area. The walk exerted a profound influence on the nesting habit of the bee. In 1971 the females tended to concentrate their burrows along the margins of the walk, especially on the lawn side.

On 31 July 1971, the number of burrows per square foot in the high density portion of the lawn was determined from 15 random samples. The number of burrows per sample ranged from 0 to 9 with an average of 4.46 per square foot.

On 30 August 1971, two square-foot samples from the lawn side of the walk were examined and in each there were 19 burrows. In each sample the majority of burrows were located within three to four inches of the edge of the walk and were close together, and some of them were interconnected. That this situation occurred was indicated by marked bees entering one burrow and emerging from another.

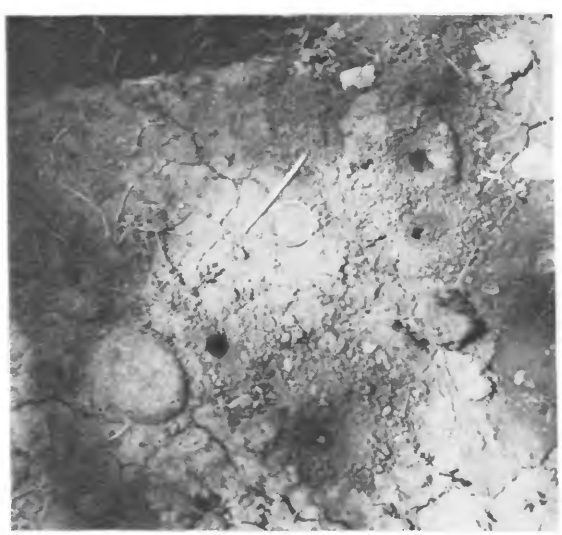

FIGURE 2.—Burrow entrances to nests of *Peponapis pruinosa* (Say) located under 12-inch board planking.

Observations conducted on 31 August 1971 revealed that the nesting site extended well beyond the lawn and the bare-soil area. In the early morning many bees were observed flying in with pollen to burrows in an adjacent area covered with a coarse grass (probably water grass).

Undoubtedly many nesting sites exist in the region. For example, on 31 July 1971, another site was discovered in the lawn of a farmstead located in a pumpkin field in the same restricted area.

Further evidence that lawns are attractive as nesting sites was obtained at Berkeley. Following experimental introductions it was found that marked females released in squash and pumpkin plantings constructed their burrows in a lawn across the street from the experimental plot (Michelbacher, Hurd, and Linsley, 1971).

Burrow construction activity occurred and working females were observed from before daylight until late evening. There is a possibility that it might even extend throughout the night. During the summer, nests in all stages of development are present. Often tumuli are associated with them. Sometimes the entrances are plugged or covered with a mound, but many were free of excavated soil. When females plug their burrows, they usually do so about one-fourth of an inch below the surface.

On 31 July and 30 August 1971 and again on 1 July and 7 July 1972, several surveys of burrows in a nest site were conducted (Table 5). In general the majority of burrows had tumuli and the presence of a tumulus is an indication of recent nest construction.

In the afternoon and early evenings there appears to be an increased activity in nest construction and repair. This may be because the bees are no longer engaged in pollen collecting and thus have more time to spend on nest development. This is indicated by an increase in fresh tumuli deposited about the openings of the burrows which, due to moisture, is darker in color than older deposits, and consequently is easy to distinguish.

TABLE 1.—*Burrows per square foot of surface in a nesting site of* Peponapis pruinosa *at Gridley, California, 10 July 1969*

Sample number	*Number of nests*	*Condition of ground cover*
1	0	Dense grass with some Bermuda grass
2	0	Thickly covered with Bermuda grass
3	8	Rye grass
4	11	Rye grass
5	3	Rye grass
6	10	Rye grass
7	2	Grass very dense and rank
8	11	Rye grass
9	0	Very dense with considerable Bermuda grass
10	8	Rye grass
Total	53	
Average	5.3	

The practice of watering the lawn each evening apparently exerted little or no adverse influence upon the nesting bees. It is also possible that the water tends to wash away the tumuli, although in some cases the tumuli melt into chimney-like structures around the entrance to the burrows. The morning after watering, females returning with pollen freely entered burrows with and without tumuli. Apparently, they do not find it necessary to make any repairs to the nest. Where tumuli were present, it is certain that some of these had been worked on after watering. Whether any of this was in response to the watering is not known. It has been determined, however, that the bees will work on their burrows until at least 2000. On 30 August 1971, the nest site was visited at 1905 during a light drizzle. The lawn had been watered lightly at 1730 and because of darkness, observations were made by flashlight. On arrival, several bees were seen in their burrows. In order to secure some measure of the amount of bee activity in their nests, two 15-minute observation periods were conducted. In the first, which lasted from 1910 to 1925, 11 bees were seen in their nests, and in the second, 1925 to 1940, 7 bees were observed. Of interest, some bees were seen in their burrows where there was no tumulus at the entrance. The use of lights did not appear to have an adverse effect on the bees.

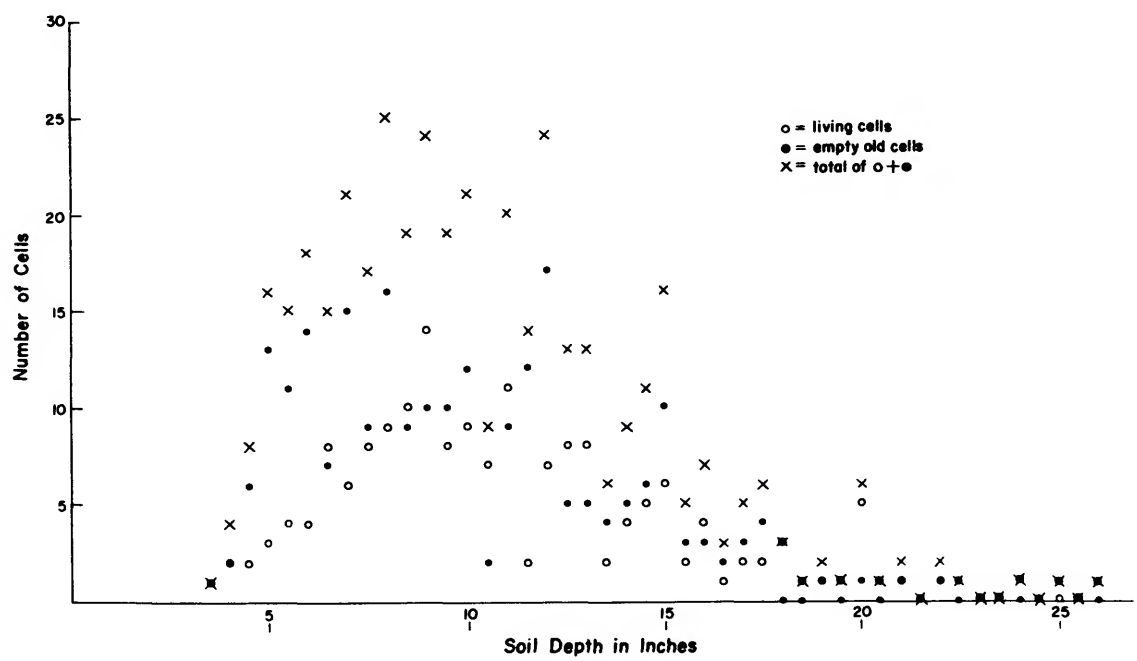

FIGURE 3.—Distribution at different levels of *Peponapis pruinosa* (Say), nest cells in a square-foot column of soil.

The nesting site was revisited the next morning, 31 August, at 0440. The temperature at 0455 was 16°C and at 0515 it dropped to 15°C. A cool breeze developed. Using flashlights, a search of burrows for bee activity was conducted. From 0445 to 0500, three bees were seen and from 0500 to 0515 only two individuals were observed. This low level of activity came as a surprise. It appears that very early in the morning bee activity is near a standstill. Foraging flight began at approximately 0508.

Where the soil is extra moist, the tumuli which are developed are deposited as small pellets. Such tumuli stand out in marked contrast to the more normal ones made of fine soil particles.

When the tumulus formed a cone about the entrance to the burrow, the soil along the inner surface of the cone was packed and smoothed in a uniform manner.

Distribution and Density of the Cells.—In order to secure some information on the distribution and number of cells, a square-foot column of soil was excavated at a nest site at Gridley on 16 March and 17 March 1970. The cells were dissected out and the data obtained plotted in Figure 3. There were 176 cells with live individuals and 231 that were empty. Cells were encountered at depths from about 3½ to 27 inches with the greatest concentration between 5 and 12 inches. Further information on the abundance of cells was obtained 9 December 1971. Prepupae were wanted for introduction investigations being conducted in New Zealand. These were excavated in the bare soil area at the nesting site where this zone was separated from the lawn by a cement walk. Again no cells were found in the first 3 inches of soil. From this level the number of cells increased and cells were found very abundant in the 8- to 12-inch zone. As expected, the greatest concentration of cells was next to the walk. This is the area where the burrows were found in most abundance during the active nesting season. In all, 6 to 7 square feet of soil were examined and 530 usable prepupae were collected. In addition some were killed in digging and many more probably escaped detection. Further, no attempt was made to recover the prepupae at the lower level. Some individuals infected with a mold or a disease were encountered. They were usually in clusters and were relatively few in comparison to the healthy individuals.

Diurnal and Seasonal Nesting Activities.—In northern California, *Peponapis pruinosa* begins field activity at about one-half to three-quarters of an hour before sunrise. For example, on 31 August 1971, at a nesting site near Gridley, the first bee was heard at 0508 hours. At this time there was just sufficient light to vaguely distinguish the color of larger objects in the area.

On a number of occasions, nesting sites were under observation in early morning to determine when the first bees initiated foraging activity. Also, observations were made in the fields to determine the time of arrival of the bees at the flowers (Table 2). Field activity closely followed the time the bees left their foraging area. Once activity is initiated, it rapidly increases and in a few minutes a constant hum develops about the nesting site. This surge of activity is paralleled by expanding activity at the flowers. The flight about the nesting areas is most impressive. This is due to the

Table 2.—*Time of earliest flight activities of* Peponapis pruinosa *at nest site and in the field at Gridley, California*

				Nesting site			*Field*		
Date	*Sunrise*	*Time*	*Temperature (°C)*	*First bee heard*	*First bee returns with pollen*	*Elapsed time (minutes)*	*First bee heard*	*First bee in flower*	*Foraging start (minutes before sunrise)*
6-25-69	0448	0415	14°	0417	0430	13	0417	0417	31
7-10-69	0500	0410	17°	0405	0419	14	0417*	0415	55
8-12-69	0540	0410	16°	0446	0455	9	0451	0453	54
8-31-71	0545	0508	15°	0508	0520	12	–	–	37
9-11-69	0552	0500	17°	0510	–	–	0515	0520	42
9-26-69	0604	0515	13°	0542	0549	7	0546	0549	22

* A steady hum over the flowers.

great concentration of burrows and the resulting numbers of females flying in and out of their burrows. Literally hundreds of females are involved and they appear to ignore persons standing in the area. Although there is a hivelike level of activity, a female has never been observed to attack a person. This, however, may not be of much comfort to a homeowner if the nesting site should occupy his lawn. It can produce an annoying situation, especially if there are children. If a child should capture a female bee, there is every likelihood of its being stung. Most parents would hesitate to allow their children to venture into this flight of bees, and unless informed are likely to undertake eradication of the bees.

The beginning of seasonal adult activity varies with the locality. Thus in the more coastal regions of central California the start of the season is later than in the hotter interior valleys. The bees are out in numbers in the Gridley area long before this situation prevails in the Berkeley region. Also, the start of activity period in a given locality varies with the season. As the season advances, the start of the foraging period begins later in the morning. The season of 1971 was delayed and a survey of two nesting sites at Gridley on 19 and 20 June revealed little or no activity. Although many bees had emerged, nest construction was not underway to any appreciable degree. It would have been impossible at that time to secure information of the type presented in Table 2.

At the time the bees commence their foraging activity, it is too dark to see what is occurring without the use of lights. In general, the lights appear to exert little influence on the bees. However, on rare occasions they react to them. On 10 July 1969, at 0400, a male bee flew to the lamp at a nesting site. At 0403 two females came out of their burrows but returned again. This was followed at 0405 by a female which emerged and flew away. At the same time another flew to the light and then away. On this day it was barely light enough to see in the flowers at 0420.

Activity at the Nesting Site.—Upon emerging the females leave the nesting area and seek nectar and protection in the flowers of their host. There is a period before the female is conditioned to build a nest and start pollen collection. The length of the prenesting period has not been fully determined. Studies by the present investigators indicate that it is of approximately two to three weeks' duration. Mathewson (1968) investigated this bee under Rhode Island conditions and reported that both sexes are abundant on *Cucurbita* blossoms during the 21 days following general emergence, but there is no evidence of nest building or pollen transport during this interval. It is this period that has been utilized in our introduction experiments since it is believed that a minimum of disruption occurs if females are moved to new areas before the nesting instinct develops and pollen collecting is initiated (Michelbacher, Hurd, and Linsley, 1968, 1971).

Thus in early season few if any bees may be found in the nesting site, while large numbers of both sexes are present in the field throughout the day, since burrow construction lags two to three weeks behind emergence. The 1971 season was a late one which resulted in a delayed appearance of the bees in comparison to other more normal years. A survey on 19 and 20 June showed an abundance of individuals in host flowers (see Tables 6 and 7). Some of the females had some pollen on the legs, but the amount was very small, and they were not flying from flower to flower. There was no evidence that they appeared to be interested in collecting pollen, and none was seen with a full pollen load. Observations at nesting sites revealed no burrow construction. The 1970 season was a more normal one and yet as late as 7 July only one female was observed in a nesting area. The 1972 season was early. In one of the nesting sites, burrow activity was well underway by 1 July. On 2 July, many burrows were under construction and the intensity of this activity was evident by the abundance of burrows with tumuli. On this date, summer squash was flowering freely and in production, but pumpkin, which is the main host, had begun blooming in only one field.

Just after dawn on 2 July, bees were most active about the nesting site, but their behavior was different from that encountered later in the season when pollen was in abundance. Although some of the females were returning to the nesting site with pollen, it soon became evident that there was not sufficient pollen and probably nectar, from squash flowers, to support the bee population present in the nesting site. Often the pollen loads appeared to be light, and the supply of pollen was apparently so limited that there was no evi-

dence of rhythm to foraging flights. Many of the females were working in their burrows, while other remained in the flowers or were seeking nectar.

Between 2 July and 7 July, the number of burrows more than doubled in the nesting areas (Table 5). The available pollen still appeared to be less than the bees could have utilized. At 0818 most of the females were coming in with pollen, although there were some with none. Between 0835 and 0915 females with light to full pollen loads were observed. Sometimes unequal distribution of the pollen on the scopa of individual bees was noted. Of the females returning to the nesting site between 1010 to 1030, 43 carried pollen, while 46 had none. In a similar survey from 1140 to 1200, 1 individual arrived with pollen and 57 were without.

On 8 July, observations on the number of females returning to the nesting site with and without pollen were continued with the following results:

Time	*Females with pollen*	*Females without pollen*	*Temperature (°C)*
0458–0513	43	3	13°
0515–0530	53	10	14°
0710–0725	95	3	18°

Since in each period some bees flew in without pollen, it is very possible that these represented individuals that were in the early stages of nest construction. Further it should be noted that the number of females entering their burrows represent but a small proportion of the individuals milling over the nesting site. However, the figures presented above do give a good index of the activity and clearly show that it increased with a rise in temperature.

Once nesting is initiated, activity in the nesting site increases rapidly and nests can be found in all stages of development, with females carrying pollen, others working on their nests, and some hovering as if searching for a site to build a nest. Such a situation was encountered at nesting sites on 24 and 25 June 1969.

Where the soil is moist, a female is capable of constructing a burrow in a relatively short period. On 9 July 1969, a female commenced a burrow at 1035 and by 1105 the excavation penetrated to the depth of one inch and a well-developed tumulus was formed. By 1250 the burrow entrance was covered with a mound. Even by the middle of July the great majority of females were collecting pollen and this activity along with nest construction appeared to be the principal occupation. Male bees are rarely encountered at the nesting area, except for individuals that have just emerged.

In an attempt to obtain comparative information on the length of time females spend in their burrows and in foraging, on 1, 30, and 31 August 1971, a number of nests were selected at random for observation. These were watched during the morning, spanning the period of major foraging activity (Table 3). The 1 August survey was conducted from 0458 to 0730. Thirteen bees were involved and the foraging flights ranged from 1 to 25 minutes, with an average of 8.8 minutes. The time spent in the burrow (excluding the one individual that never left the nest) ranged from 2 to 55 minutes, with an average of 7.6 minutes. The survey on 30 August ran from 0730 to 1000 and involved 6 bees. The foraging flight ranged from 1 to 31 minutes, with an average of 7.6 minutes. The time they remained in the burrow varied from 1 to 45 minutes, with an average of 8.1 minutes. The 31 August survey included 7 individuals and surveillance was from 0530 to 0730. The foraging flight ranged from 4 to 20 minutes, with an average of 13.3 minutes. The period in the burrow fluctuated between 4 and 31 minutes, with an average of 9.2 minutes.

The results obtained on the three surveys were in rather close agreement. A considerable variation occurred in both the length of time spent in the burrows and on foraging flights. On the 31 August survey, however, the length of the foraging period was distinctly greater than that noted on the two previous ones. The time spent in the burrows was also longer but the difference was less marked. It is believed that the decreased activity was in response to the relatively lower temperature that occurred on the morning of 31 August. The temperature at 0455 was 16°C, at 0515 it had dropped to 15°C, and at 0730 it was 17°C.

Some evidence that age is a factor influencing the length of the foraging flight was obtained on the 31 August survey. Bee number 4 was an old bee and this was indicated by the fact that her thorax was badly rubbed, the wings frayed, and the mandibles were well worn apically. Foraging

TABLE 3.—*Length of time (in minutes) spent by female* Peponapis pruinosa *in foraging and in burrows at Gridley, California, observed in 10 time periods*

Individual number	*Foraging*										*In burrow*									
	1 August 1971 (0458 to 0730)																			
1	12	7	7	5	5	13					3	53	3	2	5	4				
2	23	13	9	2	7	9	7				15	11	4	5	6	3	5			
3	17	6	4	24							15	28	3	3						
4	23	9	4	3	7	2	5	1	13	8	6	14	5	5	5	5	4	6	3	7
5	6	24	5	5	8	3	5	5	3	9	9	9	6	6	4	4	3	9	4	10
6	15	3	5	8	2	5	3	10	10	6	12	3	6	2	7	4	6	2	4	6
7	2	7	5	13	26						55	2	3	5	2					
8	7	7	10	10	4						27	4	3	5	11					
9	25	9									6	5	4							
10	19	9	9	4							16	5	4	3	2					
11	0*																			
12	18	5									3									
13	7	6	9								3	4								
	30 August 1971 (0730 to 1000)																			
1	9	9	5	7	7	8					7	4	4	4	16	5				
2	7	20	3	7	2						12	18	3	7	2					
3	9	8	2	2	1	7	9				4	10	2	1	2	1	3	45		
4	9	31	8	8	8						25	20	20	6	3					
5	0**																			
6	8	6	9	7	8	7	7	8			5	4	4	5	4	3	4	5	10	
	31 August 1971 (0530 to 0730)																			
1	14	15	12	10	17						4	4	14	5	6					
2	11	13	11	8							10	5	27	23						
3	9	11	20	8	4	9					5	3	9	4	19	5				
4	20	26	16	25							7	4	2	31						
5	12	10									7	6	5							
6	4	16	19								30	4	6	4						
7	11	10	18								7	5	6							

* Showed a number of times but never left its burrow.

** Left the burrow at 0758 and never returned.

flights of this individual were longer than for any of the others (Table 4) and averaged 33 minutes as compared to 13.3 minutes for the others.

There are probably a number of reasons which might account for the wide variation observed in the length of the foraging flight and the duration of the period spent in the burrow. The time utilized on foraging is probably influenced by age of individual, distance the bees had to go to obtain pollen, weather conditions, and the proportion of this time spent in seeking nectar. Apparently little time is required by a bee to deposit her pollen load. After a pollen trip, however, it may be necessary for the bee to spend some time on nest construction or modification. On some occasions bees could be seen working on their burrows, and this

TABLE 4.—*Numbers of female* Peponapis pruinosa *returning to burrows from early afternoon to early evening at Gridley, California, 30 August 1971*

Time period	*Number of females*		*Temperature*	
	with pollen	*without pollen*	*time*	*°C*
1300–1315	2	16	1300	26°
1315–1330	0	12		
1330–1345	0	9		
1345–1400	0	10		
1400–1415	0	9	1415	27°
1645–1700	0	3	1655	26°
1700–1715	0	2		
1715–1730	0	0	1740	23°*

* Light rain starting to fall.

activity tended to materially lengthen the time spent in the burrow.

Sometimes a female would apparently enter a burrow other than her own. When this happened the visitor usually had no pollen and left the burrow in about a minute. In other cases, competition for possession of the burrow would result and interruption of the usual trip pattern occurred. With some burrows with nest openings separated by less than an inch and obvious "landmarks" often absent, it was not surprising that some confusion would result. However, interference occurred even in instances where the entrances to burrows were more widely separated. Females often did not fly directly to their burrow. For example, one bee under observation on her last four trips would light as much as two or more feet away from her burrow. She would then begin to explore and search for her burrow. In doing so she examined a number of burrows but did not try to enter them. She continued her search and always tended to move in the general direction of her burrow. Once it was located, she readily entered it. So characteristic were her movements that she could be easily recognized on arrival at the nesting site. Other individuals displayed equally characteristic behavior.

At least within limits, the activity of the bees increases with a rise in temperature. On 1 August 1971 as the sun rose over the horizon, the nesting site was gradually but increasingly exposed to it. By 0710 about one-third of the area was in sunlight and the flight of the bees therein was noticeably faster. Such observations have been substantiated on a number of occasions. The increase in flight tempo is most marked on days when the early morning temperature is relatively low. Under such conditions, the level of activity is lower compared to later in the morning when the temperature reaches 16°C and above. There also seemed to be a rhythm to flight activity as indicated visually and by changes in the constant hum that develops over the nesting site.

Near the close of a nest survey at 1000 on 30 August it was noted that on occasions a bee was returning to her burrow without pollen. This would be expected as the day progressed, as less and less pollen was available for collection, and the females more actively seek nectar. In order to obtain more information on this subject, burrows selected at random were placed under observation at 1150 on 30 August 1971. Although there was considerable activity in the nesting site, this had diminished to a point where watching a few burrows would yield little information. To secure usable data, it was found necessary to make observations on a much larger area. From 1230 to 1245, although greatly reduced, there was still quite a hum from the bees over the nesting site. By 1300 it was markedly reduced and continued to decrease as the afternoon advanced. Between 1212 and 1255 three bees were observed coming into the nesting site with pollen, but no count was made of those returning without pollen. Starting at 1300 a record was made of the bees with and without pollen coming in and entering their burrows. The information based on 15-minute intervals is presented in Table 4. No bees with pollen were observed after the 1300 to 1315 period. A few bees without pollen continued to fly in but the number tended to decrease with the advance in time. The last bees were observed to fly in during the 1700 to 1715 interval. None were observed in the 1715 to 1730 period so observations were discontinued. Observations made at a second nesting site developed information that substantiated that shown in Table 4.

With the exceptions observed on 1 and 7 July 1972, recorded below, no female with pollen was seen to enter her burrow later than the 1300–1315 period or without pollen after 1700–1715.

Time	*Number of females*	*Temperature (°C)*
	1 July 1972	
1445–1500	5	37° 1515
1500–1515	5	
1700–1715	0	36° 1700
1715–1730	3	
1730–1745	13	36° 1745
1745–1800	22	
1800–1815	45	34° 1800
1815–1830	44	
1830–1845	38	32° 1845
1945*		29° 2000
	7 July 1972	
1700–1730	6	30° 1707
1730–1745	13	

* Area visited 1945, no bees seen. During peak of flight as many as 5 or 6 individuals seen in flight at one time. Most flights within a foot of the surface and appeared to be concentrated over thickest stand of grass. Here bees were observed to alight.

Time	*Number of females 7 July 1972*	*Temperature (°C)*
1745–1800	12	
1800–1815	5	29° 1815
1815–1830	11	
1830–1845	6	
1845–1900	1	
1900–1915	4	
1915–1930	0	26° 1930

None of the females in the above tabulation had pollen, and the data clearly show that the females were active much later into the evening than indicated in Table 4. There are several possible explanations for this behavior. Early in the season there is a possibility that females working on their nests find it necessary to seek nectar for nourishment, or the individuals involved are those that have just emerged and are stimulated to flight in a search for nectar. The flight at dusk, although unusual, is not unparalleled, for in the Cape Region of Lower California, Mexico, the squash bee *Xenoglossa mustelina* (Fox), on a number of occasions, has been observed flying at dusk and visiting the flowers of *Tecoma stans,* apparently seeking nectar (Hurd and Linsley, 1967).

The flight of *Peponapis pruinosa* at dusk is limited to early in the season, and the information in the above tabulation shows that the flight on 7 July was of less magnitude than that of 1 July. Further, it should be noted that the number of individuals involved in the flight at dusk is small as compared to the flight activity that takes place in the morning.

TABLE 5.—*Surveys of burrows in a nest site of* Peponapis pruinosa *at Gridley, California*

Time period	*Female active and seen in burrow*	*Tumulus and plugged*	*Tumulus and not plugged*	*No tumulus*	*Total burrows*
1 Jul 72					
1015–1030	5	3	25	16	49
1340–1355	1	5	36	14	56
1700–1715	1	3	42	35	81
1955–2010	0	1	30	16	47
7 Jul 72					
0855–0910	2	3	129	57	191
1430–1445	11	4	142	50	207
31 Jul 72					
1345–1400	21	29	67	58	175
1600–1615	20	13*	105	62	200
30 Aug 71					
1020–1035	3	2	59	53	126
1645–1700	5	10**	68	82	165

* 10 with entrance covered with mound.
** 7 with entrance covered with mound.

Often in early morning the bees were very sluggish, and some experienced difficulty in orienting to their nests. For example, on the morning of 31 August 1971, many bees returning to the nest site did not appear to find their burrows readily and some even dropped pollen, which accumulated noticeably on the soil about burrow entrances. At 0810 on 9 July 1969, bees returning with pollen also seemed to have difficulty orienting to their nests, although it is possible that the presence of observers in the nesting site may have interfered with the "landmarks" utilized by the bees. The disturbance of landmarks was illustrated when a homeowner who had allowed the grass to grow to the height of four to six inches cut the grass and incoming bees appeared so confused that they became "stacked" in flight over the nesting area.

COMPETITION AT THE NESTING SITE.—As far as could be determined, very little intraspecific competition takes place in a nesting site. What little competition is evident is largely among female bees rather than with other organisms. In those areas where the burrows are very concentrated, females occasionally interfered with one another and there was disruption of normal behavior. Instances were observed where a visitor would be rejected from an invaded burrow. However, no violent action was ever observed. In general, a rather harmonious relation existed, considering the large number of individuals populating the nesting sites.

Other organisms such as pillbugs *(Armadillidium)* and a small species of millipede were observed to enter the burrows, but this type of activity appeared to be tolerated by the bees. Once a large pillbug was seen to enter an occupied burrow, but the bee emerged and took off in the usual manner, although it is possible that interconnecting burrows were involved and that the bee may have bypassed the pillbug.

DIURNAL AND SEASONAL FIELD ACTIVITY.—In the Gridley area, bees begin to emerge in late May and field activity continues into October. Once emergence is initiated, it mounts rather rapidly and bees are abundant before there are sufficient host flowers to adequately accommodate all of them. At the time of the earliest emergence, some home

and commercial plantings of summer squash (zucchini, crookneck, and scallop) are in bloom, but not pumpkin, which is the major host. As a result, the available flowers are crowded with bees and many seek nectar from the flowers of morning glory (*Convolvulus arvense*) blackberry, cucumber, watermelon, and other melons. There are probably other hosts that serve this purpose but they were not observed. At this time, pollen is not an important item because there is a two- to three-week lag before the females are conditioned for nesting and pollen collecting. By then the available sources of pollen have increased to a sufficient level to maintain the bees.

In early season, males are particularly abundant and practically 100 percent of the flowers are likely to be visited.

Males spend their entire life in the field away from the nesting site. Much of the time is spent in the protection of the flowers. In the morning, they may be seen "cruising" the flowers. Their activity in the morning may lag somewhat behind the time that females commence their foraging activity. Often they may still be found sleeping in the closed flowers of the previous day. If disturbed, they reacted in a very sluggish manner. After the cruising period, the males tend to con-

TABLE 6.—*Summary of numbers of* Peponapis pruinosa *collected in 100 flower samples in fields at Gridley, California* (under "Host," Z=zucchini squash, C=crookneck squash, P=pumpkin)

Time period	*Host*	*Males*	*Females*	*Total males and females*
17 Jun 69				
0815–0850	Z	285	90	375
0850–0925	C	396	101	479
1045–1115	P	696	180	876
19 Jul 71				
0830–0845	Z	325	29	354
0855–0910	C	335	35	370
1210–1225	Z	202	22	224*
1235–1300	C	432	53	485*
1515–1530	Z	165	21	186*
1540–1600	C	339	29	368*
21 Jul 71				
0750–0810	Z	314	183	497
0815–0835	C	334	194	528
24 Jun 69				
0800–0820	Z	210	93	303
0820–0835	C	287	138	425
0850–0905	P	117	149	266
0925–0940	P	209	176	385
25 Jun 69				
0700–0725	Z	247	105	352
0725–0747	C	150	152	302
1 Jul 72				
0800–0815	Z	56	19	75
1155–1210	Z	16	2	18*
1210–1225	C	35	1	36*
1530–1600	P	255	29	284*
2 Jul 72				
0616–0639	P	214	87	301
0719–0736	Z	35	94	129
0736–0751	C	26	81	107
7 Jul 72				
0755–0810	P	90	66	156
0930–0944	P	138	41	179
1207–1230	P	152	7	159*
8 Jul 72				
0545–0602	P	165	67	232
9 Jul 69				
0855–0915	P	76	15	91
0915–0937	P	113	24	137
10 Jul 69				
0525–1550	P	188	38	226
0705–0718	C	14	19	33
0718–0726	Z	5	14	19
0930–0942	P	67	4	71
11 Aug 69				
0807–0828	P	70	4	74
0828–0845	P	54	5	59
1025–1045	P	47	2	49
1045–1105	P	35	0	35
1245–1320	P	50	3	53
10 Sep 69				
0750–0800	P	7	0	7
0837–0852	P	5	1	6
0853–0907	P	4	1	5
25 Sep 69				
0805–0820	P	0	1	1
0820–0834	P	0	5	5
0835–0850	P	0	4	4
0915–0925	P	0	0	0
0930–0937	P	0	0	0
0945–0956	P	2	0	2

* Closed flowers.

centrate in the flowers at about the time they begin to close. Mating mostly occurs in the flowers during the morning hours while the flowers are still open.

Females, although less abundant than males, are found in the flowers throughout the day in the early season, and this situation continues until the nesting instinct comes into play. Surveys conducted throughout the day on 19 June 1971 (Table 6) clearly illustrate this point. In the 1540-1600 survey, the females were as abundant as they were earlier in the day, although females often leave closed flowers and seek other protection on very hot days. As nesting activity increases, fewer and fewer are seen in the field as the day advances. Some will usually be found, however, and this is consistent with observations at the nesting site which have shown them flying in as late as 1700 to 1715 (Table 4). Also, there is always the possibility that a female may have emerged very late in the season and is not yet ready to take up nesting activity.

During the prenesting period, females as well as males may remain in the closed flowers until after sunrise. For example, on 20 June 1971, a field was visited in early morning and many of the bees were still in the previous day's flowers although sunrise had occurred at 0450. Between 0455 and 0510 the current day's new flowers were examined and 196 males and 9 females were counted, while closed flowers of the previous day

TABLE 7.—*Summary of numbers of* Peponapis pruinosa *observed in 15-minute intervals in flower samples at Gridley, California* (under "Host," Z=zucchini squash, C=crookneck squash, P=pumpkin)

Time period	*Host*	*Males*	*Females*	*Total males and females*
19 Jun 71				
0745–0800	Z	415	28	443
0806–0821	C	416	35	451
0830–0845	Z	325	29	354
0855–0910	C	335	35	370
20 Jun 71				
0455–0510	Z	196	9	205*
0515–0530	C	256	22	278*
0550–0605	Z	461	28	489
0612–0627	C	450	27	477
1 Jul 72				
0800–0815	Z	56	19	75
0815–0830	C	63	60	123
0845–0900	Z	34	9	43
0900–0915	C	71	30	101
1155–1210	Z	16	2	18**
1210–1225	C	35	1	36**
1530–1545	P	115	13	128**
2 Jul 72				
0616–0631	P	145	56	201
0719–0734	Z	33	90	123
0735–0750	C	26	81	107
7 Jul 72				
0755–0810	P	90	66	156
0930–0945	P	148	44	192
1207–1222	P	97	4	101**
8 Jul 72				
0545–0600	P	126	52	178
12 Aug 69				
0501–0516	P	24	0	24
0516–0531	P	34	2	36
0531–0546	P	71	8	79
0546–0601	P	78	7	85
25 Aug 67				
0500–0515	P	7	11	18
0515–0530	P	25	4	29
0530–0545	P	114	12	126
0545–0600	P	94	7	101
0600–0615	P	86	8	94
0615–0630	P	72	8	80
0630–0645	P	70	5	75
0645–0700	P	86	7	93
0700–0715	P	42	4	46
11 Sep 69				
0520–0535	P	3	7	10
0535–0550	P	0	10	10
0550–0605	P	4	16	20
0605–0620	P	3	17	20
0620–0635	P	4	12	16
26 Sep 69				
0550–0605	P	0	7	7
0605–0620	P	0	2	2
0620–0635	P	0	5	5
0752–0807	P	0	12	12
0807–0822	P	0	6	6

* Many bees still in closed flowers of yesterday bloom.
** Closed flowers.

produced 97 males and 19 females. When the two counts are added together, the sums are 293 males and 28 females, numbers that approximate those recorded in an 0550 to 0605 survey, which yielded 461 males and 28 females (Table 7).

In the early season, before females are abundant, males, because of their large numbers, are probably very important in carrying pollen from staminate to pistillate flowers. Those seeking nectar in staminate flowers were almost invariably covered with pollen, which adhered to their legs as well as the rest of the body, and such individuals were commonly seen taking nectar from pistillate flowers, assuring pollen transfer.

The largest number of bees found in a single flower was 21; on 17 June 1969, 19 males and 2 females were observed in a staminate pumpkin flower. In a survey conducted on 25 August 1967, numerous flowers were found with 6 or more bees. Where this occurred, at least one of the individuals was a female. In early season it is not unusual to find an average of 1 or more females per flower (Table 6). Often they are associated with a number of males.

In both early and late season, examinations of closed flowers usually revealed a few dead bees. The number is never large and the individuals usually appeared to be in perfect condition. Since the area is devoted to a wide range of crops, insecticide applications to those are suspected as the cause of death. However, no evidence of mass destruction of squash bees by pesticides was encountered.

The adult population declines as the later season advances, and as the end of the season approaches, male bees begin to disappear (Tables 6, 7). The phasing out of the males is more clearly shown in the data discussed later, relative to the investigations conducted on the Oxford Tract.

Number of Annual Generations.—At first it was believed that under California conditions two generations of *Peponapis pruinosa* might occur. As the facts developed, there appears to be but a single somewhat bimodal generation. The question arose because relatively young individuals continued to make their appearance throughout the summer. As late as 12 August 1969, two freshly emerged males were observed in a nesting site. The day before a freshly emerged male crawled up a grass stem, unable to fly. On that date most of the females coming into the nest area had worn, frayed wings, but some appeared to be newly emerged. Young individuals continued to make their appearance. On 10 September 1969, out of 139 bees netted, at a nesting site, only 12 were old bees with badly worn wings and mandibles. The remaining bees appeared to be freshly emerged females (Table 8). It was this type of information that led to speculation that there was a second generation or at least the beginning of one. However, it now appears more likely that there is but one extended generation, a provision that may insure the survival of the species during periods of adverse environmental conditions.

Oxford Tract Experiments.—Additional information on the behavior of *Peponapis pruinosa* was obtained in experiments conducted during 1971 at the Oxford Tract of the University of California, Berkeley. An important advantage of this site was the fact that continuous observations were possible. A number of varieties of squash and pumpkin were planted in the experimental plot. The 1971 season was much delayed and it was not until 25 June that the earliest varieties were coming into bloom. On 28 June one female squash bee taking nectar and two males were seen. Another male was encountered on 2 July. No further observations were made until 20 July, when, after an extensive search, a single female seeking nectar was noted. This was unexpected since in the previous year a large population had been introduced and appeared to be established. However, because of the limited population of bees, observations of 400 flowers were utilized, rather than 15-minute counts, until the end of August. Most of the flower counts were made between 0615 and 0645.

At this time some of the host varieties were

Table 8.—*Numbers and condition of female* Peponapis *pruinosa coming into nest area, Gridley, California, 10 September 1969*

Time period	*Temperature (°C)*	*Old bees**	*Young bees***	
			with pollen	*without pollen*
0840–0900	–	3	68	40
1245–1345	37°	7	0	15
1415–1515	37°	2	0	4

* Wings badly worn and stumps for mandibles.

** Wings, mandibles, and pubescence intact.

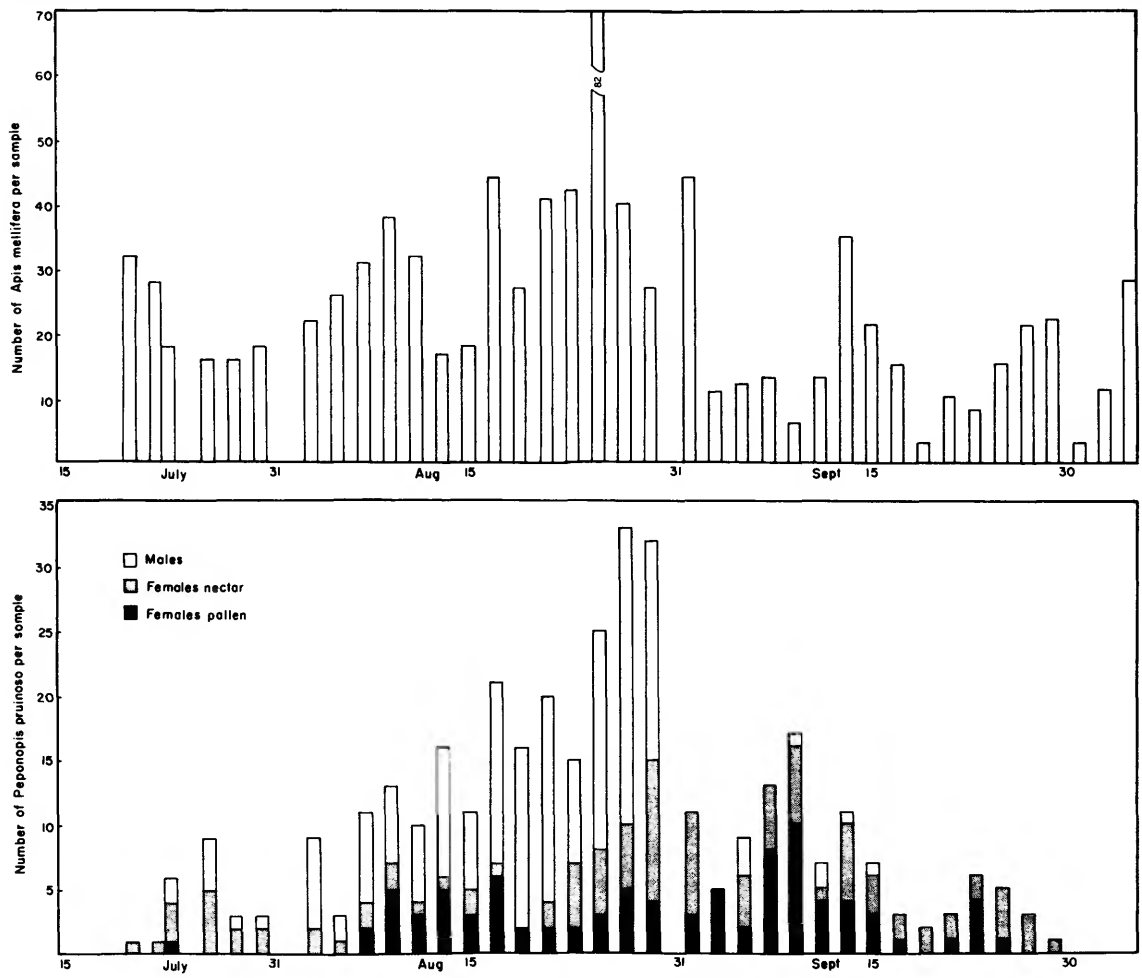

FIGURE 4.—Seasonal trends in populations of *Peponapis pruinosa* and *Apis mellifera* at flowers in experimental *Cucurbita* plantings at Oxford Tract, University of California, Berkeley.

reaching maturity, and there was a considerable decline in the number of flowers available. This fact necessitated lowering the flower counts to 200, the number used from 3 September to the end of the season. The results obtained, including that secured on 20 July, are presented in Figure 4. Despite the slow start, a relatively large adult population developed. The prenesting period was rather long, as indicated by the length of time that the females were seeking mainly nectar. It was not until early August that pollen collecting by the females came into prominence. Until the end of August male bees were encountered in much greater abundance than females. Then the male population dropped off sharply and only isolated individuals occurred thereafter, substantiating the seasonal information obtained at Gridley. The female population continued uninterrupted, but after 15 September it declined and none were found after 29 September.

In late September it was suspected that the females would visit flowers later in the day than during midseason. Based upon the behavior of other species of squash bees, it was believed that seeking nectar becomes more important than further gathering pollen (Michelbacher and Hurd,

1968). With this in mind, the planting was visited between 1145 and 1215 on 26 September. One hundred and fifty-one flowers were examined and 4 females taking nectar were observed. In addition 56 honeybees and several females of *Agapostemon texanus californicus* were seen. On 27 September the experimental plot was visited at the usual time (0615–0650). It was clear, calm, and cool and only a single honeybee was seen to enter a flower. There was no evidence of pollen disturbance. The field was again visited between 0730 and 0800. Three females were encountered drinking nectar along with 21 honeybees. The temperature at 0800 was 14°C. The temperature at the normal survey period was well above the threshold (11.1°C) for *Peponapis* activity. Evidence again indicated that in late season, delayed flower visits and the seeking of nectar are more important than pollen collecting.

On 1 October the plot was again visited between 0740 and 0810 (temperature 0810, 15°C). No squash bees were seen and there was little or no disturbance of the pollen. Furthermore, the flowers were mostly of poor quality. A final survey on 3 October produced no squash bees.

The information presented in Figure 2 clearly indicates that in the Berkeley area *Peponapis pruinosa* has but a single generation a year.

The experimental plots were again planted in 1972. The season was an early one. It should be noted that spot checks during early summer revealed a marked increase in the number of *Peponapis* encountered as compared to the previous season.

Although our investigations have concentrated on the pollination role of *Peponapis*, the importance of honeybees as pollinators of squash and pumpkin should not be minimized, even though they are poorly adapted to manipulate the relatively large-sized pollen of these plants. The abundance of honeybees and the ease of manipulation favor their effectiveness. They can also be of value where the fruiting period of squash and pumpkin extends beyond the active stage of squash bees or in areas only marginally acceptable to squash bees. This is well illustrated in the early portion of the Oxford Tract Experiments. During 1971 the number of honeybees seen was recorded along with that of the squash bees. These data are presented in Figure 4. A large honeybee population was present throughout the period of bloom. During July it was the most important pollinator and was probably responsible for the good set of squash fruits that was produced during this period. The bees were frequently seen heavily coated with pollen as they flew from staminate to pistillate flowers. There can be but little question that their activity throughout the flowering period was of sufficient intensity to result in satisfactory pollination.

In the investigations at Gridley, honeybees were never encountered in the numbers observed at the Oxford Tract; more often they were scarce.

Summary and Conclusions

1. *Peponapis pruinosa* is a gregarious ground-nesting bee with a nest site preference for flat, usually grass-covered ground which is moist during the nesting season and adjacent to or near an adequate source of pollen.

2. Like other members of the genus, females take pollen only from plants of the genus *Cucurbita*, the native wild host being *Cucurbita foetidissima*, the preferred cultivated hosts being pumpkins, summer squashes, and winter squashes in that order.

3. They are the most important pollinators of these crops.

4. In the Sacramento Valley, California, emergence of adults usually occurs in late May and activities extend into October.

5. Early in the season, males and newly emerged females spend the day taking nectar from or resting in the squash flowers, which open before sunrise and wilt toward midmorning on a clear hot day; both sexes spend the night in wilted flowers, cutting their way out near sunrise.

6. Mating occurs mostly in the flowers during the morning hours while the flowers are still open.

7. Approximately two to three weeks after emergence, females abandon the flowers for "sleeping" and begin burrow construction; shortly afterward they begin foraging for pollen.

8. Burrow construction and maintenance continue throughout the season.

9. In northern California *P. pruinosa* has few competitors at the nest site; the incidence of moldy and diseased cells was low and no major parasites or predators were encountered.

10. Honeybees (*Apis mellifera*) were the principal pollen competitors but, except at Berkeley, they were not sufficiently abundant or active early enough in the morning to provide significant competition.

11. Experiments at Berkeley proved that *Peponapis* can be introduced and established by the transport and release of prenesting adults into an area with suitable nest sites and immediately available sources of nectar and, when needed, *Cucurbita* pollen.

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