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Title: THE BIOLOGY AND BEHAVIOR OF THE ALKALI BEE
NOMIA MELANDERI COCKERELL (HYMNOPTERA:APOIDEA)

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W. P. Stephen

Nomia melanderi Cockerell is one of the most efficient pollinators of alfalfa in Eastern Oregon.

Emergence begins in June, usually reaches its peak in early July, and may continue into early August. Male emergence precedes female emergence by four or five days. For the first few weeks of this time, the males spend the morning hours patrolling the nesting area. As each new female bee emerges, many males attempt to mate with her, but most contacts are unsuccessful. Soil temperature and moisture are the prime factors influencing emergence.

After mating has been accomplished, the female bee forages in the field and returns to the bee bed in the afternoon to begin nest construction. The male also spends the afternoon in the field, returning to spend the night in clusters on plants on, or in the vicinity of

the bee bed. Some crawl under the loose soil crust, paper, sticks, rocks, or enter burrows for the night.

The female, after digging herself under the soil surface, spends the nest two or three days roughing out cells. On the third, fourth or fifth day she begins to collect pollen. She usually forages on blossoms close to the nest, tripping about 96 percent of those visited. The female gradually increases her foraging range, moving progressively further from the nest as she ages. The time required to complete each pollen collecting trip varies considerably, but averages close to 35 minutes. It takes from seven to 11 trips to complete one pollen ball and this may require from 5 1/2 to 9 hours.

The female trips the alfalfa blossom by forcing its head against the standard petal while its legs are braced against the wing petals.

Mortality is evidenced by an abrupt decline in the number of working females.

Eggs of Nomia melanderi require from 2 1/2 to 3 days to hatch. The larva passes through five instars. The fifth instar defecates after all the pollen has been consumed, and transforms into the prepupa, which passes through the winter. The following spring the prepupa transforms into the pupa which shortly develops into the mature adult.

The alkali bee uses major and minor landmarks for orientation. Larger landmarks such as haystacks, trees, fences, roads, and ditches are used to locate the bee bed. Then smaller markers such as soil clods, sticks, etc. are used to locate the individual burrow opening.

Preliminary studies suggest that the alkali bee is able to distinguish among yellow, green, blue, white and gray colors.

Temperature is usually the limiting factor in the initiation of morning activity, whereas light intensity appears to determine the time of flight cessation in the evening.

THE BIOLOGY AND BEHAVIOR OF THE ALKALI BEE NOMIA MELANDERI COCKERELL (HYMENOPTERA:APOIDEA)

by

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INTRODUCTION

The genus Nomia Latreille is represented in the New World by approximately 20 species divided among four subgenera: Epinomia Ashmead; Acunomia Cockerell; Dieunomia Cockerell; and Paranomia Michener (Cross, 1958).

Nomia (Acunomia) melanderi Cockerell is approximately two thirds as large as a honey bee and has transverse bands of green or greenish-bronze on the apical margins of the metasomal tergites. The male can readily be distinguished from the female by the long, sharp terminal antennal segment, the greatly dilated hind tibiae, which are much broader than long, and by the dense white facial pile.

Nomia melanderi occurs in restricted areas from the Rocky Mountains westward. It has been found in all of the western states north of Mexico, and into the southern parts of the interior valleys of British Columbia (Stephen, 1959). It nests in a variety of different soils, all characterized by adequate moisture content. Often these nesting sites are located in poorly-drained, lowlying alkali flats with scanty vegetation, hence the name alkali bee.

The bee is one of the most efficient pollinators of alfalfa and is largely responsible for the enormous seed yields reported from Utah (Bohart, 1947, 1950), Washington (Menke, 1954), Oregon (Stephen, 1959), and Idaho. Among the factors accounting for the success of the alkali bee as a pollinator of alfalfa are: they visit a large number of florets in a relatively short period of time; they consistently trip well over 90 percent of all florets visited; they are oligolectic on alfalfa; their populations can be increased rapidly and maintained at a high level by provision of suitable nesting conditions; they utilize waste ground for their nesting sites, thus potentially productive land is not sacrificed; their emergence can, to some extent, be controlled. In view of this, Stephen (1959) concluded that a knowledge of the habits and the life history of the alkali bee is essential, for the future of the alfalfa seed industry rests with the ability to maintain or increase their numbers.

This study was initiated in 1959 to contribute information on the life history and behavior of the alkali bee.

Since the time of seasonal emergence is extremely important to the seed producer, a knowledge of development is mandatory. Rate of development from the overwintering, prepupal stage to the adult depends primarily on soil moisture and soil temperature. Stephen (1965a) concluded that the alkali bee prepupae have distinct temperature limits within which development to the adult may proceed. No development will occur unless the temperature is above

17°C, neither will it occur when soil temperatures reach 35°C. Optimal development takes place at 29°C. Stephen (1965b) indicated that maximum emergence occurred when moisture was at 10 percent. At moisture levels above 10 percent emergence was spread over a prolonged period and mortality increased. This bears out observations in the field where excessively damp areas of the bed emerge later than the drier areas. Frick (1962) concluded that emergence was controlled mainly by temperature, and that maximum development occurred between 65°F and 80°F. He did not consider soil moisture an important factor in development.

Males begin to emerge slightly before the females and spend the morning hours patrolling the nesting site. Stephen (1965a) considers this an adaptation to insure mating at the time females emerge. Although mating has been ascribed to these initial contacts (Bohart and Cross, 1955) (Stephen, 1959), it is difficult to determine if they are successful. Once a female has mated she will repulse other males that try to mate with her. Observations of Michener and Rettenmeyer (1956) on Andrena erythronii agree with data on the alkali bee showing that males will pounce on dead bees, other males, and other species of bees, as well as on females. They often pounce upon females, whether mated or not, even sometimes on a female bringing pollen to her nest. Usually in such cases males are repulsed promptly. The most detailed description of mating in halictid bees is provided by Bohart (1950).

It is assumed that most female bees that have emerged and mated during the morning start nest construction during the afternoon and spend the night in the burrow. In contrast, the male bees aggregate on surrounding plants or under rocks, paper, or other debris on or near the nesting site. Such sleeping aggregation had been described as early as 1758 by Linnaeus (as cited by Linsley, 1962). Since Linnaeus' time, sleeping records for a wide variety of bees have been published (Banks, 1902; Bradley, 1908; Evans and Linsley, 1960; Linsley, 1958; Linsley, 1962).

The most detailed studies of the soil requirements for nesting sites of alkali bees were made by Stephen (1960, 1965b) who pointed out that soil moisture is the most critical factor governing suitability of any site for bee inhabitation, and stated that the optimum soil condition is that which permits rapid transport of sub-surface moisture through the top 12 inches of the soil, thus maintaining a moist and compact surface. These soils usually have less than 8 percent of aggregated clay-size particles.

Once the famale has selected her nesting site she begins digging. Bohart and Cross (1955) report that bees are able to dig themselves under a moist clay surface in seven to 12 minutes and that the next one inch takes 20 minutes. This data was provided by exposing burrows of a known age. However, as the nest becomes older and more complex, excavation is a tedious and difficult task.

Various materials have been introduced into the nest to facilitate its excavation. The most widely used is plaster of paris (Malyshev, 1936 and Michener et al., 1955). After the plaster hardens the cast is carefully excavated. The rate of nest construction is dependent upon the compaction of the soil and to some extent upon the individual bee. After digging ceases the bee roughs out a series of brood cells and polishes one for the reception of pollen. Typically each female builds a single nest of 15 to 20 cells in about 30 days (Bohart and Cross, 1955).

Degree of pollen-collecting specificity is difficult to determine because it depends to a large extent on the characteristics of the individual locality. The general subject of flower constancy has been comprehensively reviewed by Grant (1950).

Alkali bees prefer alfalfa pollen (Stephen, 1959) to that of other plants and will restrict their pollen collecting to it even in the presence of other plant species. In view of this, the alkali bee can be classed as an oligolectic species as defined by Linsley (1958). Alkali bees were collected on the bee beds and their pollen loads analyzed. Invariably, they were pure loads of alfalfa pollen. Other alkali bees collected in remote areas with an absence of alfalfa contained pollen from the various plants in the vicinity.

Daily pollen-collecting habits have been reported by Menke

(1954). He stated that each female bee made four to five pollen-collecting trips per day and these required four to five hours under favorable weather conditions.

Stephen (1959) pointed out that females gradually expand their range in increasingly larger circles and will rarely if ever stop to forage on closer bloom after their patterns have been established. Similar behavior has been recorded for some bumblebees (Free and Butler, 1959).

That alkali bees are important pollinators of alfalfa is well established (Tysdal, 1940; Linsley, 1946; Bohart, 1947, 1950; Menke, 1952; and Stephen, 1959). Menke (1954) emphasized that the alkali bee tends to forage close to its nest and consistently trips more than 95 percent of the alfalfa blossoms it visits. Bohart (1950) also reported tripping percentages above 90 percent for female alkali bees working in alfalfa.

Except for _Nomia_ (_Acunomia_) _melanderi_ Cockerell, biological information on the genus _Nomia_ is scarce. In spite of the abundance of published information on _Nomia_ _melanderi_, detailed data on development is still wanting. The lack of developmental information can be attributed to the difficulties encountered in rearing and observing ground-nesting bees. Early reports by Rau (1929) on _Nomia_ _triangulifera_ Vachal, and Cockerell (1934) on _Nomia_ _fedorensis_

Cockerell and *Nomia nortoni* Cresson, are brief and include little information on life histories. Cross and Bohart (1960) reported on the biologies of three species of *Nomia*, but were unable to determine accurately the total number of larval instars, although they did suggest the presence of four larval instars in *Nomia melanderi*. The most extensive works published to date on the biology of *Nomia melanderi* Cockerell are those by Bohart and Cross (1955) and Stephen (1959).

Four larval instars are inferred in the Australian ceratinine genus *Allodapula* (Syed, 1963). This number is considered to be the rule among most bees, although five larval instars have been reported for the honey bee (Bertholf, 1925) and only three larval instars are reported for *Diadasia consociata* Timberlake (Linsley *et al.*, 1952).

Literature in recent years is resplendent with behavioral studies on social bees (Carthy, 1958; Free and Butler, 1959; Johnson and Wenner, 1966; Lindauer, 1961 and 1967; von Frisch, 1958 and 1965) but a scarcity of this information exists for solitary bees.

Michener (1956, 1962, 1964 and 1965) has reported on the behavior of several solitary bee species but that on the ethology of *Andrena erythronii* is most complete. He describes the behavior of the males and females separately which is significant as male behavior is quite often overlooked.

Nest orientation has been well established (von Frisch, 1958; Lindauer, 1961; and Free and Butler, 1959) in the honeybee and bumblebees, but except for the report that Emphoropsis miserabilis (Cresson) (Stephen and Torchio, 1961) locate their nest entrances by orienting on erect plants, twigs, etc. within several yards of the nest, little information on nest orientation in solitary bees exists.

The ability of insects to discriminate between different colors was established beyond doubt fifty years ago. In 1913, von Frisch solved this problem by presenting to the bees a set of gray papers of different reflectances having one colored paper among them. The bees were trained to find food placed on the colored paper and when the food was subsequently removed, the bees always gathered on the colored paper (Lindauer, 1961 and 1967). Several studies have confirmed and enlarged on the original work by von Frisch (Hertz, 1939; Burkhardt, 1964; Lindauer, 1961 and 1967). Free and Butler (1959) have conducted similar experiments with color discrimination in bumblebees but little additional information has been added. In view of these intensive studies on social hymenoptera, it is surprising that so few color investigations have been conducted on solitary bee species.

As a result of this dearth of information on solitary bees, exploratory color discrimination experiments were undertaken with the alkali bee.

The complex of interacting physical factors which determines the period of activity of a species of solitary bees has not been determined, and few precise data relative to the subject are available (Linsley, 1958). However, a few generalizations are possible. Generally bees are sun-loving insects, thus their activity is usually between sunrise and sunset. If cloudy weather is prolonged, bees will often return to their burrow. Some social bees, especially _Bombus_ (Free and Butler, 1959), will remain active in conditions that other bees would not tolerate.

Preliminary observations on the leaf-cutter bee _Megachile rotundata_ (Fabricius) indicate that temperature is the major factor responsible for the initiation of morning activity. Conversely, light intensity appears to be the prime factor in the cessation of evening activity (Osgood[1]).

In spite of the great emphasis which is being placed in recent years on the propagation of the leaf-cutter bee, _Megachile_ _rotundata_ as a pollination of alfalfa, it is unlikely that the alkali bee will be displaced from its position as a major pollinator of alfalfa in the northwest. Maximal seed yields in the future will probably depend upon the use of both species of bees as pollinators.

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[1] C. Osgood. Personal communication.

The objectives of this study were essentially to (a) provide detailed information on the life history of the alkali bee, (b) provide emergence data, (c) determine sequence of nest construction, (d) determine degree of pollen collecting specificity, (e) record data on sleeping and mating behavior, and (f) provide preliminary data on mortality rates, nest orientation, color perception and effects of light and temperature on activity. It is hoped that this study of the biology of the alkali bee will serve as a basis for the development of optimal management practices.

The outline of this study was patterned after the suggested outline for ecological life histories of solitary bees reported by Linsley et al. (1952).

METHODS AND MATERIALS

Emergence

Knowledge of the time of emergence of alkali bees is extremely important to alfalfa seed producers in deciding whether first or second crop alfalfa should produce maximum yield. Studies on emergence were undertaken during the summers of 1958, 1959, 1960 and 1961. Eight metal cones with 30-inch diameter bases were placed on parts of two bee beds. They were checked each day at 11:00 A. M. and the number of emergent bees in each 24-hour period was recorded. The method of determining the number of emergent bees was to count the number of emergence holes present under each of the cones. After counts were made the holes were plugged so that they would not be counted the following day.

Mating and Sleeping Behavior

In order to determine where and when actual mating occurs, detailed observations were made on male behavior at the bee bed and also in the field. Late evening observations on both sexes were made on and near the bee bed to determine their sleeping habits.

Nesting Sequences

Studies were undertaken during the summers of 1961, 1963 and 1964 to determine the time and sequence of nest construction. Nests of young female bees were marked as initial nest construction began. These nests were excavated at one day intervals and the progress was recorded, thus providing a day by day record of nest construction and yielding data on the beginning of pollen collecting, the number of cells which were provisioned each day, and time of oviposition. In order to study variations in nest construction, casts were made by pouring plaster of paris into burrows of known ages; after drying each cast was carefully excavated.

Pollen Collecting

A small area of the bee bed was selected and each of 25 working female bees was marked with a different colored paint on the mesoscutum. They were collected for marking by inserting a knife blade into the soil a few inches away from the nest opening, at such an angle so as to obstruct the burrow passage at about a one and one half inch depth. The returning female could descend only a short way into the tunnel, whereupon she was picked up with a forceps and marked. After the paint had dried, she was released and the knife removed. After marking, the bees were given five days to reorient to their nest. Each of the nests containing a colored bee was marked by a correspondingly colored toothpick pushed into the soil adjacent to the nest opening. Observations were made from 6:00 A. M. to

8:30 P.M. for five nonconsecutive days, and the times of the bees departure and return were recorded. In this manner, it was possible to determine how many trips were made each day, the time needed for each trip, the time spent in the nest between trips, and the number of trips necessary to form and complete a pollen ball.

To determine the degree of specificity in their pollen collecting behavior, alkali bees were collected in areas where alfalfa was scarce and other flowering plants abundant. Each pollen-carrying bee found on a plant other than alfalfa was collected and slides were prepared of the pollen from the load and from the plant for subsequent comparison. Observations were made in the field to determine in detail how the bee trips the alfalfa blossom. The time spent on each floret and the number of visits per minute were recorded.

Age

Observations were made on the nesting site and in the field to determine the effect of age upon behavior. Females were marked with paint on the mesoscutum as soon as they started nest construction, and an identically colored marker was placed adjacent to the nest opening on which observations were made one day each week until the bee died. Observations were also made in the field one day of each week throughout the summer.

Information on the effect of age upon nesting activity was obtained by excavating burrows of different ages and comparing them.

During the summer of 1959, data on time and rate of female mortality were collected by marking off three one square yard plots in the Adrian, Oregon area, two on the Schiemer bee bed and one on the Nelson bed. After emergence was well past its peak, the number of nesting females in each plot was recorded. Each day, after activity had ceased, all holes within each plot were firmly sealed, trapping the females in their burrows. The following day all open holes were counted, and those that had not been reopened were considered to have been burrows of females whose activity had ceased, thus reflecting the rate of mortality.

Larval Development

Developmental studies on the alkali bee were carried out by removing eggs from their burrows and rearing them in the laboratory under appropriate conditions of temperature and humidity.

Eggs and pollen balls were collected after 8:00 P.M. or before 8:00 A.M. in order not to be exposed to the heat of the day. They were obtained by digging to the brood level with a shovel. Each cell was carefully opened with a knife and as soon as an egg was identified, the entire cell was carefully separated from all excess soil. The cell and its contents then were transferred to a seamless tin container previously half filled with soil from the same depth as the brood to ensure proper moisture conditions.

Six cells with eggs and pollen balls were placed into each container. These were then placed in a basement room where the temperature was maintained at 24±1 °C. Immediately after being transferred to the basement room, each cell was examined microscopically and all soil particles removed from the cell or pollen ball since it was found that fungus growth invariably resulted wherever soil particles were left in contact with pollen balls. Soil removal was achieved with a moist probing needle or a camel's hair brush gently applied to the soil particles. Movement of the pollen ball during removel of soil particles was kept to a minimum in order to reduce mortality. After cleaning, each cell was so placed in the container that it could be observed microscopically without further disturbance. Subsequently, a small soil particle was placed on the dorsum of each egg to indicate when the chorion was shed.

Moisture was maintained by keeping the lids on the seamless tin containers except when observations were made. Cells requiring moisture were usually identified by examining the feeding sites on the pollen balls and the condition of the soil surrounding the cells. If water was required, a pipette filled with water was gently applied to the soil surrounding the cell. It was found that direct addition of water to the pollen ball inevitably resulted in mortality.

Fungal growth was controlled by gently touching the affected area with a camel's hair brush moistened with a 50 percent aqueous solution of propionic acid or, if the fungus was directly on the pollen ball, a probing needle was dipped into the propionic acid solution and then used to gently scrape it off.

Data on larval development were obtained from three observations during each 24 hour period.

Nest Orientation

To determine the effect of markers on nest recognition, a small rock, stick, or soil clod approximately one to two inches high was placed adjacent to the burrow opening. It was left for five to seven days so that the bee might become conditioned to its position, after which it was moved at different times in a radius of from one to six inches from the burrow opening while the bee was foraging, and the subsequent behavior of the bee recorded.

Color Perception

Preliminary experiments in the color discrimination ability of the alkali bee were undertaken. A hole equal to the burrow opening was punched in the center of each one inch square of colored oilcloth. The colors used in this study were identified in the Rheinhold Color Atlas as follows:

Black	5H2	Purple	17A8
Blue	21A8	Red	10B8
Gray	B1, C1, D1, E1, F1	White	A1
Green	26C8	Yellow	2A8
Orange	7A8		

Some colored squares were placed singly over the nest entrances while others were placed in a checkerboard fashion. Individual bees were trained to one color which was subsequently exchanged for another. The response of the bees to the conditioning was recorded.

Flight Activity

To determine the effects of light and temperature on bee activity, temperature and light intensity data were recorded at the beginning of activity each morning and at the cessation of activity in the evening. On cloudy days when the temperature and light level were too low to permit flight, flood lights were used to arrive at activity thresholds. Recordings were made using a temperature potentiometer manufactured by the Leeds Northrup Company, Philadelphia, Pennsylvania, and a Weston Master IV lightmeter.

RESULTS

Life History

Emergence

The adult alkali bee emerges from the soil by digging a near-vertical burrow from the overwintering cell to the soil surface. These burrows usually do not coincide with new or old nesting burrows. The exit burrows can easily be distinguished from nesting burrows for they are largely back-filled with loose soil and lack a tumulus at the opening. Males appear a few days before the females but both sexes continue to emerge throughout the season. This is similar to the pattern recorded for *Andrena erythronii* in which males precede the females by as much as two days (Michener and Rettenmeyer, 1956) and is considered to be a means of insuring the fertilization of emerging females. As Stephen (1959) has pointed out, the emergence of both males and females in the Pacific Northwest is restricted primarily to mid-morning hours. Occasionally, a few bees emerge as early as 8:00 A. M. , but normally the daily peak occurs between 9:30 and 11:00 A. M. A few bees may emerge during the remainder of the day, but their numbers are insignificant.

In the Snake River Valley of Eastern Oregon, emergence may begin from early June to early July and continue into early August.

Peak emergence was determined as the day or days on which the greatest number of bees emerge. This information is of utmost importance to the alfalfa seed grower because it is imperative that he synchronize peak bloom in the alfalfa with peak emergence in the bees to insure maximum pollination. The importance of this synchronization can readily be observed in Figures 1 and 2 where the peak bee emergence occurred in mid-June in 1959 and in mid-July in 1960. Had the grower cut his first hay crop of alfalfa in 1959, his seed yield would have been reduced materially as the peak bloom of the second crop would have occurred long after the peak emergence of the bees. By this time, the bees would have established flight patterns to other pollen and nectar sources. In 1960, on the other hand, he would have greatly benefited by cutting his first crop of alfalfa and leaving the second crop for seed. Stephen (1959, 1965b) has pointed out that temperature and soil moisture are probably the two most important factors in trying to determine emergence time. He stated that temperature ranges from 65°F to 90°F can be quite closely correlated with emergence rate. He also pointed out that bees in beds in which the amount of soil moisture was above 30 percent in June did not emerge until the soil moisture level had fallen to below 25 percent. His conclusions are verified by the data in Figure 5. This bed was almost completely flooded for three days in the early spring of 1960. After the flooding, emergence cones were placed in four different localities on the bed. Number 1 was on the highest level and numbers 2, 3 and 4 at progressively lower levels of the bed. Site number 1 was not flooded and good drainage helped sites 2 and 3 to dry out quite rapidly.

Emergence began at site 1 on June 17th, peaked on the 18th and ceased on the 20th of June. At site 2, emergence started on the 26th, peaked on the 29th of June, and terminated on the 2nd of July. The emergence at site 3 occurred from July 4 to July 9th, with the peak about July 6th. Emergence at the lowest and dampest site, number 4, began on the 17th of July, reached its peak on the 19th, and terminated on the 20th of July. Data from other bee beds also show that emergence from the low-lying, poorly-drained areas peaked from three to four weeks later than from the rest of the bed. Figures 4 and 5 reflect an approximate 75 percent reduction in numbers of emerging bees in 1960 as compared to 1959. This loss is attributed to adult drowning and the increase in fungal disease resulting from excess soil moisture. In 1958, peak emergence from the higher portions of the Nelson bed occurred about June 16th (Figure 3). Emergence from site 4, the low-lying, moist part of the bed, did not begin until July 3rd and reached its peak about July 15th, approximately three weeks later than the drier parts of the bed. In 1959 similar results were obtained, the drier portion of the bed reaching peak emergence around the 16th of June and site number 4 not beginning emergence until the 16th of July, reaching its peak about the 26th.

Once emergence begins, it increases rapidly, reaches a peak and then slowly drops off (Figures 1, 3 and 4). The rate of decline is usually much slower than the rate of increase in emergence (Figure 4). An exception to this generality was recorded in 1960 (Figure 2) when the emergence peak was skewed strongly to the right. This delay in emergence was possibly influenced by the intermittant showers during the first two and one half weeks of June rather than cool temperatures for, in spite of the cloudy and rainy days in June, the mean maximum air temperatures were slightly higher than in 1959 (70.9°F vs. 69.7°F). Although no soil moisture data was collected, the entire bed appeared to have more moisture in 1960 than in 1959, and it is believed that this additional moisture delayed emergence. Emergence began on the 17th of June but did not reach a peak until the 18th of July. Emergence continued until July 31st at which time heavy rains all but terminated further activity. It was estimated that 75 percent of the female bees were trapped in their burrows and drowned as a result of this rainfall, thus accounting for the unusual activity period. The fact that the bees had reached their peak so late in the year meant that few females had realized their reproductive potential at the time of death. This resulted in a bee population about 60 percent of normal in 1961.

The weather during March, April and May appears to affect the time of emergence. June, July and August of 1960 were warmer than the corresponding months of 1959, but as can be seen by Figures 1 and 2, emergence in 1959 was much earlier. It is postulated that heavy early spring precipitation will channel off much of the later spring heat in order to evaporate the excess soil moisture. Thus the rise in soil temperature is delayed as is the onset of development. So many interacting factors are involved in the temperature, moisture, physical, and chemical condition of the soil that no serious attempt was made in this study to analyze them in their relation to emergence of the alkali bees. Stephen (1959, 1965b) has since made a thorough study of the effects of temperature on the development of the alkali bee and feels that in artificial beds some control can be exercised over most of the factors controlling emergence and that it can be accelerated by the use of heating cable, or delayed by covering the surface with insulating materials. In the larger natural beds it is a little more difficult to control emergence, but by consulting Stephen's data (1965b) it is still possible to synchronize peak bloom in the alfalfa with peak emergence of the bees. If the seed grower would keep an accurate record of the soil temperature and make periodic excavations to visually check development, he could, by consulting Stephen's data, predict a relatively accurate time for emergence. With this information it could be determined whether or

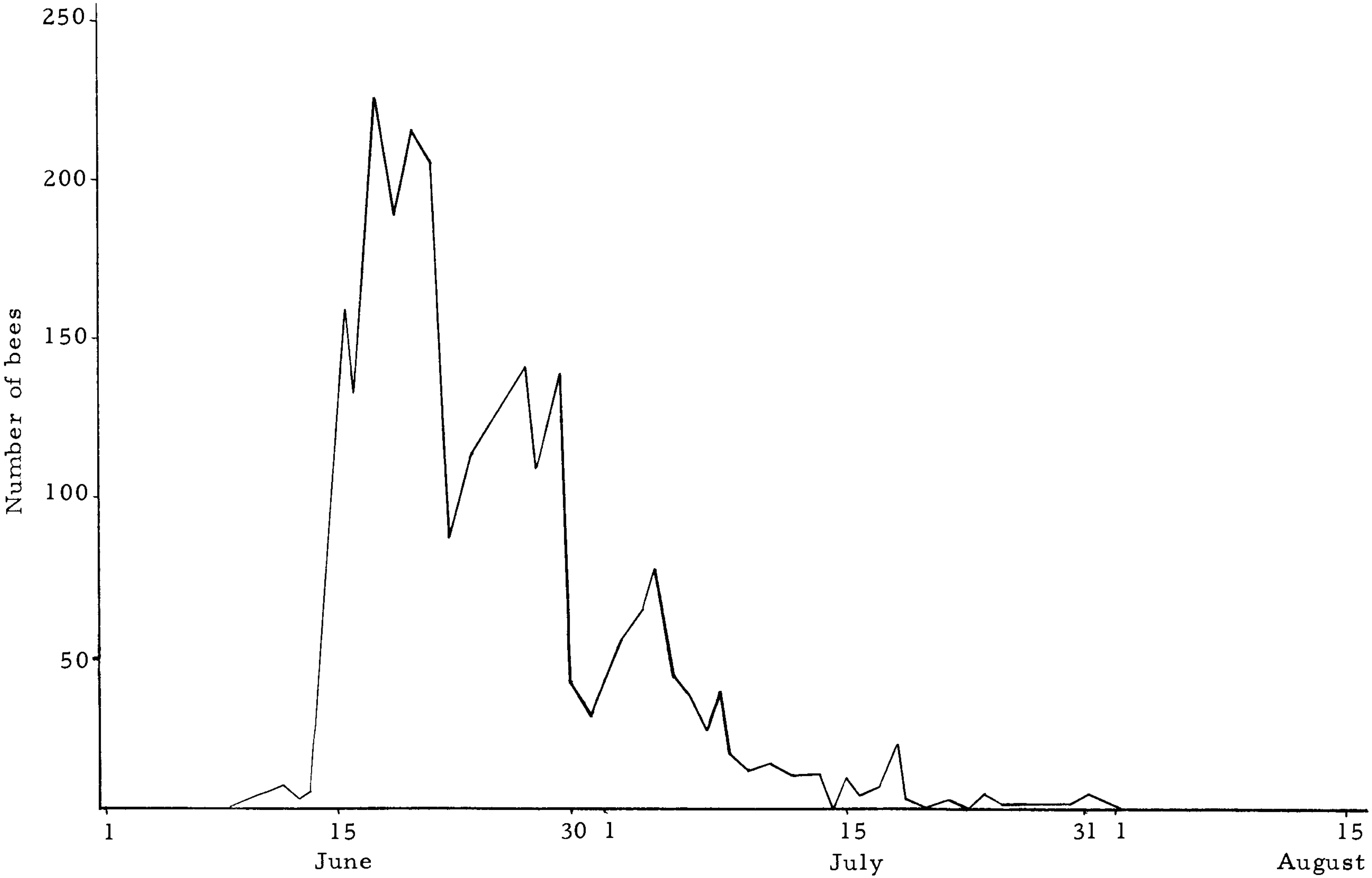

Figure 1. Alkali bee emergence -- Schiemer site 1959.

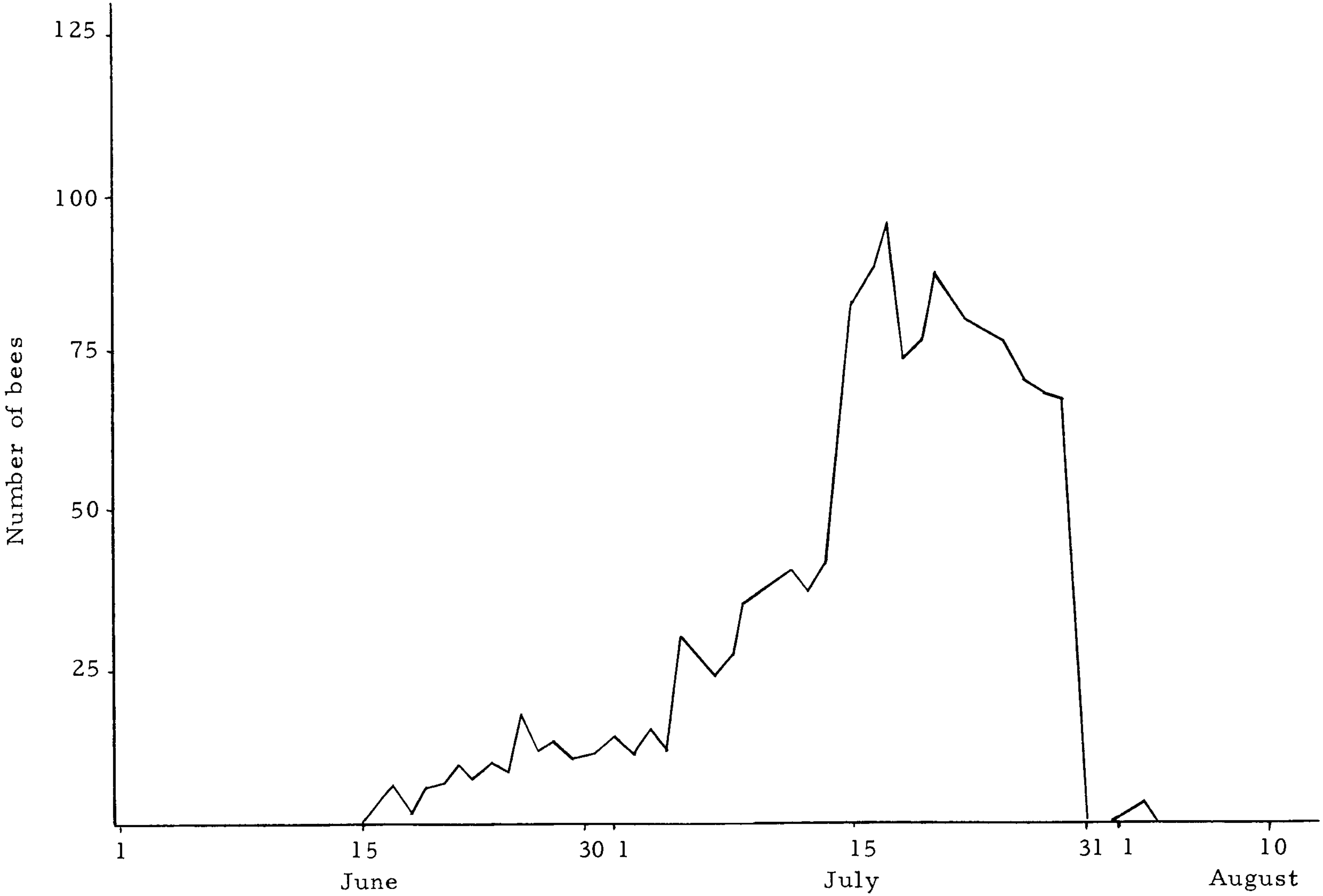

Figure 2. Alkali bee emergence -- Schiemer site 1960.

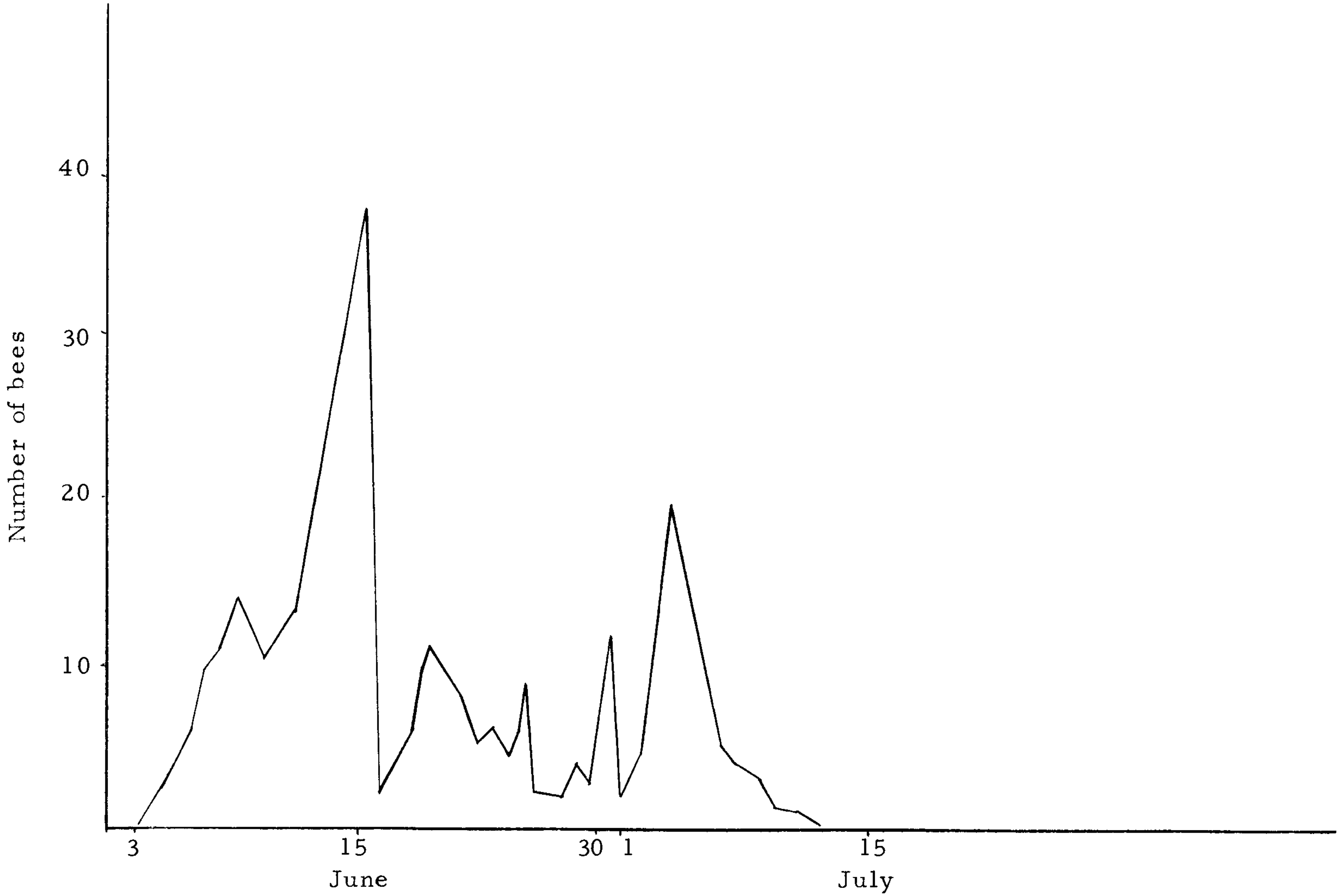

Figure 3. Alkali bee emergence -- Nelson site 1958.

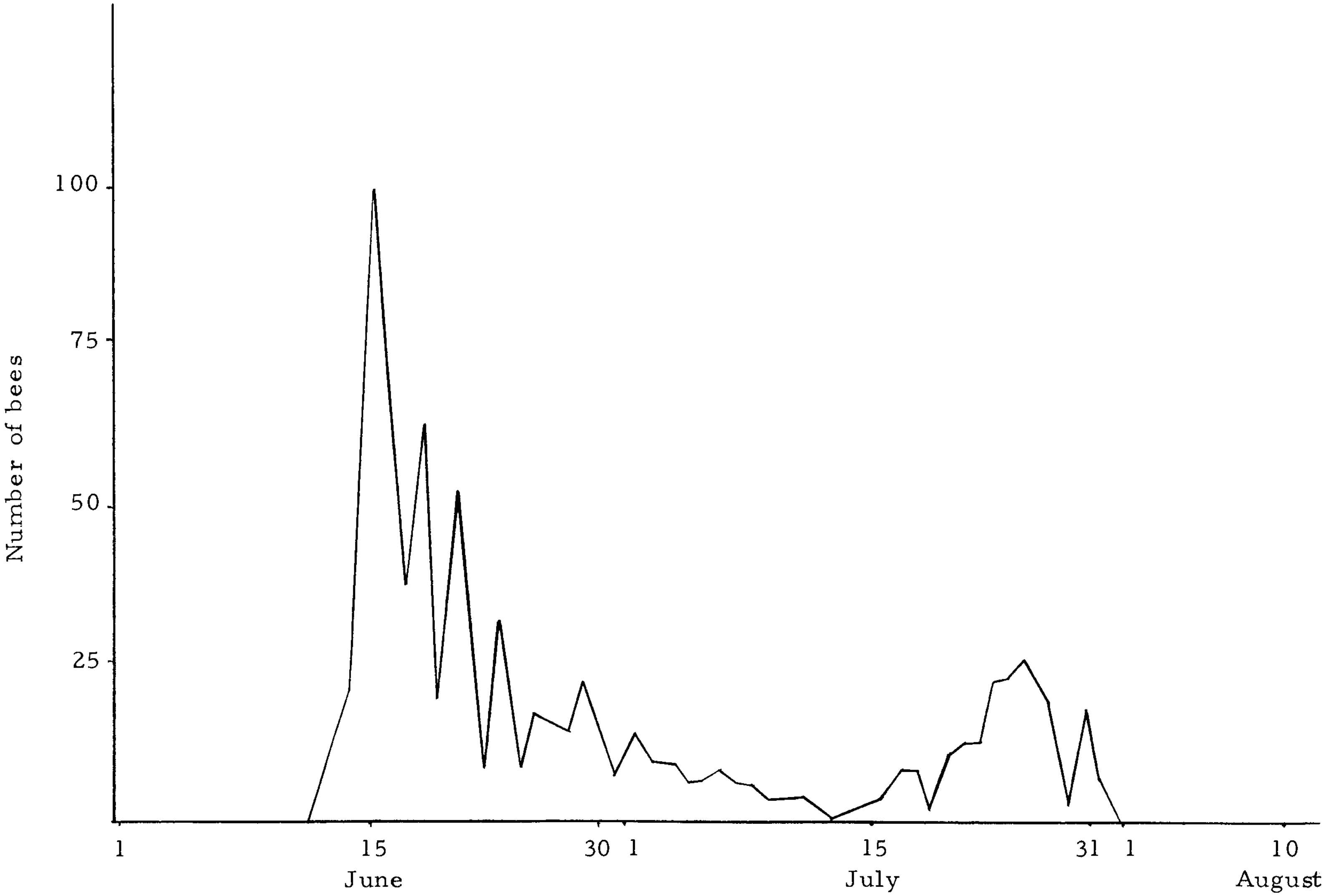

Figure 4. Alkali bee emergence -- Nelson site 1959.

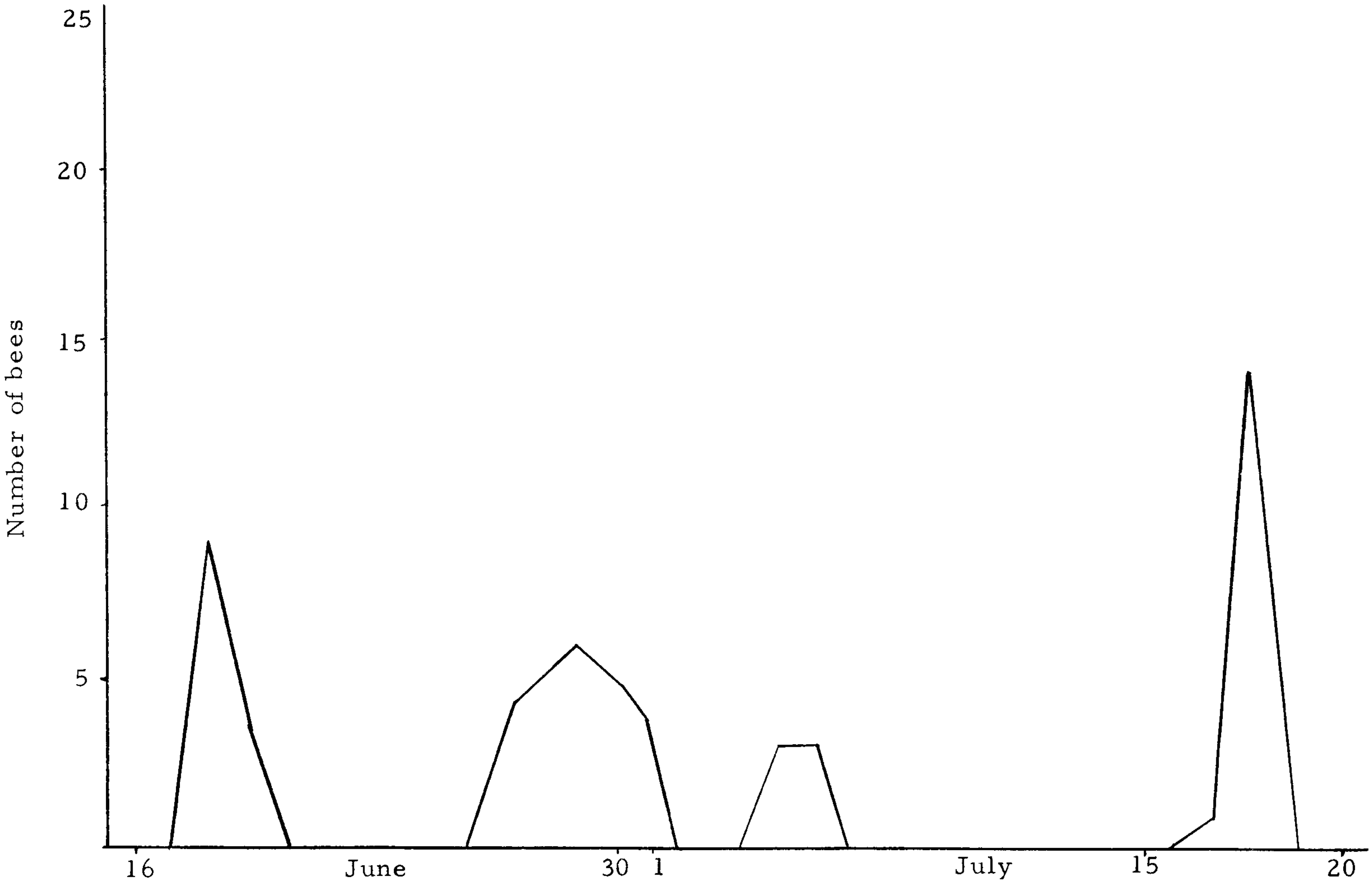

Figure 5. Alkali bee emergence -- Nelson site 1960.

not the first crop of alfalfa should be left for seed. In addition, some control over the time of flowering in alfalfa can be effected by withholding water at the proper time, thus checking vegetative growth and favoring accumulation of carbohydrates which tend to shift the plants into the fruiting condition. It is recognized that this is, at best, a rather crude attempt at synchronization, but at present about the only economical method available on the large natural beds.

Mating

The male alkali bee begins to emerge a few days before the females and spends its time flying over the bee bed, occasionally visiting sweet clover and alfalfa for nectar. Newly emergent bees spend the first few minutes preening and sunning themselves. As the wings begin to dry, the bees can be observed vibrating them and shortly thereafter they take flight. The early flights are usually quite short (a few inches to a few feet) and after three or four attempts the bee flies away. It is during this time of relative inactivity of the female that mating, or at least attempted mating, occurs. The males which patrol the nesting site are very indiscriminate, and have been observed contacting other males, tiger beetles, bombyliid flies and other species of bees. Many of these "mating" attempts are of very short duration, sometimes involving no more than initial contact. In one instance, a male bee was observed for 25 seconds trying to mate with a dead, dried, decapitated female. Usually males discover and make repeated passes at the female while she is preening herself before permanent flight. Often the female extends her wings as soon as the male makes contact, forcing him to the rear so that his forelegs grasp her around the metathorax. The female then crawls forward and easily forces the male off. Occasionally, the male grasps the female over the wings and about the thorax before she can elevate her wings. The contact may last as long as ten seconds, but in all cases closely observed the genitalia of the male was not inserted and the female resisted the male. On one occasion a male attempted copulation with a female returning to the nest with pollen. Contact lasted 10 seconds and was broken off. This was the only time a working female was observed to be disturbed for an extended period of time, for usually they are stopped only momentarily by males. During the morning hours, any female crawling about or sitting on the bee bed will be contacted repeatedly. Often five or six males will hover around each female and as soon as one departs another alights. This is especially noticeable when the wings of the female have failed to develop properly. One such female was contacted 11 times in a one and one half minute period.

Successful matings were observed on four different occasions. Each female sat stationary on the ground as the male approached from the rear and landed on her dorsum. The prothoracic legs of the male extended over her wings and about the thorax to a point just posterior to the base of her prothoracic legs. The mesothoracic legs were arranged in a similar fashion but located posterior to the base of the females' mesothoracic legs. The metathoracic legs of the male extended downward in the area of the pedicel and appeared to be directed slightly anterior under the thorax of the female, almost touching her mesothoracic legs. The head of the male was positioned near the center of the prothorax of the female. The female remained relatively motionless with her abdomen in a horizontal position. The male's abdomen extended around and under the tip of the female's, after which the female's abdominal tip lowered slightly. The male genitalia were then exposed and copulation was effected. Next, the male made a rhythmic, pulsating movement and with each pulsation the tip of the male's abdomen was thrust toward that of the female. The pulsations occurred at intervals of slightly less than one second and accompanying each pulsation an "eeep-eep-eep" sound was emitted. These four matings lasted 12, 15, 17 and 19 seconds respectively. The males broke contact and immediately flew away. The female preened herself for about five seconds, brushed her abdomen with the hind legs, flexed her wings once or twice and also flew away. During the entire mating process the female made no attempt to ward off the male but remained relatively motionless. Because the females took to flight so readily after mating, it suggests that she had flown previously.

In the majority of pre-flight mating contacts, the females start moving and struggling until freed of the male. In these easily observed pre-flight mating contacts, the genitalia were never observed to be connected nor was any sound produced. These observations suggest that the female may routinely take flight and forage for nectar prior to mating. Indeed, some may be fertilized in the field whereas others return to the bed to be mated.

Sleeping

During the first two weeks of emergence, males commonly can be found at night clustered on vegetation on or near the bee bed. They seem to show a distinct preference for sweet clover, although it is common to find them on alkali weed or other plants close by. Others can be observed under loose rock, paper, dirt clods or other material located on or near the bee bed, and occasionally some enter occupied burrows or emergence holes to spend the night. On one occasion, some shallow holes punched in the soil of the bed at 11:00 A.M. had males in them when checked at 11:00 P.M. the following day. They did not do any digging but merely used the holes for refuge.

A small population of alkali bees were maintained in Boardman, Oregon throughout the summer of 1965. During the mating period, the majority of the males spent the night on the bee bed, some of them in old emergence holes. Five of the males sleeping under the loose crusty soil surface were marked on one evening, and four of them were observed in the same areas the following night. These four returned each night at about the same time to the same sleeping site for the next three nights. After this period, very few males were seen on the bed. This was probably due to the fact that the male activity period over the bed was terminating.

Close observation of the four males indicated that each returned to the bee bed in the evening and started searching, entering old holes and going under the loose soil curst, in close proximity to their previous night's shelter. Eventually, they found their old site and entered to spend the night. This suggests that the males are capable of recognizing their sleeping site either through overt markers, or a result of a pheromone, or both.

As the season progresses, aggregations of male bees disappear. It is presumed they spread out over the fields and spend the night there, for they can be observed foraging most of the summer. Stephen[2] has suggested that this tendency to aggregate may be associated with spermatogenesis because it disappears shortly after female emergence terminates.

In areas where a partial second generation occurs, patrolling of the nesting site and aggregations again can be observed. The

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[2] W. P. Stephen. Personal communication.

males tend to aggregate and stay near the new areas of emergence. Because of the reduced numbers, aggregations are not as obvious as earlier in the year, for there are usually not more than five or six bees to a cluster.

A few young females that failed to find a nesting site were observed to behave much like sleeping males. Some crawled into holes to spend the night, while others were observed to hide under the loose soil crust and remain there all night without digging. Although females usually do not aggregate like males, three females were observed to cluster under a small piece of cardboard located on a bee bed.

Nesting Activity

After mating has occurred, the female is believed to spend a few hours foraging in the field, after which she returns to the bee bed to start nest construction. A few females have been observed searching for nesting sites just after noon, at which time they appear to be very selective. They search around dirt clods and sticks and occasionally dig at a site for a few seconds only to leave and look elsewhere. At this time of day they exhibit a definite preference for sites protected from the sun. It is possible that these shadows are mistaken for holes, for females readily accept abandoned burrows or sharp depressions as the site for their excavations. Occasional females will find an emergence hole of another bee or of the parasite Heterostylum robustum, and when they do it is rare for them to leave once they start digging. Because of this habit, potential nesting areas can be made more attractive to searching bees by punching shallow 5/16 inch diameter holes in the bed. These holes are attractive to searching females. During periods of heavy emergence they will accept these before excavating their own. As the artificial holes become older without being inhabited, they become less attractive. If a new hole is punched nearby, the bees will invaribly select the latter.

As the afternoon progresses, females, still searching for nesting sites, become more active in their search; they repeatedly enter occupied nests only to be forced out. They will often dig a burrow to a depth of two or three inches and then abandon it. By 6:30 or 7:00 P.M. they accept almost any site, many times excavating two or three inches, remaining in them overnight, only to abandon them the next morning. One evening 25 females began nest construction in holes punched with a nail, where they remained overnight. The next evening, only 13 were still occupied. Often a new female will take over an abandoned hole the next day, which makes it very difficult to follow the first two days of nest construction without marking the bees. Many females that have been unable to find a nesting site can be observed crawling around on the bed as darkness approaches.

They often enter an occupied burrow and remain in the upper part of the nest. If the resident female is not actively digging, the intruder may spend the entire night there. On the other hand, if the resident female comes into the upper part of the burrow during the night she will force the intruder out. At night, during periods of heavy emergence, the angry buzzing of females can be detected and quite frequently intruders can be observed crawling about the bed after being forced out. If an expelled female finds one of the artificial holes, she enters it and rapidly begins digging.

Once a burrowing site has been selected, the female bee chews a hole with her mandibles and pushes the loosened soil back with her forelegs. She periodically rotates in a complete circle around the new excavation. As the hole increases in depth, the pro-and mesothoracic legs appear to be used in digging; the hind legs apparently are used as stabilizers and brace the female. As the female descends into the burrow opening, the legs are in a convex position conforming to the sides of the tunnel. Throughout the process, the female can be observed rotating in the burrow with her head down. The mandibles are used to smooth out and remove any uneven areas along the burrow walls. The new soil that is loosened is passed back under the abdomen by the pro-and mesothoracic legs. When the soil accumulates and starts interferring with the digging, the female backs out of the burrow pushing the loosened soil behind her with the metathoracic legs and abdomen (Figure 7). As the tunnel progresses, the female can be observed to periodically tamp the sides of the burrow with the apical abdominal sterna to compact it. It is surprising how little soil falls back into the burrow during this process. As the burrow gets deeper, she again periodically stops digging and tamps the sides of the burrow with the underside of her abdomen. Occasionally she reverses her position and comes up head first, apparently to observe areas needing further attention, because she again changes position and comes up abdomen first and begins tamping the area she previously inspected.

The female also can be observed applying moisture to the walls of the burrow and the tumulus with the glossa. This is especially noticeable in dry soil. Often the loose soil of the tumulus will be blown away, leaving a chimney formed of the previously moistened and packed soil of the burrow wall (Figure 6).

The majority of the digging occurs during the afternoon and night, although in some instances the female may be observed pushing up fresh soil in the early morning before departing for pollen. Observations and excavations on a section of the Schiemer bed indicate that some of the loose soil excavated is used in filling subsurface cavities that may be present in the soil. In 1962, very few tumuli were in evidence on one portion of the bed that was known to be inhabited by young females. Upon excavation, it was discovered that the area had a considerable number of air pockets and mice tunnels. The bees, in digging into one of these areas, would change their direction and push all loose soil into these cavities rather than transport it to the soil surface.

The female most commonly excavates a vertical tunnel of varying depth. Bohart (1955) reports that female bees were able to dig themselves under the moist clay surface in seven to 12 minutes and that below this, progress was more rapid. He reports that the first inch took 20 minutes and the second inch took 15 minutes. As one would expect, the amount of time required in digging to a certain depth is directly correlated with the soil conditions, and the times reported by Bohart may be considerably shorter if a bee finds an old emergence hole, or longer in extremely hard soils.

During the first 24 hour period, the bee usually excavates to a depth of five to seven inches, although there are exceptions to this. The last casting in the top row at the right (Figure 8) is only four inches, and the preceeding one is nine inches long. The structure of the burrow and the number of roughed-out cells is extremely variable and the day-old castings illustrated were purposely selected to show the extremes. The roughed-out cells vary from zero to five and one-half in number four reading from left to right, top row in Figure 8. A lateral shaft leading from the verticle is usually at a depth of from three to five inches. Although roughed-out cells are common in one-day-old nests, no polished cells were found in the 50 nests examined. Bohart (1955) reports, however, that in Utah, day-old nests were found to contain polished cells. During the first 24 hours the female bee periodically leaves the burrow, presumably to feed, thereupon returning to the burrow to continue nest preparation.

Two-day-old nests characteristically contain a number of roughed-out cells and usually at least one lateral. Only two of the 50 nests examined had polished cells. When a polished cell is present, the roughed-out cells are fewer in number than in those with no polished cells. In Figure 9, the two-day-old nest shown has one polished cell and no roughed-out cells, whereas Figure 10 illustrates a two-day-old cluster with no polished cells but with six roughed-out cells. In contrast to the observations in Utah (Bohart, 1955), there was only one provisioned cell found in all two-day-old nests examined in the Eastern Oregon area.

There were a few polished cells without pollen at the end of the second day, which leads one to conclude either that the alkali bee must have polished it during the day, or the alternative, that if it were polished the previous night the bee spent the day in some task other than the gathering of pollen. The former seems more likely because it is unusual to find an unprovisioned cell in a nest at the end of a day. Excavations have shown that in the early morning most nests older than two days contained an unprovisioned, polished cell.

However, in the evening of the third day, almost without exception, the polished cells were filled with pollen balls. This would indicate the usual situation was for the bee to polish a cell sometime during the night and to provision it the next day.

The cluster formation in the two-day-old nests varies considerably, (Figures 8, 9, and 10) which is due in part to the crowded conditions of the bee bed. The depth is uniform, which is believed due to the presence of a hardpan that prevented the female bee from digging any deeper.

Figure 11, top row, shows a series of three-day-old nests, all similar in structure to those of two-day-old nests. The 45 three-day-old nests examined had a total of 17 polished cells, five of which were not provisioned. Observations on the females of these unprovisioned three-day-old nests showed that they spend the day excavating and presumably polishing the cells. Although not shown, the cluster formation is generally much more complex in three-day-old nests. Twelve of the 45 three-day-old nests contained a provisioned cell and three contained eggs at the end of that day. There is a great amount of variation in the extent of cluster formation as well as in burrow depth (Figures 11 and 12). Burrow number 4 in Figure 11 shows a rather unusual nest formation, for in three days the bee had not made any attempt at the regular cluster formation.

Ten of the 40 nests excavated after four days had two provisioned cells and 25 had only one provisioned cell each. The four-day-old nests in Figures 11 and 13 show some of the variation encountered. Burrows number 2 and 3 (left to right in Figure 11), which penetrated to a depth of nine to 10 inches, were taken from an extremely crowded bee bed. Burrow casting number 5 (top row, Figure 11) shows another burrow pattern often found in crowded areas of a bee bed. The cell clusters are located at two different levels, which suggests that lateral expansion of the clusters was restricted by cell clusters of other bees. The nest to the far right, bottom row, is approximately six inches long and is more representative of four-day-old nests located in less populated areas of the bed.

Of the 35 nests excavated after five days, 24 contained one and eight contained two provisioned cells. Two nests examined at the end of the fifth day each had a polished cell without any pollen. It would appear that some bees polish a cell during the day and do not have sufficient time to provision it. This is not surprising for under unusual conditions such as cool or stormy weather, the bees remain in the nest and rough out extra cells. In one case, a four-day-old nest had 17 roughed-out cells, with no polished or provisioned cells.

There is a tremendous variation in the amount of excavation performed by an individual bee. One five-day-old nest contained two provisioned cells with eggs, one polished cell, 13 roughed-out cells, plus a vertical excavation to a lower level, possibly for a second series of cells. Considering that the bee spent two days collecting pollen will give one some idea of the tremendous amount of digging she had accomplished in the five days. This also explains why some burrow openings may not show evidence of fresh digging for periods of nine or 10 days. It also indicates that some bees must spend a considerable time doing something other than digging or collecting pollen, or they are extremely slow in performing these tasks. Other five-day-old nests have had only one provisioned cell and one roughed-out cell.

A few five-day-old nests were found without eggs, but this was unusual and from the fifth day on, the bee generally followed the pattern reported by Bohart (1955). During the day the female: (1) provisioned a cell with a pollen ball, (2) usually excavated another cell or two during the late evening or night, (3) laid an egg on the pollen ball and sealed the cell, and (4) polished a new cell. Because most of the new pollen balls were without eggs when unearthed in the late evening but had eggs and were sealed by morning, it appears the eggs are usually laid during the late night or early morning hours. Few polished empty cells were found in the evening but these were common in the early morning. This indicates that egg-laying as well as some cell polishing takes place during the night.

Aside from the nest construction behavior in the first four or five days, the observations in Eastern Oregon generally agree with those of Bohart (1955) in Utah.

It is evident that even though a general pattern of nest construction exists, many variations occur. For example, some cells were evidently polished during the day, others were polished during the night. Some bees roughed out a large number of cells (17) during the first few days while others roughed out only two or three.

Castings of nests made where there was little or no competition for space showed the clusters to be relatively uniform in shape and depth, with the bee excavating from three and one half to five inches before constructing the lateral tunnel. In general, the lateral extended at right angles from the vertical, but in some it tended to curve and form a somewhat circular pattern.

Prior to provisioning, the female first re-works the roughed-out cell until it is 14-16mm long and 7-8mm in diameter. She then narrows the cell entrance or neck to about 5-6 mm, and lines the cell with a thin layer of clear, waxy material applied by the end of her glossa. After provisioning the cell with a pollen ball and laying an egg, she starts to seal the cell with a spiral-shaped soil plug. This is started on one side and is gradually built around the cell opening until it forms a complete spiral, then a second spiral is started on top and slightly to the center of the first. It takes five to seven spirals to completely plug the cell, and the completed plug is three to four mm in height. The female then packs soil into the neck of the cell until it is level with the floor of the lateral or chamber from which it was excavated. The total length of this soil plug varied from 10mm to 17mm in the 150 cells measured.

An unusual situation is presented in Figure 14, where the burrows of two females are interconnected. This is apparently due to the close proximity of the two nests, and if it does occur frequently during nest construction in well-populated beds, the bees must immediately seal them off.

Pollen Collecting

The female alkali bee usually does not begin collecting pollen to provision the nest until the third, fourth, or fifth day after nest construction has begun. However, in 1962, three female bees were noticed bringing in smaller than normal pollen loads on the second day. That evening the three nests were filled with plaster of paris and the following day were excavated. In two of the nests, a small pollen store was located as a small, irregular mass at the end of the main burrow. No pollen was discovered in the third nest. There were three or four roughed-out cells in each of the nests but no polished cells.

Further observations revealed that about 35 percent of the two-day-old nesting bees brought in similar small pollen loads sometime during the day. It seems unlikely that this pollen would be

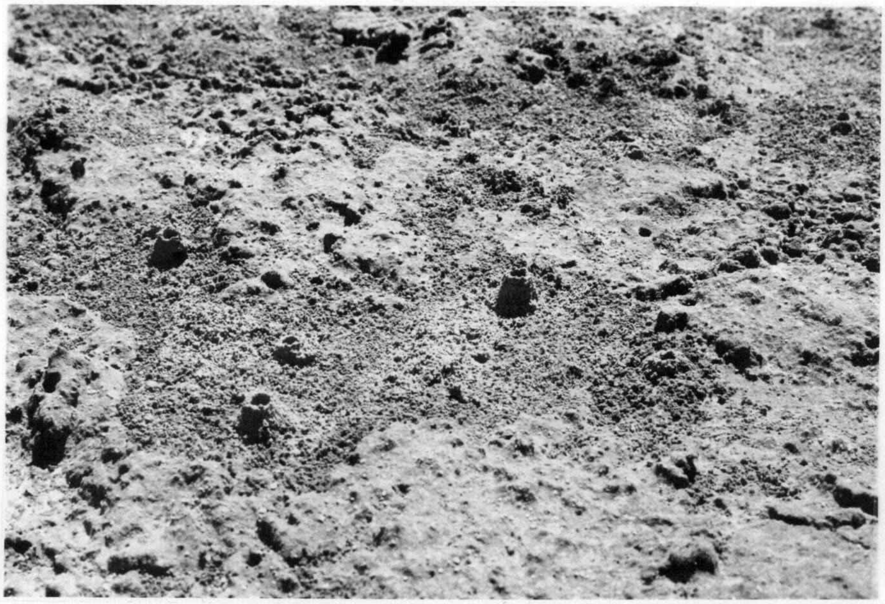
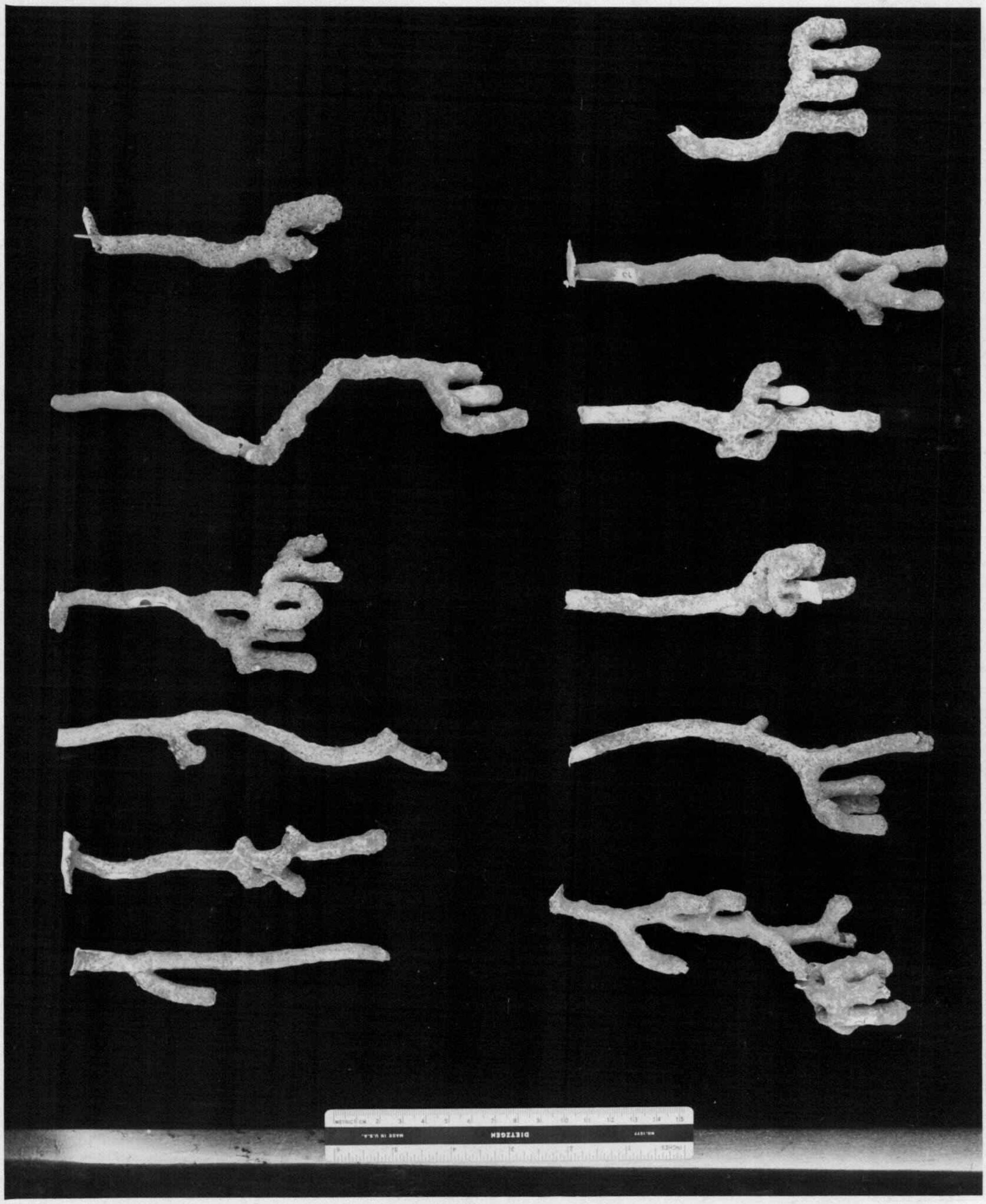


Figure 6. Alkali bee chimneys.

Figure 7. Female alkali bee pushing soil out of the burrow.

Figure 8. Top row - Plaster of paris casts of 1 day old alkali bee nests.

Bottom row - Plaster of paris casts of 2 day old alkali bee nests.


DIETZGEN

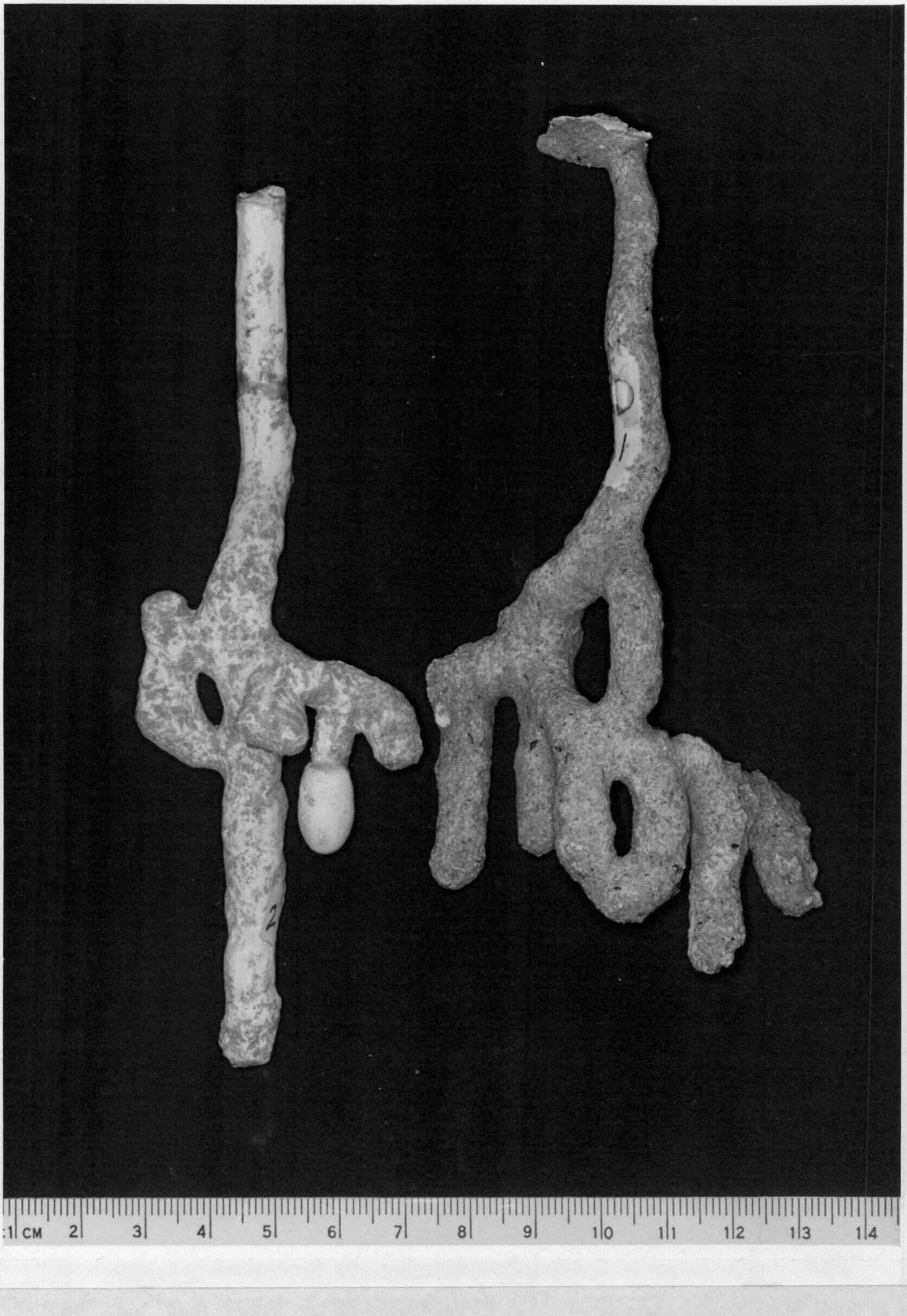


Figure 9. Comparison of a one day old nest on the right with a two day old nest on the left.

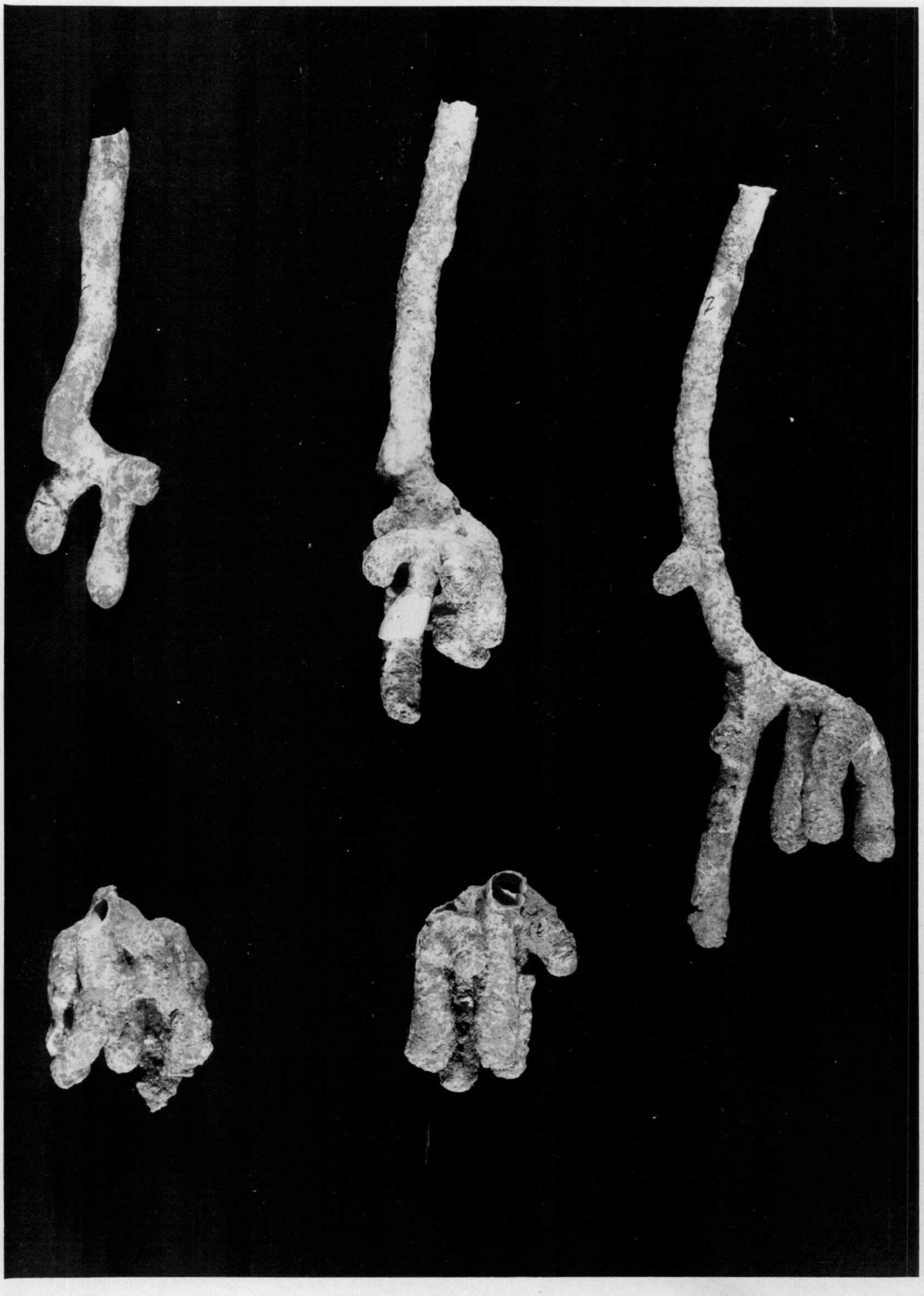
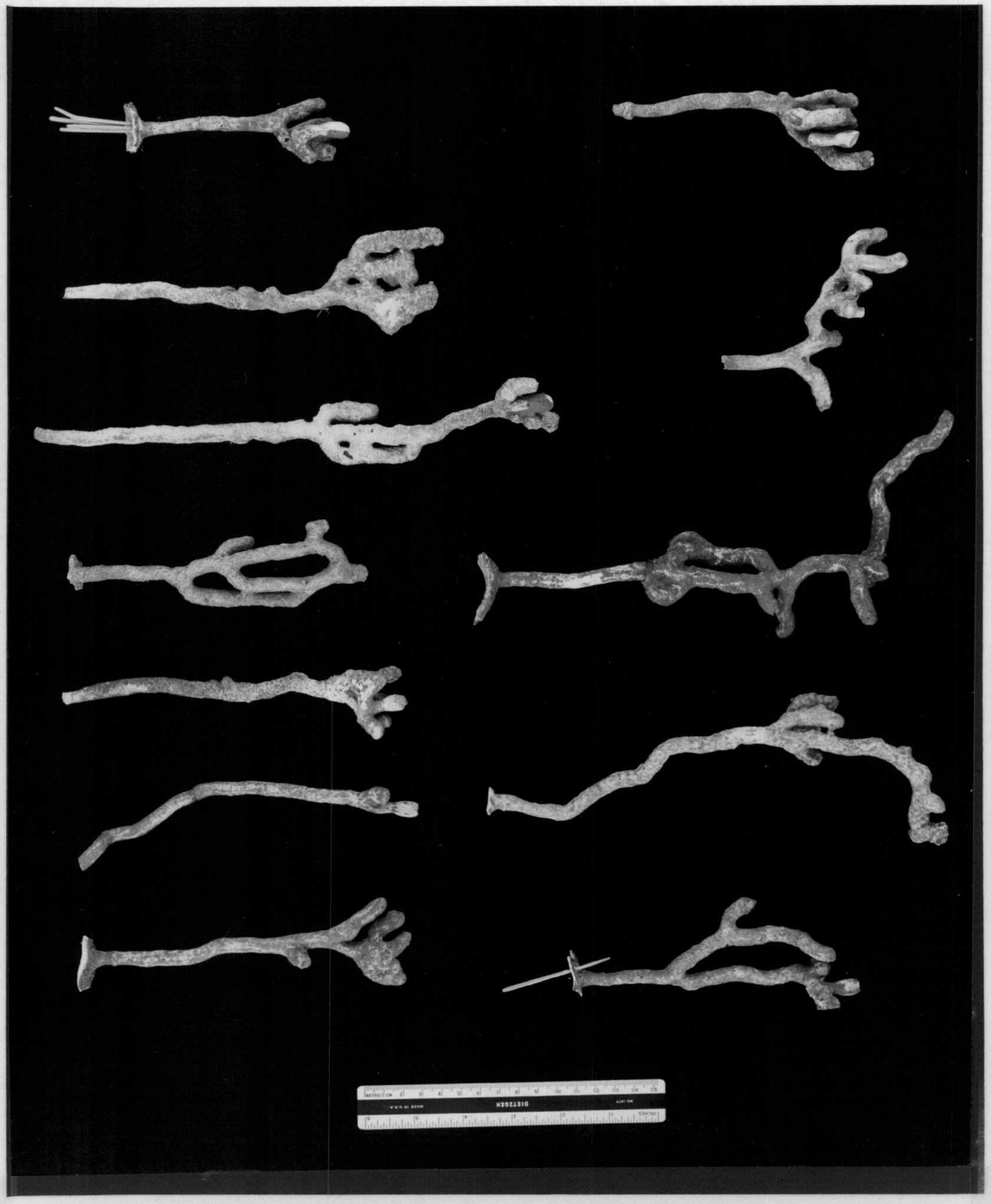


Figure 10. Two day old plaster of paris nest casts of the alkali bee.

Figure 11. Top row - Plaster of paris casts of 3 day old alkali bee nests.

Bottom row - Plaster of paris casts of 4 day old alkali bee nests.



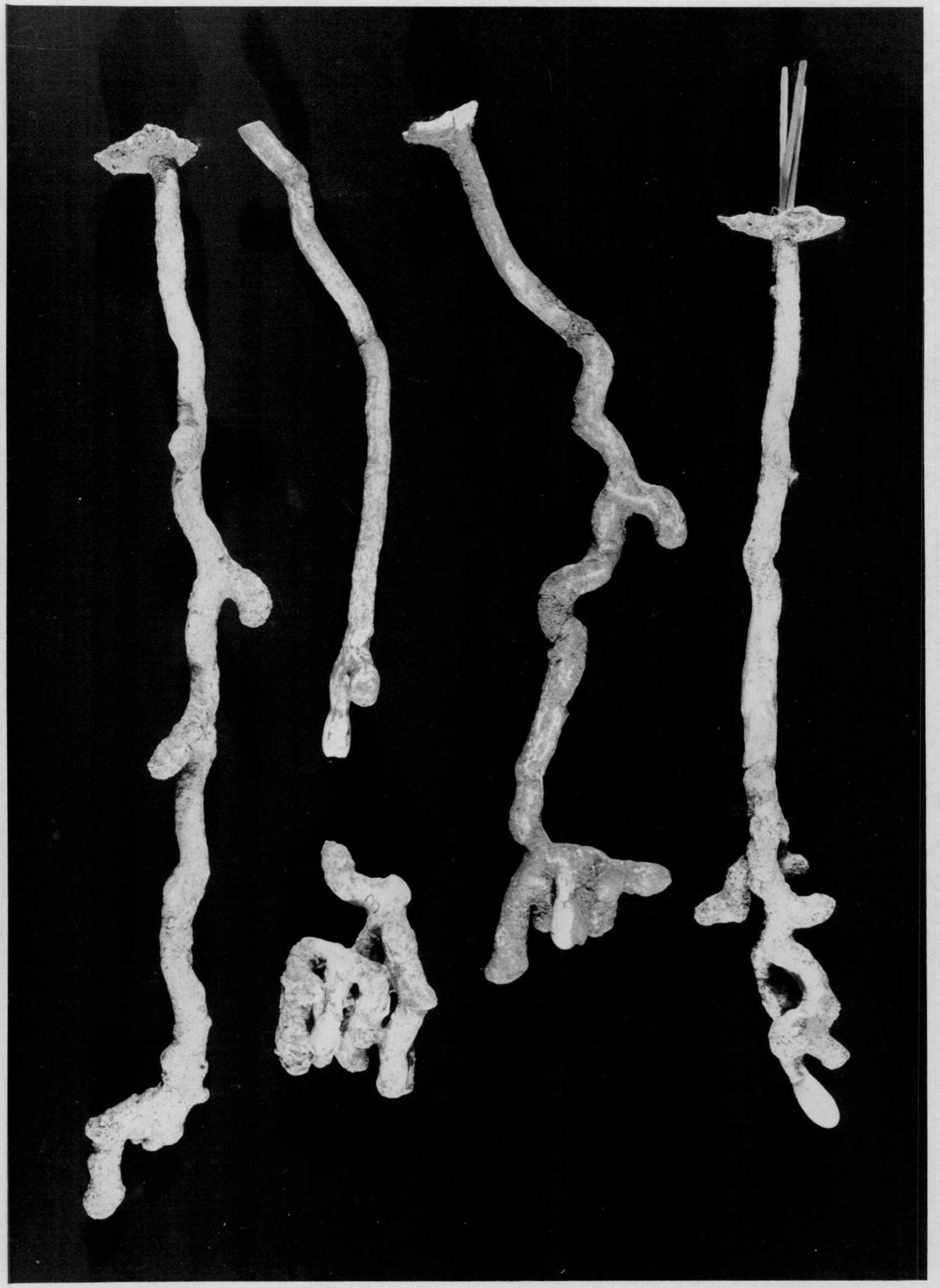


Figure 12. Comparison of three day old plaster of paris nest casts of the alkali bee.

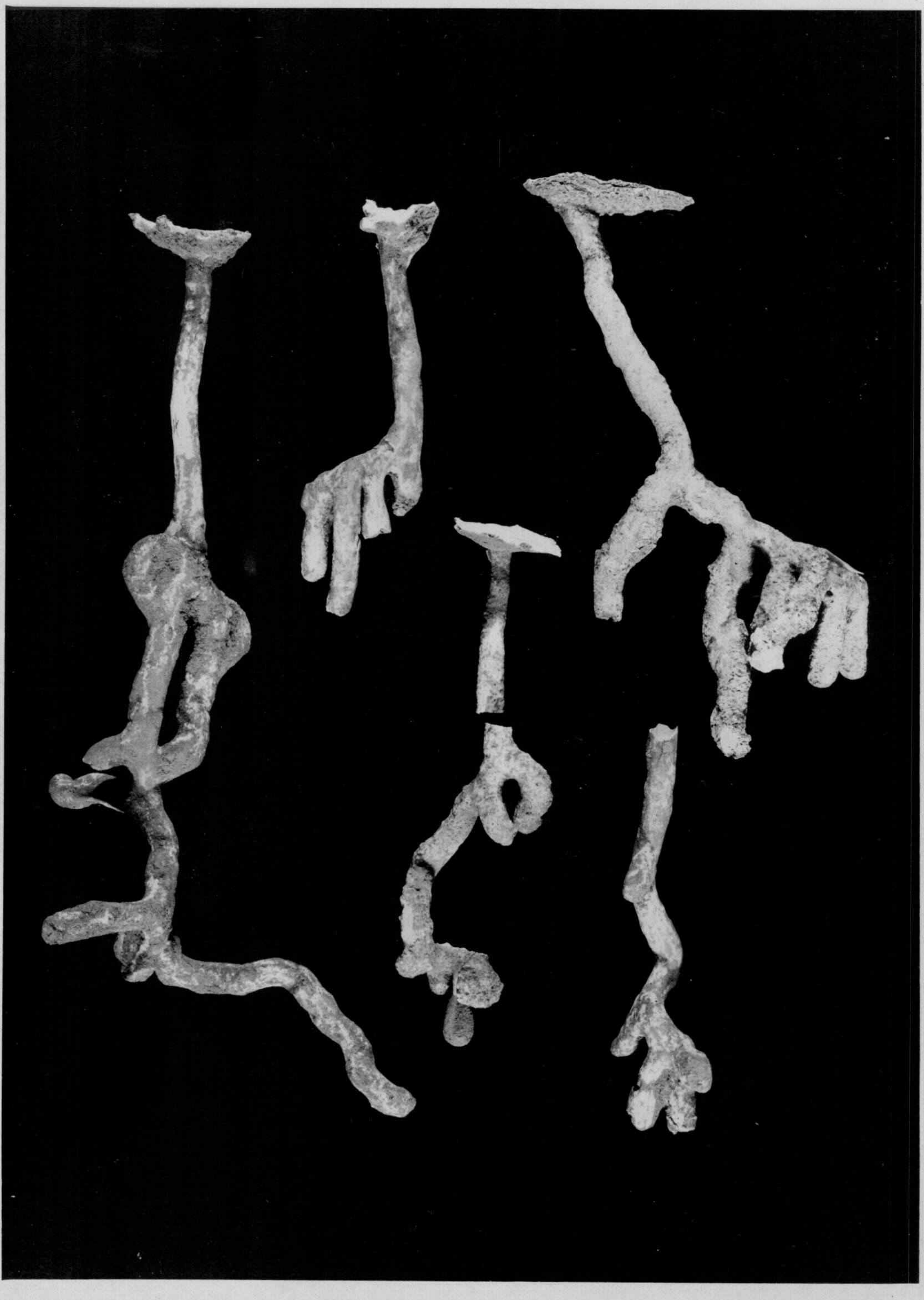


Figure 13. Comparison of four day old plaster of paris nest casts of the alkali bee.

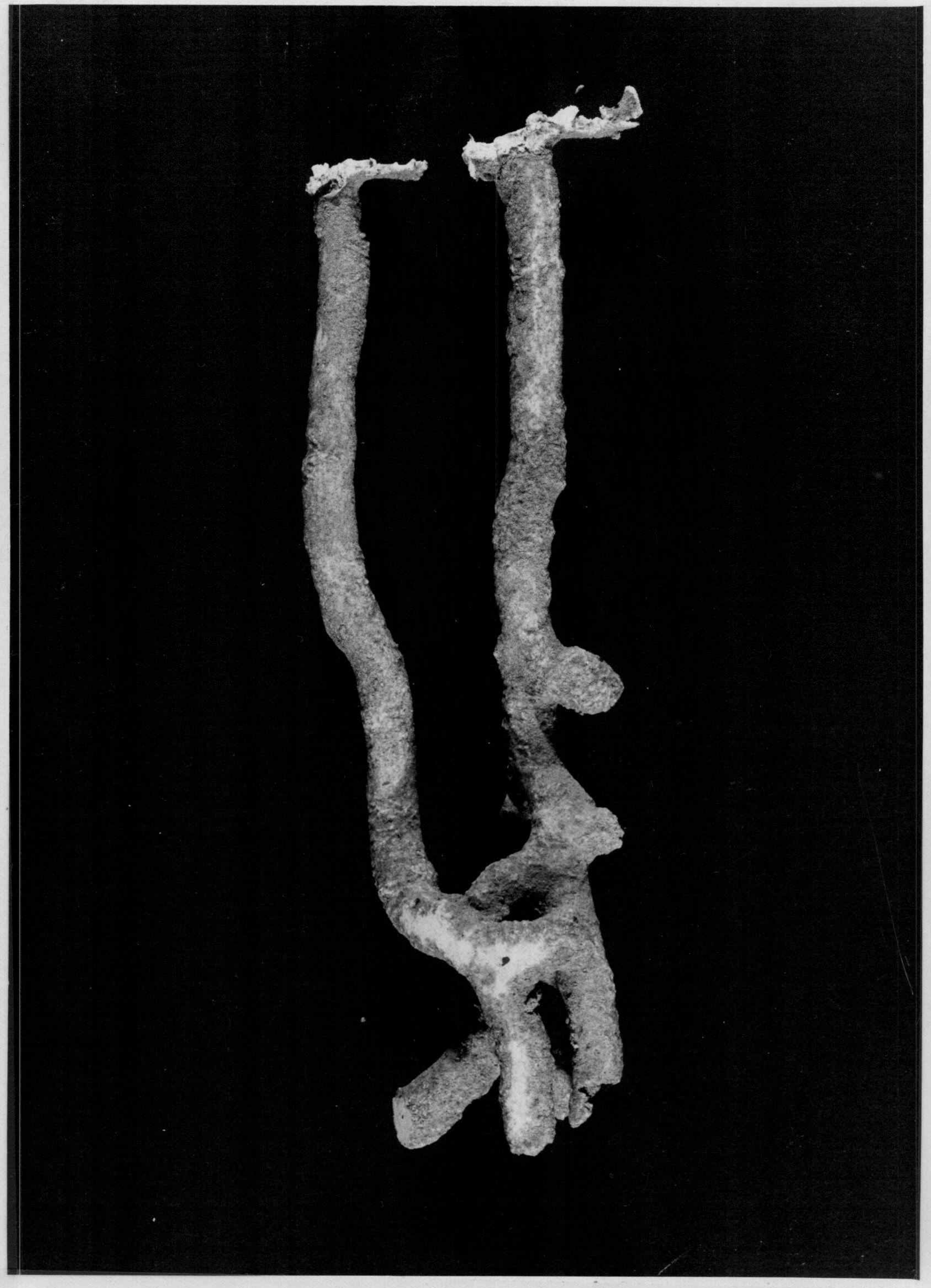


Figure 14. Plaster of paris casts of two interconnected one day old alkali bee nests.

transferred to a polished cell at a later time. Rather, it may indicate that the female alkali bee requires a protein source in her diet prior to oviposition. It is possible that most females may feed on pollen in the field and that the partial pollen loads returned to the nest may represent an unusual behavior pattern in the species. Additional investigation is needed before any definite conclusion can be reached.

Specificity. During the summer of 1962, pollen-laden female alkali bees were collected and the pollen removed to determine its source. The pollen was invariably alfalfa in areas where alfalfa bloom was available. However, in areas where there was very little or no alfalfa, it was discovered that females would collect pollen from almost any available source. The following plants are those from which alkali bees with pollen loads were taken, during the summer of 1962: yarrow, *Achillea millefolium* L.; rabbit brush, *Chrysothamnus nauseasus* (Pall.) Britt.; cleome, *Cleome platycarpa* Torr.; Canada thistle, *Cirsium arvense* Scop.; onion, *Allium cepa* L.; sun flower, *Helianthus annuus* L.; mint, *Mentha peperita* L.; yellow sweet clover, *Melilotus officinalis* (L.) Lam.; and alfalfa, *Medicago sativa* L. There was a definite preference for alfalfa and, except for sweet clover and Canada thistle, other pollen was collected only where alfalfa was rare or a considerable distance from the nesting site.

Towards the end of August, 1964, in an alfalfa field heavily infested with Canada thistle, two or three alkali bees could be observed on almost every thistle blossom. Approximately 85 percent of these bees carried alfalfa pollen and apparently were seeking nectar from the thistle. It should be mentioned that at this time the seed set was extremely heavy on the alfalfa and little bloom was present. Thus, the resulting competition for the remaining alfalfa bloom may have forced some of the bees to a less desirable forage plant.

In areas where alkali bees were visiting several plant species, each pollen load was pure or nearly so, indicating a definite flower constancy. The few cases where loads were contaminated were undoubtedly the result of the bee collecting pollen from one species of flower and visiting another to rest or gather nectar.

Linsley and MacSwain (1958) define as oligolectic those species in which the individual member, throughout the range of the population, and in the presence of other pollen sources, consistently and regularly collects pollen from a single plant species or a group of related plant species, turning to other sources, if at all, only in the face of a local absence of the pollen. Using this definition, alkali bees are oligolectic; however, it might be mentioned that any factor which reduces the attractiveness of the usual pollen source, in addition to the local absence, may force the foragers to a new plant for pollen.

Activity. Once the alkali bee has located its source of pollen and nectar, it begins a rather routine procedure of gathering pollen and nectar during the day and polishing cells or otherwise preparing the nest at night. Tables 1, 2, 3 and 4 present data collected during the summer of 1962 and 1964 on the number of pollen-collecting trips per day and the time required for each trip.

Morning emergence is to a large extent controlled by temperature, and during the summer months the first flight recorded for marked bees used in this study was 7:30 A. M. Activity gradually increased until it reached a maximum between 9:00 and 10:00 A. M. , and this level of activity continued throughout the day. The first evidence of a drop was not detected until about 4:00 P. M. and by 5:00 P. M. a noticeable drop in activity of working females was noted. By 6:00 P. M. there were few females bringing in pollen and almost all the activity was that of newly emergent females and a few males.

During July, 1964, on days with temperatures of 95°F or above, there was some activity as dusk approached; and even after dark, flashlight examination revealed females crawling around the bed searching for a nesting or overnight site. They would often enter active burrows only to be forced out by the occupant. When they encountered empty holes, they would enter and usually begin digging, but as noted previously, most would depart the next day and not return.

Female alkali bees for which records were kept foraged from five hours and 47 minutes to nine hours each day (Table 1 and 2). This contrasts with the data presented by Menke (1954), where he records that the time worked by female alkali bees in the lower Yakima Valley during 1950-1951 was about four to five hours each day under favorable weather conditions.

The data also indicate that eight to nine trips are required to form a pollen ball, and once it has been completed, the female apparently stops collecting regardless of the amount of favorable collecting time remaining. For example, bee number one (Table 2) started collecting pollen at 7:30 A.M. and after the last trip was completed (2:40 P.M.) she remained in the nest. A second bee completed her last pollen trip by 2:33 P.M., after which she too remained in the nest the rest of the day. On that same day other females made two or more trips after the earlier bees had concluded their pollen collecting. These observations substantiate Bohart and Stephen's findings that the female completes one pollen ball per day, even though in many cases there is sufficient time to make a significant start on the second. It was also noted that, as a rule, the bees that began collecting early were also the ones to terminate activity early.

There appears to be considerable variability in the length of time an individual bee requires to collect a load of pollen. Bee number four (Table 2) completed trip number three in 14 minutes, yet she required 82 minutes to complete the next trip. Bee number three (Table 1) took 15 minutes for the first trip, and 91 minutes for the sixth. Similar variations in foraging time were recorded for other bees, but such large variations were not the rule. In the nine trips made by bee number four (Table 2), the time for each load was extremely uniform, varying from 22 minutes on the second trip to a height of 36 minutes for the eighth trip, with an average duration of 29 minutes. Bee number four (Table 1) completed five of the eight trips in the identical time of 45 minutes with an eight-trip average of 44. 3 minutes. Similarly, bee number two (Table 1) completed five of the nine trips in 30 minutes with an average of 26. 1 minutes per trip.

It is rather difficult to account for these time variations. If we assume that the individual bees return to the same general area of the field to collect pollen, and there is evidence indicating this, then we must assume that there is a considerable amount of time spent doing something other than collecting pollen. If this were not the case, each trip should require approximately the same time. Field observations have revealed that often a female bee will trip 50 or 60 florets, then land on a leaf or stem and remain there for as long as two minutes. Other females that appeared completely pollen-laden were observed on flowers taking up nectar. Still others were observed tripping florets as fast as they encountered them for as long as they remained in view. Perhaps it is this inconsistency in foraging behavior that accounts for the variation in time taken to complete a pollen trip.

Stephen (1959) has pointed out that females expand their range in increasingly larger circles and rarely, if ever, stop at sites that come into bloom after their patterns have been established. Observations in Eastern Oregon tend to agree with this. Bees that have apparently passed over late-blooming alfalfa appear to continue to do this even after it comes into bloom. On the Schiemer site, bees were observed flying over 0. 3 mile of alfalfa in full bloom to forage in fields estimated to be only about 65 percent in bloom. Thus it would appear that the time needed to complete each pollen trip should gradually increase as the season progressed, but this was not the case. Where the same bees were checked three weeks later in the season, it was found that the collecting time had not changed appreciably. It may be that so little time is spent in flying to the collecting area that a little longer distance would not be detectable, or that as the bee spends more time collecting pollen she becomes more efficient, so that time spent in flying the greater distance is offset by a shorter period of actually collecting pollen.

Excavations during the day revealed that the first pollen loads are usually deposited in the cell without the addition of nectar, for the mass is extremely dry. It is assumed that nectar must be added near the time the ball is complete. Some bees were observed to leave the nest after completion of the pollen ball, and it is believed they returned with nectar to be added to the pollen or used as a source of food. However, some females did not leave the nest after their last pollen load, yet when these nests were excavated the pollen balls had the usual fluid consistency, indicating that occasionally females must bring in nectar with the last pollen load.

It was also observed that the last pollen load of some bees was appreciably smaller than the previous loads (Table 4, bee number 1). It is assumed that this small load may have been needed to complete the pollen ball, or that it was collected as a food source for the adult.

The majority of the alkali bees required nine pollen-collecting trips to complete the pollen ball (Tables 1, 2, 3 and 4); one bee (Table 4) required 11 trips, whereas two others (bee number 2, Table 4 and bee number 2, Table 2) took only eight. It was not always possible to detect if the bee returned with pollen, for occasionally the bees were well into the nest before observations could be made, and their hind legs were not visible. These are noted by question marks on the time column of Tables 1 and 2 and the time was not used in average trip computation time.

Table 1. Daily pollen collecting trips of the alkali bee to complete one pollen ball, 1962

	Bee No. 1			Bee No. 2		
	Depart	Return		Depart	Return	
1.	8:30 a. m.	9:30 a. m.	(60)	9:45 a. m.	10:00 a. m.	(15)
2.	9:45 a. m.	10:15 a. m.	(30)	10:45 a. m.	11:15 a. m.	(30)
3.	10:30 a. m.	11:00 a. m.	(30)	11:30 a. m.	12:00 noon	(30)
4.	?	11:30 a. m.		12:30 p. m.	12:50 p. m.	(20)
5.	11:45 a. m.	12:30 p. m.	(45)	1:00 p. m.	1:30 p. m.	(30)
6.	12:40 p. m.	1:10 p. m.	(30)	1:40 p. m.	2:05 p. m.	(25)
7.	1:35 p. m.	2:05 p. m.	(30)	2:30 p. m.	3:00 p. m.	(30)
8.	2:45 p. m.	3:45 p. m.	(60)	3:30 p. m.	4:00 p. m.	(30)
9.	4:15 p. m.	4:50 p. m.	(35)	4:30 p. m.	4:55 p. m.	(25)
Average pollen collecting trip time			40 min.			26. 1 min.

	Bee No. 3			Bee No. 4		
	Depart	Return		Depart	Return	
1.	9:15 a. m.	9:30 a. m.	(15)	8:00 a. m.	9:45 a. m.	(45)
2.	9:40 a. m.	10:00 a. m.	(20)	9:50 a. m.	10:15 a. m.	(25)
3.	10:15 a. m.	11:00 a. m.	(45)	10:30 a. m.	11:45 a. m.	(75)
4.	11:30 a. m.	12:00 noon	(30)	12:00 noon	12:30 p. m.	(30)
5.	12:15 p. m.	12:45 p. m.	(30)	12:45 p. m.	1:30 p. m.	(45)
6.	12:59 p. m.	2:30 p. m.	(91)	2:00 p. m.	2:45 p. m.	(45)
7.	3:30 p. m.	4:00 p. m.	(30)	3:00 p. m.	3:45 p. m.	(45)
8.	?	?		4:15 p. m.	5:00 p. m.	(45)
9.	Not complete -					
Average pollen collecting trip time			37 min.			44. 3 min.

Table 2. Daily pollen collecting trips of the alkali bee to complete one pollen ball, 1962

	Bee No. 1			Bee No. 2		
	Depart	Return		Depart	Return	
1.	7:30 a.m.	8:05 a.m.	(25)	8:34 a.m.	8:49 a.m.	(15)
2.	8:30 a.m.	8:49 a.m.	(19)	9:00 a.m.	9:32 a.m.	(32)
3.	9:00 a.m.	9:35 a.m.	(35)	9:40 a.m.	10:52 a.m.	(76)
4.	9:53 a.m.	10:10 a.m.	(17)	11:15 a.m.	11:30 a.m.	(15)
5.	10:35 a.m.	10:49 a.m.	(19)	11:45 a.m.	1:11 p.m.	(86)
6.	11:12 a.m.	11:47 a.m.	(35)	1:35 p.m.	2:10 p.m.	(35)
7.	12:11 p.m.	12:34 p.m.	(23)	2:21 p.m.	5:58 p.m.	(37)
8.	12:52 p.m.	1:15 p.m.	(23)	3:11 p.m.	4:27 p.m.	(76)
9.	1:35 p.m.	1:51 p.m.	(23)	4:54 p.m.	5:08 p.m.	(N.P.)
10.	2:26 p.m.	2:40 p.m.	?			
Average pollen collecting trip time			23.5 min.			46.5 min.

	Bee No. 3			Bee No. 4		
	Depart	Return		Depart	Return	
1.	8:45 a.m.	9:04 a.m.	(41)	8:46 a.m.	9:11 a.m.	(25)
2.	9:08 a.m.	9:37 a.m.	(29)	9:21 a.m.	9:43 a.m.	(22)
3.	9:56 a.m.	10:20 a.m.	(24)	9:49 a.m.	10:23 a.m.	(34)
4.	10:40 a.m.	11:01 a.m.	(21)	10:35 a.m.	10:58 a.m.	(23)
5.	11:12 a.m.	11:41 a.m.	(29)	11:06 a.m.	11:32 a.m.	(26)
6.	11:54 a.m.	12:20 p.m.	(34)	11:44 a.m.	12:05 p.m.	(26)
7.	12:43 p.m.	1:10 p.m.	(27)	12:13 p.m.	12:48 p.m.	(35)
8.	1:34 p.m.	2:34 p.m.	(60)	1:06 p.m.	1:42 p.m.	(36)
9.	4:54 p.m.	5:16 p.m.	?	2:00 p.m.	2:33 p.m.	(33)
Average pollen collecting trip time			33.1 min.			28.8 min.

Table 3. Daily pollen collecting trips of the alkali bee to complete one pollen ball, 1964

	Bee No. 1			Bee No. 2		
	Depart	Return		Depart	Return	
1.	9:23 a.m.	10:15 a.m.	(52)	9:20 a.m.	9:40 a.m.	(20)
2.	10:30 a.m.	11:00 a.m.	(30)	9:45 a.m.	10:20 a.m.	(35)
3.	11:10 a.m.	11:36 a.m.	(26)	10:33 a.m.	11:07 a.m.	(34)
4.	11:45 a.m.	12:15 p.m.	(30)	11:20 a.m.	11:35 a.m.	(15)
5.	12:25 p.m.	12:59 p.m.	(34)	11:42 a.m.	12:17 p.m.	(35)
6.	1:10 p.m.	1:40 p.m.	(30)	12:28 p.m.	1:11 p.m.	(43)
7.	1:55 p.m.	2:25 p.m.	(30)	1:36 p.m.	2:20 p.m.	(44)
8.	2:50 p.m.	3:16 p.m.	(26)	2:32 p.m.	3:10 p.m.	(38)
9.	4:26 p.m.	4:50 p.m.	(24)	3:25 p.m.	4:09 p.m.	(43)
10.	4:59 p.m.	5:15 p.m.	(N.P.)			
Average pollen collecting trip time			31.3 min.			34.1 min.

	Bee No. 3			Bee No. 4		
	Depart	Return		Depart	Return	
1.		10:08 a.m.		8:40 a.m.	9:34 a.m.	(65)
2.	10:30 a.m.	11:01 a.m.	(31)	10:00 a.m.	10:43 a.m.	(43)
3.	11:08 a.m.	11:43 a.m.	(35)	10:50 a.m.	11:04 a.m.	(14)
4.	11:49 a.m.	12:44 p.m.	(55)	11:10 a.m.	12:32 p.m.	(82)
5.	12:55 p.m.	1:34 p.m.	(39)	12:50 p.m.	1:26 p.m.	(36)
6.	1:48 p.m.	2:19 p.m.	(31)	1:41 p.m.	2:11 p.m.	(30)
7.	2:29 p.m.	3:13 p.m.	(42)	2:25 p.m.	3:18 p.m.	(53)
8.	3:38 p.m.	4:19 p.m.	(41)	3:41 p.m.	4:14 p.m.	(33)
9.	4:46 p.m.	5:28 p.m.	(42)	4:25 p.m.	5:04 p.m.	(99)
Average pollen collecting trip time			35.1 min.			50.5 min.

Table 4. Daily pollen collecting trips of the alkali bee to complete one pollen ball, 1964

	Bee No. 1			Bee No. 2		
	Depart	Return		Depart	Return	
1.	8:30 a. m.	9:00 a. m.	(30)	9:40 a. m.	10:11 a. m.	(31)
2.	9:22 a. m.	10:05 a. m.	(43)	10:25 a. m.	11:07 a. m.	(32)
3.	10:15 a. m.	10:45 a. m.	(30)	11:17 a. m.	12:00 noon	(43)
4.	10:52 a. m.	11:10 a. m.	(18)	12:08 p. m.	12:55 p. m.	(47)
5.	11:20 a. m.	12:00 noon	(40)	1:12 p. m.	1:58 p. m.	(46)
6.	12:16 p. m.	12:33 p. m.	(17)	2:10 p. m.	3:00 p. m.	(50)
7.	12:34 p. m.	1:20 p. m.	(35)	3:17 p. m.	4:02 p. m.	(45)
8.	1:35 p. m.	1:58 p. m.	(23)	4:32 p. m.	5:16 p. m.	(44)
9.	2:14 p. m.	2:48 p. m.	(34)			
10.	3:05 p. m.	3:40 p. m.	(35)			
11.	*4:04 p. m.	4:22 p. m.	(18)			
Average pollen collecting trip time			29. 3 min.			42. 2 min.

* Small load

The pollen is formed into a somewhat dorsally flattened ball which is positioned to one side of the cell and slightly elevated. The cell with the pollen ball is shown in Figure 19, but because of the off-center excavation, it gives an exaggerated appearance to the elevation.

Tripping. The tripping of the alfalfa flower (Figure 15) by the female alkali bee is accomplished in a variety of ways. The most commonly observed method is as follows: the bee approaches the flower from the keel side, lands and positions the meso- and metathoracic legs on the wing petals; it then braces its head and prothoracic legs on the standard petal and pushes, freeing the sexual column from its position in the keel. Occasionally, the metathoracic legs appear to remain at the sides of the bee.

Less commonly, the bee approaches from the keel side of the flower, the prothoracic and mesothoracic legs grasp the wing petals, and the head is pushed against the standard which releases the sexual column. Some bees position the mesothoracic legs at the base of the standard petal, place the metathoracic legs in contact with the wing petals, brace the head against the standard and push. The prothoracic legs are constantly in motion and as the sexual column is released, they pick up the pollen and pass it back to the hind legs. Some bees have been observed to grasp the standard with the mandibles and the wing petals with the mesothoracic and metathoracic legs; then by pushing, the flower is tripped. The prothoracic legs are again constantly in motion near the bases of the keel and standard.

On one occasion, a bee was observed tripping flowers with one prothoracic leg missing. This did not hinder it in any way. The head was pushed against the standard while the mesothoracic and metathoracic legs were in contact with the wing petals.

The female alkali bee is a highly efficient alfalfa pollinator, rarely visiting a floret without tripping it. Table 5 presents tripping data collected from 21 different bees during 1964. Four of the observations (No. 5, 6, 7 and 8) were of the same bee during succeeding one minute periods. The bees visited from two to 15 blossoms per minute with an average of 6.4 blossoms per minute. Often a bee would collect quite rapidly for several minutes, visiting nine to 12 blossoms per minute, then suddenly alight, often to remain motionless for an extended period of time, or to preen herself and arrange the pollen in a more suitable position. On the basis of 40 observations, each pollen collecting female spent from five to 15 seconds at each floret, whereas nectar collecting females had repeated five-second visitations. Two bees visited florets already tripped, and it was not possible to completely record the visitations of three others. Thus these data were not included in the calculation of the tripping percentage. The calculated tripping efficiency of 96 percent is almost identical with Menke's (1954) records of 95 percent in 1950 and 97 percent in 1951. Additional observations in 1962 on a total of 250 bees visiting 1,575 blossoms indicate tripping efficiency at 95 percent.

In 1962, observations were made on 20 male alkali bees visiting 65 blossoms of which they tripped 89 percent. This is a considerably higher figure than that reported by Menke (1954) although he did record 80 percent efficiency in 1951.

Table 5. Alfalfa tripping frequency of the alkali bee, 1964.

Nomia	Number of blossoms visited per minute	Number of blossoms tripped
1	6	6
2	12	?
3	8	8
4	6	6 - 5 to 15 seconds per blossom
5	6 (40 seconds)	6
6	4 (45 seconds)	4
7	3 (45 seconds)	2
8	10	10 - 5 seconds per blossom
9	5 (40 seconds)	5
10	6	6
11	2	1 - one already tripped
12	7	7
13	6	5 - one already tripped
14	4 (5 seconds)	4
15	9 (50 seconds)	8
16	5 (30 seconds)	5
17	3 (20 seconds)	3
18	2	2
19	9	9
20	6	6
21	5	5
22	5	5
23	15	?
24	4	4
25	12	?
Total	160	117

Average of 6.4 visits

96 percent of florets tripped

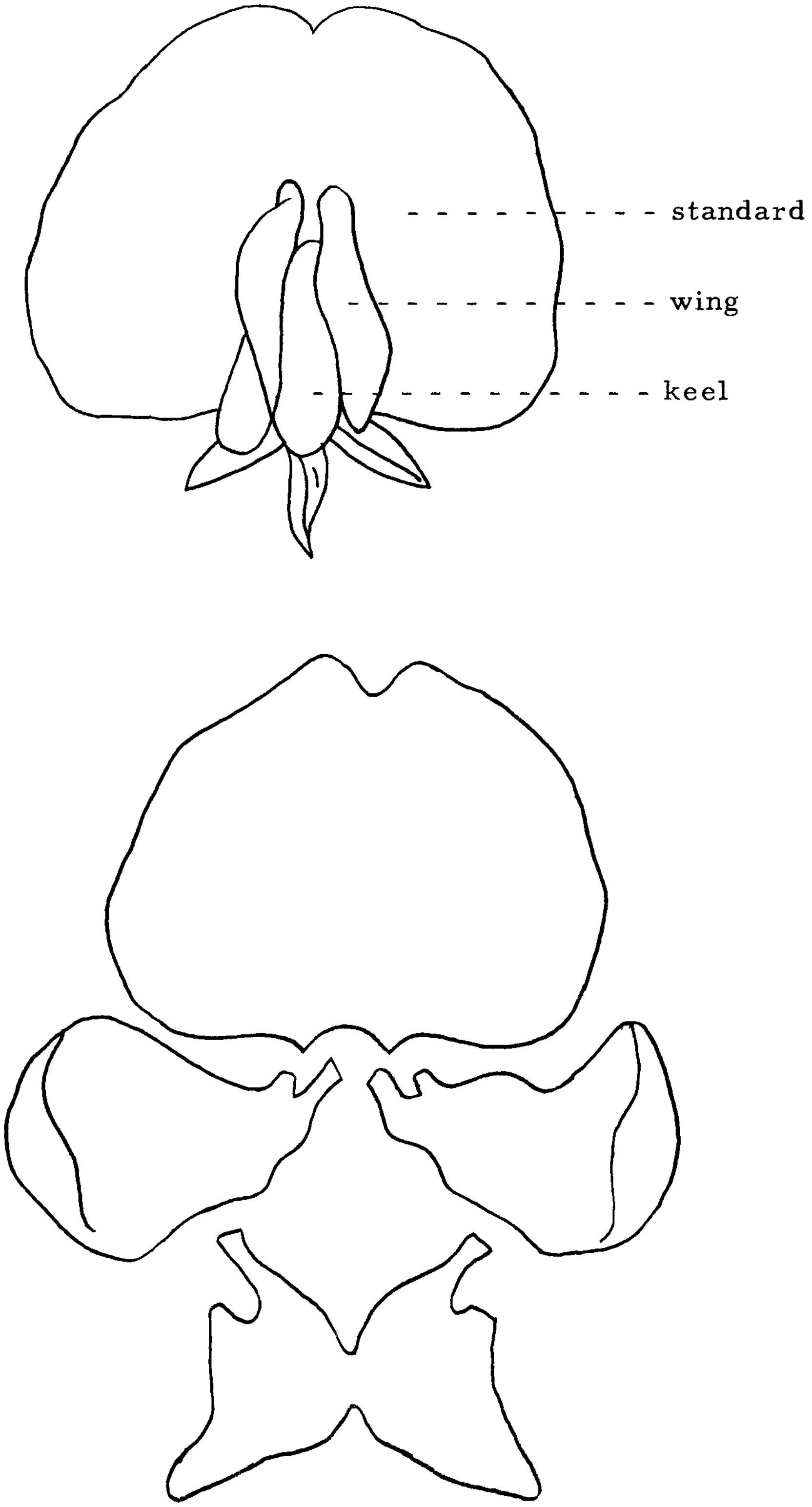


Figure 15. Legume flower.

Age

Females show signs of senility after their fifth week of activity and their behavior changes. Many working females can be observed in the field resting on stems or on the flowers. They are clumsy and often fall from flowers as they land or change position. They can be observed resting on boards or other objects at or near the site, and when they return to the nest they alight and move into the burrow entrance more slowly.

Excavations indicated the nesting behavior is also altered with age. Some of the late eggs, when viewed from above, were twisted into a slight S-shape on the pollen ball and a higher incidence of small eggs were found which invariably yield larvae which die in the first or second instar. Some of the cells had particles of dirt on the pollen ball and a few of the pollen balls had scars evidently produced by the bee's legs during oviposition. Other cells were found provisioned and sealed but lacked an egg, and some were complete but the pollen ball was about half the usual size. Still other cells had a normal-sized pollen ball and egg but the pollen ball was dry, apparently lacking nectar.

The time required to complete a pollen-collecting trip increased with age. In one specimen, it increased abruptly from an average of 30 minutes to an average of 45 minutes, between the 24th and the 26th day. The greater numbers of resting bees observed in the field suggests that this increase in pollen-collecting time is a function of this habit.

Foraging begins later in the morning and terminates earlier in the afternoon. However, this delay could be caused by the cooler morning and afternoon temperatures rather than senility.

Mortality

Under normal conditions, bee activity at a given site drops rather rapidly. Figure 16 shows the seasonal decline at three different sites, two located on the Schiemer bed and one on the Nelson bed. The two sites on the Schiemer bed show almost identical curves up to the 7th of August, but beyond this date the mortality rate was higher on site number 2. By the 9th of August, very few bees were active at site number 2 and activity ceased by August 14th. In contrast, the bees in site 1 declined slowly after the 14th of August and ceased activity on August 26th. It should be pointed out that both sites were located on a portion of the bed that had emerged first, so even though activity had ceased in these areas, there were still a fairly large number of bees working in other areas of the bed.

Activity at the Nelson site declined more slowly than that on the Schiemer bed and, as shown in Figure 16, there was a slight increase in activity between August 14th and August 18th. It is

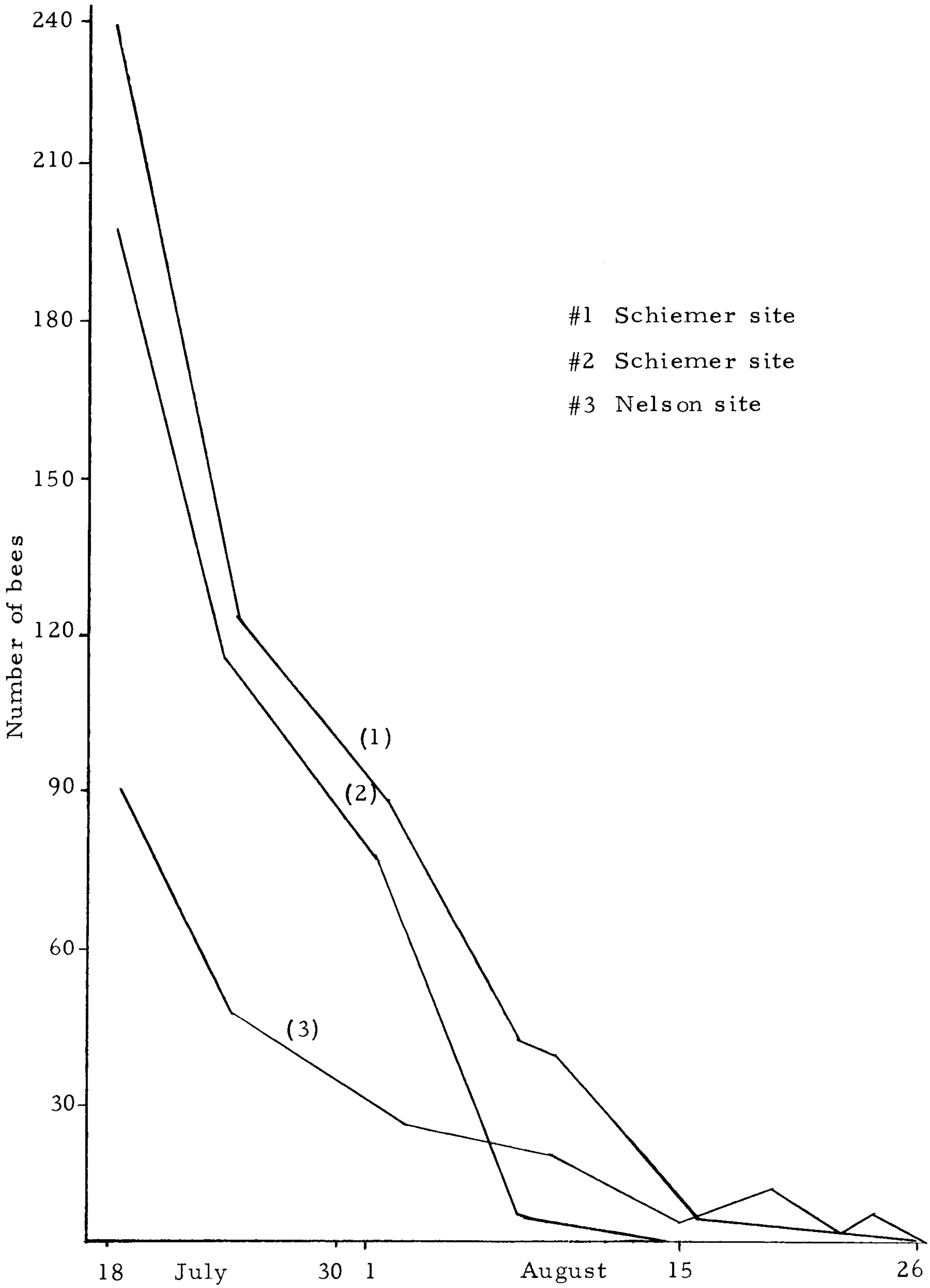


Figure 16. Mortality of the alkali bee, 1962.

possible that new females could have emerged from the damper areas of the bed and nested in the observation area. It is also possible that this increased activity represents the partial second generation reported by Bohart and Cross (1955) and Stephen (1959). In view of the uncertainty of this situation, it should receive further attention.

Larval Development

Egg

The egg of the alkali bee is strongly curved, cylindrical, and bluntly rounded at the ends (Figure 19). The chorion is thin and transparent with very indistinct mosaic sculpturing visible at 90x. The egg is slightly club-shaped, the posterior end averaging 0.20mm less than the anterior end. The length of the egg varies from 3.26mm to 4.34mm. The posterior diameter ranges from 0.57mm to 0.75mm with an average of 0.68mm. The anterior diameter ranges from 0.75mm to 0.87mm with an average of 0.78mm. Externally, the egg appears opaque and paraffin-like in texture.

The female bee attaches the posterior end of the egg near the center of the pollen ball. The anterior end is affixed near the top edge of the pollen ball in the cell, with its anterior end pointing in an upward direction. Because of the strongly-curved nature of the egg only the two ends contact the pollen ball.

Newly-deposited eggs are uniformly opaque but after a period of approximately 30 hours a transparent section starts to develop at the anterior end, and shortly thereafter at the posterior end. These areas gradually increase in length, reaching approximately 0.16mm length at maximum. At this time, it is possible to see the developing embryo; the head process is relatively distinct and shortly thereafter the gnathal segments can be determined. The embryo gradually increases in size and within 48 hours completely fills the transparent portion of the egg. By this time, it is usually possible to determine which eggs will survive.

The eggs require 60 to 72 hours to eclose. On hatching, the chorion appears to remain intact, covering the first instar larva except near the mouth where it has apparently disssolved or ruptured (Figure 17 B). The mandibles can be observed moving free of the chorion.

First Instar

The first instar larva (Figure 17 B) is distinctly segmented about 4mm in length, with the thorax, the widest part, about 0.85mm across. The head is almost circular in outline, varying from 0.66 to 0.78mm in diameter, with very indistinct features. Slight depressions can be distinguished running from the anterior mandibular articulations and converging at the mid-line of the vertex, which is lightly depressed.

The labro-clypeal area protrudes anteriorly and is very thick and fleshy in appearance. The mandibles are transparent with no trace of pigmentation visible when viewed at 80x in the early instar.

In the early stage, the mouthparts of the larva are in direct contact with the pollen ball. A fluid is present, presumably secreted by the larva, which liquifies the food material and facilitates feeding. As the larva matures, the point of contact with the pollen ball is gradually transferred from the head back to the thorax, then to the first two or three abdominal segments. When the larva is not feeding it assumes an S-shaped appearance.

The spiracles and lateral tracheal trunks are visible on eclosion. As the larva matures, the heart can be seen beating. Later, fat particles start to develop and become rather distinct in all but the first two abdominal segments. Toward the end of the first instar, the pleural area protrudes slightly, forming a transverse ridge. Although the mandibles are constantly moving, they are not used to scrape pollen from the pollen ball. Rather, the pollen is suspended in the liquid at the mouth and swallowed in the following manner: the labium is brought forward; the hypopharynx is elevated and fluid, with some pollen grains, is forced into the esophagus. The head is really the only prominent feature at this stage.

The time required for development through the first instar is one day at 24°C. This is similar to the time required under natural conditions in the bee bed.

There does not appear to be much change in the length of the first instar larva and no feeding groove is detectable on the pollen ball. Very faint pigmentation can be observed at the tips of the mandible in the latter part of this stadium.

After one day, the chorion, which has covered the first instar larva, is shed. The first rupture visible is near the frons, from which it extends dorsally and posteriorly. The chorion is forced ventrally and slightly posteriorly, and after two hours the exuvial section originally on the head can be seen on the ventrolateral margin of the second thoracic segment. The larva seems to move forward, and after six hours the exuvial section from the head is near the ninth abdominal segment. It is assumed that the chorion and first instar exuvia are shed at the same time, for the head capsule increases in size with this molt. To determine the time of molting, small particles of soil were placed on the dorsum of the head with the aid of forceps and a microscope. Because of the moist condition of the cuticle, these particles adhere closely and any change can be readily observed. It is thus possible to follow this portion of the cuticle as it is shed.

Second Instar

The second instar larva (Figure 17 C) is similar to the first. Segmentation is more evident and the features of the head are more distinct. The head capsule diameter ranges from 0.78mm to 0.88mm. The apices of the mandibles are acute. The distal tooth of the cusp is enlarged, almost giving the mandible a bifid appearance at certain angles. The articulations of the mandibles are sclerotized and the anterior recessed into pits. The maxillae appear as fleshy lobes behind the mandibles, between which can be seen the labium. All the mouth parts except the mandibles appear thick and fleshy. The antennal papillae are short, their basal widths equal to their length, and they arise from convex elevations. The epistomal suture is apparently absent. The mandibular articulations are weakly sclerotized. The anterior margin of the labrum is nearly flat, with the anterolateral margins forming slight tubercules.

The body is composed of three thoracic and nine distinct abdominal segments. A lateral transverse fleshy ridge is present over the length of the body. Slightly dorsad to this ridge are located 10 pair of spiracles, two thoracic and eight abdominal.

At 24°C this stadium lasts from 1 to 1 1/2 days. It is during this stadium that the first feeding excavation can be seen on the pollen ball. The groove measures about 2mm in length and about 1mm in width by the end of the stadium. The larva feeds on the pollen under the first abdominal segments moving from side to side. Periodically, the larva stops feeding and raises the anterior third of the body in the air (Figure 20).

Prior to molting, it stops feeding and the body is held nearly straight. The posterior third of the abdomen has a slight arch, reminiscent of the curvature of the egg.

On one occasion, an abberation in molting of the second instar was observed. The first effect was a cessation in feeding, followed by the appearance of a small droplet of fluid on the dorsum of the 6th abdominal segment. Soon thereafter, the integument ruptured at the site of the drop, gradually increasing in size until, after five hours, the old integument remained in place only on the last two abdominal segments, the head, and the venter of the larva. At this time it was easy to distinguish the old integument by its duller appearance. The rupture progressed anteriorly over the left side of the vertex and left gena. For some reason the integument did not slide off the right side of the head, and the softer left side was expanded creating a very noticeable distortion in the appearance of the head. Periodically, the swelling subsided and a normal condition was observed. After 14 hours, the larva was still unable to shed the integument from the right side of the head and the posterior abdominal segments and died shortly thereafter.

Third Instar

The third instar larva (Figure 17 E) closely resembles the second. The diameter of the head ranged from 0.87mm to 1.05mm. The apical portion of the mandible is moderately sclerotized. The cusp is covered with extremely fine teeth. Mesally the apical surface is concave. The maxillae are strongly developed with distinct palpi, the labial palpi are weak and are broader than they are long. The epistomal area forms a gentle arc between the anterior tentorial pits and is sclerotized from this point to the anterior mandibular articulation. The anterior margin of the labrum is truncate, with the anteriolateral margins forming strong tuberculate-like lobes, making the anterior surface slightly concave. The body is composed of three thoracic and nine abdominal segments . The mesothorax through the first four abdominal segments have dorsolateral margins of the dorsum elevated, giving a slight concavity to the dorsum.

The third instar larva feeds in a wider arc than that of the second. It occasionally moves forward and reaches farther down on the pollen ball. The stadium lasts for 1 to 2 1/2 days at 24°C.

Fourth Instar

The fourth instar larva (Figure 17 F) is more robust than the earlier stages. The head capsule varies from 1.11mm to 1.30mm in diameter. The antennal papillae are lightly sclerotized. The anterior mandibular articulations are heavily sclerotized. The malar margins of the mandibles are heavily sclerotized, and the cusp bears numerous fine teeth.

A small tubercle with five setae is located medially on the lateral mandibular surface. The dorsal surface of the labrum is concave, the anterior apical margin is truncate, with the anterolateral portions tuberculate. The salivarium appears as a transverse slit located anterior to the labial palpi and equidistant between them. Basally the mesal margins of the maxillae are lightly sclerotized. The maxillary palpi are one segmented and approximately as long as their basal widths.

The body tapers anteriorly and posteriorly. Two thoracic and eight pair of abdominal spiracles are still evident. This stadium undergoes a very pronounced increase in body length and the pollen is consumed at a rapid rate. A relatively large feeding area has been excavated by the time this stage is half-completed and the larva often move forward on the pollen ball and reach beyond the old feeding groove. This positions the larva in a near vertical plane with the head pointing directly towards the bottom of the cell. Apparently this has no adverse effect on the larva, for a few days later it molts to the final instar while in this inverted position. The larva is very active and if the cell and pollen ball are not carefully prepared, the larva will move to the edge of the pollen ball and occasionally fall from it. This stadium lasts from two to three days at 24 °C. On occasions where fourth instar larvae have fallen from pollen balls and have been replaced immediately, the stadium has lasted as long as nine days.

The first evidence of an impending molt in this instar is the cessation of feeding and the elevation of the anterior third of the body. First the tips of the mandibles are observed in duplicate. Within one hour the head capsule is cast, but it takes another five hours for the exuvia to be shed.

Fifth Instar

The fifth instar larva (Figure 18 G) assumes a definite C-shape attitude with the basal abdominal segments, the broadest part of the body. The head capsule is circular with the diameter through the vertex ranging from 1.40mm to 1.65mm. The mandibular tips are sclerotized and malar dentation is similar to that of the fourth instar. The midlateral surface of the mandible has a single tubercle possessing two setae. Mesally the apical surface of the mandible is concave. The epistomal suture is sclerotized from the anterior mandibular articulation to the anterior tentorial pits where the suture apparently terminates. A definite fold exists between the labrum and the clypeus but no suture is detectable. When the mandibles move, the base of the labrum is folded under the apical end of the clypeus. The lateral apices of the labrum are tuberculate, giving the anterior surface a concave appearance. The maxillae are fleshy, each with an elongate one-segmented palpus. Basally the mesal margins are lightly sclerotized. The labium is a fleshy structure extending between the maxillae. The labial papli are minute. The salivarium is located between two slightly elevated sclerotized lips and appears to extend the distance between the large lateral maxillae.

The antennal papillae are lightly sclerotized and are shorter than they are broad, with three minute but distinct wart-like bumps. Parietal bands are present.

The dorsolateral margins of the meso- and metathorax and first abdominal segment are produced to form fleshy protuberances. Ten distinct pair of lightly sclerotized spiracles are visible, two pair on the thorax and eight on the abdomen.

At 24°C the fifth instar larva takes 2 1/2 to 4 days to consume the remnants of the pollen. It then becomes very active and if the rearing cell is not large enough it may ingest soil and die. In this stage the larva is also cannabalistic. Larva have been observed to pierce the integument and feed on the body fluids of other larva placed adjacent to them. Indeed, some of them will do this even before the pollen is consumed. Almost all fifth instar larva will feed on additional pollen after completing their original store. Some have eaten almost two pollen balls and the volumetric and linear size increase is about 1 1/2 times that of a normal larva. But when they transform to the pre-pupae they are similar in size to pre-pupae that have fed on a single pollen ball. In contrast, larva that have matured on small pollen balls transform to small pre-pupae.

In two or three days the thorax resembles that of the pre-pupae, but the curvature of the posterior portion of the abdomen still gives it a C-shape.

Post Defecating Larva

From two to four days after consuming the pollen ball, the fifth instar larva begins to exude a paste-like material which it smears on the bottom half of the cell.

The venter of the ninth and tenth abdominal segments is transparent and it is possible to see the hind gut with its feces. As defecation begins, the tip of the abdomen is usually located near the bottom of the cell. The abdomen is flexed forward and upward and, as it moves, feces is smeared up the side of the cell as a broad ribbon. As it reaches half-way up the cell wall the feces is usually exhausted, although the abdomen often may be drawn farther up the wall. In other cases, waste may continue to be expelled after the abdomen has stopped. This results in a smear with a thickened tail. After a few minutes, the larva twists its abdomen to one side followed by a similar twist of the thorax, which moves it slightly to the left. Its abdomen is then straightened which causes it to slide back down into the bottom of the cell. This flexing and defecation process is repeated as the larva rotates around the entire cell, covering it with vertical fecal smears. Observations indicate there is a fixed amount of waste for each expulsion. Some smears begin at the bottom of the cell and do not extend as far up the cell wall as those that begin higher up. Within two to four minutes after expulsion new feces can be seen to enter the hind gut, even though it may be as long as one-half to four hours before the next expulsion. In a 24 hour period an average of nine vertical fecal bands are deposited. Usually the larva smears the vertical fecal bands homogeneously over the entire bottom third of the cell.

The body loses its inflated look and the dorsolateral protuberances become more prominent as defecation proceeds. The lateral ridges become very distinct and the body becomes more opaque. After defecation, the larva assumes the quiescent pre-pupal position but periodically contracts into the characteristic C-shape of the mature larva. After three to four days, it transforms permanently into the pre-pupae.

As each smear is expelled, a thin, silk-like thread can be observed extending from the anus of the larva. This is found to be embedded in the entire fecal smear. It is transparent and in most cases difficult to observe because of the presence of feces. One larva which was transferred to a new cell near the termination of defecation had covered the bottom of the cell with a weird formation of these silk-like strands. Their origin and function are unknown.

Prepupa

Nomia melanderi overwinters as a prepupa (Figure 18 H), which can resist fluctuations in temperature and moisture. The prepupa is easily distinguished from the fifth instar larva by the characteristic sharp angle between the thorax and abdomen and the sharper dorsal prominances. The cuticle is an opaque white, in contrast to the more transparent and slightly brownish cuticle of the larva.

There is no development of the prepupa until the late spring sun warms the ground at the brood-cell level (Bohart and Cross, 1955). The first visible signs of the termination of the prepupal diapause consist of a slight softening of the body wall and a less-pronounced angle between the thorax and abdomen. Shedding of the prepupal skin usually takes place in June and July. The pupa (Figure 18-I) require two to three weeks to develop into an adult.

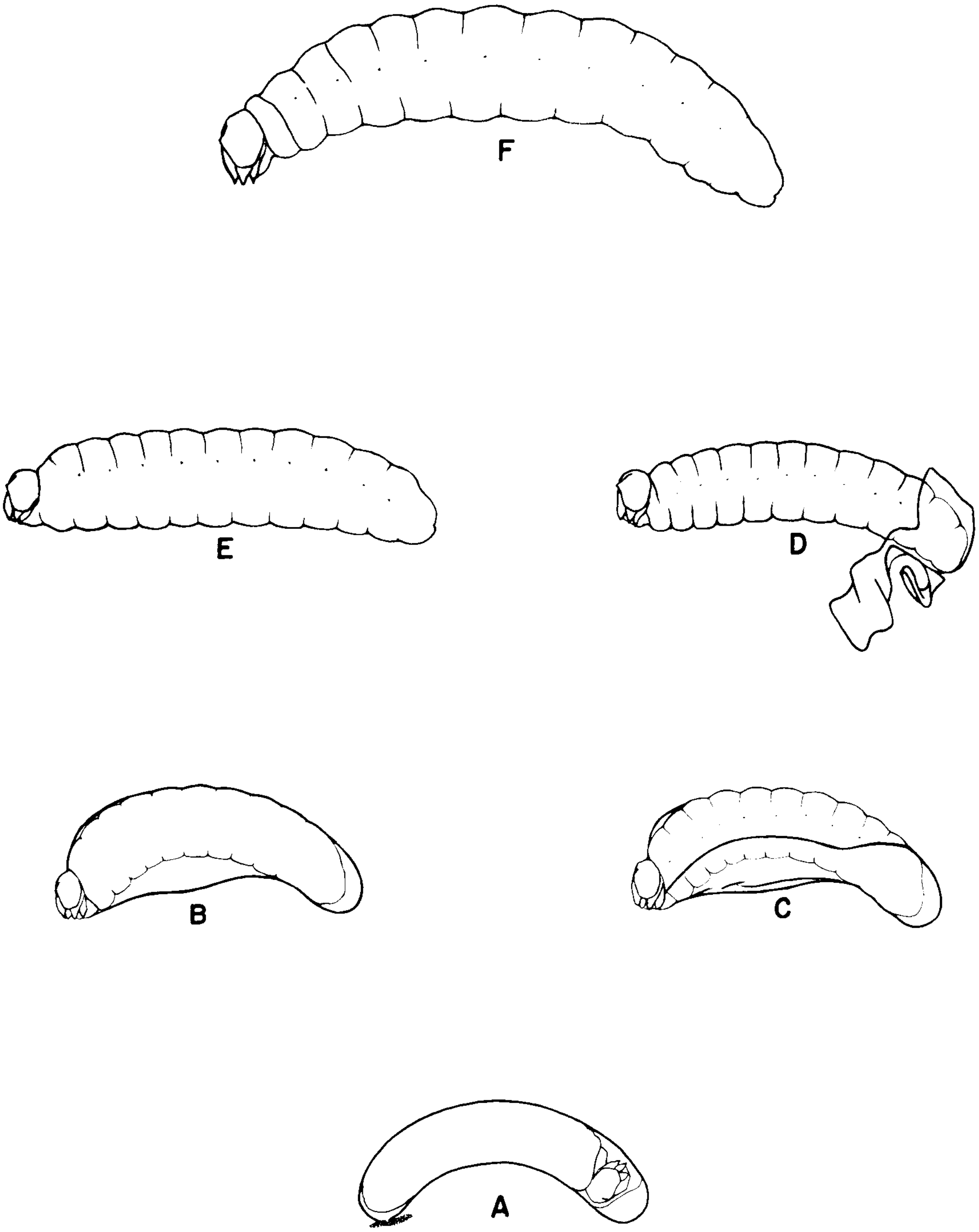


Figure 17. Immature stages of *Nomia melanderi*.

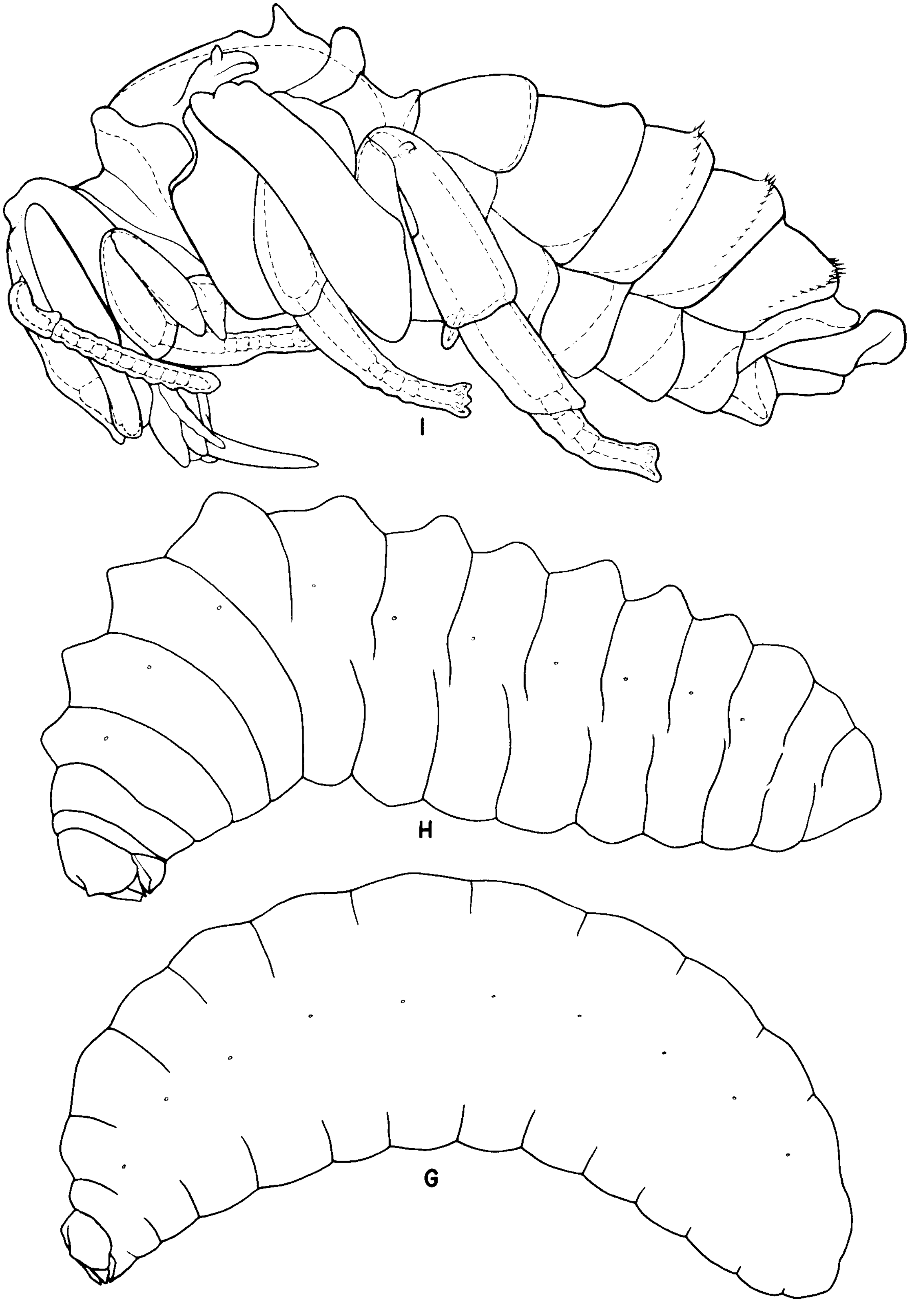


Figure 18. Immature stages of *Nomia melanderi*.

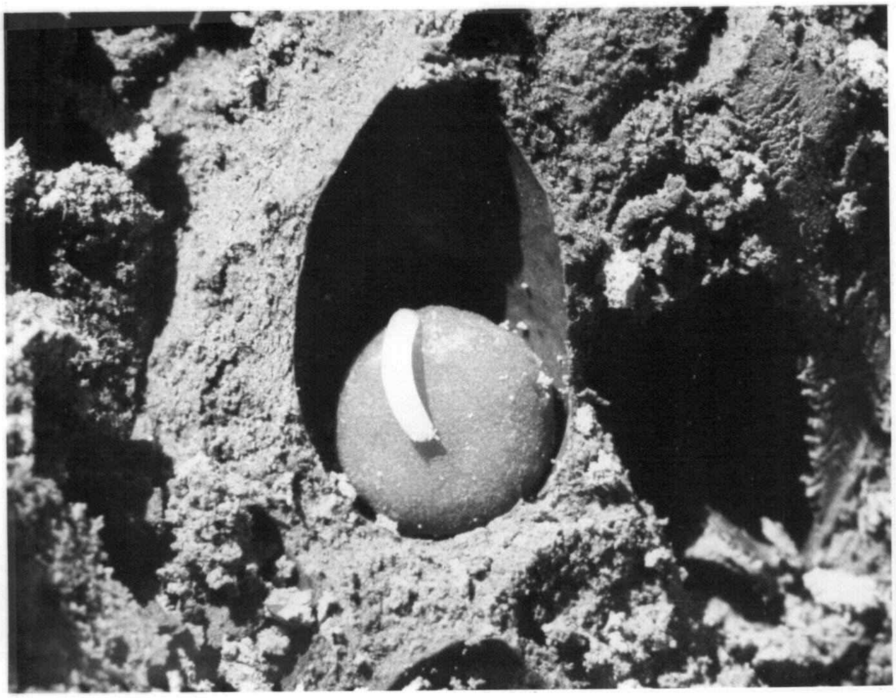


Figure 19. Alkali bee pollen ball and egg.

Figure 20. Second instar larva of the alkali bee.

Table 6. Head capsule diameter measurements of Nomia melanderi.

Date	Temp °C	Time	1	2	3	4	5	6	7	8
July 30	24°	8 P.M.	E	E	E	-	-	-	-	-
July 31	24°	8 A.M.	E	.68	E	-	-	-	-	-
" "	24°	8 P.M.	E	.82	E	-	-	-	-	-
Aug. 1	24°	8 A.M.	.68	.82	.68	-	-	-	-	-
" "	24°	8 P.M.	.68	1.04	.68	-	-	-	-	-
Aug. 2	24°	8 A.M.	.82	1.04	.80	-	-	-	-	E
" "	24°	8 P.M.	.82	1.04	.80	-	-	-	-	E
Aug. 3	24°	8 A.M.	1.04	1.04	.80	-	-	-	-	.74
" "	24°	8 P.M.	1.04	1.25	1.04	E	E	E	E	.88
Aug. 4	24°	8 A.M.	1.04	1.25	1.04	E	.72	E	E	.88
" "	24°	8 P.M.	1.04	1.25	1.04	E	.86	E	E	1.05
Aug. 5	24°	8 A.M.	1.20	1.25	1.27	E	.86	.72	.78	1.05
" "	24°	8 P.M.	1.20	1.25	1.27	E	1.04	.72	.78	1.05
Aug. 6	24°	8 A.M.	1.20	1.52	1.27	E	1.04	.88	.88	1.29
" "	24°	8 P.M.	1.20	1.52	1.27	.70	1.25	1.07	1.04	1.29
Aug. 7	23.5°	8 A.M.	1.20	1.52	1.27	.80	1.25	1.07	1.04	1.29
" "	23.5°	8 P.M.	1.48	1.52	1.56	.80	1.25	1.07	1.27	1.29
Aug. 8	24°	8 A.M.	1.48	1.52	1.56	.99	1.25	1.27	1.27	1.56
" "	24°	8 P.M.	1.48	1.52	1.56	.99	1.25	1.27	1.27	1.56
Aug. 9	25°	8 A.M.	1.48	1.52	1.56	1.20	1.56	1.27	1.27	1.56
" "	25°	8 P.M.	1.48	1.52	1.56	1.20	1.56	1.27	1.27	1.56
Aug. 10	24°	8 A.M.	1.48	1.52+	1.56+	1.20	1.56	1.56	1.56	1.56
" "	24°	8 P.M.	1.48	1.52	1.56	1.20	1.56	1.56	1.56	1.56
Aug. 11	24°	8 A.M.	1.48+	1.52	1.56	1.20	1.56	1.56	1.56	1.56
" "	24°	8 P.M.	1.48	1.52	1.56	1.56	1.56	1.56	1.56	1.56+
Aug. 12	24°	8 A.M.	1.48	1.52	1.56	1.56	1.56	1.56	1.56	1.56
" "	24°	8 P.M.	1.48	1.52*	1.56	1.56	1.56	1.56+	1.56	1.56
Aug. 13	24°	8 A.M.	1.48	1.52	1.56	1.56	1.56	1.56	1.56+	1.56
" "	24°	8 P.M.	1.48	1.52	1.56*	1.56	1.56	1.56	1.56	1.56
Aug. 14	24°	8 A.M.	1.48	1.52	1.56	1.56	1.56	1.56	1.56	1.56*
" "	24°	8 P.M.	1.48	1.52	1.56	1.56	1.56+	1.56	1.56	1.56
Aug. 15	24°	8 A.M.	1.48	PP	1.56	1.56	1.56	1.56	1.56	1.56
" "	24°	8 P.M.	1.48*		1.56	1.56	1.56	1.56*	1.56	1.56
Aug. 16	23.5°	8 A.M.	1.48		1.56	1.56	1.56	1.56	1.56	1.56
" "	24°	8 P.M.	1.48		PP	1.56	1.56	1.56	1.56	1.56
Aug. 17	24°	8 A.M.	1.48			1.56	1.56	1.56	1.56	1.56
" "	24°	8 P.M.	PP			D	1.56	PP	1.56*	PP
Aug. 18	24°	8 A.M.					1.56*		1.56	
" "	24°	8 P.M.					1.56		1.56	
Aug. 19	24°	8 A.M.					1.56		1.56	
" "	24°	8 P.M.					1.56		PP	
Aug. 20	23°	8 A.M.					1.56			
" "	24°	8 P.M.					1.56			
Aug. 21	23°	8 A.M.					PP			

+	Pollen Gone
*	Defecating
PP	Prepupae

These measurements are in millimeters.

Nest Orientation

Landmarks

One of the most interesting features of the alkali bee is the apparent ease with which the female distinguishes its nest entrance from the hundreds of nearby entrances. Females can be observed returning to their nests, usually laden with pollen, and if the nesting surface is undisturbed they move directly to their burrow and enter without any hesitation. It is rare indeed, under the normal circumstances, to see a disoriented bee. If the surface has been disturbed in some manner, confusion results, and the bee may be observed searching about for its nest. It has also been observed that female alkali bees favor excavating their burrows near or under small dirt clods or other debris located on the nesting surface, apparently to avoid the hot afternoon sun. In the presence of such markers the bees leave from, and return directly to, the burrow with minimal orientation flight. These observations led to the hypothesis that nest orientation must be strongly influenced by visual landmarks.

It was deemed possible to determine if the bees were actually using these subtle objects on which to orient to their nest by conditioning them to small markers at the burrow entrance and displacing these while the bee was in flight.

A group of 15 bees were marked individually with different colored paints. Small soil clods and small sticks were placed directly adjacent to the nest opening and the bees were left undisturbed for the next week. After the bees had been conditioned to the marker markers the following experiments were conducted:

Experiment I. This nest had a small dirt clod approximately one half inch high, one inch wide and two inches long situated directly north of the nest opening. After the female had departed from the nest to collect pollen, the dirt clod was moved four inches east of the burrow entrance. On her return, the bee flew to the south side of the displaced dirt clod and began searching for her nest. After searching on the south side for two and a half minutes, she flew up and landed on the dirt clod, walked about and flew away. Six minutes later she returned again to the south side of the dirt clod and dug for one and a half minutes before taking flight. After four minutes the bee returned to the south side for a third time and began searching for its nest. Thirty-five seconds later the bee crawled over the dirt clod and then flew to another dirt clod much smaller in size, located 10 inches to the east. It landed on the dirt clod but took flight without further searching.

The dirt clod was returned to its original position and approximately eight minutes later the bee returned, landed on the south side, and immediately entered its nest.

This same experiment was repeated eight times in four days using the same bee and relocating the clod twice each to the north, south, east and west. The bee always returned to the marker first and searched for its nest. Periodically, it would fly away only to return to the marker to resume its search.

The experiment was repeated using five different bees, and in each of the 40 trials the bee first returned to the marker.

In similar experiments, but with the marker moved eight inches away, the bees returned to the marker first 24 out of 40 times. The other 16 times they returned to their nest.

Experiment II. This experiment was conducted in the following manner: a small stick 3/4 inch in diameter and two inches long was placed adjacent to the north side of the nest opening, and a yellow spot was painted on the side of the stick facing the nest entrance. After seven days the stick was moved four inches to the north. The bee returned directly to the marker and started digging in the soil adjacent to the yellow mark. This behavior pattern was repeated in 16 tests using four different bees, all of which returned directly to the yellow area to search.

It was observed that when a marker with an irregularity such as a bump or a depression, or in the case of the sticks, a small knot, was placed adjacent to the nest entrance and then removed, the bee returned to that part of the marker to search for its nest, except when the relative compass position of the irregularity was changed.

For example, when a stick on the north side of a nest entrance was moved four inches to the north and the stick rotated so the yellow spot which normally faced south was now facing north, the bee would first return to the south side and search for its nest. If, in searching, the bee accidently found the yellow spot it showed no apparent response.

A second set of experiments was conducted to determine what effect moving the nest location would have on orientation of the bees. A metal cylinder 12 inches long and six inches in diameter as buried to ground level in a bee bed. Four evenly spaced holes were punched near the periphery of the container at approximately the four cardinal compass points. After two days bees were nesting in all four holes, but to avoid confusion three of the bees were eliminated. A soil clod approximately 1/2 inch high, 1 inch wide, and 1 inch long was placed adjacent to the east burrow and on its east side.

Experiment III. The bee was conditioned to the marker for one week and in her absence the cylinder was rotated 45° to the right. This moved the nest entrance approximately two inches and placed the soil clod southeast of the nest entrance. The bee returned directly to the dirt clod and entered its nest. Next the cylinder was rotated 90° to the right, moving the nest entrance four inches. The dirt clod was now directly south of the nest entrance. Again the bee returned to the dirt clod and entered its nest. The cylinder was rotated 180°, placing the nest entrance six inches directly west of its original position with the dirt clod on the west side of the entrance. The bee returned, flew one circular pattern over the original site, and lit near the nest entrance. She entered the nest, but immediately backed out, searched the immediate area, then took flight only to land again and re-enter the nest. Again she backed out and this time flew away. The bee returned to the original site and started digging but after 25 seconds flew away. She then returned to the soil clod, entered the nest and remained in it.

This experiment was repeated four times using the same bee, and except for three of the 180° turns, the bees were able to locate their nests.

These experiments indicate that the alkali bee orients itself to its nest primarily by visual landmarks.

During the above experiments a bee was observed searching for its nest beside a 12" x 4" x 4" box used to carry paint brushes, forcepts, etc. , used in these experiments. As the bee was pollen-laden and appeared to be using the box for orientation, it was marked. While attending to other work, the box was moved about two feet away and it was noted that the marked bee was searching for its nest at the side of the box in its new location. The box was moved back to the original position and almost immediately the marked bee was observed searching for its nest at its side. The box was then moved four feet away and again the bee was observed at the side searching for its nest. In returning it to its original position, the bee was observed following it in flight. The fact that bees become disoriented when small soil clods, etc. were moved six inches or more in the preceeding experiments, yet were able to orient to the box four feet away, is apparently a result of size.

Form Perception. Preliminary experiments were undertaken to determine the ability of the alkali bee to distinguish among various geometric figures. Experimental design was based upon Hertz (1939) conclusions that form perception in living bees was related to the degree of "brokeness" of the pattern.

Experiments in form perception with the alkali bee were conducted in the following manner: black oil cloth was cut into the following forms, each with an approximate diameter or width of 1 1/2 inches; circle, diamond, square, triangle, X, Y, and * patterns. Each pattern was glued over a white 1 1/2 inch square of oil cloth, a hold punched in the center, and then placed over the bee nest with the hole centered on the nest entrance. All other nesting bees within a six inch radius were eliminated to reduce confusion.

Experiment IV. After a bee had been conditioned to an X over its nest entrance for five days, the marker was interchanged with a diamond pattern two inches away. The bee upon returning landed on the diamond pattern and entered its nest. In other cases the X pattern was interchanged with the circle, the triangle, the square and the * pattern but in each case the bee returned and entered its nest without hesitation. Regardless of the pattern to which the bee was conditioned, when it was interchanged with other patterns the bee always returned directly to her nest rather than to the displaced marker. If the patterns were not interchanged, but the one to which the bee was conditioned was moved two inches to any side of the burrow, the bee always returned to the site of the pattern. Originally it was felt that the alkali bee was unable to distinguish these types of geometric forms, but upon further deliberation it seems more likely that the bees may have oriented on the white background rather than the patterns. Form orientation will need further study before any conclusions can be reached, but it appears to be a potentially fruitful area for research.

Color Identification

During the summers of 1960, 1961, 1962 and 1964, preliminary experiments were conducted in an effort to determine color perception in alkali bees.

In 1960, art paper of nine colors was cut into one inch squares and a hole punched in the center of each square. A green square was then placed over a bee burrow opening. The other eight -- red, blue, purple, yellow, white, black, gray and orange -- were placed adjacent to the green square, forming a checkerboard pattern similar to that in Figure 21. The pattern was left undisturbed on the bed for five days in order to determine if the bee could become conditioned to a particular colored square. On the sixth day, the green square was interchanged with a yellow square adjacent to it while the bee was foraging. Upon returning the bee went directly to the green square and started searching for its nest. After about 30 seconds the bee flew away and the squares were returned to their original positions. The bee returned directly to the green square and entered its nest. Similar results were obtained when bees were conditioned to yellow, blue, and black.

Although the bees were showing a response, the use of the art paper had to be abandoned because the colors faded rapidly in the bright sun.

In 1961, colored aluminum foil paper was substituted for the art paper, as it could be left on the bee bed for several days with no apparent fading. A test similar to that outlined above was then established. After five days the squares were interchanged as in the previous experiment. The bees usually returned to their nests without any confusion, regardless of the color that covered the burrow. The only color providing a positive response was yellow and this was not consistent. When a yellow square over the nest was interchanged with a blue square directly adjacent to it, the bees returned to the yellow square first three of 12 times; the other nine times they returned to the blue square over the nest and entered with no apparent confusion. It was observed that the metallic colors were very reflective and the reflected portion of the spectrum could be affecting the bees' orientation.

In 1961, 1962, and 1964, oil cloth was substituted for the foil paper. This largely eliminated reflection and the oil cloth was very resistent to fading. The colors used were identified in the Rheinhold Color Atlas as follows:

Black - 5H2
Blue - 21A8
Gray - C1, D1, E1, F1
Green - 26C8
Orange - 7A8
Purple - 17A8
Red 10B8
White - A1
Yellow - 2A8

The oil cloth was cut into one inch squares and a 5/16 inch diameter hole punched in the center of each. In order to test each color, the appropriate square was placed over the nest with the hole corresponding to the nest entrance. Insect pins were used to hold the square in position on the bee bed.

In the process of conducting each color test, the squares were arranged in appropriate form, and then left undisturbed for five days to allow the bee to become conditioned to them. After five days, while the bee was foraging, colored squares were interchanged or rearranged as detailed below:

Experiment 1. A bee was conditioned to a yellow square over its nest entrance, and the only other colored square was a red one located three inches to the west. There were no other bees within a three inch radius of the test bee. While the bee was foraging the two squares were interchanged. The bee returned and flew directly to the yellow square, landed, and started digging in the center hole of the square but after six seconds flew away. While the bee was away the yellow square was moved three inches to the east of the nest. Again the bee returned and landed on the yellow square, searched for its nest for approximately 14 seconds, and after walking around the edge, flew away. The yellow and red squares were then returned to their original positions and the bee, upon returning, landed on the yellow square and immediately entered its burrow. This same experiment was repeated five times and each time the bee returned to the yellow square.

Experiment 2. This experiment was essentially the same as number one except that the bee was conditioned to a green square over its nest entrance, with a yellow square located three inches to the west of the nest. While the bee was foraging, the green and yellow squares were interchanged. Upon returning, the bee flew to the green square, hovering over it for three to four seconds, then flew away. In three to four minutes the bee returned a second time, hovered over the green square for one to two seconds, then landed and started searching for its nest, digging slightly in the center of the square, and then walking around its edges. After searching for one and a half minutes the bee flew away.

The bee returned after six minutes to the green square, landed, and again began searching for its nest. She searched for three minutes and then flew away, whereupon the green square was returned to its original position. The bee returned after eight minutes and immediately landed on the green square and entered its nest. This experiment was repeated five times and in each instance the bee returned directly to the green square in search of her burrow. In four of the five experiments the bee showed no hesitation in landing on the green square, but in one case the bee hovered over the red square before landing on the green.

Experiment 3. This experiment was conducted similar to experiments 1 and 2. A bee was conditioned to a blue square over its nest. While the bee was foraging, the blue square was interchanged with a white square three inches to the west. The bee returned and landed on the blue square, walked around the edges, then walked to the center hole where she started to dig. After 30 seconds she walked around, then returned to dig again, only to leave in 60 seconds. Eight minutes later the bee returned to the blue square and spent approximately 60 seconds searching for her nest, after which she again flew away. Ten minutes later the bee returned to the blue square and spent two and a half minutes searching for its nest. She dug for 10-15 seconds, then stopped and walked around, only to return and dig again. On her departure, the squares were placed in their original positions. Upon her return, she immediately landed on the blue square and entered her nest.

This experiment was repeated five times and in each case the bee returned to the blue square to search for its nest.

Experiment 4. A fourth bee was conditioned to a white square over its nest. While the bee was foraging, the white square was interchanged with a green square located three inches away. The bee returned to the white square, walked around the edges, moved to the center hole and began to dig. She walked around for 80 seconds, returned to dig, then flew away after digging another 40 seconds. The bee then returned in five minutes and landed on the white square and spent approximately 90 seconds searching for her nest before taking to flight. The squares were then returned to the original position and the bee, upon returning, landed on the white square and entered her nest. This same experiment was repeated five times with identical results.

The previous experiments were conducted exchanging only two colored squares. To determine what effect a variety of colored squares would have on behavior, a three inch square checkerboard composed of nine different colored squares was arranged over the nest entrance.

The following abbreviations are used for various colors:

Blk - black
Bl - blue
Gr - gray
G - green
Or - orange
P - purple
R - red
W - white
Y - yellow

<u>Experiment 5</u>. In this experiment the colors were arranged on the checkerboard as indicated below and the bee was conditioned to the white square over its nest:

Blk	W	Y
G	R	P
Or	Bl	Gr

While the bee was foraging, the white square was interchanged with the green. Upon returning, the bee landed on the purple square first, but immediately flew to the white square and landed. She walked around and within four seconds started to dig at its center. Twenty seconds after landing on the white square she flew away. Upon returning a second time, the bee landed on the white square and searched for her nest. After searching for 68 seconds she flew away. The squares were returned to their original positions, and on the third return the bee landed on the purple square, walked to one side and then flew to the white square and entered her nest.

The results of these interchanges are summarized in the following table:

Conditioned color	Exchanged color	Number of 1st visits to conditioned color	Number of 1st visits to exchange colors	Number of 1st visits to other colors
White	Green	5	1	2
White	Black	6	1	1
White	Red	4	0	0
White	Purple	4	0	0
White	Yellow	3	1	0

A total of 28 trials were recorded. In 22 of the trials the bee returned first to the conditioned white color.

In three of the trials, once each with the green, black and yellow, the bee returned to the exchanged color and entered its nest. In three other trials, the bee apparently became disoriented and returned to a color other than the conditioned or exchanged color. In two cases, the bee returned first to other colors but, without leaving the vicinity of the nest, flew to the conditioned color.

Experiment 6. A bee was conditioned to a red square over its nest entrance with other colors arranged as follows:

Blk	Y	Or
P	R	W
Bl	G	Gr

While the bee was foraging, the red and white squares were interchanged. The bee returned to the white square, hovered about it for two or three seconds, then flew away. Approximately six minutes later the bee returned, hovered over the white square, landed, and entered her nest. The experiment was repeated and again the bee returned to and landed on the white square.

The red square was subsequently interchanged with the purple square while the bee was foraging. Upon her return, the bee flew to the red square but did not land. The bee then flew to the purple square, hovered above it for two to three seconds, and flew away. Upon returning, she flew to the red square, landed, and walked around the square, only to leave in 40 seconds. She returned to the purple square, landed, and searched for the burrow, which she found and entered in 30 seconds. The experiment was repeated and the bee returned to the red square first but did not land. She then returned and landed on the green square, searched for her burrow for 60 seconds, and flew away. The red square was removed to its original location. The bee returned directly to it and entered her nest.

Experiment 6 was repeated 16 times and the data are summarized in the following table:

Conditioned color	Exchanged color	Number of 1st visits to conditioned color	Number of 1st visits to exchange colors	Number of 1st visits to other colors
Red	White	2	0	0
Red	Purple	2	1	1
Red	Orange	0	2	0
Red	Green	0	1	1
Red	Yellow	0	0	2
Red	Black	1	1	0
Red	Blue	1	1	0

The bee returned to the red square first six out of 16 times, twice with the white-red interchange, twice with the purple-red interchange and once each with the blue and black square interchanges. On three other occasions the bee flew over the red square first but landed on another color.

<u>Experiment 7</u>. A bee was conditioned to a yellow square in the center of the checkerboard:

Or	W	Blk
Bl	Y	R
P	G	Gr

While the bee was foraging, the yellow square was interchanged with the green square. The bee returned directly to the yellow square and landed. After searching for its nest for approximately 50 seconds, it flew away, and the yellow square was returned to its original location. The bee returned, landed on the yellow square, and entered its nest. This same experiment was conducted four times each on the interchange of blue, green, white and red squares with yellow. In all 16 trials the bee returned and landed on the yellow square first.

<u>Experiment 8</u>. In this experiment a bee was conditioned to a blue square over its nest with other colors arranged as follows:

Blk	Gr	Or
P	Bl	W
Y	R	G

On eight different occasions, while the bee was away foraging, the blue square was interchanged, two times each with the green, yellow, red, and white squares. In six of the eight observations, the bee returned to and landed first on the blue square. Once, when the blue square was interchanged with the red and yellow squares, the bee returned and landed on these colors first.

<u>Experiment 9</u>. A bee was conditioned to a green square over its nest entrance. The checkerboard was as follows:

Or	Blk	Gr
R	G	W
Bl	Y	P

On eight different occasions, while the bee was foraging, the green square was interchanged, twice each with the red, white, blue, and yellow squares. In all eight cases the bee returned to and landed first on the green square.

To determine what effect the permanent movement of the conditioned color would have on the behavior of the alkali bee the following experiment was conducted:

Four bees were conditioned for five days to yellow squares over their nest entrances. While the bees were foraging, the yellow squares were interchanged with green ones two inches away. All the bees returned first to the yellow squares to search for their nest openings. After searching from one and a half to three minutes they would fly away, but would return after eight to 19 minutes to resume the search. One hour later one bee was observed searching four feet away from the nesting site, in an area where there were no colored squares. Two and a half hours later, one bee had located its nest, but the others had disappeared.

Observations were terminated after three and a half hours, at which time only one bee had found its burrow. Upon checking the nesting area the next morning, it was observed that two other bees had relocated their nests, but the fourth was not seen again.

These experiments suggest that the alkali bees can distinguish among yellow, green, blue, white, and sometimes red, but do not prove that they have a color sense, or color perception. The ability to distinguish among the colors used may reflect upon their ability to distinguish among different shades of gray. Thus the following experiment was conducted to determine if the alkali bees can truly perceive colors:

Experiment A. A bee was conditioned to a yellow square over its nest. This square was then surrounded by eight squares of shades of gray grading from off-white to near black. While the bee was foraging, the yellow square was interchanged twice with each of the gray squares, a total of 16 interchanges. The bee returned to the yellow square first 13 out of the 16 times. She did not return to the yellow square first when the yellow square was interchanged with the corner gray squares. When these same gray squares were placed in locations other than the corners and then interchanged with the yellow square, the bee returned to the yellow.

The test was repeated using red, blue, green, and white squares in the gray checkerboard. A total of eight interchanges were made with each colored square. Bees returned to the blue square first all eight times, regardless of its locations; to the green square first seven out of eight times; and to the white square first eight out of eight times. Bees returned to the red square first three out of eight times, landing on the gray squares over the nest four times, and on a corner square the fifth.

Stephen[3] has pointed out that a position effect has been demonstrated in other bees. Often, with corner positions, the location becomes dominant over color for the bee orienting to her nest. It may be that these four cases above are a demonstration of that "corner effect".

While these experiments suggest that alkali bees do have a color sense, it must be stressed that these experiments were of an exploratory type and need a great deal of refinement and duplication before any conclusions can be reached concerning color perception.

Color and Nest Position. A second set of experiments was conducted to see what effect the actual movement of the nest would have on orientation. This was accomplished by using a six inch diameter cylinder as indicated in the methods (Figure 6). At the time of bee emergence, small holes were punched in the soil inside the cylinder area to entice new females to nest in this area. After a female was established in each cylinder, a colored square described in the previous section was placed over the burrow entrance

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[3] W. P. Stephen. Personal communication.

and left undisturbed for one week.

Experiment I. A bee was conditioned to a yellow square over its nest entrance and no other colored squares were used in this experiment. While the bee was foraging, the cylinder was rotated approximately one quarter of a turn, which moved the nest entrance with its square approximately three inches. Upon returning, the bee approached the original position of her burrow but with little hesitation flew to the colored square and entered her nest. The same results were obtained using blue, white, red, and green squares.

Experiment II. This experiment was a repetition of Experiment I except that after the cylinder had been rotated one quarter of a turn, the colored square was removed from the nest entrance and placed back at the original nest location. In all 10 cases, twice each with the blue, yellow, green, red, and white squares, the bees returned to the colored squares and began searching for their nests. If the cylinder was not turned back to its original location in eight to 15 minutes, the bees started searching outside the cylinder. Periodically, they returned to the cylinder and started digging through the hole in the colored square. One bee excavated to a depth of three inches but did not remain in the burrow past the next morning. In one set of experiments, the cylinder was not returned to its original position and all 10 bees were lost.

Experiment III. A bee was conditioned to a green square over its nest entrance. While the bee was foraging, the cylinder was turned one half turn, placing the nest entrance with the square in place six inches away from its original location. Five different times the bees returned to the original nest location and began searching. This experiment was repeated twice with each of the red, white, yellow, and blue squares. In all trials the bees first landed and searched at the original burrow site. On three occasions, twice with the yellow square and once with the blue square, the bees eventually found their nests but after entering they came back out with their pollen and did not accept it. After eight to 15 minutes they departed and the cylinder was returned to the original position. All bees, upon returning, readily reaccepted their nests.

von Frisch has demonstrated that honey bees are red blind. The results herein reported indicate that there may be a variability in the ability of different alkali bees to perceive red. Some apparently have the ability to partially distinguish this color, whereas others have none. However, these experiments indicate that alkali bees can perceive yellow, green, blue, and white, although more careful studies must be conducted on the latter.

Hertz (1930) found that some paper absorbed ultraviolet rays and other reflected it. von Frisch (1950) stated that when ultraviolet is removed the remaining light is no longer white to the bees, but has a color complimentary to ultraviolet, probably blue-green.

Lotmar (as cited in von Frisch, 1958) however, demonstrated in his experiments with poppies that bees can recognize the reflected ultraviolet light, thus the absorbency and reflectivity of ultraviolet light by white or other colors can modify the visual stimulus of the bee in a manner quite different to that perceived by man. What may be perceived as "white" by man may appear as "white", "ultraviolet" or "blue-green" to a bee. Careful spectral analysis must be undertaken on this aspect of the problem.

Flight Activity

Temperature and Light

It is not possible to correlate the beginning and end of foraging for the day with any single factor of the environment, since several factors, such as light intensity, temperature, and humidity are all closely interrelated (Free and Butler, 1959). However, Free and Butler (1959) did conclude that bumblebees start foraging in the morning at a light intensity considerably higher than that at which they will continue foraging in the evening. They also found that both high and low temperatures can limit foraging.

In solitary bees the effects of light, temperature, and humidity are even more pronounced, for they will usually cease activity while bumblebees are still foraging. It was observed that alkali bees

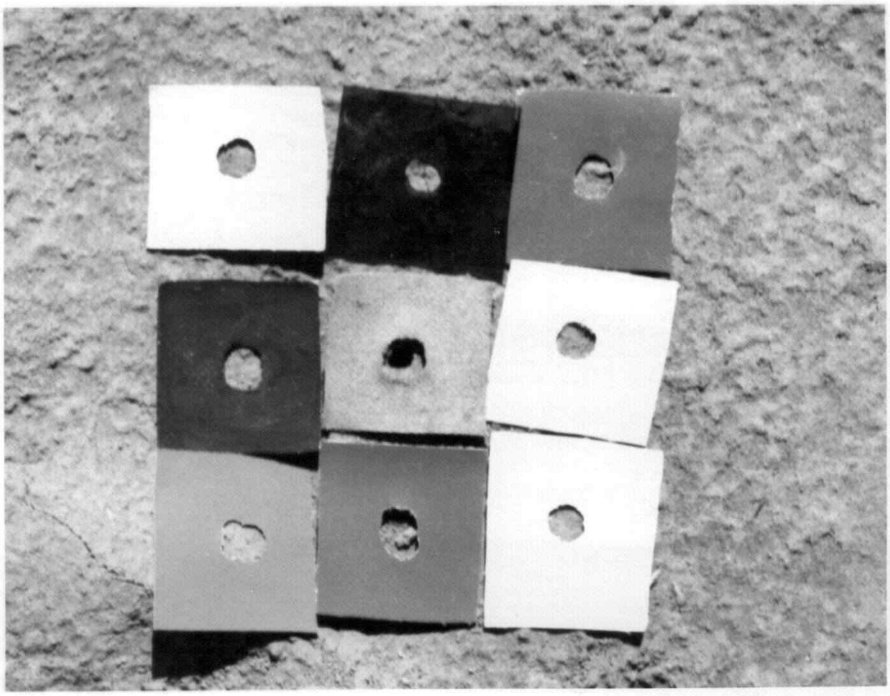

Figure 21. Colored checkerboard for alkali bee orientation study.

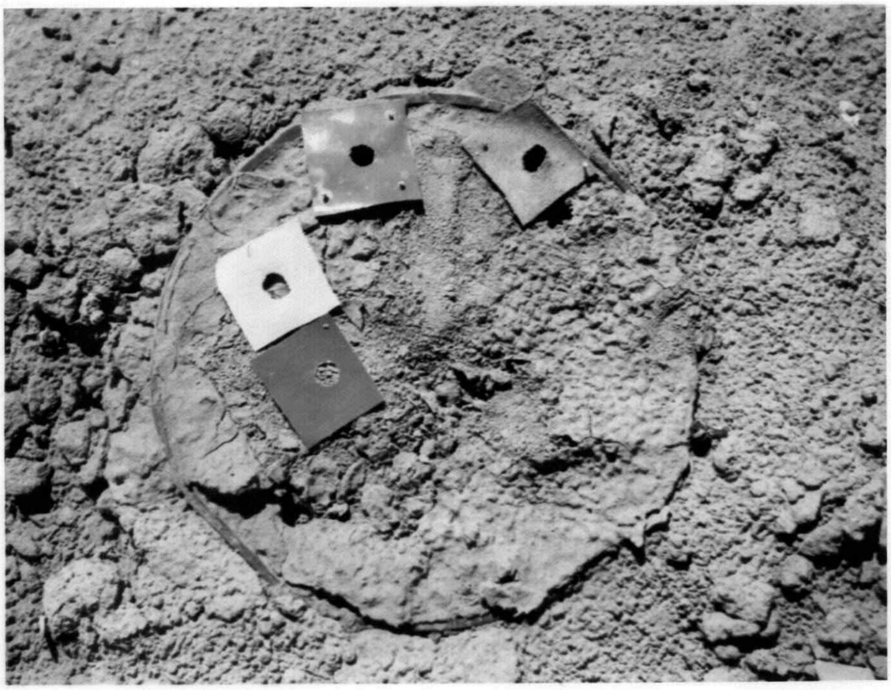

Figure 22. Cylinder *in situ*, with nests of bees within its perimeter.

began foraging in the morning at very high light intensities and did not terminate activity until almost dark. To determine what effect light and temperature had on flight activity in the alkali bee the following data were collected.

During the summer of 1965, two four-foot-square artificial alkali bee beds were placed side by side adjacent to an alfalfa field at Boardman, Oregon. During July, on several cloudy days, the bees did not emerge to forage. July 20th was overcast and there was no emergence by 10:30 A.M., at which time the light intensity was 320 foot-candles at the soil surface and the air temperature was 70.5 °F. At a depth of one inch, the temperature was 73 °F and at seven inches the temperature was 81 °F. Flood lights were installed 40 inches above the bed on the south side and positioned to shine on one of the four-foot-square beds. A plywood partition was placed between the two boxes to insure that one box would receive no light from the supplementary source. The lights were turned on at 10:40 A.M., which raised the light level at the soil surface to 1,350 foot-candles. Within 15 minutes, bees had emerged and started to fly. At 11:10 A.M. the air temperature at the soil surface under the lights had risen to 85 °F, and at one inch was 74.5 °F. The lights were turned off at 11:45 A.M. and the bees landed, crawled about on the soil surface, and re-entered their burrows. While the lights were on the bees flew short distances but returned to the illuminated area within seconds.

No foraging occurred and the major flight was back and forth across the illuminated area of the bee bed. No flight was observed on the adjacent bed.

The flood lights were then placed over the second bed and a similar result was obtained. There was flight over the bed as long as the lights were on, but inactivity when they were turned off. By noon of the same day, the air temperatures had increased to 74 °F and the temperature at the one inch depth was 77 °F on bed I. However, the soil temperature at seven inches dropped from 81° to 78 °F. The light intensity also had dropped to 295 foot-candles and a very light rain was falling. The lights were turned on over bed I, and 10 minutes afterward some of the bees emerged and began crawling around on the bed. Two minutes after emergence a few started flying, but many remained on the soil surface. The light reading at the soil surface during flight was 1370 foot-candles and the air temperature was 84 °F.

In the Boardman area bees were observed in morning flight at light intensities of 320 foot-candles and with the air temperature of 78 °F. This suggests that the temperature rather than illumination was responsible for the initiation of flight in the preceeding experiments.

In an attempt to determine the light and temperature thresholds for daily emergence of the alkali bee, data were collected at the onset of morning flight, and during the termination of flight in the evenings. The data were collected at two sites, one in Boardman, Oregon, with a limited number of female bees, and the other on a very densely populated bed near Ontario, Oregon.

At Boardman, morning emergence closely correlated with air temperature (Table 7). Flight began on seven of the eight days during which records were kept when the air temperature was between 78°F and 81.5°F. On August 2nd, flight did not begin until the air temperature had reached 92°F, but it had rained the previous night and the bed was wet.

Temperature at the one inch level also showed a very close correlation with emergence. On five of the days, the bees emerged when the temperature at the one inch level was between 80°F and 81°F. On a day with a 20 to 25 mph wind, emergence did not occur until the temperature at the one inch level had reached 85°F, indicating that a third environmental factor had become limiting. No explanation is given for the 89.3°F temperature recorded at the one inch level on July 28th. This was a bright, clear, relatively calm day, and temperature and light intensity exceeded levels recorded on other days when emergence began.

Temperatures are more uniform at the four to seven inch levels, and a good correlation between temperature at this level and emergence can be obtained. On mornings when the air temperatures are near 65 °F, bees will periodically come to the upper levels of the nest, remain at the burrow entrance for a short time, and then return to the lower levels. Similar behavior can be observed on heavily overcast days. Bees have been observed to come to the burrow entrance when the light intensity was below 210 foot-candles, but did not take flight even though the air temperature was above 74 °F. On a day when the temperature reached 78 °F and the light intensity was 250 foot-candles, some bees took to flight but activity was less than 30 percent of normal.

Light readings made at the soil surface at the peak of morning emergence in the Boardman area ranged from 320 to 1050 foot-candles. The range in light intensities in itself is not considered significant for all are considerably above the intensities recorded at the time of flight termination.

Air temperatures recorded at flight termination on July 28th through August 8th were considerably higher than temperatures at emergence, ranging from a low of 82 °F to a high of 87.5 °F (Table 7). Temperatures at one, four, and six inches also exceeded those recorded at the time of initiation of morning flight. It appears that some factor other than temperature must control flight termination. The light intensities recorded at the termination of flight appear quite uniform, usually ranging from 105 to 135 foot-candles. Data and observations suggest that light levels of this range are responsible for the cessation of flight activity. On August 2nd and August 3rd, light intensities of 230 foot-candles were recorded at the termination of flight, but other climatic conditions are considered to have been limiting. On August 2nd, it had rained and a 10 mph wind was blowing, and on the 3rd a 30 mph wind was blowing. It is assumed that the wind and light rain resulted in the termination of flight at light intensities above the usual threshold level.

Data collected in Ontario, Oregon verify the above conclusions. The first morning flight occurred at air temperatures between 69°F and 70°F, and light intensities of 225 foot-candles to 230 foot-candles at the soil surface. The air temperature at 50 percent activity was 78°F on August 6th, but to only 70°F on August 7th, and the light intensities at 50 percent activity varied from 275 foot-candles to 320 foot-candles.

Soil temperatures, on the other hand, did not vary appreciably. Flight began when temperature was 74°F at the one inch level; 73.5°F to 75°F at the four inch level; and 75°F at the six inch level. The data show that on these days flight terminated at temperatures above those recorded at the initiation of flight. Air temperature at termination ranged between 69°F to 76°F, and that at the six inch level varied between 81°F to 88°F. The light intensities at flight cessation were 29 foot-candles on one day and 36 and 43 foot-candles on the others.

These data were based on about 95 percent termination, thus, there were still a few bees flying even after it became too dark to see any flight. Although the actual temperature and light intensities recorded for initiation and cessation of flight at Boardman and Ontario differed, the same correlations are evident.

Almost without exception, flight terminates at temperatures considerably above those recorded at the initiation of flight, sometimes by as much as 17°F. However, light intensities are much lower than those present at initiation of flight, a few bees in Ontario were flying at intensities of 29 foot-candles. It was noted that flight pattern changed with decreasing light intensities of 100 foot-candles or below. Flight was restricted to within a height of three feet above the ground. As it approached 50 foot-candles, flight was usually no higher than one foot.

It is apparent that initiation of morning flight is usually temperature limited, but that the termination of flight in the evening is light-limited. The light intensity at the initiation of morning flight was always above 200 foot-candles, but it is believed that bees would have flown at a lower light intensity had temperatures been higher.

Temperatures near 65°F at the soil surface will initiate the first observable sign of bee activity. The bees come to the upper one half inch of the burrow and remain there for 15 to 40 seconds, after which they return to the lower part of the burrow. The bees are probably always active at the cell level where the soil temperature is relatively stable.

Table 7. Temperature and light thresholds for the alkali bee. Boardman, Oregon, 1965.

	Morning	Evening
July 28		
Air	81.5 °F	87.5 °F
1"	89.3 °F	102 °F
4"	82 °F	96 °F
6"	80 °F	88 °F
Light	1050 f.c.	130 f.c.
July 29		
Air	81 °F	85 °F
1"	80 °F	95 °F
4"	79 °F	92 °F
6"	80 °F	86 °F
Light	400 f.c.	120 f.c.
July 30		
Air	79.5 °F	82 °F
1"	80 °F	97 °F
4"	77 °F	92.5 °F
6"	79 °F	87 °F
Light	320 f.c.	126 f.c.
July 31		
Air	78 °F	85 °F
1"	80 °F	98 °F
4"	78 °F	94 °F
6"	79 °F	87 °F
Light	320 f.c.	105 f.c.
Aug. 1		
Air		87 °F
1"		100 °F
4"		94.2 °F
6"		87.5 °F
Light		120 f.c.

Table 7. (continued)

Aug. 2	Morning	Evening
Air	92 °F	87 °F
1"	80 °F	95 °F
4"	83 °F	90 °F
6"	83 °F	86 °F
Light	880 f. c.	230 f. c.
Aug. 3		
Air	78 °F	87 °F
1"	81 °F	96 °F
4"	77 °F	92 °F
6"	78.5 °F	87 °F
Light	320 f. c.	230 f. c.
Aug. 4		
Air	78 °F	87 °F
1"	85 °F	97 °F
4"	76 °F	91 °F
6"	77 °F	85 °F
Light	440 f. c.	135 f. c.

Table 8. Temperature and light thresholds for the alkali bee. Ontario, Oregon, 1965.

	Morning		Evening	
	1st Flight	50% Flight	50%	90%
Aug. 5				
Air			77 °F	69 °F
1"			90 °F	87 °F
4"			89 °F	89 °F
6"			89 °F	89 °F
Light			80 f. c.	30 f. c.
Aug. 6				
Air	70 °F	78 °F	76 °F	76 °F
1"	74 °F	75 °F	90 °F	89 °F
4"	75 °F	75 °F	89 °F	91 °F
6"	76 °F	76 °F	89 °F	88 °F
Light	200 f. c.	275 f. c.	95 f. c.	43 f. c.
Aug. 7				
Air	69 °F	79 °F	76 °F	76 °F
1"	74 °F	74 °F	89 °F	91 °F
4"	73.5 °F	73 °F	90 °F	91 °F
6"	75 °F	75 °F	95 °F	89 °F
Light	230 f. c.	320 f. c.		36 f. c.
Aug. 8				
Air	70 °F	72 °F		
1"	73.5 °F	74 °F		
4"	74 °F	74 °F		
6"	75 °F	75 °F		
Light	210 f. c.	300 f. c.		

SUMMARY AND CONCLUSIONS

Emergence of the alkali bee usually begins in late June or early July in the Snake River Valley of Eastern Oregon and often extends into early August. There is usually one generation per year which flies for about five to six weeks. Males precede the females by a few days. Temperature is the principal factor affecting emergence, but a high soil moisture content and a flocculated soil surface act as emergence retardents. As a result it is possible to find different emergence peaks on different parts of the same bed. Emergence on some beds may precede that on others in the same area by as much as two or three weeks. A study of emergence, as related to soil temperature and moisture conditions, would permit a grower to predict bee emergence quite accurately.

After emerging the males fly back and forth across the nesting area searching for females. By noon the males disperse into alfalfa fields to forage for nectar. As evening approaches some males enter patches of loose soil, old emergence holes or even the burrows of females; others cluster on nearby plants or under rocks or boards to spend the night. The next day the same behavior is repeated, with the males flying over the bee bed during the morning hours, waiting for females to emerge so that fertilization can be accomplished. It is believed, however, that the majority of apparent matings on the bee bed are not successful as most of the observations indicate the female struggles to free herself of the male, and the genetalia are rarely connected. In the few cases where copulation occurred, the female did not struggle to free herself and the genitalia were observed to be inserted. Abdominal pulsations could be observed in the male and a distinct sound was produced with each pulsation, it was not determined whether it came from the male or female.

On the evening after mating has occurred, the female returned to the bee bed to begin nest construction. She spent the next three or four days fashioning the nest, taking but a few short trips to the field. Pollen collection began on the third to the fifth day and a single cell was provisioned in one day. After the pollen ball was completed, an egg was laid upon it and the cell sealed with a spiral soil plug. A new cell was then polished and the procedure repeated the next day.

The exact sequence of nest construction is quite variable. Some bees roughed out only one or two cells during the three or four days preceeding pollen collecting. In these cases the bee collected pollen during the day, then laid an egg, sealed off the cell, roughed out a new cell and polished another during the night. Each morning newly excavated soil was evident at the burrow opening. Other bees excavated four to 10 rough cells before pollen collecting. They then collected pollen during the day, laid an egg, sealed off the cell, and polished a new cell during the night. After four or five days the bee may again rough-out additional cells, as evidenced by fresh digging at the burrow openings.

The shape of the cell cluster is to a large degree determined by the bee density of the bed; if the population is sparse a rather uniform cluster of 10 to 16 cells is formed, but if the density of bees is high, the cluster shape and size varies and may occur at two different levels.

The alkali bee usually starts collecting pollen on the third or fourth day after it starts construction of its nest. Both males and females are efficient alfalfa pollinators, but the female, because of her pollen collecting habit, is the most important. She usually forages on the blossoms close to the nest, normally visiting six to seven florets each minute and tripping about 96 percent of those visited. The female gradually works her way farther from the nest and once a flight pattern has been established it appears she does not change it to forage on alfalfa coming into bloom closer to the nest later in the season. Some bees have been observed flying across one-half mile of alfalfa in full bloom to forage on fields estimated to be at 60 percent bloom.

The time required to complete each pollen collecting trip varies, but the majority of trips average close to 35 minutes. Upon returning to the nest the pollen is deposited into a small mass and the bee departs for another load. It takes from seven to 11 pollen collecting trips to form one pollen ball and each ball may require from five and a half to nine hours time to complete.

The female trips the alfalfa blossom by forcing its head against the standard petal while bracing its legs on the wing petals. This frees the sexual column from its position in the keel petals.

As the alkali bee becomes older its behavior is more erratic. While visiting flowers she takes more time and crawls from flower to flower, occasionally falling off the blossom. On returning to the nest opening she will land and enter rather slowly. Senile females sometimes seal off a provisioned cell without laying eggs or without adding nectar to the pollen balls.

Mortality is evident as an abrupt decline in the number of working females.

Eggs of Nomia melanderi require from two and a half to three days to hatch at 24 ± 1°C, and has a head capsule diameter which varies from 68 to 78 mm. The first instar lasts from 12 to 24 hours. As the first instar matures, the mandibles can be observed moving back and forth and occasionally some fluid and pollen grains can be detected as they are consumed. Except for the mouth region, the larva appears to be covered with the chorion.

As the first instar exuvium and chorion are shed, the marker on the vertex can be observed to move ventrally and posteriorly. The head capsule diameter shows a definite discontinuous increase and in the second instar ranges from 78mm to 88mm. The data show that the head capsule diameters of larger first instar larvae approximate those of smaller second instar larvae, so that without actually rearing the larvae it may be difficult, if not impossible, to distinguish between the two instars. The second instar larva matures in 12 to 24 hours. A more abrupt change in size is seen in the transformation to the third instar, and the duration of the third instar is also a little longer. The changes in size are even more pronounced in the fourth and fifth instar. Individuals reared from the egg to prepupa clearly indicate that Nomia melanderi has five larval instars.

The alkali bee has a remarkable ability to locate its nest from the hundreds of nearby nests. It accomplishes this by the use of landmarks of two different types: small markers such as twigs, small rocks and soil surface differences near the burrow entrance; larger landmarks such as trees, fence posts, haystacks, roads, etc. well removed from the burrow. She must use the two in concert for she will return to almost the exact location of the burrow when the area has been scraped smooth and all openings filled. It is not known how this is accomplished.

The alkali bee is able to distinguish among yellow, green, blue, white and gray colors.

Temperature is usually the most important limiting factor in the initiation of morning activity. Conversely reduced light intensity appears to determine the time of flight cessation in the evening. There are some intricate interactions between these two factors and data suggest that either can become limiting.

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