

AN ABSTRACT OF THE THESIS OF

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Title Foraging and Nesting Behavior of the Leafcutter Bee
Megachile rotundata (Fabricius)

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The study provides the details of the ethology of Megachile rotundata (Fabricius), and presents preliminary observations on its foraging and nesting behavior. Development from prepupae to adults proceeds most rapidly at 32 degrees C., and is retarded when held at lower and higher temperatures.

Male behavior is distinct from that of the female. Mating, including the copulation process and sleeping, are described.

Requirements necessary for nesting are presented. These included: types of nesting places, natural and artificial; size range of tunnels; and the effects of competition on nesting.

Females used leaf sections from a variety of plant species in construction of their cells. Description included desirable leaf characteristics, cutting procedures used to remove leaf sections from plants and return of bees to given leaf sources. The construction of the cell cup is detailed as to leaf placement, number of leaves used,

cell dimensions, and arrangement of cells under various nesting conditions. After formation of the cell cup it is provisioned with pollen and nectar. Procedures of pollen collection, removal of pollen from the scopa, and the use of nectar for moistening the pollen mass were included as were descriptions of oviposition and cell capping. Upon completion of a cell series, the entrance to the tunnel was sealed, using leaf cuttings.

All procedures of cell construction were influenced by the age of the bee and behavioral changes noted toward the end of the flight season.

It was found that orientation to the nesting site is largely through visual association with gross characteristics of the area and that markers aided in orientation. Preliminary observations on color discrimination indicated that bees could distinguish between colors.

Foraging studies were conducted in the presence and absence of alfalfa and included notes on flower preference and pollen collecting. Flight range studies indicated that bees forage plants closest to their nesting site and increase their range as close bloom is no longer available.

Attempts made to relocate bees in new areas met with only limited success.

Morning and evening behavior of bees were characterized and climatic conditions responsible for commencement and cessation of flight outlined.

FORAGING AND NESTING BEHAVIOR OF THE
LEAFCUTTER BEE MEGACHILE ROTUNDATA (FABRICIUS)

by

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FORAGING AND NESTING BEHAVIOR OF THE
LEAFCUTTER BEE MEGACHILE ROTUNDATA (FABRICIUS)

INTRODUCTION

Megachile rotundata (Fabricius) is a member of the large, cosmopolitan leafcutter bee genus Megachile Latreille (27, p. 295). This species is native to Eurasia and its identity was confirmed in the United States from the Washington metropolitan area in 1947 (17). It has extended its range westward and has been reported in ten states from coast to coast. M. rotundata has been taken from the District of Columbia, Virginia, Pennsylvania, Kansas, Missouri, Texas, California, Utah, Idaho, Washington, Nevada, and Oregon (5; 15; 17; 35, p. 3).

Like most of the Megachile species, M. rotundata forms its nesting cells from leaf cuttings. Each cell is constructed in the form of a cup in which the female stores a mass of pollen and nectar (Figure 1). Upon this mass of provisions she lays an egg after which she seals the entrance of the cell with another piece of leaf. Cells are usually constructed in linear series and in nature are found in a variety of locations.

It is surprising that, in spite of the large number of species within the genus, little biological data have been published on this group. Most of the biological literature, at least in this country, has appeared within the last ten years. Recent interest is largely attributable to the importance of a few leafcutter bees as pollinators of

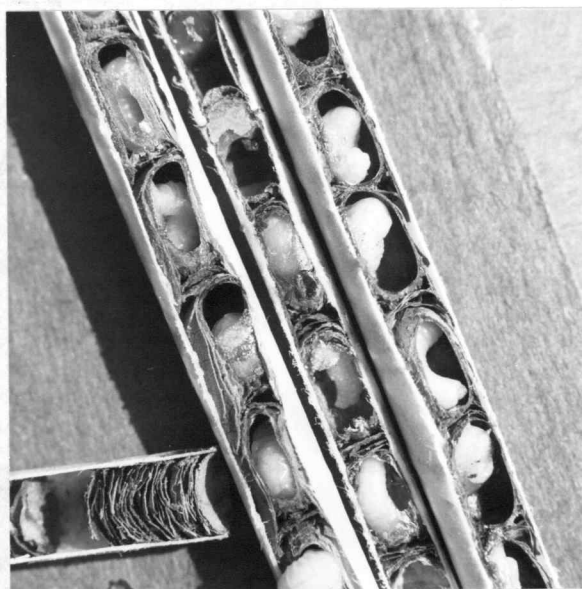


Figure 1. Longitudinal section of straws containing nesting cells and prepupae of M. rotundata.

legumes, particularly alfalfa.

Michener's (26) treatise on the biology of M. brevis brevis is the most complete study on any species within the genus. Several papers have appeared recently dealing with the biology of M. rotundata, with emphasis on management of the species for alfalfa pollination. Of these, papers by Stephen and Torchio (39), Bohart (2), and Stephen (35) are most complete.

This study is a preliminary investigation of the behavior of M. rotundata while foraging and nesting. Further, it is hoped that the knowledge of these behavioral phenomenon may contribute to a more efficient management of this bee for alfalfa pollination. Since little work of this nature has appeared in the literature, this study is designed as a contribution to the general knowledge of comparative bee behavior.

M. rotundata has many characteristics which make it a valuable tool for certain behavior studies. Females nest gregariously and readily accept artificial domiciles, making them amendable to a variety of manipulations. They are also exceptionally gentle and rarely sting, making close observations possible without danger to the observer. Bees are easily marked so that movements of an individual around the nesting site can be followed. Unfortunately, its small size and rapid movements make this bee difficult to follow in the field.

METHODS AND APPARATUS

Most of the data presented here were collected through observations at bee nesting and foraging sites in or near Boardman, Morrow County, Oregon. The town is at the center of a small, isolated, irrigation district located on the Columbia River. The farms are small and diversified, producing alfalfa, corn, watermelon and cattle in the main. A large number of old buildings and an abundance of dead Lombardy poplar provided ideal nesting sites for the species. The irrigated area around Boardman is sharply delineated from the arid, unsettled sagebrush desert about it.

Observations were conducted in a number of areas ranging from those which were arid, with little bloom, to those of high moisture, due to irrigation, with an abundance of forage plants. Studies were confined to the following five sites.

Area I was a farm in Boardman belonging to Mrs. Hazel Miller. It includes approximately 80 acres of alfalfa grown for hay, which are located adjacent to a number of older farm buildings. The combination of available food and an abundance of nesting places under the siding of farm buildings and between wood shingles of the house has resulted in large localized bee populations. Most of the observational work was done at this location.

Area II, consisted of a series of experimental alfalfa plots

located on the Boardman Bombing Range, approximately ten miles southwest of Boardman. A series of small plots of alfalfa, each 50 x 50 feet, were established in 1961 in a remote section of the open range (Figure 23). The native vegetation consists mainly of sagebrush Artemisia sp.; rabbitbrush, Chrysothamnus sp.; and grasses of various species. These plots, fourteen in number, were positioned so that they formed an L-shaped pattern with two one-mile arms. Each arm included seven plots and there was a large base plot, 50 x 100 feet, at their point of intersection. Plots in each arm were spaced at distances of 10, 20, 40, 80, 160, 240, and 320 rods from the base plot.

Area III was a desert area located five miles west of Boardman on the Boardman Bombing Range. The native vegetation was similar to that in area II, but no alfalfa was available. Several abandoned navy buildings in this area were used by leafcutter bees for nesting. These populations were used to observe foraging habits on desert plants.

Area IV was an isolated 70 acre alfalfa seed farm, located in the desert approximately 12 miles southeast of Boardman. Large populations of leafcutter bees were introduced for alfalfa pollination and situated in domiciles about the periphery of the field. Instruments to record the illumination and temperature were located in the proximity of bees at this site.

Area V consisted of a one acre plot of alfalfa at the Umatilla Branch Experiment Station, Hermiston, Oregon. Bees were established in artificial domiciles which were housed in a large protective shelter. The shelter was situated near the alfalfa so that abundant bloom was available. Studies on color determination and weather effects on flight were conducted on this bee population.

Additional observations were made on bees nesting in a variety of natural and artificial domiciles most of which are listed in the section dealing with nesting behavior. Of these domiciles those which were constructed of soda straws proved most useful because individual tunnels could be manipulated most freely. Therefore, most observations on the nesting behavior were taken at domiciles in which soda straws were the nesting medium.

Two basic types of soda straw domiciles were employed to gather data on orientation to the nesting tunnel. One type, used for color orientation studies, consisted of straws three or four inches in length contained in pint milk cartons (Figure 2). The second type consisted of a cylindrical cardboard mailing tube 2.5 inches in diameter, which was 2.5 inches in length (Figure 4). This tube was cut so that its screw top served as the bottom of the finished domicile. By removing the screw cap, observations could be made on activities at the bottom of the tunnel. The domicile was fitted with straws six millimeters in diameter, into which two one-inch pieces of 5.5 millimeter

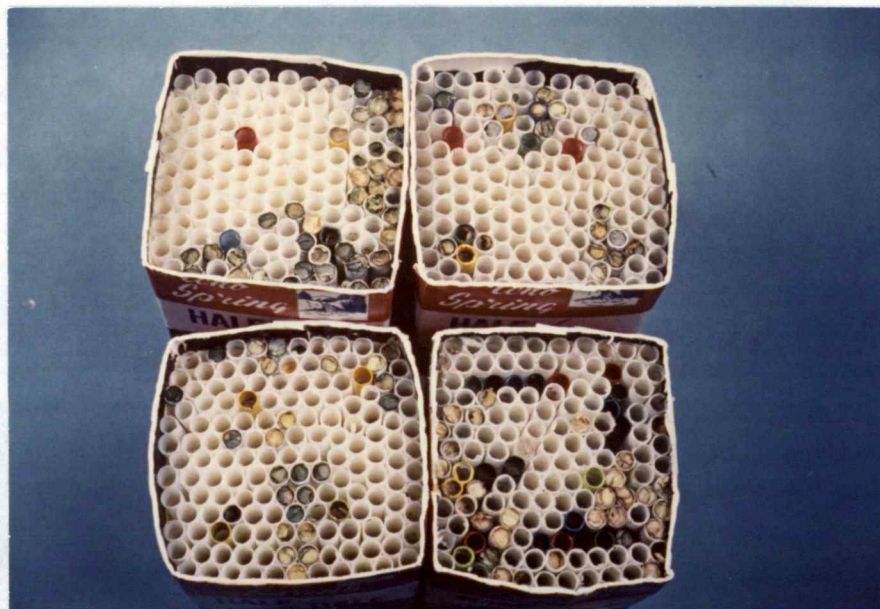


Figure 2. Straw domiciles with numbers of colored straws used for color orientation studies.

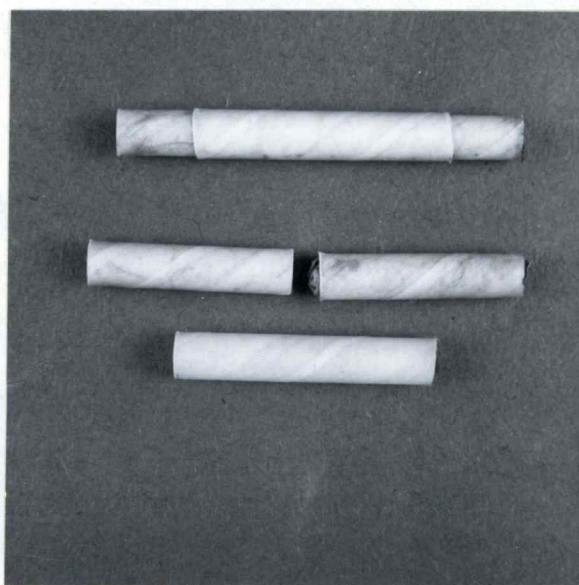


Figure 3. Divided straws used in nesting tunnel orientation studies. The bottom straw serves as a sleeve into which the two one-inch pieces (center) fit, forming the assembled unit (top).

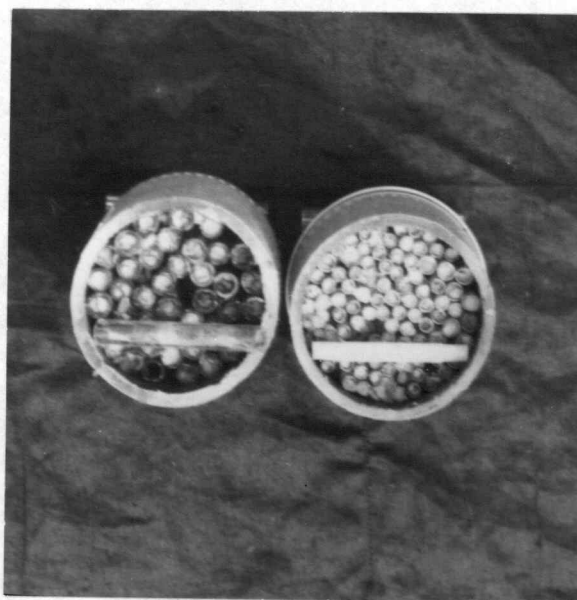


Figure 4. Modified mailing tubes, used for nesting tunnel orientation and cell construction studies, containing divided straws (Figure 3) on right, glass tubing on left. Straws and tubes filled with nesting cells of M. rotundata.

diameter straws were inserted (Figure 3). These divided straws permitted the observer to remove, displace, or exchange various portions of nesting tunnels in an attempt to determine stimuli associated with the nesting tunnel and the part it plays in bee orientation.

Cardboard mailing tubes similar in dimension to those above were filled with two inch lengths of four and one half, and six millimeter (inside diameter) glass tubing (Figure 4). These tubes could be removed, while bees were working within, thus allowing detailed observation on manner of cell construction.

Foraging range studies were conducted in area II during the summers of 1962 and 1963 to determine what distances M. rotundata would fly to obtain cell provisions. The experimental plot design is presented in Figure 23. In 1962, the number of bees in ten one-square-yard counts, representing approximately 40 plants, was recorded for each plot except the base plot in which bee counts on 60 one-square-yard counts, totaling approximately 240 plants, were made. During the summer of 1963, sampling techniques were modified so that the number of bees on approximately 32 plants was counted in each plot except the base plot in which the bees foraging 336 plants were recorded. During 1962 and 1963, each plot contained 100 blooming alfalfa plants, except the base plot, which had 504 plants.

Daily counts were made in each plot, usually between one and three P. M. because activity was at its peak during these hours.

It was necessary to establish bee populations for experimentation in areas II and V. Since females spend the night in their nesting tunnels, counts were made of the number in each domicile and these domiciles moved into experimental areas. They were permitted to emerge and take flight the following morning at the new location.

Bees brought into area II were placed in a six foot square wooden shelter located in the base plot (Figures 5, 6). Since the base plot was located at the intersection of the two rows of alfalfa plots, the bees had an equal opportunity to fly into those plots to the north or the east (Figure 23).

The effects of domicile exposure on flight activity were investigated in area IV. Domiciles containing nesting females were placed in three adjacent shelters three feet above the ground, having their entrances facing east, south, and west respectively. Bees from these shelters foraged in a large field of alfalfa just south of the nesting site.

The number of bees in each of the relocated populations was recorded by visiting nesting domiciles each night and counting bees while they were inactive. These counts were especially useful in comparing nesting populations with numbers of bees observed foraging in alfalfa plots in area II.

The details of foraging behavior, particularly the manner in which pollen was collected and transferred to the scopa, were

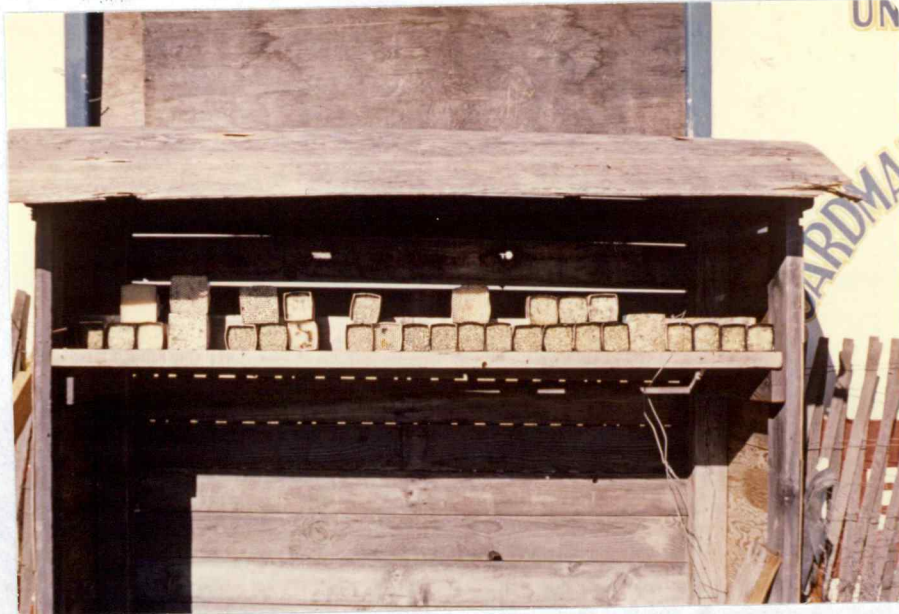


Figure 5. Shelter in base plot (Area II) containing soda straw domiciles.



Figure 6. Alfalfa plot (base plot, Figure 22) in Area II used for foraging range studies.

recorded by cinematography. These procedures are otherwise too rapid to observe.

Individual bees used in color determination and orientation studies were marked at night using quick drying lacquer paints. Since females sleep with their abdomens facing the entrance to their tunnels, a small amount of paint could easily be applied to the fifth and sixth abdominal tergites. A number of colors was used so that a given female could be easily distinguished from others. Caution had to be exercised so that only small amounts of paint were applied, otherwise, bees got paint on their wings and were unable to fly.

Straws used for color determination studies were painted by dipping them into quick drying lacquer to a depth of approximately one-half inch (Figure 2). Upon removal, they were given a few rapid shakes to remove excess paint and were permitted to dry. Color standard references were obtained, using Reinholds Color Atlas (16). Colors in this atlas referred to by number and reference to the colors used in this study are in accord with those found therein.

The effects of weather were observed in areas I, II, IV, and V. Weather data were recorded in areas IV and V, using copper-constantin thermo couples and a number 6580 Daylight Illuminometer fed to a Leeds and Northrup Company Speedomax G, model S, 60000 series recorder. Temperature measurements at various depths in nesting tubes also were made, using a Model 41TZ Tele-Thermometer made

by the Yellow Springs Instrument Company, Inc., equipped with flexible thermocouple.

NESTING BEHAVIOR

Emergence

Specimens have been collected at Sacramento and Davis, California in early May (15). Stephen (35, p. 3) reports that adults begin emerging during the latter part of May in the Columbia Basin and the first week in June in the Snake River Valley. In 1963, emergence began during the first week of June in the Boardman area.

It has been observed that bees emerged earlier in the year from nesting sites exposed to the sun than from those in shade (35, p. 3). Further, multiple generations occur more frequently when nesting domiciles are exposed to limited amounts of sun during the day. Excessive heat (greater than 35° centigrade) appears to result in high larval mortality.

Since light cannot penetrate nesting cells, temperature appeared to be the controlling environmental factor in emergence. A series of controlled temperature experiments were conducted in the laboratory from 1961-1964.

A series of tests was undertaken to determine temperature effects on the rate of development of overwintering prepupae by rearing larvae in nesting cells at various temperatures. It was found that emergence was most rapid at 32°C (21 days), being delayed at lower and higher temperatures (Figure 7; 37).

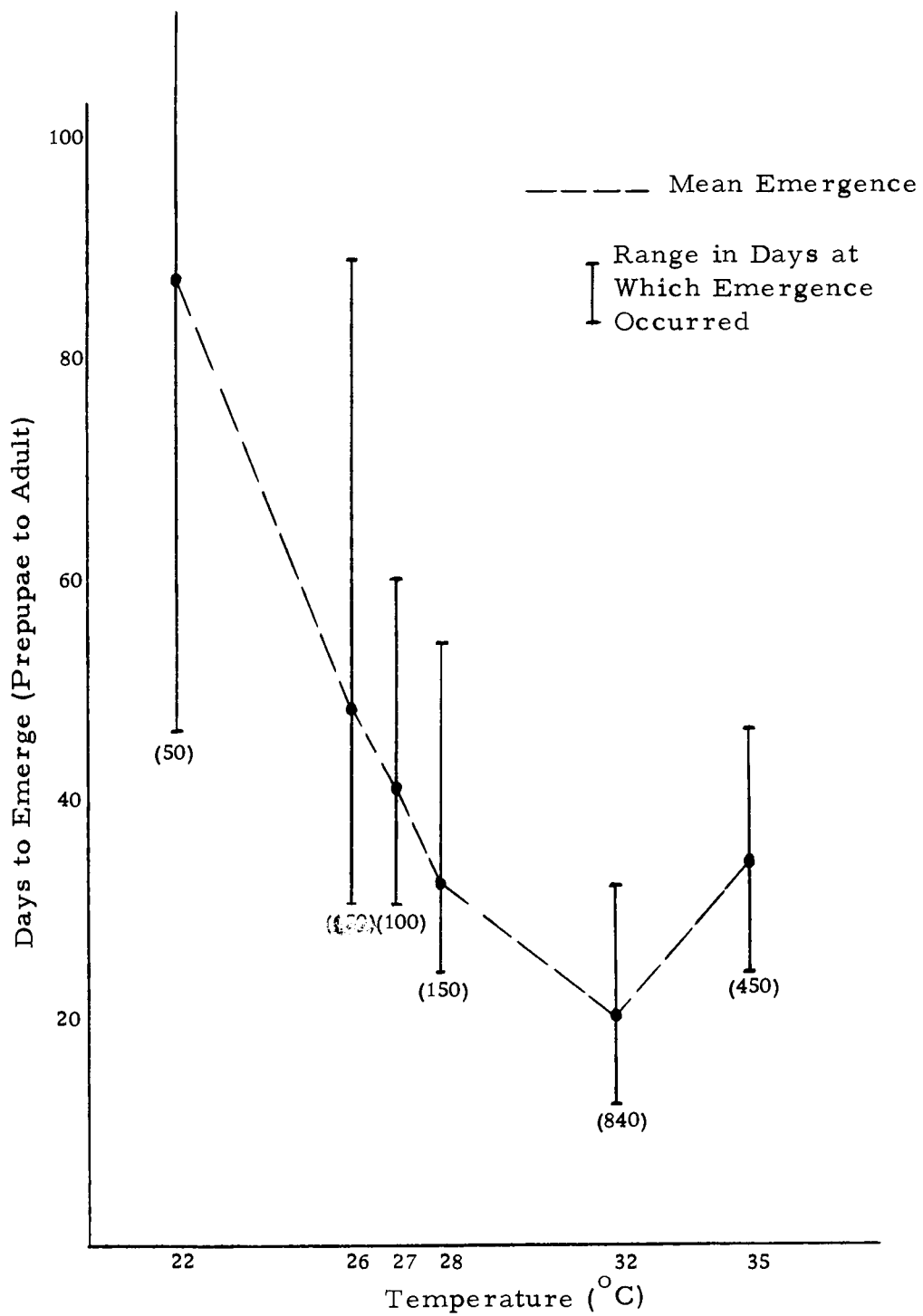


Figure 7. Effects of temperature on prepupal development. In parentheses are the number of adults which emerged at given temperatures.

It was also noted that when bees were reared in constant temperatures emergence was irregular and occurred randomly through the day (Table 1). However, if developing bees were kept at alternating temperatures, e. g. 32:22 for 12 hours each day, emergence was confined mostly to the three hour period immediately following the onset of warmer temperatures (Tables 2, 3; 38). It seems probable from the data presented in Tables 2 and 3 that a diurnal rhythm is triggered by temperature differentials, and most bees emerge during the morning hours in nature. As morning temperatures increase, adults begin chewing their way out of their nesting cells.

Table 1. Effects of constant temperatures on time of adult emergence.

Observation Time	Temperature ($^{\circ}\text{C}$)					
	35	32	28	26	22	
12 A. M.	2	--	6	6	--	
3 A. M.	--	No Data Taken			--	--
6 A. M.	6	5	17	6	3	
9 A. M.	5	9	3	16	8	
12 Noon	7	6	2	7	--	
3 P. M.	--	4	--	--	3	
6 P. M.	--	3	2	1	4	
9 P. M.	2	--	5	5	5	

Table 2. Effect of alternating temperatures on emergence
(bees kept at 22°C from 9 P. M. - 9 A. M.).

Observation Time	Temperature (°C)				
	35	32	28	26	22
12 A. M.	--	--	--	--	--
3 A. M.	--	No Data Taken			--
6 A. M.	--	--	--	--	--
9 A. M.	--	--	--	3	--
12 Noon	6	29	21	13	--
3 P. M.	--	10	4	5	--
6 P. M.	--	2	--	--	--
9 P. M.	--	--	--	--	--

Table 3. Effect of alternating temperatures on emergence
(bees kept at 22°C from 9 A. M. - 9 P. M.).

Observation Time	Temperature (°C)				
	35	32	28	26	22
12 A. M.	--	25	14	3	--
3 A. M.	--	No Data Taken			--
6 A. M.	--	15	3	6	--
9 A. M.	--	--	1	2	--
12 Noon	--	--	--	--	--
3 P. M.	--	1	--	--	--
6 P. M.	--	--	--	--	--
9 P. M.	--	--	--	--	--

Male Behavior

Data gathered from a series of laboratory emergence studies indicate that the majority of males begin emerging approximately five days before females. Their primary function is to fertilize the females, and all of their activities are devoted to this end. Males are rapid flyers and are often observed flying back and forth around nesting sites in search of sitting females. After flying for varying lengths of time, males land and other males, mistaking them for females, often pounce on them. Males frequently discontinue searching for females to sip nectar from flowers near patrolling lanes. They were not observed tripping¹ alfalfa florets by the writer, but Stephen (36) has observed a small percentage of male tripping.

Instead of entering the floret directly, males introduce their proboscis on one side of the floret between the standard and the keel. In this manner, males behave like most other bee species and are able to obtain nectar without triggering the tripping mechanism of the flower.

¹Tripping is a term applied to the release of the staminate column from the partially fused keel petals of the alfalfa floret. The staminate column is held by these petals under tension. Upon its release, the staminate column snaps quickly from the keel to a position against the standard petal. On warm, dry days an audible "snap" may be heard when a floret is tripped. For a more definitive account of the tripping process, consult Armstrong and White (1, p. 162-164).

As evening approaches males seek shelter for the night. This phenomenon, generally referred to as "sleep," has been described for males of several bee species, although few references to the "sleep" habits of species of Megachilidae appear in the literature. In the megachilid tribe Anthidiini, the males of certain species of Anthidiellum (21, p. 159-160), Anthidium (20, p. 557), and Trachusa (30, p. 74-75), sleep in the open, clinging to blades of grass using only their mandibles for support. Similar postures and habits of sleeping in the open have been reported for males of the tribe Megachilini, Chelostoma and Coelioxys (20, p. 557). However, Hirashima (In 20, p. 557) reports that males of the Megachilini genus Osmia sometimes gather in cracks for the night.

To date few observations of male sleeping habits within the genus Megachile appear in the literature. Michener (26, p. 1691) suggests that both sexes of M. brevis brevis may spend the night in curled leaves or other similar protected places but such behavior was not observed in the field.

During the summers of 1962 and 1963, males of M. rotundata were often found spending the night either alone or in aggregations of various sizes. Males "sleeping" alone will seek whatever shelter is available, and they have been observed in nesting straws, under boards, slats and shingles on houses and barns, and other sheltered niches. Most common, however, are the large aggregations of

males, which return night after night to the same location. These clusters may contain fifty to one hundred or more individuals. One cluster of fifty males was observed on June 20, 1963, spending the night under a torn piece of tar paper on the side of an old shack in Boardman, Oregon. These males returned to the same location each night and by July 23, 13 males remained. Numbers declined to 11 on July 28, until only one male was observed on August 6. It is doubtful that other males joined the cluster because of the isolation of the shack and because the number of bees in the cluster declined steadily during the period of observation.

Another aggregation of approximately one hundred individuals was observed in area IV. Proportional declines were also noted in this cluster during the same period of time as that described above.

Factors contributing to the decline in male sleeping aggregations were not determined. It could reflect normal mortality, a relocation of the sleeping place, or possibly the instinct to cluster is lost when males are no longer spermatogenic.

Mating Behavior

Mating usually takes place at the nesting site but has also been observed in the field. Females can often be observed resting in the sun on well illuminated surfaces near the nesting site, either motionless or preening their bodies with their legs. When patrolling males

approach, some females have been observed to oscillate their raised abdomens and wings simultaneously. Although this behavior was observed several times, it is apparently not essential to mating, since frequent copulations were noted when females remained motionless.

Usually males will zig-zag three or four times above resting females before pouncing on them. However, males often will proceed directly to copulation without the above premating flight activity. Copulation is exceedingly rapid, usually lasting only a fraction of a second. Due to the speed with which copulation is enacted, it is doubtful if insemination is accomplished in all attempts.

Males often hit resting females with such force as to knock them from their perch. As the mating pair fall through air, they always separate before hitting the ground and the female usually returns directly to her nesting tunnel. However, females have been noticed returning to their former resting position which suggests either multiple matings or an unsuccessful attempt at copulation. One female remained in the same position through four copulations, or attempts at such, without moving or being knocked from her position.

Rapid copulation as described above is most common in nature. However, prolonged copulations have been observed in the field under unusual circumstances. A female with an injured wing was attacked several times by males while crawling over the ground. One male landed on the dorsal surface of the female, grasping her with all six

legs. The male positioned himself so that the proboscidal fossa of his head was against the vertex and supra-antennal area of the female (24, p. 160-161). The prolegs of the male were positioned along the lateral aspects of the female's compound eyes. The middle legs grasped the female's thorax, while the male's hind legs were wrapped about the abdomen, forcing it upward to receive the male genitalia. The antennae of the male were held straight, mandibles slightly open, with wings vibrating continuously during copulation. The receptive female was observed to curve the last three abdominal segments upward to receive the male genitalia. This description was based on an observed copulation lasting 27.2 seconds, which was much longer than the majority observed. Stephen (35) has observed that small males copulating with larger females grasp the female around the neck instead of around the compound eyes. Pressure applied by the forelegs forces the female's head into a more horizontal position during copula. Since these observations are based on an anomalous mating situation, fortified by laboratory data, there is no assurance it represents the normal pattern of copulation in its detail.

Males observed definite patrolling lanes in the field and frequent copulations with females were observed on plants to either side of these lanes. Copulation has never been observed in flight.

Selection of Nesting Site

General Requirements. The gregarious nesting tendencies of Megachile rotundata often creates competition for limited nesting space and food sources, when large localized populations are propagated. Therefore, the retention of large populations depends upon the availability of suitable nesting niches and an adequate supply of pollen, nectar and leaf material in the area. Since most large bee populations develop where extensive acreages of alfalfa are grown, supplies of pollen, nectar, and leaf material are usually adequate, but a premium is placed on suitable nesting sites.

This species is adaptable to a wide range of nesting niches, rejecting only those which are too small to accommodate the bee or so large as to require an excessive number of leaves for cell construction. In all media, females preferred nesting tunnels with apertures ranging from approximately four to six millimeters. Generally the larger tunnels are used only when smaller ones are not available, but acceptance of smaller diameter tunnels is dictated by the body size of the nesting female. Only smaller females were able to occupy four millimeter tunnels.

Where prepared domiciles are not available, the bee will construct its nest in a wide variety of habitats. Cells have been taken from spaces between shingles or boards on houses and barns, nail and knot holes in buildings, tubing of all sorts, including automobile

gas lines, vacated paper and mud cells of various wasps, holes bored in dead or dying trees by various beetles, and hollow plant stems and numerous other niches.

Interest in this bee as a pollinator of alfalfa for seed has resulted in the preparation of an array of artificial domiciles. Drinking straws of various diameters have been used as nesting tunnels by gluing them to the bottom of milk cartons or some other container (Figure 8). Other commercially available domiciles include layers of corrugated cardboard fitted into boxes (Figure 9), molded polyurethane blocks containing holes (Figure 10), blocks of wood with drilled holes (Figure 11), and various other structures (Figure 12). Most of these are described in detail by Stephen (33, 34, 35, p. 8-12) and Bohart (2).

Location and Preparation. Preliminary observations indicate that females begin searching for nesting sites soon after emergence. It is assumed that they first feed on nectar and possibly may be mated.

Females are very active searchers and they have a characteristic behavior while seeking a nesting site. A female may be seen to fly slowly along the side of a building, stopping occasionally to hover before a possible nesting cavity. The bee may land when a likely niche is found and examine it by sticking its head into the aperture and moving its antennae slightly. The search may continue, or the bee may return to the same tunnel several times before accepting or

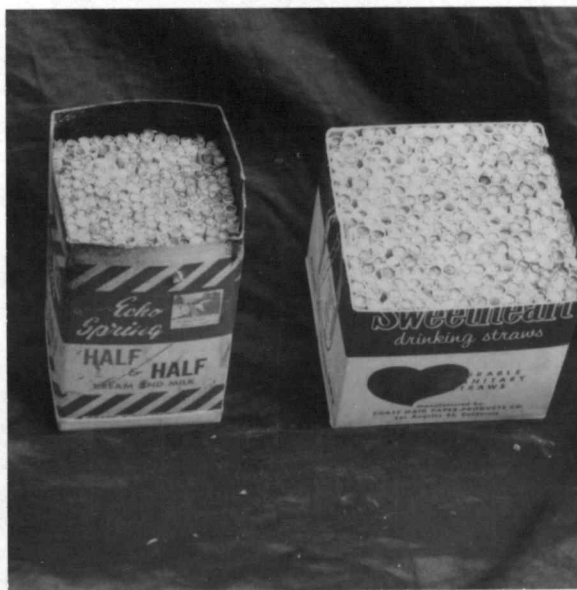


Figure 8. Soda straw domiciles filled with nesting cells of M. rotundata.

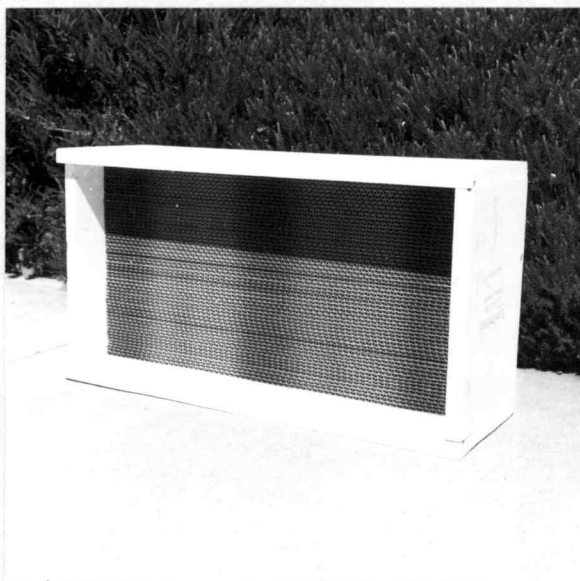


Figure 9. Commercial nesting domicile consisting of layers of corrugated cardboard.

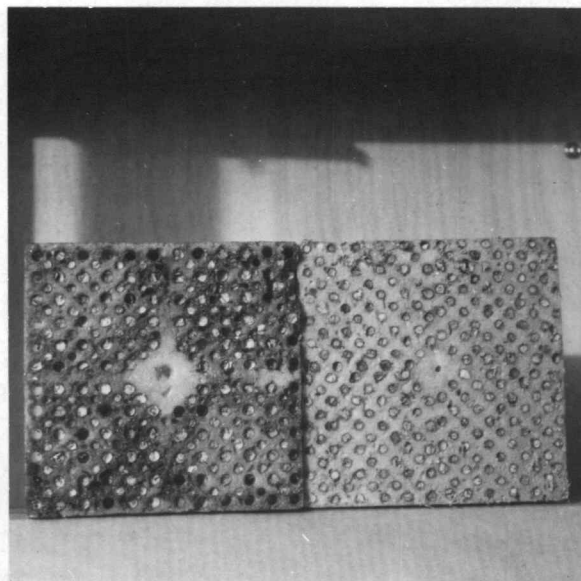


Figure 10. Commercial molded polyurethane domiciles filled with nesting cells of M. rotundata.

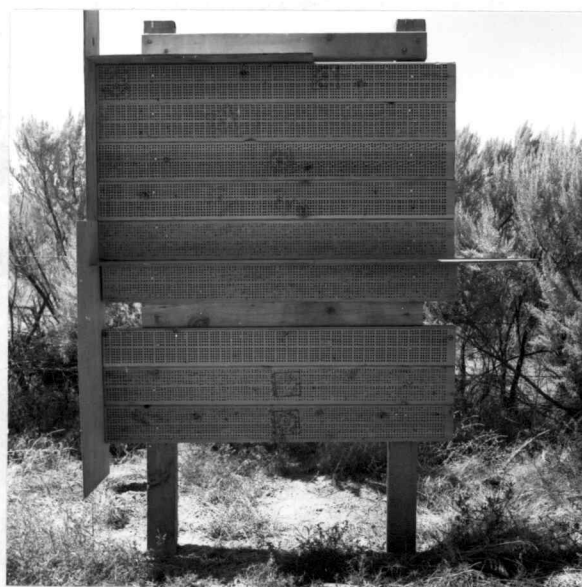


Figure 11. Commercial "alfa-bee boards" consisting of holes drilled in boards.

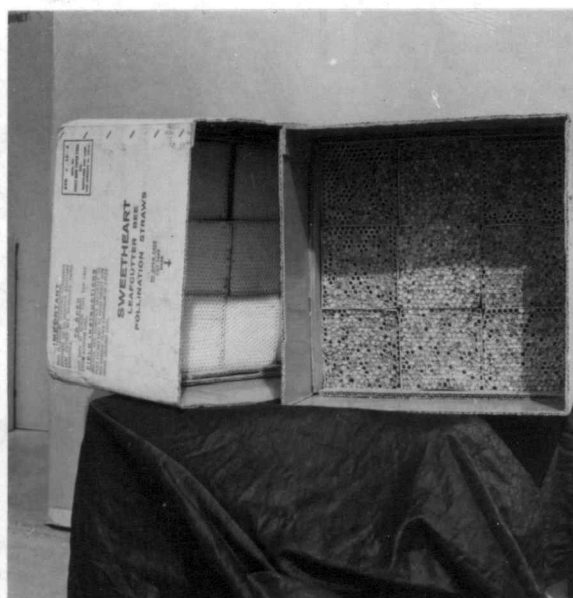


Figure 12. Commercial straw domicile units. Left unit unoccupied; right unit filled with nesting cells.

finally rejecting it. Unlike the nesting bee, she exhibits a methodical, though more leisurely, flight and may search for hours before finally selecting a nesting place. Often searching will be interrupted to obtain nectar from nearby flowers.

In areas where large numbers of artificial domiciles are available, the searching pattern is somewhat altered. The bee now is confronted with a small area containing excessive numbers of suitable nesting tunnels from which to choose. The response of searching females is highly variable. Some will land on a domicile (e.g. containing straws) and immediately enter and accept one of the straws. Others may proceed to the bottom of a straw or go only part way in before backing out and examining another. This procedure may be repeated once or several times, the bee spending different amounts of time within each straw. Once the decision is made, the female immediately begins preparing for the process of rearing its young.

Many of the older tunnels contain residues from the previous generation and "cleaning-up" procedures are necessary before new cells can be formed. However, even in new straws, the bee is seen to move up and down the straw working its mandibles and occasionally chewing around the tunnel entrance.

When overcrowded, tunnels from which some but not all emergence has taken place, may be accepted by a renesting female. In cleaning out the straw of old leaf material, she will also remove

developing larvae and unused pollen masses. Under these conditions it is not uncommon to see several live larvae in front of domiciles.

A tendency for selection of nesting sites with an easterly exposure is quite evident. The fact that these areas are first to be warmed by the morning sun is probably the major factor in this selection. It has been observed that when suitable nesting sites are available for renesting, bees will usually renest in the same area from which they emerged. Bees also tend to avoid, or are driven from, sites that get extremely hot during the day. In searching the sides of buildings, bees usually direct their observations to areas around overhanging eaves. However, this behavior could be an expression of some stimulus other than heat. For example, one artificial straw domicile was placed on the corner of an old shack and bees continued nesting in the domicile even though the temperature within the straws was above 120 degrees F., more than sufficient to kill developing larvae. This behavior may have been a reflection of competition for nesting space in the immediate area.

Competition. With the increase in local populations, the competition for nesting space often becomes keen. On several occasions large populations were seen in areas where only a limited number of nesting tunnels existed. At one site, a domicile containing approximately 250 drinking straws had a bee occupying every straw as well as a number of searching females trying to locate empty tunnels.

Bees already occupying straws sat in the entrance with only their heads protruding, mandibles open, defending their tunnel against intruding bees. On many occasions an intruding bee was observed trying to pull a defending bee from its straw. It was obvious that under these circumstances bees were unable to forage because of the constant need for protecting their nesting tunnel. When an overabundance of nesting places are available defensive behavior was not observed and bees foraged freely.

Interspecific competition for available nesting space was at times quite severe. A number of wasp species have nesting requirements similar to M. rotundata and have been observed antagonizing bees nesting in the immediate area. Some wasps constantly interfered with bee activities. In area II, Bembix occidentalis (Fox) flew around nesting sites repeatedly knocking bees out of the air as they tried to land at their nesting place. Since many species of Bembix provision their nests with flies, it is believed that leafcutter bees may be mistaken by the wasps for their usual prey. A sphecid, Trypoxylon tridentatum Packard, has been observed nesting in straws and occasionally harasses bees nesting in the same domicile.

Other insects use nesting tubes as places of concealment, or as food reservoirs. When abundant, their presence usually leads the bees to abandon the site. The European earwig is the most common of these intruders in the Boardman area. Artificial straw domiciles

that had shown good bee activity early in the summer were often completely occupied by populations of earwigs later that season. Stephen (35, p. 8) believes that earwigs also feed on the pollen provisions which are collected by the bees.

In addition to imparting a musty odor to areas inhabited by them, the physical presence of earwigs is enough to deter nesting bees. Earwigs are very difficult to extract from tunnels, which may explain why bees were never observed trying to rid their nesting site of them.

Several undetermined species of ants invade nesting sites and have been observed carrying larvae and cell provisions from the tunnels. Some of the larger ant species have been observed fighting with bees and when numerous, have caused bees to abandon the nesting site.

The influence of adult parasite activity on nesting behavior of the bee was not determined for none were host specific, nor were present in great numbers. No noticeable changes in bee behavior were observed when the Torymid parasite Monodontomerus montivagus Ashm. was present at the nesting site.

Cell Construction

Leaf Sources and Cutting. Once the female has located a suitable nesting site, she begins searching for leaves with which to

construct her first cell. Females have been observed taking leaf cuttings from a number of plant species representing several plant families. In the Boardman area these include: lilac Syringa sp.; common locust, Robinia pseudoacacia; L. round-leaved mallow; Malva rotundifolia L.; a cultivated lily, Lilium sp.; alfalfa, Medicago sativa L.; rose, Rosa sp.; white sweet clover, Melilotus alba Desv.; and goosefoot, Chenopodium sp.

No particular preference for alfalfa as a leaf source was observed although it was preferred as a pollen source. This was demonstrated in area I, where bees took leaf cuttings from a variety of plants even when the leaf source was at a greater distance than the alfalfa.

Other plants are used as leaf sources under certain conditions. For example, Stephen (36) has observed females taking sections of flower petals from ornamentals such as rose, Rosa sp.; sunflower, Helianthus annuus; L. Zinnia sp.; and Petunia sp. in the Milton-Freewater and Nyssa areas of Oregon.

Petals were taken predominantly from flowers adjacent to homes in which bees were nesting. Such was also the case with sunflowers which grew in the immediate proximity of a shed used as a nesting site. In both cases bees generally took cuttings from the nearest available sources and often ignored the same plant species when it was removed from the nesting site by some distance.

Although females did not prefer plants of a given family or species for leaf cuttings, they did demonstrate selectivity for certain leaves on a particular plant. For example, cuttings were taken from old, yellowing leaves, especially from plants in which leaves are normally thick and rigid. Females were observed on common locust cutting only those leaves which had turned yellow. It seems possible that the decreased turgidity in old leaves increases their desirability for cutting. When old leaves are not readily obtainable, bees will take cuttings from green leaves. This is especially true during the heat of the day when leaves are naturally less turgid due to high transpiration losses.

In the course of leaf cutting, a female may examine many leaves before one with desirable characteristics will be chosen. During the search she will land on a leaf margin, grasp it with all legs and move rapidly along the margin. As the bee moves, she repeatedly bites into the leaf margin with her mandibles, apparently testing the suitability of the leaf. The female may even start incisions into leaves but reject them and continue her search for others. When a suitable cutting site is found, the bee makes an incision and rapidly cuts out a circular or oval leaf piece. As the leaf portion is being cut, the bee curls it under its body with its legs. As the last few incisions are being made, the bee hangs with the leaf cutting beneath its body, held only by the leaf portion remaining to be cut. When the cutting is

complete the bee immediately takes to flight, hovering before the leaf from which it was just removed. The bee orients itself to the leaf source with short back and forth zig-zagging flights, each progressively further removed from the cutting site, before turning and flying directly to its nesting location.

On a few occasions, a given bee has been observed making an incision into a leaf margin then turning around and starting another. Females would continue at one of the incisions into the leaf and finish the cutting process at the second. It was also noted that when a large leaf vein is met, the bee usually follows the vein rather than trying to cut through it.

The time required to secure cuttings from leaves is quite variable, even among visits made to the same plant species. For example, the times required for bees to start an incision until complete excision of a portion of alfalfa leaf, varied from 5.7 seconds to 2:30 minutes with an average of 43.6 seconds. One similar cutting from round-leaf mallow took 44.5 seconds. Cuttings from lilac averaged 43.9 seconds with extremes of 19 seconds and 1:22 minutes. In contrast to the above, females took leaf cuttings from common locuts in 14.7 to 30.8 seconds, averaging only 21.8 seconds per cutting.

The wide variation in leaf cutting times appears to be influenced principally by individual leaf characteristics such as turgidity, thickness, and number of veins, as well as by the size of the leaf cutting

needed for cell construction. It is easier for bees to remove leaf cuttings from the thin, smooth leaves of the common locust than from the other plants above.

Leaf cuttings are generally taken from sources close to nesting sites regardless of the location of the food source. However, in desert areas where leaf sources are scarce, distances between nesting site and suitable leaf material may be greater than those reported below.

Bees used for foraging range studies in area II obtained most of their leaf cuttings from a one-twentieth acre alfalfa plot a few feet from their nesting site. A preference was noted, first, for plants nearest the nesting site and secondly, for certain plants within this area. Plant preference was quite evident as three or four bees would be seen taking cuttings from one plant while those around it were without bees or evidence of cutting damage.

Bee activity associated with a lilac bush in area I was observed throughout the summer of 1963. The plant had been deprived of water so that the normally thick turgid green leaves remained permanently wilted. This bush located approximately 150 feet from a large bee population was virtually without a leaf margin from which cuttings had not been taken by mid-August (Figure 13). Six feet away was another lilac bush of the same age and size but with sufficient water to retain leaf turgidity. Not a leaf cutting was taken from this bush throughout the summer.

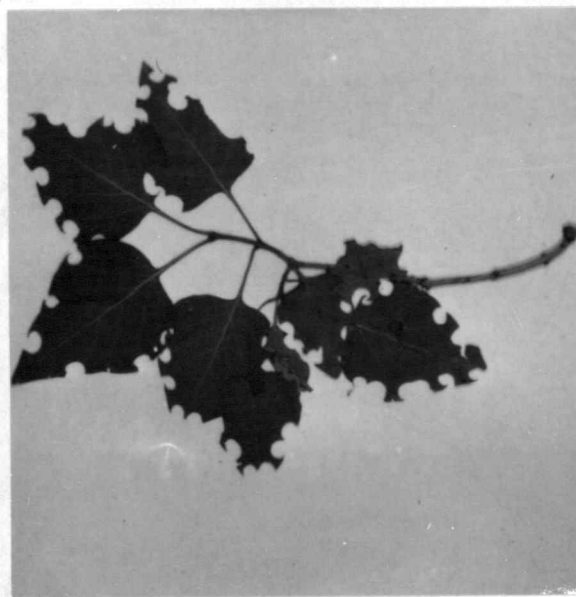


Figure 13. Twig from a lilac bush showing leaf cuttings taken from leaf margins by M. rotundata.

There has been some conjecture as to whether bees orient themselves to the location of a leaf source, for after obtaining a leaf cutting, they often return repeatedly to the same plant. The fact that numbers of females took leaf cuttings only from the wilted lilac bush when other wilted and turgid-leaved plants were available would support the contention that females orient on a single leaf source and return to it.

The factor or factors responsible for the attraction of large numbers of females to a given leaf source is not understood. It is possible that bees are attracted to the plant by a salivary secretion or by some other chemical attractant which remains after a female has taken a leaf cutting. The increase in numbers of bees at the leaf source could be due to chance, where bees seeking suitable leaf material happen upon the location, or they may have been visually attracted by bees already there. Whatever the cause, observations indicate that females return to the leaf source as long as it proves suitable for leaf cuttings.

Cell Formation. The leaf cutting is returned to the nesting site under the body of the female. It is arched so that its central position is pressed against the ventral body surface. The legs are positioned around the circumference of the leaf, and the leaf is bent in the middle so that the margins of the folded leaf almost touch. The mandibles are used to grasp the front edge of the leaf, and in this position it

forms an effective airfoil for the flying bee. As the bee approaches the nesting site, it removes its legs from their position on the leaf and uses them for landing. The leaf is then only held by the mandibles. After entering the nesting tube, the bee crawls headlong to the site of cell construction, continuing to hold the leaf only by its mandibles. She rotates in the nesting tube, using her antennae to examine the substrate and to determine placement of the new leaf. If the leaf is to be used for the base of the cell, only one half of its circumference is molded to the wall of the tube. That portion not molded to the tunnel wall is curved so as to block the tube, thus forming the bottom of the cell. However, if the leaf is needed to form the side of the cell, its entire perimeter is molded to the cavity wall.

In constructing the cell wall, the bee grasps the leaf edge with all of the legs on one side of its body and using its remaining legs and abdomen, turns the leaf over into position. Holding the leaf in place with its legs and apex of the abdomen, the bee masticates the edge of the leaf with its mandibles. During mastication, she secretes a fluid, probably of mandibular gland origin, which is used to cement the leaf to the substrate. When a particular location on the leaf is conditioned to the bee's liking, the mandibles are used to firm it tightly against the wall of the tunnel. Throughout the leaf placement process, the antennae continue to survey the work being done. As the mandibles masticate the leaf, the antennae are curved down so that they touch

the portion being manipulated.

After the leaf has been placed, the bee may rotate within the tube, presumably "checking the suitability of its work." However, on other occasions the bee backs out of its tunnel directly, without any pretense of examination.

Individual females show variability in the number of leaves used in cell cup construction. For example, one female used 14, 17, 20, 20, and 25 leaves per cup in the construction of a five cell series. The cells in a second series were composed of 8, 12, 10, 8, and 16 leaves respectively.

The dimensions of a given cell appear to be governed largely by those of the female's body. For example, a comparison between cells constructed in drinking straws of various diameters and those where space is available for making cells as large as desired, i. e., under or between boards, shows that the overall dimensions are quite similar. Since the slight variations found in interior cell dimensions correspond rather closely with the size-variation found among females of this species, it appears that the body size determines cell size. Smaller diameter apertures (four millimeters) physically impede larger bees trying to nest in them. The cells from four millimeter straws are usually not significantly longer than those from five or six millimeter tunnels, but the reduced diameter results in an average interior volume of only three-fifths of those found in six millimeter

straws. The interior volume of the cell determines the amount of pollen that is provided within, and thus the size of the adult that will develop in that cell.

That the female's body is used as an index in cell construction seems further substantiated when comparisons are made on the amounts of leaf material used in different sized nesting tunnels. For example, in tunnels four millimeters in diameter, 23.47 percent of the volume of each cell is occupied by leaf material. However, in six millimeter tunnels, leaf volume makes up 43.75 percent of the cell volume. This would indicate an attempt by the female to reduce the size of the cell to approximate her own size.

The data in Table 4 suggests that females use approximately the same number of leaves for the cell cap and cell bottom, regardless of tunnel diameter. However, there is a significant difference in the number of leaves used to construct the sides of cells. As shown in Table 4, more leaves are used in the construction of the cell sides as the tunnel diameter increases. For example, it was observed that the cell cup is composed of a single leaf layer when constructed in drinking straws of 4.0 millimeters in diameter. In 5.5 millimeter straws, the walls of the cell cups were composed of three layers of leaves.

Size of leaf cuttings used in cell construction is quite constant regardless of the size of the aperture in which nesting is taking place.

Table 4. Average number of leaves used in cell construction (range in parenthesis).

	Diameter of Tunnel			
	4 mm.	4.5 mm.	5.5 mm.	6 mm.
Aperture				
Cap	30.90 (24-40)	40.00 (26-66)	36.60 (24-58)	52.90 (34-85)
Cell				
Cap	1.80 (1-3)	1.48 (1-3)	1.52 (1-3)	1.76 (1-4)
Cell				
Sides	3.84 (2-7)	4.36 (3-6)	8.08 (6-11)	10.96 (8-16)
Cell				
Bottom	4.12 (2-10)	3.28 (2-6)	2.84 (1-6)	2.96 (1-7)

Those leaves used for cell caps and cell bottoms range between five and seven millimeters in diameter. Most of the leaves used in construction of the cell base are slightly ovate while cell cap leaves are circular. Leaves used on the sides of cells are larger than other construction leaves, are ovate in shape and measure seven by nine or ten millimeters. Greater numbers of bottom leaves are usually found in the base cell of each series. This may be because several different females started construction in the same nesting tunnel, or else it may reflect an attempt to isolate the bottom cell from the environment. Many base cells have three times the number of bottom leaves found in other cells of the series.

In constructing a cell, the female first forms the bottom three or four leaves into a basal cup (Table 4). The sides of the cup are

composed of leaves overlapping one another around the walls of the tunnel and fitted into the basal cup so that the basal leaves are usually entirely covered (Figure 1).

Series of cells are most common, although mats of closely compacted interwoven cells have been observed under siding boards of buildings (Figure 14). As Stephen and Torchio (39) point out, each female still tends to arrange her cells in normal linear fashion within the mat.

Stephen (36) has also observed situations in which females constructed cells parallel to one another. These females, unable to find more suitable nesting sites, used a shallow knot hole, approximately three-quarters of an inch deep and one inch wide, for cell construction. Because of the shallowness of the cavity, only one cell could be placed linearly, forcing females to construct their second cell beside the first. After the depression was filled with cells, all were covered over with a number of leaf cuttings.

Cell Provisioning. After the cell cup has been completed, the female begins provisioning the cell with pollen. Since most pollen and nectar gathering by M. rotundata occurs on alfalfa, the following observations have been made on bees working this crop.

Foraging bees are very active, moving quickly from floret to floret. Usually, they visit one or two florets per raceme before flying to another raceme on an adjacent plant. Pollen collecting females



Figure 14. Irregular series of nesting cells formed under the siding of an old shack.

rarely visit florets which have already been tripped and will hover around or walk over a given raceme until an untripped floret is found. Furthermore, females were always observed to trip the floret when obtaining nectar or pollen. Little time is spent at each floret where females lingered only 2.0 to 10.7 seconds, averaging 4.6 seconds per visit. Where large populations of bees are found, pollen collectors appear highly excited when unable to find untripped florets. Under these conditions, bees will revisit previously tripped florets. When untripped florets are found, the duration of visits is noticeably increased over visit times when an abundance of untripped florets is available.

Tripping is accomplished by the female using her legs to brace herself on the keel and wings of the floret, then forcing her head and proboscis along the inside edge of the standard pushing down on the keel and wings at the same time. This procedure facilitates the release of the sexual column which has been kept under tension within the enclosed keel.

When the scopa of a foraging female becomes laden with pollen grains, she returns to her nesting site. Upon landing on her straw, the female proceeds head first to the cell cup in which she will place her pollen load. Within the cup the female examines the contents with her antennae. If a pollen load had been deposited the trip before, the female will use her head to compact the pollen mass. She may or may

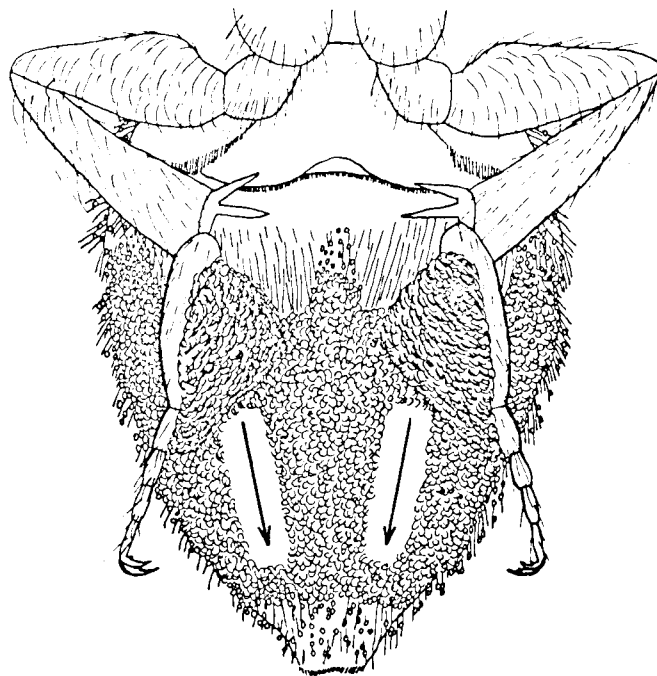
not add nectar to the pollen, depending upon its viscosity. Once the pollen mass has been compacted to her liking, the female backs out of the nesting tunnel, turns around at the entrance and backs down the cavity to her cell. In tunnels with diameters of six millimeters or greater, females are able to turn around without first backing out of the straw. In the large straws, females were observed to simply back out of the cell, somersault, and back into the cell.

After backing into her cell, the female supports herself with her fore and middle legs and uses the hind legs to remove pollen from the scopa. Pollen removal is accomplished by combing movements of the densely haired hind tarsi. As the hind legs scrape the pollen from the scopa, they move in a sifting fashion presumably to break up clumps of pollen (Figures 15, 16). Simultaneously, the hind legs spread it over one-half of the surface of the provisioning area. The following pollen load is usually deposited over the remaining one-half of the cell face. This behavior insures an even distribution of pollen over the bottom of the cell.

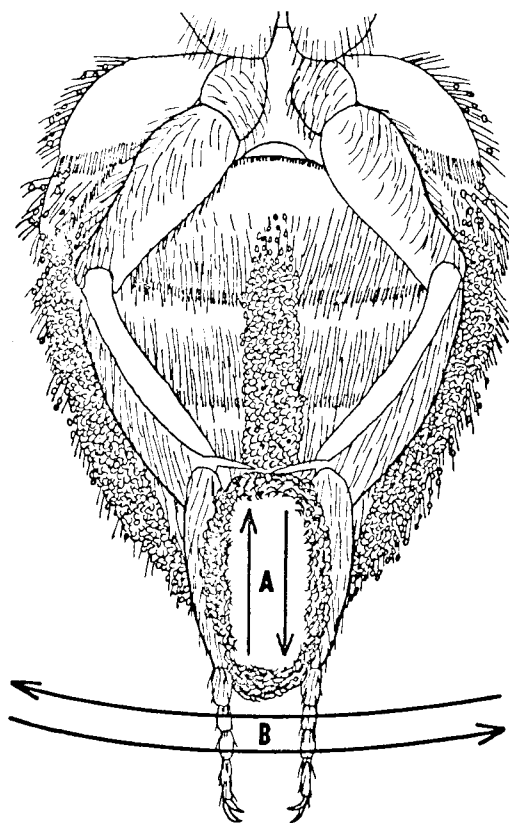
The manner in which pollen is removed from the scopa is quite similar in most females of the species. Pollen is first removed from those areas laterad of the meson leaving pollen along the meson and lateral portions of the scopa (Figure 17). It is next brushed from the peripheral portions and followed by scraping the remaining grains from the middle of the scopa (Figures 18, 19). After the bulk of

Figure 15. Ventral view of the abdomen of a female Megachile rotundata illustrating the manner by which pollen is brushed from the scopa. Arrows indicate direction in which legs are moving.

Figure 16. Ventral view of the abdomen of a female Megachile rotundata illustrating the manner in which pollen is distributed in the cell. A and B indicate simultaneous movements of the legs in the directions indicated.

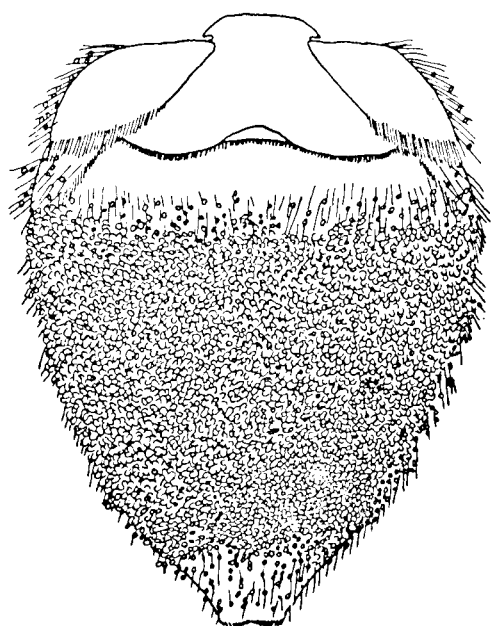


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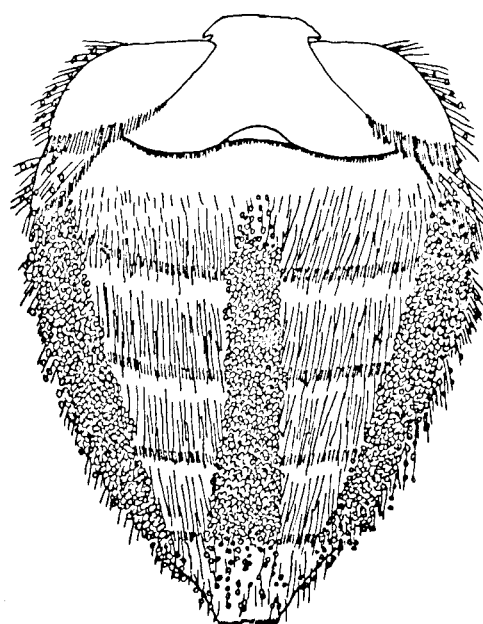


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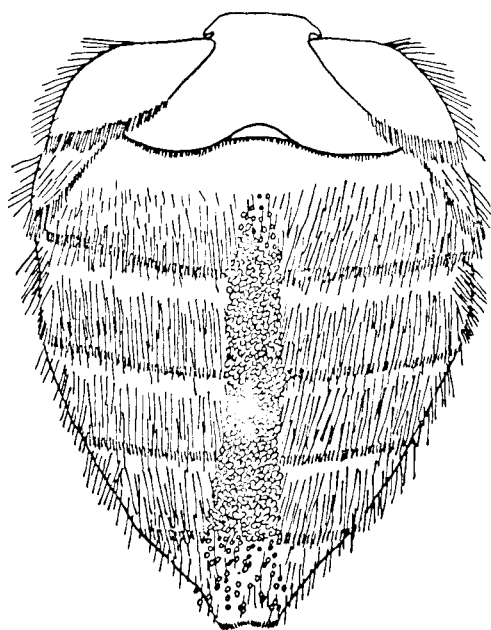
Figures 17-20 Ventral views of the abdomen
of a female Megachile rotundata
illustrating the sequential re-
moval of pollen from the scopa
by the legs.



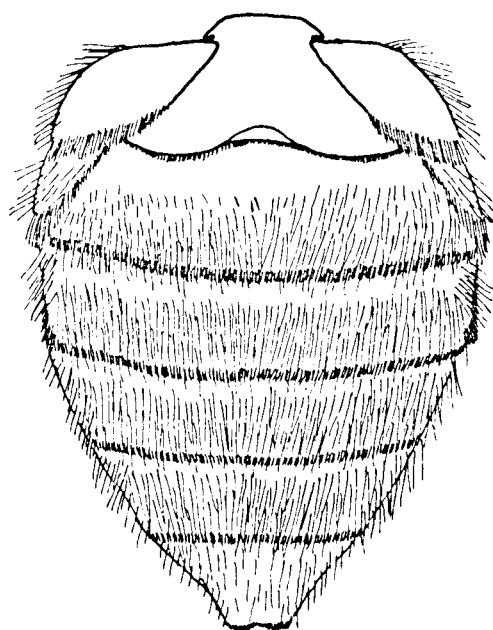
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20

pollen is removed several full length sweeps of the scopa are made (Figure 20). The female usually returns immediately to the field and pollen trips continue until about one-half of the cell volume is filled with provisions.

Nectar is used to achieve a pollen consistency suitable for larval development. Pollen masses found in most nesting cells are doughy in texture and have a thin film of nectar on the surface in which the egg is laid. On three occasions females were observed adding two consecutive nectar loads to the pollen mass before egg laying. Since the amount of surface nectar varies from cell to cell, the quantities added may depend upon the consistency of the pollen mass.

The usual number of pollen loads needed to provision a nesting cell is nine or ten (Table 6), but this varies depending upon forage conditions. On two occasions cells were followed to completion and both required nine pollen trips. Michener (26, p. 1708-1709) reports that M. brevis brevis Say required from nine to twenty pollen loads per cell. This bee is only slightly larger in size than M. rotundata but is highly polylectic. It may be that some of the pollen sources of M. brevis brevis have pollens which are not as well suited for collection as is that of alfalfa, thus requiring more pollen trips per cell. For example, pollen grains which are too large to pass between or perhaps too small to be retained between the scopal hairs would present collection difficulties. Pollen characteristics such as stickiness,

spines, or other modifications would greatly influence collection and retention within the scopa. This species has been reported foraging on members of the plant family Onagraceae having webbed pollen which may cover the scopal hairs preventing the use of spaces between the hairs. Each collecting trip does not result in full utility of available pollen transport space and more visits are required to adequately provision each cell.

Oviposition. After the pollen mass has been polished and coated with a thin layer of nectar, it is ready to receive the egg. The female backs into the cell and positions herself so that the apex of her abdomen is almost touching the pollen mass. Holding onto the upper wall of the cell she curves the apex of her abdomen up. The egg is then exuded from the body and the abdomen gradually straightens to allow proper placement of the egg on the pollen mass. The female crawls out of the cell and often is observed to back in and out or rotate within the nesting tunnel before leaving to bring in leaves for the cell cap.

Cell Capping. With provisioning and egg laying completed, one or two leaves are used to cover the cell (Table 4). These leaves are circular and slightly larger than the interior diameter of the cell. Each cap leaf is depressed into the cell and molded to the cell wall along its entire periphery. Enough space is provided between the cap and cell provisions to accommodate the rapid growing larva. After

capping the cell, the female begins the construction of another cell above the one completed if enough space is available.

Aperture Capping

Upon capping the last cell in a given series, the female begins plugging the nesting tube entrance with leaf cuttings. As each leaf is brought into the nesting tunnel, the female masticates its perimeter before fastening it to the tunnel wall and to the leaves immediately below it. Successive leaves are not placed on top of one another, but usually are arranged alternately. This staggered leaf arrangement keeps the surface of the plug slightly concave throughout most of its construction. Each bee continues to add leaves to the plug until the surface of the nesting tunnel is reached. The last few leaves used in the plug are molded tightly to the substrate and excess portions of leaves are cut off and discarded. This is especially evident when bees are nesting in drinking straws. They almost always trim the outer cap leaves so that no overlap remains, thus tightly sealing the entrance. The finished plug is flush with the surface of the medium in which the bee is nesting.

The number of leaves used to cap the entrance of the nesting tube varies from 24 to 85 (Table 4). Further, the number of leaves used to plug the aperture appears to be independent of the tunnel diameter.

In many nesting tubes gaps are present between the last cell to be constructed and the entrance plug. This space is usually quite short, but may be two, three, or more inches in length. When larger gaps occur, nesting tunnels usually contain only one, two, or in many cases, no cells at all. This behavior pattern appears to be closely associated with senility and is discussed in greater detail under the section dealing with age.

In addition to protecting cells against adverse environmental factors, entrance plugs also protect nesting cells from biotic sources. With one exception, aperture plugs were never observed to have been ruptured by bees or other insects from the outside. In this instance, birds had mutilated the domicile in search of larval bees. Entrance plugs are therefore quite important in protecting developing bees.

Age

Older bees are characterized by having pile worn from the head, thorax, and dorsum of the abdomen, making them appear quite black when compared with young bees (Figure 21). Wing margins also become quite tattered, making flight difficult.

With advancing age, behavioral changes are also noted. Cell construction is not as rapid, and leaves are often misplaced, often resulting in the deposition of unorganized leaves that fill the entire tunnel. Nesting tunnels without cells or with only a single cell are often



Figure 21. Female of M. rotundata on straw domicile.

capped by an old bee. Cell provisions are at times inadequate for larval growth, and observations have been made in which second instar larvae were found without provisions to complete development.

Associated with age-induced anomalies in the cell construction are changes in foraging activities. Old bees are much more frequently observed resting and for much longer periods of time than younger bees. In addition, the onset of morning activity is frequently delayed.

It was observed that towards the end of the flying season the behavior pattern of old as well as young bees was modified. Both were observed capping straws in which cells had not been constructed. Cells were also not constructed to the perfection observed earlier in the season, for often the cups were poorly formed or pollen provisions were inadequate.

It is difficult to account for the anomalous behavior in both old and young bees late in the season. Possibly a reduction in the mean daily temperature and cooler nights may initiate similar responses regardless of age. Deleurance (6; 7) was able to block ovary function in fertilized females of Polistes wasps by subjecting them to 0 degrees C. for 22 hours then increasing the temperature to 25 degrees C. Females treated in this manner developed behavior patterns similar to the worker caste.

A similar physiological response may be established in M. rotundata by decreasing temperatures which would then explain similar

behavior of old and young bees at the end of the flight season.

Orientation to Nesting Site

Once a bee has established herself at a nesting site, her departures for food from the site are usually direct, without further orientation. Upon returning to the nesting site, bees usually land on or in close proximity to their own tunnels on the first approach and enter directly. At times a bee may walk over a few straws, pausing to stick her head into several straws for examination before she locates and enters her own. If, however, the bee is unable to find her tunnel during the first few examinations, she will enter several others and become increasingly excited. When bees are confused, they are characteristically much more active than normal. Typically, perplexed bees hastily examine straws, take short flights after which they return to continue their search.

When nesting alone or where the number of nesting tunnels in the immediate area is small, bees seemed to have less difficulty orienting to their particular tunnel than when numbers were large. For example, in straw domiciles where each box contained from 150-250 similar straws, orientation was often difficult (Figure 8). Bees usually exhibited some difficulty in relocation even after they had constructed several cells within the same straw. However, the use of markers at these artificial domiciles reduced orientation difficulties.

A four square foot section of white, perforated acoustical tile with 2116 uniformly spaced holes was presented to a nesting bee population (Figure 22). Upon accepting a tunnel, the female presumably flew from the site to secure a leaf cutting. However, on her return she was unable to locate her nesting tunnel and became one of the large number of similarly disoriented bees hovering in front of the domicile. After about a month without orientation markers, only a few holes about the periphery had been plugged with leaf cuttings. Using black spray paint, two diagonal bands and four letters were sprayed on the white surface of the tile (Figure 22). Females began accepting holes immediately and proceeded to return with leaves for cell construction. Within two weeks, most of the holes were plugged. Bees displayed a tendency to nest in holes within or immediately adjacent to marked areas, a pattern which was also noted on wooden nesting boards sold commercially, and upon which large trade marks were stamped. Those holes around trademarked areas as well as those about knots in wood were the first to be occupied (Figure 11).

It appears that the bee orients herself, at least in part, to characteristic markings or objects at her nesting site. These general visual characteristics seem to aid the returning bee in finding the approximate location of her nesting tunnel within a given domicile. It is believed that visual orientation is used predominately by M. rotundata, for this bee seems unable to reorient when placed in an

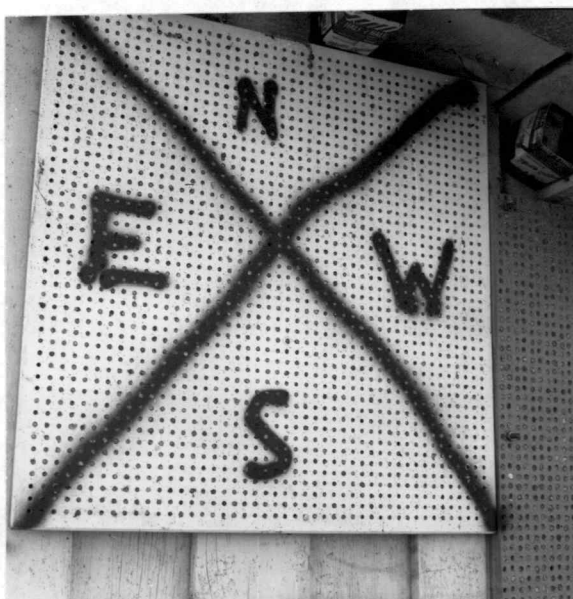


Figure 22. Section of acoustical tile used as a nesting domicile by M. rotundata. Markings were applied to aid bees in orientation to their nesting tunnels.

unfamiliar area.

After the bee has landed on the domicile, stimuli other than visual must assume predominant roles, particularly in domiciles with large numbers of identical tunnels. Perhaps secretions liberated by the bee are definitive enough to aid in locating a given tunnel. Possibly the bee is able, through tactile means, to find her own tunnel. These questions prompted the experiments described below.

Using the mailing tube domicile with divided straws described under Methods and Apparatus, a series of straw manipulations were made (Figures 3, 4). It was felt that removal or displacement of various parts of a bee's nesting tunnel would give some indication as to the nature of the stimuli associated with tunnel recognition. By replacing the outer half of an occupied straw with a new piece while the bee was foraging, it was hoped to determine if tactile and olfactory stimuli might be associated with it.

Test 1 -- The top one inch section of a straw in which a bee was nesting was replaced by another of similar length. Upon returning with a leaf, the bee walked over its own straw and then on to adjacent straws, turned and went directly into its own straw.

Test 2 -- As in test 1, except that when the top section of straw was removed, a cell, being constructed at the juncture between the top and bottom straw

sections, was somewhat disturbed. Upon its return, the bee proceeded directly to its own tunnel except that it went in and out three times before accepting it as its own and placing the leaf in the straw.

The behavior observed in Test 1 is characteristic of most bees returning to their own tunnel in an undisturbed domicile. Lack of adequate markers to aid in orientation is probably responsible for occasional misjudgment and confusion by returning bees. Test 2 indicates that disruption of the cell under construction confused the returning bee. This suggests that a tactile stimulus associated with the stage of cell construction or with the position of the cell in the tunnel may be highly significant. If the stimulus was primarily associated with an odor secreted at the tunnel entrance, it would be expected that the bee would not have accepted its tunnel when the outer half was removed.

Further experiments were undertaken to test the premise that tactile response to the cell was significant in locating the correct nesting tunnel.

Test 3 -- The bottom half of a straw in which a bee was constructing a cell was removed and replaced with a new one inch piece of straw. The bee returned with a leaf and went in and out of its own straw three times, backing out with the leaf and crawling over adjacent straws before

reentering. After the third entrance into its own straw, the bee went into one of the adjacent straws and repeated the behavior outlined above. On the fourth time, the bee left the leaf in the adjacent straw and departed from the domicile. The leaf was not placed in a manner indicative of cell construction but, rather, abandoned. It is assumed that the bee departed in confusion at being unable to locate its own straw and was not prepared to accept the new straw for nesting.

Test 4 -- The top half of a straw was removed, leaving the bottom half in situ before any bee had accepted the tunnel for nesting. The straw was accepted soon afterward and the test begun when the bee had completed the cell cup and was foraging for pollen. A one inch piece of straw was placed on top of the section in which the bee was working, thus making the tunnel the same length as those adjacent to it. The returning bee approached several times, each time walking across several straws within the area and then taking a short flight before returning. She then went into an adjacent straw, backed out, reoriented, and went into her own straw in which she deposited her pollen load.

Tests 1 and 4 demonstrate that once the bee had located its proper straw it accepts it immediately without further searching. Test 2 appears to indicate that immediate acceptance is only accomplished when the cell contents are not disturbed.

In the process of rotating or moving domiciles many bees developed unusual patterns of approaching their nesting tunnel. One bee always returned from the field to a straw which was seven straws removed from the one in which it was nesting. Upon landing on this straw, the bee would pivot 90 degrees and crawl directly to its own tunnel. It was believed that the bee's own tunnel may have been located originally at the landing place, but she now had found it at its new location, or accepted another tunnel in the same stage of construction. Instead of modifying her approach to the new site, the bee was following the stimulus that had proved successful in locating her nesting tube at its original position.

A second bee was observed capping the entrance to its nesting tunnel. While the bee was out in search of another leaf, the straw was moved two straw widths away. On the first two returns the bee was confused and examined several straws before finally locating and accepting her own. On the third and fourth trip, she was less confused and found her straw with greater rapidity. On the sixth trip the bee turned around once at its old location and went directly to the new one.

The above tests indicate that gross orientation to the nesting site is achieved predominantly by visual means. It appears that when a foraging female returns from the field, she orients first on the general characteristics of the overall nesting site. As she gets closer, the domicile imparts the orientation stimulus and she finally lands at or near her nesting tunnel. Once at her nesting tunnel, characteristics of the cell which she is constructing seem to provide the stimulus that determines final acceptance or rejection. Whether the cell stimulus is tactile, olfactory, or a combination of both is difficult to determine and further work is needed on the problem.

Color Orientation. During the summer of 1962, domiciles composed of straws of several colors were placed at two locations in the Boardman area. In some, the straws of an entire box were of one color, while in others they were mixed. There was no evident preference for one straw color over another, a conclusion also reported by Stephen (35, p. 11-12). Bees nesting in one domicile, evidently emitted an attractant which resulted in the congregation of other females in that immediate area. The acceptance and occupation of a given domicile was thus not color determined, but rather contingent on the chance occupation of a domicile by the first searching bee.

Further studies were conducted during the summer of 1963, using white straw domiciles containing a number of different colored straws (Figure 2). It was observed that bees reestablishing

themselves in the new domiciles demonstrated no preference for colored over white straws. However, this behavior could have been in part due to the bee selecting a straw in the same approximate position that it had occupied in the removed domicile.

Von Frisch (11) explained that the ability of bees to distinguish among colors does not prove that they have a color sense or color perception. Bees could be color blind, characterizing colors only by their varying shades of grey. However, von Frisch was able to show that the honeybee was able to perceive four color qualities: yellow, blue-green, blue, and ultraviolet.

The following experiments were undertaken as initial studies on the color perception ability of M. rotundata. Several domiciles were prepared, each containing different numbers and arrangements of colored straws (Figure 2).

Domicile 1 -- Four straws, a red, yellow, green, and a blue, were located approximately one inch from each of the four corners of the domicile. After two days, the domicile contained 14 nesting bees, one in each of the yellow and green straws, and twelve in white straws. Each bee nesting in the colored straws was marked.

The box was turned one quarter of a turn, moving the yellow straw five straws to the left of its original position. In spite of this displacement, the returning

bee went directly into the yellow straw without hesitation. In fact it was observed that regardless of the location of the yellow straw within the domicile, the bee always returned directly to it. This behavior was in marked contrast to other bees nesting in the domicile which were hovering in front of it unable to locate their nesting tunnels during the two hours of observation.

The domicile was then returned to its original position to enable the disoriented bees to relocate their proper straws. It was again rotated one-quarter turn and the activities of the bee working in the green straw were observed. This rotation placed the red straw at the site previously occupied by the green, and the latter approximately two inches away from its original location. Upon her return, the bee first hovered before the red straw, then flew directly to the green straw, hovered, and entered. It appears that the bee was able to distinguish green from red although not as clearly as yellow from the other colors present in the domicile. Von Frisch indicates that honeybees are unable to discern red in the color spectrum, recognizing it only as a shade of grey (11).

The tests indicate that leafcutter bees are able to distinguish among yellow, green, red, and blue. Since yellow and green have

similar wave lengths in the color spectrum, a second domicile was designed to determine if leafcutter bees could critically distinguish various shades of these colors. Von Frisch's work with honeybees demonstrated that they were unable to separate the two colors. However, Kühn and Fraenkel (18) feel that the honeybee can distinguish between the two colors for two groups of bees, one trained to the yellow portion of the color spectrum and the other to the green portion, seemed to demonstrate a preference for the color to which they had been trained.

Domicile 2 -- Four straws ranging from yellow to yellowish green: shade one (saffron yellow 4A8), shade two (yolk yellow 4B8), shade three (3C8), and shade four (30C8) were placed in a domicile and manipulated in a manner similar to that described for Domicile 1 (16). It was found that leafcutter bees were unable to distinguish among these color shades, for bees visited colored straws interchangeably when unable to locate their own.

Using Domicile 2, a purple and blue straw were used to replace shades two and four in which bees were nesting. It appeared from these experiments that blue and purple straws were distinctly different from the other colored straws and therefore immediately recognized by the returning bee. Other experiments with blue

and purple straws indicated that the bee could not distinguish between the two colors. Stephen (36) performed similar experiments in which he found bees able to distinguish red from purple and also yellow from green straws.

The bee is unable to distinguish among metallic colors such as copper, gold, and silver. Clusters of colored straws seem to be distinctive for the bee, even though the individual straw colors in the cluster are not. One cluster of four straws contained the following colors: copper, gold, Sahara 6C5, reddish-brown 8E8 (16). When the domicile was rotated, the returning bee went first to the old location of the cluster, reoriented, and flew directly to the cluster in the opposite corner of the domicile.

Many bees found their straws through trial and error when the domicile was rotated, especially when it was only a few straws away from its original position. The capacity for color recognition is sometimes difficult to distinguish from general searching. Occasionally a bee trained to a given colored straw appeared to recognize it quickly, while other bees trained to the same color are unable to detect it.

When a bee is unable to find her displaced straw, she usually flies from the nesting site, returning after a short period of time. If during this period, the straw is returned to its original position, the bee often would go directly into it, although frequently she would back out a number of times and visit adjacent straws. The bee was confused by its own nesting tube with its undisturbed cell contents. It appeared that as the length of the period in which the bee was separated from its tunnel increased, the bee exhibited more confusion and excitement. However, a few observations have been made in which the bee reaccepted its relocated tunnel immediately.

From these experiments, it is apparent that the leafcutter bee is capable of distinguishing among certain colors, but proof of actual color perception was not demonstrated. In order to demonstrate color perception in M. rotundata additional, more critical experiments must be performed.

FORAGING BEHAVIOR

Pollen Sources

Stephen and Torchio (39) and others have indicated that M. rotundata will visit alfalfa in preference to other plants within a given foraging area. This preference for one, or a limited number of plant species, is termed oligolecty and according to Stephen (34) several species of Megachile show oligolectic tendencies toward alfalfa.

The term oligolecty was proposed by Robertson (29, p. 413) to apply to those bees collecting pollen only from related plant species within a given family. In addition, he proposed the terms monolecty and polylecty to refer to those bees working a single or a number of unrelated plant species respectively. Stephen and Torchio (39) further defined those bees showing definite preferences for one or more plant species, but foraging others when they were unavailable, as being preferentially oligolectic. This term is applicable for M. rotundata.

As indicated in Table 5, M. rotundata forages a number of unrelated plant species which would tend to increase its survival potential when alfalfa is unavailable. The plant list in Table 5 is by no means complete for pollen analyses of cell provisions taken from area III yielded a variety of unidentified pollens. Possibly plants from other areas have been also overlooked.

Table 5. Plants which Megachile rotundata is reported to forage.

<u>Plant Families</u>	<u>Plant Species</u>	<u>State and Reference</u>
Boraginaceae	<u>Heliotropium oculatum</u> Heller = <u>Heliotropium curassavicum</u> L. var. <u>oculatum</u> (Hellar) I. M. Johnston ex Tidestrom	California (15)
Chenopodiaceae	<u>Salsola kali</u> L. var. <u>tenuifolia</u> Tausch	Oregon*
Compositae	<u>Chrysopsis villosa</u> (Pursh) Nutt.	Oregon*
	<u>Chrysothamnus</u> sp.	Oregon (35)
	<u>Cichorium intybus</u> L.	Oregon* Pennsylvania(15)
	<u>Centromadia pungens</u> Greene = <u>Hemizona pungens</u> (H. and A.) T. and G.	California (15)
	<u>Cosmos</u> sp.	California (15)
	<u>Machaeranthera canescens</u> (Pursh) Gray.	Oregon*
	<u>Solidago</u> sp.	California (15)
	<u>Taraxacum officinale</u> Weber	Oregon*
Cruciferae	<u>Sisymbrium altissimum</u> L.	Oregon*
Euphorbiaceae	<u>Euphorbia marginata</u> Pursh	Missouri (5)
Labiatae	<u>Mentha crispa</u> L.	Missouri (5)
	<u>Salvia greggii</u> Gray	Texas (5)
Leguminosae	<u>Melilotus</u> sp.	Utah (2)
	<u>Trifolium repens</u> L.	Utah (2)

*Plants included from this study.

Table 5 (continued)

<u>Plant Families</u>	<u>Plant Species</u>	<u>State and Reference</u>
Lythraceae	<u>Lythrum salicaria</u> L.	Texas (5)
Malvaceae	<u>Malva rotundifolia</u> L. (nectar only)	Oregon*
Plumbaginaceae	<u>Statice</u> sp.	Missouri (5)
Polygonaceae	<u>Polygonum aubertii</u> L.	California (15)
Scrophulariaceae	<u>Leucophyllum frutescens</u> Johnston	Texas (5)
	<u>Veronica longifolia</u> L.	Missouri (5)

*Plants included from this study.

Michener (26, p. 1679) found that M. brevis brevis although polylectic, demonstrated a preference for blue or purple flowers and tended to avoid the yellow. This was not the case with M. rotundata on alfalfa, for this bee did not exhibit color specificity even in varieties possessing multicolored florets. Further, no color preferences were observed in area I where M. rotundata foraged a number of plant species.

Franklin (10, p. 30) working with M. brevis and M. texana in Kansas also reported no color preferences although he noted that these bees appeared to have more difficulty tripping light colored than purple alfalfa florets. M. rotundata did not exhibit any such difficulties but there is a possibility that this may be due to varietal differences in alfalfa.

Individual bees did, however, seem to favor one plant over another, but this could reflect differences in nectar qualities rather than flower color. Such bees would visit several florets per raceme and several racemes on a given plant before moving to another plant. On a number of different occasions bees favoring a particular plant would return to it after a few visits to other plants.

Pollen Collection

As discussed in the section on cell provisioning, females work rapidly on alfalfa spending only a few seconds at each floret before

moving on to the next. However, foraging manner on composites differs considerably from above. On these plants bees usually spend more time at each flower head.

Observations on hairy golden aster, Chrysopsis villosa (Pursh) Nutt., will serve to illustrate foraging manner on composites. Upon landing on a flower, the bee rotates its body and at the same time thrusts its proboscis into many of the disk flowers. Similar behavior was reported by Michener (26, p. 1685) for M. brevis brevis. In both species the abdomen is held at about a 45 degree angle throughout foraging activities. As the body rotates, the tibiae and densely haired tarsi of the hind legs, brush the pollen from the anthers of the disk flowers. Once the tarsal hairs have become saturated with pollen the hind legs are extended and brought together. Michener (26, p. 1685-1686) suggests that pollen from the fore and middle legs is transported to the hind legs and from them to the scopa. The hind legs are lifted simultaneously and drawn forward so that the pollen is brushed onto the hairs of the scopa. On the semi-erect abdomen the sternites are separated, causing the hairs of the scopa to be spread. As the tibia and tarsi are brushed across the scopa, the pollen grains fall into the area between the hairs. In flight, the bee again lowers the abdomen parallel with the rest of the body, which serves to compress and hold the pollen securely during flight.

Pollen collecting bees rest infrequently when air temperatures

are high. As temperatures fall, there is a noticeable increase in time spent at each floret and in the frequency of rest periods. Resting bees usually land on the ground when in the field. Rest periods are usually short with the bee either remaining motionless or preening itself with its legs.

Because of their small size and rapidity of flight, foraging bees are extremely difficult to follow in the field. The number of alfalfa floret visits necessary before a bee has acquired a full load of pollen must therefore be extrapolated. One bee watched from the start of one cell to its completion required an average of 20:16 minutes to secure each of nine pollen loads (Table 6). If half of this time is devoted to movements from one floret to another and flights to and from the nesting area, then 10:08 minutes were spent visiting florets to secure each pollen load. Considering that each floret visit averages 4.6 seconds (based on 34 observed visits) then approximately 132 floret visits are necessary for each pollen load. These figures approximate those calculated by Stephen (31) for M. frigida and M. latimanus. It should be noted that these data were collected where abundant bloom was available close to the nesting site and would be expected to vary with foraging conditions. The rapidity with which M. rotundata forages enhances its value as a pollinator of alfalfa.

Bees show irregular foraging behavior when plants on which they have been foraging are suddenly removed. Such was the case in

Table 6. Time periods required to construct and provision a nesting cell.

<u>Trip</u>	<u>Material</u>	<u>In Tunnel</u>		<u>Out of Tunnel</u>	
		<u>Minutes</u>	<u>Seconds</u>	<u>Minutes</u>	<u>Seconds</u>
Before Observation Began	leaf	--	--	--	--
3	leaf	--	--	4	58
4	leaf	2	38	4	35
5	leaf	2	44	3	9
6	leaf	3	16	3	29
7	leaf	3	9	4	15
8	leaf	3	12	30	50--Bee returned at 27 minutes (nectar?)
9	leaf	4	44	5	26
10	leaf	3	28	3	19
11	leaf	3	43	3	5
12	leaf	5	1	4	44
13	leaf	6	7	4	8
14	leaf	6	16	4	4
15	leaf	3	13	21	40
16	pollen	2	11	19	10
17	pollen	2	51	22	41
18	pollen	1	35	17	9
19	pollen	3	22	17	28
20	pollen	1	58	17	57
21	pollen	0	58	18	48
22	pollen	1	18	21	35
23	pollen	1	6	28	5
24	pollen	0	42	28	5
25	nectar	0	50	26	43--Deposited nectar and polished pollen mass
26	nectar	4	0	4	36--Nectar and layed egg
27	leaf	--	--	--	-- Cell capped

Area I when an alfalfa field in which bees were working was cut for hay. Females collecting pollen in this field were forced to seek out volunteer alfalfa growing along its periphery, causing inconsistencies in the length of time necessary to obtain leaves and pollen loads. The leaf and pollen collecting periods of one such bee are given in Table 7. It will be noted from Table 7 that the length of time necessary to secure leaves and pollen is quite erratic when compared with the relative uniformity in time necessary for provisioning trips in Table 6.

Table 7. Time periods required to construct and provision a nesting cell (after foraging source removed).

<u>Trip</u>	<u>Material</u>	<u>In Tunnel</u>		<u>Out of Tunnel</u>	
		<u>Minutes</u>	<u>Seconds</u>	<u>Minutes</u>	<u>Seconds</u>
Before Observation Began	leaf	--	--	--	--
	leaf	--	--	3	51
3	leaf	2	30	2	53
4	leaf	5	58	1	40
5	---	2	0	7	8
6	leaf	3	34	25	27
7	leaf	1	6	11	31
8	leaf	4	26	1	8
9	---	1	14	7	14
10	leaf	1	43	4	16
11	leaf	4	45	7	37
12	leaf	5	47	26	42
13	leaf	7	21	4	22
14	leaf	5	31	46	31
15	pollen	2	3	16	55
16	pollen	2	56	53	48
17	pollen	3	12	End Observation	

Foraging Range

Tables 8 and 9 present data taken on bees foraging within alfalfa plots located in area II during the summers 1962 and 1963, respectively (Figure 23). The periods of observation were limited because these same alfalfa plots were also being used for similar range studies with the honeybee and alkali bee, Nomia melanderi.

The data in Table 8 indicate that daily throughout the observation period, bees foraged in the base plot and in plots six through ten: This range would correspond to 20 rods (110 yards) for those bees ranging into plot six and 40 rods (220 yards) when foraging into plot ten (Figure 23).

There were comparable numbers of bees in the base plot from September 17-21, which is reflected in similar nesting populations over these same days (Table 8). September 22 and 23 show a decline in the nesting population and also the number of bees foraging in the base plot. This decline, both in population and foraging individuals in the base plot, was attributed to the reduced amount of bloom available to the bees within the plot, forcing them to extend their range.

With only 504 blooming alfalfa plants within the base plot, the established bee population appeared to be large for the bloom available (Figure 6). In 1962 and 1963, the bees tripped all available bloom in the base plot within six days. Some new bloom appeared each morning, but after one or two hours of foraging, all bloom was again

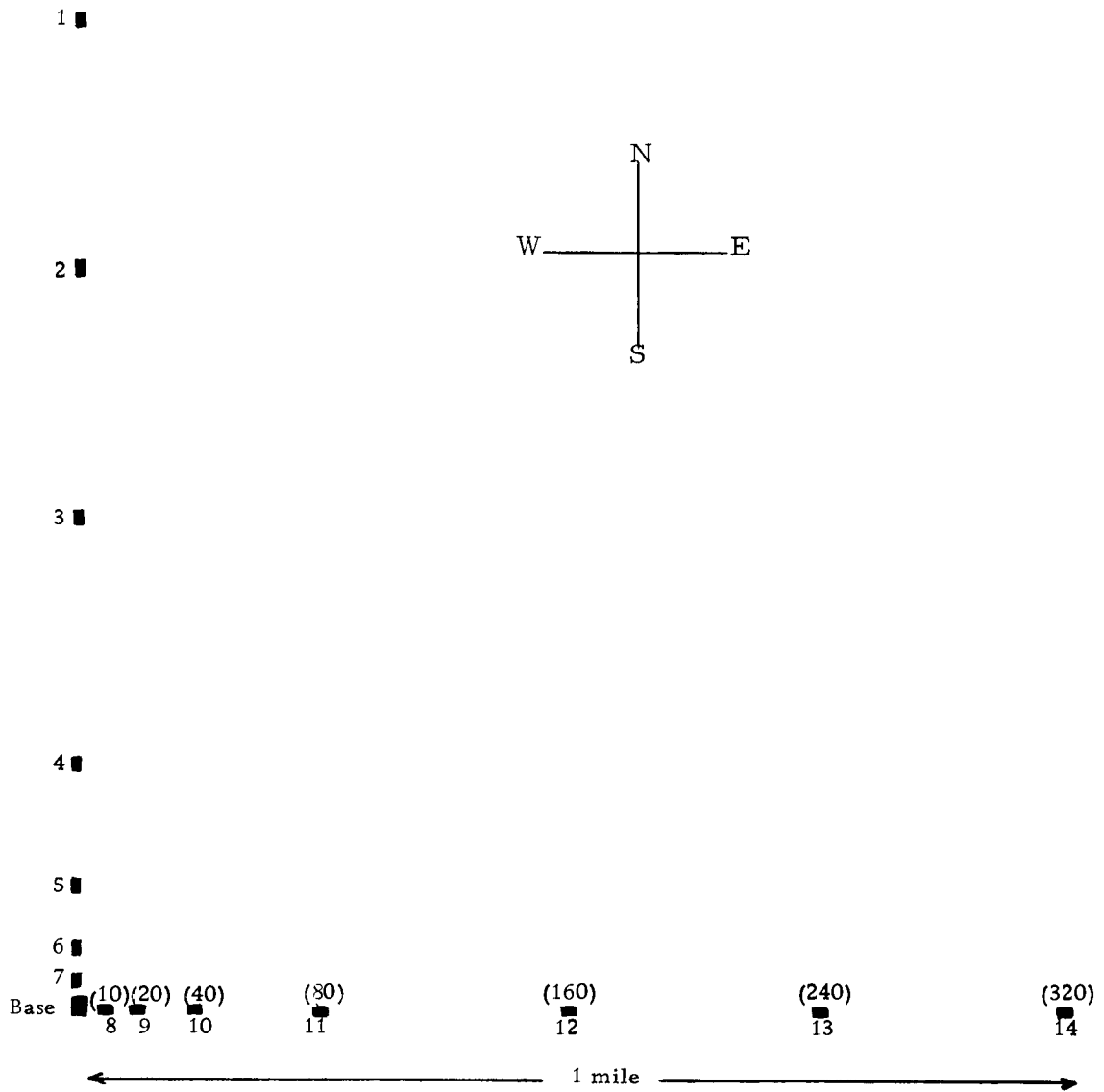


Figure 23. Boardman alfalfa plot layout (Area 2). Numbers in parentheses are distances from the base plot measured in rods. Other numbers are plot numbers. Squares indicate plots.

Table 8. Foraging range data, 1962.

	Sept. 17	Sept. 18	Sept. 19	Sept. 20	Sept. 21	Sept. 22	Sept. 23
Bee Populations --	196 ^{+50*}	227	224 ^{+321*}	274	250	202	186
Plot Numbers							
1	--	--	--	--	--	--	--
2	--	--	--	--	--	--	--
3	--	--	--	--	--	--	--
4	--	--	--	2	--	--	1
5	--	1	--	2	3	1	1
6	4	2	8	2	10	2	4
7	6	5	6	5	8	5	11
Base	13	13	13	10	15	7	6
8	9	4	9	5	10	3	9
9	7	7	3	3	7	3	3
10	2	4	1	5	6	3	3
11	--	2	--	1	3	1	--
12	--	1	--	--	--	--	--
13	--	--	--	--	--	--	--
14	--	--	--	--	--	--	--

* + the date and number of bees introduced

Table 9. Foraging range data, 1963.

	Aug. 23	Aug. 24	Aug. 25	Aug. 27	Aug. 28	Aug. 30	Sept. 4	Sept. 5
Bee Populations	+497* -- 106	+70* 210	210	169	133	135	74	64
Plot Numbers								
1	--	--	--	--	--	--	--	--
2	--	--	--	--	--	--	--	1
3	--	--	--	--	--	--	2	1
4	--	--	--	--	--	--	1	2
5	--	--	2	1	--	--	4	1
6	--	--	4	5	1	2	4	1
7	3	12	11	12	7	8	4	5
Base	21	24	26	23	26	18	15	9
8	--	5	7	5	3	4	2	2
9	1	2	5	4	7	3	2	3
10	--	1	--	--	1	3	3	1
11	--	2	2	--	--	1	1	2
12	--	--	--	--	--	--	3	8
13	--	--	--	--	--	--	4	8
14	--	--	--	--	--	--	4	1

* + the date and number of bees introduced

tripped. Little bloom in combination with the late seasonal effects appear to have contributed much to declining nesting populations and subsequent dispersal of bees towards the end of the observational periods. A similar condition was noted in 1963 (Table 9, September 4 and 5), in which the reduction in populations at the nesting site was associated with little bloom in the base plot and a wide dispersal of bees throughout the plots. It is suspected that bees found beyond two or three plots from the base did not return to the original nesting site at the base plot. They may have been searching for new nesting sites nearer plots having adequate foraging bloom. Since there were few nesting niches available in the desert and little native bloom, many of the lost bees may have died or reestablished themselves in the Boardman township about ten miles away. Occasionally, apparently lost bees were observed foraging in the plots. They were presumed to be stray bees because the plots in which they were foraging were well beyond those plots in which the majority of introduced bees were found. For example, nesting bees at the base plot ranged four plots east of the base, and no bees were observed in the fifth or sixth plots, but within the seventh a few bees were observed. Those bees in the seventh plot, which is one mile from the base, were presumed to be stray bees and were not included in the daily counts.

It was suggested above that females return repeatedly to a given source or area to secure leaf cuttings. The data in Tables 8 and 9

suggest that pollen collecting bees also oriented themselves to the plot in which they were working and returned to it on subsequent trips. This conclusion seems warranted for foraging numbers in those plots consistently frequented by bees are comparatively uniform throughout the observational period. As the bloom in plots near the nesting site was exhausted, bees moved to new foraging areas, thus accounting for dispersal noted towards the end of the period.

Bees were observed in plots other than the base plot on the day following their introduction into the experimental area in both years (Table 8, September 17; Table 9, August 23). There are at best two possible explanations for these extended ranges. If, in their original nesting location, transplanted bees had oriented themselves to particular floral locations, it is possible that upon being moved into a new area their first attempt at foraging might be to a distance comparable with that of their former floral source. It is possible that these were lost bees which happened to be foraging in these plots during the observation period.

Evaluation as to the affect of plot design on foraging behavior is difficult (Figure 23). It appears that the small plot size and wide spacing of them may produce different foraging patterns than would be observed within a solid stand of alfalfa. However, due to the small size and rapidity with which these bees forage, it would be difficult to make comparable observations in large fields. Since patterns used

by bees in search of foraging bloom have received little study, the effect of a large area with very little foraging material could introduce responses differing from those when an abundance of bloom is available. For example, if a bee searches in a generally direct course, as opposed to a random or zig-zagging manner, it is possible that she may not find the alfalfa plots in the experimental area. Chances of finding the plots are naturally greater if searching behavior is random.

Attempts were made to control stray bees as well as other endemic pollinators through the use of air and ground applications of parathion and dibrom. Netting and subsequent killing of stray leaf-cutter bees was also helpful at times. In spite of these efforts, repeated invasions by stray bees and other native pollinators interfered with the conduct of the program.

Observations were made on foraging range in other areas. A large population of M. rotundata was observed nesting near and foraging in an alfalfa field located in Area I. On July 9, 1963, this field was cut for hay. After a careful search of the area it was found that most of these bees had shifted their foraging activities from alfalfa to a one-half acre field of volunteer sweet clover, located 300 feet south of the nesting site.

Bees foraging in a solid stand of alfalfa in Area IV were observed foraging at distances of only 77 feet from their nesting shelter. It

should be noted that this observation was made in a solid stand and possibly more nearly represents foraging range when abundant bloom is available close to the nesting site. Observations indicated that bees tended to work those plants closest to the nesting site, extending their foraging range when immediate bloom was no longer available. The rapidity with which range is increased is in large part a function of bee population in a given area; that is, larger populations will increase their range faster than a small population due to more rapid utilization of available bloom.

When little foraging bloom is available and scattered over a large area, as in Area III, foraging ranges may be extensive. Maximal distances under these conditions probably are much greater than reported here.

Relocation

Several unsuccessful attempts were made in 1962 and 1963 to establish bees in Area II. Four evening introductions, totaling 1111 bees, were attempted during the summer of 1962 and of these, only 108 bees remained at the new site on the day following the last introduction. In 1963, three introductions totaling 1521 bees resulted in the establishment of only 210 bees.

The explanation for the inability to establish bees at the Boardman site and other locations when first attempted is unclear.

Observations of bee behavior on the morning following a move into a new area seem to indicate that high losses in populations occur because bees fail to re-orient to their new surroundings. Bees were observed hovering in front of their domiciles without cell provisions, obviously disoriented, trying to find their proper nesting tunnel. Many bees presumably flew away from the new area without reorienting themselves and were lost. Therefore, most attempts at relocating bees within a new area resulted in as high as eighty percent loss in bee populations.

As discussed in the section dealing with orientation, bees orient themselves by visual means to their nesting site. Therefore, when bees are brought into a new area, this visual stimulus is lost, resulting in the disoriented behavior described above. Stephen (36) relates an experiment in which domiciles containing bees were transferred at night from the edge of one alfalfa field to another located 250 to 400 yards away, but still within sight of the former nesting site. The following morning almost 100 percent of the relocated population had returned to its original nesting location. Transfers were repeated on following days but with bees first being refrigerated at 40 degrees F for periods of 24, 48, and 72 hours respectively. It was found that results were comparable with those above when not refrigerated, all bees returning to their original nesting area.

Weather conditions could be in part responsible for unsuccessful

bee introductions. Prevailing westerly winds were at times quite strong in Area II and could have sided in orientation problems for the bees. For example, during 1962, strong winds the day after one introduction were believed responsible for failure of the bees to establish.

It appeared that if a large working population was already established within an area previous to a new introduction, the percentage of introduced bees which remained in the area was much greater. An introduction of approximately 70 bees resulted in almost 100 percent of the bees remaining when a working force of 106 bees was already there. Unfortunately, similar attempts have at times proved unsuccessful.

Several methods were attempted to increase the number of bees remaining after they were moved to a new location. Cooling bees within their domiciles at 40 degrees F. for periods of from one to three days before placing them in a new area seemed to have little effect on the success of establishing them at a new site. It was thought that varying periods of cold might erase orientation patterns so that the bees would reorient when placed in the new location.

Several populations of bees were introduced into screen cages in a new area. It was reasoned that after a period of time the cage could be removed and the bees would remain within the area. Cages were constructed over blooming alfalfa plants, thus making adequate

foraging material available. Bees in general did not take well to confinement and were observed flying into the sides of cages in attempts to obtain freedom. One introduction of 168 bees into a cage in 1962 had only five living bees after three days of confinement. Most bees died in attempts to get out of the cage. Other treatments consisting of refrigeration similar to that described above and then confinement for varying lengths of time in cages also proved unsuccessful. Bohart and Pedersen (3) also observed bees attempting to free themselves when caged. They were, however, successful in establishing bee populations under caged conditions, although presumably using techniques similar to those which had failed in our experiments.

It was concluded that once adult bee populations became established at a given location, high losses followed when they were moved into a new area. This loss appeared predominately due to an inability of this bee to reorient to a new location.

With our present knowledge of M. rotundata, adult relocation is not economically advisable. However, populations have been successfully moved when bees are in immature stages. Adults then emerge and establish in the new area.

Morning and Evening Behavior

Females spend the night in their nesting tunnels while males usually spend the night clustered together in various protected places.

As evening approaches, both seek their respective overnighting places.

Females preparing for the evening make several short flights to and from the nesting site before settling down for the night. Frequently they are observed moving in and out of their nesting tubes presumably cleaning or examining it. Night is spent with the apex of the abdomen facing the tunnel entrance except in late season, when quick drops in temperature may immobilize bees before they are able to assume their normal sleeping positions.

As temperatures begin to rise in the morning, the first signs of activity are noted. There appears to be two temperature thresholds which must be reached before females begin flying each morning. The first is an activity threshold, below which little movement of the bee is observed. Once this point is reached, females begin moving their abdomens up and down or stroking their abdomens with their hind legs. Activity gradually increases until the female backs out of her tunnel usually turning around at the entrance and backing into her nesting tube again. The female remains at the tunnel entrance until her body temperature reaches the flight threshold before leaving her nest. Exit from the nesting site is usually abrupt.

The onset of morning bee activity is influenced by several other factors which may account for variations in the time at which females take flight. The depth at which a given female spends the night in her tunnel is important in determining how soon she will become active in

the morning. Usually those females which pass the night nearest the entrance of their nesting tunnels warm up more rapidly and are, therefore, first to become active in the morning. Late in the season when night temperatures are very low, morning bee activity is delayed until domiciles and bees warm from initially lower temperatures than are present during warmer periods of the flight season.

The type of medium in which the bee is nesting and the manner in which heat is conducted through it would influence how soon bees become active in the morning. Age of individual females may influence the rate of metabolic activity and subsequent flight from the nesting site.

On warm mornings, bees either leave their nesting tubes directly or hover before the entrance prior to beginning foraging activities. Often when air temperatures are not quite high enough for flying, bees may land on objects around the nesting site. Here bees are often observed to rest on bright surfaces, either sitting quietly or preening themselves with their legs. After a sufficient warming-up period, bees leave the nesting site to begin foraging activities. This resting or warming period is much more common and prolonged towards the end of the flight season as mean night and day temperatures decrease.

There is much individual variation in the time of evening flight cessation. For example, at one straw domicile, the first bee took flight 23 minutes before 50 percent of the bees in that domicile began

foraging. Comparable variation is evident in the evening when many bees are often situated for the night while other bees are still foraging or returning to the nesting site. This evening variation is possibly related to distances of foraging localities, or as Stephen (36) suggests, to age differences within the female population. The type of provisioning trip may also be a factor. For example, pollen trips require much more time than those to obtain leaves for cell construction. Since pollen trips may take as much as 20 or more minutes, females may not return to the nesting site until a full load of pollen has been collected, thus delaying evening flight cessation.

Climatic Conditions and Flight

It has long been observed that weather, particularly factors of temperature, light, and wind greatly influence flight activity of bees. Since bees vary in their requirements for these factors it was desired to delineate those necessary for flight in M. rotundata. Tests to study the effects of weather on bee activity were conducted in Area IV, using three adjacent domiciles facing south, east, and west (Test 1). Observations at these domiciles indicated that the point at which 50 percent of the population under study had taken flight (FP_{50}) was 1:25 to 2:05 hours sooner in the east shelter than in either of those facing west or south. Activity in the west and south shelters had similar FP_{50} 's each morning observations were taken. The average air

temperature one inch in front of east exposed domiciles was 85 degrees F. at morning FP_{50} compared with 74.4 degrees F. for west and south facing domiciles.

A similar test (Test 2) was conducted in Area V to determine more precisely the temperature requirements for morning activity. Domiciles in this test faced east so that bees nesting in them were affected by rapidly rising air temperatures each morning.

It was observed that there was little temperature difference two inches within straws and one inch in front of the domicile at FP_{50} (Table 10, column 3, 4). However, both readings were more than 20 degrees F. higher than the general air temperature at that time (Table 10, column 2). Once the flight threshold was reached, bees were able to fly from the east-exposed domiciles at lower general air temperatures than those in domiciles not facing the morning sun. However, females leaving radiation-warmed domiciles were often observed landing on objects near the nesting site, presumably because the general air temperature was too low for sustained flight.

The temperature rise per minute was found to be slightly higher within the straws than one inch in front of the domicile (Table 10, columns 5, 6), but both rose approximately three times faster than the general air temperature (Table 10, columns 5, 6, 8). Temperature differences at the three recording points are the result of direct solar radiation, plus effects of the shelter in which domiciles were

Table 10. Temperature and light data associated with morning FP₅₀.

1	2	3	4	5	6	7	8
Date	General Air Temp.	Air Temp. one inch in front of domicile	Air Temp. two inches in straw	°F/minute rise one inch in front of domicile	°F/minute rise two inches in straw	Foot candles of light	°F/minute rise general air temp. (data from another experiment)
Sept. 21	<68°F	88°F	87°F	.375	.500	2460	.117
Sept. 23	70°F	92°F	88°F	.216	.182	5580	.166
Sept. 24	<68°F	86°F	92°F	.242	.390	3180	.178
Sept. 25	<68°F	84°F	87°F	.311	.405	2520	.111
Sept. 26	<68°F	86°F	83°F	.471	.481	1980	----
Sept. 27	68°F	90°F	94°F	.333	.470	2820	----

placed. Domiciles were contained in wooden boxes housed within a large outer shelter. The shelter protected boxes and domiciles from prevailing westerly winds and the boxes restricted the movements of warm air from in front of the domiciles. This tended to increase temperatures each morning at a more rapid rate than the general air temperature.

In Test I, the average air temperatures in front of east exposed domiciles at FP_{50} was 85 degrees F, while those of domiciles not facing the morning sun (i. e., south, north, west) were 74.4 degrees F, or more than 10 degrees F. lower. This temperature difference at FP_{50} may be due to a more rapid rise of morning temperatures in east exposed than in other domiciles. Temperature rises in these domiciles are so rapid that they do not reflect corresponding temperature increases in the bee's body, thus there is a lag in body temperature rise with a corresponding delay in metabolic processes necessary for flight and FP_{50} . In contrast, it is believed that bees nesting in domiciles without east exposures had body temperatures which increase more closely with slowly rising air temperatures. Therefore, these bees began flying at an apparently lower air temperature than bees in east exposed domiciles above.

It was concluded from the above data that the heat provided by the rising sun was the major factor in initiating morning activity. As the sun rose in the morning, east shelters were warmed first,

therefore bees in these shelters reached FP_{50} before those in other shelters. However, it was necessary for the general air temperature to reach a flight threshold before the FP_{50} could be reached in shelters exposed to the direct rays of the morning sun.

While the initial morning flight seems predominantly dependent upon temperature, the cessation of activity in the evening appears to be influenced mainly by light intensity. Tests in Area IV revealed that when flight ceased, the air temperature in front of shelters facing east ranged from 78 to 85 degrees F. (Table 11). Flight activity terminated in those shelters with a westerly exposure at temperatures ranging from 87 to 92 degrees F. These temperatures were all well above the morning flight threshold so that temperature itself did not appear to be the limiting factor in cessation of activity in the evening.

The response of the bee to decreasing evening light intensities was sudden in all domiciles regardless of their compass exposure. Flight at the west exposed shelters lasted only 6 to 21 minutes longer than that in the shelters facing south and east. Thus, whereas temperature was the important limiting factor for morning flight, light intensities appeared to exert a limiting influence in the evening.

Cloudy weather results in little bee activity. For example, September 22, 1963 was a cloudy day in the Boardman area and the temperature at 3 P.M. reached 73 degrees F. On clear days, bee activity may be observed at this temperature, but because of cloudy conditions

Table 11. Temperature and light data associated with evening flight cessation (data recorded when 50 percent of population had returned to their domiciles for the night).

1	2	3	4	5
Date	General Air Temperature	Air Temp. one inch in front of domicile	Air Temp. two inches in straw	Foot Candles of Light
Sept. 19	75°F	78°F	82°F	576
Sept. 20	78°F	81°F	87°F	710
Sept. 21	79°F	85°F	95°F	2580
Sept. 26	79°F	84°F	87°F	660
Sept. 27	78°F	83°F	88°F	780
Sept. 28	86°F	82°F	88°F	680

no flight occurred. This data seems to suggest that dual thresholds of temperature and light intensity must be reached before flight is possible. This observation suggests that although the temperature was high enough, the light intensity was insufficient. From Table 11, it appears that light intensities above 570 foot candles are necessary for flight.

If temperature and light intensities are favorable for flight, bees continue foraging activities in spite of strong winds. This is especially true when nesting sites are in sheltered areas. Strong winds do, however, change the flight behavior of bees. On windless days flight to and from the nesting site is normally at a height of two to five feet above the ground. In contrast, on windy days, bees fly as close to the ground as possible and increase their altitude only as they near their nesting location. Upon leaving their nesting site, bees return to within a few inches of the ground for flight.

Rain showers result in cessation of flight even though other conditions are favorable. Scattered showers most of the day on September 21, 1963, caused bees to cease foraging activities at 4:30 P. M. although light and temperature were more than adequate for activity.

SUMMARY AND CONCLUSIONS

Laboratory tests indicated that 32°C was the optimal temperature for development from the diapausing prepupa to the adult. When developing bees were subjected to cool temperatures of 22°C and then moved to warmer temperatures (i. e. 26, 28, 32, 35°C) adults emerged within a three hour period immediately following the onset of warmer temperatures.

Mating and foraging behavior of the male are described. Mating usually occurs near the nesting site and copulation lasts only a fraction of a second. Single males were observed sleeping but more commonly males sleep in large aggregations in protected locations to which they return night after night.

General requirements for nesting include the presence of adequate pollen, nectar, leaf and nesting places. Of these factors the lack of suitable nesting places is most often limiting to population increase. A wide variety of nesting habitats both natural and artificial are acceptable as nesting media. Other insects often compete with bees for nesting tunnels, of which the European earwig and several ant species are the most serious.

Females utilize a number of plant species for leaf cuttings used in construction of their nesting cells. On any given plant, leaf characteristics such as age and turgidity appeared to influence the

selection of a leaf for cutting. Most leaf cuttings are taken from plants close to the nesting site and bees return to the same plant repeatedly.

The manner in which females remove cuttings from leaves was described as well as the return with the cutting to the nesting tunnel.

Details of cell construction were recorded, particularly, the manner of leaf placement in the nesting tunnel, provisioning, oviposition and subsequent capping of the cell. It was found that the number of leaves used in the formation of the cell cup increased, although not proportionally, with the diameter of the nesting tunnel. It is felt that this was an attempt by the female to reduce the size of her nesting tunnel to approximate her own body size. Females remove pollen from their scopae in the same characteristic manner each time they returned to their nesting tunnels.

After completion of a cell the female constructed another on top of it provided enough space was available. Otherwise, the entrance to the tunnel was sealed with a number of circular leaf cuttings.

The effects of late season and old age were similar, in that bees failed to construct and provision nesting cells with the exactness characteristic of other periods of adult life.

Gross orientation to the nesting site was achieved predominately by visual means. However, once at the nesting site, the characteristics of the tunnel and of the cell being constructed seemed to

provide the stimuli that determined its acceptance.

Color orientation studies indicated that M. rotundata was able to distinguish yellow, green, red and blue but tests were not sufficiently definitive to demonstrate a color sense or perception by this bee.

Although M. rotundata is oligolectic on alfalfa, it forages a number of plant species when alfalfa was unavailable. It was found that nine or ten pollen collecting trips were required to provision one nesting cell. Pollen loads were collected in from 17 to 28 minutes and trips for leaf cuttings took from three to five minutes, depending upon the distances these were from the nesting site.

Bees worked those plants closest to the nesting site, extending their range when nearby bloom was no longer available.

It was concluded that once adult bee populations became established at a given location, high losses followed when they were moved into a new area as adult transplants. This loss appeared predominately due to an inability of this bee to orient to a new location.

Morning and evening behavior was described and some of the factors affecting each were discussed. Factors such as age, depth at which females spent the night in their tunnels, time of the season and the type of medium in which females were nesting appeared to influence the time at which females took flight each morning. Delays in evening flight cessation may have been due to variations in

foraging distances, age or type of foraging trip (e. g. pollen trips take longer than those for leaves).

The effects of climatic conditions on flight indicated that while initial morning flight seems predominately dependent on temperature, the cessation of activity appears to be influenced mainly by low light intensity.

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