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The Biology of a Leafcutter Bee
(*Megachile brevis*) and Its Associates¹

BY

CHARLES D. MICHENER²

ABSTRACT

This paper presents a detailed account of the habits of the commonest leafcutter bee in Kansas. It is shown that the bee increases greatly in abundance during the warmer part of each year, there being two to four generations per year. This species is very mobile, populations regularly dispersing from certain habitats and new assemblages concentrating at other places as their food sources (flowers) change during the year. Dispersal distances up to several miles are thought to be common. Places of concentration are of two kinds, (1) nesting habitats where the sexes are equally abundant and (2) nectar habitats which hold principally males although females may be found there.

The kinds of flowers used as pollen sources are systematically diverse. Most of them are blue, purple, or whitish in color. No flower constancy was detected in bees merely sucking nectar, but in those gathering pollen there is a strong tendency for only a single kind of pollen to be gathered on any one pollen collecting trip. Exceptions were noted, however.

Nesting sites are always in pre-existing hollows, but these may be almost anywhere. Most are in weed stalks but some are in the ground or even in very dense foliage. Cell structure is also highly variable, both petals and leaves being used in most cells. The processes of cell construction, provisioning, and egg laying are described in detail. Growth and development are also described. In summer the period from egg laying to adult emergence is about a month. The species overwinters as mature larvae.

The life history of the cuckoo bee, *Coelioxys octodentata*, the principal parasite of *Megachile brevis*, is described.

A section on the possible importance of this leafcutter as a pollinator of alfalfa is included and to a considerable extent serves as a summary.

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INTRODUCTION

This work was undertaken in order to provide detailed information on the bionomics of one of our commonest North American leafcutter bees. Such information should contribute to the study of comparative behavior of bees, which ought to be pressed with the same vigor as that of comparative morphology, for it will doubtless improve our understanding of the relationships of various bee groups. Such information will also serve as a biological basis for efforts to increase the effectiveness of this bee as a pollinator of alfalfa and other crops. The work was begun primarily with this latter idea in mind for *Megachile brevis* is usually the commonest wild bee in Kansas alfalfa fields that is effective in tripping the flowers. However, since the relationships with the environment were found to be exceedingly complex and to vary from season to season, observations were made on all aspects of behavior that could be investigated with the hope that information of practical value in the effort to increase the abundance of these bees could be obtained.

The work was carried on over a period of three years, 1950 through 1952. Much of it was done in the vicinity of Lawrence, Kansas, but long series of observations at other points in the state were made, as indicated in the text.

The observations are not those of any one person; field information was gathered by several persons other than myself. Among these I wish to mention particularly Jimmy R. White, Alvaro Wille, Wallace E. La Berge, and Dr. Roland L. Fischer. Without their help the studies here reported would have required many more years.

Megachile brevis Say is a member of the subgenus *Litomegachile*. It is one of a group of very closely allied species. Mitchell (1936) separated the more distinctive species of *Litomegachile* but retained three forms as "varieties" of *brevis*. One of these "varieties," *nupta* Cresson, is presumably nothing but a rare color variant of *brevis* proper. If this is true, the name *nupta* ought to be placed in the synonymy of *brevis*.

Another of the "varieties" does not seem to intergrade with *brevis* and occupies a range from North Carolina and Mississippi to southern Florida. It is entirely sympatric with *brevis* and must therefore be regarded as a closely related but distinct species, *M. pseudo-brevis* Mitchell.

The third "variety," *onobrychidis* Cockerell, has a wide range from Nebraska and Texas to the Pacific. Over this entire area it appears to intergrade completely with bees having characteristics of *brevis* proper. It is therefore probable that a western subspecies, *M. brevis onobrychidis* Cockerell, should be recognized, although some individuals of this subspecies are indistinguishable from *brevis* proper.

The bee upon which the series of observations described below is based is therefore properly called *Megachile brevis brevis* Say. The species ranges from the Atlantic to the Pacific and from southern Florida and northern Mexico to Quebec and British Columbia. It is thus one of our most widespread bees.

Although the details of the life history will be explained later, it seems necessary to give certain background information here. *Megachile brevis*, like other members of the family Megachilidae, is a non-social insect having no worker caste. Each female constructs cells made from pieces of leaves and petals, hence the name leafcutter bee. These cells are placed in any of a wide variety of situations such as in hollow weed stalks, in curled leaves, or in holes in the ground. They may be single or in series, placed end to end. Each is provisioned with a viscous mass of honey and pollen, sufficient to provide food for the entire larval development. An egg is then laid on top of the food mass and the cell is closed with a cap made from more pieces of petals and leaves. In summer the time required for growth and development from egg laying to emergence of the adult is about a month, but larvae reaching maturity after about the middle of August cease their development, passing the winter as mature larvae which pupate and emerge as adults in the spring. The males emerge at about the same time as the females and live about as long as the latter, a situation unusual among bees.

PART I. SEASONAL HISTORY AND HABITATS

SEASONAL FLUCTUATIONS IN ABUNDANCE

Megachile brevis can be seen on flowers throughout the warm season of the year, in Lawrence from May 10 to October 1, and doubtless earlier in very mild springs and later in warm fall seasons. In southern Florida there are collecting records as early as February 9 and as late as November 22; it is possible that the species is active throughout the year there.

Because of the mobility of populations of this bee, it is difficult to obtain satisfactory data on the fluctuations in abundance during the season. A particularly attractive patch of flowers may result in a concentration of bees at almost any time, yet for miles around there may be very few bees. When the attractive patch ceases to bloom, the bees disperse, with the result that there is an apparent (but almost certainly not a real) drop in population. Moreover, the observers were often intent on watching nests or known concentrations of bees with the result that serious attempts to estimate bee abundance over large areas were not made. Furthermore, such factors as temperature, wind, and sunlight so affected the activities of the bees that two days' observation rarely gave comparable results. In spite of these difficulties considerable information on population fluctuations was gathered. For comparative purposes, this was converted to average number of *Megachile brevis* seen per half hour in the field.

In the vicinity of Lawrence this bee is not especially common and in many places, particularly early in the season, not a single specimen would be seen. However, we soon learned the most satisfactory places to look and the data is largely based on observations made in these places, although as indicated above, this introduces irregularities due to the ability of the bees to concentrate in favorable areas.

In any event, near Lawrence, the first *M. brevis* were seen on May 15 in 1950 (a not entirely fresh female which must have been active for several days), May 22 in 1951, and May 26 in 1952. A very fresh male in the Snow Entomological Museum was collected near Lawrence on May 10, 1949. During May and the entire month of June, the bees were scarce. This was particularly so in the very cool, wet June of 1951. This was the wettest June on record, with a total rainfall of 11.65 inches, resulting in great floods. During this month there was no day recorded when the average

seasons on record and therefore by middle and late summer flowers were very scarce. There is no doubt that this scarcity resulted in an apparent reduction in the bee population by dispersing it as well as in a real reduction due to the scarcity of food supplies. Counts made in early September, 1952, in the most favorable locations and in good weather, showed only six to ten *Megachile* per half hour.

Based on the three years of experience which included one extraordinarily wet and cool summer (1951) and one hot and extraordinarily dry summer (1952), it seems certain that in an ordinarily warm summer with enough precipitation to grow a normal crop of flowers, *Megachile brevis* populations in the Lawrence area would increase during the summer in approximately the manner shown in figure 1. It seems possible that in the characteristically drier regions of western Kansas, where the predominant late summer and fall flowers are yellow composites rarely utilized by this bee, the fall increase in abundance might not occur, as was the case in 1952 in Lawrence.

NUMBER OF GENERATIONS PER YEAR

The number of generations per year doubtless fluctuates with the length of the active season. Even in a single locality it is apparently not a regular or constant matter. The only generation which is relatively easily understood is the first. All bees active in May and early June seemed rather fresh. Because of the scarcity of this generation it is impossible to say how long the adult emergence period is, but the impression gained from the apparent increase in abundance of bees on flowers during May is that the emergence may continue until about the end of May. Nest construction and egg laying doubtless begin within a few days after emergence of the adults and continue for nearly their entire lives, probably at least a month. In the climatically more or less normal spring and early summer of 1952, a perfectly fresh female believed to be of the second generation was seen on June 17, and an exceedingly badly worn female, doubtless a remnant of the first generation, on July 3. In summer the egg to adult period is about a month; in the cooler weather of spring it is somewhat longer. Thus second generation individuals would be appearing more or less continuously from about June 17 until the beginning of August.

Considering the earliest offspring of each generation (thus the maximum number of generations per year), we conclude that second generation individuals emerging as early as June 17 could probably have mature third generation progeny as early as July

20 or 25. (These would thus be emerging at the same time as the last second generation individuals.) These third generation individuals could have adult progeny of the fourth generation by the end of August or early September. Their progeny would hibernate and emerge in the spring as the first generation of the following year.

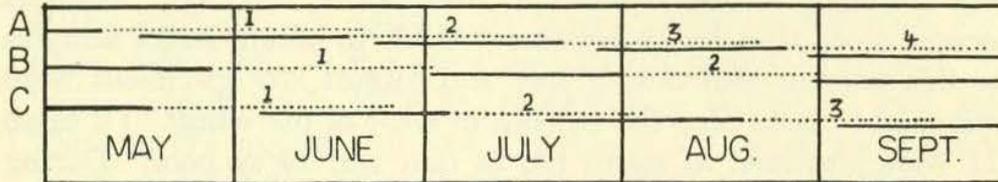


FIG. 2. Diagram showing the way in which generations become mixed, largely because of the long reproductive period of these bees. A represents a seasonal cycle of 4 generations, in which the earliest eggs of each generation give rise to the following generation. B represents a seasonal cycle of 2 generations in which the last eggs of each generation give rise to the following generation. C represents the presumably commonest situation of three generations. Solid lines represent immature stages; dotted lines adults. Generations of adults are numbered.

By contrast, considering the last offspring of each generation (thus the minimum number of generations per year) we conclude that second generation individuals emerging in late July would lay some of their last eggs well after the first week in August. Such eggs would not develop into adults until spring; thus there would be but two generations during the year. It is quite likely that some such second generation bees would survive until late August and thus be in flight at the same time as the earliest fourth generation individuals mentioned in the preceding paragraph. In short, it seems that in a year of ordinary temperatures near Lawrence, Kansas, there may be as few as two generations or as many as four; most probably go through three generations. After the first, the generations become completely mixed as shown in figure 2, because of the rather long periods (probably about a month) during which adults are active and laying eggs. One can therefore observe most adult activities, such as nest construction and provisioning, at all times from May until the first of October.

Studies of ages of population samples during 1952 support these statements. Age was judged by the amount of tattering of the wing margin; the condition of specimens was recorded as fresh, fair, or poor by comparison with drawings prepared in advance and carried in the field. Many of the bees were liberated after examination. About equal numbers of each sex fell in the various

categories, indicating that wing wear of males is about equivalent to that of females. All specimens (15) collected in May and on June 1 and 2, were fresh. Five specimens collected on June 7, and five more on June 13, were fair. On June 17, nine specimens were fair, two poor, and one (presumably second generation) fresh. Increasing numbers of fresh specimens were observed later in June and on July 3, a small sample was classified as follows: one very poor (remnant of first generation), three fresh, three fair. As bees became more abundant it became possible to obtain larger samples for this purpose and during July and August 290 specimens were examined to determine the amount of wear of the wings. Of these 111 were classified as fresh, 166 as fair, and 14 as poor. During these months there was no particular time when one category was more abundant than at other times; the summer population was a complete mixture of age groups. The small number of bees in poor condition was due to the extremely tattered wings required for this classification; only a few bees achieved sufficient wear (and sufficient age?) to be so classified.

The data for the exceedingly cool and wet spring and early summer of 1951 indicated that weather conditions influenced the rate of development and hence the number of generations. Two freshly completed nests of three cells each were found, one on May 27, one on May 29. Each was kept and the time of emergence of adults was July 11 and 12. Unfortunately all six bees which emerged were the parasite, *Coelioxys*. However, later in the summer the developmental period of the *Coelioxys* is about the same as that of *Megachile*; therefore there is good reason to believe that the cool weather slowed the developmental period of both forms from about a month to about 45 days. This surmise is supported by the field observations which show that, while very few bees could be found, only tattered individuals (presumably first generation) were seen during the first week in July. Their number was even smaller than during June, so that it appeared that the first generation nearly died out before the appearance of the second generation. Several fresh individuals were seen in the field during the second week in July. In a year such as this it would seem that the maximum possible number of generations would be three and that two might be very common. The small number of generations, in addition to the reduced reproductive activity of individual bees due to frequent periods of cloudy weather, rain, and low temperatures, would account for the low populations observed during 1951.

OVERWINTERING

As can be seen from figure 1, a very large proportion of the normal year's production consists of the overwintering individuals, and relatively few of these individuals survive to emerge the following spring. The reasons for the high winter mortality are discussed elsewhere. Overwintering occurs as fully fed mature larvae or prepupae. The factors which cause the cessation of development at this stage are not obvious, for temperatures are still high, sometimes very high, in the third and fourth weeks of August. Yet larvae which reach maturity at that time remain in that stage. They do not pupate and soon emerge as adults, as would mature larvae earlier in the season even at much lower temperatures.

The data concerning the time at which diapausing begins are as follows: An egg laid August 5, 1952, produced an adult on September 5. An egg laid approximately August 7, 1952, produced an adult at an unknown date in early September. Larvae from these eggs must have been spinning cocoons about August 16 and 18, and proceeded with their development to become adults. Eggs laid about August 17, and on August 20, 1952, developed into individuals which went into winter as mature larvae.

Twelve eggs (in several nests) which were laid on various dates from August 7 to 13, 1950, did not produce adults that year but went into winter as mature larvae. Six other larvae which had reached maturity and were beginning cocoon spinning from August 16 to 21, 1950, also went into winter as mature larvae.

Nests are still being provisioned as late as October 1; therefore all of the eggs laid from about August 7, until October 1, go to make up the overwintering generation, or first generation of the following year. It is not known exactly when pupation of this generation occurs but it is in the spring with adults emerging during the last two thirds of May.

In nests kept in the laboratory at room temperature during the winter the emergence is spread out over a long period, from October to March. Under conditions of continued warmth the diapause is apparently broken very irregularly and at widely different times.

DISPERSAL AND FAVORED HABITATS

As has already been intimated, *Megachile brevis*, unlike many solitary bees, is a highly mobile species. Since it has a long season of adult activity with several generations per year, the places which are particularly favorable at one time of the year are entirely differ-

ent from those that are favorable at other times. Not only do successive generations disperse from their regions of emergence and concentrate in the places that happen to be attractive at the moment, but it seems certain that a bee in the midst of its life and of its nest making activities may leave one area to go to another, perhaps several miles distant.

Strong indications exist of a constant shifting about of populations. Concentrations, largely of males, occur in areas of good nectar supplies even though nesting sites and pollen supplies are not available.

There are probably virtually no areas in eastern Kansas where *Megachile brevis* cannot occasionally be found. There appear to be no natural habitats which are favorable enough to attract large numbers of *Megachile* throughout the season of activity. The following sections on favorable areas where most of our studies were made are presented in order to indicate the characteristics of the places that are favorable at different seasons and in order to present the evidence for dispersal.

There are two types of favorable habitats which cause concentrations of the bees. One is called a *nesting habitat*, for it provides nesting sites and pollen sources as well as nectar. So far as is known, all plants utilized for pollen also provide nectar; at least the bees thrust their proboscides into the flowers as though sucking nectar at the same time that they collect pollen. The other is called a *nectar habitat*. It is a place where the principal flowers are highly attractive as nectar sources but are not used for pollen. Nesting sites may not be available in the vicinity. Male bees sometimes concentrate in such situations, and some female bees are found there.

NESTING HABITATS

Although the first *Megachile brevis* emerge in the vicinity of Lawrence in the first third of May, there are no known areas of concentration until the last third of May. At that time (actual observations dated May 24 to June 5) *Amorpha fruticosa* comes into bloom in low moist areas where there is no shade and often the bees concentrate on it in considerable numbers for this season. *Area 1*, where many spring observations were made, is one mile east, one mile south of Lawrence. It is a swampy spot about two acres in area full of *Amorpha fruticosa*. A railroad embankment along one side of it is covered with small rose bushes which provide leaves for nest making and with dead stalks of various large weeds, such as *Helianthus* and *Ambrosia*, which provide favorable nesting sites.

The *Amorpha* is the only source, so far as known, for pollen and nectar at this place. In early June, when this species of *Amorpha* ceases to bloom freely, the *Megachile* disappear in spite of the presence of certain flowers sometimes used by *Megachile* (e. g. *Trifolium*¹). At no subsequent time in the year, in spite of periodic observations throughout the summers of 1951 and 1952, were many *Megachile* seen in the region of Area 1, although very occasional individuals sucking nectar from *Teucrium* and *Verbena* were seen on a hill one fourth of a mile away during August.

In general, although it is occasionally a nectar source, sweet clover (*Melilotus*) is not a pollen source for *Megachile brevis*. On two occasions, however, among hundreds of patches of this plant examined, small patches of freshly blooming *Melilotus officinalis* have been found to be rather heavily used (considering the scarcity of the first generation) as pollen sources. One of these, Area 2, is four miles north of Garnett, Kansas, and bees were observed there on May 22, 28, and 29, 1951, each day abundant enough that about six could be seen per half hour of observation. This patch was on high dry land in a weedy roadside area where there were plenty of old *Helianthus* stalks for nesting sites. On June 10, only a single *Megachile* was seen there; presumably the others had left in favor of areas of *Psoralea floribunda* half a mile away or because the sweet clover became less attractive as it became older. The second area where bees were seen using *Melilotus officinalis* as a major pollen source was along the road through the sand hills four miles south of Garden City, Kansas, on June 12, 1952.

After the *Amorpha fruticosa* is no longer in full bloom the principal plant attractive to *Megachile brevis* as a pollen source is *Psoralea floribunda*, or in certain areas in southeastern Kansas (e. g., Galena and three miles east of Baxter Springs), *Psoralea psoralioides eglandulosa*. The former in particular is a widespread and common prairie plant. It occurs often in small prairie patches remaining along roadsides or railroads, but is especially abundant in large prairie acreages. In eastern Kansas the prairies are limited to high ground, usually hill tops. Thus the bees of the first generation, when the *Amorpha fruticosa* is no longer in bloom, apparently must often move distances of several miles from low wet areas to prairies covered with *Psoralea floribunda*.

The most studied prairie of this sort, Area 3, located three miles southwest of Ottawa, Kansas, is several square miles in extent. A

1. Except for the list in the section on kinds of flowers visited, generic names only are used in mentioning flowers unless two species of a genus are discussed in this paper.

few trees grow in the gullies but even there the herbaceous vegetation consists largely of prairie species. The *Psoralea floribunda* begins to bloom there at about the beginning of June and each year *Megachile* have been collected there between June 2 and 6. There are no earlier prairie flowers attractive to *Megachile* in this area. The *Psoralea* remains in bloom and serves as both a pollen and nectar source until near the end of June. In the latter part of that month *Amorpha canescens*, another prairie plant, is sometimes also used as a pollen and nectar source. As soon as the *Psoralea* is no longer in abundant bloom, however, the bees disappear from the prairie, even though *Amorpha canescens*, *Petalostemon*, and other seemingly suitable plants are in full bloom there. In Area 3, there are no suitable weed stalks for nesting, and the bees nest under bits of sod, under dried cow dung, or in fence posts. They use for nests leaves and petals of the small prairie rose as well as of various other prairie plants.

Area 4 is a floristically similar prairie of only a few acres extent located one and one half miles west and one half mile south of Lawrence. Any part of it is within a few hundred feet of such nesting sites as old *Ambrosia* and *Helianthus* stems. In this area, too, *Megachile* activity, although always slight, was limited to the season when *Psoralea floribunda* was in bloom, except for the one observation described in the following paragraph.

One of the first bits of evidence concerning migration came from the following series of observations: On August 3 and 7, Area 4 was carefully inspected for *Megachile* because of the excellent growth of seemingly suitable flowers such as *Petalostemon*. Not a specimen of *M. brevis* was seen. On these days, however, a few *M. brevis* were seen in a pasture one fourth mile away which was heavily grown up with *Vernonia*, from which the bees were gathering pollen as well as nectar and with *Symphoricarpos*, which was used only for nectar. On August 15, in the morning, this pasture was mowed and all the flowers in it cut. By noon that day several *M. brevis* of both sexes could be seen in Area 4, sucking nectar from the *Petalostemon* and from *Solidago* flowers. The next day, and subsequently, none could be found there. The inference was that the bees dispersed from the mowed pasture, some of them stopping for nectar in Area 4, but not staying since the flowers there were of rather unattractive sorts.

During the latter part of June and the first half of July the *Megachile brevis* seem very much dispersed with no areas of abundance

on native vegetation. A very few remain in the prairies where they collect pollen of *Amorpha canescens*; others are attracted by the first flowers of *Vernonia*. Introduced alfalfa (*Medicago*) is the only plant which seems to attract rather large numbers of *Megachile brevis* at this season. They were studied in numerous areas on alfalfa, but the only place worthy of special comment is known as *Area 5*. This is a two-acre patch of alfalfa surrounded by brushy and weedy creek bottoms and roadside vegetation. It is located near Blue Mound, southeast of Lawrence, Kansas. It was in full bloom when first visited on July 14, 1950, and was nearly out of bloom by August 4. During this period *Megachile brevis* was abundant collecting pollen and nectar, particularly so about July 20, when the hum of several *Megachile* could be heard at all times and at one time an estimate of 80 bees seen per half hour of observation was made. In late July, as the flowering became poorer, the *Megachile* became much scarcer.

One of the principal sources of pollen in the latter part of July and throughout most of August is *Vernonia*. This plant comes up as a perennial weed in poorly cared-for pastures, particularly in low but not swampy lands. Patches of it are very common; a few *Megachile brevis* can be found in most of them, many in some. The *Vernonia* patch most fully studied is *Area 6*, a pasture of many acres 9 miles south and 3 miles east of Lawrence. It had grown up in brush and small trees, and then a few years ago it was cleared except for certain large trees. The resulting cut brush and trees were placed in large piles scattered over the pastures. Weeds coming up in these piles were out of reach of cattle and matured and died, leaving many old weed stalks for nesting sites, in addition to scattered weed stalks elsewhere in the pasture. Sumac (*Rhus*) bushes around the pasture served as an important pollen source in 1950, especially as the *Vernonia* went out of bloom in mid-August. In 1951, the *Vernonia* was just coming into bloom at the end of July and continued until the end of August but in the warmer summer of 1952 it was blooming by mid-July and nearly out of bloom by mid-August.

Area 7 is an abandoned pasture six miles southeast of De Soto, Kansas. Since the principal pollen source is *Vernonia*, the area is attractive to *Megachile* at the same season as *Area 6*. The situation differs from that of *Area 6* principally in the great abundance of dead *Ambrosia* and *Helianthus* stalks throughout the area, forming suitable nesting places, and in the profusion of *Symphoricarpos*

which provides nectar from late July into September. *Lythrum* in a low area also serves as a nectar source. Thus as long as the *Vernonia* is in bloom this is an important nesting habitat; indeed in 1952, the only season that this area was observed, *Megachile* was more abundant here than at any other place found in eastern Kansas, possibly because of the combination of a good pollen source and many nesting places.

On July 25, 1952, most of the *Megachile* observed in this area were working on *Vernonia* flowers. By August 8, many were visiting *Symphoricarpos* for nectar, as was observed on repeated visits thereafter. By August 20, the few stragglers among *Vernonia* plants were still being visited for pollen but most of the bees in the area were visiting *Symphorocarpos* for nectar. Although, as indicated above, the abundance of *Megachile* in this area in 1952 was doubtless due to *Vernonia* and the numerous nesting places, the availability of *Symphoricarpos* nectar may be the factor that kept the bees in the area almost until the last *Vernonia* was out of bloom. By August 10, the bees were nearly gone from a *Vernonia* patch about a mile away which lacked the *Symphoricarpos*.

Area 8 is a somewhat similar pasture two miles east and eight miles south of Lawrence. It lacks the numerous nesting sites of Area 7, and the *Vernonia* is rather sparse; as at Area 6 an important pollen source is bushes of *Rhus*. Because of the abundance of *Symphoricarpos*, and in some places of *Lythrum*, the area is also a nectar habitat. Observations began in this area on August 4, 1951, when both *Vernonia* and *Rhus* were being used as pollen sources. It seemed that *Rhus* was most visited in the mornings. As this was a high dry area, the *Vernonia* ceased bloom earlier than in Area 6, so that by mid-August most of the pollen collecting was from *Rhus*, which in turn ceased its blooming in late August. Thereafter the only *Megachile brevis* seen in the area were a few sucking nectar from various flowers which are not used for pollen.

After the *Vernonia* of the pasture areas and the *Rhus* of nearby fence rows and waste land stop blooming, there is a short season when there is no really suitable abundant pollen source for *Megachile brevis* in eastern Kansas. The bees apparently disperse (see records of dispersal from Area 8 in the section on studies of marked individuals below) and can be seen sucking nectar from a very wide variety of flowers.

In 1950, a pasture (Area 9) three miles northwest of Lawrence was the site of intense activity of *Megachile brevis*. On September

5, when the place was first visited the bees were collecting pollen from both *Gutierrezia* and *Trifolium*. This activity very likely started because of the shortage of more suitable flowers. At no other place were these flowers found to be used except as an occasional nectar source. Moreover, the same flowers growing in the same place were not seen visited for pollen by *Megachile brevis* in 1951 or 1952. In 1950, however, pollen gathering continued until the *Gutierrezia* ceased flowering about September 25.

The usual pollen source after the first week in September is various species of purple *Aster* which bloom along roadsides and in pastures. In Area 10, four miles northwest of Lawrence, *Aster* began to bloom about September 6, 1950, and continued until October 7, although no *Megachile* were seen after October 1, doubtless because of cool weather. They were collecting pollen on October 1, however.

NECTAR HABITATS

It seems likely that *Megachile brevis* will, on occasion, suck nectar from almost any flower from which this bee is physically equipped to obtain nectar. Moreover, as already stated, it will obtain nectar from probably all the kinds of flowers used as pollen sources. There are, however, certain kinds of flowers not or rarely visited for pollen but very attractive to these bees as nectar sources. Patches of such flowers seem to hold wandering bees, especially males, for varying lengths of time. It is the resulting concentrations of bees not active in nest making that characterize the nectar habitats.

Areas 7 and 8 described above became nectar habitats when the pollen sources in them failed. The bees obtained the nectar principally from *Symphoricarpos*, to a lesser extent from *Lythrum*, occasionally from *Pycnanthemum*, *Bidens*, and various other plants. In each of these areas there was a considerable period when both nesting bees and those which appeared to be only sucking nectar could be found.

A small seepage space in Area 6 is a nectar habitat, often full of male bees and of some females which show no evidence of nesting in the area. Here the nectar sources are numerous and attractive before, during, and after the pollen producing plants (*Vernonia*, *Rhus*) of this area are in bloom. The plants producing the nectar are *Lythrum*, *Lippia*, *Verbena*, *Lycopus*, *Trifolium*, *Pycnanthemum*, *Teucrium*, *Ludwigia*, and *Bidens*. One or another of this series of plants is in bloom from early July to early September, and at least a few *Megachile* can be found there throughout that season.

The only area studied which was strictly a nectar habitat was *Area 11*. This is a swampy meadow about 50 yards long and 25 yards wide. It is located nine miles south of Lawrence. It is surrounded by a corn field, a bit of prairie containing neither flowers nor nesting places likely to attract *Megachile brevis*, and a sowed grass pasture. Thus there are practically no nesting sites. The meadow was full of *Lythrum* in bloom through the entire month of August, 1951, and until mid-August in the dry summer of 1952. *Megachile brevis* was the commonest bee on these flowers.

The presence of an occasional nesting *Megachile* in this area is shown by the record of a female cutting leaves there. Such scattered nesting individuals can be found almost anywhere, irrespective of the areas of concentration discussed above.

STUDIES OF MARKED INDIVIDUALS

The preceding sections show clearly that *Megachile brevis* is found in a wide variety of situations and that it concentrates in different places at different seasons. The conclusion is obvious that considerable dispersal occurs. To shed additional light on the matter, several marking studies were undertaken. Only two such studies produced significant data and even in these cases the data are meager. Both of these studies were made during August, 1951.

During the period August 4 to 20, inclusive, 148 *Megachile brevis* were marked in *Area 8*. Weather permitting, the area was visited and specimens marked every other day.

Marking was done by means of quick drying paints, spots of which were applied by means of a fine brush to bees captured in a net. All individuals marked on any one day were marked with the same color on the same part of the body. If a bee were recaptured on a subsequent day, it was marked with the color of that day, so that a bee might acquire several spots of color if it were recaptured several times. There was no evidence that the paint injured the bees. Sometimes it probably wore off, for bees were occasionally seen from which most of the paint had disappeared. However, there is no reason to believe that bees which had thus lost their identity played any large role in the results described below.

No doubt due to the change in this area from a nesting habitat in early August to a nectar habitat in the later part of the month, a considerable change in the *Megachile* population was noted. Thus from August 4 to 12 a total of 103 bees were marked, of which 67 (13.8 per day of marking) were females, 36 (7.2 per day of marking) males. From August 16 to 20, a total of 45 bees was marked,

of which 13 (4.3 per day of marking) were females, 32 (10.7 per day of marking) males. Thus the number of males marked per day increased as the area became a nectar habitat, perhaps largely due to the decrease in abundance of females which allowed the marker more time for capturing and marking males. At the same time the number of females decreased very greatly. Each day of marking usually amounted to about three hours in the field, with variations due to weather conditions. The ages of the bees varied greatly throughout the month; there was no evidence of the bees in the nectar habitat averaging younger or older than those in the nesting habitat.

Recoveries of marked bees were remarkably few. Even early in the month when pollen collecting females were often marked, only two females were seen after marking; one first marked on August 6, was marked again on August 10 and 16, another first marked on August 4, was marked again August 8. Since nest making females spend most of their time either collecting pollen or pieces of leaves, it seems that had they remained in the vicinity they would have been seen again in greater numbers. The few nests located in and around Area 8 at this time consisted of only one or two cells. The impression which we acquired is that, with *Vernonia*, the principal pollen source, rather scarce, the female nesting bees remained only long enough to finish one or two cells and then moved on. It should be pointed out that while *Rhus* was an important pollen source, we have never seen this plant alone support a population of these bees; we have always seen it used merely to supplement *Vernonia* as the latter nears the end of its flowering season.

Two additional females were recovered from among individuals marked after the middle of the month. One was merely seen in Area 8 two days after marking. By good fortune, however, one which was marked in Area 8 on August 16 was seen again on August 30 near Area 1 at a distance of 5.5 miles from the point where it was marked. This lends strong support to the idea of the great mobility of these bees. On both occasions this female was merely sucking nectar, not gathering pollen, the first time from *Symphoricarpos*, the second time from *Teucrium*. As already explained, late August is a period of poor pollen supplies for *Megachile brevis* in this region, for *Vernonia* and other midsummer pollen sources are waning, but purple *Aster*, the main autumnal pollen source, is not yet in bloom. It is quite likely that many *Megachile* spend this time wandering about.

Among males eight individuals were recovered, twice as many as among females although there were 12 less males than females marked in total. If significant, this difference between the sexes indicates that the males moved about less than the females. This is quite likely true, for because of *Symphoricarpos* Area 8 was apparently an attractive nectar habitat. Females, being probably motivated by the need for pollen with which to provision nests, would not be expected to remain long in a nectar habitat.

One male (the only one recovered more than once) was marked on August 6, recovered August 16, 18, 20, and seen on August 22 and 28. All five times after August 6, this bee was found in or around a single clump of *Symphoricarpos* bushes, showing that this individual, probably unlike most, stayed in or returned to a very restricted locality for at least 22 days.

The other marking study was conducted at Area 11, the small isolated *Lythrum* patch with practically no nesting sites or pollen sources nearby. On August 17, 1951, in one and one half hours, 55 male and four female bees were marked (all in the same way). An hour later a 15 minute survey of the area revealed 19 marked males and 4 unmarked ones. Assuming that the ratio of marked to unmarked bees in the area was as the ratio of marked to unmarked ones seen in the 15 minute survey, it was calculated that there were 12 unmarked male bees in the area, or a total of 67 males. Their age distribution was wide, as usual at this season. Of the 55 males marked, 5 were fresh, 45 in good condition, and 5 in poor condition.

Table I shows the results of similar 15 minute surveys conducted on other dates. The consistent scarcity of females in this nectar habitat is evident, as is the rather rapid disappearance of marked individuals and appearance of unmarked ones. This seems to provide additional evidence of mobility in this species.

TABLE I.—Number of marked (M) and unmarked (U) *Megachile brevis* found in 15 minute surveys of Area 11 on various dates in August, 1951. Marking was done on August 17.

		Number marked	August 17	August 20	August 22	August 29	August 31
Male	M	55	19	8	5	1	2
	U		4	6	16	7	5
Female	M	4					
	U			1			2

PART II. RELATIONS WITH FLOWERS

KINDS OF FLOWERS VISITED

Megachile brevis is commonly regarded as a highly polylectic species. For example Mitchell (1936) writes, "There are apparently few flowers which it will not visit." This is probably quite true insofar as visiting flowers for nectar is concerned, although definite preferences are exhibited for certain nectar sources.

In its pollen collecting, *Megachile brevis* is clearly rather restricted, as shown in Table II. There is some systematic significance to the limitations of the list; for example whole families like the Rosaceae are unrepresented. Yet very diverse plants such as certain of the Leguminosae and certain of the Compositae are much used. It is interesting to note that the principal pollen sources are blue or purple flowers, although such flowers may be systematically in families as diverse as the Leguminosae and the Compositae. Certain less important pollen sources are white or greenish, and one rather minor source, *Gutierrezia*, is yellow. This is interesting in view of the large number of yellow composites of the region. Many of these, such as various species of *Helianthus*, are regularly visited by many bees, including various species of *Megachile*, but they are only rarely utilized by *Megachile brevis* even for nectar.

These observations show clearly that *Megachile brevis*, in its pollen collecting, is far more restricted than such forms as *Apis* and most species of *Halictus* and *Lasioglossum*. This leads to consideration of the meaning of the terms oligolectic and polylectic. These terms were used by Robertson and subsequent workers, oligolectic bees being those which visit few kinds of flowers and polylectic ones being those which visit many kinds. Mere visiting for nectar, however, is usually not of great biological significance, and most records of visits of bees to flowers are of far less value than if additional information as to whether or not pollen was gathered were also recorded. In most bees the males and nectar sucking females visit most readily the kinds of flowers from which pollen is also gathered by the species. However, they may visit almost any flowers which provide nectar. It is in their pollen gathering that many bees are specific.

The many highly oligolectic forms known to gather pollen from only a single genus (or even species) of flower, fall at one end of a spectrum, with highly polylectic forms (e. g. *Apis*) at the other end. *Megachile brevis* falls in the midst of this spectrum.

TABLE II.—Kinds of flowers visited in Eastern Kansas by *Megachile brevis*. (x marks under pollen and nectar sources indicate relative importance; from x—one or two records only, to xxxx—of major importance.) Presumably all pollen sources are also nectar sources but this is not indicated in the table. Localities of information not obtained in vicinity of Lawrence, Kansas, are indicated under “remarks.”

Scientific name	Common name	Pollen source	Nectar source	Season	Color	Remarks
Alismataceae <i>Sagittaria</i>	Arrowhead		x	July	white	
Euphorbiaceae <i>Croton</i>	Croton		x	August	white	
Verbenaceae <i>Verbena micrantha</i>	Verbena		x	late July	white	
<i>Verbena</i>	Verbena		xx	July and August	purple	
<i>Lippia lanceolata</i> var. <i>recognita</i>	Fogfruit		x	July	whitish	
Labiatae <i>Lycopus americanus</i>	Water Horehound		xx	late July and August	whitish	
<i>Pycnanthemum flexuosum</i>	Mountain Mint		xxx	August	whitish	
<i>Teucrium canadense</i>	Wood Sage		x	August	purple	
Leguminosae <i>Astragalus</i>	Loco weed		x	June	whitish	
<i>Amorpha fruticosa</i>	False Indigo	xxx		May and early June	whitish	
<i>Amorpha canescens</i>	Lead Plant	x	xx	mid-June to mid-July	purple	
<i>Petalostemon</i>	Prairie Clover		x	July and August	white purple	
<i>Medicago sativa</i>	Alfalfa	xx		July and August	purple	
<i>Melilotus alba</i>	White Sweet Clover		x	July and August	white	
<i>Melilotus officinalis</i>	Yellow Sweet Clover	x		May and June	yellow	Locally used as an important pollen source
<i>Psoralea floribunda</i>	Wild Alfalfa	xxx		June	purple	
<i>Psoralea psoralioides</i> <i>eglandulosa</i>		xx		June	purple	South-eastern Kansas
<i>Lespedeza violacea</i>	Bush Clover	x		August	purple	
<i>Strophostyles helvola</i>	Wild Bean	x	xx	late Aug., early Sept.	red	
<i>Tephrosia virginiana</i>	Goat's Rue		x	June	red and yellow	

TABLE II—*Concluded*

Scientific name	Common name	Pollen source	Nectar source	Season	Color	Remarks
<i>Trifolium repens</i>	White Clover	xx	xxx	July to Sept.	white	In one locality, one season, important pollen source
Lythraceae <i>Lythrum alatum</i>	Winged Loosestrife		xxxx	July and August	purple	
Onagraceae <i>Ludwigia alternafolia</i>	False Loosestrife	x	xx	August	yellow	
Anacardiaceae <i>Rhus copallina</i>	Sumac	xx		August	whitish	Found used only near failing <i>Vernonia</i> patches
Umbelliferae <i>Zizia aurea</i>	Meadow Parsnip		x	late May early June	yellow	
Rubiaceae <i>Diodia teres</i>	Buttonweed		x	August	pinkish	
Caprifoliaceae <i>Symphoricarpos orbiculatus</i>	Buckbrush		xxxx	August	whitish	
Compositae <i>Coreopsis grandiflora</i>	Coreopsis		x	June	yellow	South-eastern Kansas
<i>Bidens polylepis</i>	Beggarticks		xx	late Aug., early Sept.	yellow	
<i>Helianthus annuus</i>	Sunflower		x	August	yellow	
<i>Silphium perfoliatum</i>	Cupplant		x	August	yellow	
<i>Rudbeckia serotina</i>	Black-eyed Susan		x	July	yellow	
<i>Ratibida pinnata</i>	Yellow Coneflower		x	July	yellow	
<i>Helenium autumnale</i>	Sneezeweed		x	August	yellow	
<i>Gaillardia pulchella</i>	Gaillardia		x	June	yellow-orange	Garden City Kansas
<i>Gutierrezia dracunculoides</i>	Broomweed	xx		Sept.	yellow	In one locality, one season, important pollen source
<i>Aster</i>	Aster	xxxx		Sept.	purple	
<i>Solidago</i>	Goldenrod		x	late Aug.	yellow	
<i>Eupatorium perfoliatum</i>	Boneset		x	August	whitish	
<i>Vernonia interior</i>	Ironweed	xxxx		late July and August	purple	

It should be clear that the terms oligolectic and polylectic are usually significant only in relation to pollen collecting, and that even in that reference they are only comparative terms.

NECTAR GATHERING

Bees of both sexes regularly insert their proboscides into flowers, evidently for nectar. This activity occurs throughout the lives of the adults. Individuals which had only been out of their nest for a few minutes were liberated in the midst of a patch of *Lythrum*. One of each sex alighted on *Lythrum* flowers after flying less than two feet from the point of liberation and inserted its proboscis in the ordinary and seemingly expert fashion. At the other extreme, very tattered and old individuals of both sexes are often seen sucking nectar.

Males alight on flowers almost solely in order to obtain nectar. Often in the midst of actions interpreted as searching for females they were seen to alight and suck from flowers.

Females probably suck nectar from every flower used as a pollen source. Rarely they stop only for nectar in the midst of pollen collecting. We have a record (August 9, 1950) of two females seen in Area 6 with a little *Vernonia* pollen on their scopas, but sucking nectar from *Ludwigia* flowers. Perhaps in the course of gathering pollen they wandered away from the *Vernonia* into the nectar habitat and sucked some nectar before going on to more *Vernonia*. More frequently, bees with full pollen loads are seen to stop at certain flowers and suck nectar only. This is most noticeable when nectar is gathered from kinds of flowers not used as pollen sources. Thus near Lawrence on August 19, 1950, two females with full loads of pollen from unknown but distant sources were seen to return to the vicinity of their nests. Before they went into their nests each stopped to suck from several flowers of *Diodia*. Such sucking may occur before the bees leave the vicinity of the pollen source, as shown by the following example: Near Galena, Kansas, on June 12, 1951, females were gathering pollen from *Psoralea psoralioides eglandulosa*. One with an apparently full pollen load was seen to leave the *Psoralea* and go to a *Coreopsis* head blooming among the *Psoralea*. There it sucked from several disk flowers, flew on to three more *Coreopsis* heads, to a *Psoralea* spike, to a *Coreopsis* head, to a *Psoralea*, to a *Coreopsis*, and then away. The impression was that having obtained a full pollen load, the bee sucked nectar from any convenient source, perhaps to fill its crop. That this is a common action is indicated by the frequency with which bees having full

pollen loads were seen sucking nectar but not gathering pollen. Thus bees with full loads of *Rhus* pollen were several times seen sucking from flowers of *Teucrium* or *Vernonia*.

Female bees, while looking for a nesting site, will usually stop and suck from a flower of almost any kind if it is close to their line of flight, and if a patch of flowers is encountered, they may visit several of them before going on.

It is interesting to note that nectar gathering female bees visiting alfalfa trip most of the flowers from which they suck. On various occasions females were observed to trip from all to about 70 per cent of the flowers visited. In spite of the fact that they do less work than pollen collecting individuals, they usually visit fewer flowers per minute than those which are collecting pollen. Thus one female (August 5, 1950) was observed to suck from 10 flowers per minute (average of three minutes). She tripped 21 of the 30 flowers visited. Another sucked from an average of 12 flowers per minute (in over three minutes observed) and of 34 flowers which she was watched to visit, she tripped 24. Pollen collecting females regularly trip every flower.

Males, on the other hand, often trip few or none of the alfalfa flowers visited. It would be interesting to know if each learns independently how to suck the nectar without tripping the flowers, as appears to be true of honeybee workers.

FLOWER CONSTANCY IN NECTAR GATHERING

There is no evidence of the slightest tendency for bees of either sex to restrict themselves to particular kinds of flowers as nectar sources, even for short periods of time, if several equally favorable sources are available. The following records are selected from among many to exemplify this statement: On August 13, 1951, a female which appeared to be searching for a nesting place was watched as it chanced to approach the nectar habitat in Area 6. As it encountered the low growing flowers in this area, it started going from flower to flower sucking nectar and in three minutes was seen to suck from *Lythrum*, *Vernonia*, *Croton*, *Trifolium*, and *Sagittaria*. It then wandered away continuing its original activity. Another female was seen the next day in the same place under otherwise similar circumstances to visit *Trifolium*, *Croton*, *Ludwigia*, and *Lythrum*.

In the average area, however, there is one flower distinctly more attractive as a nectar source than the others. It may or may not be a pollen source, as well.

POLLEN GATHERING

The exact mechanics of pollen gathering by female *Megachile brevis* is difficult to determine because of the rapidity of the action and the minute quantities of pollen obtained from any one flower. The following observations were made near Cherryvale, Kansas, on June 13, 1951, where numerous bees were visiting flowers of *Psoralea floribunda*. Corroborative observations have been made repeatedly on this flower.

The female bee, on landing on the flower spike, puts her proboscis into an individual flower. This opens the flower, exposing the stamens and pistil. The front tarsi are rubbed on the anthers occasionally during the process. The bee moves rapidly over the spike, working several of the flowers in this manner, then goes on to other spikes. Occasionally, after the bee has visited several flowers, the front tarsi contact the middle legs. The details are not apparent because of the rapidity of the movement but presumably pollen gathered by the front legs is transferred to the middle legs. At other times the middle tarsi can be seen to brush the venter of the thorax, where pollen must sometimes be brushed off of the anthers, or the middle legs may even be bent up over the thorax to comb the meso-scutum. Presumably the pollen gathered from the body and front legs is transferred by the middle legs to the hind legs, but this was not observed; perhaps it occurs in flight.¹ After visiting 10 or 12 flowers the bee alights on a new spike of flowers and rubs the scopa (pollen collecting hairs of the abdomen) with one rear basitarsis, or often with one after the other. At the same time the abdomen is bent upward several times, almost spasmodically, then back to its normal position. This action opens up the spaces between the groups of scopal hairs on each sternum, and pollen seems to be introduced into the spaces from the rear. Because of the way in which pollen is placed on the scopa by the hind basitarsi, a bee which is starting to gather a load of pollen may be seen to have the pollen of the scopa arranged in the V-shaped pattern shown in figure 3, each arm of the V representing the zone rubbed by the rear basitarsus of that side of the body.

On alfalfa the pollen collecting is very similar to that on *Psoralea*. When the bee inserts her proboscis, the alfalfa flower is tripped, that is, the column of stamens and pistil rapidly move up from their

1. Leg movements which probably accomplished transfer of pollen from leg to leg were noted in flight between flowers of *Vernonia*. They were also noted among sluggish individuals gathering pollen from alfalfa. Sluggish individuals are better for such observations than highly active ones.

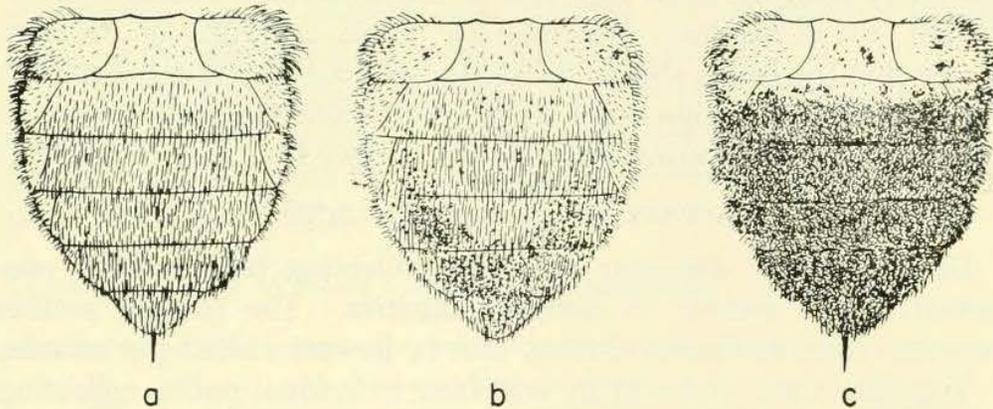


FIG. 3. Under surfaces of abdomens of females of *Megachile brevis*, showing the pollen collecting scopa. a, without pollen; b, with a little pollen; c, with a full pollen load.

original position in the keel of the flower to a position against the banner. In this process the bee's proboscis is often trapped between the column and the banner and the bee can be seen to pull loose, then reinsert the proboscis beside or behind the column. In this process also pollen is doubtless brushed off the stamens onto the under side of the thorax and head of the bee. Moreover, as the bee presses its head down into the flower, its face comes in contact with the stamens of the tripped flower. Thus pollen is probably scattered over the bee, especially over its head, more thoroughly by alfalfa than by *Psoralea*. Perhaps for this reason, bees were seen to brush their heads more when collecting from alfalfa than when collecting from *Psoralea*. After visiting several flowers a bee will cling to a flower with middle and rear legs only while brushing the front part of the body, especially the face, with the front legs. Other activity was as has been described for *Psoralea* pollen collecting.

On one occasion it was noted that when a female *Megachile* came to an alfalfa flower which had already been tripped, she immediately went on to other flowers.

The behavior of the bee is, of course, quite different on different flowers, particularly on those whose flowers occur in flat heads (Compositae) or in large masses (*Rhus*). On *Gutierrezia* a pollen collecting female tends to work with her head near the center of the flower, rotating her body around the flower head. On *Rhus* the female is noteworthy for being constantly on the move with a sort of wriggling motion over the large surface made up by the many small flowers. She appears to feed the pollen back from the front legs to the middle legs, thence to the hind legs and the scopa, rubbing

the scopa with the hind legs and at the same time raising the abdomen, just as has been described for pollen collecting on *Psoralea* except that the bee is able to do all this without stopping her motion over the flowers. Sometimes while flying from one flower mass to another or while hovering the bee rubs the two hind legs together.

RAPIDITY OF POLLEN COLLECTING

Details on the duration of pollen collecting trips will be presented in the section on nesting activities. The present section concerns rates of flower visiting, that is, flowers visited per minute.

The data were gathered by watching individual pollen collecting bees over periods as long as possible and recording the number of flowers visited each half minute of observation. The figures were then converted to flowers visited per minute.

Most of the data were obtained by observing bees collecting pollen from alfalfa. There is some evidence that the rate of collecting is higher at higher temperatures, but due to the variability found at any one temperature, the evidence is not conclusive. The greatest amount of data collected in any one temperature range (82°-85° F.) was gathered during July 1950. A total of 121 half-minute counts gave a minimum rate of 9.4 flowers visited per minute, a maximum of 24, and an average of 15.7. Of the flowers visited, over 95 per cent were tripped and therefore presumably pollinated and utilized as pollen sources. The others were merely probed by the proboscis but for some reason not tripped. These results agree reasonably well with more extensive data on this subject gathered by Franklin (1951) in Kansas and Linsley and MacSwain (1947) in California.

Data from *Psoralea floribunda*, a plant often called wild alfalfa because its flowers are similar to those of alfalfa, taken in the same temperature range indicate a higher rate of visiting flowers, possibly because tripping, required for alfalfa, is unnecessary for *Psoralea*. A total of 87 half-minute counts gave a minimum rate of 12 flowers visited per minute, a maximum of 30, and an average of 22.0.

Information on other flowers is slight, but we have records of 16 to 18 *Gutierrezia* disk flowers probed per minute, 18 to 36 *Trifolium* flowers visited per minute, and 10 to 11 *Aster* disk flowers probed per minute.

The variation in rates of visiting single kinds of flowers indicated in the preceding paragraphs is not due entirely to irregularities in flower abundance in the fields studied. There is evidence that at

the same time, place, and temperature different individuals work at different rates. Some appear sluggish, and repeatedly rest on leaves in the midst of their pollen collecting activities.

To verify this impression, data on individual bees in a single alfalfa field were gathered. The results are shown in table III. Similar data, obtained in a single patch of *Psoralea floribunda*, are presented in table IV.

TABLE III.—Rates of flower visiting by individual pollen gathering bees in a single alfalfa field.

Bee number	Flowers visited per minute			Minutes of observation
	Minimum	Maximum	Average	
1	19	20	19.3	3
2	12	18	15.7	4
3	16	17	16.3	3
4	9	15	11.3	5

TABLE IV.—Rates of flower visiting by individual pollen gathering bees in a single patch of *Psoralea*.

Bee number	Flowers visited per minute			Minutes of observation
	Minimum	Maximum	Average	
1	22	28	25.7	3
2	16	20	18.3	3.5
3	18	23	20.7	3
4	28	30	29	4

CONSTANCY IN POLLEN COLLECTING

Because of the small number of acceptable pollen sources usually available in any one area, individual pollen constancy is more difficult to judge than nectar constancy. However, one ordinarily observes pollen collecting females visiting flower after flower of the same species, and not deviating to visit other flowers, even for nectar, until a full load of pollen is gathered.

Exceptions to this general observation do occur when a bee stops using one flower and starts visiting another, but one never

sees erratic visiting of various kinds of flowers as with nectar gathering. Evidence for changes in pollen sources are as follows:

Different kinds of pollen are sometimes found in a single cell. Changes may occur in the midst of a pollen collecting trip as shown by the following two observations: In September, 1950, in Area 10 *Gutierrezia* and *Trifolium* were intermixed, both serving as pollen sources. Most pollen collecting females seemed constant to one flower or the other so far as we could observe, but on September 10, a bee which had been collecting from *Gutierrezia* flowers was seen to start visiting *Trifolium*. From then on it gathered pollen from *Trifolium* constantly, as long as it could be watched (three or four minutes). On August 11, 1950, in Area 6 a female was watched collecting *Rhus* pollen. The posterior part of its scopa was covered with *Vernonia* pollen, showing that it had changed its flower during a pollen collecting trip.

Another observation made in Area 6 concerned a bee which was nesting in a hollow dead weed stalk. For several days it had been observed bringing in the pale pollen of *Vernonia*, and had constructed three cells with that pollen. This plant, however, was becoming gradually older, with fewer fresh flowers, although there were still a great many. In the midst of provisioning the fourth cell, the bee stopped using *Vernonia* pollen and began using *Rhus*.

Additional information on flower constancy (or lack of it) was obtained in recording the activities of certain individual bees near their nests. The color of the pollen brought in was usually uniform from trip to trip. However, the bee recorded as "d", figure 8, used yellow *Rhus* pollen throughout the period of observation except that after her second pollen collecting trip for the second cell recorded in figure 8, she came in with white (*Vernonia*?) pollen. Nest "i" (figure 9) was provisioned with *Vernonia* pollen on August 11. On August 12, *Rhus* pollen was used, except that after the eighth and twelfth pollen collecting trips on that day the pollen seemed white and was probably from *Vernonia*. On August 14, the same bee used bright yellow *Rhus* pollen except for the sixth and seventh trips, which resulted in collections of white (*Vernonia*?) pollen.

PART III. MISCELLANEOUS ACTIVITIES

RELATION OF ADULT ACTIVITY TO ENVIRONMENTAL FACTORS

Very little significant information on this subject has been gathered. Much better bee subjects for such investigations are those with more permanent nests, where activity can be watched over long periods. Activity appears to be dependent upon certain relationships of temperature, light intensity, wind, and possibly other factors. On a cool day, no wind and strong sunlight are necessary to produce activity. On a cloudy day, no wind and high temperature are necessary for activity. On a windy day, sunlight and high temperature are necessary. With regard to these various factors, different bees probably have quite different thresholds of activity, for even on a rather poor day one may find a few active bees.

Quantitative data concerning these matters is almost nonexistent for *Megachile brevis*. It has been seen active at temperatures (taken in the shade of the observer's body at the level of the flowers being visited, usually one to two feet above the ground) of 76° to 100° F. Flight below 80° F. was rarely observed in summer, but in September, when generally lower temperatures prevail, it was more common. On August 21, 1950 (a clear day) a female was seen to start her work when the temperature near the nest reached 80° F.; on another such occasion the temperature reached 83° F. before the bee flew.

On three different cloudy mornings it was noted that activity did not begin until the temperature reached 85° F. Twice this was not until 11:00 a. m. or later. There is a little evidence that once the bees start to work they continue at temperatures lower than those necessary to activate them.

The hours of activity during the day vary not only with weather but of course with the season. In early August in clear weather they have been seen active as early as 8:30 a. m. and as late as 5:20 p. m. On July 27, a bee returned to its nest at 6:07 p. m. It had left 17 minutes earlier. In general, morning activity does not involve many individuals until 9:00 a. m. or later even on an ideal day.

This species has been observed flying in winds strong enough to roll a bee over and over on the ground if it happened to attempt to land in a gust. This sort of behavior was rare near Lawrence, in eastern Kansas, but in western Kansas where high winds are almost

continuous in certain seasons, it is common. Perhaps this is because the bees are forced into activity in spite of the wind.

FLIGHT

Megachile brevis is a bee that flies very rapidly with a distinct high pitched buzz audible on calm days for as much as ten or twelve feet. It is usually more easily found by means of this sound than by sight, although the sound is easily confused with that of certain bombyliid, nemistrinid, and tachinid flies as well as with that produced by certain of the other small species of *Megachile*. No difference was noted between the sound produced by males and females.

In full flight, as when females fly to and from their nests, the bees fly straight and at such a speed that the human eye can scarcely catch sight of a bee as it goes past. It is to be remembered, however, that the bee is dull colored and rather small, so that it is not easily seen. One bee was timed as making the 150 foot distance from her nest to the place where she was cutting leaves in 15 seconds. This is a rate of under 7 miles per hour. Considering that the bee quite obviously flies rather slowly as she starts her flight, gathering speed over a distance of 6 or more feet, and slows down over a similar distance at the end, the actual maximum speed is probably over 7 miles per hour but under 10. The bee is a noticeably faster flier than is *Apis*, which, however, has been reported to fly from 5.6 to 13 miles per hour by various authors.

Among flowers or elsewhere when the bees fly only short distances there is no difficulty in following their flight. Bees of either sex visiting flowers can be distinguished by sound from other bees because of the frequent brief interruptions of the flight while they rest on flowers. The characteristic buzz is therefore interrupted 9 to 36 times per minute, depending on the particular bee, kind of flower, etc.

Females searching for nesting sites can usually also be recognized by sound as they fly a sinuous or zigzag course close to the ground, investigating sticks and other possible nesting places. The flight is continuous except for irregular and often rather long interruptions while a bee crawls into a hole. In full flight to and from the nest, female bees fly two and one-half to three feet above the ground if there are no obstructions, but we have seen them fly over trees twenty feet high. They seem to do this in preference to flying through any considerable amount of shade.

MISCELLANEOUS NOTES ON BEHAVIOR

The following notes on various activities seem worth recording because they may be clues to consistent behavior patterns which may eventually be recognized:

One male was observed near Lebanon, Missouri, August 4, 1951, flying about plants of *Lespedeza violacea*. Frequently it lit on a leaf and rested for several minutes holding its forelegs up and forward.

Both sexes are often seen brushing various parts of the body with their legs. This often occurs when the bees are working flowers and probably serves to get scattered pollen off of parts of the body. We have frequently seen the eyes brushed.

In marking a male bee with quick drying enamel, paint was inadvertently got on the wings of the right side. It hardened, sticking them together. The bee could not fly. After some struggling it hooked the inner hind tibial spur between the two wings and pushed outward, straightening the leg. After repeating this several times the bee managed to peel the paint off of the wings and free them so that it could fly.

NOCTURNAL RESTING PLACES

As will be clearly shown later, females constructing nests rest in their nests at night. No positive field evidence is available on the night resting places of males or of females not constructing nests. We do know from numerous observations that they do not return to the nests in which they have developed and from which they have emerged to spend the night or for any other purpose.

In cages males and females crawl into curled leaves or similar protection to pass the night. It seems probable that they do likewise in the field.

MALE REACTIONS TO FEMALES

Curiously enough mating has never been observed in this bee. Probably it occurs very soon after emergence.

Males are often seen flying from flower to flower, not alighting but hovering for a moment over each flower, then going on to the next. The males may be very persistent in this activity or they may stop at intervals to suck nectar from certain of the flowers. We have considered this activity to be the search for females.

Males are occasionally seen to fly rapidly at females from a distance of a few inches and strike them. Females, so far as have been observed, repulse the males under such circumstances. Sev-

eral times we have observed females which were collecting pollen disturbed by males pouncing upon them.

Slightly more elaborate approaches to females have also been observed. A male sometimes hovers for several seconds two to five inches above and behind a female on a flower, then somewhat slowly, or at other times rapidly, descends upon the female. In all cases observed, the female merely flew away. If she only flies to another flower an inch or so away, the male may repeat his approach.

LONGEVITY OF ADULTS

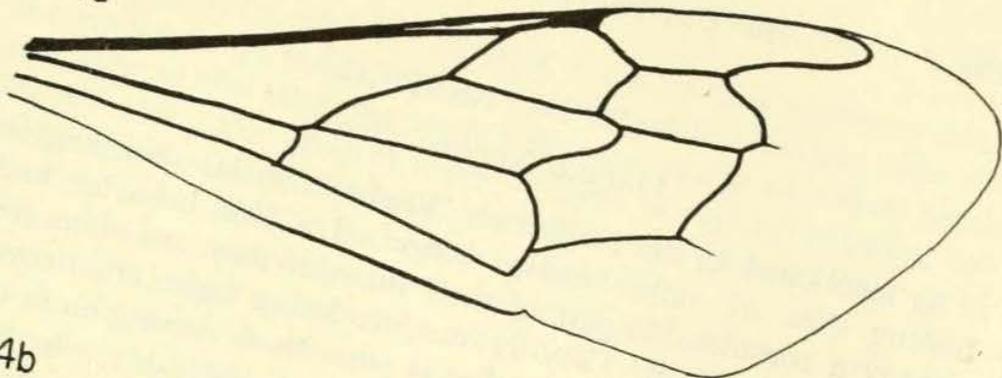
The oldest marked bee (a male) of which we have a record was last seen 22 days after the time of marking. However, there is considerable evidence that the bees actually live more nearly a month. The last eggs which will develop into fall adults are laid in early August; adults from these emerge in early September; such adults (both sexes) are active until the beginning of October (see figure 1) when they are probably killed by cold. There is some evidence that at least in cool weather longer adult life may occur. In the extraordinarily cool spring and summer of 1951, the second generation did not appear until the second week of July. Therefore, the disappearance of old and tattered first generation individuals could be observed without the complicating factor of second generation bees. Probably all first generation individuals had emerged by the last week of May, yet some still survived in the first week in July. All were females, suggesting that females survive longer than males.

Aging is shown in this species of bee in a number of ways. The wings become very much tattered in both sexes as the bees become older. This was the principal character used to judge age in the observations on age composition of populations reported under "Number of Generations Per Year." Figure 4 shows the amount of wear that occurs in wings.

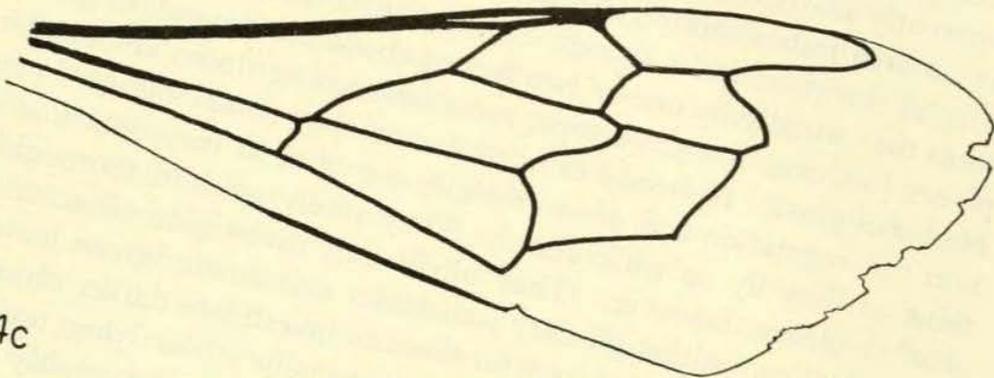
The pubescence, quite ochraceous on the dorsum of the thorax in young males and slightly so in females, loses its reddish color, the pale hairs becoming grayish white with age. This fading must occur very quickly in females, for they are not often seen in the field with ochraceous pubescence. Males, however, seem to retain this color for at least a week after emergence. Very old individuals often seem blacker than less worn ones because some of the pale hairs are broken off. This is especially true of the dorsal abdominal hairs.

The mandibles of females (but not males) show much wear. Figure 5 illustrates this.

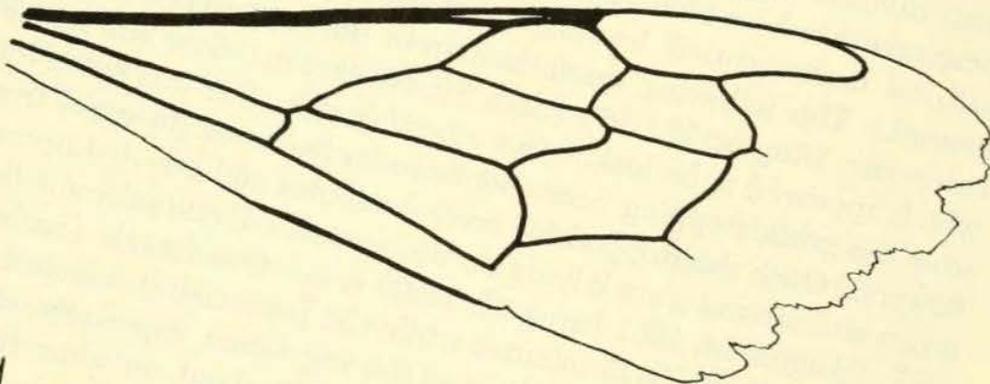
4a



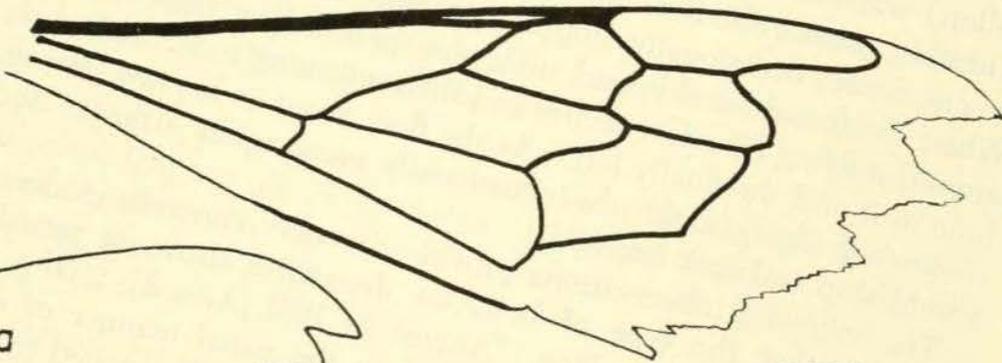
4b



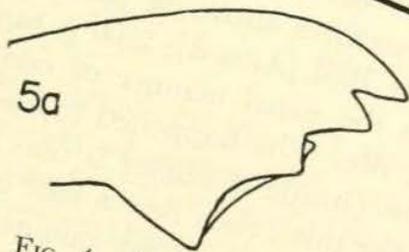
4c



4d



5a



5b

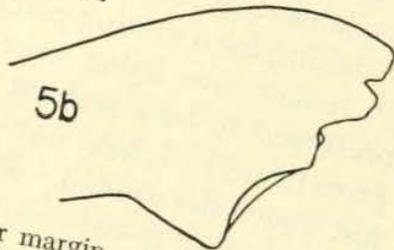


FIG. 4. Fore wings illustrating wear of outer margin. a, fresh; b, an example of the class called fair; c, an example of the class called poor; d, one of the most worn individuals studied.

FIG. 5. Mandibles of females illustrating wear. a, fresh; b, well worn.

PART IV. NESTING

FINDING NESTING SITES

As mentioned in the section on "Flight," females searching for nesting sites are rather easily recognized. This behavior must occupy a considerable part of their time for they are often seen apparently searching. They fly in a wandering flight, often covering an area rather thoroughly, but at other times moving on in one general direction even though zigzagging considerably. In bare areas they usually fly one or two inches above the ground, in grassy places just over the grass tops, sometimes going down among the blades of grass. In weedy or brushy areas they commonly go down into the vegetation and are sometimes out of sight for minutes at a time as they fly or walk about. They rarely go into thoroughly shaded places, however. They alight and investigate all sorts of small cavities. Although they sometimes nest among green leaves, there seems to be a tendency for them to investigate darker objects, such as brown curled leaves, and especially sticks lying on the ground. The following quotations from our notes exemplify this behavior: "August 13, 1951 [Area 8]; 10:30 a. m. Saw one female which appeared to be looking for a nesting site. She was flying low over the grass, stopping here and there on leaves or [to suck] from flowers. Once she stopped for several minutes and crawled up and down and around a stick lying on the ground. Eventually she flew off." "August 14, 1951 [Area 6]; 10:00 a. m. One female (without pollen) watched for 15 minutes while she presumably searched for a nesting place. She flew about in the vegetation, especially where it was dense, occasionally stopping to walk about on some stems. When she found an old dead stick, she spent a long time crawling around it flying off a few inches and then returning to it. It had no hole in it and she finally left. As she flew about in her wandering, somewhat zigzag flight, she occasionally came upon a flower and would stop and suck from it."

The following observations provide the only concrete evidence available that the type of behavior described above is actually searching for a nesting place. "August 29, 1951 [Area 8]; 2:00 p. m. [A female was flying over the grass in the usual manner of one presumed to be searching for a nesting site. She happened to approach me.] I held out a rubber tube (inside diameter 9 mm.) just above the ground. She went into the tube, then flew a foot or so away, then re-entered, went in and out five times in five minutes,

three times in the next five minutes, flying variable distances away, sometimes out of sight, between her visits. Ten minutes after she first entered the tube, she started bringing pieces of yellow petals for the nest. She brought many of them in rapid succession, but stopped and was not seen again after 4:00 p. m. [possibly because of the heat in the tube in the direct sunlight.]”

Another occasion when the “searching flight” was seen to lead to nest establishment was on August 11, 1950 (Area 6); 11:00 a. m. A female *Megachile brevis* was seen flying over the small rocks piled along the roadside. Once she left these rocks and went into the weedy pasture, searching along sticks, then returned to the rocks. At intervals she would crawl into spaces among the rocks. Finally she stayed in such a space for two minutes then left and flew all about the area (orientation flight?) well above the ground in a manner quite different from the searching flight. After this flight, she returned, then left again, flying about. This was repeated three times, one of the flights taking the bee 50 feet away. (Perhaps because of the uniform appearance of the roadside, these orientation flights were more extensive than usual.) The bee then left and after ten minutes (about 20 minutes from the time she first entered the nesting place) returned with a piece of a petal. She proceeded to construct a cell, as will be described later.

Rather different observations concerning nest establishment were made in an alfalfa field near Hutchinson, Kansas, July 26, 1950. Usual nesting sites, such as old weed stalks, were scarce in the area. A female was seen crawling in and out among the dense foliage of a deformed, fasciate plant of *Erigeron canadensis*. This bee left but soon returned to crawl around more among the leaves. After 50 minutes of this coming and going, the bee seemed to select a place, for she came back to the same spot among the leaves of the weed three times in about as many minutes, then started to bring leaves for the cell.

It is perhaps significant that among the three cases of nest establishment that we observed, the longest period required to start the work of cell construction was in the most abnormal nesting situation (among leaves of *Erigeron*).

NESTING SITES

Mitchell (1936) and Hicks (1926) both suggest that the wide variety of nesting sites reported for *M. brevis* by various workers (Reed, 1871; Packard, 1892; Rau, 1916, 1922; Hicks, 1926) may indicate that more than one species was identified as *brevis*. In view

of the similarity of various species of *Megachile* this may have been the case, but the differences in the nesting sites do not necessarily indicate this. Even greater variability in nesting sites has been observed in Kansas populations of *Megachile brevis* than was previously recorded in the literature for this species. At the season of the year when the bees are largely in the prairie patches using *Psoralea floribunda* as a food source, their nesting sites will often necessarily be different from the old weed stalks favored when the populations are in other places. Perhaps the mobility of this bee, correlated with the fact of its several annual generations, forces it to retain catholic tastes in nesting sites. That we are not dealing in Kansas with two or more related species utilizing different sites is shown by the actions of females searching for nesting places.¹ They will sometimes search along sticks and weed stalks, then search bare ground, looking into holes, then crawl into curled leaves, as though all these sites were potential nesting places to a single bee.

The great variability in nest sites observed in *Megachile brevis* is not surprising in view of the literature concerning other species of this genus. For example, *Megachile centuncularis* Linnaeus of Europe has been recorded as nesting in the soil, in rotting wood (Baysson, 1902), beneath rocks (Bellevoye, 1884), in hollow stalks and bamboo (Hardouin, 1945), and in various other situations. Smith as early as 1855 recorded a great diversity of nesting sites for this species.

As Table V shows, the nesting sites most commonly chosen, in our experience, are hollow dead weed stalks, old cornstalks, and the like, lying on the ground. I believe that most of the nests in our area are in such places but probably not as preponderant a percentage as the table at first suggests. Nests are most easily found by splitting dead stalks; it is only by observing bees that one finds nests in the soil, under prairie grass, and in like situations. The second column (nests found by observing bees) probably gives the best comparative data on the various sorts of nesting sites.

In summary, it is evident that almost any sort of small cavity may be used for nesting by this bee. The bees apparently never excavate holes. When they nest in stalks, it is almost inevitably in pithy stalks hollowed out by various borers and subsequently broken to expose the hollow. There is some evidence that the bee may clean loose debris out of such a hollow or even enlarge the hollow. The diameter of the cavity holding the cells is sometimes slightly

1. Because of the superficial similarity of various *Megachile* species, specimens have been collected frequently in all areas of study and identification checked by means of the characters detailed by Mitchell (1936).

larger than the same hollow where bees have not entered it, and bits of freshly removed pith may be found beneath the entrance.

We have never found a nest in deep shade of woods or even under a large tree or in heavy shade produced by a luxuriant growth of tall weeds. Nests are most commonly found in old broken pieces of stalk lying about where the grass and weeds are short.

The pieces of stalk may be well hidden by short grass and weeds and shaded by them, or may be entirely exposed.

TABLE V.—Nesting sites of *Megachile brevis*, and numbers of cells in nests.

Site	Nests found by observing bees	Total nests found	Number of cells per nest		
			Minimum	Maximum	Average
Dead horseweed stalks, prostrate.....	5	22	1	8	3.7
erect.....		3	1	3	2
Dead pokeweed stalks, prostrate.....	1	2	2	2	2
Dead sunflower stalks, prostrate.....	2	14	1	7	3.4
erect.....	1	4	1	5	3
Dead cornstalks, prostrate.....	7	10	1	8	5
Dead thistle stalks, prostrate.....	6	30	1	11	4.2
erect.....	1	2	4	8	6
Base of dead ironweed stalk, prostrate.....		3	1	2	1.7
Dead curled boneset leaf.....	1	1	2	2	2
Termite hole in garage door.....	1	1	8	8	8
Among dense leaves of living fasciate muletail weed.....	4	7	1	2	1.1
Among small rocks on ground.....	1	1	1	1	1
Under dry cowchips.....		3	1	3	2
Under mat of prairie grass.....	2	2	1	1	1
In holes in ground.....	4	4	1	2	1.5

The plants listed in table V are as follows: Horseweed (or giant ragweed), *Ambrosia trifida*; pokeweed, *Phytolacca decandra*; sunflower, *Helianthus annuus*, *H. tuberosus*; corn, *Zea mays*; thistle, *Cirsium* sp.; ironweed, *Vernonia interior*; boneset, *Eupatorium perfoliatum*; muletail (or horseweed, fleabane), *Erigeron canadensis*.

NEST STRUCTURE

Nests typically consist of several cells placed end to end and snugly fitted into a tubular hollow. Sometimes only a single cell is located in a hollow. When there are several cells, of course, the first constructed is the one farthest from the entrance into the cavity while the last constructed is the one closest to the entrance. The

position of the cells in a long hollow (such as a hollow stalk) varies greatly. Sometimes, even when the hollow was many centimeters long, cells were found only near the entrance, blocking the hollow and leaving most of it inaccessible and useless. At other times bees go deep into hollow stalks to construct cells. The last cell constructed may be flush with the open end of the hollow or may be deep in the hollow. Among 46 nests (in stalks) whose structure was recorded in detail, one had the last cell constructed 35 cm. from the entrance into the stalk, three had the last cell flush with entrance into the stalk, and the others were intermediate in this regard, the average distance from the entrance to the last cell constructed being 3.5 cm.

The cells are ordinarily tightly fitted together so that if a stalk containing a nest is carefully split, all the cells can be removed as a single unit. This is because the base of each cell fits inside of the apex of the preceding one. The elongate pieces of leaves and petals which form the cup of any cell extend well beyond the cap of that cell, leaving a hollow into which fit the elongate pieces which form the cup of the next cell. Often the cells of a series are so closely associated that it is necessary to break the series in order to determine how many cells are present.

Occasionally cell series constructed by two bees, or by one bee at different times, are found in the same stalk. This situation can be recognized by the old leaf and petal material of one series, compared to fresh material of the other. Sometimes in such cases there is an unoccupied space of one to several centimeters between the two series of cells.

As shown in table V, the nests are commonest in horizontal hollows (e. g. in prostrate stalks), so that the cells are usually horizontal. They are not infrequently vertical, however, with the caps upward, as in hollows of standing stalks exposed by breaking the stalk. One nest was found in which the bee entered a hole in the side of a standing stalk and turned upward, there constructing a series of vertical cells with the caps downward.

Most nests (except those few in which the last cell is flush with the entrance to the hollow) are closed at the entrance with a plug made of pieces of petals or leaves. These pieces are more or less round, like those used to cap cells, and are loosely or firmly fitted into the opening. The space between the last cell and the plug is usually empty although in one nest there was an additional plug of eight pieces of leaves just beyond the last cell and separated

from it by a millimeter or two. The distance from the last cell to the usual entrance plug varies from 2 mm. to several centimeters. Entrance plugs (in 15 nests in which they were studied) ranged from a thick plug of 20 pieces of leaves and petals to a thin one consisting of only four pieces of rose petals and another thin one of four leaflets of *Lespedeza violacea*. The average number of pieces in the 15 plugs studied was 9.3. Most of them consisted of leaves or petals of the sort used as "fillers" in cell construction but five contained pieces of rose leaves in addition to leaves of *Lespedeza* or alfalfa, making much firmer plugs.

About one third of the cell series studied were provided with no entrance plug. Sometimes this was probably due to the death of the bee or to our collecting the nest for study before her work was completed, as indicated by an incomplete last cell. In other cases, however, the last cell was complete and it appears that sometimes *Megachile brevis* does not construct an entrance plug. In few cases was an entrance plug found where only a single cell had been constructed.

NUMBER OF CELLS CONSTRUCTED

The number of cells in any one nest depends in part on the size of the space available. A small cavity may provide room for only a few cells. The right hand column of table V illustrates this point; the average number of cells per nest is higher in stems, where the long cavities provide plenty of room, than in the miscellaneous small cavities listed in the lower part of the table. The small number of cells in nests in ironweed stalks is due to the very short basal region large enough to hold *Megachile* cells.

The number of cells constructed by any single female is unknown. A series as long as 11 cells has been found, but there is no reason to believe that this is a maximum. Few nesting places provide space for very many cells; as shown in table V many single cells were constructed, even in hollow stalks where there would have been space for several cells. Since the bees move freely from place to place, a bee may construct a few cells in one place and others several miles away. Packard (1868) reports a single *Megachile* (identified, probably incorrectly, as *centuncularis* Linnaeus) that constructed 30 cells. Perhaps females of *M. brevis* construct similarly large numbers, scattering them in various places.

Study of figures 8 and 9 shows that these bees can construct and provision 1 to 1.5 cells per day. If a bee lives for 30 days, it might presumably construct 30 cells, even allowing for some bad weather.

CELL STRUCTURE

The present section contains a summary of the data obtained by dissecting 100 cells of *Megachile brevis* from 48 nests. It is well known that cup portions of cells of many leaf cutter bees are made of elongated pieces of leaves which bend inward at one end (called the base of the cell) to close it. After provisioning the cell and laying an egg, the bee closes the other end by means of round pieces of leaves, which are called the cap.

Megachile brevis follows this general pattern, using elongate pieces of leaves and petals for the cup and circular pieces for the cap. The pieces for the cup are broadly overlapped, as shown in figures 6 and 7. The pieces which form the cap are all of about the same size and shape, slightly larger than the diameter of the hollow in the cup, so that when pressed into place their edges turn up slightly and the fit is snug (figure 6).

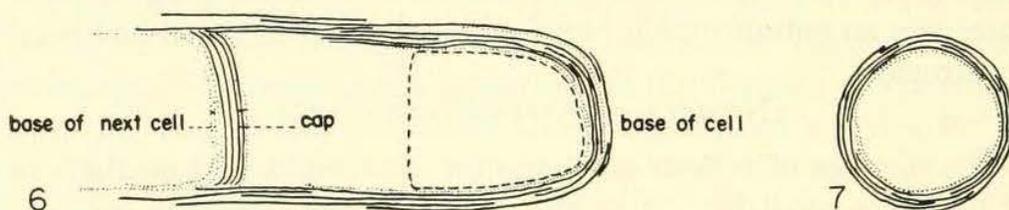


FIG. 6. Longitudinal section of cell (diagrammatic, to show make up of walls). Solid lines represent leaves; dotted lines, petals; broken line, mass of provisions.

FIG. 7. Cross-section of cell. Explanation as for figure 6.

In gathering the data on cells, the series were broken into the component cells. If round pieces adhered to the base of a cell, they were transferred to the preceding cell and considered part of the cap of that cell. This procedure is ordinarily justifiable, for the cap of one cell and the base of the next are in close contact (see figure 6). However, round pieces are sometimes found at the base of the first cell in a series. In such cases they must have been the first leaves cut and had nothing to do with any cap.

Great diversity is shown among various individuals of *Megachile brevis* as to the manner of cell construction. Part of this diversity is due to the size of the hollow in which the bee nests. The inside dimensions of the cells are quite constant, 4.2 to 5.2 mm. in diameter, 8.2-10.0 mm. in length. The dimensions of the hollows used are by no means as constant, ranging from just over 5 mm. in diameter to 10 mm. in diameter. A bee nesting in a small hollow needs to use only a few leaves and petals to construct a cell cup having the

proper inside dimensions while a bee nesting in a large cavity must carry into it many leaves and petals to form the thick walls necessary to obtain the proper inside dimensions. For example, one bee nesting in a small hollow in a weed stalk used only eight pieces to construct a cup (nest 20, table VI) while another bee nesting in a space among leaves of a fasciate *Erigeron canadensis* used 41 pieces. (nest 23, table VI). This is the bee whose record is shown as nest f, figure 9. From this record it can be seen that she really brought to the cell about 58 pieces but some were dropped through the leaves to the ground and lost, a thing which never happens in ordinary nesting places. The outside length of a cell is also variable, depending in large part on how far the walls of the cup extend beyond the cap. Most cells are from 11.5 to 14 mm. long but rarely they reach 17 mm. in length.

Additional diversity in construction is due to individual variations. Two bees working at the same place constructing nests only 10 feet apart in cavities of similar size may use quite different materials. Moreover, the cells in any one series are usually fundamentally similar but often markedly different from those in other series. As will be explained later, the bees tend to gather their construction materials largely from small "cutting places." No doubt the somewhat chance selection of these places determines in large degree the characteristics of the cells.

Almost all individuals of *Megachile brevis* make use of two or more different materials in constructing the cups of their cells. If the cavity is appreciably larger than the inside diameter of the cell, filler petals or filler leaves are the first materials to be brought in. All petals used are thin and satisfactory as fillers. The leaves most commonly used are leaflets of *Lespedeza violacea* or *Medicago* (alfalfa). These are thin, easily cut leaves often placed rather loosely in the cavity. If petals are used they often are cut first so that they form the outside of the cup, with filler leaves inside of them, although they may be intermixed to a certain extent. Major irregularities in filler material sometimes occur. Thus the second cell in nest 3, table VI had 14 *Lespedeza* leaflets on the outside, followed by five pieces of *Cassia* petals on one side of the cell, followed by nine more *Lespedeza* leaflets. As shown by the first eleven nests in table VI, leaves are more commonly used than are petals as fillers. Yet there are nests in which petals are used extensively for fillers (nests 12, 13, and 14, table VI.) and others in which petals are used exclusively or nearly so (nests 15, 17, 22, 23, table VI). Occa-

sionally nests are found in which the filler material is omitted entirely; see, for example, nests 18, 19, 20, and 21, table VI.

Inside of the filler materials are almost always placed a few firm leaves, usually cut from rose or sometimes from *Symphoricarpos*. These leaves are ordinarily the ones which provide much of the strength of the cell wall. In many species of *Megachile*, these are the only sort of leaf used in cell construction but in *M. brevis* they are usually very few in number. There are nests in which firm leaves constitute a large majority of the pieces used (e. g., first three cells of nest 13, and nests 18 to 22, table VI). On the other hand there are nests (25 to 30, table VI) in which firm leaves are altogether omitted. In nest 21, almost the whole of both cells was constructed of *Symphoricarpos* leaves. These leaves are a little thinner and more flexible than most rose leaves and presumably in this instance served both as firm leaves and filler leaves. This would explain the large number used. In nest 22, however, the 22 firm leaves recorded in table VI were all rose.

Lining petals are the last placed in the cell before pollen collecting begins. They are rather consistently present. Their number is often difficult to count in old nests, however (hence the many "+" signs in table VI), because they become soft and mushy, or later very delicate and brittle, and because at least those of the cap are often eaten by the bee larva. Lining petals are ordinarily from the same kind of flower as filler petals although they are occasionally mixed. Rarely, as in certain cells in nests 9, 10, 13, and 21, lining petals are absent and the pollen is placed in direct contact with firm leaves. Sometimes there is only a single lining petal in the cup, so that no complete lining exists (see nests 5, 9, and 21, table VI). Nest 30 is remarkable in that it contained no leaves, therefore no distinction between lining and filler petals existed. Rather than arbitrarily making a division, they are all recorded in table VI as lining petals. In three cells thin leaves, like those used for fillers, formed the lining or were among the lining petals. In table VI these leaves are listed in the column for lining petals but marked with an asterisk.

Like the materials used for the elongate pieces of the cup, those used for the round pieces of the cap are varied. Lining petals are quite consistently present, although occasionally absent (see nest 13). Filler leaves are also rather consistently present but sometimes absent. Firm leaves and filler petals are frequently absent.

In the cups, the materials are arranged in a fairly consistent man-

TABLE VI.—Materials used in the construction of cells.

Each horizontal row indicates a single cell, the figures representing the number of pieces of each material present. The first column at the left gives nest numbers, in order to show the way the cells were associated to form nests. The averages in the last row are based upon exact numbers and ignore “+” and “?” signs. A “+” indicates that the material was present but that the number of pieces was unknown. A “?” indicates that it could not be determined whether a material was present or not. In the “lining petals” column, a “*” marks figures representing thin leaves, such as those used for fillers. A blank space indicates absence of a type of material while a “—” indicates lack of information.

Nest No.	Cup					Cap				
	Lining petals	Firm leaves	Filler leaves	Filler petals	Total	Lining petals	Firm leaves	Filler leaves	Filler petals	Total
1	4	2	17		23	3		12		15
	5	3	11		19	2		4		6
	3	2	16		21	2		4		6
	5	3	19		27	3		3		6
	3	1	12		16	2	1	3		6
	3	2	11		16	2		3		5
	5+2*	2	15		24	2		3		5
2	+	11	13		—	1*	1	4		6
	+	8	9		—	?	2	1		—
	+	6	9		—	?	2	2		—
	+	8	5		—	1	4	3		8
3	5	4	19		28	3		3		6
	4	2	23	5	34	3		5	2	10
4	+	3	23		—	3	1	2		6
	4	5	23		32	2		2		4
	+	5	13		—	5	3	3		11
5	3	4	18	1	26	1		5		6
	+	3	14		—	2		1		3
	+	6	18		—	2	1	1		4
	+	4	15		—	2	2	1		5
	+	4	13		—	2	1	3		6

TABLE VI.—Continued

Nest No.	Cup					Cap				
	Lining petals	Firm leaves	Filler leaves	Filler petals	Total	Lining petals	Firm leaves	Filler leaves	Filler petals	Total
5	1	5	17		23	2	1	3		6
	?	8	21		—	2		3		5
	2	9	9		20	—	—	—	—	—
6	+	4	13	15	—	2	1	3	4	10
7	+	3	21	1	—	+	1	1		—
	+	1	23		—	+	2			—
	+	4	22	6	—	3	2	1		6
	+	4	24		—	2	1			3
	+	2	9		—	2	1	2		5
8	+	3	18		—	—	—	—	—	—
	+	4	22		—	—	—	—	—	—
	+	4	17		—	—	—	—	—	—
	+	5	16		—	—	—	—	—	—
9	2	4	22		28	—	—	—	—	—
	1	4	10	2	17	2	1	1		4
		4	19		23	1		6		7
10	?	5	5		—	?	4	4		—
	?	4	2	7	—	—	—	—	—	—
		2	8	3	13	—	—	—	—	—
11	3	3	23		29	1		3		4
12	+	5		10	—	4				4
	+	4	4	8	—	+	2			—
13		18	1		19	1	5			6
		15	5		20		2	2		4

TABLE VI.—Continued

Nest No.	Cup					Cap				
	Lining petals	Firm leaves	Filler leaves	Filler petals	Total	Lining petals	Firm leaves	Filler leaves	Filler petals	Total
13		12	9	3	24	1	2	1		4
	2	10	8	15	35	+		4		—
	5	6	7	10	28	—	—	—	—	—
14	+	4	1	2	—	—	—	—	—	—
15	4	11		8	23	—	—	—	—	—
	5	9		7	21	—	—	—	—	—
16	+	5		5	—	—	—	—	—	—
	+	4	1	7	—	—	—	—	—	—
	+	6	3	8	—	—	—	—	—	—
17	5+1*	5			11	3		8		11
	4	4		5	13	3		3		6
	3	5		3	11	1		3		4
	3	4		5	12	2		2		4
	2	4	1	3	10	2		5		7
18	5	7			12	2	5			7
19	4	14			18	3	5			8
20	+	7			—	2	2			4
	3	5			8	—	—	—	—	—
21	1	20			21		4			4
		25			25	—	—	—	—	—
22	5	22		12	39	—	—	—	—	—
23	2	10		29	41	—	—	—	—	—
24	3	3	10	2	18	—	—	—	—	—
	4	4	9	4	21	—	—	—	—	—

TABLE VI.—*Concluded*

Cup						Cap				
Nest No.	Lining petals	Firm leaves	Filler leaves	Filler petals	Total	Lining petals	Firm leaves	Filler leaves	Filler petals	Total
24	3		12	3	18	—	—	—	—	—
25	2		25		27	5		3	5	13
26	+		5	5	—	6		2		8
27	+	1	6	4	—	4		2	1	7
28	4		11	7	22	4		1		5
29	2		2	17	21	—	—	—	—	—
	3		2	19	24	—	—	—	—	—
30	33				33	—	—	—	—	—
Average	2.8 ¹	5.5	9.9	3.1	22.1	2.3	1.1	2.5	0.4	6.3

1. Nest 30 omitted from this calculation, since many of the 33 petals might best be called fillers.

ner. Thus the vertical columns of table VI are arranged from left to right in the order in which the materials are ordinarily found from the inside to the outside of the cell; however, considerable mixture often occurs so that a firm leaf may be inside a lining petal or filler leaves and petals may be somewhat intermixed. For the caps intermixture is much more the rule, the only generalization possible being that the lining petals are consistently on the inside.

The most complicated cells studied were the last three in nest 13, figure VI. All three of these cells contained four different kinds of materials, and their arrangement was far from standard. An example (the fourth cell) will be sufficient. From the inside out it contained the following: two lining petals (*Cassia*), seven firm leaves (*Rose*), six filler leaves (*Lespedeza*), two firm leaves (*Rose*), one firm leaf (*Symphorocarpos*), two filler leaves (*Lespedeza*), and 15 filler petals (*Cassia*).

The variability and complexity of the cells of *Megachile brevis* are not entirely unexpected in view of what is known of other species. Complex cell walls, consisting of layers of different materials, are well known in other species. For example several species put a layer of mud between outer and inner layers of leaves, others put a layer of masticated leaf material between outer and inner layers

of leaves. Great variation in construction materials from individual to individual is also recorded for other species and Markowsky (1933) even records a nest of *M. centuncularis* Linnaeus made without the side walls of the cells but with only partitions between the cells made of pieces of leaves. That the construction of the cells of any one nest tends to be similar in *M. centuncularis*, as in *M. brevis*, is illustrated by Markowsky's anomalous nest mentioned above and by Grandi's (1934) figures of the numbers of leaf pieces used in five cells of a single nest.

Nests for the numerical analysis shown in table VI were selected at random from those available. They were collected at various seasons of the year. The arrangement of the nests from one to 30 is intended to place nests having similar characteristics together; the commonest types are at the beginning of the table, the unusual ones near the end. All of these nests were in stalks except for number 11 which was in a hollow under a mat of prairie grass, number 22 which was in a space among pebbles, and numbers 23 and 25 which were in spaces among the dense leaves of fasciate plants of *Erigeron canadensis*.

The sizes of the leaves used in different parts of cell cup construction vary. The alfalfa leaflets used in nest 25, table VI varied from 7 mm. to 14 mm. in length. In other cell cups (not included in table VI) *Lespedeza* leaflets from 7 to 11 mm. in length and *Trifolium* leaflets 5 to 11 mm. in length were used as filler material. The smallest pieces were near the bottom of the cell.

Leaf pieces cut most of the way around (as rose leaves) also vary in size. The long firm pieces of rose leaves varied in one cell from 4.5 mm. wide and 10 mm. long to 5 mm. wide and 14.5 mm. wide. In another the extremes in sizes were 5 x 11 and 6 x 13 mm. In another cell in which *Symphorocarpus* leaves were used, the smallest long pieces were 5 x 10 mm., the largest 9 x 15 mm. In this cell the *Symphorocarpus* served both as firm leaves and filler and the large pieces were consistently on the outside of the cell, sizes becoming progressively smaller toward the inside.

From the above information the impression is inevitable that as a bee cuts leaves or petals, it selects the texture and cuts the size appropriate to the needs of the moment in fashioning its cell. The same conclusion has been independently reached by other authors (e. g., Popovici-Bazosanu, 1907) working on other species of *Megachile*. This suggests that there are delayed reactions involved, the bee reacting while cutting the leaf to stimuli received while in its nest.

It is well known (see, for example, Malyshev, 1935) that senile bees sometimes behave in unusual ways. No evidence of this was obtained in the present study because no one bee could be followed through its entire adult life. However, some peculiar structures made by *Megachile brevis* were found. The most remarkable was in a nest of two cells, the lower cell of which was normally provisioned and contained a growing larva. The upper cell, that is the second one to be constructed, consisted of a normal cell cup which was filled, not with the usual provisions, but with 40 round pieces of leaves of *Symphoricarpos*.

DURATION OF TRIPS

Much of the information on the timing of the construction and provision activities of *Megachile brevis* is summarized in figures 8 and 9. In these figures is presented the information on the comings and goings of nine different bees (a to i) watched continuously for more or less extended periods.

Bee "a" started to construct a cell between some small roadside rocks at Area 6 on August 16, 1950, at 11:00 a. m. The record (figure 8) consists solely of the 39 trips in two hours and 25 minutes required for the bee to construct the cup (bottom and side walls of the cell) from pieces of petals and leaves. For some reason which is not known, the bee never provisioned the cell.

The bee lettered "b" was first seen at 10:55 a. m. on August 21, 1952, as it flew out of an old cornstalk lying on the ground near Area 6. It was observed for a little less than an hour and a half, after which it never returned. It was neither constructing nor closing a cell, but was constructing a plug at the entrance to a series of cells that it had previously built and provisioned. This is, therefore a record of this final activity which often follows cell construction.

The bee lettered "c" was first seen at 1:19 p. m. on June 19, 1951, as it left a cell situated in a small hollow just below the surface of the ground near Lawrence, Kansas. The bee was last seen thirty-eight minutes later when it left the nest, so far as we could tell, for the last time. The record is presented, in spite of its brevity, since it is the only information available on the closing of an underground cell. The space was completely occupied by the one cell and no more cells could have been constructed here.

The bee lettered "d" was first observed at 2:12 p. m. on June 30, 1951, as it left a nest in a curled leaf of *Eupatorium perfoliatum* in

Area 6. The bee brought in about 14 leaf pieces in the next hour, then started collecting pollen. It brought in its ninth pollen load and ceased work for the night at 5:39 p. m. The next morning it resumed activities at 8:43. Observations ceased six hours and twenty minutes later as the bee was provisioning a second cell. The unusually long period at the nest (5 minutes) just before the last departure observed was due to the fact that the curled leaf had wilted some in the hot sun and the bee had trouble getting into her nest.

Nest "e" (figure 9) was found in a fasciate *Erigeron canadensis* plant in an alfalfa field at Hutchinson, Kansas. The bee was seen to enter the nest at 11:45 a. m. on July 26, 1950. The bee was collecting alfalfa pollen at the time, and in due course laid an egg and closed the cell with petals and leaves. Observations were continued for a total of 3 hours and 10 minutes.

Nest "f" was established in the same fasciate *Erigeron* as nest "e". The record shows every visit in the construction, provisioning and sealing of a cell. The first leaf was brought at 4:16 p. m. and the cell was partly constructed when the last trip of the evening terminated at 6:07 p. m. Activity began next morning at 9:35 a. m. and observations continued until the bee was caught at 6:02 p. m. after having apparently completed closing the cell.

Nest "g," also in a fasciate *Erigeron* near Hutchinson, Kansas, was located at 12:23 p. m. on August 2, 1950, as the bee entered the nest. It was observed through a series of pollen collecting trips to the beginning of closing of the cell two hours and ten minutes later, at which time the bee was taken to verify its identity.

Nest "h" was found on August 9, 1950, at 9:38 a. m. as a bee entered a hole in a dead prostrate *Ambrosia* stem in Area 6. The bee was carrying pollen when first seen, but soon after brought in petals and leaves to close the cell and to construct the cup of the next cell, and by shortly after noon was carrying pollen for the next cell. At 2:39 p. m. it started on the first trip to get petals to close this cell, the second cell to be closed this day. Petals and leaves were brought in until the last trip of the afternoon which ended at 5:30 p. m. Next morning activity started at 8:53 a. m. with bringing of more petals and leaves. At 9:36 a. m. the first pollen collecting trip started, the last one for this cell terminating at 12:19 p. m. Petals and leaves for closing the cell were then brought, and more of both were used to close the hole in the stalk. The bee was last seen about the nest at 2:12 p. m.; two hours of watching after that time indicated that the bee had left permanently.

The bee lettered "i" was found on August 11, 1950, at 12:35 p. m. as it flew from its nest in a piece of *Ambrosia* stalk lying in the grass in Area 6. The first petal to cap the cell was brought in 35 minutes later, at 1:10 p. m. and by 3:30 p. m. the cup of the next cell in the series was complete. Pollen was carried into the cell until 5:03 p. m., the last trip of the day. Next morning it was cloudy and the bee did not leave the nest until 11:15 a. m. and provisioning of the cell started the previous afternoon was not complete until 3:29 p. m. The bee then brought in a few petals and leaves, after which it seemed to cease work; it had not returned to the nest for the evening when the observer left at 5:53 p. m. The next day, August 13, threatened rain all day. The bee was seen carrying leaves, although she had only a few suitable periods during the whole day. She must have completed the next cell cup in the series, however, for after she left the nest the next day for the first time, at 10:45, she returned with pollen. Provisioning was complete and the first petal to form the cap of the cell was brought in at 1:10 p. m. on August 14.

A study of figures 8 and 9 shows some interesting things about the timing of the trips to and from the nest. The trips at the time pieces of petals and leaves are being brought to the nest are very irregular in length, varying from 20 seconds to two hours and 26 minutes. Sometimes considerable series of very short trips are made, for example there is a series of ten trips in ten minutes shown in the record of nest c. Among the data shown in figures 8 and 9, plus other records, are 335 timed trips which ended by a piece of leaf or petal being brought to the nest. Of these, 93 were trips of less than a minute in duration, 203 were trips of one to five minutes in duration, 20 were trips of six to ten minutes, 8 were of seven to fifteen minutes, three were trips of 15 to 20 minutes, and seven were trips over 20 minutes in duration.

There is no evidence as to what the bees were doing on the very long trips; possibly they might merely suck nectar. It is apparent from figures 8 and 9 as well as from examination of nests, that leaves usually are gathered in series preceded or followed by series of petals; it is unusual that a petal is brought in after a leaf and followed by another leaf, or vice versa. There is no evidence that the bees take longer to obtain leaves than petals or that the first of a series takes longer to obtain than others. As is fully confirmed by the study of nest structure presented earlier, figures 8 and 9 show that the last additions to the cup (innermost layers) are ordinarily petals as are the first or innermost layers of the cap.

The length of time spent in the nest between such trips is short, ranging from as little as 10 seconds, in cases where it was later found the bee had been merely using leaves or petals to fill excess space in the nesting cavity, to 10 minutes. In the latter cases the bee apparently merely rested in the nest. In most cases where the bee was continually active two minutes was the maximum period spent in the cell between leaf or petal gathering trips.

The foraging trips, by contrast, are of relatively uniform duration for any one nest. Thus for nests e, f, and g the trips are rather short, four and one-half to ten minutes, except for one of 23.5 minutes. This suggests that pollen can be collected rather quickly from alfalfa. By contrast, pollen collecting from *Rhus* and *Vernonia* seemed to require a longer time per trip, as can be seen, for example, from nest "d," in which the shortest trip was 10.3 minutes, the longest 29 minutes.¹ For this nest the pollen source (*Rhus*) was not near the nest (it was at least one-fourth mile away and this may account for the long duration of the trips. The length of time spent in the nest between pollen collecting trips was one to two minutes in nearly every case.

After provisioning and before bringing in further petals and leaves, a pause in outside activity consistently occurs. This is the egg laying time. The bee is in the nest from 4.5 to 9 minutes (average of 13 observations, 6.6 minutes) at this time.

Study of figures 8 and 9 suggests that unless the bee is gathering pollen, the last trips in the late afternoon tend to be rather long and to result in nothing visible being brought back to the nest.

It is also evident that when a nest is completed, it is not always, if ever, summarily abandoned; the bee often returns once or twice, carrying nothing, and buzzes about the nest or alights there before going on. In one such instance (nest f) it was noted that the bee was acting as though looking for a new nesting site. This would suggest that after one nesting cavity is filled or abandoned, the bee goes on immediately searching for another.

Besides irregularities of action already noted, there are occasional trips for which there seems to be no explanation whatever. An example is seen near the beginning of the record of nest "g". After bringing in a load of pollen, the bee left, was gone for some 45 seconds, returned with nothing visible, then left on another pollen collecting trip. On another occasion a bee in the midst of con-

1. Temperature does not seem to be well correlated with duration of pollen collecting flight.

structing the cup of a cell left the nest and rested on a leaf ten feet away for a full minute, then returned to the nest, and entered it, then left and soon brought back another leaf. The number of such irregular trips is very small, as is shown by the small number of "o" marks on figures 8 and 9.

PETAL AND LEAF CUTTING

Leafcutter bees are widely known to use rose leaves freely in constructing their cells. The broad range of leaves and petals used by *Megachile brevis* is something of a surprise, although other species are known to use both petals and leaves.¹ Table VII lists the various kinds of leaves and petals which we have seen cut by this species. Certain European authors (e. g. Hardouin, 1945) have overemphasized specificity in the kinds of leaves cut by species of *Megachile* such as *M. centuncularis* Linnaeus, a species similar to *M. brevis* in many ways. This emphasis is surprising in view of the lists of different kinds of leaves cut by various species provided in Friese's (1923) review and in much earlier papers referring to *M. centuncularis*, for example by Buysson (1902) and Ferton (1896).

As was shown in more detail in the section on nest structure, the various kinds of leaves do not fill the same needs. The petals used on the outside of the cell and the thin leaves such as those of the Leguminosae serve merely to fill up extra space. The firmer leaves, such as those of rose, give the cell its shape.

If one examines a region where *Megachile brevis* is nesting, scattered leaves or petals from which a piece has been removed by a bee will be seen. However, most of the cutting is found to be in small areas, for example a particular branch of a rose bush or a patch of *Oenothera* flowers a couple of feet square. There are no evident differences between such places which are favored for cutting and similar bushes or patches a few feet away.

The following notes made on June 14, 1951, in Area 3 illustrate this and other points: "Occasional rose petals cut by *Megachile* could be found scattered over the entire prairie. Most of the cutting, however, is concentrated in small areas two to four feet in diameter. In these places both petals and leaves are cut. The number of cuts in each little area is such that all may have been made by a single bee. One similar area where strawberry leaves

1. The author has examined a nest of *Megachile montivaga* Cresson made in a green weed stem near Eagle Rock, Los Angeles County, California. The cells in this nest were made of the pink petals of *Phlox* and leaves of poison oak, *Rhus diversiloba*, which had become red with fall coloring.

TABLE VII.—Kinds of leaves and petals utilized in nest construction.

(x indicates a single observation or a single nest, xx several observations or nests, xxx indicates repeated observation in many nests.)

Scientific name	Common name	Leaves	Petals	Remarks
Polygonaceae <i>Polygonum opelusana</i>	Smartweed	x		
Polemoniaceae <i>Phlox</i> (cultivated)	Phlox	x		
Solanaceae <i>Petunia</i>	Cultivated Petunia		x	
Rosaceae <i>Fragaria virginiana</i> <i>Fragaria</i> <i>Potentilla simplex</i> <i>Rosa suffulta</i> <i>Rosa</i>	Wild Strawberry Strawberry Cinquefoil Prairie Rose Cultivated Rose	x x x xxx xxx	xx	Important source of leaf pieces. Important source of leaf pieces.
Cassiaceae <i>Cassia chamaecrista</i>	Partridge Pea		xxx	Important source of petals
Fabaceae <i>Medicago sativa</i> <i>Lespedeza violacea</i> <i>Lespedeza virginica</i> <i>Trifolium repens</i>	Alfalfa Bush Clover Bush Clover White Clover	xx xxx x x		Whole or nearly whole leaflets used. Important source of whole or nearly whole leaflets. Nearly whole leaflets. Whole or nearly whole leaflets.
Lythraceae <i>Lythrum alatum</i>	Winged Loosestrife		x	
Crassulaceae <i>Penthorum sedoides</i>	Ditch Stonecrop	x		
Oenotheraceae <i>Ludwigia alternifolium</i> <i>Oenothera speciosa</i>	False Loosestrife White Evening Primrose	x	xx	Leaves bitten but piece not carried away.
Aceraceae <i>Acer</i> sp.	Cultivated Maple	x		Leaves of young seedling.
Caprifoliaceae <i>Symphoricarpos orbiculatus</i>	Buckbrush	xx		
Compositae <i>Zinnia</i> sp. <i>Silphium perfoliatum</i>	Cultivated Zinnia Cupplant		x x	

(*Fragaria virginiana*) were being cut was found, and another where leaves of *Potentilla simplex* were being cut. Strawberries and roses were scattered over the whole prairie." Nevertheless bees observed cutting returned unhesitatingly to their little patches.

It seems likely that an advantage of this tendency to return to a single place for leaves and petals is that it makes possible rapid gathering of these materials without the need to search on each trip.

We have seen alfalfa leaflets cut only three feet from the nest, and have seen pieces of rose leaves and leaves of *Lespedeza virginica* cut 150 to 200 feet from the nest. In the latter cases rose and *Lespedeza* leaves could have been found within ten feet of the nest. The time spent in flights of such lengths is negligible compared to that that might be spent in searching.

Figures 8 and 9 show that petal and leaf collecting trips away from the nest vary greatly in length but that the periods of time at the nest are comparatively constant. Observations of individual bees made at cutting places show that the length of time spent in cutting is rather constant, but that there is great irregularity in the length of time away from the cutting place. This indicates that the bees may spend considerable time on some trips before getting to the cutting place, for after cutting a leaf they always fly directly toward the nest. This time is perhaps spent in sucking nectar or in searching for new leaf or petal sources.

The bees cut leaves and petals with remarkable speed. The cutting is done by means of the mandibles (figure 5). We noted the cutting of a round piece of rose leaf such as is used for capping cells in 3 or 4 seconds, and timed the cutting of the longer pieces used for cup walls at 13 to 30 seconds.

Sometimes a bee cuts the first leaf it alights on but very often it flies on to leaf after leaf, as though for some reason dissatisfied. We watched one bee alight on 38 leaflets of *Lespedeza violacea* before finally cutting one off. As shown in figure 10, the bees very commonly start to cut into a leaf, and may have a piece half cut off, before abandoning it and going on to another. This hesitancy is far more noticeable when bees are not working in a repeatedly visited cutting place, but occurs even in such cutting places.

The cutting process begins with the bee resting on the edge of the leaf (or petal) with the legs of one side clinging to the upper surface of the leaf, those of the other side clinging to the under surface. The bee cuts into the edge of the leaf with its jaws, cutting in a smoothly curved line irrespective of veins in the leaf (e. g. in small

rose leaflets it cuts through the midvein, figure 10). As it cuts, the bee turns its body so that a piece of standard shape (long for the cup, round for the cap) is cut out. The middle part of the bee's body moves very little, merely rotating as the head and jaws describe an arc while the cutting goes on. As the cut is made the bee shifts its footing so that it is clinging to the piece being cut. At least in the case of an elongate piece, the piece is curled as it is cut by bending the edges away from the body of the bee. This is done as the bee shifts onto the under surface of the piece being removed,

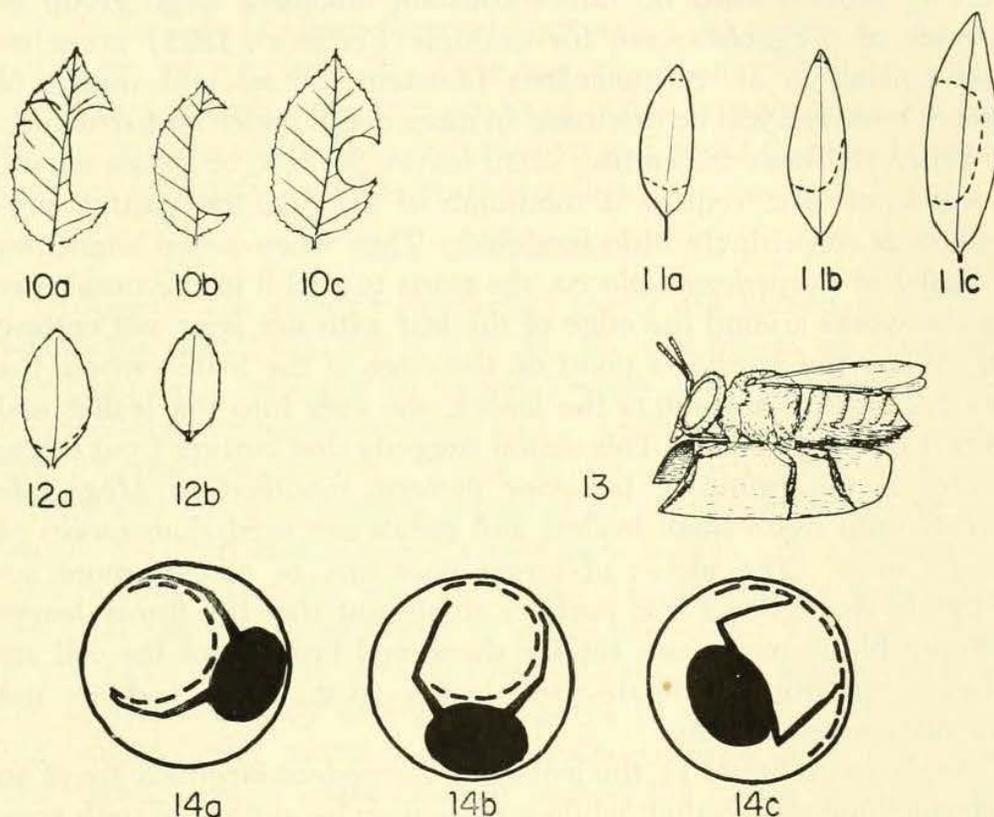


FIG. 10. Rose leaflets cut by *Megachile brevis*. a, leaflet with two incomplete cuts and one long piece removed; b, small leaflet with one long piece removed, showing that the bee cut across the midvein; c, leaflet with round piece removed.

FIG. 11. Leaflets of *Lespedeza virginica* showing the ways in which long pieces are obtained from leaflets of various sizes. a and b are common, c rare since leaflets are rarely so large.

FIG. 12. Leaflets of *Lespedeza violacea* showing ways in which they may be cut whole or nearly so for use as filler leaves.

FIG. 13. A female *Megachile brevis* showing the way in which she holds a piece of a leaf.

FIG. 14. Diagrams showing the way in which a bee places long leaf pieces to form the cell cup. The circles represent the hollow (or already partly constructed cup) seen from the open end. The leaf piece is represented by the broken lines. The bee, headed into the cell, is represented in black. The bee carries the leaf into the cell in the manner shown in a, moves sideways, as shown in b, until she gets past the edge of the leaf, as in c.

so that as the six tarsi hold the edges of the piece away from the bee's body, the center is bowed against the sternum. In every instance observed carefully (about 30 cuttings of leaves, three of petals) the piece was held in this fashion with the original under surface (of leaf) convex against the venter of the bee. As will be shown later, this results in the under surface of the leaf being outermost in the complete cell. Cutting continues around the arc characteristic of the type of piece being removed, and at the instant that the piece is severed the bee takes flight. The details of the cutting process must be rather constant among a large group of species of *Megachile*; see for example Ferton's (1893) notes on leaf cutting in *M. centuncularis* Linnaeus. Sizes and shapes of pieces removed will be discussed in more detail under nest structure.

When the bees are cutting small leaves, leaflets, or petals which, because of size, require a minimum of cutting, the cutting procedure is surprisingly little modified. Thus when a bee alights on a leaflet of *Lespedeza violacea*, she starts to curl it in the usual way as she works around the edge of the leaf with her jaws, not cutting it. When she reaches a point on the edge of the leaflet where the normal cutting arc enters the leaflet, she cuts into the leaflet and cuts it off (figure 12). This action suggests that cutting from larger leaves is the primitive behavior pattern, modified in *Megachile brevis* until more small leaflets and petals are used than pieces of larger ones. The pieces of larger ones are, of course, more accurately shaped and it is perhaps significant that the firmer leaves responsible in most cases for the shape and firmness of the cell are always cut from moderate-sized leaves (e. g., rose) and are not merely severed leaflets.

As shown in figure 11, the leaflets of *Lespedeza virginica* are of an intermediate size so that, while a piece may be cut out as with rose, more often the tip of a leaflet is cut off and dropped, then the jaws of the bee follow the leaf edge to a point near the base where they cut into the leaf and across it.

In one instance a bee was seen to cut off and carry away a small triangular piece of rose leaf left between two normal sized pieces removed previously. It is possibly significant that this was done on the last of at least ten trips of the bee to a particular cutting area.

Once the bee has cut off the leaf piece, it usually flies from one to ten feet and alights on a leaf or on the ground, remaining there as though resting for 45 to 80 seconds (average of 10 observations, 61 seconds). While resting the bee holds the leaf as previously described, curled under her body, the claws holding its margins

(figure 13). Just before flying off toward the nest, the bee, in every instance observed, rubbed her abdomen against her closed wings several times. This brief period of inactivity following cutting is often omitted but only when bees are cutting either soft and easily cut petals or leaflets which required little more than severing. Eleven cuts of *Lespedeza virginica* leaflets by a single bee¹ were observed. Of these only two leaflets were large enough to require cutting around three sides; after these two the bee rested. The others were smaller leaflets requiring less cutting (see figure 11) and the bee did not rest but flew directly to the nest, 150 feet away.

Data on how far from the nest bees will go to obtain leaves and petals are very scanty. We have seen them cut within a few feet of the nest and we have seen pieces of petals brought from 300 feet away. In view of the diversity of leaves and petals that can be used, they are probably usually obtained rather near the nest.

NEST CONSTRUCTION

Ordinarily the cells of *Megachile brevis* are placed in hollows where the actual manner of building the cell cannot be observed. We have been fortunate in finding certain nests whose cells were incompletely enclosed, enabling us to observe certain things about the construction process. Three of these nests were in spaces among the leaves of fasciate plants of *Erigeron canadensis* but one was in a curled leaf of *Eupatorium perfoliatum*. In all cases the construction technique was the same. In making the cup of the cell, elongate pieces of leaves or petals are used. The bee brings in the piece of leaf or petal curled, with the edges held away from the body, as already described (figures 13 and 14). She carries the leaf into the cavity in this position, entering head first, then she releases it and works laterally around the cavity until she gets past one edge of the leaf, as shown in the diagrams (figure 14). Additional leaves and petals are added in the same manner so that the cell wall is constructed from the outside inwards. After the bee has placed a leaf or a petal in a partially constructed cell, she works in and out and around, the abdomen moving in small, quick (respiratory?) movements. The bee may move in and out only twice, or up to five times. While doing so, she is mouthing the leaves, particularly their edges, as can be seen occasionally when she backs almost out of the cell to mouth the outer portions of the leaves. At such times it can be seen that the apex of the proboscis

1. With an observer at the nest and another at the cutting place, there was no doubt about the bee being the same one each time she was observed cutting even though she was unmarked.

is applied to the leaves although the proboscis is scarcely unfolded. Probably this activity adds the invisible quantities of adhesive apparently used in cell construction. The leaves stick together only very feebly, yet they are not entirely loose when a nest is exposed. Some species of the genus evidently stick the leaves together much more firmly (see footnote 1 in Ferton, 1898) while others may use no adhesive material at all. When this activity is finished, the bee backs out of the cell and flies away.

After the cell is complete, provisioned, and an egg laid, the bee caps the cell, using round rather than elongate pieces of petals and leaves. The cap is placed well down within the mouth of the cup. When a bee is putting in this plug, she hangs on the edge of the cup with her rear legs, the body in the cell and braced against the inner walls with the other legs, then she pushes the round piece of petal or leaf into the opening with her head and mandibles. (This closing behavior was carefully noted only once, and may vary more than indicated here.)

PROVISIONING

The partially exposed cells described in the preceding section provided an opportunity for observations of provisioning activities. When a bee returns to her cell with the scopa (the long hairs on the under side of the abdomen) full of pollen, she quickly enters the cell head first and remains in this position for 20 to 45 seconds (average of 14 observations, 28 seconds). While in this position the apex of her abdomen, which is visible inside the cell, can be seen to tremble slightly. During this time the bee is no doubt placing nectar in the cell. After this the bee quickly backs out of the cell, turns around, and backs in. When she backs out the pollen can still be seen in the scopa. Occasionally as she backs in, the beginning of probable combing motions by the rear legs to remove pollen from the scopa can be seen. She remains in the cell in this position from 40 to 65 seconds (average of 12 observations, 50 seconds), her head visible within the opening of the cell. Just before leaving the cell, the bee moves from side to side a little and often brushes the head and eyes with the front legs; then she crawls out and quickly flies away. As she leaves it can be seen that the scopa is clean.

Unless the cell is vertical, the bee consistently enters the cell with her ventral surface down during the provisioning process, not rotating on her long axis within the cell as when the cup is being constructed.

Observations of the accumulating provisions in the cell, made while the bee was away, gathering more, show them to be firm (not sticky as in opened cells) and with the surface flat, at right angles to the long axis of the cell and smooth as though tamped down.

The distance from which *Megachile brevis* will gather pollen is unknown but we have observations of pollen gathering from a few feet to one quarter mile from the nest, and circumstances often suggest that they may go much farther than this.

EGG LAYING

The behavior connected with egg laying was observed five times in cells which were sufficiently exposed that some details of the bee's activities could be seen. In each case the procedure was as described below. Minor variations in timing occur, of course, as can be judged by the variations in the length of the egg laying period shown in figures 8 and 9.

On returning from her last pollen gathering trip, the bee enters the cell head first presumably to regurgitate nectar, then backs out and backs into the cell and brushes the pollen from the scopa, just as after any other pollen collecting trip. She then comes out of the cell head first, quickly turns around at the entrance and re-enters, head first. She now works for about 50 seconds, moving about in the cell and often turning the body on a longitudinal axis so that she may be clinging to the roof of the cell (if it is horizontal) part of the time. During this period the apex of the abdomen (the only part visible) is sometimes bent downward in an unusual way. The bee then backs out of the cell, turns around, and backs in, remaining there about 45 seconds. It is during this period that the egg is laid on the surface of the mass of provisions. She then comes out head first, turns around, goes in head first again, once more working around the cell and curling the apex of the abdomen downward. This continues for about two minutes (in one case five minutes), after which the bee backs out and flies away, soon to reappear with a petal and start capping the cell.

In an ordinary nest in a weed stalk none of this activity is visible, for the hole in the stalk is large enough to allow the bee to turn around outside the cell but inside the stalk. It is interesting that in the megachilid genus *Hoplitis* (subgenus *Alcidamea*) precisely similar enterings and re-enterings occur at egg laying except that

the diameter of the hole in which the cells are constructed is so small that the bee must come all the way out of the nest in order to turn around.

FLIGHT PATTERNS AROUND NESTS AND LEAF-GATHERING PLACES

The most noticeable feature of the arrival at and departure from a nest is its rapidity. When an observer first takes his place near a nest, the returning bee may be somewhat disturbed and may fly about the vicinity or about the observer for a short time before entering the nest, but when she becomes used to the observer and her activities are undisturbed, she ordinarily flies directly toward the nest, often with a little zigzag motion in the last few feet of the approach (figure 15). If the nest is among grass or weeds the bee may or may not have an invariable route through the obstructing vegetation; the flight through it is always slow, however, compared to flight in the open. One nest located under grass on an open prairie, where landmarks are presumably poor for the bees as they are for us, was always approached from one side, the bee swinging around and then zigzagging broadly in the last eight or ten feet of the approach (figure 15). The same bee regularly approached a leaf cutting place on the prairie directly, with no zigzagging whatever, perhaps because no great precision was required, the leaf cutting area being two or three feet in diameter. The most extensive searching flight which we observed in the approach to a nest occurred in the case of a bee which nested among small rocks along a roadside. Similar small rocks had been dumped for 100 yards along the road and the rocky surface looked much the same everywhere. The bee was rarely able to approach its nest directly and often, particularly if it had been away for over five minutes, flew up and down over the rocks, often going as much as 20 feet in the wrong direction before finally narrowing its field of search and then zigzagging toward the nest. Such behavior is very striking compared

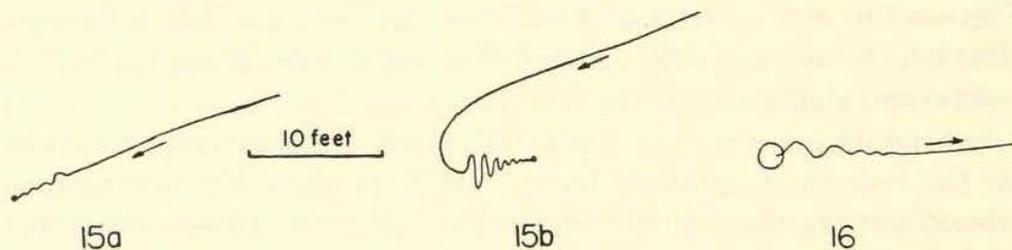


FIG. 15. Patterns of arrival at nests. a, the common pattern, in which the bee scarcely slows down to zigzag before entering the nest; b, a pattern in which a bee regularly circled and zigzagged rather broadly on the way to the nest.

FIG. 16. Flight pattern of departure from a cutting place.

to the vast majority of nests studied, to which direct approaches were made by the bees, probably because brushy and weedy situations usually provide adequate landmarks. Similar difficulty in locating a nesting site was recorded by Rau (1916) for a female nesting in a railroad tie. The bee searched the wrong tie. Presumably all the ties along the track were much alike.

In leaving the nest in favorable weather the bee comes out, immediately takes wing and is gone, usually in an essentially straight course. Occasionally in cool weather, or at the first departure in the morning, the bee crawls out of the nest and rests for a few seconds to a minute or more before flying. It was noted that in leaving her nest on the open prairie, the bee mentioned above regularly spent about two seconds zigzagging or circling over the nest site. The same bee, leaving a leaf cutting place on the prairie usually zigzagged only slightly (figure 16).

Orientation flights around a newly discovered nesting site were observed three times, and about a newly discovered cutting place once. These flights did not follow any consistent pattern such as flights of increasing length from the site or flights in increasingly large circles around it but involved merely irregular flights over the site, and in the case of the nesting places, several returns from many yards away.

From the usual nest, the pollen source is more or less definitely in a particular direction, while sources of petals and leaves are in other directions. The bee, under such circumstances, often (although by no means always) uses particular routes as she leaves the nest and returns to it. The routes of departure may or may not be identical to the routes for returning. Our notes contain numerous references to the exact way which a bee, during any one phase (e. g., pollen gathering), follows a certain course, identified for us at least by bushes, weeds, and other fixed objects. When several observers could be got in the field, it was sometimes possible for them to take stations along the line of flight from the cutting place to the nest and see that the line of flight was followed quite exactly time after time for the whole distance (150 feet).

On the other hand, we have watched a nest (d, figure 8), in which the bee rarely took the same course in leaving on its pollen collecting trips. The bee flew in a generally westerly direction for pollen but left in directions as different as north northwest and southwest and sometimes returned from directions as different as 45 degrees from the direction taken on the outward journey. The pollen source

(or sources) was at least one quarter of a mile away. The same bee, when collecting petals (mostly of *Lythrum*, one of *Cassia*?) and leaves, flew eastward, following approximately the same course each time. (There is no general rule that bees fly in the same direction for petals as for leaves; they may fly in opposite directions.)

The pollen collecting flight patterns of three bees nesting in alfalfa fields in the region of Hutchinson, Kansas, are interesting. One of the bees flew consistently northward from its nest, apparently gathering pollen from a particular part of the field, which, however, was not different so far as we could see from other parts of the field. The other two bees (one of which nested within 15 feet of the above bee and was observed on the same day) flew from their nests in many directions, apparently at random, for alfalfa pollen. These bees were able to return directly and quickly, without searching, from any direction and sometimes returned from a direction differing from the line of departure by as much as 90 degrees. All three bees flew in particular directions to gardens around nearby houses for petals and some of their leaves, but they obtained other leaves from the alfalfa plants around the nests.

CHANGES IN BEHAVIOR

Because of the mobility of *Megachile brevis* populations and the tendency of the females to construct cells in different places, we have no records of activities throughout the lives of individual bees; therefore we have no knowledge of changes which may occur in behavior during the life of a bee. However, in the brief period required for construction of single cells some observations on changes of activities are possible.

It has been noted that when the female bee concludes one phase of its activity and goes into the next, the change in behavior is abrupt and absolute. Thus when the bee finishes constructing the cell cup it promptly changes to pollen collecting behavior, and after the cell is provisioned and the egg laid, it promptly returns to leaf cutting behavior. A good example is provided by the data on nest "i" presented in figure 9. After each of the two egg layings indicated in this record, the bee, which had been flying in a generally westward direction for pollen, came out of the nest and without the slightest delay flew eastward for petals. In each case she was back to the nest with a petal within one minute. Doubtless because of previous experience in the area the bee was able to go quickly

to a petal source. Examination of figures 8 and 9 shows that first trips after changes in phases of activity average no longer than later trips. This indicates that for these bees no extensive searching for materials (petals, leaves and pollen) was necessary. The bees must have "known" of the sources of the materials at the time they left the nest. This is suggestive of a delayed reaction to previous conditioning. There is some evidence to support the idea that much behavior of aculeate Hymenoptera results from delayed reactions which were first definitely recognized among invertebrate animals by Baerends' (1941) working on *Ammophila*.

There is some evidence, meager but nonetheless suggestive, that within any one phase of its activities, changes in sources of materials are made somewhat gradually. The details of a change from collecting *Vernonia* pollen to that of *Rhus* were observed on August 11, 1950, in Area 6. The bee had been gathering pale *Vernonia* pollen for several days and had provisioned three and one half cells with it. In the midst of provisioning the fourth cell, as she left on a pollen gathering trip, she was seen to fly toward some nearby *Vernonia* and when nearly there turn and fly on a different course toward some *Rhus* bushes 100 yards away. She returned with yellow *Rhus* pollen. On her next trip, she flew again toward the *Vernonia* but quickly veered toward the *Rhus*. Thereafter she flew directly toward the *Rhus* from the nest, completing the fourth cell and provisioning two more with its pollen.

Another instance of gradual change in behavior concerns leaf cutting operations of a bee observed in Area 3 on June 16, 1951. The bee had been gathering leaves of *Lespedeza virginica* at a very rapid rate, obtaining them from a small cutting place on the prairie. An observer was at the nest, another at the cutting place, 150 feet distant. The bee made 11 trips for leaves in rapid succession, being away from the cutting place for periods of time varying from one and one-half to three minutes. On the twelfth and thirteenth trips the bee was away from the cutting place for 7.5 and 6.5 minutes. Most of this time was spent in the nest but the two observers noted that her flight time from nest to cutting place nearly doubled on these two trips although when she arrived at the cutting place, she came from the direction of the nest. On the fourteenth and fifteenth trips, the bee left the nest in the direction of the cutting place, but did not alight there. The observer there (CDM) was virtually certain that on each trip she passed the cutting place and then headed in a southerly direction; at any rate an insect that

looked and sounded like a female *Megachile brevis* arrived at the expected time (indicated by a shout from the observer at the nest) from the direction of the nest (northwest) and then headed southward. On each of these trips the bee returned to the nest with a piece of rose petal. There was no indication that she returned to the nest via the leaf cutting place. On the fifteenth trip the bee again left the nest, headed toward the leaf cutting place but was not detected there; on the sixteenth trip she left the nest headed in a more southerly direction, presumably toward the source of petals. From each of these trips she returned with a piece of rose petal.

PART V.—GROWTH AND DEVELOPMENT

TECHNIQUE OF STUDY

After the egg is laid in a cell and the cell is capped, the bee goes on to the construction and provisioning of other cells, giving no further attention to the egg or resultant larva. The developmental stages are ordinarily hidden from view. Two principal methods were used to study them. Cells, removed from the hollows in which they were constructed, were slit longitudinally on one side with a sharp blade. They could then be opened as desired for inspection of the contents. This method has serious disadvantages for the cells must be kept in a humid atmosphere to prevent desiccation of the pollen mass. Fungal growth therefore often occurs on the leaves, and later on the pollen. Moreover, the cap of the cell usually falls out. Since the larger larvae often press against the cap with their middle or posterior portions in order to force their heads down into the pollen, lack of the cap seems to cause slow feeding and sometimes larvae seem to have difficulty finding the food.

A better method consists of moving pollen mass and larva into a glass tube having an inside diameter of about 5 mm. The tube should be plugged at each end with absorbent cotton, the cotton plugs being about 10 mm. apart at their inner ends. Mold rarely grows in such containers. If they become too dry water may be added through the plugs.

Another good method consists of filling a Stender dish with paraffin, then making depressions 5 mm. in diameter and 10 mm. deep in the paraffin. Young larvae live very well in such containers, humidity being provided as needed. Visibility is very good as the lid of the Stender dish can be removed and the contents examined under a binocular. Older larvae do best in tubes, however.

Obviously all these methods involve considerable artificiality; this may account for some of the rather great variability noted in the duration of various stages. The records given below, however, omit cases where larvae were obviously away from their food for long periods or where other such avoidable abnormalities occurred.

All records of duration of stages were obtained at room temperature during August. Most larvae were observed but once each day, so that the margin of error in timing activities of short duration is great.

EGG

The egg is about three millimeters long or slightly less and 0.6 or 0.7 mm. thick (figure 18), soft and smooth on the outside, glistening white in color. It is laid on the top of the pollen mass, standing up from the surface of the pollen in a slanting position (figure 17). If the pollen mass becomes somewhat liquid, as often occurs, or if the nest is jarred in carrying it to the laboratory, the egg will slump down until it lies at full length on the pollen. This does not appear to influence development and hatching, and it may well be that the egg is often laid in this position.

It is exceedingly hard to tell when the egg hatches because the chorion or "shell" is so thin and soft and because it disappears completely after being shed. However, segmentation, muscular movements and gas filled tracheae can be seen before hatching. As soon as pollen is visible in the digestive tract, hatching must obviously have occurred. Three observations from laying time to approximate hatching time indicate that the egg stage lasts from 3 to 3.5 days.

LARVA

The larva (figures 19 to 21) is a legless whitish grub. Dorsally it is feebly brownish, and the apices of the mandibles are dark brown. Details of certain anatomical features of the mature larva are shown in a previous paper (Michener, 1953).

During the entire feeding period of the larva, from shortly after it emerges from the egg until feeding ceases on maturity, small spots which are whiter than the rest of the grayish white body can be seen through the integument. They have been seen as little as twelve hours after hatching and may appear sooner, although they are absent at the time of hatching. They are not part of the cuticle, as they can be seen moving beneath the cuticle with the movement of the tissues inside the body. After the larva finishes feeding these spots disappear and the general color of the larva becomes more white, less grayish.

The number of larval stadia has not been definitely determined. The exuviae are very delicate and are probably usually eaten soon after ecdysis.

In the first day of its life the larva is straight and lies flat on top of the pollen mass. It has thick projecting folds along each side of the body which seem to help the small larva, 3 to 4 mm. in length, to float on the often quite liquid mass of food. At this stage the larva is unable to move about to any extent. Usually on the

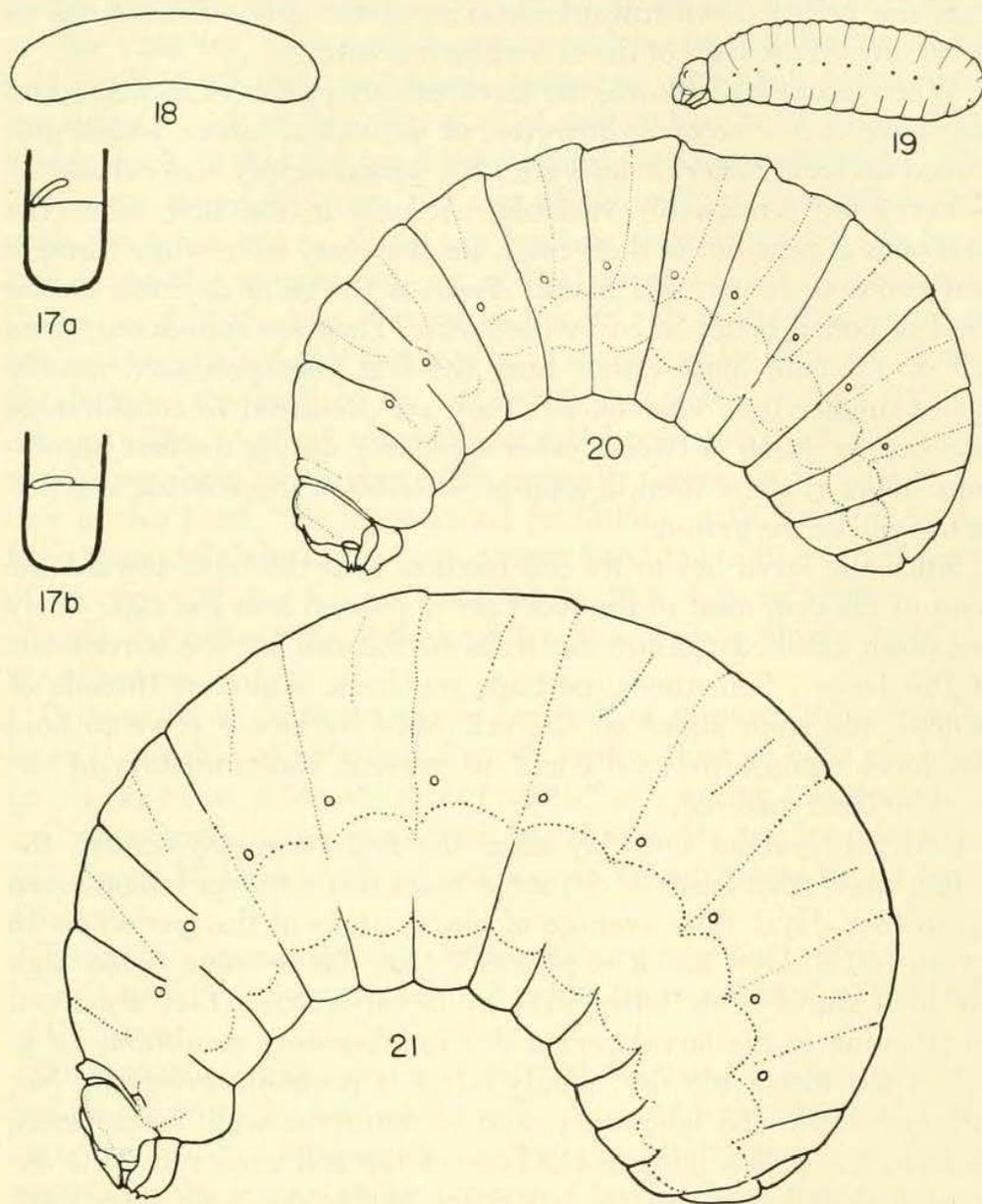


FIG. 17. Diagrams of cell cups. a, with egg standing up from edge of mass of provisions; b, with egg as usually found, lying on provisions.

FIG. 18. Egg of *Megachile brevis*.

FIG. 19-21. Larvae of *Megachile brevis*, first stage, half-grown, and mature.

second day, after what is probably the first molt, the larva becomes more curved as it eats into the pollen at one side of the cell, and the lateral folds are far less prominent. At the beginning of this stage the larva when straightened out is about 5 mm. long. As it grows the larva becomes more strongly and permanently curved (so that it cannot be straightened for measurements of length) and

eats the pollen down toward the base of the cell. Thus it has its head toward the base of the cell while it is eating.

When about half grown, the larva usually produces its first feces. We have a few records, however, of individual larvae which produced no fecal material until after the pollen supply was exhausted.

Feces are remarkably variable, not only in the time when the first ones appear but in their color, for they vary from white through testaceous to brown and black. Perhaps the color depends on the kind of pollen being eaten by the larva. They are cylindrical, often 1.0 or 1.5 mm. long, rather firm, the first ones produced usually being smaller than later ones. They are produced in considerable numbers, a dozen or twenty often appearing during the first twenty-four hours of defecation, a total of 40 or 50 or more being reached at the end of the period.

Since the larva lies in its cell feeding with the head toward the base of the cell, most of the feces are deposited near the cap. They are often crushed against the walls of the cell by the movements of the larva. Sometimes, perhaps regularly, scattered threads of whitish silk spun about on the cell walls by larvae serve to hold the feces against the walls and to prevent contamination of the food by fecal material.

Commonly about one day after the first feces are voided, the pollen mass is exhausted. In some cases this requires longer, even up to four days. The average of observations of this period on 15 larvae is 1.9 days, but it is probable that this average is too high for it is during this latter part of larval feeding that abnormal lengthening in the larval period due to laboratory conditions (e. g. pollen too moist, too dry, moldy, etc.) is probably greatest. Not infrequently in the laboratory, and in nature as well, larvae leave some of the pollen mass at the base of the cell uneaten. This unconsumed pollen consists of a pad one half to one millimeter thick in the base of the cell. It is not clear whether it is left because it has become unsuitable as food or because the larva has finished its development and needs no more food, but the latter seems probable.

After the larva has finished feeding on the pollen mass, it spends at least a day before it begins to spin its cocoon. Occasionally this period extends to three days, although the average of 14 records of this period is only 1.3 days. During this period the larva moves about considerably turning so that its head is away from the base of the cell and rasping the inner walls of the cell with its mandibles and eating some of the petals which usually form the linings of cells and which by this time have become soft and mushy. Evi-

dently the larva may reverse its position in the cell more than once at this time for cells have been opened containing larvae which had finished all their provisions, turned so that their heads were toward the cap of the cell, part of which had been eaten, then turned back so that the head was toward the base of the cell. The larva eats especially from the cap of the cell, so that petals and even the inner leaves of the cap become mere rings, for the larva can get at the centers but not at the margins of the disc-shaped pieces used in the cap. So far as known this is the first report of bee larvae eating petals and leaves. One larva was observed eating petals from the wall of its cell a full day before it had finished eating pollen. Larvae reared in artificial containers without petals and leaves seem to develop quite normally, however, in spite of the lack of this food. Under artificial conditions, with larvae removed from their cells, the entire period from hatching until the beginning of cocoon spinning ranges from 5.1 to 13.3 days in summer. As already suggested, the maximum lengths of time almost certainly are abnormal.

Perhaps throughout the entire last half of the growth period the larva is capable of spinning, for slits in the sides of cells are often found closed by a few strands of whitish silk during this period.

Cocoon spinning requires from less than a day to three days, the average of 15 individuals whose cocoon spinning was timed being 1.4 days.

The silk is spun from the slitlike salivary opening and is applied by side-to-side movements of the head and forward parts of the body of the larva.

The spinning of the cocoon starts with the larva in a position with head away from the base of the cell. As will be explained later, the cocoon consists of various layers. Presumably the larva reverses its position in the cocoon in the process of laying down each layer. As a result spinning larvae may be found in almost any position within the cocoon. After the cocoon is complete, larvae consistently take up a position with the head away from the base of the cell. In describing cocoons, therefore, the end in the base of the cell is called posterior, the end toward the cap is called anterior. This orientation is maintained in the pupal stage so that the emerging adult has its head directed toward the entrance of the nest.

After the cocoon is complete, there is a period of a day during which the larva inside the cocoon is able to seal with new silk any slit made in the cocoon for observational purposes. In one instance out of ten observed a larva was able to do this on a second day.

After this the larva appears to be unable to produce silk; at least it does not mend slits in its cocoon. It remains able to move for several days, however. The total length of the larval period after completion of the cocoon and before pupation is three to eight days (average of seven, 5.2 days) in summer; individuals of the fall generation pass the winter in this stage.

COCOON

The cocoons spun by the larvae are cylindrical with somewhat rounded ends. A randomly selected group of 15 varied from 4.3 x 8.5 mm. to 5.2 x 10.0 mm. The average width in this group was 4.75 mm., the average length, 9.06 mm. The cocoon of a partially starved larva was only 3.75 x 8 mm., but since cocoon diameter ordinarily depends on cell diameter, there probably was no relation between the starvation of this larva and the small diameter of its cocoon.

The outermost fibers of the cocoon are slender whitish or pale brown threads which form no continuous layer but attach any feces, bits of pollen, or other materials to the walls of the cell and which cause the cocoon to adhere to the inner wall of the cell except sometimes at its anterior end, where there may or may not be a small space between the anterior end of the cocoon and the cap of the cell. The outside diameter of the cocoon, therefore, is normally the same as the inside diameter of the cell.

Inside of these sparse fibers is the *outer cocoon*. In the *Coelioxys* described below it forms a complete layer, but in *Megachile brevis* the outer cocoon consists of a cap of coarse red threads covering the anterior end of the cocoon. Occasionally it is reduced to only a thread or two or is absent; more often it extends backward over the anterior end of the cocoon for a millimeter or two, and in one cocoon (out of 60 examined) the red fibers of the outer cocoon reached the middle of the cocoon. Thus the outer cocoon is always lacking from the posterior part of the cocoon.

The red fibers of the outer cocoon are coarser than those used in any other part of the cocoon. They vary greatly from cocoon to cocoon in thickness. In one the coarsest of the red fibers were .08 mm. in diameter, the finest .01 mm. in diameter with most of the fibers about .03 mm. in diameter. In another cocoon the coarsest were .04 mm., the finest .01 mm., with most of the fibers .02 mm. or less in diameter. Sometimes irregular thick places on the fibers occur so that in one cocoon whose thickest fibers were .045 mm. in diameter irregular bulges reached a thickness of .065 mm. The

fibers of the outer cocoon are very stiff, lie criss-crossing one another at irregular angles, the various thicknesses indiscriminately mixed. The outer cocoon is hard, firm, and thick in contrast to the rather delicate and thin inner cocoon.

The *inner cocoon* is firmly in contact with the outer cocoon, and the two can be pulled apart only with difficulty. Posterior to the outer cocoon, the inner cocoon is continuous with the sparse pale threads which are attached to the walls of the cell. These threads and those of the inner cocoon seem identical; they are fine, .01 to .001 mm. in diameter, pale brown, criss-cross one another irregularly, with the various sizes intermixed. The inner cocoon is spun by the larva until it is opaque, but it still appears pale brown. A few hours later it changes to a dark brown. This presumably happens when a dark brown liquid (of unknown origin) is spread by the larva on the inner surface of the inner cocoon. This liquid impregnates the inner cocoon and quickly hardens, for in every cocoon opened this portion of the inner cocoon consisted of fibers imbedded in a hard but flexible, amorphous, translucent, dark brown material which obviously must have been applied to the fibers as a liquid. This is the outer layer of the inner cocoon.

The inner layer, which is difficult to separate from the outer, is highly variable. It is always thinner than the outer layer. It may consist merely of pale brown fibers like those of the outer layer applied to the inner surface of the outer layer and giving it a silvery appearance seen from the inside. These fibers may be impregnated and joined by the amorphous brown material characteristic of the outer layer, or this material may be present only in the anterior part of the inner layer. In over 50 percent of the cocoons the inner layer does not reach the posterior end of the cocoon, but fades out short of it. In six cocoons of the 60 studied, the inner layer of the inner cocoon was absent.

Rarely there are one or more small additional "layers" of inner cocoon, sometimes mere flakes, outside the outer layer or inside of it, at the anterior end of the cocoon. These layers are impregnated with the dark brown amorphous material. Regardless of the presence of such additional layers, there is virtually always a place (sometimes conspicuous and sometimes minute) in the center of the anterior end of the cocoon where the amorphous material does not completely close the spaces among the fibers of any of the layers of the inner cocoon. This allows for ventilation of the otherwise airtight cocoon. This place corresponds to the conspicuous nipple found on the anterior end of many megachilid cocoons.

It seems probable that the inner cocoon of *Megachile* and *Coelioxys* corresponds to the entire cocoon of *Osmia* and *Hoplitis*, that the reduction of the nipple in *Megachile* and *Coelioxys* is associated with the addition of the outer cocoon, and that the addition of the tough, hard outer cocoon, especially anteriorly, is advantageous in protecting against invaders.

Complexity of the cocoon in *Megachile* may be widespread, for Micheli (1937) describes the cocoon of *Megachile nigriventris* Schenck as consisting of no less than five layers.

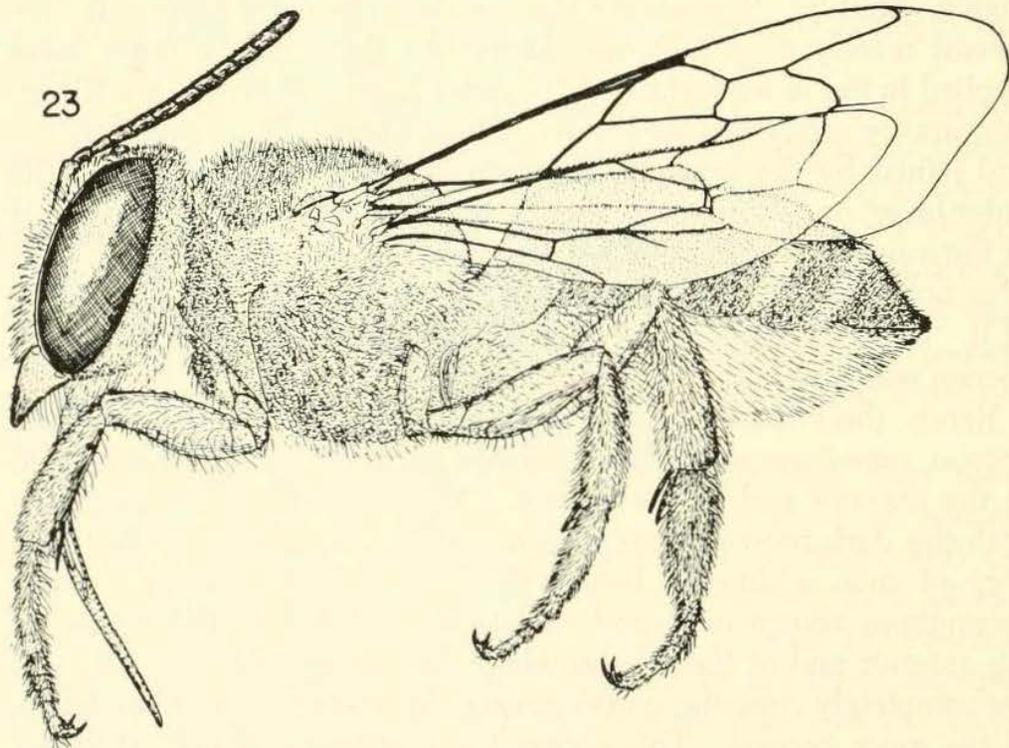
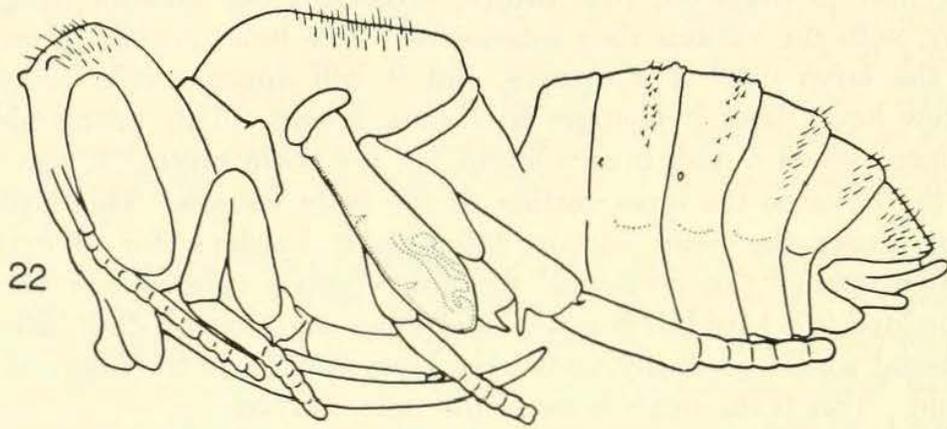


FIG. 22. Pupa of *Megachile brevis*.

FIG. 23. Adult female of *Megachile brevis*.

PUPA

The pupa lies in the cocoon with its head away from the base of the cell, that is toward the entrance of the nest. At first the pupa is entirely whitish in color but after one or two days the eyes become pink. They become gradually darker during the following several days. Then other parts of the body begin to darken, the antennae, tarsi, and tibial spurs being among the last. Finally the whole pupa becomes black. About a day before emergence of the adult, the pupa becomes soft and wrinkled in appearance.

The total pupal period ranges from 10 to 12 days (average of six, 11.2 days).

EMERGENCE

When the adult first emerges it is wet, and it may require half a day or more to dry off and expand its wings. This occurs within the cocoon. After this the apparently perfect adult remains in the cocoon from two to five days (average of 5 observations, 3.5 days), then chews its way out of the cocoon.

The adult then soon chews its way out of the cell. In so doing it commonly chews the cap and much of the cocoon into small bits. If cells are in a series, it is usual for the bees to emerge at about the same time, when the uppermost bee emerges. They leave behind them a tube of leaves and petals, the side walls of the cells, the lower or inner end of the tube being filled with the remains of cocoons and ends of cells, all broken into small pieces.

Because of the short series often available and especially because of the high rate of parasitism in long series, no significant data were gathered on whether females are usually reared in the older cells and males in the younger cells of a series.

Freshly emerged bees liberated in the field visited flowers immediately for nectar. One female stopped to suck from a *Lythrum* flower only one foot from the point where she escaped from the nest.

SUMMARY OF DEVELOPMENTAL STAGES

Making use of the data presented above, table VIII has been constructed to summarize the duration of the stages in the life history of this bee. Total figures from the time of egg laying until emergence of the adult from the cocoon are 23.9 days for the minimum column, 32.3 days for the average column and 45.8 days for the maximum column. Probably no bee achieves the minimum or maximum, as there is no reason to believe, for example, that a bee

with one stage minimum in duration would have the others minimum also. The average period from egg laying to adult emergence from the cell in the case of eight undisturbed cells was 32.2 days (minimum 30, maximum 35). This indicates that the average figures independently obtained in the laboratory for the lengths of larval stages are not greatly different from those existing in nature.

TABLE VIII.—Estimates of duration (in days) of the stages in the life history of *Megachile brevis* under summer conditions.

	Minimum	Average	Maximum
egg	3	3.2	3.5
larva			
before starting cocoon	5.1	7.7	13.3
after starting cocoon	3.9	6.7	12
pupa	10	11.2	12
adult			
before emerging	2	3.5	5
after emerging		30±	

PART VI.—THE CUCKOO BEE, COELIOXYS

SEASONAL HISTORY AND HABITATS

Perhaps the most important natural enemy of *Megachile brevis* is a bee of an allied genus, *Coelioxys octodentata* Say. This species has previously been recorded as a parasite of *M. brevis* by Hicks (1926). *Coelioxys* is a social parasite; it does not make its own nests but our species lays its eggs in the cells of *Megachile*, where its young larvae kill the young *Megachile* larvae and then eat the provisions gathered by the *Megachile*.

Much less information is available on the seasonal history of this bee than on that of *Megachile brevis*. Its season of flight is probably about the same, at least individuals have been collected near Lawrence, Kansas, from May 25 to September 25. Like the *Megachile*, the *Coelioxys* is scarce early in the season, much more abundant later. The number of generations per year is probably the same as in the *Megachile*, for available information on the rate of development of immature stages indicates that the stages are of about the same length as in the *Megachile*. The wings of the adults become tattered with wear as in *Megachile*. Overwintering, like that of *Megachile*, is in the mature larval stage in cocoons. Larvae reaching this stage after about the first week in August remain in this condition through fall and winter, as in the *Megachile*.

The habitats of the *Coelioxys* are the same as those of the *Megachile*. The *Coelioxys* seems equally mobile, appearing wherever favorable flowers are to be found, in both the nesting habitats and the nectar habitats of the *Megachile*. *Coelioxys* are often seen sucking nectar from flowers, although of course they collect no pollen. Their choice of flowers is about the same as that of nectar sucking *Megachile brevis*, although perhaps they visit yellow Compositae more frequently.

FINDING MEGACHILE NESTS

Female *Coelioxys* are sometimes seen flying over the ground or through weedy places, stopping to fly along every dead weed stalk, especially those lying on the ground. We have never seen a *Coelioxys* discover a *Megachile* nest but presume that this is the searching behavior.

EGG LAYING

Several *Megachile* nests which had been discovered by *Coelioxys* females have been observed. The *Coelioxys* returned to these nests every few hours and could fly directly to the vicinity of the nest apparently as easily as the *Megachile*. The *Coelioxys* usually alights on a twig or grass blade and remains there perfectly quiet for minutes at a time. Once one was observed to remain in such a position for 72 minutes, after which it flew away without actually going to the nest. Sometimes after the *Megachile* leaves on a pollen collecting trip the *Coelioxys* leaves its resting place and hovers at the nest entrance for a few moments before flying away. The action has not been observed by us but it seems certain that if the proper amount of pollen has been accumulated, the *Coelioxys* enters at such a time and lays its egg in a cell which is being provisioned. On one occasion observations were such that it was certain that this egg laying by the *Coelioxys* must have occurred during a one minute period following the departure of the *Megachile* for her tenth load of pollen for that cell.

In view of the ability of the *Coelioxys* to return again and again to a *Megachile* nest, having once found it, it is not surprising that whole series of *Megachile* cells or large parts of series are parasitized, while other series escape entirely.

The egg of the *Coelioxys* is deposited at the base of the pollen mass with one end of the egg inserted into the leaf or petal pieces composing the base of the cell. No doubt the slender apex of the abdomen of the female *Coelioxys* is adapted for forcing its way through the pollen for egg laying. This seems to be the common manner of ovaposition in *Coelioxys* (see Ferton, 1896; Graenicher, 1927; and Iwata, 1939) but as Ferton shows, is by no means the only one.

LARVA

The first stage larva is highly specialized with a large, sclerotized head and huge, sharply pointed jaws (figure 24). Its body is curved, not straight like the first stage *Megachile*, and its size is larger than that of *Megachile*. On hatching, the larva works its way slowly upward through the soft pollen mass, constantly opening and closing its mandibles. On reaching the surface of the pollen it continues this activity and sooner or later kills the *Megachile* with its jaws, usually within a day after the *Megachile* has hatched and while it

is still quite immobile. After killing the host larva, the *Coelioxys* continues to move about through the mass of provisions opening and closing its mandibles for as much as 24 hours.

Among first stage *Coelioxys* larvae there is considerable variation in the size of the mandibles. Possibly more than one species is involved although this is not evident from adults nor is there a clear division of the first stage larvae studied into two or more separate types.

There is considerable evidence that there are five larval stadia in *Coelioxys*. The development of the larva of both *Coelioxys* and *Megachile* will be discussed in a later paper.

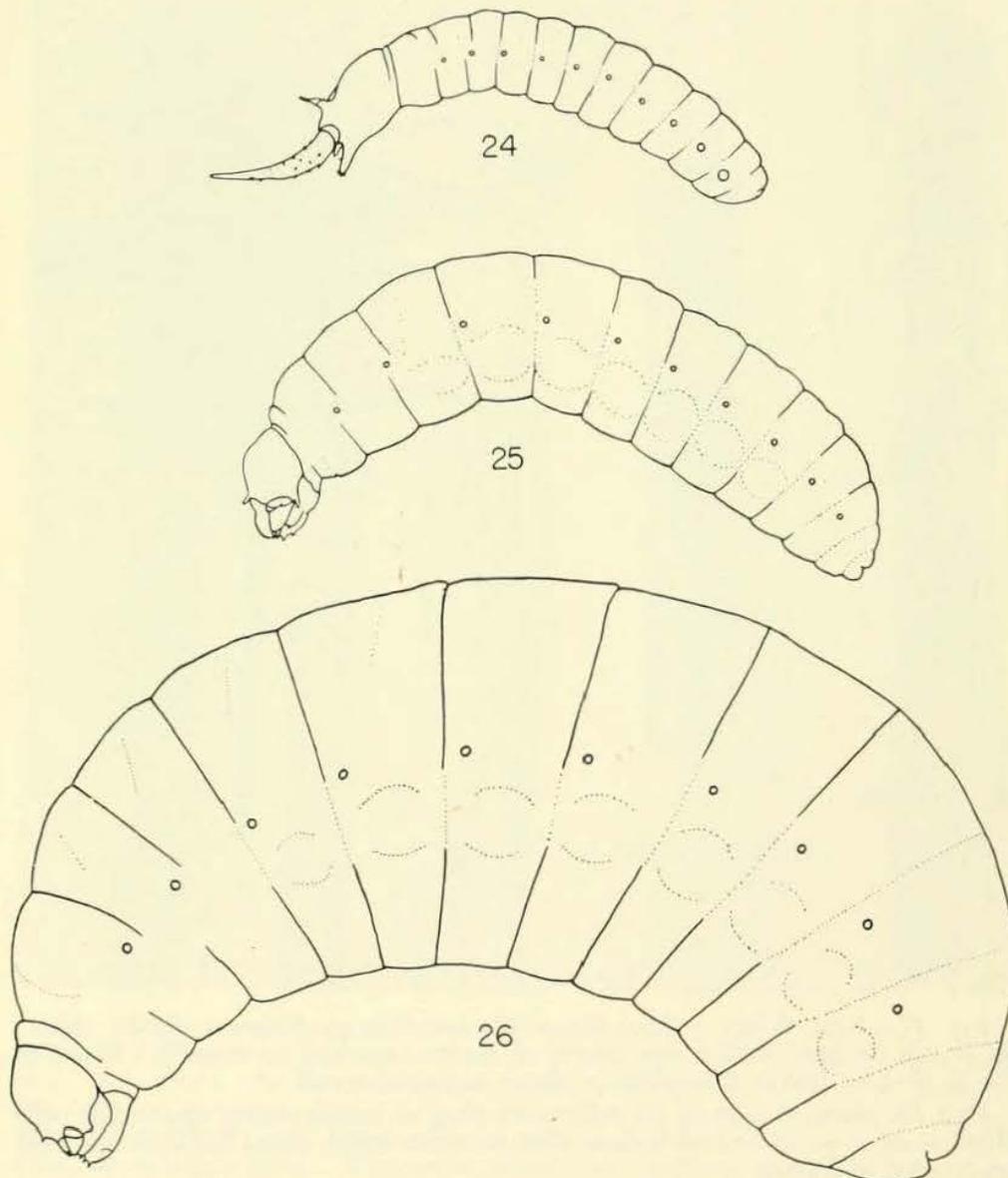


FIG. 24-26. Larvae of *Coelioxys octodentata*, first stage, half grown, and mature.

The presumed second stage larva has short but acute mandibles. One cell was opened in which the *Coelioxys* was in this stage but the *Megachile* had not been killed. This is an unusual situation, however.

Subsequent stages look much like those of *Megachile* (see Michener, 1953) and feed on the pollen from the surface toward the base, not burrowing into the pollen any more than *Megachile*. The easiest way to distinguish older larvae of *Coelioxys* from those of *Megachile* is the presence of several setae on the outer surface of each mandible (maximum of two such setae in *Megachile*) and of

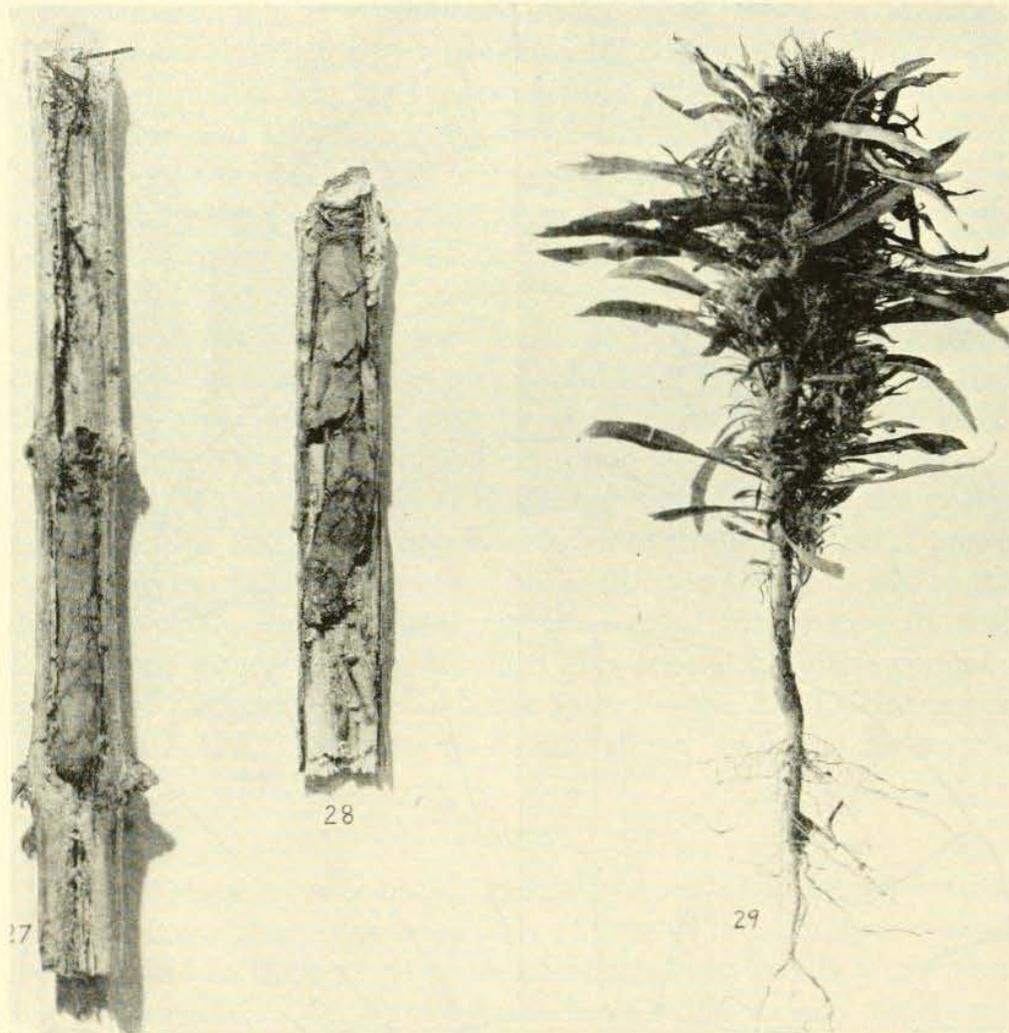


FIG. 27. Nest of four cells of *Megachile brevis* in an *Ambrosia* stalk. Opening at top plugged with a few pieces of leaves (marked by arrow). There is also a plug of leaves immediately above uppermost cell.

FIG. 28. Similar nest of six cells with plug of leaves above uppermost cell, which is so close to end of hollow that no open space exists between last cell constructed and plug.

FIG. 29. Abnormal fasciate plant of *Erigeron canadensis*. A *Megachile* cell is hidden among the dense leaves near the top of this plant.

a genal projection just behind the mandibular base which is absent in *Megachile*. The duration of the larval stages averages less than that of *Megachile*, but the number of individuals is so small that this may not be significant. Defecation often starts well before the food is gone, as in the *Megachile*, and the positions taken by the larva after the presumed second stadium as well as the orientation of the pupa is as in *Megachile*.



FIG. 30. Nests of *Megachile brevis* in various weed stalks. The scale at the left is in millimeters. a, entrance (arrow) at center, two series of three cells each, one above, the other below, entrance. No entrance plug. b, Series of five cells, no entrance plug. c, A single cell, with plug at entrance of hollow (shown by arrow). d, Series of four cells, no entrance plug. e, Series of 3 cells, no entrance plug. This series shows how hollows of varying diameters can be utilized by packing extra leaves or petals into large hollows. This nest is small in diameter at bottom, large above.

COCOON

The cocoon differs markedly from that of *Megachile brevis* in that the outer cocoon of coarse red fibers is complete, covering the entire inner cocoon. Otherwise the cocoon is as in the *Megachile*, varying widely in the coarseness of fibers and in the extent, nature, and even presence of the inner layer of the inner cocoon.

EMERGENCE

Emergence of adults occurs in the same manner as that described for *Megachile brevis*.



FIG. 31. Cell of *Megachile brevis* (marked by X) among leaves of the plant shown in figure 29.

PART VII.—NATURAL ENEMIES OF *MEGACHILE BREVIS*

SUMMER

Table IX presents data on the natural enemies of *Megachile brevis* as determined from 112 cells collected in July and August. These cells were left in the field at least until the larvae were half-grown, that is, long enough so that parasites would probably have made their attacks. Some destruction by ants and unknown predators was probably avoided by bringing the cells into the laboratory before emergence of the adults. Bees were considered to have survived if by the pupal stage no parasites were evident or if they went into winter as mature larvae with no evidence of parasites.

It is significant that not a single cell parasitized by *Coelioxys* was found in any situation other than dead stalks, and that the *Coelioxys* did not appear to search except in dead stalks, where they are often able to parasitize one cell after another in a series.

TABLE IX.—Natural enemies of *Megachile brevis*

(Based on 100 cells collected in July and August)

	<i>Percentage of larvae destroyed</i>
<i>Coelioxys octodentata</i> Say	29
<i>Leucospis affinis</i> Say (Leucospidae)	3
<i>Aprostocetus</i> sp. (Eulophidae) ¹	2
<i>Merisus</i> sp. (Pteromalidae) ¹	1
Unknown predators	5
Unknown causes (including apparent failure of bee to lay egg)	4

WINTER

We do not have sufficient data on the causes of winter mortality in *Megachile brevis*. The factors listed in table IX are probably all operative in winter as well as summer. *Coelioxys*, the principal natural enemy in summer, is just as important to the overwintering generation as to any other. There are, however, additional hazards to the overwintering brood.

Acrobat ants (*Crematogaster*) destroy many cells of the overwintering generation. The dealated queens in the fall burrow into weed stalks and often open and pass through *Megachile* cells and cocoons. Even if this treatment does not destroy the larvae, they dry out and die when exposed in this way. Colonies of the same ant are very common in dead weed stalks in the vicinity of Law-

1. Identified by Dr. B. D. Burks of the Division of Insect Detection and Identification, United States Bureau of Entomology and Plant Quarantine. Both of these species were also reared from cells parasitized by *Coelioxys octodentata*. It is possible although improbable that *Coelioxys* was the host in all cases.

rence and often destroy *Megachile* cells in the fall. Sometimes the leaf fragments are carried out so that no evidence of the nest remains.

Another major cause of winter mortality is trampling of nests by cattle and other animals, a fate much less likely during the brief period of a summer generation than during the winter months when protecting green vegetation is gone. Burning of prairie or pasture areas in spring or fall must also take a large toll of overwintering larvae.

Finally it must be admitted that some larvae die in winter for unknown reasons possibly resulting from weather conditions.

PART VIII.—POSSIBLE IMPORTANCE OF THIS BEE
AS A POLLINATOR

As explained in the introduction, the study here reported was designed, among other things, to serve as a biological basis for attempts to increase the effectiveness of a leafcutter bee, *Megachile brevis*, as a pollinator of alfalfa and other crops. By no means all of our findings are encouraging from this viewpoint and serious practical efforts along these lines have not yet been made. However, a summary of the principal facts of the life history that relate to the possible practical importance of this bee follows:

Individuals of *Megachile brevis* are effective alfalfa pollinators. Nearly every flower visited by a female while collecting pollen is tripped, therefore pollinated. Each female averages over 15 flowers per minute, and the average pollen collecting trip on alfalfa is about nine minutes long. Thus in each trip about 135 flowers are pollinated. If an average of 12 trips are required to provision a cell, 1,620 flowers would be pollinated per cell provisioned. Little is known of the number of cells a female bee provisions, but if she provisions 20, she might be responsible for pollination of 32,400 flowers. She may provision more cells; 30 is suggested as a possibility earlier in this paper in connection with other data. By comparison, the honeybee rarely trips alfalfa flowers if other pollen sources are available.

From a practical standpoint *Megachile brevis* is usually an ineffective alfalfa pollinator in Kansas and elsewhere because there are not enough of the bees in the fields. Probably the principal reason that the bees remain scarce is that there is not a continuous food supply. This bee passes through several generations per year. Thus it can build up its numbers during the summer months. However, a continuing food supply must be maintained for the various generations by a succession of suitable food plants if this build-up is to occur. A failure in the food supply causes the bees to disperse widely, as they are not bound to any permanent nesting site as are most solitary bees.

One might establish in the vicinity of an alfalfa field a succession of blooming plants providing pollen useful to the *Megachile*, such as false indigo (spring), wild alfalfa (early summer), iron weed (late summer), and wild purple asters (fall), with care being given to have at least some alfalfa in flower at all times when no one of the other plants is in bloom. Such a combination might attract and

maintain a large population of this bee. The wild plants could be mowed at the time the bees are needed for alfalfa pollination. Unfortunately the plants in the above mentioned series have different soil preferences, but some farms have the various necessary conditions. These plants could grow as weeds in pastures adjacent to the alfalfa fields or in uncultivated borders or strips.

Where such a program is impossible, one may at least attract some *Megachile* in advance of the alfalfa seed crop by stands of uncut alfalfa which would bloom prior to the seed crop or by stands of wild alfalfa. Either could be cut as the seed crop comes into bloom.

Such highly attractive nectar sources as winged loosestrife and buckbrush may also be useful in holding a *Megachile* population in the desired area.

Nesting sites can be provided by the old stalks of large weeds or even by old cornstalks, broken in one or two places, and left lying on the ground where they will not be completely shaded by trees, bushes, or growing weeds. Such nesting places should be protected from trampling by stock and from burning.

Leaves and petals for nest construction can usually be obtained in almost any situation where the other requirements for survival are present. Some rosebushes will probably be helpful, since rose leaves are much used.

Unfortunately most of the usual farming activities are opposed to the survival and increase of this bee. Sowed pastures free of weeds, elimination of weedy fence rows and of patches of prairie, burning of pastures, trampling of ground by stock, and regular cutting for hay of entire fields so that no alfalfa flowers remain all contribute toward decreasing the abundance of the bee. On the other hand, weedy and brushy pasture areas, fence rows and roadside strips where flowers and weeds can grow unmolested and where the old stalks will neither be trampled nor burned in winter, and roadside alfalfa patches which are not or only irregularly cut, all favor the development of larger populations of this bee.

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