

PSYCHE

Vol. 90

1983

No. 3

NEST BUILDING BEHAVIOR AND DEVELOPMENT
OF THE SUNFLOWER LEAFCUTTER BEE:
EUMEGACHILE (SAYAPIS) PUGNATA (SAY)
(HYMENOPTERA: MEGACHILIDAE)

BY D. R. FROLICH¹ AND F. D. PARKER
Bee Biology & Systematics Laboratory
Agricultural Research
Science & Education Administration
USDA
Utah State University, UMC 53
Logan, Utah 84322

INTRODUCTION

Eumegachile (Sayapis) pugnata (Say), formerly *Megachile (Sayapis) pugnata* Say (Mitchell 1981), is a large (13–18 mm) leafcutter bee that is widely distributed throughout the United States and southern Canada (Hurd 1979). *Eumegachile pugnata* nests in a wide variety of situations including man-made borings in wood and is easily trapped in the wild (Medler 1964, Krombein 1967, Parker & Frohlich in prep.).

Since *E. pugnata* is oligolectic to flowers of the Compositae (Tepedino & Frohlich 1982), attention has recently been directed toward developing the bee as a pollinator of commercial sunflower. Parker and Frohlich (1983) described its use in hybrid sunflower pollination; Tepedino and Frohlich (1982) discussed mortality factors, pollen utilization and sex ratio; and Frohlich (1982) described various aspects of its ecology. The purpose of this study was to

¹Current address: University of Idaho, SW Idaho Research and Extension Center, Parma, Idaho 83660.

Manuscript received by the editor March 29, 1983.

elucidate the within-nest biology of *E. pugnata*, including development, nesting and provisioning behaviors, and nest architecture.

METHODS AND MATERIALS

Within-nest behaviors were observed from a wooden box (1×1×3m) located in a green house (6×6×5m). Nests of 2 types were fastened to cardboard sheets which were then mounted onto the observation box. 1. Elderberry sticks that had been drilled (9mm diameter) and planed lengthwise, were covered with a glass plate to expose the boring; and 2. Glass tubes with plastic inserts were taped to cigarette filters to facilitate handling (8mm diameter) (Fig. 1). The end of the glass tube that served as the nest entrance was dipped in black India ink and inserted into a cork ring to allow the bee secure footing (Torchio 1972). Nests were darkened with paper slip covers until cell construction began. Removal of slip covers after the onset of nesting did not appear to affect females, though no females nested in uncovered nests. A small swamp cooler mounted above the wooden box maintained temperatures below 40°C in order to avoid egg-larval mortality due to heat buildup.

Commercial *Helianthus annuus* L. and 3 garden variety composites (Cosmos, Bachelor's Button, Callendula) were provided as pollen and nectar sources in beds of approximately equal size. Because of its usefulness in similar studies of other megachilids (Parker & Tepedino 1982, Frohlich 1983) *Oenothera hookeri* T. & G. was used as nest partition material. A tape recorder, otoscope, and stopwatch facilitated within nest observations.

As nests were completed, most were removed and replaced. Completed nests were incubated at 30°C and used to study aspects of larval development and behavior. The glass plates on the elderberry sticks were removed prior to incubation and replaced with clear plastic food wrap. The plastic inserts of the glass tube nests were also removed and provisions containing eggs were cut away and placed separately in BEEM® capsules, commonly used in electron microscopy. As each egg eclosed, the emergent instar was marked with a tiny spot of pink fluorescent Day-Glo® powder applied with a watchmaker's forceps. Disappearance of spots indicated molting and new marks were made. Larvae were inspected several times a day and various behaviors associated with each instar were observed

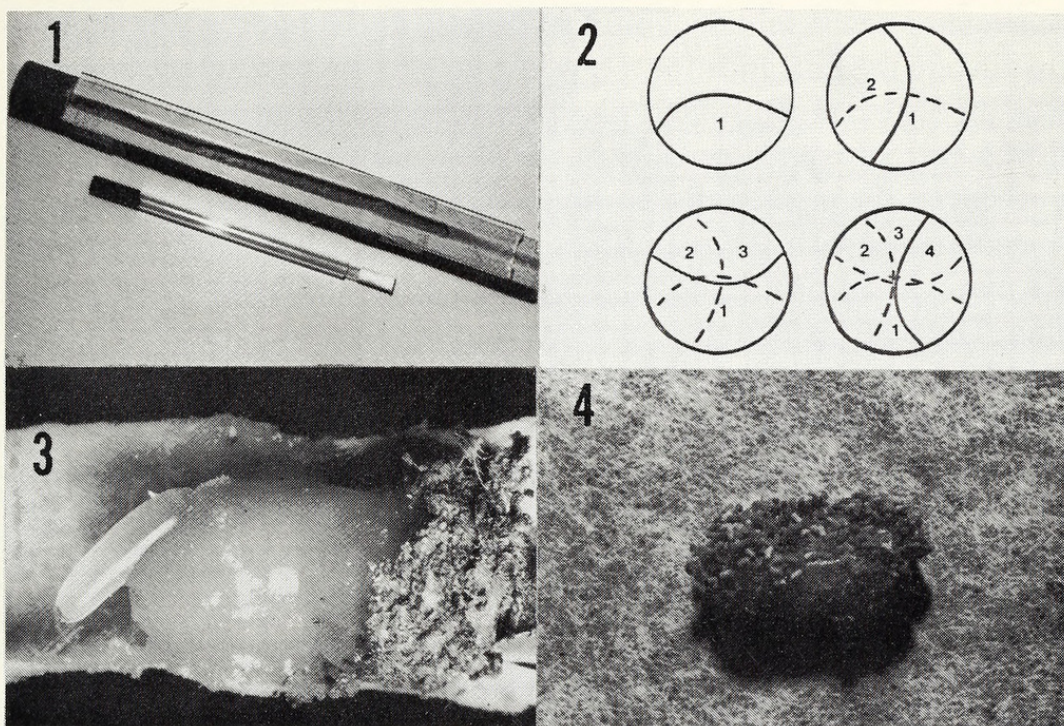


Figure 1. Glass covered stick and glass tube with plastic insert used for nests.

Figure 2. Schematic drawing showing construction of a partition. Whole leaf pieces are added in sequence (starting with No. 1) and are sealed to the nest wall, each subsequent piece partially covering the previous piece.

Figure 3. Egg in late embryogenesis, attached to provision.

Figure 4. Cocoon containing prepupal larva, showing incorporated fecal pellets.

with a dissecting microscope fitted with fiber optics lighting (to reduce heat load). Larvae that died and examples of each instar were preserved in picroformalin.

RESULTS

Within-Nest Biology

Females began nesting in the greenhouse 4 June 1981, within 3 days after release. The following is a composite account, in temporal sequence, from selection and preparation of a new nest to nest closure. Each activity discussed was observed for several different females.

Nest Selection — Preparation. Before beginning cell construction females investigated both types of potential nest substrates. Sticks and glass tubes that were not covered (darkened) in some way were either ignored or only casually inspected. Usually before pre-

paring her nest a female would sit quietly at the back of the stick or just inside the entrance for a few minutes to an hour. Once a choice was made, extraneous pith particles were picked up with the mandibles and jettisoned outside of the nest during flight. Females did not make the nest walls completely smooth but cut away gross irregularities with the mandibles and removed large pith particles. As many as 24 pith removal trips were observed before nest initiation. During this period of preparation females were especially sensitive to any activity around the nest site. On several occasions females abandoned nests when an observer approached the nest entrance. In general nesting *E. pugnata* were very wary of intruders.

Partition Building. Basal and apical partitions of each cell were constructed similarly and were composed of the same materials so construction details of each will be considered together.

After preparing her nest site for cell construction the female left the nest to retrieve a strip of *O. hookeri* leaf. The bee landed on the plant, straddling the leaf, and quickly cut, while walking backwards, a thin strip $\frac{1}{2}$ to $\frac{3}{4}$ as long as her body, and returned to the nest. After entering the nest with the unmodified leaf in her mandibles the female masticated it into a shiny ball which was pressed into the back wall, or along the floor where the cell was to be initiated. From the leaf material a thin ring of moist chewed leaf was formed around the inner circumference of the tunnel. Three to 6 trips were usually required to complete the ring. The female then left and returned with a large oval-shaped leaf piece that was carried beneath the body by all 6 legs and the mandibles.

The mandible and front legs were used to spread and position the leaf piece along a portion of the chewed ring thus closing a portion of the circle (Fig. 2). The outer edge of the unmodified leaf confluent with the ring was chewed into the ring and the 2 were sealed. The female also used her head in an extremely fast jackhammer-like motion to tamp the ring and leaf pieces together. The clypeus and proximal outer surfaces of the mandibles appeared to be the point of impact. Subsequent leaf pieces were brought in and fastened to the ring in the same manner until the base of the cell was covered (Fig. 2). Three or 4 oval-shaped leaf pieces were required to form the base of the partition. After the leaf pieces were positioned more masticated *Oenothera* strips were used to form a second ring in the

same position as the first thus further sealing the leaf pieces to the walls.

Once the second ring was in place the female continued to add to it by placing more masticated *Oenothera* on the inside of the ring and chewing and spreading it toward the center with the mandibles until a thin layer of moist leaf pulp covered the whole leaf pieces. Next, moist soil particles (not mud) were collected and placed at the base of the partition. These clods were cut into many tiny slivers which were taken singly or in groups and pressed into the pulpy partition with the mouthparts. These were then tamped in with the head as before. *Oenothera* and soil particles were retrieved alternately until the partition approached its ultimate size.

As the partition increased in thickness the periods of tamping with the head grew longer. During the last half hour of partition construction tamping often lasted as long as 5 minutes and became combined with a grooming behavior. Before tamping the female groomed the posterior portion of the abdomen with her hind legs and collected a droplet of fluid that was passed to the middle legs and then the front legs. The fore tarsi with the secretion were then used to wipe down the face and antennae; especially the clypeal and mandibular areas that came in contact with the partition during tamping. Possibly the act of tamping or packing at this point not only shaped and defined the partition but incorporated a secretion as well.

After the last leaf pulp and soil were added the concave surface of the partition was further modified. The female laid on her back and groomed the posterior portion of the abdomen and again passed a droplet of liquid to the middle and fore-legs. This time the secretion was placed between the mandibles and chewed vigorously. The female then chewed and licked the outer surface of the partition. As this was finished, provisioning ensued. No threshold or rudiment of an apical partition was laid down prior to provisioning.

Provisioning. The female first backed into the cell with a load of pollen carried on the abdominal scopa. Deposition of the first pollen load began about 3 mm in front of the basal partition and was spread backwards with the feet in the kicking motion. The pollen was removed first by the hind legs rubbing together toward the middle of the sternum. Pollen remaining on the venter between the

fore and mid-legs was scraped off initially by the mid-legs and then the fore-legs. Both pairs of legs then transferred the pollen to the hind legs where it was deposited by rubbing the legs together in a "hand washing motion." Pollen removal by the legs was aided by a complementary telescoping motion of the abdomen and elevation of sternal hairs. As the legs brushed pollen from the side, toward mid-sternum and backwards, the abdomen contracted so that the tarsi came in contact with the entire surface of the abdomen. The abdomen then elongated and the contraction-brushing motion began again.

The first load of nectar was brought in on the second provisioning trip. The female entered head first and picked up the pollen left on the first trip with her mouthparts, mixing nectar and pollen into a moist paste that she spread over the concavity in the basal partition. She then went to the nest entrance, turned around outside on the nest face, backed in, and kicked any pollen remaining from the first deposition toward the partition. Before pollen deposition this time the female arched her body into a 'U' shape, with head and abdomen as its highest points. Front legs and hind legs were placed approximately halfway up opposite walls of the nest, while mid-legs rested on the floor. The abdomen was arched and was backed into the cavity of the basal partition. Pollen removal then proceeded as before and the load fell into the concavity or onto the floor in front of the partition. On subsequent trips the female entered head first, swinging her head back and forth as she approached the provision, picking up stray pollen with her mouthparts. The dry pollen from the previous trip was then chewed and mixed with nectar to form a paste which she molded into a loaf with her mandibles. Pollen was then deposited atop the growing provision and the sequence was repeated.

Prior to nectar regurgitation, the bee usually cleaned her face and antennae, removing pollen with her front legs and passing it to her hind legs, where it was deposited along the sides of the abdomen. She also stopped just in front of the entrance and preened again before embarking on the next foraging trip.

Once the pollen loaf was approximately $\frac{1}{3}$ its ultimate size the female used the abdomen tip to plunge a shallow hole in the loaf after each pollen deposition. This hole was then filled with nectar on

the next trip and masticated. Dry pollen was deposited on it and a new hole was formed with the abdomen tip. This behavior continued until the provision was about $\frac{2}{3}$ its ultimate size whereupon the female tended to sprinkle pollen evenly over the entire surface. Nectar was also deposited more uniformly and the whole surface was chewed after each trip, incorporating pollen and nectar.

On the last few pollen trips the bee used her face to flatten the vertical surface of the pollen loaf, using a motion similar to the tamping during partition construction.

Oviposition and Cell Closure. Once the cell was provisioned the female collected an unmodified *Oenothera* strip. She masticated it into a moist ball and wiped down the floor in front of the provision, picking up loose pollen. As when making the basal partition she used the leaf pulp to form a ring around the inner circumference of the tunnel close to the edge of the pollen loaf. Two or 3 leaf gathering trips sufficed; the ring was the initiation of the apical partition.

The leaf pulp ring completed, the female made 3 or 4 more foraging bouts each time returning with only nectar. On returning from the first bout the bee plunged her mouthparts deeply into one side of the face of the provision and continued to do so in an extremely fast up and down fashion for several seconds. With the mandibles moving in a cutting fashion much of the provision was pushed to the side opposite the female. After the next trip the other side of the pollen loaf was worked in a similar fashion until the front half of the entire provision had been thoroughly kneaded. At the end of the final foraging bout the female regurgitated a large quantity of nectar onto the middle of the provision face and plunged her mandibles in an around its center until a small wet hillock was formed. The front half of the provision was thoroughly wetted with nectar and appeared much darker in color than the back half. This completed, the female turned around at the entrance, backed in and oviposited.

As she backed into the cell, she inserted her ovipositor into the upper half of the hillock, appearing to anchor to the provision. A series of pumping motions forced the egg onto the hillock where it appeared to sink into the nectar. When the egg was about halfway extruded from the female the pumping motions ceased and she pulled away, leaving the anterior portion of the egg free and at about a 45° angle (Fig. 3). During oviposition the female remained

fairly rigid with the exception of the abdominal pumping motion and a slight rocking of the body. The head was cocked downward somewhat and the antennae wiggled slightly. The whole process lasted about 60 seconds.

Immediately after oviposition the female left the nest and returned with leaf material. Most often this was a large oval-shaped piece that was sealed to the leaf pulp ring. An occasional female returned with *Oenothera* strips and added to the ring but most often the entrance to the cell was immediately closed by adding the oval-shaped pieces. Once the cell was closed, the apical partition was constructed in the same manner as the basal partition.

In almost all nests at least 1 partition, not associated with a provisioned cell, was constructed in the front of the nest to form a vestibular and an intercalary cell. This partition was constructed in the same manner as partitions defining provisioned cells, i.e., soil, leaf pulp, and whole leaf pieces were incorporated. The nest plug made to close the entrance was also constructed of the same material as partitions but was considerably thicker. The behaviors involved in plug construction were identical to those involved in partition formation. In addition to size, the closing plug differed from partitions in that it was often a series of partitions interspersed with soil and leaf pulp placed one atop the other. The outside surface of the plug was also different in that it contained much more soil than partition surfaces. Often what appeared to be pure soil was found on the outside surface of the plug, although leaf pulp was still used as the binding matrix.

Usually *E. pugnata* built 1 cell a day, but occasionally some females began provisioning a second cell. In the greenhouse *E. pugnata* provisioned cells in the morning when pollen was available and built partitions and plugs in the afternoon and early evening hours. Cell provisioning took 3.5 hours on the average. The number of pollen-nectar trips per cell varied from 36–44. Nectar and pollen deposition took roughly the same amount of time; nectar deposition = 38.7 sec. (standard deviation, $sd = 12.3$), pollen deposition = 32.4 sec. ($sd = 6.6$). Foraging trips ranged from 2 min. 28 sec. to 9 min. 22 sec. and averaged 4 min. 59 sec. ($sd = 1$ min. 38 sec.). Plug and partition construction took approximately the same amount of time as provisioning so that a nest with 1 cell, 1 intercalary partition and

a plug took about 7 hours to complete. Approximately 15 *Oenothera*, 15 soil, and 3–4 large oval leaf collecting trips were required per partition. Plug construction required roughly twice those numbers. Collection of oval leaf pieces took longer than collection of *Oenothera* strips (\bar{x} = 1 min. 23 sec., sd = 49 sec. vs \bar{x} = 40 sec., sd = 9.4 sec.) and soil collecting trips were shortest of all (\bar{x} = 22.5 sec., sd = 7.7 sec.).

In most cases females constructed nests in hollow sticks. However, when undrilled sticks, with shallow (5 mm) starter holes drilled in the side, were placed in the greenhouse for use by another bee 2 *E. pugnata* widened the cavities and nested therein.

Development

Egg Hatching. The egg, which was attached to the provision by its posterior $\frac{1}{4}$, was opaque when deposited but gradually became translucent as it developed. It measured 1–1½ mm wide anteriorly and posteriorly, 3–4 mm in length, and was straight (Fig. 3). Embryogenesis took an average of 5.1 days at 30°C (Table 1) and some structures became grossly visible through the chorion approximately 1 day before eclosion.

Eclosion usually took from 10 to 12 hours and became evident with the appearance of a clear fluid-filled area in the region of the posterior attachment. At this time the dorsal vessel, spiracles and major tracheal branches were visible. As the fluid increased in the posterior pole the embryo exhibited undulating waves that passed from anterior to posterior and perhaps aided in concentrating the fluid in the posterior region. Thus, the chorion was stretched very tightly over the head of the enclosed embryo. After fluid disappeared from the posterior pole the embryo appeared to remain quiescent for a short time. Fluid then began to collect at the anterior pole of the egg, accompanied by undulating waves moving in the opposite direction (posterior to anterior). As the chorion became tightly stretched over the posterior embryo a longitudinal-lateral split in the chorion became visible at the level of the spiracles. This rupture divided the chorion into upper and lower halves. As the pressure and peristaltic waves receded the lower half of the chorion slipped from the larva and came to lay directly between it and the pollen

mass under most of the body (except the head). The top half of the chorion including that surrounding the head seemed to dissolve. If the larva swallowed any portion of the chorion it was not evident. As eclosion continued the larva came to lay directly on top of the pollen mass, with all segments touching it, and began to feed.

Feeding Stages. The second stadium was short (Table 1) and the second instar fed differently than the other instars. The larva remained nearly motionless with the head in direct contact with food in an area of the provision that was considerably higher in fluid and nectar content than other areas. As the larva fed, a back and forth motion of the head was apparent and it appeared to suck up fluid like a small pump. The mouthparts were partially buried in the provision but almost no movement was detectable in that area during feeding.

The actual process of molting was not observed but larvae marked with powder on the dorsal side of the body were noticed lying on the old exuvium that bore the powder mark after a molt. It appeared then that the entire old integument was sloughed off and not dissolved away. The instars molted in the same manner so that after molts the body was attached to old exuviae which in turn were attached to the provision.

Ingestion of solid food, aided by the mandibles, began in the third stadium. Subsequent instars fed in a similar manner but the last instar consumed the bulk of the provision. As the larva fed, bidentate mandibles shovelled food into the mouth and appeared to be aided by a pumping motion of the head capsule. As the head capsule retracted the mandibles pulled the food in and as the head capsule extended the mandibles opened outwardly. Larvae tended to feed in bouts of approximately 5 minutes, stopping to swallow and pass food into the gut with a series of peristaltic waves between feeding bouts. As the provision was consumed the larva began to turn from white to yellow and the pollen-filled gut became visible.

The third instar began feeding in the place where the second instar fed. The fourth instar fed in the same place, hollowing out a cavity beneath itself. By the middle of the fourth stadium many larvae had become detached from the provision but were much more mobile and continued to feed. Regardless of position (attached, detached with venter on floor, detached with dorsum on floor) the last 3

Table 1. Life history and developmental times (days) for stages.

Stage	\bar{x}	sd	range	n
Oviposition to Eclosion	5.1	1.0	4-7	12
Eclosion to Solid Food	1.2	.4	1-2	12
Solid Food to First Defecation	6.5	1.9	5-9	8
First Defecation to Cocoon Spinning	14.9	2.1	10-18	19
Cocoon Spinning to Complete Cocoon	3.7	.5	3-4	11
Oviposition to Complete Cocoon	26.6	1.5	24-28	7

instars appeared to feed in a similar manner: with the body of the larva extended, the mouthparts were planted on the provision, then the body closed into a 'C' shape and several mouthfuls of food were taken in while contracting, forming a trough on the provision. The body then extended and the process was repeated in the same groove cut previously or adjacent to it so that the whole provision was systematically consumed. Feeding continued into the last stadium after the onset of defecation and lasted up to about 3 days before cocoon spinning. The time from the first ingestion of solid food (3rd instar) to first defecation (last instar) averaged 6.5 days (Table 1). The 3rd stadium averaged 1.6 days.

Defecation. Defecation began a few hours after molting into the last larval instar. The midgut in the early instars was a blind sac, not continuous with the hindgut. At the molt to the last instar the gut was connected and defecation was possible. The last instar was also distinguishable from other instars by its longer body setae.

Most of the feeding and growth took place during the last stadium. The average length of time from first defecation to the onset of cocoon spinning was 14.9 days (Table 1).

Feces were small, squat, yellow cylinders and were deposited away from the provision while feeding continued. As the provision was nearly consumed the cell began to fill with pellets and the larva smeared fresh feces on the walls instead of depositing them behind it. Defecation continued for about 3 days after feeding ceased up to

the time the cocoon was spun. Most of the pellets were incorporated into the cocoon.

Cocoon Spinning. Before fecal pellets were spun together a web-like matrix was laid down on the walls. The larva pressed its salivary lips onto various points of the walls and partitions and deposited a small droplet of material from which a short strand of silk was pulled and anchored elsewhere. The apical partition was covered with many more strands than the walls or basal partition. Most of the strands were attached anteriorly to the apical partition which was also that portion of the cell where most of the fecal pellets had been deposited. The larva anchored a pellet by holding it with the mandibles, depositing a small drop of material with the mouth, pulling away and attaching the other end to another pellet, leaf hair or portion of the wall. As the salivary component was daubed onto various structures by the salivary lips, the labium appeared to be split so that the silk was pulled through as if being threaded, and a steady pressure was maintained. The fecal pellets were spread evenly across the anterior portion of the cell and when all were anchored a cavity lined by white threads covering the entire cell had been formed. During this time the larva showed much mobility and agility, moving freely about the cell and turning completely around several times as necessary.

Once the fecal pellets were spun together more tiny strands were laid down within the cavity until a fairly dense network of threads that would be the template for the cocoon was formed. The cocoon was composed of one thin transparent and cellophane-like layer. The larva deposited the layer in one of two ways. Either a single thread was grasped with the mandibles and a clear liquid was exuded as the head moved up and down the strand or the mandibles separated 2 or more strands, depositing the liquid between them, moving the head back and forth until the layer dried. A few fecal pellets were incorporated into the matrix and flattened and spread out. No recognizable nipple was formed anteriorly. Instead, an area somewhat more transparent and of similar thickness to the rest of the cocoon was formed (Fig. 4). The average time from initiation of cocoon spinning to completed cocoon was 3.7 days (Table 1).

Pupation and Adult Emergence. On 27 July 1981, 10 overwintering larvae were placed in an incubator at 30°C in order to observe

pupation. Average time from incubation to pupation was 9.7 days (sd = 4.3, range = 7–18, n = 9). The transformation from overwintering larva to adult took an average of 22.3 days (sd = 2.9, range = 20–27, n = 6), with males completing development prior to females. Pigmentation changes were first observed in the eyes which turned yellow in approximately 11 to 13 days. At 13 to 14 days both compound eyes and ocelli had turned dark brown. Wing buds became evident and turned yellow at 11 to 14 days. Mouthparts began to darken at 15 days and had usually turned black within 16–16½ days. Coloration of general body regions started at 16 days and began with patches of integument at the bases of hairs on the vertex, frons, thoracic terga and abdominal sterna. Hairs quickly turned dark and pigmentation spread to the remaining portion of the head and thorax followed by the abdomen. Generally proximal portions of appendages changed color first with distal portions of the legs changing color last. From 16 to 20 days the body remained dull black while wings darkened. A shiny appearance to the body and hairs did not appear until just prior to ecdysis. Bees emerged from cells shortly after wings had darkened and proboscides had been retracted.

DISCUSSION

The incorporation of glandular secretions into nest linings, widespread in the Apoidea, is believed to have evolved as a mechanism to protect larvae and provisions from dehydration and/or the microbial consequences of excessively humid environs. Batra (1972, 1980), Cane (1981), and Eickwort et al. (1981) have discussed the inclusion of salivary and/or Dufour's gland components into cell linings and provisions of the 'short tongued bees' (Colletidae, Halictidae, Andrenidae) and the Anthophoridae. While the phenomenon has likely figured prominently in the evolution of these groups, little or no attention has been directed toward similar behaviors in the Megachilidae. Indeed, the evolution of the megachilidae has been viewed in a different framework. Eickwort et al. (1981) see the bulk of the megachilids (Megachilinae) as having evolved from a soil dwelling ancestor that developed the ability to gather foreign materials (leaf pieces, mud, resin, etc.) to line cells as an alternative to

glandular secretions in overcoming the constraints of humidity. While Eickwort et al.'s (1981) hypothesis of nesting evolution in the Megachilidae is interesting, more recent evidence points to the fact that glandular secretions are important features of megachild nesting biologies. Parker and Tepedino (1982) observed the application of salivary secretions to bare walls of *Osmia marginata* Michener nests. Frohlich (1983) observed the incorporation by *Osmia bruneri* Cockerell of an abdominal secretion into the provision, and also noted the application of a salivary secretion to partitions. *Dianthidium ulkei ulkei* (Cresson) also incorporates an opaque viscous substance, originating from the abdomen, into resinous cell walls and spreads the material over bare areas of the cell (Frohlich and Parker, in prep.).

Since the twig nesting megachilids probably arose from soil nesting megachilids (Eickwort et al. 1981) and since the Megachilidae is distantly related to the other soil nesting families (Michener 1974) we propose that the Megachilidae have retained the habit of using glandular secretions to line cells. It seems likely that a waterproof layer of some sort is necessary to maintain the humidity of the cell within tolerable limits. Lining cells with leaves in soils that are particularly moist would have little effect on reducing humidity and controlling fungal growth nor would lining pre-existing cavities such as twigs prevent dehydration. It is important, therefore, that we thoroughly examine the behavioral, and more importantly chemical, components of nesting in order to gain an understanding of the role of nest architecture in evolution.

The paucity of information available on the nesting biologies of other species of *Eumegachile* make it difficult to confirm (or, refute) Mitchell's (1981) recent revision of the old genus *Megachile* on the basis of behavior or nest architecture. The available data does confirm the separation of *Eumegachile* from *Megachile*, since the nest architectures of the two are radically different. *Eumegachile pugnata* nests are similar to, though somewhat more elaborate than, known nests of other species in the subgenus. Krombein (1967) reported that *E. inimica inimica* Cresson makes unlined cells with partitions of agglutinated sand a little larger than the inner circumference of the nest. *Eumegachile inimica sayi* Cresson also uses a single leafcutting as a partition but covers it with leaf pulp, incorporating five pebbles (Krombein 1967). *Eumegachile polycaris* Say lays

more than one egg per provision, makes partitions and plugs composed of leaf pulp and two layers of small compressed leaflets with no soil or pebbles, and constructs no vestibular or intercalary cells. No other biologies in the subgenus *Sayapis* are known and no biologies or nest architectures are known in the other subgenera of *Eumegachile*.

The manner in which *E. pugnata* constructs individual cells renders its adoption as a potential pollinator of commercial sunflower somewhat problematical under certain circumstances. *Eumegachile pugnata* construct cells that are separated from each other by partitions and are not surrounded by a leaf envelope. This is unfortunate because *E. pugnata* is susceptible to a chalkbrood fungus, *Ascosphaera aggregata* Skou, the treatment of which in other bees takes advantage of nest architecture. The disease sometimes decimates populations of the alfalfa leafcutting bee, *Megachile rotundata* (Fabricius), which construct cells that are completely leaf lined. During treatment, nests are opened, individual cells are separated as discrete leaf lined units, treated, and stored (Parker and Torchio 1980). When *M. rotundata* emerge only egress from individual cells is necessary and adults are not required to chew through cells containing dead larvae with infectious spores. Since *E. pugnata* are protected only by a thin cocoon and no leaf lined envelope, removal from the nest would cause excessive mortality. This "loose cell" management is also used to control various *M. rotundata* parasites. In the case of *E. pugnata* parasites could emerge from individual cells and reparasitize other cells without leaving the nest.

A second point that will have to be considered in commercial pollination is the fact that *E. pugnata* incorporates a fair amount of nectar into the provision. If growers are going to increase bee populations, sunflower cultivars that provide adequate nectar will have to be available.

Finally, one trait that makes *E. pugnata* a good candidate for sunflower pollination is its habit of provisioning cells early in the day. Male fertile sunflower cultivars dehisce overnight and in the early morning. Thus, the greatest amount of pollen is available during the time that *E. pugnata* are provisioning and pollinating flowers.

ACKNOWLEDGMENTS

Critical comments by G. C. Eickwort, V. J. Tepedino, and P. F. Torchio substantially improved and benefited our manuscript. We thank them for their conscientious efforts. Additionally, B. Peitersen, C. Schmitz, D. Veirs and T. Griswold rendered invaluable field assistance.

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