

September 2019

Use of Nest and Pollen Resources by Leafcutter Bees, Genus *Megachile* (Hymenoptera: Megachilidae) in Central Michigan

Michael F. Killewald

Michigan State University, killewam@myumanitoba.ca

Logan M. Rowe

Michigan State University, roweloga@msu.edu

Kelsey K. Graham

Michigan State University, graha252@msu.edu

Thomas J. Wood

Michigan State University, thomaswood734@gmail.com

Rufus Isaacs

Michigan State University, isaacsr@msu.edu

Follow this and additional works at: <https://scholar.valpo.edu/tgle>



Part of the [Entomology Commons](#)

Recommended Citation

Killewald, Michael F.; Rowe, Logan M.; Graham, Kelsey K.; Wood, Thomas J.; and Isaacs, Rufus 2019. "Use of Nest and Pollen Resources by Leafcutter Bees, Genus *Megachile* (Hymenoptera: Megachilidae) in Central Michigan," *The Great Lakes Entomologist*, vol 52 (1)

DOI: <https://doi.org/10.22543/0090-0222.2338>

Available at: <https://scholar.valpo.edu/tgle/vol52/iss1/8>

This Peer-Review Article is brought to you for free and open access by the Department of Biology at ValpoScholar. It has been accepted for inclusion in The Great Lakes Entomologist by an authorized administrator of ValpoScholar. For more information, please contact a ValpoScholar staff member at scholar@valpo.edu.

Use of Nest and Pollen Resources by Leafcutter Bees, Genus *Megachile* (Hymenoptera: Megachilidae) in Central Michigan

Cover Page Footnote

We thank Katie Boyd-Lee for her help in processing samples, Yajun Zhang for her help with landscape analysis, and Marisol Quintanilla for the use of her microscope to collect images of pollen. We thank Jordan Guy, Gabriela Quinlan, Meghan Milbrath, Steven Van Timmeren, Jacquelyn Albert, and Philip Fanning for their comments while preparing the manuscript. We thank the CRC station manager Jerry Skeltis and his staff for maintaining the research plots. This study was funded by the MSU Undergraduate Research Program (URP) and the Jeffrey Boettcher fund.

Use of Nest and Pollen Resources by Leafcutter Bees, Genus *Megachile* (Hymenoptera: Megachilidae) in Central Michigan

Killewald, M. F.^{1,2}*, L. M. Rowe^{1,3}, K. K. Graham¹, T. J. Wood^{1,4}, and R. Isaacs¹

¹ Department of Entomology, Michigan State University, East Lansing, MI 48824

² Department of Entomology, University of Manitoba, Winnipeg, MB R3T 2N2

³ Michigan Natural Features Inventory, 525 W. Allegan Street, Lansing, MI 48933

⁴ Laboratory of Zoology, University of Mons, 700, Mons, Belgium

*Corresponding author: (e-mail: killewam@myumanitoba.ca) (204) 474-7485

Abstract

Many landscapes throughout the Great Lakes region have experienced reductions in floral and nesting resources for bees. Identifying the resources used by bees in the family Megachilidae can be used to inform conservation programs that aim to support this group. In this study, we identified the preferred nesting substrate and size, as well as the proportion of distinct pollen types used for offspring provisioning by *Megachile* (Hymenoptera: Megachilidae) species. A total of 39 completed artificial nesting tubes were collected between July 25 and August 30, 2016. A majority of completed nests were in 4 mm diameter tubes. However, more 6 mm and 7 mm diameter nests were occupied later in the season. A total of 98 cells from 20 nests were analyzed for the composition of the pollen provisions. Nesting females gathered pollen primarily from *Trifolium repens* L.-type (70.2% of total pollen) and the majority of collection of this species occurred between July 25 and August 10. There was also frequent pollen collection from *Centaurea stoebe* (L.) (9.0%), *Rudbeckia*-type (8.4%), and *Cirsium* spp. (8.3%) with the majority of collection from these species occurring after August 10. Our results show that *Megachile* species at our mid-Michigan site exhibited strong preferences for specific nest hole sizes, and they primarily collected pollen from non-native plants. This information can inform efforts to build local populations of these summer-active bees using combined nesting and foraging resources.

Keywords: Pollen identification, pollinator, bee, stem, nest

Leafcutter bees (Hymenoptera: Megachilidae) are important pollinators of alfalfa (*Medicago sativa* L.), clover (*Trifolium* spp.), cranberry (*Vaccinium macrocarpon* Aiton), sunflower (*Helianthus* spp.), and many wildflower species (Hobbs and Lilly 1954, Stephen and Osgood 1965b, Osgood 1974, Tepedino and Frohlich 1982, Cane et al. 1996, Pitts-Singer and Cane 2011, Richards 2015). In the wild, *Megachile* are highly adaptive, utilizing a wide range of nesting materials, including plant stems, soil, and logs, as well as man-made structures (Hobbs and Lilly 1954). Because of this plasticity, there has been increasing interest in managing these species near cropland to bolster pollination services. To manage *Megachile* species, artificial cavities of various sizes can be placed around croplands to encourage nesting. However, regionally specific information on nesting and floral resources used by different species of *Megachile* is needed to optimize efforts to increase local abundances of this genus.

Most *Megachile* use leaf material to make their nests in decaying logs or inside the hollow stems of plants, but some species make their nests underground (Hobbs and Lilly 1954, Gibbs et al. 2017). The inner walls of the nest are lined with cut leaf material to form a cell (Frolich and Parker 1983), with some species using masticated leaf material and soil (Medler 1964). They then provision this cell with pollen and nectar before laying an egg and finally sealing the cell with more leaf material (Ivanochko 1979). This process is repeated several times from the back to the front of the cavity until it is full of completed cells. Once the nest is full of completed cells, an endcap of leaf material is added to protect their offspring. Once the endcap is added, the nest is now completed and the female begins another (Frolich and Parker 1983, Peterson and Artz 2014). Within the Great Lakes region, the natural nesting biology of several species of *Megachile* is well studied, and we can use this foundation to inform selection of nesting materials for management (Medler and Koerber 1958, Medler

1959, 1964, Medler and Lussenhop 1968). Nesting habits of some commonly managed *Megachile*, such as *M. rotundata* (Fabricius), may vary significantly, as they are known to nest in cavities with diameters as variable as 3–4 mm (O'Neill et al. 2010) to 6–7 mm in diameter (Stephen and Osgood 1965a). But we still know relatively little about the optimal nesting materials that should be provided to bolster local populations of *Megachile* in general (instead of targeting specific species). Clarifying the optimal materials and sizes to provide *Megachile* species in the Great Lakes region will therefore optimize efforts by growers and conservationists to increase local populations.

Similarly, the floral resources used by *Megachile* species in the Great Lakes region are not well studied, and a better understanding of resource use could aid in increasing local abundance of *Megachile*. Although lists of visited plants for different *Megachile* species exist (Ascher and Pickering 2019), there is little information on which plants this genus uses for pollen foraging specifically, as these plant associations are often more restrictive than those plants visited for nectar (Williams 2003). It has been shown that some *Megachile* species often provision nests with pollen from a restricted number of plant species, such as Asteraceae or Fabaceae species (Tepedino and Frohlich 1982, O'Neill et al. 2004), and that this number of plant species may be further restricted when factors such as intensive agriculture reduce floral abundance and diversity in the area (Rich and Woodruff 1996). Pollen resources are critical for brood development (Nelson et al. 1972), and clarifying the pollen provisioning behavior of this group of bees is needed to better understand their resource requirements.

Pollen analysis can be used to identify dietary preferences and host-species fidelity in bees (Beil et al. 2008). Most traditional collection methods revolve around hours of searching for individual bees in the field. However, pollen analysis of trap nests allows researchers to passively monitor the diet of cavity nesting bees with minimal time spent in the field and removes floral associations that are used for nectaring only. Given that pollen provisioning preferences of *Megachile* species are not well studied in the Great Lakes region, understanding the pollen use and nesting preferences of this group is important for their management.

At a site in central Michigan where multiple native wildflower species were established to evaluate their use by bees (Rowe et al. 2018), we addressed the following questions: 1) What nest diameters are utilized by the *Megachile* species at this site?

and 2) What are the primary pollen species collected by these bees?

Methods

Study site. This research was conducted during the summer of 2016 at the Clarksville Research Center (CRC) located near Clarksville, MI (42.873390, -85.258496). Fifty-three native wildflower species (S1) were established in individual plots replicated four times, across a three-acre area (Rowe et al. 2018). Within a 1 km radius of the study site, the landscape was dominated by non-rewarding agricultural land (54.1%), but also included 20.3% of rewarding agricultural land, 10.4% forests, 7.3% of developed land, 3.5% wetlands, 3.2% fallow agricultural land, and 0.7% other classification types (Fig. 1). Non-rewarding agricultural land is comprised of crops that do not produce resources that are generally used by bees. Corn, oats, rye and sorghum are included in the non-rewarding agricultural land category. Similarly, rewarding agricultural land is comprised of crops that produce resources generally used by bees, such as alfalfa, cucumbers, clover, wildflowers, and apples. These data were extracted from the Crop Data Layer (USDA National Agricultural Statistics Service Cropland Data Layer 2016) with 30 m spatial resolution using ArcGIS 10.2.2 (ESRI 2014). Full details of the site layout, plant species used, and experimental design can be found in Rowe et al. (2018).

Nest boxes. To identify preferences for nest tube diameter and material, four nesting boxes containing a variety of materials were placed at CRC in May 2016 (Fig. 2). Each nest box was made from a plastic mail tote (Uline, Pleasant Prairie, WI) that was 18 x 13 x 12" in size and contained four sizes of cardboard nesting tube (4, 5, 6, and 7 mm inside diameter) in bundles of 62 nests (Jonesville Paper Tube Company, Jonesville, MI), a reusable wooden nest tray with 8 mm inside nest diameter containing a total of 72 available holes (Crown Bees, Woodinville, WA), and a cluster of 12 pieces of bamboo with hole diameters ranging from 8–16 mm. Nests were secured inside the nesting box with a piece of 2 x 3" wood oriented vertically and zip ties holding the nesting substrate to the wood. During the summer of 2015, only four *Megachile* were collected during the season long bee surveys carried out by Rowe et al. (2018). To encourage nesting, 131 overwintering *Megachile* cocoons were placed in each nesting box in early May. Most of the released cocoons were of *M. rotundata*, but other overwintering *Megachile* species could have been released as well since most unopened *Megachile* cocoons can-

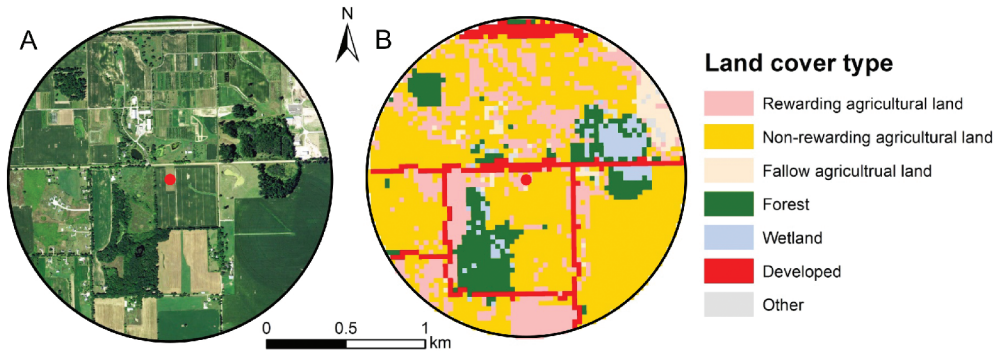


Figure 1. A. An aerial image with a 1km radius around the Clarksville Research Station (CRC) with a 1m resolution. B. An aerial view of the site with different landscape classifications. The image was extracted from Crop Data Layer (USDA National Agricultural Statistics Service Cropland Data Layer 2016) with 30 m spatial resolution using ArcGIS 10.2.2 (ESRI, 2014).

not be identified to species. Of the released cocoons at each nesting box, 44% were 4mm, 47% were 6–8 mm, and 10% were 8–10 mm. These cocoons were originally collected from nests in a native bee hotel at Michigan State University, in which *M. rotundata* and *M.*

pugnata (Say) were commonly observed nesting (Gibbs et al. 2017).

Nest sampling. Nest boxes were checked weekly from May until September for completed nests, which were removed and replaced with new nests to maintain a consistent number of available cavities throughout



Figure 2. One of the four nest boxes placed at the Clarksville Research Center (CRC) in the summer of 2016. Artificial nesting material inside the box includes four sizes of cardboard nests (4, 5, 6, and 7 mm inside diameter), a reusable wood block (8 mm inside diameter), and 12 bamboo nests with varying diameters from 8-20 mm.

the season. *Megachile* nests were assigned a week category based on the collection date so trends in nesting and pollen could be visualized. Week one marked the first completed nest and week 4 marked the end of nesting. A week was considered Monday–Sunday, with July 25, August 1, August 8, August 15, 2016 marking the beginning of weeks 1–4, respectively. All collected nests were placed into a -23°C freezer within 2 hours after collection to terminate larval development.

Analysis of pollen from nests. Pollen was isolated by removing plant material and placing the pollen ball into a 1.5 mL centrifuge tube. These samples were then stored in a -23°C freezer before further processing. For each week of nesting, alternating cells were analyzed for five nests. To better visualize features of the pollen grains, some selected samples were processed using acetolysis according to Louveaux et al. (1978) and Jones (2014). The remaining samples that were not processed with acetolysis were processed according to Westrich and Schmidt (1986). Samples were diluted with 70% ethanol, vortexed, and immediately a subsample was pipetted onto a microscope slide. A piece of fuschin gel was heated and then a cover slip was added to the center of each pollen sample (Westrich and Schmidt 1986). Amounts of ethanol were varied to keep a consistent amount of pollen on the microscope slides for identification, ranging from 250 μl to 1 mL, with full pollen loads receiving 1 mL of ethanol and minimal pollen loads receiving 250 μl .

For both processing methods, volumes of pollen species were visually estimated (Folk 1951) for each pollen load. Pollen species were identified to the lowest taxonomic rank using Sawyer (1981) and a reference collection that was processed using similar methods. Pollen slides processed with acetolysis were identified using a reference collection that was also processed with acetolysis. Likewise, non-acetolysed samples were only compared to a non-acetolysed reference sample. For the non-acetolysed samples, pollen species were identified against a reference collection of 254 plant

species collected across Michigan. The acetolysed samples were compared to a reference collection of 73 plant species collected across Michigan. Pictures of pollen species from both reference collections are available online (<https://www.flickr.com/photos/161453633@N02/collections>). If the identity of the pollen species was not certain, similar pollen grains were lumped into type categories or lowest taxonomic level possible. Reference collections included plants established in the wildflower planting (Rowe et al. 2018).

Results

A total of 39 completed *Megachile* nests were collected during the sampling period between July 25 and August 15, 2016 (Fig. 3). The *Megachile* at our site nested more frequently in 4 mm nests than any other diameter, with almost 50% of the nesting in this tube size. However, later in the nesting season, after August 10, more 6 mm and 7 mm nests were utilized than 4 mm nests. No *Megachile* nests were found in the 5mm cardboard tubes or the wooden nesting block, and only 6 completed bamboo nests were collected at the site. The total number of completed nests of each size are summarized in Table 1.

Half of the collected nests were randomly selected for pollen analysis, totaling 98 cells from 20 nests. Pollen analysis identified seven distinct pollen types: *Trifolium repens* L.-type, *Centaurea stoebe* (Linnaeus), *Rudbeckia*-type, *Cirsium* spp., *Trifolium pretense* L., Unknown pollen, and *Lotus corniculatus* (Linnaeus). Over the entire nesting season, *Megachile* species primarily collected *T. repens*-type (70.2%), *C. stoebe* (8.9%), *Rudbeckia*-type (8.4%), and *Cirsium* pollen (8.3%). All other pollen types were present in < 3% abundance. Most of the pollen species identified from nests were not collected from the sown plant species. However, *Rudbeckia*-type pollen could be a sown species, with only 4 sown species having a similar pollen structure. Similarly, *C. stoebe* and *L. corniculatus* were sown, but

Table 1. Number of nests of each size completed by *Megachile* spp. at the Clarksville Research Center during 2016.

Nesting substrate (inside diameter)	Total nests completed	Percent of total nests
Paper tube (4 mm)	20	48.8
Paper tube (5 mm)	0	0
Paper tube (6 mm)	9	22.0
Paper tube (7 mm)	6	14.6
Wood block (8 mm)	0	0
Bamboo (8-10 mm)	6	14.6

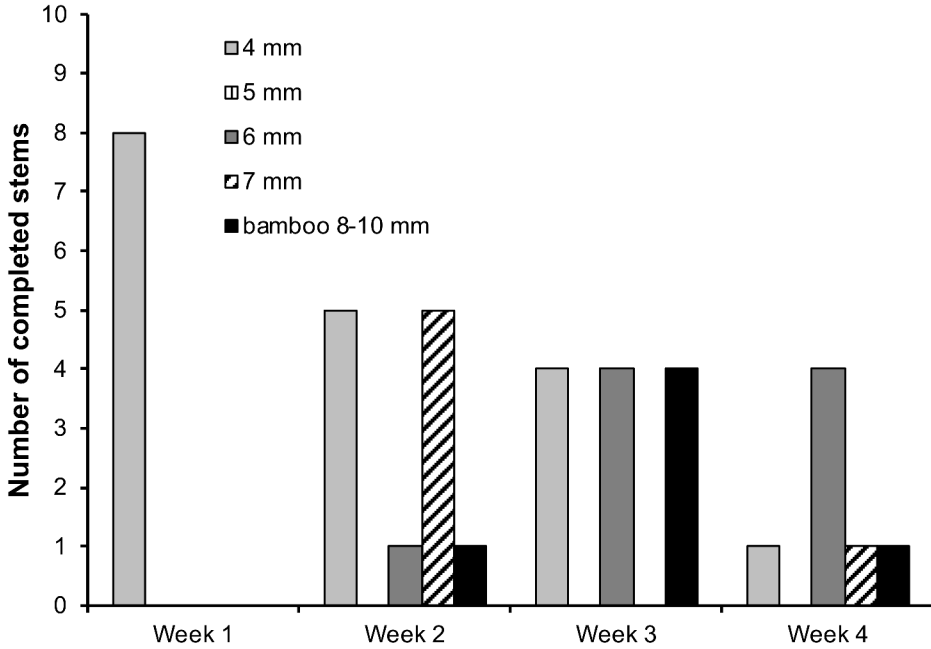


Figure 3. The number of completed nests collected per week at the Clarksville Research Center (CRC) during the summer of 2016.

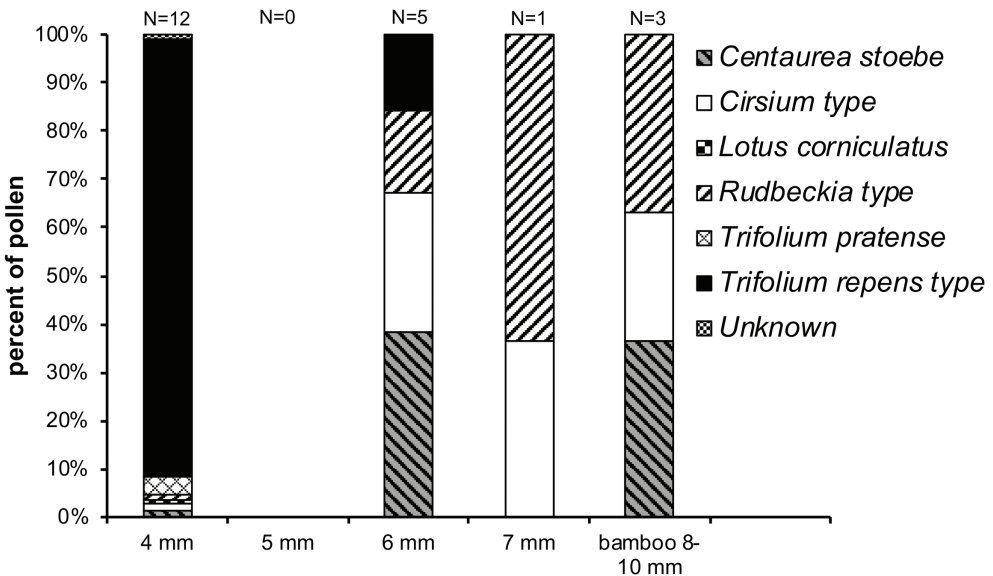


Figure 4. Pollen composition of each nest size. Nests were collected at the Clarksville Research Center during the summer of 2016.

Table 2. Identified pollen groups with their taxonomic constituents from *Megachile* nests collected at the Clarksville Research Center during 2016.

pollen type	order	Family	genus	species
<i>Lotus corniculatus</i>	Fabales	Fabaceae	<i>Lotus</i>	<i>corniculatus</i>
<i>Trifolium pratense</i>	Fabales	Fabaceae	<i>Trifolium</i>	<i>pratense</i>
<i>Trifolium repens</i> -type	Fabales	Fabaceae	<i>Trifolium</i>	
			<i>Medicago</i>	
			<i>Melilotus</i>	
<i>Centaurea stoebe</i>	Asterales	Asteraceae	<i>Centaurea</i>	<i>stoebe</i>
<i>Cirsium</i>	Asterales	Asteraceae	<i>Cirsium</i>	
<i>Rudbeckia</i> -type	Asterales	Asteraceae	<i>Rudbeckia</i>	
			<i>Coreopsis</i>	
			<i>Echinacea</i>	
			<i>Ratibida</i>	

there was also an abundance of these species in the surrounding landscape. A summary of pollen composition of each nest size is available in Fig. 4.

The pollen species utilized by nesting *Megachile* varied throughout the season. *Megachile* species used Fabaceae pollen almost exclusively (100% in week 1 and 81.6% in week 2) early in the nesting season. However, in weeks 3 and 4, *Megachile* species utilized more Asteraceae pollen than in previous weeks. Abundances of Fabaceae pollen (*T. repens*-type, *T. pratense*, and *L. corniculatus*) decreased over time from 100% in week 1, to 81.6% in week 2, to 29.8% in week 3, and finally increased slightly in week 4 to 62.1%. This trend was mostly driven by *T. repens*-type. The abundance of

T. repens-type declined from 95.8% in week 1 to 29.7% in week 3, but increased slightly to 57.1% in week 4. Abundances of Asteraceae pollen (*Cirsium*, *Rudbeckia*-type, and *C. stoebe*) increased from 18% in week 2, to 68.2% in week 3, and finally decreased to 36.4% in week 4. Pollen constituents for the type pollens are included in Table 2. A figure of pollen composition by stem size and week is available in Fig. 5.

Discussion

We found that the *Megachile* species at our site used mostly 4 mm nests early in the season (week 1) and then utilized mostly larger nests (>6 mm) later in the season (weeks 3 and 4). We also found that the

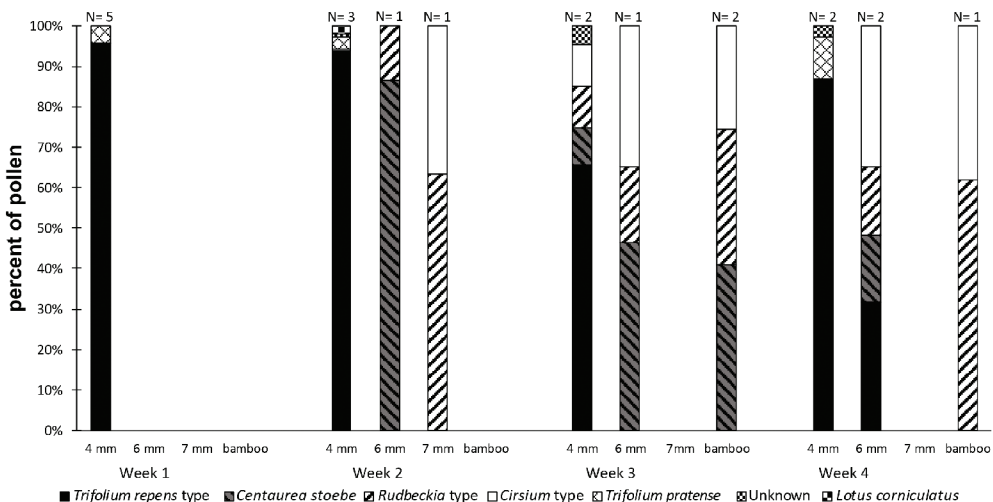


Figure 5. Pollen composition of each cavity size separated by weeks of nesting. Nests were collected at the Clarksville Research Center during the summer of 2016.

Table 3. Species of *Megachile* that were collected at the Clarksville Research Center during the summer of 2016 from the Rowe et al. (2018) study. Intertegular distance is averaged from 3 specimens collected at the site. If 3 specimens were not collected, then other specimens collected in Michigan's Lower Peninsula were measured. Standard error is given in parenthesis to the right of the average intertegular distance.

species	number collected	average intertegular distance mm	known nest size	flight time	floral preference	floral records	other info	citation
<i>M. rotundata</i>	8	2.44 (0.03)	4-7mm	July 20-August 8	Generalist but forages mainly on Fabaceae	<i>Asclepias verticillata</i> , <i>Lotus corniculatus</i> , <i>Pycnanthemum virginianum</i>	actively managed for alfalfa pollination, Common in MSU trap nests	Stephen and Osgood, 1965a, Gerber and Klostermeyer, 1972, Pits-Singer and Cane, 2011, Gibbs et al., 2017
<i>M. pugnata</i>	3	2.69 (0.09)	7-9mm	July 7-August 22	Asteraceae	<i>Coreopsis palmata</i> , <i>Echinacea purpurea</i>	uses masticated rather than cut leaf material for nest construction. Common in MSU trap nests	Medler, 1964, Tepedino and Frohlich, 1982, Frolich and Parker, 1983, Gibbs et al. 2017
<i>M. frugalis</i>	2	2.69 (0.08)	unknown	July 7-August 3	Generalist	<i>Asclepias tuberosa</i> , <i>Verbena stricta</i>	limited information available, Gibbs et al., 2017 only lists county records in Michigan	Rowe et al. 2018, Ascher and Pickering, 2019
<i>M. mucida</i>	2	3.41 (0.07)	8mm	June-16	Generalist but floral visitation records limited	<i>Penstemon digitalis</i>	emergence among the earliest of the <i>Megachile</i> species in Michigan, ground nesting	Gibbs, 2017, Gibbs et al. 2017
<i>M. brevis</i>	1	2.74 (0.04)	8-9mm	August-16	Generalist but forages on more Asteraceae than other families	<i>Rhus copallinum</i>	one study (Michender, 1953) found a female to nest inside a 9 mm rubber tube placed on the ground	Michener, 1953, Medler and Lussenhop, 1968
<i>M. mendica</i>	1	3.20 (0.07)	6.4-12.7mm	June-16	Generalist but forages on more Asteraceae than other families	<i>Lotus corniculatus</i>	nests in soil, but will accept trap nests. Krombein (1967) found one nest of this species inside a cavity 4.8 mm inside diameter, but it appears that use of nests this size are rare.	Krombein, 1967, Baker et al. 1985

Megachile at the study site primarily forage from *T. repens*-type (Fabaceae family) pollen early in the nesting season (weeks 1 and 2), but then use a mix of Asteraceae pollen later in the nesting season (weeks 3 and 4). For areas where *Megachile* species are managed for pollination services of specific crops, managers can use this information to inform their nest material and plant selection.

A shift in nesting resources and pollen preference likely indicates that different species are utilizing different resources. Seven species of *Megachile* were recorded at this site during the same growing season (Rowe et al. 2018), with *M. rotundata* being the most dominant species and *M. pugnata* being the second most common (Table 3). *Megachile rotundata* tend to nest in 4 mm inside diameter tubes (Klostermeyer and Gerber 1969), but will accept tubes ranging from 4–7 mm (Stephen and Osgood 1965a). Although this species will visit a wide range of flowers, it tends to forage on Fabaceae, especially members of *Medicago*, *Melilotus*, and *Trifolium* (O'Neill et al. 2004, Pitts-Singer and Cane 2011, Ascher and Pickering 2019). *Megachile rotundata* is the smallest *Megachile* species found at the site, and the only species found to use 4 mm nests (O'Neill et al. 2010). *Megachile rotundata* is also common within the nests at MSU that our nesting boxes were seeded with (Gibbs et al. 2017). Given the pollen foraging habits, local abundance, and willingness to use smaller cavities, *M. rotundata* is the most likely occupant of the 4 mm nests found at our site.

The second most common species at the site, *M. pugnata*, will nest in 7 mm inside diameter tubes (Tepedino and Frohlich 1982), but will use a range of tube sizes from 7–9 mm (Medler 1964, Frohlich and Parker 1983). *Megachile pugnata* is common in both Michigan's Lower Peninsula and the MSU trap nests that the nesting boxes were seeded with (Gibbs et al. 2017). *Megachile pugnata* displays stronger pollen preferences than *M. rotundata*. One study found that *M. pugnata* uses almost exclusively Asteraceae pollen, with only 0.6 to 2.5% of collected pollen not belonging to this family (Tepedino and Frohlich 1982). The use of larger diameter cavities, preference of Asteraceae pollen, and local abundance makes *M. pugnata* a likely occupant of the larger nest sizes.

Two specimens of both *Megachile frugalis* (Cresson) and *Megachile mucida* (Cresson) were also collected at the site during the summer of 2016. Little information is known about these species, but given floral records (Ascher and Pickering 2019), both species appear to visit a wide range of flowers. It is unknown what sizes of cavities *M. frugalis* will utilize. *Megachile mucida* is found to

nest in the ground (Gibbs 2017), and is quite common in mid-Michigan. The emergence of *M. mucida* is among the earliest of the *Megachile* species found in Michigan. Given the ground nesting behavior of *M. mucida*, it is likely not a candidate for the larger diameter stems collected at our site.

Two other species of *Megachile*, *M. brevis* (Say) and *M. mendica* (Cresson), were also found at the site in 2016, but only one specimen of each species was collected. The biology of *Megachile brevis* is well documented in Kansas by Michener (1953). However, its nesting preferences are not well known, as he did not document the nest diameters used by this species, other than a single female accepted a 9 mm rubber tube when placed on the ground. The nesting biology of *Megachile mendica* is summarized in Baker et al. (1985), where they found that *M. mendica* accepted trap nests ranging from 6.4–9.5 mm, but a majority of nests were 8 mm inside diameter. Given floral visitation data, it appears that both *M. brevis* and *M. mendica* are generalists. However, both species show more floral associations within the Asteraceae family than other families (Ascher and Pickering 2019).

The exact identity of the nest occupants cannot be known for certain, but given floral visitation data and previous nesting studies, we believe that the occupants of the 4 mm nests were *M. rotundata*. The occupants of the larger diameters of nests are less clear, but is most likely *M. pugnata* given their abundance and oligolecty on Asteraceae pollen. *Megachile mucida* is not a likely candidate for the larger diameter stems due to its ground nesting behavior. However, it is not clear whether this species would accept artificial cavities given the option. Although the other nesting species cannot be discredited completely, they are much less common and more general in their foraging preferences than *M. pugnata*.

Our findings also suggest that nesting *Megachile* species did not utilize the majority of sown wildflowers. However, due to the difficulty of pollen identification and lack of published keys, some pollen species had to be lumped into a type category. For instance, *T. repens*-type pollen could be from a number of Fabaceae species; though, there were no Fabaceae species with *T. repens*-type pollen in the wildflower planting at our site. However, *Melilotus* and *Medicago* have a similar pollen structure to *T. repens*-type and are often lumped together (Sawyer 1981). Both of these genera were not sown, but were found within 100 m of the nest boxes, and could be possible sources of *T. repens*-type pollen. Similarly, *Rudbeckia*-type pollen could also be another Asteraceae pollen other than

Rudbeckia, and there were planted members of the Asteraceae family with a similar pollen structure in bloom during the nesting season: *Coreopsis palmata* (Nutt.), *Echinacea purpurea* (L.), *Ratibida pinnata* (Vent.), and *Rudbeckia hirta* (L.). It is therefore possible that *Rudbeckia* type pollen found in nests were from the planted species; however, overall collection of *Rudbeckia* type pollen was low.

The non-sown resources are likely more effective at local recruitment and retention of *Megachile* due to their preferences for them. Unfortunately, since some of the pollen species had to be grouped together, we cannot be certain which pollen species were the most useful. Given that many of the collected pollen species are weedy and widespread, lack of pollen resources may not be a large concern for *Megachile* in this region.

Acknowledgments

We thank Katie Boyd-Lee for her help in processing samples, Yajun Zhang for her help with landscape analysis, and Marisol Quintanilla for the use of her microscope to collect images of pollen. We thank Jordan Guy, Gabriela Quinlan, Meghan Milbrath, Steven Van Timmeren, Jacquelyn Albert, and Philip Fanning for their comments while preparing the manuscript. We thank the CRC station manager Jerry Skeltis and his staff for maintaining the research plots. This study was funded by the MSU Undergraduate Research Program (URP) and the Jeffrey Boettcher fund.

Literature Cited

- Ascher, J. S. and J. Pickering. 2019.** Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila). http://www.discoverlife.org/mp/20q?guide=Apoidea_species.
- Baker, J. R., E. D. Kuhn, and S. B. Bambara. 1985.** Nests and immature stages of leafcutter bees (Hymenoptera: Megachilidae). *Journal of the Kansas Entomological Society* 58: 290–313.
- Beil, M., H. Horn, and A. Schwabe. 2008.** Analysis of pollen loads in a wild bee community (Hymenoptera: Apidae) – a method for elucidating habitat use and foraging distances. *Apidologie* 39: 456–467.
- Cane, J. H., D. Schifffhauer, and L. J. Kerwin. 1996.** Pollination, foraging, and nesting ecology of the leaf-cutting bee *Megachile* (*Delomegachile*) *addenda* (Hymenoptera: Megachilidae) on cranberry beds. *Annals of the Entomological Society of America* 89: 361–367.
- ESRI. 2014.** ArcGIS Desktop: Release 10. Environmental Systems Research Institute, Redlands, CA.
- Folk, R. L. 1951.** A comparison chart for visual percentage estimation. *Journal of Sedimentary Petrology* 21: 32:33.
- Frolich, D. R., and F. D. Parker. 1983.** Nest building behavior and development of the sunflower leafcutter bee *Eumegachile* (*Sayapis*) *pugnata* (Say) (Hymenoptera: Megachilidae). *Psyche* 90: 193–210.
- Gerber, H. S. and Klostermeyer, E. C. 1972.** Factors affecting the sex ratio and nesting behavior of the alfalfa leafcutting bee. Washington Agricultural Experiment Station Washington State University, Pullman, WA.
- Gibbs, J. 2017.** Notes on the nests of *Augochloropsis metallica fulgida* and *Megachile mucida* in central Michigan (Hymenoptera: Halictidae, Megachilidae). *The Great Lakes Entomologist* 50: 17–24.
- Gibbs, J., J. S. Ascher, M. G. Rightmyer, and R. Isaacs. 2017.** The bees of Michigan (Hymenoptera: Apoidea: Anthophila), with notes on distribution, taxonomy, pollination, and natural history. *Zootaxa* 4352: 001–160.
- Hobbs, G. A., and C. E. Lilly. 1954.** Ecology of species on *Megachile* Latreille in the mixed prairie region of southern Alberta with special reference to pollination of alfalfa. *Ecology* 35: 453–462.
- Ivanochko, M. 1979.** Taxonomy, biology and alfalfa pollinating potential of Canadian leaf-cutter bees—genus *Megachile* Latreille (Hymenoptera: Megachilidae). M.S. thesis. McGill University, Quebec.
- Jones, G.D. 2014.** Pollen analyses for pollination research, acetolysis. *Journal of Pollination Ecology* 13: 203–217.
- Klostermeyer, E. C., and H. S. Gerber. 1969.** Nesting behavior of *Megachile rotundata* (Hymenoptera: Megachilidae) monitored with an event recorder. *Annals of the Entomological Society of America* 62: 1321–1325.
- Krombein, K. V. 1967.** Trap-nesting wasps and bees: life histories and nest associates. Smithsonian Press.
- Louveaux, J. A. Maurizio, and G. Vorwohl. 1978.** Methods of melissopalynology. *Bee World* 59: 139–157.
- Medler, J. T. 1959.** A note on *Megachile centuncularis* (Linn.) in Wisconsin (Hymenoptera: Megachilidae). *The Canadian Entomologist* 91:113–115.
- Medler, J. T. 1964.** A note on *Megachile* (*Sayapis*) *pugnata pugnata* Say in trap-nests in Wisconsin (Hymenoptera: Megachilidae). *The Canadian Entomologist* 96: 918–921.

- Medler, J. T. and Koerber T. W. 1958.** Biology of *Megachile relativa* Cresson (Hymenoptera, Megachilidae) in trap-nests in Wisconsin. *Annals of the Entomological Society of America* 51: 337–344.
- Medler, J. T., and Lussenhop, J. F. 1968.** Leafcutter bees of Wisconsin. *University of Wisconsin Research Bulletin* 274: 3–80.
- Michener, C. D. 1953.** The biology of the leafcutter bee (*Megachile brevis*) and its associates. *University of Kansas Science Bulletin* 35: 1659–1745.
- Nelson, E. V., Roberts, R. B., and Stephen, W. P. 1972.** Rearing larvae of the leaf-cutter bee *Megachile rotundata* on artificial diets. *Journal of Apicultural Research* 11: 153–156.
- O'Neill, K. M., R. P. O'Neill, S. Blodgett, and J. Fultz. 2004.** Composition of pollen loads of *Megachile rotundata* in relation to flower diversity (Hymenoptera: Megachilidae). *Journal of the Kansas Entomological Society* 77: 619–625.
- O'Neill, K. M., A. M. Pearce, R. P. O'Neill, and R. S. Miller. 2010.** Offspring size and sex ratio variation in a feral population of alfalfa leafcutting bee (Hymenoptera: Megachilidae). *Annals of the Entomological Society of America* 103: 775–784.
- Osgood, C. E. 1974.** Relocation of nesting populations of *Megachile rotundata*, an important pollinator of alfalfa. *Journal of Apicultural Research* 13: 67–73.
- Peterson, S. S., and D. R. Artz. 2014.** Production of solitary bees for pollination in the United States. Elsevier Inc. 653–681.
- Pitts-Singer, T. L., and J. H. Cane. 2011.** The alfalfa leafcutting bee, *Megachile rotundata*: the world's most intensively managed solitary bee. *Annual Review of Entomology* 56: 221–237.
- Rich, T. C. G., and E. R. Woodruff. 1996.** Changes in the vascular plant floras of England and Scotland Between 1930–1960 and 1987–1988: The BSBI monitoring scheme. *Biological Conservation* 75: 217–229.
- Richards, K. W. 2015.** The alfalfa leafcutter bee, *Megachile rotundata*: a potential pollinator for some annual forage clovers. *Journal of Apicultural Research* 34: 115–121.
- Rowe, L., D. Gibson, D. Landis, J. Gibbs, and R. Isaacs. 2018.** A comparison of drought-tolerant prairie plants to support managed and wild bees in conservation programs. *Environmental Entomology* 47: 1128–1142.
- Sawyer, R. 1981.** Pollen identification for beekeepers. Northern Tree Books, West Yorkshire, England.
- Stephen, W. P., and C. E. Osgood. 1965a.** Influence of tunnel size and nesting medium on sex ratios in a leaf-cutter bee, *Megachile rotundata*. *Journal of Economic Entomology* 58: 965–986.
- Stephen, W. P., and C. E. Osgood. 1965b.** The induction of emergence in leaf-cutter bee *Megachile rotundata* an important pollinator of alfalfa. *Journal of Economic Entomology* 58: 284–286.
- Tepedino, V. J., and D. R. Frohlich. 1982.** Mortality factors, pollen utilization, and sex ratio in *Megachile pugnata* Say (Hymenoptera: Megachilidae), a candidate for commercial sunflower pollination. *New York Entomological Society* 90: 269–274.
- USDA National Agricultural Statistics Service Cropland Data Layer. 2016.** Published crop-specific data layer. <https://nassgeodata.gmu.edu/CropScape/>
- Westrich, P., and K. Schmidt. 1986.** Methoden und Anwendungsgebiete der Pollenanalyse bei Wildbienen (Hymenoptera, Apoidea). *Linzer biologische Beiträge* 18: 341–360.
- Williams, N. M. 2003.** Use of novel pollen species by specialist and generalist solitary bees (Hymenoptera: Megachilidae). *Oecologia* 134: 228–237.

S1. List of the sown plant species at the Clarksville Research Center. Pollen type refers to the morphological group that each plant species would be placed into based on their pollen structure.

plant species	plant family	pollen type	bloom time relative to nest construction
<i>Lotus corniculatus</i>	Fabaceae	<i>Lotus</i> sp.	during
<i>Oenothera fruticosa</i>	Onagraceae	<i>Oenothera</i> sp.	during
<i>Achillea millefolium</i>	Asteraceae	<i>Aster</i> type	during
<i>Asclepias syriaca</i>	Asclepiadaceae	<i>Asclepias</i> sp.	during
<i>Ceanothus americanus</i>	Rhamnaceae	<i>Ceanothus</i> sp.	during
<i>Asclepias tuberosa</i>	Asclepiadaceae	<i>Asclepias</i> sp.	during
<i>Potentilla arguta</i>	Rosaceae	<i>Potentilla</i> sp.	during
<i>Rudbeckia hirta</i>	Asteraceae	<i>Rudbeckia</i> type	during
<i>Campanula rotundifolia</i>	Campanulaceae	<i>Campanula</i> sp.	during
<i>Amorpha canescens</i>	Fabaceae	<i>Amorpha</i> sp.	during
<i>Coreopsis palmata</i>	Asteraceae	<i>Rudbeckia</i> type	during
<i>Hypericum prolificum</i>	Clusiaceae	<i>Hypericum</i> sp.	during
<i>Monarda fistulosa</i>	Lamiaceae	<i>Monarda</i> sp.	during
<i>Hieracium gronovii</i>	Asteraceae	<i>Taraxacum</i> type	during
<i>Pycnanthemum virginianum</i>	Lamiaceae	<i>Pycnanthemum</i> sp.	during
<i>Verbena stricta</i>	Verbenaceae	<i>Verbena</i> sp.	during
<i>Chamerion angustifolium</i>	Onagraceae	<i>Chamerion</i> sp.	during
<i>Centaurea stoebe micranthos</i>	Asteraceae	<i>Centaurea</i> type	during
<i>Solidago nemoralis</i>	Asteraceae	<i>Aster</i> type	during
<i>Asclepias verticillata</i>	Asclepiadaceae	<i>Asclepias</i> sp.	during
<i>Dalea purpurea</i>	Fabaceae	<i>Dalea</i> sp.	during
<i>Ratibida pinnata</i>	Asteraceae	<i>Rudbeckia</i> type	during
<i>Pycnanthemum pilosum</i>	Lamiaceae	<i>Pycnanthemum</i> sp.	during
<i>Liatris cylindracea</i>	Asteraceae	<i>Rudbeckia</i> type	during
<i>Echinacea purpurea</i>	Asteraceae	<i>Rudbeckia</i> type	during
<i>Eryngium yuccifolium</i>	Apiaceae	<i>Eryngium</i> sp.	during
<i>Monarda punctata</i>	Lamiaceae	<i>Monarda</i> sp.	during
<i>Helianthus occidentalis</i>	Asteraceae	<i>Helianthus</i> type	during
<i>Solidago juncea</i>	Asteraceae	<i>Rudbeckia</i> type	during
<i>Silphium integrifolium</i>	Asteraceae	<i>Helianthus</i> type	during
<i>Silphium terebinthinaceum</i>	Asteraceae	<i>Helianthus</i> type	during
<i>Rhus copallinum</i>	Anacardiaceae	<i>Rhus</i> sp.	during
<i>Lespedeza hirta</i>	Fabaceae	<i>Lespedeza</i> sp.	during
<i>Lespedeza capitata</i>	Fabaceae	<i>Lespedeza</i> sp.	during
<i>Coreopsis tripteris</i>	Asteraceae	<i>Rudbeckia</i> type	during
<i>Packera obovata</i>	Asteraceae	<i>Aster</i> type	before
<i>Potentilla simplex</i>	Rosaceae	<i>Potentilla</i> sp.	before
<i>Lupinus perennis</i>	Fabaceae	<i>Lupinus</i> sp.	before
<i>Penstemon hirsutus</i>	Plantaginaceae	<i>Penstemon</i> sp.	before
<i>Heuchera richardsonii</i>	Saxifragaceae	<i>Heuchera</i> sp.	before
<i>Coreopsis lanceolata</i>	Asteraceae	<i>Rudbeckia</i> type	before
<i>Tradescantia ohioensis</i>	Commelinaceae	<i>Tradescantia</i> sp.	before
<i>Baptisia alba</i> var. <i>macrophylla</i>	Fabaceae	<i>Baptisia</i> sp.	before
<i>Penstemon digitalis</i>	Plantaginaceae	<i>Penstemon</i> sp.	before
<i>Rosa carolina</i>	Rosaceae	<i>Rosa</i> sp.	before
<i>Dasiphora fruticosa</i>	Rosaceae	<i>Dasiphora</i> sp.	after
<i>Helianthus strumosus</i>	Asteraceae	<i>Helianthus</i> type	after
<i>Liatris aspera</i>	Asteraceae	<i>Rudbeckia</i> type	after
<i>Oenothera biennis</i>	Onagraceae	<i>Oenothera</i> sp.	after
<i>Oligoneuron rigidum</i>	Asteraceae	<i>Aster</i> type	after
<i>Symphotrichum sericeum</i>	Asteraceae	<i>Aster</i> type	after
<i>Symphotrichum oolentangiense</i>	Asteraceae	<i>Aster</i> type	after
<i>Solidago speciosa</i>	Asteraceae	<i>Rudbeckia</i> type	after