

A survey and historical comparison of the Megachilidae (Insecta: Hymenoptera) of Itasca  
State Park, Minnesota

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## **Abstract**

The University of Minnesota Insect Collection holds a rich collection of bees from Itasca State Park, Minnesota, in 1937 and 1938. This collection formed the historical baseline data for comparison with a new survey conducted from 2011-2013. Bees were collected with timed net surveys and trap nests at eight different sites within the park. Megachilidae were the focal family for the current study, due to their importance as commercial pollinators and their unique nesting habits. Species richness and diversity of Megachilidae in the new survey were both significantly lower than that of the historical collection, and remained lower (but not significantly) when species accumulation curves were extrapolated to estimate the true species richness. Eleven species in the historical collection were not rediscovered, while three species not previously collected in Itasca State Park were found in 2011-13. Some possible explanations for this apparent decline are discussed.

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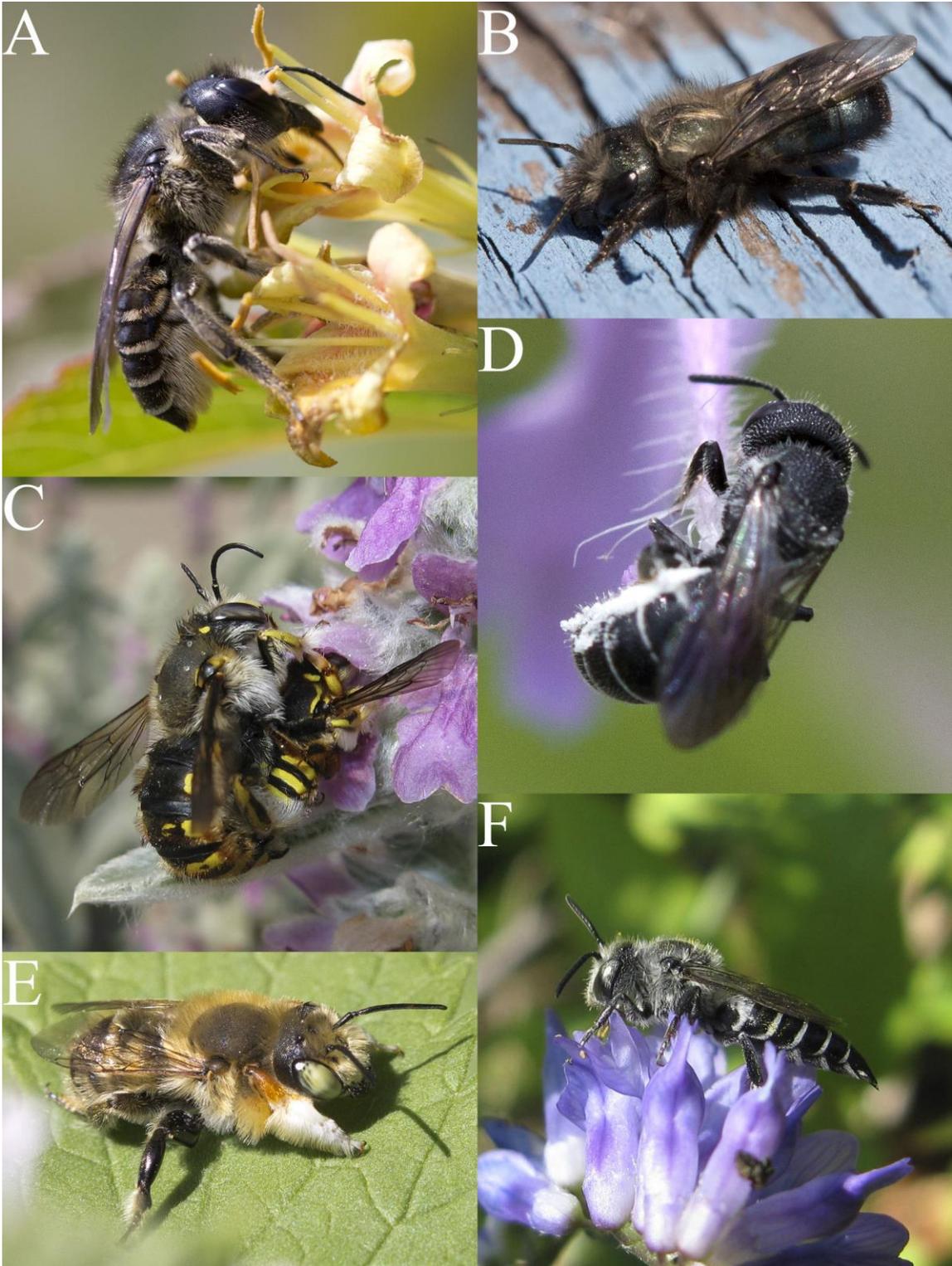
## Chapter 1

### Literature Review

#### *Natural history of Megachilidae*

According to a recent study by Danforth et al. (2006), Megachilidae is one of the more primitive bee families. Together with the Apidae, they form a monophyletic group called the “long-tongued bees” for their commonly elongated mouthparts, a group which may be sister to all other bees. Megachilidae is distinguished from Apidae and other bees by several easily seen, definitive characters: with a few Palearctic exceptions, all megachilids have two submarginal cells in the forewing and, except for cleptoparasitic genera, pollen-carrying hairs (scopa) on the metasomal sterna. Other bee families more commonly have three submarginal cells (although some genera can have two) and scopa on the hind legs, never on the metasoma. As a more subjective character, megachilids usually have large, powerful mandibles and, consequently, a bigger head than most other bees (Fig. 1).

There are slightly more than 4,000 described species of Megachilidae worldwide and 600 in the United States, making it the third-largest of seven recognized bee families (Ascher and Pickering 2012). All of these species are solitary, although some will nest gregariously (Cane et al. 1996; Eickwort 1975; Hefetz and Tengo 1992; Pitts-Singer and Cane 2011). A generalized, univoltine solitary bee life cycle begins when adult bees emerge from the nest in spring or summer. Mating occurs soon after emergence, followed by nesting. Once a suitable nesting place is found, the female bee constructs a



**Figure 1** Diversity in Megachilidae. A) Female *Megachile inermis* Provancher, showing metasomal scopa and large jaws typical of Megachilidae. B) Female *Osmia lignaria* Say, a commercial orchard pollinator. C) European wool carder bees, *Anthidium manicatum* L. D) Female *Heriades* sp., one of the smallest megachilids. E) Male *M. latimanus* Say with dilated, pale forelegs typical of *Megachile* males. F) Female *Coelioxys* sp., a cleptoparasite.

number of separate cells (usually in a linear series), each provisioned with a mass of pollen moistened with nectar, upon which she lays one egg. The nesting period lasts from one to two months. Over the remainder of the year, the larvae in the nest eat their pollen provisions and grow until winter, at which point they enter diapause. Bees that fly in the spring typically complete their development over the summer and diapause as dormant adults, while bees that fly in the summer diapause as advanced larvae (called prepupae) and complete their development the following year. The bees emerge at roughly the same time every year. Depending on the species and local climate, some bees may be bivoltine.

Among bees, there is much variation within the basic pattern of nesting behaviors. This is especially true of Megachilidae, where the greatest diversity in nesting sites and nest construction materials exists. Solitary bee nesting can be broadly divided into two categories: ground-nesting bees dig a burrow in soil, and cavity-nesting bees use aboveground tunnels, either finding existing tunnels (such as those left by wood-boring beetles) or excavating their own. Ground-nesting is the primitive state for bees (Litman et al. 2011), and probably the most common in the world bee fauna. Extrapolating from known nesting biologies, about 64% of non-parasitic bees are thought to be ground-nesting. In contrast, only about 17% of Megachilidae are ground-nesting (Cane and Neff 2011). Of the 36% of all bees that are cavity-nesting, almost half are Megachilidae (calculated from Cane and Neff 2011).

Megachilidae are distinct from other bees, even other cavity-nesting Apidae and Colletidae, in the incorporation of foreign material into the nest structure. Where other

bees use a glandular secretion to line the nest and protect it from moisture and disease (Hefetz 1987), most Megachilidae collect a wide variety of materials from the environment to use for this purpose (Fig. 2). These materials can include mud, resin, sand or gravel, wood chips, plant fibers, leaf pulp (Cane et al. 2007), and/or flower petals (Rozen et al. 2010) in the large, diverse genus *Osmia* alone. Leafcutter bees in the genus *Megachile* may also use large, intact pieces of cut leaves, and the primitive Lithurgini use no lining at all (Rust et al. 2004). Equally diverse are the substrates in which megachilid bees build their nests. Some are ground-nesting; these bees usually dig shallow horizontal tunnels a few centimeters below the surface, in contrast to the usually deep nests of other ground-nesting bees (Cane and Neff 2011). Aboveground cavity-nesting megachilids commonly nest in wood or hollow plant stems, and less commonly in rock crevices, abandoned nests of other Hymenoptera, snail shells, plant galls (Cane et al. 2007), old, dried dung pats (Cane 2012), or active termite nests (Messer 1984).



**Figure 2** Nesting diversity in Megachilidae. A) *Osmia lignaria* nest with dried mud cell partitions in wood block. B) *Osmia tersula* Cockerell nest with chewed leaf pulp cell partitions in bamboo reed. C) *Hoplitis albifrons* Kirby nest with chewed leaf pulp and loose gravel cell partitions in bamboo reed. D) *Heriades carinata* Cresson nest with hardened resin cell partitions in wood block. E) *Megachile relativa* Cresson nest with cells enclosed in cut leaf fragments, in bamboo reed. F) *Megachile pugnata* Say nest with chewed leaf pulp and dried mud cell partitions.

### *Value of Megachilidae as pollinators*

As honey bees are increasingly embattled with pests, disease, and the stress of moving cross-country to pollinate almonds, the need for additional, alternative pollinators that can ease the burden on honey bees is greater than ever before (Allen-Wardell et al. 1998). Megachilids, with their great diversity of nesting habits, emergence times, and floral hosts, seem ideally suited to the task.

Excluding social bees, there are more species of Megachilidae currently managed for commercial crop pollination than any other bee family. Although ground-nesting bees can be successfully reared in large numbers and used for crop pollination (Cane 2008), this is much easier to accomplish with aboveground cavity-nesting bees such as most Megachilidae. Wood- and stem-nesting bees will readily adopt man-made structures, which can be easily moved, opened, cleaned, stocked with purchased bees, and re-used from year to year. These structures can be further tailored to attract specific pollinators of interest. Wood blocks containing only holes of 7-8 mm diameter, for instance, are ideal for nesting *Osmia lignaria* (Tepedino and Torchio 1989; Torchio 1982), while *Megachile rotundata* Fabricius is more successful in holes of 5-7 mm diameter (Gerber and Klostermeyer 1972). A brief overview of managed megachilid pollinators follows.

The alfalfa leafcutter bee, *Megachile rotundata* (reviewed in Pitts-Singer and Cane 2011), was the first solitary bee intensively managed for commercial pollination, starting around the 1970s. Prior to the discovery and development of this bee, alfalfa pollination was dependent on honey bees, which can pollinate the crop but are not very efficient. Alfalfa pollination requires “tripping” the stamens in the flower, which forcefully strike

the potential pollinator to disperse pollen. Honey bees try to avoid this mechanism, but alfalfa leafcutters are far less careful, greatly increasing their pollination efficiency. Owing to this behavior, alfalfa leafcutters may be responsible for up to 2/3 of world alfalfa seed production, in spite of their lower total populations and shorter flight periods (Pitts-Singer 2008).

Bees in the genus *Osmia* make up the rest of the Megachilidae managed as pollinators. The native blue orchard bee, *Osmia lignaria*, is an early spring bee that pollinates apples, pears (Torchio 1985), cherries (Bosch et al. 2006), and almonds (Torchio 1981) with greater efficiency than honey bees. Their effectiveness is due in part to the bees' tolerance of cool spring temperatures and precipitation, allowing them to forage while honey bees stay in the hive, potentially missing days of crop bloom (Bosch et al. 2006). *Osmia lignaria* is probably the second most intensively managed solitary bee (after *M. rotundata*) and is used in orchards across the United States and Canada. *Osmia cornuta* Latreille and *O. cornifrons* Radoszkowski are similarly managed in Europe and Japan, respectively (reviewed in Bosch and Kemp 2002), and have also been introduced into the United States, although the native *O. lignaria* is still a better pollinator there (Abel et al. 2003; Torchio and Asensio 1985). *Osmia californica* Cresson and *O. aglaia* Sandhouse are promising species being developed as managed pollinators on the West Coast of the United States.

### *Bees in decline*

Much recent attention is directed at declines in honey bees, but they are not the only bees struggling. Bumble bees are especially well-studied, and the declines of several once-

common species are well documented. Colla and Packer (2008) found significant decreases in seven bumble bee species across the eastern United States and Canada when compared with previous surveys in the same locations, and an increase in only four species. The subgenus *Bombus* seems the most affected, including *Bombus affinis*, *B. terricola*, their social parasite *B. (Psithyrus) ashtoni*, and *B. occidentalis*. *Bombus franklini* may already be extinct (Berenbaum et al. 2007). Grixti et al. (2009) found reduced geographic distributions of four species in Illinois when compared with museum collections, and the complete absence of another four. Most recently, Cameron et al. (2011) surveyed sites across the entire United States and found significant declines in abundance and distribution of four target species (*B. affinis*, *B. terricola*, *B. occidentalis*, and *B. pensylvanicus*) while their four co-occurring reference species remained unchanged, based on extensive museum records. They also found increased levels of infection by the gut parasite *Nosema bombi* and reduced genetic diversity in declining species. The situation is even worse in Europe, with as many as three species already extinct in Britain and four in continental Europe, and many more suffering significant range reductions over the last century (Goulson et al. 2008; Kosior et al. 2007; Williams 1982). Dupont et al. (2011), using detailed records of bumble bees visiting red clover fields in Funen, Denmark from 1930-34, documented declines not only in species diversity but also in absolute abundance of long-tongued species. Long-tongued bumble bees are thought to be more vulnerable to the effects of habitat loss due to shorter flight distances and more limited flower preferences.

In contrast, comparative studies using historical records of solitary bees are relatively sparse and the overall picture is less clear. The earliest such study was by Marlin and

LaBerge (2001), who collected bees on 24 plant species around Carlinville, Illinois from 1970-72. This survey was compared to earlier work by Charles Robertson in the same area from 1884-1916. Most species found by Robertson were recollected by Marlin and LaBerge; of those that were not found, many were specialists on plants that were not sampled by Marlin and LaBerge due to time restrictions. The two collections had a fairly high degree of similarity, leading the authors to conclude that the native bee fauna was stable and could remain intact despite increased agricultural and urban development. However, a few formerly common species were absent from the 1970-72 collection, and in closing the authors suggested that a third survey of Carlinville be made.

Grixti and Packer (2006) surveyed solitary bees in a 1.2-hectare field in Ontario, Canada from 2002-03, and compared their results with a 1968-69 survey in the same field. Contrary to expectations, they found a significant *increase* in species richness, diversity, and evenness over the 34-year period. However, similarity between the two collections was very low, suggesting a high amount of species turnover. The authors attributed these findings to ecological succession and diversification in the plant community, and possibly range expansion by bee species spreading northward due to global warming.

These two studies suggest a generally resilient population of solitary bees, but a survey of bees visiting *Andira inermis* trees near Liberia, Costa Rica from 1972-2004 paints a different picture (Frankie et al. 2009). The researchers reported a drop from about 70 species in 1972 down to 31 species in 2004. Megachilidae were especially adversely affected, falling from 34 species in 1972 to less than ten from 1996-2004, with the remaining species also less abundant. Urban expansion and destruction of wooded areas

important to cavity-nesting bees were undoubtedly the causes of these declines (Frankie et al. 2009).

Most recently, Burkle et al. (2013) revisited Carlinville, Illinois in 2009 and 2010, with a focus on plant-pollinator interactions that occur from March through May. They observed phenology and bee visitation of 26 spring-blooming woodland forbs that were studied by Robertson in the 1800s. All 26 plants were found, but only 54 bee species were re-collected of the 109 found by Robertson, and only 125 of 532 (24%) plant-pollinator interactions remained intact, though this was somewhat mitigated by 121 new interactions. Specialist bees, cleptoparasites, cavity-nesting bees (Megachilidae), and bees with historically weak plant interactions were especially prone to extirpation. (A weak plant-pollinator interaction is one with short phenological overlap between bee flight and flower bloom.) Alarmingly, they also found that many of the surviving interactions are significantly weaker than they were in Robertson's day. Average peak bee activity was 11 days earlier while peak bloom was only 9.5 days earlier, and average bee flight times were 22.5 days shorter while bloom times were 8 days shorter, creating greater phenological mismatch. Pollinator redundancy and fidelity also decreased, at least on *Claytonia virginica*. The authors conclude that while this plant-pollinator interaction network is flexible, it is weakened by habitat loss and phenological changes, and highly vulnerable to further stress. This is in sharp contrast to the findings of Marlin and LaBerge (2001) in 1970-72. Burkle et al. compared bee species richness on *C. virginica* and found no difference from the 1800s to the 1970s, but it fell by over half from the 1970s to 2009-10, paralleling agricultural intensification and loss of woodland habitat.

A similar situation exists in Europe. Tanács et al. (2009) compared results from five different surveys in alfalfa fields of Hungary, spanning the years 1954-2007. A sharp decline in some *Eucera* and *Tetralonia* species (Apidae: Anthophorinae) was observed between 1956 and 1967, and these species persisted in low numbers up to 2007, due perhaps to the advent of intensive pesticide use, cultivation of large alfalfa monocultures, and the resulting removal of nesting sites and weeds these generalist bees would normally use to supplement their diet. This was mirrored by an increase in alfalfa-specialist bees such as *Melitta leporina*, and later by bumble bees, though it is not known why bumble bee abundance should increase (Tanács et al. 2009).

Banaszak et al. (2003) conducted three surveys 10 years apart in six different habitat types of western Poland, and found fairly stable bee communities despite the influence of agricultural expansion. Natural plant succession at one site caused a significant decline in bee species diversity and density as flowering plants were replaced by trees and shrubs. But the opposite scenario also occurred when some trees were removed from a shelterbelt, and bee diversity increased as flowering plants moved in. Although there was no general trend of decline across all bees, three bumble bee species significantly declined over the 20-year study period, and three solitary bees increased.

Finally, Patiny et al. (2009) report that the once-common European leafcutter bee *Megachile parietina* Geoffroy has suffered significant range reductions compared to its known historical distribution. It would seem from these studies that declines of solitary bees are a real issue of concern, yet are unpredictable and may be locally restricted. Particular groups or species of concern should be identified by comparing declines

between studies in different regions. The current study seeks to investigate bee species richness in a novel, protected park area.

## Chapter 2

### The Megachilidae of Itasca State Park

#### Introduction

Bees in decline have been a major topic of concern in recent years, beginning with *The Forgotten Pollinators* (Buchmann and Nabhan 1996), and becoming a media sensation when the honey bee Colony Collapse Disorder was discovered in 2006. Although the term “CCD” only applies to honey bees, wild bees are also suffering losses when compared with historical data. This has been well-studied in bumble bees, with particular species of concern identified (Berenbaum et al. 2007; Cameron et al. 2011; Colla and Packer 2008; Goulson et al. 2008; Grixti et al. 2009; Kosior et al. 2007; Williams 1982). Trends are not so consistent for the remaining wild bees. Some studies documented clear species declines (Burkle et al. 2013; Frankie et al. 2009), some found little change or a blend of declines and increases (Banaszak et al. 2003; Marlin and LaBerge 2001; Tanács et al. 2009), and at least one documented an increase in bee species richness and diversity (Grixti and Packer 2006).

More research is needed to confirm wild bee declines, and determine what the primary factors precipitating those declines are and which species or groups should be considered of particular concern. A substantial historical collection of bees from Itasca State Park, Minnesota, a protected pine forest and wetland area since 1891, provided an opportunity to resurvey the site and compare bee fauna across time. The family Megachilidae was the focus of this study, although other bees were collected and will be analyzed in a future

publication. Megachilidae were selected because of their importance as managed pollinators (Bosch and Kemp 2002; Pitts-Singer and Cane 2011) and their possibly greater sensitivity to habitat changes (Frankie et al. 2009; Grixti and Packer 2006).

### *Itasca State Park*

The University of Minnesota has a long history of collecting at Itasca State Park, making this an ideal location at which to study changes in bee populations. Itasca State Park covers about 132 square kilometers in northern Minnesota, primarily within southern Clearwater County but touching northern Becker and Hubbard Counties. It is important to distinguish Itasca State Park from Itasca County, which is actually located over 60 kilometers to the east. The park is heavily forested with pine and aspen, and also contains numerous lakes and wetlands. Bee collecting for the present study focused on roadsides, paths, and clearings, where flowers were most abundant.

The University of Minnesota Insect Collection contains at least 1,394 bees from the park, including 289 Megachilidae, from 1911 to 1986. For unknown reasons, most of this collecting took place in the early years, and steadily dropped off after about 1940, even though the University continues to maintain the Itasca Biological Station and Laboratories and holds summer session classes there to this day.

The years 1937 and 1938 represent a peak in bee collecting, coinciding with a time when three of Clarence Mickel's graduate students (H.R. Dodge, A.E. Pritchard, and H.E. Milliron) were with him while he was teaching a summer course in Field Zoology. 698 bees, including 170 Megachilidae, were collected during those two years. A majority of

these bees (64%) were collected by Mickel and his graduate students; Milliron was especially prolific, accounting for just over 50% of the 1937-38 bees. The other bees were collected by Mickel's Field Zoology students, comprising 59 known individuals over both years.

Although there are no class syllabi available for this Field Zoology course (only a brief mention in the 1937-38 University of Minnesota Bulletin, available on the UMN Digital Conservancy), it seems likely that Mickel assigned an insect collection for his class, and the bees (along with other insects) were collected to fulfill that requirement. Milliron was at the park while studying methods of rearing a local caddisfly and its ichneumonid parasitoid, and indicated that he did some collecting via sweeping vegetation while searching for the parasitoid (Mickel and Milliron 1939). It is unlikely that all the bees were incidentally collected during this search, but it does give an important clue to the methods Milliron used. Later in his career, Milliron published several papers on bumble bees, but clearly his interest in bees started long before.

### *Project objectives*

The purpose of this project was twofold. First, to conduct a survey of Itasca State Park, Minnesota, and assess current species richness of the megachilid bees. And second, to compare results with bees in the University of Minnesota Insect Collection, collected in the same location from 1937-38. It is through historical comparisons such as this that changes in species composition can be detected, and if necessary, conservation practices developed.

## Materials and Methods

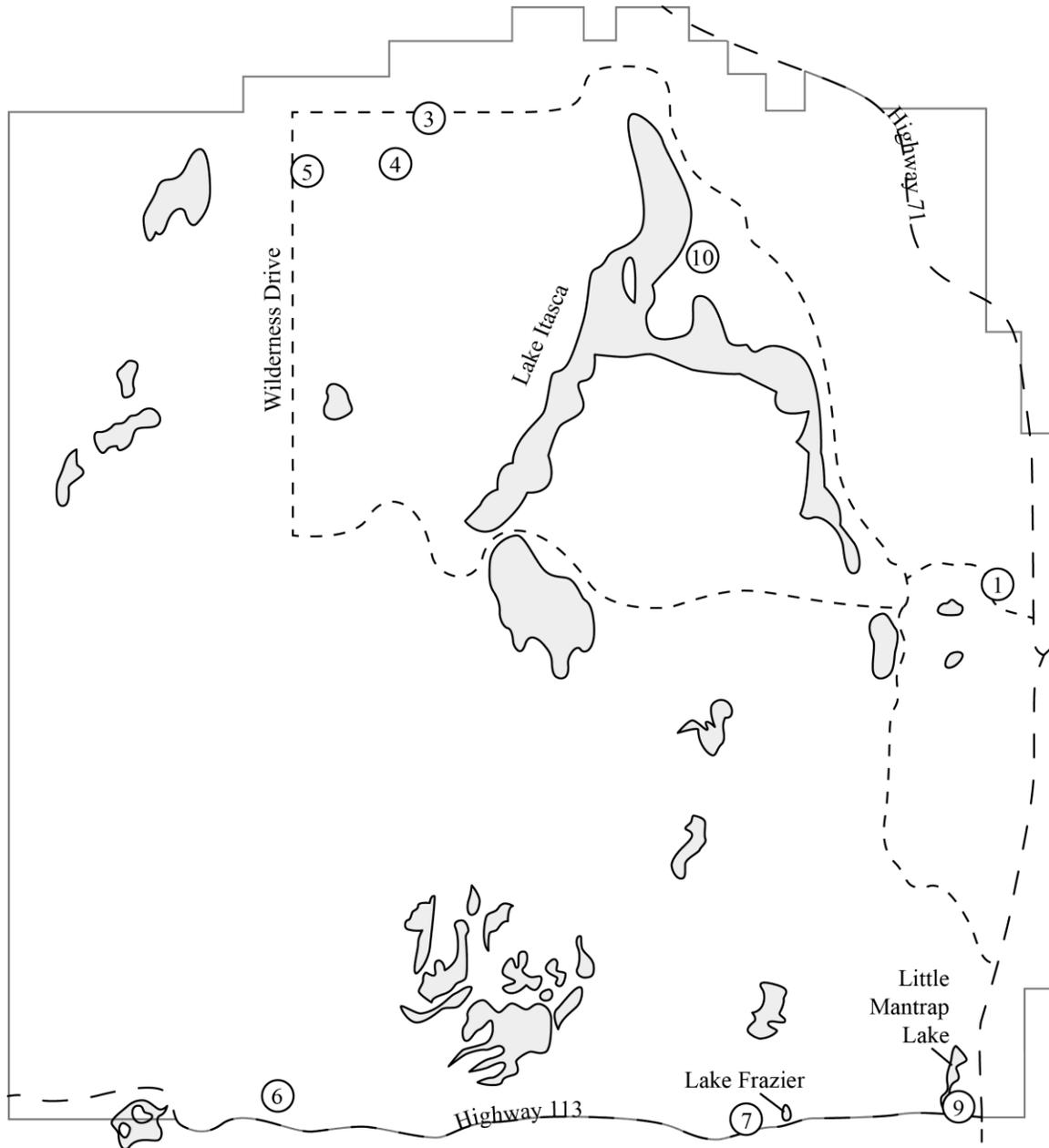
### *Study sites*

In 2010, an initial trap nest trial was conducted on the southern edge of the University of Minnesota Biological Station and Laboratories (UMBSL) grounds. A cleared strip of land, about 600 m long, was chosen for study because it receives ample direct sunlight, contains abundant floral resources, and has several large patches of bare, exposed soil, all conditions favorable to bees. *Trifolium* spp., *Erigeron* spp., *Berteroa incana*, and *Melilotus officinalis* were the most common flowering plants in this area. The site suffers major disturbance when it is mowed in late June to control plant growth, destroying many of the flowers, but it is mostly recovered by mid-July.

In preparation for the 2011 field season, I examined Google Earth satellite images of Itasca State Park to locate clearings where flowers and bees would likely be found. Seven study sites throughout the park were found and deemed suitable for trap nesting and/or net collecting in addition to the 2010 UMBSL site, which is henceforth designated as site 10 (Fig. 3). Sites 2 and 8 were unsuitable and were not sampled. Sites suitable for nets were larger and contained more flowers than trap nest-only sites. The study sites, eight in total (three net and trap nest sites, two net-only, and three trap nest-only), represented a wide range of the habitat conditions found in Itasca State Park.

Site 1, the most densely forested location, was on a service road directly adjacent to a small lake, a short distance from the eastern park boundary. It was chosen for the early

spring-blooming willows next to the lake; later in the spring, *Trillium grandiflorum* and other wildflowers bloom along the overgrown road.



**Figure 3** Selected study sites in Itasca State Park. Roads (dotted lines) and park borders (gray lines) are approximate. GPS coordinates are as follows: 1) 47°11.491'N, 95°9.045'W 3) 47°14.282'N, 95°14.145'W 4) 47°14.004'N, 95°14.433'W 5) 47°13.967'N, 95°15.210'W 6) 47°8.330'N, 95°15.311'W 7) 47°8.244'N, 95°11.227'W 9) 47°8.330'N, 95°9.348'W 10) 47°13.509'N, 95°11.553'W

Site 4 was in a large (>5000 m<sup>2</sup>), dry forest clearing alongside another overgrown service road north and west of Lake Itasca. *Trifolium* spp., *Fragaria* spp., and *Achillea millefolium* dominated along the road. The east end of the clearing was mostly tall ferns, but the west end had only low vegetation, including *Vaccinium* spp., *Rubus* (*Rubus*) spp., and *Cirsium discolor* among many other flowers. Sites 3 and 5 were to the east and west of site 4, respectively, in smaller clearings along the same path, with similar vegetation.

Site 6 was a roughly 0.36 km<sup>2</sup> expanse of rolling hills covered in grass and young pines, interspersed with small ponds, near the southwestern corner of the park. According to old maps at UMBSL, the site used to be a farm, perhaps as recently as the 1950s (Jon Ross, personal communication). It is now in the process of being restored to pine forest, but at the moment remains a mostly open meadow dominated by *Solidago* spp., *Campanula rotundifolia*, and *Leucanthemum vulgare*.

Site 7 was just west of Lake Frazier, near the middle of the southern edge of the park, along a forested trail used for snowmobiles in the winter and along the side of Highway 113. *Rubus* and *Fragaria* were extremely abundant in the forested area, while *Melilotus officinalis* was most common along the sunny roadside. Old stone foundations and the presence of ornamental lilac bushes and irises indicated that a homestead once existed here.

Site 9 was in the southeastern corner of the park near Little Mantrap Lake, including part of the same snowmobile trail as site 7, a small, dry clearing where the trail starts and ends, and some roadsides along Highway 113. *Ranunculus acris* was very common in

the clearing. *Agastache foeniculum* and *Centaurea stoebe* grew near or among the trees, and *Melilotus officinalis* once again dominated the roadside.

### *Trap nests*

In 2010, six trap nests were set up at roughly 100 meter intervals along the clearing of site 10. In 2011, the two most successful nests of the previous year (those with the most bees nesting inside) were left in place, and the other four plus one extra were moved one each to sites 1, 3, 5, 6, and 7. The same sites were used in 2012, except the nest at site 1 was moved to site 9, and two nests were set up at site 6 and only one at 10. This was done based on observed usage rates of the nests in 2011; the nests were moved where they might have the greatest chance of success. No trap nests were set up in 2013.

Trap nests were made and housed in shelters based on the observation block design of Hallett (2001), but scaled to 3/5 the given dimensions to hold 18 blocks each instead of 50 (Fig. 4). The fronts of nest blocks were painted solid blue or black initially, but after several unfinished nest constructions in adjacent tunnels were seen at the end of 2010, I concluded there was not enough visual contrast, causing the bees to mistakenly enter the wrong tunnels. In 2011 and 2012, the fronts of nest blocks were painted with a series of random



**Figure 4** Observation block trap nest with bamboo bundle.

shapes in white, yellow, blue, or black to help distinguish tunnel entrances. Shelter boxes were painted with a few broad blue stripes to increase long-distance visibility to bees. The shelters were attached to 5-foot (1.5 m) metal garden stakes pounded into the ground, holding the shelters about 4 feet (1.2 m) above the surface. The stakes were regularly smeared with a thin layer of petroleum jelly and the immediate area cleared of tall vegetation to discourage ants and spiders from climbing up. When possible, the shelters were placed in dry ground with sparse vegetation, oriented to face east or southeast, with trees to the west to provide shade in the afternoon.

In 2011 and 2012, bundles of bamboo were also attached to the top of each shelter box (Fig. 4). Bamboo of 0.5" (1.27 cm) average outer diameter was cut into 12-22 cm lengths and held in 6" (15.24 cm) diameter plastic pipe segments, wide enough to fit 50 to 60 bamboo sticks inside. The pipe served as a shelter and was secured to the wooden shelter box with steel wire.

Nests were set up on-site in April and retrieved in September or October, when the bees had finished nesting. Over the winter, cocoons and prepupae were removed from the nests, put in individual gelatin capsules, labeled (Fig. 5), and stored at 4° C until spring, at which time they were kept at outdoor temperatures until emergence. Bees were collected as they emerged. Photographs taken of the undisturbed nests, combined with the individually labeled capsules, allowed accurate tracking of a specimen's original position and nest construction, which aided in identification.



**Figure 5** Labeling system for trap nest bees. Each block or reed is assigned a number. Each tunnel in a block is assigned a letter A-H, (bamboo is assigned a lowercase ‘b’) and each cell is numbered in order of construction. Labeled bees can be matched with nest photos to assist in identification. Letters ran in reverse order in 2012.

### *Net surveys*

Net collecting was performed at sites 4, 6, 7, 9, and 10 in 2011 and 2012, and at 1, 3, 4, 5, 6, 7, and 10 in 2013. Different sites were sampled in 2013 based on bloom. Site 9, for instance, has very little blooming in the spring but is very rich in summer, while site 1 is the opposite.

In 2011, seven two-day collecting trips were made every 2-3 weeks, during which each site was sampled twice, once early in the day (loosely defined as 10:00 to 1:00) and once later (1:00 to 5:00). The dates of these trips were May 25-26, June 6-7, June 25-26, July 16-17, August 8-9, August 30-31, and September 17-18.

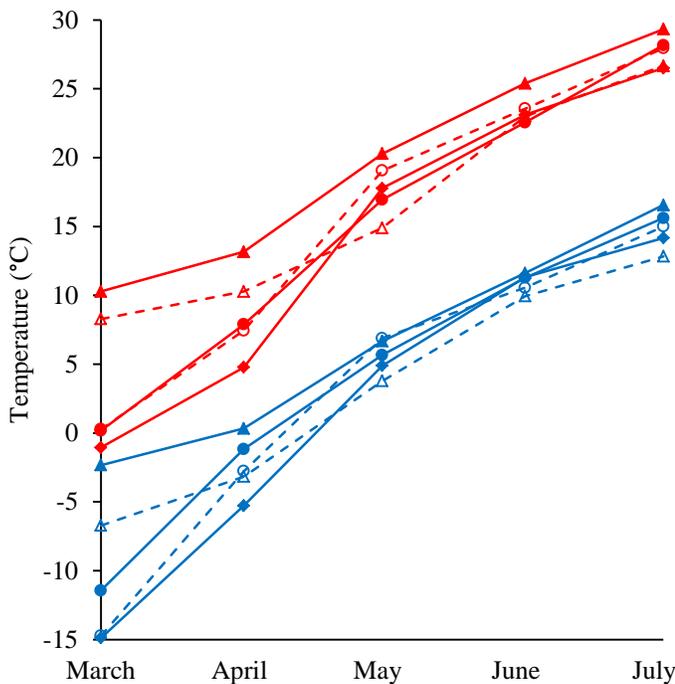
Each sample was timed at 15 minutes of sweeping flowers for foraging bees. Upon arriving at the site, I and one or two other collectors spread out in search of flowers in bloom. When a patch of flowers was encountered, the timer started and the collector

walked through, sweeping the flowers with broad, quick strokes of the net as he or she moved. The timer was stopped and the net checked for bees if a bee was seen to be captured, if a different flower species was encountered, or at regular intervals if neither of these things occurred. Most captured bees were put in plastic vials, separated by the flower on which they were collected, and euthanized via freezing, to be pinned later. Bees that are easily identifiable on sight (for example, *Osmia lignaria*) were recorded and released, after being marked with a spot of nail polish on the thorax to avoid recapture. The timer was also stopped while moving between flowers, so the sample reflects only the diversity of bees present on flowers, not flower density. Collectors continued moving from flower to flower until they had a combined collecting effort of 15 minutes (with three collectors, this equated to 5 minutes per person). Care was taken not to sweep the same flower more than once in the same sample if enough other flowers were available.

Weather conditions proved to be an unpredictable, sometimes ruinous factor on the 2011 collecting trips, especially late in the season, and the number of Megachilidae captured was unsatisfactory. To mitigate this problem, as well as focus more collecting effort in June and July (when Mickel's class was held), the collecting schedule was revised for 2012. I lived on-site at the UMN Biological Station and Laboratories from May 30 to August 5. Except for the week of June 10-16, which was cool and rainy, and July 15-21, I performed 15 net samples per week. Net collecting protocol was the same as it was in 2011, except the time per sample was reduced to 10 minutes since I was working alone. A 10-minute sample with one collector working typically took between 45 and 90 minutes including handling and walking time, depending on flower density and the number of bees found. Sites were sampled evenly so that at no time was one site much

more heavily sampled than the others, or too heavily skewed towards early or late samples.

It was my original intention to collect only in 2011 and 2012, to correspond with the two years of museum specimens with which I would compare data. However, while beginning data analysis, I noticed that the species richness of my collection was much lower than it was historically, and that many of the species missing in my collection were early spring-flying bees such as *Osmia*. The spring of 2012 was exceptionally warm



**Figure 6** Average monthly high (red) and low (blue) temperatures in Park Rapids, MN, about 15 km south of Itasca State Park. Filled diamonds = 2013, filled triangles = 2012, filled circles = 2011, open triangles = 1938, open circles = 1937. Note that 2012 was much warmer than any other year, and 2013 was cooler. 1938 also had an exceptionally warm spring, but experienced a four-day cold snap in May which pulled the average temperature down (data not shown). Source: NOAA National Climatic Data Center.

(Fig. 6), raising the possibility that these species were missing not because they did not exist, but because their flight period had already ended by the time I started collecting.

Therefore, I performed three more weeks of net collecting from May 26 to June 15 of 2013. The spring of 2013 was exceptionally cold (Fig. 6), allowing me to collect at

the same calendar time as previous years, yet much earlier phenologically. Methods were the same as in 2012, except that the time per sample was reduced to 5 minutes. This was done to allow coverage of more sites in a single day, since there were often fewer flowers blooming per site than is typical for summer. If enough flowers were available, then two consecutive samples were performed at the same site, effectively generating a 10-minute sample. Sites were still sampled evenly, however, based on the number of 5-minute samples taken.

### *Specimen processing*

All bees collected were pinned and labeled with date and approximate time of collection, GPS coordinates of the study site, and the plant they were collected on. They were identified to species using the keys in Mitchell (1962), Sandhouse (1939), and on DiscoverLife (<http://www.discoverlife.org>). Terry Griswold and Molly Rightmyer assisted in the identification of some particularly difficult specimens. All specimens will be accessioned in the University of Minnesota Insect Collection.

### *Statistical analysis*

EstimateS (Colwell 2013) was used to calculate Fisher's log series alpha statistic for species richness, and the exponential Shannon and inverse Simpson indices for species diversity. Fisher's alpha was chosen because it is a pure richness measure with no evenness component, so it is insensitive to collector bias (a condition where common species may be ignored once several individuals have been captured, artificially increasing the relative abundance of rare species) (Magurran 1988). With so much of

Mickel and Milliron's actual collection methods left up to hints and speculation, bias cannot be ruled out as a confounding factor. Fisher's alpha is also insensitive to small sample sizes (Magurran 1988), an important consideration when dealing with Megachilidae alone, which is one of the less well-represented bee families in this collection with only 170 individuals. Chi-squared tests were performed to verify that the data fit the log series distribution, following methods in Magurran (1988). The exponential Shannon and inverse Simpson indices were chosen as standard measures of diversity, including an evenness component, on the recommendation of Colwell (personal communication). The Shannon index is more affected by differences in species richness, while the Simpson index is more affected by evenness, and is more sensitive to bias and small sample sizes.

Data were loaded into EstimateS as sample-based, with species in rows and days of collection as samples in columns. To obtain standard deviations of the richness and diversity indices, they were computed 100 times, randomizing samples with replacement for each run. It should be noted that randomizing with replacement naturally produces datasets with lower species richness and diversity than the full dataset, as some samples will be selected more than once and others not at all. However, general trends are preserved. *P*-values were obtained by running *t*-tests in R statistical software.

EstimateS was also used to generate species accumulation curves for both datasets. A species accumulation curve shows the rate of discovery of new species as a function of collecting effort. Neither curve visibly reached an asymptote, suggesting that additional collecting would have revealed more species. For this reason, the curves were

extrapolated to 150 samples, slightly less than triple the reference sample size, to allow estimation of the total species richness, including undiscovered species. Colwell (2013) does not recommend extrapolation beyond this, as the variance increases greatly. The curves were generated separately from the diversity indices, without randomization, based on recommendations in the EstimateS User's Guide and personal communication with Colwell.

## Results

### *Net surveys*

Net collecting in 2011-13 produced a collection comparable to that of 1937-38. Twenty-one Megachilidae were collected in 2011, 143 in 2012, and 25 in 2013, for a total of 189 bees, compared with 170 from 1937-38. Although the 2011-13 collection was somewhat

Species	1937-1938	2011-2013	Species	1937-1938	2011-2013
<i>Ashmeadiella buconis</i>	1	0	<i>Megachile melanophaea</i>	2	5
<i>Coelioxys alternata</i>	1	1	<i>Megachile montivaga</i>	2	0
<i>Coelioxys funeraria</i>	1	0	<i>Megachile pugnata</i>	3	13
<i>Coelioxys modesta</i>	0	1	<i>Megachile relativa</i>	26	52
<i>Coelioxys moesta</i>	1	1	<i>Osmia albiventris</i>	0	2
<i>Coelioxys rufitarsis</i>	2	0	<i>Osmia atriventris</i>	23	14
<i>Heriades carinata</i>	2	23	<i>Osmia bucephala</i>	3	3
<i>Heriades variolosa</i>	1	11	<i>Osmia collinsiae</i>	5	0
<i>Hoplitis albifrons</i>	3	4	<i>Osmia conjuncta</i>	2	0
<i>Hoplitis pilosifrons</i>	5	1	<i>Osmia distincta</i>	7	0
<i>Hoplitis producta</i>	3	3	<i>Osmia lignaria</i>	0	12
<i>Hoplitis spoliata</i>	4	2	<i>Osmia proxima</i>	17	1
<i>Hoplitis truncata</i>	0	2	<i>Osmia simillima</i>	8	7
<i>Megachile campanulae</i>	2	4	<i>Osmia tersula</i>	3	6
<i>Megachile frigida</i>	9	0	<i>Osmia virga</i>	4	0
<i>Megachile gemula</i>	1	3	<i>Stelis lateralis</i>	2	0
<i>Megachile inermis</i>	11	18	Total species	30	23
<i>Megachile latimanus</i>	16	0	Total individuals	170	189

**Table 1** Species counts of Megachilidae in the 1937-38 collection and the 2011-13 collection. Eleven species are unique to 1937-38, and four are unique to 2011-13 (but see Results).

larger in terms of individuals, they were closer when the data were converted to sample-based: bees were collected on 53 days in 2011-13, and 51 days in 1937-38.

23 species were found in 2011-13 and 30 in 1937-38. Eleven species in the 1937-38 collection were not found in 2011-13, and four species not present in the 1937-38 collection were found in 2011-13. Of these four species, three (*Coelioxys modesta* Smith, *Osmia albiventris* Cresson, and *O. lignaria*) were new species not previously collected from Itasca State Park; the other one (*Hoplitis truncata* Cresson) is in the University of Minnesota Insect Collection from Itasca State Park, only not from 1937 or 1938. Two additional species (*Coelioxys porterae* Cockerell and *C. sodalis* Cresson) are in the University of Minnesota Insect Collection from Itasca State Park, but are not present in either the 1937-38 or 2011-13 collections. The collections are summarized in Table 1.

A

Class	Individuals upper boundary	Species observed	Species expected	$\chi^2$	$p$
1	2.5	13	14.6365	0.183	
2	4.5	7	5.0164	0.7844	
3	8.5	4	4.5959	0.0773	
4	16.5	3	3.4152	0.0505	
5	32.5	3	1.7902	0.8176	
		30	29.4542	1.9127	0.7518

B

Class	Individuals upper boundary	Species observed	Species expected	$\chi^2$	$p$
1	2.5	8	9.8179	0.3366	
2	4.5	5	3.5432	0.599	
3	8.5	3	3.4806	0.0664	
4	16.5	4	2.9677	0.3591	
5	32.5	2	2.0307	0.0005	
6	64.5	1	0.9371	0.0042	
		23	22.7771	1.3657	0.928

**Table 2** Chi-squared tests to verify goodness of fit with the log series. Under this distribution, there are expected to be many rare species with only one or two individuals in the collection, and a few common species with many individuals. (A) 1937-38 collection, (B) 2011-13 collection.

### *Richness and diversity indices*

Neither dataset differed significantly from the species distribution expected of the log series (Table 2), allowing the use of Fisher's alpha as a meaningful measure of species richness. There were highly significant differences between 1937-38 and 2011-13 for all three indices examined (Table 3). In all cases, the 2011-13 collection had lower species richness and species diversity than the 1937-38 collection.

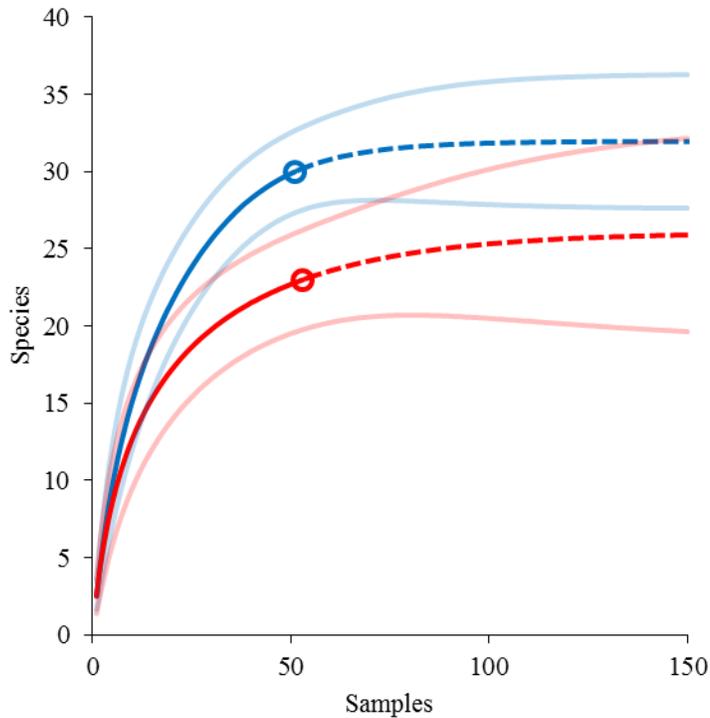
### *Species accumulation curves*

Neither species accumulation curves for 1937-38 or 2011-13 visibly reached an asymptote by the time all samples were included. This indicates that sampling was inadequate to capture the true species richness of Itasca State Park at the time of collection. However, after extrapolating the curves to 150 samples, both reached clear asymptotes. The asymptote, representing the estimated true species richness, in 1937-38 was about 32 species, and in 2011-13 it was about 26 species (Fig. 7).

The 2011-13 curve lies clearly below the 1937-38 curve at all points. The difference is obviously significant close to the reference sample, as the 95% confidence intervals do not overlap. However, the variance of these curves naturally increases with further extrapolation, causing the confidence intervals to expand and overlap at the far end of the

	Fisher's $\alpha$	exp Shannon	inv Simpson
1937-38	9.22 (1.2)	16.71 (1.18)	12.0 (1.02)
2011-13	5.88 (0.77)	11.67 (1.25)	7.98 (1.13)
<i>p</i>	<0.0001	<0.0001	<0.0001

**Table 3** Mean Fisher's alpha, exponential Shannon, and inverse Simpson indices from 100 randomized runs with replacement. Standard deviations are given in parentheses. *P*-values reflect significant differences between the 1937-38 and 2011-13 datasets for all indices examined.



**Figure 7** Species accumulation curves for the 1937-38 collection (blue line) and the 2011-13 collection (red line). 95% confidence intervals are shown in pale blue and pale red, respectively. Open circles mark the reference sample (51 and 53, respectively); extrapolation beyond this point is shown by dotted lines.

graph. Determining statistical significance of extrapolated species accumulation curves with overlapping confidence intervals is a difficult problem for which there is currently no formal method (Colwell et al. 2012). The most that can be said is that the estimated true species richness of 1937-38 is visibly lower than that of

2011-13.

### *Trap nests*

A total of 674 solitary bee cells were completed in 194 different trap nest tunnels over the years 2010-2012. Of these cells, 475 bees were successfully reared to the adult stage. Nine bee species were identified, of which eight were Megachilidae. *Osmia tersula* and *O. lignaria* were extremely abundant, making up 40.7% and 26.8% of all nests founded, respectively (40.2% and 41.7% of individual cells).

Only 26 bees were reared from the 2010 trap nests, all *O. tersula* (Table A1). This is most likely due to all six trap nests being set up at the same site, within about 450 meters of each other. When seven trap nests were set up at various sites throughout the park in 2011, there was a dramatic increase in both the number of nests founded and the number of bee species reared (Table A2). *Megachile pugnata* was very common that year, founding 36.9% of all 2011 nests (16.3% of individual cells). 2012 saw similar trends, only there was a dramatic drop in the abundance of *M. pugnata* despite the addition of a second nest at site 6, where they were most common in 2011 (Table A3). The cause of this drop is not known. There was also a very high rate of parasitism of *O. tersula* by *Sapyga martinii* Smith (Hymenoptera: Sapygidae) compared with previous years (47.4% total mortality vs. 17.7% and 38.1% in 2011 and 2010; most mortality of *O. tersula* was due to *S. martinii*).

No species were reared from the trap nests that were not detected in the net surveys. However, the abundance of *Osmia tersula* and *O. lignaria* in the trap nests does suggest that they are much more common in Itasca State Park than indicated by the net data.

## **Discussion**

The results of my collecting in 2011-13 all point to a decline in Megachilidae at Itasca State Park sometime in the last 75 years. All richness and diversity indices examined were lower in 2011-13 than in the past, with very high statistical significance. The species accumulation curves were also highly significantly different at the reference sample, and although formal analysis cannot be performed on the extrapolated true richness estimates, this difference might be maintained. The curves remain roughly

parallel, and the difference in species richness at the reference sample (30 vs. 23, or seven species) is not much less than the estimated true richness (32 vs. 26 species).

Of the eleven species in the 1937-38 collection that were missing in the 2011-13 collection, six (*Osmia collinsiae* Robertson, *O. conjuncta* Cresson, *O. distincta* Cresson, *O. virga* Sandhouse, *Stelis lateralis* Cresson, and *Megachile frigida* Smith) were collected early in the year (the first three weeks of June). The remaining five species are all rare, represented by just one or two individuals, with the notable exception of *Megachile latimanus*, represented by 16 individuals. Beyond simple presence and absence, one formerly common spring bee (*Osmia proxima* Cresson) was reduced from 17 individuals in 1937-38 to just one male found in 2011. Only *M. latimanus* experienced a drop in abundance as large as this.

This possible bias toward early species led me to suspect that they were missing not because they did not exist, but only because they were done flying by the time I began collecting in 2012, due to the early spring that year. However, collecting in the spring of 2013 failed to turn up any of the missing species, despite excellent phenological timing. Collecting in 2012 began just after the dandelions had finished blooming, while collecting in 2013 ended near this same point and began much earlier. This would indicate that the missing species are either truly missing, or less abundant than they used to be. Two of the missing early species (*O. conjuncta*, *S. lateralis*) were rare in 1937-38, but others should have been found if they were still common.

This apparent decline is troubling because Itasca State Park has been a protected area since it was established in 1891. The park's immediate surroundings, while not

protected, are not heavily developed either. The usual factors blamed for bee declines—agricultural intensification, pesticide misuse, and habitat loss—cannot have played major roles in this case. What, then, could be responsible for a loss of species?

First, it should be noted that sampling artifacts cannot be completely ruled out. For instance, it is not known exactly where in the park Milliron and the others did their collecting, or on which plant species the bees were found. While I attempted to cover a large area of the park with my study sites, sampling every flower species in every accessible large clearing I found, it is possible that they collected in different areas or on different plants supporting different bee species. The western and central areas, in particular, were not sampled in 2011-13, mainly due to difficulty of access and lack of obvious clearings. Willows (*Salix* spp.) were also not sampled because they had finished blooming by the time collecting began, and various other wildflowers reported from the park (*Desmodium*, *Helianthus*, *Verbena*) were not found during the collecting period.

Collector bias is another possible confounding factor. The 1937-38 collection did not fit the log series distribution nearly as well as the 2011-13 collection, nor were certain common species (*Megachile relativa*) collected in nearly so great of numbers. This might be evidence of bias or simply that species evenness was higher in the past. If bias did exist, the actual number of bees found would be higher than the number retained in the collection. With a larger true sample size, more rare species would be present than expected for the collection, which would explain many of the missing species in a future collection of comparable size. However, it is hard to believe that Clarence Mickel's Field Zoology students would be able to distinguish rare and common bee species in the field.

Mickel himself and H.E. Milliron, as workers in Hymenoptera, might have known the difference, but at least half of the collection should be relatively free of bias.

Assuming that my coverage of the park in 2011-13 was comprehensive and unbiased, however, some possible explanations can be offered. Banaszak et al. (2003) documented a major decline in bee species richness at one of their study sites, which they attributed to ecological succession. The site, a xerothermic grassland which was once subject to plowing and grazing, has been protected since the establishment of Wielkopolska National Park in 1957. This allowed the protected grassland to be colonized by woody plants, decreasing the number of flowering herbs available for bees. Grixti and Packer (2006) also attributed changes in the bee species community in Ontario to ecological succession and global warming. While they documented an increase in species richness, rather than a decline, many of the bee species present at their study site 34 years ago were not rediscovered. Species richness only increased because of an influx of new species.

Over the last 75 years, certain areas of Itasca State Park have also undergone ecological succession. Aerial photos from 1939 were obtained from the Minnesota Department of Natural Resources and compared with 2011 Google Earth satellite images to evaluate changes in tree cover. Five sites have obvious differences. Site 6, an old farm, was probably cropland in 1939, and is now grassland dotted with young pines. Site 7 had what might have been a homestead in a 4,300 m<sup>2</sup> clearing, which is now almost completely forested. And site 10, the UMN Biological Station and Laboratories, appears to be much more densely forested now than it was in 1939. The last two sites, 4 and 9, were completely forested in 1939 and must have been cleared sometime later. The fact

that site 10 was much more open in the past is especially significant, as this is likely where Milliron and Mickel did a large part of their collecting.

This situation—the establishment of a protected area, and the conversion of formerly disturbed grassland to young forest—bears many similarities to that of Banaszak et al. (2003). Even the time frame is similar, if the farm at site 6 was abandoned sometime in the 1950's. It should be noted, however, that none of the other sites studied by Banaszak et al. (2003) experienced declines such as this. If the decline in species richness at Itasca State Park is due to the protection of formerly disturbed areas, the lost species may persist in the surrounding, unprotected area. Gixti and Packer (2006) also found many new species to offset declines of others. Only three new species were discovered in Itasca State Park, but perhaps with time, more would appear and eventually replace the original Megachilidae species community.

Another possible explanation is the appearance of one of the new species: *Osmia lignaria*. This species was extremely common in 2011-13, especially in the trap nests, but was not detected in 1937-38, even though Itasca State Park is within its native range. It is possible that the park was once part of a gap in *O. lignaria*'s range, or that *O. lignaria* was less common in the past and was simply missed. Either way, the likely reason for its appearance is the development of the species as a commercial pollinator (see Bosch and Kemp 2002). *Osmia lignaria* nests and cocoons are bought and sold across the United States and Canada for orchard pollination, which would greatly accelerate range expansion. If the species was not originally present in Itasca State Park, its introduction could conceivably have adverse effects on bees with similar biology.

Tepedino and Torchio (1994) observed frequent nest usurpation among *O. lignaria* females in a greenhouse. As many as 25% of all nests started were at some point usurped, and 75% of all nesting females usurped at least one nest. The propensity to usurp nests was significantly correlated with body weight and size, with larger bees more likely to usurp nests. Usurpation occurred irrespective of nearby, unoccupied tunnels. Although the study was conducted in a greenhouse with *O. lignaria* the only species present, it is reasonable to assume that wild populations might usurp the nests of other species with similar nesting habits. And because *O. lignaria* is one of the largest *Osmia* species in Itasca State Park, it could successfully usurp and defend the nests of most other species (the one possible exception being *Osmia bucephala* Cresson). Unfortunately, the nesting habits of most of the missing *Osmia* species are not known, so it cannot be determined if competition between these species and *O. lignaria* could exist. Meanwhile, some species still present (*O. albiventris*, *O. bucephala*) are known to have similar nesting habits to *O. lignaria* (Cane et al. 2007), yet no evidence of nest usurpation of other species by *O. lignaria* was seen in the trap nests. This hypothesis also does not explain the disappearance of summer bees such as *Megachile frigida* and *M. latimanus*. Regardless, with the growing use and spread of *O. lignaria* as a commercial pollinator, it is a topic worth further investigation.

Perhaps a more likely scenario involves pathogen spillover from commercial to wild populations. This phenomenon has been demonstrated in bumble bees, and is one of the main suspected reasons for their decline (Meeus et al. 2011). Managed *O. lignaria* populations are known to be affected by chalkbrood fungus (Youssef et al. 1985) and hairy-fingered mites (Krombein 1962), besides various cleptoparasites (Torchio 1989;

Torchio and Bosch 1992). Chalkbrood and cleptoparasites were usually scarce in my trap nests (the main exception being the *Sapyga martinii* on *Osmia tersula* in 2012), but hairy-fingered mites (*Chaetodactylus* sp.) were quite common among *O. lignaria* in all years. The mites were not seen on any other species in the trap nests, but two males of *Hoplitis albifrons*, each carrying several *Chaetodactylus* sp., were collected in 2011. It would be most informative if the nests of more species could be found and parasite and pathogen loads could be evaluated.

All of this remains speculation, however; the causes of the decline of Megachilidae in Itasca State Park over the last 75 years are not truly known. In the near future, I plan to include other families of bees in this analysis; this may shed more light on possible causes. But it is a troubling problem if even bees in remote, protected areas can be affected by declines. Perhaps this is an important reminder that human activity can have far-reaching, indirect effects we may not even suspect.

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## Appendix A

### Trap Nest Data

Species	Site	Nest	♀	♂	N
<i>O. tersula</i>	10b	2D	0	1	1
<i>O. tersula</i>	10b	2F	5	0	6
<i>O. tersula</i>	10c	3C	0	0	1
<i>O. tersula</i>	10c	3D	0	0	1
<i>O. tersula</i>	10c	3E	0	0	2
<i>O. tersula</i>	10c	3F	3	0	7
<i>O. tersula</i>	10c	4B	2	1	3
<i>O. tersula</i>	10c	4C	0	0	2
<i>O. tersula</i>	10c	4E	7	0	8
<i>O. tersula</i>	10d	4F	4	0	6
<i>O. tersula</i>	10e	1C	0	1	2
<i>O. tersula</i>	10e	1D	0	1	1
<i>O. tersula</i>	10e	1E	0	1	2
<i>O. tersula</i>		Total	21	5	42

**Table A1** Bees completing development to adulthood in 2010 trap nests. See Fig. 3 for nest numbering diagram. N is the total number of completed cells in the nest, including those that did not complete development.

Species	Site	Nest	♀	♂	?	N	Species	Site	Nest	♀	♂	?	N
<i>H. albifrons</i>	7	11b	1	0	0	3	<i>O. lignaria</i>	3	7C	0	2	3	6
<i>H. albifrons</i>	7	20b	1	1	0	3	<i>O. lignaria</i>	3	8A	0	0	1	1
<i>H. albifrons</i>	7	22b	1	4	0	6	<i>O. lignaria</i>	3	10B	0	2	7	9
<i>H. albifrons</i>	7	24b	1	1	0	2	<i>O. lignaria</i>	3	11b	0	2	0	2
<i>H. albifrons</i>	7	40b	0	0	0	1	<i>O. lignaria</i>	5	1C	3	4	2	10
<i>M. pugnata</i>	5	3b	0	2	0	3	<i>O. lignaria</i>	5	1D	0	0	0	1
<i>C. alternata</i>	5	3b	1	0	0	-	<i>O. lignaria</i>	5	2A	2	0	1	5
<i>M. pugnata</i>	5	4b	1	0	0	1	<i>O. lignaria</i>	5	2C	0	0	3	3
<i>M. pugnata</i>	5	5b	0	1	0	1	<i>O. lignaria</i>	5	2D	1	3	3	7
<i>M. pugnata</i>	5	7b	0	1	0	1	<i>O. lignaria</i>	5	3A	1	0	4	6
<i>M. pugnata</i>	5	9b	1	1	0	2	<i>O. lignaria</i>	5	3F	1	2	2	6
<i>M. pugnata</i>	5	10b	0	1	0	1	<i>O. lignaria</i>	5	4E	0	1	4	7
<i>M. pugnata</i>	5	12b	0	0	0	1	<i>O. lignaria</i>	5	5A	0	0	1	1
<i>C. alternata</i>	5	12b	0	1	0	-	<i>O. lignaria</i>	5	6A	2	3	1	6
<i>M. pugnata</i>	5	13b	0	0	0	1	<i>O. lignaria</i>	5	6F	0	0	3	3
<i>M. pugnata</i>	5	14b	0	1	0	2	<i>O. lignaria</i>	5	8A	1	0	3	4
<i>M. pugnata</i>	6a	1b	1	0	0	1	<i>O. lignaria</i>	6a	2A	1	2	6	13
<i>M. pugnata</i>	6a	2b	0	0	0	1	<i>O. lignaria</i>	6a	2D	0	1	1	4
<i>M. pugnata</i>	6a	3b	0	2	0	2	<i>O. lignaria</i>	6a	7D	1	1	2	4
<i>M. pugnata</i>	6a	5b	0	1	0	1	<i>O. lignaria</i>	6a	7E	0	2	3	5
<i>M. pugnata</i>	6a	6b	1	1	0	2	<i>O. tersula</i>	3	7b	0	3	0	3
<i>M. pugnata</i>	6a	7b	1	0	0	1	<i>O. tersula</i>	3	10b	1	4	0	5
<i>M. pugnata</i>	6a	8b	0	0	0	1	<i>O. tersula</i>	3	12b	0	1	0	1
<i>M. pugnata</i>	6a	10b	2	0	0	2	<i>O. tersula</i>	5	7F	0	2	0	3
<i>M. pugnata</i>	6a	11b	0	0	0	1	<i>O. tersula</i>	5	6b	2	1	0	3
<i>M. pugnata</i>	6a	12b	0	2	0	2	<i>O. tersula</i>	5	8b	1	0	0	1
<i>M. pugnata</i>	6a	13b	2	0	0	2	<i>O. tersula</i>	5	11b	0	0	0	6
<i>M. pugnata</i>	6a	14b	0	1	0	1	<i>O. tersula</i>	5	15b	5	1	0	6
<i>M. pugnata</i>	6a	15b	0	1	0	1	<i>O. tersula</i>	6a	9b	0	1	0	1
<i>M. pugnata</i>	6a	17b	0	0	0	1	<i>O. tersula</i>	6a	29b	0	5	0	5
<i>M. pugnata</i>	6a	18b	1	0	0	1	<i>O. tersula</i>	6a	37b	0	1	0	1
<i>M. pugnata</i>	6a	19b	0	1	0	2	<i>O. tersula</i>	7	1B	0	3	0	5
<i>M. pugnata</i>	6a	20b	0	1	0	1	<i>O. tersula</i>	7	1C	3	2	0	6
<i>M. pugnata</i>	6a	21b	2	0	0	2	<i>O. tersula</i>	7	1E	1	1	0	2
<i>M. pugnata</i>	6a	22b	0	1	0	1	<i>O. tersula</i>	7	1b	0	1	0	1
<i>M. pugnata</i>	6a	23b	0	1	0	1	<i>O. tersula</i>	7	2b	0	1	0	1
<i>M. pugnata</i>	6a	24b	0	2	0	2	<i>O. tersula</i>	7	3b	1	1	0	2
<i>M. pugnata</i>	6a	25b	1	0	0	3	<i>O. tersula</i>	7	4b	3	0	0	3
<i>M. pugnata</i>	6a	26b	1	0	0	1	<i>O. tersula</i>	7	5b	3	1	0	4

<i>M. pugnata</i>	6a	27b	0	0	0	1	<i>O. tersula</i>	7	6b	1	1	0	2
<i>M. pugnata</i>	6a	28b	0	0	0	1	<i>O. tersula</i>	7	8b	1	2	0	5
<i>M. pugnata</i>	6a	31b	0	1	0	1	<i>O. tersula</i>	7	9b	3	0	0	4
<i>M. pugnata</i>	6a	32b	1	0	0	1	<i>O. tersula</i>	7	10b	1	0	0	1
<i>M. pugnata</i>	6a	33b	0	1	0	2	<i>O. tersula</i>	7	13b	2	5	0	8
<i>M. pugnata</i>	6a	36b	0	1	0	3	<i>O. tersula</i>	7	14b	1	2	0	4
<i>M. pugnata</i>	6a	38b	0	1	0	1	<i>O. tersula</i>	7	15b	0	8	0	9
<i>M. pugnata</i>	6a	39b	0	0	0	1	<i>O. tersula</i>	7	17b	1	4	0	5
<i>M. pugnata</i>	7	1F	1	2	0	3	<i>O. tersula</i>	7	18b	0	1	0	1
<i>M. relativa</i>	5	2b	0	2	0	2	<i>O. tersula</i>	7	21b	1	0	0	1
<i>M. relativa</i>	6a	4F	2	2	0	10	<i>O. tersula</i>	7	25b	2	1	0	3
<i>M. relativa</i>	6a	7F	0	1	0	1	<i>O. tersula</i>	7	26b	2	0	0	2
<i>O. lignaria</i>	1	3D	0	5	2	7	<i>O. tersula</i>	7	27b	2	3	0	5
<i>O. lignaria</i>	1	3F	0	4	3	10	<i>O. tersula</i>	7	28b	0	0	0	4
<i>O. lignaria</i>	3	5B	1	1	7	11	<i>H. albifrons</i>	Total	4	6	0	15	
<i>O. lignaria</i>	3	5E	0	1	4	10	<i>M. pugnata</i>	Total	16	27	0	60	
<i>O. lignaria</i>	3	6D	0	2	2	5	<i>C. alternata</i>	Total	1	1	0	-	
<i>O. lignaria</i>	3	7A	1	4	6	11	<i>M. relativa</i>	Total	2	5	0	13	
<i>O. lignaria</i>	3	7B	0	1	2	9	<i>O. lignaria</i>	Total	15	26	76	166	
							<i>O. tersula</i>	Total	37	56	0	113	

**Table A2** Bees completing development to adulthood in 2011 trap nests. See Fig. 3 for nest numbering diagram. ? are bees that escaped their gelatin capsules before the sex could be determined. N is the total number of completed cells in the nest, including those that did not complete development.

Species	Site	Nest	♀	♂	?	N	Species	Site	Nest	♀	♂	?	N
<i>He. carinata</i>	6a	1B	2	0	0	3	<i>O. tersula</i>	3	4b	1	1	0	6
<i>He. carinata</i>	6a	1C	1	0	0	1	<i>O. tersula</i>	3	6b	4	0	0	7
<i>Ho. albifrons</i>	3	7b	0	2	0	3	<i>O. tersula</i>	3	5b	0	0	0	2
<i>Hylaeus</i> sp.	5	13b	0	0	0	3	<i>O. tersula</i>	3	8b	0	1	0	3
<i>M. pugnata</i>	6a	1b	1	1	0	2	<i>O. tersula</i>	3	9b	0	2	0	2
<i>M. pugnata</i>	6a	2b	0	0	0	1	<i>O. tersula</i>	5	3b	3	3	0	7
<i>M. pugnata</i>	6a	3b	0	0	0	1	<i>O. tersula</i>	5	5b	2	1	0	8
<i>M. relativa</i>	5	14b	0	4	0	5	<i>O. tersula</i>	5	8b	5	3	0	8
<i>M. relativa</i>	5	15b	0	0	0	1	<i>O. tersula</i>	5	12b	5	0	0	8
<i>M. relativa</i>	5	17b	0	3	0	4	<i>O. tersula</i>	5	16b	0	0	0	2
<i>M. relativa</i>	5	20b	0	1	0	3	<i>O. tersula</i>	7	10b	0	1	0	1
<i>O. albiventris</i>	5	2A	2	1	0	7	<i>O. tersula</i>	7	12b	0	1	0	2
<i>O. lignaria</i>	3	3D	1	0	0	2	<i>O. tersula</i>	7	14b	4	2	0	6
<i>O. lignaria</i>	3	4A	2	0	0	2	<i>O. tersula</i>	7	18b	0	1	0	1
<i>O. lignaria</i>	3	4D	1	0	0	2	<i>O. tersula</i>	7	20b	1	1	0	2
<i>O. lignaria</i>	3	5B	1	0	0	1	<i>O. tersula</i>	7	22b	0	0	0	1
<i>O. lignaria</i>	3	5C	0	0	0	1	<i>O. tersula</i>	7	24b	0	0	0	1
<i>O. lignaria</i>	3	9D	1	0	0	1	<i>O. tersula</i>	9	6A	0	1	0	4
<i>O. lignaria</i>	3	10B	1	0	0	3	<i>O. tersula</i>	9	2b	1	0	0	6
<i>O. lignaria</i>	5	4A	1	0	1	4	<i>O. tersula</i>	9	3b	2	0	0	5
<i>O. lignaria</i>	5	4D	2	0	0	2	<i>O. tersula</i>	9	5b	0	0	0	1
<i>O. lignaria</i>	5	6A	1	0	0	1	<i>O. tersula</i>	9	6b	3	0	0	4
<i>O. lignaria</i>	7	3D	2	0	0	2	<i>O. tersula</i>	9	8b	0	1	0	3
<i>O. lignaria</i>	7	4A	2	2	0	5	<i>O. tersula</i>	9	9b	0	0	0	3
<i>O. lignaria</i>	7	4F	3	2	1	6	<i>O. tersula</i>	9	12b	0	2	0	5
<i>O. lignaria</i>	7	6B	3	1	0	4	<i>O. tersula</i>	9	15b	1	0	0	2
<i>O. lignaria</i>	7	6C	4	4	0	11	<i>O. tersula</i>	10h	7b	0	2	0	5
<i>O. lignaria</i>	7	6D	1	0	0	1	<i>O. tersula</i>	10h	8b	2	0	0	3
<i>O. lignaria</i>	7	6F	5	6	0	12	<i>O. tersula</i>	10h	9b	0	0	0	3
<i>O. lignaria</i>	9	2A	1	0	0	1	<i>O. tersula</i>	10h	15b	0	1	0	2
<i>O. lignaria</i>	9	3A	3	0	0	4	<i>O. tersula</i>	10h	22b	1	0	0	1
<i>O. lignaria</i>	9	4B	8	6	0	14	<i>He. carinata</i>	Total		3	0	0	4
<i>O. lignaria</i>	9	7A	4	4	1	10	<i>Ho. albifrons</i>	Total		0	2	0	3
<i>O. lignaria</i>	9	7B	3	4	0	7	<i>Hylaeus</i> sp.	Total		0	0	0	3
<i>O. lignaria</i>	9	7D	0	1	0	2	<i>M. pugnata</i>	Total		1	1	0	4
<i>O. lignaria</i>	9	7E	0	5	0	6	<i>M. relativa</i>	Total		0	8	0	13
<i>O. lignaria</i>	9	7F	3	7	0	11	<i>O. albiventris</i>	Total		2	1	0	7
<i>O. tersula</i>	3	1b	0	1	0	1	<i>O. lignaria</i>	Total		53	42	3	115
<i>O. tersula</i>	3	2b	1	0	0	1	<i>O. tersula</i>	Total		36	25	0	116

**Table A3** Bees completing development to adulthood in 2012 trap nests. See Fig. 3 for nest numbering diagram. ? are bees that escaped their gelatin capsules before the sex could be determined. N is the total number of completed cells in the nest, including those that did not complete development.

## Appendix B

### Net Collection Data

Genus	Species	Sex	Site	Date	Time	Collected On
<i>Coelioxys</i>	<i>alternata</i>	female	4	7/16/12	12:20 PM	<i>Solidago</i>
<i>Coelioxys</i>	<i>modesta</i>	female	7	7/9/12	3:30 PM	<i>Melilotus officinalis</i>
<i>Coelioxys</i>	<i>moesta</i>	female	7	7/13/12	2:00 PM	<i>Melilotus officinalis</i>
<i>Heriades</i>	<i>carinata</i>	male	4	7/16/12	12:20 PM	<i>Melilotus officinalis</i>
<i>Heriades</i>	<i>carinata</i>	male	6	7/13/12	4:00 PM	<i>Melilotus officinalis</i>
<i>Heriades</i>	<i>carinata</i>	male	7	6/22/12	10:45 AM	<i>Rubus (Rubus)</i>
<i>Heriades</i>	<i>carinata</i>	female	7	6/30/12	3:45 PM	<i>Melilotus officinalis</i>
<i>Heriades</i>	<i>carinata</i>	female	7	7/2/12	12:20 PM	<i>Melilotus officinalis</i>
<i>Heriades</i>	<i>carinata</i>	female	7	7/2/12	12:20 PM	<i>Melilotus officinalis</i>
<i>Heriades</i>	<i>carinata</i>	male	7	7/2/12	12:20 PM	<i>Melilotus officinalis</i>
<i>Heriades</i>	<i>carinata</i>	female	7	7/3/12	4:20 PM	<i>Melilotus officinalis</i>
<i>Heriades</i>	<i>carinata</i>	female	7	7/3/12	4:20 PM	<i>Melilotus officinalis</i>
<i>Heriades</i>	<i>carinata</i>	female	7	7/4/12	12:20 PM	<i>Melilotus officinalis</i>
<i>Heriades</i>	<i>carinata</i>	female	7	7/5/12	2:00 PM	<i>Melilotus officinalis</i>
<i>Heriades</i>	<i>carinata</i>	female	7	7/5/12	2:00 PM	<i>Melilotus officinalis</i>
<i>Heriades</i>	<i>carinata</i>	female	7	7/7/12	12:20 PM	<i>Melilotus officinalis</i>
<i>Heriades</i>	<i>carinata</i>	female	7	7/7/12	12:20 PM	<i>Potentilla recta</i>
<i>Heriades</i>	<i>carinata</i>	female	7	7/9/12	3:30 PM	<i>Melilotus officinalis</i>
<i>Heriades</i>	<i>carinata</i>	female	7	7/9/12	3:30 PM	<i>Melilotus officinalis</i>
<i>Heriades</i>	<i>carinata</i>	female	7	7/13/12	2:00 PM	<i>Melilotus officinalis</i>
<i>Heriades</i>	<i>carinata</i>	female	7	7/13/12	2:00 PM	<i>Melilotus officinalis</i>
<i>Heriades</i>	<i>carinata</i>	female	9	7/16/11	3:20 PM	<i>Melilotus officinalis</i>
<i>Heriades</i>	<i>carinata</i>	female	9	7/27/12	11:50 AM	<i>Melilotus officinalis</i>
<i>Heriades</i>	<i>carinata</i>	female	10	7/10/12	10:45 AM	<i>Trifolium repens</i>
<i>Heriades</i>	<i>carinata</i>	female	10	7/12/12	4:00 PM	<i>Melilotus officinalis</i>
<i>Heriades</i>	<i>carinata</i>	female	10	8/2/12	12:30 PM	<i>Solidago</i>
<i>Heriades</i>	<i>variolosa</i>	female	4	7/17/11	12:45 PM	
<i>Heriades</i>	<i>variolosa</i>	female	4	6/29/12	2:40 PM	<i>Achillea millefolium</i>
<i>Heriades</i>	<i>variolosa</i>	male	4	7/1/12	3:00 PM	<i>Achillea millefolium</i>
<i>Heriades</i>	<i>variolosa</i>	male	4	7/1/12	3:00 PM	<i>Achillea millefolium</i>
<i>Heriades</i>	<i>variolosa</i>	male	4	7/11/12	2:20 PM	<i>Trifolium repens</i>
<i>Heriades</i>	<i>variolosa</i>	male	7	7/2/12	12:20 PM	<i>Solidago</i>
<i>Heriades</i>	<i>variolosa</i>	male	7	7/2/12	12:20 PM	<i>Rhus typhina</i>
<i>Heriades</i>	<i>variolosa</i>	male	7	7/4/12	12:20 PM	<i>Solidago</i>
<i>Heriades</i>	<i>variolosa</i>	male	7	7/4/12	12:20 PM	<i>Solidago</i>
<i>Heriades</i>	<i>variolosa</i>	female	7	7/5/12	2:00 PM	<i>Solidago</i>
<i>Heriades</i>	<i>variolosa</i>	female	7	7/7/12	12:20 PM	<i>Potentilla recta</i>
<i>Hoplitis</i>	<i>albifrons</i>	male	3	6/10/13	12:40 PM	<i>Taraxacum officinale</i>
<i>Hoplitis</i>	<i>albifrons</i>	male	4	6/10/13	2:00 PM	<i>Taraxacum officinale</i>
<i>Hoplitis</i>	<i>albifrons</i>	male	7	6/7/11	10:45 AM	<i>Convallaria majalis</i>
<i>Hoplitis</i>	<i>albifrons</i>	male	7	6/7/11	4:30 PM	<i>Taraxacum officinale</i>
<i>Hoplitis</i>	<i>pilosifrons</i>	male	4	6/6/11	3:20 PM	<i>Fragaria</i>
<i>Hoplitis</i>	<i>producta</i>	male	6	7/13/12	4:00 PM	<i>Geum aleppicum</i>
<i>Hoplitis</i>	<i>producta</i>	male	9	6/5/12	12:45 PM	<i>Rubus (Rubus)</i>

<i>Hoplitis</i>	<i>producta</i>	male	9	6/28/12	2:30 PM	<i>Trifolium repens</i>
<i>Hoplitis</i>	<i>spoliata</i>	female	6	7/11/12	12:15 PM	<i>Trifolium hybridum</i>
<i>Hoplitis</i>	<i>spoliata</i>	female	7	7/16/11	1:30 PM	<i>Centaurea stoebe</i>
<i>Hoplitis</i>	<i>truncata</i>	male	4	6/7/12	3:00 PM	<i>Rubus (Rubus)</i>
<i>Hoplitis</i>	<i>truncata</i>	male	6	6/6/12	1:20 PM	<i>Ranunculus acris</i>
<i>Megachile</i>	<i>campanulae</i>	male	4	7/5/12	10:20 AM	<i>Achillea millefolium</i>
<i>Megachile</i>	<i>campanulae</i>	female	4	7/25/12	3:20 PM	<i>Achillea millefolium</i>
<i>Megachile</i>	<i>campanulae</i>	male	6	7/13/12	4:00 PM	<i>Solidago</i>
<i>Megachile</i>	<i>campanulae</i>	female	9	7/16/11	4:00 PM	<i>Trifolium pratense</i>
<i>Megachile</i>	<i>gemula</i>	male	4	6/7/12	3:00 PM	<i>Vicia americana</i>
<i>Megachile</i>	<i>gemula</i>	female	4	6/27/12	12:30 PM	<i>Achillea millefolium</i>
<i>Megachile</i>	<i>gemula</i>	female	6	6/8/12	1:00 PM	<i>Leucanthemum vulgare</i>
<i>Megachile</i>	<i>inermis</i>	female	4	6/29/12	2:40 PM	<i>Achillea millefolium</i>
<i>Megachile</i>	<i>inermis</i>	male	4	7/1/12	3:00 PM	<i>Trifolium repens</i>
<i>Megachile</i>	<i>inermis</i>	male	4	7/4/12	10:10 AM	<i>Prunella vulgaris</i>
<i>Megachile</i>	<i>inermis</i>	female	4	7/9/12	11:00 AM	<i>Solidago</i>
<i>Megachile</i>	<i>inermis</i>	female	4	7/24/12	10:35 AM	<i>Cirsium discolor</i>
<i>Megachile</i>	<i>inermis</i>	female	4	7/29/12	11:15 AM	<i>Cirsium discolor</i>
<i>Megachile</i>	<i>inermis</i>	female	4	8/2/12	4:00 PM	<i>Cirsium discolor</i>
<i>Megachile</i>	<i>inermis</i>	female	6	8/8/11	3:00 PM	<i>Cirsium</i>
<i>Megachile</i>	<i>inermis</i>	female	6	7/7/12	10:30 AM	<i>Rhus glabra</i>
<i>Megachile</i>	<i>inermis</i>	male	6	7/10/12	2:00 PM	<i>Trifolium hybridum</i>
<i>Megachile</i>	<i>inermis</i>	female	6	8/3/12	12:15 PM	<i>Cirsium discolor</i>
<i>Megachile</i>	<i>inermis</i>	female	7	8/8/11	1:40 PM	<i>Cirsium</i>
<i>Megachile</i>	<i>inermis</i>	male	7	7/2/12	12:20 PM	<i>Melilotus officinalis</i>
<i>Megachile</i>	<i>inermis</i>	male	7	7/5/12	2:00 PM	<i>Melilotus officinalis</i>
<i>Megachile</i>	<i>inermis</i>	male	7	7/9/12	3:30 PM	<i>Trifolium hybridum</i>
<i>Megachile</i>	<i>inermis</i>	male	7	7/11/12	10:30 AM	<i>Trifolium hybridum</i>
<i>Megachile</i>	<i>inermis</i>	male	9	6/28/12	2:30 PM	<i>Achillea millefolium</i>
<i>Megachile</i>	<i>inermis</i>	male	9	7/13/12	12:25 PM	<i>Agastache foeniculum</i>
<i>Megachile</i>	<i>melanophaea</i>	female	4	6/27/12	12:30 PM	<i>Trifolium repens</i>
<i>Megachile</i>	<i>melanophaea</i>	male	6	6/15/12	11:45 AM	<i>Leucanthemum vulgare</i>
<i>Megachile</i>	<i>melanophaea</i>	male	6	6/25/12	11:00 AM	<i>Campanula rotundifolia</i>
<i>Megachile</i>	<i>melanophaea</i>	male	10	6/18/12	2:10 PM	<i>Melilotus officinalis</i>
<i>Megachile</i>	<i>melanophaea</i>	male	10	6/18/12	2:10 PM	<i>Melilotus officinalis</i>
<i>Megachile</i>	<i>pugnata</i>	male	4	6/29/12	2:40 PM	<i>Achillea millefolium</i>
<i>Megachile</i>	<i>pugnata</i>	female	4	7/1/12	3:00 PM	<i>Achillea millefolium</i>
<i>Megachile</i>	<i>pugnata</i>	male	4	7/1/12	3:00 PM	<i>Achillea millefolium</i>
<i>Megachile</i>	<i>pugnata</i>	male	4	7/4/12	10:10 AM	<i>Achillea millefolium</i>
<i>Megachile</i>	<i>pugnata</i>	male	4	7/4/12	10:10 AM	<i>Achillea millefolium</i>
<i>Megachile</i>	<i>pugnata</i>	female	4	7/5/12	10:20 AM	<i>Achillea millefolium</i>
<i>Megachile</i>	<i>pugnata</i>	female	4	7/9/12	11:00 AM	<i>Achillea millefolium</i>
<i>Megachile</i>	<i>pugnata</i>	female	4	7/29/12	11:15 AM	<i>Campanula rotundifolia</i>
<i>Megachile</i>	<i>pugnata</i>	male	7	7/2/12	12:20 PM	<i>Asclepias</i>
<i>Megachile</i>	<i>pugnata</i>	male	7	7/4/12	12:20 PM	<i>Rudbeckia hirta</i>
<i>Megachile</i>	<i>pugnata</i>	male	7	7/5/12	2:00 PM	<i>Rudbeckia hirta</i>
<i>Megachile</i>	<i>pugnata</i>	male	7	7/11/12	10:30 AM	<i>Melilotus officinalis</i>
<i>Megachile</i>	<i>pugnata</i>	female	7	7/27/12	1:20 PM	<i>Melilotus officinalis</i>
<i>Megachile</i>	<i>relativa</i>	male	4	7/17/11	12:45 PM	

<i>Megachile relativa</i>	female	4	8/31/11	5:00 PM	<i>Symphytotrichum</i>
<i>Megachile relativa</i>	female	4	7/1/12	3:00 PM	<i>Achillea millefolium</i>
<i>Megachile relativa</i>	male	4	7/4/12	10:10 AM	<i>Achillea millefolium</i>
<i>Megachile relativa</i>	female	4	7/4/12	10:10 AM	<i>Achillea millefolium</i>
<i>Megachile relativa</i>	male	4	7/5/12	10:20 AM	<i>Achillea millefolium</i>
<i>Megachile relativa</i>	female	4	7/5/12	10:20 AM	<i>Ranunculus acris</i>
<i>Megachile relativa</i>	female	4	7/11/12	2:20 PM	<i>Achillea millefolium</i>
<i>Megachile relativa</i>	female	4	7/16/12	12:20 PM	<i>Melilotus officinalis</i>
<i>Megachile relativa</i>	female	4	7/24/12	10:35 AM	<i>Solidago</i>
<i>Megachile relativa</i>	female	4	7/29/12	11:15 AM	<i>Solidago</i>
<i>Megachile relativa</i>	female	6	8/9/11	1:00 PM	<i>Solidago</i>
<i>Megachile relativa</i>	male	6	6/8/12	1:00 PM	<i>Leucanthemum vulgare</i>
<i>Megachile relativa</i>	male	6	6/21/12	3:45 PM	<i>Leucanthemum vulgare</i>
<i>Megachile relativa</i>	male	6	6/21/12	3:45 PM	<i>Ranunculus acris</i>
<i>Megachile relativa</i>	female	6	6/25/12	11:00 AM	<i>Leucanthemum vulgare</i>
<i>Megachile relativa</i>	female	6	7/7/12	10:30 AM	<i>Rhus glabra</i>
<i>Megachile relativa</i>	female	6	7/10/12	2:00 PM	<i>Solidago</i>
<i>Megachile relativa</i>	female	6	7/10/12	2:00 PM	<i>Solidago</i>
<i>Megachile relativa</i>	male	6	7/11/12	12:15 PM	<i>Achillea millefolium</i>
<i>Megachile relativa</i>	female	7	8/8/11	1:40 PM	<i>Solidago</i>
<i>Megachile relativa</i>	female	7	8/9/11	12:30 PM	<i>Solidago</i>
<i>Megachile relativa</i>	male	7	6/8/12	10:50 AM	<i>Rubus (Rubus)</i>
<i>Megachile relativa</i>	male	7	6/8/12	10:50 AM	<i>Rubus (Rubus)</i>
<i>Megachile relativa</i>	male	7	6/16/12	4:15 PM	<i>Rubus (Idaeobatus)</i>
<i>Megachile relativa</i>	male	7	6/22/12	10:45 AM	<i>Erigeron</i>
<i>Megachile relativa</i>	male	7	6/22/12	10:45 AM	<i>Rubus (Rubus)</i>
<i>Megachile relativa</i>	male	7	7/2/12	12:20 PM	<i>Melilotus officinalis</i>
<i>Megachile relativa</i>	male	7	7/2/12	12:20 PM	<i>Potentilla recta</i>
<i>Megachile relativa</i>	female	7	7/2/12	12:20 PM	<i>Melilotus officinalis</i>
<i>Megachile relativa</i>	male	7	7/3/12	4:20 PM	<i>Melilotus officinalis</i>
<i>Megachile relativa</i>	female	7	7/3/12	4:20 PM	<i>Melilotus officinalis</i>
<i>Megachile relativa</i>	female	7	7/7/12	12:20 PM	<i>Potentilla recta</i>
<i>Megachile relativa</i>	female	7	7/7/12	12:20 PM	<i>Ranunculus acris</i>
<i>Megachile relativa</i>	female	7	7/7/12	12:20 PM	<i>Ranunculus acris</i>
<i>Megachile relativa</i>	male	7	7/9/12	3:30 PM	<i>Solidago</i>
<i>Megachile relativa</i>	male	7	7/9/12	3:30 PM	<i>Melilotus officinalis</i>
<i>Megachile relativa</i>	female	7	7/9/12	3:30 PM	<i>Trifolium hybridum</i>
<i>Megachile relativa</i>	female	7	7/9/12	3:30 PM	<i>Melilotus officinalis</i>
<i>Megachile relativa</i>	male	7	7/11/12	10:30 AM	<i>Melilotus officinalis</i>
<i>Megachile relativa</i>	male	7	7/13/12	2:00 PM	<i>Trifolium repens</i>
<i>Megachile relativa</i>	female	7	7/13/12	2:00 PM	<i>Melilotus officinalis</i>
<i>Megachile relativa</i>	female	7	7/21/12	10:45 AM	<i>Melilotus officinalis</i>
<i>Megachile relativa</i>	female	7	7/21/12	10:45 AM	<i>Melilotus officinalis</i>
<i>Megachile relativa</i>	female	7	8/1/12	12:40 PM	<i>Symphytotrichum</i>
<i>Megachile relativa</i>	female	9	7/17/11	10:30 AM	<i>Campanula rotundifolia</i>
<i>Megachile relativa</i>	male	9	6/21/12	2:30 PM	<i>Berteroa incana</i>
<i>Megachile relativa</i>	male	9	7/5/12	12:30 PM	<i>Achillea millefolium</i>
<i>Megachile relativa</i>	female	9	7/10/12	12:30 PM	<i>Ranunculus acris</i>
<i>Megachile relativa</i>	male	9	7/28/12	2:30 PM	<i>Centaurea stoebe</i>

<i>Megachile</i>	<i>relativa</i>	female	10	6/18/12	2:10 PM	<i>Erigeron</i>
<i>Megachile</i>	<i>relativa</i>	female	10	7/7/12	4:00 PM	<i>Melilotus officinalis</i>
<i>Osmia</i>	<i>albiventris</i>	female	4	6/6/12	1:20 PM	<i>Rubus (Rubus)</i>
<i>Osmia</i>	<i>albiventris</i>	female	4	6/7/12	3:00 PM	<i>Rubus (Rubus)</i>
<i>Osmia</i>	<i>atriventris</i>	female	3	6/13/13	1:00 PM	<i>Fragaria</i>
<i>Osmia</i>	<i>atriventris</i>	female	4	7/4/12	10:10 AM	<i>Trifolium repens</i>
<i>Osmia</i>	<i>atriventris</i>	female	4	6/10/13	2:00 PM	<i>Taraxacum officinale</i>
<i>Osmia</i>	<i>atriventris</i>	male	5	6/8/13	4:30 PM	<i>Taraxacum officinale</i>
<i>Osmia</i>	<i>atriventris</i>	female	5	6/13/13	2:30 PM	<i>Fragaria</i>
<i>Osmia</i>	<i>atriventris</i>	female	5	6/13/13	2:30 PM	<i>Fragaria</i>
<i>Osmia</i>	<i>atriventris</i>	female	7	6/2/12	3:15 PM	<i>Rubus (Rubus)</i>
<i>Osmia</i>	<i>atriventris</i>	female	7	6/8/12	10:50 AM	<i>Rubus (Rubus)</i>
<i>Osmia</i>	<i>atriventris</i>	female	7	7/3/12	4:20 PM	<i>Trifolium hybridum</i>
<i>Osmia</i>	<i>atriventris</i>	female	7	7/7/12	12:20 PM	<i>Potentilla recta</i>
<i>Osmia</i>	<i>atriventris</i>	female	7	6/2/13	3:20 PM	<i>Taraxacum officinale</i>
<i>Osmia</i>	<i>atriventris</i>	male	7	6/13/13	4:15 PM	<i>Rubus</i>
<i>Osmia</i>	<i>atriventris</i>	female	10	5/25/11	3:00 PM	<i>Taraxacum officinale</i>
<i>Osmia</i>	<i>atriventris</i>	female	10	7/10/12	10:45 AM	<i>Trifolium repens</i>
<i>Osmia</i>	<i>bucephala</i>	female	4	6/6/11	3:20 PM	<i>Astragalus</i>
<i>Osmia</i>	<i>bucephala</i>	female	5	6/13/13	2:30 PM	<i>Fragaria</i>
<i>Osmia</i>	<i>bucephala</i>	female	7	6/8/12	10:50 AM	<i>Rubus (Rubus)</i>
<i>Osmia</i>	<i>lignaria</i>	female	1	6/11/13	3:30 PM	<i>Viola pubescens</i>
<i>Osmia</i>	<i>lignaria</i>	female	3	6/10/13	1:08 PM	<i>Taraxacum officinale</i>
<i>Osmia</i>	<i>lignaria</i>	female	3	6/13/13	1:30 PM	<i>Thalictrum dioicum</i>
<i>Osmia</i>	<i>lignaria</i>	female	3	6/13/13	1:50 PM	<i>Taraxacum officinale</i>
<i>Osmia</i>	<i>lignaria</i>	female	4	6/7/13	3:00 PM	<i>Taraxacum officinale</i>
<i>Osmia</i>	<i>lignaria</i>	female	4	6/7/13	3:00 PM	<i>Vaccinium</i>
<i>Osmia</i>	<i>lignaria</i>	female	4	6/13/13	12:00 PM	<i>Taraxacum officinale</i>
<i>Osmia</i>	<i>lignaria</i>	female	4	6/13/13	12:35 PM	<i>Vaccinium</i>
<i>Osmia</i>	<i>lignaria</i>	female	5	6/7/13	1:30 PM	<i>Taraxacum officinale</i>
<i>Osmia</i>	<i>lignaria</i>	female	10	6/6/11	2:00 PM	gathering mud
<i>Osmia</i>	<i>lignaria</i>	female	10	6/4/12	3:10 PM	<i>Trifolium repens</i>
<i>Osmia</i>	<i>lignaria</i>	female	10	6/7/13	4:45 PM	<i>Taraxacum officinale</i>
<i>Osmia</i>	<i>proxima</i>	male	4	6/6/11	3:20 PM	
<i>Osmia</i>	<i>simillima</i>	male	3	6/6/13	11:00 AM	<i>Taraxacum officinale</i>
<i>Osmia</i>	<i>simillima</i>	female	4	6/7/11	12:45 PM	
<i>Osmia</i>	<i>simillima</i>	female	4	6/13/13	11:30 AM	<i>Fragaria</i>
<i>Osmia</i>	<i>simillima</i>	male	5	6/13/13	2:30 PM	<i>Fragaria</i>
<i>Osmia</i>	<i>simillima</i>	female	6	6/25/12	11:00 AM	Lamiaceae
<i>Osmia</i>	<i>simillima</i>	female	10	6/18/12	2:10 PM	<i>Trifolium repens</i>
<i>Osmia</i>	<i>simillima</i>	female	10	6/24/12	12:00 PM	<i>Trifolium repens</i>
<i>Osmia</i>	<i>tersula</i>	female	4	6/7/11	12:45 PM	<i>Fragaria</i>
<i>Osmia</i>	<i>tersula</i>	female	4	6/7/13	3:00 PM	<i>Fragaria</i>
<i>Osmia</i>	<i>tersula</i>	female	6	6/10/13	4:10 PM	<i>Fragaria</i>
<i>Osmia</i>	<i>tersula</i>	female	7	6/2/12	3:15 PM	<i>Rubus (Rubus)</i>
<i>Osmia</i>	<i>tersula</i>	female	7	6/8/12	10:50 AM	<i>Rubus (Rubus)</i>
<i>Osmia</i>	<i>tersula</i>	female	7	6/16/12	4:15 PM	<i>Rubus (Rubus)</i>