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On the vertical distribution of bees in a temperate deciduous forest

MICHAEL D. ULYSHEN,[1] VILLU SOON[2] and JAMES L. HANULA[1] [1]USDA Forest Service, Southern Research Station, Athens, GA, USA and [2]Deparment of Zoology, Institute of Ecology and Earth Sciences, University of Tartu, Tartu, Estonia

Abstract. 1. Despite a growing interest in forest canopy biology, very few studies have examined the vertical distribution of forest bees. In this study, bees were sampled using 12 pairs of flight-intercept traps suspended in the canopy (≥15 m) and near the ground (0.5 m) in a bottomland hardwood forest in the southeastern United States.

2. In total, 6653 bees from 5 families and 71 species were captured. *Augochlora pura* (Say) (Halictidae), accounted for over 91% of all bees collected and was over 40 times more abundant on average in the canopy than near the ground.

3. Even after removing *A. pura* from the dataset, bee abundance, richness and Shannon's diversity were considerably higher in the canopy than near the ground.

4. According to both non-metric multidimensional scaling and analysis of similarities, the bee community in the canopy was distinct from that near the ground. Based on indicator species analysis, *A. pura*, *Lasioglossum imitatum* (Smith), *Lasioglossum versatum* sensu Mitch., and *Lasioglossum zephyrum* (Smith) were significantly associated with the canopy whereas *Andrena personata* Robertson and *Lasioglossum macoupinense* (Robertson) were significantly associated with the ground.

5. *Augochlora pura* was consistently more abundant in the canopy than near the ground throughout the season, but was more so in mid-to-late summer (i.e., June–September), a period coinciding with low floral resource availability. As a group, the remaining bee community exhibited a similar pattern.

6. We suspect that bees frequent the canopy, particularly during times of low nectar and pollen availability, to acquire non-floral resources such as honeydew and sap.

Key words. Arboreal, arthropods, biodiversity, bottomland hardwood forests, floodplains, insects, pollinators, sweat bees, vertical stratification, wetlands, window traps.

Introduction

Our current understanding of arthropod diversity and ecology near the forest floor, although incomplete, far exceeds what is known about life in the forest canopy. Only within the last few decades have concentrated efforts been made to study arthropods and other organisms in the crowns of forest trees. These studies suggest that while arthropods are generally equally or more diverse in the canopy than near the ground in tropical rainforests (e.g., Erwin, 1982; Intachat & Holloway, 2000; Stork & Grimbacher, 2006) the opposite pattern is more often observed in temperate deciduous forests (Nielsen, 1987; Preisser *et al.*, 1998; Le Corff & Marquis, 1999; Ulyshen & Hanula, 2007; Pucci, 2008; Hirao *et al.*, 2009). However, it is clear from several studies (e.g., Vance *et al.*, 2003, 2007; Ulyshen & Hanula, 2007; Pucci, 2008) that canopies of temperate deciduous forests support distinct faunas as well.

Few intensive efforts have been made to study the vertical distribution patterns of bees in forests of any type. In a comparison of bees at two heights (18–27 vs. 3–8 m) in a Panamanian rainforest, Roubik (1993) found that most species were equally or

Correspondence: Michael D. Ulyshen, USDA Forest Service, Southern Research Station, 320 Green Street, Athens, GA 30602, USA. E-mail: mulyshen@hotmail.com

more common near the ground than in the canopy and suggested that most bee species found in the canopy are more opportunistic than specialised. Similar studies have not been conducted in temperate deciduous forests but Sobek *et al.* (2009) found two of the three species of cavity-nesting bees collected in a German broadleaved forest to be more common in the canopy.

Most trees in temperate deciduous forests are wind-pollinated and only members of a few genera (e.g., *Acer*, *Prunus*, etc.) are pollinated by insects (Elton, 1966). Furthermore, almost all trees, regardless of pollination mechanism, and most understory plants (Heinrich, 1976; Schemske *et al.*, 1978), bloom early in the year before or during leaf expansion. With few exceptions (Kudo *et al.*, 2008), late-season flowering plants are confined to canopy gaps, forest edges and other disturbed areas receiving direct sunlight (Heinrich, 1976).

How forest-dwelling bees cope with these seasonal declines and changing distributions of floral resources remains largely unknown. Some bees may forage long distances when necessary, perhaps beyond the boundaries of the forest, to acquire nectar and pollen. Others may supplement their diets with non-floral resources (Elton, 1966) available nearby. For example, bees have long been known to feed on honeydew, sap and other sugar sources in the absence of flowers (e.g., Trelease, 1881; Burton, 1891; Santas, 1983; and references therein; Konrad *et al.*, 2009; and references therein). These resources are most readily available in the forest canopy, but information on the vertical distribution patterns of bees is lacking. In a recent study investigating the vertical distribution of beetles in a bottomland hardwood forest in the southeastern United States (Ulyshen & Hanula, 2007), a large number of bees were collected, providing an opportunity to better understand the spatial distribution patterns of this important fauna. Here, we compare the abundance, species richness, diversity, evenness and composition of bees collected in the canopy and near the ground in that study.

Methods

Sampling took place in Scull Shoals Experimental Forest, a mature bottomland hardwood forest within the Oconee National Forest in Oglethorpe County, Georgia (see Ulyshen & Hanula, 2007 for a map of the study area). The upper canopy was dominated by willow oak (*Quercus phellos* L.), water oak (*Q. nigra* L.), sweetgum (*Liquidambar styraciflua* L.), sycamore (*Platanus occidentalis* L.), loblolly pine (*Pinus taeda* L.), river birch (*Betula nigra* L.) and several less common species. Hop-hornbeam [*Ostrya virginiana* (Mill.) K. Koch] was common in the lower canopy reaching heights of about 10 m. As pollinators were not the original focus of this project, no effort was made to record flowering trees, shrubs or herbs.

We selected 12 dominant overstory trees (average height 31.67 ± 0.88 m, range 29–36 m) from the four most common tree species (i.e., three trees per species) in our study area which were *Q. phellos* L., *L. styraciflua* L., *P. occidentalis* L. and *P. taeda* L. We chose trees with suitable limbs for hanging traps and that also offered unobstructed space through which to raise and lower traps. Each tree had one trap suspended in the canopy and one suspended near ground level for a total of 12 traps at each height. In February, before the trees put out leaves, a slingshot attached to a fishing reel was used to send a small lead weight over the highest limb possible in each tree. Heavier ropes were then pulled over the limbs and were later used to pull traps into the canopy. Our goal was to suspend each trap above the lowest leaf-bearing branch in each tree. A light-weight rope was tied to the side of each trap and attached to a stake in the ground to ensure that the traps were raised to the same height each time and to aid in pulling them down. They were measured at the end of the study to determine trap heights (average height 18.83 ± 0.95 m, range 15–24 m). At each location, a second trap was suspended 0.5 m above the ground directly below the canopy trap from a metal pole driven into the ground.

The traps were made by cutting grooves halfway down the middle of two clear plastic vanes (20 × 30 cm) and sliding them together to create a + shaped barrier. The top of this barrier had a wire attached for hanging the trap and the bottom was wired to a white plastic bucket (diameter 16 cm, depth 15 cm). A hole (diameter 1.7 cm) in the side of the bucket covered with fine wire mesh (< 1 mm) prevented the traps from overflowing during rain storms. Propylene glycol was added to the buckets to kill and preserve the catch. The average horizontal distance between pairs of traps was 290 m (range, 11–915 m). The traps were operated continuously from April 5 to June 28 and again from July 12 to October 4, 2005. Because trapping began shortly after or during bud break, depending on tree species, and ended shortly before leaf fall, we sampled during most of the growing season. Samples were collected every 2 weeks. Insects were stored in 70% ethanol and bees were later separated and identified by VS and JLH as described by Mitchell (1960, 1962). *Lasioglossum* spp. were identified by J. Gibbs (York University, Toronto, Ontario). Voucher specimens are currently held in the research collection of JLH but will eventually be given to the Georgia Museum of Natural History.

Moran's *I* and Geary's *c* spatial autocorrelation coefficients (Legendre & Fortin, 1989) were calculated to test for autocorrelation among the 12 trapping locations (i.e., the canopy and ground samples were pooled for each tree). The trapping locations were significantly autocorrelated (i.e., not independent) based on $\log_{10}(x + 1)$-transformed abundance data according to Moran's *I* and on Shannon's diversity data according to both Moran's *I* and Geary's *c* (data not shown). Consequently, traditional statistical tests (e.g., paired *t*-tests) were not used to compare the number of bees captured at the two heights. Non-metric multidimensional scaling (NMS) (to qualitatively compare community composition between heights) and indicator species analysis (to quantitatively identify species significantly associated with one of the heights) were carried out on $\log_{10}(x + 1)$-transformed abundance data using PC-ORD (McCune & Mefford, 2006). These analyses were performed on a dataset from which species present in fewer than three samples had been removed, as recommended by McCune and Grace (2002). The same data set was used in PAST (Hammer *et al.*, 2001) to perform analysis of similarities (ANOSIM) with 10 000 permutations using a Bray–Curtis distance measure to quantitatively compare bee community similarity between heights.

Results

We collected 6653 bees from 5 families and 71 species (Appendix A). The traps in the canopy produced 6300 specimens and 57 species while those near the ground produced 353 specimens and 47 species. *Augochlora pura* (Say) accounted for over 91% of all bees collected and was over 40 times more abundant on average in the canopy than near the ground (Table 1).

Bee abundance and richness were generally higher in the canopy than near the ground (Table 2). Diversity and evenness exhibited the opposite pattern (Table 2) due to the fact that *A. pura* accounted for 94% of bees collected in the canopy compared to only 41% of bees collected near the ground (Appendix A). After removing *A. pura* from the dataset, abundance, richness and diversity were higher in the canopy than near the ground and evenness differed little between the two heights (Table 2).

Augochlora pura was consistently more abundant in the canopy than near the ground throughout the season, but was more so in mid-summer (i.e., June–September) when there was a pronounced increase in the number of *A. pura* in the canopy (Fig. 1). Aside from being more abundant near the ground than in the canopy in late April, the remaining bee community, as a group, exhibited a similar pattern (Fig. 2).

According to both NMS [final stress 12.5, within the acceptable range for ecological data (McCune & Grace, 2002)] (Fig. 3) and ANOSIM ($R = 0.87$, $P < 0.0001$), the bee community in the canopy was distinct from that near the ground. Based on indicator species analysis, four species [*A. pura*, *Lasioglossum imitatum* (Smith), *Lasioglossum versatum* sensu Mitch., and *Lasioglossum zephyrum* (Smith)] were found to be significantly associated with the canopy and two [*Andrena personata* Robertson and *Lasioglossum macoupinense* (Robertson)] were found to be significantly associated with the ground (Table 1).

Discussion

We found bees to be more abundant, species rich and diverse (after excluding *A. pura* from the dataset) in the canopy than near the ground. These results cannot be attributed to flower visitation alone because bees were highly active in the canopy throughout the season, even when trees were not producing nectar or pollen.

Table 2. Mean ± SE ($n = 12$) abundance, richness, Shannon's diversity and evenness of bees captured in flight-intercept traps suspended in the canopy (≥15 m) and near the ground (0.5 m) at our study site. Separate calculations were made for each; either including or excluding *Augochlora pura*, the most abundant species collected.

	Canopy	Ground
Abundance (including *A. pura*)	525.00 ± 96.69	29.42 ± 5.85
Abundance (excluding *A. pura*)	31.75 ± 6.27	17.33 ± 3.34
Richness (including *A. pura*)	13.58 ± 0.96	9.25 ± 1.30
Richness (excluding *A. pura*)	12.58 ± 0.96	8.33 ± 1.27
Diversity (including *A. pura*)	0.45 ± 0.09	1.64 ± 0.10
Diversity (excluding *A. pura*)	2.14 ± 0.06	1.74 ± 0.14
Evenness (including *A. pura*)	0.18 ± 0.04	0.80 ± 0.03
Evenness (excluding *A. pura*)	0.86 ± 0.01	0.89 ± 0.02

Certain cavity- and wood-nesting bee species may preferentially or occasionally nest in the canopy. For instance, some wood-nesting bees in Costa Rica nest more commonly in the crowns of dead trees than in the crowns of living trees or near the ground (Thiele, 2005). Furthermore, Sobek *et al.* (2009) collected more cavity-nesting bees in the canopy than near the ground in a German broadleaved forest. While the species most strongly associated with the canopy in this study, *A. pura*, nests in wood, it seems doubtful that nesting conditions are suitable ≥15 m above the ground considering the species prefers to nest in moderately moist logs that are shaded (Stockhammer,1966). We observed an *Apis mellifera* hive in a tree cavity 10–15 m above the ground which demonstrates that at least some of the bees collected may have been nesting in the canopy.

The importance of honeydew, sap and other non-floral sugar sources to bees has long been recognised, particularly by beekeepers. For example, over 65% of the honey produced by *A. mellifera* in Greece is derived from honeydew produced by at least 32 species of insects (Santas, 1983). These resources become especially important to bees during times of low flower availability. This was demonstrated particularly well in a recent field cage experiment in which the solitary bee *Osmia bicornis* (L.) [= *O. rufa* (L.)] was provided a nectar source (i.e., oilseed rape) alone, one of two aphid honeydew sources alone [colonies of *Myzus persicae* (Sulzer) or *Brevicoryne brassicae* (L.)], or a combination of nectar and honeydew (Konrad *et al.*, 2009). When provided

Table 1. Mean ± SE ($n = 12$) abundance of bee species found by indicator species analysis to be significantly associated with either the canopy (≥15 m) or ground (0.5 m) at our study site.

Species	Canopy	Ground	Indicator value	*P*-value
Andrena personata Robertson	0.33 ± 0.14	2.58 ± 0.81	61.0	0.01
Augochlora pura (Say)	493.25 ± 91.96	12.08 ± 2.81	73.0	< 0.01
Lasioglossum imitatum (Smith)	1.67 ± 0.58	0.08 ± 0.08	54.1	0.01
Lasioglossum macoupinense (Robertson)	0.17 ± 0.11	1.58 ± 0.38	65.7	< 0.01
Lasioglossum versatum sensu Mitch	7.00 ± 1.68	0.83 ± 0.42	82.1	< 0.01
Lasioglossum zephyrum (Smith)	1.83 ± 1.16	0 ± 0	41.7	0.04

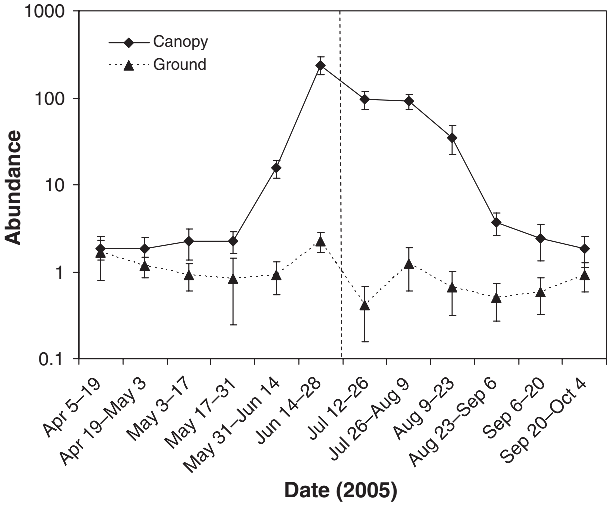

Fig. 1. Mean ± SE (n = 12) abundance of *Augochlora pura* in the canopy (≥15 m) and near the ground (0.5 m) at our study site. The dotted vertical line indicates a missing sampling period.

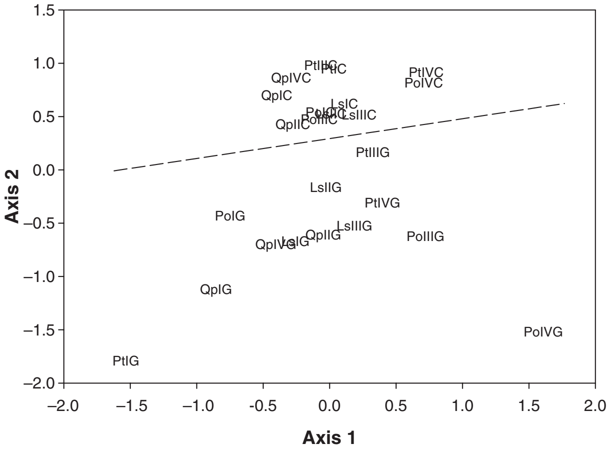

Fig. 3. Non-metric multidimensional scaling plot showing symbols for the different sampling locations. The letters comprising each symbol refer to tree species (Qp = *Quercus phellos*, Pt = *Pinus taeda*, Po = *Platanus occidentalis* and Ls = *Liquidambar styraciflua*), tree number (roman numerals) and trap height (G = ground, C = canopy). The closer two symbols appear in this figure, the more similar the bee communities were at those locations. The dashed line separates canopy locations (top) from ground locations (bottom).

with both nectar and honeydew, *O. bicornis* consumed only nectar. However, when provided with only a single honeydew type, 47% of *O. bicornis* consumed honeydew produced by *M. persicae* and 3% consumed honeydew produced by *B. brassicae*. These results show that bees will readily supplement their diets with honeydew in the absence of nectar. As honeydew producing insects are likely more abundant in the canopy than near the ground (Moran & Southwood, 1982; Wardhaugh *et al*., 2006), we suspect the same phenomenon in large part explains why we observed so many more bees in the canopy during mid-summer when nectar availability was low.

All four bee species found to be significantly associated with the canopy in this study have been observed feeding on honeydew. *Augochlora pura* and related species are known to do so (Eaton & Kaufman, 2007) and there have been reports of *A. pura* feeding from nectar glands on leaves as well (Trelease, 1881). Similarly, Batra (1966) reported that *L. zephyrum*, '…licked the honeydew on stems and leaves of suckers of *Populus deltoides* that were infested with aphids'. Likewise, Michener (1966) noted that *L. versatum* and *L. imitatum* utilised honeydew produced by the aphid *Anoecia corni* feeding on leaves of *Cornus asperifolia* from October 19 to 22 when most flowers were dead. Consequently, we strongly suspect that honeydew, though less nutritious than floral nectar (Lee *et al*., 2004), is readily available in the canopy throughout the season and plays an important role in providing food for these and perhaps many other forest-dwelling bee species.

Overall, bees were more numerous in the canopy but 14 species were collected only near the ground (Appendix A). Ten of these were singletons and two were doubletons. Just two species, *A. personata* and *L. macoupinense*, which were collected at both heights, were found to be significantly associated with the ground. *Andrena personata* is a ground-nester with preferences for rosaceous, umbelliferous and salicaceous plants (Miliczky, 1988; and references therein). Although information on the nesting habits of *L. macoupinense* could not be found, it is presumably a ground-nester like most halictids (Sakagami & Michener, 1962). However, nesting habits probably have little bearing on vertical distribution patterns. For example, all three species of *Lasioglossum* significantly associated with the canopy in this study are ground-nesters (Batra, 1966; Michener, 1966; Wcislo, 1997). In a paper dealing with the vertical distribution of bees in Panama, Roubik (1993) suggested that some bee species are physiologically incapable of tolerating the exposed conditions in

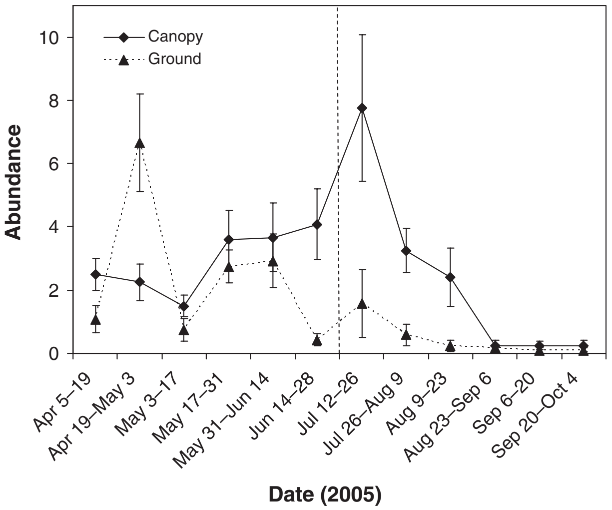

Fig. 2. Mean ± SE (n = 12) abundance of bees (excluding *Augochlora pura*) in the canopy (≥15 m) and near the ground (0.5 m) at our study site. The dotted vertical line indicates a missing sampling period.

the forest canopy causing them to be largely absent from the upper reaches of the forest. Future research may reveal a similar physiological basis for the vertical distribution patterns observed for *A. personata* and *L. macoupinense* in the present study.

While the results from both NMS and ANOSIM indicate that the bee community in the canopy was distinct from that near the ground, and certain species were only collected at one of the two heights, we have no reason to believe that any species collected in this study is restricted to a particular stratum. Roubik (1993) warns, 'If bee foraging behaviour, including stratum association, is largely the product of foraging experience, a short-term observation of a few months or at one site could lead to serious misconceptions regarding when and where these pollinators are likely to be found'. Clearly, more research will be needed before any definitive conclusions can be reached.

While *A. pura* was by far the most commonly collected bee species in this study, it cannot be said that *A. pura* is necessarily the most common species in the forest. For example, our traps may have been more effective at collecting *A. pura* than other bee species. Although flight-intercept traps are rarely used to sample bee communities (e.g., Westphal *et al.*, 2008), the particular design employed in this study, perhaps due to the white buckets (Campbell & Hanula, 2007), was quite productive and may have utility in future bee surveys.

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Appendix A. Bees collected using flight-intercept traps suspended in the canopy (≥15 m) and near the ground (0.5 m) at our study site.

Family	Species	Canopy	Ground	Total
Andrenidae	*Andrena banksi* Malloch	3	0	3
	Andrena confederata Viereck	1	0	1
	Andrena cressonii Robertson	9	4	13
	Andrena fragilis Smith	1	0	1
	Andrena hippotes Robertson	3	1	4
	Andrena ilicis Mitchell	1	3	4
	Andrena imitatrix Cresson	17	17	34
	Andrena mendica Mitchell	4	1	5
	Andrena nasonii Robertson	2	1	3
	Andrena obscuripennis Smith	0	1	1
	Andrena perplexa Smith	2	2	4
	Andrena personata Robertson	4	31	35
	Andrena sp. 13	1	0	1
	Andrena sp. 14	2	0	2
	Andrena sp. 15	1	0	1
	Andrena sp. 16	1	0	1
Apidae	*Anthophora abrupta* Say	2	1	3
	Apis mellifera Linnaeus	22	11	33
	Bombus bimaculatus Cresson	5	1	6
	Bombus citrinus (Smith)	1	0	1
	Bombus griseocollis (DeGeer)	3	1	4
	Bombus impatiens Cresson	12	2	14
	Bombus pensylvanicus (DeGeer)	1	0	1
	Ceratina calcarata Robertson	22	6	28
	Ceratina metallica Smith	0	1	1
	Habropoda laboriosa (Fabricius)	0	1	1
	Melissodes bimaculata (Lepeletier)	1	0	1
	Nomada ovata (Robertson)	0	1	1

Appendix A. *Continued*

Family	Species	Canopy	Ground	Total
	Nomada parva Robertson	0	1	1
	Nomada perplexa Cresson	0	1	1
	Xylocopa virginica (Linnaeus)	2	1	3
Colletidae	*Colletes inaequalis* Say	0	2	2
	Colletes nudus Robertson	0	1	1
	Colletes thoracicus Smith	1	1	2
	Hylaeus floridanus (Robertson)	0	1	1
	Hylaeus georgicus (Cockerell)	3	1	4
	Hylaeus grossicornis (Swenk & Cockerell)	1	1	2
	Hylaeus hydrangeae Mitchell	1	0	1
	Hylaeus illinoisensis (Robertson)	1	0	1
	Hylaeus modestus Say	4	1	5
	Hylaeus sparsus (Cresson)	1	1	2
	Hylaeus teleporus (Lovell)	7	0	7
Halictidae	*Augochlora pura* (Say)	5919	145	6064
	Augochlora sp.	1	0	1
	Augochlorella striata (Provancher)	75	49	124
	Halictus ligatus Say	2	0	2
	Halictus rubicundus (Christ)	0	2	2
	Halictus sp. 2	2	1	3
	Lasioglossum atlanticum (Mitchell)	1	0	1
	Lasioglossum bruneri (Crawford)	1	0	1
	Lasioglossum coeruleum (Robertson)	4	1	5
	Lasioglossum coreopsis (Robertson)	1	0	1
	Lasioglossum disparile (Cresson)	2	0	2
	Lasioglossum fuscipenne (Smith)	2	1	3
	Lasioglossum imitatum (Smith)	20	1	21
	Lasioglossum macoupinense (Robertson)	2	19	21
	Lasioglossum oblongum (Lovell)	8	2	10
	Lasioglossum versatum sensu Mitch	84	10	94
	Lasioglossum zephyrum (Smith)	22	0	22
	Lasioglossum spp.	2	5	7
	Sphecodes carolinus Mitchell	1	1	2
Megachilidae	*Hoplitis producta* (Cresson)	1	0	1
	Hoplitis simplex (Cresson)	0	7	7
	Megachile mendica Cresson	2	0	2
	Megachile sculpturalis Smith	1	0	1
	Megachile xylocopoides Smith	1	0	1
	Osmia atriventris Cresson	2	4	6
	Osmia chalybea Smith	0	1	1
	Osmia georgica Cresson	0	3	3
	Osmia lignaria Say	0	1	1
	Osmia pumila Cresson	2	2	4
Total		6300	353	6653