

Wild Bees (Hymenoptera: Apoidea: Anthophila) of the Michigan Highbush Blueberry Agroecosystem

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ABSTRACT Highbush blueberry (*Vaccinium corymbosum* L.) is a native North American crop dependent upon pollen movement by bees for high fruit set and large berries. Commercial blueberry farms use honey bees (*Apis mellifera* L.) to provide pollination services, but there is concern regarding their long-term sustainability as crop pollinators. We conducted a 3-yr study at 15 farms to identify the bee community associated with the blueberry agroecosystem in Michigan to improve our understanding of this community and to better target conservation practices. Pan trapping and direct observation were used to determine the relative abundance and diversity of wild bees before, during, and after bloom. We found at least 166 species, representing 30 genera and five families, 112 of which were active during bloom. Most bees captured were solitary, soil-nesting bees. Most species were from subfamily Halictinae (family Halictidae) and genus *Andrena* (family Andrenidae). *Andrena carolina* Viereck, a specialist on Ericaceae, was the most abundant native bee species collected during blueberry bloom. Several native *Osmia* species that were present in low abundance during bloom are potential targets for management. Honey bees were more often captured in white than in yellow traps, regardless of trap position in the field. Wild bees were more often captured in field perimeters than interiors, but they did not respond differentially to trap color. We report seven new state records for Michigan, including significant range extensions, and three new floral record associations. Implications for the conservation of native bees in this agricultural system are discussed.

KEY WORDS native bee conservation, pan trapping

Highbush blueberry (*Vaccinium corymbosum* L.) is a native North American crop dependent upon bees for moving pollen between flowers, thus enhancing fruit set and berry size (McGregor 1976, Free 1993, MacKenzie 1997, Delaplane and Mayer 2000). Many native bee species are known to pollinate *Vaccinium* blueberries, including several *Andrena*, *Osmia*, and *Bombus* species, and *Colletes validus* Cresson in eastern North America (Cane and Payne 1993, MacKenzie and Eickwort 1996, Drummond and Stubbs 1997), and *Habropoda laboriosa* (F.) in the southeastern United States (Sampson and Cane 2000). Some are able to sonicate, or buzz-pollinate, the porous anthers of *Vaccinium* flowers (Buchmann 1983) and will forage under cool weather conditions (Heinrich 2004). Many of these species visit more flowers per minute and deposit more pollen per visit than honey bees, *Apis mellifera* L. (Dogterom 1999, Sampson and Cane 2000, Javorek et al. 2002, Sampson et al. 2004).

Before the current large-scale production of highbush blueberry, native bees and feral honey bees were largely responsible for its pollination (Marucci and Moulter 1977, DeGrandi-Hoffman 1987). When com-

mercial acreage increased and pest management practices grew more intensive, it became necessary for growers to supplement wild pollinators with managed honey bee colonies. Although honey bees are not the most efficient bees at pollinating *Vaccinium* (Javorek et al. 2002), adequate pollination of highbush blueberry can be achieved when they are sufficiently abundant (Dogterom and Winston 1999, Dedej and Delaplane 2003). Hence, honey bees have become indispensable in commercial highbush blueberry production as in many other bee-dependent crops (Dorr and Martin 1966, Southwick and Southwick 1992, Roubik 1996).

Since the late 1980s, there have been concerns about the state of the honey bee industry in the United States (Torchio 1990, Watanabe 1994, DeGrandi-Hoffman 2003). After recent reports of colony collapse disorder, in which beekeepers find hives full of honey but few bees (Cox-Foster et al. 2007, Oldroyd 2007), it is clear that a more diverse pollination strategy would be beneficial to the long-term sustainability of crops that require insect-mediated pollination (Torchio 1990, Allen-Wardell et al. 1998, Stubbs and Drummond 2001). A first step toward that goal is to determine the community of bees present in agroecosystems (Cane and Tepedino 2001, NAS 2007). Conservation efforts should begin with faunal surveys that increase our knowledge of the identities, distribution,

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phenology, nesting biology, and floral associations of the taxa to be conserved.

To our knowledge, there has been no comprehensive survey of native bees in Michigan blueberry fields, even though Michigan is the leading producer of blueberries in the United States with 7,500 ha (18,500 acres) in production (USDA–NASS 2004). Surveys of native bees associated with lowbush blueberry production in British Columbia (MacKenzie and Winston 1984) and Maine (Drummond and Stubbs 1997), rabbiteye blueberry in South Carolina (Cane and Payne 1993, Sampson and Cane 2000), and highbush blueberry in upstate New York (MacKenzie and Eickwort 1996) have been conducted previously. These studies have focused on bees foraging during blueberry bloom, but many of these species are likely to be present before or after blueberry bloom, or during both periods, using other flowering plant species. To help conserve and eventually increase their abundance, these insects require floral resources, nesting habitat, and protection from insecticides aimed at pest insects outside of the bloom period of the crop. Consequently, it will be important to identify which of the abundant bees foraging on blueberry flowers are also present before and after bloom.

Previous faunal surveys in blueberry production regions predict that different key species associated with *Vaccinium* pollination will be abundant in different areas. In British Columbia, the most common species visiting lowbush blueberry was *Bombus mixtus* Cresson (MacKenzie and Winston 1984). In Maine, the wild bee community was dominated by genera *Bombus* and *Andrena* (Drummond and Stubbs 1997). In South Carolina, the dominant species was the blueberry bee *Habropoda laboriosa* (F.), to which most of the crop pollination was attributed when present (Cane and Payne 1993, Sampson and Cane 2000). In upstate New York, two species of *Andrena*, *A. (Andrena) carolina* and *A. (Melandrena) carlini* Cockerell, were the most abundant (MacKenzie and Eickwort 1996). *A. carolina* is a known *Vaccinium* specialist (LaBerge 1980, cited therein as *A. longifacies*) found abundantly only in association with Ericaceae, including deerberry (*Vaccinium stamineum* L.) (Cane et al. 1985, cited therein as *A. longifacies*) in addition to blueberries. *A. carlini*, a relatively large and generally abundant species across much of eastern North America, is not a specialist on Ericaceae but is known to forage on *Vaccinium* in large numbers as do related species of subgenus *Melandrena* such as *A. vicina* Smith and *A. regularis* Malloch. Based on distributional and floral records published by Mitchell (1960, 1962) and in subsequent revisions of *Andrena* (Bouseman and LaBerge 1979, LaBerge 1980) and in subsequent regional studies of *Bombus* (e.g., Medler and Carney 1963), we predicted that the bee community in Michigan blueberry would be most similar to that reported by MacKenzie and Eickwort (1996).

In this study, pan trapping, direct observation, and pollen analysis from bee specimens were used to determine the relative abundance and diversity of wild bees associated with highbush blueberry agroecosys-

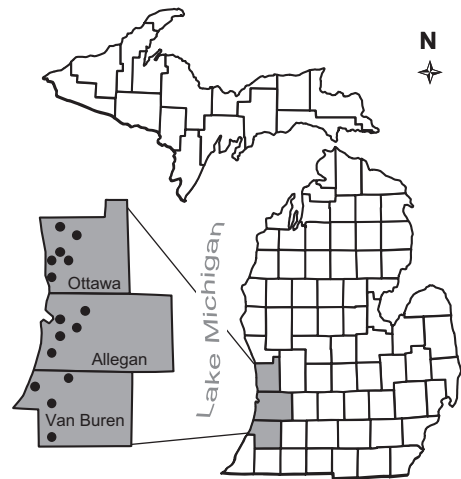


Fig. 1. Location of the 15 blueberry fields in three southwest Michigan counties where bee collections were made during 2004–2006.

tems in southwestern Michigan before, during, and after bloom. We also compared captures of native bees in white and yellow pan traps placed at field borders or interiors to determine optimal methods for pan trapping native bees in this agricultural system.

Materials and Methods

A 3-yr study was conducted to identify the species composition and phenology of bees at 13 commercial blueberry farms and two semiabandoned blueberry fields located in the highbush blueberry production region of southwest Michigan (Fig. 1). Six sites were located in Ottawa County, five in Allegan County, and four in Van Buren County. Each sampled field was at least 3 km away from any other sampled field in this study.

Bees were monitored passively using pan traps, and those bees visiting blueberry flowers were determined during timed observations. To determine the relative fidelity of the most dominant bee species to blueberry, the proportion of *Vaccinium* pollen carried was determined from bees collected in pan traps and while foraging on blueberry flowers. Bee sampling was conducted when weather conditions met the following criteria: minimum temperature of 13°C with clear or partly cloudy skies or 17°C with any sky condition other than rain (Pywell et al. 2005).

Pan Trapping. Sampling was conducted during the growing seasons of 2004–2006. Because of longitudinal differences in bloom phenologies, all sites were not sampled on the same days but instead were divided into three sampling groups based on the county in which they were located. For each trapping event, sites in Van Buren County were always sampled first, followed by the sites in Allegan and then Ottawa counties on subsequent days according to bloom phenology and weather. Because of varying early spring weather conditions from year to year, trapping during

bloom was conducted twice in 2004 (16 May–3 June), three times in 2005 (16–25 May), and twice in 2006 (17–31 May) at each field. Prebloom trapping was conducted once in 2005 (15–21 April) and in 2006 (19–26 April) in each field, but not in 2004. Postbloom trapping was conducted twice in 2004 (15 June–4 September) and three times in 2005 (22 June–15 September) and 2006 (12 June–10 August).

Pan traps were constructed from 355-ml white and yellow plastic bowls (Amscan, Inc., Elmsford, NY) mounted onto 2.7-cm-diameter polyvinyl chloride (PVC) poles stabilized with rebar. Traps were half filled with a 2% soap solution (Dawn dish soap, Procter & Gamble, Cincinnati, OH) to a level with a surface area of ≈ 133 cm². Five pairs of white and yellow pan traps mounted on 1.2-m PVC poles were placed 5 m apart along each of two transects running perpendicular to the orientation of the rows. One transect was established within 1 m of the field edge and the other was established 25 m into the field. Traps were set out between 0800 and 1200 h and were collected between 1600 and 2000 h for a minimum trapping period of 6 h on days when suitable weather conditions, as described above, were met.

After the sampling period, pan trap contents were strained into plastic bags and stored in a -12°C freezer for later processing. Specimens were thawed at room temperature before washing in a 70% ethanol solution. Honey bees were separated out and counted and then stored in a 70% ethanol solution. When pollen was present on wild bees collected during bloom, pollen samples were taken (see below), and then bees were placed in a mesh bag through which a hairdryer was used to fluff-dry their hair before pinning for identification (Droege 2008).

To determine the degree to which our sampling protocol accurately reflects the bee community, species accumulation curves were generated based on randomized resampling of bee trapping observations with 1,000 permutations in R 3.2.1, and the bootstrap estimate was used to estimate species richness each year (using the “specaccum” function in the “vegan” package; Colwell and Coddington 1994). A two-way analysis of variance (ANOVA) (PROC GLM, SAS 9.1, SAS Institutes, Cary, NC) was conducted to examine the response of bees to trap position in the field (edge versus interior) and trap color (white versus yellow), by using Tukey’s means separation. The analysis was repeated for each of the three sampling years. This model was used to determine the response of wild bee abundance ($\log n + 1$), species richness and diversity (Shannon–Wiener H'), and honey bee abundance to trap position and color. The abundances of eight of the most common bee species that have been recorded foraging on blueberry (Mitchell 1960, 1962; Hurd 1979, MacKenzie and Eickwort 1996; this study) were pooled across years and also tested for their response to trap position and trap color.

Direct Bee Observations. Timed observations of bees visiting blueberry flowers were conducted at three of the commercial sites and at the two semia-bandoned blueberry farms in 2004–2006. Fifteen ran-

domly selected bushes were observed for 1 min each, on three occasions during bloom in each field. Observations were conducted during times when conditions were suitable for bee activity, as described above. Bees were identified as honey bees, bumble bees, or other wild bees. The other wild bees were collected for identification ($n = 62$).

Species Identifications. Preliminary identifications of bees were made using three published dichotomous keys (Mitchell 1960, 1962; Michener et al. 1994) and the online keys available through www.discoverlife.org. Further identifications and verifications for most species recorded, including the new state records, were made by comparison with voucher specimens at the American Museum of Natural History, Division of Invertebrate Zoology. Sam Droege of the USGS Patuxent Wildlife Research Center identified or verified many of the *Hylaeus* and *Lasioglossum* (*Dialictus*) species. Voucher specimens are deposited in the Albert J. Cook Arthropod Research Collection at Michigan State University.

Pollen Analysis. Pollen samples were brushed from corbiculae of honey bees and scopae of all other bees collected during timed observations and in pan traps, by using a fine paint brush. Each pollen sample was stained using melted basic fuchsin gel on glass microscope slides (Kearns and Inouye 1993). Pollen slides were examined under a $400\times$ light microscope and the number of tetrad pollen grains (i.e., *Vaccinium*) out of 100 was recorded. The proportion of *Vaccinium* pollen was calculated for each sampled bee, and these values were averaged for each bee species from which pollen was collected.

Results

Over 3 yr across the 15 farms, we collected 12,637 bees in pan traps, representing at least 167 species, including *A. mellifera*, belonging to 30 genera and five families (Table 1). Each site was sampled 17 times, representing $>1,300$ d of trapping effort. The species accumulation curves created using pan trapping data were similar for the 3 yr and approached an asymptote (Fig. 2). Bootstrap estimates of the entire species pool suggest that we captured $\approx 88\%$ of the species predicted to be present each year (Fig. 2). This indicates that pan trapping effort was sufficient to represent most of the community of bees likely to be captured in pan traps in this habitat.

Bee Community Structure. During bloom, the most abundant groups of wild bees captured were halictid (mostly tribe Halictini) and andrenid (only genus *Andrena*) bees at 44 and 43% of wild bee individuals and 37 and 35% of wild bee species, respectively (Table 2). The next most abundant group of wild bees included three species of *Ceratina* (Apidae) (10% of individuals) (Table 2). Seven species of *Bombus* spp. were caught in low numbers (Table 1). Colletidae and Megachilidae were captured with less frequency (2 and 1% of individuals, respectively), but 10% of the

Table 1. Bee species collected in pan traps from 15 blueberry fields in SW Michigan over a period of 3 yr from 2004 to 2006

Family species	Pre (n = 2)		Bloom (n = 7)		Post (n = 8)		Total	No. yr captured (n = 3)
	♀	♂	♀	♂	♀	♂		
Andrenidae								
<i>Andrena alleghaniensis</i> Viereck	0	0	20	27	2	0	49	3
<i>A. andrenoides</i> (Cresson)	0	0	0	1	0	0	1	1
<i>A. arabis</i> Robertson	2	6	0	1	0	0	9	2
<i>A. barbilabris</i> (Kirby)	2	4	10	0	0	0	16	2
<i>A. bisulcatus</i> Viereck	5	0	0	0	4	0	9	2
<i>A. carlini</i> Cockerell	43	57	133	0	0	0	233	3
<i>A. carolina</i> Viereck	32	366	446	87	4	0	935	3
<i>A. ceanothi</i> Viereck	0	2	14	1	1	0	18	3
<i>A. clarkella</i> (Kirby)	2	0	1	0	0	0	3	2
<i>A. commoda</i> Smith	0	0	4	0	0	0	4	2
<i>A. confederata</i> Viereck	0	0	0	1	0	0	1	1
<i>A. crataegi</i> Robertson	1	0	12	32	3	0	48	3
<i>A. cressonii</i> Robertson	33	28	43	4	6	0	114	3
<i>A. dunningi</i> Cockerell ^a	0	0	1	0	0	0	1	1
<i>A. erigeniae</i> Robertson	0	8	2	0	0	1	11	2
<i>A. erythrogaster</i> (Ashmead)	2	7	1	0	0	0	10	2
<i>A. erythronii</i> Robertson	9	3	1	0	0	0	13	2
<i>A. forbesii</i> Robertson	11	2	12	0	0	0	25	3
<i>A. frigida</i> Smith	4	0	0	0	0	0	4	2
<i>A. germanii</i> Robertson	0	0	0	0	1	0	1	1
<i>A. hiliaris</i> Smith	0	0	0	3	0	0	3	1
<i>A. hippotes</i> Robertson	4	3	13	4	0	0	24	3
<i>A. hirticincta</i> Provancher	0	0	0	0	0	2	2	1
<i>A. imitatrix</i> Cresson	0	5	0	78	0	1	84	3
<i>A. imitatrix</i> or <i>morrisonella</i> ^b	8	0	54	0	0	0	62	3
<i>A. integra</i> Smith	0	0	2	0	0	0	2	1
<i>A. mandibularis</i> Robertson	0	0	2	0	0	0	2	1
<i>A. mariae</i> Robertson	0	0	1	0	0	0	1	1
<i>A. melanochroa</i> Cockerell	0	1	0	0	0	0	1	1
<i>A. milwaukeeensis</i> Graenicher	0	0	1	0	0	0	1	1
<i>A. miserabilis</i> Cresson	75	35	101	0	1	0	212	3
<i>A. morrisonella</i> Viereck	0	0	10	1	1	0	12	3
<i>A. nasonii</i> Robertson	35	66	28	4	1	0	134	3
<i>A. neonana</i> Viereck	0	0	1	0	1	0	2	2
<i>A. nigrae</i> Robertson	0	0	14	0	0	0	14	2
<i>A. nigrihirta</i> (Ashmead)	36	26	11	0	1	0	74	3
<i>A. nivalis</i> Smith	0	0	1	0	0	0	1	1
<i>A. nuda</i> Robertson	0	9	23	3	9	0	44	3
<i>A. perplexa</i> Smith	2	1	9	16	1	0	29	3
<i>A. persimulata</i> Viereck	0	0	1	0	0	0	1	1
<i>A. placata</i> Mitchell	0	0	0	0	5	3	8	1
<i>A. platyparia</i> Robertson	0	0	0	0	1	0	1	1
<i>A. pruni</i> Robertson	0	1	3	1	0	0	5	3
<i>A. rehni</i> Viereck	0	0	2	0	2	0	4	2
<i>A. robertsonii</i> Dalla Torre	0	0	4	0	0	0	4	3
<i>A. rugosa</i> Robertson	2	2	20	0	0	0	24	3
<i>A. salictaria</i> Robertson	0	1	6	0	0	0	7	2
<i>A. signundi</i> Cockerell	2	0	0	0	0	0	2	1
<i>A. spiraeana</i> Robertson	0	0	0	1	0	0	1	1
<i>A. vicina</i> Smith	13	26	117	15	0	0	171	3
<i>A. wellesleyana</i> Robertson	5	0	0	0	0	0	5	2
<i>A. wilkella</i> (Kirby) (exotic)	0	0	0	0	2	9	11	1
<i>A. (Melandrena) spp.</i> ^b	2	7	3	1	0	0	13	2
<i>A. (Trachandrena) spp.</i> ^b	2	0	8	0	0	0	10	2
<i>Andrena spp.</i> ^b	1	4	2	0	0	1	8	3
<i>Calliopsis andreniformis</i> Smith	0	0	0	0	3	1	4	3
<i>Perdita octomaculata</i> (Say)	0	0	0	0	1	0	1	1
<i>Pseudopanurgus nebrascensis</i> (Crawford)	0	0	0	0	3	0	3	1
Apidae								
<i>Anthophora terminalis</i> Cresson	0	0	0	0	2	3	5	2
<i>Bombus bimaculatus</i> Cresson	0	0	9	0	0	0	9	2
<i>B. citrinus</i> (Smith)	0	0	16	0	2	1	19	2
<i>B. fervidus</i> (F.)	0	0	6	0	1	0	7	3
<i>B. grisocollis</i> (DeGeer)	0	0	7	0	3	0	10	2
<i>B. impatiens</i> (Cresson)	1	0	2	1	8	7	19	3
<i>B. perplexus</i> Cresson	1	0	4	0	1	2	8	3

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Table 1. Continued

Family species	Pre (n = 2)		Bloom (n = 7)		Post (n = 8)		Total	No. yr captured (n = 3)
	♀	♂	♀	♂	♀	♂		
<i>B. vagans</i> Smith	0	0	0	0	1	0	1	1
<i>Ceratina calcarata</i> Robertson ♂	-	390	-	50	-	47	487	3
<i>C. calcarata</i> ♀ or <i>dupla</i> ♀ ^b	137	-	122	-	367	-	626	3
<i>C. dupla</i> Say ♂	-	35	-	11	-	16	62	3
<i>C. strenua</i> Smith	18	32	14	1	105	7	177	3
<i>Eucera atriventris</i> (Smith)	0	0	1	0	0	0	1	1
<i>E. hamata</i> (Bradley)	0	0	0	0	2	1	3	1
<i>Melissodes agilis</i> Cresson	0	0	0	0	1	0	1	1
<i>M. apicata</i> Lovell and Cockerell	0	0	0	0	1	0	1	1
<i>M. bimaculata</i> Lepeletier	0	0	0	0	6	5	11	3
<i>M. communis</i> Cresson	0	0	0	0	3	0	3	1
<i>M. druriella</i> (Kirby) [= <i>rustica</i> (Say)]	0	0	0	0	3	0	3	1
<i>M. trinodis</i> Robertson	0	0	0	0	2	1	3	2
<i>M. (Eumelissodes) spp.</i> ^b	0	0	0	1	5	5	11	3
<i>Nomada cf. denticulata</i> Robertson	0	0	2	0	0	0	2	1
<i>N. cf. depressa</i> Cresson	3	0	0	0	0	0	3	1
<i>N. cressonii</i> Robertson	0	0	1	0	0	0	1	1
<i>N. luteoloides</i> Robertson	6	1	0	0	0	0	7	1
<i>N. maculata</i> Cresson	6	11	1	0	0	0	18	1
<i>N. obliterated</i> Cresson	1	1	0	0	0	0	2	1
<i>N. ovata</i> (Robertson)	0	0	0	1	0	0	1	1
<i>N. pygmaea</i> Cresson	0	1	0	0	0	0	1	1
<i>N. ruficornis</i> species group ^b	156	0	92	0	40	0	288	3
<i>Triepeolus lunatus</i> (Say)	0	0	0	0	1	0	1	1
<i>Xylocopa virginica virginica</i> (L.)	0	0	1	2	0	0	3	2
Colletidae ^c								
<i>Colletes inaequalis</i> Say	1	39	18	0	0	0	58	2
<i>C. simulans armatus</i> Patton	0	0	0	0	1	1	2	2
<i>C. thoracicus</i> Smith	18	0	13	16	0	0	47	3
<i>C. validus</i> Cresson	0	0	2	0	0	0	2	1
<i>Hylaeus affinis</i> (Smith)	15	2	1	3	33	3	57	3
<i>H. affinis</i> or <i>modestus</i> Say ^b	2	1	0	0	0	2	5	2
<i>H. annulatus</i> (L.) [= <i>ellipticus</i> (Kirby)]	0	0	0	0	2	0	2	2
<i>H. (Prosopis) sp. B</i>	0	0	0	0	1	0	1	1
<i>H. illinoisensis</i> Robertson or sp. A	13	0	4	0	17	0	34	3
<i>H. mesillae</i> (Cockerell)	1	0	1	0	1	0	3	1
<i>H. verticalis</i> (Cresson)	0	0	0	0	1	0	1	1
Halictidae ^d								
<i>Agapostemon sericeus</i> (Frster)	1	0	8	0	3	2	14	3
<i>A. splendens</i> (Lepeletier)	0	0	3	0	0	6	9	2
<i>A. texanus</i> Cresson	0	0	3	0	1	0	4	2
<i>A. virescens</i> (F.)	0	0	11	0	18	4	33	3
<i>Augochlora pura</i> (Say)	10	0	68	0	9	6	93	3
<i>Augochlorella aurata</i> (Smith) [= <i>striata</i>]	34	0	174	0	118	20	346	3
<i>Augochloropsis metallica</i> (F.)	0	0	1	0	0	0	1	1
<i>Halictus confusus</i> Smith	5	0	33	0	15	1	54	3
<i>H. ligatus</i> Say	1	0	50	0	52	19	122	3
<i>H. parallelus</i> Say	0	0	5	0	4	1	10	3
<i>H. rubicundus</i> (Christ)	1	0	13	0	2	1	17	3
<i>Lasioglossum acuminatum</i> McGinley	1	0	12	0	1	1	15	3
<i>L. admirandum</i> (Sandhouse) ^e	7	0	45	0	25	0	77	3
<i>L. anomalum</i> (Robertson)	0	0	7	0	5	0	12	3
<i>L. athabascense</i> (Sandhouse)	1	0	0	0	0	0	1	1
<i>L. bruneri</i> (Crawford)	1	0	4	0	4	0	9	3
<i>L. cattellae</i> (Ellis)	0	0	2	0	0	0	2	2
<i>L. coeruleum</i> (Robertson)	3	0	17	0	4	0	24	3
<i>L. coriaceum</i> (Smith)	4	0	90	0	12	0	106	3
<i>L. cressonii</i> (Robertson)	3	0	113	0	27	0	143	3
<i>L. fattigi</i> (Mitchell) or <i>apocyni</i> (Mitchell)	0	0	1	0	0	0	1	1
<i>L. forbesii</i> (Robertson)	1	0	0	0	0	1	2	2
<i>L. fuscipenne</i> (Smith)	1	0	6	0	1	0	8	3
<i>L. illinoense</i> (Robertson)	0	0	1	0	2	0	3	2
<i>L. imitatum</i> (Smith)	161	0	124	0	64	0	349	3
<i>L. leucozonium</i> (Schrank) (exotic) ^f	0	0	155	0	255	220	630	3
<i>L. lineatulum</i> (Crawford)	2	0	10	0	0	0	12	2
<i>L. lustrans</i> (Cockerell)	0	0	0	0	2	0	2	2
<i>L. nelumbonis</i> (Robertson)	0	0	1	0	0	0	1	1
<i>L. nigroviride</i> (Graenicher)	0	0	7	0	0	0	7	2
<i>L. nymphaearum</i> (Robertson)	0	0	4	0	3	0	7	3

Continued on following page

Table 1. Continued

Family species	Pre (n = 2)		Bloom (n = 7)		Post (n = 8)		Total	No. yr captured (n = 3)
	♀	♂	♀	♂	♀	♂		
<i>L. nymphale</i> (Smith)	1	0	0	0	0	0	1	1
<i>L. oblongum</i> (Lovell)	0	0	3	0	3	0	6	3
<i>L. obscurum</i> (Robertson)	0	0	1	0	0	0	1	1
<i>L. pectorale</i> (Smith)	0	0	39	0	67	1	107	3
<i>L. pilosum</i> (Smith)	94	0	264	0	124	11	493	3
<i>L. quebecense</i> (Crawford)	7	0	22	0	3	0	32	3
<i>L. rohweri</i> (Ellis)	7	0	79	0	14	0	100	3
<i>L. rohweri</i> or <i>lineatulum</i> ^b	3	0	3	0	1	0	7	2
<i>L. tegulare</i> (Robertson)	1	0	27	0	19	2	49	3
<i>L. versans</i> (Lovell)	0	0	6	0	2	0	8	3
<i>L. vierecki</i> (Crawford)	7	0	7	0	36	1	51	3
<i>L. (Dialictus)</i> unknown sp. 1 ^b	1	0	2	0	1	0	4	3
<i>L. (Dialictus)</i> unknown sp. 2 ^b	0	0	3	0	0	0	3	2
<i>L. (Dialictus)</i> unknown sp. 3 ^b	0	0	2	0	3	0	5	1
<i>L. (Dialictus)</i> unknown sp. 4 ^b	0	0	0	0	1	0	1	1
<i>L. (Dialictus)</i> spp. ^b	0	0	3	0	2	8	13	3
<i>L. (Evylaeus)</i> spp. ^b	0	0	2	0	1	1	4	2
<i>Sphécodes confertus</i> Say	1	0	1	0	1	0	3	2
<i>S. cf. cressonii</i> (Robertson)	0	0	0	0	4	0	4	1
<i>S. mandibularis</i> Cresson	0	0	0	0	3	0	3	1
<i>S. ranunculi</i> Robertson	0	0	1	0	0	0	1	1
<i>Sphécodes</i> spp. ^b	9	0	8	0	21	0	38	3
Megachilidae								
<i>Anthidium manicatum</i> (L.) (exotic)	0	0	0	0	2	6	8	2
<i>Chelostoma philadelphia</i> (Robertson)	0	0	0	0	0	1	1	1
<i>Coelioxys</i> sp.	0	0	0	0	1	0	1	1
<i>Dianthidium simile</i> (Cresson)	0	0	0	0	7	10	17	2
<i>Heriades variolosus</i> (Cresson)	0	0	0	0	1	0	1	1
<i>Hoplitis pilosifrons</i> (Cresson)	0	0	0	1	0	1	2	2
<i>H. producta</i> (Cresson)	0	0	2	0	1	0	3	1
<i>H. spoliata</i> (Provancher)	0	0	1	0	0	0	1	1
<i>Megachile addenda</i> Cresson	0	0	0	1	0	2	3	2
<i>M. brevis</i> Say	0	0	0	0	0	2	2	2
<i>M. centuncularis</i> (L.) ^g	0	0	0	0	1	0	1	1
<i>M. cf. gemula</i> Cresson	0	0	1	0	0	0	1	1
<i>M. mendica</i> Cresson	0	0	0	0	9	0	9	2
<i>M. montivaga</i> Cresson	0	0	0	0	1	0	1	1
<i>M. pugnata</i> Say	0	0	0	2	3	2	7	3
<i>M. relativa</i> Cresson	0	0	0	0	0	1	1	1
<i>M. rotundata</i> (F.) (exotic)	0	0	0	1	1	0	2	2
<i>Osmia atriventris</i> Cresson	3	18	0	0	1	0	22	2
<i>O. atriventris</i> or <i>pumila</i> ^b	10	152	8	1	0	0	171	3
<i>O. atriventris</i> or <i>virga</i> ^b	0	0	0	0	1	0	1	1
<i>O. bucephala</i> Cresson	7	21	5	1	3	0	37	3
<i>O. conjuncta</i> Cresson	3	3	2	0	1	0	9	2
<i>O. distincta</i> Cresson	0	1	0	0	1	0	2	1
<i>O. felti</i> Cockerell	0	0	0	0	1	0	1	1
<i>O. georgica</i> Cresson	0	0	0	0	1	0	1	1
<i>O. lignaria</i> Say	5	4	0	0	0	0	9	2
<i>O. pumila</i> Cresson	5	22	3	0	4	0	34	2
<i>O. simillima</i> Smith	1	0	0	0	0	0	1	1
<i>O. subfasciata</i> Mitchell	0	8	0	0	0	0	8	1
<i>O. virga</i> Sandhouse	0	4	0	0	0	0	4	1
<i>Osmia</i> spp. ^b	7	13	8	2	4	0	34	3
Non- <i>Apis</i> abundance	1,115	1,428	2,927	372	1,640	450	7,932	
No. of non- <i>Apis</i> species (♀ + ♂)		76		112		105	166	
<i>A. mellifera</i> L. abundance (♀ only)		24		4,580		101	4,705	
Total bee abundance		2,567		7,879		2,191	12,637	

Samples were taken before (pre), during (bloom), and after (post) blueberry bloom (*n* is number of pan trapping periods).

^a Additional males may have been overlooked due to identification difficulties.

^b Not counted as an additional species because it is either imprecise or redundant.

^c Most of the *Hylaeus* species were determined or verified by S. Droege.

^d Most of the *Lasioglossum (Dialictus)* species were determined or verified by S. Droege.

^e Separation of *Lasioglossum admirandum* (Sandhouse) from other species such as *Lasioglossum atlanticum* (Mitchell) remains uncertain pending completion of molecular studies by J. Gibbs (personal communication).

^f Exotic status has only recently been hypothesized (Giles and Ascher 2006) and corroborated (Zayed and Packer 2007).

^g Native status uncertain (see Giles and Ascher 2006).

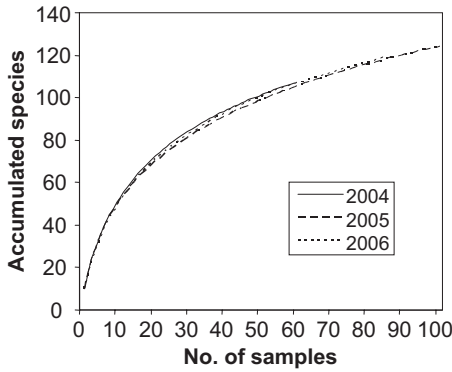


Fig. 2. Species accumulation curves generated from 1,000 permutations each of the 2004, 2005, and 2006 pan trap sampling data. Listed in order from 2004 to 2006, the bootstrap estimate of the entire species pool was 123 ± 4 , 142 ± 5 , and 136 ± 5 , respectively, with $\approx 88\%$ of the species accounted for in our samples each year.

wild bee species caught during bloom were megachilids (Table 2). The most species-rich genera were *Andrena* at 54 species, followed by *Lasioglossum*, with at least 30 species (Table 1). The overall proportion of bees within each family remained relatively stable from year to year, even though fewer bees were trapped during bloom in 2006 compared with the other years, likely due to cooler spring weather conditions in that year.

At least 112 wild bee species were captured in pan traps during blueberry bloom over the 3 yr (Table 1). Except for bees in the cleptoparasitic genera (e.g., *Nomada* and *Sphecodes*), most of these species are

potential pollinators of blueberry. By far the most abundant non-*Apis* species captured at this time of the season was the *Vaccinium* specialist *A. carolina* (16% of the total wild bee abundance). *Lasioglossum pilosum* (Smith) composed 8% of the samples, followed by *Augochlorella aurata* (Smith) and *Lasioglossum leucozonium* (Schrank) at 5%. These three species are consistently abundant in bee faunal studies of eastern North America (e.g., Giles and Ascher 2006). Eight species represented 3–4% of trapped bees, 18 species were abundant between 1 and 2%, and the rest (72 species) were present at <1% of the total.

The dominant non-*Apis* native bee species that were observed visiting blueberry flowers every year and are reported to forage on *Vaccinium* (Mitchell 1960, 1962; Hurd 1979; MacKenzie and Eickwort 1996) were *A. carolina*, *A. carlini*, *A. vicina*, *Ceratina calcarata* Robertson or *dupla* Say (the females are not readily distinguishable; there were many more male *C. calcarata* than there were *C. dupla*), *A. aurata* [recently synonymized with *Augochlorella striata* (Provancher)], *Lasioglossum coriaceum* (Smith), *Lasioglossum imitatum* (Smith), and *L. pilosum*. All except for *C. calcarata* are ground nesting bees (Michener 2000). All of these species were also present in samples collected before bloom in 2005 and 2006 (Table 1) and likely would have been present before bloom in 2004, but no prebloom sampling was conducted in 2004. Four of these species are eusocial, have lengthy flight seasons, and were therefore also present after bloom in samples taken in all 3 yr: *A. aurata*, *Bombus* spp., *L. imitatum*, and *L. pilosum* (Table 1). The activity period of three of the most abundant species throughout the season (Fig. 3), reveals

Table 2. Proportion of species and individuals with respect to taxonomic and ecological groupings of non-*Apis* bees collected in highbush blueberry fields in southwest Michigan from 2004 to 2006

Category	Proportion of species			Proportion of individuals		
	Pre (n = 76)	Bloom (n = 112)	Post (n = 106)	Pre (n = 2568)	Bloom (n = 3302)	Post (n = 2116)
Families						
Andrenidae	0.31	0.35	0.20	0.39	0.43	0.03
Apidae	0.17	0.13	0.17	0.32	0.10	0.31
Colletidae	0.08	0.05	0.07	0.04	0.02	0.03
Halictidae	0.32	0.37	0.34	0.15	0.44	0.59
Megachilidae	0.13	0.10	0.22	0.10	0.01	0.03
Exotic/native						
Exotic	0	0.02	0.04	0	0.05	0.23
Native	1.00	0.98	0.96	1.00	0.86	0.71
Floral specificity						
Oligolectic	0.08	0.05	0.11	0.18	0.17	0.02
Polylectic	0.74	0.82	0.77	0.61	0.73	0.91
Nesting substrates						
Cavity	0.15	0.14	0.25	0.04	0.02	0.03
Wood/pith	0.10	0.07	0.10	0.26	0.08	0.29
Soil	0.63	0.73	0.59	0.55	0.85	0.61
Other	0	0	0.01	0	0	0.01
Sociality						
Social	0.22	0.26	0.24	0.13	0.32	0.32
Solitary ^a	0.66	0.64	0.68	0.72	0.63	0.63
Parasitic	0.12	0.06	0.06	0.08	0.03	0.03

Notes that pre indicates collections made before crop bloom; bloom indicates collections made during crop bloom; and post indicates collections made after crop bloom; where groups do not sum to 100, attribute is unknown for some species.

^a This is a broad category including communal or otherwise weakly social but not eusocial species.

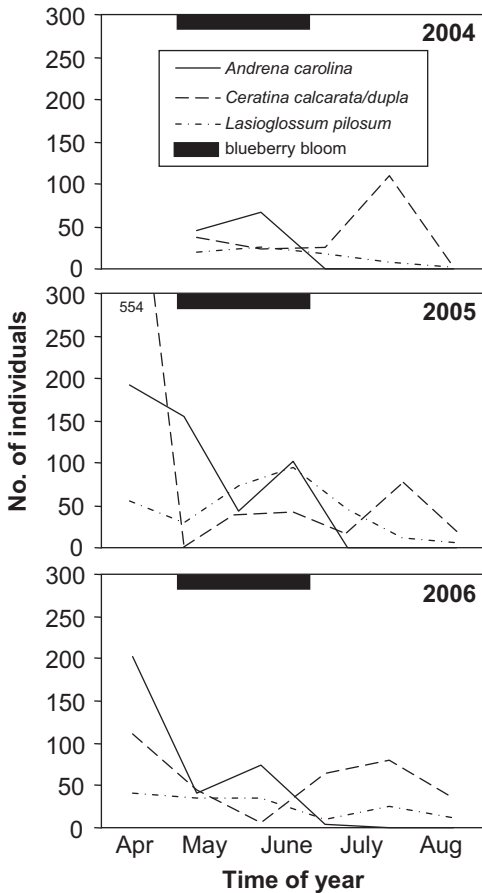


Fig. 3. Relative abundance throughout the season of the three most abundant native bee species reported to forage on *Vaccinium* spp. that were trapped in 15 highbush blueberry fields in southwest Michigan from 2004 to 2006. The black bar denotes the approximate timing of blueberry bloom.

that *A. carolina* is present in blueberry fields before and during bloom, but not afterward, because its flight season is restricted by the bloom period of its sole pollen sources (blueberries and related Ericaceae). *C. calcarata* or *C. dupla* had two peaks, one in spring and the other during summer, whereas *L. pilosum* was found in all samples, declining through the summer. *A. mellifera* was by far the most abundant species trapped during blueberry bloom (58%), but was much less abundant before hives were placed next to the crop (1%) and after bloom when hives were removed again (4%). This suggests that most of the honey bees captured at these sites were from managed colonies, even at those sites that were semiabandoned.

Exotic bees excluding honey bees were rare before and during bloom but composed 23% of the bees captured in postbloom samples (Table 2). Native bees considered to be oligolectic were most abundant before (18% of individuals) and during bloom (17% of individuals); however, the largest number of species considered to be oligolectic were captured after bloom (11% of species versus 5% during), many of

which are likely specialists on Asteraceae (Hurd 1979) (Table 2). Soil nesters were the most abundant and species-rich nesting guild of bees captured during each trapping period. Cavity nesters were the second most species-rich followed by wood or pith nesters, but the abundance of wood or pith nesters was greater than that of the cavity nesters (Table 2). Solitary bees outnumbered social bees throughout the growing season and were most abundant before blueberry bloom, whereas social bees were more abundant during and after blueberry bloom, an expected result as the abundance of workers from social colonies increases through the summer, whereas only queens are present in early spring. Across this study, most of the bees captured were solitary, soil-nesting bees. The greatest number of species collected were Halictinae, all of which were polylectic, and *Andrena*, which included both oligolectic and polylectic species.

Direct Observations of Bees Foraging on Blueberry. From timed observations made in commercial and semiabandoned blueberry fields during bloom, honey bees far outnumbered non-*Apis* bees in commercial fields, with >30-fold greater abundance. In semiabandoned fields, where no honey bee hives were installed, but where drift from commercial fields stocked with honey bees is possible, the ratio of honey bees to wild bees was 3:1. During these observations, we collected 62 non-*Apis* bees visiting blueberry from 21 species across 10 genera. The most abundant non-*Apis* bees observed visiting bloom were *A. carolina* and *A. carlini*, followed by *Bombus bimaculatus* Cresson and *A. vicina*. Additional records of bee visitation to *Vaccinium* are newly documented: *Agapostemon sericeus* (Förster) (pollen obtained from a single specimen, but frequently observed foraging), *Andrena miserabilis* Cresson (pollen obtained from specimens in pan traps; Table 3), *Andrena morrisonella* Viereck (observed visiting, but almost no pollen was collected; Table 3), *Lasioglossum acuminatum* McGinley (observed visiting, but no pollen was obtained), one *Nomada* species, and one *Sphecodes* species (both collected while nectaring on blueberry).

Pollen Analysis. *A. carolina* showed a high level of floral constancy for *Vaccinium*; nearly all specimens were found to carry $\approx 100\%$ pure *Vaccinium* pollen ($n = 37$, Table 3). *Andrena vicina* ($n = 12$) and *A. carlini* ($n = 12$) carried pure loads of *Vaccinium* pollen in about half of the specimens (0.40 and 0.53, respectively; Table 3). Specimens labeled as *Andrena* sp. 2, which probably included mostly *A. carolina* (these were specimens from which pollen was obtained before they were assigned an ID number and so could not be tracked to species identity), were more likely to carry 100% pure *Vaccinium* pollen than pollen from other species ($n = 15$, on average 0.72; Table 3). Few samples of other species were analyzed for pollen composition due to the low numbers collected, but the data agree with previous records (e.g., Hurd 1979) that several species of *Colletes* and several halictine species also collect *Vaccinium* pollen (Table 3).

New Species Range Extensions. During the 3 yr of collecting, we found eight new species that have never

Table 3. Wild bees collected or captured during blueberry bloom at 15 farms in SW Michigan in 2004–2006 from which pollen was obtained and examined for the presence of *Vaccinium* pollen

Family species	No. specimens sampled for <i>Vaccinium</i> pollen	Proportion <i>Vaccinium</i> pollen	Proportion of total wild bees collected in pan traps during bloom	No. specimens collected while foraging on blueberry	Floral records ^a
Andrenidae					
<i>Andrena carlini</i>	12	0.40	0.04	11	H; M&E
<i>A. carolina</i>	37	0.99	0.16	13	H; M&E
<i>A. cressonii</i>	3	0	0.01		
<i>A. imitatrix</i> or <i>morrisonella</i>	6	0.01	0.02	1	New floral record this study
<i>A. miserabilis</i>	7	0.13	0.03		New floral record this study
<i>A. morrisonella</i>	1	0	<0.01		
<i>A. nasonii</i>	2	0	<0.01		
<i>A. perplexa</i>	1	0	<0.01		
<i>A. vicina</i>	12	0.53	0.04	6	M; H; M&E
<i>Andrena</i> sp. 1 (large)	3	0.21			
<i>Andrena</i> sp. 2 (medium)	15	0.72			
<i>Andrena</i> sp. 3 (small)	1	0.03			
<i>A. (Melandrena)</i> sp.	1	0.02			
<i>A. (Trachandrena)</i> sp.	3	<0.01			
Colletidae					
<i>Colletes inaequalis</i>	1	0.99	<0.01		M&E
<i>C. thoracicus</i>	3	0.36	<0.01		H
<i>C. validus</i>	2	0.65	<0.01		M; H
Halictidae					
<i>Agapostemon sericeus</i>	1	0.50	<0.01		New floral record this study
<i>Augochlora pura</i>	1	0.90	0.02	1	M; H; M&E
<i>Augochlorella aurata</i>	2	0.49	0.05	1	M; H; M&E
<i>Halictus rubicundus</i>	1	0.02	<0.01	1	M&E
<i>Lasioglossum coriaceum</i>	6	0.53	0.03		M&E
<i>L. (Evyllaesus)</i> sp.	1	0.14		1	
All other wild species (n = 94)			0.56		

^a M, Mitchell (1960, 1962); H, Hurd (1979); M&E, MacKenzie and Eickwort (1996).

been recorded in southwest Michigan (Table 4). Seven are new state records and are new northern extensions of their previously recorded ranges. It is particularly surprising that *Andrena confederata* Vierdeck and *Andrena hiliaris* Smith were found this far north (see Table 4 for details). The remaining species, *A. nigrae* Robertson, is newly detected in southern Michigan, having been reported previously in the northeastern portion of the lower peninsula of Michigan (Ribble 1974) (Table 4).

Response of Bees to Trap Position and Color. Wild bees were more likely to be caught in edge traps than in interior traps in all 3 yr (2004: $F_{1,58} = 5.85, P = 0.02$; 2005: $F_{1,58} = 8.17, P = 0.006$; 2006: $F_{1,58} = 11.35, P = 0.001$) (Fig. 4). Wild bee richness followed a similar pattern with a greater number of species caught in traps placed at the edge than in the interior (2004: $F_{1,58} = 7.01, P = 0.01$; 2005: $F_{1,58} = 6.05, P = 0.02$; 2006: $F_{1,58} = 12.85, P = 0.0007$). Wild bee abundance (Fig. 4) or species richness did not vary with trap color in any of the 3 yr ($P > 0.05$). In contrast, honey bees responded to trap color and were more likely to be caught in white than yellow traps in all years (2004: $F_{1,58} = 7.15, P = 0.01$; 2005: $F_{1,58} = 14.35, P = 0.0004$; 2006: $F_{1,58} = 12.18, P = 0.009$) (Fig. 4); however, their captures did not vary significantly with trap position ($P > 0.05$).

The response of individual native bee species to trap position and color varied across the eight most abundant species known to forage on *Vaccinium* that were present in each year. *A. vicina* ($F_{1,57} = 7.27, P = 0.009$)

and *L. coriaceum* ($F_{1,57} = 7.03, P = 0.01$) were more often captured in white than yellow traps, whereas *A. carolina* was more often captured in yellow than white traps ($F_{1,57} = 7.62, P = 0.008$). *C. calcarata* or *dupla* ($F_{1,57} = 10.87, P = 0.002$), *A. aurata* ($F_{1,57} = 8.84, P = 0.004$), and *L. pilosum* ($F_{1,57} = 4.44, P = 0.04$) were all more often captured in traps at the field edge rather than the interior. *A. carlini* and *L. imitatum*, the other two abundant wild bee species known to forage on blueberry, showed no affinity for either trap color or position in the fields ($P > 0.05$).

Discussion

This study provides a comprehensive view of the pollinator community in Michigan blueberry fields, documents the most common native species pollinating blueberry, and describes effective methods for passive monitoring of these bees. In total, 166 wild bee species were trapped throughout the growing season in and around blueberry fields, with the majority of these species tending to be rare (one to two specimens) and not occurring in every year of the study (Table 1). During blueberry bloom, 112 wild bee species were trapped over 3 yr, varying between 69 and 82 species each year. Of the native bees captured during bloom, soil-nesting *Andrena* and Halictinae were the most abundant, with the genus *Andrena* being the most species-rich taxon (54 species, Table 1). This finding agrees with a previous study of bees associated with highbush blueberry in upstate New

Table 4. New species range extensions for bees captured in pan traps in Michigan blueberry fields in 2004–2006

Family species	Sites details	Latitude/longitude	Notes
Andrenidae			
<i>Andrena confederata</i>	Allegan Co., Saugatuck Twp., 2 mi ESE of Douglas, Michigan	42° 37.589/086° 10.117	Occurrence of this species in Michigan is quite surprising as Bouseman and LaBerge (1979, map Fig. 10) reported this species north only to southern Illinois, southern New York, and southern New England. One specimen was found at this semi-abandoned site.
<i>Andrena hiliaris</i>	Allegan Co., Ganges Twp., 3 mi WSW of Fennville, Michigan	42° 34.917/086° 09.107	Occurrence of this species in Michigan is surprising, because Bouseman and LaBerge (1979) (map fig. 7) record this "relatively rare, southeastern" species from inland states north only to Missouri and West Virginia and from Atlantic Coastal states north only to southern New York and southern New England. Their records of <i>A. hiliaris</i> from Ithaca in Central New York are believed to be incorrect, because putative specimens in the Cornell University collection were found by J.S.A. to be misdetermined. The identification of <i>A. hiliaris</i> from Michigan was verified by direct comparison to reliably determined <i>A. hiliaris</i> and <i>Andrena illini</i> Bouseman & LaBerge (similar species to <i>A. hiliaris</i> known from Indiana and northern Illinois) specimens. Three specimens were found at this semiabandoned site.
<i>Andrena neonana</i>	Allegan Co., Saugatuck Twp., 2 mi ESE of Douglas, Michigan; Van Buren Co., Covert Twp., 1.2 mi NW of Toquin, MI	42° 37.589/086° 10.117; 42° 16.075/086° 13.997	New state record. One specimen was found at each of two sites. Allegan site was semiabandoned, the other was commercially managed.
<i>Andrena nigrae</i>	Allegan Co., Ganges Twp., 3 mi WSW of Fennville, MI; Ottawa Co., Park Twp., 4 mi WNW of Holland, MI	42° 34.917/086° 09.107; 42° 49.122/086° 10.236	New site records; previously found in the northeastern Lower Peninsula of Michigan (Ribble, 1968: map 8). Ten specimens were collected at the Allegan site, a semiabandoned field; four specimens were collected at the other site, a commercial field.
<i>Pseudopanurgus nebrascensis</i>	Allegan Co., Ganges Twp., 1.3 mi NNE of Glenn, MI; Van Buren Co., Covert Twp., 1.2 mi NW of Toquin, MI	42° 32.148/086° 12.896; 42° 16.075/086° 13.997	New state record. Two specimens collected in Allegan, one in Van Buren; both sites are commercial fields.
Apidae			
<i>Eucera atriventris</i>	Allegan Co., Ganges Twp., 3 mi WSW of Fennville, MI	42° 34.917/086° 09.107	New state record. One specimen from a semiabandoned field.
<i>Melissodes apicata</i>	Allegan Co., Saugatuck Twp., 2 mi ESE of Douglas, MI	42° 37.589/086° 10.117	New state record. Specialist on <i>Pontederia cordata</i> L.; found at a semiabandoned site near the Kalamazoo river.
Megachilidae			
<i>Osmia virga</i>	Allegan Co., Laketown Twp., 4 mi NE of Saugatuck, MI; Allegan Co., Saugatuck Twp., 2 mi ESE of Douglas, MI; Ottawa Co., Park Twp., 4.5 mi NW Holland, MI	42° 41.677/086° 08.920; 42° 37.589/086° 10.117; 42° 50.604/086° 09.902	New state record. Probable specialist on Ericaceae (M. Arduser, personal communication). One specimen was found at each site. The site near Douglas is semiabandoned. The others are commercial fields.

All known state occurrences for these species, including the new Michigan records, can be found on global bee maps at www.discoverlife.org.

York (MacKenzie and Eickwort 1996) and expands the list of species present in the highbush blueberry habitat. The most abundant *Vaccinium* foragers identified in our samples were three *Andrena* spp. (*A. carolina*, *A. carlini*, and *A. vicina*), the species complex of *C. calcarata/dupla* and four halictid species (*A. aurata*, *L. coriaceum*, *L. imitatum*, and *L. pilosum*). All were present before bloom and five were also present after bloom, as predicted based on knowledge of their flight seasons (Mitchell 1960, 1962; Giles and Ascher 2006). Activity periods that extend beyond crop

bloom suggest a need for noncrop floral resources to help support populations of bees nesting in or near blueberry fields. For the *Vaccinium* specialist *A. carolina* these include other *Vaccinium* species such as deerberry (Cane et al. 1985) found within the range of *A. carolina*, but not in Michigan (USDA–NRCS 2008).

Native bee abundance and species richness were greater in traps placed at the edges of blueberry fields than at the interior. This finding corresponds to previous studies of native bees in agricultural systems that

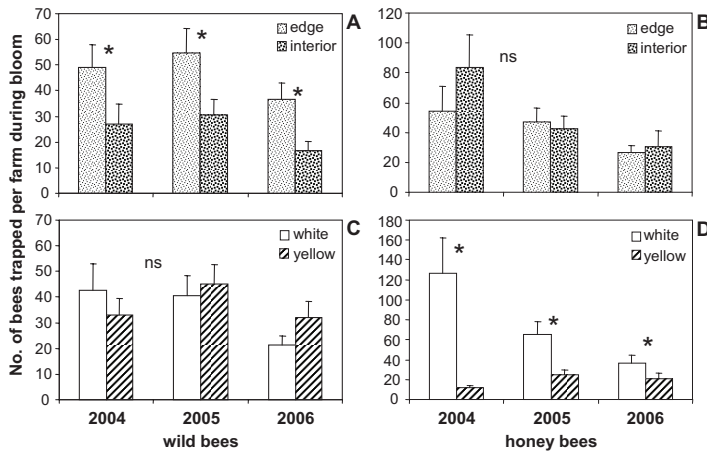


Fig. 4. Wild bee and honey bee response to (A and B, respectively) trap placement (edge versus field interior) and (C and D, respectively) pan trap color (white versus yellow) across three years during bloom in highbush blueberry fields in southwestern Michigan. Stars indicate significantly different means within each year ($P < 0.05$); ns, not significant.

have repeatedly found greater native bee abundance and diversity at field edges, presumably closer to nesting sites and alternative foraging material (e.g., Cane 2001). Although abundance of the blueberry specialist *A. carolina* followed this pattern, individuals were also collected inside fields. The timing of this species' emergence and adult activity coincides closely with *Vaccinium* bloom (including that of later-blooming deerberry where this occurs), and we have observed nesting sites of this and other *Andrena* in soil within fields (J.K.T., unpublished data; also see Osgood 1972). These life history traits of *A. carolina* and other *Andrena* may facilitate their survival in commercial blueberry farms. Whereas generalist bees present before or after bloom could be negatively affected by insecticide applications and other management practices administered at these times, the specialist *A. carolina* likely builds nests primarily during bloom when only bee-safe pest management practices are used, allowing it to provision nests with minimal exposure to detrimental crop management practices. At the community level, conservation strategies that reduce the impact of postbloom pest management practices on nontarget insects are needed to protect wild bees with extended flight periods (including all eusocial species) that contribute to blueberry pollination.

This 3-yr study of the bee community associated with highbush blueberry agriculture demonstrated the utility of pan traps to monitor and describe the bee community over time. Pan trapping was effective at detecting rare species and provided an estimate of the relative abundance of the common species. Honey bees and native bees associated with *Vaccinium* were more likely to be captured in white pan traps than yellow. This could be due to the similarity in color between the white blueberry flowers and the white traps, because individual bees tend to remain constant in their foraging effort, collecting nectar and pollen from a single species of flower (Wilson and Stine 1996). Leong and Thorp (1999) found that male and

female *Andrena pulverea* Viereck (cited as *Andrena limnanthis* Timberlake), an oligolectic bee of white-flowering *Limnanthes douglasii rosea* (Benth.) Mason, were more often captured in white pan traps than in blue or yellow traps. An exception to the floral constancy/sensory preference of oligoletes hypothesis for explaining pan trap color preference in our study is *A. carolina*, a known specialist of *Vaccinium* spp. This species was often seen foraging on blueberry, with almost pure *Vaccinium* pollen on specimens collected in pan traps, but it was captured more often in yellow pan traps than in white (Table 5). More research is needed to explore the degree to which preferences for flower color affects response of native bees to pan traps.

A. mellifera was the most abundant bee species captured during bloom, composing one third to one half of all bee individuals captured in pan traps. The ratio of honey bees to native bees was much higher in the commercial fields during bloom, reflecting the growers' practice of stocking fields with honey bee hives. Before bloom, honey bees were rarely found (Table 1) and this was also the case after bloom when hives are removed from fields. The apparent lack of feral honey bee colonies remaining near blueberry fields in southwest Michigan emphasizes the dependence of highbush blueberry production on managed honey bees and the need for conservation practices aimed at encouraging native bees associated with blueberry habitat.

For native crops such as blueberry, particularly those that require sonication to release pollen, pollen-collecting native bees are likely to provide an important component of the pollen deposition that increases crop yields. This will be important when weather conditions do not favor foraging by *A. mellifera*, as often occurs during the early spring bloom period of blueberry. Bumble bees are known to remain active at lower temperatures than honey bees (Heinrich 2004). This and their more efficient pollination of blueberry

flowers (Javorek et al. 2002) has led to the use of commercially reared colonies of *B. impatiens* by some growers to augment natural populations that are scarce during blueberry bloom. In this survey, relatively few bumble bees were captured during bloom, although we found seven species including *B. impatiens* and the social parasite *B. citrinus* (Table 1). The low numbers are likely a reflection of both their ability to avoid being captured in pan traps and their natural phenology.

Future studies aimed at conservation of native pollinators in highbush blueberry of the Great Lakes region should target the several *Andrena* species that emerge before bloom, some of which also have been reported as the most numerous native pollinator in apple orchards in upstate New York (Gardner and Ascher 2006; also see Atwood 1933). These include the specialist *A. (Andrena) carolina* and the relatively large *Andrena (Melandrena)* species *A. carlini* and *A. vicina* in southwestern Michigan, and likely also the related species *A. nivalis* and *A. regularis* at more northern sites (Bouseman and LaBerge 1979). Managing *Andrena* for crop pollination will be challenging because it is not known how to consistently induce and enhance their nesting aggregations in soil. *Osmia atriventris* Cresson or *pumila* Cresson are the most abundant mason bees present in spring (Table 1) and will nest in preformed cavities (Cane et al. 2007); so, these species may have more immediate potential as managed pollinators of highbush blueberry.

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