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ECOLOGY AND CONSERVATION OF WILD BEES ASSOCIATED WITH HIGHBUSH BLUEBERRY FARMS IN MICHIGAN

By

Julianna Kristen Tuell

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ABSTRACT

ECOLOGY AND CONSERVATION OF WILD BEES ASSOCIATED WITH HIGHBUSH BLUEBERRY FARMS IN MICHIGAN

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The objectives of these studies were: 1) to develop a method for pan trapping bees in highbush blueberry (Ericaceae: *Vaccinium corymbosum* L.); 2) to describe the structure of the endemic bee community associated with blueberry and determine to what extent wild bees contribute to its pollination; 3) to examine the relationship between wild bee community structure and both local habitat features and pest management practices; 4) to evaluate native perennial plants for attracting bees; and 5) to examine blueberry bee community structure in the context of landscape spatial scales. Pan traps elevated in the canopy of flowering blueberry collected more bees than traps placed on the ground or above the canopy. This method was used at 15 blueberry farms in southwest Michigan to characterize the bee community present prior, during, and after blueberry bloom for three years (2004-6). Honey bees, primarily from rented hives, comprised 50-66% of all the bees captured in pan traps each year during bloom. The remainder were wild bees, mainly soil nesting bees in the families Andrenidae and Halictidae. *Andrena carolina*, a solitary bee that is oligolectic on Ericaceae, was the most abundant species captured in pan traps during bloom (14%). Bees collected while foraging (n = 22 species) and pollen carried by bees in pan traps (n = 126 specimens) were used to confirm which bees were foraging on blueberry. In pan trap samples during bloom, there was high species turnover from year to year with 79 species recorded on average each year out of a total of 120 species over the three years. Wild bees were more often captured in traps at the field edge than in the interior. In simple linear regressions (SLR) of bees and field characteristics, bee species richness increased with flowering plant species in 2005, and declined with the local frequency of adjacent blueberry fields. Bee diversity (H') was also lower in fields with more nearby blueberry fields. Native bee abundance and richness in 2004 along with bee diversity in 2005 declined with increasing insecticide program toxicity (IPT). In a redundancy analysis of the same characters, IPT explained the greatest amount of variation in the bee species data in 2004, and vegetation attributes explained variation in the species in 2005 and 2006. Of the 43 native perennial plants that were evaluated, all but 2 were visited at least once by non-*Apis* bees (n = 1393), but there were 9 that were visited most frequently. Floral area explained 33% of the bee diversity at particular plant species. The response of wild bees to the proportion of different landscape types around blueberry fields was evaluated at 5 nested scales using 250, 500, 750, 1000, and 1500 m radius circles. Forest margins (<10 m from the forest edge), human settlement, annual cropland, and blueberry plantations were the most abundant landscape types at each of the spatial scales. Total bee abundance, richness, and diversity did not vary significantly with any of 6 categories of land use at any of the spatial scales, however, *A. carolina* responded to the proportion of human settlement at the 1500 m scale, and *Ceratina calcarata/dupla* responded to the proportion of blueberry plantations and semi-natural habitat at the 250 m scale. Three of 4 blueberry fruit yield attributes increased with the proportion of blueberry habitat and decreased with the proportion of semi-natural habitat within 500 m of the focal field. Implications for the conservation of native bees and their importance in blueberry pollination are discussed.

DEDICATION

To Matthew

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Julianna Tuell

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INTRODUCTION

Arthropod-mediated pollination is an evolved mutualism in most angiosperms (Willemstein 1987) and is an essential ecosystem service that directly contributes to plant productivity in natural and agricultural landscapes (Kevan 1991, Kearns and Inouye 1997, Nabhan and Buchmann 1997, Kevan and Phillips 2001, Potts et al. 2003, Fontaine et al. 2006). Ecosystem services are "the conditions and processes through which natural ecosystems, and the species that make them up, sustain and fulfill human life" (Daily 1997). Many agricultural crops require insect-mediated pollination for economical yields, and this is usually provided by bees (Free 1993, Delaplane and Mayer 2000). It has been estimated that 35% of global crop yields of fruit, vegetables, and seeds are dependent upon bee-mediated pollination (Klein et al. 2006).

For crops that require pollination, large commercial farms typically rely on thousands of honey bee (*Apis mellifera* L.) colonies that are trucked in to the fields by itinerate beekeepers. However, there are more than 4000 other bee species that are native to North America (Michener 2000) and contribute to crop pollination at an estimated value of $3.07 billion of fruit and vegetables in the United States annually (Losey and Vaughan 2006). There is growing concern about the health of both honey bee and wild bee populations around the world (Allen-Wardell et al. 1998), and the conservation of wild bees may be viewed as a strategy towards sustainable crop pollination (Southwick and Southwick 1992, Kevan and Phillips 2001, Klein et al. 2006). Bee conservation efforts have been underway for more than a decade in Europe (Edwards 1996), but there has been relatively little awareness of the need for pollinator conservation in the US. A recent report from the National Academy of Sciences (2006) has highlighted that we know very little about the status of pollinators in North America.

This review will include: 1) a brief history and current status of crop pollination by bees in North America; 2) the biology of non-*Apis* bees; 3) agricultural practices that are likely to affect endemic bee communities; 4) the influence of habitat quality and surrounding land use on endemic insect communities in agricultural ecosystems; and 5) the pollination requirements of highbush blueberry (*Vaccinium corymbosum* L.).

HISTORY AND CURRENT STATUS OF CROP POLLINATION IN NORTH AMERICA

Honey bees – the first managed pollinator. Honey bees are native to the Eurasian continent and have been managed for pollination for the past 50 years (DeGrandi-Hoffman 2003). Honey and beeswax production have been important to human civilization for thousands of years, as seen in Neolithic rock paintings, ancient Egyptian hieroglyphics, and in the writing of Aristotle, Virgil and Pliny (Martin and McGregor 1973). Recognition of the role of bees in plant pollination was not reported until 1682, and formally documented by Koelreuter in 1761 (as cited in Martin and McGregor 1973). The first record of honey bees (*Apis mellifera* L.) being introduced into North America from Europe is from 1607 when early settlers brought them to Jamestown for their honey and wax production (DeGrandi-Hoffman 2003). Thomas Jefferson wrote in 1788 that native Americans called honey bees the "white man's flies" as they were often used as indicators of nearby European settlements (as cited in DeGrandi-Hoffman 2003).

Part of the evolution in thinking about honey bees as crop pollinators was in response to evolving agricultural practices. Transition from the small polycultural family farms in relatively complex landscape matrices prior to the Great Depression and World War II to the large monocultural and highly mechanized corporate farms in relatively simple landscape matrices resulted in greater dependence on managed pollinators. In a polycultural setting, native bees living in the vicinity were often plentiful enough to provide crop pollination services and honey bees were kept for the honey and wax they produced, contributing incidentally to crop pollination. In the current monocultural model of farming, blocks of flowering crops have become too large for endemic bees to pollinate, and so the practice of transporting thousands of honey bee hives to pollinate these vast plantations is now common (see DeGrandi-Hoffman 2003 for a succinct review of honey bee history in North America). Indeed, the annual economic value of honey bees in North America is estimated to be $14.6 billion (Morse and Calderone 2000) ($17.1 billion when adjusted for inflation to represent 2006 dollars).

The majority of honey bee workers are nectar foragers and are typically not the most efficient pollinators of crop plants (Westerkamp 1991). However, they make up for their relatively low pollination efficiency in many crops by being available in great numbers (Dogterom and Winston 1999). Interest in pollination by native and/or non-managed pollinators is increasing as evidence mounts that many crops benefit from visits by native bees (Torchio 1994). For instance, some crops have floral morphologies that make them better suited to native bees that can sonicate, or vibrate, the anthers to release pollen (e.g. members of the Solanaceae and Ericaceae families) (Buchmann 1983, Morandin et al. 2001b). Other crops may have sufficient open floral morphology to allow easy nectar access and pollen transfer, but they bloom in early spring when weather conditions are highly variable and often colder than when honey bees are apt to forage (e.g. cherry, apple, and early varieties of blueberry) (Boyle and Philogene 1983). Many native solitary bee species that emerge in synchrony with the bloom of particular native crop plants are well-adapted to these conditions (MacKenzie and Averill 1995, MacKenzie and Eickwort 1996, Javorek et al. 2002). A foraging behavior, called trap-lining, or foraging along a row instead of across rows, can also limit honey bee pollination potential in crops that provide the greatest yield when cross-pollinated, such as those that are planted with male pollenizers (apples) or in alternating rows of a different cultivar (e.g. rabbiteye blueberries, *V. ashei*). There is some recent evidence that the presence of native bees has a synergistic effect on honey bee pollination of sunflowers for the production of hybrid seed, by causing trap-lining honey bees to be disrupted (Greenleaf and Kremen 2006).

Challenges to traditional beekeeping. Over the past 20-30 years, a combination of parasitic mites and diseases of honey bees have rapidly reduced the number of beekeepers and the number of hives available for pollination. Winter mortality in honey bee colonies in the United States has dramatically increased since the accidental introduction of two parasitic mites: tracheal mites (*Acarapis woodi*) in 1984 and Varroa mites (*Varroa destructor* (listed as *V. jacobsoni* in Frazier et al. 2000)) in 1987 (Frazier et al. 2000). There are few effective treatments against the mites, and this has led to concerns about chemical resistance (Frazier et al. 2000). Also, a number of debilitating diseases, that affect mainly the brood in a hive, also pose tremendous challenges to beekeepers (Free 1993). More recently, a mysterious ailment called "Colony Collapse Disorder," in which the bees disappear from hives, has caused many commercial beekeepers to lose large portions of their overwintering stock (Gill 2007).

In addition to disease and mite problems, "Africanized" bees are another significant concern for the already beleaguered beekeeping industry. Africanized bees result from the hybridization of a European subspecies with an African subspecies (*Apis mellifera scutellata*). The African subspecies is more easily irritated and aggressive and swarms with greater frequency than the European subspecies, making Africanized colonies particularly dangerous to nearby workers and livestock (Visscher et al. 1997). Since 1956 when 24 swarms of imported *A. m. scutellata* escaped in Brazil, it was predicted that they would eventually arrive in the United States (Martin and McGregor 1973). Hybridized or "Africanized" bees entered Texas in 1990, and have since spread to all the states bordering Mexico (Visscher et al. 1997). Although further encroachment into the US has been much slower than predicted, Africanized bees have hybridized with both wild and domesticated honey bee populations throughout the agricultural region of southern California, causing many beekeepers to go out of business there. As a result hive shortages have occurred in some areas (Visscher et al. 1997). Since a large proportion of available hives in the U.S. pass through the California almond crop, it was predicted that eventually the Africanized bee would spread further (DeGrandi-Hoffman 2003), and recently, Africanized bees have been detected in southern Oklahoma, southwestern Arkansas, and Florida (DeGrandi-Hoffman et al. 2006).

Other managed bees. While honey bees are by far the most important and abundant managed pollinators, there are several other bee species that are managed and used for crop pollination. Commercially reared bumble bee colonies have been used in greenhouses with much success (Morandin et al. 2001a, Morandin et al. 2001b), but they have also been evaluated and used to pollinate crops in outdoor settings (Bohart 1972, Stubbs and Drummond 2001a). In natural systems, bumble bee queens produced at the end of the summer overwinter, emerging in early spring to initiate a colony. Most commercial colonies were originally started by collecting wild *Bombus* queens and then manipulating them into beginning their colony much earlier than they would in nature, so that workers are available to pollinate early blooming crops (Kearns and Thomson 2001).

Several solitary nesting bees are managed or encouraged to nest near agricultural fields as well. The alkali bee, *Nomia melanderi*, is encouraged to nest near alfalfa fields by providing the right kind of soil in which it will nest (Bohart 1972). Various mason and leafcutting bees have been encouraged to nest near agricultural fields by providing manmade straws or blocks of wood drilled with holes. Some growers will incubate the bees during the winter and then place them in ambient conditions in time for emergence with a particular crop bloom. Mason bee species that have been managed for pollination of fruit crops include the horn-faced bee (*Osmia cornifrons*) (Bohart 1972) and the blue orchard mason bee (*O. lignaria*) in cherry orchards (Bosch and Kemp 2001), *O. lignaria* in almond orchards (Bosch et al. 2000), and *O. atriventris* in lowbush blueberry heaths (Drummond and Stubbs 1997a). *Osmia lignaria propinqua* has been evaluated for the pollination of meadowfoam (*Limnanthes alba*) (Jahns and Jolliff 1991), while the alfalfa leafcutter bee (*Megachile rotundata*) has been managed for pollination of alfalfa (Bohart

1972) and lowbush blueberry (MacKenzie and Javorek 1997, Stubbs and Drummond 1997a). Overall, these studies indicate that there are several non-*Apis* managed bees that could serve as effective alternatives or supplements to honey bee pollination for some crops.

AN OVERVIEW OF THE BIOLOGY OF NON-*APIS* BEES

Taxonomy and morphology. Bees are Hymenoptera in the superfamily Apoidea, and are closely related to sphecid wasps (Michener 2000). The main difference between bees and their close relatives, aside from morphological differences, is that they provision their nests with pollen mixed with nectar, as opposed to prey items. This behavior, along with morphological characters such as plumose hairs that attract electrostatically charged pollen (Vaknin et al. 2000) and dense pollen-carrying hairs on their hind legs, thorax, or abdomen called scopa (Michener et al. 1994) make them an important group of pollinators. *Apis mellifera* is just one of more than 4000 different species of bees found in North America (Michener 2000). In Michigan, 398 species have been recorded, consisting of 48 genera in 6 families (Mitchell 1960, Hurd, Jr. 1979, Michener et al. 1994).

Bees can be broadly grouped by family according to tongue length, and those with the shortest tongues are thought to be most closely related to sphecid wasps. There are 5 main families of bees in Michigan. In order from shortest to longest tongues, they are: Colletidae (2 genera, 32 species), Andrenidae (5 genera, 91 species), Halictidae (13 genera, 104 species), Megachilidae (11 genera, 72 species), and Apidae (16 genera, 98 species) (Mitchell 1960, Hurd, Jr. 1979, Michener 2000). The details of bee biology described below are paraphrased from Michener's *The Bees of the World* (2000), unless otherwise noted.

Social guilds. Bees can be divided into ecological guilds in several ways. One way is to consider their sociality. Bees can be solitary with each female provisioning a nest containing her own offspring, communal with several females sharing the same nest entrance but provisioning for their own offspring, semi-social with one to a few queens and a number of female workers that may or may not lay some of their own eggs, social with one queen and many female workers who are unlikely to lay their own eggs, or cleptoparasitic or cuckoo bees with females laying their eggs in the nests of other bees.

Most species of bees are solitary, producing one generation per year. Many of them nest in large aggregations. Males and females of solitary bees usually emerge at about the same time from overwintering as adults or pupa, though there is often some degree of protandry. Upon emergence they mate, and females either excavate or locate a suitable nest in which to lay their eggs. The eggs develop into adults that emerge the following season. Communal nesting is somewhat similar except for the shared nest entrance and because the females will often take turns guarding the entrance. Many solitary bees emerge in synchrony with particular plants and are considered to be oligolectic, i.e. they collect pollen from plants within a single genus or family.

Semi-social and social bees produce multiple generations per season, and probably as a consequence, they visit plants from multiple families across a broad temporal range. There is a continuum of behaviors from some of the more loosely-social groups of halictid bees, to the very highly eusocial behavior of honey bees. Division of labor in semi-social bees can be very flexible. Except for the special case of honey bees, who maintain a perennial colony, in general, female social bees emerge from overwintering already mated to begin the establishment of a new nest. Queens must forage until the first set of workers emerge. Towards the end of the season, drones and new queens are produced, they mate, and then the new queens find an overwintering site.

Nesting guilds. Another way to group bees is by nesting behavior. Most bee species excavate nests in soil. Soil nesting bees can be found in every bee family except for the Megachilidae. Most megachild bees nest in preexisting cavities such as beetle galleries in logs and use mud, pieces of leaves, or plant fibers to create nest cells. They can be easily encouraged to nest in manmade straws or blocks of wood drilled with holes (Shepherd et al. 2003). Other megachilids use pebbles and resin to construct nests that they attach to a substrate. Bumble bees (*Bombus* spp.) in the family Apidae nest in well-insulated, preexisting cavities and many prefer abandoned rodent burrows or grassy tussocks (Goulson 2003). Carpenter bees, also in the family Apidae, excavate nests in solid wood (*Xylocopa* spp.) or in pithy plant stems (*Ceratina* spp.).

Both social and nesting guilds are important to consider in bee conservation efforts. For instance, bees that produce multiple generations throughout the season are likely to be constrained by the availability of season-long foraging resources and intensity of agricultural practices, such as pesticide use. Likewise, bees that nest in preexisting cavities are likely to be constrained by the availability of nesting sites.

AGRICULTURAL PRACTICES LIKELY TO AFFECT ENDEMIC BEES

Agricultural intensification. Mechanized agriculture and the introduction of inexpensive pesticides developed during World War II significantly impacted crop production methods, with the effect that more land was put into production, planted in large monocultures, and maintained with heavy machinery and broad-spectrum pesticides (Martin and McGregor 1973). While opportunities for pollination services increased with these changes in crop production, beekeeping as an occupation became less profitable in the US and some other countries in the 1950s and 60s due in part to these different land use patterns that resulted in reduced year-long foraging habitats for bees (Martin and McGregor 1973). By the 1970s, it was recognized that intensive land use was a major limiting factor to commercial beekeeping and to the conservation of valuable native bee resources (Martin and McGregor 1973). Effects of agricultural intensification include direct and indirect risks to bees from pesticide use and the destruction and fragmentation of natural habitats.

Pesticide poisoning to bees is an important problem facing beekeepers (Martin and McGregor 1973) and the dangers of pesticides, in particular insecticides, to pollinators are well documented (Johansen 1977, Johansen and Mayer 1990, Stevenson 2003, Chauzat et al. 2006). Some herbicides are also poisonous to bees, but use of them is more a concern with regard to the destruction of potential foraging resources (Kevan 1999). Most studies have dealt with toxicity and hazards of direct exposure of honey bees to pesticides, but these results do not necessarily transfer well to other bees (Johansen and Mayer 1990, Riedl et al. 2006). Less known and often overlooked are the sublethal effects that reduce longevity and adversely affect foraging, memory and navigational abilities of some bees (Kevan 1999, Stevenson 2003, Chauzat et al. 2006, Desneux et al. 2007). One hypothesis about "Colony Collapse Disorder" is that a new neonicotinoid insecticide, imidacloprid, is causing the sublethal effect of memory loss, with the result that upon exposure, honey bees are unable to find their way back to the hive (Gill 2007). Evidence for sublethal effects of neonicotinoids has been recently presented for both honey bees (Suchail et al. 2001) and bumble bees (Morandin and Winston 2003).

Pressure to reduce the use of organophosphate and other broad-spectrum insecticides in US agriculture has increased with the implementation of the Food Quality Protection Act of 1996. With the adoption of integrated pest management programs designed to protect and enhance populations of non-target, beneficial insects and reduce environmental impact, grower awareness about pesticide risks has increased. In crops that rely on insect pollination, it is recommended that growers generally not apply insecticides during bloom (McGregor 1976, Johansen and Mayer 1990). However, there are relatively few studies on the response of native pollinators to the use of broad-spectrum insecticides within typical pest management programs.

Although the risk of bee kill from insecticides in agroecosystems has been reduced, there have been instances in Canada and in the US in which major losses of bees have occurred due to pest management activities in urban and arboreal landscapes. These have typically been associated with widespread mosquito control programs (Kevan 1999). Although not measured, the effects to populations of native bees have been expected to be severe (Kevan 1999), but there is little information relating specifically to the effects on non-*Apis* pollinators. In one documented case, application of the organophosphate fenitrothion to reduce defoliation of spruce by budworms in eastern Canada also devastated the native bee pollinators of adjacent lowbush blueberry and other native flora (Kevan and Plowright 1989). The reduction in fruit set in these plants reduced the amount of resources available to other animals and created broad disruption to the ecosystem. These ecosystem effects support the idea that pollinators can be used as sensitive bioindicators of habitat degredation (Kevan 1999).

HABITAT QUALITY AND LAND USE

Declines in abundance of pollinators and other beneficial insects are thought to be the result of habitat loss and fragmentation due to anthropogenic land use and agricultural practices associated with pest management (Kremen et al. 2002, Tscharntke et al. 2005, Biesmeijer et al. 2006). Many studies have examined the relationship between local habitat resources and the abundance and diversity of pollinators (Kells et al. 2001, Klein et al. 2004, Ricketts 2004, Forup and Memmott 2005, Pywell et al. 2005, Shuler et al. 2005, Hegland and Boeke 2006, Pollard and Holland 2006, Marshall et al. 2006). Other studies have looked at pollinator abundance and diversity in relation to landscape characteristics on larger spatial scales (Steffan-Dewenter et al. 2002, Westphal et al. 2003, Westphal et al. 2006, Winfree et al. 2006, Chacoff and Aizen 2006). In general, reduced natural communities of pollinators have been found to limit pollination and reduce crop yields (i.e. the desired ecosystem service) (Kremen et al. 2002). This has also been documented in lowbush blueberry heaths in eastern Canada and Maine (Kevan et al. 1997) and recently in highland coffee production in Indonesia (Klein et al. 2003).

Habitat quality. Most beekeepers move their hives of *A. mellifera* several times throughout a growing season to follow the crops that need pollination services and to provide their bees with alternative foraging when those crops are finished blooming. This is not possible for native bees, yet alternative foraging resources are often required to complete their life cycle. Generally regarded as weeds in crop production systems, the value of non-crop forage to pollinators and other anthophiles is high. Flowering plants have been considered for use in agricultural settings to help conserve populations of beneficial insects, including insect natural enemies (Bugg et al. 1989, Maingay et al. 1991, Bugg and Waddington 1994, Pontin et al. 2006) and pollinators (Patten et al. 1993, Kearns and Inouye 1997, Carreck and Williams 1997). Flowering plants frequently have been recommended for attracting beneficial insects in agricultural settings to reduce pest populations (Baggen and Gurr 1998, Baggen et al. 1999, Begum et al. 2006). A few studies in North America have evaluated native plants for their attraction to bees (Patten et al. 1993, Frankie et al. 2005), and some studies in the United Kingdom have evaluated pollinator attraction to cultivated (Comba et al. 1999a) and to native or naturalized (Comba et al. 1999b) flowering plants.

The effects of intensive agricultural practices on potential nesting, mating and foraging habitats for bees (and other beneficial fauna) have been recognized everywhere agriculture is practiced (Kevan 1999, Tscharntke et al. 2005, Klein et al. 2006, Winfree et al. 2006). A number of studies in agricultural systems have suggested that uncropped, flower-rich habitats directly adjacent to crop fields will increase diversity and abundance of beneficial insects in the field (Long et al. 1998, Kells et al. 2001, Croxton et al. 2002, Pywell et al. 2005, Marshall et al. 2006), and that hedges adjacent to agricultural fields in particular can hold high arthropod diversity (Pollard and Holland 2006). The creation of flower-rich field borders to provide refuge habitats that might stimulate populations of beneficial insects such as adophagous hoverflies (Syrphidae), ladybird beetles (Coccinellidae), pollinators and parasitoids (Hymentoptera) has been examined in a few cropping systems (Bugg et al. 1989, Maingay et al. 1991, Bugg and Waddington 1994, Pontin et al. 2006). In California, farmers are planting borders of flowering plants and perennial grasses around their crops in order to attract beneficial insects (Long et al. 1998). In England, resource strips and set-asides have been studied for their ability to provide resources in agricultural landscapes for bumble bees (Corbet et al. 1994, Croxton et al. 2002, Carvell et al. 2006, Carvell et al. 2007), and in Sweden one study found that grassland adjacent to agricultural fields provides a source of butterflies and bumble bees in adjacent agricultural landscapes (Ockinger and Smith 2007).

The encroachment of development and intensive agricultural methods has lead to fragmentation and scarcity of natural habitats (Edwards 1996, Westrich 1996). This disturbance is at odds with the needs of stem and ground-nesting bees and of bumble bees that prefer abandoned field-mice dens and tall grass for their nest sites (Goulson 2003). Availability of habitats for foraging and nest building is the key limiting factor for native pollinator populations (Matheson 1996).

Land use effects and proximity to natural habitat. Kremen et al. (2002) compared bee abundance and diversity of native bees among melon farms that were classified as organic-near (organic management surrounded by over 30% natural habitat within a 1km radius of the field), organic-far (organic management surrounded by <1% natural habitat within a 1km radius), or conventional-far (conventional management surrounded by <1% natural habitat within a 1km radius). These authors found that proximity to natural habitat and diversity of native bees were key to sustainable pollination of the melon crops. Because bee abundance and community assemblage naturally fluctuate from year to year, they found that overall bee diversity was more important than any particular bee species for ensuring that the melon flowers were pollinated (Kremen et al. 2002).

Landscape context has been examined for many insects of relevance to agriculture, and several studies have examined the effects of landscape matrix quality in relation to biological control and biodiversity in and around crops. In Sweden, increasing landscape diversity around cereal fields corresponded with a decrease in the establishment of the bird cherry-oat aphid, *Rhopalosiphum padi*, due to increased biological control agents inhabiting field margins (Ostman et al. 2001). In South Dakota alfalfa fields, the quality of the landscape surrounding the field explained a greater proportion of the variation in predator abundance than did the aphid populations within the field (Elliott et al. 2002). In southern Mexico coffee plantations, ground-foraging ant diversity was greater in more complex landscape matrices (Perfecto and Vandermeer 2002). These studies support the concept of landscape complexity as a driver of biodiversity and improved biologically-based food production.

The spatial scale of plant-insect interactions is based on the biology and behavior of the organism(s) in question (Thies and Tscharntke 1999, Steffan-Dewenter 2002, Thies et al. 2002). The foraging range of most native bees is unknown. However, for those that are, the size of the bee and the relative fragmentation of the habitats used for nesting, mating and foraging appear to determine their range (Westrich 1996, Osborne et al. 1999, Svensson et al. 2000, Goulson 2003). Recently, Tscharntke and Brandl (2004) reviewed the current literature on population dynamics theory and trophic interactions from a landscape perspective in relation to plant-insect interactions. They concluded that the fragmentation of landscapes is important to consider when studying any plant-insect interactions.

Bumble bees as a case study. Although bumble bee (*Bombus* spp.) nests can be difficult to locate in the wild, the habitat requirements and foraging ranges of some bumble bee species have been well studied compared to most other non-*Apis* bees. In a landscape scale microsatellite study in England, *B. terrestris* and *B. pascuorum* were found to have different nest densities and foraging ranges; *B. pascuorum* had more nests per area and a smaller foraging range of less than 312 m versus *B. terrestris*, which will forage up to 625 m from its nest (Darvill et al. 2004). Another study found that marked *B. terrestris* workers could be recaptured while foraging on highly abundant resources, i.e. crop plants, at distances up to 1750 m from their nest compared to *B. muscuorum* that tended to forage in patches that were closer to their nest (Walther-Hellwig and Frankl 2000). A study in Sweden found that bumble bees were most likely found in forest and field boundaries and in uncultivated open landscapes (Svensson et al. 2000), and that while different species preferred different habitats, the preferred nesting sites were withered grass and tussocks for all species.

POLLINATION REQUIREMENTS OF BLUEBERRY

Blueberry production in Michigan. Highbush blueberry (*V. corymbosum*) is one of several cultivated species of Ericaceae plants grown in the United States. Its growth habit is upright and bushes can reach more than 2 m high. It is planted in rows, and a field can remain in production for more than 50 years when care is taken in annual pruning. Large block plantings of single varieties are common to facilitate cultivation and harvesting (Morrow 1943, Free 1993), although this limits opportunities for cross-pollination. Blueberries are dark bluish-black berries that are both hand- and mechanically-harvested, with the first few pickings typically done by hand. In Michigan, early cultivars of highbush blueberry begin to bloom in early May, and the latest blooming cultivars finish by mid-June.

Michigan is the top producer of highbush blueberry in the U.S.; it has 18,500 acres in production in 2003 (2003-2004 Michigan Fruit Inventory) with a farm gate value of ~\$90 million per year. Most of the acreage is located in southwest Michigan in five counties that border Lake Michigan and benefit from weather moderated by the large body of fresh water. The top three cultivars in terms of acreage are 'Jersey,' 'Bluecrop,' and 'Rubel,' although much of the 'Jersey' and 'Rubel' acreage was planted prior to the 1970s (2003-2004 Michigan Fruit Inventory).

Pollination requirements of highbush blueberry. It is well-established that highbush blueberry flowers require the transfer of pollen by insects, but that they do not require cross-pollination. Merrill (1936) was the first to examine the pollination requirements of the highbush blueberry and concluded that yields from self-pollination were as satisfactory as cross-pollination. Later studies found that depending on the cultivar, cross-pollination may produce slightly larger berries (Schaub and Baver 1942, Morrow 1943, Meader and Darrow 1947) and faster ripening fruit than those that are self-pollinated (Dorr and Martin 1966). As proof of its need for pollen transfer by bees, Dorr and Martin (1966) and Brewer et al. (1969) found that blueberry bushes that were caged to exclude bees produced an eighth of the yield produced by bushes caged with bees.

Up until the early 1950s, most blueberry growers apparently obtained adequate pollination from native bees, because it was not common for them to rent honey bee hives. However, by 1965 growers felt that 'Jersey,' the predominant commercial cultivar in production at the time, had been decreasing in yield and that this reduction seemed to coincide with increasing pesticide use (Dorr and Martin 1966). Anecdotal evidence suggests that, prior to cultural changes that included clean cultivation and the widespread use of pesticides, native bees had been abundant pollinators of blueberry in Michigan. Because of this perceived decline in native bees, honey bee pollination activity on blueberry was examined and found to be adequate when supplied in sufficient numbers (Dorr and Martin 1966, and more recently in rabbiteye blueberry by Dedej and Delaplane 2003). Placement of hives singly and evenly within a blueberry plantation was recommended, because it was observed that pollination by honey bees was best close to the hive (Martin and McGregor 1973).

In the meantime, new cultivars have been introduced with new studies to determine whether there is a benefit of cross-pollination. Dogterom et al. (2000) documented that yields and development of outcrossed 'Bluecrop' bushes versus self-pollinated bushes were not significantly different. This corresponds with an earlier study by MacKenzie (1997) in which cross-pollination in 'Bluecrop' was of no benefit over self pollination, while two other cultivars ('Patriot' and "Northland') were differentially benefited, again indicating that any effect of cross-pollination is cultivar-dependent.

Dogterom et al. (2000) also found that 125 pollen tetrads were sufficient to produce maximum fruit set and minimize the time to ripen in a for 'Bluecrop.' Based on the known pollen deposition levels of honey bees (range of 5-20 tetrads/visit) and many native bees (range of 6-107 tetrads/visit) in lowbush blueberry (*V. angustifoilum*) it is clear that multiple visits from pollinators would be required to provide the optimum number of pollen tetrads (Javorek et al. 2002).

Efficiency of honey bees vs. native bees. Although most growers rely on the pollination services of honey bees in Michigan blueberry production, a variety of commercial pollination alternatives are slowly becoming available and affordable (Free 1993, Torchio 1994, Roubik 1996, Winston 1998). Honey bees are not the most efficient pollinators for every crop (Bohart 1972). Depending on their handling, some *A. mellifera* colonies can be induced to be better pollen foragers, but there is some question as to whether that would really make them better pollinators. For example, Dogterom and Winston (1999) found that honey bee colonies deprived of pollen increased pollen foraging, but not in adjacent *V. corymbosum* (cultivar 'Bluecrop') fields. On the contrary, nectar foraging honey bees were more likely to visit *V. corymbosum* and were probably providing pollination services as a secondary effect of nectar foraging (Dogterom and Winston 1999).

Other bees that do not produce harvestable honey have been managed commercially or experimentally as alternative pollinators to honey bees, and several are particularly important and proven to be consistently effective pollinators of some crops (Martin and McGregor 1973, Torchio 1990). Floral morphology can sometimes prevent direct access to nectar (Delaplane and Mayer 2000) and highbush blueberry and other blueberry species fall into this category with their long corolla tubes. Bees with longer tongues such as bumble bees, or bees that are small enough to climb inside the flower such as many halictids, may have an easier time manipulating flowers with long corolla tubes (Delaplane and Mayer 2000). In addition, pollen is more easily accessed from the porous anthers of the blueberry blossom via sonication (or buzz-pollination) achieved by some native bees such as bumble bees through vibration of their wing muscles upon landing on the flower (Buchmann 1983, Morandin et al. 2001b). Another advantage of non-*Apis* pollinators, even those not able to sonicate flowers, is that some, such as the alfalfa leaf-cutting bee (*Megachile rotundata* and other species), will begin foraging earlier in the day during cooler temperatures when *A. mellifera* are not yet active (Delaplane and Mayer 2000, Goulson 2003).

Other managed blueberry pollinators. There are other pollinators with a high degree of potential for pollination of blueberry, and studies have already been conducted to evaluate a few non-*Apis* bees for management in these blueberry crops. An orchard mason bee (*Osmia ribifloris*, family Megachilidae) was found to be an effective managed pollinator for rabbiteye blueberry (*Vaccinium ashei*) in the southeastern U.S. (Sampson et al. 2006). *Osmia ribifloris* and two other megachilids, *Osmia atriventris* and the alfalfa leafcutting bee, *Megachile rotundata*, were found to be effective managed pollinators for lowbush blueberry (*Vaccinium angustifolium*) pollination in Maine (Drummond and Stubbs 1997a, Stubbs and Drummond 1997a, Stubbs and Drummond 1997b). *Anthophora pilipes villosula* and commercially reared *Bombus impatiens*, both in the family Apidae, were also shown to be promising alternative managed bees for the pollination of lowbush blueberry (Stubbs and Drummond 2000, Stubbs and Drummond 2001a).

Community studies of blueberry pollinators. A handful of native bee community studies have been conducted in cultivated blueberry fields. One study identified the three main bee taxa visiting rabbiteye blueberry in southeastern US, which were honey bees, several species of bumble bees, and a solitary bee, *Habropoda laboriosa* (Cane and Payne 1993). The bee community of lowbush blueberry in Maine was sampled by Drummond and Stubbs (1997b), but the community composition was not reported in detail. Two studies were conducted in highbush blueberry, one as part of a survey of native bees in multiple berry crops in the Lower Fraser Valley of British Columbia, Canada (MacKenzie and Winston 1984), and another in upstate New York (MacKenzie and Eickwort 1996). A detailed listing of bee species collected in New York was provided, and a total of 42 species were observed, with the three most abundant species being honey bees, and two solitary andrenid bees, *Andrena carlini* and *Andrena carolina* (MacKenzie and Eickwort 1996). These studies demonstrate the variation that is typically observed from one blueberry production region to another.

FOCUS OF THIS PROJECT

The rich natural habitats that often surround Michigan croplands may provide the appropriate habitat for nesting, mating and alternate nectar and pollen resources for non-*Apis* bees. But to date, there has been no systematic survey of bees associated with Michigan blueberry. There is significant potential for conservation of native bees in and around *V. corymbosum* fields, to provide a pollinator community that is more reliable during early spring weather conditions and that can provide sustainable pollination services to the blueberry crop during the relatively short window of opportunity for pollination in Michigan. Bee-toxic pesticides are generally avoided during blueberry bloom, but insecticide use later in the season may be suppressing the long-term growth of native bee populations in and around fruit crops. Habitat quality and non-crop habitat surrounding fields may buffer against intensive management practices within fields.

My objectives were: (1) to determine optimum pan-trap placement for capturing bees in highbush blueberry; (2) to characterize the native bee community and to determine the degree to which native species contribute to pollination of blueberries in Michigan; (3) to determine which commercial production practices and local habitat attributes surrounding *V. corymbosum* fields are related to the abundance and diversity of native bees within the fields during bloom; (4) to evaluate native perennial plants for their relative attractiveness to Michigan bee species; and (5) to determine at what spatial scale landscape complexity affects bee abundance and diversity in highbush blueberry fields.

CHAPTER 2:

ELEVATED PAN TRAPS FOR MONITORING BEES IN CROP CANOPIES: RESPONSE OF BLUEBERRY POLLINATORS

INTRODUCTION

Bees are highly visual insects that respond to visible and UV color patterns on flowers (Chittka and Menzel 1992, Kevan et al. 1996, Gumbert 2000). This attraction to color can be exploited for monitoring bee populations by the use of passive colored pan traps that provide an inexpensive method to capture bees (Aizen and Feinsinger 1994, Leong and Thorp 1999, Baum et al. 2006). Pan traps are made from colored receptacles holding a dilute, aqueous soap solution to trap bees. These traps are typically plastic party bowls (15 cm diameter) or condiment cups (6 cm diameter) that are already colored. Or they may be painted with fluorescent paint (LeBuhn et al. 2002).

The pan trapping approach has important advantages compared to more traditional bee collection methods that use nets or aspirators. Pan traps eliminate collector bias, which is particularly important when comparing data across different studies or when using multiple collectors in the same study. They also provide an inexpensive method for sampling bee populations using consistent, easily replicated sampling intensity. Finally, collectors with minimal training can sample over a longer period of time and at multiple sites simultaneously. As with any sampling method, there are some drawbacks: pan traps may be biased toward attracting some bee taxa over others, and they do not allow determination of direct relationships between bee and flower species. In combination with other methods, however, pan trapping can be very effective. Williams et al. (2001) recommend their use in combination with netting and trap nesting methods for monitoring bee communities.

The use of pan traps to monitor bee communities is a recent development, but it is increasingly used as a sampling tool by researchers in natural landscapes and in studies comparing bee abundance in urban versus natural landscapes. For example, Leong and Thorp (1999) used blue, white, and yellow bowl traps to sample the bee community associated with a natural vernal pool plant community in California. McIntyre and Hostetler (2001) used blue and yellow pans to compare the bee communities associated with urban land use in southwest U.S. desert ecosystems and surrounding natural habitats. Russell et al. (2005) used light blue, dark blue, yellow, and white bowls to compare bee communities associated with powerline easements and grasslands in Massachusetts. Brosi et al. (2007) used pan traps to monitor the bee community associated with pastureland among forest fragments in Costa Rica. In all of these studies, the traps were placed directly on the ground among open, or low-growing vegetation. This deployment of pan traps is appropriate for many natural habitats and so is generally recommended (see: http://online.sfsu.edu/~beeplot/).

The majority of monitoring for native bees has been in natural habitats, often with little to no overhead plant canopy (e.g. extensive sampling for bees with pan traps has been conducted in the Grand Staircase-Escalante National Monument by T. Griswold et al., unpublished data). However, if this technique is applied in agricultural habitats, it will be important to consider that many crops have a vertical structure. Canopy structure has been found to be important when monitoring for pest insects, including several *Rhagoletis* flies (Diptera: Tephritidae). Vertical placement of traps has significant implications for monitoring apple maggot fly (Drummond et al. 1984), blueberry maggot fly (Teixeira and Polavarapu 2001), and the eastern cherry fruit fly (Pelz-Stelinski et al. 2006). Mature highbush blueberry (*Vaccinium corymbosum*) plants can reach over 2 m, with the majority of flowers produced in the upper half of the plant, so it is expected that pan traps placed on the ground would be less visible to bees than traps placed in the canopy where most bee foraging occurs.

The goal of this study was to determine the response of bees to vertical placement of traps relative to the canopy of highbush blueberry plants, with the expectation that pan traps in the highbush blueberry canopy would capture more bees than traps placed on the ground or above the canopy. I also tested whether three colors of commercially-available plastic bowls varied in the abundance and diversity of bees collected. Specifically, I was interested in determining whether bee species foraging on *Vaccinium* responded differently to height and color than species not known to forage on *Vaccinium.* I also compared timed observations, a method used in previous studies of bees foraging in blueberry fields, with pan trapping on the same day.

MATERIALS AND METHODS

Response of bees to trap height. This study was conducted in a highbush blueberry planting (*V. corymbosum*) at the Trevor Nichols Research Complex near Fennville, Michigan in May of 2004 and 2005. The height of yellow pan traps was varied within the canopy of the blueberry plants by placing traps on the ground or on different lengths of PVC pipe stabilized with rebar. Traps were placed on the ground, mounted 1/3rd of the way up in the canopy (between 0.46-0.6 m), 2/3rds of the way up in the canopy (between 0.9-1.2 m), or above the canopy (between 1.5-1.8 m). Traps were spaced 5 m apart and arranged in a 4 x 6 Latin square design, with six replications.

In 2004 the study was conducted on 19 May in a mature stand (cv. 'Rubel') with an average height of 1.5 m. In 2005 the study was repeated on 25 May and conducted in two blocks in the mature planting described above, and two blocks in a younger, adjacent plantation (cv. 'Bluecrop'), that had an average height of 1 m. Traps were deployed during full bloom from 10:00-19:00 h, 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 traps were constructed from 355 ml yellow plastic bowls (sunshine yellow, Amscan, Inc., Elmsford, NY) with a PVC coupler (female, double-ended, accepting 2.7 cm PVC) glued to the bottom of each bowl using plumber's cement so that the bowls could be mounted onto PVC poles of 2.7 cm diameter. The PVC poles were stabilized by slipping them over 0.6 m lengths of rebar that were pounded 0.3 m into the ground. Each pan was half filled (approx. 150 ml) with a 2% unscented soap solution (Dawn® dish soap, Procter & Gamble, Cincinnati, OH). Insects collected in the pans were strained into plastic bags, which were then stored in a cooler for transport to a -12°C freezer for later processing. Specimens were thawed at room temperature, washed in 70% ethanol, and then placed in a mesh bag through which they were fluffed and dried with a hairdryer before pinning and identification (LeBuhn et al. 2002).

Preliminary identifications of bees were made using two published dichotomous keys (Mitchell 1960, Michener et al. 1994) and the online key available through www.Discoverlife.org. Verification and further identifications were made by Dr. J.S.

Ascher of the American Museum of Natural History, Division of Invertebrate Zoology. Voucher specimens are held in the Albert J. Cook Arthropod Research Collection at Michigan State University.

Assumptions for equal variance (Levene's test) and normality (Shapiro-Wilk test) were met without transformation of the 2004 bee abundance data, which were tested in relation to trap placement using a mixed model analysis of variance (PROC MIXED, SAS V9.1). Trap height was the fixed effect and replicate (n = 6) was the random effect. In 2005, bee abundance was summed across the six traps of each treatment (ground, 1/3rd canopy, 2/3rd canopy, and above canopy) within each block, and then data were square-root transformed to meet assumptions of normality (Shapiro-Wilk test) and equal variance (Levene's test). A mixed model ANOVA with trap height as the fixed effect and block (n = 4) as the random effect was used to determine whether bee abundance varied significantly with trap placement. Also in 2005, andrenid and halictid bee abundance were examined separately using the same methods as for the complete bee fauna. The Tukey-Kramer means separation test was conducted for all analyses.

Response of bees to trap color. Blue, white, and yellow bowls (marine blue, snow white, and sunshine yellow, respectively; Amscan, Inc., Elmsford, NY) were compared during bloom on 19 May 2004 at the same highbush blueberry (cv. 'Rubel') planting described above. Traps were mounted with PVC couplers on 1.2 m lengths of PVC pipe as described above, were spaced 5 m apart, and arranged in a 3 x 6 Latin square design (six replications), from 10:00-19:00 h when minimum weather conditions for bee activity were met (see above). Specimen handling and identification methods used were the same as in the height study. Bee abundance was normally distributed without transformation and was analyzed to determine whether bee captures varied among trap colors, using a mixed model ANOVA with trap color as the fixed effect and replicate as the random effect. A Pearson chi-square analysis was conducted to determine 1) whether *Vaccinium* foragers were more likely to be collected in one color over the other, and 2) whether andrenids and halictids preferred one color over the others.

Comparison of pan trap sampling to timed observations. On 2 and 7 June 2005, 20 pan traps were deployed between 8:00 and 16:00 hrs at a semi-abandoned blueberry field near Douglas, Michigan. Pan traps were elevated on PVC poles as described previously, to within 2/3rd of the highbush blueberry canopy. Meanwhile, 15 1-min observations were made four times (8:00-9:00, 10:00-11:00, 12:00-13:00, and 14:00-15:00 hrs) on each day at blueberry bushes in the same field. Bees collected in pan traps were identified to genus or species using the methods described above. Bees observed foraging on blueberry were identified to genus (with the exception of genera in the Tribe Augochlorini) or species when only one species was known to be present in the area (e.g. *Apis mellifera* and *Xylocopa virginica virginica*). Abundance and generic composition of the samples were compared.

RESULTS

Response of bees to trap height. In 2004, bee captures varied significantly with trap height ($F_{3,15} = 9.17$, $P = 0.001$) (Figure 2.1), and the number of bees recovered from traps 1/3rd of the way up the blueberry canopy was significantly greater than traps placed at the other three levels (Tukey-Cramer $P<0.05$). Andrenid and halictid bees were the predominant groups collected, comprising 41 and 32% of the total number of bees collected, respectively.

When the study was repeated in 2005, including the adjustment of traps relative to a shorter blueberry stand in two of the replicates, the trend for traps in the canopy to collect more bees than those on the ground or above the canopy remained (Figure 2.1), but the number of bees captured was not significantly different among trap positions in the canopy ($F_{3,9} = 3.16$, $P = 0.08$). Andrenid and halictid bees were trapped in different proportions from the year before (28 and 66% of the total number of bees collected, respectively), and I examined how andrenids and halictids responded to trap height. Andrenid bees were found to vary significantly with trap height ($F_{3,9} = 6.93$, $P = 0.01$) (Figure 2.2), and were significantly more abundant among the bees captured in the canopy level traps compared to those on the ground or above the canopy (Figure 2.2). In contrast, halictid bee captures did not vary significantly with trap placement ($F_{3,9} = 2.36$, $P = 0.14$) (Figure 2.2).

Bees in the family Andrenidae, of which *Andrena carolina* (cited as *A. longifacies* in LaBerge 1980) is a specialist on *Vaccinium*, were always recovered from mid-canopy traps, but less often from ground level or above canopy traps (Table 2.1). Both *Apis mellifera* (honey bees) and the bumble bee *Bombus impatiens* were recovered only from traps elevated above the ground (Table 2.1). Smaller bees such as *Ceratina* spp. and *Hylaeus affinis* were found primarily in ground and mid-canopy traps. However, many of the small *Lasioglossum (Dialictis)* spp. were found more often in mid-canopy and above canopy traps. Eighteen bee species were present in both years of this study, suggesting they are common in this location during blueberry bloom. There were 6 unique bee species captured in 2004 and 20 unique species captured in 2005, although the total increase in the number of species captured between years was likely the result of increased sampling effort in 2005 (Table 2.1).

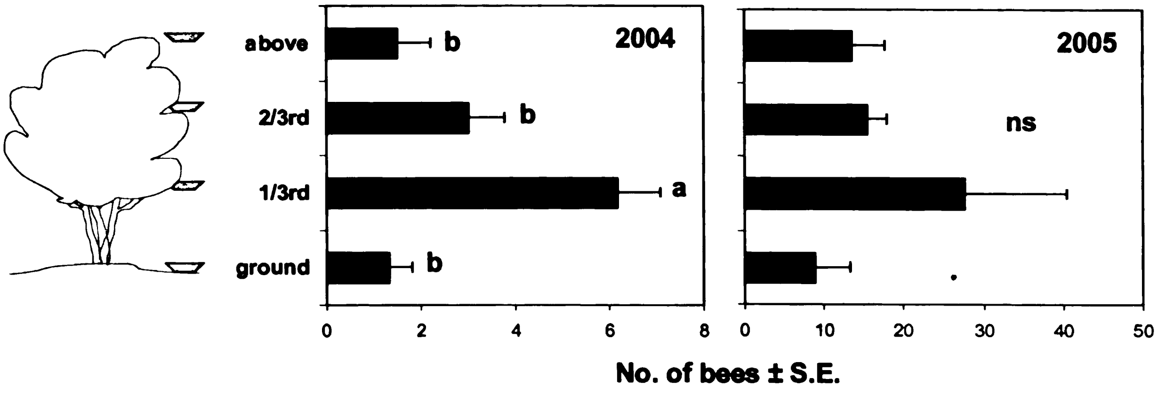

Figure 2.1. Average number of bees recovered from pan traps placed on the ground or elevated 1/3rd, 2/3rd, or above the canopy within highbush blueberry stands in 2004 and 2005. Bars with the same letter are not significantly different from one another (Tukey-Kramer means separation, P<0.05).

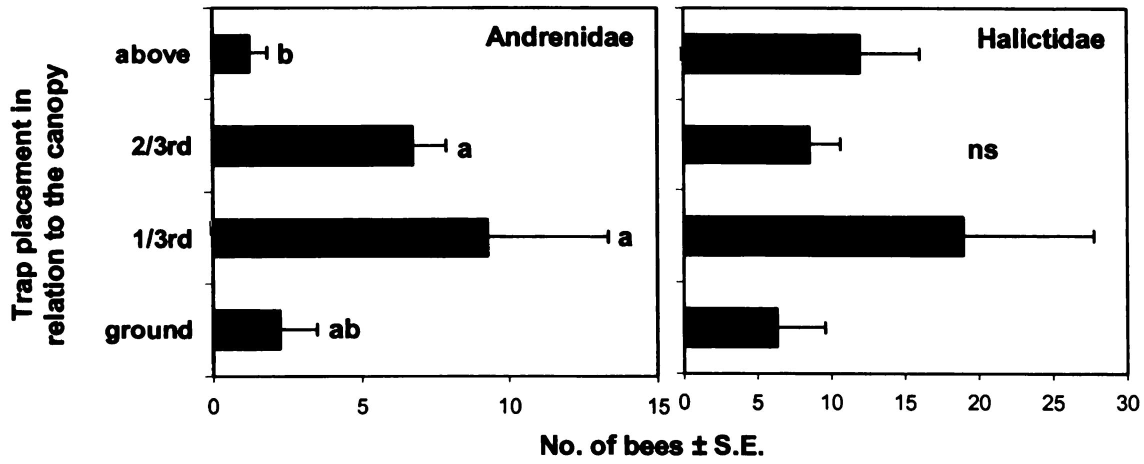

Figure 2.2. Average number of bees in the families Andrenidae and Halictidae recovered from pan traps placed on the ground or elevated 1/3rd, 2/3rd, or above the canopy within highbush blueberry stands in 2005. Means with different letters are significantly different from one another (Tukey-Kramer means separation, P<0.05).

Table 2.1. Bee species recovered from pan traps placed either on the ground, in mid-canopy (0.46 to 1.2 m), or above the canopy (1.5 to 1.8 m) in a highbush blueberry field during bloom near Fennville, Michigan in 2004-05. A (✓) indicates the year in which each species was collected. Presence of female (♀) or male (♂) bees is indicated by an x.

Family	**2004**	**2005**	**ground level**		**mid-canopy**		**above canopy**	
Species			♀	♂	♀	♂	♀	♂
Andrenidae								
Andrena algida		✓			x			
Andrena arabis		✓			x			
Andrena carlini†‡	✓	✓	x		x		x	
Andrena carolina†‡	✓	✓			x			
Andrena commoda		✓			x			
Andrena cressonii	✓	✓	x		x			
Andrena forbesii†	✓				x			
Andrena hippotes†		✓			x			
Andrena imitatrix† or *morrisonella**	✓	✓			x		x	
Andrena miserabilis	✓	✓	x		x		x	
Andrena morrisonella		✓			x			
Andrena nasonii	✓	✓	x		x			
Andrena perplexa	✓				x			
Andrena vicina†‡	✓	✓			x		x	
Andrena sp.	✓	✓			x	X		
Apidae								
Apis mellifera†	✓	✓			x		x	
Bombus impatiens†		✓					x	
Ceratina calcarata		✓		x		X		
Ceratina calcarata or *dupla*†*	✓	✓	x		x		x	
Ceratina dupla†		✓		x				
Ceratina strenua†	✓		x		x			
Eucera hamata		✓						
Colletidae								
Hylaeus affinis	✓	✓		x	x	X		
Halictidae								
Agapostemon virescens		✓	x		x		x	
Augochlorella aurata (=striata)†‡	✓	✓	x		x		x	
Dufourea marginata	✓		x					
Halictus confusus‡	✓	✓	x		x			
Halictus ligatus	✓	✓			x		x	
Halictus rubicundus‡		✓			x			
Lasioglossum admirandum		✓	x		x		x	
Lasioglossum anomalum		✓					x	
Lasioglossum coriaceum‡	✓				x		x	
Lasioglossum cressonii‡		✓			x		x	
Lasioglossum imitatum‡		✓	x		x		x	
Lasioglossum leucozonium	✓	✓			x		x	
Lasioglossum nymphaearum		✓			x			
Lasioglossum pectorale		✓			x			
Lasioglossum pilosum	✓	✓	x		x		x	
Lasioglossum quebecense‡		✓			x			

Family	**2004**	**2005**	**ground level**		**mid-canopy**		**above canopy**	
Species			♀	♂	♀	♂	♀	♂
Lasioglossum rohweri	✓	✓			x		x	
Lasioglossum tegulare		✓			x		x	
Lasioglossum spp.		✓					x	
Sphecodes dichrous	✓				x			
Sphecodes spp.	✓	✓			x		x	
Total # of species:	**24**	**38**						
No. of unique species:	**6**	**20**						
Total # bees:	**72**	**278**						

†*Vaccinium* floral record noted by Hurd, Jr. (1979). ‡*Vaccinium* floral record based on collections made by MacKenzie and Eickwort (1996) on highbush blueberry in the Finger Lakes area of central New York.
*These specimens could not be distinguished from one another: *Andrena imitatrix* and *A. morrisonella* are difficult to distinguish when hair on the thorax has been matted down after being wet; *Ceratina calcarata* and *C. dupla* females are morphologically indistinct.

Response of bees to trap color. Bee captures, both overall abundance and species richness, did not vary significantly with trap color ($F_{2,10} = 0.31$, $P = 0.74$) (Table 2.2). The lowest number of bee species associated with *Vaccinium* was trapped in the blue traps, with only two species of *Andrena*, compared to six and seven species in the white and yellow traps, respectively (Table 2.2). Andrenid bees were more likely to be found in white bowls, whereas halictid bees were more likely to be found in blue bowls (df = 2, $\chi^2 = 8.75$, $P = 0.01$). However, there was no significant relationship between trap color and whether bees trapped were known to forage on *Vaccinium* (df = 2, $\chi^2 = 2.22$, $P = 0.33$).

Comparison of pan trap sampling to timed observations. A total of 320 pan-trap hours and 2 hours of observations were made over the two days of sampling. Pan trap samples contained more species but fewer specimens compared with the number of bees observed while foraging on blueberry (Table 2.3). The number of honey bees observed foraging was 13 times greater than the number collected in traps (Table 2.3). *Xylocopa virginica virginica* was only observed foraging and was not captured in pan traps, as was a species of *Megachile*. Parasitic bee species were captured in pan traps, but not observed foraging on blueberry blooms (e.g. *Nomada* and *Sphecodes* spp., Table 2.3). A single bumble bee was collected in a pan trap, but no bumble bees were observed foraging on *Vaccinium* during timed observations.

Table 2.2. Number and species diversity of bees recovered from blue, white, or yellow pan traps elevated 1.2 m in the canopy of a mature highbush blueberry stand during bloom near Fennville, Michigan in 2004. All specimens were female unless otherwise noted.

Family **Species**	**blue**	**white**	**yellow**	**total**
Andrenidae				
Andrena carlini†‡	8	10	3	21
Andrena carolina†‡			1	1
Andrena commoda		1		1
Andrena hippotes†			1	1
Andrena imitatrix†* *or morrisonella**			1	1
Andrena mandibularis			1	1
Andrena miserabilis		6		6
Andrena nasonii		2	2	4
Andrena perplexa	1			1
Andrena vicina†‡		2	1	3
Andrena sp.		1		1
Apidae				
Apis mellifera†‡	5	8	8	21
Ceratina calcarata‡ (♂ only)	1			1
Ceratina calcarata†* or *dupla*†‡*		1		1
Eucera hamata (♂ only)	3			3
Colletidae				
Colletes thoracicus†		1		1
Halictidae				
Agapostemon texanus	1			1
Agapostemon virescens	1		1	2
Augochlorella striata†‡	1			1
Halictus confusus‡			2	2
Halictus ligatus	3	1	1	5
Halictus rubicundus‡		1		1
Lasioglossum admirandum		2	1	3
Lasioglossum cressonii‡			1	1
Lasioglossum imitatum‡	1	1		2
Lasioglossum leucozonium	4	1		5
Lasioglossum pilosum‡	3	1	4	8
Lasioglossum rohweri		1	1	2
Lasioglossum sp.	3			3
Total abundance:	**35**	**40**	**29**	**104**
Total no. of species:	**13**	**16**	**15**	**29**
No. of species previously recorded on *Vaccinium*:	**6**	**8**	**9**	**15**

†*Vaccinium* floral record noted by Hurd, Jr. (1979). ‡*Vaccinium* floral record based on collections made by MacKenzie and Eickwort (1996) on highbush blueberry in the Finger Lakes area of central New York. *These specimens could not be distinguished from one another: *Andrena imitatrix* and *A. morrisonella* are difficult to distinguish when hair on the thorax has been matted down after being wet; *Ceratina calcarata* and *C. dupla* females are morphologically indistinct.

Table 2.3. Comparison of bees captured in pan traps placed in the blueberry canopy with bees observed foraging on blueberry during timed observations, over two days of sampling in a southwest Michigan blueberry field in 2005.

Pan-trapped bees	Pan Trap total	Observation total	Bees observed while foraging on blueberry
Apis mellifera	15	201	*Apis mellifera*
Bombus impatiens	1	0	
Xylocopa virginica	0	8	*Xylocopa virginica*
Ceratina calcarata/dupla	15	1	*Ceratina* sp.
Ceratina strenua	2	-	
Nomada sp.	1	0	
Andrena sp.	1	1	*Andrena* sp.
Andrena carlini	7	29	*Andrena carlini/vicina*
Andrena carolina	4	14	*Andrena carolina*
Andrena hippotes	1	-	
Andrena nasonii	1	-	
Andrena vicina	1	-	
Colletes sp.	1	11	*Colletes* sp.
Hylaeus sp.	3	1	*Hylaeus* sp.
Augochlora pura	6	5	Augochlorini
Augochlorella sp.	1	-	
Halictus confusus	4	6	*Halictus* sp.
Halictus parallelus	1	-	
Halictus rubicundus	2	-	
Lasioglossum bruneri	2	26	*Lasioglossum* sp.
Lasioglossum coriaceum	4	-	
Lasioglossum leucozonium	2	-	
Lasioglossum pilosum	6	-	
Sphecodes sp.	1	0	
Megachile sp.	0	1	*Megachile* sp.
Osmia spp.	2	1	*Osmia* sp.
Total:	**84**	**305**	
Minimum no. of species:	**24**	**13***	

*This is a conservative estimate based on the generic level listed here. A more liberal and perhaps more accurate estimate would be 18 species, based on what was collected in pan traps and what is found in the floral record literature (see Appendix C).

DISCUSSION

Response of bees to trap height. Bee captures were greatest in traps elevated in the blueberry canopy versus those placed on the ground or above the canopy. Members of the bee family Andrenidae, many of whom tend to be oligolectic (Michener 2000), were more likely to be found in the canopy traps nearer to the blooms on which they were presumably foraging before they were captured. In contrast, halictid bees, which tend to be polylectic (Michener 2000), were not confined to the canopy traps, presumably because they were more likely to be searching a broader area for forage. Future studies that use pan traps to monitor bee communities associated with plants that have a vertical structure, in which other sampling methods may be difficult (e.g. net sampling) or time consuming (e.g. observations), should consider placement of pan traps in the canopy. The optimum height to obtain samples with the highest bee abundance and diversity should be tested for each plant community.

Response of bees to trap color. Known *Vaccinium*-foraging bees did not exhibit marked preferences for trap color, but andrenid bees preferred white traps and halictid bees preferred blue traps. Leong and Thorp (1999) found that male and female *Andrena limnanthis*, an oligolectic bee of white-flowering *Limnanthes douglasii rosea* (Benth.) Mason, were most attracted to white pan traps over blue or yellow. Additionally they found that non-*A. limnanthis* bees, consisting of generalist and specialist species of yellow-colored flowers, were most attracted to yellow pan traps. In contrast, I found that known *Vaccinium*-foragers, not necessarily all specialists on this plant genus, were found in similar abundance in white, blue, and yellow traps. However, andrenid species found in this study were more likely to be found in white traps (although, curiously, the one

Vaccinium specialist, *A. carolina*, was only found in yellow traps – see also Chapter 3). I also found that halictids, a group of bees that tend to be generalists, favored blue traps over white and yellow, whereas honey bees showed no significant preference (Table 2.2, but see Chapter 3, Figure 3.8).

Comparison of pan trapping and timed observations. More bees were observed foraging on blueberry flowers during the same time period in which pan trap sampling was being conducted, but species richness was greater in the pan traps. *Apis mellifera* was 13 times more abundant at blueberry flowers than in pan traps. Species composition was similar between the methods, although parasitic bees were only caught in pan traps and *Xylocopa virginica virginica* was only observed while foraging. That more species were collected in pan traps than on blueberry, could be a result of sampling at a single plant species as opposed to sampling at any other plants that may have been blooming in the landscape. However, when this crop is in bloom, it is the most abundant floral resource in this landscape (personal observation).

Pan trapping and honey bees. *Apis mellifera* (honey bees) are often rarely caught in studies that use pan traps, so it has been generally assumed that pan traps are not a good method for monitoring honey bees (Cane et al. 2001). Recently in southern Costa Rica, honey bees were rarely caught in pan traps whereas they were collected in great abundance in netting samples (Brosi et al. 2007). When intensive net sampling was compared with pan trapping for bees in northern Virginia, only a single honey bee was captured in pan traps compared with 204 honey bees netted or observed foraging in the same area (Roulston et al. 2007). Both of these studies placed pans directly on the ground and the lack of honey bees in ground level traps in this study follows that pattern.

However, honey bees were captured with similar frequency to other bee species in the height study (Table 2.1), and in greater frequency than other bee species in the pan trap color experiment (Table 2.2), when traps were elevated in the canopy. This emphasizes the need to place pan traps in the appropriate niche used by bees for foraging when deploying this method for monitoring bees.

Conclusion. The use of pan traps has important advantages compared to more traditional bee collection methods. Pan traps eliminate collector bias, are relatively inexpensive, are easily replicated, and can be used over a longer period of time at multiple sites simultaneously. Although pan traps may be biased toward some bee taxa over others, in combination with other methods, pan trapping can be very effective for monitoring bee communities (Kearns and Inouye 1993, pg 269). This study aimed to optimize pan trapping methods for monitoring the bee community in a crop that has a vertical structure. From the results presented here, I suggest that attention should be given to vertical plant structure and that elevated pan traps may ensure the greatest abundance and diversity of bees in pans.

CHAPTER 3:

NATIVE BEES ASSOCIATED WITH THE HIGHBUSH BLUEBERRY AGROECOSYSTEM IN MICHIGAN

INTRODUCTION

Highbush blueberry (*Vaccinium corymbosum* L.) is a native North American crop that is dependent upon pollination for optimum yields (McGregor 1976, Free 1993, Delaplane and Mayer 2000). A number of native bee species, such as several *Andrena*, *Osmia*, and especially *Bombus* spp., are efficient pollinators of *Vaccinium*. Some are able to sonicate the porous anthers of *Vaccinium* flowers or will forage under cooler weather conditions than honey bees (Buchmann 1983, Heinrich 2004). Some visit more flowers per minute and deposit more tetrads per visit than honey bees (Dogterom 1999, Sampson and Cane 2000, Javorek et al. 2002, Sampson et al. 2006). Together, these traits make native bees efficient pollinators of blueberry.

Prior to the current large-scale production of highbush blueberry, endemic native bees and feral honey bees were largely responsible for its pollination (Marucci and Moulter 1977, DeGrandi-Hoffman 1987). It became necessary for commercial growers to supplement wild pollinators with managed honey bee (*Apis mellifera*) hives when commercial acreage increased and pest management practices grew more intensive, including the use of herbicides to clear vegetation surrounding fields that would have supported wild pollinators when the crop was not in bloom. Although honey bees are not the most efficient at pollinating *Vaccinium*, when there are enough of them, adequate pollination can be achieved (Dogterom and Winston 1999, Dedej and Delaplane 2003). Therefore, honey bees have become indispensable for most crops that require pollination to produce profitable yields (Southwick and Southwick 1992, Roubik 1996) including blueberry (Dorr and Martin 1966). In the mid-sixties, Wood (1965) reported that bumble bees and solitary bees were common in North America, but usually not in adequate numbers to pollinate commercial crops.

About the time that honey bees began to be managed extensively and transported across the U.S. for pollination, beekeepers began to face annual hive losses due to several illnesses and parasitic mite infestations, such that by the late 1980s and early 1990s,.there was concern about the state of the honey bee industry (Torchio 1990, Watanabe 1994, DeGrandi-Hoffman 2003). As of this writing, honey bees are threatened with a mysterious ailment called "colony collapse disorder," in which beekeepers find hives full of honey but with no bees (New York Times, February 2007). In the winter of 2006-7, some beekeepers have reported losses of up to 90% of their colonies. It remains to be seen how this will impact crop pollination, and whether these beekeepers will recover quickly from these losses.

At the same time, there has been increasing concern over the perceived loss of pollinator biodiversity around the world, with a call for studies to better understand the current extent of pollinator populations, including native bees (Kearns 1998, Allen-Wardell et al. 1998, Cane and Tepedino 2001, National Academy of Sciences 2006). Surveys of native bees associated with lowbush blueberry production in 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 prior to and/or after blueberry bloom, which means that in order to help conserve and eventually increase their abundance, they require floral resources, nesting habitat, and protection from production practices aimed at pest insects outside of the bloom period of the crop. To my knowledge, no native bee survey on Michigan blueberry has been conducted, even though Michigan is the leading producer of blueberries in the U.S., with 18,500 acres in production (USDA 2004) valued at ~$90 million per year.

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 agroecosystems in southwest Michigan before, during, and after bloom.

MATERIALS AND METHODS

A three-year study was conducted to characterize the bee community active during blueberry bloom at 13 commercial blueberry farms and 2 semi-abandoned blueberry fields located in the highbush blueberry production region of southwest Michigan (Figure 3.1). Six sites were located in Ottawa County, north of Holland, Michigan, five sites were located in Allegan County, and the remaining four sites were located in Van Buren County (see Appendix A). Each sampled field was at least 3 km away from any others in this study.

Passive collections of bees were made using pan traps (Chapter 2) and direct collections of bees were made during timed observations. To determine which bees were pollinating blueberry, the proportion of *Vaccinium* pollen was analyzed 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).

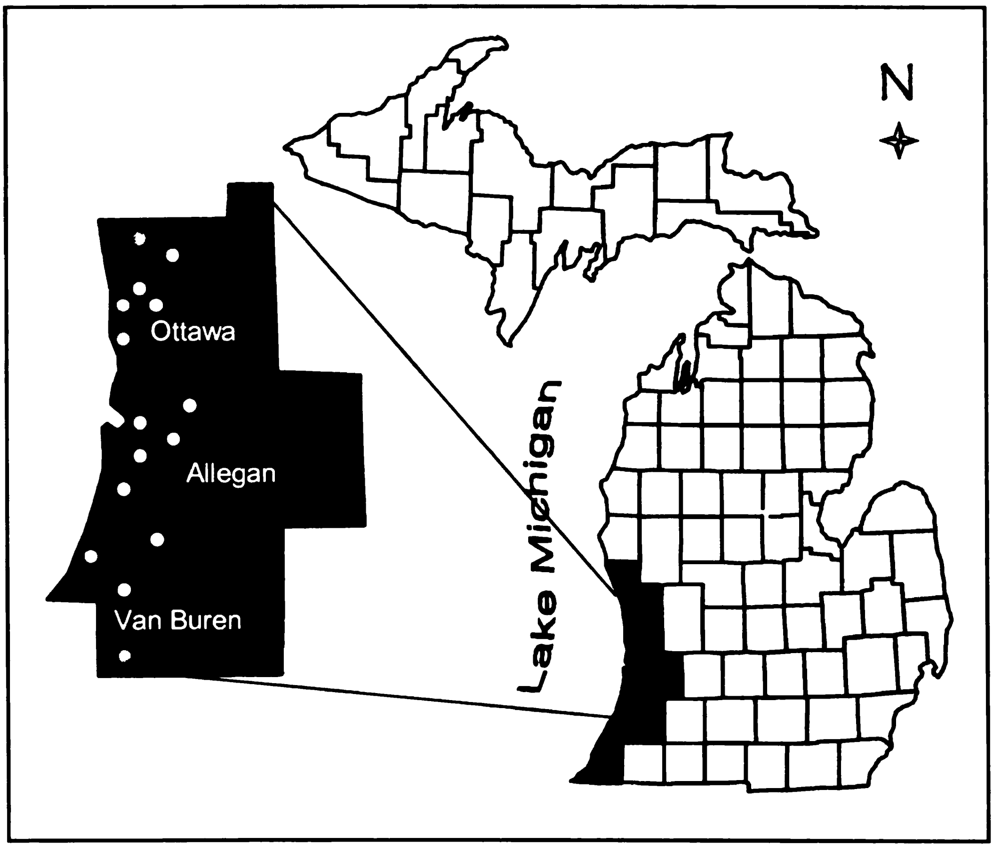

Figure 3.1. Location of 15 bee collection sites in relation to the top five blueberry producing counties in Michigan. Van Buren, Ottawa, and Allegan Counties are 1st, 2nd, and 3rd in blueberry acreage in Michigan with 7550, 5300, and 2750 acres, respectively (USDA 2004). This figure is presented in color.

Pan trapping. Each of the fifteen farms was sampled during bloom (2004-06) using pan traps (Table 3.1). Due to varying weather conditions from year to year, trapping was conducted two (2004, 2006) or three (2005) times during bloom in each field. Pre-bloom pan trapping was conducted in 2005-6 and an additional post-bloom pan trapping sample was conducted in 2005-6.

Table 3.1. Dates between which pan trapping was conducted in Michigan blueberry fields prior to blueberry bloom (Pre-bloom), during blueberry bloom (Bloom), and after blueberry bloom (Post-bloom), and the number of times traps were deployed in each field during each time period (n).

Year	Pre-bloom	n	Bloom	n	Post-bloom	n
2004	n/a	-	16 May – 3 June	2	15 June – 4 Sept	2
2005	15 – 21 April	1	16 – 25 May	3	22 June – 15 Sept	3
2006	19 – 26 April	1	17 – 31 May	2	12 June – 10 August	3

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 8:00-12:00 h and were collected between 16:00-20:00 h for a minimum trapping period of 6 h on days when suitable weather conditions, as described above, were met.

Pan traps half filled with a 2% unscented soap solution (Dawn® dish soap, Procter & Gamble, Cincinnati, OH), were constructed from 355 ml white and yellow plastic bowls (Amscan, Inc., Elmsford, NY) mounted onto 2.7 diameter PVC poles stabilized with rebar (see Chapter 2, page 37). 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 prior to washing in a 70% ethanol solution. Honey bees were separated out and counted, then stored in 70% ethanol solution. Pollen samples were taken (when present) from bees collected during bloom, then wild bees were placed in a mesh bag through which they were fluffed and dried with a hairdryer before pinning and identification.

Species accumulation curves were based on randomized re-sampling of bee trapping observations with 100 permutations in R 3.2.1 ("vegan" package, specaccum function). A 2-way analysis of variance (PROC GLM, SAS 9.1) was conducted to examine the response of bees to trap position in the field (edge vs. interior) and trap color (white vs. yellow) by year with Tukey means separation. This model was used to test the response of native (non-*Apis*) bee abundance (log n+1), native bee species richness, native bee diversity (Shannon-Wiener H'), and honey bee abundance. The abundance of eight of the most common species that have been recorded foraging on blueberry (Hurd, Jr. 1979, MacKenzie and Eickwort 1996, and data from this study) was pooled across years and also tested for response to trap position and color.

Pollen analysis. Pollen samples were brushed from corbiculae on honey bees and scopa on all other bees collected during timed observations and in pan traps, using a fine paint brush. Each pollen sample was stained by mixing with melted basic fuschin gel on glass microscope slides (Kearns and Inouye 1993). Pollen slides were examined under a 400x light microscope and the number of tetrad pollen grains (i.e. *Vaccinium*) out of 100 was recorded. The proportion of *Vaccinium* pollen was calculated per bee and averaged over each bee species from which pollen was collected.

Direct bee observations. Timed observations of bees visiting blueberry flowers were conducted at three of the commercial sites and at the two semi-abandoned blueberry farms in 2004-06. Fifteen randomly selected bushes were observed for one minute each, on three occasions during bloom in each field. Observations were conducted during times when conditions were suitable for bee activity. Bees were identified as honey bees, bumble bees, or "other" bees. "Other" bees were collected for identification (n = 62).

Species identifications. Preliminary identifications of bees were made using two published dichotomous keys (Mitchell 1960, Michener et al. 1994) and the online key available through www.discoverlife.org. Further identifications and verifications were made by J.S. Ascher of the American Museum of Natural History, Division of Invertebrate Zoology. Voucher specimens are held in the Albert J. Cook Arthropod Research Collection at Michigan State University (See Appendix B).

RESULTS

Over three years across the 15 farms, 7929 bees were collected in pan traps, representing at least 174 species, in five families and 30 genera (Table 3.2). Each site was sampled 17 times, representing more than 1300 pan-days of trapping effort. Species accumulation curves created using pan trapping data collected during bloom in 2004 approached an asymptote (Figure 3.2), indicating that pan trapping effort was sufficient to represent the community of bees likely to be captured in pan traps in this habitat.

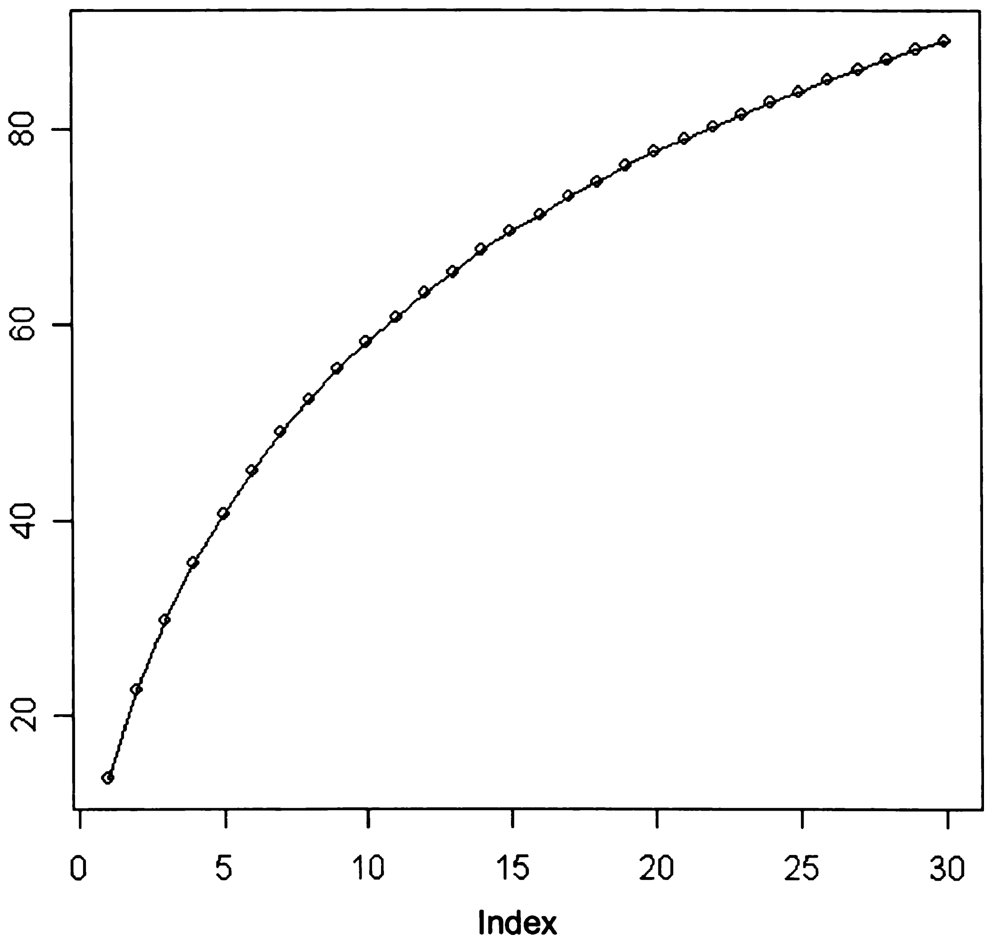

Figure 3.2. Species accumulation curve generated from 100 permutations of the 2004 pan trap sampling data. Species curves generated from 2005-6 data were similar.

Table 3.2. Bee species collected in pan traps in blueberry fields in southwest Michigan over a period of three years beginning in 2004. Samples were taken prior to blueberry bloom (pre), during bloom (bloom), and after bloom (post).

Family	**2004**		**2005**			**2006**			
	bloom	**post**	**pre**	**bloom**	**post**	**pre**	**bloom**	**post**	
Species n =	2	2	1	3	3	1	2	3	**total**
Andrenidae									
Andrena (Melandrena) sp.	-	-	-	-	-	1	-	-	1
Andrena algida	1	-	27	1	-	9	1	-	39
Andrena alleghaniensis	3	-	-	8	-	-	9	2	22
Andrena arabis	-	-	1	-	-	1	-	-	2
Andrena barbilabris	-	-	1	8	-	1	2	-	12
Andrena bisalicis	-	-	-	1	1	5	5	4	16
Andrena carlini	59	-	21	60	-	21	18	-	179
Andrena carolina	114	-	19	237	-	14	101	4	489
Andrena ceanothi	4	-	-	2	-	-	8	1	15
Andrena clarkella	-	-	1	1	-	1	-	-	3
Andrena commoda	2	-	-	2	-	-	-	-	4
Andrena crataegi	7	-	-	1	-	-	3	3	14
Andrena cressonii	9	2	27	22	1	4	9	3	77
Andrena dunningi	1	-	-	-	-	-	-	-	1
Andrena erigeniae	-	-	-	2	-	-	-	-	2
Andrena erythrogaster	-	-	1	1	-	1	-	-	3
Andrena erythronii	-	-	8	-	-	1	1	-	10
Andrena forbesii	5	-	6	-	-	5	7	-	23
Andrena frigida	-	-	2	-	-	2	-	-	4
Andrena geranii	-	-	-	-	-	-	-	1	1
Andrena hippotes	5	-	2	4	-	2	4	-	17
Andrena hirticincta	-	2	-	-	-	-	-	-	2
Andrena imitatrix or *morrisonella*	8	-	5	27	-	3	19	-	62
Andrena integra	2	-	-	-	-	-	-	-	2
Andrena mandibularis	-	-	-	2	-	-	-	-	2
Andrena mariae	1	-	-	-	-	-	-	-	1
Andrena milwaukeensis	1	-	-	-	-	-	-	-	1
Andrena miserabilis	9	-	19	45	-	56	37	1	167
Andrena morrisonella	3	-	-	4	-	-	3	1	11
Andrena nasonii	7	-	22	12	-	14	9	1	65
Andrena neonana	1	-	-	-	-	-	-	1	2
Andrena nigrae	3	-	-	-	-	-	5	-	8
Andrena nivalis	1	-	-	-	-	-	-	-	1
Andrena nuda	15	-	-	2	-	-	6	9	32
Andrena perplexa	7	-	-	1	-	2	1	1	12
Andrena persimulata	-	-	-	-	-	-	1	-	1
Andrena placata	-	5	-	-	-	-	-	-	5
Andrena platypaea	-	-	-	-	-	-	-	1	1
Andrena pruni	2	-	-	1	-	-	-		3
Andrena rehni	2	-	-	-	-	-	-	-	2
Andrena robertsonii	1	-	-	1	-	-	2	-	4

	2004		2005			2006			
	bloom	**post**	**pre**	**bloom**	**post**	**pre**	**bloom**	**post**	**total**
Andrena rugosa	10	-	1	4	-	1	6	-	22
Andrena salictaria	1	-	-	5	-	-	-	-	6
Andrena sigmundi	-	-	-	-	-	2	-	-	2
Andrena sp. (females only)	-	-	3	-	-	-	-	-	3
Andrena spp. (males only)	70	4	361	138	-	304	70	10	957
Andrena thespii	-	-	-	-	-	-	2	-	2
Andrena tridans	-	-	1	-	-	-	-	-	1
Andrena vicina	49	-	7	43	-	6	24	-	129
Andrena wellesleyana	-	-	4	-	-	1	-	-	5
Andrena wilkella	-	-	-	-	-	-	-	3	3
Calliopsis andreniformis	-	1	-	-	1	-	-	1	3
Perdita octomaculata	-	-	-	-	1	-	-	-	1
Pseudopanurgus nebrascensis	-	-	-	-	3	-	-	-	3
Apidae (except for *Apis mellifera,*which is shown at the end of the table)									
(Anthophorini) spp.	-	-	-	1	3	-	-	-	4
Anthophora terminalis	-	8	-	-	-	-	-	2	10
Bombus bimaculatus	6	-	-	-	-	-	2	-	8
Bombus citrinus	16	1	-	-	-	-	1	1	19
Bombus fervidus	-	1	-	3	-	-	2	-	6
Bombus griseocollis	3	1	-	-	-	-	4	3	11
Bombus impatiens	2	-	-	2	10	-	-	5	19
Bombus perplexus	4	1	-	-	1	1	-	2	9
Bombus vagans	-	1	-	-	-	-	-		1
Ceratina calcarata (males only)	3	23	296	13	22	94	32	7	490
Ceratina calcarata or *dupla* (females only)	56	162	123	54	89	17	13	160	674
Ceratina dupla (males only)	1		34	7	1	1	3	15	62
Ceratina strenua	9	45	39	6	31	11	-	39	180
Eucera atriventris	1	-	-	-	-	-	-	-	1
Eucera hamata	-	-	-	-	-	-	-	3	3
Melissodes agilis	-	-	-	-	1	-	-	-	1
Melissodes apicata	-	2	-	-	-	-	-	-	2
Melissodes bimaculata	-	5	-	-	3	-	-	1	9
Melissodes communis	-	3	-	-	-	-	-	-	3
Melissodes druriella	-	-	-	-	3	-	-	-	3
Melissodes spp.	-	6	-	-	3	-	-	1	10
Melissodes tridonis	-	1	-	-	-	-	-	2	3
Nomada cressonii	-	-	-	1	-	-	-	-	1
Nomada denticulata	-	-	-	2	-	-	-	-	2
Nomada depressa	-	-	3	-	-	-	-	-	3
Nomada luteoloides	-	-	7	-	-	-	-	-	7
Nomada maculata	-	-	17	1	-	-	-	-	18
Nomada obliterata	-	-	2	-	-	-	-	-	2

	2004		2005			2006			
	bloom	post	pre	bloom	post	pre	bloom	post	total
Nomada ovata	-	-	-	1	-	-	-	-	1
Nomada pygmaea	-	-	1	-	-	-	-	-	1
Nomada spp.	32	-	86	47	1	70	13	40	289
Triepeolus lunatus	-	1	-	-	-	-	-	-	1
Xylocopa virginica virginica	2	-	-	1	-	-	-	-	3
Colletidae									
Colletes inaequalis	-	-	39	15	1	-	3	-	58
Colletes sp.	-	1	2	-	-	-	-	-	3
Colletes thoracicus	24	-	4	4	-	14	1	-	47
Colletes validus	-	-	-	2	-	-	-	-	2
Hylaeus affinis	2	37	-	3	36	-	1	5	84
Hylaeus rudbeckiae	-	-	-	3	2	-	2	26	33
Hylaeus sp.	-	-	-	-	1	-	-	-	1
Halictidae									
Agapostemon sericeus	1	2	1	3	-	-	4	3	14
Agapostemon splendens	2	4	-	1	2	-	-	-	9
Agapostemon texanus	-	-	-	2	1	-	1	-	4
Agapostemon virescens	3	9	-	5	10	-	3	3	33
Augochlora pura	42	3	10	13	11	-	11	1	91
Augochlorella aurata	58	56	16	32	36	15	64	47	324
Augochlorella gratiosa	10	2	-	-	-	-	-	-	12
Augochloropsis sumptuosa	1	-	-	-	-	-	-	-	1
Dufourea marginata	-	-	-	-	1	-	-	-	1
Halictus confusus	2	6	5	27	6	-	4	4	54
Halictus ligatus	19	33	-	20	35	1	10	9	127
Halictus parallelus	2	3	-	1	-	-	2	2	10
Halictus rubicundus	3	2	-	7	-	1	3	1	17
Lasioglossum (Dialictus) spp.	-	11	-	-	-	-	-	6	17
Lasioglossum (Evylaeus) spp.	8	4	-	-	-	-	-	-	12
Lasioglossum acuminatum	4	-	-	3	1	1	5	1	15
Lasioglossum admirandum	27	6	5	13	14	6	19	16	106
Lasioglossum anomalum	1	1	-	4	3	-	1	1	11
Lasioglossum athabascense	-	-	-	-	-	1	-	-	1
Lasioglossum boreale	2	-	1	-	1	-	-	-	4
Lasioglossum bruneri	3	2	-	1	1	1	-	1	9
Lasioglossum coeruleum	8	-	2	5	3	1	4	1	24
Lasioglossum coriaceum	61	2	3	17	3	1	12	7	106
Lasioglossum cressonii	79	3	-	17	6	3	17	19	144
Lasioglossum fattigi	1	-	-	1	1	-	-	-	3
Lasioglossum forbesii	-	-	-	-	1	1	-	-	2

	2004		2005			2006			
	bloom	**post**	**pre**	**bloom**	**post**	**pre**	**bloom**	**post**	**total**
Lasioglossum fuscipenne	5	-	-	1	-	1	1	1	9
Lasioglossum illinoense	-	-	-	-	-	-	-	1	1
Lasioglossum imitatum	25	12	23	72	10	138	21	42	343
Lasioglossum leucozonium	68	136	-	27	171	-	56	174	632
Lasioglossum nelumonis	1	-	-	-	-	-	-	-	1
Lasioglossum nigroviride	3	-	-	-	-	-	3	-	6
Lasioglossum nymphaearum	1	2	-	1	1	-	2	-	7
Lasioglossum nymphale	-	-	1	-	-	-	-	-	1
Lasioglossum oblongum	2	-	-	-	-	-	-	-	2
Lasioglossum pectorale	3	14	-	14	24	-	11	25	91
Lasioglossum pilosum	45	26	54	147	62	40	67	46	487
Lasioglossum quebecense	8	1	3	6	-	3	7	3	31
Lasioglossum rohweri	47	6	7	28	3	2	14	5	112
Lasioglossum spp.	-	-	1	-	9	-	-	-	10
Lasioglossum suvianae	-	-	-	-	1	-	-	-	1
Lasioglossum tegulare	6	2	-	5	5	1	14	14	47
Lasioglossum versans	1	-	-	-	-	-	1	-	2
Lasioglossum vierecki	1	6	3	6	13	4	-	17	50
Sphecodes confertus	1	1	1	-	-	-	-	-	3
Sphecodes cressonii	-	-	-	-	4	-	-	-	4
Sphecodes mandibularis	-	-	-	-	3	-	-	-	3
Sphecodes ranunculi	1	-	-	-	-	-	-	-	1
Sphecodes spp.	4	6	5	1	14	4	2	6	42
Megachilidae									
Anthidium manicatum	-	5	-	-	-	-	-	3	8
Ashmeadiella sp.	-	-	-	1	-	-	-	-	1
Coelioxys sp.	-	-	-	-	1	-	-	-	1
Dianthidium simile	-	14	-	-	2	-	-	-	16
Heriades leavitti	-	-	-	-	-	-	-	1	1
Heriades variolosus	-	1	-	-	-	-	-	-	1
Hoplitis producta	-	-	-	2	1	-	-	-	3
Hoplitis spoliata	-	-	-	1	-	-	-	-	1
Megachile albatarsis	-	-	-	-	1	-	-	7	8
Megachile brevis	-	-	-	-	-	-	-	1	1
Megachile centuncularis	-	-	-	-	1	-	-	-	1
Megachile mendica	-	-	-	-	1	-	-	-	1
Megachile montivaga	-	1	-	-	-	-	-	-	1
Megachile pugnata	-	5	-	-	-	-	-	-	5
Megachile rotundata	-	-	-	-	1	-	-	-	1
Megachile spp.	2	1	-	2	1	-	1	6	13
Osmia a/m/p	8	3	116	2	-	-	1		130
Osmia atriventris	-	-	6	-	-	15	-	2	23
Osmia atriventris or *pumila*	-	-	-	-	-	25	-	-	25

Osmia bucephala	3	-	16	2	-	8	1	3	33
Osmia conjuncta	-	-	5	2	-	-	-	1	8
Osmia distincta	-	-	-	-	-	1	-	1	2
Osmia felti	-	-	-	-	-	-	-	1	1
Osmia georgica	-	-	-	-	-	-	-	1	1
Osmia lignaria	-	-	7	-	-	1	-	-	8
Osmia michiganensis or *illinoensis*	-	-	3	-	-	1	1	-	5
Osmia pumila	-	-	3	3	-	23	-	4	33
Osmia simillima	-	-	-	-	-	1	-	-	1
Osmia spp.	-	-	5	2	1	-	1	-	9
Osmia subfasciata	-	-	7	-	-	-	-	-	7
Osmia virga	-	-	-	-	-	4	-	-	4

	2004		**2005**			**2006**			
	bloom	**post**	**pre**	**bloom**	**post**	**pre**	**bloom**	**post**	**total**
Abundance (without *A. mellifera*):	1136	704	1501	1298	681	969	794	846	7929
Apis mellifera abundance:	2382	40	16	1347	6	8	851	55	4705
								Total abundance:	12634
No. of species:	86	58	61	84	62	59	70	73	
Shannon-Wiener H' (calculated without *A. mellifera*):	3.54	2.86	2.78	3.25	2.91	2.63	3.41	3.05	
								Total no. species:	175

Bee community structure. *Apis mellifera* was the most abundant species trapped during bloom, with all other bees comprising one third to one half captured during bloom. Most of the non-*Apis* bees in the family Apidae were *Ceratina* species. Although *Bombus* spp. were caught in low numbers, 7 species are represented (Table 3.2). Bees in the families Andrenidae (between 34-46%) and Halictidae (45-55%) were among the most abundant native bees trapped during blueberry bloom in all three years (Figure 3.3). The most speciose genus was *Andrena* at 49 species, followed by at least 28 *Lasioglossum* spp. (Table 3.2). Bees in families Colletidae and Megachilidae were rare in the pan trapping samples each year. The overall proportion of bees within each family remained relatively stable from year to year, however, fewer bees were trapped during bloom in 2006 compared to the other years, likely due to cooler spring weather conditions in that year.

Looking at bees across the entire season by nesting guild, soil nesters were the most abundant bees collected each year (66-75%), followed by pithy stem nesters (15-21%) (Figure 3.4). Cleptoparasitic bees and cavity nesting bees were in equal abundance all three years (between 5-6%) (Figure 3.4). More rare were wood-boring bees (e.g. *Xylocopa virginica virginica*), and pebble and resin nest builders (e.g. *Dianthidium simile*) (<1-2%).

By far the most abundant non-*Apis* species captured during bloom over the three years at 14% of the total bee abundance was the *Vaccinium* specialist, *Andrena carolina* (Table 3.3). *Lasioglossum pilosum* comprised 8% of the total, followed by *Augochlorella aurata* and *L. leucozonium* at 5% (Table 3.3). Eight species were abundant between 3-4%, 18 species were abundant between 1-2%, and the rest (90 species) were present at less than 1% of the total. A total of 120 bee species were trapped in bowl traps during blueberry bloom over the three years (Table 3.3).

The eight most abundant native bee species present every year during bloom that are known to forage on *Vaccinium* were *Andrena carolina*, *An. carlini*, *An. vicina*, *Ceratina calcarata* (or *dupla*; the females are indistinguishable, however there were many more male *C. calcarata* than there were *C. dupla*), *Augochlorella aurata* (which includes the species formerly known as *Au. striata*), *Lasioglossum (L.) coriaceum*, *L. (Dialictus) imitatum*, and *L. (Dialictus) pilosum*. All except for *C. calcarata* are ground nesting bees (Michener 2000). All of these species were also present prior to bloom (2005 and 2006, Figure 3.5). Five of these species were also present after bloom: *Au. aurata*, *Bombus* spp., *C. calcarata/dupla*, *L. imitatum*, and *L. pilosum* (2004-06, Figure 3.5).

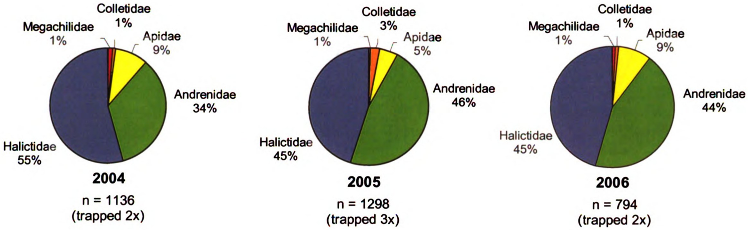

Figure. 3.3. Proportion of wild (non-*Apis*) bees by family trapped during blueberry bloom at 15 farms in southwest Michigan from 2004-06. This figure is presented in color.

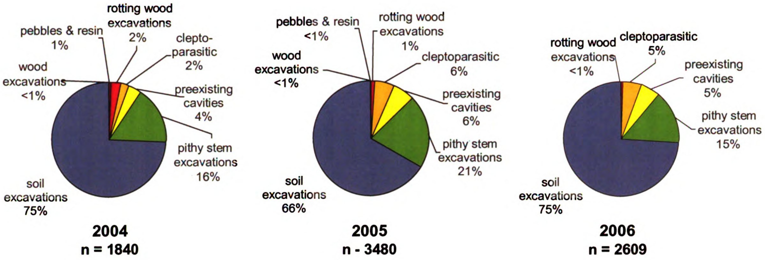

Figure 3.4. Proportion of wild (non-*Apis*) bees in each nesting guild trapped throughout the season across 15 blueberry farms in southwest Michigan over three years. Nesting biology is after Michener (2000). This figure is presented in color.

Table 3.3. Species of native bees (n = 120 species and 3228 specimens) listed in order of most to least abundant over three years of collecting during bloom in 15 southwest Michigan blueberry farms from 2004-06.

Family	**Species**	**proportion of bees collected**
Andrenidae	*Andrena carolina*[1,2,3]	0.14
Halictidae	*Lasioglossum pilosum*[2]	0.08
Halictidae	*Augochlorella aurata*[1,2,3]	0.05
Halictidae	*Lasioglossum leucozonium*	0.05
Andrenidae	*Andrena carlini*[1,2,3]	0.04
Apidae	*Ceratina calcarata* or *dupla* (females only) [1,2,3]	0.04
Halictidae	*Lasioglossum imitatum*[2,3]	0.04
Andrenidae	*Andrena vicina*[1,2,3]	0.04
Halictidae	*Lasioglossum cressonii*[2,3]	0.04
Apidae	*Nomada* spp. [3]	0.03
Andrenidae	*Andrena miserabilis*[3]	0.03
Halictidae	*Lasioglossum coriaceum*[2]	0.03
Halictidae	*Lasioglossum rohweri*	0.03
Halictidae	*Augochlora pura*[1,2,3]	0.02
Halictidae	*Lasioglossum admirandum*	0.02
Andrenidae	*Andrena imitatrix* or *morrisonella*[3]	0.02
Halictidae	*Halictus ligatus*	0.02
Apidae	*Ceratina calcarata* (males only)	0.01
Andrenidae	*Andrena cressonii*	0.01
Halictidae	*Halictus confusus*[2,3]	0.01
Colletidae	*Colletes thoracicus*[1,3]	0.01
Andrenidae	*Andrena nasonii*	0.01
Halictidae	*Lasioglossum pectorale*	0.01
Halictidae	*Lasioglossum tegulare*	0.01
Andrenidae	*Andrena nuda*	0.01
Halictidae	*Lasioglossum quebecense*[2]	0.01
Andrenidae	*Andrena alleghaniensis*	0.01
Andrenidae	*Andrena rugosa*[2]	0.01
Colletidae	*Colletes inaequalis*[2,3]	0.01
Apidae	*Bombus citrinus*	0.01
Halictidae	*Lasioglossum coeruleum*	0.01
	All other species (n = 90) present at <1%	0.19

[1] *Vaccinium* floral record in Hurd (1979).

[2] *Vaccinium* floral record in MacKenzie and Eickwort (1996).

[3] *Vaccinium* record in this study either from pollen samples or direct observations (Tables 3.4 and 3.5).

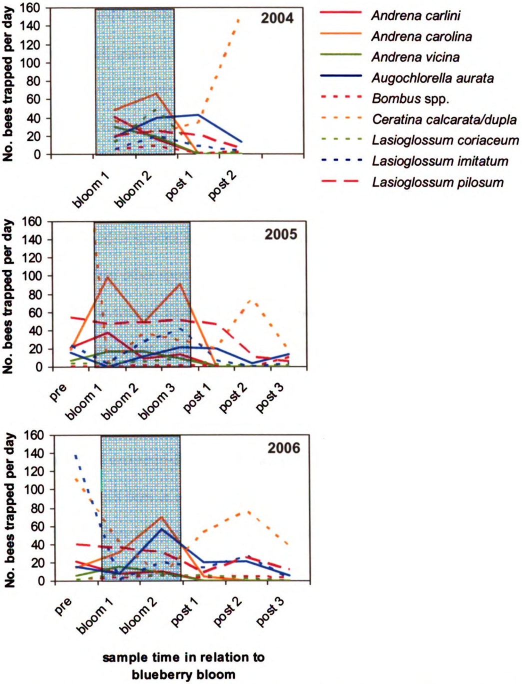

Figure 3.5. Incidence throughout the season of the most abundant native bee species that are known to forage on *Vaccinium* spp. plus all the *Bombus* spp. that were trapped throughout the study in fifteen highbush blueberry fields in southwest Michigan from 2004-06. The shaded area denotes blueberry bloom. This figure is presented in color.

Pollen analysis. *Andrena carolina* showed a high level of floral constancy for *Vaccinium*; nearly all specimens were found to carry ~100% pure *Vaccinium* pollen (n=37, Table 3.4). *A. 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 3.4). The species group labeled *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 could later be tracked to species identity), were more likely to carry 100% pure *Vaccinium* pollen than other species of pollen (n = 15, on average 0.72, Table 3.4). Very few samples of other species were analyzed for pollen composition, but the data agree with previous records (Hurd, Jr. 1979) that several species of *Colletes* and several halictid species also collect *Vaccinium* pollen (Table 3.4).

Direct observations of bees foraging on blueberry. From timed observations made in commercial and semi-abandoned blueberry fields during bloom, honey bees far outnumbered non-*Apis* bees in commercial fields by almost 33:1 (Figure 3.6). In semi-abandoned fields, where no honey bee hives were installed, the ratio of honey bees to wild bees was 3:1. During these observations, I collected 62 non-*Apis* bees visiting blueberry for a total of 10 genera and 21 species (Table 3.5). The most abundant non-*Apis* bees observed visiting bloom were *Andrena carolina* and *An. carlini*, followed by *Bombus bimaculatus* and *An. vicina* (Table 3.5). Three species and two genera are reported foraging on *Vaccinium* for the first time: *An. miserabilis* (pollen record, Table 3.4), *An. morrisonella*, *Lasioglossum acuminatum*, one *Nomada* and one *Sphecodes* species (collected while foraging on blueberry, Table 3.5).

Table 3.4. Proportion of *Vaccinium* pollen on the bodies of the most commonly collected native bees found in Michigan blueberry fields in 2004 and 2005 (n = 126).

Species	**Family**	**n**	**prop *Vaccinium* pollen**
Andrena carolina	Andrenidae	37	0.99
Colletes inaequalis	Colletidae	1	0.99
Augochlora pura	Halictidae	1	0.90
Andrena sp.2 (medium)	Andrenidae	15	0.72
Colletes validus	Colletidae	2	0.65
Apis mellifera	Apidae	5	0.62
Andrena vicina	Andrenidae	12	0.53
Lasioglossum coriaceum	Halictidae	6	0.53
Agapostemon sericeus	Halictidae	1	0.50
Augochlorella aurata	Halictidae	2	0.49
Andrena carlini	Andrenidae	12	0.40
Colletes thoracicus	Colletidae	3	0.36
Andrena sp.1 (large)	Andrenidae	3	0.21
Lasioglossum (Evylaeus) sp.	Halictidae	1	0.14
Andrena miserabilis†	Andrenidae	7	0.13
Andrena sp.3 (small)	Andrenidae	1	0.03
Andrena (Melandrena) sp.	Andrenidae	1	0.02
Halictus rubicundus	Halictidae	1	0.02
Andrena imitatrix or *morrisonella*	Andrenidae	6	0.01
Andrena (Trachandrena) sp.	Andrenidae	3	<0.01
Andrena cressonii	Andrenidae	3	0
Andrena morrisonella	Andrenidae	1	0
Andrena nasonii	Andrenidae	2	0
Andrena perplexa	Andrenidae	1	0

† New pollen record.

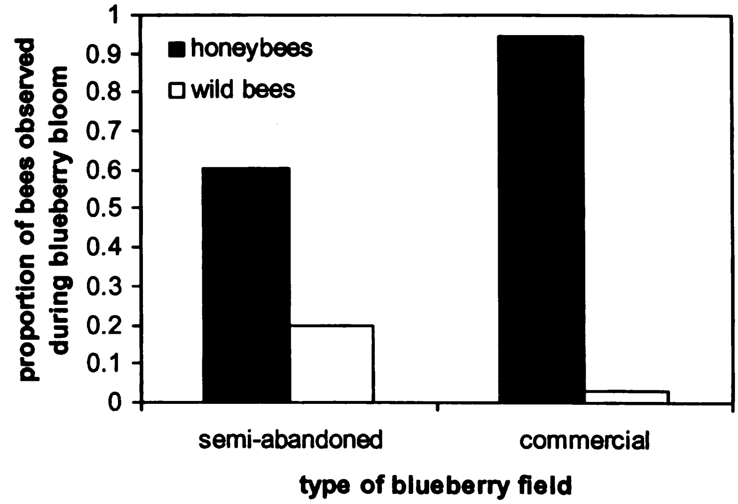

Figure 3.6. Proportion of honey bees and wild bees observed during blueberry bloom at semi-abandoned and commercial blueberry fields in southwest Michigan, 2004-06.

Table 3.5. Non-*Apis* bee species collected while foraging on blueberry blooms in Michigan in 2004-06.

Family Species	No. bees
Andrenidae	
Andrena carlini	11
Andrena carolina	13
Andrena morrisonella†	1
Andrena nivalis	1
Andrena sp. (male)	1
Andrena vicina	6
Apidae	
Bombus bimaculatus	7
Bombus griseocollis	1
Bombus impatiens	2
Bombus perplexus	4
Nomada sp.†	1
Xylocopa virginica virginica	1
Halictidae	
Augochlora pura	1
Augochlorella aurata	1
Halictus confusus	2
Halictus rubicundus	1
Lasioglossum acuminatum†	1
Lasioglossum cressonii	3
Lasioglossum imitatum	1
Lasioglossum sp.	1
Sphecodes sp.†	1
Megachilidae	
Osmia bucephala	1
Total:	**62**

†New floral records.

New species range extensions. Out of the three years of collecting, I obtained seven new species that have never been recorded in southwest Michigan (Table 3.6). Six are new state records, and are new northern extensions of their previously recorded ranges. One specimen, *Andrena nigrae*, is new to southern Michigan, having been reported previously in the northeastern portion of the lower peninsula of Michigan (Table 3.6).

Table 3.6. New species range extensions for bees captured in pan traps in Michigan blueberry fields in 2004-06.

Family	Species	Notes
Andrenidae	*Andrena neonana*	Van Buren County; new state record. (USA: CT MI IL IN OH NY NJ DC TN NC GA FL AR TX)
Andrenidae	*Andrena nigrae*	Allegan County; new site record; previously found in the northeastern lower peninsula of MI. (CAN: SK AB USA: ME CT MI IL IN OH NY NJ PA MD VA DC TN NC MS AL GA FL MN IA MO AR ND SD NE KS OK TX CO UT ID WA)
Andrenidae	*Andrena tridens*	Van Buren County; new state record. (CAN:? ON? USA: MA RI CT WI MI IL IN OH NY NJ PA MD WV VA DC TN NC AL GA MN IA NE KS)
Andrenidae	*Pseudopanurgus nebrascensis*	Allegan and Van Buren Counties; new state record. (CAN: NS NB ON MB AB USA: NENG[-RI] WI MI IL IN NY NJ NC MS FL MN ND SD NE TX? CO)
Apidae	*Eucera atriventris*	Allegan County; new state record. (USA: MA CT WI MI IL OH KY NY NJ PA MD DE VA DC NC GA MN IA)
Apidae	*Melissodes apicata*	Allegan County; new state record, specialist on *Pontederia cordata* [pickerelweed]. (USA: ME NH MA CT MI IL NY NJ MD DC NC GA FL)
Megachilidae	*Osmia virga*	Van Buren County; new state record, specialist on Ericaceae. (USA: ME MA CT WI MI IN NY NJ PA MD DE WV VA NC)

Notes: In parentheses are the previous known state and province records for these species per J.S. Ascher, personal communication.

Response of bees to trap position and color. Native bees were more likely to be caught in edge traps than in interior traps in all three years (2004 $F_{1,58} = 5.85$, $P = 0.02$; 2005 $F_{1,58} = 8.17$, $P = 0.006$; 2006 $F_{1,58} = 11.35$, $P = 0.001$) (Figure 3.7). Native bee richness followed a similar pattern with a greater number of species associated with traps placed at the edge of the field (2004 $F_{1,58} = 7.01$, $P = 0.01$; 2005 $F_{1,58} = 6.05$, $P = 0.02$; 2006 $F_{1,58} = 12.85$, $P = 0.0007$). Native bee diversity (Shannon-Wiener H') was also greater at field perimeters than in the interiors in 2004 ($F_{1,58} = 6.17$, $P = 0.02$) and 2006 ($F_{1,58} = 8.06$, $P = 0.006$), but there was no significant difference between positions in 2005 ($F_{1,58} = 1.82$, $P = 0.18$). Bee abundance, species richness, and diversity did not vary with trap color in any of the three years ($P>0.5$). On the contrary, honey bees were more likely to be caught in white traps (2004 $F_{1,58} = 7.15$, $P = 0.01$; 2005 $F_{1,58} = 14.35$, $P = 0.0004$; 2006 $F_{3,56} = 12.18$, $P = 0.009$) (Figure 3.8), and in 2006 they were more frequently caught in interior traps than in edge traps ($F_{1,58} = 5.77$, $P = 0.02$), but otherwise their capture did not vary with trap position ($P>0.05$).

Individual native species response to trap position and color varied across the eight most abundant species known to forage on *Vaccinium* that were present in each year (Table 3.7). Species responding significantly to color were trapped more frequently in white over yellow traps, except for *Andrena carolina*, which was more often captured in yellow traps (Table 3.7). In three species, more bees were trapped at the field edge than the interior (Table 3.7).

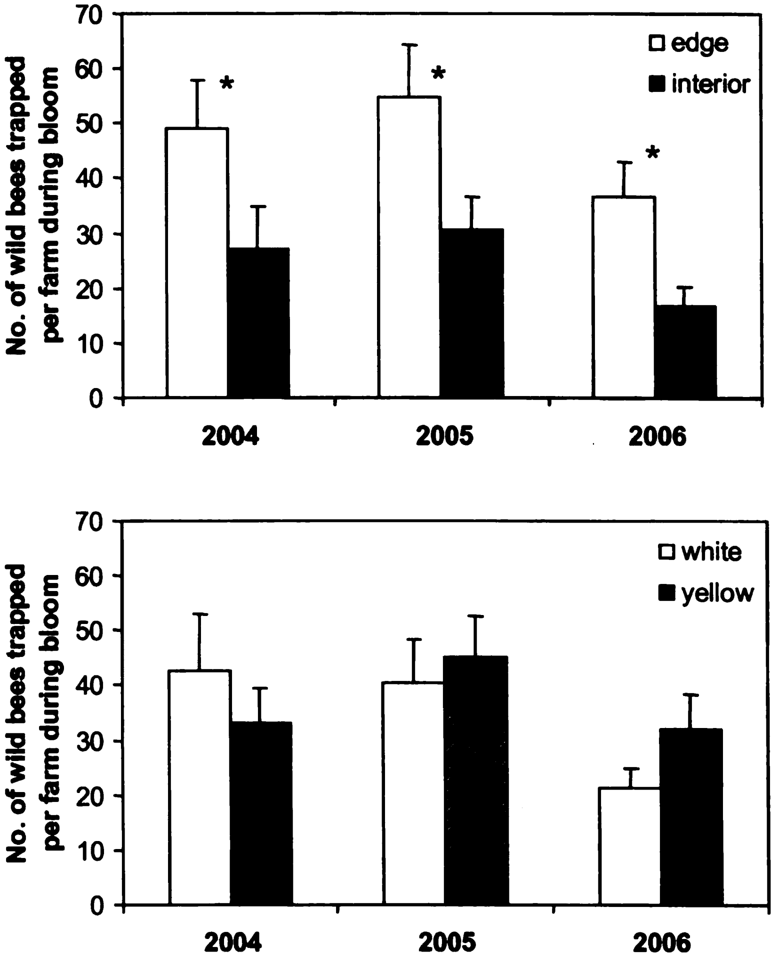

Figure 3.7. Native bee response to trap placement (edge vs. interior of the field) and color (white vs. yellow) across three years during bloom in highbush blueberry fields in southwest Michigan. Stars indicate significantly different means within each year ($P < 0.05$). This figure is presented in color.

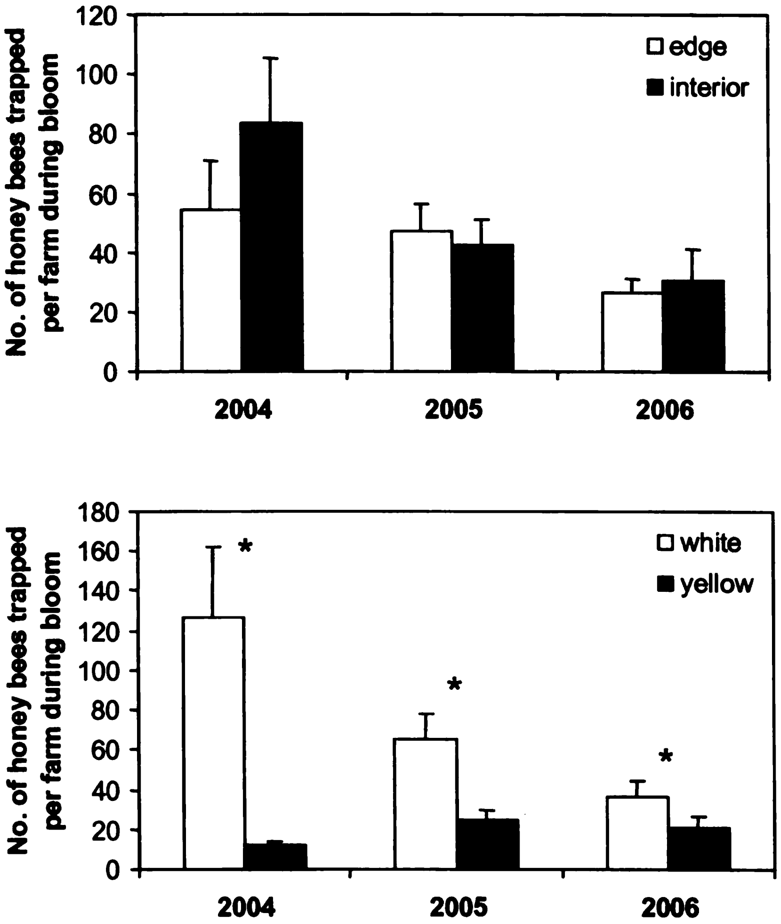

Figure 3.8. Honey bee response to trap placement (edge vs. interior of the field) and color (white vs. yellow) across three years during bloom in highbush blueberry fields in southwest Michigan. Stars indicate significantly different means within each year ($P < 0.05$). This figure is presented in color.

Table 3.7. ANOVA results of the response to pan trap position (edge vs. field interior) and color (white vs. yellow) of the eight most abundant native bees known to forage on *Vaccinium*. Data across three years (2004-06) from 13 commercial and 2 semi-abandoned blueberry fields in southwest Michigan are pooled in the analysis.

		position		**color**		
Family	**Species**	**$F_{1,57}$**	**P**	**$F_{1,57}$**	**P**	**Tukey† (P < 0.05)**
Andrenidae	*Andrena carolina*	1.53	0.22	7.62	**0.008**	yellow
Andrenidae	*An. carlini*‡	0.50	0.48	2.33	0.13	ns
Andrenidae	*An. Vicina*‡	0.30	0.59	7.27	**0.009**	white
Apidae	*Ceratina calcarata or dupla*	10.87	**0.002**	0.03	0.87	edge
Halictidae	*Augochlorella aurata*‡	8.84	**0.004**	0.99	0.32	edge
Halictidae	*Lasioglossum coriaceum*‡	0.41	0.52	7.03	**0.01**	white
Halictidae	*L. imitatum*	0.93	0.34	0.03	0.86	ns
Halictidae	*L. pilosum*	4.44	**0.04**	3.13	0.08	edge

†The last column shows the trap attributes that were associated with significantly greater bee abundance for each bee species in pairwise comparisons of edge vs. interior and white vs. yellow; (ns) means neither comparison was significant.

‡Log (n+1) transformed prior to analysis to fit assumptions of normality and equal variance.

DISCUSSION

Bee community associated with blueberry. *Apis mellifera* was the most abundant species captured during bloom at all sites, comprising one third to one half of all bees captured in pan traps. During observations in commercial and semi-abandoned fields that were in bloom, honey bees out numbered native bees by almost 20:1 in commercial fields, whereas they were 3 times more abundant as native bees in semi-abandoned fields in which managed honey bee hives were absent (Figure 3.6). This suggests that the blueberry production region is abundant with honey bees during bloom, because even at locations without managed hives, there were still honey bees present. Prior to bloom and the addition of managed hives, honey bees were rarely found (Table 3.2) and this was also the case after bloom when hives are removed from fields. The lack of feral honey bee colonies remaining near the blueberry fields emphasizes the dependence of highbush blueberry production on native bees or managed honey bees (National Academy of Sciences 2007).

In total, at least 174 species of non-*Apis* bees were trapped throughout the growing season in and around blueberry fields, with the majority of these species tending to be rare (1-2 specimens) and not appearing in every year of the study (Table 3.2). Of the native bees captured during bloom, soil nesting bees in the families Andrenidae and Halictidae were the most abundant, with the genus *Andrena* being the most speciose (49 species, Table 3.2). This finding agrees with a previous study of bees associated with highbush blueberry in upstate New York (MacKenzie and Eickwort 1996, see also Appendix C). The most abundant known *Vaccinium* foragers were three *Andrena* spp. (*An. carolina*, *An. carlini*, and *An. vicina*), the species complex of *Ceratina calcarata/dupla* and four halictid species (*Augochlorella aurata*, *Lasioglossum (L.) coriaceum*, *L. (Dialictus) imitatum*, and *L. (D.) pilosum*. All were present prior to bloom and five were also present after bloom (Figure 3.5). Their long activity period indicates that floral resources available to bees beyond the bloom period of the crop can help support populations of these bees that are likely to be contributing to blueberry pollination.

New ecological records. Direct observation and collection of bees foraging on blueberry, as well as pollen load analysis, revealed three new species and two new genera never before recorded on *Vaccinium* spp. (Table 3.4 and 3.5) Also, I report seven new species range extensions. Intensive studies such as this can reveal changes in species distributions and are essential for conservation planning.

Response of bees to trap position. Native bee abundance, richness, and diversity were all greater in traps placed at the edge of the field. This finding corresponds to previous studies of native bees in agricultural systems in which it has been repeatedly noted that bee abundance and diversity is highest at field edges, where presumably most bee nesting will be found (Cane 2001). However, although abundance of the blueberry specialist *Andrena carolina* followed this pattern, it was not significantly confined to the field edge and individuals were collected inside the field. The timing of its emergence and activity as an adult coincided closely with blueberry bloom, and this may provide an important advantage related to survival in commercial blueberry farms. Whereas bees that are present longer before or after bloom could be negatively affected by insecticide applications and other management practices in the field, *An. carolina* may be able to build nests in blueberry fields before the time when more intensive pest management practices begin. I explore this idea in later chapters.

Response of bees to trap color. Honey bees were more likely to be captured in white traps, regardless of their position in the field. Likewise, native bees associated with *Vaccinium* species were also more likely to be captured in white pan traps. This could be due to the apparent similarity in color between the white blueberry flowers and the white traps, since individual bees tend to remain constant in their foraging effort, collecting nectar and pollen from a single species of flower (Wilson and Stine 1996). As stated in the previous chapter, Leong and Thorp (1999) found that male and female *Andrena limnanthis*, an oligolectic bee of white-flowering *Limnanthes douglasii rosea* (Benth.) Mason, were most attracted to white pan traps over blue or yellow. The glaring exception to the floral constancy hypothesis for explaining pan trap color preference is *An.*

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. More research is needed to explore the degree to which flower color affects bee response to pan traps.

Conclusion. When the National Academy of Sciences published a recent pollinator status report (2007), the message was clear: we know alarmingly little about the status of pollinators in North America. Agricultural land far exceeds the acreage currently in wildlife reserves, and the potential for conservation in agroecosystems of beneficial organisms is great. For native crops such as blueberry, pollen collecting native bees are likely be important for yields, particularly when weather conditions are ill-favored for foraging by the European honey bee, *Apis mellifera.* In this study, I found that 30-50% of all the bees captured in pan traps during bloom were non-*Apis* bees, and that the proportion of bees in each family and nesting guild remained stable across the three years.

Conservation efforts need to begin with a faunal survey. This three year study of the bee community associated with highbush blueberry agriculture demonstrated the utility of pan traps to monitor bee populations toward that end. Pan trapping revealed the level of rarity of many of the bee species and gave a good estimate of the relative abundance of the common species. Compared to other faunal surveys such as those by MacKenzie and Eickwort (1996) and Drummond and Stubbs (1997) on lowbush blueberry, studies that rely on netting or observations alone may be biased towards rare species. Future studies aimed at conservation of native pollinators in blueberry should target the several *Andrena* spp. that emerge prior to bloom, as well as *Osmia bucephala*, which may turn out to be a good candidate for solitary bee management.

CHAPTER 4:

RESPONSE OF NATIVE BEES TO HABITAT QUALITY AND PRODUCTION PRACTICES IN HIGHBUSH BLUEBERRY

INTRODUCTION

Insect communities endemic to agricultural landscapes are subjected to regular disturbances associated with crop production. Growers face the challenge of producing a product free of pest damage, while doing as little harm as possible to beneficial insects such as pollinators. Unlike managed honey bees, wild bees are entirely dependent upon the agricultural landscape and adjacent habitat, nesting and foraging in and around crop fields (Free 1993, Williams and Kremen, 2007). Habitat features within and adjacent to crop fields, and the management practices applied to crop fields are all expected to affect the native bee community providing crop pollination.

Highbush blueberry (*Vaccinium corymbosum* L.) is native to North America and requires bee-mediated pollination for economically viable yields (Free 1993, Delaplane and Mayer 2000). Managed honey bees are typically rented by growers each year, but they are less efficient pollinators than many native bees (Sampson and Cane 2000, Javorek et al. 2002) and are declining due to diseases and mites (Watanabe 1994). Native bee behavior and ecology are better adapted to blueberry flower morphology and cooler weather conditions common during bloom (MacKenzie and Eickwort 1996, Batra 1997, Heinrich 2004). Therefore, native bees are likely to contribute to the pollination of this crop, particularly when honey bees are inhibited from foraging during inclement weather.

Blueberry bloom lasts 4-6 weeks depending on the number of cultivars on a particular farm. In contrast, native bee life cycles extend beyond blueberry bloom and are likely to be affected by management practices and surrounding habitat features (Kremen et al. 2002, Kim et al. 2006, Holzschuh et al. 2007). Bee diversity is positively correlated with flowering plant species richness in natural habitats such as temperate grasslands (Hegland and Boeke 2006) and Mediterranean landscapes (Potts et al. 2003). Various studies in agricultural systems have suggested that uncropped, flower-rich habitats directly adjacent to crop fields will increase diversity and abundance of beneficial insects in the field (Long et al. 1998, Kells et al. 2001, Croxton et al. 2002, Pywell et al. 2005, Marshall et al. 2006), and that hedges adjacent to agricultural fields in particular can support high arthropod diversity (Pollard and Holland 2006). Conversely, habitats in which pest management practices are more intensive are likely to have a negative impact on the structure of the endemic bee community (Shuler et al. 2005, Gabriel and Tscharntke 2007).

Application of insecticides with high toxicity to bees has been shown to have direct negative impacts on pollinators and other non-target insects that are found in crop fields (Kevan and Plowright 1989, Johansen and Mayer 1990, Riedl et al. 2006). While the direct toxicity may be known for honey bees, the lethal and sublethal effects of various pesticides on native bees are not as well understood, and measurements are typically taken under controlled laboratory conditions (Stark and Banks 2003, Desneux et al. 2007). Field studies to determine how a typical insecticide program may be impacting the endemic bee community are uncommon. Kremen et al. (2004) lumped insecticides into 4 categories based on the LD50 for honey bees and their known residual activity, then used field areas and number of applications to create an index of insecticide use on watermelon farms. They found no significant relationship between their index and pollination services to the crop. In another study, a binomial variable of pesticides/no-pesticides was used to examine how the density of bees visiting squash flowers was related to insecticide use, and again, there was no significant relationship (Shuler et al. 2005). In general, management intensity has been regarded as a combination of pest management practices, including cultivation to reduce weeds in and around fields, and proximity to semi-natural habitat, with a pattern of greater abundance and diversity associated with nearby semi-natural habitats and a reduction in diversity associated with conventional versus organic production systems (Kremen et al. 2002, Kremen et al. 2004, Shuler et al. 2005, Kim et al. 2006).

I have previously identified a community of native bees that pollinate highbush blueberry in southwest Michigan (Chapter 3). Here my objective was to investigate which components of the conventional highbush blueberry cropping system are driving native bee abundance, richness, and diversity in blueberry agroecosystems.

MATERIALS AND METHODS

Thirteen commercial and two semi-abandoned highbush blueberry farms located at least 3 km away from one another in southwest Michigan were sampled for bees using pan traps in 2004-06. Due to varying weather conditions from year to year, trapping was conducted two (2004, 2006) or three (2005) times during bloom in each field. 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 8:00-12:00 h and were collected between 16:00-20:00 h for a minimum trapping period of 6 hours on days 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 traps filled halfway with a 2% unscented soap solution (Dawn® dish soap, Procter & Gamble, Cincinnati, OH), were constructed from 355 ml white and yellow plastic bowls (Amscan, Inc., Elmsford, NY) mounted onto 2.7 diameter PVC poles stabilized with rebar (see Chapter 2, page 37). After the sampling period concluded, pan trap contents were strained into plastic bags and stored in a -12°C freezer for later processing. Specimens were thawed at room temperature prior to washing in a 70% ethanol solution. Honey bees were separated out and counted, then stored in 70% ethanol solution. All other bees were placed in a mesh bag through which they were fluffed and dried with a hairdryer before pinning and identification.

Species identifications. Preliminary identifications of bees to the lowest possible taxonomic group were made using two published dichotomous keys (Mitchell 1960, Michener et al. 1994) and the online key available through www.Discoverlife.org. Further identifications and verifications were made by J.S. Ascher of the American Museum of Natural History, Division of Invertebrate Zoology. Voucher specimens are held in the Albert J. Cook Arthropod Research Collection at Michigan State University.

Habitat features. Habitat features around each field were characterized at 45 degree intervals starting at the northern edge of the field, for a total of 8 areas sampled (Figure 4.1). This method was used because the habitat bordering the blueberry fields often was different from one end to the other of a particular field edge. Features were assigned a 1 if present and a 0 if absent and summed over the eight directions (i.e. if tree

lines were present in three 45 degree directions, the score for tree lines would be 3). There were 11 categories of attributes used (Table 4.1).

Flowering plant species in the adjacent habitats were identified and recorded four times throughout the season each year between April and August in 2004-6. In addition, five randomly placed 5 m transects were used to assess the abundance of potential foraging resources in the field perimeter adjacent to bee sampling sites in 2005-6, by multiplying the number of flowers in a contiguous patch touching each transect by the area of a single bloom in the patch, and then summing all the patch areas per transect. The area of a single bloom, including bracts in the case of members of the family Asteraceae, was estimated by measuring the widest diameter of an open flower perpendicular to the stigma and using the diameter to calculate the area of a circle.

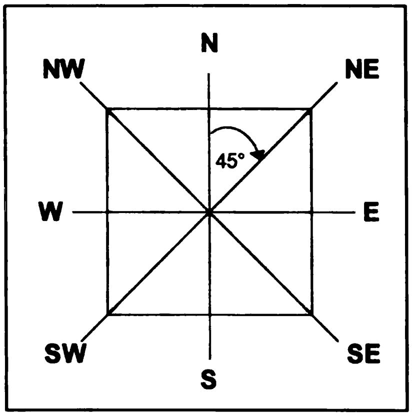

Figure 4.1. Diagram of habitat feature sampling method around the perimeter of blueberry fields, depicted here as the shaded square.

Table 4.1. Categories of habitat features used to characterize the habitat immediately surrounding highbush blueberry fields where bees were sampled in southwest Michigan from 2004-06.

Habitat feature	**Description**
Blueberry	Commercial or semi-abandoned blueberry fields
Other perennial crop	Fruit orchards, usually apple
Annual crop	Field crops
Meadow/scrubland/fallow	Any area that contained non-crop vegetation that was rarely disturbed during the growing season (i.e. mown once or twice)
Tree line	Trees planted as wind breaks along and between crop fields
Ditch	Drainage ditches that may be dry for part of the season
Pond	Manmade and used for irrigation
Deciduous woods	Woodlots varying from open to semi-closed canopy
Other woods	Mixed deciduous and coniferous, or coniferous only woodlots varying from open to semi-closed canopy
Settlement	Houses surrounded by yards that may or may not contain flower gardens; some commercial property.
Road	Blacktop or gravel

Management practices. The management intensity of non-crop vegetation was characterized under the crop canopy, between crop rows, in the perimeter immediately adjacent to the crop, and in the surrounding adjacent habitats. Intensity was based on categorical divisions of management with greater vegetation disturbance assigned higher numerical values (Table 4.2). The overall score of vegetation management intensity within each category was summed to obtain a total vegetation management score for each field.

Insecticide application records for 2003-05 were obtained for each field sampled for bees. The insecticide products used, their chemical name, their chemical class, their targeted pests, and their published LD_{50} for honey bees are listed in Table 4.3. Kilograms of active ingredient (AI) applied per hectare was calculated by dividing the application rate by the percent AI for each product used. To obtain an insecticide program toxicity (IPT) score for each field for each season, the AI per hectare for each application was divided by its LD_{50} for honey bees, and this was summed for all insecticide applications applied to each field during each year.

$$\text{insecticide program toxicity} = \sum \frac{\text{amount of active ingredient (kg) / Ha}}{LD_{50}\text{ for honeybees}}$$

The LD_{50} for honey bees was used because it is the most complete data set and should be generally representative of the response of other bees in the community to insecticides. With this equation, as the LD_{50} decreases, the IPT score increases. Likewise, if more AI is used, the IPT score increases. This score was used to determine the relationship between insecticide use and wild bee abundance and diversity during crop bloom of the following year. A second toxicity score was calculated by dividing kg/Ha of AI by 1, 2, or 3 based on the toxicity to bees rating listed in the 2007 Michigan Fruit Management Guide (Table 4.3), where Highly Toxic = 1, Moderately Toxic = 2, and Relatively Safe = 3. This order was chosen to match the relationship between the bee variables described above for the first IPT score.

Table 4.2. Areas in which non-crop vegetation was managed in and around focal blueberry fields in southwest Michigan and how they were scored for intensity.

Areas of non-crop vegetation management	**Description of categories for scoring vegetation management intensity**
under crop canopy	1 = 0-50% bare ground 2 = 50-75% bare ground 3 = 75-90% bare ground 4 = 90-99% bare ground 5 = 100% bare ground
between crop rows	1 = mown vegetation 2 = herbicide 3 = tilled
crop field perimeter	1 = untended 2 = mown vegetation 3 = herbicide 4 = tilled
adjacent habitat	1 = untended 2 = management of strip adjacent to field 3 = management to edge of adjacent habitat 4 = management into adjacent habitat 5 = clearing of adjacent habitat

Table 4.3. Insecticides used by blueberry growers in southwest Michigan whose farms were sampled for bees in 2004-06.

Material	**Active Ingredient**	**Chemical Class**	**Targeted pests***	**LD_{50} µg/bee†**	**Tox‡**
Diazinon 50 WP	diazinon	organophosphate	CBFW, CFW, BBM, OBLR, BBA	0.14	T
Guthion 50 WP	azinphos-methyl	organophosphate	CBFW, CFW, OBLR	0.06	T
Imidan 70 WP	phosmet	organophosphate	BBM, JB, OBLR	0.61	T
Aqua Malathion 8 EC, 8 F , LV	malathion	organophosphate	BBM, JB, BBA	0.27	T
Lannate 2.4 LV, 90 SP	methomyl	carbamate	BBA, WMTM	0.08	T
Sevin 50 W, 80 WSP	carbaryl	carbamate	BBM, JB, OBLR, PC	1.5	T
Sevin XLR+	carbaryl	carbamate	BBM, JB, OBLR	26.7	T
Asana XL 0.66 EC	esfenvalerate	pyrethroid	CBFW, CFW, BBM, JB, OBLR, BBA	0.06	T
Provado 1.6 F	imidacloprid	neonicotinoid	BBM, JB, BBA	0.0179	T
Spintor 2 SC	spinosad	naturalyte	BBM	0.025	M
Confirm 2 F	tebufenozide	insect growth regulator	CBFW, CFW, OBLR	234	S
Dipel	*Bacillus thuringiensis*	biological	CBFW, CFW, OBLR	nd	S

*As indicated in the 2007 Michigan Fruit Management Guide (http://web1.msue.msu.edu/pestpubs/E154/01-TOC.pdf). CBFW = cranberry fruitworm; CFW = cherry fruitworm; JB = Japanese beetle; BBM = blueberry maggot; OBLR = obliquebanded leafroller; BBM = blueberry maggot; JP = Japanese beetle; BBA = blueberry aphid; WMTM = white-marked tussock moth; PC = plum curculio.

†LD_{50} for honey bees; nd = no data. ‡Level of toxicity assigned by the 2007 Michigan Fruit Management Guide; T = highly toxic to bees, M = moderately toxic, S = relatively safe.

Statistical analyses. The Mantel test ("vegan" package for R 2.3.1) was used to compare pairwise bee community similarity indices (Jaccard, Bray-Curtis, and Morisita-Horn) with pairwise geographic distances between each of the fifteen blueberry farms. Spatial autocorrelation in non-pairwise variables (bee abundance, species richness, Shannon-Weiner and Simpson's diversity indices) was assessed with Moran's I ("ape" package for R 2.3.1).

Simple linear regression analysis was conducted between wild bee abundance, species richness, diversity (Shannon-Wiener H'), abundance of *Andrena carolina*, *Lasioglossum coriaceum*, *Ceratina calcarata/dupla* females, *Andrena carlini*, and *Augochlorella aurata* were regressed and 4 different habitat features: flowering plant richness, adjacent blueberry, adjacent deciduous woods, and adjacent ditches (PROC REG, SAS 9.1). Bees in the categories described above were also regressed separately against 3 different management intensity indexes: the IPT score based on the LD_{50} values, the IPT score based on the toxicity rankings, and vegetation management intensity (PROC REG, SAS 9.1).

For each year, a redundancy analysis (RDA in CANOCO 4.5) was conducted using all the bee species collected for which there is a *Vaccinium* floral record and the following environmental variables: insecticide program toxicity, vegetation management intensity, the number of flowering plant species, and adjacent ditches, treelines, deciduous woods, other woods (mixed or conifer), blueberry fields, annual crop fields, other flowering perennial crops, ponds, meadows, roads, and settlements. RDA is a form of canonical analysis that is an extension of multiple linear regression, which assumes Y (species data) and X (in this case habitat attributes and management intensity variables) are linearly related. It may also be seen as an extension of principal components analysis with the ordination of Y constrained in such a way that the resulting ordination vectors are linear combinations of the variables in X (Legendre and Legendre 1998). Thus, it enables analysis of the effect of multiple potential explanatory variables on a community of many bee species.

RESULTS

Independence of sites. Bee communities at the sampled fields were considered to be independent based on the results of the Mantel test for community similarity ($Z = 1729.3$, $df = 14$, $p = 0.143$). Likewise, bee abundance, species richness, Shannon-Weiner and Simpson's diversity indices assessed with Moran's I were not significant indicating no spatial autocorrelation among sites ($I < 0.514$, $df = 13$, $p > 0.05$).

Response of wild bee communities to habitat features. At least 84 flowering plant species were found in the habitats adjacent to the blueberry fields in which bees were trapped, with 32% of the species being found at single sites (Table 4.4). Increasing bee species richness was associated with increasing plant species richness in 2005 only (Figure 4.2e). Bee abundance, species richness, and diversity did not vary significantly with flowering plant abundance in 2005 or 2006.

Bee abundance, species richness, and diversity also did not vary significantly with vegetation management intensity, proximity to ditches, or deciduous woodland in all years. However, with more blueberry fields in the surrounding habitat, bee species richness and diversity declined significantly in 2004 and 2005 (Figure 4.3). Also, bee abundance and species richness declined with increasing values of both measures of IPT in 2004 and 2005 (Figures 4.4 a-b, d-e and 4.5 a-b, d-e). Likewise, bee diversity declined significantly with increasing IPT scores in 2005 (Figure 4.5h).

Table 4.4. Plant species found in the perimeter of blueberry fields sampled for bees in southwest Michigan. Nomenclature and U.S. nativity based on the USDA-NRCS Plants Database at http://plants.usda.gov (last accessed 15 July 2007).

Family	Scientific Name	Native vs. exotic	No. of farms where present
Apiaceae	*Cicuta maculata*	native	1
Apiaceae	*Daucus carota*	exotic	3
Apocynaceae	*Apocynum androsaemifolium*	native	1
Asclepiadaceae	*Asclepias syriaca*	native	2
Asteraceae	*Achillea millefolium*	exotic	10
Asteraceae	*Centaurea maculosa*	exotic	1
Asteraceae	*Chrysanthemum leucanthemum*	exotic	8
Asteraceae	*Cichorium intybus*	exotic	1
Asteraceae	*Crepis capillaris*	exotic	5
Asteraceae	*Erigeron annuus*	native	6
Asteraceae	*Erigeron philadelphicus*	native	2
Asteraceae	*Eupatorium perfoliatum*	native	1
Asteraceae	*Hieracium aurantiacum*	exotic	2
Asteraceae	*Hieracium* sp.	native and exotic	12
Asteraceae	*Hypochoeris radicata*	exotic	1
Asteraceae	*Rudbeckia hirta*	native	6
Asteraceae	*Senecio vulgaris*	exotic	1
Asteraceae	*Solidago* sp.	native	15
Asteraceae	*Sonchus* sp.	exotic	1
Asteraceae	*Taraxacum officinale*	exotic	15
Balsaminaceae	*Impatiens capensis*	native	1
Bignoniaceae	*Campsis radicans*	native	1
Brassicaceae	*Alliaria officinalis*	exotic	1
Brassicaceae	*Barbarea vulgaris*	exotic	9
Brassicaceae	*Berteroa incana*	exotic	4
Campanulaceae,	*Lobelia* sp.	native	3
Caprifolaceae	*Sambucus* sp.	native	9
Caprifoliaceae	*Lonicera* sp.	native and exotic	1
Caryophyllaceae	*Cerastium vulgatum*	exotic	14
Caryophyllaceae	*Dianthus armeria*	exotic	5
Caryophyllaceae	*Silene pratensis*	exotic	6
Clusiaceae	*Hypericum perforatum*	exotic	7
Cornaceae	*Cornus* sp.	native	1
Elaeagnaceae	*Elaeagnus umbellata*	exotic	1
Fabaceae	*Medicago lupulina*	exotic	13
Fabaceae	*Melilotus alba*	exotic	2
Fabaceae	*Melilotus officinalis*	exotic	3
Fabaceae	*Trifolium arvense*	exotic	2
Fabaceae	*Trifolium dubium*	exotic	5
Fabaceae	*Trifolium hybridum*	exotic	3
Fabaceae	*Trifolium incarnatum*	exotic	1
Fabaceae	*Trifolium pratense*	exotic	11
Fabaceae	*Trifolium procumbens*	exotic	2
Fabaceae	*Trifolium repens*	exotic	13
Fabaceae	*Vicia cracca*	exotic	2

Gentianaceae	*Centaurium pulchellum*	exotic	1
Geraniaceae	*Geranium* sp.	native and exotic	1
Iridaceae	*Iris* sp.	native and exotic	1
Iridaceae	*Sisyrinchium* sp.	native	3
Laminaceae	*Lamium purpureum*	exotic	5
Laminaceae	*Monarda fistulosa*	native	1
Laminaceae	*Prunella vulgaris*	native	3
Lauraceae	*Sassafras albidum*	native	2
Liliaceae	*Lilium* sp.	native and exotic	1
Liliaceae	*Maianthemum canadense*	native	3
Lythraceae	*Lythrum salicaria*	exotic	1
Onagraceae	*Oenothera biennis*	native	2
Oxalidaceae	*Oxalis stricta* or *europa*	native	8
Plantaginaceae	*Plantago major*	native	3
Polygonaceae	*Polygonum persicaria*	unknown	2
Polygonaceae	*Rumex acetosella*	exotic	13
Polygonaceae	*Rumex crispus*	exotic	4
Ranunculaceae	*Ranunculus abortivus*	native	2
Ranunculaceae	*Ranunculus acris*	native and exotic	1
Rosaceae	*Fragaria virginiana*	native	4
Rosaceae	*Potentilla recta*	exotic	6
Rosaceae	*Potentilla simplex*	native	2
Rosaceae	*Prunus* sp.	native and exotic	4
Rosaceae	*Rosa palustris*	native	3
Rosaceae	*Rubus* sp.	native	15
Rosaceae	*Spiraea alba*	native	1
Rubiaceae	*Galium* sp.	exotic	1
Salicaceae	*Salix* sp.	native and exotic	8
Scrophulariaceae	*Nuttallanthus canadensis* (formerly: *Linaria canadensis*)	native	1
Scrophulariaceae	*Mimulus* sp.	native	1
Scrophulariaceae	*Penstemon* sp.	native	2
Scrophulariaceae	*Verbascum blattaria*	exotic	3
Scrophulariaceae	*Verbascum thapsus*	exotic	2
Solanaceae	*Solanum carolinense*	native	3
Solanaceae	*Solanum dulcamara*	exotic	3
Solanaceae	*Solanum nigrum*	exotic	4
Violaceae	*Viola kitaibelliana*	exotic	6
Violaceae	*Viola* sp.	native and exotic	7

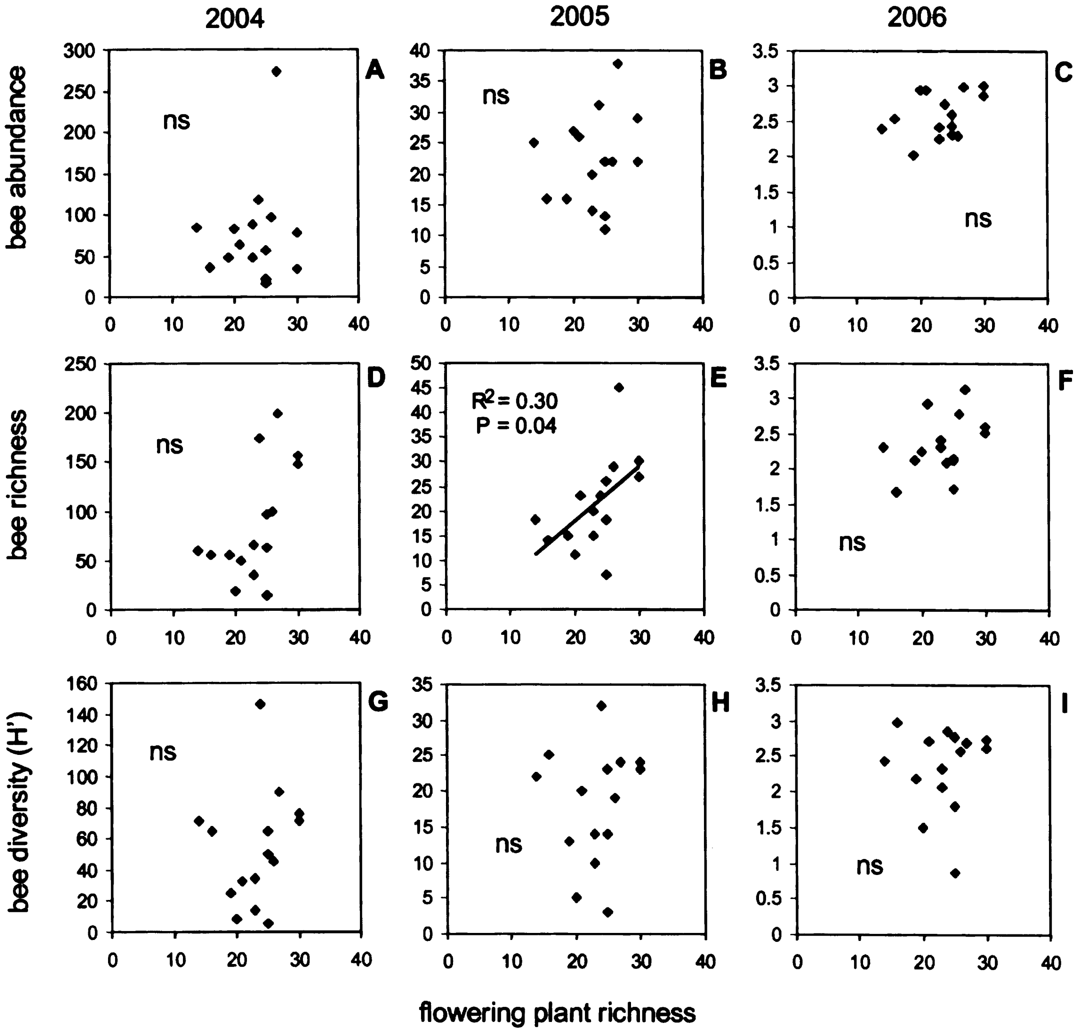

Figure 4.2. Regression analyses of wild (non-*Apis*) bee abundance (A, B, C), bee species richness (D, E, F), and bee diversity (G, H, I) with the number of flowering plant species found in the field margin at 15 farms in southwest Michigan. Except for bee richness in 2005, flowering plant species richness was not a significant factor in explaining bee abundance, richness or diversity. ns = not significant at $P < 0.05$.

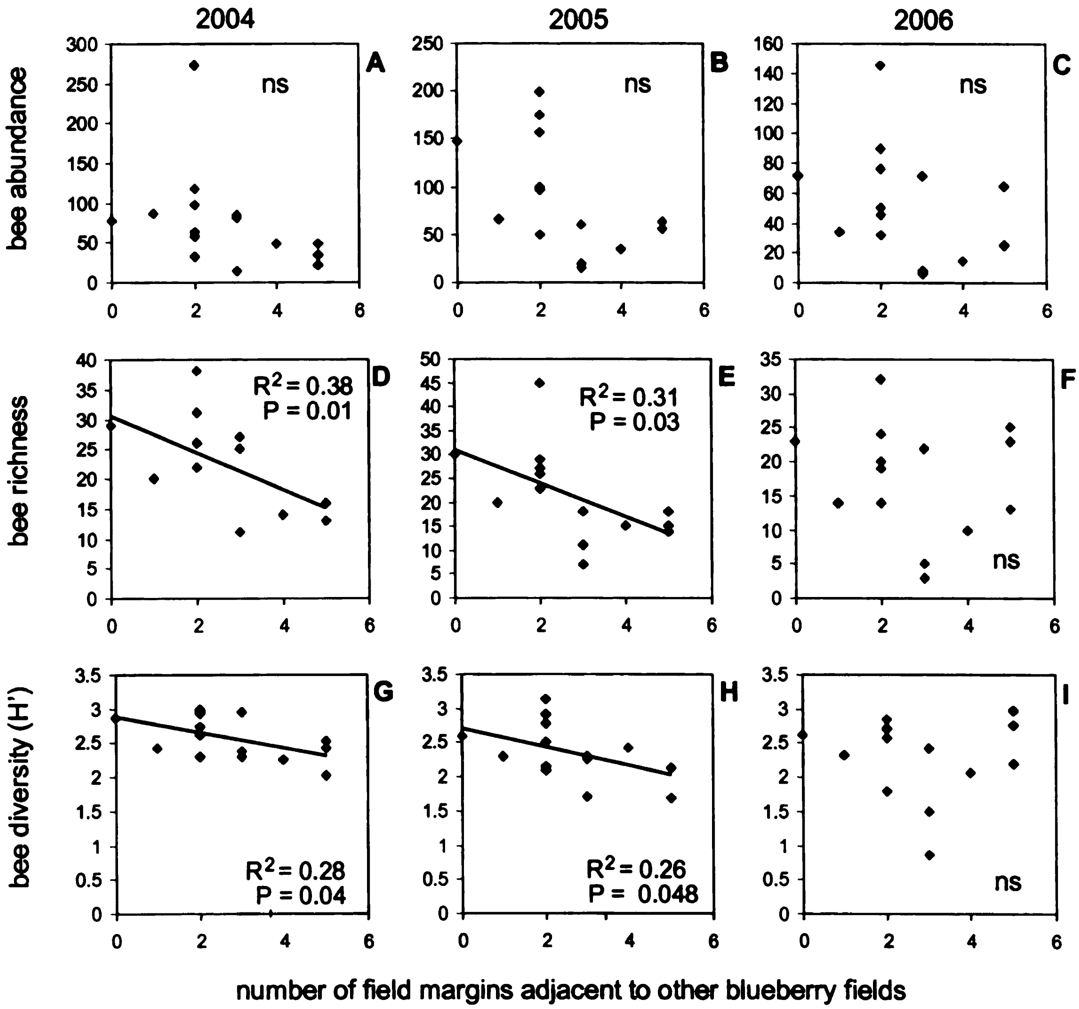

Figure 4.3. Regression analyses of wild bee abundance (A, B, C), bee species richness (D, E, F), and bee diversity (G, H, I) in relation to the number field margins bordered by blueberry fields in eight 45 degree directions (see Materials and Methods for details). ns = not significant at $P < 0.05$.

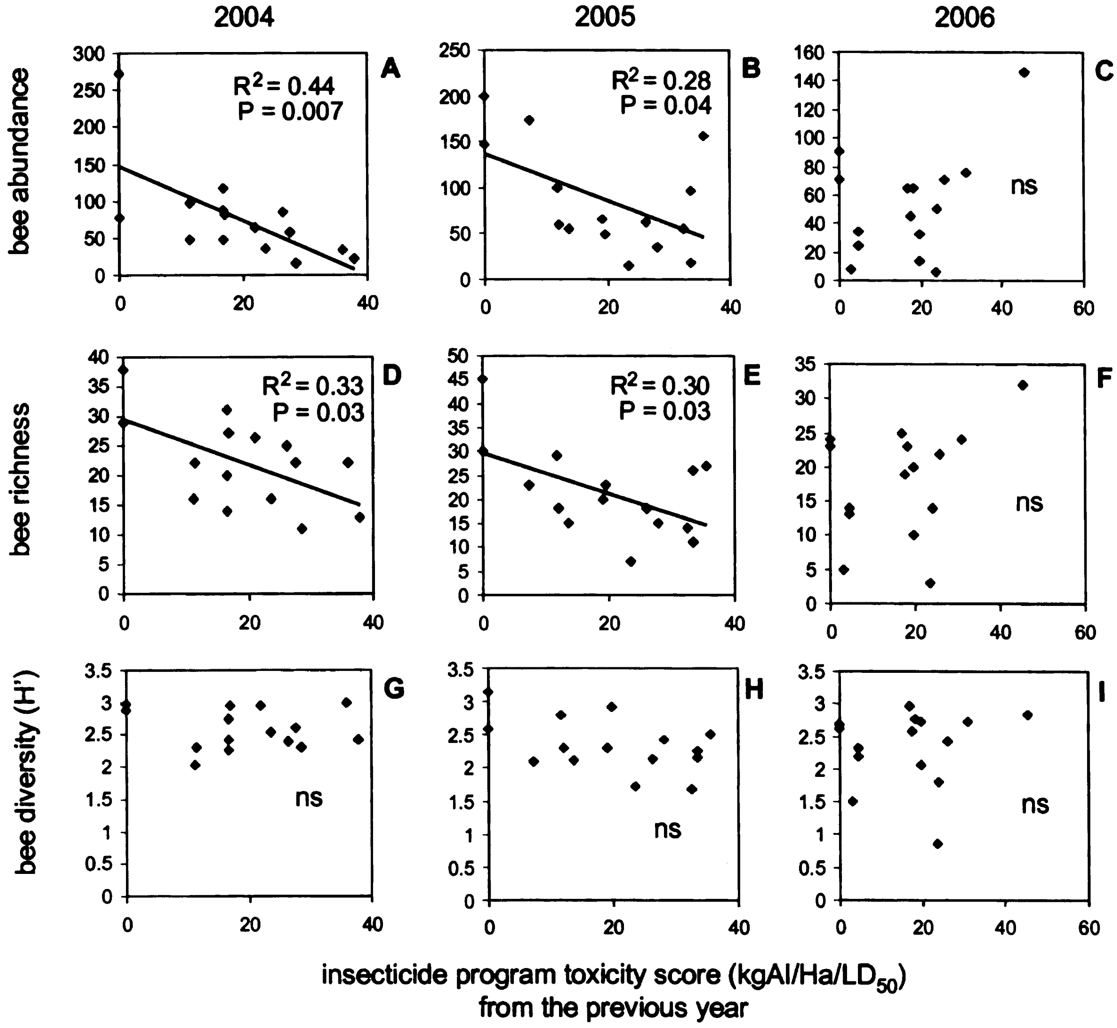

Figure 4.4. Regression analyses of wild bee abundance (A, B, C), bee species richness (D, E, F), and bee diversity (G, H, I) in relation to the insecticide program toxicity score based on LD_{50} for honey bees from the year previous to bee sampling (see Materials and Methods for details). ns = not significant at $P < 0.05$.

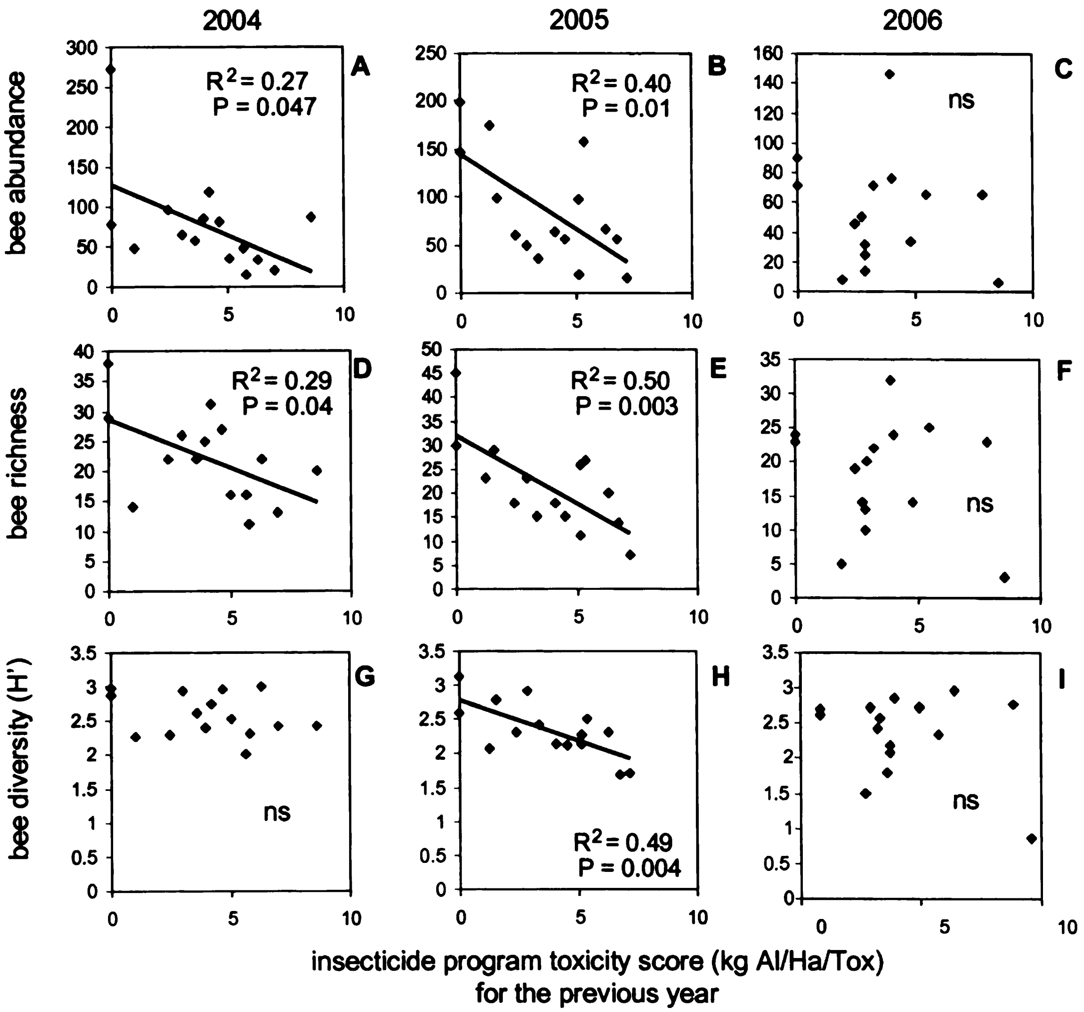

Figure 4.5. Regression analyses of wild bee abundance (A, B, C), bee species richness (D, E, F), and bee diversity (G, H, I) with the insecticide program toxicity score based on ratings in the 2007 Michigan Fruit Management Guide from the year prior to bee sampling (see Materials and Methods for details). ns = not significant at $P < 0.05$.

Response of the most common blueberry foraging bees to management practices and habitat features. The 5 most common *Vaccinium* foraging bees responded differently to management practices and habitat features within and among years. *Augochlorella aurata* was less abundant at sites with more intensive insect pest management programs and more intensive management of vegetation in and around fields (Table 4.5, 2004). However, it was more abundant at sites surrounded by a greater number of ditches. Likewise, *Andrena carlini* was less abundant at sites with more intensive insect pest management, but was either more or less abundant with increased vegetation management intensity depending on the year (Table 4.5, 2004 and 2006). Greater captures of *An. carlini* were found with increasing numbers of field margins containing ditches (2004), but not with greater flowering plant richness (2006). Abundance of *Lasioglossum coriaceum* increased positively with the proportion of adjacent woodland (2005), and with flowering plant richness (2006). *Ceratina calcarata/dupla* was less abundant in fields surrounded by more blueberry fields (2005). One of the most common bees found in blueberry fields, *Andrena carolina*, did not respond significantly to any of the variables tested.

Table 4.5. Regression coefficients for simple linear regressions of the 5 most abundant native bee blueberry foragers and management or habitat variables at 15 blueberry farms in southwest Michigan. R^2 values that are significant are in bold followed by their associated P-value in parentheses and +/- indicating the slope of the linear regression.

Management or habitat variables	**2004**	**2005**	**2006**
a) kgAI/Ha/LD$_{50}$			
Andrena carolina	0.15	0.04	0.20
Lasioglossum coriaceum	0.23	0.001	0.05
Ceratina calcarata or *dupla* (♀ only)	0.10	0.16	0.02
Andrena carlini	0.24	0.002	0.002
Augochlorella aurata	**0.35 (0.02) -**	0.16	0.04
b) kgAI/Ha/ToxRate			
Andrena carolina	0.10	0.04	0.01
Lasioglossum coriaceum	0.23	0.01	0.005
Ceratina calcarata or *dupla* (♀ only)	0.06	0.18	0.08
Andrena carlini	**0.29 (0.04) -**	0.03	0.001
Augochlorella aurata	**0.27 (0.046) -**	0.21	0.03
c) Vegetation management intensity			
Andrena carolina	0.0004	0.19	0.16
Lasioglossum coriaceum	**0.30 (0.04) -**	0.04	0.0005
Ceratina calcarata or *dupla* (♀ only)	0.09	0.15	0.09
Andrena carlini	**0.32 (0.03) -**	0.02	**0.39 (0.01) +**
Augochlorella aurata	**0.34 (0.02) -**	0.14	0.0004
d) Adjacent deciduous woods			
Andrena carolina	0.02	0.01	0.23
Lasioglossum coriaceum	0.14	**0.29 (0.04) +**	0.04
Ceratina calcarata or *dupla* (♀ only)	0.04	0.03	0.02
Andrena carlini	0.17	0.23	0.20
Augochlorella aurata	0.18	0.20	0.22
e) Adjacent ditches			
Andrena carolina	0.04	0.16	0.12
Lasioglossum coriaceum	**0.32 (0.03) +**	0.04	0.07
Ceratina calcarata or *dupla* (♀ only)	0.001	0.12	0.11
Andrena carlini	**0.29 (0.04) +**	0	0.03
Augochlorella aurata	0.20	0.27	0.13
f) Adjacent blueberry fields			
Andrena carolina	0.01	0.04	0.004
Lasioglossum coriaceum	0.02	0.008	0.09
Ceratina calcarata or *dupla* (♀ only)	0.24	**0.30 (0.03) -**	0.04
Andrena carlini	0.02	0.08	0.007
Augochlorella aurata	0.06	0.03	0.02
g) Flowering plant species richness			
Andrena carolina	0.11	0.0013	0.04
Lasioglossum coriaceum	0.03	0.12	**0.27 (0.047) +**
Ceratina calcarata or *dupla* (♀ only)	0.0001	0.24	0.9
Andrena carlini	0.06	0.21	**0.41 (0.01) -**
Augochlorella aurata	0.05	0.09	0.02

Comparison of bee species and habitat attributes using RDA. In 2004, the IPT score (kgAI/Ha/Tox) was the most significant explanatory variable for the species abundances in that year (Table 4.6). The abundance of most bee species was negatively correlated with this variable (Figure 4.6). Although not statistically significant in the RDA, the negative trend between bee species and greater pest management intensity appeared again in both 2005 and 2006 (Figures 4.7-8). In 2005, bee species abundance varied significantly with 5 variables: most bee species were negatively correlated with increasing vegetation management intensity and proximity to other flowering perennial crops, but positively correlated with the number of flowering plant species found in field perimeters and proximity to deciduous woods and ditches (Table 4.6, Figure 4.7). The number of flowering plant species in field perimeters and proximity to deciduous woods were also significantly correlated with species abundance in 2006 (Table 4.6, Figure 4.8). Increasing vegetation management intensity was negatively correlated with most bee species in all years (Figures 4.6-8). Most species were positively correlated with habitat variables associated with foraging or nesting resources, such as woodland habitat and ditches, and were negatively correlated with habitats in which pest management was more intensive (Figure 4.6-8).

Table 4.6. Summary of the RDA analyses of bee community abundance in blueberry fields by year. The λ values from greatest to least refer to the order in which the variables were added based on how well they explain the species data. Results of the Monte Carlo permutation test for each addition of an explanatory effect is listed in the P column along with its corresponding F-statistic. Significant probability values (< 0.05) are highlighted in bold.

	2004			**2005**			**2006**		
Variable	**λ**	**P**	**F**	**λ**	**P**	**F**	**λ**	**P**	**F**
Insecticide program score (kgAI/Ha/tox-rating)	0.19	**0.006**	3.01	0.03	0.526	0.88	0.06	0.506	0.94
Treelines	0.11	0.070	1.92	0.04	0.378	1.08	0.07	0.31	1.20
Ditches	0.1	0.074	1.81	0.09	**0.04**	2.24	0.05	0.58	0.76
Meadows	0.08	0.122	1.65	0.05	0.358	1.13	0.07	1.00	0.00
Ponds	0.07	0.248	1.32	0.04	0.41	1.41	0.06	0.438	1.09
No. of flowering plant species	0.06	0.276	1.28	0.17	**0.02**	2.6	0.13	**0.01**	2.15
Deciduous woods	0.06	0.330	1.29	0.13	**0.006**	2.68	0.14	**0.02**	2.08
Vegetation management intensity	0.05	0.342	1.22	0.11	**0.02**	2.39	0.07	0.242	1.27
Blueberry fields	0.06	0.344	1.11	0.03	0.48	0.93	0.05	0.426	1.05
Annual crops	0.05	0.406	1.04	0.03	1.00	0.0	0.04	0.552	0.69
Flowering perennial crop	0.04	0.492	0.95	0.13	**0.014**	2.21	0.07	0.23	1.30
Other woodland	0.04	0.566	0.8	0.04	0.468	0.99	0.09	0.094	1.48
Settlement	0.03	0.708	0.45	0.04	0.506	0.91	0.05	0.386	1.09
Road	0.06	1.00	0.00	0.07	0.1	2.2	0.05	0.518	0.89

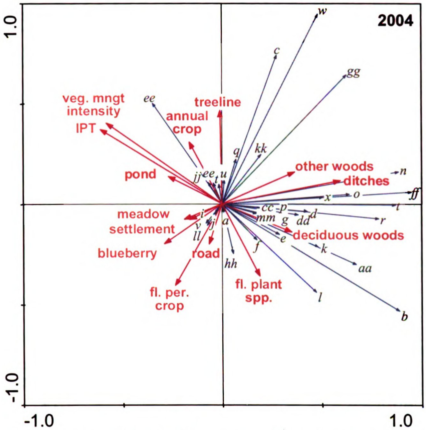

Figure 4.6. Redundancy analysis of the abundance of 38 bee species known to forage on *Vaccinium* and 13 environmental characters, including two measurements of crop management intensity at 15 blueberry farms in southwest Michigan in 2004. Blue lines represent different bee species. Red lines indicate environmental characters. See text for details on environmental characters. Key to species: a = *Agapostemon sericeus*, b = *Andrena carlini*, c = *An. carolina*, d = *An. crataegi*, f = *An. hippotes*, g = *An. imitatrix* or *morrisonella*, i = *An. nivalis*, j = *An. pruni*, k = *An. rugosa*, l = *An. vicina*, m = *Augochlora pura*, n = *Augochlorella aurata*, o = *Au. gratiosa*, p = *Augochloropsis sumptuosa*, q = *Bombus bimaculatus*, r = *B. citrinus*, t = *B. griseocollis*, u = *B. impatiens*, v = *B. perplexus*, w = *Ceratina calcarata/dupla*, x = *C. strenua*, aa = *C. thoracicus*, cc = *Halictus confusus*, dd = *H. rubicundus*, ee = *Lasioglossum acuminatum*, ff = *L. coriaceum*, gg = *L. cressonii*, hh = *L. imitatum*, ii = *L. pilosum*, jj = *L. quebecense*, kk = *Osmia atriventris/pumila*, ll = *O. bucephala*, mm = *Xylocopa v. virginica*. This figure is presented in color.

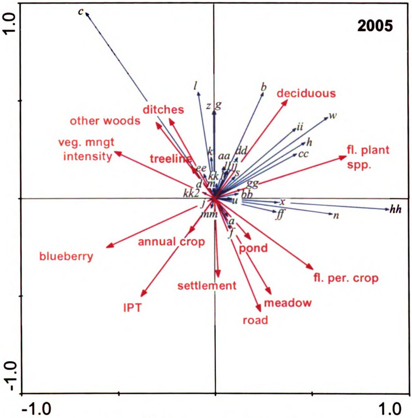

Figure 4.7. Redundancy analysis of 30 bee species known to forage on *Vaccinium* and 13 environmental characters, including two measurements of crop management intensity at 15 blueberry farms in southwest Michigan in 2005. Blue lines represent different bee species. Red lines indicate environmental characters. See text for details on environmental characters. Key to species: a = *Agapostemon sericeus*, b = *Andrena carlini*, c = *An. carolina*, d = *An. crataegi*, f = *An. hippotes*, g = *An. imitatrix* or *morrisonella*, h = *An. miserabilis*, j = *An. pruni*, k = *An. rugosa*, l = *An. vicina*, m = *Augochlora pura*, n = *Augochlorella aurata*, s = *Bombus fervidus*, u = *B. impatiens*, w = *Ceratina calcarata/dupla*, x = *C. strenua*, z = *Colletes inaequalis*, aa = *C. thoracicus*, bb = *C. validus*, cc = *Halictus confusus*, dd= *H. rubicundus*, ee = *Lasioglossum acuminatum*, ff = *L. coriaceum*, gg = *L. cressonii*, hh = *L. imitatum*, ii = *L. pilosum*, jj = *L. quebecense*, kk1 = *Osmia atriventris*, kk2 = *O. pumila*, ll = *O. bucephala*, mm = *Xylocopa v. virginica*. This figure is presented in color.

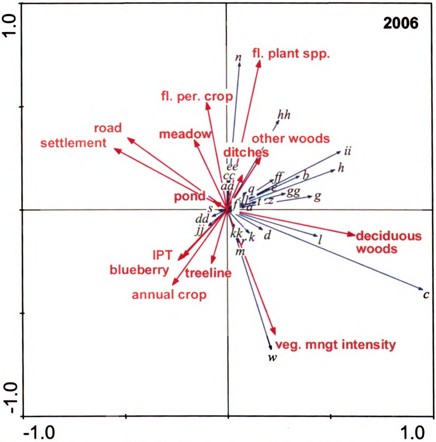

Figure 4.8. Redundancy analysis of 28 bee species known to forage on *Vaccinium* and 13 environmental characters, including two measurements of crop management intensity at 15 blueberry farms in southwest Michigan in 2006. Blue lines represent different bee species. Red lines indicate environmental characters. See text for details on environmental characters. Key to species: a = *Agapostemon sericeus*, b = *Andrena carlini*, c = *An. carolina*, d = *An. crataegi*, e = *An. forbesii*, f = *An. hippotes*, g = *An. imitatrix* or *morrisonella*, h = *An. miserabilis*, k = *An. rugosa*, l = *An. vicina*, m = *Augochlora pura*, n = *Augochlorella aurata*, q = *Bombus bimaculatus*, r = *B. citrinus*, s = *B. fervidus*, t = *B. griseocollis*, w = *Ceratina calcarata/dupla*, z = *C. inaequalis*, aa = *Colletes thoracicus*, cc = *Halictus confusus*, dd = *H. rubicundus*, ee = *Lasioglossum acuminatum*, ff = *L. coriaceum*, gg = *L. cressonii*, hh = *L. imitatum*, ii = *L. pilosum*, jj = *L. quebecense*, kk = *Osmia atriventris* or *pumila*, ll = *O. bucephala*. This figure is presented in color.

DISCUSSION

Within a conventional cropping system, it is expected that there will be variation among farms in terms of soils and hydrology, the distribution of habitat features surrounding crop fields, and in the way individual growers choose to manage their farmland. Previous studies have shown that broad categorizations of crop management systems, such as the division of management practices into conventional versus organic, reveal effects of this farm variation on the accompanying bee communities, with lower bee diversity and abundance in conventional farms (Kremen et al. 2002, Shuler et al. 2005, Kim et al. 2006, Holzschuh et al. 2007, Gabriel and Tscharntke 2007). This study aimed to determine which components of conventional crop systems are driving bee community structure in highbush blueberry.

It is clear from toxicological studies that insecticides can have both lethal and sub-lethal effects on bees (Johansen and Mayer 1990, Desneux et al. 2007) and that insecticides applied for pest management can have negative impacts on non-target arthropods at the community level (Kevan and Plowright 1989, Stark and Banks 2003). While growers of crops that require bee pollination typically avoid spraying insecticides during bloom (Riedl et al. 2006), field studies to determine how a typical insecticide program may be impacting native bee communities are uncommon and have been unable to show direct relationships between insecticide use and the structure of the bee community (Kremen et al. 2004, Shuler et al. 2005).

Previous attempts to use indices or simple binomial categories of insecticide use intensity have not found any relationship between insecticide application intensity throughout the growing season and the endemic bee community (Kremen et al. 2004, Shuler et al. 2005). The two indices of insecticide program toxicity developed here revealed significant negative relationships between the intensity of insecticide programs applied to blueberry fields and the bee community present during bloom the following year, in two out of three years. Either of these indices could be applied to pest management programs to allow growers to assess the risk of their management practices to bees, and to identify pesticide applications that could be removed or replaced with a less toxic alternative.

Crop management intensity is a combination of pest management practices, including cultivation to reduce weeds in and around fields and proximity to semi-natural habitat, with a pattern of greater abundance and diversity of bees in fields near semi-natural habitats and lower bee diversity in conventional versus organic production systems (Kremen et al. 2002, Kremen et al. 2004, Shuler et al. 2005, Kim et al. 2006, Holzschuh et al. 2007). I found that blueberry fields surrounded by similar crop habitat, i.e other blueberry fields, were likely to have bee communities that were less speciose and less diverse. This effect could be due to landscape homogeneity, and is likely to be an important part of the explanation for variation in bee community structure.

This study also revealed a reduction in the abundance during bloom of bees that are known to forage on blueberry with increasing crop management intensity measurements, including the intensity of weed management and the abundance of other adjacent crop fields. These findings suggest that the insecticide program intensity, while a key variable affecting the structure of native bee communities in crop fields is one of many factors that combine to affect the suitability of crop fields for these insects.

Flower-rich habitats and other semi-natural landscapes adjacent to crop fields are associated with a greater abundance and diversity of beneficial insects in agricultural landscapes (Long et al. 1998, Kells et al. 2001, Croxton et al. 2002, Ricketts 2004, Pywell et al. 2005, Marshall et al. 2006). A similar pattern in the bee community was observed in the fields sampled here, with the abundance of blueberry foraging bees being higher in fields having greater floral species richness. In addition, fields adjacent to habitats likely to contain floral and nesting resources, such as woodlands and ditches, were positively correlated with the abundance of blueberry foragers during bloom.

Conclusions. A number of indices have been developed to determine or predict the effects of pesticides on human health and the environment (e.g. Kovach et al. 1992), but not with specific respect to their potential impact on bees (although see Kremen et al. 2004). There is evidence that accidental drift of insecticides into non-target areas can be detrimental to native bee populations (Kevan and Plowright 1989), and there are a number of studies that have compared conventional vs. organic crop management systems showing that bees are typically more abundant and more diverse on organic farms (Kremen et al. 2002, Kremen et al. 2004, Shuler et al. 2005, Kim et al. 2006). But most agricultural land is managed conventionally and there is a wide variation in management styles within the broad category of "conventional."

Further work still needs to be done to examine what it is about conventional farms that make them more or less hospitable to bees. We need metrics to measure the response of native bees to insecticide use in conventional agricultural landscapes. For conservation of diverse bee communities, habitat heterogeneity appears to be an important piece of the puzzle. For conservation of specific crop pollinators, attention to their phenology with regard to floral resources beyond crop bloom and nesting resources in protected areas will be important. Agricultural landscapes have great potential for the protection of pollinators, particularly in cropland dependent upon them. Further studies are needed to better understand where native bees are nesting in agricultural lands and which sets of flowering plants should be used to supplement floral resources throughout the growing season.

CHAPTER 5:

COMPARISON OF NATIVE PLANTS FOR USE IN AGRICULTURAL BEE CONSERVATION PROGRAMS IN THE MID-WESTERN U.S.

INTRODUCTION

Pollination is critical to the productivity of many agricultural crops (McGregor 1976, Free 1993, Kearns 1998, Kevan and Phillips 2001). A recent review found that of 115 cultivated plants grown for fruit, vegetable, or seed production, 87 depend upon animal-mediated pollination, comprising 35% of global crop production yields (Klein et al. 2006). Non-managed wild bees are estimated to be responsible for pollination contributing $3.07 billion of fruits and vegetables in the United States annually (Losey and Vaughan 2006). Until recently, little attention was paid to pollinators in biodiversity conservation programs for managed and non-managed ecosystems (Buchmann and Nabhan 1996, Kearns and Inouye 1997). However, concerns over declines in insect biodiversity, thought to be caused by habitat loss and fragmentation as a result of agricultural intensification and other anthropogenic land use changes, have emphasized the importance of natural ecosystem services, including pollination (Westrich 1996, Kremen et al. 2002, Tscharntke et al. 2005, Biesmeijer et al. 2006).

Plant productivity in natural and agricultural systems has been linked to pollinator abundance and diversity, leading to an increased awareness of the services pollinators provide in these ecosystems and greater attention on strategies that can support their populations (Allen-Wardell et al. 1998, Kevan and Phillips 2001, Javorek et al. 2002, Kremen et al. 2002, Klein et al. 2003, Potts et al. 2003, Fontaine et al. 2006). At the same time, the availability of managed *Apis mellifera* colonies that are used to provide pollination services is declining because of diseases and parasites (Torchio 1990, Watanabe 1994). This increases the importance of conserving wild bees, as part of growers' strategies for achieving sustainable crop pollination (Southwick and Southwick 1992, Kevan and Phillips 2001, Klein et al. 2006).

The suitability of an ecosystem for bees depends on the ecology of each bee species in the community, including bee phenology, foraging range, and the availability of suitable foraging and nesting resources within that range (Kearns and Inouye 1997, Cane 2001). For some bees, foraging resources are needed during a brief window in time, with these bees typically emerging in synchrony with specific plant species. Those that are multivoltine (e.g. many halictine bees) or social (e.g. bumble bees) require resources throughout the season, and benefit from floral resources that are distributed in time as well as in space (Michener 2000). Hence, conservation of plant-pollinator interactions requires a community rather than an individual species approach (Kearns 1998), in which appropriate plant species are selected to provide resources for bees with diverse ecological attributes (Potts et al. 2003).

Conservation programs that increase farmland biodiversity are expected to achieve greatest adoption if they are designed to address multiple needs. Most bee species require flowering plant resources through a longer time period than when the crop is in bloom and so flowering plants have been evaluated for supporting crop pollination by insects (Patten et al. 1993, Kearns and Inouye 1997, Carreck and Williams 1997). Flowering plants have also been evaluated for use in agricultural settings to help enhance biological control (Bugg et al. 1989, Maingay et al. 1991, Bugg and Waddington 1994, Pontin et al. 2006, see also reviews by Landis et al. 2000 and Gurr et al. 2003). Plants that can provide resources for both groups of beneficial insects should provide greater economic return to growers and should also increase the likelihood that they will be included in conservation programs designed to enhance arthropod-mediated ecosystem services.

Typically, non-native flowering annuals are recommended for attracting beneficial insects in agricultural settings to reduce pest populations (Baggen and Gurr 1998, Baggen et al. 1999, Begum et al. 2006). However these often require yearly sowing, and would not be suitable for projects that also aim to conserve or restore native plants and the beneficial insects associated with them. Perennial plants offer the potential of creating a more stable habitat within and around farm land to enhance beneficial insects, and a selection of plant species that bloom throughout the growing season is expected to support beneficial insect communities better than a single sowing of an annual plant species.

A few studies in North America have evaluated native plants for their attraction to bees (Patten et al. 1993, Frankie et al. 2005), and some studies in the United Kingdom have evaluated pollinator attraction to cultivated (Comba et al. 1999a) and to native or naturalized (Comba et al. 1999b) flowering plants. However, selection of native plants from these studies as part of a conservation or restoration project aiming to enhance pollinator populations is challenging because different plant species were tested in different years and at different sites. Given the variability in weather, soils, and climate found between study sites, direct comparison of plant species at the same site is expected to provide a more robust comparison of relative plant suitability for pollinator conservation (Patten et al. 1993, Gustafson et al. 2005). As part of a project designed to evaluate native Midwestern USA prairie and savanna plants for their support of natural enemies (Fiedler and Landis 2006a), I compared 43 native flowering plants for their attraction to bees. The goal of the combined projects was to identify plants that could be used in a multi-purpose ecosystem services enhancement program. Here I report on which plants were visited most frequently by bees and whether simple floral characteristics can be used as indicators of a plant's degree of attraction to bees.

MATERIALS AND METHODS

Study site and plants. The study site was established on a former agricultural field with Marlette fine sandy loam, previously managed in a corn and soybean rotation, at the Michigan State University Entomology Research Farm in Ingham County, Michigan, USA. Forty three native plant species were established in 1 m^2 blocks spaced 6 m apart with a background planting of orchard grass (*Dactylis glomerata* L.). The plots were established using a randomized complete block design with five replicates of each plant species. These plants were evaluated for their relative attractiveness to bees. Plant nomenclature follows Voss (1996) and plant taxonomy follows Judd (2002). Native plant species were selected for study using the following criteria: 1) native Michigan perennial plant, 2) adapted to agricultural field conditions (e.g. full sun, moderate drought tolerance), 3) species representing a diversity of bloom periods, 4) species from a variety of plant families, with varied flower color and morphology easily accessible by natural enemies, 5) forb or shrub species formerly found in Michigan oak savanna and prairie, and 6) local genotypic plants commercially available in Michigan.

Three, five or eight plugs of the perennials were planted per plot, depending on the growth habit of each species, to maximize plant density within the plot. Planting occurred during the fall of 2003. Plots were maintained as described in Fiedler and Landis (2006a).

Plant measurements. Floral area per meter square, corolla width, and corolla depth during peak bloom were recorded from each plant species evaluated. To estimate floral area per meter square of each plot, the number of open flowers per plot was counted weekly and multiplied by the average area of ten representative flowers or clusters based digital images taken at the site (Coolpix 4800, Nikon, Melville, NY), with a ruler for reference in each image. Digital images were prepared for analysis by converting flower images into white space (Knoll 2000) using Adobe Photoshop 6.0 software. ScionImage freeware (Alpha 4.0.3.2, www.scioncorp.com) was used to calculate individual floral area based on the converted images.

Floral morphology was measured on young, open flowers with intact stamens using a Spot Imaging System (v.3.5.9 Diagnostic Instruments, Inc. Sterling Heights, Michigan) in combination with an Olympus SZX12 stereoscope. Corolla width and depth were measured on five flowers per species to the nearest 0.01 cm. For plants in the Asteraceae, one young, open disc flower was measured per flower head, and for species with florets, one floret was measured. Width was measured at the point where the corolla fused and depth was measured from the point of corolla fusion to nectaries (exceptions are described in Fiedler and Landis (2006b)). Corolla depth was recorded as zero in species with nectaries located at the point where petals attach to the gynoecium.

Vacuum sampling for bees. All floral visitors were collected weekly from 4 May – 27 September 2005 from flowering plants one week before, the week of, and one week after peak bloom between 0930-1330 EST on calm, sunny days. Samples collected prior to, during, and after the week of peak bloom (hereafter called "full bloom period"), based on the weekly counts of the number of open flowers on each plant species, were used in the analyses. A fine white mesh bag (Kaplan Simon Co., Braintree, MA) was placed over the intake on a leaf blower (Stihl BG55, Norfolk, VA) modified into a vacuum and plots were vacuumed until all flowers were sampled. Each sample was frozen, and bees were subsequently sorted and identified to the lowest taxonomic level using the key of Michener et al. (1994) and the online key to eastern North American bee species at www.Discoverlife.org. The number of bees per sample was recorded and averaged over the number of collections made during peak bloom per plot for analyses. For eight plant species, one or more of the plots were not in bloom during the three sampling visits and so the average was taken across the total number of plots sampled.

Bee observations. Timed observations of bees visiting each plot in bloom were conducted from 1 June – 17 August 2005 between 1000 – 1700 EST on sunny, calm days when vacuum sampling was not taking place. Each plot was observed once during peak bloom for 5 minutes, for a total of 5 replicate observations per plant species. Bees visiting the plants during this time were either recorded and identified to the lowest taxonomic level (usually genus) *in situ* or collected with a modified Dustbuster™ insect vacuum (BioQuip Products, Rancho Dominguez, CA) for subsequent identification using the keys described above. No samples were taken from the earliest blooming species (*Sambucus racemosa* L.) and the last four blooming species (*Solidago riddellii* Frank ex Riddell, *S. speciosa* Nutt., *Aster novae-angliae* L., and *A. laevis* L.).

Statistical analysis. Analysis of variance with Tukey-Kramer adjusted means separation (PROC MIXED, SAS v 8.02) was used to examine differences among plant species in the number of non-*Apis* bees that visited plants within early, middle, and late blooming periods for both the vacuum samples and timed observations. Simple linear regression analyses (PROC REG, SAS 9.1) were conducted with each pair of floral characters to check for autocorrelations, then a multiple linear regression analysis (PROC REG, SAS v 8.02) was conducted on the bees obtained during vacuum sampling to determine whether bee abundance (honey bees, bumble bees, wild bees other than bumble bees, and all wild bees) and richness (number of different bee taxa represented in the samples collected from each plant species) varied with any of the three floral characteristics (average floral area during full bloom, corolla width, and corolla depth).

RESULTS

Attractiveness of plants. The number of bees collected during vacuum sampling increased over the course of the 2005 growing season. Across all the plants in each of the three seasonal groupings, there was an average of 3.5 ± 0.1, 22.6 ± 5.7, and 69.8 ± 20.2 bees per plant species in the early, mid, and late season samples, respectively (Figure 5.1). There was an associated increase in the richness of bees collected, with average number of bee taxa collected of 2.3 ± 0.5, 4.8 ± 0.8, and 7.1 ± 1.2 per plant species in the early, mid, and late season groups, respectively (Figure 5.1).

A total of 875 honey bees and 1393 wild bees was collected via vacuum sampling. The most abundant wild bee was *Bombus impatiens*, comprising 62% of the wild bees collected. *Lasioglossum admirandum* (93, 6%), *Hylaeus affinis* (71, 5%), *Agapostemon virescens* (66, 5%), *Halictus ligatus* (50, 4%), *Ceratina calcarata/dupla* females (38, 3%), and *Xylocopa virginica virginica* (34, 3%) were the next most abundant wild bee species (Table 5.1). Honey bees were assumed to be from seven managed hives that were within 200 m of the study site.

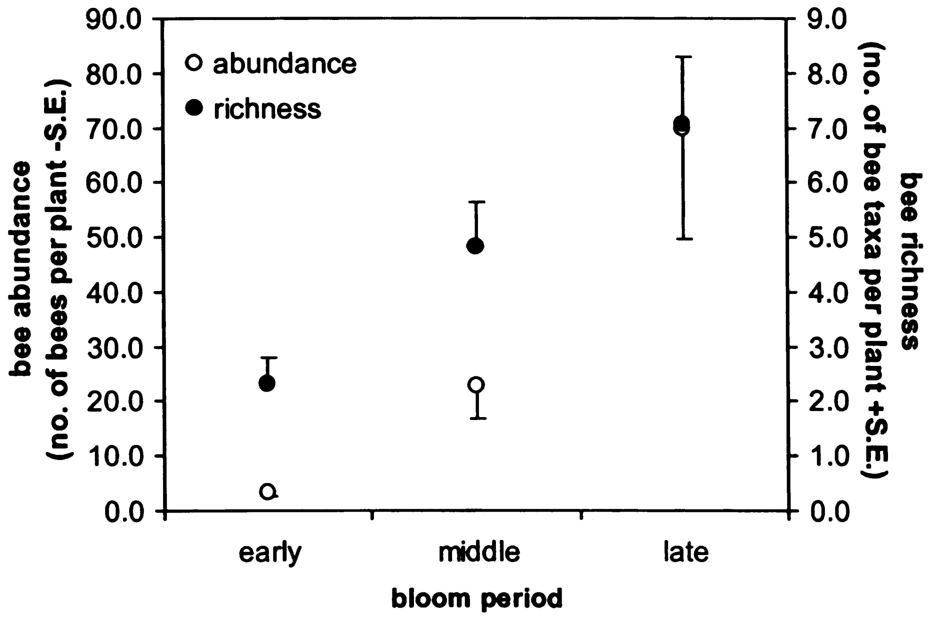

Figure 5.1. Average abundance (number of bees per plant species) and richness (number of bee taxa per plant species) of all wild (non-*Apis*) bees collected at native plants in 2005 in Ingham Co., Michigan via vacuum sampling during peak bloom. Samples are grouped by peak bloom periods: early (mid-May – June), middle (July – mid-August), and late (mid-August – September).

Table 5
families
Lamina
after ea

Plant fam

Species
Andrenid
Andrena
helianth
Andrena
Apidae
Bombus
bimacu
Bombus
Bombus
Bombus
griseoc
Bombus
Ceratina
calcara
(♀)
Ceratina
(♂)
Melissod
bimacu
Melissod
Nomada
Triepeol
concav
Triepeol
Triepeol
pectora
Triepeol
remigat
Xylocop
virgini
Colletid
Hylaeus
Hylaeus
Hylaeus
Hylaeus
Hylaeus
rudbec
Hylaeus
Halictid
Agapost
splende

Table 5.1. Bees collected during 3 vacuum sampling periods during peak bloom at a research plot of 43 native prairie forb species in Ingham County, Michigan. Shown here are plants in families (A) Asteraceae, (B) Apiaceae, (C) Apocynaceae, (D) Asclepiadaceae, (E) Campanulaceae, (F) Caprifolaceae, (G) Fabaceae, (H) Geraniaceae, (I) Hydrophyllaceae, (J) Laminaceae, (K) Liliaceae, (M) Ranunculaceae, (N) Rhamnaceae, (O) Rosaceae, (P) Rubiaceae, (Q) Saxifragaceae, (R) Scrophulariaceae, and (S) Verbenaceae. The date in parentheses after each plant name indicates when it was in peak bloom in 2005.

Plant family*	A												B			C	D		E	F	G			H	I	J		K	M		N	O				P	Q	R			S	
Species	*Aster laevis* L. (27-Sep)	*Aster novae-angliae* L. (20-Sep)	*Cacalia atriplicifolia* L. (23-Aug)	*Coreopsis lanceolata* L. (21-Jun)	*Eupatorium perfoliatum* L. (23-Aug)	*Helianthus strumosis* L. (30-Aug)	*Liatris aspera* Michx. (30-Aug)	*Ratibida pinnata* (Vent.) Barnh. (2-Aug)	*Silphium perfoliatum* L. (23-Aug)	*Solidago riddellii* Frank ex Riddell (13-Sep)	*Solidago speciosa* Nutt. (20-Sep)	*Vernonia missurica* Raf. (23-Aug)	*Angelica atropurpurea* L. (14-Jun)	*Heracleum maximum* Bartr. (21-Jun)	*Zizia aurea* (L.) Koch (6-Jun)	*Apocynum cannabinum* L. (12-Jul)	*Asclepias incarnata* L. (2-Aug)	*Asclepias tuberosa* L. (12-Jul)	*Lobelia siphilitica* L. (23-Aug)	*Sambucus racemosa* L. (10-May)	*Amorpha canescens* Pursh (2-Aug)	*Desmodium canadense* (L.) DC. (9-Aug)	*Lespedeza hirta* (L.) Hornem. (30-Aug)	*Geranium maculatum* L. (31-May)	*Hydrophyllum virginianum* L. (6-Jun)	*Agastache nepetoides* (L.) Kuntze (16-Aug)	*Monarda punctata* L. (16-Aug)	*Allium cernuum* Roth (9-Aug)	*Anemone canadensis* L. (14-Jun)	*Aquilegia canadensis* L. (6-Jun)	*Ceanothus americanus* L. (12-Jul)	*Fragaria virginiana* Duchesne (24-May)	*Potentilla fruticosa* auct. non L. (12-Jul)	*Rosa setigera* Michx. (12-Jul)	*Spiraea alba* Duroi (9-Aug)	*Cephalanthus occidentalis* L. (19-Jul)	*Heuchera americana* L. (21-Jun)	*Penstemon hirsutus* (L.) Willd. (14-Jun)	*Scrophularia marilandica* L. (27 Jul)	*Veronicastrum virginicum* (L.) Farw. (2-Aug)	*Verbena stricta* Vent. (2-Aug)	**total for all plants**
Andrenidae																																										
Andrena helianthiformis	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
Andrena spp.	-	3	-	-	-	-	-	-	-	7	1	-	-	-	1	1	1	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	17
Apidae																																										
Bombus bimaculatus	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	3
Bombus citrinus	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
Bombus fervidus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
Bombus griseocollis	-	-	-	-	-	-	-	3	4	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11
Bombus impatiens	13	12	37	-	6	8	57	7	233	19	69	20	-	-	-	-	-	1	136	-	2	1	7	-	-	91	5	13	-	-	-	-	-	4	22	3	-	-	21	66	5	858
Ceratina calcarata/dupla (♀)	-	1	-	-	1	-	-	1	1	2	-	2	-	-	-	-	-	-	20	-	1	-	-	-	1	-	-	-	-	-	-	1	-	-	-	-	-	4	-	1	2	38
Ceratina dupla (♂)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Melissodes bimaculata	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	3
Melissodes spp.	-	-	1	-	6	6	-	3	2	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	21
Nomada spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Triepeolus concavus	-	1	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3
Triepeolus lunatus	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Triepeolus pectoralis	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Triepeolus remigatus	-	-	-	-	-	-	-	5	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7
Xylocopa v. virginica	-	-	-	-	-	-	-	1	-	1	2	-	-	-	-	-	23	-	-	-	-	-	-	-	-	-	6	-	-	-	-	-	-	-	-	-	-	1	-	-	-	34
Colletidae																																										
Hylaeus affinis	-	-	-	-	2	-	-	-	-	13	-	-	-	-	2	4	1	-	3	-	-	-	-	-	-	-	-	-	-	-	1	-	21	-	24	-	-	-	-	-	-	71
Hylaeus annulatus	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	4
Hylaeus mesillae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	8
Hylaeus modestus	-	-	-	-	-	-	-	-	-	1	-	-	-	1	1	1	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5
Hylaeus rudbeckiae	-	-	-	-	-	-	-	-	-	7	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	10
Hylaeus sp.	-	-	-	-	2	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	6
Halictidae																																										
Agapostemon splendens	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1

	Aster laevis	*Aster novae-angliae*	*Cacalia atriplicifolia*	*Coreopsis lanceolata*	*Eupatorium perfoliatum*	*Helianthus strumosis*	*Liatris aspera*	*Ratibida pinnata*	*Silphium perfoliatum*	*Solidago riddellii*	*Solidago speciosa*	*Vernonia missurica*	*Angelica atropurpurea*	*Heracleum maximum*	*Zizia aurea*	*Apocynum cannabinum*	*Asclepias incarnata*	*Asclepias tuberosa*	*Lobelia siphilitica*	*Sambucus racemosa*	*Amorpha canescens*	*Desmodium canadense*	*Lespedeza hirta*	*Geranium maculatum*	*Hydrophyllum virginianum*	*Agastache nepetoides*	*Monarda punctata*	*Allium cernuum*	*Anemone canadensis*	*Aquilegia canadensis*	*Ceanothus americanus*	*Fragaria virginiana*	*Potentilla fruticosa*	*Rosa setigera*	*Spiraea alba*	*Cephalanthus occidentalis*	*Heuchera americana*	*Penstemon hirsutus*	*Scrophularia marilandica*	*Veronicastrum virginicum*	*Verbena stricta*	**total**
Agapostemon virescens	3	4	-	-	3	2	1	-	23	19	-	6	-	-	-	-	-	-	2	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	66
Augochlorella aurata	-	-	-	-	2	-	-	1	-	1	-	-	-	-	1	-	-	1	5	-	-	-	-	-	1	-	-	-	-	-	-	2	-	-	-	-	3	-	-	-	-	17
Halictus confusus	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	4
Halictus ligatus	-	-	5	-	5	1	-	33	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	50
Halictus parallelus	-	-	-	-	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3
Halictus rubicundus	-	-	-	-	2	-	-	-	-	1	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1	1	-	9
Lasioglossum acuminatum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1	-	-	3
Lasioglossum admirandum	-	1	1	1	3	-	-	1	-	10	8	-	1	1	2	1	3	2	14	-	8	1	-	-	-	2	-	7	2	2	1	-	3	-	1	1	3	1	8	4	-	93
Lasioglossum coriaceum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	2
Lasioglossum cressonii	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Lasioglossum leucozonium	-	1	-	1	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4
Lasioglossum nymphaearum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1
Lasioglossum pilosum	-	-	1	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	3	-	-	-	-	-	-	-	-	9
Lasioglossum rohweri	-	-	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-	-	-	-	-	1	-	-	5
Lasioglossum sp. 1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Lasioglossum sp. 2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Lasioglossum tegulare	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1
Megachilidae																																										
Anthidium manicatum	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Megachile pugnata	-	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
Megachile sp.	-	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
No. of non-*Apis* bees:	**16**	**23**	**48**	**2**	**33**	**19**	**58**	**58**	**272**	**90**	**84**	**32**	**1**	**3**	**13**	**10**	**34**	**4**	**186**	**1**	**13**	**2**	**7**	**1**	**4**	**97**	**12**	**24**	**3**	**2**	**2**	**3**	**41**	**6**	**50**	**6**	**6**	**7**	**32**	**72**	**8**	**1393**
No. of non-*Apis* bee species:	**2**	**7**	**8**	**2**	**11**	**5**	**2**	**12**	**13**	**17**	**7**	**7**	**1**	**3**	**7**	**6**	**7**	**3**	**10**	**1**	**5**	**2**	**1**	**1**	**4**	**6**	**3**	**4**	**2**	**1**	**2**	**2**	**12**	**3**	**5**	**4**	**2**	**4**	**5**	**4**	**3**	**44**
No. of *Apis mellifera*:	2	12	2	-	22	-	-	2	10	178	89	9	-	-	1	10	197	11	1	-	-	-	-	-	-	8	23	106	-	-	-	-	1	6	19	-	-	5	3	140	18	875

* Not shown are *Senecio obovatus* Muhl. ex Willd (Asteraceae) and *Oenothera biennis* L. (Onagraceae), from which no bees were collected.

All but two of the plant species evaluated in this study had at least one wild bee visitor collected from or observed on them. No bees were collected from *Senecio obovatus* and *Oenothera biennis*. Most of the plants were visited at low frequency by bees (Table 5.1), while a smaller sub-set were visited by relatively greater numbers of bees. Bees were more often collected or observed on plants in the following families: Asteraceae, Asclepiadaceae, Campanulaceae, Laminaceae, Liliaceae, Rosaceae, and Scrophulariaceae (Table 5.1). The average number of bees sampled was determined for each plant species from the five observational samples and the fifteen vacuum samples. From these values, plant species that were visited by 5 or more bees on average during the samples were considered highly attractive species (Frankie et al. 2005). Based on this criterion, wild bees were most attracted to 9 of the native plants: *Potentilla fruticosa* auct. non L., *Scrophularia marilandica* L., *Veronicastrum virginicum* (L.) Farw., *Ratibida pinnata* (Vent.) Barnh., *Agastache nepetoides* (L.) Kuntze, *Silphium perfoliatum* L., *Lobelia siphilitica* L., *Solidago riddellii* Frank ex Riddell, and *Solidago speciosa* Nutt. (Figure 5.2A). Honey bees visited 26 out of 43 native plants and based on the same criteria developed by Frankie et al. (2005), they were most attracted to 5 plant species: *Asclepias incarnata* L., *V. virginicum*, *Allium cernuum* Roth, *S. riddellii*, and *S. speciosa* (Figure 5.2B).

When the three periods of the growing season were considered separately, the most attractive plants that bloomed early, middle and late in the season were identified. Vacuum sampling of plants that bloomed during the early season revealed that relatively few bees were collected, but that wild bees were most abundant at *Zizia aurea* (L.) Koch ($F_{12,48} = 3.46$, $P = 0.001$) (Table 5.2). The most attractive mid-season blooming plants using this method were *P. fruticosa*, *A. incarnata*, *V. virginicum*, *R. pinnata*, and *Spiraea alba* Duroi ($F_{18,71} = 9.93$, $P < 0.0001$) (Table 5.2). The most attractive late season plants were *A. nepetoides*, *S. perfoliatum*, *L. siphilitica*, and *S. riddellii*, and *S. speciosa* ($F_{15,57} = 16.83$, $P < 0.0001$) (Table 5.2).

From timed observations during the early season, wild bees were most attracted to *Fragaria virginiana* Duchesne and *Coreopsis lanceolata* L. ($F_{11,35} = 7.38$, $p < 0.0001$) (Figure 5.3A). Of the mid-season plants, wild bees were most frequently seen at *P. fruticosa*, *S. marilandica V. virginicum*, and *R. pinnata* ($F_{18,62} = 10.65$, $p < 0.0001$) (Figure 5.3A). During the late season bloom period, wild bees were most attracted to *A. nepetoides*, *S. perfoliatum* and *L. siphilitica* ($F_{11,37} = 16.07$, $P < 0.0001$) (Figure 5.3A). Honey bees were observed visiting *Scrophularia marilandica* at much higher rates than from samples taken with the vacuum (Figure 5.3B).

When the proportion of wild bees captured during vacuum sampling was regressed against the proportion of wild bees observed during timed observations, in order to compare methods, the methods appeared to be moderately similar with a regression coefficient of 0.51 (Figure 5.4A). However, examination of the data in Figure 5.4 shows that the observational method was biased toward recording more bees on *Potentilla fruticosa*, and that the vacuum sampling method was biased toward collecting more bees on *Lobelia siphilitica*. Excluding these two outliers increased the regression coefficient to 0.86 with a slope of 1.24. *Scrophularia marilandica* was the outlier for honey bees, with more honey bees recorded during observations than collected while vacuum sampling. Excluding this outlier provided a regression coefficient of 0.86 with a slope of 1.27.

Relationship between floral characteristics and bee abundance. The native plants evaluated in this study ranged in their peak bloom period from the first week in May to the first week of October. The range of peak bloom covered by these plants indicates the temporal range of mostly herbaceous flowering resources achievable with a combination of native plants (Table 5.2). Early blooming plants typically had the smallest average floral area, with the overall size of floral area increasing toward the end of the season among species (Table 5.2). Average corolla width and depth of the flowers tested did not vary among species throughout the season.

Floral characteristics only explained 14% of the variation in all wild bee abundance, 14% of the variation in bumble bee abundance, and 13% of the abundance of wild bees other than bumble bees, with floral area being the significant parameter (Table 5.3). Almost none of the variation in honey bee abundance could be predicted by floral characteristics (Table 5.3). However, the number of different wild bee species visiting the tested plants could be explained by floral characteristics, which explained 33% of the variation in bee diversity, suggesting that floral area may be used to indicate potential bee diversity at particular plants (Table 5.3).

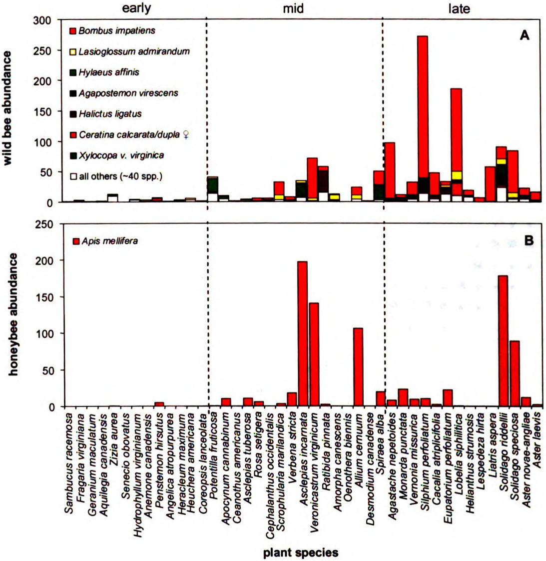

Figure 5.2. Total number of (A) wild bees, and (B) honey bees collected during 15, 30 sec vacuum samples for floral visitors at 43 native plants in Ingham Co., Michigan in 2005. Plants are organized from left to right by bloom phenology in 2005. Blue lines represent different bee species. Red lines indicate environmental characters. This figure is presented in color.

Table 5.2. Floral attributes, bloom period, and the average number of wild bees collected during vacuum sampling for floral visitors during peak bloom of each plant in 2005. Plants are listed in order of bloom.

Species*	Family**	Floral area (cm^2)	Corolla width (mm)	Corolla depth (mm)	Bloom Period***																					Average no. wild bees†
					May					Jun				Jul				Aug					Sep			
Early Season																										
Sambucus racemosa	F	821.3	1.0	0.0	▪	■	▪	—																		0.07 **b**
Fragaria virginiana	O	730.6	3.7	0.0		—	▪	■	▪	—																0.20 **ab**
Geranium maculatum	H	364.5	2.7	0.0				▪	■	▪	—	—														0.07 **b**
Aquilegia Canadensis	M	373.3	6.0	22.3				—	▪	■	▪	—	—													0.13 **b**
Zizia aurea	B	682.7	1.0	0.0			—	—	▪	■	▪	—														0.87 **a**
Senecio obovatus	A	667.4	5.2	0.7				—	▪	■	▪	—														0 **b**
Hydrophyllum virginianum	I	868.1	4.1	5.5					▪	■	▪															0.40 **ab**
Anemone Canadensis	M	556.3	2.3	0.0					—	▪	■	▪	▪	—	—											0.20 **ab**
Penstemon hirsutus	R	610.4	2.2	18.2						▪	■	▪														0.47 **ab**
Angelica atropurpurea	B	274.2	1.3	0.0						▪	■	▪	—													0.07 **b**
Heracleum maximum	B	115.3	1.3	0.0						—	■	▪	▪													0.25 **ab**
Heuchera Americana	Q	327.3	3.0	2.0						—	▪	■	▪	—	—											0.40 **ab**
Coreopsis lanceolata	A	494.3	0.9	5.1							▪	■	▪	—	—	—	—	—	—	—	—	—				0.13 **b**
Mid Season																										
Potentilla fruticosa	O	974.6	4.2	0.0							—	—	▪	▪	■	▪	▪	—	—	—	—	—	—	—	—	2.73 **bcd**
Apocynum cannabinum	C	428.0	1.6	1.8								—	▪	▪	■	▪	—	—								0.67 **cd**
Ceanothus americana	N	128.9	1.2	0.0									—	▪	■	—	—	—								0.25 **cd**
Asclepias tuberose	D	344.4	0.3	1.6										▪	■	▪	—	—	—	—	—					0.27 **cd**
Rosa setigera	O	725.7	3.9	0.0										▪	■	▪										0.46 **cd**
Cephalanthus occidentalis	P	55.1	1.7	7.0											▪	■	▪	—	—							0.60 **cd**
Scrophularia marilandica	R	168.2	3.3	4.1									—	—	▪	▪	■	▪	—	—	—	—				2.13 **bcd**
Verbena stricta	S	492.7	0.9	5.1										—	—	▪	▪	■	▪	—	—	—				0.53 **cd**
Asclepias incarnate	D	1408.0	0.2	0.8										—	—	▪	▪	■	▪	—						2.27 **bc**
Veronicastrum virginicum	R	774.3	1.3	3.8												—	▪	■	▪	—						4.80 **ab**
Ratibida pinnata	A	3865.6	0.7	2.3												—	▪	■	▪	▪	—					3.87 **a**
Amorpha canescens	G	18.2	0.5	0.0												▪	▪	■	▪	—	—	—	—			0.87 **cd**

Table 5.2. Continued.

Species*	Family**	Floral area (cm²)	Corolla width (mm)	Corolla depth (mm)	Bloom Period*** May	Jun	Jul	Aug	Sep	Average no. wild bees†
Oenethera biennis	L	123.9	3.1	28.9			— ▪	▪ ■ ▪ — —		0 d
Allium cernuum	K	910.9	1.8	0.0			—	▪ ■ ▪ ▪ —	—	1.60 bcd
Desmodium canadense	G	139.6	0.8	0.0			—	▪ ■ ▪ —		0.13 d
Spiraea alba	O	213.3	2.0	0.0				▪ ■ ▪ ▪ —	—	3.33 bc
Late Season										
Agastache nepetoides	J	2766.4	1.4	6.3			—	▪ ▪ ■ ▪ ▪	—	6.47 cd
Monarda punctata	J	473.0	13.1	2.4			—	▪ ▪ ■ ▪ ▪	— — — —	0.80 cd
Vernonia missurica	A	586.6	0.9	7.0				— ▪ ■ ▪ —	—	2.13 cd
Silphium perfoliatum	A	3870.9	5.6	1.2			—	— — ▪ ■ ▪	—	18.13 a
Cacalia atriplicifolia	A	612.1	1.0	6.4				— ▪ ▪ ■ ▪	— —	3.20 cd
Eupatorium perfoliatum	A	5878.2	0.5	2.1				— — ▪ ■ ▪	— —	2.20 cd
Lobelia siphilitica	E	829.3	0.3	2.6			—	— — ▪ ■ ▪	— — —	12.40 ab
Helianthus strumosis	A	3132.5	5.4	1.2			—	— — — ▪ ■	▪ — —	1.27 cd
Lespedeza hirta	G	96.3	0.7	0.0				— ▪ ■	▪	0.47 d
Liatris aspera	A	370.9	1.5	8.3				— ▪ ■	▪ — —	3.87 cd
Solidago riddellii	A	878.3	0.6	2.9					▪ ■ ▪ —	6.00 bc
Solidago speciosa	A	3814.2	0.6	3.8					— ▪ ■ ▪ —	5.60 cd
Aster novae-angliae	A	1232.5	0.7	4.7					— ▪ ■ ▪ —	1.53 cd
Aster laevis	A	623.9	0.8	4.7					— ▪ ■ ▪	1.07 cd

* All natives are perennials except for *O. biennis*, which is a biennial.

** Codes for plant families: A = Asteraceae, B = Apiaceae, C = Apocynaceae, D = Asclepiadaceae, E = Campanulaceae, F = Caprifolaceae, G = Fabaceae, H = Geraniaceae, I = Hydrophyllaceae, J = Laminaceae, K = Liliaceae, L = Onagraceae, M = Ranunculaceae, N = Rhamnaceae, O = Rosaceae, P = Rubiaceae, Q = Saxifragaceae, R = Scrophulariaceae, S = Verbenaceae

*** Key for bloom period: ■ = peak bloom date, ▪ = full bloom, — = sparse bloom

† Averages followed by different letters are significantly different (Tukey means separation).

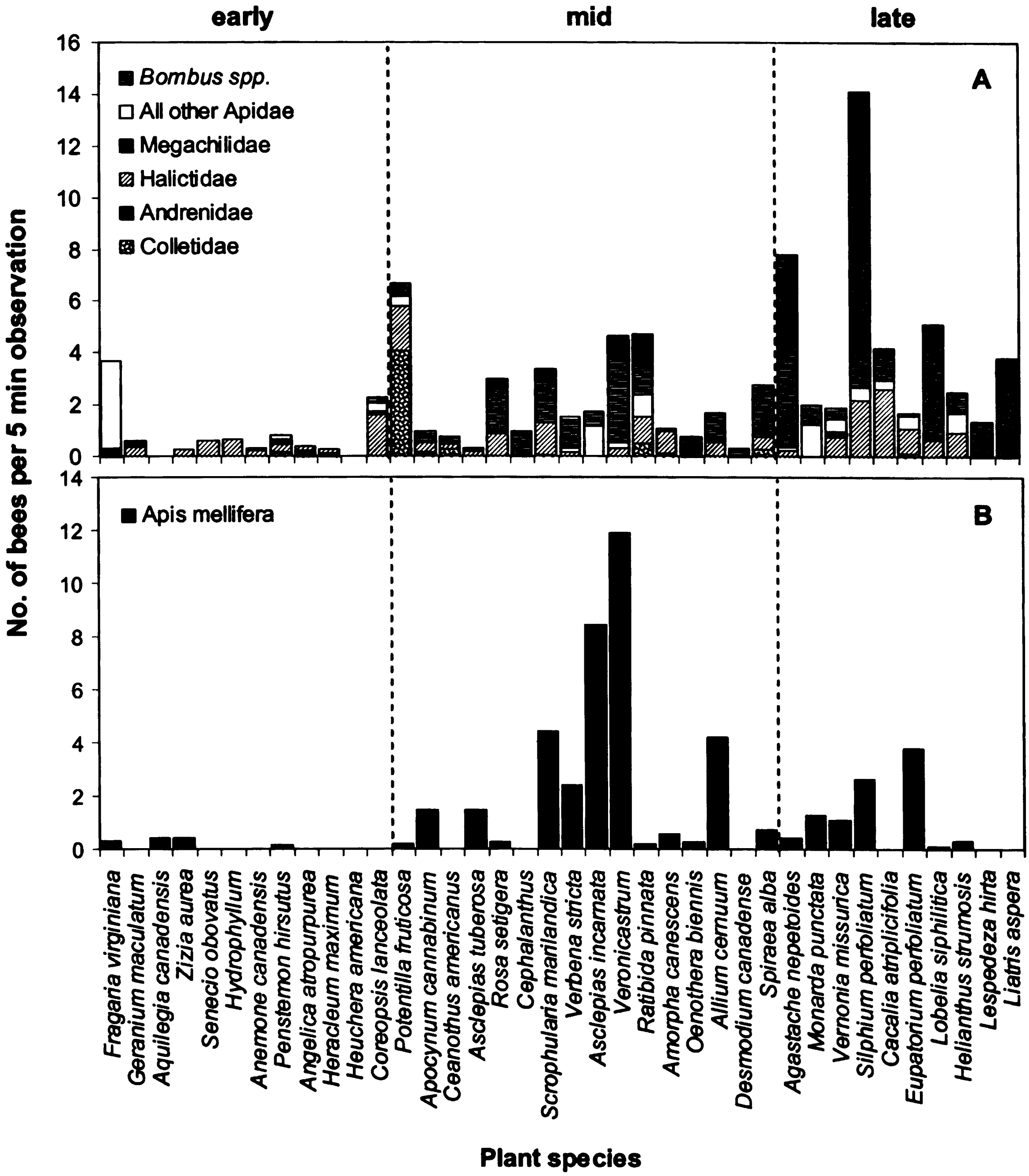

Figure 5.3. Average number of (A) wild bees, and (B) honey bees noted during 5 timed observations. Observations were not made at the earliest (*Sambucus racemosa*) and latest (two species each of *Solidago* and *Aster*) blooming species in the study. Plants are organized from left to right by bloom phenology in 2005.

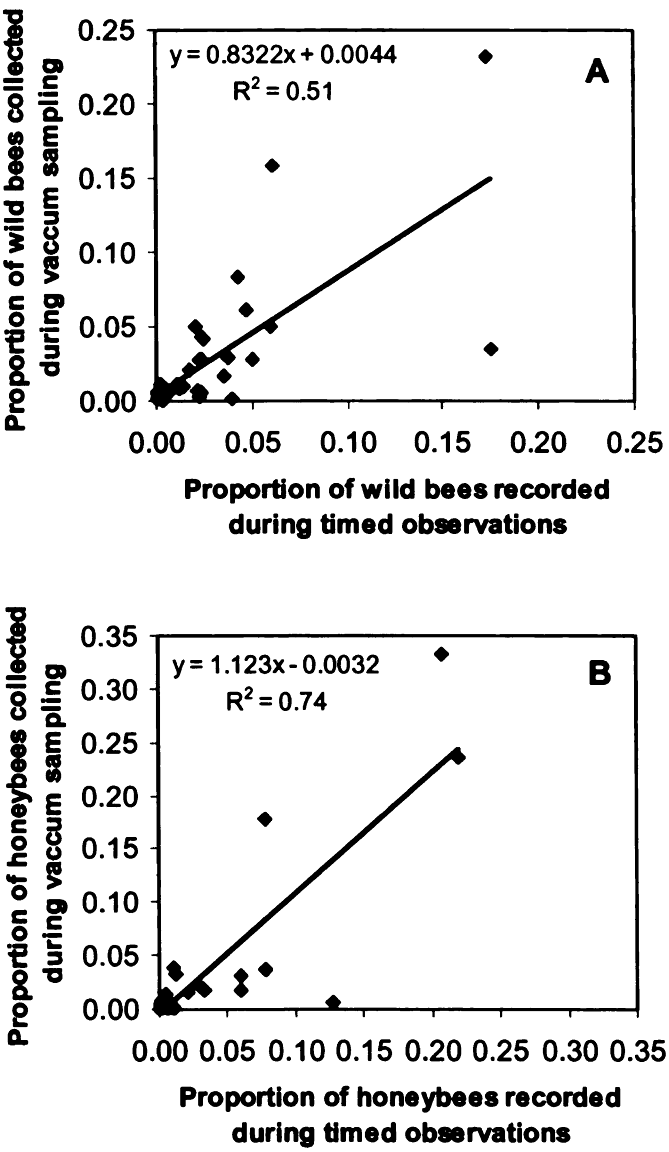

Figure 5.4. Comparison of bee sampling methods using simple linear regression of (A) the proportion of wild bees and (B) the proportion of honey bees caught or recorded using each method at 38 of the plant species tested in Ingham County, Michigan in 2005.

Table 5.3. Results of multiple linear regressions of the abundance and diversity of bees collected at native flowering plants during peak bloom against three floral characters. Significant regression coefficients ($P < 0.05$) and probability values less than 0.05 are highlighted in bold.

	Overall model			**Parameter estimate probabilities**		
Variable	R^2	$F_{3,39}$	P	**floral area**	**corolla width**	**corolla depth**
Bee abundance						
Honey bees (*A. mellifera*)	0.05	0.69	0.56	0.54	0.29	0.65
Bumble bees (*Bombus* spp.)	0.14	2.18	0.11	**0.02**	0.57	0.99
Wild bees other than bumble bees	0.13	2.01	0.13	**0.03**	0.86	0.44
All wild bees	0.14	2.08	0.12	**0.03**	0.69	0.61
Bee diversity						
No. of wild bee species	**0.28**	5.09	0.005	**0.001**	0.45	0.42

DISCUSSION

With increasing concern about the suitability of agricultural landscapes for wild pollinators (Buchmann and Nabhan 1996, National Academy of Sciences 2006) and other beneficial insects (Baggen and Gurr 1998, Landis et al. 2000, Begum et al. 2006), conservation activities are expected to increase in agricultural lands. Agricultural habitats can be inhospitable for beneficial insects during much of the growing season due to intensive management practices. Intensification of agricultural systems over the past fifty years has led to declines in native bee populations through various mechanisms (Osborne et al. 1991, Matheson 1994, Allen-Wardell et al. 1998, Stubbs and Drummond 2001b). The most important of these are the use of agrochemicals for pest control and the loss of field margins and hedgerows, resulting in habitat fragmentation and a reduction in flower abundance and diversity in farm landscapes (Buchmann and Nabhan 1996, Kearns 1998, Steffan-Dewenter and Tscharntke 1999). This loss of plant diversity translates into both spatial and temporal gaps in the availability of floral resources (Matheson 1994). By integrating flowering plants that support native bees into farms, growers of pollination-dependent crops may receive greater pollination services when the crop is in bloom (Matheson 1994).

Most species of native bees that are endemic in agricultural landscapes require nectar and pollen resources beyond those that a crop plant may provide. Because of this, conservation of bees on farmland will require that they have access to plants that provide suitable flowers throughout the growing season. The investment required to create a managed season-long area of flowering plants would suggest that optimizing the suitability of the plant species for local pollinators will give the greatest return on that investment in terms of pollinator conservation and benefit to the crop. Based on two sampling methods, this study has identified 14 native perennial plants to which wild bees in southern Michigan show affinity. These plants were originally selected to be suitable for use by natural enemies, so their use in an agricultural setting could promote pollination and biological control, the two main ecosystem services provided to agriculture by arthropods.

Plants in this study were divided into early, middle, and late-blooming groups, and we found increasing bee abundance and diversity as the season progressed. This temporal pattern in bee abundance at flowers mirrors the availability of floral resources, variation in weather (Pywell et al. 2005) and population growth of multivoltine and social bees later in the season (Buchmann and Nabhan 1996). By taking this approach, plants that attracted relatively few bees in the spring were not being compared to those in bloom during the warmer summer months when social bee colony size was greatest. In their peak bloom order, the plants frequented the most by bees were: *Fragaria virginiana*, *Zizia aurea*, *Coreopsis lanceolata*, *Potentilla fruticosa*, *Scrophularia marilandica*, *Asclepias incarnata*, *Veronicastrum virginicum*, *Ratibida pinnata*, *Spiraea alba*, *Agastache nepetoides*, *Silphium perfoliatum*, *Lobelia siphilitica*, *Solidago riddellii*, and *Solidago speciosa* (Table 5.2, Figure 5.3). These plants are representatives from seven different plant families: five species of Asteraceae, three Rosaceae, two Scrophulariaceae, and one each of Apiaceae, Asclepiadaceae, Campanulaceae, and Laminaceae. All of these families contain species of plants that have been shown to be attractive to bumble bees and other wild bees (Corbet et al. 1994, Frankie et al. 2005, Carvell et al. 2006).

Because this study was designed primarily to address the issue of providing attractive floral resources for natural enemies, a vacuum sampling method was used to collect insects. While this is an unconventional method for monitoring bees, results from timed observations were similar for most plant species to those obtained during vacuum sampling. Vacuum sampling could be considered for use across a large set of field sites as a rapid and reproducible method to obtain a fairly accurate representation of the bee community.

It was unexpected that so few bees in the families Andrenidae and Megachilidae were collected in the samples. However, the time of year when this study was conducted may account for their absence. For instance, many andrenid and megachilid bees emerge early in spring, and are solitary univoltine species, thus their period of activity may not have overlapped with this study. Future studies should include blooming woody plants that provide floral resources early in the spring to help support early-season pollinators

(Matheson 1994). Also, floral resources alone are not enough to sustain populations of bees; nesting resources are also needed. It may be that this site is depauperate of the kind of nesting resources required by cavity nesting bees in the family Megachilidae.

Of the three floral attributes measured in this study, floral area was the most explanatory factor related to the abundance of bees other than honey bees. This finding suggests that unlike honey bees, that receive information from hive mates about rewarding patches, wild bees maximize reward for their foraging efforts by seeking patches with greater floral area. This finding agrees with previous studies showing that pollinating insects concentrate their foraging in dense patches of flowers (Thomson 1981, Westphal et al. 2003, Hegland and Totland 2005, Hegland and Boeke 2006). Plants with greater average floral area were also more likely to have greater wild bee diversity (Table 5.2). Together, these results suggest that floral area might be a simple indicator of a bee's potential attraction.

Recent studies have linked plant community diversity to pollinator community diversity in natural systems (Potts et al. 2003), and long term declines in bee pollinated plants have been linked to declines in pollinators (Biesmeijer et al. 2006). Further evidence comes from experimental studies that have shown that pollinator diversity is linked to the persistence of plant communities (Fontaine et al. 2006), In agricultural systems, diverse pollinator communities can increase productivity in crops such as sunflowers (Greenleaf and Kremen 2006), watermelon (Kremen et al. 2002), and coffee (Klein et al. 2003), so enhancing pollinator diversity is a worthwhile goal for managers of land on which pollinator-dependent crops are grown.

The link between pollinator and plant diversity support the continued development of native perennial plants for use within beneficial insect conservation programs in agricultural settings. Perennial plants may have higher initial planting costs than annuals and take some time to mature and reach their potential floral area, but there are long-term benefits. In addition to providing resources for pollinators (Pywell et al. 2005, Carvell et al. 2006) and insect natural enemies (Landis et al. 2000, Colley and Luna 2000, Gurr et al. 2003), these plant species are adapted to the local environment (Gustafson et al. 2005), and can also provide aesthetic value to the landscape (Goulder and Kennedy 1997).

A first step toward conservation of native bees on farmland is to determine which plants are most suitable for providing foraging resources at different times of the growing season. The results from this direct comparison of co-blooming plants can be combined with the findings of Fiedler and Landis (2007a, 2007b) related to natural enemy attraction. Using these two studies, future research should evaluate a combination of highly suitable plants to provide overlapping bloom periods from late spring through the rest of the season. Such a combined floral planting can then be tested for its utility in conserving beneficial insects within agricultural settings, with the ultimate aim of improving sustainable pollination of crops that depend on bees for this important component of yield.

CHAPTER 6:

RESPONSE OF NATIVE BEES TO LAND USE PATTERNS IN BLUEBERRY AGROECOSYSTEMS

INTRODUCTION

Concern over perceived worldwide pollinator declines and their relationship to anthropogenic land use change have been the driving force behind a number of landscape level studies of bee abundance and diversity. The response of bee communities to anthropogenic land use and proximity to natural areas has been documented around the world. In California, Kremen et al. (2002) found that both conventional and organic watermelon fields far from adjacent natural habitat had low wild bee community diversity and had to be supplemented with honey bees, whereas fields near natural habitat had sufficient pollination by native bees. In Germany, potted flowering plants were placed next to cereal fields within landscape matrices containing varying proportions of semi-natural habitat. Bees were attracted to these plants according to their body size and nesting guild, with long-range foraging bees responding to the degree of semi-natural habitat at larger spatial scales than bees with shorter foraging ranges (Steffan-Dewenter et al. 2002). However, Westphal et al. (2003) found that bumble bees were more likely to respond to the percentage of mass-flowering crops than to nearby semi-natural habitat and found that bumble bee foraging duration decreased and colony growth increased where forage resources were abundant near their nests (Westphal et al. 2006). In Costa Rica, pastures near forest patches had a greater abundance and diversity of native meliponine bees than those distant from the forest (Brosi et al. 2007), and fruit set of coffee plants was greater near larger adjacent tropical forest fragments (Ricketts 2004, Ricketts et al. 2004). In Argentinian grapefruit plantations, flower-visiting insects also were most abundant in fields bordering premontane subtropical forests (Chacoff and Aizen 2006).

The effect of land use on pollinator communities in urban settings was explored recently in Arizona, California, and New Jersey. Desert pollinator communities were in residential areas with xeric landscaping were found to be more diverse than turf-based yards, but most diverse in areas on the fringe of the metropolitan area of Phoenix (McIntyre and Hostetler 2001). In northern California, both native and exotic bees (e.g. *Apis mellifera*) preferred native over exotic flowering plants on a percent basis, even though exotic plants far outnumbered the natives in the two urban areas studied (Frankie et al. 2005). In southern New Jersey, more bee species were found in agricultural and residential developments than in extensive pine-barren forests (Winfree et al. 2007).

Several studies have examined the response of cavity-nesting bees and wasps to spatial scale. Tylianakis et al. (2006) found that most cavity nesting bees and wasps responded to landscape quality at small scales in Ecuador, while Klein et al. (2006) found that diversity and parasitism of trap-nesting Hymenoptera were greater in agroforestry adjacent to rainforests in Indonesia. In Germany, the abundance of trap-nesting bees, wasps, and their natural enemies increased with greater percent semi-natural habitats within a radius of 750 m, but decreased with increasing landscape scale up to 3 km (Steffan-Dewenter, 2002).

The underlying pattern in most of these studies is that land use affects bee abundance and/or diversity at various spatial scales based on the bees' potential use of resources, its mobility or foraging range, and proximity to nesting habitat. In southwest

Michigan, where most highbush blueberry (*Vaccinium corymbosum*) production occurs, land use has changed dramatically over the past 30-40 years, towards a greater percentage of developed land. Because native bees are a significant component of the pollinating community in blueberry fields, and blueberry is a long-lived perennial crop, the system is well suited to native bee community studies in a landscape context. My objectives were: (1) to examine the pattern of bee abundance and diversity across 15 highbush blueberry farms in the context of landscape structure and scale, and (2) to determine whether blueberry pollination was affected by landscape characteristics.

METHODS

Thirteen commercial and two semi-abandoned highbush blueberry farms located at least 3 km away from one another in southwest Michigan, were sampled during bloom in 2004-06 using pan traps. Due to varying weather conditions from year to year, trapping was conducted two (2004, 2006) or three (2005) times during bloom in each field. Trapping occurred between 16 May – 3 June in 2004, 16 – 25 May in 2005, and 17 – 31 May in 2006.

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 8:00-12:00 h and were collected between 16:00-20:00 h for a minimum trapping period of 6 hours on days 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 traps filled halfway with a 2% unscented soap solution (Dawn® dish soap, Procter & Gable, Cincinnati, OH), were constructed from 355 ml white and yellow plastic bowls (Amscan, Inc., Elmsford, NY) mounted onto 2.7 diameter PVC poles stabilized with rebar (see Chapter 2, page 37). After the sampling period concluded, pan trap contents were strained into plastic bags and stored in a -12°C freezer for later processing. Specimens were thawed at room temperature prior to washing in a 70% ethanol solution. Honey bees were separated out and counted, then stored in 70% ethanol solution. All other bees were placed in a mesh bag through which they were fluffed and dried with a hairdryer before pinning and identification.

Species identifications. Preliminary identifications of bees to the lowest possible taxonomic group were made using two published dichotomous keys (Mitchell 1960, Michener et al. 1994) and the online key available through www.Discoverlife.org. Further identifications and verifications were made by J.S. Ascher of the American Museum of Natural History, Division of Invertebrate Zoology. Voucher specimens are held in the Albert J. Cook Arthropod Research Collection at Michigan State University (see Appendix B).

Yield assessments. To compare fruit set and yield on blueberry clusters exposed or not exposed to pollinators, five unopened flower clusters on two separate branches on ten blueberry bushes within 1 m of the field edge were tagged. On each cluster, the number of flowers were counted, then one set of clusters was covered per bush with fine mesh netting (bridal veil) to exclude floral visitors. When bloom was finished, the mesh was removed and the number of fruit set per cluster was counted on all the marked branches. After the terminal berry was ripe and the other berries were starting to turn blue, all the berries from the clusters on the marked branches were harvested. Berries were counted and weighed to obtain an average berry weight. The diameter of the largest berry from each sample was measured with a caliper, then the berry was squashed to extract its seeds. This was done in a plastic zip bag so that seeds could easily be felt and seen through the bag and counted.

Quantification of landscape features. Aerial photos taken during the summer of 2005 at a precision level of 1:5000 were downloaded from the USDA Geospatial Data Gateway (http://datagateway.nrcs.usda.gov/GatewayHome.html) and imported into ArcMap (Arc GIS 9, ESRI). A handheld GPS unit (SportTrak Pro, Magellan Navigation, Inc., Santa Clara, CA) was used to record coordinates for each of the field sites, and then coordinates were added to the ArcGIS file. Because bumble bees are very rare in my bee collection and honey bees are presumed to be from managed hives, I choose to make the maximum radius of the area of concern 1500 meters because most native bees are assumed not to forage further than this. Thus, site inspections were conducted within a 1500 m radius of the focal field and aerial photos were digitized and labeled accordingly (see Table 6.1 for description of landscape categories used). Circles with radii of 250, 500, 750, and 1000 were overlaid on the images, and the area calculated for each digital piece of land in the resulting nested areas (Figure 6.1). Landscape categories used in regression analyses were percent: (1) forest margins, (2) settlement, (3) annual cropland, (4) blueberry crop habitat, (5) open uncultivated (pasture/meadow/fallow/scrubland, ditches/tree lines, field margins, and vegetation near water), and (6) semi-natural habitats (which are groups 1 and 5 added together) (Table 6.1).

Statistical analyses. The Mantel test ("vegan" package for R 2.3.1) was used to compare pairwise bee community similarity indices (Jaccard, Bray-Curtis, and Morisita-Horn) with pairwise geographic distances between each of the fifteen blueberry farms. Spatial autocorrelation in non-pairwise variables (bee abundance, species richness, Shannon-Weiner and Simpson's diversity indices) was assessed with Moran's I ("ape" package for R 2.3.1).

Simple linear regressions (PROC REG, SAS 9.1) at each spatial scale were conducted between the bees collected during bloom (overall abundance, richness, and diversity) and to each of the 6 land use groupings (see above). Similarly, the abundances of each the 5 of the most abundant blueberry foragers were also regressed against the 6 different groupings. The difference between the fruit set, weight, diameter, and seed count from clusters that were open pollinated and those from which pollinators were excluded was used in regression analyses (PROC REG, SAS 9.1) to determine the relationship between the change in those aspects of fruit development and landscape context using the 6 land use groups above.

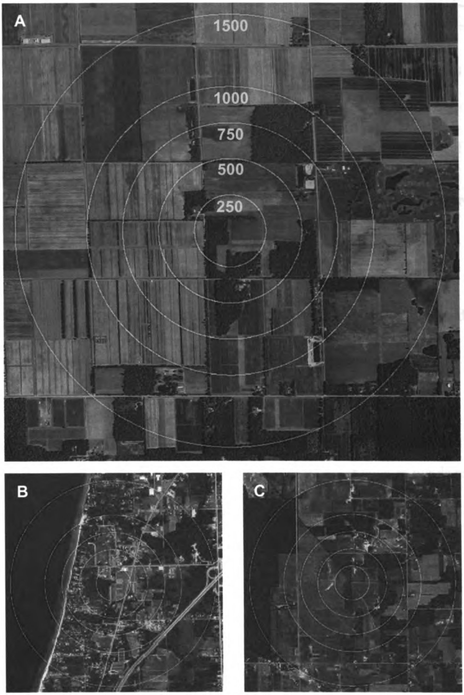

Figure 6.1. Examples of the aerial photographs used to digitize landscape features; (A) is a site with a high proportion of annual and nursery crops and depicts the 5 different radius (meters) sectors used in the analyses, (B) is a site near Lake Michigan (to the west) with a high proportion of settlement area, and (C) is a site with a high proportion of blueberry plantations. Images from USDA-NRCS Geospatial Data Gateway (http://datagateway.nrcs.usda.gov/GatewayHome.html last accessed 8/14/2007). This figure is presented in color.

Table 6.1. Categories of landscape types used in the digitization of aerial photos.

Habitat type	**Description**
Blueberry plantations	commercial and semi-abandoned highbush blueberry
Perennial crops	other perennial crops, including vineyards and nurseries
Annual crops	annual crops
Pastures	grazing pastures
Open uncultivated	including meadows, scrubland, fallow and other ruderal areas
Ditches and treelines	running along or bisecting agricultural land
Other field margins	margins along agricultural land other than ditches and tree lines
Forest/woodland margin	<10 m from forest edge
Forest/woodland interior	>10 m from forest edge
Settlement	suburban development including golf courses and a landfill
Road	paved or dirt
Train tracks	abandoned or still in use
Utility	areas cleared for powerlines
shoreline	vegetation along Lake Michigan
wetlands	usually vegetation along a river
Other vegetation near water	vegetation along inland bodies of water such as ponds and lakes
open water	open bodies of water including lakes, ponds, and rivers

RESULTS

Independence and landscape composition of sites. Bee communities at the sampled fields were considered to be independent based on the results of the Mantel test for community similarity (Z = 1729.3, df = 14, p = 0.14). Likewise, bee abundance, species richness, Shannon-Weiner and Simpson's diversity indices assessed with Moran's I were not significant indicating no spatial autocorrelation among sites (I < 0.514, df = 13, p > 0.05).

Farms selected for this study varied in the proportion of each measured land use type in the surrounding landscape (Table 6.2). The most abundant landscape types were forest margins and settlements, which accounted for an average of 22 and 21%, respectively, of the total area of all habitats at the 1500 m spatial scale (Table 6.2). Annual cropland and blueberry plantations each comprised 13% of the land within a 1500 m radius of the fields (Table 6.2). All other landscape types accounted for the remaining area at the 1500 m spatial scale (Table 6.2).

Response of bees to landscape scale. Total bee abundance (log n+1), species richness, and diversity did not vary significantly with any of the 6 landscape categories at any of the spatial scales (Table 6.3). However, 34% of the variation in the abundance of *Andrena carolina*, a *Vaccinium* specialist, at the 1500 m scale was explained by the proportion of settlements, with there being more *A. carolina* with a greater proportion of settlement area (Figure 6.2). Variation in the abundance of bees in the species group *Ceratina calcarata/dupla* was explained by the proportion of blueberry fields at the 250 and 500 m spatial scales (35 and 28% respectively), with fewer bees associated with higher proportions of blueberry farmland (Table 6.3, Figure 6.3b). Also, *C. calcarata/*

dupla increased in abundance with more semi-natural habitat at the 250 m spatial scale with 28% of the variation explained by this landscape category (Figure 6.3d).

Table 6.2. Composition and quantification of the 1500 m radius landscape sectors in southwestern Michigan. Data were gathered by field inspection. Means ± S.E., minimum, and maximum are given for 15 study sites.

	Area (%) of landscape		
Landscape type	**Average**	**Minimum**	**Maximum**
Forest margin (10 m deep)	22.48 ± 3.11	5.39	44.56
Settlement	20.64 ± 2.53	6.00	36.99
Annual crops	13.08 ± 3.05	0	37.79
Blueberry plantations	12.71 ± 3.39	0.08	45.06
Forest interior (>10 m)	7.98 ± 0.85	3.35	13.69
Open uncultivated†	7.33 ± 0.81	0.78	12.50
Perennial crops and nurseries	5.25 ± 3.17	0	38.82
Open water	3.04 ± 1.53	0.25	23.51
Road	2.07 ± 0.18	1.25	3.50
Ditches and tree lines†	1.65 ± 0.38	0.02	4.18
Other field margins†	1.54 ± 0.31	0.58	5.70
Pasture†	1.06 ± 0.60	0	8.62
Vegetation near water†	0.63 ± 0.49	0	7.39
Wetland	0.49 ± 0.49	0	7.30
Conifer plantation	0.30 ± 0.24	0	3.65
Utility and train tracks	0.25 ± 0.21	0	3.22

† Landscape categories that were grouped together as semi-natural habitat.

Table 6.3. Regression coefficients for wild bee abundance, species richness, diversity, and the 5 most abundant *Vaccinium*-foragers averaged over three years and the proportion of (a) forest margin, (b) settlement, (c) annual cropland, (d) blueberry plantations, (e) semi-natural habitat, and (f) semi-natural and forest margins together at 5 spatial scales. Significant ($P < 0.05$) r^2 values are in bold and the slope indicated in parentheses.

	250 m	**500 m**	**750 m**	**1000 m**	**1500 m**
a) Forest margin (10 m deep)					
log (wild bee abundance +1)	0.08	0.02	0.05	0.06	0.06
wild bee species richness	0.03	0.02	0.05	0.02	0.02
wild bee diversity (H')	0.0002	0.03	0.09	0.07	0.04
Andrena carolina	0.12	0.008	0.005	0.02	0.0003
Lasioglossum coriaceum	0.0002	0.19	0.16	0.08	0.05
Ceratina calcarata or *dupla* (♀ only)	0.16	0.02	0.003	0.006	0.003
Andrena carlini	0.01	0.02	0.004	0.004	0.02
Augochlorella aurata	0.001	0.05	0.04	0.04	0.06
b) Settlement					
log (wild bee abundance +1)	0.02	0.002	0.006	0.02	0.08
wild bee species richness	0.04	0	0.002	0.007	0.03
wild bee diversity (H')	0.14	0.10	0.007	0.005	0.005
Andrena carolina	0.0002	0.008	0.02	0.08	**0.34 (+)**
Lasioglossum coriaceum	0.05	0.04	0.02	0.01	0.0004
Ceratina calcarata or *dupla* (♀ only)	0.02	0.007	0.0009	0.002	0.005
Andrena carlini	0.10	0.001	0.001	0.003	0
Augochlorella aurata	0.004	0.06	0.08	0.09	0.13
c) Annual crop					
log (wild bee abundance +1)	0.004	0.001	0.01	0.04	0.10
wild bee species richness	0.0004	0.003	0.02	0.04	0.09
wild bee diversity (H')	0.05	0.04	0.0002	0.008	0.05
Andrena carolina	0.004	0.0001	0.0002	0.0007	0.009
Lasioglossum coriaceum	0.06	0.04	0.09	0.11	0.17
Ceratina calcarata or *dupla* (♀ only)	0.0006	0.07	0.02	0.006	0.004
Andrena carlini	0.0006	0.0001	0.02	0.04	0.05
Augochlorella aurata	0.02	0.0004	0.02	0.02	0.005
d) Blueberry					
log (wild bee abundance +1)	0.06	0.007	0.0002	0.0002	0.0001
wild bee species richness	0.17	0.04	0.01	0.006	0.003
wild bee diversity (H')	0.14	0.01	0	0.007	0.02
Andrena carolina	0.0004	0.01	0.006	0.002	0.006
Lasioglossum coriaceum	0.0005	0.003	0.009	0.02	0.02
Ceratina calcarata or *dupla* (♀ only)	**0.35 (-)**	**0.28 (-)**	0.17	0.12	0.10
Andrena carlini	0.005	0.006	0.02	0.03	0.04
Augochlorella aurata	0.04	0.09	0.08	0.08	0.08
e) Semi-natural					
log (wild bee abundance +1)	0.03	0.004	0.002	0.007	0.03
wild bee species richness	0.11	0.01	0.03	0.008	0
wild bee diversity (H')	0.06	0	0.04	0.03	0.02
Andrena carolina	0.005	0.002	0.02	0.11	0.21
Lasioglossum coriaceum	0.008	0.0001	0.05	0.02	0.005
Ceratina calcarata or *dupla* (♀ only)	0.13	0.02	0.10	0.15	0.24
Andrena carlini	0.01	0.002	0.006	0.0001	0.02
Augochlorella aurata	0.01	0.003	0.007	0.03	0.05

f) Semi-natural + forest margins					
log (wild bee abundance +1)	0.08	0.01	0.006	0.04	0.06
wild bee species richness	0.17	0.002	0.002	0.0007	0.005
wild bee diversity (H')	0.07	0.005	0.0001	0.0005	0.0002
Andrena carolina	0.04	0	0.03	0.10	0.09
Lasioglossum coriaceum	0.01	0.04	0.0003	0.006	0.03
Ceratina calcarata or *dupla* (♀ only)	**0.28 (+)**	0.03	0.10	0.11	0.08
Andrena carlini	0.005	0.0001	0.001	0.0007	0.03
Augochlorella aurata	0.008	0.001	0.03	0.06	0.08

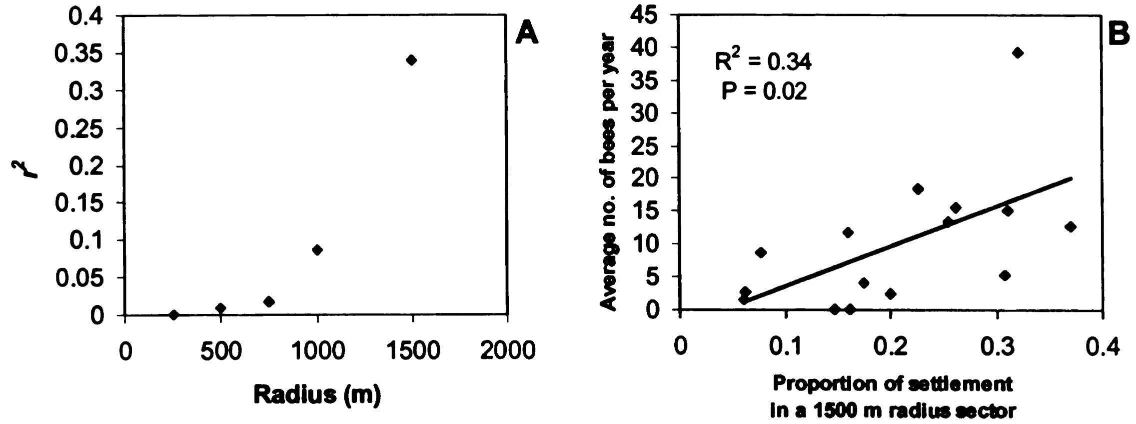

Figure 6.2. Scale-dependent effect of landscape structure on the number of *Andrena carolina* bees collected in pan traps at 15 highbush blueberry fields in southwestern Michigan. The graph on the left (A) shows the regression coefficients for the average number of bees and the proportion of human settlement at each of the 5 spatial scales. The graph on the right (B) shows a simple linear regression of the spatial scale with the highest r^2 value for *A. carolina* and the proportion of human settlement.

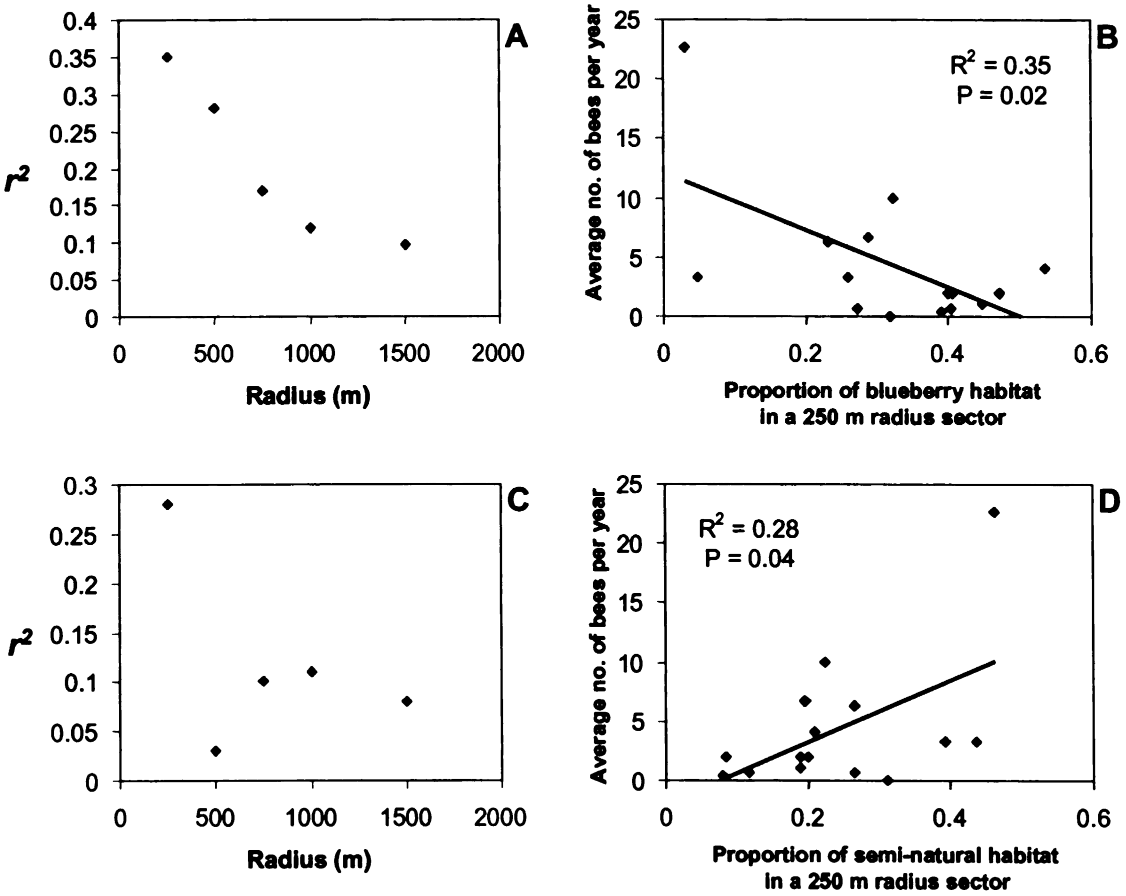

Figure 6.3. Scale dependent effects of landscape structure on the number of *Ceratina calcarata* or *dupla* (they are morphologically indistinguishable) female bees collected in pan traps at 15 highbush blueberry fields in southwestern Michigan. The graphs on the left show the regression coefficients for the average number of bees and the proportion of (A) blueberry habitat or (C) semi-natural habitat at each of the 5 spatial scales. The graphs on the right show simple linear regressions of the spatial scales with the highest r^2 value for *C. calcarata/dupla* and the proportion of (B) blueberry habitat or (D) semi-natural habitat.

Response of fruit set, size, and weight to landscape scale. Three of the four fruit attributes, used as a measure of pollination, varied significantly with the proportion of the landscape containing blueberry fields. Regression coefficient (R^2) values for the proportion of the difference between open-pollinated and pollinator-excluded fruit set at harvest were highest at the 500 m scale (Figure 6.4b), while fruit weight per berry (Figure 6.4d) and diameters of the largest berry (Figure 6.4f) were highest at the 250 m scale, all increasing with the proportion of blueberry habitat (Figure 6.4). Berry weight and fruit diameter decreased with a greater proportion of open uncultivated habitats at the 250 and 500 m scales respectively (Figure 6.5b,d). Finally, berry weight and fruit diameter decreased with a greater proportion of semi-natural habitat at the 500 m spatial scale (Figure 6.6b,d). This result was found even though there was no significant correlation between land used for blueberry production or in semi-natural habitat..

Table 6.4. Regression coefficients for the proportion of fruit set at harvest, fruit weight per berry at harvest, diameter of the largest berry, and the number of seeds per largest berry averaged over three years and the proportion of (a) forest margin, (b) settlement, (c) annual cropland, (d) blueberry plantations, (e) semi-natural habitat, and (f) semi-natural and forest margins together at 5 spatial scales. Significant ($P < 0.05$) R^2 values are in bold; slope indicated in parentheses.

	250 m	**500 m**	**750 m**	**1000 m**	**1500 m**
a) Forest margin (10 m deep)					
proportion of fruit set at harvest	0.08	0.0003	0.005	0.001	0.06
weight per berry	0.05	0.06	0.01	0.009	0.02
diameter of largest berry	0.006	0.05	0.03	0.006	0.0002
no. of seeds in largest berry	0.04	0.0003	0.0005	0	0.02
b) Settlement					
proportion of fruit set at harvest	0.13	0.05	0.04	0.4	0.01
weight per berry	0.02	0.008	0	0.01	0.02
diameter of largest berry	0.005	0	0.01	0.07	0.06
no. of seeds in largest berry	0.006	0	0.003	0.03	0.03
c) Annual crop					
proportion of fruit set at harvest	0.007	0.04	0.04	0.03	0.05
weight per berry	0.07	0.07	0.05	0.07	0.009
diameter of largest berry	0	0.004	0.008	0.03	0.001
no. of seeds in largest berry	0.02	0.01	0.02	0.005	0.01
d) Blueberry					
proportion of fruit set at harvest	0.13	**0.34** (+)	0.26	0.19	0.16
weight per berry	**0.47** (+)	0.21	0.18	0.19	0.14
diameter of largest berry	**0.27** (+)	0.17	0.20	0.24	0.21
no. of seeds in largest berry	0.06	0.009	0.02	0.05	0.04
e) Semi-natural					
proportion of fruit set at harvest	0.06	0.05	0.13	0.13	0.12
weight per berry	**0.58** (-)	**0.58** (-)	**0.32** (-)	0.26	0.10
diameter of largest berry	0.22	0.26 (-)	0.22	0.12	0.05
no. of seeds in largest berry	0.04	0.05	0.04	0.009	0.004
f) Semi-natural + forest margins					
proportion of fruit set at harvest	0.13	0.05	0.09	0.06	0.008
weight per berry	**0.50** (-)	**0.58** (-)	0.21	0.18	0.08
diameter of largest berry	0.21	0.26 (-)	0.12	0.04	0.02
no. of seeds in largest berry	0.08	0.05	0.03	0.004	0.01

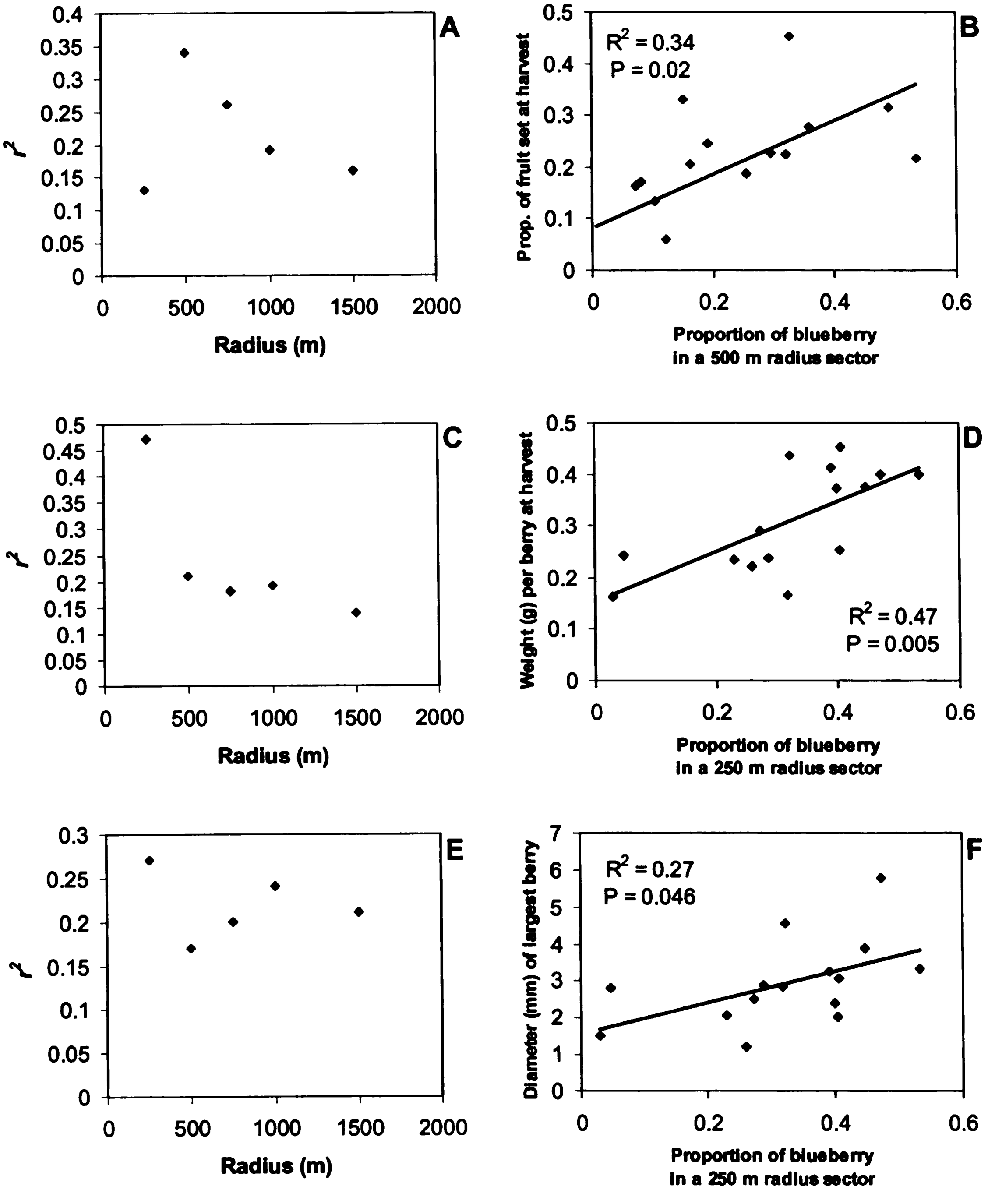

Figure 6.4. Scale-dependent effects of the proportion of the landscape in blueberry production on three different fruit attributes at harvest at 15 highbush blueberry fields in southwestern Michigan. Graphs on the left show the regression coefficients for (A) proportion of fruit set, (C) weight per berry, and (E) diameter of largest berry and the proportion of blueberry habitat at each of 5 spatial scales. Graphs on the right show simple linear regressions of the spatial scales with the highest r^2 value for (B) proportion of fruit set, (D) weight per berry, and (F) diameter of largest berry and the proportion of blueberry habitat.

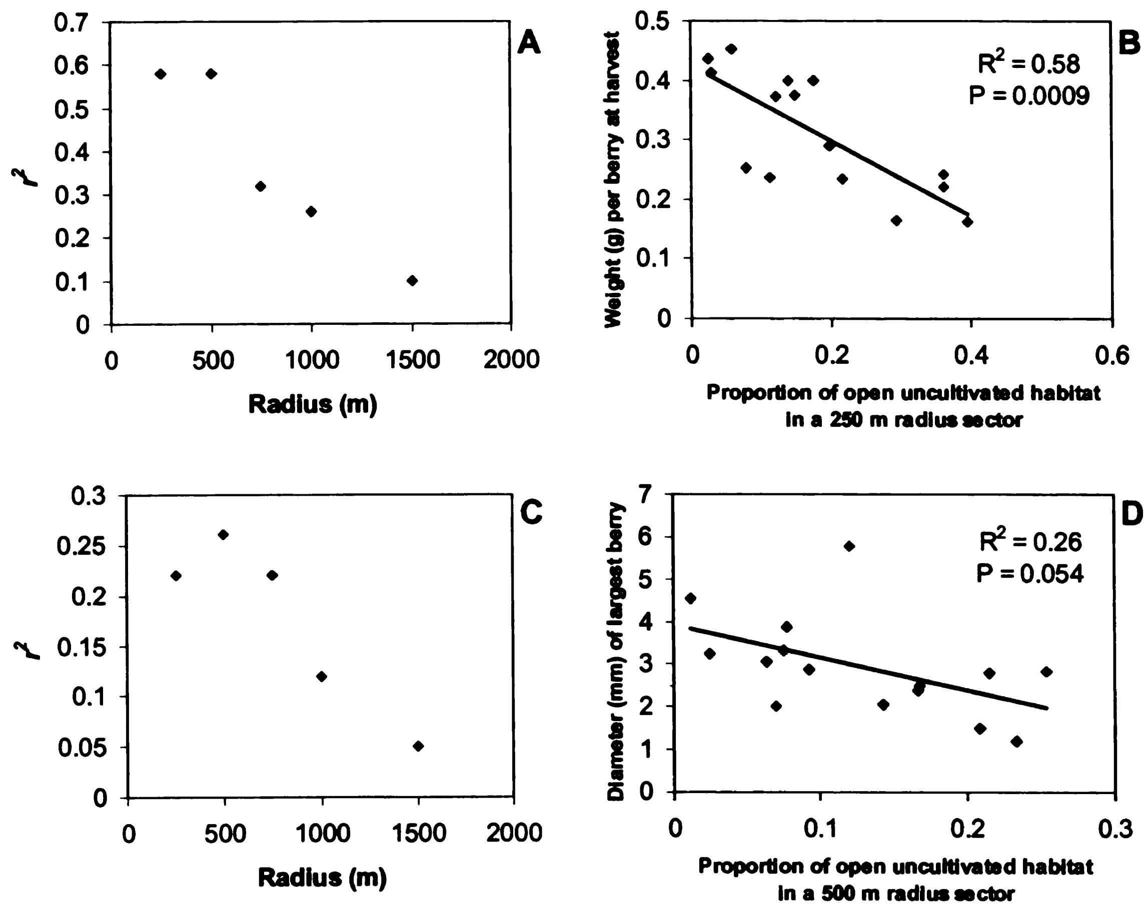

Figure 6.5. Scale-dependent effects of the proportion of open uncultivated land on two different fruit attributes at harvest at 15 highbush blueberry fields in southwestern Michigan. Graphs on the left show the regression coefficients for (A) weight per berry and (C) diameter of largest berry and the proportion of open uncultivated habitat at each of 5 spatial scales. Graphs on the right show simple linear regressions of the spatial scales with the highest r^2 value for (B) weight per berry and (D) diameter of largest berry and the proportion of open uncultivated habitat.

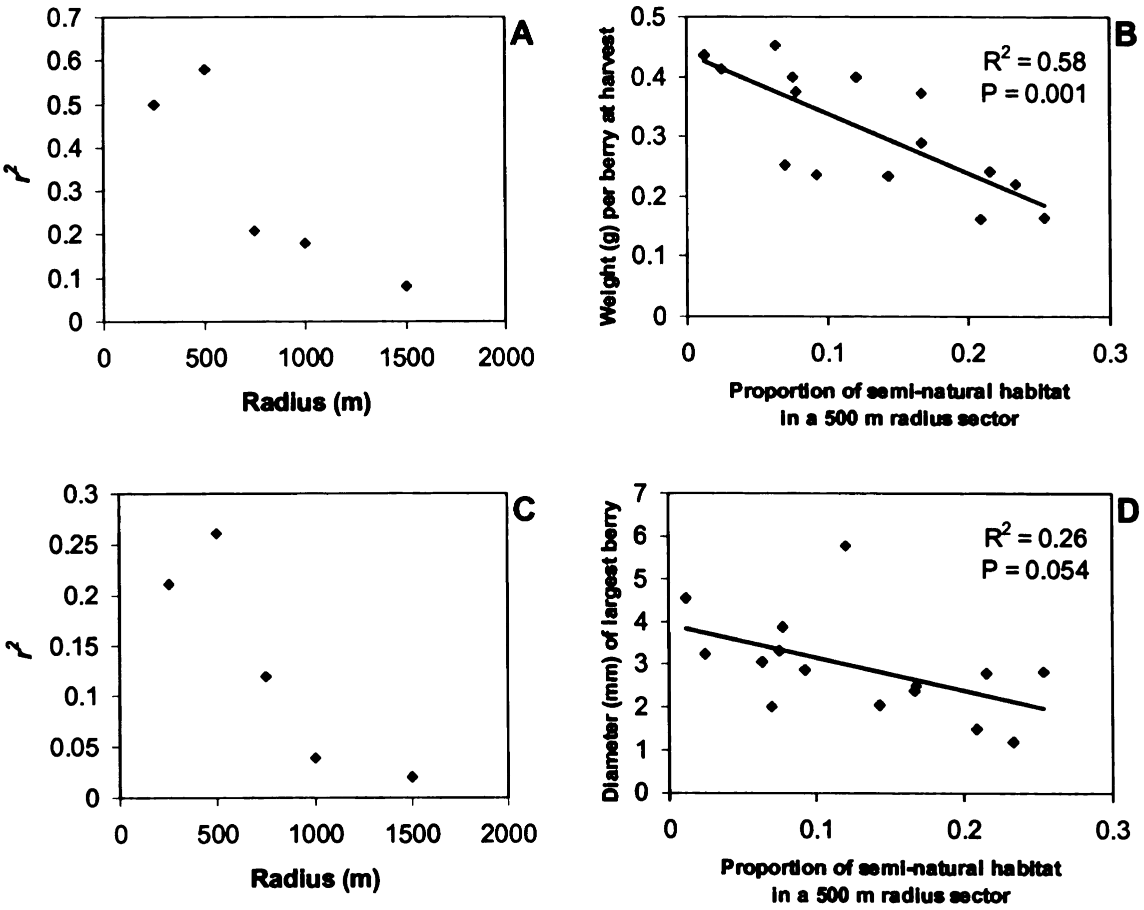

Figure 6.6. Scale-dependent effects of the proportion of semi-natural land, including woodland habitat, on two different fruit attributes at harvest at 15 highbush blueberry fields in southwestern Michigan. Graphs on the left show the regression coefficients for (A) weight per berry and (C) diameter of largest berry and the proportion of semi-natural habitat at each of 5 spatial scales. Graphs on the right show simple linear regressions of the spatial scales with the highest r^2 value for (B) weight per berry and (D) diameter of largest berry and the proportion of semi-natural habitat.

DISCUSSION

Bees and their relatives have been shown to respond to habitat features in the landscape at various scales depending on their known or expected foraging range and the quality of the surrounding habitat (Perfecto and Vandermeer 2002, Steffan-Dewenter 2002, Steffan-Dewenter et al. 2002, Ricketts 2004, Klein et al. 2006, Veddeler et al. 2006). The proportion of the landscape that is semi-natural has been the strongest predictor of bee abundance, presumably because this provides nesting sites and non-managed habitat for bees. Bees with long foraging ranges such as honey bees have been shown to respond to landscape features up to 3000 m from sampled fields, whereas smaller, solitary bees with shorter foraging ranges, respond to landscape features within 750 m (Steffan-Dewenter et al. 2002, Klein et al. 2004).

In this study, where any honey bees collected were presumed to be from managed hives temporarily present in the landscape, and where bumble bees were infrequently collected, most of the bee species collected during blueberry bloom were solitary or semi-social. Measurements of abundance, richness, or diversity of wild bees showed no significant relationship to any of the landscape features examined, which is unexpected considering previous studies (Steffan-Dewenter et al. 2002, Klein et al. 2006, Veddeler et al. 2006.

Despite the lack of response of the whole bee community to landscape variation, some individual bee species that are known to forage on blueberry varied significantly with the surrounding landscape. Members of the species complex *Ceratina calcarata/dupla* were more abundant in habitats with a higher proportion of semi-natural landscape at the 250 m scale. This fits well with the idea that the smaller the bee, the smaller its foraging range. This bee is one of the smallest species in Michigan (5-7 mm), and is a semi-social carpenter bee that nests in pithy stems (Michener 2000). Thus, its size and the fact that semi-natural habitat is likely to contain a high proportion of its nesting resource, could explain this relationship. *Ceratina calcarata/dupla* were less abundant in habitats with a high proportion of blueberry fields at the 250 m spatial scale. This could be due to the intensive management of plants in crops margins, i.e. the destruction of nesting resources, or that management practices such as insecticide use after bloom are reducing the number of bees that survive to the following year.

In contrast to the expected response by solitary bees to landscape complexity, the main blueberry specialist bee species found in this region, *Andrena carolina*, was more abundant in habitats containing a greater proportion of human settlement at the 1500 m spatial scale. At first, this appears to support the Winfree et al. (2007) finding that some bees may benefit from the floral diversity and nesting opportunities provided by non-natural, residential landscapes. However, because *A. carolina* is a solitary, soil-nesting species (Michener 2000) and is a blueberry specialist (MacKenzie and Eickwort 1996), one would expect this bee to be more highly correlated with blueberry field abundance and to have a relatively short foraging range, considering the results of Steffan-Dewenter et al. (2002). On the contrary, this result suggests that the foraging range of this species may be farther than expected, allowing it to use habitat containing a wide variety of plant species for forage. It is possible that *A. carolina* is capable of foraging up to a much greater distance than expected by the average foraging range of solitary bees (Steffan-Dewenter et al. 2002).

Pollination of blueberry, measured as the difference in fruit set, berry weight, and diameter of the largest berry, between open pollinated and pollinator-excluded flower clusters, increased with the area of surrounding blueberry plantations. This seems to indicate that blueberry habitat, typically containing a high proportion of managed honey bees is beneficial to production of this crop. Honey bees were the most abundant species of bee collected in the pan traps during bloom and were the most abundant kind of bee observed visiting blooms (see Chapter 3).

Fruit weight and diameter decreased with the proportion of open-uncultivated and semi-natural habitats within 500 m of the focal field. One explanation for this result is that there may not have been enough bees either native, rented, or as spillover from neighboring farms in fields that were surrounded by more semi-natural habitat (i.e. the fields may have been too isolated). This result suggests that wild pollinators residing in adjacent habitats may be contributing little to pollination in intensive highbush blueberry production, contrary to other studies in which adjacent semi-natural habitat and its associated diversity of wild bees resulted in higher fruit or seed set (Steffan-Dewenter and Tscharntke 1999, Ricketts et al. 2004).

Conclusion. This is the first study of which I am aware to look at the response of several solitary soil-nesting or semi-social dwarf carpenter bee species and their response to landscape context at different spatial scales. In most of the sampled fields, honey bees outnumbered any other kind of bee by two or three to one, and honey bees were unlikely to be greatly affected by landscape context since they were only brought in for crop bloom. In this situation, the presence of honeybees may make it difficult to measure the effect of native bees on commercial blueberry pollination. Further studies to examine resource partitioning between different bee species, similar to that by Greenleaf and Kremen (2006) in sunflower, would be helpful in describing what role native bees play in the pollination of this crop for which certain native bee species, such as *Bombus* spp., are efficient pollinators.

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APPENDIX A:

GPS COORDINATES FOR FIELD SITES

Table A. GPS coordinates for the 15 blueberry fields in southwest Michigan in which bees were sampled between 2004-6.

Site	Code	N	W
1	GAL	42°16.075	086°13.997
2	DGJ	42°20.869	086°13.355
3	DGS	42°21.885	086°17.217
4	BOD	42°24.749	086°06.378
5	EAR	42°32.148	086°12.896
6	FEL	42°34.917	086°09.107
7	DOU	42°37.589	086°10.117
8	DJS	42°41.677	086°08.920
9	DJP	42°43.631	086°06.638
10	BOW	42°49.122	086°10.236
11	WAS	42°50.604	086°09.902
12	STA	42°52.051	086°07.578
13	CAR	42°52.905	086°09.369
14	TIL	42°57.208	086°06.568
15	RAN	42°59.413	086°09.451

APPENDIX B:

LIST OF VOUCHER SPECIMENS

Table B. List of voucher specimens. The ID column refers to the unique number assigned to each specimen. Key to determinations: A = J.S. Ascher; L = J.C.W. Langdon; T = J.K. Tuell.

ID	Date Collected	Family	*Genus*	*species*	sex	det
40506	5/16/2004	Andrenidae	*Andrena*	*algida*	f	A
40644	6/3/2004	Andrenidae	*Andrena*	*alleghaniensis*	f	A
52049	4/21/2005	Andrenidae	*Andrena*	*arabis*	f	A
50972	5/16/2005	Andrenidae	*Andrena*	*barbilabris*	f	A
52024	6/30/2005	Andrenidae	*Andrena*	*bisalicis*	f	A
40109	5/15/2004	Andrenidae	*Andrena*	*carlini*	f	A
40921	5/25/2004	Andrenidae	*Andrena*	*carolina*	f	A
41023	5/25/2004	Andrenidae	*Andrena*	*ceanothi*	f	A
53791	4/21/2005	Andrenidae	*Andrena*	*clarkella*	f	A
40181	5/19/2004	Andrenidae	*Andrena*	*commoda*	f	A
40311	5/19/2004	Andrenidae	*Andrena*	*crataegi*	f	A
41046	8/19/2004	Andrenidae	*Andrena*	*cressonii*	f	A
40707	5/26/2004	Andrenidae	*Andrena*	*dunningi*	f	A
50364	5/25/2005	Andrenidae	*Andrena*	*erigeniae*	f	A
50925	5/16/2005	Andrenidae	*Andrena*	*erythrogaster*	f	A
40389	5/16/2004	Andrenidae	*Andrena*	*forbesii*	f	A
50023	4/16/2005	Andrenidae	*Andrena*	*frigida*	f	A
61776	6/12/2006	Andrenidae	Andrena	*geranii*	f	A
41499	6/3/2004	Andrenidae	*Andrena*	*hippotes*	f	A
42461	8/19/2004	Andrenidae	*Andrena*	*hirticincta*	m	A
40988	5/25/2004	Andrenidae	*Andrena*	*imitatrix or morrisonella*	f	A
41236	5/25/2004	Andrenidae	*Andrena*	*integra*	f	A
40169	5/15/2004	Andrenidae	*Andrena*	*mandibularis*	f	A
40385	5/16/2004	Andrenidae	*Andrena*	*mariae*	f	A
41118	5/26/2004	Andrenidae	*Andrena*	*milwaukeensis*	f	A
40150	5/15/2004	Andrenidae	*Andrena*	*miserabilis*	f	A
40098	5/25/2004	Andrenidae	*Andrena*	*morrisonella*	f	A
40151	5/15/2004	Andrenidae	*Andrena*	*nasonii*	f	A
40992	5/25/2004	Andrenidae	*Andrena*	*neonana*	f	A
41289	5/25/2004	Andrenidae	*Andrena*	*nigrae*	f	A
40104	6/2/2004	Andrenidae	*Andrena*	*nivalis*	f	A
41300	5/26/2004	Andrenidae	*Andrena*	*nuda*	f	A
40572	5/16/2004	Andrenidae	*Andrena*	*perplexa*	f	A
60617	5/17/2006	Andrenidae	Andrena	*persimulata*	f	A
41768	8/19/2004	Andrenidae	*Andrena*	*placata*	f	A
61800	6/12/2006	Andrenidae	Andrena	*platypaea*	f	A
41698	6/3/2004	Andrenidae	*Andrena*	*pruni*	f	A
40300	5/19/2004	Andrenidae	*Andrena*	*rehni*	f	A
40995	5/25/2004	Andrenidae	*Andrena*	*robertsonii*	f	A
40575	5/16/2004	Andrenidae	*Andrena*	*rugosa*	f	A
40306	5/19/2004	Andrenidae	*Andrena*	*salictaria*	f	A
62286	4/24/2006	Andrenidae	Andrena	*sigmundi*	f	A
40979	5/25/2004	Andrenidae	*Andrena*	*spiraeana*	f	A
60030	5/26/2006	Andrenidae	Andrena	*thespii*	f	A

ID	Date Collected	Family	*Genus*	*species*	sex	det
52666	4/16/2005	Andrenidae	*Andrena*	*tridans*	f	A
40401	5/16/2004	Andrenidae	*Andrena*	*vicina*	f	A
52662	4/16/2005	Andrenidae	*Andrena*	*violae*	f	A
52232	4/21/2005	Andrenidae	*Andrena*	*wellesleyana*	f	A
61845	6/12/2006	Andrenidae	Andrena	*wilkella*	f	A
41395	9/4/2004	Andrenidae	*Calliopsis*	*andreniformis*	f	A
53902	9/15/2005	Andrenidae	*Perdita*	*octomaculata*	f	A
41795	8/19/2004	Andrenidae	*Pseudopanurgus*	*nebrascensis*	f	A
41527	6/3/2004	Apidae	*(Eucera)*	*atriventris*	f	A
61726	6/12/2006	Apidae	*(Eucera)*	*hamata*	f	A
61272	7/6/2006	Apidae	*Anthophora*	*terminalis*	f	A
40240	5/15/2004	Apidae	*Apis*	*mellifera*	f	T
41620	6/2/2004	Apidae	*Bombus*	*bimaculatus*	f	A
41515	5/25/2004	Apidae	*Bombus*	*citrinus*	f	A
42529	8/19/2004	Apidae	*Bombus*	*fervidus*	f	A
40320	5/19/2004	Apidae	*Bombus*	*griseocollis*	f	A
40321	5/29/2004	Apidae	*Bombus*	*impatiens*	f	A
40771	6/2/2004	Apidae	*Bombus*	*perplexus*	f	A
42396	8/19/2004	Apidae	*Bombus*	*vagans*	f	A
40528	5/19/2004	Apidae	*Ceratina*	*calcarata*	m	T
40364	5/19/2004	Apidae	*Ceratina*	*dupla*	m	T
40843	6/3/2004	Apidae	*Ceratina*	*strenua*	f	T
53333	9/15/2005	Apidae	*Melissodes*	*agilis*	f	A
42405	7/15/2004	Apidae	*Melissodes*	*apicata*	m	A
41156	7/29/2004	Apidae	*Melissodes*	*bimaculata*	m	A
41388	9/4/2004	Apidae	*Melissodes*	*communis*		A
42420	8/16/2004	Apidae	*Melissodes*	*desponsa*	f	T
53897	9/15/2005	Apidae	*Melissodes*	*druriella*	f	A
42407	7/23/2004	Apidae	*Melissodes*	*tridonis*	f	A
53143	5/10/2005	Apidae	*Nomada*	*cf. armatella*	m	A
53104	5/21/2005	Apidae	*Nomada*	*cressonii*	m	A
53589	5/10/2005	Apidae	*Nomada*	*denticulata*	f	A
52838	4/16/2005	Apidae	*Nomada*	*luteoloides*	f	A
53586	5/10/2005	Apidae	*Nomada*	*maculata*	f	A
52833	4/16/2005	Apidae	*Nomada*	*obliterata*	f	A
53103	5/21/2005	Apidae	*Nomada*	*ovata*	m	A
53573	4/21/2005	Apidae	*Nomada*	*pygmaea*	m	A
42398	8/22/2004	Apidae	*Triepeolus*	*lunatus*	f	T
42425	5/25/2004	Apidae	*Xylocopa*	*virginica virginica*	m	A
41403	5/25/2004	Colletidae	*Colletes*	*thoracicus*	m	L
41180	5/26/2004	Colletidae	*Hylaeus*	*affinis*	f	L
50639	5/21/2005	Colletidae	*Hylaeus*	*rudbeckiae*	f	L
41790	8/19/2004	Halictidae	*Agapostemon*	*sericeus*	m	L
40881	6/3/2004	Halictidae	*Agapostemon*	*splendens*	f	L
40185	5/19/2004	Halictidae	*Agapostemon*	*texanus*	f	L
40993	5/25/2004	Halictidae	*Agapostemon*	*virescens*	f	L
42267	8/22/2004	Halictidae	*Augochlora*	*pura*	f	L
41220	5/25/2004	Halictidae	*Augochlorella*	*aurata*	f	L

ID	Date Collected	Family	*Genus*	*species*	sex	det
42303	8/19/2004	Halictidae	*Augochlorella*	*gratiosa*	f	L
40239	5/19/2004	Halictidae	*Dufourea*	*marginata*	f	L
40238	5/19/2004	Halictidae	*Halictus*	*confusus*	f	A
42100	8/22/2004	Halictidae	*Halictus*	*ligatus*	m	L
40538	5/16/2004	Halictidae	*Halictus*	*parallelus*	f	A
42075	8/19/2004	Halictidae	*Halictus*	*rubicundus*	m	L
40923	5/25/2004	Halictidae	*Lasioglossum*	*acuminatum*	f	A
41309	9/4/2004	Halictidae	*Lasioglossum*	*admirandum*	f	L
41720	6/3/2004	Halictidae	*Lasioglossum*	*anomalum*	f	L
40726	5/16/2004	Halictidae	*Lasioglossum*	*boreale*	f	L
40355	5/19/2004	Halictidae	*Lasioglossum*	*bruneri*	f	L
41788	8/19/2004	Halictidae	*Lasioglossum*	*coeruleum*	f	L
40231	5/15/2004	Halictidae	*Lasioglossum*	*coriaceum*	f	L
40815	6/3/2004	Halictidae	*Lasioglossum*	*cressonii*	f	A
50245	5/25/2005	Halictidae	*Lasioglossum*	*fattigi*	f	L
40325	5/29/2004	Halictidae	*Lasioglossum*	*fuscipenne*	f	A
61399	7/6/2006	Halictidae	Lasioglossum	*illinoense*	f	A
41967	7/15/2004	Halictidae	*Lasioglossum*	*imitatum*	f	A
40326	5/16/2004	Halictidae	*Lasioglossum*	*leucozonium*	f	A
41657	5/25/2004	Halictidae	*Lasioglossum*	*nelumonis*	f	A
41286	6/3/2004	Halictidae	*Lasioglossum*	*nigroviride*	f	A
42527	8/19/2004	Halictidae	*Lasioglossum*	*nymphaearum*	f	L
52304	4/21/2005	Halictidae	*Lasioglossum*	*nymphale*	f	L
41637	5/25/2004	Halictidae	*Lasioglossum*	*oblongum*	f	A
40489	5/19/2004	Halictidae	*Lasioglossum*	*pectorale*	f	A
40825	6/3/2004	Halictidae	*Lasioglossum*	*pilosum*	f	A
40819	6/3/2004	Halictidae	*Lasioglossum*	*quebecense*	f	A
40711	6/3/2004	Halictidae	*Lasioglossum*	*rohweri*	f	L
51784	6/29/2005	Halictidae	*Lasioglossum*	*suvianae*	m	L
40813	6/3/2004	Halictidae	*Lasioglossum*	*tegulare*	f	A
60621	5/17/2006	Halictidae	Lasioglossum	*versans*	f	L
42465	7/15/2004	Halictidae	*Lasioglossum*	*vierecki*	f	A
42322	7/15/2004	Halictidae	*Sphecodes*	*confertus*	f	A
40220	5/19/2004	Halictidae	*Sphecodes*	*dichrous*	f	A
40738	5/16/2004	Halictidae	*Sphecodes*	*ranunculi*	f	A
54122	6/9/2005	Megachilidae	*Anthidium*	*manicatum*	f	T
52104	5/21/2005	Megachilidae	*Ashmeadiella*	sp.	m	L
51465	6/29/2005	Megachilidae	*Dianthidium*	*simile*	f	T
61626	6/12/2006	Megachilidae	Heriades	*leavitti*	m	L
42495	8/16/2004	Megachilidae	*Heriades*	*variolosus*	f	A
51481	5/21/2005	Megachilidae	*Hoplitis*	*producta*	f	A
51482	5/21/2005	Megachilidae	*Hoplitis*	*spoliata*	m	A
50414	5/25/2005	Megachilidae	*Megachile*	*(Xanthosarus)* sp.	m	A
53895	9/15/2005	Megachilidae	*Megachile*	*albatarsis*	f	T
41406	7/29/2004	Megachilidae	*Megachile*	*campanulae*	f	T
51466	6/29/2005	Megachilidae	*Megachile*	*centuncularis*	f	A
53156	9/15/2005	Megachilidae	*Megachile*	*mendica*	f	T
41511	7/29/2004	Megachilidae	*Megachile*	*montivaga*	f	A

ID	**Date Collected**	**Family**	***Genus***	***species***	**sex**	**det**
41416	9/4/2004	Megachilidae	*Megachile*	*mucida*	f	T
42502	8/16/2004	Megachilidae	*Megachile*	*pugnata*	f	A
51471	6/29/2005	Megachilidae	*Megachile*	*rotundata*	f	A
50062	4/16/2005	Megachilidae	*Osmia*	*atriventris*	m	L
40096	5/25/2004	Megachilidae	*Osmia*	*bucephala*	f	T
52102	5/21/2005	Megachilidae	*Osmia*	*conjuncta*	f	L
61472	6/12/2006	Megachilidae	Osmia	*distincta*	f	A
61654	6/12/2006	Megachilidae	Osmia	*felti*	f	A
61350	7/6/2006	Megachilidae	Osmia	*georgica*	f	A
51490	4/15/2005	Megachilidae	*Osmia*	*lignaria*	m	A
51484	4/15/2005	Megachilidae	*Osmia*	*michiganensis or illinoensis*	f	L
50678	5/21/2005	Megachilidae	*Osmia*	*pumila*	f	A
62608	4/26/2006	Megachilidae	Osmia	*simillima*	m	A
50011	4/16/2005	Megachilidae	*Osmia*	*subfasciata?*	m	L
60994	4/24/2006	Megachilidae	Osmia	*virga*	m	A

APPENDIX C:

A RECORD OF BEE SPECIES ASSOCIATED WITH *VACCINIUM* SPP. IN MICHIGAN

Table C. Bee species for which there are either pollen, nectar, or floral visitation records on *Vaccinium* spp. The first two records were compiled from Mitchell (M-1960) and Hurd (H-1979). The third record is from a single community study in highbush blueberry in upstate New York reported by MacKenzie and Eickwort (M&E-1996). The last record is from observations and collections made in highbush blueberry in this dissertation (T - 2004-6).

Family **species**	**M - 1960**	**H - 1979**	**M&E - 1996**	**T - 2004-6**
Andrenidae				
Andrena bradleyi		✓		
Andrena carlini carlini		✓	✓	✓
Andrena carolina		✓	✓	✓
Andrena crataegi	✓	✓		
Andrena forbesii	✓	✓	✓	
Andrena hilaris	✓	✓		
Andrena hippotes	✓	✓		
Andrena imitatrix	✓	✓		
Andrena kalmiae		✓		
Andrena melanochroa		✓		
Andrena milwaukeensis			✓	
Andrena miranda	✓	✓		
Andrena miserabilis				✓
Andrena morrisonella				✓
Andrena nivalis			✓	✓
Andrena pruni			✓	
Andrena regularis	✓	✓		
Andrena rugosa			✓	
Andrena rugosignata			✓	
Andrena sayi	✓	✓		
Andrena sigmundi	✓	✓		
Andrena thaspii	✓	✓		
Andrena transnigra		✓		
Andrena vicina	✓	✓	✓	✓

Family **species**	**M - 1960**	**H - 1979**	**M&E - 1996**	**T - 2004-6**
Andrenidae cont.				
Andrena wilkella	✓	✓		
Apidae				
Anthophora ursina ursina		✓		
Apis mellifera	✓	✓	✓	✓
Andrena affinis	✓	✓		
Bombus bimaculatus	✓	✓	✓	✓
Bombus borealis	✓	✓		
Bombus fervidus	✓	✓	✓	
Bombus fraternus	✓	✓		
Bombus griseocollis	✓	✓		✓
Bombus impatiens	✓	✓	✓	✓
Bombus nevadensis auricomus	✓	✓	✓	
Bombus pennsylvanicus	✓	✓		
Bombus perplexus	✓	✓	✓	✓
Bombus rufocinctus	✓	✓		
Bombus ternarius	✓	✓		
Bombus terricola	✓	✓	✓	
Bombus vagans	✓	✓	✓	
Bombus ashtoni			✓	
Bombus fernaldae			✓	
Ceratina calcarata			✓	
Ceratina dupla	✓	✓	✓	
Ceratina strenua		✓	✓	
Habropoda laboriosa laboriosa		✓		
Xylocopa virginica (virginica virginica in K)	✓	✓	✓	✓
Colletidae				
Colletes inaequalis			✓	✓

Family species	M - 1960	H - 1979	M&E - 1996	T - 2004-6
Colletidae cont.				
Colletes thoracicus		✓		✓
Colletes validus	✓	✓		✓
Halictidae				
Agapostemon sericeus				✓
Augochlora pura pura	✓	✓	✓	✓
Augochlorella aurata (=striata)	✓	✓	✓	✓
Augochlorella gratiosa	✓	✓		
Augochloropsis metallica			✓	
Augochloropsis sumptuosa		✓	✓	
Halictus confusus			✓	✓
Halictus rubicundus			✓	✓
Lasioglossum (Dialictus) cressonii			✓	✓
Lasioglossum (Dialictus) imitatum (=imatatus)			✓	✓
Lasioglossum (Dialictus) pilosum (=pilosus)			✓	
Lasioglossum (Dialictus) smilacinae			✓	
Lasioglossum (Dialictus) versatus			✓	
Lasioglossum (Dialictus) zephyrus			✓	
Lasioglossum (Evylaeus) foxii			✓	
Lasioglossum (Evylaeus) quebecense (=quebecensis)			✓	
Lasioglossum (L.)acuminatum				✓
Lasioglossum (L.)coriaceum			✓	
Sphecodes sp.				✓
Megachilidae				
Hoplitis truncata truncata	✓	✓		
Megachile addenda	✓	✓		
Megachile brevis psudobrevis	✓	✓		
Megachile gemula gemula	✓	✓		
Megachile ingenua		✓		

Family **species**	**M - 1960**	**H - 1979**	**M&E - 1996**	**T - 2004-6**
Megachilidae cont.				
Megachile mendica mendica	✓	✓		
Megachile (Chalicodoma) exilis parexilis		✓		
Megachile (Chalicodoma) georgica		✓		
Megachile (Chalicodoma) rugifrons		✓		
Nomada spp.				✓
Osmia atriventris	✓	✓	✓	
Osmia bucephala		✓	✓	✓
Osmia chalybea		✓		
Osmia inermis		✓		
Osmia inspergens	✓	✓		
Osmia pumila	✓	✓		
Osmia sandhouseae		✓		
Mellitidae				
Macropis nuda	✓	✓		
Total species:	42	61	41	26