An Assessment of Non-Apis Bees as Fruit and Vegetable Crop Pollinators in Southwest Virginia

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Abstract

Declines in pollinators around the globe, notably the loss of honey bees (*Apis mellifera* L.) to Colony Collapse Disorder, coupled with a dearth of quantitative data on non-*Apis* bee pollinators, led to this dissertation research, which documents the role of non-*Apis* bees in crop pollination in southwest Virginia. Major findings of this first study of its kind in the region were that non-*Apis* bees provided the majority of pollination—measured by visitation—for several economically important entomophilous crops (apple, blueberry, caneberry, and cucurbits); diverse bee populations may be helping to stabilize pollination service (105 species on crop flowers); landscape factors were better predictors of non-*Apis* bees in the genera *Andrena*, *Bombus*, and *Osmia* were as constant as honey bees when foraging on apple.

Non-*Apis*, primarily native, bees made up between 68% (in caneberries) and 83% (in cucurbits) of bees observed visiting crop flowers. While 37–59 species visited crop flowers, there was low correspondence between bee communities across or within crop systems ("within crop" Jaccard similarity indices for richness ranged from 0.12–0.28). Bee community diversity on crop flowers may help stabilize pollination service if one or more species declines temporally or spatially. A few species were especially important in each crop: *Andrena barbara* in apple; *Andrena carlini* and *A. vicina* in blueberry; *Lasioglossum leucozonium* in caneberry; and *Peponapis pruinosa* and *Bombus impatiens* in cucurbits. Eight species collected were Virginia state records.

In models testing effects of farm management and landscape on non-*Apis* crop pollination service, percent deciduous forest was positively correlated in apple, blueberry, and squash, but at different scales. For apple and blueberry, pollination service declined with an increase in utilized

alternative forage but was positively related to habitat heterogeneity. For squash, percent native plants also related positively, possibly due to increased presence of bumble bees in late summer.

Species collected from both bowl traps and flowers was as low as 22% and overall site bee diversity had no effect on crop pollination service, highlighting the value in pollination research of monitoring bees on flowers.

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CHAPTER 1 Introduction

Declines in pollinator populations around the globe, the recent loss of honey bees (Apis mellifera L.) to Colony Collapse Disorder, and increased awareness of the lack of baseline data regarding pollinators other than honey bees for crops and other ecosystems has led to a surge in interest in non-Apis pollinators (Cane and Tepedino 2001, Kevan and Viana 2003, NRC 2007, Hackett et al. 2010, Potts et al. 2010). Though we generally view the European (or western) honey bee as our most important pollinator, native and introduced non-Apis bees provide the majority of pollination services for many crops in the United States (Richards 1993, 2008). In Virginia, most research on bee pollinators has focused on honey bees, bumble bees, Bombus spp. (family Apidae), the orchard mason bee, Osmia lignaria Say (family Megachilidae), and two species of squash bees, Peponapis pruinosa Say and Xenoglossa strenua Cresson (family Apidae), although nearly 500 species of bees inhabit the state (Shimanuki 1977, Reichelderfer and Caron 1979, Cantwell 1980, Fell and Robinson 1981, Rajotte and Fell 1982, Fell 1986, 1995, 1999, Kraemer and Favi 2005, Shuler et al. 2005, Burley 2007). I investigated the role of non-Apis bees in pollination of entomophilous crops in Virginia throughout the growing season, from April to August. I monitored bee visitors to crop flowers in apple, blueberry, caneberry (raspberry, blackberry, and black raspberry), and several cucurbits (summer and winter squash, cucumber, melon, and watermelon) in Virginia. I tested the influence of farm management and landscape features on pollination services provided by non-Apis bees. To gain some sense of native bee foraging habits when visiting crops, I tested the floral constancy of the most important groups of bees visiting apple.

While the role of native bees as crop pollinators has been studied regionally, no baseline data exist for southwest Virginia. Research in northern Virginia, Maryland, New Jersey, Pennsylvania, and New York indicates that non-*Apis* bees may provide the majority of crop pollination for some crops and pollination "insurance" during periods of honey bee decline (Winfree et al. 2007a, Winfree et al. 2007b, Winfree et al. 2008). The influence of farm management and landscape features on squash bees has been well-studied in northern Virginia (Shuler et al. 2005, Julier and Roulston 2009). In southeast Virginia, pollen choice of the mason bee, *Osmia lignaria*, was investigated, highlighting the importance of native tree pollen in the diet of this superb fruit tree pollinator (Kraemer and Favi 2005). In southwest Virginia, crop

pollination research has focused on honey bees, with studies in apple and sunflower, and to a lesser extent on *Bombus* spp. in apple (Fell and Robinson 1981, Fell 1986, 1999). No studies have been published regarding bee populations and crops throughout the growing season.

Within this context, the goals of this research were to gauge the relative importance of non-*Apis* (primarily native) and *Apis* bees in crop pollination in southwest Virginia, determine the floral constancy of some of the most important non-*Apis* fruit tree pollinators relative to honey bees, gain understanding of forage as competition for pollinators or as beneficial habitat, determine farm management and landscape factors that affect crop pollination by bees, and compare the use of derived habitat metrics with field measured metrics in predicting pollination service.

To gauge the relative importance of non-Apis bees in crop pollination (Chapter 3), I monitored crop flower visitation at farms in southwest Virginia from April to August in 2008 and 2009: five apple, seven blueberry, five caneberry, and sixteen cucurbit sites. Bees were grouped into the following categories recognizable on sight: honey bees, bumble bees (Bombus spp.), carpenter bees (Xylocopa virgnica L.), medium bees (about the size of honey bees), and small bees. Following observation at flower, bees were collected from flowers with nets, and later identified to species or genus to determine the richness of species visiting crops. One hundred five non-Apis bees were found on crop flowers, with between 37 and 59 species per crop. Bowl traps with soapy water were also used to collect bees from the site, for better understanding of overall site species richness, and as part of a broader monitoring program coordinated by the U.S. Geological Survey. Crop flower visitation by medium and larger bees was assumed to be as effective or more effective than honey bees (based on research on the most important medium and larger bees visiting these crops) and provided a measure of non-Apis bee pollination service for comparison with honey bee visitation. Non-Apis bees provided the majority of pollination in apple, blueberry, caneberry, cucumber, and squash, and an equivalent amount of melon pollination as honey bees. Honey bee colonies were present at some farms, so the influence of colonies on honey bee presence at flower was also tested. Honey bee colony presence in crop fields had no effect on the number of honey bees visiting crop flowers.

To better understand the foraging habits of important non-*Apis* pollinators (Chapter 4), I compared the pollen loads of the four most important bee genera pollinating apple. One reason honey bees are considered especially good pollinators is their floral constancy, so I compared the

floral constancy of *Apis* with the three most important non-*Apis* genera pollinating apple: *Andrena, Bombus*, and *Osmia*. I collected bees from apple flowers and counted the number of apple and non-apple pollen grains they carried. I also monitored visitation to alternative forage (non-apple plants in flower during apple bloom) at each site to gain insights into possible competitive effects of alternative forage with apple for pollinators. I found that any competitive effects were negligible for those bees visiting apple flowers and that there were no significant differences in the floral constancy of *Andrena, Apis, Bombus*, or *Osmia*.

The presence of bees on crop flowers may be influenced by many factors: the natural distribution of species associated with forage and nesting sites, farm management practices, annual weather and cycles of predator and parasite populations. Factors that can be relatively easily measured include land cover available from national image-based datasets, such as the Multi-Resolution Land Characteristics Consortium's National Land Cover Dataset 2001(NLCD) (Soil Survey Staff 2004 (2008)) and farm management practices. I tested the use of a model to predict bee pollination service with landscape and farm management factors based on our largest dataset (squash) for other crops (Chapter 5), with flower visitation by medium and larger non-*Apis* bees as a measure of pollination service. I found that the squash-based model was not validated with other crop data, so investigated the factors important for the second largest dataset, apple combined with blueberry. I found that percent forested habitat correlated with pollination service in most crops, and that habitat heterogeneity, percent natives, and crop richness were the best predictors in some crops, but not others.

The following literature review (Chapter 2) examines basic pollination concepts, the importance of bee pollinators for crops and ecosystems globally, prior research on non-*Apis* bee crop pollinators in the U.S., and pollination of apples, blueberries, caneberries, and cucurbits in Virginia. In subsequent chapters, "we" includes my co-authors on manuscripts in preparation for publication.

CHAPTER 2 Literature review

2.1 The mechanics of pollination

Pollination is the movement of the male gametes contained in plant pollen to female gametes of the same species, which can lead to sexual reproduction if fertilization (fusion of the male and female gametes) occurs. Sexual reproduction ensures mixing of genes, which does not occur when plants propagate themselves through asexual means, such as budding or division. Abiotic forces such as wind (anemophily) and water (hydrophily), aid pollination, but insects and other organisms (biotic pollination) provide the vast majority of terrestrial plant pollination. Waser and Ollerton (2006) give a history of animal pollination research in *Plant-pollinator Interactions: From Specialization to Generalization*. Due to receptivity (female flowers may be receptive for limited periods of time), limits of pollen viability, or cross-pollination needs, pollination does not always lead to fertilization.

Plants may be self-fertile or self-infertile. In the former case, a plant sets fruit or seed from its own pollen—self-pollination. Self-infertile plants require cross-pollination with pollen from other plants of the same species for successful fertilization (Free 1993, Delaplane and Mayer 2000c). Many self-fertile plants, however, have developed mechanisms to promote cross-pollination similar to self-infertile plants, and may produce more or better quality fruit with cross-pollination. Pollination requirements often vary within one species, with some varieties more dependent on cross-pollination than others. Most apple, blueberry, cherry, kiwi, persimmon, sunflower, and caneberry varieties require cross-pollination from other varieties for optimum fruit set (McGregor 1976, Torchio 1988, Free 1993, Delaplane and Mayer 2000c, McConkey 2009, Raintree_Nursery 2010). Crop pollination requirements are described in more detail below within the section on crops studied (2.6).

2.2 Mutualism–floral rewards attract pollinators

Most animal-mediated pollination is based on mutualistic relationships between plants and animals whereby plants provide nutrients or other resources (floral rewards) and pollinators transfer pollen within one plant or from one plant to another while utilizing the plants' resources

(Buchmann and Nabhan 1996, Kearns and Inouye 1997). Floral rewards include pollen (protein source), nectar (sugar source), oil (nest provisioning, mating), resin (waterproofing in nest construction, potentially prophylactic anti-bacterial and anti-fungal properties), wax and plant parts (nest construction), compounds that carry scents or other attractants used by some species in attracting mates or transferred during mating, and shelter (nesting sites, temporary protection, or, in some cases, heat) (Duffield et al. 1984, Kearns and Inouye 1993, Rasmussen and Olesen 2000, Cseke et al. 2007, Harder and Barrett 2007, Johnson 2010). Attractants such as scent or appearance (such as orchids that mimic female bees) may not always lead to any real reward for the visitors (Gill 1989, Peter and Johnson 2008).

When insects continue to visit a given type of flower, the floral reward is generally greater in terms of energy gained than energy lost in travel and collecting, but not too great to discourage movement between more flowers (Waddington 1996, Rodrigues-Girones and Santamaria 2007, Whitney and Glover 2007). Differences in quality of nectar are known to affect visitation by various bees due to energy needs and competition (Heinrich 1979, Biernaskie and Gegear 2007, Goulson et al. 2007). If nectar rewards in terms of sugar are very high, pollinators may visit fewer flowers (Pankiw et al. 2001, Feldlaufer et al. 2004). For example, a bat pollinated plant produces large quantities of nectar that may provide all the resource needs of a bee, but eliminate the need for the bee to visit another plant (Marten-Rodriguez et al. 2009).

Depending on resource availability in a region and in plants throughout a day, visitation may be partitioned. Larger bees may visit rewarding flowers before smaller bees if they can fly earlier (in cooler temperatures). A long-tongued bee may use less energy to gather nectar, so utilize a floral resource that a shorter-tongued bee would only use when better resources are no longer available (Heinrich 1979). In Kevan and Baker's (1983) review of insects as flower visitors and pollinators, the authors describe relationships between nectar type and visitor type (lapping flies, short-tongued bees, long-tongued bees, and butterflies/moths), flower type (open bowl, actinomorphic, zygomorphic, and stereomorphic), percentage sugars (ranges between 10 to 80 percent), sugar ratios (sucrose relative to glucose and fructose), and volume. Some flower spikes tend to have more nectar in lower flowers, and bees tend to move up the stalk until the amount is too low (at which point they move to another stalk) (Heinrich 1979). This allows bees to conserve energy (avoid flying far between flowers), while effectively transferring pollen for

the plants. Turtlehead flowers (*Chelone* spp.) produce large quantities of concentrated nectar, but their flower structure prevents gathering by all but bumble bees.

Besides sugar ratios, composition of amino acids, proteins, lipids, antioxidants, alkaloids, vitamins, organic acids, allantoin/allantoic acid, dextrins, and inorganic materials (minerals) also affects visitation (Kevan and Baker 1983). Some nectar is composed of sugars that are toxic to bees, but not to other insects (Adler 2000). Kevan and Baker (1983) point out that nectars used by moths, butterflies, and wasps tend to be richer in amino acids than nectars used by bees and flies that also consume pollen, and birds and bats that also consume insects. Proteins in nectar are presumed to have an enzymatic function for insects without proteinases, such as moths and butterflies. Lipids are more common in nectar used by Hymenoptera and may serve to decrease evaporation of nectar.

Pollen likewise attracts various groups based on varying characteristics, such as protein content, ratios of lipid and starch content, or oils that can help grains hold together and to pollencarrying hairs (Stanley and Linskens 1974, Roulston and Buchmann 2000). Roulston and colleagues (2000) and Roulston and Cane (2000) reviewed the relationships between pollen nutrients, digestibility, and pollinators, noting that protein content may be as high as 61%, but that it remains unclear if this is related more to energy required for pollen tube growth for fertilization or pollinator preference. Pollenkitt is an external lipid coating that helps pollen stick to stigmas and insects. Chemicals volatile in pollenkitt attract bees and may be the main attractant for oligolectic (specialist) bees (Pacini and Hesse 2005). Pollen composition also affects palatability and limits its use. Although percent protein has been correlated with life spans of bees, percent protein, as mentioned above, may relate more to pollen tube growth than pollinator rewards (Schmidt et al. 1987, Roulston et al. 2000). Pollen also contains enzymes for protein digestion, and phagostimulants that may help bees determine pollen from non-pollen materials (Kearns and Inouye 1993, Hanna and Schmidt 2004). Pollen presentation, the time period in which pollen is shed, also affects visitation and, for the flower, cross-pollination (Percival 1955, Waddington 1996, Castellanos et al. 2006).

Other floral products and structures benefit or deter pollinators. Oils secreted by some flowers separately from nectar are mixed with pollen fed to young by some flower visitors (Steiner and Whitehead 1990, Aguiar and Melo 2009). Male euglossine bees gather volatile compounds from orchids that are used to attract females (Teichert et al. 2009). Some

antioxidants within nectars may prevent lipids from becoming rancid or serve other functions (Baker and Baker 1983). The minerals found in nectar from some onions apparently deter use by honey bees, though they may attract other insects (Baker and Baker 1983, Delaplane and Mayer 2000c). Cucurbit flowers provide overnight shelter to male squash bees (Willis and Kevan 1995). Skunk cabbage produces heat in late winter and early spring that attracts pollinators (Buchmann and Nabhan 1996). Some bowl shaped flowers in the arctic collect solar energy for basking insects (Hocking and Sharplin 1965).

2.3 Importance of pollinators in crop production and ecosystem services

About 35% of global crop production depends on animal-mediated pollination (Kevan and Viana 2003, Klein et al. 2007). In the 1980s, when honey bee declines due to tracheal (Acarapis woodi (Rennie)) and varroa (Varroa destructor Anderson and Trueman) mites became a major concern, the USDA estimated that honey bees were the primary pollinators for about 15% of the world's crops (Buchmann and Nabhan 1996). Managed bees are recognized as the most economically important pollinators worldwide, with honey bees, and a few other managed bee species pollinating the vast majority of animal pollinated plants in our diet. The value of non-managed native pollinators in crop production and in other ecosystem services has also recently received attention (Kearns et al. 1998, Tscharntke et al. 2005, Winfree et al. 2007b). Estimates of the value of honey bee pollination in the U.S., based on associated crop values, range from \$6.8 billion to \$16.4 billion (in 2003 dollars), while one estimate of the value of fruit and vegetable crops dependent on native pollinators, primarily native bees, is \$3.07 billion, between one half and one sixth the value of honey bees (Morse and Calderone 2000, Losey and Vaughan 2006). However, Allsop and colleagues suggest that the cost of replacement of pollinator services may be a better way of valuing pollinator services since it is more likely to include the value of wild, non-managed species that tend to be undervalued, as well as managed pollinators (Allsopp et al. 2008).

Rising agricultural demand for bees due to increasing crop acreages, recent declines in honey bee colonies, and parallel declines of native bee populations and associated plant communities, has led to concern about a potential global pollination crisis (Kevan and Viana 2003, Ghazoul 2005, Eardley et al. 2006, Klein et al. 2007, Winfree 2008). Over the past fifty years, demand for managed honey bees has increased 45% while cultivation of crops dependent

on pollinators has grown nearly 300% (Aizen and Harder 2009). In 2005, due to expanded almond acreage combined with honey bee shortages associated with disease, the U.S. government allowed importation of honey bees from outside North America for the first time since 1922. In 1922, passage of the Honeybee Act banned such importation to prevent inadvertent importation of honey bee pests and diseases (Kearney 2006). A long-term study of plants and their pollinators in the Netherlands and Britain revealed parallel declines in plants, bees and syrphid flies since the 1980s—plants dependent on the declining pollinator species declined relative to other plant species (Biesmeijer et al. 2006).

In 2007, the National Research Council of the U.S. National Academy of Sciences reported the need for more baseline data on native bee pollinators, particularly in the U.S. (NRC 2007). Scientists concerned about the loss of wild bee populations have documented the ecosystem services that non-managed bees provide through crop pollination and within wild plant and animal communities (Allen-Wardell et al. 1998a, Cox-Foster et al. 2008, Le Conte and Navajas 2008, Tuell et al. 2008, Byrne and Fitzpatrick 2009). Recent research has also demonstrated the economic importance of native bees in indirect pollination services through their interaction with honey bees and the role of diversity in ecosystem stability (Balvanera et al. 2005, Fontaine et al. 2006a, Greenleaf and Kremen 2006b, Aizen et al. 2008b).

2.4 Non-Apis bees important for crop pollination

Bees other than honey bees important for crop pollination may be introduced or augmented in crops in a variety of ways, though they are not managed intensively in colonies as are honey bees. Other than bumble bees, most non-*Apis* species important for pollination are solitary bees. Research on specific native pollinators in the eastern U.S. has focused on bees listed in Table 2.1. In addition to those listed in the table, a survey of native pollinators in apple orchards in New York found mining bees (family Andrenidae), carpenter bees (family Apidae, subfamily Xylocopinae), cellophane bees (family Colletidae) and sweat bees (family Halictidae) to be the most abundant pollinator species besides honey bees in the orchards—only one mason bee (*Osmia lignaria*) was found (Gardner and Ascher 2006).

Сгор	Bee	Notes and Sources	
cucurbits	squash bees, Peponapis	non-managed wild species, specialists on cucurbits (Kevan et al. 1988, Willis and	
	pruinosa Say and Xenoglossa		
	strenua Cresson	Kevan 1995, Shuler et al. 2005, Sampson et	
		al. 2007, Julier and Roulston 2009)	
fruit	orchard mason bee, Osmia	populations in orchards augmented with	
trees,	lignaria Say	commercially available larvae or with	
brassicas		provision of nesting sites (Abel et al. 2003,	
		Kemp and Bosch 2005, Kraemer and Favi	
		2005, Gardner and Ascher 2006, Sheffield et	
		al. 2008a)	
blueberry	orchard mason bees, Osmia	being studied and promoted as managed	
	ribifloris Cresson, O. lignaria	species (Rust and Osgood 1993, Sampson et	
	Say, O. chalybea Smith, O. virga	al. 2004b, Sampson et al. 2009)	
southern blueberry bee, (Cane and Pa		(Cane and Payne 1991, Cane 1994, 1996b)	
	Habropoda laboriosa Fab.		
	bumble bees, Bombus impatiens	(Cane and Payne 1991, Sampson and Spiers	
	Cresson and other species	2000, Stubbs and Drummond 2001, Javorek	
		et al. 2002, Velthuis and van Doorn 2006)	
	eastern carpenter bee, Xylocopa	(Cane and Payne 1991, Dedej and Delaplane	
	virginica L.	2004, Sampson et al. 2004a)	
	mining or andrenid bees,	(Tuell et al. 2009)	
	Andrena spp.		
	alfalfa leafcutting bee,	(Stubbs and Drummond 1996b, Pitts-Singer	
	Megachile rotundata F.	and Cane 2011)	
deerberry	melittid bee, Melitta americana	sonicates to collect and distribute pollen from	
	Smith	deerberry (Cane et al. 1985)	
cranberry	bumble bees, Bombus affinis	(Mohr and Kevan 1987, Patten et al. 1993,	
	Cresson and other species	Mackenzie and Averill 1995, Loose et al.	
		2005, Evans and Spivak 2006)	
	leafcutting bee, Megachile	(Cane et al. 1996, Loose et al. 2005)	
	addenda Cresson		

Table 2.1 A few non-*Apis* bees important for crop pollination that have been studied in the eastern United States and Canada.

2.4.1 Managed non-Apis bees important for crop pollination

Cane (1996a) and Richards (1993) described the most important non-*Apis* bees managed for crop pollination in North America. Management of those species involves rearing colonies, as in the case of bumble bees; providing nesting material that may be collected once nesting is complete, stored to protect from predators and parasites, and shipped to growers in the larval or

pupal stage within the nesting material; or creation of suitable ground nesting sites (Jahns and Jolliff 1991, Gathmann and Tscharntke 1997, Havenith 2000, Cane 2006, Cane et al. 2007). Managed bees include bumble bees, *Bombus terrestris* L., *Bombus impatiens* Cresson, and *Bombus occidentalis* Greene; the alkali bee, *Nomia melanderi* Cockerell (family Halictidae); the alfalfa leafcutting bee, *Megachile rotundata* Fabricius (family Megachilidae); and various mason bees, *Osmia* spp. (Table 2.1).

Managed bumble bees are used for cranberry and greenhouse tomato pollination, plants that require sonication for pollen release, a service honey bees do not perform (Cane et al. 1993, Westendorp and McCutcheon 2001, Winter et al. 2006). Sonication in bees is vibration of the flight muscles that causes pollen to be released from poricidal anthers, also known as buzz pollination (King and Buchmann 2003). Honey bees can vibrate their muscles, but the frequencies produced are not adequate for pollen release. King and Buchmann found that the structure of a bee's exoskeleton affects the natural frequencies produced, including harmonic vibrations, and determines the sonication ability found in many non-*Apis* bees. In Virginia, bumble bees and sweat bees are often seen and heard buzz pollinating plants in the Solanaceae, nightshade family (tomatoes, peppers, eggplants, potatoes, and many wild nightshade species) and Ericaceae, heath family (blueberries, cranberries, and many other edible and non-edible heath species).

The alkali bee (native to the northwestern U.S.) and alfalfa leafcutting bee (native to Europe) are both used for pollinating alfalfa for seed production in the northwest U.S. and in Canada (Delaplane and Mayer 2000a, Cane 2002, Pitts-Singer and James 2005, Cane 2008, Pitts-Singer and Bosch 2010). Since establishment of techniques for creating suitable ground-nesting sites for the alkali bee and introduction of the alfalfa leafcutting bee in Canada, alfalfa seed yields there increased from about 50 kg/ha, when honey bees were the primary pollinators, to 350 kg/ha (Richards 1993). The alkali bee is also used for onion seed production (Delaplane and Mayer 2000b).

Mason bees, *Osmia* spp., are recognized as excellent pollinators, important in North America and many other parts of the world primarily for pollination of apples, pears, almonds, cherries, caneberries, blueberries, and other tree fruits, but also for rape pollination (Torchio 1988, Gathmann et al. 1994, Bosch and Kemp 1999, Delaplane and Mayer 2000e, Havenith 2000, Sekita 2000, Kemp and Bosch 2002, Abel et al. 2003, Li et al. 2004, Monzon et al. 2004,

Cane 2005a, b, Bosch et al. 2006, Gardner and Ascher 2006, Krunic and Stanisavljevic 2006a, Sheffield et al. 2008a, Steffan-Dewenter and Schiele 2008, Matsumoto et al. 2009, Sampson et al. 2009). Bosch and Kemp (2002) provide a review of *Osmia* research, evaluating them as crop pollinators.

2.4.2 Non-managed bees important for pollination

Wild bees are often listed among the pollinators for various crops in McGregor's *Insect Pollination of Cultivated Crop Plants* (McGregor 1976). The importance of native bees in pollinating crops such as blueberries, cranberries, and squash is well documented (Tepedino 1981, Rozen and Ayala 1987, Cane and Payne 1991, Stubbs and Drummond 1997, Canto-Aguilar and Parra-Tabla 2000, Stubbs and Drummond 2001, Sampson et al. 2004b, Brevis et al. 2005, Loose et al. 2005, Pinkus-Rendon et al. 2005, Shuler et al. 2005, Evans and Spivak 2006, Velthuis and van Doorn 2006).

As described earlier, non-managed native bees were found to provide the majority of crop pollination in peppers, tomatoes and watermelon in New Jersey and Pennsylvania (Winfree et al. 2008) and native bees were the most common pollinators in New York apple orchards (Gardner and Ascher 2006). Plants in the nightshade family, such as tomato, potato, pepper, and eggplant, need sonication for pollen release. Many ericaceous species (blueberries, cranberries, deerberries, and huckleberries) also depend on sonication for pollen release. Though honey bees drum anthers to successfully release pollen of some flowers, they do not sonicate (Cane et al. 1993, King and Buchmann 2003). Where wind is not adequate for pollination, many of these crops and their wild relatives depend on bumble bees and solitary bees for sonication (Cane et al. 1985, Buchmann and Cane 1989). Crops like apple that flower in early spring, benefit from native bees that are more active in adverse weather conditions than honey bees (Vicens and Bosch 2000b, Gardner 2006). The life cycles of specialist bees like the squash bees and southern blueberry bee correspond with the flowering of their wild and cultivated hosts (cucurbits and blueberries) (Tepedino 1981, Cane and Payne 1988, Willis and Kevan 1995, Sampson and Cane 2000).

Recent research has revealed an indirect but significant role for native bees in the pollination of sunflowers in California that may be relevant for crops requiring cross-pollination for optimum fruit or seed set. Greenleaf and Kremen (2006b) showed that honey bee interactions

with native bees led to significantly higher pollination success in hybrid sunflower seed production, an economically important crop in California that is grown using male fertile and male sterile (sometimes referred to as female) cultivars. Pollen is only produced by the male fertile cultivar, and pollen must be carried to the "female" cultivars for hybrid seed to be produced. A given honey bee may forage on either nectar or pollen, or both (Fell 1986, Free 1993, Drezner-Levy et al. 2009). Individual honey bees tend to specialize on pollen or nectar, with pollen foragers not typically moving from male fertile to male sterile (pollenless) flowers, though nectar foragers would go to either. In the Greenleaf and Kremen (2006b) study, a honey bee was more likely to visit male sterile (female) flowers if she interacted with a native bee. Honey bees were observed carrying more pollen in fields with a higher diversity (not simply higher numbers) of native bees. This interaction led to significantly higher yields, valued at nearly a third of the overall crop production. This indirect role may be important in other crops that require cross-pollination for optimum yields, such as apples, blueberries, and caneberries. In France, a complementary relationship between honey bees and other bees occurred in strawberry pollination. Honey bees pollinated apical stigmata of strawberries, while small non-Apis bees pollinated basal stigmata (Chagnon et al. 1993).

2.5 Bee diversity, land management, and habitat research

In 1997, concern regarding managed and feral honey bee declines in North America led the Society for Conservation Biology to commission a team of scientists and resource managers led by Gary Nabhan to review evidence regarding the potential consequences of pollinator declines on biodiversity and food crop yields (Allen-Wardell et al. 1998b). The team's report presented research and conservation needs regarding wild pollinator populations and connections with managed agricultural and urban environments. Studies of native pollinators, particularly bees, have found that proximity to natural habitat, size of forager (related to foraging distance), and cultivation practices affect their presence in agricultural lands (Brandhorst 1943, Torchio 1988, Richards 1993, Freitas and Paxton 1998, Canto-Aguilar and Parra-Tabla 2000, Kremen et al. 2002, Steffan-Dewenter and Tscharntke 2002, Kremen et al. 2004, Kraemer and Favi 2005, Roulston and Goodell 2011). As pollinator communities worldwide decline, the need to protect and improve harborage to support native pollinators increases. The following section examines some effects of these factors on bee pollinators in crops.

2.5.1 Landscape features affecting bee pollinator populations

Landscapes surrounding agricultural lands naturally affect bee populations found in crops since these areas provide habitat for nesting and forage. The presence of natural areas and organically managed buffer strips adjacent to croplands correlates with increased pollinator diversity and crop success in some landscapes (Klein et al. 2004, Greenleaf and Kremen 2006a, Kim et al. 2006, Holzschuh et al. 2008). Carvell and colleagues (2004, 2007) investigated relationships between bumble bee pollinators and various types of "agri-environment schemes" (primarily buffer strips) adjacent to agricultural land. Carvell's studies found that forage planted adjacent to farms was effective in attracting bumble bees and that species mix affected the types of bumble bee flower visitors. The study addressed concerns about declines in bumble bee populations and did not investigate related impacts on crop visitation. Sheffield investigated the habitat needs of cavity-nesting (primarily megachilid) bees pollinating apple and augmentation of lupine populations to support *Osmia lignaria* outside the apple bloom period (Sheffield et al. 2008a, Sheffield et al. 2008b). Loose and colleagues (2005) investigated conservation and land management needs of native bees in cranberry production, and promoted management to support bee populations associated with adjacent land. They described the benefits to cranberry growers of refocusing management from crops to include landscapes that support important pollinators of cranberry. They also advocated simply protecting forage and nesting sites and avoiding insecticide use in those areas.

A study on the effects of human disturbance on bee communities found greater bee diversity associated with human land use versus natural areas in a forested landscape (Winfree et al. 2007a). In related research, habitat heterogeneity surrounding agricultural land was more important for bee diversity and crop visitation than land cover type or farming methods (organic or conventional) (Winfree et al. 2008). Research on squash bees found that irrigation and soil types were correlated with bees on squash flowers (Julier and Roulston 2009). In a review of resources regulating wild bee populations, Roulston and Goodell (2011) emphasized the importance of floral resources. These findings suggest that managing for pollination services requires site specific information.

The role of diversity, in general, for ensuring ecosystem services and providing ecosystem stability has also been investigated (Kearns et al. 1998, Kremen et al. 2004, Fontaine

et al. 2006a, Fontaine et al. 2006b, Losey and Vaughan 2006). Pumpkin yield was associated with greater bee diversity, but not greater bee abundance in one study (Hoehn et al. 2008). Proportions of natural habitat were found to correlate with bee diversity in European systemsthe greater the extent of habitat, the greater the diversity of bees (Klein et al. 2004). In the 1970s, Moldenke investigated co-evolution of bees and plants in North America and found the greatest diversity of bees in the Chihauhuan and Sonoran deserts, close to 900 species at the time, while biotic regions dominated by forests had between 425 and 450 species, generally, though California forests had 600 species (Moldenke 1979). Motten (1986) studied the effects on wildflower seed set of competition between pollinators in an eastern deciduous forest. Various researchers have investigated the effects of habitat fragmentation and invasive species on bee communities (Steffan-Dewenter and Tscharntke 2002, Tallamy 2004, Tscharntke and Brandl 2004, Townsend and Levey 2005, Lopes and Buzato 2007, Taki et al. 2007, Rundlof et al. 2008, Steffan-Dewenter and Schiele 2008). Tuell and colleagues (2008) studied visitation to native plants planted to provide alternative habitat for bees adjacent to agricultural lands. They found that floral abundance was the most important factor explaining non-Apis bee presence (Tuell et al. 2008).

2.6 Pollination of crops in Virginia

2.6.1 Fruits, cucurbits, forage, and oilseed

Crops in Virginia dependent on bees for pollination are primarily fruits, cucurbits, and some forage and oilseed, while pollination of legumes and nightshade crops is enhanced by bees (MAAREC 2000, McConkey 2009, USDA-NASS 2009). Fruit crops cultivated in Virginia that are bee pollinated include apple, pear, peach, almond, nectarine, apricot, plum, cherry, blueberry, caneberry (raspberry, blackberry, black raspberry, dewberry), strawberry, loganberry, elderberry, gooseberry, persimmon, serviceberry, passion flower (Maypops), and hardy kiwi. Many of these require cross-pollination for optimum fruit and seed set (McGregor 1976, Free 1993, Fell 1995). Planting guidelines that can help ensure cross-pollination are discussed below. The primary vegetable, forage, and oilseed crops pollinated by bees are summer and winter squash (including pumpkin), cucumber, watermelon, cantaloupe, tomato, alfalfa, clover (red and crimson grown for seed) and sunflower, though some varieties, particularly many cucumber varieties, are self-pollinating. A small amount of tomato production in Virginia is greenhouse production, but no

information on the use of bees is included in agricultural statistics (bumble bees are typically used for pollination in greenhouse tomato production). Legumes such as alfalfa and clover require bee pollination for seed set, but are grown for hay or forage to a greater extent than seed in Virginia. Most other cultivated legumes (peas, beans, etc.) and nightshades (tomato, eggplant, and pepper) are self-pollinating, though their pollination may be enhanced by wind, and bees may visit their flowers and also enhance seed set. Brassicas, such as rapeseed, mustard, broccoli, and cabbage, are not grown for seed in Virginia, so bee visitation is not directly relevant to Virginia farmers. Among forage crops, buckwheat requires insect pollination and attracts a tremendous variety of pollinators, including bees, though some farmers grow it as a cover crop, tilling or cutting it prior to seed-set (Taylor and Obendorf 2001, Jacquemart et al. 2007, Carre et al. 2009). Ginseng, an alternative crop in Virginia, is self-fertile, but its seed-set is enhanced by bee and syrphid fly pollination (Mooney and McGraw 2007).

2.6.2 Honey bee colony recommendations for crop pollination

The number of honey bee colonies recommended to ensure adequate pollination varies by crop and sometimes by cultivar (McGregor 1976, Free 1993, Delaplane and Mayer 2000c). In Virginia, the number of honey bee colonies recommended ranges from one colony per two acres (0.8 hectares) for most tree fruits to one colony per three to five acres (1.2 to 2.0 hectares) for pumpkin and squash (Fell 1995, 1999). 'Delicious' apples and plums often require more hives per acre due to self-incompatibility, which can be addressed by careful planting design (discussed below) (Fell and Robinson 1981). Pear nectar normally has very low sugar content, so higher numbers of hives are generally recommended (Free 1993, Delaplane and Mayer 2000c, Monzon et al. 2004). Presumably, the increased competition for nectar and pollen of pear increases flower visitation (Delaplane and Mayer 2000c). Honey bee colonies are not generally recommended for peach and nectarine pollination, primarily because hand thinning, required with heavy set, is costly, but also because there is little competition from other flowers very early in the season (Fell 1995). As dwarf varieties replace standard sized trees, and density of plantings increase, higher numbers of colonies are recommended. Fell (1995, 1999) provided the following rules of thumb for farmers to determine if they have enough honey bees for adequate pollination. For fruit trees, he recommended spending 30 seconds to count the number of bees on one tree on a warm, sunny day in the middle of the day. Minimally, 8 to 12 bees observed during

this period would indicate enough bees are present in the orchard. For pumpkins and squash, he recommended counting bees visiting 25 female flowers at about 8:30 a.m. on a sunny day. If 10 to 15 bees are observed, there are likely adequate numbers of bees for good pollination. Such estimates should be made at varying distances from hives, if hives are present, and an average measurement calculated to estimate bee presence. Generally, hives placed in orchards should be grouped four to eight per site and distributed throughout a farm so that trees are never more than 91 to 137 m (100 to 150 yards) from a set of colonies. Fell also recommended placing hives on hive stands to increase foraging under adverse weather conditions.

2.6.3 Cross-pollination

Fruit set of some crops is greatly enhanced with cross-pollination (McGregor 1976, Free 1993, Delaplane and Mayer 2000c). For example, pollination of 'Red Delicious' apples and many other varieties of apples can be improved by planting crab apples within the target variety. Such plants, which provide pollen to ensure or enhance cross-pollination or, in dioecious plants, a male cultivar counterpoint to a female cultivar, are termed pollenizers. Nurseries provide lists of appropriate pollenizers for all varieties requiring or benefitting from a specific pollenizer or from cross-pollination. There is tremendous diversity in the cross-pollination needs of cultivated crops. Within one species, one cultivar may be self-fertile, while another may need crosspollination with one or more other cultivars/varieties. In some species, some varieties are incompatible with other varieties, whether due to unreceptive stigmas or timing of flowering. Some crops are dioecious, with male flowers on separate plants from female flowers, so care must be taken to ensure adequate numbers of male plants are interspersed with female plants. For some hybrid crops like sunflower and seedless watermelon, male sterile varieties are planted with male fertile pollenizer varieties for desirable traits. Plants with flowers that have both male and female parts are called hermaphrodites, but in some flowers, like apples, female and male flower parts may be active at different times (a mechanism that enhances cross-pollination). Research on the foraging behavior of bees has led to recommendations to intersperse apple pollenizers, rather than plant them in separate rows (which had been recommended for ease of harvest) (Fell and Robinson 1981, Brevis et al. 2005). Besides apples, crops that have varieties requiring or benefitting from cross-pollination include blueberries, cherries, kiwis, persimmons, sunflowers, caneberries, pawpaw, and hemp (McGregor 1976, Free 1993, McConkey 2009).

2.6.4 Measuring pollination effectiveness

Teasing out the role of individual bee species in pollinating a particular crop requires consideration of a variety of factors that influence pollination effectiveness. Besides monitoring flower visitation time and frequency, other measures of effectiveness are the amount of pollen deposited on flowers, the number of pollen grains that germinate, and the number of grains needed for well-formed fruit and adequate seed set in relation to visiting rates and pollen loads (Dafni 1992, Kearns and Inouye 1993). Detailed analyses of pollen loads, pollen deposition, germination rates, body size, and behavior have been incorporated into models to estimate pollination rates and effectiveness (Winfree et al. 2007b).

The successful pollination of many plants requires multiple visits. If not adequately pollinated, the developing ovary (or ovaries) may abort or grow into malformed fruit. For watermelon, for example, Winfree and colleagues (2007b) estimate 1400 pollen grains are needed for optimal fruit set. This estimate is based on research by Stanghellini and colleagues (Stanghellini et al. 1997, 1998) on average number of pollen grains deposited by bumble bees and honey bees making about 12 and 18 visits, respectively, for successful pollination of watermelon. Winfree and colleagues (2007b) counted pollen grains deposited by other bee visitors to watermelon to estimate numbers of visits required by various species for successful pollination. Generally, the larger the bee, the greater the number of pollen grains deposited per flower visit. However, behavior while visiting a flower and other flowers in a given landscape also affects pollination effectiveness. Combined with research on pollen loads, body size, and behavior, flower visitor counts can provide a cost-effective proxy for pollination activity.

2.6.4.1 Flower constancy

Flower constancy refers to the behavior of bees, or other creatures, focusing their attention on one type of flower for a period of time, despite the availability of other forage (Waser 1986, Waser and Ollerton 2006). Much research has investigated this behavior in order to understand how bees learn, what attracts them to certain flowers (scent, for example), the evolution of plants and insects, and how these issues relate to pollination effectiveness (Waser 1998, Raguso 2004, Waser and Ollerton 2006, Wolfe and Sowell 2006). Efficiency (energy conserved) associated with predictable floral rewards is one reason bees might specialize

(visiting an unknown flower entails greater risk of not finding adequate reward in terms of nectar or pollen) (Heinrich 1975, 1979, Dafni 1992, Goulson et al. 2007). Flower constancy is generally beneficial for plant pollination, since the more constant a bee to a given flower type, the more likely it will transfer the appropriate pollen for fertilization. Honey bees are renowned for their floral constancy, not only because one particular bee will tend to visit one type of flower until resources are depleted, but because she or her sisters may recruit sisters to forage at the same type of flower when rewards are high (Cakmak et al. 2000, Caron 2000). However, when alternative forage competes for the attention of honey bees, this recruitment behavior can draw honey bees away from crop flowers. It is generally assumed that buffer zones with a variety of floral resources around agricultural fields benefit bees by providing alternative forage when a crop is not flowering (Kleijn et al. 2006). However, research on apple pollination indicated that honey bees foraging on dandelion in apple orchards tended not to visit apple flowers, and vice versa, and farmers have been encouraged to remove dandelions and other competition by mowing or using selective herbicides (Free 1993). Also, bees and beneficial insects within crop rows may be inadvertently hurt by insecticides sprayed on crops.

While for many bees flower constancy may change as resources change (a given bee will shift its visits to a different type of flower when resources decline), some bees are specialists, or oligoleges, exhibiting a preference for pollen from one plant species, genus, or family, though they may gather nectar from various species (Minckley 2008). The two species of squash bees in Virginia, *Peponapis pruinosa* and *Xenoglossa strenua*, generally only collect pollen from flowers in the Cucurbitaceae (squash family). Understanding the foraging habits of bees, whether they are generalist or oligolectic species, provides insight into habitat needs and may help improve land management to support bee diversity.

2.6.4.2 Pollination efficiency and effectiveness

Pollination efficiency can refer to the energy used by bees as they forage (energy spent versus energy gained—the bee perspective) or to the speed and time a bee takes pollinating flowers (the plant or farmer perspective). Honey bees are considered effective pollinators because of their easily transportable high numbers and constancy when introduced to a crop at an appropriate time. Also, on an annual basis, honey bees in introduced hives may be more reliable than unmanaged bees—relatively easily replaced, so less affected (in practical farming terms) by

climate and other environmental conditions outside our control. However, on a per bee basis, they can be both less efficient and less effective than other bee species, depending on the crop. Floral preference (relating to floral structure or nutrition), foraging habits (timing of visits in relation to fertilization/receptivity, nectar or pollen collecting, accessing nectar in relation to picking up and depositing pollen), physical attributes (tongue length, size, pollen carrying structures/packing, speed or frequency of visits, sonication ability), and other factors can influence effectiveness (Dafni 1992, Free 1993, Buchmann and Nabhan 1996, Delaplane and Mayer 2000c, Adler and Irwin 2006).

2.6.5 Apple, blueberry, caneberry, and cucurbit cultivation in Virginia

Most of the information in the following sections is drawn from Delaplane and Mayer's Crop Pollination by Bees, John Free's Insect Pollination of Crops, McGregor's Insect Pollination of Crop Plants and Virginia Tech's Virginia Fruit Page (McGregor 1976, Free 1993, Delaplane and Mayer 2000c, Pfeiffer 2010). For apples, much is drawn from Marini's Virginia Cooperative Extension publication Growing Apples in Virginia (Marini 2009). For blueberries, much of the information comes from a Virginia Cooperative Extension publication by Bratsch and Pattison (2009), Specialty Crop Profile: Blueberries, as well as Pritts and Hancock's (1992) Highbush Blueberry Production Guide. For both blueberries and caneberries, an additional resource is The Mid-Atlantic Berry Guide 2010-2011 coordinated by Demchak (2010) at Pennsylvania State University in cooperation with fruit specialists from Rutgers University, the University of Delaware, the University of Maryland, Virginia Tech, and West Virginia University. For cucurbits, additional information was drawn from crop profiles developed at Virginia Tech (Schooley et al. 2005a, Schooley et al. 2005b, c, d). Citations included in this section reflect only resources other than these. Of the primary research crops for this study, annual production values from the Agricultural Statistics Board for crops in Virginia were only available for apples (\$37.7 million in 2008), cucumbers (\$4.3 million in 2005), and watermelon (\$3.6 million in 2005) (USDA-NASS 2006, ERS 2009, USDA-NASS 2009).

Of respondents to a 2006 survey of berry (small fruit) producers throughout Virginia, 52% produce strawberries (not considered in this study), 48% percent produce blueberries, 41% produce blackberries, 26% produce summer-bearing raspberries, 25% produce fall-bearing (primocane) raspberries, and 8% produce other berry crops such as elderberry and gooseberry (Monson 2008). Monson (2008) noted that tobacco buyout payments to farmers primarily in the south and southwestern parts of the state due to the 2004 Fair and Equitable Tobacco Reform Act provide a source of financing for farmers converting from tobacco to other crops. He noted that as land prices rise and acreage devoted to farming is reduced, high-value crops like small fruits may provide a viable alternative to tobacco or lower value crops. The development of the wine industry in Virginia has also led to increased use of berry crops for dessert and blended types of wines (Virginia_Wine 2010).

Although these crops flower and produce at different times, they all come in a range of varieties from early to late season, or can be planted in succession. Plants that require cross-pollination should be paired with varieties with overlapping flowering times. By cultivating early to late varieties, or planting vegetable crops in succession, farmers extend their growing seasons, and also gain some assurance that their whole crop will not be affected by adverse weather conditions or pests.

2.6.5.1 Apple

Apple, *Malus domestica*, is the most important tree fruit in Virginia economically; 105 million kilograms were produced in 2008, with a utilized production value of \$37.7 million (USDA-NASS 2009). Utilized production is produce that is marketed (versus harvested). The Virginia State Apple Board estimates that the apple industry contributes \$235 million annually to Virginia's economy (VAGA 2010). Of about 3000 apple cultivars available worldwide, the most popular cultivars in Virginia are Fuji, Golden Delicious, Red Delicious, Winesap, Gala, Granny Smith, Rome, York, Ginger Gold, Jonathan, and Stayman. Other varieties recommended by the Virginia Cooperative Extension are Lodi, Earlycrisp, Redfree, Jonagold, Empire, and Arkansas Black (Marini 2009). Cultivation of heirloom varieties is increasing, both for eating and for cider production. Foggy Ridge Cider, one of the study sites for this project, grows 36 different heirloom varieties for producing high-end hard cider: Ashmead's Kernel, Black Limbertwig, Burford Red Flesh, Cannon Pearmain, Cox's Orange Pippin, Dabinett, Dymock Red, Father Abraham, Golden Harvey, Graniwinkle, Grimes Golden, Harrison, Kingston Black, Kinnard's Choice, Muscadet de Berney, Nehou, Newtown Pippin, Norfolk Beefing, Northern Spy, Parmar, Pitmaston Pineapple, Pomme de Gris, Ralls Janet, Rhode Island Greening, Ribston Pippin, Roxburry Russett, Smith's Cider, Stoke Red, Tremlett's Bitter (Geneva), Virginia Beauty, Virginia Hewe's Crab, White Winter Pearmain, and Winter Banana (Flynt and Flynt 2010).

Apples produce the best fruit when nighttime temperatures are cool at harvest time (at or below 15°C), at elevations above 250 m in Virginia. Most apple production in Virginia is in the foothills and mountains of the western and southwestern parts of the state, particularly the Shenandoah Valley, where diseases associated with high humidity and warm temperatures are less pervasive than in more lowland areas.

Nearly all varieties of apple require cross-pollination. Pollenizers, commonly crab apples, should be planted within 30 m of the target crop. When triploid varieties are grown, two diploid varieties with overlapping bloom times must also be planted to ensure that all three varieties fruit. Flowers of crab apples bloom on one-year old wood, so trees should be pruned immediately after flowering. Studies of honey bee behavior have found that bees tend to work up and down rows rather than across them, therefore planting recommendations encourage interspersing pollenizers rather than separate rows (which had been promoted previously for ease of harvest). Variety, planting, and care information is available from state Cooperative Extension programs, as well as from fruit tree nurseries. Varieties are grafted onto rootstock selected for various traits—primarily size (standard, semi-dwarf, and dwarf), disease resistance, and fruitfulness.

Apples bloom in Virginia from mid-April to early May, depending on the variety and weather conditions. Free (1993) stated that the optimum temperature for fertilization and pollen tube growth is between 18 and 27°C. Flower clusters include an average of six flowers, with the central "king" bud opening first. Flowers remain open for several days, with the most effective pollination occurring within three days of bloom. At least six of ten ovaries must develop for well-formed fruit. Bees collect nectar and pollen from the flowers. Free highlighted research by Brittain (1933) and Menke (1952) that indicated solitary bees are particularly valuable pollinators because they are mainly pollen foragers and, among andrenids, they have the habit of inserting their heads into the middle of the cluster of stamens and wrapping their abdomens around anthers (Figure 2.1).



Figure 2.1. Honey bee (left) and andrenid bees (center and right) foraging on apple flowers.

2.6.5.2 Blueberry

Much research in the last two decades has highlighted beneficial properties of blueberries, as well as caneberries, particularly anti-oxidant activity and inhibition of carcinogenesis. Increased awareness of these health benefits has led to increased consumption of berries (Seeram and Heber 2007, Zafra-Stone et al. 2007, Huntley 2009, USHBC 2010). Blueberries in Virginia are generally sold as pick-your-own (U-Pick) and there are about 24 hectares in production, with most farms about one half to one hectare (Monson 2008, O'Dell 2010). Highbush blueberry, *Vaccinium corymbosum*, is the most widely planted species in Virginia. Only one farm in my study cultivates primarily rabbiteye blueberry, *V. ashei*, and none grow the other commercial variety, lowbush blueberry, *V. angustifolium*. Of 42 varieties described in the *Mid-Atlantic Berry Guide*, about fourteen highbush and three rabbiteye varieties grow on farms I visited. Bratsch and Pattison (2009) listed twenty-five recommended cultivars for Virginia, but only seventeen for the mountain region. Highbush varieties grown at farms I visited include Berkley, Bluecrop, Bluehaven, Bluejay, Blueray, Duke, Jersey, Nelson, Northland, Patriot, Sara, Spartan, Spectra, and Toro. Rabbiteye varieties include Climax, Premier, and Tifblue.

Blueberries flower at roughly the same time as apples in Virginia, from mid-April to mid-May, though the length of time for each bush is generally longer than for each apple tree. Blueberry inflorescences are indeterminant, continuing to produce new buds and flowers on shoots extending above the first flowers. Although most highbush varieties and three varieties of rabbiteye are self-fertile, cross-pollination increases both fruit size and yields, and leads to earlier fruiting. Care must be taken to plant not only two or more cultivars, but also those that flower and mature at the same time, to ensure cross-pollination and ease (cost-effectiveness) of harvest.

2.6.5.3 Caneberries

Caneberries, *Rubus* spp., are also known as brambles and include raspberries, blackberries, and black raspberries. They are becoming more widely cultivated in Virginia, in part due to the development of primocane varieties, in part due to increased awareness of their health benefits, and in part due to their high value (Seeram and Heber 2007, Zafra-Stone et al. 2007, Monson 2008, Shukitt-Hale et al. 2009). Primocane, or fall-bearing, varieties produce fruit on the first year's growth and begin bearing in late July, continuing to flower and produce fruit until frost. Summer-bearing, or floricane, varieties, bear fruit on second year's growth that ripens within a three to four week period in June and July. Summer-bearing varieties produce heavier crops in a shorter period of time. For farmers picking and selling at markets, this more intensive production involves relatively lower picking costs. With the development of primocane varieties, management is less costly, but picking is less efficient. Primocane varieties can be mowed down at the end of the season, while floricanes must be hand-pruned. Many native bees nest over winter in the canes, so it may be beneficial for farmers growing primarily primocane varieties to maintain some wild types or floricane species, or simply keep cut canes on site until overwintering bees have a chance to emerge.

Caneberries in Virginia start flowering in May and continue flowering through frost, though a species or variety may have a flush of flowers for two to three weeks, while others, particularly the primocane varieties, may flower continuously until frost. Most commercial varieties are self-fertile, but cross-pollination improves fruit weight and shape. The optimum pollination period for raspberries is the first day of bloom and for blackberries is the first two days of bloom. Bees, and many other insects, as well as hummingbirds, visit the flowers, which produce both nectar and pollen. Like blueberry, the inflorescences are indeterminate, producing new flowers above older flowers and formed fruit.

2.6.5.4 Cucurbits

Cucurbits in this study include squash (summer and winter varieties), *Cucurbita* spp. (*C. pepo, C. maxima, C. mixta*, and *C. moschata*); cucumber, *Cucumis sativus*; melon (cantaloupe,

muskmelon), *C. melo*; and watermelon, *Citrullus lanatus*. Many cucurbits are monoecious, with separate male (staminate) and female (pistillate) flowers on the same plant, but some are andromonoecious (with male and hermaphrodite flowers on the same plant). Staminate (male) flowers produce both pollen and nectar, while pistillate (female) flowers produce only nectar. Gynoecious varieties of cucumber have been developed with about 70% female flowers (in most monoecious varieties, there are many more male than female flowers). Most cucurbits require insect pollination for cross-pollination or self-fertilization (to carry pollen from male flowers to female flowers within one plant), but some parthenocarpic varieties that do not require pollination have been developed in cucumbers.

Cucurbita species all originated in the New World, where western honey bees, *Apis mellifera*, were not introduced until Europeans began to settle in the region. They have two oligolectic pollinators, *Peponapis pruinosa* and *Xenoglossa strenua*, in Virginia, and related specialists in other parts of North America. The other cucurbits, cucumber, cantaloupe, and watermelon, are Old World crops (Kerje and Grum 2000, Dane and Liu 2007). Cucurbit flowers are open in the mornings, generally, for one day only, so optimum pollination occurs in the morning. Summer squash, cucumbers, melon, and watermelon are often planted in succession, not only for continual production, but as a pest management strategy (particularly to address problems associated with the squash vine borer).

2.7 Native analogs of bee pollinated crops in Virginia

Many of the crops studied here have wild relatives that may support native bee populations. Table 2.2 lists the crops and some of their wild relatives. An asterisk indicates a crop investigated for this project. Many of these crops were wholly or partially cultivated from their wild relatives. The native relatives may have limited distribution and not all of those listed are found in southwestern Virginia. Understanding connections between our cultivated crops and native flora may help improve public appreciation of the relevance of biodiversity to our wellbeing and the evolutionary connections between our crops and native pollinators. Table 2.2 Cultivated crops, edible (culinary or medicinal) wild relatives and related native forage in Virginia (Moerman 2010, NRCS 2010, Weiboldt 2010).

	Wild Mid-Atlantic Relatives	Wild Relatives
Crop, Genus	of the Same Genus	in Other Genera,
		Same Family
t		
apple ^a , <i>Malus</i> ^o	crab apple, <i>Malus</i> spp.	serviceberry,
pear, Pyrus		Amelanchier spp.;
quince, Cydonia ^c		hawthorn, Crataegus
cherry, plum, peach,	Allegheny plum, <i>P. allegheniensis</i> ;	spp.; crab apple,
apricot, almond,	American plum, P. americana; Chickasaw	Malus spp.;
Prunus	plum, <i>P. angustifolia</i> ; hortulan plum, <i>P</i> .	chokeberry, <i>Photinia</i>
	hortulana; beach plum, P. maritima; pin	spp. (formerly Aronia)
	cherry, <i>P. pensylvanica</i> ; black cherry, <i>P.</i>	
	serotina; choke cherry, P.virginiana	
raspberry ^a ,	garden dewberry, R. aboriginum; Allegheny	
blackberry ^a , black	blackberry, R. allegheniensis; oldfield	
raspberry, Rubus	blackberry, R. alumnus; sawtooth blackberry,	
	<i>R. argutus</i> ; Bailey's dewberry, <i>R</i> .	
	baileyanus; Kittatiny blackberry, R.	
	<i>bellobatus</i> ; smooth blackberry, <i>R</i> .	
	canadensis; sand blackberry, R. cuneiformis;	
	DC dewberry, R. fecundus; woodland	
	dewberry, <i>R</i> . <i>felix</i> ; northern dewberry, <i>R</i> .	
	flagellaris; yankee blackberry, R. frondosus;	
	bristly dewberry, R. hispidus; American red	
	raspberry, R. idaeus; Watauga River	
	blackberry, R. immanis; upland dewberry, R.	
	invisus; plains blackberry, R. laudatus;	
	bottomland dewberry, R. leviculus; Long's	
	blackberry, R. longii; Michigan dewberry, R.	
	michiganensis; Missouri dewberry, R.	
	missouricus; kinnickinnick dewberry, R.	
	multifer; black raspberry, R. occidentalis;	
	purpleflowering raspberry, R. odoratus;	
	highbush blackberry, R. ostryifolius;	
	Chesapeake blackberry, R. pascuus;	
	Pennsylvania blackberry, R. pensilvanicus;	
	upland blackberry, R. pergratus; Smithfield	
	blackberry, R. pernagaeus; Philadelphia	
	blackberry, R. philadelphicus; tangled	
	dewberry, R. plexus; plaitleaf dewberry, R.	
	plicatifolius; tree blackberry, R. probabilis;	
	Plymouth blackberry, R. randolphiorum;	
	recurved blackberry, R. recurvans; Lucretia	
Wild Mid Atlantic Polativos		Wild Relatives
-----------------------------	---------------------------------------------------------------	------------------------------
Crop, Genus	of the Same Genus	in Other Genera,
	of the Same Ochus	Same Family
	dewberry, R. roribaccus; James River	
	blackberry, <i>R. rosarius</i> ; Steele's dewberry,	
	<i>R. steelei</i> ; branched blackberry, <i>R. suus</i> ;	
	southern dewberry, <i>R. trivialis</i> ;	
6	ROSSULARIACEAE (GOOSEBERRY FAMI	LY)
gooseberry &	American black currant, <i>R. americanum</i> ;	
currant, Ribes	eastern prickly gooseberry, R. cynosbati;	
	skunk currant, R. glandulosum; hairystem	
	gooseberry, <i>R. hirtellum</i> ; prickly currant, <i>R</i> .	
	lacustre; Missouri gooseberry, R.	
	missouriense; red currant, R. triste;	
	EBENACEAE (EBONY FAMILY)	
persimmon,	persimmon, Diospyros virginiana	
Diospyros		
	ERICACEAE (HEATH FAMILY)	
blueberry ^a ,	lowbush blueberry, V. angustifolium;	kinnickinnick,
cranberry,	farkleberry, V. arboreum; New Jersey	Arctostaphylos uva-
Vaccinium	blueberry, V. caesariense; highbush	ursi; leatherleaf,
	blueberry, V. corymbosum; creeping	Chamaedaphne
	blueberry, V. crassifolium; Elliot's blueberry,	<i>calyculata</i> ; trailing
	V. elliottii; southern mountain cranberry, V.	arbutus, <i>Epigaea</i>
	<i>ervthrocarpum</i> : southern blueberry, V.	<i>repens</i> : eastern
	formosum: black highbush blueberry, V.	teaberry. Gaultheria
	fuscatum cranberry V macrocarpon	procumbens.
	velvetleaf huckleberry V myrtilloides small	procumo eno,
	cranberry V oxycoccus: Blue Ridge	
	blueberry V pallidum: upland highbush	
	blueberry V simulatum: deerberry V	
	stamineum: small blueberry V tenellum	
huckleberry	black G baccata: box G brachveera:	
Gaylussacia	dwarf G dumosa: blue G frondosa	
Gayiassacia	$\Delta MONACEAE (CUSTADD ADD E EAMILY)$	
powpow Asimina	anonaceae (COSTARD-AFFEE FAMIL I)
pawpaw, Asiminu	sinannower pawpaw, A. purvijioru	
1111000	 CADDIEOLIACEAE (HONEVSUCKI E EAMIL	V)
aldarbarry	red alderberry S. reasonage	viburnum Viburnum
Samhuang	red elderberry, S. racemosa	viburnum, viburnum
Sambucus		spp.
canadensis		``
	Missouri courd C fastidiarius) wild one with a s
summer/winter	Niissouri goura, C. <i>Joetidissima</i>	wild cucumber,
squash, Cucurbita		Echinocystis lobata;
watermelon,		Guadeloupe
Citrullus		cucumber, Melothria

Crop Copys	Crop, Genus Wild Mid-Atlantic Relatives of the Same Genus				
Crop, Genus					
cantaloupe		<i>pendula</i> · bur			
cucumber <i>Cucumis</i>		cucumber Sicvos			
cucumber, cucumus		angulatus			
	ASTERACEAE (ASTER FAMILY)	angulalus			
sunflower,	Jerusalem sunchoke, <i>H. tuberosus</i>	coneflower, Echinacea			
Helianthus annuus		spp.			
	FABACEAE (LEGUME FAMILY)				
clover, Trifolium	T. reflexum; T. virginicum	jointvetch,			
spp.		Aeschynomene			
alfalfa, medick, &		virginica; hogpeanut,			
bur-clover,		Amphicarpaea			
Medicago		bracteata; groundnut,			
crown vetch,		Apios americana;			
Coronilla		milkvetch, Astragalus			
sweetclover,		spp.; wild indigo,			
Melilotus		Baptisia spp.; butterfly			
lespedeza,	L. angustifolia; L. capitata; L. frutescens; L.	pea, Centrosema			
Lespedeza	hirta; L. procumbens; L. repens; L. stuevei;	virginianum; redbud,			
1	L. violacea; L. virginica	Cercis canadensis;			
vetch, Vicia	American, V. Americana; Carolina, V.	sensitive pea,			
,	caroliana	Chamaecrista spp.;			
pea, Lathyrus	marsh pea, L. palustris; tiny pea, L. pusillus;	butterfly pea, Clitoria			
F,	veiny pea. L. venosus	mariana; tick-trefoil,			
		Desmodium spp.; wild			
birdsfoot trefoil	American birdsfoot trefoil <i>L</i> unifoliolatus	lupine, Lupinus			
Lotus		perennis; Senna spp.;			
20000		goat's rue, Tephrosia			
		spp.; bush pea,			
		Thermopsis mollis;			
		American wisteria,			
		Wisteria frutescens			
POLYGONACEAE (BUCKWHEAT FAMILY)					
buckwheat,		buckwheat,			
Fagopyrum		Eriogonum allenii;			
		smartweed, bindweed,			
		knotweed, Polygonum			
		spp.; dock, <i>Rumex</i> spp.			
^a crops included in thi	s study				
^b some <i>Malus</i> spp. we	ere formerly classified as Pyrus spp.				
^c Cydonia has been cl	assified as <i>Pyrus</i> in the past				

CHAPTER 3 Bee pollinators of entomophilous crops in southwest Virginia

3.1 Introduction

Better understanding of non-*Apis* bees important for crop pollination is needed in the face of potential pollinator declines around the globe (Potts et al. 2010), increasing acreage of pollinator dependent crops (Aizen et al. 2008a), and the lack of baseline data regarding crop pollinators other than honey bees and a few other managed species (NRC 2007). In Virginia, little is known about the relative importance of non-*Apis* bees pollinating entomophilous crops, other than squash bees (*Peponapis pruinosa* (Say) and *Xenoglossa strenua* (Cresson)) and bumble bees (*Bombus* spp.) for cucurbits (Shuler et al. 2005, Julier and Roulston 2009), though the region is home to nearly 500 species of bees. The western honey bee, *Apis mellifera* L., is generally assumed to be the primary pollinator of entomophilous crops in Virginia, adding an estimated \$23 million in 2002 to the value of apple production alone in Virginia, according to the Virginia Department of Agriculture and Consumer Services (VDACS 2010). However, this valuable pollination service may be substantially provided by non-*Apis* bees (Losey and Vaughan 2006).

Research in eastern North America has highlighted the abundance or pollination efficiency of native and introduced non-*Apis* bees in a variety of entomophilous crops, including apple (Brittain 1933, Kuhn and Ambrose 1984, Thomson and Goodell 2001, Gardner 2006, Gardner and Ascher 2006, Sheffield et al. 2008a); blueberry, cranberry, and deerberry (Cane et al. 1985, Cane and Payne 1991, Batra 1994, Cane 1994, Mackenzie and Averill 1995, Cane 1996b, Drummond and Stubbs 1996, Stubbs and Drummond 1996a, 1997, Stubbs et al. 1997, Stubbs and Drummond 2001, Javorek et al. 2002, Brevis et al. 2005, Loose et al. 2005, Evans and Spivak 2006, Tuell et al. 2009); cucumber, squash, and watermelon (Stanghellini et al. 1997, 1998, Winfree et al. 2007b, Winfree et al. 2008); and tomato (Morandin et al. 2001a, Morandin et al. 2001b, Velthuis and van Doorn 2006, Winfree et al. 2008). Findings in northern Virginia, Maryland, New Jersey, Pennsylvania, and New York indicate that non-*Apis* bees may provide the majority of crop pollination for some crops and pollination "insurance" during periods of honey bee decline (Winfree et al. 2007b, Winfree et al. 2008). No baseline data regarding non-*Apis* bee crop pollinators or their relative importance in crop production are available for southwest Virginia. Research in Virginia has focused on honey bees, bumble bees, the orchard mason bee, *Osmia lignaria* Say, and the two species of squash bees mentioned above, *Peponapis pruinosa* and *Xenoglossa strenua* (Shimanuki 1977, Reichelderfer and Caron 1979, Cantwell 1980, Fell and Robinson 1981, Rajotte and Fell 1982, Fell 1986, Cane and Payne 1991, Fell 1995, 1999, Kraemer and Favi 2005, Shuler et al. 2005, Burley 2007). Little is known about other species pollinating crops and potentially stabilizing pollination services, irrespective of honey bee status.

One mechanism of pollination "insurance" highlighted by Winfree and Kremen (2009) is biodiversity. Ecosystems with higher species richness are more stable in response to disturbance, where greater redundancy in terms of ecosytem functioning can compensate for the decline in one or more species over time or space (Kremen et al. 2002, Klein et al. 2003). We expected that the diversity of bee crop pollinators would be more similar within crop systems than between crops and over time.

Foraging behavior, body size, hairiness, and other factors influence the effectiveness of various pollinators. *Andrena* (mining), *Bombus* (bumble), *Megachile* (leaf-cutting) and *Osmia* (mason or orchard) species are at least as effective, and often more effective, than honey bees in fruit tree and berry pollination (Torchio 1988, Stubbs and Drummond 1996b, 1997, 2001, Davis et al. 2002, Javorek et al. 2002, Monzon et al. 2004, Krunic and Stanisavljevic 2006b). Squash bees and bumble bees are more effective in some cucurbits than honey bees (Tepedino 1981, Willis and Kevan 1995, Stanghellini et al. 1997, Canto-Aguilar and Parra-Tabla 2000, Sampson et al. 2007, Julier and Roulston 2009). Nevertheless, the large number of honey bees introduced in colonies at appropriate times can compensate for the lower pollination effectiveness of individual honey bees (McGregor 1976, Free 1993, Delaplane and Mayer 2000c, Rader et al. 2009).

To gain better understanding of bee pollination of entomophilous crops in southwest Virginia, we monitored crop flower visits at farms with apple, blueberry, caneberry, and/or cucurbit crops, comparing visitation by non-*Apis* bees to visitation by honey bees. Because honey bee hives were present on some farms, we also tested for effects of hives on honey bee abundance at flowers. Research focused on the following questions:

 What is the contribution of non-*Apis* bees to crop pollination in Virginia relative to honey bees?

- 2) Are non-*Apis* bee crop pollinator populations similar in terms of species composition within the same entomophilous crops in Virginia?
- 3) How do bee crop pollinator populations change through the growing season?

3.2 Methods

3.2.1 Research sites and field visits

Study sites were farms within a 65 km radius of Blacksburg, Virginia (Figure 3.1). All were commercial farms, except Kentland, which is a Virginia Tech research farm. Research sites included five for apple, seven for blueberry (highbush blueberry except for Windrush farm, which grows only rabbiteye blueberry, and Bob Pond, with 5% rabbiteye blueberry), sixteen for various cucurbits (summer squash, winter squash, pumpkin, cucumber, cantaloupe, and watermelon), and five for various caneberries (raspberry, black raspberry, and blackberry).



Figure 3.1 Map of crop pollination research sites (2007 to 2010) in relation to Blacksburg and the state of Virginia.

Research crop area ranged from 0.5 to 40 hectares, with farms ranging in size from 0.5 to 170 hectares (Appendix A). Sites were visited multiple times where bloom time permitted (Appendix B). Apple and blueberry farms were visited once each season (due to limited bloom period) in April and May. Two additional apple and five additional blueberry farms were visited in 2009. Caneberry was primarily monitored in 2009, with one visit to farms with primarily floricane varieties (early season varieties) and two visits to farms with primocane varieties (extended season varieties with continuous bloom to frost) in June to July. Cucurbit farms were visited in June to August. Those with early plantings were generally visited three times in 2008 and the rest were visited twice. All cucurbit sites were visited twice in 2009. All cucurbit farms grew squash, while some also grew cucumber and/or melon (cantaloupe and/or watermelon) (Appendix A).

3.2.2 Sampling procedure

Flowers were observed when honey bees were active, generally when temperatures were above 21° C (70° F), cloud cover was less than 35%, and wind was less than 3 Beaufort (gentle breeze) (Giles 2010). Due to the short sampling window for apple and blueberry, sampling in those crops included a few relatively cool spring overcast days; as long as honey bees were clearly active, sampling was conducted. Based on the flower visitation monitoring method described by Winfree (2008), crop flowers were observed for 45 seconds at meter intervals along a 40 m transect for apples, blueberries, and caneberries in 2008 and 2009, for cucurbits in 2008, and along a 20 m transect for cucurbits in 2009. Transect length for cucurbits was reduced in 2009 to ensure all crops were sampled in the morning. Number of flowers observed within a one m^2 area was estimated and bee visitation counted using the following categories: honey bee, bumble bee, carpenter bee, medium bee, and small bee. Medium bees were at least three-quarters the size of a typical worker honey bee, about 10 mm or larger. Small bees were less than threequarters the size of a honey bee, approximately 9 mm or less. For apple, blueberry, and caneberry, transects were sampled in the morning and afternoon (during the time periods 10 a.m. to noon and 1 to 3 p.m.). For cucurbits, sampling was begun between 8:30 and 9:00 a.m., as long as the temperature had reached 21° C, and completed as quickly as possible (generally by noon or 1 p.m.), depending on the number of crops at a site, since cucurbit flowers generally close by

early afternoon. While bumble bees and squash bees are active much earlier, we began sampling in mid-morning to cover the time period when all bees that use cucurbits would be active simultaneously. Beginning sampling in mid-morning was aimed at including the greatest diversity of bees visiting squash, since honey bees and many of the smaller bees are active by mid-morning, though it may have underestimated the role of bumble bees and squash bees (active much earlier). Where multiple crops were grown, squash was sampled first, followed by other cucurbits and then caneberry. Bees were collected with an insect net for 15 minutes following observation, killed with ethyl acetate fumes in kill jars, and later identified to species or genus. Temperature, relative humidity, cloud cover, and wind speed based on the Beaufort scale were recorded prior to monitoring.

3.2.3 Data analysis

Three primary analyses were carried out, one to test for the effect of hive presence on honey bee density on each crop, one to compare visitation between honey bees and medium to large bees on each crop, and one to examine species diversity among and between crops. In the first two analyses, the dependent variable was the total number of bees observed divided by the total number of flowers observed during a 45 second observation period. The overall statistical model was an analysis of variance (ANOVA), general linear model. For testing the effect of hives on honey bee density, observation year and hive presence (as well as their interaction) were included as fixed categorical variables. Sampling event per site per year (each site was sampled 2-3 times for most crops) was treated as an ordinal variable. Site was included as a random effect.

For comparing visitation rates between bee types (honey bees versus medium to large bees), year and bee type (and their interaction), as well as sampling event within a crop, were included as fixed variables. Site and transect within site were included as random effects. These analyses were carried out using JMP Version 8.0.1 (SAS Institute, Cary, NC) statistical software.

For examining differences in species composition, we calculated Bray-Curtis and Jaccard similarity indices for all pairs of crops using EstimateS software (Colwell 2009). The Bray-Curtis index derives from the relative abundance of each species in each sample, influenced primarily by common species, while the Jaccard index is based on presence/absence. The indices range from zero to one, with values closer to one indicating greater similarity. We

tested two questions: 1) is bee community richness (Jaccard) or diversity (Bray-Curtis) more similar within crops than across crops? and 2) is community richness or diversity more similar within the same crop season? We used mean values for all crop pairings for comparison to account for different numbers of sites per crop. We used Kruskal-Wallis and Wilcoxon tests to compare Bray-Curtis means (non-parametric tests) and Student's t and Tukey-Kramer HSD to compare Jaccard means with JMP statistical software.

3.3 Results

3.3.1 Summary of bees collected

Twenty-two hundred bees were netted from crop flowers from 2008 to 2010. The average number of non-*Apis* species collected per farm from crop flowers ranged from 12 to 19 and total species per crop ranged from 43 to 59 (Table 3.1). Genera with the highest number of species on crops were *Andrena*, *Bombus*, *Lasioglossum*, and *Osmia* (Table 3.2). One hundred six species were collected from crop flowers, including *Apis mellifera*. The most commonly collected species (20 or more specimens), organized by first date collected, are listed in Figure 3.2. Some halictid bees (*Halictus* and *Lasioglossum* species) and *Andrena*, *Nomada*, and *Sphecodes* have not been identified to species, so the species number may be slightly larger. Of those identified, ten species were netted from all four crops: *Apis mellifera*, *Augochlora pura*, *Bombus bimaculatus*, *Bombus griseocollis*, *Bombus impatiens*, *Bombus perplexus*, *Ceratina calcarata*, *Halictus confusus*, *Halictus ligatus*, and *Xylocopa virginica*. About half of the most abundant species were collected from late April through August or September, including eight of the species found on all crops (all but *Bombus perplexus* and *Xylocopa virginica*). Appendix C

Crop	No. of	Average bee species collected	Total spp.
	farms	from flowers per farm (±SD)	from flowers
Apple	5	19±6	53
Blueberry	7	19±5	59
Caneberry	5	12±5	47
Cucurbit	16	14±6	43

Table 3.1 Average number of bee species per farm collected from flowers in a 2008-2010 study of crop pollination in southwest Virginia.



Figure 3.2 First to last date the most commonly collected non-*Apis* species (20 or more specimens) were collected at research sites in southwest Virginia in 2006–2009.

Genus	All Crops	Apple	Blueberry	Caneberry	Cucurbits
Agapostemon	3	1		2	1
Andrena	26	22	14	5	1
Anthidium	1	-	-	-	1
Anthophora	1	-	-	-	1
Augochlora	1	1	1	1	1
Augochlorella	2	-	1	1	2
Augochloropsis	2	-	1	-	2
Bombus	9	5	8	5	6
Calliopsis	1	1	-	-	1
Ceratina	3	3	2	2	3
Colletes	3	2	2	1	1
Halictus	5	2	4	3	5
Hoplitis	1	-	-	1	-
Hylaeus	2	-	-	2	-
Lasioglossum	22	6	12	8	14
Megachile	2	-	-	2	2
Melissodes	1	-	-	-	-
Nomada	7	3	5	1	-
Osmia	8	5	7	2	-
Peponapis	1	-	-	-	1
Sphecodes	1	1	1	-	-
Triepeolus	1	-	-	-	-
Xenoglossa	1	-	-	-	-
Xylocopa	1	1	1	1	1
Total netted	105	53	59	37	43

Table 3.2 Number of non-*Apis* bee species per genus collected from crop flowers at farms in southwest Virginia in 2008-2009.

provides two timelines of all bees collected and identified (not just the most commonly collected), one organized by first date collected and the second alphabetically, and a list of bees associated with farm crops.

3.3.2 Influence of honey bee hives on honey bee visits to crop flowers

Honey bees were present on all farms and on all crop flowers except blueberry flowers at one blueberry farm, while honey bee hives were not uniformly present (Table 3.3 and Appendix D). The presence of honey bee hives had no significant effect on the number of honey bees per flower for cucumber, melon (which included cantaloupe and watermelon), or squash (Figure 3.3). There were too few data points to test for significant differences in apple, blueberry, or caneberry, but honey bee numbers were higher at blueberry sites without hives (Figure 3.3). The effects of hives introduced only at crop time on honey bee presence on crop flowers could not be tested.

Crop	Sites w/	Sites w/o	Sites w/hives introduced
	hives	hives	only at crop time
Apple	4	1	2
Blueberry	2	5	1
Caneberry	2	3	0
Cucurbit	9	4	1

Table 3.3 Presence of honey bee hives at southwest Virginia research sites in 2008-2009.



Figure 3.3 Effects of honey bee hive presence on number of honey bees observed per crop flower at farms in southwest Virginia in 2008 and 2009.

3.3.3 Relative abundance of honey bees and non-*Apis* bees visiting apple, blueberry, caneberry, and cucurbit flowers

Non-*Apis* bees made up between 68% (in caneberries) and 83% (in cucurbits) of bees observed visiting crop flowers in 2008 and 2009 (Figure 3.4). Excluding small bees and carpenter bees, which may not be as effective pollinators as honey bees, bumble bees and non-*Apis* medium bees made up between 43% and 75% of all bees observed on flowers: 62% in apples, 60% in blueberries, 43% in caneberries, and 75% in cucurbits. When only honey,



Figure 3.4 Percentages of honey bees, bumble bees, carpenter bees, medium bees, and small bees observed visiting crop flowers at southwest Virginia farms in 2008 and 2009.

bumble, and medium bees are considered, non-*Apis* bees made up between 54% and 76% of bees observed on flowers: 71% in apples, 76% in blueberries, 54% in caneberries, and 73% in cucurbits (Figure 3.5). Crop flower visits by medium and bumble bees were significantly higher than visits by honey bees in apple, blueberry, caneberry, cucumber, and squash, while no significant difference was found for melon (cantaloupe and watermelon) (Figure 3.6). Overall flower visitation was significantly higher in 2008 for apple, caneberry, melon, and squash, but no difference was found for blueberry and cucumber (Figure 3.7).



Figure 3.5 Percentages of honey bees, bumble bees, and medium bees observed visiting crop flowers at southwest Virginia farms in 2008 and 2009.



Figure 3.6 Comparison of honey bee versus combined bumble and medium (non-*Apis*) bee visits to crop flowers on farms in southwest Virginia in 2008 and 2009.



Figure 3.7 Differences in bee visits to crop flowers between 2008 and 2009 on farms in southwest Virginia.

3.3.3.1 Most common bees on crops through the growing season

Apple and blueberry flowers were monitored in April and May, caneberry in June, and successive plantings of cucurbits from June through August. The relative abundance of bees in crops varied with crop flowering through the season, with the greatest percentage of honey bees in June when caneberry were in full bloom and cucurbits had begun flowering (Figure 3.8).

The most abundant non-*Apis* medium to larger bees visiting apple, blueberry, and caneberry flowers were *Andrena* (andrenid bees), *Bombus*, and *Osmia* (mason or orchard bees) (Figure 3.9 and Table 3.4). Other abundant genera in cucurbits with medium-sized species were *Agaopostemon* and *Melissodes*.

While some genera were especially important for each crop, some species were collected in much greater abundance than others (Table 3.5). A few species stand out for their high numbers. In apple, *Andrena barbara* alone made up 18% of all specimens collected. In blueberry, *Andrena carlini* and *A. vicina* made up 20% of all specimens collected. *Lasioglossum leucozonium*, a bee that would fit in the small bee category, made up 16% of all caneberry specimens. In cucurbits, *Bombus impatiens* made up 10% of all specimens collected (86% of all *Bombus* spp. collected from cucurbits), second only to *Peponapis pruinosa* (the most abundant based on visual counts).



Figure 3.8 Percentage of bee types, by month, observed visiting crop flowers at farms in southwest Virginia in 2008 and 2009.



Andrena

Bombus

Osmia

Peponapis

Figure 3.9 The most common non-*Apis* genera on crop flowers on farms in southwest Virginia in 2008-2009.

Genus ^a	Apple	Blueberry	Caneberry	Cucurbits	
Agapostemon	1	0	5	30	
Andrena	212	156	13	1	
Anthidium	0	0	0	1	
Anthophora	0	0	0	1	
Augochlora	2	9	4	66	
Augochlorella	0	3	1	14	
Augochloropsis	0	1	0	3	
Bombus	19	52	28	308	
Calliopsis	1	0	0	10	
Ceratina	19	12	7	30	
Colletes	4	8	1	1	
Halictus	4	14	9	10	
Hoplitis	0	0	2	0	
Hylaeus	0	0	2	0	
Lasioglossum	9	24	13	200	
Megachile	0	0	3	6	
Melissodes	0	0	0	26	
Nomada	4	9	1	0	
Osmia	23	31	5	0	
Peponapis^b	0	0	0	160	
Sphecodes	1	1	0	0	
Triepeolus	0	0	0	7	
Xenoglossa	0	0	0	3	
Xylocopa	7	20	2	2	
Total netted	306	340	96	879	
^a The most common	<i>ly collected</i> n	nedium and larg	ger genera are sh	own in bold.	
^b <i>Peponapis</i> was undercollected relative to its abundance because it was easily					

Table 3.4 Number of non-*Apis* bees, by genera, collected from crop flowers at farms in southwest Virginia in 2008 and 2009.

Table 3.5 Bee species with ten or more specimens collected from flowers and/or bowl traps associated with crops on farms in southwest Virginia in 2008-2009.

recognized. It was actually the most common bee in cucurbits.

	Farm Type			
Bee species	Apple	Blueberry	Caneberry	Cucurbit
Agapostemon sericeus	1	1	50	10
Agapostemon virescens	12	28	91	238
Andrena barbara	139	4	2	0
Andrena carlini	38	84	0	0
Andrena crataegi	17	14	2	2
Andrena erigeniae	5	13	0	0
Andrena forbesii	7	3	0	0
Andrena illini	13	4	0	0

	Farm Type			
Bee species	Apple	Blueberry	Caneberry	Cucurbi
Andrena miserabilis	10	3	0	0
Andrena nasonii	19	16	12	1
Andrena perplexa	23	8	0	0
Andrena pruni	6	9	0	0
Andrena vicina	34	59	0	1
Andrena violae	16	10	0	0
Augochlora pura	3	10	6	91
Augochlorella aurata	3	38	67	67
Augochlorella persimilis	0	0	1	14
Augochloropsis metallica	0	1	6	6
Bombus bimaculatus	9	26	6	23
Bombus griseocollis	12	6	2	24
Bombus impatiens	46	12	23	416
Bombus perplexus	1	3	5	8
Bombus sandersoni	8	11	0	2
Bombus vagans	0	2	1	12
Calliopsis andreniformis	1	11	95	55
Ceratina calcarata	21	27	41	27
Ceratina dupla	3	4	19	25
Ceratina strenua	2	12	55	20
Colletes inaequalis	5	7	0	0
Halictus confusus	4	6	10	19
Halictus ligatus	2	19	61	97
Halictus parallelus	0	1	3	18
Halictus rubicundus	8	7	15	2
Hoplitis producta	0	4	36	0
Hylaeus modestus/affinis	0	0	12	9
Lasioglossum mitchelli	5	13	24	174
Lasioglossum bruneri	0	2	0	14
Lasioglossum callidum	2	10	20	172
Lasioglossum coriaceum	0	5	12	8
Lasioglossum ellisiae	2	1	15	0
Lasioglossum illinoense	0	0	3	59
Lasioglossum imitatum	5	9	4	132
Lasioglossum leucozonium	2	6	193	116
Lasioglossum oceanicum	0	2	0	59
Lasioglossum pectorale	2	12	18	21
Lasioglossum pilosum	4	10	47	336
Lasioglossum pruinosum	0	0	5	5
Lasioglossum sp.	12	3	16	162
Lasioglossum tegulare	9	17	54	238
Lasioglossum versatum	1	9	54	118
Lasioglossum viridatum	0	0	23	0
Lasioglossum zephyrum	0	0	0	25
0	-	-	-	

	Farm Type			
Bee species	Apple	Blueberry	Caneberry	Cucurbit
Megachile mendica	0	0	6	20
Melissodes bimaculata	0	0	4	135
Melitoma taurea	0	0	8	26
Osmia cornifrons	30	11	5	0
Osmia georgica	4	6	3	2
Osmia lignaria	28	4	1	0
Osmia pumila	9	15	6	1
Osmia taurus	8	10	0	0
Peponapis pruinosa	0	0	4	234
Xylocopa virginica	9	21	2	2

3.3.3.2 Species richness and diversity between and among crops

Within crop Bray-Curtis average community similarity was 0.33 for apple, 0.13 for blueberry, 0.14 for caneberry, and 0.27 for cucurbits (Figure 3.10). For Jaccard, within crop average community similarity was 0.28 for apple, 0.12 for blueberry, 0.21 for caneberry, and 0.23 for cucurbits (Figure 3.11). Similarity in diversity or richness was not significantly greater



Figure 3.10 Similarity of bee community diversity (minimum, maximum, median, and upper and lower quartiles) within and between crops at farms in 2008-2009 southwest Virginia crop pollination study. Crops were apple (app), blueberry (blu), caneberry (can), and cucurbit (cuc).

within crops (such as apple to apple) or among crops within the same season (apple and blueberry were grouped in one season and caneberry and cucurbit in another) (Table 3.6, Table 3.7, and Table 3.8).



Figure 3.11 Similarity of bee community richness (minimum, maximum, median, and upper and lower quartiles) within and between crops at farms in 2008-2009 southwest Virginia crop pollination study. Crops were apple (app), blueberry (blu), caneberry (can), and cucurbit (cuc).

Table 3.6 Wilcoxon/Kruskal-Wallis tests comparing Bray-Curtis similarity indices for crop bee community diversity in a 2008-2009 pollination study in southwest Virginia.

Test	ChiSquare	DF	Prob>ChiSq		
Within vs. across crops ^a	< 0.001	1	0.98		
Within season vs. across season ^b	1.74	2	0.42		
^a Within crop comparisons were apple to apple, blueberry to blueberry, caneberry to					
caneberry, and cucurbit to cucurbit.					
^b Within season crops were apple with blueberry or caneberry with cucurbits.					

Table 3.7 Student t-test comparing Jaccard similarity indices for crop bee community richness within and across crops in a 2008-2009 pollination study in southwest Virginia.

Level		Jaccard index mean			
Within crops ^a	A^{b}	0.18			
Across crops	А	0.15			
^a Within crop comparisons were apple to apple, blueberry to blueberry,					
caneberry to caneberry, and cucurbit to cucurbit.					
^b Levels not connected by the	same letter are sig	gnificantly different (α =0.05).			

Level		Jaccard index mean		
Within apple-blueberry season	A^{a}	0.18		
Within caneberry-cucurbit season	А	0.17		
Between seasons	А	0.14		
^a Levels not connected by the same letter are significantly different (α =0.05).				

Table 3.8 Student t-test comparing Jaccard similarity indices for crop bee species richness between crop seasons in a 2008-2009 pollination study in southwest Virginia.

3.3.1 Bee pollinators in apple

The abundance of bee types and species visiting apple flowers varied greatly among the five apple sites (Figure 3.12). All but King Brothers Orchard had honey bee hives. Non-*Apis* medium bees made up the majority of visitors at all but one farm, where honey bees were the primary flower visitors.



Figure 3.12 Bee types observed on apple flowers at farms in southwest Virginia in 2008 and 2009.

Fifty-three non-*Apis* bee species were collected from apple flowers, along with *Apis mellifera*. Only *Andrena vicina* and *Bombus impatiens* were found at all five study sites; *Andrena carlini*, *Andrena miserabilis*, *Xylocopa virginica*, *Andrena perplexa*, and *Osmia pumila* were found at four of five sites; and *Andrena barbara*, *Andrena crataegi*, *Andrena forbesii*, *Andrena illini*, *Andrena pruni*, *Bombus bimaculatus*, *Osmia cornifrons*, *Osmia lignaria*, and *Ceratina calcarata* were found at three of five sites. Forty-nine percent of species were found at only one or two sites.

3.3.2 Bee pollinators in blueberries

The abundance of bee types and species visiting blueberry flowers also varied greatly among blueberry sites (Figure 3.13). Bob Pond and Sinking Creek had honey bee hives on site, but Crow's Nest and Windrush had hives on neighboring properties within 0.5-1 km of blueberry crops. Fifty-nine non-*Apis* bee species were collected from blueberry flowers, along with *Apis mellifera*. None was collected from all seven sites; *Andrena carlini, Bombus bimaculatus*, and *Xylocopa virginica* were collected from six sites; *Andrena nasonii, Andrena vicina, Augochlora pura, Augochlorella aurata, Bombus griseocollis, Bombus sandersoni, Colletes inaequalis,* and *Osmia taurus* were collected from five sites; and *Bombus impatiens, Halictus ligatus, Lasioglossum mitchelli, Lasioglossum callidum, Lasioglossum coriaceum, Lasioglossum versatum, and Osmia georgica* were collected from four sites. Seventy-one percent of species netted on crop flowers were found at three or fewer of seven sites.



Figure 3.13 Bee types observed on blueberry flowers at farms in southwest Virginia in 2008 and 2009.

3.3.3 Bee pollinators in caneberries

The abundance of bee types and species visiting caneberry flowers also varied greatly among caneberry sites (Figure 3.14). Eggers, Five Penny, and Kentland had honey bee colonies on site, and Crow's Nest had colonies on neighboring property within 0.5 km of caneberry crops. Thirty-seven non-*Apis* bee species were collected from caneberry flowers, along with *Apis mellifera*. Only *Augochlorella aurata* was collected from all five sites; *Agapostemon virescens*, *Bombus impatiens*, *Ceratina strenua*, *Halictus ligatus*, *and Megachile mendica* were collected from four sites; and *Bombus bimaculatus*, *Ceratina calcarata*, *Halictus rubicundus*, *Hoplitis producta*, *Hylaeus modestus/affinis*, *Lasioglossum coriaceum*, *Lasioglossum imitatum*, *and Lasioglossum leucozonium*, were collected from three sites. Fifty-nine percent of species netted on crop flowers were found at two or fewer sites.



Figure 3.14 Bee types observed on caneberry flowers at farms in southwest Virginia in 2008 and 2009.

3.3.4 Bee pollinators in cucurbits

Cucurbit sites varied greatly in terms of size, types of cucurbits grown, and numbers of varieties grown, but squash was a common denominator at all sixteen sites. Nine of these had honey bee hives (Five Penny, Greenstar, Jeter, Kentland, Layman, Martin, Seven Springs, Stonecrop, and Tom's Creek), and honey bees were observed on crop flowers at all sites (Figure 3.15). Forty-seven species were collected from cucurbit flowers, which included summer squash,

cucumber, winter squash (including pumpkin), cantaloupe, and watermelon. Only *Augochlora pura*, *Bombus impatiens*, *Lasioglossum pilosum*, and *Peponapis pruinosa* were collected from all sixteen sites; *Lasioglossum tegulare* was collected from fifteen sites; *Lasioglossum mitchelli* and *Lasioglossum leucozonium* were collected from fourteen sites; *Agapostemon virescens*, *Augochlorella aurata*, *Lasioglossum callidum*, and *Lasioglossum versatum* were collected from thirteen sites; and *Lasioglossum imitatum*, *Halictus ligatus*, *Calliopsis andreniformis*, *Melissodes bimaculata*, *Bombus griseocollis*, *Lasioglossum oceanicum*, and *Lasioglossum illinoense* were found at between twelve and nine sites. Fifty-seven percent of species collected from crop flowers were netted at only fifty percent or less of sites (8 or fewer).



Figure 3.15 Bee types observed on cucurbit flowers at farms in southwest Virginia in 2008 and 2009.

3.4 Discussion

Non-*Apis* bees in Virginia provided more than half the crop pollination service generally assumed to be provided by honey bees. Visitation to crop flowers by non-*Apis* medium and bumble bees was significantly higher than visitation by honey bees in apple, blueberry, caneberry, cucumber, and squash; and equaled honey bee visitation to melon flowers. Other research on bee crop pollinators in eastern North America has also found high abundance of non-*Apis* bees on several of these crops, but this is the first study to investigate bee visitation at crops

throughout the growing season (Cane and Payne 1991, Cane 1996a, Shuler et al. 2005, Gardner and Ascher 2006, Greenleaf and Kremen 2006a, Winfree et al. 2007b, Winfree et al. 2008, Julier and Roulston 2009).

The relative importance of bee groups changed through the growing season, with non-*Apis* bees making up between 60 and 90% of bees observed on flowers in April, May, July, and August, while honey bees made up about 60% in June. The percentage of bumble bees grew tremendously over the growing season, from less than 10% in April to more than 50% in August, not surprising given the growth cycle of their annual colonies.

The presence of honey bee hives had no effect on honey bee presence on flowers in cucumber, melon, or squash, but could not be tested for apple, blueberry, or caneberry. Honey bees are generally most effective as pollinators when introduced to a crop at peak flowering time, due to their floral constancy and recruitment behaviors (McGregor 1976, Free 1993, Caron 2000, Delaplane and Mayer 2000d). When present year-round, they will scout the surrounding landscape for best resources and may ignore crops if better resources are available (Todd and McGregor 1960, Visscher and Seeley 1982, Jay 1986).

Several genera with many medium and larger species were especially important for each crop: *Andrena*, *Bombus*, and *Osmia* in apple and blueberry; *Andrena* and *Bombus* in caneberry; and *Peponapis*, *Bombus*, and *Melissodes* in cucurbits. Halictid bees (*Agapostemon*, *Augochlora*, *Augochlorella*, and *Lasioglossum*) and small carpenter bees (*Ceratina*) were also collected in abundance from crop flowers. Some halictid bees are about the size of honey bees, but most fit into the small bee category. Crop systems appeared to be dominated by a small number of pollinator species: *Andrena barbara* in apple; *Andrena carlini* and *A. vicina* in blueberry; *Lasioglossum leucozonium* in caneberry; and *Peponapis pruinosa* and *Bombus impatiens* in cucurbits.

Basing the importance of bees on their frequency of visitation ignores differences in pollination effectiveness. In particular, research on the effectiveness of *Bombus* and *Osmia* (manageable species) indicates that a few hundred provide the equivalent pollination service of thousands of honey bees; a four-fold greater effectiveness for *Andrena*; and much greater effectiveness for the pollen specialists *Peponapis* and *Xenoglossa* (Tepedino 1981, Kuhn and Ambrose 1984, Richards 1993, Bosch and Blas 1994, Cane 1996a, Stanghellini et al. 1997, 1998, Bosch and Kemp 1999, Canto-Aguilar and Parra-Tabla 2000, Delaplane and Mayer 2000e,

Sampson and Cane 2000, Vicens and Bosch 2000a, Thomson and Goodell 2001, Javorek et al. 2002, Kemp and Bosch 2002, Fuchs and Muller 2004, Ladurner et al. 2004, Cane 2005b, Gardner 2006, Velthuis and van Doorn 2006, Hoehn et al. 2008). Although Javorek and colleagues (2002) measured the effectiveness of Andrena, less research has focused on the pollination effectiveness of ground-nesting bees that cannot easily be managed. Much work has nevertheless recognized the importance of andrenid bees in crop pollination, especially springflowering fruit crops (McGregor 1976, Jones and Little 1983, Free 1993, MacKenzie and Eickwort 1996, Delaplane and Mayer 2000c, Havenith 2000, Davis et al. 2002, Tepedino et al. 2007, Tuell et al. 2009). Batra (1999) conducted a detailed study of Andrena fenningeri, promoting its use as an orchard pollinator and proposing techniques for introducing and helping to maintain populations on site. Regarding the pollination effectiveness of other non-Apis crop pollinators found in this study, Kremen and colleagues (2002) documented pollen deposition on watermelon flowers by native bees, including those grouped as small bees in this study, for modeling effectiveness of a complex of wild bees. More commonly, researchers have documented the diversity and abundance of wild bees in crops and the positive correlations between bee diversity and improved pollination (Chagnon et al. 1993, Greenleaf and Kremen 2006b, Greenleaf and Kremen 2006a, Winfree and Kremen 2009).

Examination of differences in species composition showed tremendous variability not only between crops, but also within the same crop systems. Overall the Bray-Curtis indices of bee community diversity and Jaccard indices of bee community richness were closer to zero than one, an indication of less similarity, with the highest indices within crops for apple and blueberry about 0.3 and lowest for caneberry and cucurbit about 0.1. Comparisons of similarity indices indicated no significant differences within and across crops or seasons. We expected similarity within crops to be much greater.

The diversity of bees within the same crop systems suggests that non-*Apis* bees are also greatly enhancing the stability of pollination services in Virginia. When comparing bee species composition at different sites for the same crop, the percentages of the same species collected from all sites are extremely low: 4% for apple, 0% for blueberry (5% at all but one blueberry site), 3% for caneberry, and 9% for cucurbits. Between 49 and 79% of all species were found at only half or fewer sites within the same crop system. Looking at visitation to all crops, of 106 bee species netted from crop flowers, only 10 (9%), including *Apis mellifera*, were found in all

four cropping systems. Given the seasonal longevity of the study, from April through August, the different composition through the growing season is not surprising. Many non-*Apis* bees are active as adults for short periods of time and species composition changes through the season. The variability within crops, not just seasonally, indicates that a wide range of bee species support pollination of entomophilous crops produced in Virginia and that the loss or decline of any given species would not likely affect pollination overall, e.g. the diversity of non-*Apis* bee crop pollinators stabilizes pollination services through time. These ecosystem services (direct pollination and stabilization of pollination service over time) should be recognized and supported in conservation planning.

3.4.1 Conclusion

Non-*Apis* bees are providing a significant proportion of pollination of entomophilous crops in southwest Virginia, contributing at least 50% in all crops studied. This service was dominated within each crop by a few bee species. At the same time, between 43 and 49 species of non-*Apis* bees visited flowers in each crop system, with very little overlap of species between sites. This tremendous diversity of bees suggests that non-*Apis* bees are also providing stability to pollination services, ensuring pollination if one or more species declines over time or space. It is important to note that while 60% of bees observed on flowers in June were honey bees, during the rest of the growing season, non-*Apis* bees made up between 60–90% of bees on crop flowers. Clearly, non-*Apis* bees are major contributors to crop pollination in Virginia and the mid-Atlantic region and must be considered in management efforts aimed at ensuring adequate crop pollination.

CHAPTER 4 Pollen loads of bee pollinators on apple flowers

4.1 Introduction

In combination with their easily transportable large numbers, a prime reason honey bees are considered especially good crop pollinators is their floral constancy. Once a honey bee colony begins foraging on a given crop, its workers will forage on that same crop until resources are depleted or another more abundant resource leads them to collectively shift (Waser 1986, Dafni 1992). The foraging habits of other bees are more variable, though some species, genera, and families are oligolectic, foraging on pollen of one species or one family of plants, such as squash bees (Peponapis and Xenoglossa spp.) foraging on Cucurbitaceae (Waser 1986). While there is some indication mason or orchard bees, Osmia spp., prefer Rosaceae pollen (the family to which apples, cherries, plums, pears, and almonds belong), they collect from a wide range of plant families (Marquez et al. 1994, Kraemer and Favi 2005). Bumble bees, *Bombus* spp., tend to forage on a small group of species at any given time, avoiding wasting energy visiting untested resources or because of a limited capacity to remember multiple traits (Heinrich 1975, 1979, Waddington et al. 1981, Gegear and Thomson 2004, Gegear and Laverty 2005). Relatively little is known about non-Apis apple pollinators in southwest Virginia, which include an abundance of bumble bees, and mining bees, Andrena spp., as well as mason bees. Bombus and Andrena species, like Osmia, are active in early spring and at relatively cool temperatures, making them well-suited for apple pollination (Batra 1999, Delaplane and Mayer 2000e, Havenith 2000, Vicens and Bosch 2000a, b, Ladurner et al. 2004, Wittmann et al. 2005, Gardner 2006, Tepedino et al. 2007). This study investigates the floral constancy of the primary apple pollinators found visiting apple flowers in southwest Virginia, comparing pollen loads of the four most important genera: Andrena, Apis, Bombus, and Osmia.

Among apple pollinators, honey bees and mason bees have been well-studied since they are managed (Fell and Robinson 1981, Fell et al. 1983, Batra 1998, Delaplane and Mayer 2000e, Dag et al. 2005, Finta 2005). Bosch and Kemp's (2002) review of research evaluating mason bees as crop pollinators highlights the criteria used in measuring pollination effectiveness: stigma contact and pollen deposition, visitation rates (flowers visited in a given time period),

flowers visited per tree, and frequency of movement between rows or cultivars. Effective fertilization may also be affected by pollen viability (which may be reduced depending on time carried or packing by bees, or application of fungicides by farmers) and the receptivity period of the stigma (Fell et al. 1983, Kearns and Inouye 1993, Soltesz 1997). In apples, many cultivars are self-incompatible, so pollen deposition on stigmas may not equate with pollination effectiveness, but has been used as a practical method for comparing pollinators (Thomson and Goodell 2001, Bosch and Kemp 2003).

Other issues making inferences about pollination effectiveness based on pollen loads difficult relate to foraging habits and differences in pollen carrying structures of various bees. Pollen loads vary depending on the particular point of a given foraging trip and the type of forage (pollen or nectar). Depending on the crop, nectar and pollen foragers may tend to forage greater distances or times, affecting pollen viability (Vaissiere et al. 1996). These issues can render relative size of pollen loads meaningless as a measure of pollination effectiveness.

Techniques that could measure pollination effectiveness of each bee species would examine only unpacked pollen collected from head, thorax, or abdominal hairs or counts of pollen deposited and/or germinated on stigmas, rather than pollen loads (Dafni 1992, Kearns and Inouye 1993, Dafni and Firmage 2000). One technique for pollen collection to estimate pollination effectiveness involves removing pollen-carrying legs to eliminate packed pollen (non-viable pollen) from samples. Abdomens could likewise be removed from megachilid bees, such as *Osmia* spp. Figure 4.1 shows the pollen carrying legs of an andrenid bee in contrast to the abdominal scopa of a megachilid bee (*Osmia* sp.) shown in Figure 4.2. For this study, legs and abdomens were not removed and percentages of pollen loads are used to compare floral constancy, as an indication of potential pollination effectiveness and as a source of information about foraging habits of important apple pollinators (Thomson and Goodell 2001).

Alternative forage may compete with apple for pollinators, such as white clover, *Trifolium repens*, and dandelion, *Taraxacum officinale*, but alternative forage and nesting habitat is required to support wild bees (Free 1993, MacRae et al. 2005, Sheffield et al. 2008a, Sheffield et al. 2008b, Potts et al. 2010). Recent investigations into causes of Colony Collapse Disorder have also highlighted diet impact on honey bee health and the potential negative impacts of limited floral diversity on bees placed in large scale monoculture crops (Alaux et al. 2010, vanEngelsdorp and Meixner 2010). Regarding wild bees, Batra (1999) evaluated the first native



Figure 4.1 Ventral view of pollen laden hind legs and abdomen (left) of *Andrena barbara* and close-up of hind leg with pollen (right). Bee collected in 2008 from an apple flower, Doe Creek orchard in southwest Virginia.



Figure 4.2 Ventral view of *Osmia lignaria* showing abdominal scopa (pollen-carrying hairs) and close-up (right). Bee collected in 2009 from an apple flower, Foggy Ridge Cider orchard in southwest Virginia.

bee to emerge in early spring in the Beltsville, Maryland area, *Andrena fennigeri*, as an orchard pollinator. Her research showed that alternative forage, particularly maple (*Acer*) and willow (*Salix*) supported bees before orchard flowers opened.

We investigated pollen loads of bees visiting apple flowers in orchards in southwest Virginia and alternative forage in close proximity to the orchard. Percentages of apple pollen carried by *Apis mellifera* versus non-*Apis* bees and the number of other types of pollen carried by bees visiting apple flowers provided measures for comparing potential pollination effectiveness of the three most important non-*Apis* genera pollinating apple flowers—*Andrena*, *Bombus*, and *Osmia*—with *Apis*. They also provided an indication of the foraging habits of important apple pollinators during apple bloom.

4.2 Methods

The study sites, apple orchards within a 65 km radius of Blacksburg, Virginia, were visited between 23 and 29 April 2009 and 12 to 22 April 2010 (flowering was about 10 days earlier in 2010 compared with 2008 and 2009). Pollen sampling sites included Doe Creek Orchard (Giles County), Ikenberry Orchards (Botetourt County), King Brothers Orchard (Roanoke County), Kentland Farm (Montgomery County)(2010 only) and Foggy Ridge Cider (Carroll County). Sampling was conducted when temperatures were at least 22°C, winds were less than 3 Beaufort (calm to light breeze), and honey bees were active. Conditions were sunny at all sites except Foggy Ridge in 2009, where it was overcast, but bright, and honey bees (as well as other bees) were active. According to Vicens and Bosch (2006b), honey bees are not active below 500 lux and a typical overcast day provides between 10,000 and 25,000 lux. Based on honey bee activity that day and estimated solar radiation, conditions at Foggy Ridge Cider were comparable with other sites.

Bees were collected from apple flowers and placed into vials of 70% ethyl alcohol (15 ml for *Bombus* and 5 to 10 ml for all other specimens). Pollen loads were separated from bees by vortexing samples for 30 seconds, then sonicating for 120 seconds (Solid State Ultrasonic FS-28 sonicator by Fisher-Scientific, Waltham, MA). The alcohol with pollen loads was decanted into 15 ml clinical centrifuge tubes and centrifuged in a Clay Adams Dynac (Block Scientific, Bohemia, NY) centrifuge for 5 minutes at 2000 RPM to concentrate pollen granules into pellets. Supernatant was removed, discarded, and the remaining liquid evaporated in a warm sand bath at 60°C until pellets were dry, between 2-3 hours.

In preparation for pollen grain counting using a Bright-Line hemacytometer (Hausser Scientific, Horsham, PA), pellets were rehydrated with premeasured quantities of distilled water, dislodged and broken up with a glass Pasteur pipette (rinsed with distilled water between samples), and pollen was resuspended with an air displacement pipette (sonication to resuspend grains jettisoned too much pollen onto the sides of the centrifuge tube). Sixty µl of water was

added to pellets initially. This was the smallest amount of water that provided enough liquid for loading both sides of a hemacytometer twice. Based on visual observation of opacity, additional measured amounts of water were added, as needed, until a good counting density was achieved. Ten to 15 μ l subsamples (15 μ l when more than 60 μ l of water were added to pellets) were pipetted onto each side of a hemacytometer, and pollen grains in four 1 mm² grids (each with a volume of 0.1 μ l) were counted on each side. This provided 8 grid counts on one slide. This step was repeated, providing a total of 16 grid counts for each bee sampled.

Apple pollen was identified initially using reference slides and verified with photographs of samples reviewed by Dr. Karen Goodell of Ohio State University and Mia Park of Cornell University (personal communications, 1 and 2 September 2010). Pollen counts noted apple pollen, non-apple pollen, and dehydrated grains (these could be apple or a number of other plants) (Figure 4.3). With 2010 samples, drawings of pollen types in each subsample were used to tally a total number of non-apple pollen types carried by each bee sampled, not including the dehydrated grains. In 2009, non-apple types per subsample were recorded, but without keeping track of specific pollen types within the whole sample. Therefore, only 2010 data were used to compare pollen types in data analysis. Based on forage data collected, images of pollen of the most commonly visited plants were found in PalDat, an online palynological database and compared with non-apple pollen types in samples (Buchner and Weber 2000 onwards). Pollen grains were also identified with Sawyer's (1981) *Pollen Identification for Beekeepers*.



Figure 4.3 Pollen grains collected from bees visiting apple flowers at Doe Creek Orchards in Giles County, Virginia in 2010. The largest grain is pine, the three triangular grains are apple, and the smallest oval shaped grain is an unidentified dehydrated grain. Alternative forage species—plants in flower at the time of apple bloom—were recorded within orchards and along orchard perimeters, along with observations of bee visitors. Alternative forage was surveyed between morning and afternoon observation of bee visitation at flowers (Chapter 3). Vegetation at each site was also characterized with point-intercept transects and with land cover data from Landsat Thematic Mapper imagery used to compare site vegetative characteristics in relation to bee diversity, but these data are examined in more detail in Chapter 5. In this chapter, species in flower and their bee visitors are listed and discussed in relation to pollen loads.

4.2.1 Data analysis

Analyses were based on hydrated pollen grains, which comprised about 90% of each sample (Figure 4.3). Percent apple pollen and number of non-apple pollen types carried in pollen loads by *Apis*, *Andrena*, *Bombus*, and *Osmia* were compared using Welch's ANOVA (for unequal variances) and ANOVA (JMP 1989-2009). The number of pollen types was compared only with 2010 data.

4.3 Results

4.3.1 Percent target pollen and number of non-apple pollen types carried by bees visiting apple flowers

No significant differences were found at the p=0.05 level in percent apple pollen carried in 2009 (p=0.10) or 2010 (p=0.27). There was no significant difference in the number of types of pollen carried (p=0.03). Table 4.1 shows, by genus, mean percent apple pollen carried by bees collected in 2009 and 2010 and the maximum number of non-apple pollen types they carried in 2010.

Mean percent apple pollen was also compared by genus across sites. Significant differences were found only for *Bombus* (p=0.002). Based on Tukey-Kramer HSD comparison of means, *Bombus* at Foggy Ridge carried significantly lower percent apple pollen (about 85% versus between 95 and 99% at all other sites). Of nine *Bombus* from Foggy Ridge in 2010, four carried between 5 and 15% dandelion (*Taraxacum officinale*) pollen and one carried about 33% purple deadnettle, *Lamium purpureum*, with the rest of their pollen loads (about 65 to 90%)

composed of apple pollen. The other four of nine bees at Foggy Ridge carried between 90 and 97% apple pollen.

Dandelion, *Taraxacum officinale*, and purple deadnettle, *Lamium purpureum* were the most common non-apple pollen types found in somewhat high numbers in a few samples (Figure 4.4). Of 147 bees sampled in 2010, 19 (13%) carried more than 10% non-apple pollen. Fourteen of those with more than 10% non-apple pollen carried between 5 and 32% dandelion pollen, three carried between 9–20% of unidentified pollen that may be violet (*Viola sp.*), bittercress (*Cardamine* sp.) or bittersweet (*Berberis* sp.), two carried 5% pine pollen (plus 5% dandelion), and one carried about 33% purple deadnettle pollen.

Table 4.1 Percent apple pollen and number of types of non-apple pollen found on bees collected from apple flowers at Doe Creek, Foggy Ridge Cider, Ikenberry, Kentland, and King Brothers orchards in southwest Virginia in 2009 and 2010.

Genus		Mean % per µl sul	apple po psample (Maximum number of non- apple pollen types				
	Ν	2009	Ν	2010	per bee (2010) ^d			
<i>Andrena</i> ^a	11	94±0.02	43	96±6.8	5			
Apis	5	97±0.03	36	97±4.7	4			
Bombus ^b	5	88±0.03	39	94±7.9	4			
<i>Osmia</i> ^c	5	86±0.03	29	96±5.0	4			

^a Andrena species were A. barbara, A. bimaculatus, A. carlini, A. dunningi, A. fenningeri, A. heraclei, A. perplexa, A. thoracica, and A. tridens

^b Bombus species were B. bimaculatus, B. griseocollis, B. impatiens, B. perplexus, and B. sandersoni. ^c Osmia species were O. cornifrons, O. lignaria, and O. taurus.

^d The maximum number of non-apple pollen types identified among hydrated grains for each bee sampled. Dehydrated grains may have included additional unidentified pollen types.



Figure 4.4 Pollen grains viewed on a hemacytometer showing apple, dandelion and pine. Grains from *Andrena carlini* collected in southwest Virginia from an apple flower at Ikenberry Orchards on 23 April 2009. The pine pollen shown here is smaller than most observed. The size in Figure 4.3 was more typical.

4.3.2 Bee presence on alternative forage flowers

During apple blossom in 2009 and 2010, 36 other plant species in 22 families (Table 4.2) were observed in flower within orchards or along their perimeter. Since bee foraging distances extend well beyond the orchard boundaries, these flowers represent a portion of the alternative forage available to bees at these sites, somewhat favoring herbaceous species since the orchards are kept open (mown) (Gardner 2006, Greenleaf et al. 2007, Matsumoto et al. 2009). Visitation to flowers was noted and, combined with the pollen load information in Section 4.3.1 above, provides an indication of foraging behavior related to apple pollination. Although only two species, dandelion and purple deadnettle, were observed in all five orchards, most of the plants are common throughout the region and most would likely be found within a kilometer of orchard boundaries.

Number of alternative forage species in flower ranged from eight at Doe Creek to 23 at Kentland, but the percentage of species in flower visited by bees at sites was between 68–75%, fairly uniform across sites. All five bee groups were observed only on dandelion and redbud,

Plant Spacios	Common Nomo	Herb/	No.	Bee Visitors					
Fiant Species		Woody	Sites	Η	B	С	Μ	S	
ACERACEAE (maple family)									
Acer pensylvanicum	striped maple	W	1					+	
ASTERACEAE (aster family)									
Packera sp.	groundsel	h	1					Ŧ	
Sonchus arvensis ^a	sowthistle	h	1		+		+	+	
Taraxacum officinale ^a	dandelion	h	5	+	+	+	+	+	
BERBERIDACEAE (barberry family)									
<i>Berberis thunbergii</i> ^{<i>a</i>} (i) ^b	Japanese barberry	W	1				+	+	
BETULACEAE (birch family)									
Betula sp.	birch	W	1						
BRASSICACEAE (mustard family)									
Alliaria petiolata ^a (i)	garlic mustard	h	2				+	+	
Brassica sp.ª	mustard	h	4	+		+	+	+	
Capsella bursa-pastoris ^a	shepherd's purse	h	3				+	+	
Cardamine hirsute ^a	hairy bittercress	h	2						
CARYOPHYLLACEAE (pink)									
Stellaria media ^a	chickweed	h	4						
CORNACEAE (dogwood family)									
Cornus florida	flowering dogwood	W	4		+		+	+	

Table 4.2 Plants in flower during apple bloom in 2009 and 2010 in orchards in southwest Virginia visited by honey (H), bumble (B), carpenter (C), medium (M), or small (S) bees.

Diant Spacing	Common Nomo	Herb/	No.	Bee Visitors					
Flant Species	Common Name	Woody	Sites	Η	B	С	Μ	S	
ELA	ter family)								
<i>Elaeagnus umbellata</i> ^a (i)	autumn olive	W	1	+	+		+	+	
FABACEAE (legume family)									
Cercis canadensis	eastern redbud	W	2	+	+	+	+	+	
Robinia pseudoacacia	black locust	W	1						
Trifolium repens ^a	white clover	h	1	+	+		+		
FUN	IARIACEAE (fumito	ry family)							
Corydalis flavula	corydalis	h	1						
GERANIACEAE (geranium family)									
Erodium cicutarium ^a	storksbill	h	1						
Geranium columbinum ^a	longstalk cranesbill	h	2						
JUG	LANDACEAE (waln	ut family)							
<i>Carya</i> sp.	hickory	W	1						
LAMIACEAE (mint family)									
Glechoma hederacea ^a	ground ivy	h	3		+	+	+		
Lamium amplexicaule ^a	henbit	h	3						
Lamium purpureum ^a	purple deadnettle	h	5	+	+			+	
LAURACEAE (laurel family)									
Sassafras albidum	sassafras	W	4					+	
	LILIACEAE (lily fa	mily)							
Uvularia sp.	bellwort	h	1						
POL	EMONIACEAE (phl	lox family)							
Phlox subulata	moss phlox	h	1						
PORT	ULACACEAE (purs	lane family	y)						
Claytonia virginica springbeauty h 1									
RANUNCULACEAE (buttercup family)									
Ranunculus abortivus	ranunculus	h	1						
	ROSACEAE (rose fa	mily)							
Amelianchier sp.	serviceberry	W	1						
Chaenomeles sp. ^a	flowering quince	W	1						
Fragaria virginiana	wild strawberry	h	3					+	
Potentilla sp.	cinquefoil	h	2					+	
Prunus sp.	cherry	W	2	+	+		+	+	
RI	JBIACEAE (bedstrav	v family)							
Diodia teres	buttonweed	h	1						
SCROPHULARIACEAE (figwort family)									
Veronica arvensis ^a	corn speedwell	h	3					+	
	VIOLACEAE (violet f	family)							
<i>Viola</i> sp.	violet	h	4					+	
^a Non-native species.									
^b Invasive species indicate	d by (i) (VADCR 2011	l).							

Cercis canadensis, and all but carpenter bees on autumn olive, *Elaeagnus umbellata*, and cherry, *Prunus* sp. Small and medium bees were observed on more types of forage than any other bees, on 51% and 35% of species, respectively, reflecting the greater species diversity of small and medium bees. Honey and bumble bees were seen on 19% and 24% of species, respectively, while carpenter bees were observed on 11%.

About half the plants in flower were non-native species (*Prunus* and *Potentilla* include both native and non-native species), but more than half those observed with bee visitors were non-native (about 47% for small bees, 70% for medium bees, 75% for carpenter bees, 67% for bumble bees, and 71% for honey bees) (Table 4.2). A much larger percentage, about 60%, of the herbaceous species found are introduced (non-native) species, compared with woody species, about 23%.

Families with abundant species and bee visitors were Asteraceae (aster), Brassicaceae (mustard), Fabaceae (legume or pea), and Lamiaceae (mint) (Table 4.2). Within those families, all but redbud (*Cercis canadensis*), which was observed with all bee types and black locust (*Robinia pseudoacacia*), which had no visitors while observed, are herbaceous. All of the herbaceous species in those families except groundsel (*Packera* sp.) are introduced. *Prunus* was the only other species in the Rosaceae (the rose family and same family as apple) observed with bees other than small bees.

Honey, bumble, and medium bees were observed on only 33% of alternative forage species in flower during apple bloom (Table 4.2) All three bee groups were only seen on four species: dandelion, autumn olive, redbud, and white clover.

4.4 Discussion

Analysis of pollen loads carried by *Apis, Andrena, Bombus,* and *Osmia* visiting apple flowers indicates that during apple bloom in southwest Virginia there is little difference in floral constancy between these bee genera. Apple pollen comprised 86–97% of pollen loads carried by bees visiting apple flowers. When these groups of bees forage on apple, alternative forage is a negligible source of competition to apple for pollinators. Since only pollen loads of apple foragers were examined, this does not mean apple is always preferred.

Regarding alternative forage, only two of 36 plant species were observed with all five bee groups, dandelion and redbud, while only two additional species were seen with all but carpenter

bees, autumn olive and cherry (all tree species except dandelion). Honey bees and bumble bees were seen on the lowest percentage of plants (19 and 24%, respectively), while medium and small bees were seen on 35 and 51%, respectively. These proportions parallel the species diversity of each group, except honey bees.

Fontaine (2008) found diet breadth of bumble bees is a flexible trait dependent on resource availability and that greater competition tends to lead to greater specialization. The floral constancy of bees that visited apple may relate to the relatively narrow range (8–32 species per site) of alternative forage available during apple bloom. However, Marquez and colleagues (1994) found that pollen loads of *Osmia cornuta* in apple orchards were primarily apple (92–94%), though they appeared to prefer *Prunus* (in their study, almond) when not in apple orchards, indicating the floral constancy of *Osmia cornuta* foraging on apple. In this southwest Virginia study, the most abundant non-apple pollens carried were dandelion and purple deadnettle. The composition of pollen loads would vary pre- and post- apple bloom, time periods not examined in this study. Ideally, study of alternative forage would examine flowers available before and after crop bloom and compare apple flower visitors with those dependent on earlier and later pollen and nectar sources, as Batra (1999) did for *Andrena fennigeri*. Also, pollen loads of bees collected on alternative forage prior, during, and after apple bloom would be compared with loads and species of bees collected from apple flowers. Such an approach would better illuminate foraging habits as they relate to apple pollination.

Forage without bees observed may provide pollen and nectar resources at other times. Black locust, *Robinia pseudoacacia*, and serviceberry, *Amelanchier* spp., for example, are known to attract bees and other pollinators, but no bees were observed visiting their flowers during apple bloom. It was probably not optimal foraging time for those flowers. Servicebery was near the end of its bloom period and black locust just beginning its bloom period.

Tree pollen is known to be important for early spring bees such as *Osmia* and *Andrena*, yet few bees were observed on other tree flowers during apple bloom (Batra 1999, Kraemer and Favi 2005, Wittmann et al. 2005). Batra's (1999) work highlighted the importance of maple (*Acer*) species, in particular, for bees emerging in very early spring in the piedmont of Maryland. Other than striped maple, an understory tree, no maple trees were still in flower during apple bloom in this Virginia mountains study, differing from Batra's piedmont Maryland study. In
apple orchards studied, 70% of the alternative forage species were herbaceous, most of those introduced, possibly providing lower volumes of pollen or nectar than tree species.

Land supporting alternative forage near orchards is important for providing nectar and pollen resources when crops are not flowering and also for nesting habitat. Forest, meadow, and open land close to orchards provide nesting sites for cavity-nesting bees (*Osmia* and feral honey bees) and for ground-nesting bees (*Bombus* and *Andrena*), yet compete little for pollinators during apple bloom. Steffan-Dewenter and colleagues found that nesting sites limited the numbers of *Osmia rufa* more than other factors such as resource availability or parasitism in orchard meadows in Germany (Steffan-Dewenter and Schiele 2008). The habitat needs of ground-nesting bees like *Bombus* and *Andrena* differ from cavity-nesting bees like *Osmia*, with many andrenid bees nesting in open ground (that warms from solar radiation more quickly in spring), while many *Bombus* nest in vegetated areas, with preference for abandoned mouse nests. Studies of honey bee foraging have found foragers in greatest density closest to the hive (Free 1993, Tepedino et al. 2007).

4.5 Conclusion

The primary non-*Apis* bee pollinators of apple, bees in the genera *Andrena*, *Bombus*, and *Osmia*, were as constant to apple flowers as honey bees during apple bloom in southwest Virginia. Alternative forage was found to be a negligible source of competition for bee pollinators that were foraging on apple. Rather than emphasizing alternative forage as competition, educators could emphasize the benefits non-crop plants and buffer lands provide as nesting habitat and resources for diverse, healthy diets for a variety of bees that pollinate crops.

CHAPTER 5 Influence of landscape and farm management on pollination service provided by *non-Apis* bees for entomophilous crops in southwest Virginia

5.1 Introduction

Decline in bee populations around the globe has led to increased interest in monitoring non-*Apis* bees that support crop pollination and perform other ecosystem services (Chan et al. 2006, Losey and Vaughan 2006, NRC 2007, Isaacs et al. 2009, Potts et al. 2010). The presence and diversity of bees as pollinators on crops and within surrounding landscapes is influenced by many factors, including the variety and extent of crops; management practices for the crop and surrounding lands; and landscape features that provide nesting sites and other habitat needs or are associated with the natural distribution of a species (such as latitude and elevation) (Kremen 2005, Tscharntke et al. 2005, Kohler et al. 2007a, Kohler et al. 2007b, Kohler et al. 2007c, Concepcion et al. 2008, Roulston and Goodell 2010). Given the vital pollination services non-*Apis* bees provide, understanding more about factors influencing their presence on crops and surrounding lands can help guide farm management and conservation planning.

Agricultural land use intensification that reduces semi-natural habitat has been found to reduce presence of bees on crops, particularly in large-scale monoculture crop systems (Kremen et al. 2004, Greenleaf and Kremen 2006a, Holzschuh et al. 2007, Meyer et al. 2007). Steffan-Dewenter and colleagues (2002) investigated impacts of habitat fragmentation on solitary, bumble, and honey bees and found that solitary bees respond to habitat changes at a smaller scale (up to 750 m) compared to bumble bees and honey bees (up to 3000 m). Other researchers (Klein et al. 2004, Kleijn and van Langevelde 2006) found that solitary bee diversity on crops was affected by the availability of semi-natural habitat between 300–1000 m of crops. Lonsdorf and colleagues (2009) tested a model predicting pollination service based on estimates of nesting and floral resources and found that the model worked in areas where resources were more uniform and less well where fine-scale differences were not easily accounted for in the model.

Within the mid-Atlantic, Winfree and colleagues (2007a, 2007b, 2008) investigated the influence of farm management and landscape features in Pennsylvania and New Jersey on bee presence at summer crop flowers (muskmelon, pepper, tomato, and watermelon) and found that habitat heterogeneity was more important than farm management practices such as pesticide

usage or the intensity of land use. Shuler and colleagues (2005) and Julier and Roulston (2009) tested factors more likely to affect ground-nesting bees such as tilling, irrigation, and percent clay in soils in research on squash bees in Virginia and surrounding areas. They found that tillage was correlated with fewer bees in one study, while having no effect in another. Irrigation was positively correlated and clay soils negatively correlated with bee presence on flowers.

The presence of bees on crop flowers may be influenced not only by land management practices, habitat heterogeneity, and annual weather patterns, but also by existing population sizes, disease patterns associated with climate, and cycles of predator and parasite populations (Potts et al. 2010). Alternative forage that blooms before, during, or after crop flowering can be managed by farmers, so schemes to support pollinator diversity promote the planting of forage that provides pollen and nectar throughout the growing season (Kleijn et al. 2006, Concepcion et al. 2008, Scherr and McNeely 2008, Redpath et al. 2010). Recent research on honey bees has also highlighted the importance of floral diversity for overall bee health (Alaux et al. 2010). Pollinator diversity associated with landscape diversity is generally expected to stabilize pollination service by ensuring a pool of species is available that could functionally replace or supplement services if a species declines or is lost (Ricketts et al. 2008, Lonsdorf et al. 2009, Winfree and Kremen 2009).

To gain better understanding of farm management and landscape influences on pollination services provided by non-*Apis* bees in southwest Virginia, we investigated pollination service throughout the growing season, from early spring in apple and blueberry, through summer in caneberry and cucurbits. Developing a model based on our largest dataset, cucurbits, we tested its prediction value in the other cropping systems. The most abundant medium and larger bees found on these crops are known to be equally or more effective in pollinating them as honey bees: *Bombus* and *Andrena* in apple, blueberry, and caneberry; and *Peponapis* and *Bombus* in cucurbits (Tepedino 1981, Torchio 1988, Willis and Kevan 1995, Stubbs and Drummond 1996b, Stanghellini et al. 1997, Stubbs and Drummond 1997, Canto-Aguilar and Parra-Tabla 2000, Stubbs and Drummond 2001, Davis et al. 2002, Javorek et al. 2002, Monzon et al. 2004, Krunic and Stanisavljevic 2006b, Sampson et al. 2007, Julier and Roulston 2009). We therefore focused attention on medium-sized and larger non-*Apis* bees as a conservative measure of pollination service provided by non-*Apis* bees. Our aim was to understand which

factors have the most influence on pollination services in this region in order to improve conservation planning and farm management that supports bee populations.

Habitat factors were measured in the field, derived from aerial imagery (national land cover datasets), and estimated from farmer surveys. It is generally not feasible to measure vegetative cover in the field for large distances due to time constraints and limited accessibility to lands surrounding farms. If national land cover estimates provide useful habitat information, their use might facilitate a cost-effective method for delineating habitat that supports bee populations and crop pollination services.

Bees tend to forage as close as possible to their nests, depending on the quality of resources available, but may be affected by landscape context at different scales (Free 1993, Steffan-Dewenter et al. 2002, Klein et al. 2004, Kleijn et al. 2006). Gathmann found the maximum foraging distance of 16 solitary bee species ranged between 150 and 600 m from nest sites (Gathmann and Tscharntke 2002). Honey bees commonly forage within about 800 m of their colony (but have been found to travel as far as 13 km) (McGregor 1976, Eickwort and Ginsberg 1980). The preferred foraging distances of bees relates to body size, with larger bees, such as bumble bees, traveling greater distances. Maximum bee foraging distance has been found to increase non-linearly with body size, with larger bees foraging a disproportionately larger distance than smaller bees (Greenleaf et al. 2007).

Factors expected to relate positively to pollination service were those that supported greater floral diversity or abundance, such as the number of crops grown, use of irrigation, the number of plant genera or alternative forage species on sites, and habitat heterogeneity (a greater number of habitat types would be expected to have a greater diversity of flora) (Westerkamp and Gottsberger 2001, Wojcik et al. 2008). While irrigation may increase floral abundance and nectar flow, it could also negatively impact ground-nesting bees by increasing moisture levels and potentially supporting fungal growth that can kill larvae and pupae, but those potential negative impacts would be limited to bees nesting within crop rows. Alternative forage could also relate negatively, as a source of competition with crops for pollinators.

Farm size could have a positive or negative effect on non-*Apis* bee pollination services depending on how crops within rows and land surrounding farms is managed and has generally been found to be more important in areas with large monocultural cropping systems, much larger than those found in the mid-Atlantic region (Kremen et al. 2002, Kremen et al. 2004). Insecticide

use, fungicide use, and presence of honey bee colonies could negatively relate to non-*Apis* bee presence at flowers, due to toxicity of insecticides, possible toxicity of fungicides, and potential displacement by honey bees at flower (Fell et al. 1983, Frazier et al. 2008, Mullin et al. 2010). However, honey bee colony presence may benefit non-*Apis* bees if they engender more cautious use of pesticides by farmers.

Nesting and resource needs vary among species. About 70% of solitary bees are groundnesting, with the remaining 30% cavity-nesting. Forest habitat could benefit cavity-nesting bees if nesting sites are limited (Steffan-Dewenter and Schiele 2008). Bumble bees often utilize abandoned mouse nests for their own nests, which can be found in both pasture and forest, while many ground-nesting bees choose sites with good exposure to the sun (that warm up earlier in spring and may stay drier) (Michener 2000). Many bees emerging in early spring depend on trees for food resources since fewer herbaceous plants bloom at that time, while some species specialize on spring herbs. Forested landscapes are not tilled, as pasture might be, so may provide refuge from tilling. A higher percentage of native plants would generally indicate a higher quality habitat and because native plants have co-evolved with native bees, they would be expected to better support native bee populations than recently introduced species. Native plants have been found to support much greater diversity of Lepidopteran species in the mid-Atlantic, so we expected native plants near farms to positively relate to crop pollination services (Steffan-Dewenter 2003, Tallamy 2004).

In addition to the relatively broad scale habitat factors examined with national land cover datatsets, we examined impacts of alternative forage, one of the most easily managed landscape features, on some of the most important non-*Apis* crop pollinators—bees in the genera *Bombus*, *Andrena*, *Osmia*, and *Peponapis*. Due to the high level of landscape disturbance in some farm systems, alternative forage close to crop systems is generally herbaceous, so can be managed within short time spans. We wanted to understand if alternative forage is likely to be more important in supporting bee visitation to crops or in drawing pollinators away from crops through competition (Abel and Wilson 1998, Dale and Polasky 2007, Karanja et al. 2010).

We also investigated connections between general diversity of bees on site with pollination service. One way to measure overall site species diversity is with the use of bowl traps. This method is promoted by the U.S. Geological Survey for ease of repeatability and for being less biased by the skills or interests of collectors using nets (Droege 2009, 2010). It is not

biasfree, however, since certain bees tend to avoid the bowls (Cane et al. 2000). We were interested in two questions: 1) does the richness or diversity of bees collected in bowl traps relate to pollination services? and 2) to what extent do bee species collected in bowls parallel those visiting flowers?

5.2 Methods

5.2.1 Research sites, field visits, and sampling procedure

See sections 3.2.1 and 3.2.2 for research site descriptions, a map of site locations, field visit details, and sampling procedure.

5.2.2 Habitat factors

Field measurements of habitat included vegetative cover and forage (species in flower that could provide nectar or pollen resources). Farmers provided data on farm and land management practices. We also tested the use of habitat metrics derived from aerial imagery and datasets that are free and readily available online: the national Multi-Resolution Land Characteristics Consortium's National Land Cover Dataset 2001(NLCD) (Soil Survey Staff 2004 (2008)) and the National Elevation Dataset (USGS 2001). Derived habitat metrics that may relate to bee species diversity and presence on crop flowers included percent forest cover, percent pasture, and habitat heterogeneity.

5.2.2.1 Land cover

Land cover metrics from National Land Cover Dataset 2001 (NLCD) and elevation data from the National Elevation dataset were extracted in zones extending 500 m and 1500 m from the center of croplands with ArcMap (ESRI 1999-2009, USGS 2001). In addition, we analyzed vegetation in the field with 40 m point intercept transects. We estimated cover in three transects at each site extending from the edge of crop fields and oriented from the field center to the north, southeast, and southwest, where possible, and to the closest degree when those directions were inaccessible (due to fencing or other obstructions). Multiplying each point of the transect that touched a given plant (point intercept) by 2.5 yielded percent cover estimates by genus or species (grasses and sedges were grouped as a general category). McCune and Grace (2002) indicated that point intercept vegetation transects are acceptable substitutes for full scale percent cover estimates, but require much less time in the field.

NLCD land cover estimates are standard national categories, ranging from open water to deciduous or evergreen forest, or developed (urban). Appendix G lists standard national detailed descriptions of categories and Figure 5.1 shows one apple site with the NLCD cover classes mapped within 500 m and 1500 m buffer zones (Homer et al. 2004). Percent pasture/hay and percent deciduous forest were used in land cover analysis. In addition, Shannon habitat heterogeneity indices were calculated based on all land cover types within the 500 and 1500 m zones (McCune and Grace 2002, Fernandez et al. 2003). The Shannon-Wiener diversity index for habitat heterogeneity (H') was calculated using the equation

$H' = -\sum P_i ln[P_i])$

where P equals the relative proportion of each category (i).



Figure 5.1 Foggy Ridge Cider field site in Carroll County, Virginia, with National Land Cover Data 2001 cover classes.

5.2.2.2 Alternative forage

Bees were monitored visiting alternative forage-plants in flower in the landscape surrounding study crops that could provide nectar or pollen as alternative food sources for bees—to gain an understanding of how alternative forage might hinder or help crop pollination. Plants in flower at the same time as crops and their bee visitors were surveyed on the same days crop flower visitors were monitored. Due to variability in the number of crops surveyed and the wide range in farm and forage patch size, sampling ranged from early morning to mid-afternoon. The number of species in flower, in combination with percent cover data from the point intercept vegetation transects, was used to quantify the overall plant diversity of the site. Time, temperature, relative humidity, and wind speed based on the Beaufort system were noted at the time surveying was begun (Giles 2010). Bee visitors to plants in flower were recorded based on the same categories described in Chapter 3: honey bee, bumble bee, carpenter bee, medium bee, and small bee. If accessible following observation, bees were netted at flower, and length of collection time recorded (some plants were inaccessible due to fencing or other impediments). The number of genera found in vegetation transects, the percent native cover, the percent invasive species, the number of species of alternative forage, and the number of alternative forage crops visited by bees were calculated.

5.2.2.3 Farm size and farm management practices

Farmers were surveyed regarding farm size and management practices (Appendix F). Surveys recorded crop hectares; number of crops and crop varieties grown; presence/absence and time of introduction of honey bee colonies; weed management strategies; and use of irrigation, chemical fertilizers, mineral fertilizers, herbicides, insecticides (conventional or organic), and fungicides.

5.2.3 Site bee species richness

Based largely on methods recommended by the Beltsville, Maryland Bee Monitoring Lab of the U.S. Geological Survey (USGS) in the Handy Bee Manual, bees were collected with bowl traps and netting at flower (Droege 2009, 2009 (2010)). Fifteen bowl traps (96 ml Solo brand cups with 70 mm diameter lip, 35 mm height, and 52 mm diameter base filled with soapy water) were placed at each site upon arrival, alternating fluorescent blue, fluorescent yellow, and white bowls, every 5 m along a 45 m transect, where possible, or within a rectangular area where rows were shorter than 45 m. Fluorescent blue and fluorescent yellow pigments were mixed with silica flat paint base (all from Guerra Paint and Pigment Corporation, New York) before being painted on the interior of bowl traps. The USGS recommendation increased from 15 to 30 bowl traps per site after this study was begun. Non-bee insects collected in bowl trap samples were discarded. In addition to bees collected in bowl traps, bees were netted from crop and forage flowers. Bees were netted from crop flowers for 15 minutes after crops had been observed for flower visitation (Chapter 3). Bees were also netted from forage flowers following observation of bee visitation to crops, generally for 1–2 minutes in forage patches less than a half m² and up to 5 minutes for larger patches.

Bee diversity was examined in terms of species collected in bowl traps and by net, and by calculating a separate Shannon-Wiener diversity index for bee species collected by bowl and by net at each site by crop, using the same equations presented in section 5.2.2.1, substituting species for land cover type (McCune and Grace 2002).

5.2.4 Data analysis

A best fitting model relating non-*Apis* bee pollination service to landscape and farm management practices was developed with stepwise linear regression and evaluated with SAS JMP 8.0.1 software and the corrected Akaike's Information Criteria (AICc) (Hurvich and Tsai 1989, JMP 1989-2009). The best fitting model in the stepwise procedure is based on several criteria: the statistical significance of variables, the percent of variation explained (R-square), and the number of variables (smaller numbers of variables being better). Up to 56 best models were generated for each set of variables, with up to five variables per set. To create a best overall model, we used data from our largest dataset, squash (13 sites), and included only variables that are potentially meaningful across crops (Table 5.1). We then tested the model's predictive value for the other crop datasets: apple, blueberry, and caneberry. This method was chosen rather than combining datasets due to different amounts of sampling in crops and changing faunas across the season. The statistical model was considered predictive if coefficients in the test set were within one standard deviation of the original coefficients, a Student's t-test indicated no difference between the test and original coefficients, or statistically significant coefficients in the original model were also statistically significant in the test group (Power 1993, Zar 2010). We developed

a separate model for apple combined with blueberry when the squash model was not validated, in order to investigate factors important for those crops. Due to the small number of apple, blueberry, and caneberry sites, separate models for each crop were not developed.

Variable	Definition	Justification				
Farm management factors						
Crop hectares	Study crop hectares	Crop extent				
Total crops ^a	Types of crops grown	Floral diversity				
Total crop varieties	Varieties of study crop	Floral diversity				
Irrigation ^b	Irrigation employed ^c	Floral abundance				
Weed control	Weeds controlled with herbicide, mowing, grazing, cultivation, or mulch in crop rows during crop flowering ^c	Floral competition				
Insecticidee	Insecticides applied ^c	Direct impact (lethal)				
Fungicide ^e	Fungicides applied ^c	Potential toxicity				
Honey bee colonies	Honey bee colonies present ^c	Potential displacement				
Landscape factors						
Elevation ^e	Elevation (in meters) NED ^d	Habitat				
Plant genera	Plant genera in transects and alternative forage surveys	Floral diversity				
Alternative forage ^{ae}	ternative forage ^{ae} Plant species in flower at the same time as crops					
Visited forage ^a	Alternative forage observed with bees	Floral competition				
% invasive plants	Percent invasive plants in transects	Habitat quality				
% native plants	Percent native plants in transects	Habitat quality				
% pasture/hay 500 m ^{ae}	Percent land pasture or hay NLCD ^d	Habitat quality				
% pasture/hay 1500 m	Percent land pasture or hay NLCD ^d	Habitat quality				
% decid. forest 500 m ^a	Percent land deciduous forest NLCD ^d	Habitat quality				
% dec. forest 1500 m	Percent land deciduous forest NLCD ^d	Habitat quality				
Heterogeneity 500 m ^a	Shannon habitat heterogeneity NLCD ^d	Habitat quality				
Heterogeneity 1500 m	Shannon habitat heterogeneity NLCD ^d	Habitat quality				

Table 5.1 Farm management and landscape variables used for model development in a 2007–2009 study of non-*Apis* bee pollination service at farms in southwest Virginia.

^aVariables removed prior to squash model testing when found to have Pearson Correlation Coefficients of 0.65 or above in pairwise comparisons.

^bIrrigation was not included in the model because all squash farms were irrigated. ^cBinary variables with values of 0 or 1.

^dImagery sources: National Elevation Database (NED) and National Landcover Dataset 2001 (NLCD) (USGS 2001, 2007).

^eVariables removed prior to apple and blueberry model testing based on pairwise comparisons.

Prior to model development, one of the variables in pairs of highly correlated variables was removed (those with Pearson correlation coefficients of 0.65 or above) (Guisan and

Zimmermann 2000) (Table 5.2 and Table 5.3). In choosing between correlated variables, we retained those that correlated with more than one other variable when that occurred.

Non-*Apis* bee pollination service was defined as the total number of medium and bumble bees observed divided by the total number of flowers observed for a 45 second observation period. Least square means of bees per flower were calculated with an analysis of variance (ANOVA), general linear model. To calculate visitation rates, year and bee type (and their interaction), as well as sampling event within a crop, were included as fixed variables. Sampling event per site per year (each site was sampled two to three times for most crops) was treated as an ordinal variable. Site and transect within site were included as random effects.

Table 5.2 Correlations between variables retained and removed for squash model development in a 2007–2009 study of non-*Apis* bee pollination service at farms in southwest Virginia.

Variable retained	Correlations ^a	Variables removed			
Habitat heterogeneity 1500 m	-0.88	% deciduous forest 500 m			
Plant genera	0.85, -0.80, -0.70	Altern. forage, habitat het. 500 m, insect.			
Weed control	1, -0.80	Insecticide, total crops			
% deciduous forest 1500 m	-0.75	% deciduous forest 500 m			
% pasture/hay 1500 m	-0.81, 0.64 ^b	% dec. forest 500 m, % pasture/hay 500 m			
^a Pearson's Correlation Coefficient in pairwise comparisons of all predictor variables.					
^b The 500m percent pasture/hay was removed even though it was slightly less than 0.65 since					
the 1500 m percent pasture/hay	was retained.				

Table 5.3 Correlations between variables retained and removed for apple/blueberry model development in a 2007–2009 study of non-*Apis* bee pollination service at farms in southwest Virginia.

Variable retained	Correlations ^a	Variables removed
Visited forage	1 ^b	Alternative forage
Heterogeneity 1500 m	-0.88, 0.76	% dec. forest 1500 m, % pasture/hay 1500 m
% deciduous forest 500 m	-0.87	% pasture/hay 500 m, % dec. forest 1500 m
Hectares	-0.74	Alternative forage
Percent native	0.69	Elevation

^aPearson's Correlation Coefficient in pairwise comparisons of all predictor variables. ^bThe number of visited forage species and alternative forage species was equal in apple and blueberry.

We also tested the effects of species richness and diversity on non-*Apis* bee pollination service, based on bees collected in bowl traps and collected from flower, as well as overall site data. General linear models (ANOVA) were used to test the effects of species richness and

diversity (Shannon diversity index for bee species) on pollination service, with crop as covariate. Pollination service data were transformed (exponeniated -0.06) to meet assumptions of normality.

All analyses were carried out using JMP Version 8.0.1 (SAS Institute, Cary, NC) statistical software.

5.3 Results

5.3.1 Crop pollination service model based on squash data

The best model for non-*Apis* bee crop pollination service based on the squash dataset retained two landscape factors: percent deciduous forest (1500 m buffer area) and percent native plants. Neither coefficient was significant at the p=0.05 level (p=0.06 for percent forest and p=0.20 for percent native plants), but percent deciduous forest was significant at the p=0.10 level. The model developed was:

y = 0.09 + 0.004 percent deciduous forest 1500 m + 0.005 percent native plants

The positive coefficients indicate that both deciduous forest 1500 m and percent native plants relate positively to non-*Apis* bee presence on squash flowers. Compared with other models generated, it had the second lowest AICc, highest R- squared value, and smallest root mean square error (RMSE), indicating good fit (Table 5.4). Neither this model nor the other best fitting models based on AICc were significant at the p=0.05 level. Of variables in the other models shown in Table 5.4, only plant genera was also positively related to non-*Apis* bee

Table 5.4 Variables in the best six squash models for farm management and landscape effects on non-*Apis* bee pollination services in 2008–2009 southwest Virginia crop pollination study.

Squash model variables	R ²	RMSE	AICc ^a	Model Prob > F
% deciduous forest 1500 m	0.24	0.14	-7.65	0.09
% deciduous forest 1500 m, % native ^b	0.36	0.13	-5.60	0.10
% pasture/hay 1500 m	0.11	0.15	-5.49	0.28
Habitat heterogeneity 1500 m	0.10	0.15	-5.47	0.28
Plant genera, % decid. forest 1500 m*	0.35	0.14	-5.27	0.12
% native	0.09	0.15	-5.26	0.32

^aSorted by AICc (corrected Akaike's Information Criteria) value. A lower value indicates a better fitting model.

^bBest fitting model from stepwise linear regression.

*Asterisk indicates significant variable or model (α =0.05).

presence on crop flowers based on a positive coefficient. Coefficients for both percent pasture/hay and habitat heterogeneity were negative.

5.3.1.1 Squash model validation

The squash model was not validated when tested on the other crop data. We compared coefficients generated from apple, blueberry, and caneberry datasets to the coefficients in the squash model. Though the squash model coefficients were not significant at the p=0.05 level, we compared test models at the 0.10 level for deciduous forest, but none were significant (Table 5.5). None of the test coefficients were within one standard error of the squash model coefficients (Table 5.6). A Student's t-test of differences between coefficients found that the squash coefficients were significantly different from the other three (Table 5.7).

Table 5.5 Significance of model variables in 2008–2009 crop pollination study in southwest Virginia.

	Prob > F					
Variable	squash	apple	blueberry	caneberry		
% deciduous forest	0.06*	0.62	0.24	0.72		
% native	0.20	0.86	0.46	0.95		
*Significant at the p=0.	10 level.					

Table 5.6 Model coefficients in a 2008–2009 southwest Virginia crop pollination study.

	Coefficients & squash standard error (x1000) ^a					
Variable	squash ± SE	apple	blueberry	caneberry		
% deciduous forest	36.10 ± 1.74	0.14	0.14	0.00		
% native	5.07 ± 3.66	0.05	0.05	0.00		
^a Multiplied by 1000 fo	r ease of interpretati	on.				

Table 5.7 Student's t-test comparing differences between crop pollination service model coefficients in a 2008–2009 southwest Virginia crop pollination study.

Level	Mean			
Squash	4.34E-03 A ^a			
Apple	9.07E-05 B			
Blueberry	1.65E-05 B			
Caneberry	1.10E-07 B			
^a Levels not connecte	^a Levels not connected by the same letter are significantly different.			

5.3.1 Crop pollination service model based on apple and blueberry data

The best model for crop pollination service based on the combined apple and blueberry datasets retained three landscape variables: visited forage (p=0.005), percent deciduous forest 500 m (p=0.06), and habitat heterogeneity 500 m (p=0.01). The model was statistically significant (p=0.01) and both visited forage and habitat heterogeneity were significant at the p=0.05 level. The model equation was:

y = 0.005 - 0.0009 visited forage + 0.00009 % deciduous forest 500 m + 0.025 habitat heterogeneity 500 m

The model coefficients indicate a negative relationship between pollination service and visited forage and a positive relationship with deciduous forest 500 m and habitat heterogeneity 500 m. This model does not have the lowest AICc, highest R-square value, or smallest root mean square error, but among statistically significant models, it has the smallest number of variables with a very high R-square value of 0.71 and the second smallest root mean square error (Table 5.8).

The two other variables retained in models with low AICc values were crop varieties and 1500 m habitat heterogeneity. Coefficients for crop varieties were positive in the three models that include it, while the coefficient for 1500 m habitat heterogeneity was negative, indicating positive and negative correlations, respectively, with crop pollination service by non-*Apis* bees.

Table 5.8 Variables in the best six apple and blueberry models for farm management and	
landscape effects on non-Apis bee pollination services in 2008–2009 southwest Virginia stud	y.

Apple and blueberry model variables	\mathbb{R}^2	RMSE	AICc ^a	Model Prob > F			
Crop varieties*, % invasive*, habitat	0.88	0.002	-91.50	0.002*			
heterogeneity 500 m* & 1500 m*							
Crop var.*, % invas.*, habitat het. 500 m*	0.75	0.003	-91.44	0.01*			
Visited forage	0.33	0.004	-90.67	0.05			
Visited forage*, habitat het. 500 m	0.54	0.004	-90.51	0.03*			
Crop varieties	0.31	0.004	-90.43	0.06			
Visited forage*, % dec. forest 500 m,	0.71	0.003	-89.92	0.01*			
habitat heterogeneity 500 m ^{*b}							
^a Sorted by AICc (corrected Akaike's Information Criteria) value. A lower value							
indicates a better fitting model.							

^bBest fitting model from stepwise linear regression.

*Asterisk indicates significant variable or model (α =0.05).

5.3.2 Alternative forage visited by bees

The number of alternative forage species increased from 32 during apple flowering to167 during cucurbit flowering, while the percentage of alternative forage plants visited by bees across the growing season changed little, ranging from 40 to 59% (Table 5.9). Appendix E lists all alternative forage species in flower, plants that received bee visitors, the number of sites with each plant species, growth habit (herbaceous or woody), origin (native or introduced), and invasiveness in the mid-Atlantic region. Honey bees made up between 11 and 26% of the bee types visiting alternative forage (Table 5.10and Figure 5.2). Small bees made up nearly half of the visitors to alternative forage in blueberry, and a third of visitors observed on forage associated with other crops, while the relative abundance on alternative forage of medium bees was greatest in apples, and that of bumble bees greatest in caneberry and cucurbits (Table 5.10 and Figure 5.2).

Concerning bumble bee foraging, nine species were found visiting crops and forage during this study. One species, *Bombus impatiens*, made up the vast majority of those collected, mainly in July and August from cucurbits (Table 5.11). While all species visited alternative forage, relative proportions in crops and alternative forage varied greatly by species. *Bombus bimaculatus* and *B. sandersoni* were more abundant in blueberry (Table 5.12).

Table 5.9 Alternative forage species in flower at the time of crop bloom and the percentage observed with bee visitors. Farms in southwest Virginia in 2009.

	Apple	Blueberry	Caneberry	Cucurbit
	(Api	ril-May)	(June)	(June-Aug.)
Alternative forage species in flower	32	39	68	167
Percent observed with bee visitors	53%	54%	40%	56%

Table 5.10 Number of alternative forage species visited by various bee groups during crop bloom at farms in southwest Virginia in 2009.

Bee	Apple	Blueberry	Caneberry	Cucurbit
group	(Apr	ril-May)	(June)	(June-Aug.)
Honey	7	4	11	42
Bumble	4	6	16	47
Carpenter	2	3	2	11
Medium	9	9	6	39
Small	13	19	16	67



Figure 5.2 Percent of bee types observed visiting alternative forage at the time crops were in flower in 2009.

Table 5.11 Number of *Bombus* species collected through the growing seasons in 2008 and 2009 at farms in southwest Virginia from crops and alternative forage.

	Apr	May	Jun	Jul	Aug	Sep	TOTAL
B. auricomus	2	1	1	0	0	0	4
B. bimaculatus	12	23	17	8	2	0	62
B. fervidus	1	1	1	0	3	0	6
B. griseocollis	2	6	12	12	1	0	33
B. impatiens	9	13	48	121	269	1	461
B. pensylvanicus	0	0	1	0	0	0	1
B. perplexus	1	3	4	7	2	0	17
B. sandersoni	4	11	0	2	0	0	17
B. vagans	0	2	5	5	3	0	15

Table 5.12 Numbers of *Bombus* collected in 2008–2009 from flowers at farms in southwest Virginia.

	Apple	Blueberry	Caneberry	Cucurbits	Other (Spp.) ^a			
B. auricomus	-	2	-	-	2 (2)			
B. bimaculatus	5	23	6	13	15 (12)			
B. fervidus	1	1	-	-	4 (4)			
B. griseocollis	1	6	2	13	11 (6)			
B. impatiens	8	10	23	370	50 (25)			
B. pensylvanicus	-	-	1	-	-			
B. perplexus	1	3	5	5	3 (3)			
B. sandersoni	4	10	-	1	2 (2)			
B. vagans	-	2	1	4	8 (8)			
^a Number of non-cro	^a Number of non-crop (alternative) species in parentheses.							

For apples and blueberries, the most important non-*Apis* pollinators besides *Bombus* were *Andrena* and *Osmia*. For cucurbits, *Peponapis pruinosa* was the most important non-*Apis* pollinator along with *Bombus* species. *Andrena* was collected from the most types of alternative forage, paralleling the genus' diversity and the larger quantity collected overall, primarily during April and May, when alternative forage diversity was lowest (Table 5.13 and Table 5.14).

Table 5.13 Numbers of *Andrena*, *Osmia*, and *Peponapis* collected during the 2008 and 2009 growing season at farms in southwest Virginia from crops and alternative forage flowers.

	Apr	May	Jun	Jul	Aug	Sep	TOTAL
Andrena	285	311	18	10	7	5	636
Osmia	45	60	11	3	3	1	123
Peponapis	-	-	18	111	108	1	238

Table 5.14 Numbers of *Andrena*, *Osmia*, and *Peponapis* collected from flowers in 2008–2009 at farms in southwest Virginia.

	Apple	Blueberry	Caneberry	Cucurbits	Other (Spp.) ^a
Andrena	278	214	39	2	103 (22)
Osmia	34	53	17	4	15 (9)
Peponapis	-	-	4 ^b	232	$2(2^{\circ})$

^aNumber of non-crop (alternative) species in parentheses.

^bNo *Peponapis* were seen on caneberry, but four were collected in bowl traps.

Peponapis were on two species in the morning glory, Convolvulaceae, family.

5.3.3 Effects of species richness or diversity on pollination service

Neither site species richness nor diversity had a significant effect on non-*Apis* bee pollination service when tested based on bowl trap, species netted only from crop flowers, or all species collected from sites (including alternative forage) (Table 5.15).

Table 5.15 Effects of farm bee species richness and diversity on pollination service in a 2008–2009 southwest Virginia pollination study.

	Overall ^a Prob>F	Bowl trap Prob>F	Netted from crop flowers Prob>F				
Bee species richness	0.67	0.97	0.69				
Bee diversity	0.47	0.67	0.17				
^a Includes bees collected from bowl traps, crop flowers, and alternative forage.							

5.3.3.1 Species richness based on bowl trap and netting

Overall diversity paralleled richness at flowers in apple, blueberry, and caneberry, but not in cucurbits (Table 5.16). Bowl trap diversity generally increased through the growing season (from apple through cucurbit flowering). No bees were collected from bowl traps at two sites, one apple and one blueberry, and there was low correspondence between species collected in bowls and species netted on crop flowers. Of 162 species, percentage of species collected from both methods combined was 22% in apple, 47% in blueberry, 32% in caneberry and 47% in cucurbits.

		Bowl	trap]	Netted f	rom crop	(Overall ^a		
Farm	Ν	spp.	Shan. div ^b	Ν	spp.	Shan. div.	spp.	Shan. div.		
Apple										
Kentland	82	29	2.91	166	29	2.67	55	3.31		
Foggy Ridge	0	0	n/a	119	21	3.01	29	3.04		
Doe Creek	18	9	1.90	101	18	2.68	31	2.92		
King Bros.	16	3	0.83	96	17	2.52	25	2.75		
Ikenberry	17	9	1.99	138	14	1.44	23	1.94		
			Blue	eberry						
Crows Nest	119	33	1.80	82	23	2.21	48	3.30		
Sinking Creek	65	23	1.83	111	27	2.63	44	3.27		
McKee	40	16	1.56	34	17	2.73	31	3.20		
Windrush	10	7	1.43	27	14	2.58	23	3.03		
Bob Pond	33	14	1.58	82	22	2.53	31	2.90		
Woodall	12	6	1.38	40	14	2.36	20	2.74		
Eggers	0	0	n/a	40	16	2.51	18	2.59		
			Can	eberry	7					
Kentland	394	42	2.95	91	20	2.66	47	3.03		
Crows Nest	272	25	2.57	16	27	2.44	34	2.73		
Eggers	49	13	1.97	17	10	1.90	20	2.47		
			Cuc	urbits						
Greenstar	146	27	2.86	91	9	1.57	51	3.36		
Stonecrop	65	20	2.49	127	9	1.91	38	3.22		
Raines	207	27	2.43	77	26	2.63	45	3.05		
Toms Creek	183	27	2.64	70	18	2.46	43	3.03		
Seven Spring	176	24	2.60	172	16	2.18	37	2.98		
Kentland	160	22	2.80	59	16	2.22	31	2.95		
Craig Creek	217	21	2.68	46	20	2.30	32	2.91		
Layman	409	32	2.60	59	25	2.36	41	2.86		
Ikenberry	61	23	2.86	80	15	1.90	29	2.85		

Table 5.16 Numbers of bee species collected from farms in a 2008–2009 pollination study in southwest Virginia.

	Bowl trap]	Netted from crop			Overall ^a	
Farm	Ν	spp.	Shan. div^b	Ν	spp.	Shan. div.	spp.	Shan. div.	
Jeter	133	21	2.50	71	13	2.16	27	2.69	
Martin	114	17	2.12	177	17	2.21	31	2.64	
Five Penny	168	26	2.61	69	15	1.41	34	2.63	
King	38	14	2.38	91	10	1.34	19	2.09	
^a Sorted by overall diversity (bees from bowls and netted on crops and alternative forage.)									

^bShannon diversity index calculated based on species in each crop.

5.4 Discussion

Landscape factors were found to have greater impact than farm management practices on non-Apis pollination service, though different factors were more important depending on the crop and/or season. Percent deciduous forest was positively correlated to be presence in apple, blueberry, and cucurbits, while in apple and blueberry habitat heterogeneity was also positively related. However, percent deciduous forest correlated for cucurbits within the 1500 m area, while for apple and blueberry that correlation was for the 500 m area. In both datasets, 1500 m and 500 m deciduous forest factors were negatively correlated with one another (Table 5.2 and Table 5.3). This negative correlation implies that effects of forest cover on pollination service likely varies with scale. Effects of forest cover may also be related to structural differences among crops and the nesting habits of pollinators (Williams et al. 2010). Apple and blueberry are permanent woody crops, while cucurbits are annuals. Among the most abundant pollinators of apple, blueberry, and cucurbits, *Osmia* (early spring species) are the only cavity nesters, so deciduous forest in close proximity to apple and blueberry could relate to increased nesting sites and greater abundance of Osmia. Crop proximity to natural habitat has been found to be important in other pollination research, though this was the first study to examine crop pollination across growing seasons (Kremen et al. 2002, Kremen et al. 2004, Kim et al. 2006, Ricketts et al. 2008). Besides nesting sites for cavity-nesting species, deciduous forest may provide food resources for bee populations that pollinate crops and refuge during cultivation or other disturbance associated with farming. Habitat heterogeneity is an indicator of diverse land cover types within close proximity to crops and could be associated with changing land use on farms. In general, greater species diversity is associated with greater habitat diversity (Westerkamp and Gottsberger 2001, Westphal et al. 2004, Winfree et al. 2007a, Steffan-Dewenter and Westphal 2008). Visited forage, the number of alternative forage species visited,

was negatively related to pollination service in apple and blueberry, suggesting that alternative forage may compete with those crops. To what extent that competition reduces crop pollination is unclear, since such a large proportion of apple and blueberry pollination service was provided by non-*Apis* bees.

Among field-measured habitat characteristics (the number of plant genera, the number of alternative forage species visited by bees, the percent invasive plants, and the percent native plants), only percent natives correlated with pollination service, and only in cucurbits, the season of greatest floral diversity. In general, greater plant diversity is associated with greater insect diversity (Wilson 1992). Tallamy found that native caterpillars depend on native plants to a much greater extent than introduced plant species (Tallamy 2004). In cucurbits, since squash bees depend primarily on squash flowers, the positive effects of floral diversity on pollination service are likely associated with bumble bees, whose colony numbers are highest in summer.

Regarding alternative forage, further study could elucidate the extent these forage plants compete with target crops for pollinators and to what extent they provide balance in bee diets. Visitation to alternative forage by the various bee groups paralleled the relative diversity of each group, with the exception of honey bees. Honey bees comprised 11–26% of bees observed on alternative forage flowers, likely reflecting relative abundance of honey bees in the total bee population. Recent research on honey bee health indicates that the narrow diet of honey bees in monocultures negatively impacts their health (Conte and Ellis 2008, Alaux et al. 2010). This may be true for other non-specialist bees. Research on the impact of pollen and nectar resources on larval development in bees has highlighted the qualitative differences that impact larval growth (Roulston and Cane 2000, Roulston et al. 2000, Roulston and Cane 2002). In this study, about 50% of the available alternative forage from May through August was visited by bees. Ideally, these resources would have been inventoried and monitored prior to and following the crop flowering period to better gauge the extent the plants supported crop pollinators versus created competition for the study crop. More in-depth study is needed on the importance of herbaceous and woody plant nectar and pollen resources for the diversity of bees in crop lands in order to provide sound recommendations to farmers and land managers seeking to support bee diversity (Roulston and Goodell 2011).

Bee species richness and diversity were not found to correspond with pollination service. We found only between 22 and 47% of species in common when comparing richness of bees

collected from bowl traps with species collected from flowers, highlighting the importance of observing bees at flower and netting from flower for understanding crop pollinator populations.

5.5 Conclusion

Landscape features were better predictors than farm management practices of non-*Apis* bee pollination service in farms in southwest Virginia, while at the same time no one model predicted service across crops. For the annual crops studied, cucurbits, percent forest within a 1500 m area was positively related to pollination service, while for apple and blueberry, perennial woody crops that depend on a cavity-nesting genus, deciduous forest within 500 m was positively related. The percentage of alternative forage visited by bees changed little over the growing season, despite a large growth in the number of species. The correspondence between bee species collected in bowl traps and those netted on flower was as low as 22% and overall site species richness and diversity did not correspond with pollination service. The lack of correspondence between species collected from bowl traps and from flowers, or between overall site species richness or diversity with pollination service, underscores the value of observing and collecting bees on flowers for understanding potential pollination service.

CHAPTER 6 Conclusion

6.1 Role of native bees in crop pollination in southwest Virginia

Non-*Apis*, primarily native, bees comprised between 60 and 90% of bees visiting entomophilous crop flowers throughout the growing season in Virginia, except in June, when honey bees were more predominant (60%). Based on a very conservative measure of non-*Apis* pollination service—crop flower visitation by medium and bumble bees—non-*Apis* bees provided more than 50% (on average 68–83%) of pollination services when compared with honey bees in all crops except melon (where they provided an equal amount of service). Honey bee decline due to Colony Collapse Disorder has raised public awareness of global pollinator decline, yet we still generally assume that honey bees are our most important pollinators. This is the first study highlighting the great extent of non-*Apis* bee crop pollination throughout the growing season in Virginia. Other research has highlighted the importance of non-*Apis* bees in crop pollination in other parts of the eastern seaboard (Section 2.4).

A tremendous diversity of non-*Apis* bees help ensure the successful pollination of crops in southwest Virginia (105 species were collected from crop flowers). With sampling conducted in a minute fraction of southwest Virginia (less than 100 hectares), nearly one third of the known species in the state, 162 of 485 species, were documented visiting crops, visiting forage near crops, or collected in bowl traps. The diversity of bees visiting crops was as great within the same crop (between sites) as across crops, indicating that non-*Apis* bees are also important in stabilizing pollination services, generally, regardless of the status of honey bees. The genera *Osmia, Andrena*, and *Bombus* were most important for the early spring crops, apple and blueberry, *Peponapis* and *Bombus* were most important for summer crops, while honey bees were most abundant during caneberry bloom, and were especially important on early varieties of cucurbits that flowered before *Peponapis* emerged.

Among bees collected, eight species were Virginia state records: *Bombus sandersoni* Franklin, 1913; *Coelioxys rufitarsis* Smith, 1854; *Holcopasites calliopsidis* (Linsley, 1943); *Lasioglossum apocyni* (Mitchell 1960); *Lasioglossum ellisiae* (Sandhouse, 1924); and *Melissodes communis* Cresson, 1878; *Osmia texana* Cresson, 1872; and *Triepeolus simplex*

Robertson, 1903. *Coelioxys rufitarsis* and *Osmia texana* have also been collected in Clarke County, Virginia (T'ai Roulston, personal communication, 10 February 2011). While bees are often collected and identified to family, this is the first study in southwest Virginia to document species of bees visiting a full seasonal spectrum of entomophilous crops and surrounding vegetation through two full growing seasons. These baseline data are the first available for this region. They provide a valuable reference point for monitoring bee diversity through time, accessible to other researchers through Discover Life, an online database of bee records managed in part by the U.S. Geological Survey Bee Monitoring Lab (Droege et al. 2011). The seasonal timeline of dates bees were first and last collected from mid-April through September can guide future research with more focused study of seasonal vegetation and land management relating to bee populations.

While bowl trapping is promoted as a relatively unbiased sampling method that is easily repeatable, this study found only between 22 and 47% of the species collected in bowls were also collected from flowers. During apple bloom, many bowl traps remained empty after a full day. Bowl traps in this study provided information about bee diversity among sites, but observation of visitation and collecting bees from flowers provided more reliable information about bee pollinators of crops. Neither bee species richness nor diversity was found to correspond with pollination service. Although a few species identified at crop flowers were particularly abundant, the lack of similarity among bee communities within the same crop systems suggests that management efforts to support crop pollination should involve site specific research. Developing standardized sampling procedures for monitoring bees at crop flowers, as has been done for bowl trap monitoring, would allow for easier comparison of study results across regions.

Study of pollen loads (Chapter 4) revealed that during apple bloom, the three most important non-*Apis* genera of bees pollinating apple—*Andrena*, *Bombus*, and *Osmia*—share a common level of floral constancy with *Apis*. Alternative forage did not compete with apple bloom, but more study is needed to understand what plants support bee populations before and after apple bloom, as well as other crops.

6.2 Farm and landscape management

Models testing the influence of farm management practices and landscape features on non-*Apis* bee crop pollination service indicated that landscape features were better predictors of service than farm management factors and that the importance of factors varied by crop. The relative abundance of deciduous forest was important in apple, blueberry, and cucurbits, but at different scales. Effects of scale likely relate to the nesting and foraging habits of particular bee populations at each site. Both the lack of community similarity within crop systems (Chapter 3) and lack of effect of bee diversity or richness on pollination service (Chapter 5) highlight the importance of examining bee populations within each site in order to improve landscape management to support pollination services. In their review of factors regulating bee populations, Roulston and Goodell (2011) emphasize the direct effect of floral resources. Further research could investigate scale-related factors affecting specific bee populations found to be important for pollination at given sites and/or for various crops.

6.3 Do we need to conserve habitat?

Protecting a diversity of habitat types around farms helps support bee populations. A large percentage of bees collected were not found on crops, so likely depend on alternative forage. These bees support other ecosystem services, helping to ensure pollination of non-cultivated plants that provide food and shelter for other wildlife, and maintain the plant systems that support our watersheds.

All the study crops have native relatives (Table 2.2). To what extent are the bees that pollinate our cultivated crops related to those that pollinate their wild relatives? More systematic investigation of alternative forage visitors could help illuminate evolutionary connections that support crop pollination. Would increased cultivation of wild relatives help attract pollinators to crops?

6.4 Further research

Many questions remain regarding the role of non-*Apis* bees in crop pollination in the region and how best to support bee populations. Further investigations could test the use of landscape metrics in predicting pollination service at other sites. The role of alternative forage before and after crop flowering needs further study. Do crops grown in early spring, a time of

limited wild foraging resources, promote bee populations for later crops? Male bees often exhibit protandry, emerging earlier than females. Do they depend on alternative forage more than females? Although peaches generally are adequately pollinated without the addition of managed species in this region, they may be important as forage before apple bloom. Can successional plantings in perennial or annual cropping systems support bee populations or improve pollination services? Introduction of primocane berries has increased berry production in the region. However, some cavity nesters like small carpenter bees nest in old canes. With primocane production, canes are cut in fall or winter to encourage new growth. Are cavity nesting bees nest site limited in agricultural areas? To what extent can leaving or moving post-harvest crop debris, such as cane, contribute to supporting pollinator populations? Should we be recommending that farmers maintain some floricane varieties or keep cut primocanes on site over winter for nesting? Deciduous forest within 500 m of apple and blueberry was correlated with pollination service, but deciduous forest within 500 m of my study sites was negatively correlated with forest within 1500 m. How does forest cover relate to cavity-nesting bees (Osmia spp.) versus ground-nesting bees (Andrena and Bombus spp.) important in apple pollination? If cavity nesters are limited by nesting sites, how do nest boxes compare with natural forest in supporting bee populations? Is predation or parasitism greater in nest boxes or forest over time? Since a majority of non-Apis bees are ground-nesters, what practices can be used to improve or protect ground-nesting sites? How do practices to improve nesting habitat of these two primary groups of pollinators support or hurt the other groups, as well as honey bees? Does the presence of honey bee hives on farms affect farmer use of pesticides and thereby benefit non-Apis bee populations? These and other questions warrant more study. For the time being, protecting diverse habitats surrounding farmlands can help ensure that native bees continue to support the bountiful harvest and beautiful watersheds that nourish our lives.

Appendix A: 2008 and 2009 research sites, crop hectares, and county locations

Farms and crops visited in both 2008 and 2009 are indicated by "8-9." Those visited only in 2008 or 2009 are shown by "8" or "9." Counties shown in parentheses: Botetourt (B), Carroll (Ca), Craig (Cr), Floyd (F), Montgomery (M), and Roanoke (R).

Research Sites in 2008 and 2009°	hectares ^a	apple	blueberry	caneberry	summer squash	winter squash	cucumber	melon	watermelon
Bob Pond Blueberry Farm (G)	4		8-9						
Craig Creek Farm (Cr)	0.5				8-9	8-9			
Crow's Nest (M)	4		8-9	9					
DeHart Farm (F)	1				8		8		
Doe Creek Orchard(G)	40	8-9							
Eggers Farm (F)	1		9	9					
Five Penny Farm (F) ^d	1			9	8-9	8-9		9	9
Foggy Ridge Cider(Ca)	6	9							
Full Circle Organic Farm (F)	0.5				8				
Greenstar Farm (M)	0.5				8-9	8-9	8-9		
Ikenberry Orchards (B)	9	8-9			8-9	9			
Jeter Farm (R)	3				8-9				
Kentland Farm (M)	1	8-9		8-9	8-9	8-9	8-9	8-9	8-9
King Brothers Orchard (F)	5	9							
King Farm (M)	0.5				8-9		8-9		
Layman Farm (B)	6				8-9	8-9	8-9	8-9	8-9
Martin Farm (B)	1				8-9	8-9	8-9	8-9	
McKee Farm (F)	0.5		9						
Raines Farm (Cr)	2				8-9	8-9	8-9	8	
Seven Springs Farm (F)	2				8-9	8-9	8-9		
Sinking Creek Farm (G)	0.5		8-9						
Stonecrop Farm (G)	1				8-9	8-9	8-9		
Tom's Creek Farm (M)	2				8-9	8-9	8-9	8	
Windrush Blueberry Farm (G) 1			9						
Woodall Farm (Cr) 1			9						
Total Sites by Crop in 2008			3	1	15	10	10	5	2
Total Sites by Crop in 2009	5	7	4	13	10	9	4	3	
^a Hectares shown are those with res other crops not dependent on insect	earch ts for j	crops pollina	, and o ation.	do not	inclu	de hec	tares	in cor	n or

^c Some bee species data was collected in 2007 for apples and caneberries at Kentland Farm, blueberries and caneberries at Crow's Nest, and caneberries at two other sites. ^d Five Penny has two sites, one of which is Five Penny Quarry (or Five Penny Q).

Appendix B: Site visit dates and geographic coordinates

Site visit dates for monitoring bee flower visitation at farm sites in southwest Virginia in 2008 and 2009 and geographic coordinates of sites (in second table below).

Site visit dates and transects per date							
Сгор	Farm	Date	Number of transects ^a				
Apple	Doe Creek	5/1/08	2				
	Foggy Ridge Cider	4/25/09	2				
		4/29/09	2				
	Ikenberry	4/24/08	2				
		4/26/08	2				
		4/23/09	2				
	Kentland	5/2/08	2				
		4/26/09	2				
	King Brothers	4/27/09	2				
Blueberry	Bob Pond	5/9/08	1				
		5/13/08	2				
		5/26/08	2				
		4/24/09	2				
	Crow's Nest	5/7/08	2				
		4/28/09	2				
	Eggers	5/7/09	2				
	McKee	5/7/09	1				
		5/9/09	1				
	Sinking Creek	5/5/08	3				
		5/14/08	1				
		5/1/09	2				
	Windrush	5/8/09	2				
	Woodall	5/2/09	2				
Caneberry	Craig Creek	6/21/09	1				
	Crow's Nest	5/30/09	1				
		7/14/09	1				
	Eggers	5/29/09	2				
	Five Penny	7/3/09	1				
		8/5/09	1				
	Kentland	8/8/08	1				
		7/14/09	2				
		8/3/09	2				
Cucurbit	Craig Creek	7/7/08	1				
		7/30/08	1				
		6/21/09	4				
		7/22/09	4				
	DeHart	8/1/08	2				
	Five Penny	6/25/08	2				
		7/16/08	1				

Сгор	Farm	Date	Number of transects ^a
Cucurbit (continued)		7/3/09	1
		8/5/09	1
	Five Penny Quarry	8/14/08	1
		7/4/09	2
		8/5/09	4
	Full Circle	7/9/08	1
		7/31/08	1
	Greenstar	6/30/08	1
		7/11/08	1
		7/29/08	3
		6/24/09	1
		7/23/09	1
	Ikenberry	6/20/08	1
	2	7/22/08	1
		6/23/09	1
		7/24/09	2
	Jeter	7/15/08	1
		8/6/08	1
		7/2/09	1
		8/4/09	2
	Kentland	8/8/08	1
		8/13/08	2
		8/3/09	4
	King	7/10/08	2
	C	8/4/08	2
		7/8/09	2
		8/7/09	1
	Layman	6/22/08	2
	2	6/23/08	2
		7/22/08	4
		7/24/08	1
		8/15/08	1
		8/18/08	3
		6/22/09	3
		7/18/09	4
	Martin	6/19/08	3
		7/24/08	1
		8/19/08	1
		6/15/09	4
		7/15/09	5
	Raines	7/14/08	3
		8/5/08	3
		8/20/08	3
		6/27/09	2
		7/27/09	$\overline{2}$

Сгор	Farm	Date	Number of transects ^a				
Cucurbit (continued)	Seven Springs	7/2/08	1				
		7/17/08	3				
		8/21/08	2				
		6/25/09	2				
		7/28/09	3				
	Stonecrop	8/7/08	3				
		6/19/09	1				
		7/19/09	3				
	Tom's Creek	6/13/08	3				
		6/24/08	1				
		7/3/08	2				
		7/21/08	3				
		7/23/08	2				
		6/18/09	1				
		7/9/09	1				
		8/6/09	1				
^a Transects generally had 40 observation points in 2008 and 2009. Cucurbit transects							
in 2009 had 20 observation	ion points.						

Geographic Coordinates of Research Sites								
North American Datum 1983, UTM Zone 17 North								
Site	Crop	Easting	Northing					
Doe Creek	apple	537321.8198	4131488.848					
Foggy Ridge Cider	apple	542156.5284	4069326.333					
Ikenberry	apple	591723.2114	4146107.351					
Kentland	apple	536067.9952	4117165.28					
King Orchard	apple	571878.509	4107210.341					
Bob Pond	blueberry	513781.6453	4141562.561					
Crows Nest	blueberry	545236.2198	4119046.201					
Eggers	blueberry	559196.7232	4086056.036					
McKee	blueberry	546609.3386	4090947.073					
Sinking Creek	blueberry	548425.2007	4130729.943					
Windrush	blueberry	539996.6214	4125281.87					
Woodall	blueberry	559260.6012	4140430.225					
Craig Creek	caneberry	580310.2811	4152011.803					
Crow's Nest	caneberry	545236.2198	4119046.201					
Eggers	caneberry	559136.394	4085987.091					
Five Penny	caneberry	569669.4786	4084709.467					
Kentland	caneberry	536207.854	4117937.845					
Craig Creek	cucurbit	580303.0782	4152011.803					
Five Penny	cucurbit	569693.7444	4084685.493					
Five Penny Quarry	cucurbit	565916.0543	4084925.455					

Geographic Coordinates of Research Sites							
North American Datum 1983, UTM Zone 17 North							
Site	Сгор	Easting	Northing				
Full Circle	cucurbit	564625.3741	4090451.276				
Greenstar	cucurbit	547974.0034	4121023.293				
Ikenberry	cucurbit	591580.6601	4146039.55				
Jeter (2008)	cucurbit	600419.0318	4132605.013				
Jeter (2009)	cucurbit	600666.3694	4133653.833				
Kentland	cucurbit	538558.8731	4117165.356				
King	cucurbit	578427.1322	4114229.407				
Layman	cucurbit	595444.2633	4150145.354				
Martin	cucurbit	601354.5478	4154918.885				
Raines	cucurbit	551357.0007	4132442.342				
Seven Springs	cucurbit	569723.3837	4097142.596				
Stonecrop	cucurbit	535731.849	4123784.537				
Tom's Creek	cucurbit	549121.0491	4122984.714				

Appendix C1-C3: Timelines of all bees collected and species associated with farm type

The following bees were collected from farms in southwest Virginia between 2007 and 2010. Timelines show the first to last dates bees were collected, first organized by date (C1, pages 92–95) and then alphabetically by species (C2, pages 96–99). C3, pages 100–103 list species associated with farm type (apple, blueberry, caneberry, and cucurbit), collected from crops and alternative forage by net or bowl. Voucher specimens are deposited in the Virginia Tech Entomology Department Insect Collection.

Appendix C1: Timeline of bees collected, listed by first date collected, page 1 of 4.



Appendix C1: Timeline of bees collected, listed by first date collected, page 2 of 4.

Andrena bisalicis Sphecodes sp. Lasioglossum pilosum Lasioglossum coriaceum Lasioglossum callidum Halictus parallelus Bombus fervidus Agapostemon texanus Lasioglossum versatum Lasioglossum tegulare Lasioglossum pectorale Lasioglossum foxii Lasioglossum forbesii Lasioglossum ellisiae Lasioglossum cressonii Lasioglossum mitchelli Colletes thoracicus Calliopsis and reniformis Andrena personata Andrena mandibularis Andrena erigeniae Andrena cressonii Osmia subfasciata Osmia georgica Lasioglossum quebecense Andrena nasonii Andrena commoda Agapostemon virescens Agapostemon sericeus Ceratina dupla Osmia virga Osmia pumila Osmia bucephala Osmia atriventris Nomada maculata Colletes inaequalis Bombus auricomus Andrena violae Andrena pruni



Appendix C1: Timeline of bees collected, listed by first date collected, page 3 of 4.



Appendix C1: Timeline of bees collected, listed by first date collected, page 4 of 4.

Melissodes denticulata Melissodes desponsa Lasioglossum lineatulum Lasioglossum (viridatum) Melissodes trinodis Lasioglossum lustrans Osmia texana Holcopasites calliopsidis Coelioxys octodentata Paranthidium jugatorium Coelioxys sayi Andrena aliciae Svastra obliqua Osmia chalybea Nomada vegana Coelioxys rufitarsis Coelioxys moesta Triepeolus simplex Megachile brevis Triepeolus lunatus Lasioglossum nelumbonis Colletes latitarsis Lasioglossum anomalum Xenoglossa strenua Melissodes communis Megachile campanulae Heriades carinatus Melissodes bimaculata Triepeolus remigatus Ptilothrix bombiformis Lasioglossum pruinosum Lasioglossum coeruleum Hylaeus mesillae Anthophora bomboides Lasioglossum versans Lasioglossum apocyni Megachile mendica Megachile rotundata Megachile latimanus Lasioglossum obscurum Heriades variolosus



Appendix C2: Timeline of bees collected, listed alphabetically by species, page 1 of 4.



Appendix C2: Timeline of bees collected, listed **alphabetically by species**, page 2 of 4.


Appendix C2: Timeline of bees collected, listed **alphabetically by species**, page 3 of 4.

Lasioglossum zephyrum Lasioglossum viridatum Lasioglossum versatum Lasioglossum versans Lasioglossum truncatum Lasioglossum tegulare Lasioglossum quebecense Lasioglossum pruinosum Lasioglossum pilosum Lasioglossum pectorale Lasioglossum obscurum Lasioglossum oceanicum Lasioglossum nelumbonis Lasioglossum macoupinense Lasioglossum lustrans Lasioglossum lineatulum Lasioglossum leucozonium Lasioglossum imitatum Lasioglossum illinoense Lasioglossum fuscipenne Lasioglossum foxii Lasioglossum forbesii Lasioglossum ellisiae Lasioglossum cressonii Lasioglossum coriaceum Lasioglossum coreopsis Lasioglossum coeruleum Lasioglossum callidum Lasioglossum mitchelli Lasioglossum apocyni Lasioglossum anomalum Lasioglossum (viridatum) Hylaeus modestus/affinis Hylaeus mesillae Hylaeus affinis Hoplitis spoliata Hoplitis producta Hoplitis pilosifrons



Appendix C2: Timeline of bees collected, listed alphabetically by species, page 4 of 4.

Xylocopa virginica Xenoglossa strenua Triepeolus simplex Triepeolus remigatus Triepeolus lunatus Svastra obliqua Stelis lateralis Sphecodes sp. Ptilothrix bombiformis Peponapis pruinosa Paranthidium jugatorium Osmia virga Osmia texana Osmia taurus Osmia subfasciata Osmia pumila Osmia lignaria Osmia georgica Osmia cornifrons Osmia collinsiae Osmia chalybea Osmia bucephala Osmia atriventris Nomada vegana Nomada superba Nomada maculata Nomada luteoloides Nomada imbricata Nomada composita Melitoma taurea Melissodes trinodis Melissodes desponsa Melissodes denticulata Melissodes communis Melissodes bimaculata Megachile rotundata Megachile pugnata Megachile mendica Megachile latimanus Megachile gemula Megachile campanulae Megachile brevis



Appendix C3: Bees associated with farm type (collected by net or bowl on crops or alternative forage), page 1 of 4.

	Farm Type									
Bee species	Apple	Blueberry	Caneberry	Cucurbit						
Agapostemon sericeus	1	1	50	10						
Agapostemon texanus	0	1	1	2						
Agapostemon virescens	12	28	91	238						
Andrena aliciae	0	0	0	1						
Andrena alleghaniensis	0	2	0	1						
Andrena barbara	139	4	2	0						
Andrena bimaculatus	3	0	0	0						
Andrena bisalicis	1	0	0	0						
Andrena brevipalpis	0	0	0	1						
Andrena carlini	38	84	0	0						
Andrena carolina	0	1	0	0						
Andrena commoda	1	1	7	0						
Andrena confederata	1	0	0	0						
Andrena cornelli	1	0	0	0						
Andrena crataegi	17	14	2	2						
Andrena cressonii	0	2	0	0						
Andrena dunningi	6	2	0	0						
Andrena erigeniae	5	13	0	0						
Andrena fenningeri	8	0	0	0						
Andrena forbesii	7	3	0	0						
Andrena heraclei	1	0	0	0						
Andrena hippotes	0	0	1	0						
Andrena illini	13	4	0	0						
Andrena imitatrix	3	5	0	0						
Andrena mandibularis	1	0	0	0						
Andrena mariae	4	2	0	0						
Andrena miserabilis	10	3	0	0						
Andrena nasonii	19	16	12	1						
Andrena perplexa	23	8	0	0						
Andrena personata	4	2	0	0						
Andrena pruni	6	9	0	0						
Andrena rugosa	2	0	0	0						
Andrena sayi	1	0	0	0						
Andrena sp.	7	9	0	6						
Andrena spiraeana	0	0	0	7						
Andrena tridens	6	0	0	0						
Andrena vicina	34	59	0	1						
Andrena violae	16	10	0	0						
Andrena wilkella	0	1	0	3						
Anthidium manicatum	0	0	0	5						

		Farn	n Type	
Bee species	Apple	Blueberry	Caneberry	Cucurb
Anthidium oblongatum	0	0	0	1
Anthophora abrupta	0	0	0	1
Anthophora bomboides	0	0	0	7
Anthophora terminalis	0	0	0	2
Apis mellifera	79	9	19	75
Augochlora pura	3	10	6	91
Augochlorella aurata	3	38	67	67
Augochlorella persimilis	0	0	1	14
Augochloropsis metallica	0	1	6	6
Bombus auricomus	1	2	0	1
Bombus bimaculatus	9	26	6	23
Bombus fervidus	0	1	1	3
Bombus griseocollis	12	6	2	24
Bombus impatiens	46	12	23	416
Bombus pensylvanicus	0	0	0	1
Bombus perplexus	1	3	5	8
Bombus sandersoni	8	11	0	2
Bombus vagans	0	2	1	12
Calliopsis andreniformis	1	11	95	55
Ceratina calcarata	21	27	41	27
Ceratina dupla	3	4	19	25
Ceratina dupla/calcarata	0	0	0	2
Ceratina strenua	2	12	55	20
Coelioxys moesta	0	0	0	1
Coelioxys octodentata	0	0	0	2
Coelioxys rufitarsis	0	0	0	2
Coelioxys sayi	0	0	0	1
Colletes inaequalis	5	7	0	0
Colletes latitarsis	0	0	2	5
Colletes thoracicus	2	2	0	0
Eucera hamata	0	2	0	2
Halictus confusus	4	6	10	19
Halictus foxii	1	0	0	0
Halictus ligatus	2	19	61	97
Halictus ligatus/poeyi	0	0	0	2
Halictus parallelus	0	1	3	18
Halictus rubicundus	8	7	15	2
Heriades carinatus	0	0	0	1
Heriades variolosus	0	0	0	1
Holcopasites calliopsidis	0	0	1	0
Hoplitis pilosifrons	1	0	4	1
Hoplitis producta	0	4	36	0
Hoplitis spoliata	0	1	0	1
Hylaeus affinis	0	0	0	2

		Farm	n Type	
Bee species	Apple	Blueberry	Caneberry	Cucurbit
Hylaeus mesillae	0	0	0	1
Hylaeus modestus	0	0	1	2
Hylaeus modestus/affinis	0	0	12	9
Lasioglossum (viridatum)	0	0	4	0
Lasioglossum anomalum	0	0	0	1
Lasioglossum apocyni	0	0	0	1
Lasioglossum mitchelli	5	13	24	174
Lasioglossum bruneri	0	2	0	14
Lasioglossum callidum	2	10	20	172
Lasioglossum coeruleum	0	0	0	6
Lasioglossum coreopsis	0	1	0	1
Lasioglossum coriaceum	0	5	12	8
Lasioglossum cressonii	1	0	2	3
Lasioglossum ellisiae	2	1	15	0
Lasioglossum forbesii	1	1	0	0
Lasioglossum foxii	3	2	0	0
Lasioglossum fuscipenne	0	1	0	1
Lasioglossum illinoense	0	0	3	59
Lasioglossum imitatum	5	9	4	132
Lasioglossum leucozonium	2	6	193	116
Lasioglossum lineatulum	0	0	1	0
Lasioglossum lustrans	0	0	0	3
Lasioglossum macoupinense	0	0	0	1
Lasioglossum nelumbonis	0	0	0	2
Lasioglossum oceanicum	0	2	0	59
Lasioglossum obscurum	0	0	0	1
Lasioglossum pectorale	2	12	18	21
Lasioglossum pilosum	4	10	47	336
Lasioglossum platyparium	0	0	0	1
Lasioglossum pruinosum	0	0	5	5
Lasioglossum quebecense	1	1	0	0
Lasioglossum sp.	12	3	16	162
Lasioglossum tegulare	9	17	54	238
Lasioglossum truncatum	0	0	2	1
Lasioglossum versans	0	0	0	2
Lasioglossum versatum	1	9	54	118
Lasioglossum viridatum	0	0	23	0
Lasioglossum zephyrum	0	0	0	25
Megachile brevis	0	0	2	2
Megachile campanulae	0	0	0	3
Megachile gemula	0	0	0	0
Megachile latimanus	0	0	0	3
Megachile mendica	0	0	6	20
Megachile pugnata	0	0	1	6

		Farn	1 Туре	
Bee species	Apple	Blueberry	Caneberry	Cucurbit
Megachile rotundata	0	0	1	4
Melissodes bimaculata	0	0	4	135
Melissodes communis	0	0	0	3
Melissodes denticulata	0	0	0	2
Melissodes desponsa	0	0	1	1
Melissodes trinodis	0	0	0	4
Melitoma taurea	0	0	8	26
<i>Nomada</i> sp.	4	8	1	1
Nomada composita	0	1	0	0
Nomada imbricata	0	1	0	0
Nomada luteoloides	4	5	0	0
Nomada maculata	4	4	0	0
Nomada superba	1	0	0	0
Nomada vegana	0	0	0	1
Osmia albiventris	1	0	0	0
Osmia atriventris	0	4	0	0
Osmia bucephala	0	2	0	0
Osmia chalybea	0	0	0	3
Osmia collinsiae	0	0	0	0
Osmia cornifrons	30	11	5	0
Osmia georgica	4	6	3	2
Osmia lignaria	28	4	1	0
Osmia pumila	9	15	6	1
Osmia subfasciata	1	3	0	1
Osmia taurus	8	10	0	0
Osmia texana	0	0	2	0
Osmia virga	0	3	0	0
Paranthidium jugatorium	0	0	0	1
Peponapis pruinosa	0	0	4	234
Ptilothrix bombiformis	0	0	0	1
Sphecodes sp.	0	4	1	3
Stelis lateralis	0	0	5	0
Svastra obliqua	0	0	0	2
Triepeolus lunatus	0	0	0	2
Triepeolus remigatus	0	0	0	9
Triepeolus simplex	0	0	0	1
Xenoglossa strenua	0	0	0	3
Xylocopa virginica	9	21	2	2

Site & crop	Hives ^a	No. of	Bee ratio	Bumble +	Honey
		trans.	honey : bum.+med.	medium	
Apple			(sorted high to low)	bees/100 fl	owers±SD
Doe Creek	yes	2	12.00	1.9±3.6	22.8±14.8
Ikenberry	yes ^a	6	0.68	18.5 ± 25.2	12.6±13.6
King Brothers	no	2	0.40	8.7±9.2	3.5 ± 7.0
Foggy Ridge	yes ^a	4	0.29	11.1±10.9	3.2 ± 5.3
Kentland	yes	4	0.07	20.5 ± 28.7	1.5±5.6
Blueberry				bees/1000 f	lowers±SD
Windrush	no	2	3.22	2.3±2.9	7.4±3.9
Crow's Nest	no ^b	4	2.54	2.4 ± 3.9	6.1±8.8
Bob Pond	yes ^a	7	0.99	9.6±14.0	9.5±18.9
Sinking Creek	yes	6	0.83	7.8±11.3	6.5±14.6
Eggers	no	2	0.64	9.1±8.3	5.8 ± 5.0
Woodall	no	2	0.17	7.5±5.8	1.3 ± 2.8
McKee	no	2	0.00	13.8±11.9	0
Caneberry				bees/10 flo	owers±SD
Craig Creek	no	1	10.24	2.1±3.6	21.5±9.4
Crow's Nest	no ^b	2	9.36	1.4 ± 2.5	13.1±9.3
Eggers	no	2	3.69	1.3 ± 2.6	4.8 ± 4.8
Five Penny	yes	1	0.53	6.8±8.7	3.6 ± 4.8
Kentland	yes	5	0.35	9.9±16.3	3.5±5.8
Cucurbit				bees/10 flo	owers±SD
Layman (cms) ^d	yes ^a	20	1.52	2.1 ± 4.4	3.2 ± 5.4
Martin (cms)	n,y°	14	1.42	1.9 ± 5.1	2.7 ± 4.3
Craig Creek (cms)	no	10	0.50	1.8 ± 4.2	0.9 ± 2.4
Greenstar (cs)	yes	7	0.45	5.5 ± 8.5	2.5 ± 5.6
Ikenberry (s)	no	5	0.41	3.2 ± 5.6	1.3 ± 2.2
Five Penny (cs)	yes	5	0.39	6.7±12.4	2.6 ± 3.3
King (cs)	no	7	0.38	3.4±6.1	1.3 ± 2.6
Five Penny Q(cms) no	7	0.35	2.3 ± 4.5	0.8±1.5
Seven Springs (cs)	yes	11	0.27	3.3 ± 5.7	0.9 ± 2.5
DeHart (cs)	no	2	0.21	5.7±6.9	1.2 ± 2.9
Jeter (s)	yes	5	0.11	6.6±10.8	0.7±1.9
Kentland (cms)	yes	7	0.11	3.8±6.3	0.4±0.9
Raines (cms)	no	13	0.09	5.6±10.8	0.5 ± 1.4
Full Circle (s)	no	2	0.03	5.8 ± 6.1	0.2±0.9
Stonecrop (cs)	yes	7	0.02	4.2±7.6	0.1±0.3
Tom's Creek (cms)) ves	14	0.81	2.1 ± 5.1	1.7 ± 3.7

Appendix D: Hive presence, bee ratios, and bees per flower by crop and farm at crop flowers at farms in southwest Virginia in 2008–2009.

^aHives introduced at crop flowering time.

^bHives not present on site, but within 0.5 km of crop.

"No hives in 2008, but introduced permanent hives in 2009.

^dCrops grown: c=cucumber; m=melon (canteloupe or watermelon); s=squash.

Appendix E: Alternative forage in flower during target crop bloom

Plants observed in flower during crop bloom at farm sites in southwest Virginia during the 2008 and 2009 growing seasons. Plants in bold were observed with bee visitors. Family abbreviations explained in separate table below. Types listed are cultivated (c), herbaceous (h), shrub or small tree (s), and tree (t). Origins are introduced (i), native (n), invasive (v), and for genera with both native and introduced species observed (b). Some crops are native to the Americas, but introduced to Virginia, such as tomato.

				Crop Sites					
Species	Common name	Fam- ily	All sites	Apple	Blueberry	Caneberry	Cucurbit	Type	Origin
Abelmoschus esculentus	okra	Malv.	3	-	-	-	3	c	i
Abutilon theophrasti	velvetleaf	Malv.	3	-	-	-	3	h	i
Acer pensylvanicum	striped maple	Acer.	1	1	-	-	-	S	n
Achillea millefolium	yarrow	Aste.	14	-	-	4	10	h	i
Aegopodium podagraria	bishop's weed	Apia.	1	-	-	-	1	с	i
Agastache scrophulariifolia	purple giant hyssop	Lami.	2	-	-	-	2	h	n
Agrimonia gryposepala	agrimony	Rosa.	4	-	-	-	3	h	n
Ailanthus altissima	tree-of-heaven	Sima.	1	-	-	-	1	t	v
Alcea rosea	hollyhock	Malv.	1	-	-	-	1	с	i
Alliaria petiolata	garlic mustard	Bras.	5	2	2	1	-	h	v
Allium cepa	onion	Lili.	3	-	-	1	2	c	i
Allium odorum	Chinese leeks	Lili.	2	-	-	-	2	с	i
Allium porrum	leek	Lili.	1	-	-	-	1	с	i
Allium vineale	wild garlic	Lili.	3	-	-	-	3	h	i
Amaranthus hybridus	pigweed	Amar.	12	-	-	-	12	h	n
Ambrosia artemisiifolia	ragweed	Aste.	4	-	-	-	4	h	n
Ambrosia trifida	great ragweed	Aste.	2	-	-	-	2	h	n
Amelianchier sp.	serviceberry	Rosa.	1	1	-	-	-	s	n
Amphicarpaea bracteata	hog peanut	Faba.	2	-	-	-	2	h	n
Anagallis arvensis	sweet pimpernel	Prim.	1	-	-	-	1	h	i
Anemone virginiana	thimbleweed	Ranu.	1	-	-	-	1	h	n
Anethum graveolens	dill	Apia.	5	-	-	-	5	с	i
Antennaria sp.	pussytoes	Aste.	1	-	1	-	-	h	n
Anthemis arvensis	wild chamomile	Aste.	2	-	-	-	2	h	i
Antirrhinum majus	snapdragon	Scro.	1	-	-	-	1	с	i
Apocynum cannabinum	dogbane	Apoc.	6	-	-	1	5	h	n
Arabidopsis thaliana	mouseear cress	Bras.	1	-	1	-	-	h	i
Arctium lappa	burdock	Aste.	10	-	-	1	9	h	i
Asclepias syriaca	common milkweed	Ascl.	10	-	-	1	9	h	n
Asclepias tuberosa	butterfly milkweed	Ascl.		-	-	-	2	h	n
Asparagus officinalis	asparagus	Lili.	2	-	-	-	2	c	i
Aster sp.	aster	Aste.	1	-	-	-	1	h	n
Bellis perennis	English daisy	Aste.	1	-	-	-	1	с	i

			Crop Sites						
Species	Common name	Fam- ilv	All sites	Apple	Blueberry	Caneberry	Cucurbit	Type	Origin
Berberis thunbergii	Iananese barberry	Berb.	2	1	1	-	-	s	v
Betula sp.	birch	Betu.	1	1	-	-	-	t	n
Bidens sp.	beggarticks	Aste.	1	-	-	-	1	h	b
Borago officinalis	borage	Bora.	2	-	-	-	2	с	i
Bracteantha bracteata	strawflower	Aste.	2	-	-	-	2	с	i
Brassica oleracea	collards, broccoli	Bras.	3	-	-	-	3	с	i
Brassica rapa	mustard, turnips	Bras.	2	-	-	1	1	с	i
Brassica sp.	mustard	Bras.	18	4	6	2	6	h	i
Buddleja davidii	butterflybush	Budd.	1	-	-	-	1	s	v
Calendula officinalis	calendula	Aste.	2	-	-	-	2	c	i
Calystegia/Convolvulus sp.	bindweed	Conv.	11	-	-	1	10	h	n
Campanulastrum americanum	American bellflower	Camp.	1	-	-	-	1	h	n
Capsella bursa-pastoris	shepherd's purse	Bras.	5	1	2	-	2	h	i
Capsicum annuum	pepper	Sola.	11	-	-	1	10	с	i
Carya sp.	hickory	Jugl.	1	1	-	-	-	t	n
Catalpa speciosa	catalpa	Bign.	1	-	-	-	1	t	n
Celosia sp.	cock's comb	Amar.	1	-	-	-	1	c	i
Centaurea cyanus	bachelor button	Aste.	2	-	-	-	2	h	i
Centaurea stoebe	spotted knapweed	Aste.	7	-	-	1	6	h	v
Cercis canadensis	eastern redbud	Faba.	2	2	-	-	-	s	n
Chenopodium album	lambsquarters	Chen.	9	-	-	1	8	h	n
Chrysanthemum sp.	chrysanthemum	Aste.	1	-	-	-	1	с	i
Cichorium intybus	chicory	Aste.	15	-	-	1	14	h	i
Cirsium arvense	Canada thistle	Aste.	3	-	-	-	3	h	v
Cirsium sp.	thistle	Aste.	8	-	-	-	8	h	v
Claytonia virginica	springbeauty	Port.	3	1	2	-	-	h	n
Clematis sp.	virgin's bower	Ranu.	12	-	-	1	7	v	n
Cleome spinosa	cleome	Capp.	1	-	-	-	1	с	i
Clinopodium vulgare	wild basil	Lami.	14	-	-	3	8	h	n
Commelina communis	common dayflower	Comm.	1	-	-	-	1	h	i
Conyza canadensis	marestail, horseweed	Aste.	4	-	-	-	4	h	n
Coreopsis tinctoria	tickseed	Aste.	1	-	-	-	1	h	n
Coriandrum sativum	cilantro	Apia.	5	-	-	-	4	с	i
Cornus florida	flowering dogwood	Corn.	10	4	6	-	-	s	n
Cornus sericea	red-osier dogwood	Corn.	2	-	-	-	1	s	n
Corydalis flavula	corydalis	Fuma.	1	1	-	-	-	h	n
Cosmos bipinnatus	cosmos	Aste.	1	-	-	-	1	c	i
Cosmos sulphureus	orange cosmos	Aste.	1	-	-	-	1	c	i
Crataegus sp.	hawthorn	Rosa.	1	-	-	-	1	S	n
Cucumis sativus	cucumber	Cucu.	5	-	-	-	5	c	i
Dahlia sp.	dahlia	Aste.	3	-	-	-	2	c	i
Datura stramonium	jimsonweed	Sola.	7	-	-	-	5	h	i
Daucus carota	Queen Anne's lace	Apia.	28	-	-	3	15	h	i

				Crop Sites					
Species	Common name	Fam- ily	All sites	Apple	Blueberry	Caneberry	Cucurbit	Type	Origin
Delphinium sp.	larkspur	Ranu.	2	-	-	-	1	с	i
Desmodium sp.	ticktrefoil	Faba.	8	-	-	2	6	h	n
Dianthus armeria	Deptford pink	Cary.	11	-	-	1	6	h	i
Diodia teres	buttonweed	Rubi.	1	1	-	-	-	h	n
Dipsacus fullonum	teasel	Dips.	6	-	-	-	4	h	v
Duchesnia indica	false strawberry	Rosa.	1	-	-	-	1	h	i
Echinacea purpurea	purple coneflower	Aste.	4	-	-	-	2	с	b
Elaeagnus umbellata	autumn olive	Elae.	2	1	1	-	-	s	v
Erigeron philadelphicus	fleabane	Aste.	31	-	1	4	15	h	n
Erodium cicutarium	storksbill	Gera.	3	1	1	-	1	h	i
Eryngium sp.	sea holly	Apia.	0	-	-	-	1	h	i
Euonymus atropurpureus	eastern wahoo	Cela.	1	-	-	-	1	s	i
Eupatoriadelphus fistulosus	Joe-pye weed	Aste.	9	-	-	-	5	h	n
Eupatorium sp.	snakeroot	Aste.	2	-	-	-	2	h	n
Euphorbia corollata	flowering spurge	Euph.	2	-	-	-	1	h	n
Fagopyrum esculentum	buckwheat	Poly.	11	-	-	-	7	с	i
Fragaria virginiana	wild strawberry	Rosa.	8	3	5	-	-	h	n
Galinsoga quadriradiata	hairy galinsoga	Aste.	18	-	-	3	10	h	i
Galium sp.	bedstraw	Rubi.	4	-	-	-	2	h	n
Galium verum	vellow bedstraw	Rubi.	1	-	-	-	1	h	n
Gaura biennis	gaura	Onag.	4	-	-	-	4	h	n
Geranium carolinianum	smallflower cranesbill	Gera.	2	-	-	-	2	h	n
Geranium columbinum	longstalk cranesbill	Gera.	2	1	1	-	-	h	i
Geranium maculatum	wild geranium	Gera.	2	-	1	1	-	h	n
Geranium molle	dove's foot cranesbill	Gera.	3	-	2	1	-	h	i
Geum sp.	avens	Rosa.	1	-	-	-	1	h	n
Gladiolus sp.	gladiola	Lili.	1	-	-	-	1	h	i
Glechoma hederacea	ground ivv	Lami.	9	2	4	1	2	h	i
Glycine max	sovbean	Faba.	1	-	_	-	1	с	i
Helianthus sp.	sunflower	Aste.	8	-	-	1	5	h	n
Heliopsis helianthoides	oxeve sunflower	Aste.	7	-	-	-	5	h	n
Hemerocallis sp.	davlilv	Lili.	3	-	-	-	2	с	i
Hesperis matronalis	dame's rocket	Bras.	6	-	1	1	3	h	i
Hibiscus trionum	flower-of-an-hour	Malv.	3	-	-	-	2	h	i
Hieracium paniculatum	panicled hawkweed	Aste.	8	-	-	1	4	h	n
Hieracium sp.	hawkweed	Aste.	7	-	-	2	5	h	n
Hylotelephium telephium	sedum	Cras.	1	-	-	-	1	c	i
Hypericum perforatum	St. Johnswort	Clus.	11	-	-	2	8	h	i
Hypericum prolificum	shrubby St. Johnswort	Clus.	1	-	-	-	1	s	n
Impatiens capensis	jewelweed	Bals.	8	-	-	-	6	h	n
Ipomoea pandurata	wild potato vine	Conv.	2	-	-	-	1	h	n
Ipomoea purpurea	morning glory	Conv.	3	-	-	-	2	c	i
Kniphofia uvaria	red hot poker	Lili.	1	-	-	-	1	c	i
A V	1 I								·

			Crop Sites						
Species	Common name	Fam- ily	All sites	Apple	Blueberry	Caneberry	Cucurbit	Type	Origin
Lactuca canadensis	wild lettuce	Aste.	2	-	-	-	2	h	n
Lamium amplexicaule	henbit	Lami.	1	-	-	1	-	h	i
Lamium purpureum	purple deadnettle	Lami.	9	3	6	-	-	h	i
Lathyrus latifolia	perennial pea	Faba.	4	-	-	-	3	h	i
Lavandula sp.	lavender	Lami.	1	-	-	-	1	с	i
Leonurus cardiaca	motherwort	Lami.	2	-	-	-	2	h	i
Lepidium sp.	pepperweed	Bras.	3	-	-	2	1	h	b
Leucanthemum vulgare	oxeye daisy	Aste.	22	-	1	3	11	h	i
Ligustrum sinense	Chinese privet	Olea.	2	-	-	-	1	S	v
Limonium sp.	statice	Plum.	4	-	-	-	2	с	i
Liriodendron tulipifera	tuliptree	Magn.	1	-	-	1	-	t	n
Lobelia spicata	spiked lobelia	Camp.	2	-	-	-	2	h	n
Lobularia maritima	sweet alyssum	Bras.	4	-	-	2	2	с	i
Lonicera japonica	Japanese honeysuckle	Capr.	4	-	-	-	4	v	v
Lonicera sp.	bush honeysuckle	Capr.	4	-	2	-	2	S	v
Lotus corniculatus	birdsfoot trefoil	Faba.	1	-	-	-	1	h	i
Luffa operculata	luffa	Cucu.	2	-	-	-	1	с	i
Lycopus sp.	bugleweed	Lami.	1	-	-	-	1	h	n
Lysimachia sp.	yellow loosestrife	Prim.	2	-	-	-	2	h	n
Malus sp.	apple, crab apple	Rosa.	3	-	3	-	-	t	b
Malva neglecta	common mallow	Malv.	8	-	-	-	7	h	i
Matricaria recutita	chamomile	Aste.	6	-	-	-	4	с	i
Medicago lupulina	black medick	Faba.	11	-	-	1	7	h	i
Medicago sativa	alfalfa	Faba.	5	-	-	-	5	с	i
Melilotus officinalis	yellow sweet clover	Faba.	10	-	-	-	7	h	i
Melissa officinalis	lemon balm	Lami.	1	-	-	-	1	с	i
Mentha sp.	mint	Lami.	1	-	-	-	1	c	i
Mentha spicata	spearmint	Lami.	6	-	-	-	4	h	i
Mimulus ringens	monkeyflower	Scro.	3	-	-	-	2	h	n
Mollugo verticillata	carpetweed	Moll.	1	-	-	-	1	h	n
Momordica charantia	bitter melon	Cucu.	2	-	-	-	1	с	i
Monarda didyma	beebalm	Lami.	1	-	-	-	1	с	n
Monarda fistulosa	wild bergamot	Lami.	7	-	-	-	4	с	n
Nasturtium officinale	watercress	Bras.	1	-	1	-	-	h	i
Nepeta cataria	catnip	Lami.	4	-	-	1	2	с	i
Nicotiana sp.	nicotiana	Sola.	2	-	-	-	1	с	i
Ocimum basilicum	basil	Lami.	2	-	-	-	2	С	i
Oenothera sp.	primrose	Onag.	7	-	-	-	6	h	n
Origanum vulgare	oregano	Lami.	2	-	-	1	1	с	i
Oxalis rubra	oxalis	Oxal.	1	-	-	-	1	c	i
Oxalis sp.	wood sorrel	Oxal.	22	-	3	3	11	h	i
Packera sp.	groundsel	Aste.	2	1	1	-	-	h	n
Papaver sp.	рорру	Papa.	2	-	-	-	1	с	i

			Crop Sites						
Species	Common name	Fam- ily	All sites	Apple	Blueberry	Caneberry	Cucurbit	Type	Origin
Penstemon digitalis	foxglove beardtongue	Scro.	2	-	-	-	1	h	n
Petroselinum crispum	parsley	Apia.	1	-	-	-	1	с	i
Phaseolus vulgaris	bean	Faba.	13	-	-	1	10	c	i
Phlox paniculata	garden phlox	Pole.	3	-	-	-	2	h	n
Phlox subulata	moss phlox	Pole.	1	1	-	-	-	h	n
Physalis philadelphica	tomatillo	Sola.	5	-	-	-	5	c	i
Physalis virginiana	Virg. groundcherry	Sola.	11	-	-	2	8	h	n
Phytolacca americana	pokeweed	Phyt.	20	-	-	4	13	h	n
Pisum sativum	garden pea	Faba.	4	-	-	-	3	c	i
Plantago lanceolata	narrowleaf plantain	Plan.	21	-	-	4	12	h	i
Polygonum convolvulus	climbing buckwheat	Poly.	6	-	-	-	5	v	i
Polygonum sp.	smartweed	Poly.	26	-	-	4	14	h	b
Portulaca oleracea	purslane	Port.	6	-	-	-	4	h	i
Potentilla sp.	cinquefoil	Rosa.	17	2	6	2	5	h	b
Prunella vulgaris	heal-all	Lami.	7	-	-	1	5	h	i
Prunus sp.	cherry	Rosa.	2	1	1	-	-	S	b
Pueraria montana	kudzu	Faba.	1	-	-	-	1	v	v
Pycnanthemum tenuifolium	narrowleaf mtn.mint	Lami.	3	-	-	-	2	h	n
Ranunculus abortivus	ranunculus	Ranu.	2	1	1	-	-	h	n
Ranunculus bulbosus	buttercup	Ranu.	5	-	3	1	1	h	i
Robinia pseudoacacia	black locust	Faba.	1	1	-	-	-	t	n
Rosa multiflora	multiflora rose	Rosa.	3	-	-	2	1	S	V
Rosa palustris	swamp rose	Rosa.	2	-	-	-	1	h	n
Rubus allegheniensis	blackberry	Rosa.	8	-	1	1	5	S	n
Rubus flagellaris	dewberry	Rosa.	2	-	1	-	1	S	n
Rubus sp.	blackberry	Rosa.	2	-	-	-	2	S	n
Rudbeckia fulgida/hirta	blackeyed Susan	Aste.	7	-	-	1	4	h	n
Rudbeckia laciniata	orange coneflower	Aste.	4	-	-	-	3	h	n
Rudbeckia triloba	browneyed Susan	Aste.	1	-	-	-	1	h	n
Ruellia caroliniensis	wild petunia	Acan.	1	-	-	-	1	h	n
Rumex obtusifolius	broad-leaved dock	Poly.	3	-	-	-	3	h	i
Salvia nemorosa	meadow sage	Lami.	1	-	1	-	-	с	i
Salvia officinalis	sage	Lami.	2	-	-	-	1	С	i
Sambucus nigra	elderberry	Capr.	8	-	-	3	4	S	n
Saponaria officinalis	bouncingbet	Cary.	9	-	-	1	5	h	i
Sassafras albidum	sassafras	Laur.	5	3	2	-	-	t	n
Schizachyrium scoparium	little bluestem	Poac.	1	-	-	-	1	g	n
Securigera varia	crownvetch	Faba.	15	-	-	1	9	h	i
Sedum ternatum	stonecrop	Cras.	1	-	-	-	1	h	n
Sida spinosa	prickly sida	Malv.	2	-	-	-	2	h	n
Silene latifolia	campion	Cary.	4	-	-	-	4	h	1
Silene sp.	campion, catchfly	Cary.	2	-	-	-	2	h	b
Silene vulgaris	bladder campion	Cary.	1	-	1	-	-	h	1

			Crop Sites						
Species	Common name	Fam- ily	All sites	Apple	Blueberry	Caneberry	Cucurbit	Type	Origin
Silphium trifoliatum	whorled rosinweed	Aste.	4	-	-	-	3	h	n
Sisyrinchium angustifolium	blue-eyed grass	Irid.	1	-	-	-	1	h	n
Sium suave	water parsnip	Apia.	2	-	-	-	2	h	n
Smallanthus uvedalius	hairy leafcup	Aste.	2	-	-	-	2	h	n
Solanum carolinense	horsenettle	Sola.	28	-	-	3	15	h	n
Solanum lycopersicum	tomato	Sola.	27	-	-	2	14	c	i
Solanum melongena	eggplant	Sola.	12	-	-	1	8	c	i
Solanum ptycanthum	black nightshade	Sola.	10	-	-	3	6	h	n
Solanum tuberosum	potato	Sola.	6	-	-	1	3	c	i
Solidago sp.	goldenrod	Aste.	6	-	-	-	5	h	n
Sonchus arvensis	sowthistle	Aste.	12	-	-	2	8	h	i
Stachys byzantina	lambsear	Lami.	1	-	-	-	1	c	i
Stellaria graminea	lesser stitchwort	Cary.	2	-	-	-	1	h	i
Stellaria media	chickweed	Cary.	13	3	7	1	2	h	i
Stellaria pubera	star chickweed	Cary.	1	-	1	-	-	h	n
Tagetes sp.	marigold	Aste.	3	-	-	-	3	h	i
Tanacetum parthenium	feverfew	Aste.	2	-	-	-	1	с	i
Tanacetum vulgare	tansy	Aste.	1	-	-	-	1	с	i
Taraxacum officinale	dandelion	Aste.	36	5	6	3	15	h	i
Teucrium canadense	American germander	Lami.	10	-	-	2	5	h	n
Thalictrum pubescens	tall meadow rue	Ranu.	1	-	-	-	1	h	n
Thymus vulgaris	thyme	Lami.	3	-	-	-	3	c	i
Tithonia rotundifolia	Mexican sunflower	Aste.	3	-	-	-	2	с	i
Tragopogon dubius	oysterplant	Aste.	1	-	-	1	-	h	i
Trifolium incarnatum	crimson clover	Faba.	1	-	-	-	1	с	i
Trifolium pratense	purple clover	Faba.	31	-	-	5	14	h	i
Trifolium repens	white clover	Faba.	34	-	-	5	16	h	i
Triodanus perfoliata	Venus' looking-glass	Camp.	2	-	-	-	1	h	n
Tropaeolum sp.	nasturtium	Trop.	1	-	-	-	1	c	i
Uvularia sp.	bellwort	Lili.	1	1	-	-	-	h	n
Verbascum blattaria	moth mullein	Scro.	13	-	-	3	8	h	i
Verbascum thapsus	common mullein	Scro.	5	-	-	-	5	h	i
Verbena hastata	vervain	Verb.	3	-	-	-	2	h	n
Verbena urticifolia	white vervain	Verb.	9	-	-	-	7	h	n
Verbesina alternifolia	wingstem	Aste.	3	-	-	-	3	h	n
Verbesina occidentalis	wingstem	Aste.	1	-	-	-	1	h	n
Verbesina sp.	wingstem	Aste.	6	-	-	1	5	h	n
Vernonia noveboracensis	New York ironweed	Aste.	6	-	-	-	4	h	n
Veronica arvensis	corn speedwell	Scro.	12	3	4	1	3	h	i
Veronica officinalis	common speedwell	Scro.	1	-	-	1	-	h	i
Viburnum prunifolium	blackhaw viburnum	Capr.	4	1	2	-	1	S	n
Vicia sativa	common vetch	Faba.	4	-	-	-	4	h	i
Vicia villosa	hairy vetch	Faba.	8	-	-	2	6	h	i

				Crop Sites					
Species	Common name	Fam- ily	All sites	Apple	Blueberry	Caneberry	Cucurbit	Type	Origin
Viola sp.	violet	Viol.	9	3	6	-	-	h	n
Yucca filamentosa	yucca	Agav.	2	-	-	-	1	h	n
Zea mays	corn	Poac.	11	-	-	-	9	с	c
Zinnia sp.	zinnia	Aste.	3	-	-	-	2	c	c

Abbre-	Plant	Common	Abbre-	Plant	Common
viation	family	name	viation	family	name
Acan.	Acanthaceae	acanthus	Fuma.	Fumariaceae	fumitory
Acer.	Aceraceae	maple	Gera.	Geraniaceae	geranium
Agav.	Agavaceae	agave	Irid.	Iridaceae	iris
Amar.	Amaranthaceae	amaranth	Jugl.	Juglandaceae	walnut
Apia.	Apiaceae	parsley	Lami.	Lamiaceae	mint
Apoc.	Apocynaceae	dogbane	Laur.	Lauraceae	laurel
Ascl.	Asclepiadaceae	milkweed	Lili.	Liliaceae	lily
Aste.	Asteraceae	aster	Magn.	Magnoliaceae	magnolia
Bals.	Balsaminaceae	balsam	Malv.	Malvaceae	mallow
Berb.	Berberidaceae	barberry	Moll.	Molluginaceae	carpetweed
Betu.	Betulaceae	birch	Olea.	Oleaceae	olive
Bign.	Bignoniaceae	trumpet-creeper	Onag.	Onagraceae	primrose
Bora.	Boraginaceae	borage	Oxal.	Oxalidaceae	wood-sorrel
Bras.	Brassicaceae	mustard	Papa.	Papaveraceae	рорру
Budd.	Buddlejaceae	butterflybush	Phyt.	Phytolaccaceae	pokeweed
Camp.	Campanulaceae	bellflower	Plan.	Plantaginaceae	plantain
Capp.	Capparaceae	caper	Plum.	Plumbaginaceae	leadwort
Capr.	Caprifoliaceae	honeysuckle	Poac.	Poaceae	grass
Cary.	Caryophyllaceae	pink	Pole.	Polemoniaceae	phlox
Cela.	Celastraceae	bittersweet	Poly.	Polygonaceae	buckwheat
Chen.	Chenopodiaceae	chenopod	Port.	Portulacaceae	purslane
Clus.	Clusiaceae	mangosteen	Prim.	Primulaceae	primrose
Comm.	Commelinaceae	spiderwort	Ranu.	Ranunculaceae	buttercup
Conv.	Convolvulaceae	morning glory	Rosa.	Rosaceae	rose
Corn.	Cornaceae	dogwood	Rubi.	Rubiaceae	madder
Cras.	Crassulaceae	orpine	Scro.	Scrophulariaceae	figwort
Cucu.	Cucurbitaceae	cucurbit	Sima.	Simaroubaceae	quassia
Dips.	Dipsacaceae	teasel	Sola.	Solanaceae	nightshade
Elae.	Elaeagnaceae	oleaster	Trop.	Tropaeolaceae	nasturtium
Euph.	Euphorbiaceae	spurge	Verb.	Verbenaceae	verbena
Faba.	Fabaceae	legume	Viol.	Violaceae	violet

Appendix F: Survey form for farm management practices

Farm owner(s):	 Farm:
Farm crops & size:	County:
Address:	Date:
Crop	Other comments
Varieties	
Crop acres	
Irrigated (how often)?	
Fertilizers?	
Fertil. appln times	
Common pests	
Pesticides used? herb/ fung/pesticide	
Pestic. appln times	
Fallow (how often)?	
Cover crop(s)?	
No. & cond. h-bee col's	
H-bee col brought in	

Appendix G: National Land Cover Dataset 2001 land cover class descriptions (for classes at study sites in southwest Virginia, as found in Homer et al 2004). Used under Fair Use, 2011.

Name	Class Description
Open Water	All areas of open water, generally with less than 25% cover of vegetation or
	soil.
Developed,	Includes areas with a mixture of some constructed materials, but mostly
Open Space	vegetation in the form of lawn grasses. Impervious surfaces account for less
	than 20 percent of total cover. These areas most commonly include large-lot
	single-family housing units, parks, golf courses, and vegetation planted in
	developed settings for recreation, erosion control, or aesthetic purposes.
Developed,	Includes areas with a mixture of constructed materials and vegetation.
Low	Impervious surfaces account for 20–49 percent of total cover. These areas
Intensity	most commonly include single-family housing units.
Developed,	Includes areas with a mixture of constructed materials and vegetation.
Medium	Impervious surfaces account for 50–79 percent of the total cover. These
Intensity	areas most commonly include single-family housing units.
Developed,	Includes highly developed areas where people reside or work in high
High	numbers. Examples include apartment complexes, row houses and
Intensity	commercial/industrial. Impervious surfaces account for 80 to100 percent of
	the total cover.
Barren Land	Barren areas of bedrock, desert pavement, scarps, talus, slides, volcanic
	material, glacial debris, sand dunes, strip mines, gravel pits and other
	accumulations of earthen material. Generally, vegetation accounts for less
	than 15% of total cover.
Deciduous	Areas dominated by trees generally greater than 5 meters tall, and greater
Forest	than 20% of total vegetation cover. More than 75 percent of the tree species
	shed foliage simultaneously in response to seasonal change.
Evergreen	Areas dominated by trees generally greater than 5 meters tall, and greater
Forest	than 20% of total vegetation cover. More than 75 percent of the tree species
	maintain their leaves all year. Canopy is never without green foliage.
Mixed	Areas dominated by trees generally greater than 5 meters tall, and greater
Forest	than 20% of total vegetation cover. Neither deciduous nor evergreen species
	are greater than 75 percent of total tree cover.
Shrub/Scrub	Areas dominated by shrubs; less than 5 meters tall with shrub canopy
	typically greater than 20% of total vegetation. This class includes true
	shrubs, young trees in an early successional stage or trees stunted from
	environmental conditions.
Grassland/	Areas dominated by graminoid or herbaceous vegetation, generally greater
Herbaceous	than 80% of total vegetation. These areas are not subject to intensive
	management such as tilling, but can be utilized for grazing.
Pasture Hay	Areas of grasses, legumes, or grass-legume mixtures planted for livestock
	grazing or the production of seed or hay crops, typically on a perennial cycle.
	Pasture/hay vegetation accounts for greater than 20 percent of total
	vegetation.

Name	Class Description
Cultivated	Areas used for the production of annual crops, such as corn, soybeans,
Crops	vegetables, tobacco, and cotton, and also perennial woody crops such as
	orchards and vineyards. Crop vegetation accounts for greater than 20 percent
	of total vegetation. This class also includes all land being actively tilled.
Woody	Areas where forest or shrubland vegetation accounts for greater than 20
Wetlands	percent of vegetative cover and the soil or substrate is periodically saturated
	with or covered with water.
Emergent	Areas where perennial herbaceous vegetation accounts for greater than 80
Herbaceous	percent of vegetative cover and the soil or substrate is periodically saturated
Wetlands	with or covered with water.

Appendix H: Additional acknowledgements

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