BEE ABUNDANCE AND DIVERSITY IN BERRY AGRICULTURE

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Abstract

I studied the abundance, diversity and dispersal patterns of managed and wild bee populations in and around commercial highbush blueberry and cranberry fields in the Fraser Valley of British Columbia, and assessed their potential as pollinators of these crops by determining which groups of bees had the greatest impact on crop yield.

I found greater species diversity than previous studies but bee diversity was not correlated to berry weight. Bumble bees dispersed well within both crops. Other wild bees were well-distributed in blueberry fields but generally remained at cranberry field edges. Wild bee abundance was correlated between fields and surrounding areas, suggesting that wild bees were readily able to cross into fields although bee abundance varied greatly between fields. Blueberry and cranberry weight were related to bumble bee abundance but not to honey or other wild bee abundance. Bumble bees are recommended as potential alternative pollinators of these crops.

Keywords: *Apis*; *Bombus*; bee diversity; blueberry; cranberry

To my Mummy, Baba, Flavs and Jadon.

You are my life.

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Chapter 1: Introduction

Expanding human population and increasing expectations of higher living standards have driven agriculture towards higher-acreage growing operations, denser plantings and high-intensity pesticide use (Backman and Tiainen 2002). This intensification of agricultural practices may destroy bee nesting and hibernation sites and natural food resources, decreasing wild bee populations (Free 1993; Williams 1982; Macfarlane, Griffin and Read 1983). Pushed by these pressures, North American agriculture attempted to meet crop pollination requirements by the sole use of the only historically available managed pollinator, the introduced European honey bee, rather than relying on native wild bees and introduced alternative pollinators.

1.1 General Pollination Requirements

Pollination is the transfer of pollen from an anther to the stigma. Pollen travels down the style to the ovule where fertilisation occurs. The pollen grain and ovule fuse to form an embryo which develops into a seed. The ovary around the seed matures after fertilisation to form a fruit (Meeuse and Morris 1984).

Plants may be self pollinated or may rely on an external vector to transfer pollen from anther to stigma. Cross pollination, pollen transfer between flowers of different individuals of the same species, increases the heterozygosity of a plant's offspring, hiding deleterious alleles and increasing offspring vigour and is mandatory for seed production in self incompatible plants (Kearns and Inouye 1997). Each plant species has an optimal number of pollen grains that need to be deposited on the stigma to produce maximum seed and fruit set, in turn maximising fruit size and weight. Competition between pollen grains results in genetically superior seeds since the most vigorous pollen grains will travel fastest down the style to fertilise the ovule (Kearns and Inouye 1997). Insufficient deposition of pollen can lead to reduced seed and fruit production (Kearns and Inouye 1997).

At least 67% of modern flowering plants depend on insect pollination (Kearns and Inouye 1997) with bees being the most common insect pollinators. There are between 20 000 and 40 000 species of bees worldwide (Kearns and Inouye 1997), each of which have specific emergence times, life spans, nesting habitats, temperature ranges in which they can forage, floral preferences and foraging behaviour (Bosch and Kemp 2002). Thus pollinator and plant must be spatially, temporally and behaviourally adapted for each other.

Generalist flowers are pollinated by a wide range of pollinators while specialist flowers rely on a narrower range of pollinators. Generalist flowers will have a greater variety of visitors but any single visitor may not be particularly effective. Specialist flowers attempt to exclude visitors that could either rob resources without pollinating the plant or are less effective, providing minimal pollination for the amount of resources consumed. Factors such as flower size, colour, scent or accessibility of rewards may determine which pollinators visit (Bosch and Kemp 2002; Kearns and Inouye 1997). Some flowers hide nectar rewards so that only bees with a specific tongue length can access them while others have specialized pollen release mechanisms, such as poricidal anthers, that can not be triggered by specific bees (Kearns and Inouye 1997). Effective pollinators will facilitate the outcrossing of a plant's genes and maximise seed and fruit production.

1.2 Crop Pollination and Alternative Pollinators

Thirty percent of human food requires or benefits from bee pollination but not all pollinators work equally well for all crops (Kearns and Inouye 1997). A paucity of appropriate pollinators can lead to inadequate seed set which in turn can lead to smaller, often lopsided fruit having reduced market value (Birmingham 2003). Understanding specific pollination requirements of a crop can lead to improved management practices and in turn influence crop yields.

Alfalfa seed production dropped drastically in the Canadian prairies in the 1940's as fields became larger and more intensively managed, eliminating nesting sites for native bees (Kevan and Phillips 2001). By the 1950's small fields yielded 1000kg/ha but large fields yielded only 15kg/ha where there were too few native bees to pollinate anything but the periphery of the field (Kevan and Phillips 2001). Alfalfa is poorly pollinated by honey bees since they quickly learn to steal nectar from the sides of the flower, avoiding tripping the pollen dispensing mechanism and attempts to use this species yielded no improvement in crop production (Kearns and Inouye 1997). *Megachile rotundata* and *Nomia melanderi* are now regularly used to pollinate alfalfa, with much better success than honeybees (Kearns and Inouye 1997; Kevan and Phillips 2001). "Megachileculture" is now worth about $6 million CDN per year in the Canadian prairies alone with economic benefits estimated at 35% of annual crop production (Kevan and Phillips 2001).

Greenhouse tomato pollination used to rely on human workers using hand-held electronic vibrators, an extremely costly method (Kevan and Phillips 2001). Attempts to introduce honeybee colonies were ineffective since honeybees were unable to extract pollen from tomato anthers. Artificially reared bumblebee colonies are now brought in and are the sole pollinators of greenhouse tomatoes, greatly reducing pollination costs and producing superior fruit (Birmingham 2003; Kevan and Phillips 2001). The greenhouse tomato industry is worth $200 million CDN annually in British Columbia alone (Birmingham 2003). The value of "bombiculture" has not been assessed but is estimated at millions of dollars worldwide (Kevan and Phillips 2001)

Osmia spp. are now commonly used throughout the United States to pollinate fruit trees, increasing orchard yields (Bosch and Kemp 2002). Honeybees are minimally attracted to fruit trees and quickly learn to 'side-work' flowers, robbing nectar without making contact with the stigma, thus not pollinating the crop (Bosch and Kemp 2002). *Osmia spp.* make stigmatic contact almost 100% of the time, increasing seed set and therefore producing larger, rounder fruit with increased market value (Bosch and Kemp 2002; Narcis and Bosch 2000).

1.3 Blueberry and Cranberry Pollination

The introduced managed honey bee (*Apis mellifera* L.) has been the primary pollinator of most North American crops but many wild bee species might be better suited as pollinators of specific crops, including highbush blueberry and cranberry (Ericaceae: *Vaccinium corymbosum*, *Vaccinium macrocarpon*). Both are major crops in the Fraser Valley of British Columbia, Canada (BCCGA 2003; Dogterom, Winston and Mukai 2000). B.C. is the second largest producer of highbush blueberries in the world, and accounts for 97% of Canadian production, and 99% of B.C.'s production comes from the Fraser Valley. In 2002, B.C. produced 16.7 million kg of highbush blueberries with a farm gate value of over $44.2 million (MAFF 2003). Cranberries are one of British Columbia's largest berry crops by both volume and value, with over 340,000,000 kg produced in the lower Fraser Valley and on Vancouver Island annually, accounting for approximately 12% of cranberry production in North America. (BCCGA 2003).

However, both blueberry and cranberry yields may be less than optimal in the Fraser Valley. 'Small berry syndrome', common in certain regions of the Fraser Valley and is presumed to be caused by insufficient pollination (Dogterom, personal communications). Likewise, cranberries may be setting as little as 30% of their optimal yield (Sweeney, personal communications).

1.3.1 Pollination Requirements

Highbush blueberries and cranberries (Ericaceae: *Vaccinium corymbosum*, *Vaccinium macrocarpon*) benefit from bee pollination to increase fruit set, seed number, berry size and weight, and decrease ripening time (reviewed by Free 1993; McGregor 1976). Unvisited cranberry flowers rarely set fruit (Cane and Schiffhauer 2001).

Blueberry flower stigmatic loading with pollen is positively correlated with increased fruit set, seed number, berry weight and shorter ripening time (Dogterom, Winston and Mukai 2000; Free 1993; Stubbs and Drummond 2001). Highbush blueberries var. 'bluecrop' required deposition of 125 pollen tetrads per stigma for optimal fruit quality (Dogterom, Winston and Mukai 2000), and therefore flowers must be visited numerous times by pollinators that deposit considerably fewer than 125 pollen grains per visit to produce a large blueberry. Honey bees, for example, deposit between five to 20 grains per visit (Javorek et al. 2002).

Cranberries require deposition of eight pollen tetrads per stigma for optimal fruit set, and fruit mass increases only slightly with more than eight tetrads. Seed number is maximised with 16 pollen tetrads (Cane and Schiffhauer 2001; 2003).

Greater seed number increases size and weight of many fruit including apple (Blazek and Hlusickova 2006), kiwifruit (Hopping 1976), pear (Hong et. al 1991), cucumber (Nitsch 1952), strawberry (Nitsch 1950), and tomato (Bell, Spooner-Hart, and Haigh 2006). Ultimately, it is crop yield, which is largely determined by fruit size and weight, which is most important to the grower. Most studies have found that better-pollinated blueberries have more mature seeds and in turn have larger, faster ripening berries, but a few studies have failed to find a relationship between blueberry size and seed number (reviewed by Free 1993). Varieties vary in setting different amounts of fruit without pollination (0 – 45%, Free 1993), having different average size of well pollinated fruits (Brewer and Dobson 1969) and possibly having different mean ovule numbers (Elizabeth Elle, Margriet Dogterom, personal communications) and therefore need to be analysed individually. It is important to determine if berry weight is directly linked to pollination through seed number, and not just a factor of other variables such as amount of rain, temperature, or amount of sunlight.

There also is a positive relationship between cranberry seed number and berry size (Eaton 1966; Filmer, Marucci and Moulter 1958; Rigby and Dana 1971; Sarracino and Vorsa 1991) but the relationship between seed number and berry weight has not been investigated. Confirming the relationship between seed number and berry weight would allow the use of berry weight as an indication of pollination level and further demonstrate the importance of pollination to the grower.

Blueberries bloom early in the spring when cool, wet weather conditions often prevail (O'Toole 1993; Javorek et al. 2002, Winston and Graf 1982) and many species of bees have not emerged. Some managed pollinators can be made available in early spring through artificial rearing practices, but may have limited foraging activity unless capable of flight and foraging under cool spring conditions (Javorek 1996).

Blueberries and cranberries have poricidal anthers, a pollen dispensing mechanism that allows small amounts of pollen to be released at a time through a pore at the tip of the anther (Buchmann 1983). The buzz pollination practiced by most wild bees (*Bombus*, *Andrena*, *Halictus*, *Osmia*, *Lasioglossum*, *Agapostemon*, etc) is the most effective method of removing pollen from poricidal anthers (Free 1993; Sampson 1993; Buchmann 1983), whereby a bee contracts and relaxes her indirect flight muscles thereby vibrating the pollen out of the pore (Buchmann 1983; Free 1993). Honey bees and *Megachile spp.* do not buzz pollinate, but instead use their legs to 'drum' pollen from poricidal anthers (Buchman 1983; Javorek et al. 2002; Cane, Schiffhauer and Kervin 1996; MacKenzie 1994). A direct comparison has not been made between buzz pollination and drumming of pollen grains but it is generally believed that buzz pollination results in release of larger amounts of pollen (Free 1993; Sampson 1993; Buchmann 1983). Honey bees have been observed drumming cranberry flowers when collecting pollen (less than 2% of honey bee cranberry pollen foragers), but have not been observed drumming any other species of *Vaccinium* (Cane, MacKenzie and Schiffhauer 1993), and removal and delivery of pollen by honeybees from poricidal anthers has been shown to be low (Cane and Schiffhauer 2001; Dogterom and Winston 1999; Javorek et al. 2002; MacKenzie 1994). Since only some bee species are capable of buzz pollination, it is important to determine whether these species are present in large enough numbers in commercial fields to promote fruit production.

1.3.2 Honey Bee Pollination

Managed honey bees, *Apis mellifera*, are excellent generalist pollinators but are inefficient on some crops with specialised pollination requirements (O'Toole 1993). In spite of their limitations, honey bees are commonly used for commercial blueberry and cranberry pollination due to their availability and economics (McGregor 1976; Free 1993; Kevan 1977) but their effectiveness on blueberries and cranberry is questionable (MacKenzie 1994). Reliance on honey bees as the sole pollinator of blueberries and cranberries faces several challenges including the limitations of weather conditions, preferences for non-crop bloom, and infrequent collection of blueberry and cranberry pollen, qualities that must be weighed against honey bee affordability and availability.

Honey bee foraging ability is diminished by the cool, wet weather conditions that prevail during blueberry bloom (Javorek et al. 2002; Winston and Graf 1982). They are unable to fly in rain, rarely forage in temperatures below 16°C, and colony growth ceases below 10°C (Heinrich 1979).

Individual honey bee foragers specialise on either pollen or nectar collection. Pollen-foraging bees pollinate 6 times more blueberry flowers than nectar foragers since they have more pollen grains on their bodies (Javorek et al. 2002) but honey bee pollen foragers collected blueberry pollen only 3 to 7% of the time, almost invariably collecting pollen from other floral sources (Dogterom and Winston 1999; Stubbs and Drummond 2001). Honey bee nectar foragers readily forage on blueberry flowers but the proportion of blueberry pollen on their bodies did not exceed 13%, foragers had fewer than 100 grains on their bodies, and they only deposited between 5 – 20 grains per floral visit (Dogterom and Winston 1999; Javorek et al. 2002). These pollen grains may be transferred to a stigma but are too few to produce an optimally sized berry as 125 grains must be deposited to produce desired yields (Dogterom, Winston and Mukai 2000), so multiple visits by honeybees would be required. Honey bee nectar foragers have slower visitation rates than most other bees found foraging on blueberries (Javorek et al. 2002).

Beekeepers generally report that honey bee colonies placed in cranberry fields fare poorly (Cane, MacKenzie and Schiffhauer 1993; Marucci 1967). Honey bees do not readily visit cranberries due to the flower's low nectar rewards (Cane and Schiffhauer 1997), preferring other plants flowering nearby (Cane, Schiffhauer and Kervin 1996; Farrar and Bain 1946; Kevan et al. 1983; Marucci 1967; Marucci and Moulter 1977). Honey bee presence can have no detectable effect on fruit or seed set (Kevan et al. 1983) though they did increase berry size in caged pollination experiments (Farrar and Bain 1946).

Honey bees can forage for cranberry nectar directly but also rob nectar by side-working flowers from above, not making contact with the stigma (Cane, MacKenzie and Schiffhauer 1993; Cane and Schiffhauer 2003; Cane and Schiffhauer 2001; MacKenzie 1994). Only 41.4% of honey bee nectar foragers contacted the cranberry stigma, while 95.9% of bumble bees did so when foraging for nectar (MacKenzie 1994).

Honey bee pollen foragers were 64% better pollinators than non-thieving nectar foragers since they more often delivered over eight pollen tetrads (Cane and Schiffhauer 2001). Cane and Schiffhauer (2001) calculated that 77% of flowers visited by pollen foragers but only 47% of flowers visited by nectar foragers that made stigmatic contact would set fruit.

Honey bees rarely and unpredictably forage for pollen on cranberry (Cane, MacKenzie and Schiffhauer 1993; Farrar and Bain 1946; MacKenzie 1994). From 0% to 98% of pollen collected by honey bees was from cranberry and the proportion of foragers collecting cranberry pollen varied significantly from year to year, between neighbouring fields in the same year, or even between different colonies in the same field (Cane, MacKenzie and Schiffhauer 1993; MacKenzie 1994; Shimanuki, Lehnert and Stricker 1967).

Experiments with honey bees often are conducted in cages to force foragers to collect cranberry pollen (Cane and Schiffhauer 2001; Cane and Schiffhauer 2003; MacKenzie 1994). Caged honey bees provided satisfactory pollination (Farrar and Bain 1946) but nectar robbers were more abundant in field conditions (Cane and Schiffhauer 2003). Twenty percent of foragers in a cage but only 2% of neighbouring non-caged foragers collected cranberry pollen (Cane, MacKenzie and Schiffhauer 1993). As few as 1.5 % and 3.2 % of honey bees collected pollen from cranberry under open field conditions (MacKenzie 1994; Shaw, Shaw and Weidhaas 1956).

However, honey bee colonies are easily transported and can be brought into a field at the time of bloom with minimal effort, at a cost of $55 to $60 (Cdn) per colony for blueberry pollination and $90 to $115 (Cdn) per colony for cranberry pollination in

2005 (Paul VanWestendorp, personal communications). The difference in rental cost is due to the greater stress put on honey bee colonies when foraging on cranberry. Other managed pollinators such as bumble bees (*Bombus spp.*) and mason bees (*Osmia spp.*) are more costly, difficult to manage or transport, or simply unavailable commercially (Cane, Schiffhauer and Kervin 1996; McGregor 1976; Free 1993; Kearns and Inouye 1997).

1.3.3 Wild Pollinators

Many species of non-*Apis* pollinators are more effective than honey bees at pollinating blueberries and cranberries and can be an important source of improved and sustainable berry production. The usefulness of alternative pollinators is determined by both pollination effectiveness and economics.

Bumble bees (*Bombus spp.*) can forage in moderate to heavy rain, starting earlier in the morning and at temperatures below 10°C that limit *A. mellifera* (Free 1993; Heinrich 1979; Stubbs and Drummond 2001). Non-*Apis* bees foraging on blueberry flowers collect both nectar and pollen (Javorek et. al, 2002) and therefore are likely to have sufficient pollen grains on their bodies to produce large berries. This is reflected in pollination rates that are higher than those of *A. mellifera*. *Bombus spp.* queens pollinated 6.5 flowers, *Bombus spp.* workers pollinated 5.4 flowers, *Andrena spp.* pollinated 3.6 flowers, *M. rotundata* pollinated 3.4 flowers, and *Halictus spp.* pollinated 2.7 flowers in the time that it would take *A. mellifera* to pollinate 1 flower. These taxa also deposited more pollen grains per flower pollinated. One honey bee would have to visit a flower 2.2 times to deposit the same amount of pollen as a single visit from *Halictus spp.*, 4.0 times to equal one *Andrena spp.* visit, and 4.3 times to equal a single visit from a *Bombus spp.* queen (Javorek et al. 2002).

Multiplying pollination rate by the number of pollen grains deposited per flower suggests even larger differences in overall pollination ability between pollinator taxa. Taken together, these measures suggest that non-*Apis* bees are pollinating more flowers in any given time period and are pollinating each of these flowers better than *A. mellifera*.

Many wild bee species collect cranberry pollen, especially bumble bees (Cane, MacKenzie and Schiffhauer 1993; Cane, Schiffhauer and Kervin 1996; Kevan et al 1983; MackKenzie 1994; MacKenzie and Winston 1984; Winston and Graff 1982). Cranberries exposed to pollination by bumble bees had increased yields, larger fruit and more seeds per berry than cranberries to which only smaller insects had access (Mohr and Kevan 1987). *Bombus afinis* deposited a mean of 61 pollen tetrads per cranberry flower visited, *Megachile addenda* 28 pollen tetrads, *M. rotundata* 15 pollen tetrads and *Apis mellifera* pollen foragers 10 pollen tetrads, while unpollinated flowers had a mean of one pollen tetrad per stigma (Cane, Schiffhauer and Kervin 1996; Cane and Schiffhauer 2003). *B. affinis* were calculated to produce greater percent yield and mass of cranberries than *M. rotundata* and *A. mellifera* and greater number of seeds than *M. addenda*, *M. rotundata* and *A. mellifera* (Cane and Schiffhauer 2003). Between 48% to 74% of bumble bees but only 3% to 16% of honey bees were found gathering cranberry pollen (MacKenzie 1994; Winston and Graf 1982). Bumble bees also forage significantly faster than honey bees, visiting more flowers per minute (MacKenzie 1994).

Megachile addenda were found nesting in fields in New Jersey and all female *M. addenda* and *M. rotundata* were found collecting cranberry nectar and pollen exclusively to provision their nests (Cane, MacKenzie and Schiffhauer 1993; Cane and Schiffhauer 2003; Cane, Schiffhauer and Kervin 1996). Cane, Schiffhauer and Kervin (1996) calculated that one female *M. addenda* would produce 645 to 720 cranberries per nest cell she provisioned, and therefore this species can be a valuable pollinator of cranberries even without active management.

Bumble bees not only collect blueberry and cranberry pollen, but often are abundant (Cane and Schiffhauer 2003; Free 1993; Winston and Graf 1982). *Bombus affinis* were naturally abundant in cranberry fields in New Jersey (Cane and Schiffhauer 2003). In one area there were averages of seven leaf-cutting bees (*Megachile spp.*) and 1107 bumble bees per hectare, mostly *Bombus impatiens*, which were considered sufficient to provide more than adequate pollination (Hutson 1925).

Wild bees could pollinate small or moderate sized fields within easy access of uncultivated land where they nest, but there may not be sufficient wild bees to pollinate large fields (Free 1993; Kevan et al 1983; MacKenzie and Averill 1995; MacKenzie and Winston 1984; Mohr and Kevan 1987; Filmer and Doehlert 1959). Decreased wild bee abundances may be caused by spraying of pesticides (Kevan 1977), or increasing agricultural acreage causing loss of wild habitat where bees nest (Westrich 1996). A relationship between bee abundances of a particular group of pollinators and berry weight would identify which groups of bees are affecting the largest proportion of blueberry and cranberry pollination and whether these bees are sufficiently abundant for adequate pollination. This would permit identifying factors that are associated with abundance of these groups of bees, and thereby permit us to increase their populations in fields where populations are too low for optimal pollination.

1.3.4 Bee Distribution, Diversity and Local and Large Scale Factors

Edges are defined as the boundaries between two distinct habitat or vegetation types (Rand, Tylianakis and Tscharntke 2006). The edges between agricultural fields and the surrounding habitat can act as barriers to movement at a landscape level for arthropods including Araneae, Coleoptera, Diptera, Hemiptera and Lepidoptera (Bedford and Usher 1994; Van Wilgenburg, Maxerolle and Hobson 2001; Wratten et al. 2003). Both slow dispersing arthropods such as carabids and fast flying arthropods with larger foraging ranges and strong eyesight can be affected by edges such as fences, hedgerows, open gaps or lines of dense or sparse trees (Bedford and Usher 1994; Wratten et al. 2003). However, bees must routinely travel between their nests and forage patches through unrewarding matrix and may be better adapted to crossing over edges than other arthropods (Cane 2001). We need to determine if wild bees will enter into blueberry and cranberry fields before attempting to increase their abundance surrounding fields through improved habitat, as providing safe nesting sites surrounding fields may or may not increase bee populations within fields themselves depending on if the edge of the field is acting as a barrier to bee movement.

Some arthropods may cross into fields from the surrounding habitat but may not disperse well in the field itself. Bedford and Usher (1994) found that certain groups of arthropods have limited dispersal in agricultural fields, dropping in diversity and abundance in as little as 5m from the edge of adjacent lands. Similarly, specific groups of bees have been found to decrease in abundance with increasing distance from field edges while other groups are evenly dispersed (Klein, Steffan-Dewenter and Tscharntke 2003; Morandin and Winston 2005). Different species of bees have different maximum dispersal distances ranging from less than 50m to more than 2km (Gathmann and Tcsharntke 2002; Walther-Hellwig and Frankl 2000; Westrich 1996), therefore, the ability of wild bees to disperse into agricultural lands may depend on the bee species. Uneven distribution of wild bees with short dispersal ranges would lead to uneven pollination of crops; therefore it is important to assess bee dispersal within fields if even pollination is to be achieved throughout the entire area.

Unlike most other common invertebrate pollinators, bees are central-place foragers, having to return to a specific nesting location between foraging bouts (Cane 2001; Stephens and Krebs 1986). This method of foraging requires more energy and therefore nesting sites must be located within a feasible distance from all needed resources, such as nest building materials and nectar and pollen sources (Stephens and Krebs 1986; Westrich 1996). Close proximity of nesting sites to crops and all other resources becomes imperative in agricultural landscapes, where natural habitat is scarce, if wild bees are to pollinate crops (Westrich 1996).

Alternate forage can be important to bee populations before, during and after crop bloom. Bees must have alternate forage available in close proximity to their nesting sites before and after crop bloom if bee adult life span does not coincide precisely with crop bloom (Backman and Tiainene 2002; Klein, Steffan-Dewenter and Tscharntke 2003; MacKenzie and Winston 1984). This can be provided as either flowering weeds or as alternate crops with non-concurrent bloom times. During crop bloom, non-crop flowering plant (weed) abundance and bee diversity and abundance have been correlated in several other cropping systems due to the preference of many bee species for diverse floral resources (Backman and Tiainene 2002). For instance, flowering weed cover was the most important predictor of both wild bee abundance and species richness in canola fields (Morandin 2005). Similarly, solitary bee diversity and abundance were positively correlated with increased bloom cover of herbs in coffee plantations (Klein, Steffan-Dewenter and Tscharntke 2003) and in Finland, increased bumble bee abundance was associated with abundance of dicotyledonous flowers in neighbouring patches of farmland (Backman and Tiainen 2002). Increasing flowering weed cover in blueberry and cranberry fields could enhance berry production if flowering weed abundance increases bee abundance and diversity and if bee abundance and diversity increase crop yield. The concept of promoting flowering weed growth during crop bloom is controversial, as traditionally these flowers have been viewed as competitors for the bees' attention (Laverty and Hiemstra 1998; Lipecki 2006). However, increased flowering weed abundance could reduce costs for the grower in the form of reduced mowing, mulching and herbicide spraying. Alternately, increased flowering weeds could compete with crops for soil nutrient, water and sunlight (Lehoczky, Reisinger and Komives 2005; Lipecki 2006)

Both bee abundance and diversity may be important for pollination and increased crop yield (Javorek et al. 2002; Klein, Steffan-Dewenter and Tscharntke 2003). Having a diverse bee fauna would allow for numerous species of bees, with different emergence times, to provide pollination over the entire blooming period of a crop if the life span of any one abundant bee species does not coincide precisely and consistently over years with crop bloom. Also, different bee species forage optimally at different times of day, temperature and weather conditions and may even prefer different heights of bloom (Bosch and Kemp 2002; Heinrich 1979; Roubik 1993), therefore having numerous species would ensure maximum pollination regardless of what time of day, where on the plant or under what weather conditions flowers open. A correlation between bee diversity and berry weight would indicate if numerous bee species are required for optimal pollination.

It must be determined if large scale factors, such as differences between fields and amount of surrounding natural habitat or local scale factors such as distance from the edge of the field and weed diversity have the greatest impact on bee abundance if we are to encourage wild bee populations in agricultural lands.

In this thesis I investigated bee abundance and diversity in highbush blueberry and cranberry fields and their relation to bee abundance surrounding the fields, distance from the edge of the field, and weed abundance. I also assessed how bee abundance and diversity related to mean blueberry and cranberry weight and how berry weight related to number of mature seeds.

Chapter 2: Bee Diversity and Abundance in Blueberry and Cranberry Agriculture

2.1 Objectives

The overall objectives of this thesis were to assess bee abundance and diversity in highbush blueberry and cranberry fields with relation to bee abundance in the surrounding area, distance from the edge of the field, and weed abundance, and to determine if bee abundance or diversity were correlated with berry weight or seed set.

2.2 Methods

I sampled bees in six highbush blueberry (*Vaccinium corymbosum* L.) and five cranberry (*Vaccinium macrocarpon* Ait.) fields in the Fraser Valley of British Columbia, Canada in 2003 and 2004.

2.2.1 Field Layout

In 2003, nine sampling sites were located at each field, and in 2004, eight sampling sites were located at each field. In both years, six of these sampling sites were located diagonally within each field from one corner to the other such that the sites were equidistant to each other to determine if bees were dispersing evenly throughout the field. The edge was sampled at either three sites (2003) or two sites (2004) (Figure 2.1). At each of these sampling sites bees were pan trapped, visually observed and sweep netted, and weed abundance and berry weight assessed. I predicted a large fluctuation in wild bee abundance, but not honey bee abundance, between years and a decrease in bee abundance with increasing distance from the edge of the field.

The edge was designated as the side of the field that had the most natural vegetation ('vegetated edge'). The amount and type of natural vegetation varied among fields ranging from a mere fringe of somewhat longer, unmowed grass to a much larger area with many mature trees and heavy undergrowth. I hypothesised that the vegetated edge would be the location where most of the wild bees would be nesting and therefore coming from. I expected bees to be able to cross in and out of the field readily since their foraging behaviour likely makes them better adapted to crossing over edges than other arthropods (Cane 2001).

The amount of natural to semi-natural habitat and agricultural land surrounding the fields also varied greatly among fields. All blueberry and cranberry fields had other blueberry and cranberry fields along at least one edge but the habitat surrounding the other edges varied from predominantly agricultural to much larger expanses of trees or shrubs.

There was a large variation in the size and shape of the fields varying from 0.5 hectares to 2.8 hectares (1.9 ha ± 0.4 ha) in blueberry fields and from 0.7 hectares to 7.4 hectares (3.0 ha ± 1.2 ha) in cranberry fields and from almost square to a long thin rectangle. Eight different varieties of blueberries were planted in the fields to varying extents: Bluecrop, Duke, June, Nortland, Patriot, Unknowns 1, 2, 3. Bluecrop was the only variety that was planted in more than one field. Stevens variety was planted in all cranberry bogs. I expected different fields to have significant differences in bee abundance.

Honey bee colonies were placed in five of the six blueberry fields and four of the five cranberry fields. Number and location of colonies are shown in Table 2.1.

2.2.2 Sampling Techniques

I used a combination of pan trapping, sweep netting and visual observations to provide robust measures of bee abundance (Cane 2001).

2.2.2.1 Pan Trapping

One trap was set out at each sampling site, consisting of three large pans, one yellow (39 x 28cm; $\lambda = 450$), one white (29 x 21cm; $\lambda = 0$) and one blue (37 x 26cm; $\lambda = 600$). These three colours were used to reduce bias in species caught due to colour preference (Leong and Thorp 1999). Sizes differed as per availability of pans but did not bias results since the three colours were pooled together for all analyses. Each pan was filled with 4cm of water, six large drops of glycerol (~ 0.5ml) to reduce water tension, and approximately 5ml of honey previously dissolved in water. Pan traps were elevated on wooden stands to the height of bloom in blueberry fields and were placed directly on the ground, on top of the cranberry plants in cranberry fields.

In blueberry fields, the traps were set out when a field was 20% in bloom until it was 80% out of bloom. The first traps were set out on April 15th in 2003 and April 3rd in 2004. Bees were collected from the traps every 3 days. In cranberry fields, the traps were set out when a field was 30% in bloom until it was 50% out of bloom. The first traps were set out on June 19th in 2003 and June 11th in 2004. Bees were collected from the traps every four days in 2003 and every three days in 2004. In 2003 the traps were immediately refilled after collection, providing continuous trapping. In 2004 the traps were turned over and left empty for four days after each collection. All specimens were preserved in the field in 70% ethanol and brought back to the laboratory for later pinning, sexing and identification. All bees were identified to species wherever possible, with the exception of *Lasioglossum* (*Dialictus*) which were identified to sub-genus.

2.2.2.2 Visual Observations

Visual observations were made in addition to pan trapping, to quantify the number of bee visits to blueberry and cranberry flowers. Visual observations were conducted by marking the corners of a 1m x 1m quadrat of blooming blueberry or cranberry plants in 2003 at each sampling site and a 2m x 1m quadrat of blooming blueberry plants and 2m x 2m quadrat of blooming cranberry plants in 2004. Visual observations in blueberry fields were conducted by treating the bush as if it were a flat vertical surface. I recorded every bee foraging within the quadrat over a 15 minute period and identified it as either a honey, bumble or other wild bee (herein 'other' bee).

Visual observations were conducted twice in five blueberry fields and once in one blueberry field in 2003 and four times in four blueberry fields and three times in two blueberry fields in 2004. Visual observations were conducted once per cranberry field in each year. Visual observations were done between 1000hrs and 1600hrs, the peak bee foraging hours and whenever possible under sunny weather conditions and temperatures above 12°C when bees were most active (Kevan, 1975).

2.2.2.3 Sweep Netting

A 10m transect was designated at each sampling site both within the field and in the edge. Transects followed crop rows in blueberry fields and ran parallel to the longest edge of the field in cranberry fields and parallel to the nearest edge in field edges. In 2003 I or an assistant walked the length of the transect sweeping above the crop on one side, then turning around at the end of the transect and walking the length of the transect again, sweeping the other side. In this way, 20m were swept at each sampling site. I walked briskly in blueberry fields but slowly in cranberry fields to avoid damaging the crop resulting in approximately 40 sweeps per transect in blueberry and 150 sweeps per transect in cranberry. In 2004, I walked up and down the length of the transect continuously for 5 minutes actively sweeping at all bees observed in order to improve my sweep catching.

Sweeps were conducted immediately following the 15 minutes of visual observations. All specimens were placed in an ethyl acetate kill jar in 2003 and cyanide kill jars in 2004 and brought back to the laboratory for later identification. All bees were identified to species wherever possible, with the exception of *Lasioglossum* (Dialictus) which were identified to sub-genus.

2.2.3 Weed Abundance

I assessed weed abundance once per year at each sampling site, during crop bloom. Six one-meter-square quadrats were assessed at each sampling site, two at either end of the transect and two in the middle. I visually estimated what percent of each quadrat was covered by non-crop bloom. I hypothesised that sampling locations with greater weed abundance would also have greater bee abundance.

2.2.4 Crop Yield

In 2004, I marked two 15cm blueberry stems per sampling site with flagging tape during crop bloom. The 15cm were measured from the tip of a stem close to the top of the bush. The number of flowers was counted at the time of selection.

Two weeks after the end of bloom I covered each stem with a mesh bag to prevent birds and blueberry pickers from eating or collecting the blueberries and to catch any blueberries that fell off. Ripe blueberries were collected into plastic bags once a week and the mesh bag replaced. The blueberries were brought back to the laboratory, weighed, then frozen.

Later, I selected the stem that had the most berries from each sampling site to ensure a large enough sample size of berries. For each date that blueberries were collected from this stem, two blueberries were randomly selected to determine the number of seeds. These two blueberries were examined with a dissecting microscope and all mature, viable seeds were counted (see Dogterom, Winston and Mukai 2000). In addition, all seeds (viable, aborted and unpollinated) from one blueberry at each sampling site were counted to determine the maximum number of potential mature seeds.

In 2004, I marked 10 cranberry uprights with flagging tape at each sampling site, during crop bloom, selecting uprights with 2 to 5 flowers. The developing cranberries were collected two months after bloom was over. The cranberries were brought back to the laboratory, weighed, their colour recorded (white, ¼ red, ½ red, ¾ red, red), then frozen.

Later, three of the ten uprights per sampling site were randomly selected and all cranberries examined with a dissecting microscope to count the number of mature, viable seeds. Mature seeds were defined as dark brown, round, deeply invaginated, and more than 0.2mm in length. All ovules (mature seeds, aborted seeds and unpollinated ovules) from one randomly chosen cranberry at each sampling site were counted to determine the maximum number of potential mature seeds. I predicted a correlation between berry weight and bee diversity, and a relationship between both berry weight and wild bee abundance and number of mature seeds per berry.

2.2.5 Statistical Analysis

Bees were separated into three categories for abundance analyses: honey bees, bumble bees, and 'other' bees. Bumble bees were categorised separately from other wild bees because of their abundance and potential importance as an alternate pollinator to commercial honey bees.

A Chi-Squared test was used to compare honey, bumble and 'other' bee abundances between sampling methods: pan trapping, sweep netting and visual observations. Data from all sampling sites were pooled within each bee category and sampling method to test the hypothesis that similar proportions of bees (*Apis*, *Bombus*, 'other' bees) would be found among the three sampling methods.

Bee abundance was analysed using ANOVA with a split plot in time design since repeated measures were taken on the same fields and sampling sites (Steel, Torrie and Dickey 1997). Field was the main plot and sampling site was the sub-plot with year as the repeated measure. Interactions between these variables were also tested. The model, using shorthand notation was:

log (Bee Abundance) = Field(R) SS Field*SS(R) Year Year*SS

where Field = the different fields we sampled in

SS = the sampling sites sampled in each field

Year = the two years in which bees were sampled

R = random effect representing experiment units on blocks

ProcMixed was used to fit this model (SAS 9.1, SAS Institute Inc. 2003). Sampling sites were treated as categorical since both linear and non-linear variations in bee abundance between sampling sites were of interest. Pan trapped, visually observed and sweep netted bee abundances were analysed separately in blueberry fields but were averaged together per sampling site in cranberry fields since the Chi-Squared test showed no difference between these three sampling methods in cranberry. Sampling sites were not nested in fields since nesting would imply that different sites within a field were replicates of each other but instead each sampling site represented a distinct proportional distance into the field from its edge. A significant effect of site would be interpreted as bees not dispersing well throughout the fields and instead preferring specific locations within the fields, potentially leading to uneven pollination. Differences in sampling effort were controlled for by dividing bee abundance by the number of times an area was sampled to produce mean bee abundance per sampling location and for the size of the area sampled for visually observed bee abundance in 2004 by dividing by the area sampled to produce mean bee abundance per meter squared. For this and all subsequent analyses, ά = 0.05. Data were log transformed to improve normality and heterogeneity of variance but all graphs are of non-transformed data.

The above analysis was repeated with the two outermost sampling sites averaged together (0% and 100%), the next two sampling sites averaged together (20% and 80%) and the centre two sites averaged together (40% and 60%). This tested for bees dispersing well at either end of the field but not the centre, i.e. it took into account that bees might arrive at the field from the nearest edge rather than the designated vegetated edge.

Weed abundance between fields, sampling sites, years and interactions between these variables also were analysed with ANOVA with fields set as a random effect and sites and years considered fixed (SAS 9.1, SAS Institute Inc. 2003).

Variance components were estimated to determine how variation in bee abundance was partitioned between each effect, demonstrating whether large scale (field), small scale (sampling site) or temporal (year) effects had the greatest influence on variation in bee abundance. Variance components were used since both random and fixed sources of variation were present in the model.

Partial correlation analysis (SAS 9.1, SAS Institute Inc. 2003) was used to determine whether mean bee abundance was correlated between edges and fields and to test whether weed abundance and bee abundance were correlated after accounting for variation due to sampling over two years. Linear regression (SAS 9.1, SAS Institute Inc. 2003) was used to determine whether bee abundance affected mean berry weight and whether mean berry weight was determined by the number of mature seeds per berry. A Bonferroni correction was used for blueberry data to control for multiple regressions between bee abundance and berry weight when analysing each variety separately. Correlation analysis (SAS 9.1, SAS Institute Inc. 2003) was used to determine whether mean bumble bee abundance was correlated with mean 'other' bee abundance in blueberry fields and multiple regression analysis was used to determine if bumble bee or 'other' bee abundance had a greater influence on mean blueberry weight wherever both bee categories were significantly related to blueberry weight.

Shannon-Wiener diversity (H) and Shannon evenness indices were calculated for each field and correlated with mean berry weight (SAS 9.1, SAS Institute Inc. 2003) to determine whether bee diversity was related to the size of berries produced. The Shannon-Wiener diversity index was calculated as:

$$H = -\sum_{i=1}^{S} p_i \ln p_i$$

where: H = Shannon-Wiener diversity index

S = the total number of species in the community

p_i = proportion of S made up of the ith species

The Shannon-Wiener diversity index was chosen over Simpson's diversity index since it favours rare species and would be less likely to undervalue the contribution of small numbers of bees of certain species. It is also more commonly used and allowed comparison of diversity values from previous studies in this field.

2.3 Results

2.3.1 Bee Species Captured

A total of 15,646 bees were caught by pan trapping and sweep netting in highbush blueberry fields in 2003 and 2004. Of these, 11,272 were honey bees, 2,742 were bumble bees in at least 13 species and 1632 were 'other' bees in at least 47 species (Table 2.2). Of these, four genera and 19 individuals were parasitic bees.

A total of 4,919 bees were caught by pan trapping and sweep netting in cranberry fields in 2003 and 2004. Of these, 3028 were honey bees, 1168 were bumble bees representing at least 10 species and 723 were 'other' bees of at least 36 species (Table 2.3). Of these, 5 genera and 35 individuals were parasitic bees. Parasitic bees are not likely to contribute significantly to pollination since they lay their eggs in cells provisioned by other species of bees and do not collect pollen themselves (Westrich 1996).

2.3.2 Sampling Techniques

Proportional abundances of the three bee categories between the three sampling methods were significantly different in blueberry fields ($x^2 < 0.0001$) but there was no consistent direction of bias. For example, honey bees were overrepresented in pan traps in four fields but underrepresented in two when compared to visual observations. Therefore, the data from the three sampling techniques could not be pooled for blueberry fields. There was no significant difference in proportional abundances of the three bee categories between the three sampling methods in cranberry fields ($x^2 = 0.18$) and so bees captured with different methodologies were combined for all cranberry analyses presented below.

2.3.3 Bee Distribution

In blueberry fields there was a significant difference in the abundance of pan trapped honey bees between sampling sites when analysed from the edge with the most natural vegetation ($F_{5,25} = 3.92$, $P = 0.0092$) (Figure 2.2, Table 2.4). There were no significant differences between sampling sites for abundance of visually observed or sweep netted honey bees or for bumble bees or 'other' bees with any sampling method. There were no significant differences for any bee category with any sampling method when analysed from the nearest edge (Figure 2.3).

In cranberry fields there was a significant difference between sampling sites for abundance of 'other' bees when analysed from both the edge with the most natural vegetation (Figure 2.4, Table 2.5) and from the nearest edge (Figure 2.5). There were no significant differences between sampling sites for either honey or bumble bee abundance.

In blueberry fields bee abundance was significantly different between years for all bees caught in sweep nets, for honey and 'other' bees (but not bumble bees) collected in pan traps and visually observed 'other' bees (Table 2.4). In cranberry fields there was a significant difference between years for honey bees and 'other' bees but not for bumble bees (Table 2.5). There was never a significant interaction between year and sampling site for either crop therefore sampling site data are presented as averages across years, showing the consistent difference among sites.

The amount of variation in bee abundance among fields (Figure2.6, Figure 2.7) was always substantially greater than among sampling sites within fields (Figure2.2, Figure2.4). Variation in bee abundance among fields was greater than variation in bee abundance between years and the variation in the interaction between fields and sampling sites, fields and years, sampling sites and years, and fields, sampling sites and years for all bee categories except sweep netted honey bees and other bees in blueberry fields and for bumble bees in cranberry fields (Table 2.6, Table 2.7).

2.3.4 Edge/Field Correlation

In blueberry fields mean number of honey and bumble bees caught in edge and field pan traps were significantly correlated, with a trend towards significance for 'other' bees (Figure 2.8) but the correlation for pan trapped honey bees was due to an outlier and the correlation became non-significant once it was removed ($r = 0.21$, $P = 0.58$). Only bumble bee abundances were correlated between edge and field when visually observed, and both bumble and 'other' bee abundances correlated between edge and field when sweep netted. In cranberries edge and field honey and 'other' bee abundances were significantly correlated with a trend towards significance for bumble bee abundances (Figure 2.9).

2.3.5 Weed Abundance and Bee Abundance

Weed abundance was consistently low in both blueberry and cranberry fields (blueberry fields: mean ± SE = 2.6 $cm^2/m^2 \pm 0.52$ cm^2/m^2; cranberry fields: mean ± SE = 2.1 $cm^2/m^2 \pm 1.3$ cm^2/m^2). Weed abundance was not significantly different between blueberry fields ($F_{5,25} = 1.35$, $P = 0.26$) or cranberry fields ($F_{4,20} = 1.78$, $P = 0.152$) or between sampling sites (blueberry fields: $F_{5,25} = 1.25$, $P = 0.23$; cranberry fields: $F_{5,20} = 1.04$, $P = 0.449$). There was no correlation between weed and bee abundance in blueberry fields in any of the three bee categories with any of the three sampling methods or in cranberry fields (Figure 2.10, Figure 2.11).

2.3.6 Bee Abundance vs. Berry Weight

Mean blueberry weight was related to bumble bee abundance measured by all 3 sampling methods, with 'other' bee abundance in pan traps, but not with honey bee abundance measured by any sampling method (Figure 2.12, Table 2.8) when all blueberry varieties were pooled together. Bumble bee and 'other' bee abundance were positively correlated with each other in blueberry pan traps ($r = 0.54$, $P < 0.0001$) but not in blueberry visual observations ($r = 0.06$, $P = 0.61$) or sweep netting ($r = -0.007$, $P = 0.95$). Multiple regression of both bumble and other bee abundance with berry weight maintained a marginal positive relationship between pan trapped bumble bee abundance and blueberry weight ($P = 0.095$) but the relationship between pan trapped 'other' bee abundance and blueberry weight became non-significant ($P = 0.23$), suggesting that the significant correlation between other bee abundance in pan traps and blueberry weight was simply due to the correlation between bumble bee and other bee abundance.

When analysing each blueberry variety separately, Bluecrop mean berry weight was significantly related to bumble bee abundance by all three sampling methods, and 'other' bee abundance by visual observations. Bumble bee and 'other' bee abundance in Bluecrop fields were positively correlated for both pan trapped ($r = 0.59$, $P = 0.022$) and visually observed data ($r = 0.68$, $P = 0.005$) but not for sweep netted data ($r = 0.25$, $P = 0.37$). Multiple regression showed a highly significant positive relationship between visually observed bumble bee abundance and blueberry weight ($P = 0.004$) but the relationship between visually observed 'other' bee abundance and blueberry weight became non-significant ($P = 0.19$). Mean berry weight for all other varieties was not related to bee abundance for any of the three bee categories (Table 2.8).

There was a significant relationship between mean cranberry weight and bumble bee abundance but not between mean cranberry weight and honey bee or 'other' bee abundance (Figure 2.13).

2.3.7 Number of Mature Seeds vs. Blueberry Weight

The mean number of total ovules (mature seeds, aborted seeds, unpollinated ovules) per blueberry ranged from 67 to 124 among varieties (Table 2.9). There was a positive relationship between blueberry weight and number of mature seeds both overall, and when analysing each variety separately (Table 2.10, Figure 2.14). The mean number of ovules per cranberry was 38.4 (SE = 1.14, n = 30). There was a positive relationship between cranberry weight and number of mature seeds (Figure 2.15) ($r^2 = 0.2758$, $P < 0.0001$)

2.3.8 Shannon-Wiener Diversity and Evenness Indices

Shannon-Wiener diversity and Shannon evenness indices for each field are presented in tables 2.11 and 2.12. There was no significant correlation between either blueberry weight or cranberry weight and Shannon-Wiener diversity of bees (blueberry: $r = 0.194$, $P = 0.6765$, df = 1; cranberry: $r = 0.041$, $P = 0.9478$) or evenness indices (blueberry: $r = 0.278$, $P = 0.5455$, df = 1; cranberry: $r = 0.174$, $P = 0.7794$).

2.4 Tables

Table 2.1: Number, location and proximity of honey bee colonies in six blueberry fields and five cranberry bogs. Location of colonies indicates which sampling site colonies were closest to. Distance from the nearest sampling site is given in meters. N/A indicates that no colonies were placed in the field.

Blueberry Field	# of Colonies	Distance (m)	Location
1	10	37	80%
2	36	77	80%
3	32	10	100%
4	N/A	N/A	N/A
5	48	23	80%
6	21	10	80%

Cranberry Field	# of Colonies	Distance (m)	Location
1	263	450	100%
2	N/A	N/A	N/A
3	243	190	40%
4	82	277	100%
5	56	83	0%

Table 2.2: Abundance of each bee species caught in highbush blueberry fields in 2003 and 2004, combined across years and sampling methods. Parasitic species are indicated by an asterisk (*) beside their name.

Species	Abund	Species	Abund
Andrena angustitarsata	15	*Bombus mixtus*	883
Andrena candida	2	*Bombus nevadensis*	12
Andrena cupreotincta	5	*Bombus occidentalis*	26
Andrena halinii	7	*Bombus rufocinctus*	309
Andrena hemileuca	209	*Bombus sitkensis*	41
Andrena hippotes	1	*Bombus vosnesenskii*	19
Andrena miranda	21	*Bombus spp.*	14
Andrena miserabilis	55	*Ceratina acantha*	37
Andrena nigrocaerulea	9	**Coelioxys porterae*	1
Andrena nivalis	2	*Halictus confusus*	2
Andrena perarmata	39	*Halictus rubicundus*	103
Anrena prunorum	9	*Lasioglossum (Dialictus) spp.*	509
Andrena saliciflоris	45	*Lasioglossum pacificum*	1
Andrena transnigra	13	*Lasioglossum zonulum*	52
Andrena vicina	237	*Lasioglossum spp.*	5
Andrena sp 1	1	*Megachile gemula*	1
Andrena sp 2	4	*Megachile melanophaea*	3
Andrena sp 3	4	**Nomada sp.*	1
Andrena sp 4	7	*Osmia albalateralis*	1
Andrena sp 5	8	*Osmia bucephala*	1
Andrena sp 6	1	*Osmia caerulescens*	2
Andrena sp 8	1	*Osmia dolerosa*	58
Andrena sp 9	1	*Osmia lignaria*	31
Andrena spp.	102	*Osmia pusilla*	5
Apis mellifera	11272	*Osmia tristella*	4
Bombus appositus	2	**Psithyrus insularis*	2
Bombus californicus	4	**Sphecodes sp 1*	6
Bombus centralis	1	**Sphecodes sp 2*	6
Bombus flavifrons	810	**Sphecodes sp 3*	2
Bombus impatiens	5	**Sphecodes sp 4*	1
Bombus melanopygus	616		

Table 2.3: Abundance of each bee species caught in cranberry fields in 2003 and 2004, combined across years and sampling methods. Parasitic species are indicated by an asterisk (*) beside their name.

Species	Abund	Species	Abund
Agapostemon texanus	1	*Halictus rubicundus*	40
Andrena candida	2	*Hoplitis producta subgracilis*	2
Andrena salicifloris	2	*Hoplitis sp.*	1
Andrena sp 1	1	*Hylaeus modestus citriaifrons*	19
Andrena sp 5	1	*Lasioglossum Dialictus spp*	427
Andrena sp 8	2	*Lasioglossum zonulum*	50
Andrena spp.	4	*Megachile frigida*	4
Anthidium manicatum	1	*Megachile gemula*	36
Anthophora terminalis	1	*Megachile melanophaea*	43
Apis mellifera	3028	*Megachile perihirta*	4
Bombus flavifrons	263	*Megachile rotundata*	3
Bombus insularis	4	*Melissodes spp.*	4
Bombus melanopygus	93	**Nomada sp.*	1
Bombus mixtus	639	*Osmia caerulescens*	3
Bombus nevadensis	4	*Osmia dolerosa*	5
Bombus occidentalis	2	*Osmia potentillae*	1
Bombus rufocinctus	78	*Osmia pusilla*	1
Bombus sitkensis	34	*Osmia tristella*	1
Bombus vosnesenskii	30	**Psithyrus insularis*	1
Bombus spp.	21	**Sphecodes sp 1*	6
Ceratina acantha	8	**Sphecodes sp 2*	7
**Coelioxys porterae*	8	**Sphecodes sp 3*	10
Colletes sp.	2	**Stelis lateralis*	2
Halictus confusus	19		

Table 2.4: *F* and *P*-values for split plot in time Analysis of Variance of bee abundance in blueberry fields with sampling site (SS), year (Yr) and the interaction between the two (Yr*SS) as fixed effects. Three sampling methods and three bee categories were analysed for proportional distance into the field from the edge with the most natural vegetation and the nearest edge. *P*-values are shown in parentheses.

	Vegetated Edge				Nearest Edge		
Pan Trapped	***Apis***	***Bombus***	**'Other'**		***Apis***	***Bombus***	**'Other'**
SS df(5,25)	3.92 *(0.0092)	0.58 (0.7152)	0.17 (0.9714)	SS df(2,10)	2.95 (0.0982)	0.93 (0.4251)	0.19 (0.8332)
Yr df(1,30)	8.91 *(0.0056)	1.85 (0.1845)	6.37 *(0.0171)	Yr df(1,51)	7.81 *(0.0073)	1.99 (0.1649)	5.01 *(0.0295)
Yr*SS df(1,30)	0.58 (0.7137)	0.59 (0.7085)	0.98 (0.4433)	Yr*SS df(2,51)	0.52 (0.5993)	1.30 (0.2818)	0.32 (0.7299)

Visually Observed	***Apis***	***Bombus***	**'Other'**		***Apis***	***Bombus***	**'Other'**
SS df(5,25)	1.87 (0.1353)	1.51 (0.2233)	0.46 (0.7992)	SS df(2,10)	0.47 (0.6366)	1.95 (0.1929)	0.73 (0.5047)
Yr df(1,30)	1.51 (0.2293)	2.04 (0.1636)	14.13 *(0.0007)	Yr df(1,51)	1.19 (0.2802)	1.14 (0.2915)	14.29 *(0.0004)
Yr*SS df(1,30)	1.49 (0.2217)	2.04 (0.101)	0.96 (0.4591)	Yr*SS df(2,51)	2.42 (0.0989)	1.14 (0.3281)	0.16 (0.8504)

Sweep Netted	***Apis***	***Bombus***	**'Other'**		***Apis***	***Bombus***	**'Other'**
SS df(5,25)	0.67 (0.6487)	0.73 (0.6056)	0.69 (0.6371)	SS df(2,10)	0.44 (0.6532)	0.96 (0.4154)	0.25 (0.7854)
Yr df(1,30)	113.05 *(<0.0001)	11.11 *(0.0023)	13.05 *(0.0011)	Yr df(1,51)	112.78 *(<0.0001)	11.70 *(0.0012)	12.47 *(0.0009)
Yr*SS df(1,30)	1.11 (0.3763)	0.37 (0.8666)	1.21 (0.3296)	Yr*SS df(2,51)	0.61 (0.5487)	0.39 (0.6766)	0.07 (0.9344)

Table 2.5: F and P-values for split plot in time Analysis of Variance of bee abundance in cranberry fields with sampling site (SS), year (Yr) and the interaction between the two (Yr*SS) as fixed effects. Three bee categories were analysed for proportional distance into the field from the edge with the most natural vegetation and the nearest edge. *P*-values are shown in parentheses.

	Vegetated Edge				**Nearest Edge**		
	Apis	***Bombus***	**'Other'**		***Apis***	***Bombus***	**'Other'**
SS	0.44	0.82	3.25	SS	0.38	0.25	4.78
df(5,25)	(0.8161)	(0.5478)	*(0.0262)	df(2,10)	(0.6932)	(0.782)	*(0.043)
Yr	4.86	0.18	5.93	Yr	5.22	0.18	5.71
df(1,30)	*(0.0373)	(0.6763)	*(0.0227)	df(1,51)	*(0.0275)	(0.675)	*(0.0214)
Yr*SS	0.15	1.41	0.62	Yr*SS	0.03	2.29	0.67
df(1,30)	(0.9782)	(0.255)	(0.687)	df(2,51)	(0.9708)	(0.1142)	(0.5181)

Table 2.6: Percent Variance of Components for bee abundance with blueberry fields (Field), sampling site (SS), year (Yr), and the interaction between variables (Field*SS, Field*Yr, SS*Yr, Field*SS*Yr). Three sampling methods and three bee categories were analysed to determine how variation in bee abundance was partitioned between each effect.

Pan Trapped	***Apis***	***Bombus***	**'Other'**
Field	65	43	50
SS	5	0	0
Field*SS	2	4	17
Yr	2	0	3
Field*Yr	16	39	10
SS*Yr	0	2	2
Field*SS*Yr	10	12	19

Visually Observed	***Apis***	***Bombus***	**'Other'**
Field	54	86	27
SS	1	0	0
Field*SS	15	6	0
Yr	0	0	13
Field*Yr	11	1	26
SS*Yr	4	1	2
Field*SS*Yr	14	6	32

Sweep Netted	***Apis***	***Bombus***	**'Other'**
Field	6	65	17
SS	0	1	0
Field*SS	4	1	0
Yr	64	4	10
Field*Yr	14	18	39
SS*Yr	2	0	5
Field*SS*Yr	10	13	30

Table 2.7: Percent Variance of Components for bee abundance in cranberries with field (Field), sampling site (SS), year (Yr), and the interaction between variables (Field*SS, Field*Yr, SS*Yr, Field*SS*Yr). Three bee categories were analysed to determine how variation in bee abundance was partitioned between each effect. Bee sampling methods were pooled when no significant difference was found in proportional abundances of the three bee categories between the three sampling methods.

	Apis	*Bombus*	'Other'
Field	61	29	40
SS	0	0	10
Field*SS	8	0	6
Year	2	0	5
Field*Year	10	5	9
SS*Year	0	4	0
Field*SS*Year	18	62	30

Table 2.8: r^2 and Bonferroni corrected *P*-values for regression between berry weight and *Apis*, *Bombus*, and 'other' bee abundance for all blueberry varieties together and each variety separately for pan trapped, visually observed and sweep netted data. N/A indicates that insufficient data was available to conduct a regression analysis, either due to a single sampling site for the variety or due to absence of bees.

		Apis		***Bombus***		**'Other'**	
Sampling Method	**Variety**	r^2	*P*	r^2	*P*	r^2	*P*
Pan Trapped	All	0.0048	0.6633	0.1438	0.0133	0.1131	0.0294
	Bluecrop	0.1868	0.6462	0.6297	0.0024	0.2481	0.3528
	Duke	0.6223	1.0000	0.9324	1.0000	0.9978	0.1812
	June	0.032	1.0000	0.4065	1.0000	0.6255	0.3660
	Nortland	0.0674	1.0000	0.0496	1.0000	0.0244	1.0000
	Patriot	0.5516	0.9030	0.1687	1.0000	0.4247	1.0000
	Unknown 1	N/A	N/A	N/A	N/A	N/A	N/A
	Unknown 2	N/A	N/A	N/A	N/A	N/A	N/A
	Unknown 3	0.035	1.0000	0.6646	0.2880	0.5701	0.4956
Visually Observed	All	0.0041	0.6857	0.4502	<.0001	0.0065	0.6106
	Bluecrop	0.3072	0.1920	0.7282	0.0006	0.5281	0.0126
	Duke	0.6402	1.0000	0.9978	0.1812	0	N/A
	June	0.2635	1.0000	0.0448	1.0000	0.3709	1.0000
	Nortland	0.0056	1.0000	0.0805	1.0000	0.2471	1.0000
	Patriot	0.0132	1.0000	0.0564	1.0000	0.0382	1.0000
	Unknown 1	N/A	N/A	N/A	N/A	N/A	N/A
	Unknown 2	N/A	N/A	N/A	N/A	N/A	N/A
	Unknown 3	0.0087	1.0000	0.5989	0.4254	0.6793	0.2616
Sweep Netted	All	0.0118	0.4929	0.443	<.0001	0.0556	0.1326
	Bluecrop	0.3135	0.1800	0.7376	0.0006	0.1489	0.9330
	Duke	0.9798	0.5454	0	N/A	0	N/A
	June	0.1403	1.0000	0.2367	1.0000	0	N/A
	Nortland	0.0213	1.0000	0.0003	1.0000	0.0888	1.0000
	Patriot	0.0001	1.0000	0.029	1.0000	0.0008	1.0000
	Unknown 1	N/A	N/A	N/A	N/A	N/A	N/A
	Unknown 2	N/A	N/A	N/A	N/A	N/A	N/A
	Unknown 3	0.3462	1.0000	0.6136	0.3918	0.0002	1.0000

Table 2.9: Mean total # of ovules (mature seeds, aborted seeds and unpollinated ovules) for eight varieties of highbush blueberries

Variety	Mean # of Ovules	n	SE
Bluecrop	124.47	15	3.49
Duke	88.67	3	6.89
June	94.17	6	3.02
Nortland	95.80	5	4.93
Patriot	71.83	6	2.54
Unknown 1	67.00	1	-
Unknown 2	135.00	1	-
Unknown 3	120.83	6	2.80

Table 2.10: Regression values between mature seed number and weight of corresponding berries for eight varieties of highbush blueberries.

Variety	n	Mean Berry Weight	SE	Mean # of Mature Seeds	SE	r^2	*P*
Bluecrop	189	1.50	0.06	8.48	0.71	0.56	<.0001
Duke	17	1.52	0.07	8.12	0.85	0.28	0.0294
June	83	0.77	0.05	6.12	0.96	0.76	<.0001
Nortland	44	0.86	0.06	3.25	0.51	0.59	<.0001
Patriot	82	1.24	0.08	1.68	0.25	0.59	<.0001
Unknown 1	4	1.22	0.24	1.75	1.44	0.93	0.0336
Unknown 2	6	1.36	0.22	19.83	3.83	0.64	0.0549
Unknown 3	67	1.08	0.09	3.09	0.66	0.79	<.0001

Table 2.11: Shannon-Wiener diversity and Shannon evenness indices for bees caught in six highbush blueberry fields in 2003 and 2004.

Field	Year	Diversity	Evenness
Field 1	2003	1.13	0.38
	2004	0.94	0.33
Field 2	2003	1.12	0.35
	2004	0.82	0.26
Field 3	2003	0.43	0.14
	2004	0.50	0.16
Field 4	2003	2.65	0.74
	2004	2.23	0.76
Field 5	2003	1.78	0.51
	2004	1.67	0.62
Field 6	2003	0.94	0.28
	2004	0.68	0.28

Table 2.12: Shannon-Wiener diversity and Shannon evenness indices for bees caught in five cranberry fields in 2003 and 2004.

Field	Year	Diversity	Evenness
Field 1	2003	2.02	0.59
	2004	1.32	0.44
Field 2	2003	1.79	0.62
	2004	1.81	0.64
Field 3	2003	0.91	0.35
	2004	0.71	0.28
Field 4	2003	0.52	0.19
	2004	0.78	0.33
Field 5	2003	1.64	0.61
	2004	1.62	0.61

2.5 Figures

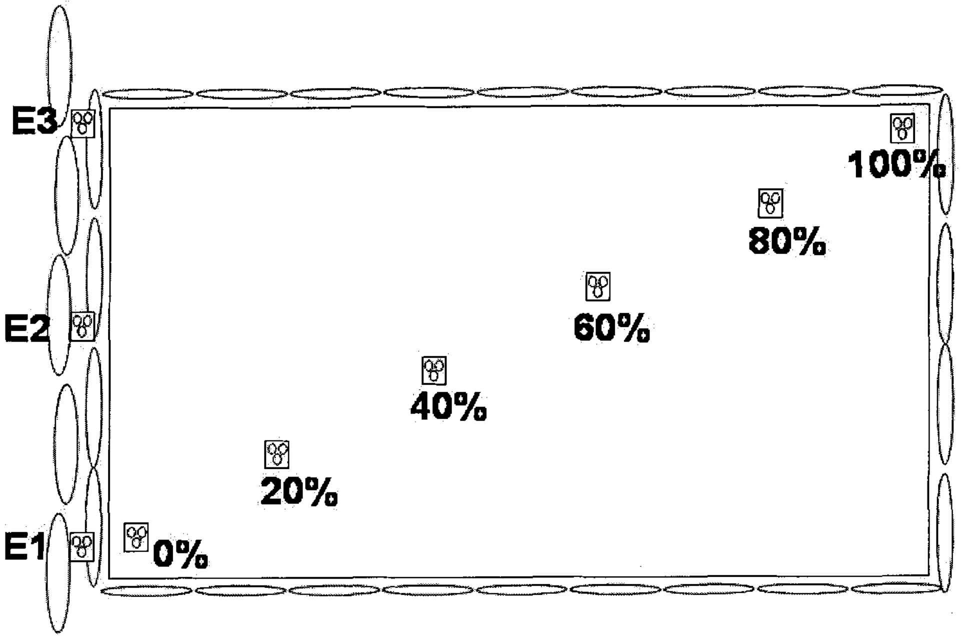

Figure 2.1: Blueberry and cranberry field layout showing locations of sampling sites with relation to the designated vegetated edge. E1, E2 and E3 are the three edge sites and 0% through 100% are the six sites in the field at varying percent distance into the field.

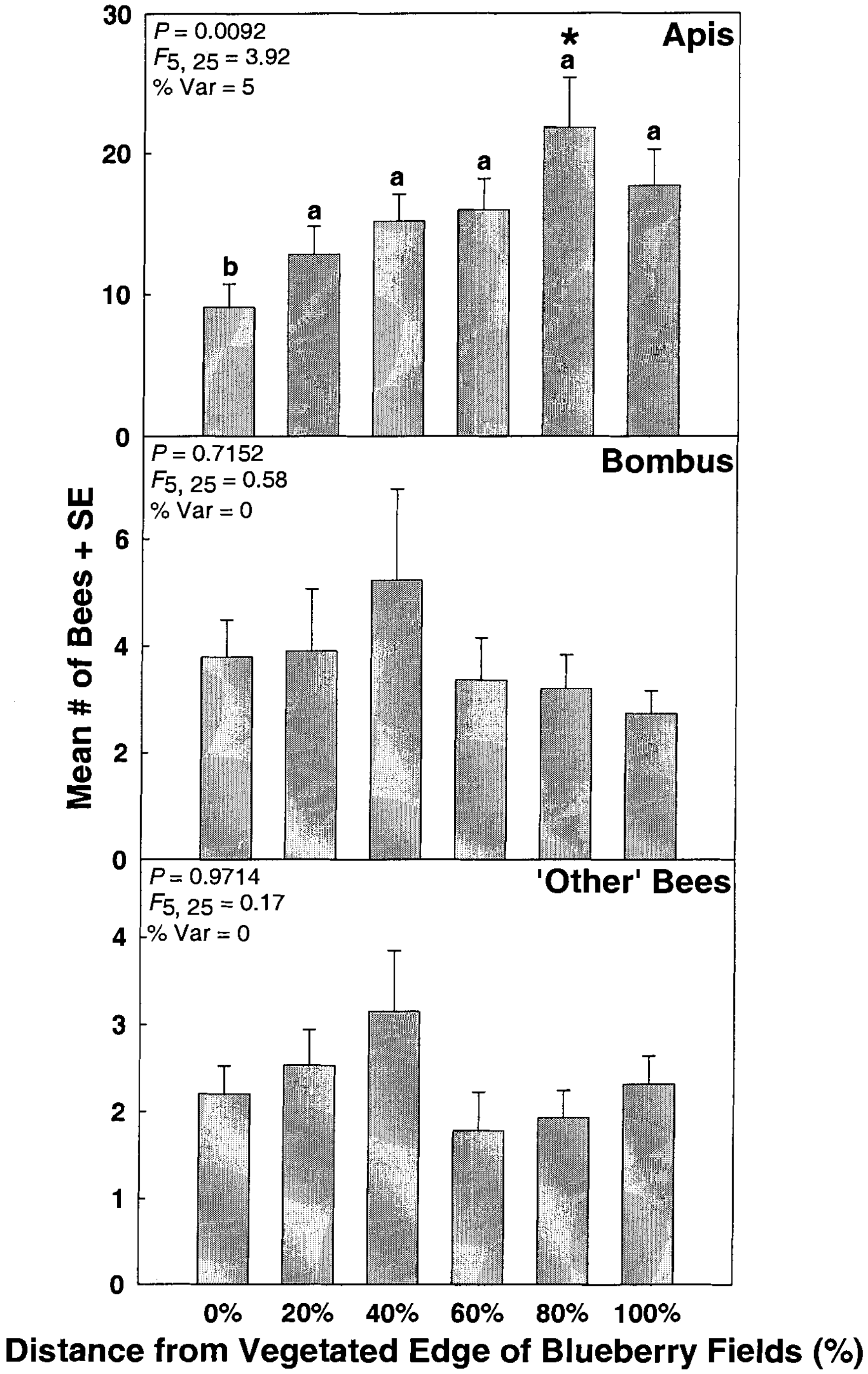

Figure 2.2: Mean number of bees pan trapped at six distances into highbush blueberry fields. Six fields were sampled in both 2003 and 2004 at proportional distances from the edge of the field with the most natural vegetation and analysed using ANOVA. The sampling site closest to the majority of honey bee colonies is indicated by an asterisk (*). Years were averaged together as no interaction between year and field was found. Bars topped by the same letter indicate no significant difference between distances. % Var indicates the percent of the total variation in bee abundance due to sampling site effect.

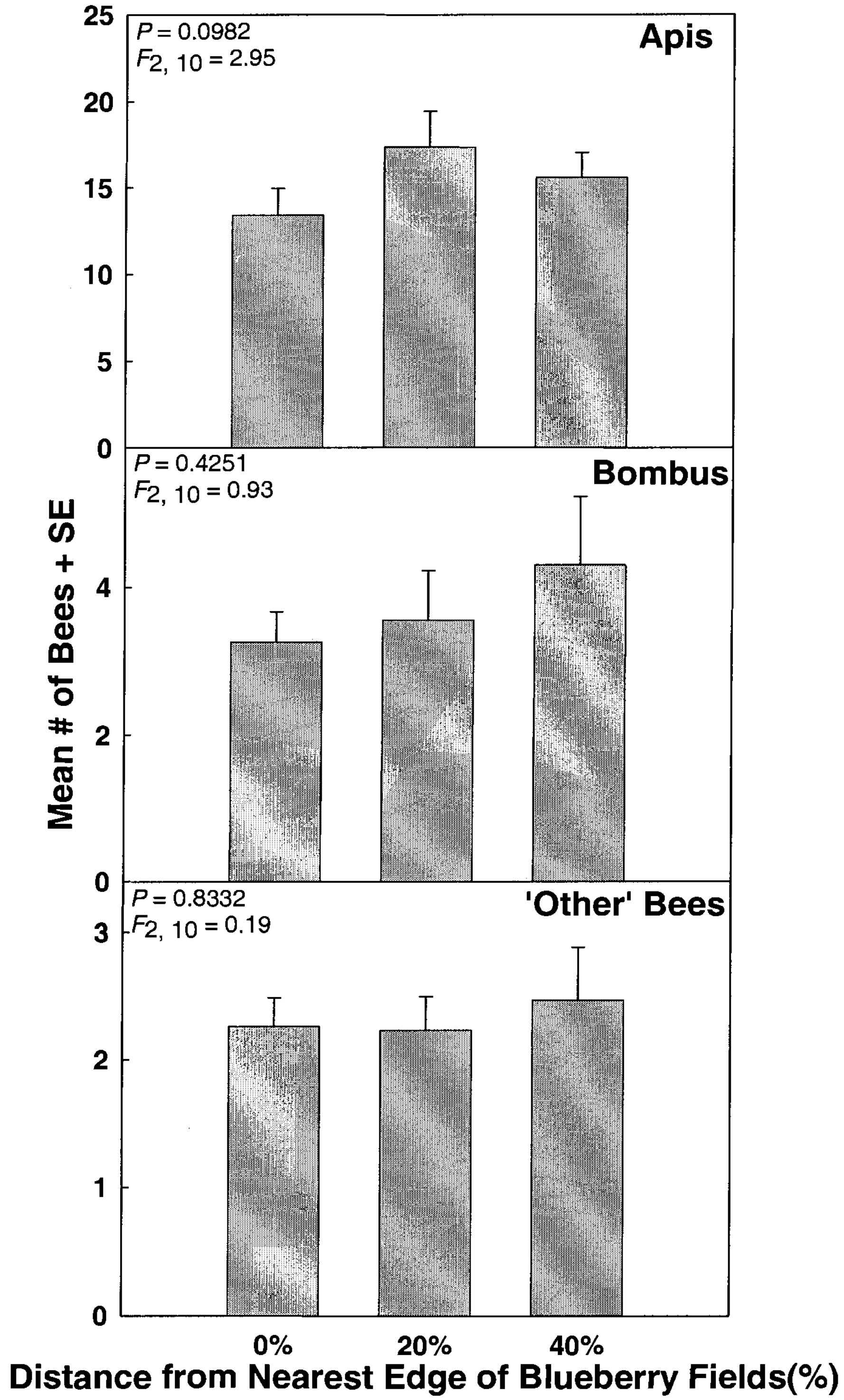

Figure 2.3: Mean number of bees pan trapped at proportional distances from the nearest edge of highbush blueberry fields. Six fields were sampled in both 2003 and 2004 and analysed using ANOVA. Years were averaged together as no interaction between year and field was found.

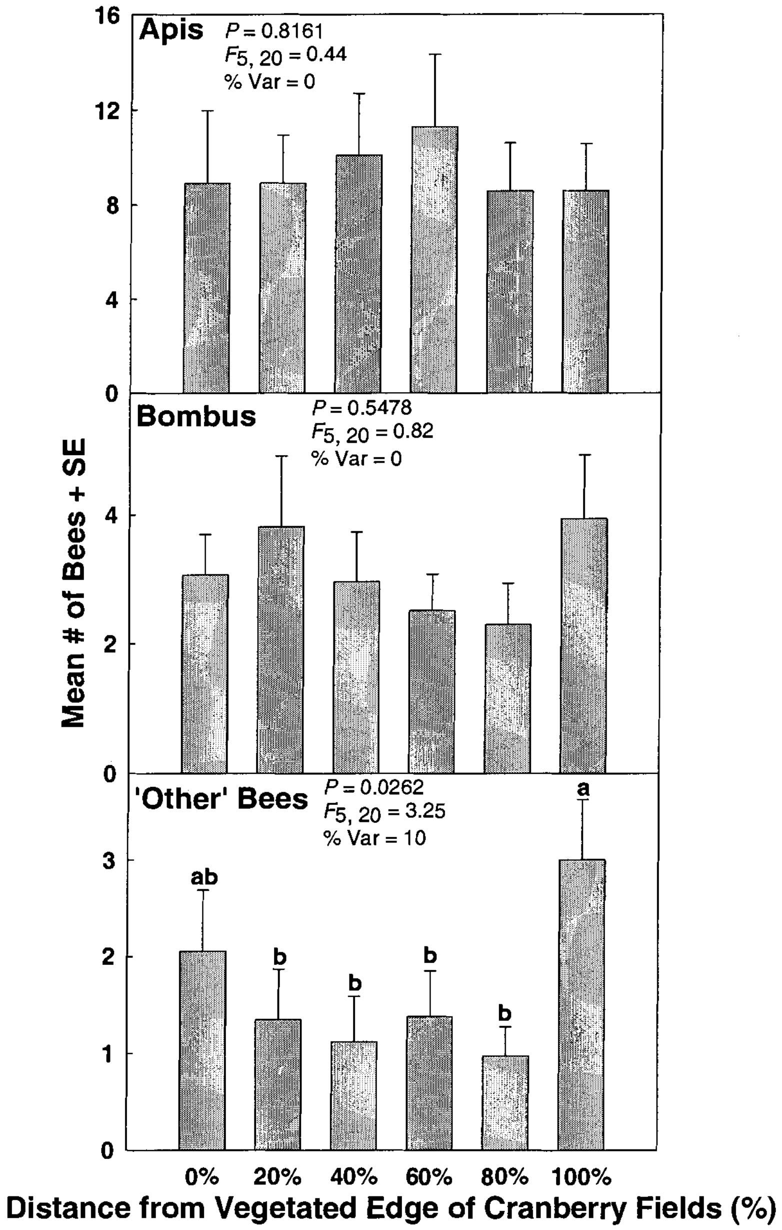

Figure 2.4: Mean number of bees pan trapped, visually observed and sweep netted at six distances into cranberry fields. The three sampling methods were averaged as no difference in proportions of bee categories was found. Five fields were sampled in both 2003 and 2004 at proportional distances from the edge of the field with the most natural vegetation and analysed using ANOVA. Years were averaged together as no interaction between year and field was found. Bars topped by the same letter indicate no significant difference between distances. % Var indicates the percent of the total variation in bee abundance due to sampling site effect.

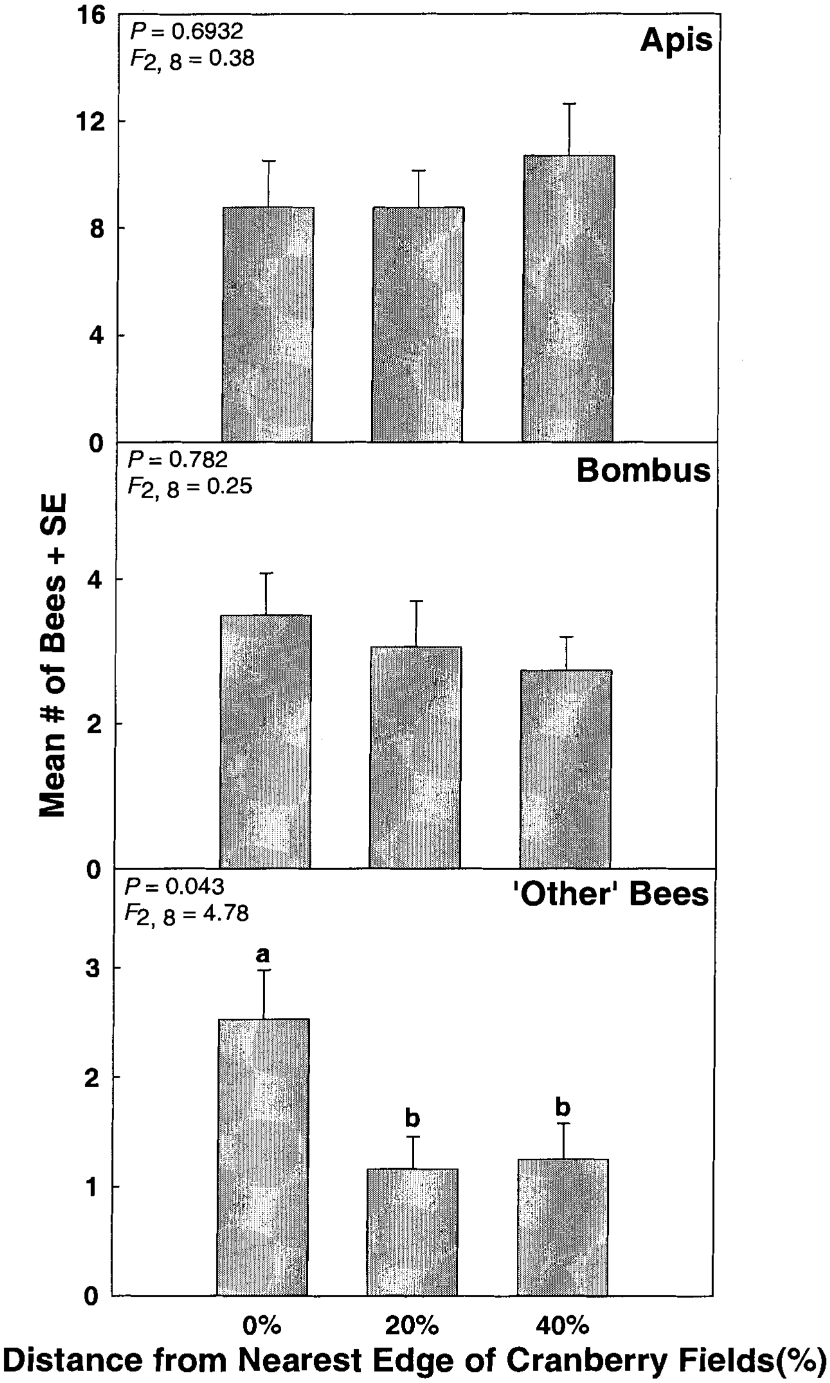

Figure 2.5: Mean number of bees pan trapped, visually observed and sweep netted at proportional distances from the nearest edge of cranberry fields. The three sampling methods were averaged as no differences in proportions of bee categories were found. Five fields were sampled in both 2003 and 2004 and analysed using ANOVA. Years were averaged together as no interaction between year and field was found. Bars topped by the same letter indicate no significant difference between distances.

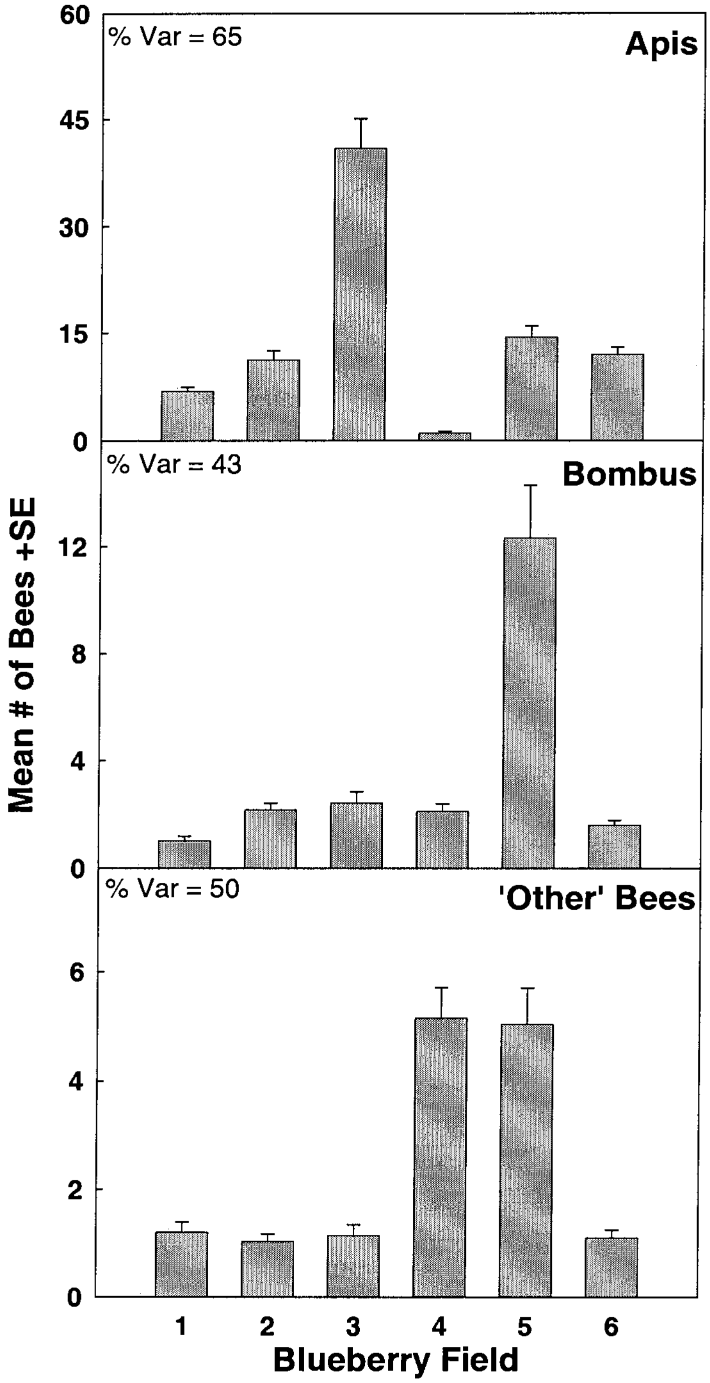

Figure 2.6: Mean number of bees pan trapped in six highbush blueberry fields. Means were generated from pan traps in six locations in each field in both 2003 and 2004. Years were averaged together as no interaction between year and field was found. Visually observed and sweep netted data are similar to pan trapped data and are not presented. % Var indicates the percent of the total variation in bee abundance due to field effect.

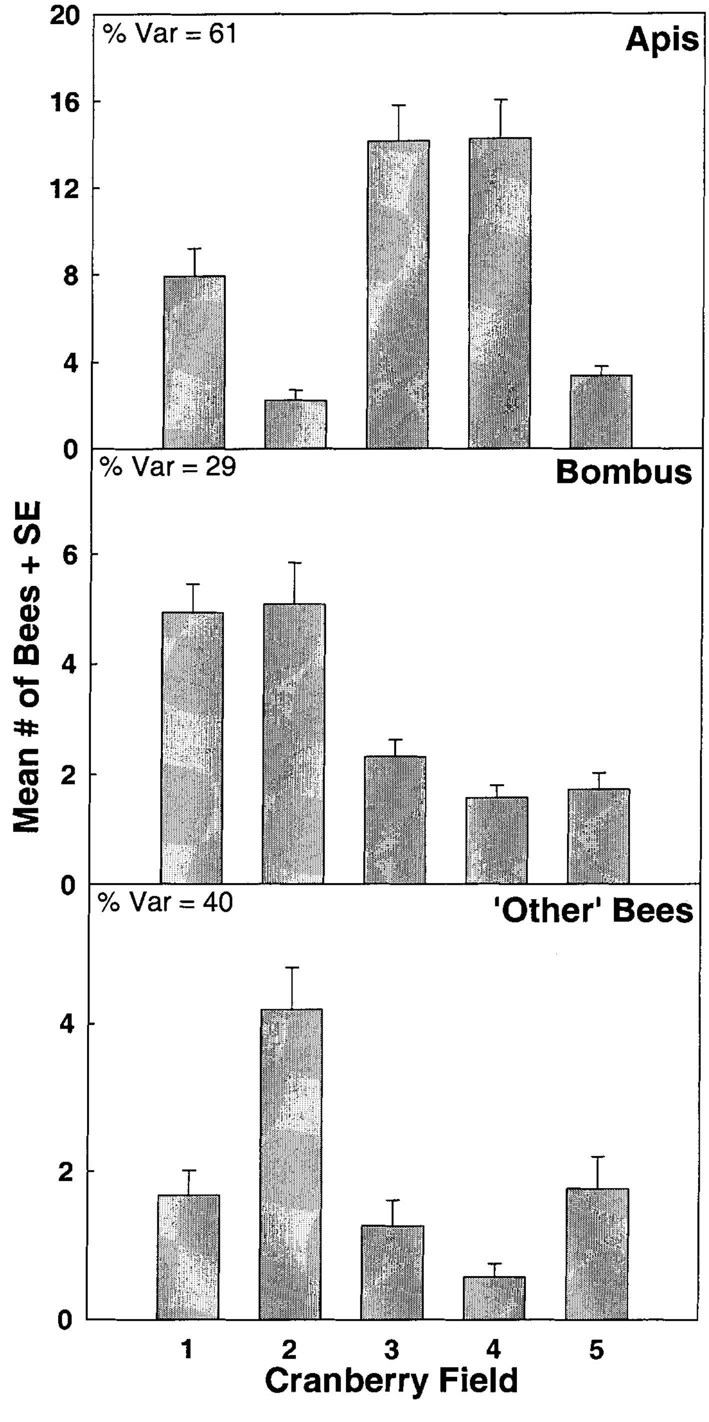

Figure 2.7: Mean number of bees pan trapped, visually observed and sweep netted in five cranberry fields. The three sampling methods were averaged as no difference in proportions of bee categories were found. Means were generated from sampling sites at six locations in each field in both 2003 and 2004. Years were averaged together as no interaction between year and field was found. % Var indicates the percent of the total variation in bee abundance due to field effect.

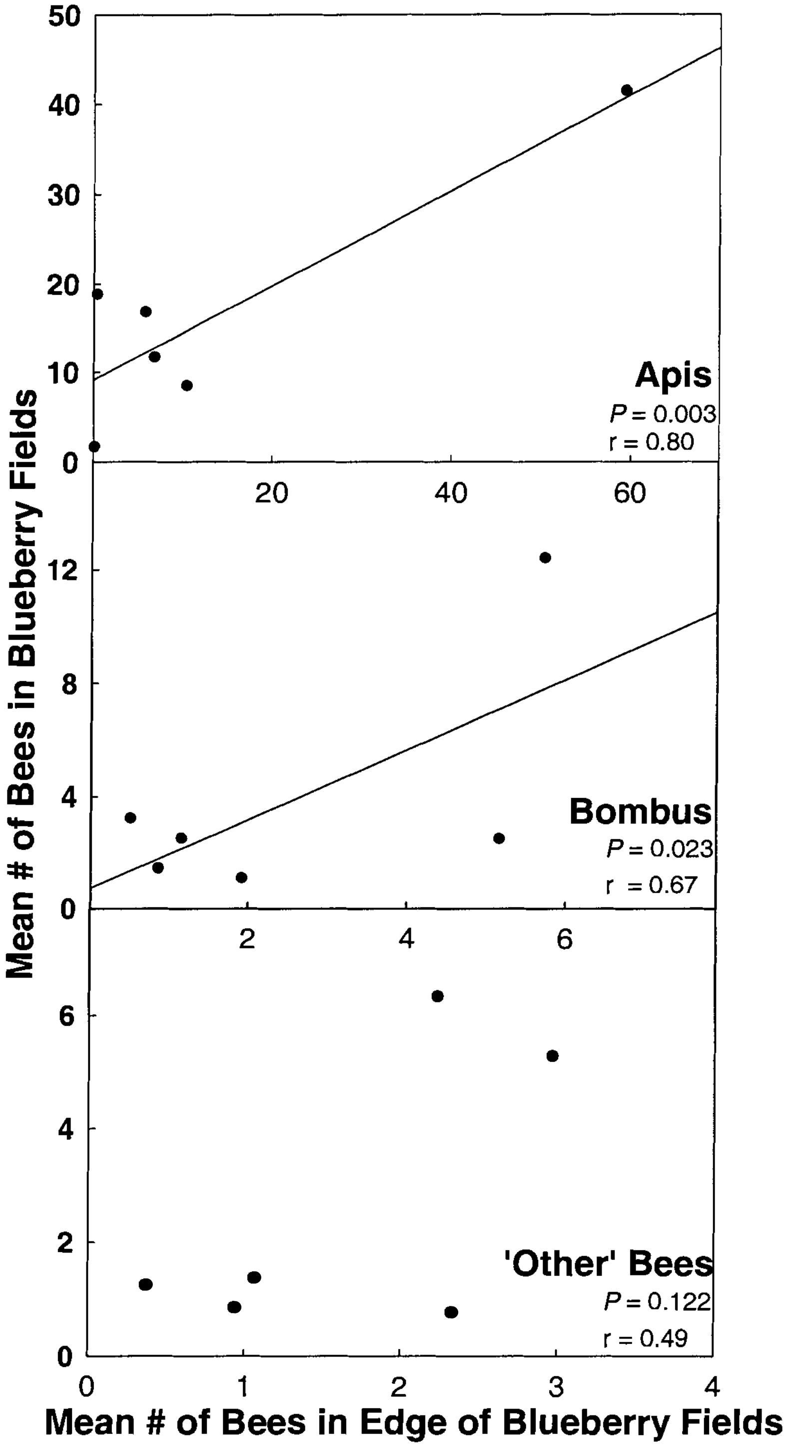

Figure 2.8: Partial correlation between edge and field pan trapped bees in highbush blueberry fields. Six sampling sites in each field were averaged and three (in 2003) or two (in 2004) sampling sites in each edge were averaged.

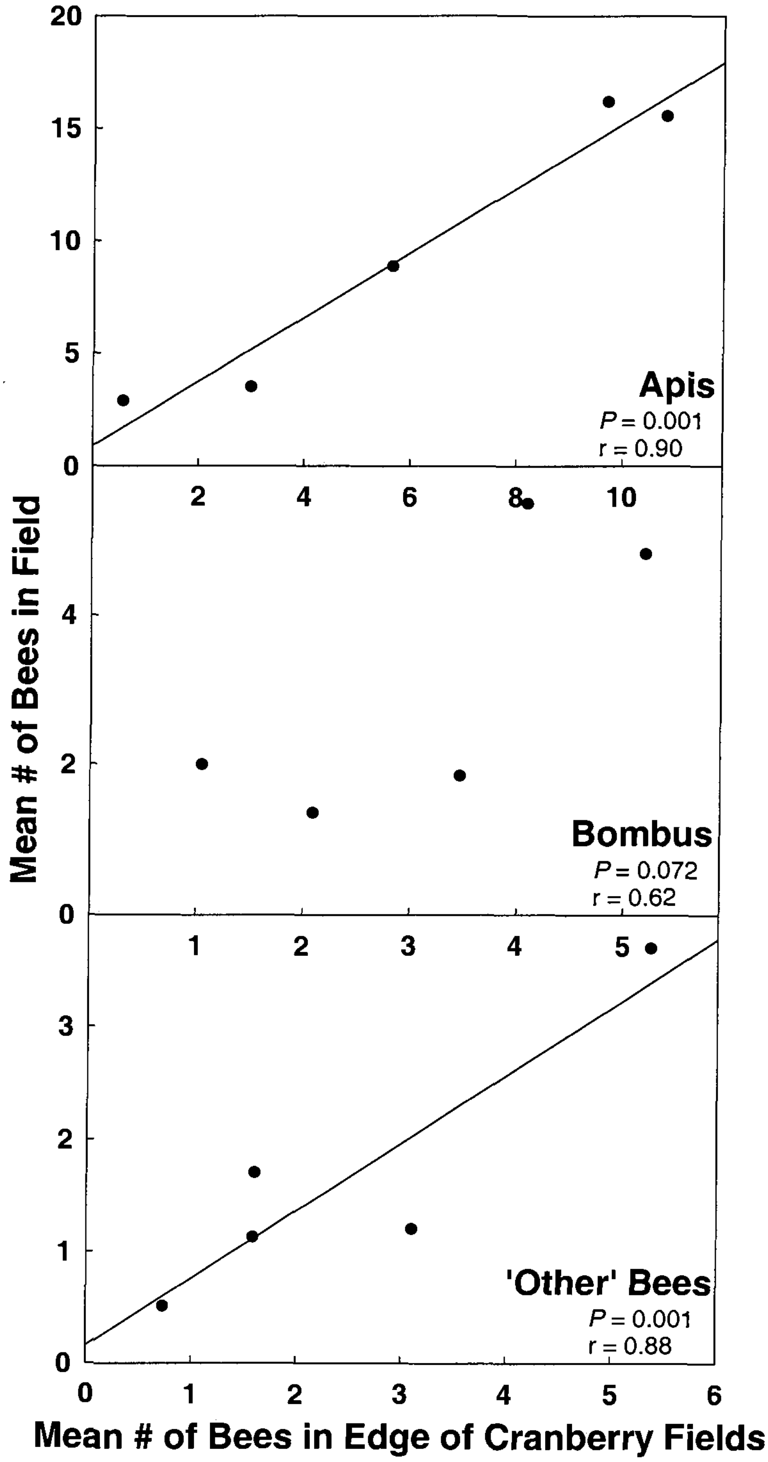

Figure 2.9: Partial correlation between edge and field pan trapped, visually observed and sweep netted bees in cranberry fields. The three sampling methods were averaged when no difference in proportions of bee categories were found. Six sampling sites in each field were averaged and three (in 2003) or two (2004) sampling sites in each edge were averaged.

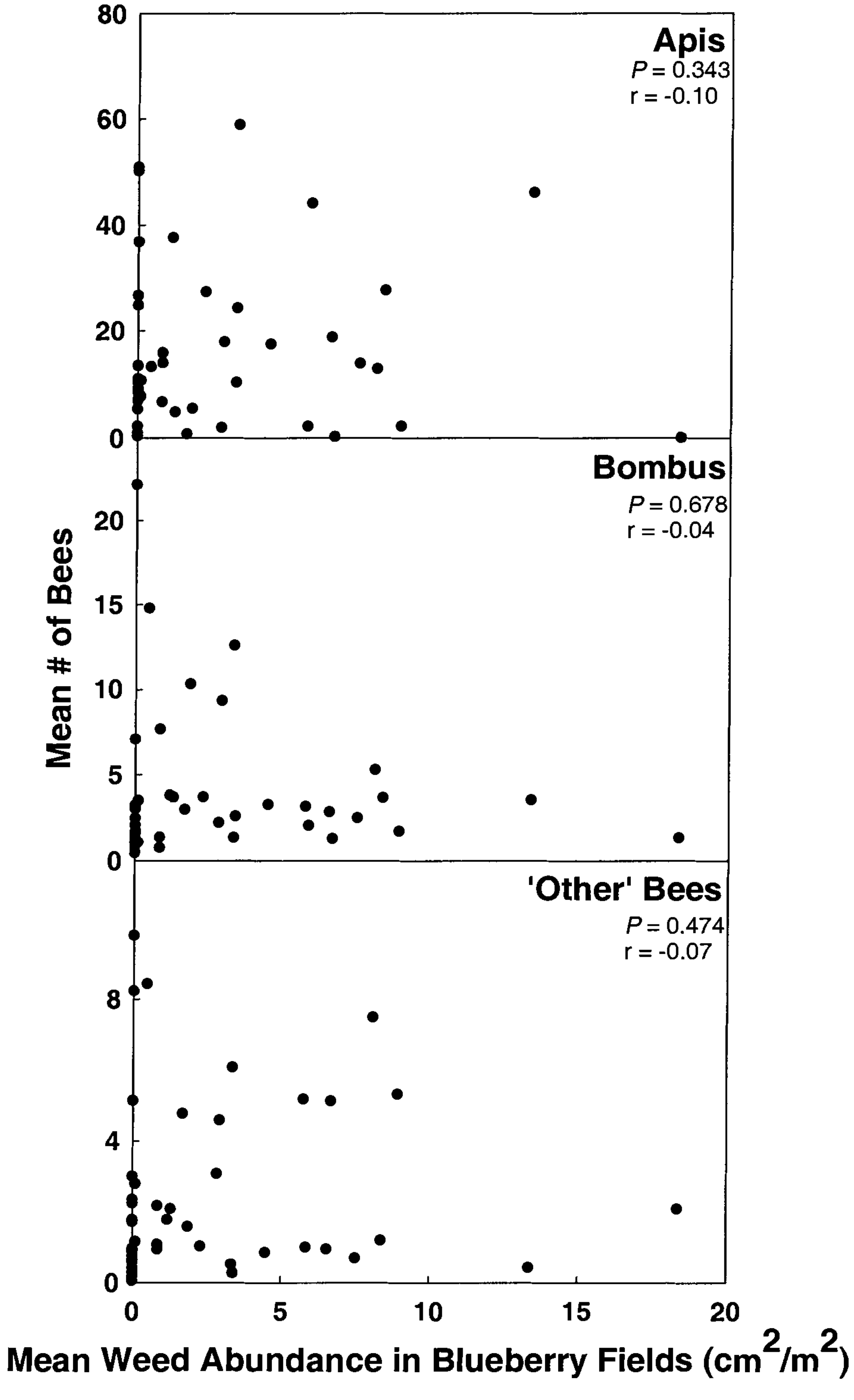

Figure 2.10: Lack of correlation between mean weed abundance (cm^2/m^2) vs. mean number of bees pan trapped in highbush blueberry fields.

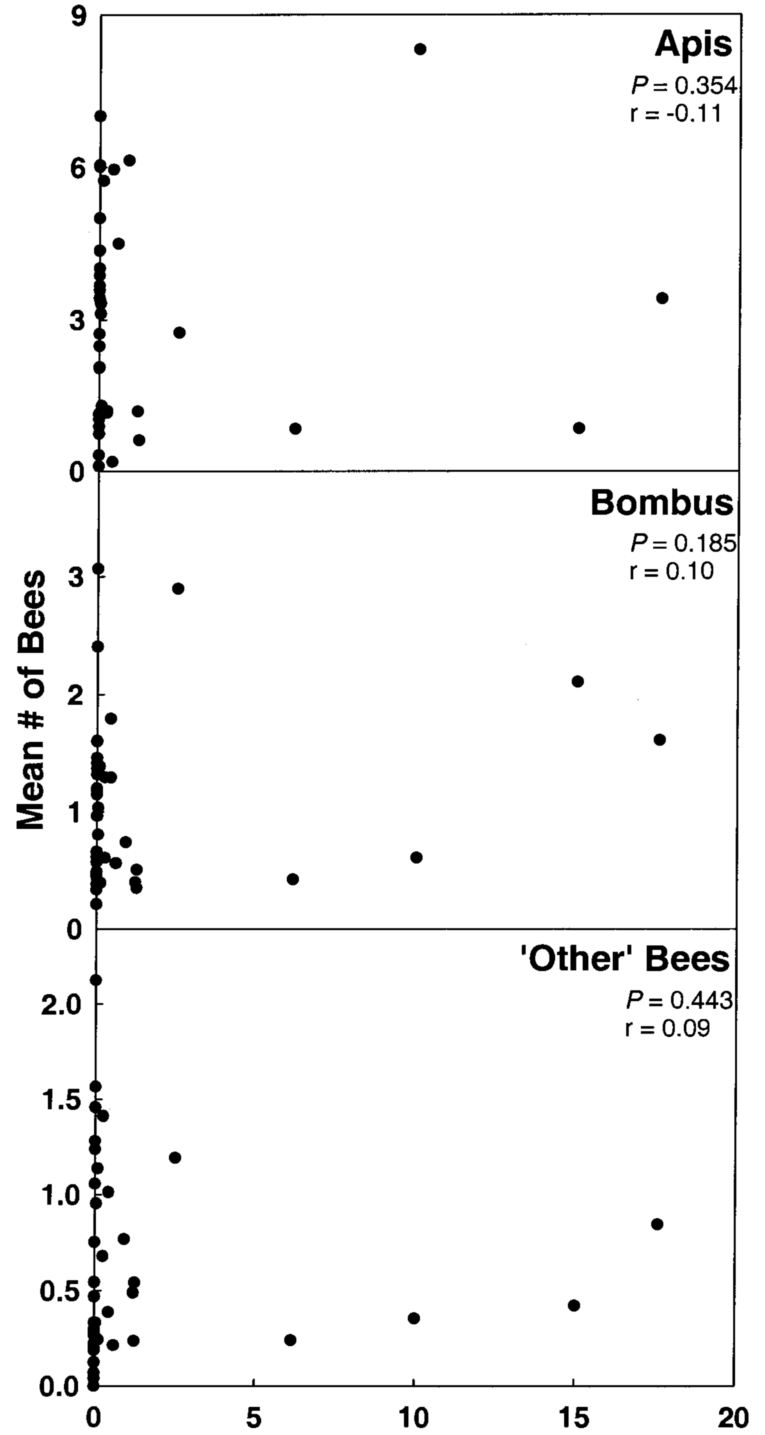

Figure 2.11: Lack of correlation between mean weed abundance (cm^2/m^2) vs. mean number of bees in cranberry fields.

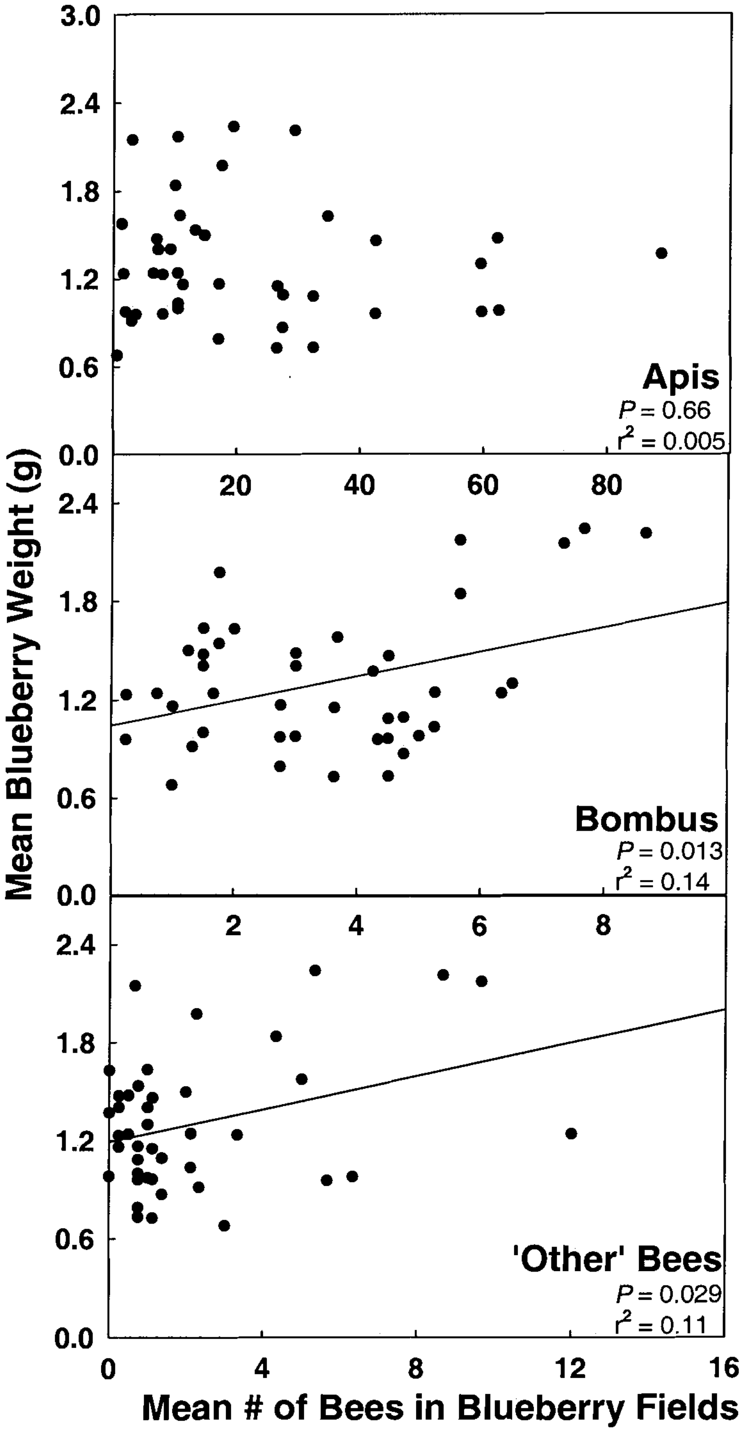

Figure 2.12: Regression between mean number of bees pan trapped in field sampling sites in highbush blueberry fields vs. mean blueberry weight (g).

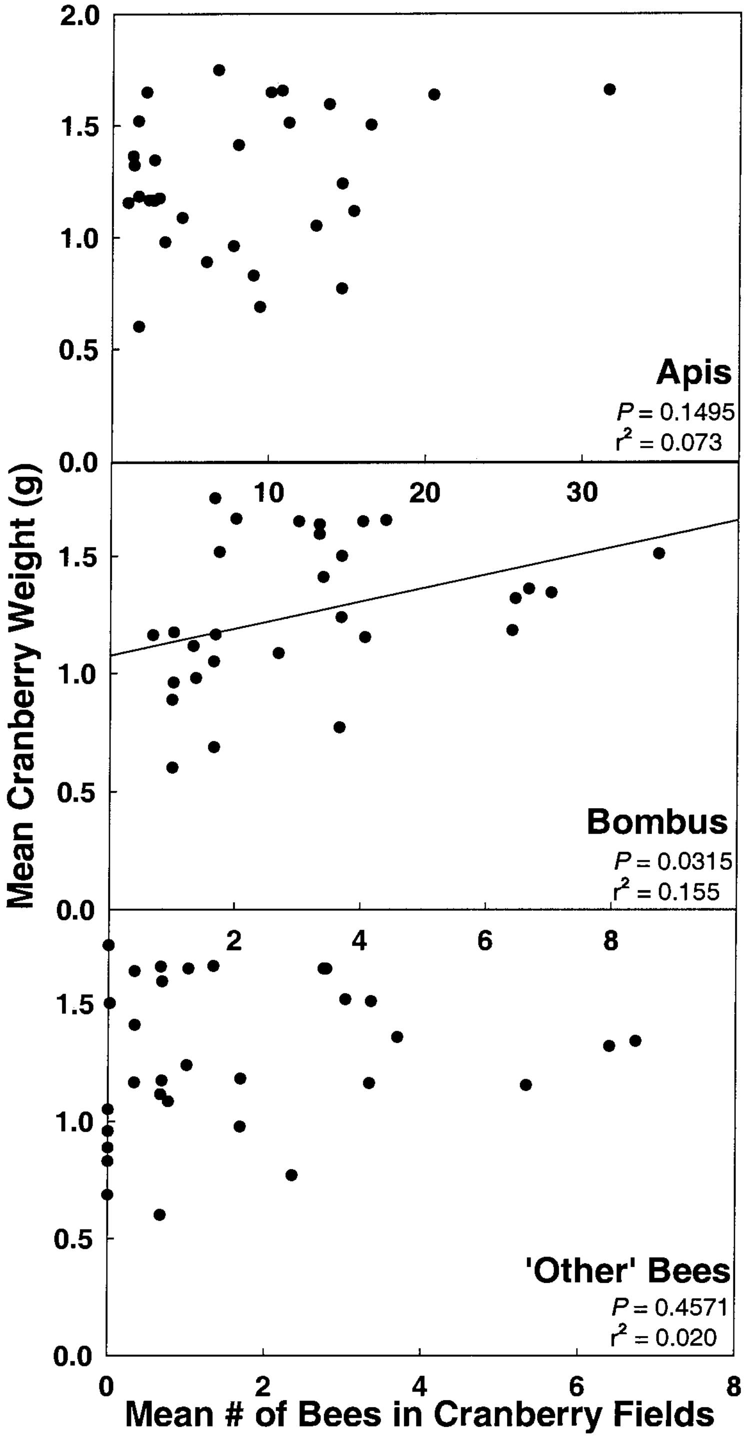

Figure 2.13: Regression between mean number of bees pan trapped, visually observed and sweep netted in field sampling sites in cranberry fields vs. mean cranberry weight (g). The three sampling methods were averaged as no difference in proportions of bee categories were found.

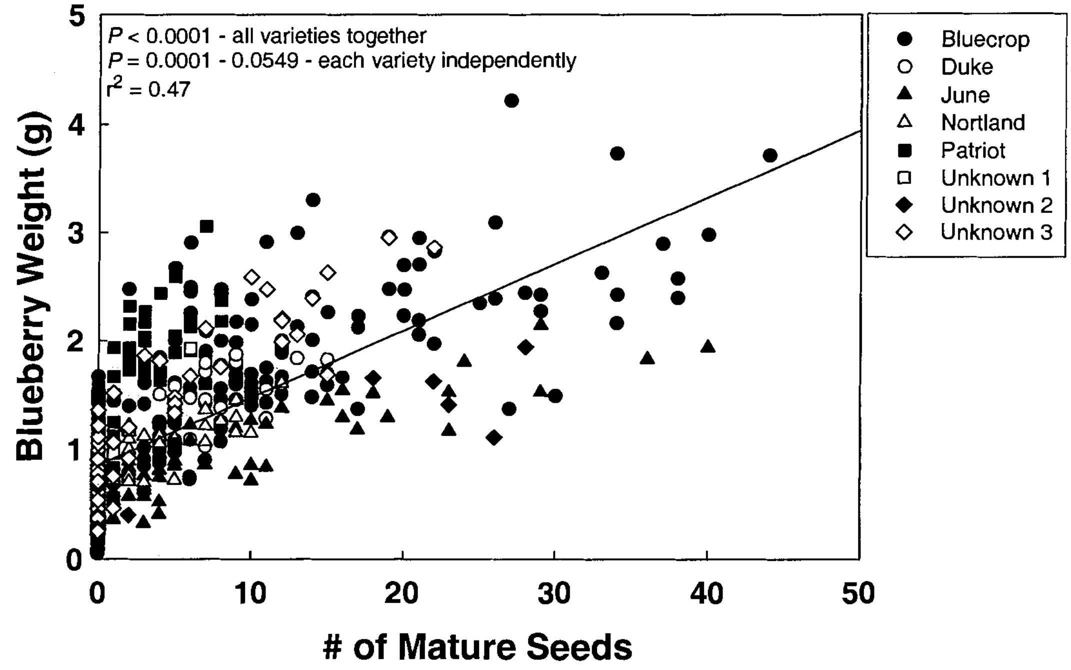

Figure 2.14: Blueberry weight (g) vs. number of mature seeds per berry. The regression line is for all blueberry varieties pooled together ($P < 0.0001$, $r^2 = 0.47$). Individual varieties were also analysed separately. See Table 2.8 for individual r^2 and P-values.

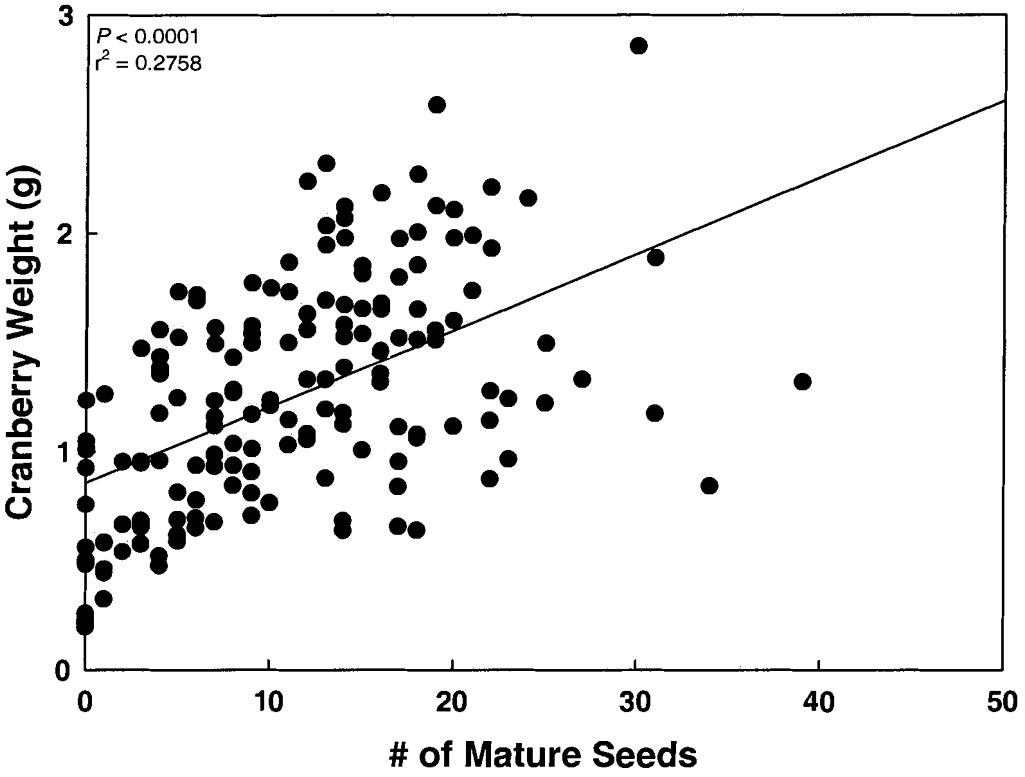

Figure 2.15: Cranberry weight (g) vs. number of mature seeds per berry.

Chapter 3: Discussion

I examined managed and wild bee abundance, dispersal, diversity and their effect on crop yield over two years in highbush blueberry and cranberry fields in the Fraser Valley of British Columbia. I found greater species diversity than previous studies in this region. Wild bees dispersed well within blueberry fields and bumble and honey bees dispersed well within cranberry fields but ‘other’ bees as a group remained at field edges. All bees were readily able to cross into fields from the surrounding area but bee abundance between fields varied greatly.

Blueberry and cranberry weight were related to bumble bee abundance but not to honey or ‘other’ bee abundance. Diversity and evenness of bees were not correlated to berry weight in either crop. Overall, these results suggest that bumble bees are the most important pollinator for these crops.

3.1 Bee Species Captured

The introduced honey bee was by far the most abundant species, not surprising since managed colonies are rented and placed in highbush blueberry and cranberry fields for pollination. *Bombus mixtus* was the second most abundant species in both crops.

Other studies also have found bumble bees to be naturally abundant in blueberry and cranberry fields (Cane and Payne 1993; Cane and Schiffhauer 2003; Cane, Schiffhauer and Kervin 1996; Dedej and Delaplane 2003; Hutson 1925; Javorek, MacKenzie and Vander Kloet 2002; MacKenzie and Winston 1984; Winston and Graf

1982). However, overall my species list contrasts sharply with those found in previous studies in this region. I found considerably more species of bees and higher proportions of 'other' bees than either of the previous two studies conducted on wild bees in blueberry and cranberry fields in the Fraser Valley.

MacKenzie and Winston (1984) and Winston and Graf (1982) found only five and four species of bumble bees and 9 and 17 individual non-*Bombus* wild bees respectively in blueberry fields and only four species of bumble bees each and zero and one species respectively of non-*Bombus* wild bees represented by a single individual in cranberry fields. More detailed non-*Bombus* wild bee data were not presented. In contrast, I found 13 species of bumble bees and over 47 species of 'other' bees in blueberry fields and 10 species of bumble bees and over 36 species of 'other' bees in cranberry fields.

This sharp difference in number of species may reflect an actual increase in bee diversity and abundance over 20 years, but more likely was due to my increased sampling effort and greater variety of sampling techniques. The previous two studies sampled only three fields of each crop and did not use pan traps to assess bees. Pan trapping allows for sampling over a longer period of time and, since many wild bees are small, they may have easily been underrepresented in sweep netting and visual observations in previous studies. Increasing the number of bees caught increases the number of rare bees caught, in turn increasing the number of species caught. Out of the 60 species and 4374 individual wild bees caught in blueberry fields, 36 species were represented by less than 10 individuals and out of the 46 species and 1891 individual wild bees caught in cranberry fields, 31 species were represented by less than 10 individuals. Not only were fewer bees collected in both previous studies, but the ratio of ‘other’ bees to bumble bees was considerably greater in my study.

In blueberry fields in the south-eastern United States, 27 species of bees were caught in the south-eastern United States over seven years and a much larger geographic region comprised of nine states. Here again, other wild bees, excluding honey bees, bumble bees and *Habropoda laboriosa*, made up only 4% of total bee numbers (Cane and Payne 1993). My number of species in blueberry fields was more similar to that found in central New York where 42 bee species were collected, but, in contrast to most blueberry field studies, that study had considerably more ‘other’ bees, making up between 63 to 86% of bees collected (MacKenzie and Eickwort 1996). Similarly, in cranberry I found considerably more non-*Bombus* wild bees than studies in Ontario (Kevan et al. 1983) and Massachusetts (MacKenzie and Averill 1995). The ratio of bumble bees to ‘other’ bees in my cranberry fields was much closer to the ratio in abandoned and natural cranberry fields than in commercial fields (MacKenzie and Averill 1995).

Even though bumble bees were abundant in all Fraser Valley studies, the species of bumble bee most abundant or even present varied greatly from year to year. *Bombus mixtus* was either the most or second most abundant species of bumble bee in all four years that studies were conducted in the Fraser Valley: 1981, 1982, 2003 and 2004 (Winston and Graf 1982; MacKenzie and Winston 1984, and this thesis), but the second most abundant bumble bee in my study, *Bombus flavifrons*, was represented by 19 individuals in blueberry fields in 1982 (MacKenzie and Winston 1984), was absent from blueberry fields in 1981 (Winston and Graf 1982) and was represented by a maximum of

2 individuals in cranberry fields in 1981 (Winston and Graf 1982) and a single individual in cranberry fields in 1982 (MacKenzie and Winston 1984).

Bombus occidentalis was the second most abundant bumble bee in blueberry fields in 1981 (Winston and Graf 1982), but made up less than 6% of the *Bombus* collected in 1982 (as *Bombus terricola*) (MacKenzie and Winston 1984) and less than 1% of the *Bombus* collected in my study, even though the studies in 1981 and 1982 were conducted in the same fields. Likewise *Bombus occidentalis* was the most abundant bee in cranberry fields in 1982 and second most abundant bee in 1981 (MacKenzie and Winston 1984; Winston and Graf 1982), but was represented by 2 individuals in cranberry fields in 2003 and was absent in 2004. *Bombus occidentalis* was also very low in abundance in urban habitats adjacent to this region (Tommasi *et al.* 2004). This drop in abundance could be due to a *Nosema* outbreak from imported colonies (Thorp and Shepherd 2005). Still, bumble bees as a group were consistently abundant in spite of population fluctuations of individual species.

3.2 Bee Distribution and Local Scale Factors

The difference in honey bee abundance between sampling locations within blueberry fields showed that honey bees may not be dispersing well in these fields. Honey bee numbers were significantly different between blueberry field sampling locations in pan traps but not in sweep netting or visual observations. Analysing honey bee abundance from the nearest edge instead of the area with the most natural vegetation showed no significant difference between sampling sites. However, although honey bees were not preferentially caught in pan traps at the edge of the field, they were likely to be caught in pan traps closest to their colonies. Honey bee colonies were placed in five of the six blueberry fields. In four of these five fields, colonies were placed closest to the sampling site that corresponded to a distance of 80% into the field from the edge with the most natural vegetation, and honey bee abundance was highest at this distance (Table 2.1, Figure 2.2). Previous studies also found a decrease in honey bee abundance with increasing distance from the colony (Aras et al. 1996).

In contrast, honey bees dispersed well within cranberry fields. No differences between sampling sites were detected. This also contrasts with previous cranberry studies that found honey bees did not disperse well, rarely being seen more than 100m and never being seen beyond 200m from their colonies (Kevan *et al.* 1983). In all of my cranberry fields honey bees would have had to travel well over 200m from their colonies to access the furthest sample site, and at least 190m to access the nearest sampling site in all but one field (Table 2.1). Perhaps this difference in dispersal was due to the greater number of honey bee colonies placed in my fields (2.8 colonies/ha in Kevan et al. (1983) vs. a mean of 4.9 colonies/ha in my study), although both are within the recommended colony density for cranberry (2 to 5 colonies/ha) (Le Duc and Turcotte 2004; McGregor 1976).

All sampling methods showed bumble bees were well-dispersed within blueberry fields. Similarly, bumble bees dispersed well in cranberry fields as indicated by their abundance at both the edges and centers of the fields. This is not surprising since bumble bees have been observed to forage as far away as 1750m from their nesting sites (Walther-Hellwig and Frankl 2000) and foraging bouts as far as 5km from their nests could be energetically feasible if floral resources are sufficiently rewarding (Heinrich 1979). Analysing bee abundance from the nearest edge of blueberry fields instead of the area with the most natural vegetation showed no significant difference for any bee category or sampling method.

'Other' bee numbers were not significantly different between sampling locations in blueberry fields with any sampling method. It does not appear that wild bees were concentrating at the edges, but instead dispersed well throughout the fields. Previous studies also found evenly dispersed wild bee abundances throughout blueberry fields (Aras et al. 1996).

However, 'other' bees were more abundant near edges of cranberry fields than they were at 20% or 40% into the field. Unlike honey bees and bumble bees, 'other' bees did not disperse well into cranberry fields, remaining at the periphery. Therefore, as a group 'other' bees were not a good alternative as cranberry pollinators since they would provide uneven pollination, despite the fact that they were common in most fields. This difference in dispersal of 'other' bees between blueberry and cranberry fields might be influenced by the large number of *Lasioglossum* (Dialictus) in my samples (66% of 'other' bees in cranberry fields vs. 31% of 'other' bees in blueberry fields). Bee flight distance has been positively correlated to bee body length (Gathmann and Tscharntke 2002). Very small bees such as *Lasioglossum* (Dialictus) may not travel larger distances readily. Precise flight distances for *Lasioglossum* (Dialictus) would need to be determined to verify the reason for their limited dispersal. To the best of my knowledge, no other study has directly investigated wild bee dispersal in cranberry fields.

The lack of correlation between weeds and bee abundance in these blueberry and cranberry fields was most likely due to the very low weed abundance throughout all of these fields. All blueberry fields in this study were either mowed or sprayed with herbicides and all cranberry fields were sprayed with herbicides to prevent the growth of weeds. Low weed abundance has been previously found in cranberry (MacKenzie 1994), but, to the best of my knowledge, a similar analysis has not been conducted to census weed abundance in blueberry fields. Past studies have found that bee abundance was highly correlated to weed abundance in agricultural settings (Backman and Tiainen 2002; Klein, Steffan-Dewenter and Tscharntke 2003; Morandin 2005). Although I found no correlation, it is quite possible that sampling in blueberry and cranberry fields with larger variation in weed abundance could yield a correlation between bee and weed abundance. In fact, new recommendations that weeds not be eliminated from within crops have been proposed (Laverty and Hiemstra 1998). If weed abundance and bee abundance are positively correlated in blueberry and cranberry fields, then it would be beneficial to growers to increase the number of weeds in their fields, therefore possibly increasing the number of bees thus enhancing pollination.

The lack of significant difference between years for pan trapped and visually observed bumble bee populations in blueberry fields and in cranberry fields suggests that while individual species may vary, general abundance is consistent, contrary to previous studies in which overall bumble bee abundance was shown to be variable between years (Cane and Payne 1993; MacKenzie and Averill 1995; MacKenzie and Winston 1984; Stubbs and Drummond 1997). Variation in wild bee abundance among fields was greater than variation in wild bee abundance between years, showing that variation in wild bee abundance between years is not as important a factor as large scale landscape level factors. This further suggests that variation between years may not be as drastic as other studies have implied. The significant difference between years for all sweep netted bees in blueberry fields was likely due to the modifications made to my sweep netting technique in 2004, consequently catching many more bees compared to 2003. My study suggests that honey bee abundance can be variable even with similar numbers of colonies.

The consistency between years for bumble bees in both crops could indicate that they may be a more reliable pollinator than even honey bees and would further support the case for bumble bees as excellent alternate pollinators. Bumble bees are able to forage in adverse weather conditions that can limit honey bee foraging and that may have contributed to the variability in honey bee numbers between years (Free 1993; Heinrich 1979; Stubbs and Drummond 2001). However, it should be noted that the current study was only conducted over two years. Sampling over several years would reduce the chance of a type two error and reveal whether my conclusion that bumble bee abundance does not vary from year to year is sound.

3.3 Bee Abundance and Large Scale Factors

Bee numbers were highly variable among both blueberry and cranberry fields. Other published studies also indicate that different fields can vary greatly in bee abundance. Up to 11-fold differences in bumble bee abundance have been found between two blueberry fields in the same region (Cane and Payne 1993; MacKenzie and Winston 1984; Winston & Graf 1982). Likewise, two different cranberry fields in a given region can have between a two- to eight-fold difference in bumble bee abundance (Kevan et al 1983; MacKenzie and Averill 1995; MacKenzie and Winston 1984; Winston and Graf 1982). The large variation in bee abundance among both blueberry and cranberry fields and the much smaller variation within fields indicates that large scale factors, such as surrounding habitat and subsequent availability of nesting sites and alternate forage before and after crop bloom, are likely important in determining wild bee abundance. This was also suggested in previous studies (MacKenzie and Winston 1984; Mohr & Kevan 1987; Williams 1982; Winston & Graf 1982). However, both large and local scale factors, such as distance from the edge of the field and weed abundance, are important for 'other' bees in cranberry fields, as indicated by their uneven distribution within fields.

I propose that the amount of natural vegetation surrounding fields, such as forested areas, is the greatest factor determining wild bee abundance. In blueberry, fields four and five and, in cranberry, fields one and two had greater amounts of natural habitat surrounding the fields and also greater abundance of wild bees than did other fields which were surrounded predominantly by agricultural lands (Ratti, personal observations). A GIS analysis of the amount of natural vegetation surrounding these fields could provide valuable information as to required wild bee habitat and could indicate reasons for the large variation between fields.

Other studies have proposed that destruction of nesting sites and loss of habitat are decreasing wild bee populations in agricultural lands (Hutson 1925; MacKenzie and Averill 1995; MacKenzie and Winston 1984; Mohr and Kevan 1987; Williams 1982; Winston and Graf 1982), but few studies have thoroughly investigated this issue directly. For example, *Megachile addenda* nest in dikes surrounding commercial cranberry fields in New Jersey and require red maple leaves to line their nests (Cane, Schiffhauer and Kervin 2003), but the nesting requirements and flight distances for many bees are not well known (Westrich 1996; Williams 1982). Variation in honey bee abundance between fields was likely due to the quantity and location of honey bee colonies with honey bees foraging closest to their colonies in blueberry fields (Figure 2.2) and with fewer honey bees caught in fields with the fewest or no colonies for both crops (Table 2.4, Figure 2.6, Figure 2.7).

The edge of the field is not a barrier to bee movement. In blueberry fields, bumble bee abundance was highly correlated between edge and field pan traps and there was a trend towards significance for pan trapped 'other' bee abundance. In cranberry bogs, honey and 'other' bee abundance also was correlated between edge and field sampling sites, with a trend towards a correlation for bumble bees. Since the edge was not a nectar rich environment, bees were likely trapped while just passing through, or wild bees may have been using it for nesting locations.

Visual observations in blueberry provided no correlation of either honey or 'other' bee abundance between field and edge sites, possibly because of the low amount of weeds in most field edges. Visual observations were counted as bees foraging on a flower. Since few to no flowers were blooming in many of the field edges, few bees were observed foraging in this location.

Sweep netted bumble and 'other' bees in blueberry fields were correlated between edge and field sampling sites since I did not restrict my collection to bees foraging on bloom and collected bees just flying through the area. Sweep netted honey bees showed a trend towards significance between abundance at edge and field sampling sites.

The lack of correlation between honey bee abundance in fields and field edges in blueberry is likely an indication of honey bees not foraging in or landing in pan traps in field edges instead of an inability of honey bees to cross into the edge of the field from the field itself. Honey bees were routinely seen flying from the field into adjacent lands and back again (Ratti, personal observations). In each crop, one field had no honey bee colonies, although honey bees were still present, further demonstrating that honey bees are travelling into these fields from nearby areas (Table 2.1, Fig 2.2). The outlier was due to one particular field, field 3, which routinely had very large numbers of honey bees caught in edge pan traps. This could possibly be due to the lack of alternate forage in the surrounding area. This field had non-flowering crops and tilled fields adjacent to it (Ratti, personal observations).

The ability of bees to travel between crops and the surrounding area would suggest that increasing wild bee abundances in surrounding habitat where they are most likely to be able to nest, also would increase bee abundance in blueberry or cranberry fields themselves. Morandin et al. (in press) found that wild bee abundance was greater in canola fields surrounded by greater amounts of untilled pastureland than in low pastureland fields, further suggesting that wild bees readily cross into canola fields from adjacent pasturelands.

3.4 Bee Abundance and Berry Weight

The relationship between bumble bee abundance and mean berry weight and lack of a similar relationship between honey bee abundance and mean berry weight indicates strongly that bumble bees may be better pollinators of commercial highbush blueberries and cranberries, and may already be responsible for a large percentage of pollination (Javorek et. al 2002). The current bumble bee populations in some of these fields, particularly some of the blueberry fields, are likely more than sufficient to adequately pollinate the crop as shown by the large berry weight in these fields.

Previous studies have found bumble bees to be better blueberry and cranberry pollinators than honey bees (Cane, Schiffhauer and Kervin 1996; Cane and Schiffhauer 2003; Javorek et. al 2002; MacKenzie 1994; Stubbs and Drummond 2001), therefore lower numbers of bumble bees than honey bees are needed to pollinate a crop effectively. I found that a blueberry field with 6 bumble bees per pan trap had greater mean berry weight than a field with 62 honey bees per pan trap but fewer bumble bees, even though they were both the same variety, suggesting that considerably lower numbers of bumble bees than honey bees are needed to pollinate a crop effectively. Caged pollination studies like those that have already been conducted with honey bees, with different densities of bumble bees for a given area of blueberry or cranberry bloom, would be useful in determining the precise minimum number of bumble bees needed for maximum berry pollination.

In cranberry fields bumble bees delivered six times more pollen tetrads per visit and it was estimated that they would pollinate an extra two cranberries per stem over legitimate (non-robbing) honey bee foragers (Cane and Schiffhauer 2003). Bumble bees also have been directly related to increased fruit set and seed set in cranberry (Kevan et al 1983). I found that a cranberry field with 5 bumble bees per sampling site had greater mean berry weight than a field with 10 honey bees per sampling site but fewer bumble bees, suggesting that fewer bumble bees than honey bees are needed to pollinate a cranberry field effectively.

Pan trapped 'other' bees also were significantly related to blueberry weight, but this relationship was due to the significant correlation between pan trapped bumble bee and 'other' bee abundance. Multiple regression analysis of pan trapped bumble bees and ‘other’ bees and blueberry weight showed no significant relationship between ‘other’ bee abundance and blueberry weight. Visually observed and sweep netted ‘other’ bees were not related to blueberry weight. Bumble and ‘other’ bees were correlated likely because they respond to similar environmental factors. Fields with areas of natural habitat that supports larger bumble bee populations likely also contains habitat that supports ‘other’ bees. Factors such as availability of alternate forage or other nesting resources could equally affect bumble and ‘other’ bees. Furthermore, it’s possible that fields with higher abundances of bumble bees had either reduced or more responsible pesticide use which would simultaneously be advantageous to ‘other’ bees but may not have as significant an impact on honey bee colonies which can be closed up during times of heavy spraying.

I analysed bee abundance data by separating blueberries into varieties since different varieties are known to have different relationships between seed number and berry size (Brewer and Dobson 1969). Only the ‘Bluecrop’ variety was found in multiple fields (three fields) and, since the greatest difference in bee abundance was found between fields, instead of within fields, ‘Bluecrop’ serves as the best single variety in this study to more closely examine bee abundance and crop yield. Bumble bee abundance was highly related to ‘Bluecrop’ berry weight for all three sampling methods, whereas honey bee abundance was not related to ‘Bluecrop’ berry weight and ‘other’ bee abundance was related to ‘Bluecrop’ berry weight only for visually observed data. Again, the relationship between visually observed ‘other’ bee abundance and ‘Bluecrop’ berry weight was due to the correlation between visually observed bumble and ‘other’ bee abundance since multiple regression analysis of visually observed bumble bees and ‘other’ bees and blueberry weight showed no significant relationship between 'other' bee abundance and blueberry weight.

Some studies have concluded that wild bees are not numerous enough to pollinate blueberry or cranberry crops but did not measure the relationship between wild bee abundance and crop yield (MacKenzie and Winston 1984; Winston and Graf 1982). My study has demonstrated that existing bumble bee populations may already be providing superior pollination over honey bees and may be sufficient to pollinate blueberry and cranberry crops.

3.5 Number of Mature Seeds vs. Berry Weight

I found significant positive relationships between both blueberry and cranberry weight and number of mature seeds. Bigger berries are due to more mature seeds which in turn have been shown to be due to better pollination (Cane and Schiffhauer 2001; 2003; Dogterom, Winston and Mukai 2000; Eaton 1966; Filmer, Marucci and Moulter 1958; Free 1993; Rigby and Dana 1971; Sarracino and Vorsa 1991; Stubbs and Drummond 2001). The significant relationship between mature seed number and berry weight enabled the use of berry weight as a measure of pollination.

3.6 Shannon-Wiener Diversity and Shannon Evenness Indices

Species diversity in blueberry and cranberry fields was considerably higher in the current study than in past studies (MacKenzie and Winston 1984; Winston and Graf 1982). Only my least diverse blueberry field had a diversity value in the range of MacKenzie and Winston's (1984) highest diversity value. However, my more diverse fields were comparable to diversity found by MacKenzie and Eickwort in central New York (1996). My lowest diversity value in cranberry fields was higher than MacKenzie and Winston's (1984) highest diversity value. However, it was comparable to diversity found by MacKenzie and Averill (1995).

The greater diversity of bees in the current study as compared to the two previous studies in this region (MacKenzie and Winston 1984; Winston and Graf 1982), is most likely explained by my greater sampling effort. However, sampling effort does not explain the similarity in diversity between the current study and those conducted in Eastern Canada (MacKenzie and Averill 1995) and central New York (MacKenzie and Eickwort 1996) since these two studies caught considerably fewer bees than the current study. It's possible that there is genuinely a more diverse bee fauna in Eastern Canada and the North-eastern United States than in the temperate rain forests of British Columbia since higher diversity of bees is generally found in more arid regions (Griswold unpublished data; McIntyre and Hostetler 2001).

The lack of correlation between berry weight and bee diversity or evenness indicates that for monoculture crops like blueberries and cranberries, having low abundances of a lot of different bees is not as beneficial as having large numbers of a few species of bees, or perhaps even one species, that pollinate well. The efficiency and longevity of bumble bee colonies likely reduces the importance of bee diversity in these particular cropping systems. Bumble bee queens were present concurrently with the beginning of blueberry bloom and bumble bee workers were numerous and highly active well through to the end of cranberry bloom. The abundance of all species of bumble bees would have to drop significantly before the sequential emergence of 'other' bees would prove important to crop yield.

A varied bee fauna could prove important in systems where the life span of one particular pollinator does not consistently encompass the entire bloom period of the crops. Different species of bees have different emergence times, therefore a diverse bee fauna is more likely to ensure that some bees are present during bloom if environmental factors such as rain fall or temperature have differential effects on timing of bloom and bee emergence.

Also, increased genetic diversity protects a population from parasitism (Baer and Schmid-Hempel 1999; Brown and Schmid-Hempel 2003). Specific disease or parasite outbreaks can drastically decrease the abundance of one, or a group of closely related species of bees but are much less likely to decrease the abundance of several genera of bees. Large numbers of a few species will produce maximum yield but a diverse bee fauna would ensure at least a certain level of pollination should the most effective pollinators decrease in abundance or be unavailable during crop bloom (Klein, Steffan-Dewenter and Tscharntke 2003).

3.7 Management Implications

This study has provided evidence that bumble bees are important pollinators of highbush blueberry and cranberry crops. Bumble bee abundance was related to berry weight in both blueberry and cranberry fields. Honey and 'other' bee abundance were not indicators of berry weight in either crop. Bumble bees dispersed well in both crops, but 'other' bees did so only in blueberry fields. All bees were readily able to cross into fields from the surrounding areas but bee abundance varied greatly between fields. Thus, these results suggest good potential for commercial blueberry and cranberry crops to be pollinated by bumble bees in the Fraser Valley.

Bumble bees were the most abundant genus of non-*Apis* bees in both crops and as a group were consistently abundant from year to year in spite of population fluctuations of individual species between my study and the previous two studies conducted in this area. Bumble bees are therefore likely a reliable source of berry pollination. If particular species of bumble bee species decline in a certain year, other species will likely be able to maintain suitable pollination service.

I noted a marked decrease of *Bombus occidentalis* between my and previous studies. *B. occidentalis* population decreases have been previously noted and are suspected to be due to a *Nosema* outbreak from imported bumble bee colonies used for greenhouse pollination (Thorp and Shepherd 2005). Further census of *B. occidentalis* would determine if populations are returning to pre-outbreak levels, are continuing to decrease or have reached a new equilibrium at a much lower population level.

Introduced invasive bumble bee species can out-compete native bumble bee species for floral resources and nesting sites, as has been shown with the introduced *Bombus terrestris* and native bumble bees in Japan (Inari et al. 2005; Velthuis and Van Doorn 2006). Consequently, the finding of *Bombus impatiens* in blueberry fields is of some concern. I found five individuals, including one queen. *B. impatiens* is not native to British Columbia and could displace native bumble bee species should it become established in the wild. *B. impatiens* colonies are imported and used for pollination in tomato greenhouses which have unscreened vents, and foraging external to greenhouses is common (Whittington and Winston 2003; Whittington and Winston 2004). Precautions to prevent the establishment of viable populations outside the greenhouse environment include the use of queen excluders to prevent queens from exiting the colonies but queen excluders that are not properly fastened or are removed by greenhouse employees to enhance the workers' ability to enter and leave the hive allow queens to exit (Birmingham, personal communications). My finding of a *B. impatiens* queen supports the likelihood that these non-native bees are or soon will be established in the wild.

Bumble bees are longer lived than solitary bees, with colonies lasting over the course of a summer (Heinrich 1979). Maintaining healthy bumble bee populations would require continuous availability of floral resources throughout the colony's life cycle (Cane 2001; Heinrich 1979). Planting of non-crop flowers before and after crop bloom could benefit bumble bee populations, and therefore crop yield, in situations where other floral resources are not available at these times. Alternatively, a mixed cropping strategy utilizing crops with non-concurrent bloom times, such as blueberry, raspberry and cranberry, within bumble bee flight range would benefit bumble bee populations while maximising food productivity, provided that adequate nesting sites are available.

There were four and five genera of parasitic bees found in blueberry and cranberry fields respectively. The effects of parasitic bee populations and also non-bee parasites of bees should be investigated in more detail since parasites can negatively impact wild and domesticated bee populations, even though their abundance was low in the current study.

3.8 Summary

In conclusion, this study has provided evidence of the potential of bumble bees to provide effective highbush blueberry and cranberry pollination. The managed honey bee, although convenient, is not delivering the best pollination service. In contrast, bumble bees are excellent pollinators of blueberries and cranberries and are likely already carrying out a large portion of the pollination in some of these fields. Their abundance, dispersal and readiness to travel into fields from surrounding areas further support their use as berry pollinators.

Future research should be directed at increasing natural bumble bee abundance in blueberry and cranberry fields. Both large and small scale factors such as the amount of natural habitat surrounding blueberry and cranberry fields and available bumble bee nesting sites and alternate forage should be further investigated to assess their roles in determining bee population size and blueberry and cranberry pollination.

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Appendix

Table A.1: Abundance of each bee species caught in strawberry fields in 2003, combined across two fields and sampling methods. Parasitic species are indicated by an asterisk (*) beside their name.

Species	**Abundance**
Andrena nigrocaerulae	1
Andrena perarmata	1
Andrena salicifloris	2
Andrena sp.3	2
Andrena sp.6	1
Andrena sp.7	2
Andrena spp.	3
Apis mellifera	114
Bombus californicus	2
Bombus flavifrons	33
Bombus impatiens	1
Bombus melanopygus	24
Bombus mixtus	193
Bombus occidentalis	2
Bombus rufocinctus	59
Bombus sp.	1
Ceratina acantha	5
Halictus rubicundus	13
Lasioglossum athabascense	1
Lasioglossum Dialictus spp.	18
Lasioglossum olympiae	2
Lasioglossum zonulum	51
Osmia bucephala	1
Osmia dolerosa	1
Osmia pusilla	1
**Sphecodes sp.1*	1
Total	**535**

Figure A.1: Mean number of insects visually observed foraging in strawberry fields in 2003.