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NATIVE BEE DIVERSITY AND POLLEN FORAGING SPECIFICITY IN
CULTIVATED Highbush Blueberry (Ericaceae: *Vaccinium*
corymbosum L.) plantings in Rhode Island

BY

ZACHARY SCOTT

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE
REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE
IN
BIOLOGICAL SCIENCES

UNIVERSITY OF RHODE ISLAND

2016

MASTER OF SCIENCE THESIS

OF

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UNIVERSITY OF RHODE ISLAND

2016

ABSTRACT

Approximately 87% of flowering plants in the world are pollinated by animals. Bees are some of the most economically and ecologically important pollinators, necessary for the production of about one third of all crops. One such crop is highbush blueberry, grown throughout Rhode Island in small acreages. I conducted a survey of the bee species foraging on managed blueberry farms throughout Rhode Island, and analyzed their preference for blueberry pollen. I identified species using the DiscoverLife bee guides and confirmed the determinations with a taxonomist. I analyzed pollen loads, calculating percent blueberry pollen collected to determine which species were the most specific when in blueberry patches.

Most bee species nest underground. *Andrena* spp. are known to typically prefer sandy soils near forest edges or openings, but individual species data tends to focus on the biology and behavior of the bee and not soil characteristics. We discovered nests of *Andrena crataegi* Robertson underneath apple trees while collecting bees from commercial and research highbush blueberry plantings in Rhode Island. We identified the soil texture, percent organic matter, bulk density, and pH of the soil at the nest site. Depending on depth, the soil was found to be either silt loam or silt, percent organic matter ranged from 2.6-8.4%, bulk density ranged from 1.0-1.5 g/cm³, and pH ranged from 4.8-5.0. Further study is required to better understand the nesting requirements of this bee, with consideration of how site specific characteristics influence the agriculturally significant bee species in an area.

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PREFACE

The chapters of this thesis are being submitted in manuscript format. Chapter one, “Native Bee Diversity and Pollen Foraging Specificity in Cultivated Highbush Blueberry (Ericaceae: *Vaccinium corymbosum* L.) Plantings in Rhode Island” has been accepted to Environmental Entomology with co-authors Howard Ginsberg and Steven R. Alm. Chapter two, "Soil Characteristics of an *Andrena crataegi* Roberston (Hymenoptera: Andrenidae) Nesting Site" includes soil data for this native pollinator's nesting habitat.

TABLE OF CONTENTS

ABSTRACT	ii
ACKNOWLEDGEMENTS	iii
PREFACE	iv
TABLE OF CONTENTS	v
LIST OF FIGURES AND TABLES	vi
CHAPTER 1	1
ABSTRACT	2
INTRODUCTION	3
METHODS	5
RESULTS	7
DISCUSSION	9
ACKNOWLEDGEMENTS	15
REFERENCES CITED	16
FIGURES AND TABLES	20
CHAPTER 2	33
ABSTRACT	34
INTRODUCTION	35
METHODS	36
RESULTS	38
DISCUSSION	38
ACKNOWLEDGEMENTS	41
REFERENCES CITED	42
FIGURES AND TABLES	43
APPENDIX	47

LIST OF FIGURES AND TABLES

FIGURE OR TABLE	PAGE
Chapter One	
Table 1. Bee species and numbers collected from <i>Vaccinium corymbosum</i> , East Farm, Kingston, RI, May 19 - June 4, 2014.	20
Table 2. Bee species and numbers collected from <i>Vaccinium corymbosum</i> , May 13 – June 4, 2015.	22
Table 3. Number of bees (in order of most frequently collected to least in 2014 and 2015) with the largest blueberry pollen loads at each sampled primary farm. From left to right, farms with greatest number of important blueberry pollinators to fewest... .	27
Figure 1. Blueberry sampling sites: 1. Manfredi Farms, Westerly, RI; 2. East Farm, Kingston, RI; 3. The Farmer’s Daughter, Wakefield, RI; 4. Smith’s Berry Farm, Saunderstown, RI; 5. Peter Morgan, North Kingstown; 6. Narrow Lane Orchard, North Kingstown, RI; 7. Macomber’s Blueberry Farm, Coventry, RI; 8. Pippin Orchard, Cranston, RI; 9. Dame Family Farm, Johnston, RI; 10. Barden Family Farm, North Scituate, RI; 11. Harmony Farms, North Scituate, RI; 12. Jaswell’s Farm, Smithfield, RI; 13. Sweet Berry Farm, Middletown, RI; 14. Hart Family Farm, Tiverton, RI; 15. Boughs and Berries, Little Compton, RI.....	29
Figure 2. Mean (+SE) total blueberry grains collected by the ten most frequently collected bee species in 2014 and 2015. From left to right in order of most frequently collected to least. Means followed by the same letter are not significantly different (Tukey’s HSD test, $\alpha = 0.05$)... ..	30

Figure 3. Mean (+SE) percent blueberry pollen by the ten most frequently collected bee species collected in 2014 and 2015. From left to right, in order of most frequently collected to least. Means followed by the same letter are not significantly different (Tukey's HSD test, $\alpha = 0.05$). 31

Figure 4. Mean (+SE) total pollen grains collected by the ten most frequently collected bee species in 2014 and 2015. From left to right in order of most frequently collected to least. Means followed by the same letter are not significantly different (Tukey's HSD test, $\alpha = 0.05$). 32

Chapter Two

Figure 1. Emergence traps placed over *A. crataegi* nest entrances..... 43

Figure 2. Close up view of the tibial spur of *A. crataegi*. 44

Figure 3. Golf course cup changer used to obtain soil from the nest site. 45

Table 1. Mean soil characteristics of three samples at an *A. crataegi* nest site. 46

Appendix

Table 1. Bee species and numbers collected from *Vaccinium corymbosum*, May 17 – June 1, 2016.. 52

CHAPTER 1

“Native Bee Diversity and Pollen Foraging Specificity in Cultivated Highbush Blueberry (Ericaceae: *Vaccinium corymbosum* L.) Plantings in Rhode Island”

by

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Accepted in Environmental Entomology

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ABSTRACT

We identified 41 species of native bees from a total of 1083 specimens collected at cultivated highbush blueberry plantings throughout Rhode Island in 2014 and 2015. *Andrena* spp., *Bombus* spp. and *Xylocopa virginica* (L.) were collected most often. *Bombus griseocollis* (DeGeer), *B. impatiens* Cresson, *B. bimaculatus* Cresson, *B. perplexus* Cresson, and *Andrena vicina* Smith collected the largest mean numbers of blueberry pollen tetrads. The largest mean percent blueberry pollen loads were carried by the miner bees *Andrena bradleyi* Viereck (91%), *A. carolina* Viereck (90%), and *Colletes validus* Cresson (87%). The largest mean total pollen grain loads were carried by *B. griseocollis* (549,844), *B. impatiens* (389,558), *X. virginica* (233,500), and *B. bimaculatus* (193,132). *Xylocopa virginica* was the fourth and fifth most commonly collected bee species in 2014 and 2015 respectively. They exhibit nectar robbing and females carried relatively low blueberry pollen loads (mean 33%). Overall we found 10 species of bees to be the primary pollinators of blueberry in Rhode Island.

INTRODUCTION

The importance of pollinators to blueberry production has been well documented (Brewer and Dobson 1969, MacKenzie 1997, Dogterom et al. 2000). At least 80% of highbush blueberry flowers must set fruit to result in a commercial crop (MacKenzie 1997). Blueberry flowers only release pollen from small pores or slits in the anthers, and pollen is most effectively removed by sonication, commonly referred to as buzz pollination (Free 1993, De Luca and Valleho-Marin 2013). Bees that buzz-pollinate are especially effective at pollinating blueberry, and many native bee species, including those in the genera *Andrena* and *Bombus*, have evolved this adaptation (Javorek et al. 2002). Pollination increases the number of blossoms that set fruit, seed number and fruit size (Brewer and Dobson 1969). Fruit size and seed number decreases in flowers that are pollinated later, so there is an advantage to having flowers pollinated early in the season (Brewer and Dobson 1969). Pollination from more distantly related cultivars leads to larger berries that ripen earlier (Dogterom et al. 2000). When artificially pollinated with outcrossed pollen, fruit mass increased significantly as 10, 25, and 125 pollen tetrads were used, but did not change when 300 (the maximum amount one flower can receive) were added (Dogterom et al. 2000). Days to ripening also decreased with pollen load increase (Dogterom et al. 2000). This suggests there is an advantage to growing cultivars that are distantly related. It is also important for growers to keep in mind that blueberry cultivars flower early, mid-, or late during the approximately three week bloom period in Rhode Island and cultivars must be in bloom at the same time to take advantage of cross pollination. (McGregor 1976, Eck et al. 1990).

Recent research has improved our knowledge of which species are important blueberry pollinators. Moisan-Deserres et al. (2014) found that species from the genera *Bombus* and *Andrena* collected large amounts of lowbush blueberry pollen, with two *Andrena* species (*A. carolina* Viereck and *A. bradleyi* Viereck) collecting nearly 100 percent lowbush blueberry pollen (monolectic). *Bombus* species collected the largest pollen loads. Bushmann and Drummond (2015) found that *Andrena* spp. were the most numerous wild bees foraging in lowbush blueberries in Maine. The efficacy of bumble bees as lowbush blueberry pollinators has already been documented (Javorek et al. 2002, Drummond 2012), and Bushmann and Drummond (2015) did not want to deplete the bumble bee populations of the region in their study. Stubbs et al. (1992) also found that *A. bradleyi* and *A. carlini* Cockerell collected more than 95% lowbush blueberry pollen. At the other end of the spectrum, *A. vicina* Smith is a polylectic bee with 69 genera of plants listed as sources of pollen and nectar (Stubbs et al. 1992).

A study of rabbiteye blueberry, *Vaccinium virgatum* Aiton pollinators found that three taxa were often abundant: the honey bee, *Apis mellifera* L.; queens of four bumble bee species, and the eastern blueberry bee, *Habropoda laboriosa* F. (Cane and Payne 1993). Carpenter bees, *Xylocopa virginica* (L.), were also commonly seen. However, they always robbed nectar by cutting holes in the corolla to sip nectar without collecting pollen (Cane and Payne 1993). Honey bees were the only other species observed to use these holes, and over 90% of them were observed exhibiting this behavior during mid- to late-flowering season (Cane and Payne 1993). Another study of nectar robbery in rabbiteye blueberry showed that increased numbers of floral

visits by carpenter and honey bees yielded stigmatic loads equal to one visit by *H. laboriosa* and that nectar robbery had no overall effect on fruit set (Sampson et al. 2004).

Our growing awareness of the importance of native pollinators to agricultural systems highlights the need to know which species are present in a crop system, and their importance for pollinating the desired crop. This will allow growers to manage habitat and forage to attract the most important pollinators. Our objectives were to identify the native bee highbush blueberry pollinators in Rhode Island and determine the amounts of blueberry and pollen from all plant species they collected.

METHODS

Pollinator collections 2014. From 19 May to 4 June 2014, pollinators were collected for 30 min, 9 mornings and afternoons, along eight 50 m transects in a 1,457 m² highbush blueberry planting at the University of Rhode Island's East Farm, Kingston, RI. The planting consists of early ('Earlyblue', 'Bluetta', 'Collins', 'Reka') mid- ('Bluehaven', 'Blueray', 'Bluejay', 'Bluecrop', 'Northland', 'Bluegold', 'Jersey', 'Chandler') and late ('Darrow', 'Herbert', 'Lateblue') ripening cultivars of different ages planted 1.5 by 2.4 m apart. Pollinators visiting blueberry flowers were collected with nets, killed with ethyl acetate in jars and placed in labeled containers in a freezer until they were pinned and labeled. All specimens were determined to the species level. Specimens were further separated into male, female and for the genus *Bombus* into queens and workers.

Pollinator Collections 2015. From 13 May to 5 June 2015, pollinators were collected as they visited blueberry flowers using 50 ml snap cap plastic vials. Three individuals collected bees as they walked 50-70 m transects along different rows of blueberries for 15 minutes. Six commercial and one agricultural experiment station blueberry plantings throughout Rhode Island (Fig. 1) were sampled in both the morning and afternoon for four to eight collections at each site. Sites with less cultivar diversity were sampled fewer times due to the shorter bloom period. The same technique using two collectors for 15 minutes was conducted at eight additional commercial plantings for one to three mid-day collections between 26 May and 5 June 2015 (Fig. 1). Bees were kept in the vials used to collect them to prevent any cross contamination of pollen. They were transported in a cooler to a laboratory to be frozen, pinned and labeled with site, date, and time collected. Specimens were then identified under a dissecting microscope to species and verified by S. Bushmann (University of Maine) or S. Droege (USGS Patuxent Wildlife Research Center).

Pollen Analysis. Pollen loads were analyzed according to methodology adapted from Louveaux et al. (1978) and Moisan-Deserres et al. (2014). One leg with pollen was removed from each specimen with scissors and placed in 1 ml of a staining solution (1% Gram's fuchsin solution, Sigma-Aldrich, St. Louis, MO; 5% Tween 20, Sigma-Aldrich, St. Louis, MO; 94% double distilled water). The leg and pollen was vortexed for 30 seconds and 1 μ l was placed on an improved Neubauer hemocytometer (Hausser Scientific, Horsham, PA) where the total number of blueberry and other plant pollen types (Moore and Webb 1978 and Moore et al. 1991) were counted on a computer screen connected to a camera attached to a Olympus

SZX stereo microscope (600×). We then calculated the total pollen load per bee (excluding pollen on the body) as well as the percent blueberry pollen collected. We did not use the formula provided by the manufacturer of the hemocytometer since we found that blueberry pollen is considerably larger (35 - 71 μm) than blood cells (6 - 8 μm) and pollen was often clumped outside of the counting grid when the manufacturer's directions were followed. Placing 1 μl directly on the grid allowed us to count all pollen grains and tetrads.

Diversity analysis. To calculate species richness and the Shannon-Weiner and Simpson's indices of diversity, sampling effort was equalized to two mornings and two afternoons at each site.

Statistical Analysis. To evaluate differences in mean *Vaccinium* pollen tetrads, and mean total pollen loads for each species, counts of pollen grains and tetrads were log transformed. To evaluate differences in mean percent *Vaccinium* pollen tetrads, data were arcsine square root transformed. Both transformations sufficiently normalized the data. We used Welch's ANOVA's because of across-species heterogeneity in variances. Following a significant ANOVA, Tukey's HSD test was used for mean separation (JMP, SAS Institute, 2015).

RESULTS

Pollinator collections. One hundred and fifty pollinators were collected and identified to 17 species at East Farm in 2014 (Table 1). *Andrena vicina* and *Bombus bimaculatus* were the most prevalent species (25 and 24% of the total number

collected respectively) followed by *A. carlini* Cockerell, *Xylocopa virginica*, *B. griseocollis* and *B. perplexus* (Table 1).

Nine hundred and thirty-three pollinators were collected and identified to 40 species in 2015 (Table 2.). All species collected in 2014 were also collected in 2015 except for *Nomada maculata* Cresson, a kleptoparasite of andrenid bees, which was not collected in 2015. As in 2014, *Andrena vicina* and *Bombus bimaculatus* were again the most common species (17% and 16% of the total respectively) along with *B. impatiens* (15%) followed by *B. griseocolis*, *Xylocopa virginica*, *A. carolina*, *B. perplexus*, and *A. carlini* (Table 2).

The Shannon-Weiner and Simpson's diversity indexes ranged from 1.68 to 2.42 and 0.74 to 0.90 respectively (Table 3). Narrow Lane Orchard had the highest Shannon-Wiener index (2.42) and the highest Simpson's index (0.90). Macomber Farm had the highest species richness (17) and the second highest Shannon-Wiener index (2.26). East Farm (Agricultural Experiment Station) had the second highest species richness along with Narrow Lane Orchard (16) (Table 3).

Blueberry and Total Pollen collections. The species with the largest mean number of blueberry pollen tetrads ranked as follows: *Bombus griseocollis* (318,240), *B. impatiens* (243,500), *B. bimaculatus* (145,739), *B. perplexus* (89,121), *A. vicina* (70,100), *X. virginica* (34,066), *A. bradleyi* (29,125), *A. carolina* (28,212), *Colletes validus* (28,000), and *A. carlini* (21,882) (Fig. 2). *Bombus griseocollis* collected significantly more blueberry pollen tetrads than any other species except *B. impatiens* ($F = 29.39$, $df = 9, 551$, $P < 0.001$) (Fig. 2).

Species with the largest percent blueberry pollen loads were: *Andrena bradleyi* (91%), *A. carolina* (90%), *Colletes validus* (87%), *Bombus bimaculatus* (82%), *B. perplexus* (74%), *B. griseocollis* (73%), *B. impatiens* (72%), *A. vicina* (69%), *A. carlini* (51%), and *Xylocopa virginica* (33%) (Fig. 3). *Andrena carolina* collected the largest mean percentage of blueberry pollen, but it was not significantly greater than *A. bradleyi*, *C. validus*, *B. bimaculatus* or *B. perplexus*. *Andrena carolina* did collect a significantly greater percentage of blueberry pollen than *A. vicina*, *B. impatiens*, *B. griseocollis*, *X. virginica*, *A. carlini* ($F = 12.92$, $df = 9, 549$, $P < 0.001$) (Fig. 3).

The largest mean total pollen grains and tetrads were carried by: *Bombus griseocollis* (549,844), *B. impatiens* (389,558), *Xylocopa virginica* (233,500), *B. bimaculatus* (193,132), *B. perplexus* (143,000), *Andrena vicina* (130,187), *A. carlini* (84,800), *A. carolina* (33,353), *A. bradleyi* (31,750) and *C. validus* (29,556) (Fig. 4). *Bombus griseocollis* collected significantly more total pollen grains and tetrads than any other species except *B. impatiens* ($F = 30.15$, $df = 9, 583$, $P < 0.001$) (Fig. 4).

Total number of the top ten blueberry pollinators (based on largest blueberry pollen loads) for each of the primary farms and based on the same number of collection periods ranged from a high of 124 at Dame Farm to a low of 31 at Sweet Berry Farm (Table 3). The Dame and Jaswell Farms are located in northern Rhode Island and are the most rural locations we sampled.

DISCUSSION

The most frequently collected pollinators on highbush blueberry include *Bombus* spp., the carpenter bee *Xylocopa virginica*, and bees in the families

Andrenidae and Halictidae (MacKenzie and Eickwort 1996, Isaacs and Kirk 2010, Bushmann and Drummond 2015). The most frequently collected species in our study were: *Andrena vicina* (199), *Bombus bimaculatus* (190), *B. impatiens* (154), *B. griseocollis* (103), *Xylocopa virginica* (103), *A. carolina* (83), *B. perplexus* (71) and *A. carlini* (68).

Andrena vicina is a polylectic bee that prefers *Prunus*, *Salix*, *Crataegus*, and *Vaccinium* (Bouseman and LaBerge 1979) but has a host list of 40+ species of plants (Ascher and Pickering, 2015). Stubbs et al. (1992) listed 69 genera of plants as sources of pollen and/or nectar for this bee. Since female *A. vicina* are active from early May until late June, they, along with other blueberry-foraging bees must seek other pollen sources when blueberry is not available (Miliczky and Osgood 1995). Miliczky and Osgood (1995) studied the bionomics of *A. vicina* in Maine and Washington and found a perennial nesting aggregation in a suburban lawn in Edmonds, WA while bees in Maine nested within fields managed for commercial blueberry production. Each nest consisted of a near-vertical main burrow with as many as 13 cells dispersed around its lower end at depths of 15 to 36 cm. Provision masses consisted of flattened spheres of pollen moistened with nectar and varied considerably in size. *A. vicina* overwinters as an adult in the natal cell (Miliczky and Osgood 1995). It is worth noting that potential habitat and forage is present within 400 m of the East Farm blueberry planting in the form of considerable swards of turfgrass and apple and crabapple orchards.

Bombus bimaculatus emerges in early spring (Colla and Dumesh 2010). Its habitats are listed as close to or within wooded areas, urban parks and gardens (Colla

and Dumesch 2010). It nests underground and for most colonies, the life cycle is completed by the middle of summer (Lavery and Harder 1988).

Bombus impatiens also emerges in early spring and can be found in wooded areas, open fields, urban parks and gardens, and wetlands (Colla and Dumesch 2010). It is a generalist species, visiting over 100 native plant genera throughout its range. This is necessary because of their long colony life cycle which extends into autumn and spans the flowering periods of many plant species. (Colla and Dumesch 2010).

Bombus griseocollis exhibits late spring emergence (Colla and Dumesch 2010). Its habitats includes open farmland and fields, urban parks and gardens, and wetlands (Colla and Dumesch 2010). Nests are usually on the ground surface and most colonies are completed by mid-summer (Lavery and Harder 1988).

Xylocopa virginica has a long colony life cycle, with many females living two years. In March and April males defend areas near the nest and mate with females. Females construct nests in unfinished wood, and nests can be reused for many generations (Gerling and Hermann 1978). *Xylocopa virginica* has nectar robbing tendencies, relatively low blueberry pollen loads, and pollen transfer efficiency is low (2.5 pollen tetrads deposited per visit, Benjamin and Winfree 2014). Despite these shortcomings, the large number of these pollinators and possible ease of increasing numbers by providing unfinished wood nesting sites around blueberry plantings, suggests more research on the importance of this bee as a blueberry pollinator is needed.

Andrena carolina is considered to be a *Vaccinium* specialist, present in blueberry fields before and during bloom, but not afterward because its flight season

is restricted by the bloom period of its sole pollen sources (blueberry and related Ericaceae) (Tuell et al. 2009).

Bombus perplexus emerges in early spring and can be found in wooded areas, urban parks and gardens, and wetlands (Colla and Dumesht 2010). It nests on the ground surface and in hollow logs and trees (Lavery and Harder 1988).

Andrena carlini is a relatively large and abundant species across much of eastern North America (Tuell et al. 2009). It is not a specialist on Ericaceae but about half of the specimens collected by Tuell et al. (2009) were carrying pure loads of *Vaccinium*.

Bushmann and Drummond (2015) collected 124 species of bees in lowbush blueberry, *Vaccinium angustifolium* Aiton, in Maine. However, they used bee bowls to sample bees, some of which may not have been pollinating blueberry. This total is considerably higher than the 38 species that Stubbs et al. (1992) collected in Maine lowbush blueberry fields. MacKenzie and Eickwort (1996) collected 42 species of bees in highbush blueberry in New York State, with six species having 10 or more specimens. MacKenzie and Winston (1984) collected only 15 species of bees on cultivated blueberry, raspberry and cranberry in British Columbia, Canada, versus 48 species on natural flowers. Their study also points out that natural vegetation may be more attractive to native pollinators than a desired crop and one must be careful in recommending to growers planting or conserving native vegetation that may compete with blueberry pollination.

Benjamin and Winfree (2014) studied honey and native bee pollination in commercial highbush blueberry in New Jersey. They found that the European honey

bee, *Apis mellifera* L. deposited a median of 18.5 tetrads of pollen during a nectar-collecting visit, 24 tetrads during a pollen-collecting visit and 0.5 tetrads during a secondary nectar-robbing visit. They also found that pollen tetrads deposited by *Bombus* spp., large *Andrena* spp., medium *Andrena* spp. and *Xylocopa virginica* were 23.5, 9.0, 11.5, and 2.5 tetrads respectively. All of their study sites were stocked with domesticated honey bees at densities of 2.5-7.5 hives ha⁻¹. Honey bees provided 86% and native bees 14% of the pollination. Conversely, Winfree et al. (2007) found that native bees were the most important pollinators and alone were sufficient to pollinate commercially grown watermelons in New Jersey and Pennsylvania. Previous studies have shown that native bees contribute to crop pollination at farms near natural habitat, but not in more intensively used agricultural areas (Kremen et al. 2004, Klein et al. 2007). Bees that sonicate flowers when collecting pollen, including those in the genera *Bombus*, *Andrena*, *Colletes*, and *Xylocopa virginica*, are more effective at removing pollen from poricidal anthers, which may result in more efficient pollination on a per-visit basis (Buchmann 1983, Javorek et al. 2002).

Our study sites were relatively small (0.08 – 0.8 ha) and native bees are probably adequate for pollination. Only four farms had honey bee hives. Rhode Island growers should be able to increase their pollination by stocking domesticated honey bees and increasing habitat and forage for native bees beyond blueberry bloom. The largest number of important native bee blueberry pollinators were found in northern Rhode Island. The greater numbers most likely result, in part, from habitat differences among the various sampled farms. Other possible contributing factors include other crops grown at these farms, soil types, and pesticide applications that might affect

native bee populations. Further research at these locations may help to explain the reasons for the larger populations of native bee blueberry pollinators found there.

In order to determine the direct pollination effectiveness of the ten most commonly collected bees in Rhode Island, per-visit pollen deposition rates could be calculated as in Benjamin and Winfree (2014) to determine which of the most common species is the most effective pollinator.

The Shannon-Weiner diversity indexes we calculated (1.68 – 2.42) were slightly lower in most locations than those calculated by MacKenzie and Eickwort (1996) from highbush blueberry sites in Central New York (2.4 in a commercial plot to 2.57 in a natural forest). They were higher than the indexes MacKenzie and Winston (1984) calculated from commercial blueberry fields in British Columbia (0.48 – 0.61). The lower native bee species richness and diversity in that region may be due to some biotic (e. g. disease, habitat) or abiotic factors (e. g. pesticides). It is interesting that no *Andrena* spp. were collected in that study.

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Table 1. Bee species and numbers collected from *Vaccinium corymbosum*, East Farm, Kingston, RI, May 19 - June 4, 2014

Family:	Genus and species	No. of			<i>Bombus</i> only	
					Queens	Workers
Andrenidae	<i>Andrena vicina</i> Smith	38	20	18		
Apidae	<i>Bombus bimaculatus</i> Cresson	37			7	30
Andrenidae	<i>Andrena carlini</i> Cockerell	13		13		
Apidae	<i>Xylocopa virginica</i> (L.)	12	8	4		
Apidae	<i>Bombus griseocollis</i> (DeGeer)	11			11	0
Apidae	<i>Bombus perplexus</i> Cresson	11			6	5
Apidae	<i>Bombus impatiens</i> Cresson	8			7	1
Andrenidae	<i>Andrena carolina</i> Viereck	6		6		
Andrenidae	<i>Andrena bradleyi</i> Viereck	4		4		
Andrenidae	<i>Andrena dunningi</i> Cockerell	2		2		
Andrenidae	<i>Andrena nivalis</i> Smith	2	1	1		

Table 1. (continued)

Family:	Genus and species	No. of Individuals	Male	Female	<i>Bombus</i> only	
					Queens	Workers
Andrenidae	<i>Andrena imitatrix</i> Cresson	1		1		
Apidae	<i>Nomada maculata</i> Cresson	1		1		
Halictidae	<i>Halictus confusus</i> Smith	1		1		
Halictidae	<i>Lasioglossum quebecense</i> (Crawford)	1		1		
Andrenidae	<i>Andrena pruni</i> Robertson	1	1			
Total		150				

Table 2. Bee species and numbers collected from *Vaccinium corymbosum*, May 13 – June 4, 2015.

Family	Genus and species	No. of individuals	Males	Females	<i>Bombus</i> only	
					Queens	Workers
Andrenidae	<i>Andrena vicina</i> Smith	161	5	156		
Apidae	<i>Bombus bimaculatus</i> Cresson	153			38	114
Apidae	<i>Bombus impatiens</i> Cresson	146			138	8
Apidae	<i>Bombus griseocollis</i> (DeGeer)	92			91	1
Apidae	<i>Xylocopa virginica</i> (L.)	91	39	52		
Andrenidae	<i>Andrena carolina</i> Viereck	77	3	74		
Apidae	<i>Bombus perplexus</i> (Cresson)	60			19	41
Andrenidae	<i>Andrena carlini</i> Cockerell	55		55		

Table 2. (continued)

Family	Genus and species	No. of individuals	Males	Females	<i>Bombus</i> only	
					Queens	Workers
Andrenidae	<i>Andrena bradleyi</i> Viereck	15	1	14		
Andrenidae	<i>Andrena crataegi</i> Robertson	14	7	7		
Colletidae	<i>Colletes validus</i> Cresson	10		10		
Halictidae	<i>Lasioglossum quebecense</i> (Crawford)	6		6		
Andrenidae	<i>Andrena imitatrix</i> Cresson	6		6		
Andrenidae	<i>Andrena nivalis</i> Smith	5		5		
Andrenidae	<i>Andrena bisalicis</i> Viereck	3		3		
Andrenidae	<i>Andrena pruni</i> Robertson	3		3		

Table 2. (continued)

Family	Genus and species	No. of individuals	Males	Females	<i>Bombus</i> only	
					Queens	Workers
Apidae	<i>Bombus vagans</i> Smith	3			2	1
Colletidae	<i>Colletes thoracicus</i> Smith	3	1	2		
Halictidae	<i>Lasioglossum versatum</i> (Robertson)	3		3		
Andrenidae	<i>Andrena mandibularis</i> Robertson	2		2		
Halictidae	<i>Augochloropsis metallica</i> (F.)	2	1	1		
Colletidae	<i>Colletes inaequalis</i> Say	2		2		
Halictidae	<i>Halictus confusus</i> Smith	2		2		
Megachilidae	<i>Osmia bucephala</i> Cresson	2		2		

Table 2. (continued)

Family	Genus and species	No. of individuals	Males	Females	<i>Bombus</i> only	
					Queens	Workers
Megachilidae	<i>Osmia cornifrons</i> (Radoszkowski)	2		2		
Halictidae	<i>Agapostemon sericeus</i> (Forster)	1		1		
Andrenidae	<i>Andrena barbilabris</i> (Kirby)	1		1		
Andrenidae	<i>Andrena cornelli</i> Viereck	1		1		
Andrenidae	<i>Andrena dunningi</i> Cockerell	1		1		
Andrenidae	<i>Andrena hippotes</i> Robertson	1		1		
Andrenidae	<i>Andrena milwaukeensis</i> Graenicher	1		1		
Andrenidae	<i>Andrena miserabilis</i> Cresson	1		1		

Table 2. (continued)

Family	Genus and species	No. of individuals	Males	Females	<i>Bombus</i> only	
					Queens	Workers
Andrenidae	<i>Andrena perplexa</i> Smith	1		1		
Halictidae	<i>Augochlorella aurata</i> (Smith)	1		1		
Halictidae	<i>Augochlora pura</i> (Say)	1	1			
Apidae	<i>Ceratina calcarata</i> Robertson	1		1		
Halictidae	<i>Halictus rubicundus</i> (Christ)	1		1		
Halictidae	<i>Lasioglossum nymphaerum</i> (Cockerell)	1		1		
Apidae	<i>Nomada cressonii</i> Robertson	1	1			
Megachilidae	<i>Osmia inspergens</i> Lovell and Cockerell	1		1		
Total		933				

Table 3. Diversity indexes and number of bees (in order of most frequently collected to least in 2014 and 2015) with the largest blueberry pollen loads at each sampled primary farm. From left to right, farms with greatest number of important blueberry pollinators to fewest.

Species	Dame	Jaswell	East Farm	Macomber	Boughs & Berries	Narrow Lane Orchard	Sweet Berry Farm
<i>A. vicina</i>	41	51	17	9	1	8	6
<i>B. impatiens</i>	26	30	3	13	26	6	3
<i>B. bimaculatus</i>	14	6	21	13	16	6	11
<i>B. perplexus</i>	15	2	5	3	4	3	0
<i>B. griseocollis</i>	3	3	4	1	26	1	2
<i>X. virginica</i>	2	9	13	19	1	7	7
<i>A. carlini</i>	5	9	8	4	3	2	2

Table 3. (continued)

Species	Dame	Jaswell	East Farm	Macomber	Boughs & Berries	Narrow Lane Orchard	Sweet Berry Farm
<i>A. bradleyi</i>	1	0	5	1	1	0	0
<i>A. carolina</i>	16	4	10	1	0	3	0
<i>C. validus</i>	1	2	0	6	0	0	0
Total	124	116	86	70	78	36	31
Species Richness	14	11	16	17	13	16	9
Shannon-Weiner	1.97	1.68	2.33	2.26	1.74	2.42	1.89
Simpson's Index	0.821	0.738	0.884	0.871	0.771	0.902	0.837

Figure 1: Blueberry sampling sites: 1. Manfredi Farms, Westerly, RI; 2. East Farm, Kingston, RI; 3. The Farmer’s Daughter, Wakefield, RI; 4. Smith’s Berry Farm, Saunderstown, RI; 5. Peter Morgan, North Kingstown; 6. Narrow Lane Orchard, North Kingstown, RI; 7. Macomber’s Blueberry Farm, Coventry, RI; 8. Pippin Orchard, Cranston, RI; 9. Dame Family Farm, Johnston, RI; 10. Barden Family Farm, North Scituate, RI; 11. Harmony Farms, North Scituate, RI; 12. Jaswell’s Farm, Smithfield, RI; 13. Sweet Berry Farm, Middletown, RI; 14. Hart Family Farm, Tiverton, RI; 15. Boughs and Berries, Little Compton, RI.

Figure 2: Mean (+SE) total blueberry tetrads collected by the ten most frequently collected bee species in 2014 and 2015. From left to right in order of most frequently collected to least. Means followed by the same letter are not significantly different (Tukey's HSD test, $\alpha = 0.05$).

Figure 3: Mean (+SE) percent blueberry pollen by the ten most frequently collected bee species collected in 2014 and 2015. From left to right, in order of most frequently collected to least. Means followed by the same letter are not significantly different (Tukey's HSD test, $\alpha = 0.05$).

Figure 4: Mean (+SE) total pollen grains and tetrads collected by the ten most frequently collected bee species in 2014 and 2015. From left to right in order of most frequently collected to least. Means followed by the same letter are not significantly different (Tukey's HSD test, $\alpha = 0.05$).

CHAPTER 2

“Soil Characteristics of an *Andrena crataegi* Roberston (Hymenoptera: Andrenidae) Nesting Site”

by

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ABSTRACT

Most bee species nest underground. *Andrena* spp. are known to typically prefer sandy soils near forest edges or openings, but individual species data tend to focus on the biology and behavior of the bee and not soil characteristics. We discovered nests of *Andrena crataegi* Robertson underneath apple trees while collecting bees from commercial and research highbush blueberry plantings in Rhode Island. We identified the soil texture, percent organic matter, bulk density, and pH of the soil at the nest site. Depending on depth, the soil was found to be either silt loam or silt, percent organic matter ranged from 2.6-8.4%, bulk density ranged from 1.0-1.5 g/cm³, and pH ranged from 4.8-5.0. Further study is required to better understand the nesting requirements of this bee, with consideration of how site specific characteristics influence the agriculturally significant bee species in an area.

INTRODUCTION

The majority of bee species are solitary ground nesters (Linsley 1958). The nesting requirements for bees varies considerably among species, with well-drained soil being the only factor generally influencing nest site selection in ground nesting bees (Linsley 1958). The presence of bare ground is an important factor in determining the dominant species and overall bee community in an area (Potts et al. 2005). Soil compaction can also affect where bees nest, but the diversity of individual preferences by species makes quantifying the suitability of a site for nesting difficult (Sardiñas and Kremen 2014). Bees in the genus *Andrena* generally prefer forest edges or openings, and sandy soil (Linsley 1958, Cane 1991). This general knowledge is suitable for locating nesting resources on a farm, but specific habitat data for individual species may be necessary when considering protecting bees of conservation concern. In this study we used soil analysis techniques to increase our understanding of characteristics that could be used to identify habitat preferences of *Andrena crataegi* Robertson.

A. crataegi was found foraging on highbush blueberry at Narrow Lane orchard, N. Kingstown, RI in 2015. Nests were located directly adjacent to the blueberry planting, underneath a row of apple trees. We made a note of the location and returned to collect soil data in order to learn more about this species' nesting requirements in addition to what is known from Osgood (1989).

METHODS

Collection and Identification. The nest site was located at Narrow Lane orchard in North Kingstown, RI, owned by Steven Grenier and Sharon Slagle. After

finding the nest site we placed three emergence traps (Fig. 1) over the entrances on May 27, 2015 and left them overnight. The next morning we retrieved them, finding as many as 11 bees in one trap. Specimens were pinned and labeled, and species identification was determined by sending several photographs to Sam Droege, M.S. at the USGS Patuxent Wildlife Research Center in Maryland. Photos were taken with an Olympus OM-D E-M10 camera mounted on an Olympus SZ dissection microscope. The key feature discerning *A. crataegi* from similar species are its distinctly curved rear-tibial spurs (Fig. 2).

Soil Sampling and Analysis. We used a golf course cup changer (Fig. 3) to remove soil samples from three areas at the nest site, in 10 cm increments down to 40 cm deep, measuring with a ruler to get four 10 cm samples from each location. We took samples from underneath the apple trees where the nests were found, staying at least one meter away from the trunks to reduce the chances of harming the roots. Samples were labeled and stored in plastic freezer bags.

We measured bulk density by dividing the mass of the soil by the volume of the sample, first removing moisture by heating at 105°C overnight in a laboratory oven (Soiltest Inc., Evanston, IL). We determined pH by taking 10 g of the mixed soil sample and suspending it in 10 ml of distilled water, obtaining the reading from an AB 15 pH meter (Fisher Scientific, Waltham, MA) after fifteen minutes.

To determine percent organic matter, we put a 10 g subsample of each dried soil sample into a ceramic crucible and recorded the initial weight. Next we placed the samples into a muffle furnace at 550°C for 5 hours to burn off the organic matter,

letting them cool overnight. They were weighed immediately after removal, with the difference being the total amount of organic matter used to calculate the percentage.

To determine soil texture we measured the percent sand and silt. We assumed clay to be 5% throughout as recommended by Dr. Mark Stolt (University of Rhode Island Department of Natural Resource Science). To measure sand and silt, we first sifted our samples through a number 10 sieve (2 mm mesh openings) to remove the rocks, then weighed out a 10 g subsample for each sample into a 250 ml Nalgene™ bottle. We added 10 ml of Calgon solution (35.7 g (NaPO_3)₆ and 7.94 g of Na_2CO_3 in 1 liter of distilled water) to break up the soil particles, then added distilled water until the bottle was 2/3rds full. We then placed the bottles in a shaker on low speed overnight. Next, we poured each sample through a number 270 sieve (0.053 mm mesh openings) to remove silt and clay particles, using distilled water as needed to rinse out the entire bottle and a spray bottle to wash the silt through the sieve. We then used the spray bottle with distilled water to rinse the sand out of the sieve into weighed beakers, pouring off the excess water once the sand settled. We put the beakers into an oven at 105°C for at least 12 hours to completely dry them, then put the sand through a number 270 sieve again to dry sift. Dry sifting removes any leftover silt from the rinsing process. After obtaining the final mass of the sand, soil texture was determined for each sample using the USDA's soil texture calculator (http://www.nrcs.usda.gov/wps/portal/nrcs/detail/soils/survey/?cid=nrcs142p2_054167).

RESULTS

Soil from 0-10 cm deep was classified as silt loam, and from 11-40 cm was classified as silt (Table 1). Bulk density increased with depth, as expected with the increasing mass of soil above. It was measured as 1.0 g/cm³ at 0-10 cm deep, 1.2 g/cm³ at 11-20 cm deep, 1.3 g/cm³ at 21-30 cm deep, and 1.5 g/cm³ at 31-40 cm deep (Table 1). pH was similar throughout, 5.0 at 0-10 cm deep, 4.8 from 11-30 cm deep, and 5.0 again at 31-40 cm deep (Table 1). Percent organic matter was the highest (8.4%) from 0-10 cm deep, 3.7% from 11-20 cm deep, 2.6% from 21-30 cm deep, and 2.9% at 31-40 cm deep (Table 1).

DISCUSSION

A. crataegi is widely distributed, ranging throughout the entire continental U.S. and parts of southern Canada (<http://www.discoverlife.org/mp/20m?kind=Andrena+crataegi>). This species is a communally nesting bee (Osgood 1989), meaning females share a nest with one or more entrances but each individual female makes her own brood cells and provisions pollen for her eggs. This behavior is different from that of semi-social and eusocial species where there is division of labor in the nest (Michener 2007). Osgood (1989) described the biology of *A. crataegi* from a nest site in a commercial lowbush blueberry (*Vaccinium angustifolium* Aiton) field in Maine. Brood cells were found at depths between 33 and 53 centimeters and were mostly concentrated around 38 centimeters deep. Three nests were excavated in this study. One nest with a single entrance was excavated on 3 July 1973. Eleven females were provisioning cells in this communal nest. Twenty-nine cells were recovered: 19 containing *A. crataegi* larvae, 2

containing larvae of a cleptoparasitic *Nomada* sp., and 8 cells were in various stages of completion. In order to avoid disturbing nearby nests to be studied later, the author mentions that some cells of this nest were probably missed. Osgood (1989) excavated a second nest in early September where fifty-four cells were recovered (15 adult male *A. crataegi*, 14 adult female *A. crataegi*, 8 adult *Nomada cressonii*, 4 males and 4 females, and 17 contained larvae of an undetermined species of bombyliid). The largest nest excavated on 20 September contained four entrances, but the number of provisioning females could not be determined. This nest had been used for more than one year. Of the cells recovered, 16 contained adults of *A. crataegi* (11 males and 5 females), two contained adults of *N. cressonii* (1 male and 1 female) and one contained a bombyliid larva (Osgood 1989).

The soil texture results are somewhat surprising, as the literature suggests Andrenidae species primarily prefer sandy soils (Cane 1991). Results, however, varied among species from 34.4 to 87.7% sand (Cane 1991). It appears that *A. crataegi* has soil preferences outside of the known typical range for Andrenids, which is not well known. The data in this study is limited in scope, but *A. crataegi* females will often occupy the same nest site they hatched in (Osgood 1989) as many bee species do (Linsley 1958). It is possible to collect more data from the same site in the future.

Looking at general soil surface factors such as percent organic matter may prove useful for future research goals as a way to classify soils for overall ground nesting bee nest selection preferences. Osgood (1972) attributed percent organic carbon in the O (organic) horizon as the best determining factor for nesting, with nest sites having from 6.7-10.6% and nearby control areas without nests had 12.6-20.4%.

Osgood suggested that a deep organic layer would be more difficult for bees to dig through. The study included sites known to be inhabited by bees from the families Colletidae, Andrenidae (including *A. crataegi*), Halictidae and Megachilidae. Our results were within the range for nest sites found by Osgood (1972). With further study, percent organic matter could prove to be a useful characteristic for categorizing where bees prefer to nest.

It is important to note the lack of standardized methods for quantifying the nesting habitats of bees (Sardiñas and Kremen 2014), suggesting that a more concentrated collaborative effort may be required if we are to fully understand the significance of nesting resources in determining the community composition of bee species.

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Figure 1. Emergence traps placed over *A. crataegi* nest entrances.

Figure 2. Close up of the tibial spur of *A. crataegi*.

Figure 3. Golf course cup changer used to obtain soil from the nest site.

Table 1. Mean soil characteristics of three samples at an *A. crataegi* nest site.

Depth	Bulk Density						
(cm)	(g/cm³)	% Sand	% Silt	% Clay	pH	% OM	Classification
0-10	1.0	25.2	69.8	5.0	5.0	8.4	Silt loam
11 to 20	1.2	12.8	82.2	5.0	4.8	3.7	Silt
21 to 30	1.3	13.5	81.5	5.0	4.8	2.6	Silt
31-40	1.5	12.4	82.6	5.0	5.0	2.9	Silt

APPENDIX

“Additional pollinator species data for cultivated highbush blueberry in Rhode Island”

by

Zachary Scott and Steven R. Alm

INTRODUCTION

This appendix is a continuation of chapter one of my thesis, intended to expand the dataset another year in order to facilitate the continuation of the research questions brought up during the completion of my thesis work.

METHODS

Pollinator Collections 2016. From 17 May to 1 June 2016, pollinators were collected with 50 ml plastic snap cap vials as they visited blueberry flowers. Only bees seen foraging on the plants were caught and only one bee was caught per vial. Collections were made on 50-70 m transects down rows of blueberry bushes. Sites were sampled by two or three collectors for 15 minutes each. 11 commercial plantings and 1 research planting were sampled, all of which were previously sampled in 2015 (Fig 1). Each site was sampled once in the morning and once in the afternoon during the bloom period. Bees were stored in a cooler for transport back to the lab, where they were frozen, pinned and labeled. Specimens were identified with dissecting microscopes. Pollen was removed and stored with the same methods as chapter one, but not analyzed for the appendix due to time constraints.

RESULTS

I collected an additional 389 specimens in 2016, comprising 27 species. Five species: *Andrena tridens* Robertson, *Lasioglossum acuminatum* McGinley, *Lasioglossum oblongum* (Lovell), *Osmia lignaria* Say, and *Osmia virga* Sandhouse, had not been collected previously, bringing the total species collected on Rhode Island highbush blueberry to 46. Only one individual of each species new to this study was collected, so they are presumably uncommon in Rhode Island or are not typically

found on blueberry. Nine of the ten most commonly collected species in 2015 were still the collected the most frequently, with the one exception being *Colletes validus*, which was replaced by *Lasioblossum quebescense*, a species found to be relatively common in 2015. The order of the most common species was different in 2016, however, possibly due to sampling more extensively at farms that had been visited less often in 2015.

DISCUSSION

The relative consistency of the common species suggest they are typically dominant in Rhode Island highbush blueberry, and this abundant subset of the total species found likely provides the most pollination services (Winfrey et al. 2015). My pollen specificity data from chapter one supports this. Different species compositions at individual farms may cause variability in the quality of pollination provided at that farm. This thesis has identified the most important native bee pollinators of Rhode Island highbush blueberry.

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Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. *Ecol lett.* 18:626-635.

Table 1. Bee species and numbers collected from *Vaccinium corymbosum*, May 17 – June 1, 2016.

Family:	Genus and species	No. of			<i>Bombus</i> only	
		Individuals	Male	Female	Queens	Workers
Apidae	<i>Xylocopa virginica</i>	102	24	78		
Apidae	<i>Bombus bimaculatus</i>	60			19	41
Apidae	<i>Bombus impatiens</i>	53			51	2
Apidae	<i>Bombus griseocollis</i>	52			52	
Andrenidae	<i>Andrena carolina</i>	36	2	34		
Andrenidae	<i>Andrena carlini</i>	23		23		
Andrenidae	<i>Andrena vicina</i>	14	3	11		
Apidae	<i>Bombus perplexus</i>	11			6	5
Andrenidae	<i>Andrena bradleyi</i>	9		9		
Halictidae	<i>Lasioglossum quebecense</i>	6		6		
Colletidae	<i>Colletes validus</i>	3		3		
Andrenidae	<i>Andrena imitatrix</i>	2		2		

Table 1. (continued)

Family:	Genus and species	No. of			<i>Bombus</i> only	
		Individuals	Male	Female	Queens	Workers
Andrenidae	<i>Andrena nivalis</i>	2		2		
Halictidae	<i>Halictus rubicundus</i>	2		2		
Megachilidae	<i>Osmia bucephala</i>	2		2		
Halictidae	<i>Agopostemon sericeus</i>	1		1		
Andrenidae	<i>Andrena crataegi</i>	1	1			
Andrenidae	<i>Andrena tridens</i> Robertson	1		1		
Halictidae	<i>Augochlora pura</i>	1		1		
Colletidae	<i>Colletes inaequalis</i>	1		1		
Halictidae	<i>Halictus confusus</i>	1		1		
Halictidae	<i>Lasioglossum acuminatum</i> McGinley	1		1		
Halictidae	<i>Lasioglossum oblongum</i> (Lovell)	1		1		
Apidae	<i>Nomada gracilis</i> Cresson	1		1		

Table 1. (continued)

Family:	Genus and species	No. of			<i>Bombus</i> only	
		Individuals	Male	Female	Queens	Workers
Apidae	<i>Nomada maculata</i>	1	1			
Megachilidae	<i>Osmia lignaria</i> Say	1		1		
Megachilidae	<i>Osmia virga</i> Sandhouse	1		1		
	Total	389				