Effects of Honey Bee (Hymenoptera: Apidae) and Bumble Bee (Hymenoptera: Apidae) Presence on Cranberry (Ericales: Ericaceae) Pollination

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ABSTRACT Honey bees, *Apis mellifera* L., are frequently used to pollinate commercial cranberries, *Vaccinium macrocarpon* Ait., but information is lacking on the relative contribution of honey bees and native bees, the effects of surrounding vegetation on bee visitation, and on optimal timing for honey bee introduction. We begin with a descriptive study of numbers of honey bees, bumble bees, and other bees visiting cranberry blossoms, and their subsequent effect on cranberry yield, on three cranberry properties in 1999. The property surrounded by agricultural land, as opposed to wetlands and woodlands, had fewer numbers of all bee types. In 2000, one property did not introduce honey bee colonies, providing an opportunity to document the effect of lack of honey bees on yield. With no honey bees, plants along the edge of the bed had significantly higher berry weights compared with nonedge plants, suggesting that wild pollinators were only effective along the edge. Comparing the same bed between 1999, with three honey bee colonies per acre, and 2000, with no honey bees, we found a significant reduction in average berry size. In 2000, we compared stigma loading on properties with and without honey bees. Significantly more stigmas received the minimum number of tetrads required for fruit set on the property with honey bees. Significantly more tetrads were deposited during mid-bloom compared with early bloom, indicating that mid-bloom was the best time to have honey bees present. This study emphasizes the importance and effectiveness of honey bees as pollinators of commercial size cranberry plantings.

KEY WORDS honey bees, cranberries, pollination, bumble bees

Ensuring adequate and reliable pollination for commercial properties of cranberries, *Vaccinium macrocarpon* Ait., is critical for fruit yield and quality (Marucci 1967, Eck 1990), but relying on natural populations of bees (bumble bees, feral honey bees, and solitary bees) may not provide sufficient pollination. Previous studies indicate that bumble bees (*Bombus* spp.) are the most efficient bee pollinator of cranberries (Macfarlane 1995). However, naturally nesting bumble bee colonies are not a reliable source of pollinators because their nesting sites are limited by habitat disturbance and agricultural practices in the areas surrounding cranberry properties because most bumble bees make their nests underground (Free 1993). Although some cranberry growers purchase bumble bee colonies, the majority of growers rent honey bee colonies to ensure adequate pollination. Honey bees are not the most efficient cranberry pollinators because they are more likely than other bees to collect only nectar, thereby not helping with pollen transfer (Marucci 1967, Kevan et al. 1984). Honey bees also forage on whatever is the most prolific and abundant flower source in the area because of their recruitment through the dance language (Seeley 1986). Large numbers of bees within honey bee colonies compensate for their lack of efficiency as cranberry pollinators because more bees are able to visit more flowers, particularly on large cranberry properties (Free 1993). However, there are still questions concerning the relative contribution of honey bees and native bees to cranberry pollination, the effects of surrounding vegetation on bee visitation, and the timing of honey bee colony introduction into cranberry properties to maximize yield.

The usual practice in the United States is to place two honey bee, *Apis mellifera* L., colonies per acre of cranberries and to leave the colonies in place for the duration of bloom. In Wisconsin, cranberry bloom typically lasts from mid-June to early July (Eck 1990). However, it is not known whether increasing the number of honey bee colonies above the usual two per acre would increase yield. There are also questions about what is the most effective time to have honey bees present on the cranberry beds.

Land use in areas surrounding the cranberry bed is another factor that may alter cranberry pollination. If a cranberry bed, or other agricultural crop, is surrounded by undisturbed areas such as woods or wetlands, there may be more native pollinators because of an increase in potential nesting areas (Ricketts et al.

2004). Honey bee activity on cranberry beds also may increase when cranberry beds are surrounded by undisturbed areas because the honey bees tend to remain on the crop when there are fewer weedy plants in the surrounding areas that are more attractive to honey bees than cranberries. Conversely, cranberry properties surrounded by agricultural and disturbed areas have fewer naturally nesting bumble bees and are often home to plants such as clover, *Trifolium* spp. L., sweet clover, *Melilotus officinalis* L., and alfalfa, *Medicago sativa* L., that are highly attractive to foraging honey bees. On these properties, honey bees could tend to not forage on the cranberries, resulting in decreased pollination and cranberry yield.

Materials and Methods

Sites. In 1999, cranberry flower visitation was observed on four cranberry beds at three different properties (owned by different growers). The cranberry beds were ≈230 by 50 m, and each bed had at least 16 honey colonies situated within 100 m of it. We examined one bed each of Stevens and Pilgrims varieties at property 1, which were ≈600 m from each other. We examined one bed of Pilgrims variety at property 2, and one bed of Stevens variety at property 3. In 1999, property 1 had three honey bee colonies per acre. Properties 2 and 3 had two colonies per acre.

In 2000, we were not able to access property 3, so we examined one bed of Stevens variety on both properties 1 and 2. The Stevens variety bed at property 1 was the same for 1999 and 2000. In 2000, property 1 had no honey bees colonies brought onto the property. Property 2 had two honey bee colonies per acre.

Properties 1 and 3 were located in Monroe County, Wisconsin. Property 2 was located nearby in Jackson County. Properties 1 and 2 were surrounded by wooded areas and wetlands. Property 3 was surrounded by some wooded areas, some housing, and mostly agricultural land, such as alfalfa and clover fields. All properties were within 5 km of each other.

Bloom progression was monitored at all sites by counting 100 flowers that were categorized as closed, open, or out of bloom (after petal fall). We randomly chose stalks along the same transect used for visitation observations and counted flowers until we reached 100. The percentage of open flowers equaled the percentage in bloom; for example, 25% in bloom means 75% of the flowers have not yet opened. As bloom progresses, a particular plant has more flowers that have dropped their petals than open flowers, so the percentage out of bloom can be determined from the percentage of flowers that have dropped their petals. For example, 25% out of bloom means that 25% of the flowers have dropped their petals. A typical cranberry bloom lasts 2 to 4 wk.

Visitation. Cranberry flower visitation was assessed by counting flower visitors within 1 m of a transect down the middle of a cranberry bed, usually along an irrigation pipe. The transect followed the length of the cranberry bed (≈230 m). Observers noted the numbers and types of flower visitors encountered. Flower visitors were categorized as honey bees, bumble bees, or other bees (Megachilidae, Halictidae, and Anthophoridae). The presence or absence of pollen loads on the bees was noted. Observations took place only on warm, sunny days. In 1999, observations took place on 18 June (early bloom), 24 June (mid-bloom), and 28 June and 2 July (late bloom). Transects were conducted approximately once every 2 h (five times per day) and were synchronized by variety so that two beds of the same variety on different properties were observed simultaneously with 60 total transect observations. In 2000, transects were repeated from two to four times a day, every 3 to 4 d, weather permitting, with 33 total transect observations between 19 June and 11 July, corresponding with early, mid-, and late bloom at properties 1 and 2.

Yield. Yield in 1999 and 2000 was assessed by collecting cranberries from 20-cm^2 plots within 3 m of the same transects used for foraging activity observations. From each transect, four plots were chosen within 5 m of the edge of the bed (edge plots) and six were chosen toward the middle of the bed (nonedge plots). All berries were weighed. Yield in both years was assessed using average weight of individual berries.

Stigma Loading. In 2000, stigmas from cranberry flowers of approximately the same age were collected during early, mid-, and late bloom along the same transect lines in the same beds used for visitation observations from both properties. All flowers were at least 3 d old as determined by stigmatic protrusion beyond the anther cone (Rigby and Dana 1972). Collection dates at the two properties varied because bloom progression was different on the two properties. For early bloom, stigmas were collected from property 1 when cranberry flowers were 25% in bloom (23 June) and from the property 2 when cranberry flowers were 18% in bloom (14 June). For mid-bloom, stigmas were collected from property 1 when cranberry flowers were 16% out of bloom (30 June) and from property 2 when cranberry flowers were 25% out of bloom (27 June). For late bloom, stigmas were collected from property 1 when cranberry flowers were 40% out of bloom (3 July) and from property 2 when cranberry flowers were 45% out of bloom (30 June). All flowers were at least 5 m in from the edge of the bed. Stigmas were stained by placing them in glycerin jelly with fuschsin on microscope slides. Slides were viewed with a light microscope and pollen tetrads on each stigma were counted.

Statistical Analysis. There were a limited number of cranberry growers that would allow us access to cranberry properties, and within those properties we were allowed to inspect only one or two cranberry beds; therefore, the visitation and cross-property yield data were limited to a descriptive nature. Yield data comparing the same property across years was analyzed using one-way analysis of variance (ANOVA) tests with JMP software (SAS Institute 1994). Log likelihood chi-square tests were used to compare proportions of bumble bees and honey bees carrying pollen on each property for each year using JMP software (SAS Institute 1994). Stigma loading at the two prop-

Table 1. Bee visitation (means ± SD) to two varieties of cranberry in Wisconsin in 1999 and 2000 (flowers per 100 m^2)

Property	Bloom time	Colonies/acre	1999						2000			
			Pilgrims variety			Stevens variety			Stevens variety			
			Honey bees	Bumble bees	Other bees[a]	Honey bees	Bumble bees	Other bees[a]	Colonies/acre	Honey bees	Bumble bees	Other bees[a]
1	Early	3	52.84 ± 27.78	3.97 ± 1.16	0.26 ± 0.24	33.62 ± 19.45	2.59 ± 1.43	0.09 ± 0.19	0	0	0.87 ± 0.53	0.61 ± 0.66
	Mid		54.65 ± 7.63	2.67 ± 1.03	0.17 ± 0.24	39.57 ± 19.68	0.43 ± 0.00	0.17 ± 0.39		0	0.29 ± 0.71	0.22 ± 0.36
	Late		48.19 ± 30.02	1.72 ± 1.29	0.26 ± 0.39	18.53 ± 15.74	1.29 ± 1.49	0		0	1.30 ± 0.43	0
	Overall		51.90 ± 22.42	2.79 ± 1.44	0.23 ± 0.28	30.57 ± 19.33	1.44 ± 1.44	0.09 ± 0.24		0	0.71 ± 0.77	0.31 ± 0.50
2	Early	2	31.89 ± 11.95	2.73 ± 1.00	0	—	—	—	2	4.89 ± 1.52	0.22 ± 0.25	1.16 ± 0.91
	Mid		26.43 ± 17.21	1.94 ± 1.27	0.26 ± 0.39	—	—	—		18.09 ± 4.33	0.52 ± 0.36	1.65 ± 0.36
	Late		17.71 ± 17.07	0.26 ± 0.24	0	—	—	—		18.57 ± 13.18	0.65 ± 0.66	0.13 ± 0.21
	Overall		25.35 ± 15.66	1.64 ± 1.38	0.09 ± 0.25	—	—	—		15.56 ± 11.11	0.53 ± 0.53	0.78 ± 0.81
3	Early	2	—	—	—	2.44 ± 2.06	0.17 ± 0.24	0		—	—	
	Mid		—	—	—	0.70 ± 0.50	0.44 ± 0.53	0.09 ± 0.20		—	—	
	Late		—	—	—	22.97 ± 22.09	1.48 ± 1.18	0		—	—	
	Overall		—	—	—	8.70 ± 15.82	0.70 ± 0.92	0.03 ± 0.11		—	—	

Bee visitation was averaged on a bee per m^2 basis and summarized as the number of bees seen per 100 m^2.

[a] Other bees included unidentified species from the families Megachilidae, Halictidae, and Anthophoridae.

Table 2. Comparison of the percentage of total honey bees and bumble bees observed with visible pollen loads along transects on two varieties of cranberry in Wisconsin in 1999 and 2000

Property	Honey bee colonies/acre	1999				Honey bee colonies/acre	2000	
		Pilgrims variety		Stevens variety			Stevens variety	
		% honey bees with pollen	% bumble bees with pollen	% honey bees with pollen	% bumble bees with pollen		% honey bees with pollen	% bumble bees with pollen
1	3	15a (778, 15)	84b (42, 15)	25a (458, 15)	57b (22, 15)	0	0 (0, 14)	74 (23, 14)
2	2	11a (380, 15)	40b (25, 15)			2	33a (680, 19)	48a (23, 19)
3	2			37a (131, 15)	62a (10, 15)			

Numbers in parentheses refer to total number of bees observed along a 1- by 230-m transect and the total number of transect observations. Statistical comparisons were made between honey bees and bumble bees within each property, on each variety, and for each year, except for property 1 in 2000 when no honey bee colonies were introduced. Percentages of honey bees and bumble bees, within a variety, followed by different letters are significantly different ($P < 0.001$; Log likelihood chi-square tests).

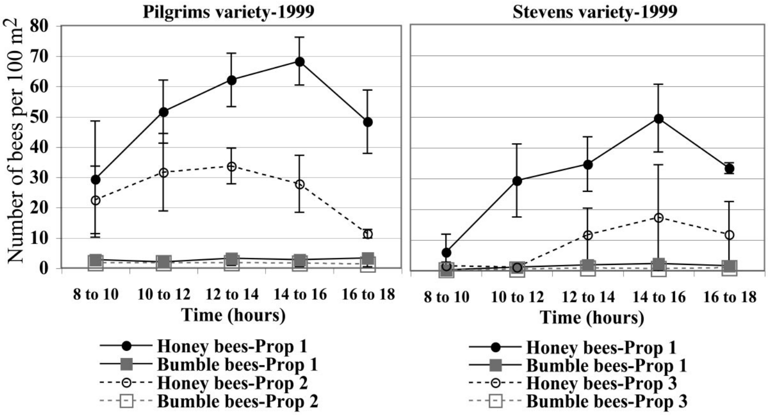

Fig. 1. Bee visitation, 1999. Number of honey bees and bumble bees seen visiting cranberry flowers per 100 m^2 at different hours of the day averaged over all bloom times (means ± SEM) in three properties in Wisconsin.

erties was examined for the percentage of stigmas that had eight or more pollen grains during early, mid-, and late bloom. Stigma loading was examined for differences between properties by using one-way ANOVA tests with JMP software (SAS Institute 1994). The data for the numbers of pollen grains per stigma were normalized using a common log + 1 transformation (Sokal and Rohlf 1995).

Results

Visitation. In 1999, more honey bees were observed visiting both Pilgrims and Stevens varieties on property 1 compared with the same variety on property 2 or 3 (Table 1). Because of the lack of replication, it was not possible to determine whether the difference in visitation was because of the number of honey bee colonies per acre (three colonies per acre on property 1 versus two colonies per acre on properties 2 and 3) or because of some difference in management practices (e.g., fertilization, irrigation, or pest control). However, more honey bees were observed on property 1 through early, mid-, and late bloom, and throughout the day (Table 2; Fig. 1). Honey bee visitation rates were particularly low for property 3, the property surrounded by agricultural fields. Numbers of bumble bees and other wild native bees visiting both varieties of cranberries were relatively low but showed a more consistent pattern throughout the day than honey bees whose peak activity was in late afternoon (Fig. 1).

In 2000, no honey bees were seen visiting Stevens variety on property 1, which had not rented honey bee colonies that year, although a few honey bees were seen foraging on clover alongside the cranberry bed. In contrast, 15.56 ± 11.11 (mean ± SD) honey bees/100 m^2 were observed on Stevens variety on property 2, with two honey bee colonies per acre (Table 1). There were similar numbers of bumble bees and other wild native bees on both properties (Table 1). The daily foraging patterns were similar to those in 1999 (Fig. 2).

In 1999 on Pilgrims variety at both properties, a significantly greater proportion of bumble bees were observed carrying pollen compared with honey bees (Table 2). On Stevens variety the same year, a significantly greater proportion of bumble bees had pollen loads on property 1 but not on property 3. In 2000, on the Stevens bed at property 2, there was no significant difference in the proportion of bees carrying pollen loads.

Yield. In 1999, the average berry weights of both Pilgrims and Stevens varieties on all three properties ranged from 1.4 to 1.6 g (Table 3). In 2000, the average berry weight of Stevens variety on property 2 was 1.16 ± 0.43 g and on property 1, with no honey bees present, average weight was 0.83 ± 0.39 g. The yield data correspond with the visitation data: cranberry beds where a higher number of honey bees were observed visiting flowers had higher yields compared with beds where fewer or no honey bees were observed visiting flowers. The lowest yield was seen on the Stevens bed on property 1 where no honey bee visitation had been observed.

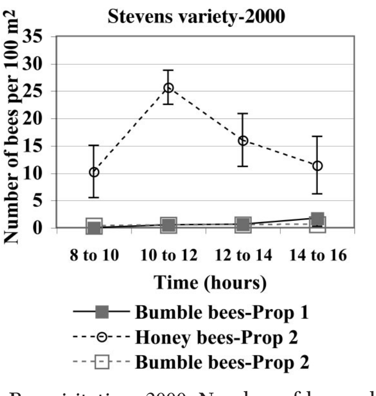

Fig. 2. Bee visitation, 2000. Number of honey bees and bumble bees per 100 m^2 seen visiting cranberry flowers at different hours of the day averaged over all bloom times (means ± SEM) in two properties in Wisconsin.

Table 3. Cranberry yield from two varieties as weight of individual cranberries (means ± SD) in 1999 and 2000 in Wisconsin

Property	Honey bee colonies/acre	Pilgrims, 1999 (g)	Stevens, 1999 (g)	Honey bee colonies/acre	Stevens, 2000 (g)	1999 vs. 2000 Stevens comparison (g)
1	3	1.57 ± 0.43	1.60 ± 0.44	0	0.83 ± 0.39	F = 681.14; df = 1, 799; P = <0.0001
2	2	1.49 ± 0.46		2	1.16 ± 0.43	
3	2		1.37 ± 0.47			

Cranberries were collected from 10 plots that were 20 cm^2 along transects through cranberry beds.

Comparing the same cranberry bed from property 1, which had honey bees present in 1999 and no honey bees in 2000, average yield was nearly double in 1999 (1.60 ± 0.44 versus 0.83 ± 0.39 g). This difference was highly significant (Table 3). In 1999, there was no difference in yield between edge and nonedge plots within property 1 when honey bees were present (Table 4). However, in 2000, when no honey bee colonies were introduced, edge plots had significantly higher berry weights than nonedge plots within the same Stevens bed (Table 4).

Stigma Loading. In 2000, there was no significant difference between the numbers of pollen grains deposited on cranberry flower stigmas on property 2 with honey bees and property 1 without honey bees during early bloom ($F = 0.04$; df = 1, 59; $P = 0.84$) (Fig. 3). However, during both mid- and late blooms, there were significantly more pollen grains deposited on stigmas on the property with honey bees (mid-bloom: $F = 20.68$; df = 1, 57; $P < 0.0001$; late bloom: $F = 4.26$; df = 1, 60; $P < 0.05$). This difference was most evident during mid-bloom when more flowers were open.

Cane and Schiffhauer (2001) showed that eight pollen grain tetrads was the minimum number required for cranberry fruit set and that any number of tetrads greater than eight was superfluous in regards to fruit set. Examination of stigma loading at the two properties for the percentage of stigmas that had eight or more pollen grains during early, mid-, and late bloom revealed that the property with honey bees had a higher percentage of flowers that received sufficient pollination for fruit set during mid-bloom ($\chi^2 = 6.273$; df = 1, 57; $P = 0.0123$) (Fig. 4). This difference was not significant during early ($\chi^2 = 0.123$; df = 1, 59; $P = 0.7267$) or late bloom ($\chi^2 = 2.886$; df = 1, 60; $P = 0.0893$). The difference between the two properties was greatest during mid-bloom, indicating that there were not sufficient numbers of wild pollinators to successfully pollinate the great number of blooms open during mid-bloom on the property without honey bees, the time of greatest open flower density on cranberry beds.

Table 4. Cranberry yield as weight of individual cranberries (means ± SD) in different locations within a cranberry bed for Stevens variety on property 1 during 1999 and 2000 in Wisconsin

Location in cranberry bed	Yield (g) with three honey bee colonies/acre[a]	Yield (g) with no honey bee colonies[b]
Edge	1.53 ± 0.45	0.90 ± 0.41
Nonedge	1.63 ± 0.46	0.78 ± 0.37
	F = 3.53; df = 1, 418; P = 0.06	F = 9.17; df = 1, 396; P = 0.003

[a] Data are from 1999.
[b] Data are from 2000.

Discussion

This study shows that on large cranberry properties, the presence of honey bee colonies increases cranberry yield. The best support for this conclusion comes from our comparison of cranberry yield on the same bed of Stevens variety between 1999 when three honey bees colonies per acre were present and 2000 when no colonies were brought into the same property. In 2000, no honey bees were observed foraging on the beds and the average individual cranberry weight was reduced by approximately half compared with when honey bee colonies were present. This could potentially lead to a significant reduction in the number of bushels produced by the cranberry grower.

In 2000, more stigmas received the minimum number of pollen tetrads required for fruit set at property 2 than at property 1, indicating that without honey bees, more fruit did not set because of insufficient pollination. However, >50% of the examined stigmas on property 1 without honey bees had enough pollen tetrads for fruit set. Wild native bees, such as bumble bees, leafcutter bees, and sweat bees, were probably responsible for some of the pollen deposition. Few bumble bees, and fewer other bees, were observed visiting the cranberries on all three properties. It is possible that the numbers of open flowers were low enough during early and late bloom for the small numbers of wild native bees to be able to visit most of

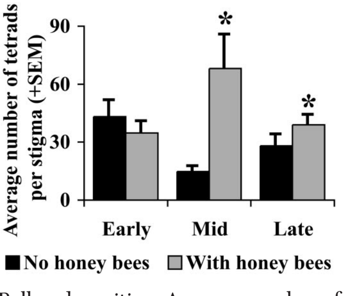

Fig. 3. Pollen deposition. Average number of pollen tetrads on each examined stigma (means ± SEM) is displayed for different bloom stages (early, mid-, and late bloom) for a property with no added honey bees and a property with two honey bee colonies per acre in 2000 in Wisconsin. For ANOVAs, all data were transformed using $\log_{10} + 1$ transformation. Asterisk (*) indicates significant difference as determined by ANOVA.

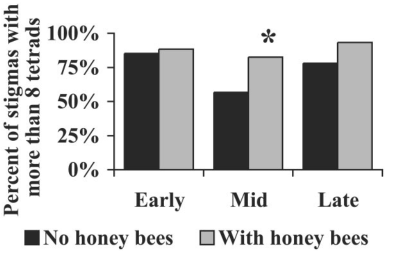

Fig. 4. Percentage of stigmas with more than eight tetrads. Percentage of stigmas with more than eight tetrads for different bloom stages (early, mid-, and late bloom) for a property with no added honey bees and a property with honey bee colonies in Wisconsin in 2000. Asterisk (*) indicates significant difference as determined by chi-square test.

the flowers. At mid-bloom, with many more flowers present on the bed, bumble bee numbers were possibly too low to provide sufficient pollination of cranberry flowers.

One question cranberry growers often ask is when is the best time to introduce honey bee colonies. Most sources recommend having honey bees present during the duration of the bloom (Eck 1990). However, there is conflicting information on the optimal timing for honey bee placement. Some recommend placement during early bloom (Marucci and Moulter 1978), and some during mid-bloom (Moeller 1973). One way to address this question is from our data on stigma loading. Comparing the property with honey bees and the property with no honey bees in 2000, a higher percentage of flowers received the required number of pollen grains for optimum fertilization during mid-bloom and late bloom with honey bee presence. Thus, honey bees may not be as critical during early bloom. The benefits of honey bee presence are realized predominantly during mid- and late bloom.

In 2000, the greater berry weight in edge plots on property 1 with no honey bees suggests that wild native bee pollinators may have been more prevalent on the edge of beds and were less likely to forage in the middle of beds. Our results support the prediction that when no honey bees are brought in, any honey bees or other native bees that are present in the surrounding area reach the edges of the cranberry beds, but they may not be present in sufficient numbers to forage throughout the interior areas of the cranberry beds. The lack of differences between edge and non-edge plots on property 1 with three honey bee colonies per acre in 1999 and the presence of these differences in 2000 when no honey bees were introduced also shows that honey bee presence provided more uniform levels of pollination across the entire cranberry bed than wild native bee pollinators. An examination of stigma loading at specific locations within a cranberry bed is needed before pollination levels can be confirmed as the cause of these differences.

Surrounding vegetation seemed to have an effect on visitation rates of all bee types. The property that was surrounded by agricultural land (property 3) tended to have lower visitation from all bee types than the properties that were surrounded with wooded areas and wetlands (properties 1 and 2). The lower numbers of honey bees were possibly caused by honey bees foraging on agricultural and weedy vegetation surrounding the cranberry property instead of the cranberry flowers. Property 3 also had the lowest yield of all observed properties. However, this property experienced a hail storm before harvest. We cannot determine whether the lower yield was due to inferior pollination or other factors such as weather.

Although not always statistically significant, the higher percentage of bumble bees carrying pollen loads compared with honey bees on most cranberry beds corroborates the superiority of bumble bees as cranberry pollinators on an individual bee-by-bee basis (Macfarlane 1995). Although bumble bees more consistently collected pollen, their numbers were not great enough to provide reliable pollination.

In summary, honey bees are effective pollinators of cranberries when sufficient numbers are brought into an area, particularly during mid- and late bloom. The number of honey bee colonies needed will be greater if the beds are surrounded by disturbed areas because of both the attractiveness of these areas to foraging honey bees and the decrease in the number of wild native pollinators. Smaller properties surrounded by wooded areas may be able to rely more heavily on wild native pollinators.

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