Bee (Hymenoptera: Apoidea) Diversity and Abundance on Cranberry in Southeastern Massachusetts

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ABSTRACT Diversity and abundance of bee pollinators foraging on cranberry in southeastern Massachusetts were studied from 1990 to 1992. Both collections and observations of bees were used to compare the effects of habitat, bog location and size, and year. Although there was a high diversity of native bee pollinators, the abundance of most was very low except for a few bumble bee species and honey bees. Nonapid bees were more abundant and diverse on abandoned and natural bogs than on cultivated bogs; bumble bees were similarly abundant and diverse in the three habitats; and honey bees were present in large numbers only on cultivated bogs where colonies had been placed. In 1991, some sites had more bumble bees than honey bees even though colonies were present. Small, cultivated bogs tended to have more native bees than did large, cultivated bogs. Native bee populations seemed to be affected by weather and site attributes such as cropping history and surrounding vegetation. Bumble bees might be useful as managed pollinators of cranberry.

KEY WORDS pollination, native bees, cranberry

CULTIVATION OF THE American cranberry, *Vaccinium macrocarpon* Aiton, one of the few fruit crops native to North America, began in the early 1800s, making it the first species of *Vaccinium* to be grown commercially (Vander Kloet 1988, Eck 1990). Today, it is an important high-value crop in Massachusetts, Wisconsin, New Jersey, and the Pacific Northwest. Cranberry requires insect-mediated pollen transfer and, thus, pollination is an essential component of cranberry cultivation (McGregor 1976, Eck 1990).

Although cranberry is a native plant, very little is known about its native bee pollinators. Bumble bees were abundant pollinators of cultivated cranberry in New Jersey (Hutson 1926, Roberts 1979), Massachusetts (Franklin 1950), Ontario (Kevan et al. 1983), and British Columbia (Winston & Graf 1982, MacKenzie & Winston 1984), yet bees other than Apidae (honey bees and bumble bees) were seen rarely in these studies. It must be noted that the diversity and abundance of bees is known to be lower in cultivated areas than in natural, uncultivated areas (MacKenzie & Winston 1984, Scott-Dupree & Winston 1987), where management practices such as pesticide use and habitat destruction have been implicated in the decline of bee pollinators (NRCC 1981; MacKenzie & Winston 1984; Kevan et al. 1990a, b). However, only one small natural bog has been surveyed for bees. In southern Ontario, honey bees and bumble bees were the dominant cranberry pollinators on this site, although, in the second of a 2-yr study, bees other than Apidae (mainly Dialictus species) made up >25% of the bees collected (Reader 1975, 1977).

This apparent paucity of native bees foraging on cranberry is surprising, considering the great diversity of bee pollinators found on other cultivated species of *Vaccinium*. From 25 to 69 bee species foraged on lowbush blueberry in various studies (Boulanger et al. 1967, Kevan 1975, Finnamore & Neary 1978, Miliczky & Osgood 1979, Stubbs et al. 1992). Twenty-six species were collected foraging on rabbiteye blueberry in the southeastern United States (Cane & Payne 1993) and 46 species on highbush blueberry in central New York (MacKenzie 1994).

It is impossible to discern whether past studies truly reflect bee populations on cranberries. Our study investigated the diversity and abundance of bee pollinators of cranberry in the growing area of southeastern Massachusetts. The objectives of the research were to compare pollinator abundance and diversity on cultivated and uncultivated areas, to assess bee populations on cultivated bogs throughout the cranberry growing area of southeastern Massachusetts, to compare bee populations on cultivated habitats over a 3-yr period, and to evaluate native bee species for use as managed pollinators of cranberry.

Materials and Methods

The study was conducted in the cranberry growing area of southeastern Massachusetts during

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Table 1. Types of cranberry bogs used for bee diversity and abundance studies in southeastern Massachusetts in 1990, 1991, and 1992

Site[a]	Year of sampling	Size, ha	Cultivar[b]	Location	Comments
C1	1990, 1991, 1992	4.4	EB, some H, many others	SE	Experiment station, many cultivar plots
C2	1990, 1991, 1992	20.6	EB, H	SW	
C3	1990, 1991, 1992	2.3	EB, H	Cape Cod	
C4	1991	28.9	EB, H	SE	
C5	1991	2.0	EB, some native	Central	Isolated in state forest, no honey bees
C6	1991	1.5	EB, H	NE	Plus 2.0 ha new vines
C7	1991	10.1	EB, H	NE	
C8	1991	17.6	EB, H	NW	
C9	1991	36.4	EB, H	NW	2.0 ha H surrounded by 16.5 ha EB
C10	1991	1.4	EB, trace H	Cape Cod	Observations only
A1	1990	1.4	unknown	SW	
A2	1990	1.2	unknown	SW	
A3	1990	1.4	unknown	Cape Cod	
N1	1990	0.2[c]	Native	Cape Cod	In sand dunes
N2	1990	0.4	Native	Cape Cod	In sand dunes

[a] C denotes cultivated bogs, A abandoned bogs, and N natural bogs.
[b] EB refers to Early Black, H to Howes, and Native to cranberry plants that grow naturally.
[c] Total area of four small bogs that were close together. Bog used for sampling was ≈ 0.1 ha.

bloom from mid-June to mid-July in 1990, 1991, and 1992. The weather in 1990 and 1992 was generally cool and wet, whereas 1991 was warm and dry (weather statistics recorded at the Cranberry Experiment Station, East Wareham, MA). Over the 3 yr, 15 collection sites were used representing the following three habitat types: (1) 10 cultivated bogs (C1 through C10), (2) three previously cultivated cranberry bogs that had been abandoned for at least 2 yr (A1, A2, A3), and (3) two natural sites (N1 and N2). Site descriptions and experimental uses are given in Table 1 and locations in Fig. 1. Honey bee colonies were placed next to all cultivated bogs except C5, which was near an apiary.

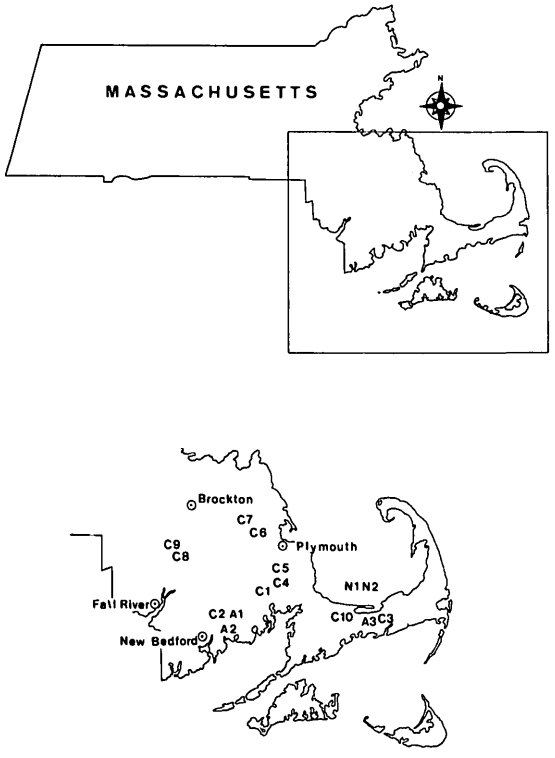

Fig. 1. Location of experimental sites in the cranberry growing area of southeastern Massachusetts (box on upper map) used for bee diversity and abundance studies. C indicates cultivated bogs, A abandoned bogs, and N natural sites.

In 1990 and 1991, observations and collections were made three times during cranberry bloom at the specified sites (Table 1). Observations only were made in 1992 at sites C1, C2, and C3. Collections were used to evaluate bee diversity and abundance, and observations were used exclusively for abundance measurements.

Collections. As many bees as possible were captured with either an insect net or jar as the individual collecting moved throughout the bog for 15 min in 1990 and for 10 min in 1991. All bees, including honey bees, foraging on cranberry bloom were collected. The bees were killed and taken to the laboratory and pinned. All bees were identified to species, and specimens were placed in the Cornell University Insect Collection (Lot number 1200). The Shannon–Wiener Diversity Index (H') was calculated, both with and without honey bees, from these data (Margalef 1958). Capture rates (bees per minute) were calculated as one method of comparing bee abundance on the different sites.

Observations. Observations of bee visits to cranberry flowers were used as a second measure of abundance. In 1990, a 0.25-m^2 template was laid gently on a flowering bog and all honey bees, bumble bees, and other native bees foraging on flowers in this area in 10 min were recorded. The number of flowers in the square was counted (because of the large numbers of flowers, estimates rather than exact counts were made). In 1991 and 1992, a 1-m^2 template was used and observations were recorded for 5 min. At each site, counts were repeated at six randomly chosen locations for each

Table 2. Bees collected foraging on cranberry from three habitats in southeastern Massachusetts in 1990

Family Species	Site							
	C1	C2	C3	A1	A2	A3	N1	N2
Apidae								
Apis mellifera	40	36	71	8	31	20	11	5
Bombus affinis	—	6	1	1	4	1	—	2
Bombus bimaculatus	2	4	8	7	12	3	2	5
Bombus impatiens	3	3	17	18	10	—	6	20
Bombus perplexus	3	2	4	2	2	3	—	2
Bombus terricola	—	5	—	11	9	—	—	—
Bombus vagans vagans	1	2	2	3	—	1	—	3
Other *Bombus* (2 spp.)	—	1a	2a	—	—	—	1a	1b
Total *Bombus* (8 spp.)	9	23	34	43	37	8	9	33
Andrenidae *Andrena* (5 spp.)	—	1b	—	3cde	4ae	—	1c	—
Anthophoridae (2 spp.)	—	—	—	—	1a	—	1b	—
Halictidae								
Dialictus admirandus	—	—	—	—	—	—	3	15
Other *Dialictus* (4 spp.)	—	—	—	5ac	2c	—	4bd	3b
Evylaeus cinctipes	—	—	—	6	7	—	—	—
Lasioglossum (3 spp.)	—	—	—	2c	4abc	—	—	—
Other Halictids (7 spp.)	—	—	1g	3bdf	1d	3ade	1c	—
Megachilidae (3 spp.)	—	1b	1a	—	—	2bc	—	—
Melittidae *Melitta* near *americana*	—	—	1	—	—	1	2	—
Bees other than Apidae (27 spp.)	0	2	3	19	19	6	12	18
Total bees (36 spp.)	49	61	108	69	87	34	32	56

C refers to cultivated bogs, A to abandoned bogs, and N to natural bogs. — indicates no individuals of that group were collected. In a row, letters after the numbers of bees collected refer to the species in each family. For Apidae, other *Bombus*, a is *B. griseocollis* and b is *B. rufocinctus;* for Andrenidae, *Andrena,* a is *A. carlini,* b is *A. cressonii,* c is *A. carolina,* d is *A. nivalis,* and e is *A. vicina;* for Anthophoridae, a is *Xylocopa virginica* and b is *Ceratina dupla/calcarata* (could not distinguish between these species); for Halictidae, other *Dialictus,* a is *D. lineatulus,* b is *D. marinus,* c is *D. rohweri,* and d is *D.* sp. 1; for Halictidae, *Lasioglossum* a is *L. acuminatum,* b is *L. athabascense,* and c is *L. coriaceum;* and for Halictidae, other Halictids, a is *Agapostemon sericeus,* b is *Agapostemon texanus,* c is *Augochlorella striata,* d is *Augochloropsis metallica,* e is *Halictus confusus,* f is *Halictus rubicundus,* and g is *Sphecodes minor;* and for Megachilidae, a is *Megachile frigida,* b is *Megachile gemula,* and c is *Osmia atriventris.*

time period in all 3 yr. From these data, abundance measures for all 3 yr (bees per minute per square meter), and the number of bees per flower (bees per minute per flower) for 1990, were calculated.

Habitat Comparisons. In 1990, three cultivated bogs (C1, C2, and C3), three abandoned bogs (A1, A2, and A3), and two natural bogs (N1 and N2) were used to assess the effects of habitat on bee diversity and abundance. Diversity among habitats was evaluated by comparing the numbers of bees collected and the Shannon–Wiener diversity indices. The abundance of bees was compared by nested analysis of variance (ANOVA) (capture rates: habitat, week [habitat] and observations: habitat, week [habitat, site]) and Tukey's multiple comparison test where appropriate (SAS Institute 1985).

Distributions of Bees on Cultivated Bogs. In 1991, collections were made at nine cultivated bogs and observations were made at 10 bogs. Bee diversity was evaluated as above. Bee abundance, using both capture rates and observations, was compared by ANOVA and Tukey's multiple comparison test where appropriate (SAS Institute 1985). In addition, the effect of field size on bee abundance was evaluated by placing each bog into one of two categories, small (<5 ha, four bogs for capture rates and five for observations) and large (>10 ha, five bogs for both measures). Results were analyzed by two-way ANOVA (size and week) and Tukey's multiple comparison test (SAS Institute 1985).

Yearly Variation. Three cultivated sites (C1, C2, and C3) were used in all 3 yr of the study. Bee observations for all 3 yr and capture rates for 1991 and 1992 were compared by nested ANOVA (year, site [year], week [site]) and Tukey's multiple comparison test where appropriate (SAS Institute 1985). Bee diversity was compared for 1991 and 1992 as previously described.

Results

Habitats. Thirty-six species of bees in six families were collected on cranberry bogs in southeastern Massachusetts in 1990 (Table 2). Honey bees and bumble bees (Apidae) were common in all three habitats (comprising 97.7, 76.8, and 65.9% of the bees collected in cultivated, abandoned, and natural habitats, respectively). Bumble bees made up the most of the Apidae collected on abandoned (59.2%) and natural habitats (72.4%) compared with only 31.0% on cultivated bogs where honey bee colonies had been placed. *Bombus impatiens* Cresson was the most commonly collected bumble bee in all three habitats, and *B. bimaculatus* Cresson, although less numerous than *B. impatiens,* was also common. *B. terricola* Kirby was commonly collected only on the abandoned

Table 3. Shannon-Wiener diversity index, H', of bees collected foraging on cranberries in southeastern Massachusetts in 1990 and 1991

Habitat	Site	Size, ha	1990	1991
Cultivated	1	4.4	1.31 (0.72)[a]	1.00 (0.84)
	2	20.6	2.00 (1.50)	1.54 (1.19)
	3	2.3	1.63 (1.20)	1.47 (1.67)
	4	28.9		1.66 (1.30)
	5	2.0		1.67 (1.82)
	6	1.5		1.29 (1.51)
	7	10.1		1.40 (1.00)
	8	17.6		2.00 (2.00)
	9	36.4		1.28 (1.51)
Abandoned	1	1.4	2.25 (2.35)	
	2	1.2	2.25 (2.10)	
	3	1.4	2.17 (1.57)	
Natural	1	0.2	2.11 (2.03)	
	2	0.4	1.62 (1.77)	

$H' = \Sigma\ p_i(\ln p_i)$ where p_i = proportion of the *ith* species in the sample.

[a] Index calculated only with native bees, the index in parentheses was calculated with honey bees included.

Table 5. Floral and bee densities on cranberry bogs in southeastern Massachusetts in 1990

Category	*n*	Floral density	Bee density
		flowers/m^2	Bees/min/flower[a]
Habitat			
Cultivated	54	1,457a[b]	0.0002
Abandoned	54	791b	0.0019
Natural	36	378c	0.0051
Pooled SEM		40	0.0014
Week			
1	48	524b	0.0029
2	48	1,123a	0.0023
3	48	1,165a	0.0010
Pooled SEM		39	0.0014

[a] Numbers of bees includes honey bees, bumble bees, and other bee species.

[b] $P < 0.05$ from ANOVA *F* test; in a column for each category of either capture rates or observations, different letters indicate significant differences in means by Tukey's multiple comparison test.

bogs. Bees other than Apidae were rare on cultivated bogs, comprising 2.3% of the collected bees with only one specimen each of five species; but were more common in the other two habitats, 19 species comprising 23.2% of the collected bees on abandoned bogs and seven species comprising 34.1% on natural bogs. Most of the other bee species were rare, and the only were species of Halictidae collected in numbers. *Dialictus admirandus* (Sandhouse) was fairly common on one of the natural bogs and *Evylaeus cinctipes* (Provancher) was collected on two of the abandoned bogs.

Diversity as measured by the Shannon–Weiner diversity index tended to be highest on abandoned bogs, intermediate on natural bogs, and lowest on cultivated bogs, although sites did vary (Table 3). Bee abundance also varied by habitat, both in capture rates and observations (Table 4). Capture rates showed honey bees to be more abundant on cultivated bogs, natural bogs had fewer total bees, and bumble bees were similarly represented on all three habitats. Results from observations were similar, except that natural bogs had more bees in total (reflecting the greater numbers of bees other than Apidae) than did the other two habitats. More honey bees were captured in week 3 than in the previous 2 wk, whereas similar numbers of bumble bees and total bees were captured in all 3 wk. From the observations, total numbers of bees were significantly greater in the 3rd wk than in the first 2 wk, and honey bees and bumble bees were more abundant in the 3rd wk than in the first (Table 4). The numbers of flowers varied by habitat (Table 5). Cultivated bogs had more flowers than did abandoned sites, which had more than natural sites. Week 1 had fewer flowers than did weeks 2 and 3. There were no differences in the numbers of bees per minute per flower.

Cultivated Bogs. Twenty-three species of bees in five families were collected from cultivated bogs in 1991 (Table 6). Honey bees and bumble bees

Table 4. Bee abundance on cranberry bogs in southeastern Massachusetts in 1990

Category	Capture rates, bees/min				Observations, bees/m^2/min			
	n	Honey bees	Bumble bees	Total bees[a]	*n*	Honey bees	Bumble bees	Total bees[a]
Habitat								
Cultivated	9	0.9a[b]	0.4	1.4a	54	0.24a	0.10	0.34b
Abandoned	9	0.3b	0.5	1.1a	54	0.13ab	0.13	0.30b
Natural	6	0.1b	0.3	0.5b	36	0.08b	0.11	0.58a
Pooled SEM		0.1	0.1	0.2		0.04	0.03	0.06
Week								
1	8	0.4b	0.3	0.8	48	0.07b	0.04b	0.18b
2	8	0.4b	0.6	1.2	48	0.13ab	0.12ab	0.31b
3	8	0.7a	0.3	1.2	48	0.26a	0.17a	0.67a
Pooled SEM		0.1	0.1	0.2		0.04	0.03	0.06

[a] Total numbers of bees includes honey bees, bumble bees, and other bee species.

[b] $P < 0.05$ from ANOVA *F* test; in a column for each category, different letters indicate significant differences in means by Tukey's multiple comparison test.

Table 6. Bees collected from nine cultivated cranberry bogs in southeastern Massachusetts in 1991

Family Species	Site								
	C6	C5	C3	C1	C7	C8	C2	C4	C9
Apidae									
Apis mellifera	11	15	20	61	42	20	61	57	6
Bombus affinis	4	—	—	—	6	2	3	3	10
Bombus bimaculatus	10	7	11	10	1	3	14	6	—
Bombus impatiens	37	—	36	10	4	17	10	12	4
Bombus perplexus	7	3	1	1	—	6	2	3	—
Bombus terricola	1	—	3	—	5	4	1	4	13
Bombus vagans vagans	5	24	—	—	1	6	1	7	—
Other *Bombus* (2 spp.)	—	—	6ab	—	—	1a	—	—	5a
Total *Bombus* (8 spp.)	64	34	57	21	17	39	31	35	32
Andrenidae *Andrena* (3 spp.)	—	—	1c	—	—	3ab	2ac	—	—
Halictidae (8 spp.)	—	8bceh	3adf	—	—	2gh	—	—	—
Megachilidae (2 spp.)	—	—	—	—	3b	—	—	1a	—
Melittidae *Melitta* near *americana*	0	4	2	1	—	—	—	—	—
Bees other than Apidae (14 spp.)	0	15	6	1	0	6	2	0	0
Total bees (23 spp.)	75	64	83	83	59	65	94	92	38

Sites arranged according to increasing size from left to right; C6, C5, C3, and C1 are small (<5.0 ha) and C7, C8, C2, C4, and C9 are large (>10 ha). — indicates that no individuals of that group were collected. In each row, letters after the numbers of bees collected refer to the species in each family. For Apidae, other *Bombus*, a is *B. griseocollis* and b is *B. rufocinctus;* for Andrenidae, *Andrena*, a is *A. crataegi*, b is *A. nuda*, and c is *A. vicina;* for Halictidae, a is *Agapostemon sericeus*, b is *Augochlorella striata*, c is *Dialictus admirandus*, d is *Dialictus pilosus*, e is *Dialictus* sp. C, e is *Evylaeus cinctipes*, f is *Halictus confusus*, and g is *Halictus rubicundus;* and for Megachilidae, a is *Megachile texana* and b is *Osmia atriventris*.

comprised a large percentage of the collections at all nine sites, and other bees were rare on all sites except C5, where other bees comprised 23.4% of the collection. That bog was small and isolated in the middle of a state forest. Overall, bumble bees made up 50.5% of the collections and, on five bogs, were collected in greater numbers than were honey bees. Once again, *B. impatiens* was the most common species collected, with B. bimaculatus also numerous. On site C5 (the small, isolated bog), *B. vagans vagans* Smith was the most common bumble bee. None of the other bees was commonly collected at any of the nine sites. The Shannon–Wiener diversity index ranged from 1.00 to 2.00 on the nine cultivated sites (Table 3). There was no obvious effect of bog size on bee diversity based on either collection or diversity indices (Tables 3 and 6).

Bee abundance varied among the different sites (Table 7). In capture rates, honey bees were more abundant at sites C1, C2, and C4 than at C9 and C6, and bumble bees were more abundant at site C6 and C3 than at sites C1 and C7. Total numbers of bees captured were greater on bogs C3, C1, C2, and C4 than on C9. The results of observations were similar, C9 having fewer honey bees than C1, C7, C2, and C4, and bumble bees were more abundant on sites C10, C6, and C3 than C1, C7, C4, and C9. Site C9, the largest bog surveyed (35.4 ha), had fewer total numbers of bees than six of the other sites. Samples from that bog were taken from a 2.0-ha area of the late cultivar, 'Howes', that was surrounded on all sides by 16.5 ha of the early cultivar, 'Early Black'. This distribution may have affected bee foraging. From these results, it does not appear that bog location affected bee distri-

Table 7. Abundance of bees foraging on cultivated cranberry in southeastern Massachusetts in 1991

Site	Capture rates, bees/min			Observations, bees/m^2/min		
	Honey bees	Bumble bees	Total bees	Honey bees	Bumble bees	Total bees
C10	—	—	—	0.35abc	0.57a	0.98a
C6	0.4c	2.1a	2.5ab	0.12bc	0.55a	0.68ab
C5	0.5bc	1.1ab	2.0ab	0.05bc	0.23ab	0.37bc
C3	0.7abc	1.9a	2.7a	0.31abc	0.54a	0.87ab
C1	2.0a	0.7b	2.7a	0.62a	0.12b	0.78ab
C7	1.4abc	0.6b	2.0ab	0.40ab	0.04b	0.44abc
C8	0.7abc	1.3ab	2.2ab	0.17bc	0.28ab	0.44abc
C2	2.0a	1.0ab	3.1a	0.68a	0.25ab	0.94a
C4	1.9ab	1.2ab	3.1a	0.57a	0.12b	0.69ab
C9	0.2c	1.1ab	1.3b	0.01c	0.04b	0.05c
Pooled SEM	0.3	0.2	0.3	0.08	0.08	0.12

Sites are arranged according to increasing size from top to bottom; C10, C6, C5, C3, and C1 are small (<5 ha) and C7, C8, C2, C4, and C9 are large (>10 ha). — indicates no data, only observations were done on C10. Total bees includes honey bees, bumble bees, and other bees. $P < 0.05$ from analysis of variance F test; in a column, different letters indicate significant differences in means by Tukey's multiple comparison test.

Table 8. Bee abundance on three cultivated cranberry bogs by site, bloom period, and year

Category	Capture rates, bees/min				Observations, bees/m²/min			
	n	Honey bees	Bumble bees	Total bees	*n*	Honey bees	Bumble bees	Total bees
Year								
1990	9	0.9b	0.4b	1.4b	54	0.24b	0.11a	0.34b
1991	9	1.6a	1.2a	2.8a	54	0.54a	0.31a	0.86a
1992		—	—	—	54	0.43ab	0.10b	0.55b
Pooled SEM		0.1	0.1	0.1		0.06	0.02	0.07
Site								
C1	6	1.4	0.4c	1.8	54	0.34	0.05b	0.40b
C2	6	1.4	0.8b	2.2	54	0.47	0.13b	0.61ab
C3	6	1.0	1.2a	2.3	54	0.45	0.23a	0.69a
Pooled SEM		0.2	0.1	0.2		0.06	0.03	0.07
Week								
1	6	1.2	0.7	1.9	54	0.33	0.11b	0.45b
2	6	0.9	0.9	1.9	54	0.42	0.18b	0.61ab
3	6	1.6	0.9	2.5	54	0.45	0.23a	0.69a
Pooled SEM		0.2	0.1	0.2		0.06	0.03	0.07

Total numbers of bees includes honey bees, bumble bees, and other bee species. — Indicates no data, only observations were made in 1992. $P < 0.05$ from ANOVA F test; in a column for each category, different letters indicate significant differences in means by Tukey's multiple comparison test.

bution; rather, specific site attributes such as size, adjacent vegetation, and cropping history were probably important.

Capture rates on small bogs were similar to those on large bogs for honey bees (1.5 compared with 1.0 bees per minute, respectively, pooled SEM 0.2), bumble bees (1.5 versus 1.0, pooled SEM 0.2) and total bees (2.5 versus 2.3, pooled SEM 0.2). From the observations, the numbers of honey bees on small bogs was similar to those on large bogs (0.29 versus 0.36 bees per square meter per minute, respectively, pooled SEM 0.04), but both bumble bee numbers (0.40 versus 0.15, pooled SEM 0.04) and total numbers of bees (0.73 versus 0.52, pooled SEM 0.06) were greater on small bogs compared to large ones. There were no significant differences in capture rates during the 3 wk of bloom for honey bees (1.0, 1.3, and 1.3, bees per minute for weeks 1, 2, and 3, respectively, pooled SEM 0.02), bumble bees (1.0, 1.3, and 1.3, pooled SEM 0.1), and total numbers of bees (2.0, 2.4, and 1.6, pooled SEM 0.2). However, by the observation method, there were significantly fewer honey bees (0.25, 0.25, and 0.49 bees per square meter per minute for weeks 1, 2, and 3, respectively, pooled SEM 0.05) and total numbers of bees (0.45, 0.52, and 0.90, pooled SEM 0.07) in weeks 1 and 2 than in week 3; and fewer bumble bees in week 1 than week 3 (0.19, 0.25, and 0.39, pooled SEM 0.04).

Yearly Variation. Diversity of bees as measured by the Shannon–Wiener diversity index dropped on all three bogs from 1990 to 1991 when only native bees were used to calculate the index (Table 3). In addition, more bees were collected in 1991 except for fewer honey bees at site C3 (Tables 2 and 6). Bee abundance did vary in the different years; in general, bees were more abundant in 1991 than in 1990 and 1992 (Table 8). By capture rates, all three categories (honey bees, bumble bees, and total bees) were greater in 1991 than 1990. By observation, honey bees were more abundant in 1991 than in 1990, bumble bees were less abundant in 1992 than in the other 2 yr, and total numbers of bees were more abundant in 1991 than in the other 2 yr. Although observed numbers of honey bees were similar among the three sites, more bumble bees were observed at site C3 than at the other two sites in both years, and total numbers of bees were greater in 1992 than in 1990. By observations, there were greater numbers of bumble bees and total numbers of bees in the 3rd wk than in the 1st wk.

Discussion

The diversity of bees, both on cultivated and uncultivated cranberries in Massachusetts reported in this study, is similar to that seen with other cultivated *Vaccinium* species, and much higher than reported previously on cranberry. The 41 bee species collected from cranberry compares favorably to the 25 to 60 species reported from other cultivated *Vaccinium* species (Boulanger et al. 1967, Kevan 1975, Finnamore & Neary 1978, Miliczky & Osgood 1979, Stubbs et al. 1992, Cane & Payne 1993, MacKenzie 1994).

In our study, eight species of bumble bees and 18 species of bees in four families other than Apidae were collected from cultivated cranberry bogs, with a further 14 species and one additional bee family from abandoned and natural bogs. This diversity is much greater than the past literature indicates. In 1923, in New Jersey, only one species each of Andrena and Megachile were collected, whereas bumble bees, primarily *B. impatiens*, were numerous (Hutson 1926). Seven species of bumble bees foraged on cultivated cranberry bogs in Mas-

sachusetts (Franklin 1950). The only native bees collected from cranberries in British Columbia were four species of bumble bees (Winston & Graf 1982, MacKenzie & Winston 1984), and in Ontario, bumble bees (four species) comprised the majority of the native bees; a few halictids (three species) were also collected (Kevan et al. 1983). On a small natural bog in southern Ontario, Reader (1975, 1977) collected five bumble bee species, a few Andrena individuals, and three genera of Halictidae (the number of species is not indicated). In addition, diversity indices ranged from 0.10 to 0.40 on British Columbian bogs (MacKenzie & Winston 1984) compared with 1.00–2.00 in our study.

It should be noted that of past studies, two were located outside the natural range of cranberries (British Columbia) (Winston & Graf 1982, MacKenzie & Winson 1984) and one at its edge (Ontario) (Kevan et al. 1983), and, in addition, the studies on a natural bog were also located in Ontario (Reader 1975, 1977). The natural range of cranberry extends from Newfoundland west to central Minnesota, south to northern Illinois, northern Ohio and central Indiana, and in the Appalachian Mountains to Tennessee and North Carolina (Vander Kloet 1988). Diversity of cranberry pollinators might be expected to be low in areas outside the natural range of the plant. The cranberry producing region in Massachusetts is located in the middle of the natural range of cranberry. In addition, cranberry has been cultivated since the early 1800s and some of our research sites had been in cultivation for many years and the natural sites present for hundreds of years. Therefore, it is not unexpected that we identified greater bee diversity on cranberry than had been previously known.

The abundance of bumble bees on the cranberry bogs in Massachusetts was surprisingly high, and nonapid bees were of low abundance in most cases. In 1992, bumble bees exceeded 0.5 bees per square meter per minute on three commercial bogs and 0.2 on six of them, and on all cultivated bogs, nonapid bees were <0.1 bees per square meter per minute (Table 7). In 1926, Hutson estimated that 0.12 bumble bees per square meter was sufficient for good pollination of a cranberry crop, and Roberts (1979) found few bees from families other than Apidae (0.007/m^2 compared with 0.026/m^2 for bumble bees and 0.057/m^2 for honey bees) foraging on cranberry in New Jersey. Bumble bee abundance in British Columbia was also high, averaging nearly 0.5 bees per square meter per minute over the season (MacKenzie & Winston 1984). Native bee populations tend to fluctuate widely from year to year and site to site within a year (McGregor 1976, MacKenzie & Winston 1984, Cane & Payne 1993, Free 1993). In this study, bee abundance was highest in 1991 and lower in 1990 and 1992; weather patterns probably accounted for these differences. Even in the years with poor weather, however, bumble bees were generally abundant on the cultivated bogs in Massachusetts, and appear to be able to maintain their populations in this highly managed cropping system. This surprising abundance of bumble bees perhaps can be attributed to the large natural areas of mixed forest that typically surround most of the bogs in Massachusetts. In addition, most Massachusetts bogs are very irregular in shape, often having long fingers and corners that jut into the surrounding vegetation. These areas probably act as natural flight paths and nesting habitat for bumble bees.

It must be noted that only cultivated bogs were used for all but two of the previous studies on cranberry pollinator diversity. Past research has shown that natural vegetation supports a much more diverse bee fauna than do berry crops (MacKenzie & Winston 1984) and tree fruits (Scott-Dupree & Winston 1987). This pattern is expected as natural areas also have a much greater diversity of flowering plants on which pollinators can forage and more nesting sites. In this study, the bee visitors of same plant species were compared in three different habitats with natural sites supporting a more diverse nonapid bee fauna than did cultivated sites.

Overall, the differences in diversity and abundance seen here between cultivated and noncultivated cranberry bogs and between large and small bogs are probably due to such factors as habitat destruction and pesticide use on these cultivated sites, especially for the smaller solitary species which usually have localized foraging ranges around their nest sites (Batra 1984, Eickwort & Ginsberg 1980) and which are more sensitive to pesticide exposure (Johansen 1972, Plowright & Thaler 1978, NRCC 1981, Johansen et al. 1983, Mayer & Johansen 1991). The fact that smaller bogs tended to have more native bees supports this conclusion. From our study we conclude that bumble bees are the only native bees that showed any potential to be developed as managed cranberry pollinators, and methods of enhancing the uncultivated areas surrounding commercial bogs to both maintain and encourage wild bee populations should be investigated.

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