Comparative Pollination Effectiveness Among Bees (Hymenoptera: Apoidea) on Lowbush Blueberry (Ericaceae: *Vaccinium angustifolium*)

S. K. JAVOREK,[1] K. E. MACKENZIE, AND S. P. VANDER KLOET[2]

Atlantic Food and Horticulture Research Station, Agriculture and Agri-Food Canada, 32 Main Street, Kentville, Nova Scotia, Canada B4N 1J5

Ann. Entomol. Soc. Am. 95(3): 345–351 (2002)

ABSTRACT The pollination effectiveness (floral visitation rate, percentage of flowers pollinated, and pollen deposition) of indigenous and introduced bees visiting lowbush blueberry (*Vaccinium angustifolium* Aiton) was studied in Nova Scotia from 1992 to 1994. Floral visitation rate alone was not a good indicator of pollination effectiveness, as not all floral visits resulted in successful pollination events. As a group, pollen-harvesting taxa pollinated >85% of flowers visited as compared with under 25% for nectar foragers. Equivalencies derived from floral visitation rates and pollination percentages show that the most effective pollen-harvesters, *Bombus* spp. queens and *Andrena* spp., would pollinate 6.5 and 3.6 flowers, respectively, in the time it would take a nectar-foraging honey bee, *Apis mellifera* L., to pollinate a single flower. Average pollen deposition for nectar-foragers (*A. mellifera* and *Megachile rotundata* F.) did not exceed 13 tetrads per visit, which was significantly less than all pollen-harvesters. Among pollen-harvesters, *Bombus* spp. workers, *M. rotundata* and *Halictus* spp. deposited moderate stigmatic loads (34, 28, and 26 tetrads, respectively), whereas *Bombus* spp. queens and *Andrena* spp. deposited >45 tetrads per single visit. Pollination equivalencies show *A. mellifera* would have to visit a flower four times to deposit the same amount of pollen as single visits by *Bombus* spp. queens or *Andrena* spp.

KEY WORDS *Bombus*, *Andrena*, *Apis*, honey bee, *Megachile*, blueberry

LOWBUSH BLUEBERRY (*Vaccinium angustifolium* Aiton) is an endemic North American shrub that ranges from Newfoundland west to southern Manitoba and Minnesota, south to northern Illinois, PA, and Delaware, and in the mountains to Virginia (Vander Kloet 1988). Within this range, native stands have been developed into a major horticultural crop in Maine, Atlantic Canada, and the Saguenay-Lac St. Jean region of Quebec.

Lowbush blueberry production depends on bees to facilitate cross-pollination among the mosaic of predominantly self-sterile genotypes (clones) that typify commercial blueberry fields. The flowers of *V. angustifolium* are well adapted for buzz-pollination (Buchmann 1983) as anther dehiscence is terminal via apical pores that face inward toward the style. The white to pink petals of the flower are fused to form a 5- to 7-mm bell-shaped corolla that houses two whorls of five stamens inserted at the base of the corolla around a much longer style terminated by the stigma (Vander Kloet 1988). To reach the nectaries located at the base of the style, a bee must insert its tongue between the filaments.

A diverse assemblage of indigenous bees is associated with pollination of lowbush blueberry (Boulanger et al. 1967, Finnemore and Neary 1978, Stubbs et al. 1992, Sampson 1993). Females of many genera, such as *Andrena*, *Bombus*, *Halictus*, *Agapostomon*, *Augochlora*, *Augochlorella* and *Lasioglossum*, are behaviorally adapted to foraging at *V. angustifolium* as they routinely sonicate flowers to harvest pollen (Sampson 1993). Furthermore, individuals of many of these indigenous genera forage in the marginal weather conditions that are often prevalent during the spring *V. angustifolium* flowering period (Bigras-Hoet et al. 1972). Improvements in crop management and increasing field size have produced more flowers than can be satisfactorily pollinated by wild bee populations (Chiasson and Argall 1996, Ismial 1987). It is common practice to supplement indigenous bee populations with honey bees (*Apis mellifera* L.) (Ismial 1987), and more recently, alfalfa leafcutting bees (*Megachile rotundata* F.) (Argall et al. 1996). Both of these species lack the foraging adaptations of indigenous pollinators, as they do not buzz-pollinate and are often adversely affected by weather conditions during bloom. Although honey bees readily forage for nectar at *V. angustifolium*, the crop is rarely used as a pollen source (Lesaffre et al. 1975, MacKenzie et al. 1996).

[1] E-mail: javoreks@em.agr.ca.
[2] Department of Biology, Acadia University, Wolfville, NS, Canada B0P 1X0.

Because they do not collect pollen, there may be a problem intrinsic to pollination of lowbush blueberries by honey bees (Mohr and Kevan 1987, Parker et al. 1987). In contrast, floral morphology does not deter *M. rotundata* (females) from harvesting pollen at *V. angustifolium* (Javorek 1996).

Differences in pollination efficacy have been observed among bees foraging on other commercially important *Vaccinium* species. Cane and Payne (1990) demonstrated differential pollination effectiveness of bees visiting rabbiteye blueberry (*Vaccinium ashei* Reade). Single visits to virgin flowers from the indigenous genera *Habropoda* and *Bombus* resulted in greater fruit set than single visits from *A. mellifera.* Based on foraging density and estimates of relative pollination efficiency on cranberry (*Vaccinium macrocarpon* L.), Macfarlane et al. (1994) estimated pollen and nectar collecting honey bees were equivalent to 0. 5 and 0.05 bumblebees, respectively. On highbush blueberry (*Vaccinium corymbosum* L.), bumble bees deposited more pollen per single visit than honey bees, while honey bees and mason bees (*Osmia lignaria propinqua* Cresson) deposited similar stigmatic loads (Dogterom 1999). In cage experiments where *V. angustifolium* stems were presented to bees, Stubbs and Drummond (1997) found the average amount of pollen deposited per single visit was similar for *A. mellifera* (11.6 tetrads) and *Bombus impatiens* Cresson workers (16.0 tetrads) whereas *M. rotundata* and *Osima atriventris* Cresson deposited 23.1 and 33.8 tetrads, respectively.

Within the blueberries, *Vaccinium* Section *Cyanococcus,* stigmatic loading is positively correlated with fruit set (Dogterom 1999; K.E.M., unpublished data), seed number (Dogterom 1999) and fruit weight (Aalders and Hall 1961, Eaton 1967, Bigras-Hoet et al. 1972, Jackson et al. 1972). Given these fundamental relationships, differences in pollination effectiveness (the rate of successful pollination events and the amount of pollen transferred per visit) among bees must be considered an important factor in lowbush blueberry production. However, the pollination effectiveness of bees visiting lowbush blueberry under field conditions has only been inferred from indirect measures such as floral visitation rate, behavior and abundance, with little objective data to quantify taxon-specific pollination success and levels of pollen transfer. The purpose of this paper is to assess the efficacy of different bee taxa in transferring pollen to receptive stigmata in field populations of *V. angustifolium.*

Materials and Methods

Study Sites and Pollinators. From 1992 to 1994, pollinator effectiveness studies were conducted from early to mid-June in three commercial lowbush blueberry fields located in the Debert area, Colchester County, Nova Scotia (45° 28' N, 63° 30' W). Field size and introduction of managed bees were as follows: field A (9 ha), 10 honey bee colonies, field B (7 ha), two leafcutting bee shelters (75,000 bees per shelter), and field C (12 ha), 25 honey bee colonies and two leafcutting bee shelters (75,000 bees per shelter). Indigenous bees were abundant at all three sites. Floral visitation rates, pollination percentages (percentage of floral visits resulting in pollen deposition), and stigmatic loading were determined for the major bee taxa present, including the introduced species *A. mellifera* (workers) and *M. rotundata* (males and females) and females of the indigenous genera *Andrena* spp. (moderate to large species: 10–14 mm), *Bombus* spp (queens: *B. impatiens* Cresson, *B. perplexus* Cresson, *B. ternarius* Say, *B. terricola* Kirby, *B. vagans* Smith; workers: *B. ternarius, B. terricola*) and *Halictus* spp. (*H. rubicundus* Christ, *H. confusus* Smith). Voucher specimens are deposited in the collection at the Agriculture and Agri-Food Canada, Atlantic Food and Horticulture Research Center, Kentville, Nova Scotia, Canada.

Data were collected on warm (>20°C) sunny or partly sunny days between 1030 and 1530 hours. All three fields were visited on the same day with multiple sampling days each year (range, 5–8 sampling days per year). The order of field visitation was arranged so that individual sites were visited at different times of the day on consecutive sampling dates. For example, the first field visited on the first sampling date became the second visited on the second sampling date and so on. Two individuals were responsible for data collection during this study. To ensure consistency, one individual monitored floral visitation rates while the second individual observed flowers for pollinator visitation.

Floral Visitation Rate. Individual foraging bees were tracked for 3 min at an unobtrusive distance of ≈1 m. The number of flowers visited was recorded for each bee. This resulted in 591 min of monitoring floral visitation over the course of the study. Floral visitation rates (flowers visited per minute) were calculated as the number of floral visits divided by the duration of the observation period. The foraging task (nectar-collecting versus pollen-harvesting) and, where appropriate, pollen-harvesting technique (sonication versus nonsonication) was noted.

Pollination Percentages and Pollen Deposition. Before the onset of bloom, pollinator exclusion cages (25 cm long by 25cm wide by 40 cm high) were positioned over groups of *V. angustifolium* stems (≈50 stems per cage). In each year, 15 cages were placed both peripherally and centrally in each field and near *M. rotundata* shelters and *A. mellifera* colonies. A total of 150 exclusion cages were in place in each year of the study.

During bloom, exclusion cages were removed singly to expose virgin *V. angustifolium* flowers to foraging bees. Following this, flowers were monitored for pollinator approach. During this "sit and wait" study, 4,380 min were spent watching flowers for pollinator visitation. To ensure the immediate foraging history of the individual bee on the crop (1) nectar foraging bees were observed visiting a minimum of 15 blueberry flowers before visiting target flowers and (2) all pollen foragers were deemed to have substantial pollen loads. Following visitation, stigmata were detached from

flowers by a mid-style cut and placed in a drop of basic fuchsin gel (500 ml water, 150 ml glycerine, 14 g gelatin and a few crystals of basic fuchsin stain; modified from Beattie 1971) and positioned on a microscope slide. Bee taxon, foraging task and foraging technique were recorded on each slide. As a control, this procedure was repeated on single unvisited flowers adjacent to visited flowers to test for pollen contamination. Stigmata were viewed under light microscopy (400×) and classified as pollinated (*Vaccinium* pollen present) or not pollinated (no *Vaccinium* pollen). The pollination percentage for each taxon was calculated as the number of pollinated stigmata divided by the total number of flowers visited. The number of *V. angustifolium* pollen tetrads (group of four pollen grains) on stigmatic surfaces was then counted to determine the amount of pollen deposited per visit. Only successful pollination events were used to calculate mean pollen deposition for each bee taxon.

Pollinator Equivalencies. Data from this study were used to calculate the relative pollination equivalencies among bee taxa in terms of (1) pollination rate (floral visitation rate × pollination percentage = flowers pollinated per minute) and (2) pollen deposition per single visit. The relative number of flowers pollinated per unit time was expressed as the quotient of any two taxon-specific floral pollination rates. The quotient of any two mean pollen deposition values indicated the number of floral visits required by one taxon to deposit the equivalent stigmatic load as another.

Statistical Analysis. The effect of year, field, and taxon on floral visitation rate was assessed using a full factorial design (PROC GLM, SAS Institute 1990). As neither year, field nor interactions were significant, data were pooled and mean floral visitation rates among taxa were compared by one-way analysis of variance (ANOVA), followed by Tukey's studentized range test ($P < 0.05$) (PROC GLM, SAS Institute 1990).

Maximum likelihood ANOVA (PROC CATMOD, SAS Institute 1990) was used to detect the influence of year, field, and taxon on pollination percentage. Since only taxon was significant, all data were combined and analyzed using maximum likelihood ANOVA followed by contrasts ($P < 0.05$) to determine differences in pollination percentages among taxa (PROC CATMOD, SAS Institute 1990).

Following a log transformation of data to equalize variances, a full factorial design (PROC GLM, SAS Institute 1990) was used to investigate the effect of year, field, and taxon on pollen deposition. Since only taxon was significant, data were pooled and subjected to one-way ANOVA followed by Tukey's studentized range test to investigate differences in mean stigmatic loading among bee taxa for cases where at least one *Vaccinium* pollen tetrad was deposited (PROC GLM, SAS Institute 1990).

Nonlinear regression was used to investigate the relationship between mean pollen deposition per single visit (of cases where at least one pollen tetrad was deposited) and pollination percentage (PROC NONLIN, SAS Institute 1990).

Table 1. Floral visitation rates for bees sequentially visiting *Vaccinium angustifolium* flowers on commercial lowbush blueberry fields

Taxon	No. individuals	Foraging task	Flowers visited per minute	
			Mean ± SE	Range
Apis mellifera	27	Nectar	8.0 ± 0.4b	3–13
Megachile rotundata (♂)	28	Nectar	4.1 ± 0.3c	1–7
Megachile rotundata (♀)	25	Nectar	4.3 ± 0.3c	1–7
Megachile rotundata (♀)	29	Pollen	7.6 ± 0.3b	3–11
Bombus spp. (queens)	33	Pollen	12.8 ± 0.5a	7–16
Bombus spp. (workers)	21	Pollen	11.2 ± 0.6a	5–15
Andrena spp.	22	Pollen	7.2 ± 0.3b	4–10
Halictus spp.	12	Pollen	6.1 ± 0.3b	4–8

Means with the same letter do not significantly differ at $P < 0.05$ (ANOVA, Tukey's studentized range test).

All statistical summaries are given as mean ± SE.

Results

Foraging Task and Technique. *V. angustifolium* pollinators considered in this study were divided into two groups based on foraging task: (1) nectar-collectors: *A. mellifera* (workers) and *M. rotundata* (males and newly released females) and (2) pollen-harvesters (including bees that simultaneously forage for nectar and pollen): *Andrena* spp., *Bombus* spp. (queens and workers), *Halictus* spp. and *M. rotundata* (females). Among the pollen collectors, *Andrena* spp., *Bombus* spp. and *Halictus* spp. sonicated *V. angustifolium* flowers, whereas *M. rotundata* physically manipulated the porose anthers with their forelegs to harvest pollen.

Floral Visitation Rate. There were significant differences in floral visitation rates among bee taxa visiting *V. angustifolium* ($F = 62.53$, df = 7, $P < 0.0001$) (Table 1). *Bombus* spp. (queens and workers) had the fastest floral visitation rates. This was partly due to their habitat of sequentially visiting many flowers as they moved in an upward spiral on a single inflorescence. Floral visitation rate does not appear to be broadly related to foraging task as nectar-collecting *A. mellifera* visited similar numbers of flowers per minute as pollen-harvesting *M. rotundata*, *Andrena* spp. and *Halictus* spp.

Pollination Percentages. Pollination percentage comparisons with unvisited flowers were significant for all bees examined, indicating that each taxon makes a positive contribution to *V. angustifolium* pollination. There were significant differences in pollination percentages among bee taxa (maximum likelihood ANOVA, $\chi^2 = 179.00$, df = 8, $P < 0.0001$) (Table 2). As a group, pollen foraging bees (mean pollination percentage = 91.8%, $n = 151$ visits) were more reliable than nectar foragers (mean pollination percentage = 19.1%, $n = 133$ visits) when pollinating virgin *V. angustifolium* flowers.

Pollen Deposition. Stigmatic loads associated with single visits by all taxa examined were significantly larger than controls (unvisited flowers that had pollen on the stigma), which averaged only 1.3 ± 0.2 pollen tetrads per stigma. For flowers receiving at least one

Table 2. Percentage of visits by bees that result in successful pollination events at virgin *Vaccinium angustifolium* flowers

Taxon	No. individuals	Foraging task	Visits at virgin flowers		
			Pollinated	Not pollinated	% pollinated
Apis mellifera	42	Nectar	10	32	24b
Megachile rotundata (♂)	54	Nectar	8	46	15b
Megachile rotundata (♀)	37	Nectar	7	30	19b
Megachile rotundata (♀)	47	Pollen	40	7	85a
Bombus spp. (queens)	31	Pollen	30	1	97a
Bombus spp. (workers)	25	Pollen	23	2	92a
Andrena spp.	27	Pollen	26	1	96a
Halictus spp.	21	Pollen	18	3	85a
Control	179	—	179	169	6c

Percentages with the same letter do not significantly differ at $P < 0.05$ (least likelihood ANOVA, contrasts).

Vaccinium pollen tetrad, mean pollen deposition differed significantly among bee taxa (ANOVA, $F = 148.63$, df = 8, $P < 0.0001$; data log transformed to equalize variances, Bartlett's test $\chi^2 = 6.33$, df = 8, $P = 0.61$) (Table 3). All pollen-harvesting taxa delivered more pollen per single visit than nectar-collectors. Among pollen-harvesting bees, *Bombus* spp. queens and *Andrena* spp. deposited more pollen than *Halictus* spp. and *M. rotundata.*

Pollinator Equivalencies. Combining floral visitation rate with pollination percentage yielded the pollination rate (*V. angustifolium* flowers pollinated per minute) for each taxon. Pollen-harvesting *Bombus* spp. queens successfully pollinated 12.4 flowers per minute followed by *Bombus* spp. workers (10.3), *Andrena* spp. (6.9), *M. rotundata* (6.5), and *Halictus* spp. (5.2). Among the nectar-foragers, *A. mellifera* pollinated 1.9 flowers per minute followed by female and male *M. rotundata* at 0.8 and 0.7 flowers per minute, respectively. Table 4 shows the pollination rate equivalency matrix for bees foraging at *V. angustifolium.* For example, a *Bombus* spp. queen will pollinate 6.5 flowers in the same time it takes for *A. mellifera* to pollinate a single flower.

Table 5 shows the pollen deposition equivalency matrix for bees foraging at *V. angustifolium.* For example, *A. mellifera* must visit a flower 4.3 times to deposit the same amount of pollen as a single visit by a *Bombus* spp. queen. Comparison between managed pollinators reveals *A. mellifera* would have visit a flower 2.4 times to deposit an equivalent stigmatic load as a single visit by pollen harvesting *M. rotundata.*

Pollen Deposition Versus Pollination Percentage. Data were submitted to nonlinear regression using a simple exponential function. The resulting exponential equation was $y = 308.451(1\text{-}e^{0.113x})$, where y is pollination percentage and x is pollen tetrads deposited in a single visit, satisfactorily described the relationship between pollination percentage and pollen deposition ($r^2 = 0.98$) (Fig 1). The amount of pollen deposited per single visit was significantly related to pollination percentage ($F = 184.45$, df = 7, $P < 0.0001$). Bees that deposited small amounts of pollen do not do this consistently from flower to flower. Instead, many of their floral visits failed to result in successful pollination events. Alternatively, bees that deposited relatively large amounts of pollen (>25 tetrads) per single visit seldom failed (<15% of visits) to pollinate *V. angustifolium* flowers.

Table 3. Pollen deposition by bees resulting from single visits at virgin *Vaccinium angustifoilium* flowers

Taxon	No. individuals	Foraging task	Pollen deposited per single visit	
			Mean ± SE	Range
Apis mellifera	10	Nectar	11.7 ± 1.7d	5–20
Megachile rotundata (♂)	8	Nectar	11.6 ± 1.4d	6–17
Megachile rotundata (♀)	7	Nectar	12.9 ± 1.4d	7–19
Megachile rotundata (♀)	40	Pollen	27.8 ± 1.6c	8–61
Bombus spp. (queens)	30	Pollen	50.6 ± 3.1a	28–107
Bombus spp. (workers)	23	Pollen	34.3 ± 1.9bc	21–51
Andrena spp.	26	Pollen	46.2 ± 2.7ab	20–92
Halictus spp.	18	Pollen	25.8 ± 1.9c	12–44
Control	10	—	1.3 ± 0.2e	1–2

Means with the same letter do not significantly differ at $P < 0.05$ (Tukey's studentized range test following square root transformation).

Discussion

Considerable variation in pollination efficacy was found among bee taxa visiting *V. angustifolium.* Effectiveness (pollination percentage and pollen deposition) was clearly linked to the foraging task of the visiting bee, with pollen-harvesters far superior to their nectar co-foragers. Differences in pollination

Table 4. Pollination rate equivalency matrix for bees foraging at *Vaccinium angustifolium*

Taxa	1	2	3	4	5	6	7	8
1. *A. mellifera*	1.0	—	—	—	—	—		
2. *M. rotundata* (♂)	0.4	1.0	—	—	—	—	—	—
3. *M. rotundata* (♀N)	0.4	1.1	1.0	—	—	—	—	—
4. *M. rotundata* (♀P)	3.4	9.3	8.1	1.0	—	—	—	—
5. *Bombus* spp. (Q)	6.5	17.7	15.5	1.9	1.0	—	—	—
6. *Bombus* spp. (W)	5.4	14.7	12.9	1.6	0.8	1.0	—	—
7. *Andrena* spp.	3.6	9.9	8.6	1.1	0.6	0.7	1.0	—
8. *Halictus* spp.	2.7	7.4	6.5	0.8	0.4	0.5	0.8	1.0

Pollination rate comparisons with taxa occupying the highest column tier represented down columns as the equivalent number of flowers pollinated per unit time as the taxa in the far left column. N, nectar; P, pollen; Q, queen; W, worker.

Table 5. Pollination deposition equivalency matrix for bees foraging at *Vaccinium angustifolium*

Taxa	1	2	3	4	5	6	7	8
1. *A. mellifera*	1.0	—	—	—	—	—	—	—
2. *M. rotundata* (♂)	1.0	1.0	—	—	—	—	—	—
3. *M. rotundata* (♀N)	1.1	1.1	1.0	—	—	—	—	—
4. *M. rotundata* (♀P)	2.4	2.4	2.3	1.0	—	—	—	—
5. *Bombus* spp. (Q)	4.3	4.4	3.9	1.8	1.0	—	—	—
6. *Bombus* spp. (W)	2.9	3.0	2.7	1.2	0.7	1.0	—	—
7. *Andrena* spp.	4.0	4.0	3.6	1.7	0.9	1.3	1.0	—
8. *Halictus* spp.	2.2	2.2	2.0	0.9	0.5	0.7	0.6	1.0

Pollen deposition comparisons represented down columns as the number of successful floral visits required by taxa occupying the highest tier in the column to deliver an equivalent stigmatic load as the taxa in the far left column. N, nectar; P, pollen; Q, queen; W, worker.

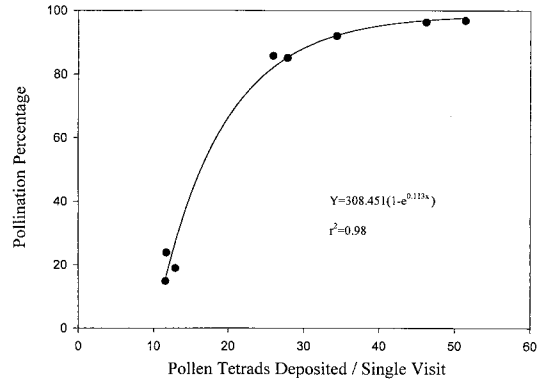

Fig. 1. Relationship between pollination percentage and the mean number pollen tetrads deposited per single visit by bees at *Vaccinium angustifolium.*

effectiveness based on foraging task were illustrated by *M. rotundata.* Upon release, *M. rotundata* (females) initially visit blueberry flowers for nectar. These visits were characterized by low pollination percentages with relatively small amounts of pollen being transferred to receptive stigmata. Following nest initiation, *M. rotundata* (females) routinely visited blueberry flowers for pollen resulting in significant increases in the percentage of pollinated flowers and stigmatic loading.

Nonparasitic indigenous taxa (*Andrena, Bombus, Colletes, Halictus, Lasioglossum, Evylaeus, Dialictus, Augochlora, Augochlorella, Osmia*) use *V. angustifolium* as a pollen source. Honey bees are not prone to harvest pollen from the poricidal anthers of *V. angustifolium.* Only 2–10% of honey bees found on commercial blueberry fields collect *Vaccinium* pollen (Lesaffre et al. 1975, MacKenzie et al. 1996). While foraging for nectar, honey bees and leafcutting bees do not provide sufficient agitation of the porose anthers to cause a large amounts of pollen to be released and, as a result, transport relatively few *Vaccinium* pollen grains on their integument among flowers (Mohr and Kevan 1987, Parker et al. 1987, Javorek 1996). Unlike honey bees, leafcutting bees released on commercial blueberry fields are not deterred from harvesting pollen at *V. angustifolium* as a high percentage of natal cells are provisioned with *Vaccinium* pollen (Javorek 1996, Stubbs et al. 1994).

Of the bees observed in this study, *M. rotundata* (females) were the only pollen-harvesting bees that did not sonicate *V. angustifolium* flowers to remove pollen. Despite this, these bees displayed comparable pollination percentages while depositing similar amounts of pollen per visit as some sonicating taxa. This demonstrates that while sonication is a highly effective means of pollen removal, it is not a prerequisite for effective pollination of *V. angustifolium.* Therefore, the value of this leafcutting bee as a pollinator of lowbush blueberry is not limited by pollination effectiveness, as is the case for *A. mellifera.* Instead, the primary disadvantage to the use of *M. rotundata* is environmental, as it requires warmer air temperatures to initiate flight, thus limiting the hours and days it will forage as compared with other pollinators (Javorek 1996).

With the exception of *Bombus* spp. queens and workers, which visit significantly more flowers per minute, many taxa (*Andrena* spp., *Halictus* spp., *A. mellifera* and female *M. rotundata*) exhibit similar floral visitation rate. However, it is evident from this study that floral visitation at *V. angustifolium* is not synonymous with pollination. As such, the interpretation of taxon-specific pollination efficiency based solely on floral visitation rates (Wood 1965; Marucci and Moulter 1977) is misleading as it fails to incorporate differences in pollination percentages that exist among taxa. The average pollination percentage of pollen harvesting bees was six times greater than nectar foragers. All pollen- harvesting bees tested had pollination percentages exceeding 85%, with *Bombus* spp. (queens) and *Andrena* spp. over 95%. In contrast, nectar foragers had pollination percentages below 25%. When we consider the number of flowers pollinated per minute, the pollination contribution of pollen-harvesting bees ranged from three to six times the number of flowers per minute compared with the most effective of the nectar-foragers tested, *A. mellifera.*

The quality of a floral visit (stigmatic pollen load per visit) also varied considerably among taxa. As a group, pollen foraging bees deposited three times the amount of pollen per single visit than did *A. mellifera. Andrena* spp. and *Bombus* spp. are the most effective bees depositing on average, >45 tetrads per visit. Interestingly, the introduced species *M. rotundata* (females) showed moderate pollen deposition comparable to that of *Bombus* spp. workers and *Halictus* spp. It should be noted here that the first *Bombus* spp. workers of the season appear during the mid- to late stages of the *V. angustifolium* flowering period. They are small compared with queens and have little foraging experience. This combination of smaller size and naivete, may account for differences in pollination efficiency observed between *Bombus* spp. queens and workers.

Although complicating factors such as inter-flower selfing (Ballington and Galletta 1978, Vander Kloet

and Cabilio 1984, Vander Kloet and Lyrene 1987), low pollen viability (Vander Kloet 1983) and the prevalence of male and female sterility (Aalders and Hall 1961) make it difficult to define optimal pollen deposition levels under field conditions, the inherent benefits of greater pollen loading and in turn, more efficient pollinators, are clear. Within the blueberries (*Vaccinium* Section *Cyanococcus*), stigmatic loading is positively correlated with fruit set (Dogterom 1999, K.E.M., unpublished data), seed number (Dogterom 1999), and fruit weight (Aalders and Hall 1961, Bigras-Hoet et al. 1972, Jackson et al. 1972). Using compatible donor pollen under controlled conditions, increasing stigmatic loads from 10 to 50 tetrads increased *V. angustifolium* fruit set by >25% (K.E.M., unpublished data). The differences in pollen deposition observed among taxa should have a strong bearing on the quantity of fruit produced. Single visits by *A. mellifera* and *M. rotundata* (males) that deposit relatively few tetrads per visit (≈12) should be much less likely to set a fruit as compared with more efficient pollinators. It must be acknowledged that these data do not incorporate the effects of taxon-specific foraging patterns (specifically, movement within versus among clones) on the proportion of compatible pollen delivered. Further study is needed to elucidate what bearing foraging patterns of different taxa have on outcrossing between *V. angustifolium* clones.

Although possible to set fruit from a single compatible pollen tetrad, larger stigmatic loads result in more ovules being fertilized and therefore more seed set (S.P.V.K., unpublished data). In open pollinated plants in natural settings, small berries (80–140 mg) contain 5 ± 3 viable seeds, medium-sized berries (≈0.33 gm) have 18 ± 6 viable seeds, and large berries (0.66 gm) have 32 ± 24 viable seeds (Vander Kloet and Austin-Smith 1987). Floral visitation by more effective pollinators (pollen-harvesting females of *Andrena* spp., *Bombus* spp., *Halictus* spp., and *M. rotundata*), given adequate environmental conditions over the growing season, could potentially result in heavier fruit and thus would contribute more on a berry-to-berry basis toward yield. Small stigmatic loads associated with single visits by *A. mellifera* and *M. rotundata* (males), would result in fewer seeds set and thus predestine fruit to relatively small size.

Pollen deposition equivalencies derived in this study show that flowers would require multiple visits by *A. mellifera* to receive comparable amounts of pollen deposited by a single visit by indigenous genera or pollen-harvesting *M. rotundata.* Therefore, to compensate for poor quality single visits, pollen would have to be sequentially added to stigmata following initial pollination to promote greater fruit set and subsequent berry size. Following initial pollination, repeat visits to flowers must occur before fertilization, after which stigmata are no longer receptive. Under field conditions this occurs within 2 d of pollination (S.P.V.K., unpublished data). The probability of successive visits depends on a combination of floral density, pollinator abundance, and available flight window. Data obtained from 17 commercial blueberry fields in Nova Scotia and New Brunswick show that 34% (range, 12–60%) of pollinated flowers receive <15 pollen tetrads per stigma over their period of receptivity (Javorek unpublish. data). Such stigmatic loads are clearly characteristic of single visits by relatively poor pollinators. Therefore, it is apparent that under current pollination practices many flowers at the time of fertilization had received only single visits (1) emphasizing the importance of individual pollinator efficiency and (2) indicating that in many situations current *A. mellifera* stocking rates may be low.

The positive relationship between *A. mellifera* foraging density and fruit set, seed set and berry weight (Aras et al. 1996) indicates that honey bee abundance can mitigate the effects of low individual pollination effectiveness. Although greater fruit set can at least be partially attributed to more flowers being visited, increased seed number and berry weight associated with more honey bee foragers must be attributed to larger stigmatic loads resulting from repeat floral visitation.

Recent studies have evaluated lowbush blueberry pollination based solely on bee abundance (Eaton 1992, 1997). Although not stated, these studies hinge on the underlying assumption of the relative equality of each member of the pollination guild. As an artifact of this line of investigation, the superior individual pollination contribution of many indigenous bees is often under-represented as their foraging densities are often eclipsed by higher honey bee numbers. To correct this oversight in the future, bee abundance should be combined with measures of relative pollinator effectiveness to more accurately assess the pollination contribution of a specific pollinator guild.

In addition to clearly showing significant differences in pollination effectiveness among bees visiting *V. angustifolium,* this paper highlights the value of the diverse suite of indigenous pollinators associated with this crop. As such, there is a need for research to establish the ecological underpinnings that define indigenous bee abundance and diversity within lowbush blueberry agro-ecosystems so management practices can be adopted that promote their conservation and enhancement.

Acknowledgments

We thank Trish Javorek and Troy Whidden for field and laboratory assistance, Dan Ryan for statistical support, and Jim Cane and Michael Hardman for their constructive review of this paper. We appreciate the cooperation of the Wild Blueberry Producers Association of Nova Scotia and the blueberry growers who allowed access to the fields. The Canada/Nova Scotia Agri-Food Development Agreement provided project funding. This is article is contribution number 2225 from the Atlantic Food and Horticulture Research Center of Agriculture and Agri-Food Canada.

References Cited

Aalders, L. E., and I. V. Hall. 1961. Pollen incompatibility and fruit set in lowbush blueberry. Can. J. Genet. Cytol. 3: 300–307.

Aras, P., D. de Olivera, and L. Savoie. 1996. Effect of a honey bee (Hymenoptera: Apidae) gradient on the pollination and yield of lowbush blueberry. J. Econ. Entomol. 89: 1080–1083.

Argall, J., K. E. MacKenzie, S. K. Javorek, and G. Chiasson. 1996. Alfalfa leafcutting bees for the pollination of wild blueberries. Wild blueberry fact sheet B.7.0. Canada/ New Brunswick Agreement on Economic Diversification, New Brunswick Department of Agriculture and Rural Development, Fredericton, New Brunswick.

Ballington, J. R., and G. J. Galletta. 1978. Comparative cross-ability of four diploid *Vaccinium* species. J. Am. Soc. Hortic. Sci. 103: 554–560.

Beattie, A. J. 1971. A technique for the study of insect-borne pollen. Pan-Pac. Entomol. 47: 82.

Bigras-Hoet, F., L. Hout, and L. J. Jobin. 1972. La pollinisation du bleuet au Lac-St-Jean. I. R⊥le de l'abeille domestique, *Apis mellifera* L. Ann. Soc. Entomol. Que. 17: 138–169.

Boulanger, L. W., G. W. Wood, E. A. Osgood, and C. O. Dirks. 1967. Native bees associated with the lowbush blueberry in Maine and Eastern Canada. Technical Bulletin 26. Maine Agriculture Experiment Station, Orono, ME.

Buchmann, S. L. 1983. Buzz pollination in angiosperms, pp. 73–113. *In* C. E. Jones and R. J. Little (eds.), Handbook of experimental pollination biology. Van Nostrand Reinhold, New York.

Cane, J. H., and J. A. Payne. 1990. Native bee pollinates rabbiteye blueberry. 37: 4. Highlights of Agricultural Research, Alabama Agricultural Experiment Station, Auburn University, Alabama.

Chiasson, G., and J. Argall. 1996. Pollination of wild blueberries. Wild blueberry fact sheet number B.1.0. Canada/ New Brunswick Agreement on Economic Diversification, New Brunswick Department of Agriculture and Rural Development, Fredericton, New Brunswick.

Dogterom, M. H. 1999. Pollination by four species of bees on highbush blueberry. Ph.D. dissertation, Simon Fraser University, Burnaby, British Columbia.

Eaton, G. W. 1967. The relationship between seed number and berry weight in open-pollinated highbush blueberries. HortScience 2: 14–15.

Eaton, L. J. 1992. Effect of pollinator number on fruit set and yield of lowbush blueberry. Can. Beek. 32–34.

Eaton, L. J. 1997. Relationships of pollinator numbers in blueberry fields to fruit development and yields. Acta Hortic. 446: 181–188.

Finnemore, A. T., and M. E. Neary. 1978. Blueberry pollinators of Nova Scotia, with a checklist of the blueberry pollinators in Eastern Canada and North Eastern United States. Ann. Soc. Entomol. Que. 23: 168–181.

Ismial, A. A. 1987. Honey bees and blueberry pollination. Cooperative Extension Service Publication 2079. University of Maine, Orono, ME.

Jackson, L. P., L. E. Aalders, and I. V. Hall. 1972. Berry size and seed number in commercial low-bush blueberry fields of Nova Scotia. Nat. Can. 99: 615–619.

Javorek, S. K. 1996. The potential of the alfalfa leafcutting bee *Megachile rotundata* F. (Hymenoptera: Megachilidae) as a pollinator of lowbush blueberry (*Vaccinium angustifolium* Ait, *V. mytilloides* Michx.) M.Sc. thesis, Acadia University, Wolfville, Nova Scotia.

Lesaffre, O., B. Dupont, and J. M. Perron. 1975. M 74 thode simple pour comparer l'activité la planche de vol de différentes ruches d'abeilles domestiques. Ann. Soc. Entomol. Que. 20: 180–187.

Macfarlane, R. P., L. A. Royce, B.K.W. Wyatt, and D. F. Mayer. 1994. Evaluation of commercial bumble bee colonies for cranberry pollination. Melanderia 50: 13–19.

MacKenzie, K. E., D. Rogers, D. Nelson, and S. K. Javorek. 1996. Pollination of lowbush blueberry: improving honey bee pollination of lowbush blueberry. Final report. Nova Scotia Agricultural Development -Technology Development. Program. Nova Scotia Department of Agriculture and Marketing, Truro, NS.

Marucci, P. E., and H. J. Moulter. 1977. Blueberry pollination in New Jersey. Acta Hortic. 61: 175–186.

Mohr, N. A., and P. G. Kevan. 1987. Pollinators and pollination requirements of lowbush blueberry (*Vaccinium angustifolium* Ait. And *V. myrtilloides* Michx.) and cranberry (*V. macrocarpon* Ait.) in Ontario with notes on highbush blueberry (*V. corymbosum* L.) and lingonberry (*V. vitis-ideae* L.). Proc. Entomol. Soc. Ont. 118: 149–154.

Parker, F. D., S.W.T. Batra, and V. J. Tepedino. 1987. New pollinators for our crops. Agric. Zool. Rev. 2: 279–307.

Sampson, B. J. 1993. Pollination of lowbush blueberry, (*Vaccinium angustifolium* Aiton) by bees (Hymenoptera: Apoidea) in Nova Scotia. M.Sc. thesis, Acadia University, Wolfville, Nova Scotia.

SAS Institute. 1990. SAS/STAT user's guide, version 6: 4th ed. SAS Institute, Cary, NC.

Stubbs, C. S., and F. A. Drummond. 1997. Blueberry and cranberry (*Vaccinium* spp.) pollination: a comparison of managed and native bee foraging behavior. Proceedings, International Symposium on Pollination. Acta Hort. 437: 341–344.

Stubbs, C. S., H. A. Jacobson, E. A. Osgood, and F. A. Drummond. 1992. Alternative forage plants for native (wild) bees associated with lowbush blueberry, *Vaccinium* spp., in Maine. Maine Agriculture Experiment Station Technical Bulletin 148. University of Maine, Orono, ME.

Stubbs, C. S., F. A. Drummond, and E. A. Osgood. 1994. *Osmia ribifloris biedermannii* and *Megachile rotundata* (Hymenoptera: Megachilidae) introduced into the lowbush blueberry agroecosystem in Maine. J. Kans. Entomol. Soc. 67: 173–185.

Vander Kloet, S. P. 1983. The relationship between seed number and pollen viability ion *Vaccinium corymbosum* L. Hort Science 18: 225–226.

Vander Kloet, S. P. 1988. The genus *Vaccinium* in North America. publication 1828. Agriculture Canada, Ottawa, Ontario.

Vander Kloet, S. P., and P. Austin-Smith. 1987. Energetics, patterns and timing of seed dispersal in *Vaccinium* section *Cyanococcus.* Am. Midl. Nat. 115: 386–396.

Vander Kloet, S. P., and P. Cabilio. 1984. Annual variation in seed production in a population of *Vaccinium corymbosum* L. Bul. Torr. Bot. Club 111: 483–488.

Vander Kloet, S. P., and P. M. Lyrene. 1987. Self-incompatibility in diploid, tetraploid and hexaploid *Vaccinium corymbosum.* Can. J. Bot. 65: 660–665.

Wood, G. W. 1965. Note on the activity of native pollinators in relation to the bloom period of lowbush blueberry. J. Econ. Entomol. 58: 777.

Received for publication 8 May 2001; accepted 19 November 2001.