# Commercial Bumble Bee *Bombus impatiens* (Hymenoptera: Apidae) as a Pollinator in Lowbush Blueberry (Ericale: Ericaceae) Fields

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**ABSTRACT**   Here, we evaluate the potential of the bumble bee *Bombus impatiens* Cresson, obtained from commercial colonies, as a pollen vector for lowbush blueberry, *Vaccinium augustifolium* Aiton. We wanted to gain insight into the relationships between pollination by introduced bumble bees, the categories of seeds produced, and the weight and the maturity of the blueberries. The effect of *B. impatiens* foraging in blueberry stands was measured quantitatively through fruit set and seed set analysis. We created a density gradient of *B. impatiens* by clustering 72 small hives at the southern extremity of blueberry fields located in Girardville (49° 00′ N, 72° 33′ W), Quebec, Canada. Observers recorded plant and insect data in 52 plots of 1 by 10 m, distributed at distances ranging from 25 to 1,500 m from the hives. From these data, we evaluated the fruit set rate, the weight and maturity of the berries, and the number of seed structures per berry, including true seeds of large, medium, and small size, pseudo-seeds, and ovules. Positive correlations were found between the density of *B. impatiens* and fruit set as well as the number of large seeds per berry. Large seeds influenced the weight and maturity of berries. *B. impatiens* acted as a "near-nest central forager" and increased fruit set and seed production up to 100 and 150 m respectively, from the hives.

**KEY WORDS**   bumble bee, *Bombus impatiens*, lowbush blueberry production, *Vaccinium angustifolium*, pollination

Lowbush blueberry, *Vaccinium augustifolium* Aiton, is a weakly self-fertile plant (Aalders and Hall 1961) that requires cross-pollination to produce a good blueberry crop (Karmo et al. 1959, Wood 1968). The near self-sterility and hercogamy of lowbush blueberry are mechanisms that promote allopollination. More specifically, its pendent flowers open downward and possess a cone-shaped stigma located below the stamens, thus acting to prevent self-fertilization via hercogamy. Pollen grains slide by gravity on the smooth walls of this cone and cannot easily attain the stigmatic surface, which faces the ground (Eck 1988). This particular structure of the flower, which is not anemophilous, makes pollination very difficult without insects (Eck 1988). Indeed, it is because of these mechanisms and the need for cross-pollination between blueberry clones that the presence of pollen vectors, mostly bees, explains >80% of the lowbush blueberry fruit production (Lee 1958, Karmo et al. 1959, Aras et al. 1996). Current intensive agricultural practices help create a large mass of homogeneous flowers that bloom in synchrony. This overabundance of flowers, combined with a decrease in the native insect fauna through habitat loss and pesticide use (Wood and Wood 1962, Kevan 1975, CNRC 1981, MacKenzie and Winston 1984, Payette and de Oliveira 1989) reduces the pollinator to flower ratio within the crop as well as within neighboring populations of wild plant species that share the same functional pollinators. In these systems, the native pollinator community is no longer sufficient, and its density is too unpredictable from year to year to ensure adequate pollination of crops (Boulanger et al. 1967, MacKenzie and Winston 1984, Eck 1988). The phenomena described above are in part responsible for the introduction of pollinating insects in blueberry crops, particularly the honey bee, *Apis mellifera* L. (McGregor 1976, Free 1993). In the Lac-Saint-Jean region of Québec, Canada, this trend has increased following studies, in particular, that of Aras et al. (1996), which showed that the introduction of hives in a blueberry stand significantly increases blueberry production. Indeed, improved pollination results in a greater number of seeds per fruit, which is associated with a shorter maturation time and a greater fruit weight (Aalders and Hall 1961, Wood 1968, Jackson et al. 1972, Aras et al. 1996). With the arrival of *Varroa destructor* Anderson & Trueman in Québec, it has become more difficult for apiculturists to provide pollination services to cover the 21,918 ha of blueberry fields (MAPAQ 2005) in Québec. This has thus created the need for alternatives to exclusive use of *A. mellifera* as pollen vector.

Bumble bees occur in large numbers in boggy habitats and have probably coevolved with this type of

vegetation (Heinrich 2004). Consequently, there is a strong likelihood that reciprocal adaptation has made the bumble bee an ideal pollinator of the blueberry. The bumble bee's physiological, morphological, and behavioral characteristics support this claim. Its great fidelity to the blueberry culture (Whidden 1996, Stubbs and Drummond 2001), buzz-pollination capabilities, foraging speed (Bigras-Huot et al. 1973, Stubbs and Drummond 2001, Javorek et al. 2002), and propensity to deposit large pollen loads on stigmas have been demonstrated previously (Javorek et al. 2002). Also, as an endothermic species (Willmer 1983), the bumble bee forages in diverse meteorological conditions and for a longer times than the honey bee (Pesson and Louveaux 1984, Desjardins 2003). Nevertheless, these characteristics are still only potential indications of the bumble bee's pollinating effectiveness.

Here, we quantify the effect of a density gradient of commercial bumble bees on fruit set and the number of seeds per fruit in blueberry fields. We also elucidate the relationship between pollination by *B. impatiens* and the weight and maturity of berries, through their association with categories of seed structures produced, including true seeds of large, medium, and small size, pseudo-seeds, and ovules. Finally, we characterize the worker bee's foraging dispersal and assess the area of maximal pollination.

## Materials and Methods

Our experimental sites were located in the blueberry stand of the Girardville Forest Cooperative (49° 00′ N, 72° 33′ W), Lac-Saint-Jean region, Québec. Its total area is 209 ha. This research was carried out during the blueberry flowering period (28 May–20 June 2001), in a 20-ha area in its first year of production. The two fields studied were about the same form and size (10 ha each), arranged longitudinally, and extended northward >2 km. They were separated from each other by a 10-m-wide Jack pine, *Pinus divaricata* Aiton, strip. These fields are composed primarily of *Vaccinium augustifolium* Aiton. We chose methods that are similar to those of Aras et al. (1996). Grouping 72 small hives at the southern end of the blueberry fields created a gradient in introduced *B. impatiens* density. These bumble bees ($200 per colony of ≈200 individuals), obtained from APIPOL sen.c. (Laval, Québec, Canada), were placed in an open area situated in the Jack pine strip separating the two fields. At the end of the blueberry flowering period a colony was composed of 30 bumble bees, on average. Observations were made in 52 open plots 1 by 10 m oriented with the long axis running east–west. Pairs of plots were set in each field at the following distances: 25, 50, 100, 150, 200, 300, 400, 500, 600, 700, 800, 1,200, and 1,500 m away from the hives. Within each field, the pair of plots for a given distance from the hives were placed 15 m apart.

Twice a day (0900–1200 and 1300–1600 hours), three observers made a systematic insect survey in all plots for a total of 50 surveys per plot over the flowering period. Each survey consisted of having an observer walk slowly westerly along the east–west axis of the plot, at constant speed for 10 s. Consequently, sampling was mainly conducted upwind (primarily east–west), thus diminishing the effect of human presence on bumble bees. It is recognized that bumble bees' sense of smell is relatively well developed. When walking downwind the bumble bees seem to detect and fly away from observers (D.de O., unpublished data). During their walk, observers recorded the number of insects foraging on blueberry flowers for each of the following groups: *B. impatiens*, native bumble bees (mainly *B. ternarius* and *terricola*), solitary bees (Megachilidae, Andrenidae, Halictidae, and Colletidae), and other pollinators (Coleoptera, Diptera, Lepidoptera, and other Hymenoptera).

Floral density was evaluated in each plot by multiplying the estimated number of blueberry stems by the average number of flowers per stem. To estimate the number of blueberry stems per plot, we counted the stems present in four randomly located subplots of 25 by 25 cm within each plot. The determination of the floral potential (see below) was used to ascertain the average number of flowers per blueberry stem.

In spring, to determine fruit set (percentage of flowers producing a fruit), we randomly selected and tagged 25 blueberry stems in each plot. At mid-bloom, floral potential was determined on each of these stems by counting all floral buds, open flowers, and ovaries (if corollas were missing). This was then related to fruit numbers in mid-July, the period of summer coinciding with the end of physiological pruning caused by a poor pollination (Young 1951, Stephenson 1981).

In each plot, berries were collected just before the commercial harvest of the stand. Fruits were frozen to be able to examine them over an extended period. From randomly selected samples of 25 frozen blueberries per plot, we weighed and recorded the color of the berries as an index of maturity. Their color development being very rapid (≈ 4 d, Young [1951]), as soon as the fruit showed some red, blue, or both pigmentations we considered them as mature, giving binary type data (mature or immature). We extracted and categorized seed structures by using a stereobinocular microscope with a micrometric calibration ocular. Seed structures (Fig. 1) were classified into five categories: 1) filled large-sized seeds measuring >1.3 mm in length (length, $1.42 \pm 0.07$ mm; thickness, $0.70 \pm 0.07$ mm; weight, $0.417 \pm 0.077$ mg); 2) filled medium-sized seeds measuring between 1 and 1.3 mm in length (length, $1.18 \pm 0.07$ mm; thickness, $0.61 \pm 0.07$ mm; weight, $0.279 \pm 0.072$ mg); 3) filled small-sized seeds measuring <1 mm in length (length, $0.87 \pm 0.08$ mm; thickness, $0.48 \pm 0.12$ mm; weight, $0.136 \pm 0.059$ mg); 4) pseudo-seeds of irregular shape measuring >0.75 mm (length, $0.97 \pm 0.21$ mm; thickness, $0.36 \pm 0.08$ mm; weight, $0.115 \pm 0.047$ mg); and 5) ovules, not filled measuring <0.75 mm.

Statistical analyses were done using SAS (SAS Institute 1998). Correlations and regressions were used to relate *B. impatiens* density with each of the seed structure categories and to describe the relationship
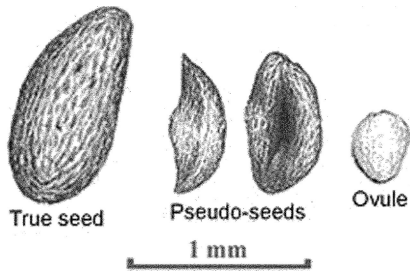
**Fig. 1.** Illustration of a true seed (filled shape, length >0.75 mm), pseudo-seeds (irregular shape, length >0.75 mm), and an ovule (not filled, length <0.75 mm) of lowbush blueberry fruit.



**Fig. 2.** Density of *B. impatiens* and native fauna as a function of distance from the hives. Observed variables are total number of *B. impatiens* and native fauna foraging within a plot ($n = 50$ surveys of 10 s each per plot). Average assessed from four plots per distance ($n = 28$): two fields by two (1 by 10-m) plots per distance.

between these seed categories and berry weight and maturity (logistic regression). The weight of the seeds was subtracted from the weight of the fruit to avoid all possibility of covariance. Explanatory variables to be used in the final analysis were chosen using multiple regression analyses with backward variable selection (Kleinbaum et al. 1998). The double asymptotic and logarithmic models were chosen to represent the influence of B. *impatiens* on blueberry production, as discussed in previous studies. Stubbs and Drummond (1997) demonstrated that the expected outcome of a "near-nest central forager" is best represented by the double asymptotic model form:

production factor =

$$A + B \, (1 + \exp^{(C+D*\text{distance from domicile})})$$

where *A* is theoretical background pollination represented by the upper asymptote and *B* is the increase in pollination caused by the introduced forager. Aras et al. (1996) established that the relationship between pollinator density and studied blueberry production parameters is logarithmic. Least-squares method was used to assess the linearity assumption (linear regression) and to choose the best-fitting models. Logarithmic, exponential and square-root transformations were performed to satisfy normality and linearity assumptions. For the whole analyses, homoscedastic and normality assumptions were verified with the first and second moment specification and Shapiro–Wilk tests, respectively. For the multiple regressions, collinearity was verified using the variance inflation factor and tolerance and with analyses of the correlation matrix between the predictors.

## Results

Uniformity in the dispersion of native pollinators (Fig. 2) and the lack of significant correlations with other potentially explanatory variables and production parameters (Table 1) strongly suggest that *B. impatiens* density influences blueberry production.

**Insect Dispersal.** *B. impatiens* density decreased progressively as a function of the hive distance, whereas native bee distribution was homogeneous throughout the fields (Fig. 2). None of the *B. impatiens*
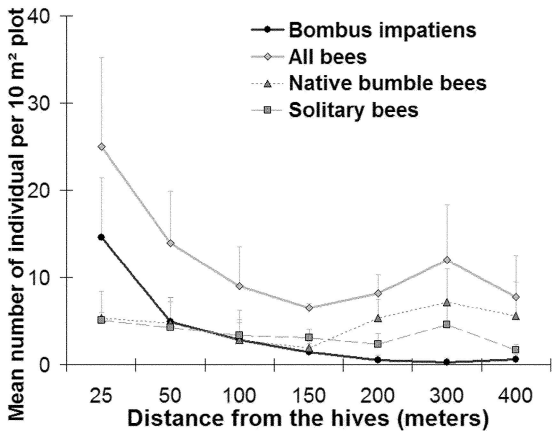
workers were seen foraging further than 400 m from the colonies.

**Fruit Set.** Correlations analyses showed that both solitary bees and *B. impatiens* significantly influenced fruit set (Table 1), but a subsequent multiple regression analysis showed that only *B. impatiens* density was significantly correlated with fruit set. Twenty-one percent of the variation in fruit set was explained by the density of *B. impatiens* in the blueberry field ($R^2 = 0.21$, $P \leq 0.05$, $n = 24$). The relationship between these two variables is logarithmic; thus, a greater increase in fruit set is observed at low bumble bee densities (Fig. 3). The double asymptotic model allowed us to assign the highest fruit set at 54% up to 100 m from the hives and the background pollinator level to 42% (Fig. 4). *B. impatiens* enhanced mean fruit set by 12% over background pollinator level.

**Pollinator Value through Ovule Fertilization.** The presence of introduced bumble bees was only significantly associated with large seeds (Table 2). Their relationship is logarithmic (Fig. 5). The density of *B. impatiens* accounts for 41% of the variation in the number of this category of seeds per berry ($R^2 = 0.41$,

**Table 1.** Pearson correlation coefficients between the potentially explanatory variables and the studied production factors

|  | Fruit set rate | Large seeds/berry |
|---|---|---|
| *B. impatiens* | 0.46* | 0.64*** |
| Native bumble bees | −0.09 NS | −0.22 NS |
| Solitary bees | 0.42* | 0.27 NS |
| All bees | 0.34 NS | 0.35 NS |
| Other pollinators | 0.24 NS | −0.03 NS |
| Flowers/m² | 0.25 NS | 0.26 NS |
| Stems/m² | 0.20 NS | 0.02 NS |
| Distance from the field's edge | −0.31 NS | 0.11 NS |

NS, not-significant at $\alpha = 0.05$; *, significant at $\alpha = 0.05$; and ***, significant at $\alpha = 0.001$.
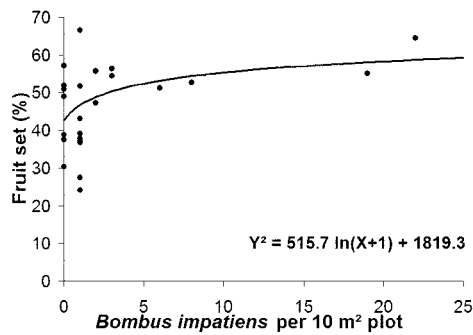
**Fig. 3.** Relationship between lowbush blueberry fruit set and the density of *B. impatiens*. Observed variables are total number of *B. impatiens* foraging ($n = 50$ surveys of 10 s each per plot) and fruit set ($n = 25$) within a 1 by 10-m plot ($n = 24$).

**Table 2.** Pearson correlation coefficients between *B. impatiens*, weight, and maturity of berries and the number of seeds per berry, for each of the seed structure categories

| | Seeds | | | Pseudo-seeds | Ovules |
|---|---|---|---|---|---|
| | Large | Medium | Small | | |
| *B. impatiens* | 0.64*** | −0.33 NS | −0.16 NS | 0.11 NS | −0.18 NS |
| Wt | 0.72**** | 0.26** | 0.03 NS | −0.02 NS | −0.45**** |
| Maturity | 0.26** | 0.29** | 0.15 NS | 0.06 NS | −0.24* |

NS, not-significant at $\alpha = 0.05$; *, significant at $\alpha = 0.05$; **, significant at $\alpha = 0.01$; ***, significant at $\alpha = 0.001$; and ****, significant at $\alpha = 0.0001$.

was positively correlated to its large ($r = 0.30$, $P = 0.05$, $n = 95$) and medium seed content ($r = 0.33$, $P = 0.01$, $n = 95$) (Table 2).

## Discussion

**Insect Dispersal.** *B. impatiens* workers in this study had a limited foraging range (400 m), which ranks them between *Megachile rotundata* (F.) who rarely forage >60 m (Stubbs and Drummond 1997) and the honey bee, which forages >5 km from the hives (Aras et al. 1996). The advantage of proximity foraging is that it ensures pollination of the target culture, but an inconvenience is that it complicates hive placement in large blueberry fields. Bumble bee hives would need a greater deployment than honey bee hives, which are most often agglomerated to the edge of the field. We did not see any *A. mellifera* or native *B. impatiens* in our study site, the distribution area of the latter being limited to latitudes further south than Lac-Saint-Jean (Laverty and Harder1988).

**Fruit Set.** Although *B. impatiens* foraged as far as 400 m from their colony, we obtained the highest rate
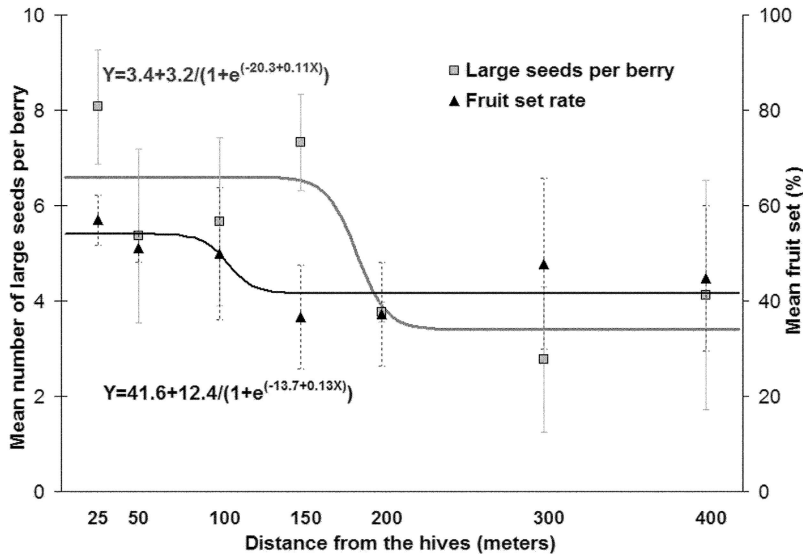
$P \le 0.001$, $n = 28$). The double asymptotic model reveals that the introduced bumble bee doubled the mean number of large seeds per berry: background pollination level accounts for 3.4 large seeds per berry versus 6.6 up to 150 m from the hives (Fig. 4).

**Influence of Seeds on Berry Weight and Maturity.** Numbers of large- ($r = 0.72$, $P = 0.0001$, $n = 104$) and medium ($r = 0.26$, $P = 0.01$, $n = 104$)-sized seeds were significantly correlated to fruit weight (Table 2). Multiple regression analysis showed that only the large seeds are significantly associated with berry weight. Fifty-four percent of the variation in fruit weight can be explained by the number of large seeds a fruit contains ($R^2 = 0.54$, $P < 0.0001$, $n = 104$). The relationship between these two variables shows a rapid and constant increase, followed by a berry weight leveling off at ≈30 seeds (Fig. 6). Maturity of a berry



**Fig. 4.** Average number of large seeds per berry and fruit set as a function of the distance from the hives. Observed variables are fruit set ($n = 25$) and seed set ($n = 25$) per plot. Average assessed from four plots per distance ($n = 28$): two fields by two (1 by 10-m) plots per distance.
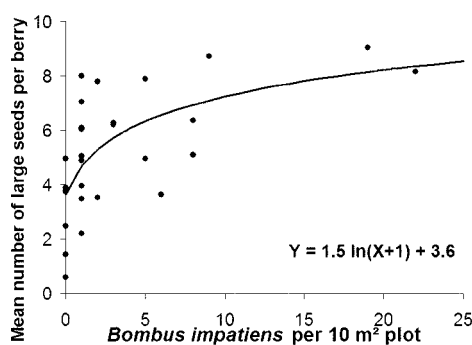
**Fig. 5.** Relationship between large seed content of blueberries and *B. impatiens* density. Observed variables are total number of *B. impatiens* foraging ($n = 50$ surveys of 10 s each per plot) and seed set ($n = 25$), within a 1 by 10-m plot ($n = 28$).

of fruit set up to 100 m from the hives. At this distance, *B. impatiens* density was three individuals per 10 $m^2$ and resulted in a fruit set increase of 29%. This density coincided with the end of the curve inflection in the logarithmic relationship between *B. impatiens* and fruit set. Fruit set increased more slowly after that point. Thus, we consider densities equal or greater than three individuals, corresponding to 0.06 individual per 10 $m^2$ per 10-s survey, as optimal to maximize fruit set under our experimental conditions (floral density of 835 flowers per $m^2$). The strong presence of native insect fauna and the rapid increases in fruit set that occurred at low pollinator densities may have caused the effect of *B. impatiens* to be underestimated, compared with another blueberry stand or another year where native pollinators might be less abundant. Here, the introduction of 2,160 (72 colonies × 30 individuals per colony) bumble bees resulted in a maximal fruit set on an area of 3.14 ha (pi × maximal fruit set radius from colonies$^2$ = $3.1416 \times (100 \text{ m})^2$), or the equivalent of 688 individuals per hectare. If we consider that the market price for a colony of 250 individuals is between $150 and $200 (Apipol and Koppert Canada, commercial bumble bee sellers) costs would approach $400 to $500/ha to achieve maximal and relatively secure pollination, *B. impatiens* being relatively active in extreme meteorological con-
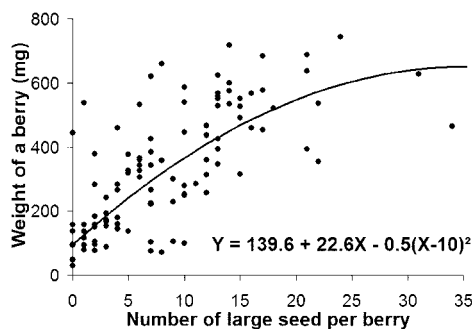


**Fig. 6.** Relationship between weight of a lowbush blueberry fruit and its large seed content ($n = 104$).

ditions (Desjardins 2003). Comparatively, berry producers would pay $400/ha for *A. mellifera* and $223/ha for *M. rotundata* (**MAPAQ** 1997) at the recommended density of four hives per hectare and 50,000 individuals per hectare, respectively. The price calculated for *M. rotundata* includes all the equipment costs amortized over a 10-yr period, the yearly offspring recovery (evaluated to 60%), nest extraction, and incubation. The producer's time and energy to manage *M. rotundata* throughout the annual cycle have not been considered.

**Pollinator Value through Ovule Fertilization.** The density of commercially available bumble bees explains 41% of the variation in large seed number per berry (Fig. 5). The association with large-sized seeds confirms *B. impatiens* pollinating efficiency, because a good pollinator produces more large-sized seeds per berry (Aras et al. 1996, Dogterom et al. 2000). Based on the relationship between the number of large seeds and berry weight (Fig. 6), bumble bee density within 150 m of the hives doubled the fruit's seed content and brought about a weight gain of 45%; an increase from 195 to 283 mg near the hives. This high-quality pollination could be caused by a superior pollinator density and/or by the efficiency of the pollinator. These two options lead to the same result: a greater pollen load, also possibly of higher genetic heterogeneity, on the stigma of flowers. The capacity of *B. impatiens* to enhance large seeds per berry up to 150 m from the hives, but fruit set only up to 100 m, demonstrates that the quality pollination obtained is not because of a higher density but rather because of a superior pollination efficiency. At lower densities of *B. impatiens*, fewer flowers were visited giving a lower fruit set rate, but these flowers still received an effective pollination as shown by the greater number of large seeds. The resulting berries contained a higher number of large seeds. The density of hair covering a bumble bee's body, which facilitates pollen adherence, and the bumble bees foraging behavior, including its buzz-pollinating ability, both contribute to its pollinating efficacy; both promote allopollination and the deposition of a greater pollen load per visit as demonstrated by Javorek et al. (2002).

This improved pollen load could lead to the fertilization of ovules by genetically "superior" pollen grains (Cruden 1997), through pollen competition in the style (Mulcahy and Mulcahy 1987) or from pollen of better genetic compatibility (higher heterogeneity of pollen). This would promote the formation of viable seeds that are of greater size (Jackson et al. 1972, Ehlenfeldt 1996, Dogterom et al. 2000). Ehlenfeldt (1996) suggests that pollen vigor, defined by the speed of growth of its pollen tube in the style, has a direct effect upon the resulting seeds, which are of greater size and higher viability. It is recognized that certain crossings produce seeds of greater size. This phenomenon, called the xenic effect, is observed in many plant species (Freytag 1979, de Oliveira et al. 1983, Colbert and de Oliveira 1990).

**Influence of Seeds on Weight and Maturity of Berry.** Seeds contain growth hormones essential to fruit set and development to maturity (Nitsch 1952). These hormones are mainly found in the albumen (Nitsch 1952), the tissue that is responsible for a large part of the variation in volume of the mature seed (Bell 1957, Anisimova and Shamrov 2000). Our observations demonstrate large seeds to be the only seed category which positively influence fruit weight and therefore the primary growth hormonal source. Large- and medium-sized seeds seem to have a similar influence on berry maturity. It is important to mention that comparisons of the seed content between green and ripe blueberries are difficult. When our observations were made, the development of the embryo, and likely the seed as well (Anisimova and Shamrov 2000), had ended ≈15 d earlier (Young 1951). Nevertheless, it seemed that the large seeds were darker (at least their seed coat) and more compact and thus smaller in ripe blueberries. It is natural for a seed, nearing its maturation, to eliminate a certain amount of water to improve its potential to survive over time. It is possibly at this moment that berry seeds changed color, from beige to orange-brown. This reduction may have resulted in an overestimation of the larger seeds in green blueberries, leading to a weaker correlation between fruit maturity and large seeds.

**Conclusions.** Under these experimental conditions, lowbush blueberry benefits from cross-pollination by *B. impatiens.* The addition of this pollinator to native insects increased lowbush blueberry fruit set and large seed set. Large seeds were the only category that had a positive influence on fruit weight, whereas maturity was associated with equal strength to large- and medium-sized seeds. It is plausible that the relationship between *B. impatiens* pollination and seeds of larger size indicates a variation in genetic compatibility between clones as expressed by seeds of varying sizes.

The commercial *B. impatiens* acted as a near-nest forager and was an effective pollinator up to 100 m from the hives. Based on these results, a deployment of the hives throughout the fields and a density of 688 *B. impatiens* per hectare are recommended to the blueberry grower for optimal pollination effectiveness.

## Acknowledgments

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