Research Article

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Insect pollinators of haskap (Lonicera caerulea L.: Caprifoliaceae) in subarctic Canada

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Abstract: Recently, the Yukon has seen a large growth in agricultural activity. Crops of commercial interest for local consumption and the export market include domestic berries, especially haskap (Lonicera caerulea L.). However, information on the pollination of these crops in our northern climate is lacking. To begin addressing this knowledge gap, we characterized foraging habits of on-farm bees in southwest Yukon by: 1) identifying pollen collected by bees occupying solitary bee houses; and 2) identifying and counting insect visitors to haskap flowers. Results show that cavity-nesting bees collect a wide variety of pollen including pollen from haskap, and that bumble bees (Bombus spp.) were much more common on haskap flowers than domestic honey bees (Apis mellifera L.), other bee species, syrphid flies, and butterflies. The number of bumble bees per haskap flower was also higher than reported elsewhere in Canada. The ability of bumble bees to be active in cool temperatures and the proximity of the study farms to natural ecosystems likely explain the prevalence of bumble bees in this study. In Yukon, it is still possible to support insect pollinators by maintaining natural areas among agricultural lands. Such undeveloped lands are, at present, typical of agricultural landscapes in subarctic Canada.

Keywords: Bumble bee; Honey bee; Pollination; Solitary bee; Berry

1 Introduction

Since the mid-1980s, interest in commercial agriculture in subarctic Canada has steadily grown. As of 2017, there were over 15,500 ha of land disposed for agricultural use in Yukon, of which 70% was within 60 km of the largest urban centre, Whitehorse (Government of Yukon 2018). The land disposition process remains active in Yukon, facilitating the conversion of public lands to privately owned agricultural lands. On a landscape scale, agricultural development in Yukon is relatively young, intertwined with tracts of original forest, riparian habitat, and grasslands. Elsewhere, conversion of natural areas to agricultural and urban use has been associated with fewer insect pollinators (Harrison et al. 2017; Vanbergen 2013). In Yukon, native flora and fauna are still commonly found adjacent to and within cultivated fields. This is potentially advantageous for crops benefitting from insect pollinators.

According to Statistics Canada (2017), the allocation of land north of 60°N for fruits and berries doubled from 2011 to 2016. In Yukon, the most prominent berry crop of commercial interest is haskap (Lonicera caerulea L.: Caprifoliaceae). It is a relatively new food crop for North America, although it is well known for its health-related benefits in Russia and Japan, where it is also grown (Celli et al. 2014). With the development of varieties that produce larger and better-tasting berries, combined with its cold hardiness and relative lack of associated pests (Bors et al. 2012), haskap appears to be a good choice for commercial production.

Despite the relative ease with which haskap grows, there are extrinsic factors that affect yields. One of these is its dependence on insects for pollination. Haskap is self-incompatible, requiring cross-pollination of two compatible varieties to set fruit (Bors et al. 2012). The blooming period, typically from mid-May to early June, determines which insect species are available for pollination. Frier et al. (2016a) noted that haskap has early stigma receptivity, high nectar production, high floral longevity and long anthesis, and surmised that haskap employs...
a generalist pollination strategy to maximize use of the limited number of pollinators available in spring.

Two studies have looked at insect pollinators on haskap at locations in Canada. One was undertaken near Birch Hills, Saskatchewan (52.97° N, 105.42° W) by Frier et al. (2016b) and the other was undertaken near Blockhouse, Nova Scotia (44.45° N, 64.42° W) by Olmstead (2019). Both studies found that, overall, domestic honey bees (Apis mellifera L.: Apidae) were in higher numbers on haskap flowers than other bees. Of the native bees, bumble bees (Bombus spp. Latreille: Apidae) were the most common on haskap flowers.

In this study, we document insect pollinators frequenting haskap flowers in a relatively young agricultural landscape situated in a subarctic environment to: 1) document and compare the activity of native and non-native (managed) pollinators; 2) compare the abundance of native pollinators on haskap in Yukon to published data collected from more southerly locations (Frier et al. 2016b; Olmstead 2019); and 3) discuss implications of the findings for local crop pollination.

2 Methods

The study took place at five different farms within 100 km of Whitehorse, Yukon (60.721° N, 135.057° W). No pesticides were used at any of the study sites. Table 1 lists coordinates, size and other characteristics of each study site. Farm A allocated 4 ha for haskap production within a 7.3 ha parcel of land. The plantation was bordered by mixed white spruce (Picea glauca (Moench): Pinaceae)–aspen (Populus tremuloides Michx.: Salicaceae) forest to the east, white spruce–aspen–willow (Salix spp. L.: Salicaceae) to the west, cultivated land to the north, and pasture to the south. On Farm B, haskap formed a small portion of the berry crops. The area also had hedgerows of willows, lodgepole pine (Pinus contorta Doug.: Pinaceae) and caragana (Caragana arborescens Lam.: Fabaceae). There were fallow fields to the north and west. Mixed riparian forest existed beyond the fields and to the southeast. Farm C had 8.1 ha of their 16.2 ha area planted in haskap. Except for a few black currants (Ribes nigrum L.: Grossulariaceae), crops were not harvested from the remaining land. The land had previously been used as pasture, and fallow fields still existed to the north and east of the plantation. Lodgepole pine-dominated forest occurred to the south and west. Farm D was the only unfenced plantation. It was bordered by mixed white spruce–aspen riparian forest to the south and east, mixed forest to the north, and a cultivated field of grain to the west. Farm E had a remnant copse of aspen–spruce forest within the plantation. Land to the north and west was open shrub willow, with extensive wetlands beyond to the west. Mixed white spruce–aspen forest abuts the plantation to the south, and a strip of dense willow shrubs separates the field from the roadside to the east.

In 2017, three of the five farms had honey bee hives. Farm A introduced eleven honey bee hives in early spring of 2017, placing them temporarily at the east and west end of the haskap plantation for the growing season. Farm C also introduced 15 honey bee hives in 2017, placing them temporarily near the centre of their haskap plantation from early spring through summer. Farm D had eight established honey bee hives in an enclosure 360 m from the berry plantation. These hives remained at the farm throughout the year.

To determine whether solitary cavity-nesting bees collect pollen from haskap, we installed eight bee blocks (“trap-nests”) on each farm. Installation of bee blocks took place between 22 April and 20 May 2016. These were

| Farm | Coordinates (decimal degrees) | Elevation (m) | Size of plantation (ha) | Haskap planted (year) | Other domestic berry crops |
|------|------------------------------|--------------|------------------------|----------------------|--------------------------|
| A    | 60.861° -135.552°            | 655          | 7.3                    | 2014                 | none                     |
| B    | 60.847° -135.339°            | 650          | 2.7                    | 2012                 | raspberries (Rubus idaeus L.), black currants (Ribes nigrum L.), red currants (Ribes rubrum L.), domestic strawberries (Fragaria L.) and saskatoons (Amelanchier alnifolia (Nutt.)) |
| C    | 60.842° -135.312°            | 640          | 16.2                   | 2014                 | black currants           |
| D    | 60.945° -135.096°            | 640          | 0.8                    | 2010                 | black currants           |
| E    | 61.154° -135.369°            | 775          | 1.0                    | 2012                 | raspberries, black currants, saskatoons |

Table 1: Characteristics of each study site. “Size of plantation” refers to entire plantation area; haskap made up only a portion of this area in each farm (see Methods), with the remainder not planted or devoted to other crops.
cut from untreated white spruce sourced from a local mill. Bee blocks were mounted on posts or trees within 1 m of ground level, and wherever possible, oriented with hole entrances facing south. They were spaced anywhere from 12 to 103 m apart, depending on configuration of plantation and availability of existing posts or trees for mounting. Each bee block had 60 holes, 20 holes each of diameters 6.4 mm, 7.9 mm, and 9.5 mm. Having different diameters was intended to accommodate different sizes of cavity nesters. Each hole was 15 cm deep and spaced 1.9 cm from adjacent holes. Prior to installation, we lined 30 of the 60 holes in each block with removable paper nesting straws. We designed the bee block and gave Yukonstruct of Whitehorse permission to post the building plans (Yukonstruct 2019).

The straws were removed in September, housed in an unheated garage in Whitehorse until late October, and then brought to a laboratory for dissection and identification of the contents. Bee cocoons from these nests were housed in an incubator until emergence or death of adults, 1–2 years later. For overwintering, cocoons were kept at temperatures between 2 and 5°C until early December (2016) or November (2017), after which temperatures were gradually raised to a 20°C/10°C daily cycle for emergence. Emerging specimens were killed by being placed in a freezer, and these along with any adult bees that failed to emerge from cocoons were pinned and identified to genus or species when possible using Michener et al. (1994), Sheffield et al. (2011), and Dumesh & Sheffield (2014). Specimens are stored in the Forrest lab’s collection at the University of Ottawa. Any inhabitants of the remaining 30 unlined holes of each bee block were left in situ to perpetuate local populations.

Pollen used by each bee occupant was identified by taking a minimum of one pollen sample from each bee nest (straw). When possible, we sampled any unconsumed pollen remaining in the nest at the time of sampling. These pollen samples were slide-mounted with basic fuchsine gel (Kearns & Inouye 1993). When no pollen remained in the straw, we sampled frass (bee fecal pellets) instead. Bees digest only the internal contents of pollen grains, so the outer walls, which retain the important identifying features, can be used for identification (Scott 1996). Frass was placed in a drop of water on a microscope slide to soften for a few minutes and the pellets were teased apart using a metal probe or forceps. The slide was placed on a heating plate to evaporate the remaining water. Then a cube of fuchsin gel was placed on the evaporated sample and a cover slip was placed on top of the fuchsin gel. The heat melted the fuschin gel and thereby stained the pollen walls in the sample. The pollen and frass samples were then compared to a comprehensive local reference collection for identification. Each sample contained several hundred pollen grains, which were scanned at 100–400 x magnification under a light microscope by at least two observers, who assessed whether each identified pollen type was a “major” (>25% by volume) or “minor” (<25% but >5%; i.e., likely not simply a contaminant) constituent of the sample. Although some pollen types could not be confidently distinguished from one another, haskap pollen is distinctive and could not be confused with any other locally occurring pollen.

To determine which pollinators were most active on the haskap, we surveyed pollinators on haskap at each farm by scanning all flowers for insects while walking slowly along transects. The rate of walking was slower when the density of flowers was higher. Average rate was 16 m per minute. The method is adapted from Ward et al. (2014), Pollard et al. (1977) and Vaissière et al. (2011). Between 29 May and 7 June, the numbers of bumble bees (Bombus spp.), honey bees (Apis mellifera), other bee species (families Megachilidae, Halictidae, Colletidae, Andrenidae), syrphid flies (family Syrphidae) and butterflies (superfamily Papilionoidea) were counted on haskap flowers. No other insect taxa were recorded on the flowers. We counted the flower visitors along all rows at Farms B and E. For the other farms with larger haskap plantations, we counted a subset of four rows. All surveys were conducted on two separate dates 6–9 days apart, with the intent of having surveys overlap with timing of peak flowering. Data were collected on the distance and number of bushes surveyed. The number of flowers on 2–5 randomly selected bushes was also counted at each site. These data were used to approximate the number of flowers per metre, assuming that the number of flowers per bush was fairly uniform within each farm; within each farm the bushes were the same age and grown under the same conditions (e.g., soil, irrigation, fertilizer). The number of flower visitors per metre was divided by the number of flowers per metre to give estimates of visitation rate (flower visitors per metre) and, as in Vaissière et al. (2011), no time duration is incorporated into the calculation. Insect counts were conducted between 1100 h and 1700 h at ambient temperatures between 15°C and 18°C, wind velocity below 40 km/h, and in the absence of precipitation.

To compare abundances of the five visitor taxa, while accounting for the repeated surveys at each farm, we modeled the number of visitors observed as a function of taxon (bumble bees, honey bees, other bees, syrphid flies, or butterflies) and farm (coded as a fixed factor due to the limited number of farms). Individual surveys were
the replicates. We used a negative binomial model, fitted using the function glm.nb in the R v. 3.4.2 (R Core Team 2017) package MASS (Venables & Ripley 2002), because of the overdispersed nature of the count data. Significance of the “taxon” term was tested using a likelihood-ratio test. Pairwise comparisons of the abundances of different taxa were computed using the emmeans function of the emmeans R package (Lenth 2019), which employs the Tukey method to correct for multiple testing. To assess the variation among farms in number of insect visitors per metre, which usually covaries with flower density, we plotted the number of insects per metre vs. the number of flowers per metre.

To produce data comparable to Frier et al. (2016b), the number of bumble bees per 400 flowers was estimated by dividing the average number of bumble bees per metre by average number of flowers per metre and multiplying this by 400. The comparison gives insight on whether the frequency of bumble bees on haskap is similar across different latitudes and different agricultural settings.

3 Results

Four genera of cavity-nesting bees were identified (Table 2): mason bees (one species each of Osmia Panzer: Megachilidae and Hoplitis Klug: Megachilidae), leafcutter bees (two species of Megachile Latreille: Megachilidae) and masked bees (a single species of Hylaeus, likely H. annulus (L.): Colletidae). Pollen from haskap was only found in nests of Osmia mason bees. Table 2 summarizes the pollen composition of each nest. In addition to haskap, mason bees gathered pollen from legumes (Fabaceae) and mustards (Brassicaceae), and to a lesser degree, fireweed (Chamerion angustifolium (L.): Onagraceae) and composites (Asteraceae). We suspect that species from the rose family (Rosaceae) contributed substantially to the pollen contents of mason bee nests, but identification of these pollen grains was inconclusive. The leafcutter bees collected pollen primarily from composites and fireweed. The pollen in the sole masked bee nest was primarily composed of mustards, with composites forming a smaller component.

Characteristics of the surveyed transects at each farm appear in Table 3. The distance surveyed varied depending on the farm, ranging from 98 m at Farm B to 1640 m at Farm C. The number of bushes encountered along the rows varied widely, from 83 bushes at Farm B to 1700 bushes at Farm A. The number of blooming flowers on bushes was much higher at Farm D than all other farms.

Flower-visitor taxa varied markedly in their relative abundance on haskap flowers (χ² = 59.8, df = 4, p < 0.0001; Figure 1). Specifically, bumble bees were much more common than any other insect group on haskap flowers (p < 0.0001 in all four pairwise comparisons), making up an average of 73.4% (s.d. = 19.9%, n = 10 surveys) of all visits. All bumble bees observed on haskap flowers were queens. Syrphid flies (ψ = 3.1 ± 13.0%) were the only other taxon observed on haskap flowers at all five farms; this taxon was significantly more abundant than butterflies (p < 0.0001) and “other bees” (p = 0.03), but not significantly different in abundance from honey bees (p = 0.97). Honey bees (ψ = 7.5 ± 10.3%) and other bees (ψ = 5.4 ± 10.5%) were similar in overall abundance (p = 0.15) and were observed at three and four farms respectively. Butterflies (ψ = 0.6 ± 1.4%) were by far the least common visitor taxon (all pairwise comparisons p < 0.03), observed on haskap flowers on only two farms.

When limiting the descriptive statistics to the three sites (Farms A, C, and D) with honey bee hives, bumble bees (ψ = 73.2 ± 24.9%) were still the most abundant flower visitors. These were followed by honey bees (ψ = 12.5 ± 10.8%), then other bees (ψ = 3.1 ± 6.6%), syrphid flies (ψ = 10.9 ± 10.5%) and butterflies (ψ = 0.3 ± 0.6%).

Overall, the most common pollinators on haskaps were bumble bees, ranging from 96% of insects on haskap flowers at Farm A on 6 June to 32% of insects on haskap flowers at Farm D on 5 June (Figure 1). The greatest change in percent bumble bees also occurred at Farm D, where bumble bees dropped from 60% to 32% of insect pollinators between surveys. During the second survey, peak flowering had passed, as evidenced by many dropped flower corollas. At this time, many bumble bees were feeding on wild strawberry flowers (Fragaria virginiana Duchesne: Rosaceae) at the base of the haskap plants. The least common insect pollinators were butterflies, represented by Canada tiger swallowtails (Papilio canadensis Rothschild and Jordan: Papilionidae) at Farms D and E. Honey bees were only detected during counts at farms where hives were present, though they were observed at Farm B (without hives) on other occasions.

The number of flower visitors increased with the number of flowers (Figure 2). This is based on the counts of insects conducted on the same day the numbers of flowers were tallied. These limited data suggest that study sites did not differ greatly in the number of insect visitors per flower. Farm E, which did not have honey bees, appears to have at least as many visitors per flower as farms with honey bees (Figure 2).

The overall abundance of insect pollinators ranged from 0.013 insects per metre for Farm A on 1 June to 0.28
insects per metre for Farm D on 29 May (Figure 3). The estimated number of insects per 1000 flowers ranged from 0.072 for Farm A on 1 June to 0.55 for Farm B on 31 May (Table 3). The number of bumble bees ranged from 0.02 per 400 flowers for Farm A to 0.13 bumble bees per 400 flowers for Farm B. These last values are given as “per 400 flowers” to ease comparison with Frier et al.’s (2016b) study.

4 Discussion

This study indicates that native insects have a prominent role in pollinating domestic berry plants in subarctic boreal Canada. Although our study in Yukon counted floral visitors, and not all floral visitors are necessarily pollinators, Frier et al. (2016b) and Olmstead (2019)
demonstrated that honey bees, bumble bees and mason bees pollinate haskap when they visit the flowers. The contribution to pollination on haskap in Yukon is inconsistent among solitary cavity-nesting bees, with Osmia at only one of the four farms at which they occurred showing an affinity for haskap. However, bumble bees consistently outnumbered all other groups of flower visitors, including honey bees. This contrasts with results from Saskatchewan (Frier et al. 2016b) and from Nova Scotia (Olmstead 2019) and cannot be explained by the stocking density of honey bees. The Yukon sites with honey bees had a higher stocking density of hives (>1.8 hives per ha) than the Nova Scotia and Saskatchewan sites (0.4–0.8 hives per ha). In Saskatchewan, honey bees outnumbered bumble bees on haskap flowers except in early morning (0600 h to 0700 h) and late evening (1900 h to 2000 h). During the warmest part of the day (1000 h to 1600 h), honey bees outnumbered bumble bees by about four to one (Frier et al. 2016b). In Nova Scotia, counts of floral visitors along transects indicated that honey bees and bumble bees were encountered at similar rates in one year, but honey bees outnumbered bumblebees by about three to one the following year. The Saskatchewan study showed that, per individual, bumble bees are more efficient at pollinating haskap than are honey bees. Nevertheless, the collective contribution to pollination by honey bees can be higher than that of bumble bees when hives are introduced (Frier et al. 2016b) and honey bees outnumber bumble bees on flowers. In this Yukon study, bumble bees outnumbered
honey bees at flowers in all five studied haskap plantations.

Study sites in Yukon were > 850 km further north than the Saskatchewan site and >1700 km further north than the Nova Scotia sites. According to data gathered from 1982 to 2012, temperatures were much cooler at the Yukon study area (May: $x = 6.8^\circ C$; June: $x = 11.7^\circ C$) than the Saskatchewan study site (May: $x = 10.7^\circ C$; June: $x = 15.3^\circ C$; Climate-Data.org 2019) and the Nova Scotia sites. Olmstead (2019) reported an average of $11.3^\circ C$ during the month of May in the years he counted bees on haskap flowers in Nova Scotia. The ability of bumble bees to remain active in cooler temperatures has been well documented (Lundberg 1980; Heinrich 2004) and is one explanation for the greater relative abundance of bumble bees on haskap flowers in Yukon.

A second possible explanation for the greater relative abundance of bumble bees on haskap flowers in Yukon is that there were more bumble bees available in Yukon for the equivalent number of haskap flowers at the other study sites. The estimated number of bumble bees per 400 flowers in Yukon ranged from 0.02 to 0.13 and was far greater than the number recorded in the Saskatchewan study, where the average number of bumble bees per 400 flowers (also recorded by scan sampling) was less than 0.003 (Frier et al. 2016b). (Data on the number of bees per flower were not available from the Nova Scotia sites for comparison.) Bumble bees do appear to be more abundant in the Yukon’s agricultural landscape, where there is high retention of natural habitat. The haskap plantations in the Yukon study were 0.8 to 16.2 ha in size and situated in a landscape where undeveloped land dominates. By contrast, the Saskatchewan study took place on a 30 ha orchard in a heavily altered landscape dominated by quarter sections of canola, alfalfa and wheat (Frier et al. 2016b). The location of the haskap plantations in the Yukon study had features that are known to be beneficial to bees. The smallest plantations in our dataset did have the greatest numbers of insects per metre; however, because these also had the highest flower density, it is unclear what effect plantation size actually had on abundance of flower visitors. Higher abundance of native pollinators is associated with landscapes in close proximity to natural ecosystems (Morandin and Winston 2006), with riparian strips (Cole et al. 2015), and a smaller proportion of agricultural area (Bartomeus et al. 2014; Connelly et al. 2015). Smaller plantations are also associated with a higher proportion of wild pollinators (Isaacs and Kirk 2010). Because foraging distances for bumble bees are typically less than 110 m (Elliot 2009; Geib et al. 2015; Woodcock 2012), plants in smaller fields are more likely than those in larger fields to be visited by bumble bees whose nests are located outside of the farm fields.

During the flowering period of haskap, the number of insect pollinators available may limit fruit production. At this time, bumble bee queens are collecting pollen and nectar to establish colonies and bumble bee populations are at their lowest levels. Soon after, bumble bee populations grow as worker bees are produced and emerge from each colony (Williams et al. 2014). Complex landscapes where forage resources are available throughout the growing season (Persson and Smith 2013) would support bumble bee colonies in producing a sufficient number of queens to overwinter and pollinate haskap flowers the following spring. If Yukon is able to maintain natural areas in amongst and within agricultural land, this will be advantageous to crops that benefit from insect pollination and potentially beneficial to the conservation of insect pollinators. During this study, one species of conservation concern, Bombus occidentalis mckayi Ashmead: Apidae (COSEWIC 2014), was among the bumble bees feeding on haskap flowers.

We recommend further study on the abundance and diversity of bumble bees and other flower visitors on berry crops situated in different climates and landscapes with varying levels of agricultural alteration to better understand the role of native insects in the pollination of domestic crops, and the habitats that support them. Future studies could also explore the role of haskap in supporting bumble bees early in the growing season in areas where food may be limiting, such as cultivated lands. Providing nesting habitat for wild, solitary bees near haskap crops may help support local populations of insects such as mason bees, which may also occasionally visit haskap flowers. However, our data suggest that such interventions are unlikely to contribute measurably to haskap pollination, provided bumble bee populations remain healthy.

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