Environmental Entomology, 50(4), 2021, 968–981
doi: 10.1093/ee/nvab045
Advance Access Publication Date: 17 May 2021
Research

Pollinator Ecology and Management

Hoary Squash Bees (*Eucera pruinosa*: Hymenoptera: Apidae) Provide Abundant and Reliable Pollination Services to *Cucurbita* Crops in Ontario (Canada)

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Subject Editor: Gloria DeGrandi-Hoffman

Received 17 February 2021; Editorial decision 14 April 2021

Abstract

The increasing demand for insect-pollinated crops highlights the need for crop pollination paradigms that include all available pollinators. In North America, *Cucurbita* crops (pumpkin, squash) depend on both wild (solitary and *Bombus* spp.: Hymenoptera: Apidae) and managed honey bees (*Apis mellifera* L. 1758: Hymenoptera: Apidae) for pollination. Temporal and spatial differences in abundance may determine which bee taxa are the most important pollinators of *Cucurbita* crops. We surveyed bees visiting *Cucurbita* crop flowers on 19 farms over four years (2015–2018) during the crop flowering period (July 1–August 30 from 06:00–12:00). All the farms surveyed had hoary squash bees (*Eucera pruinosa* (Say, 1867), and most also had some combination of honey bees, bumble bees (*Bombus* spp.), or other wild bees present on their *Cucurbita* crop flowers. All four bee taxa were present on about two-thirds of farms. Spatially and temporally, wild bees were more abundant on *Cucurbita* crop flowers than managed honey bees. Hoary squash bees were the most abundant wild bees, maintaining their abundance relative to other wild bee taxa year-over-year. Male hoary squash bees were both more frequently and consistently seen visiting crop flowers than females in all years. Peak activity of hoary squash bees and bumble bees coincided with the daily crop pollination window, whereas peak activity of honey bees and other wild bees occurred after that window. In addition to elucidating the ecological interactions among wild and managed pollinators on *Cucurbita* crops, our work provides a novel practical way to evaluate pollinator abundance using a crop-centered benchmark framework.

Key words: crop pollination window, wild bees, pollinator benchmarks, *Cucurbita* crop pollination services

People depend upon a wide variety of crops for their food, fuel, fiber, medicines, and cultural expression (IPBES 2016). Around 76% of these crops require or benefit from, the pollination services of pollinators, including bees and other insects (Klein *et al.* 2007, Rader *et al.* 2016). Although there are over 20,555 bee species known worldwide, most of which are unmanaged, wild species (Orr *et al.* 2021), only 2% of these species account for almost 80% of all visits by wild bees to agricultural crops across years, crops, and locations within biogeographical regions (Kleijn *et al.* 2015). Where wild bees are present on farms, their pollination services provide no-cost alternatives to renting or purchasing managed bees and may compensate for the loss of honey bee pollination services (Winfree *et al.* 2007).

At a time when demand for insect-pollinated crops is increasing greatly, the supply of managed bees is not keeping pace with demand (Aizen *et al.* 2008, Aizen and Harder 2009, Aizen *et al.* 2019). Furthermore, declines in both pollinator abundance and richness are well documented with a parallel risk of decline in pollination services to both wild and crop plants (Biesmeijer *et al.* 2006, Burkle *et al.* 2013, Kerr *et al.* 2015, IPBES 2016, Zattara and Aizen 2021).

Diverse bee communities can provide complementarity and improve pollination of crops because of differences in dietary specialization, activity periods, flower handling behavior, movement within the crops, and annual population fluctuations (Garibaldi *et al.* 2013, Isaacs *et al.* 2017). Increased bee species richness, including both wild and managed species, improves the resilience of crop pollination services by protecting against year-over-year population changes in any single species caused by weather events, disease infestation, or availability of managed pollinators (Kevan *et al.* 1990, Kremen *et al.*

2002, Winfree *et al.* 2007, Garibaldi *et al.* 2013, Vanbergen and Initiative 2013, Mallinger and Gratton 2015, IPBES 2016) and can provide additive or even synergistic improvements in yield (Hoehn *et al.* 2008, Brittain *et al.* 2013a; Garibaldi *et al.* 2013).

To preserve biodiversity among crop pollinators and maintain crop pollination services, close attention should be paid to the well-being of wild species within agricultural contexts, where they may be under the greatest threat from loss of habitat and exposure to pesticides (Kremen *et al.* 2002, Rundlöf *et al.* 2008, IPBES 2016, Willis Chan *et al.* 2019, Pindar *et al.* 2020). As such, we urgently need strong ecological data that documents the role of specific bee taxa in the pollination of specific crops, including how those roles may vary spatially and temporally and how individual taxa within the community of bees visiting a crop may impact each other.

As a case in point, *Cucurbita* crops (Cucurbitaceae, pumpkin, and squash) are of great cultural, nutritional, and economic importance in human food systems (Dornan 2009, FAOSTAT 2013, Boyd *et al.* 2014, Mailvaganan 2018). These crops have separate staminate (male) and pistillate (female) flowers that bloom for a single morning (Nepi and Pacini 1993), making them entirely dependent on insects, primarily bees, for pollination (Hurd *et al.* 1971, Graças Vidal *et al.* 2010). To attract insects, *Cucurbita pepo* flowers produce copious quantities of sucrose-dominant, amino acid-rich nectar that becomes available at flower opening (Ashworth and Galetto 2001, Nepi *et al.* 2001, Chatt *et al.* 2018). Staminate *C. pepo* flowers also produce many (~16,000–49,000 grains) large (136 µm diameter), spiny, and oily pollen grains (Willis 1991, Lau and Stephenson 1993, Graças Vidal *et al.* 2010, Willis Chan 2020).

To produce fruit, bees must visit *Cucurbita* flowers not only during the flowering period but also within the more limited seasonal and daily pollination windows. The seasonal pollination window for *Cucurbita* crops begins about ten days into the flowering period when both staminate and pistillate flowers are present on the vines and is limited by the amount of time needed by plants postpollination to mature fruit (Fig. 1; Stapleton *et al.* 2000, Westerfield 2014). The timing of flower opening (dawn) and the availability of viable pollen on staminate flowers define the daily pollination window, which may close long before blooms wilt (Tepedino 1981, Willis 1991, Cane *et al.* 2011, Phillips and Gardiner 2015, Willis Chan 2020).

In North America, important pollinators of *Cucurbita* crops include the western honey bee (*Apis mellifera* Linnaeus,1758), bumble bees (*Bombus* spp.), and the hoary squash bee (*Eucera pruinosa* (Say, 1867)) (Hurd *et al.* 1971, Shuler *et al.* 2005, Julier and Roulston 2009, Phillips and Gardiner 2015, McGrady *et al.* 2019). However, a wide variety of insects, including beetles, stingless bees, other solitary bees, moths, and ants, also visit the flowers of both wild and cultivated *Cucurbita* across the range where they are grown (Meléndez-Ramirez *et al.* 2002, Krug *et al.* 2010, Sinu *et al.* 2017, Delgado-Carrillo *et al.* 2018).

Both honey bees and bumble bees are generalist corbiculate bee taxa that visit *Cucurbita* flowers primarily for nectar (Percival 1947, Artz and Nault 2011, Brochu *et al.* 2020). They also tend to avoid or discard passively accumulated *Cucurbita* pollen, likely because they have difficulty packing it into their corbiculae due to the spininess, oiliness, and large size of the pollen grains (Percival 1947, Michelbacher *et al.* 1964, Parker 1981, Tepedino 1981, Lunau *et al.* 2015, Brochu *et al.* 2020).

Managed honey bees can provide adequate pollination services to *Cucurbita* crops (Phillips and Gardiner 2015, McGrady *et al.* 2019, but see Petersen *et al.* 2013), but those services may become increasingly costly because global crop pollination demands already outstrip honey bee supply (Aizen and Harder 2009).

Bumble bees are excellent *Cucurbita* crop pollinators, depositing more pollen grains per stigma and contacting the stigma more often than hoary squash bees or honey bees in a single flower visit (Artz and Nault 2011). Although several bumble bee species are in decline, the range and relative abundance of the common eastern bumble bee (*Bombus impatiens* Cresson, 1863: Hymenoptera: Apidae), the species most commonly found on *Cucurbita* crops in eastern North America, is increasing (Cameron *et al.* 2011, Colla *et al.* 2012). *Bombus impatiens* is also commercially reared as a managed pollinator for crop pollination in North America, although it is used mostly in greenhouse crops in Ontario (Woodcock 2012).

Unlike honey bees or bumble bees, hoary squash bees are strict specialists on *Cucurbita* spp., depending on plants in this genus for pollen to feed their larvae (Hurd and Linsley 1964). As *Cucurbita* pollen specialists, hoary squash bees are also efficient pollinators of these crops (Tepedino 1981, Willis 1991, Cane *et al.* 2011, Phillips and Gardiner 2015), and female hoary squash bees have evolved structural modifications such as smooth, stout, unbranched scopal hairs that support and adhere to the large, spiny, and oily *Cucurbita* pollen (Roberts and Vallespir 1978).

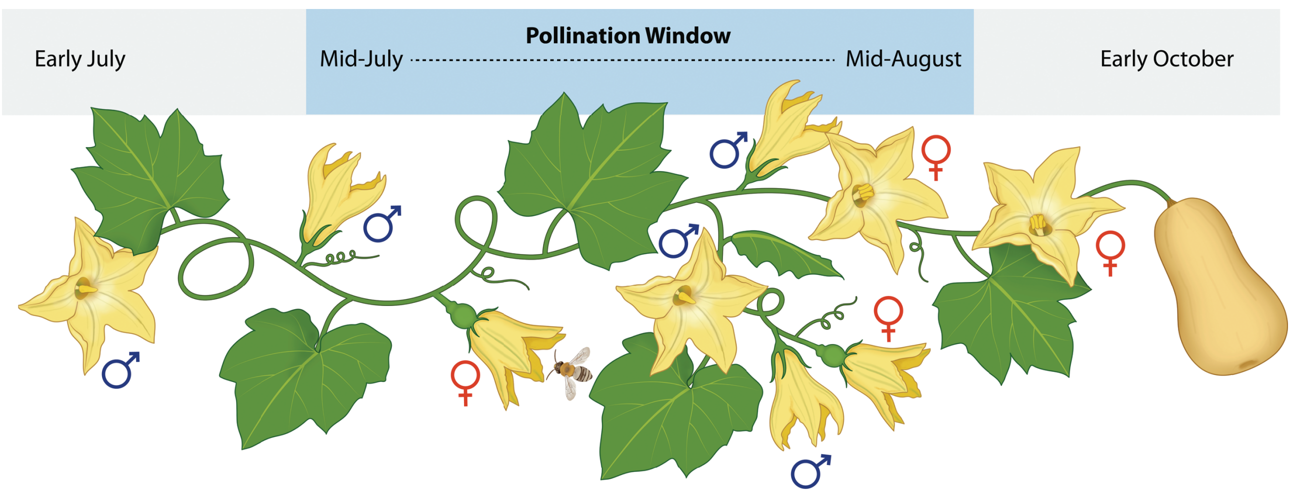

Fig. 1. The flowering season of *Cucurbita* crops in Ontario showing the seasonal pollination window during which both staminate (male) and pistillate (female) flowers are present and there is enough time postpollination for the plant to produce a mature fruit.

Hoary squash bees are both common and widespread on *Cucurbita* crops in Ontario and elsewhere in the northeastern United States (Kevan 2000, Julier and Roulston 2009, Artz *et al.* 2011, Artz and Nault 2011, Petersen *et al.* 2013, Phillips and Gardiner 2015, McGrady *et al.* 2019, Appenfeller *et al.* 2020). Female hoary squash bees forage for pollen exclusively on *Cucurbita* crops in large parts of their range where no wild *Cucurbita* species are found (López-Uribe *et al.* 2016). Although they are a solitary species in which each female excavates its own nest, hoary squash bees often establish sizeable local populations by nesting in large aggregations within or close to crop fields (Mathewson 1968, Hurd *et al.* 1974, Kevan *et al.* 1988). Male hoary squash bees may be more important than females as pollinators of *Cucurbita* crops (Artz and Nault 2011, Cane *et al.* 2011).

Variation in the abundance and richness of bee species on a crop may be related to the attractiveness of the crop and the suitability of the surrounding landscape to provide nesting habitat and floral resources before and after crop bloom (Laverty & Plowright 1988, Kevan *et al.* 1990, Kremen *et al.* 2002, Sheffield *et al.* 2008, Kennedy *et al.* 2013, Vanbergen and Initiative 2013). Farm management practices, including supplementation with managed honey bees, pesticide use, tillage, field size, and irrigation practices, may also affect the abundance of wild bee species on *Cucurbita* flowers (Shuler *et al.* 2005, Julier and Roulston 2009, Artz *et al.* 2011, Ullmann *et al.* 2016, Skidmore *et al.* 2019, Willis Chan *et al.* 2019, Willis Chan and Raine 2021).

Species-specific phenology may determine the seasonal activity patterns of different bee species on crop flowers (Willis and Kevan 1995, Minahan and Brunet 2018). Such seasonal activity cycles may also be driven by intrinsic behavior resulting in bees that are active at different times during the season (Cane and Payne 1993, Packer *et al.* 2007). For example, many generalist bee taxa, such as bumble bees and honey bees, are active throughout the temperate growing season (April–October) while more specialized oligolectic bees are restricted in their seasonal activity to the flowering period of their pollen host (Linsley 1958, Thorp 1979). Seasonally, hoary squash bee activity corresponds well with the flowering period of *Cucurbita* crops in Ontario (Willis and Kevan 1995).

Daily activity cycles of individual bee taxa on a crop are likely to be affected by microclimatic conditions and how these interact with interspecific differences in bee physiology and behavior (Willmer and Stone 2004). For example, the diurnal foraging activity patterns of hoary squash bees are closely synchronized with the opening and closing of *Cucurbita* flowers (Mathewson 1968, Hurd *et al.* 1974, Willis & Kevan 1995).

Honey bees, bumble bees, hoary squash bees, and other wild bee species form the community of bees that could visit and potentially pollinate the flowers of *Cucurbita* crops. When all these taxa are present on a farm their efficacy as *Cucurbita* crop pollinators will likely depend on their abundance during the seasonal and daily crop pollination windows (Willis Chan 2020).

In Ontario, *Cucurbita* producers are guided by government pollination recommendations, and crop insurance claims are contingent upon them being followed. Current recommendations include a required honey bee stocking rate (1 managed hive/0.4–1.2 ha for fields larger than 0.8 ha), but provide no guidelines regarding the pollination services provided by wild bees. To ground-truth these recommendations, we studied the pollinator communities visiting *Cucurbita* crops in Ontario and compared them to communities visiting these crops elsewhere in eastern North America.

Our objectives in this study are to 1) characterize the daily and seasonal *Cucurbita* crop pollination window for Ontario; 2) evaluate spatial and temporal variation in abundance of bee taxa visiting *Cucurbita* crops flowers in Ontario and determine if inter-taxa interactions occur; 3) develop abundance benchmarks for growers that reflect the pollination windows; and 4) compare the relative abundance of bee taxa visiting *Cucurbita* crop flowers across jurisdictions in the northeastern United States and Canada. This work is important because it clarifies the relative importance of wild and managed bee taxa in the pollination of *Cucurbita* crops, describes the variability associated with pollination services in this crop both spatially and temporally, and provides specific evidence-based recommendations to update pollination guidelines for those crops in Ontario.

Materials and Methods

Characterizing the Crop Pollination Window

The seasonal pollination window was estimated to begin when pistillate (female) flowers began to be produced on the vines and to end at the point after which there was insufficient time for pollinated flowers to develop into mature fruit (Stapleton *et al.* 2000, Westerfield 2014, Fig. 1).

The daily pollination window was defined as beginning at dawn (*ca.* 06:00) when pollen becomes available on the synandria of staminate flowers as they open, and ending when both the synandria are depleted of pollen (Willis Chan 2020) and pollen deposition on the gynecia of pistillate flowers is complete (Tepedino 1981, Willis 1991, Phillips and Gardiner 2015). To measure pollen depletion, we collected synandria from 614 staminate *Cucurbita* crop flowers (*Cucurbita pepo*, pumpkins, no information about varieties) at hourly intervals from 06:00 (anthesis) to 12:00 (flower wilt) on 13 collection days over four seasons (2015–2018) (Supp Table 1 [online only]). The day before each collection, ten unopened flowers were taped to allow the synandria to dehisce while preventing access by bees. These flowers were designated 'predawn' samples and contained their maximum pollen load. The next day the corolla was cut away and the predawn synandria were removed from flowers with a razor blade, put into a 2 ml microcentrifuge tubes to which 0.5 ml 70% ethanol was added. At each hourly interval (06:00–12:00) thereafter, ten more synandria were collected in the same way. In the lab, the tubes were microcentrifuged (Eppendorf 5417C) at 2500 rpm for three minutes to dislodge pollen grains from the synandrium. Synandria were then removed and checked to ensure that all pollen had been dislodged. Then 1.5 ml of 50% glycerin was added to the remaining pollen-alcohol suspension to increase its viscosity (ensuring pollen grains remained in suspension longer). After thorough mixing with a Fisherbrand Mini Vortex Mixer, pollen counts were made by taking five 10-μL aliquots from each tube (i.e., five aliquots per synandrium) and counting all pollen grains in each aliquot under a microscope (25× magnification). The number of pollen grains per aliquot was averaged across the aliquots for each synandrium and the mean was related back to the full volume of the suspension (2 ml) to provide a pollen count per synandrium (synandrium count = mean aliquot count × 2 ml × 1000 μl/ml/10 μl). For each time interval within a day, the mean pollen count was calculated by averaging across all ten synandria collected. Data were averaged across all observation days to characterize daily patterns of pollen depletion (Supp Table 1 [online only]).

Bee Census

A census of bees visiting *Cucurbita* crop flowers was taken on 19 farms across Ontario during the flowering season (mid-July to end of August) over four seasons (2015–2018) to determine the abundance of the taxa observed (Supp Fig. 1 [online only]). All counts were made in pumpkin fields of 1.5 ha or more. Due to constraints of time and distance, and because permission was not always granted to work on farms from year-to-year, sampling was uneven across farms, years, and/or times (Supp Table 2 [online only]). Eleven farms (#6 9–13, 15–19) were sampled in a single year, two farms (#1, 14) were sampled in 2 yr, two farms (#2, 5) were sampled for 3 yr, and four farms (#3, 4, 7, 8) were sampled for 4 yr.

On each census day, bee counts were made along the edges of fields or along rows of pumpkins to avoid damaging the crop. At hourly time intervals (06:00 to 12:00), the observer walked along counting the number of bees seen in the first 25 flowers. This was repeated on three other nonoverlapping sets of 25 flowers further along the row or edge, resulting in four sets of 25 flower counts per hour on each observation day. Censuses were made during four two-week periods beginning 1 July to 31 August, for a total of 1581 counts of 25 flowers across all farms, dates, and times (Supp Table 2 [online only]).

Without capturing them, bees observed in flowers were visually categorized as honey bees, hoary squash bees, bumble bees, or other wild bees. We use the common name 'hoary squash bee' for *Eucera pruinosa* because there is no other recognized common name for the species and in translation the Latin '*pruinosa*' means frost-like. No further classification was undertaken for bumble bees or other wild bees. All bumble bees observed were assumed wild as the use of commercial managed *B. impatiens* outside of greenhouses is uncommon in Ontario (Woodcock 2012). No data were collected about the location of honey bee hives. Hoary squash bees were easily recognized as they are the only species of squash bee found in Ontario. The sex of hoary squash bees was determined by observing obvious morphological differences: females are larger and have distinctive

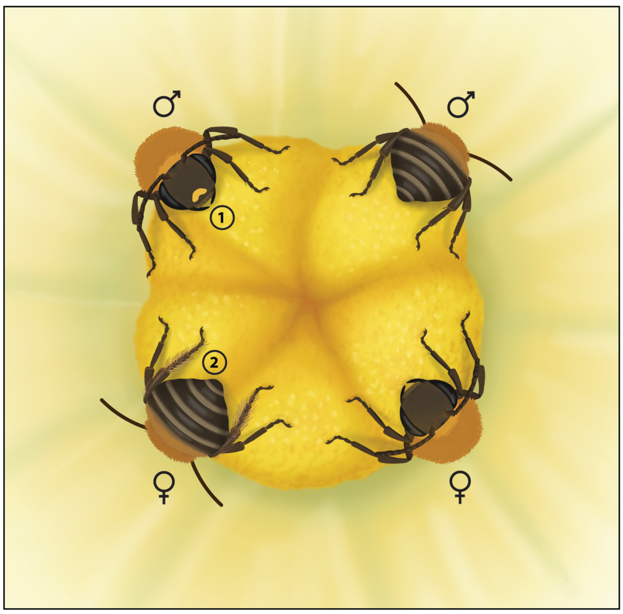

Fig. 2. Anterior and posterior views of male (above) and female (below) hoary squash bees (*Eucera pruinosa*) on the gynecium of a *Cucurbita* crop flower showing their clear identifying features. Male hoary squash bees have a whitish-yellow marking on their clypeus that is clearly visible in the anterior view (1). Females lack this facial marking but have hairy scopa on their hind legs which are visible in the posterior view (2) (males lack scopa). Illustration designed by D.S.W.C. from photographs and drawn by Ann Sanderson. Used with permission.

hairy scopae on their hind legs, and males have a white mark on the clypeus which is absent in females (Hurd and Linsley 1964) (Fig. 2).

Grower Benchmarks

To calculate bee abundance benchmarks for growers, we created a restricted data set that included only bee census observations made during the season (mid-July to mid-August) and daily (06:00–08:00) pollination windows (Supp Table 2 [online only]). Median and mean (±SE) counts were calculated to provide abundance benchmarks for each bee taxon (hoary squash bees, wild bumble bees, other wild bees, honey bees), for male and female hoary squash bees, and for total numbers of bees visiting *Cucurbita* crop flowers. The abundance benchmark for each taxon was then related to the total abundance of visiting bees and expressed as a percentage of the total population.

Statistical Analysis

All statistical analyses were carried out using a general linear mixed model approach in SAS University Edition (Version 3.8). To analyze how pollen counts on the synandria of staminate *Cucurbita* flowers changed over time, we used the model: pollen count = time, with no repeated measures or random variables. The data did not permit analysis of other effects.

To characterize how abundance of bee taxa (hoary squash bees, honey bees, wild bumble bees, and other wild bees) or hoary squash bee sexes visiting *Cucurbita* crop flowers changed over time, we used the full model: Abundance of bee taxon A = Year + Time + Year*Time + Abundance of bee taxon B + Abundance of bee taxon C + Abundance of bee taxon D, the random effect of Farm, repeated measure of Period (Table 1). Because the inclusion of the year*time interaction in the model caused least-squares means to be inestimable (likely due to uneven sampling), the year*time interaction was excluded from the model. Period was removed as a repeated measure for the abundance of bumble bees to achieve model convergence (Table 1).

Because sampling across farms, years, dates, and times was necessarily unbalanced (Supp Table 2 [online only]), variance components were estimated using the restricted maximum likelihood method (REML) to calculate least squares means and standard errors. Model effects and post hoc pairwise comparisons of differences between model effect levels used the Satterthwaite method for determining the degrees of freedom. All post hoc pairwise comparisons used Tukey–Kramer adjusted *P*-values to compensate for multiple comparisons and unbalanced sampling. Conclusions about significant differences in *post hoc* comparisons were based on the least square (lsmeans) rather than the observed means as they are more statistically reliable where sampling is unbalanced. The significance threshold (α) in all tests was 0.05.

Results

Characterizing the Crop Pollination Window

The seasonal pollination window was estimated to begin in mid-July when pistillate (female) flowers began to be produced and to end in mid-August after which there was insufficient time for pollinated flowers to develop into mature fruit (Fig. 1).

The daily pollination window was defined by the depletion of pollen grains on the synandria of *Cucurbita* flowers as a result of bee activity. The pollen load on flowers was depleted quickly over time within the daily flowering period (Fig. 3; Table 1a; Supp Table 3

Table 1. Model information for each dependent variable in this study. For bee taxon variables (hoary squash bees, bumble bees, other wild bees, honey bees, total bees) include the full data set (19 farms, 4 yrs, 4 seasonal periods, and 7 daily time intervals) from Ontario, Canada, 2015–2018. In models (b–e), (g), and (h), farm was a random effect and period of the season was a repeated measure. For model (f), the repeated measure of period was removed from the model to achieve model convergence

Model	N Obs.	AIC	Effect	F value	p value
a) **Pollen Count** = Time	614	13795.9	Time	$F_{7,606} = 32.99$	<0.0001
b) **Total Bees** = Year + Time	1581	10205.9	Year	$F_{3,1516} = 3.33$	0.0188
			Time	$F_{6,1515} = 3.99$	0.0006
c) **Total Hoary Squash Bees** = Year + Time + Honey Bees + Bumble Bees + Other Wild Bees	1577	9791.3	Year	$F_{3,1529} = 16.11$	<0.0001
			Time	$F_{6,1547} = 0.65$	0.6864
			Bumble Bees	$F_{1,1555} = 2.07$	0.1500
			Other Wild Bees	$F_{1,1561} = 4.13$	0.0429
			Honey Bees	$F_{1,1559} = 0.83$	0.3613
d) **Male Hoary Squash Bees** = Year + Time + Honey Bees + Bumble Bees + Other Wild Bees	1577	9062.4	Year	$F_{3,1502} = 3.54$	0.0142
			Time	$F_{6,1549} = 1.21$	0.2976
			Bumble Bees	$F_{1,1558} = 2.20$	0.1384
			Other Wild Bees	$F_{1,1563} = 3.07$	0.0798
			Honey Bees	$F_{1,1562} = 1.61$	0.2041
e) **Female Hoary Squash Bees** = Year + Time + Honey Bees + Bumble Bees + Other Wild Bees	1577	6665.4	Year	$F_{3,1544} = 67.47$	<0.0001
			Time	$F_{6,1546} = 2.98$	0.0068
			Bumble Bees	$F_{1,1553} = 0.52$	0.4699
			Other Wild Bees	$F_{1,1559} = 3.15$	0.0763
			Honey Bees	$F_{1,1557} = 0.08$	0.7753
f) **Bumble Bees** = Year + Time + Hoary Squash Bees + Other Wild Bees + Honey Bees (no repeated measure)	1577	4898.9	Year	$F_{3,1153} = 28.38$	<0.0001
			Time	$F_{6,1551} = 2.97$	0.0069
			Hoary Squash Bees	$F_{1,1502} = 1.90$	0.1688
			Other Wild Bees	$F_{1,1541} = 6.49$	0.0109
			Honey Bees	$F_{1,1553} = 0.20$	0.6544
g) **Other Wild Bees** = Year + Time + Hoary Squash Bees + Bumble Bees + Honey Bees	1577	5070.5	Year	$F_{3,1454} = 17.87$	<0.0001
			Time	$F_{6,1551} = 5.17$	<0.0001
			Hoary Squash Bees	$F_{1,1558} = 4.32$	0.0378
			Bumble Bees	$F_{1,1560} = 7.16$	0.0075
			Honey Bees	$F_{1,1564} = 1.40$	0.2375
h) **Honey Bees** = Year + Time + Hoary Squash Bees + Other Wild Bees + Bumble Bees	1577	7669.9	Year	$F_{3,1397} = 64.12$	<0.0001
			Time	$F_{6,1551} = 14.30$	<0.0001
			Hoary Squash Bees	$F_{1,1554} = 0.82$	0.3649
			Bumble Bees	$F_{1,1561} = 0.27$	0.6060
			Other Wild Bees	$F_{1,1563} = 1.41$	0.2352

[online only]). As predawn flower pollen loads did not differ significantly from those at 06:00 (Supp Table 4 [online only]), we inferred that pollen depletion (and the daily pollination window) began at 06:00. Pollen availability decreased by 66.1% between the 06:00 and 07:00 intervals (Fig. 3; Supp Tables 3 and 4 [online only]) and was fully depleted by 08:00 (as there were no significant differences in the quantity of pollen remaining on the synandria between the 07:00 and 08:00 intervals or between any subsequent intervals: Fig. 3; Supp Table 4 [online only]).

Bee Census

There was a significant effect of year and time on the overall total abundance of bees in the 25-flower count (Table 1b). On average, we found many more wild bees (5.44 ± 0.15: 75.3%) than managed honey bees (1.78 ± 0.08: 24.7%) visiting each set of 25 *Cucurbita* crop flowers (Fig. 4b, c). Hoary squash bees (4.46 ± 0.15) were more abundant visitors to *Cucurbita* crop flowers than honey bees (1.78 ± 0.08), wild bumble bees (0.50 ± 0.03), and other wild bees (Fig. 4b; Supp Table 5 [online only]). Male hoary squash bees (3.18 ± 0.12: 71.3%) were significantly more abundant than females (1.28 ± 0.06: 28.7%) in the 25-flower counts with a male-biased mean sex ratio across all years (male:female = 2.48: Fig. 4a). There were no significant differences in the abundance of bumble bees and other wild bees (Supp Table 5 [online only]).

Variation by Farm

We observed at least two bee taxa visiting *Cucurbita* crop flowers on all 19 farms and most farms (13 farms; 68.4%) had all four bee taxa (hoary squash bees, bumble bees, other wild bees, and honey bees) (Fig. 5).

While hoary squash bees were present at all locations surveyed, their abundance relative to the other bee visitors on *Cucurbita* crop flowers varied from fewer than 5% of flower visitors on one farm (#1) to more than 85% of visitors on three other farms (#17–19) (Fig. 5). Hoary squash bee relative abundance was higher than all the other bee taxa combined on 11 (57.9%) farms (#9–19: Fig. 5).

Bumble bees and other wild bees were observed visiting *Cucurbita* crop flowers on 17 farms (89.5%) and 14 farms (73.7%), respectively (Fig. 5). However, even the combined relative abundance of these two wild bee taxa was lower than that of hoary squash bees on 17 farms (89.5%; Fig. 5).

Honey bees were present on *Cucurbita* crop flowers on 18 farms (94.7%; Fig. 5). They were less abundant than hoary squash bees on 14 farms (73.7%), but more abundant on the other five farms (26.3%: #1–3, 5, 6; Fig. 5).

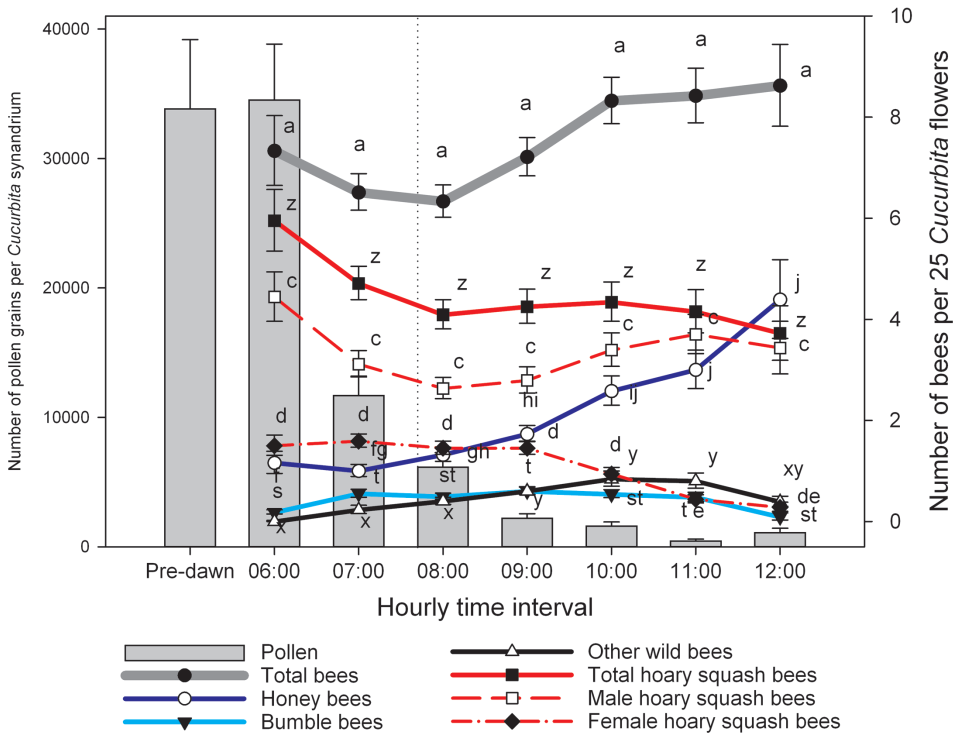

Fig. 3. Pollen depletion (bar graph) and bee abundance by taxa and hoary squash bee sex (line graph) during the daily flowering period (06:00–12:00) of *Cucurbita* crops in Ontario, Canada. The end of the daily crop pollination window (08:00) is indicated with a dotted vertical line. Pre-dawn pollen counts represent the maximum quantity of pollen available on a *Cucurbita* synandrium before bees began to forage. Data presented are means ± standard errors. Points with the same letter are not significantly different. No comparison among lines is intended. Significant differences among the pollen loads on synandria are presented in Supp Table 3 and 4 [online only].

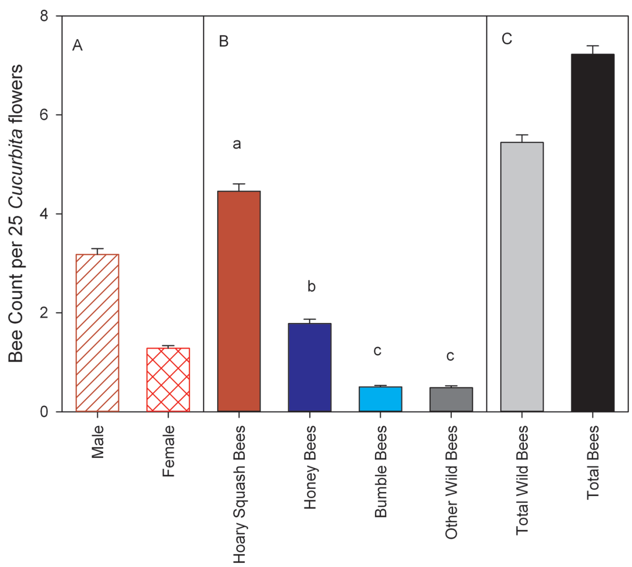

Fig. 4. The overall abundance of (A) hoary squash bee males and females, (B) each bee taxon (hoary squash bees, bumble bees, other wild bees, and honey bees), (C) total wild bees (including all taxa but honey bees) and total bees visiting *Cucurbita* crops in Ontario. Means (± standard error) are aggregated from samples taken across 19 farms and 4 yrs (2015–2018) throughout the daily (06:00–12:00) and seasonal flowering period (early July to end of August).

Annual Variation

The total number of bees visiting *Cucurbita* crop flowers varied by year (Table 1b). This pattern was driven by a significant increase in total bee abundance on crop flowers between 2015 and 2016, with no further significant increases thereafter (Fig. 6; Supp Tables 6 and 7 [online only]).

The abundance of hoary squash bees fluctuated significantly by year (Fig. 6; Table 1c), driven mostly by more substantial fluctuations in the female rather than the male population (Table 1; Supp Tables 6 and 7 [online only]). Female and male hoary squash bee abundance on *Cucurbita* crop flowers did not fluctuate in the same way by year (Table 1d, e). The magnitude of the mean fluctuation in abundance between consecutive years for females was 1.92 ± 0.38 bees per 25 flowers. Male hoary squash bee populations did not fluctuate between consecutive years but there were more males in 2018 than at the beginning of our observation period in 2015 (Fig. 6; Table 1d; Supp Tables 6 and 7 [online only]).

Bumble bee abundance was affected by year (Table 1f), with a small but significant increase in abundance between 2017 and 2018 (Fig. 6; Supp Tables 6 and 8 [online only])

The abundance of other wild bees on *Cucurbita* crop flowers also varied significantly with a year (Table 1g), being significantly higher in 2015 and 2018 compared to either 2016 or 2017 (Fig. 6; Supp Tables 6 and 8 [online only]).

Honey bee abundance on *Cucurbita* crop flowers also fluctuated between years (Table 1h), rising substantially from 2016 to 2017 before decreasing back to 2016 levels in 2018 (Fig. 6; Supp Tables 6 and 8 [online only]).

Daily Variation

Total bee abundance observed on *Cucurbita* crop flowers varied substantially during the daily flowering period (Table 1b), rising significantly from 06:00–08:00 until 10:00 with no significant change thereafter (Fig. 3; Supp Tables 9 and 10 [online only]).

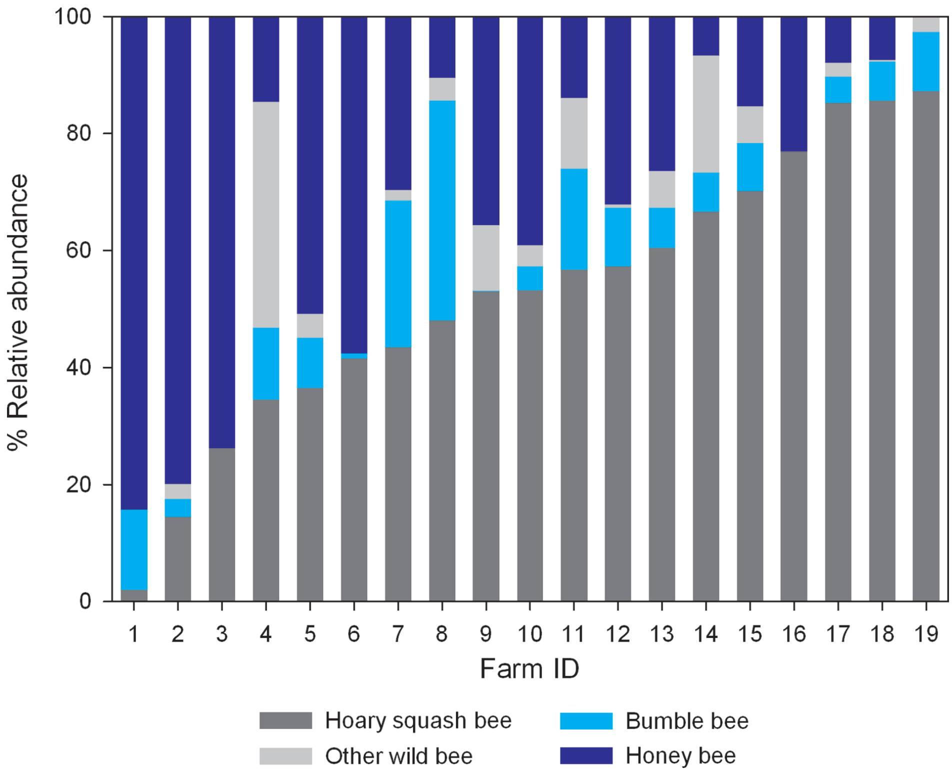

Fig. 5. Relative abundance of each bee taxon (hoary squash bees, bumble bees, other wild bees, honey bees) observed visiting *Cucurbita* crop flowers by farm. Observations were made during the daily (06:00–12:00) and seasonal (July 1–August 30) flowering period of the crop on farms in Ontario, Canada surveyed from 2015–2018. Farms are arranged from least (left) to greatest (right) relative abundance of hoary squash bees. Farms 6,9–13,15–19 were surveyed for 1 yr, farms 1 & 14 were surveyed for 2 yrs, farms 2 & 5 were surveyed for 3 yrs, and farms 3, 4, 7 & 8 were surveyed for 4 yrs.

Table 2. Pollination window benchmarks for each bee taxon (hoary squash bees, honey bees, bumble bees, and other wild bees) or groups of bee taxa (total wild bees, total bees) per 25 *Cucurbita* crop flowers on farms in Ontario, Canada. The total wild bee group includes all bee taxa except honey bees. All benchmarks are aggregated across 19 farms and four years (2015–2018), for the seasonal (mid-July to mid-Aug.) and daily (06:00–08:00) pollination windows. The percentage (relative) abundance of each bee taxon = bee taxon count / total bee count on 25 *Cucurbita* crop flowers × 100%

Variable	N		Abundance		Percentage Abundance
	Counts	Bees	Median Benchmark	Mean Benchmark (± SE)	Mean Benchmark (± SE)
Hoary squash bees	655	3148	3	5.80 ± 0.28	75.9 ± 3.7%
Honey bees	655	765	0	1.40 ± 0.12	18.3 ± 1.6%
Bumble bees	655	221	0	0.40 ± 0.04	5.2 ± 0.5%
Other wild bees	655	37	0	0.07 ± 0.01	0.9 ± 0.1%
Total wild bees	655	3406	4	6.24 ± 0.28	81.7 ± 3.7%
Total bees	655	4171	5	7.64 ± 0.31	100%

Hoary squash bees were already at peak numbers when the flowers first opened at 06:00, and their overall abundance did not vary significantly over the course of the morning (Fig. 3; Table 1c). However, the abundance of female hoary squash bees on flowers decreased by 11:00 during the morning (Table 1e; Supp Tables 9 and 11 [online only]), while the numbers of male hoary squash abundance did not vary significantly during the morning (Fig. 3; Table 1d; Supp Table 9 [online only]).

Bumble bee abundance was significantly affected by time (Table 1f), increasing from 06:00 to 07:00 with little change thereafter (Supp Tables 9 and 12 [online only]).

The abundance of other wild bees also varied with time (Table 1g), increasing from very low abundance at the start of the morning to peak levels between 09:00–12:00 (Supp Tables 9 and 13 [online only]) - more than three hours after hoary squash bee peak abundance and two hours after bumble bee peak abundance.

Honey bee abundance increased slowly over the daily flowering period with apparent peak abundance from 10:00 until flowers were closed at 12:00 (Table 1h). Abundance significantly increased from flower opening (06:00) to 08:00, and again from 08:00 to 10, with no further increases between 10:00 and 12:00 (Supp Tables 9 and 14 [online only]).

Inter-taxa Effects

The number of honey bees visiting *Cucurbita* crop flowers did not significantly affect the abundance of any other bee taxa (Table 1h).

Both hoary squash bee and bumble bee abundance had a significant effect on the abundance of the other wild bees (Table 1g). There was a weak, but significant, negative correlation between the abundance of hoary squash bees and other wild bee taxa (Pearson's r = −0.0999, $P < 0.0001$) and a weak positive correlation between bumble bee and other wild bee abundance (Pearson's $r = 0.0665$, $P = 0.0082$). The abundance of hoary squash bees did not affect the abundance of either bumble bees or honey bees on *Cucurbita* crop flowers (Table 1f, h).

Grower Benchmarks

Median and mean bee abundance benchmarks per 25 flowers for the *Cucurbita* crop pollination window (mid-July to mid-August; 06:00–08:00) in Ontario are presented in Table 3. The mean abundance benchmark for total bees was considerably higher than the median value because the mean is more sensitive to the occurrence of higher visitation rates on some farms.

The relative abundance of wild bees (77 ± 2%) was much higher than managed honey bees (23 ± 2%) within the bee visitor population on *Cucurbita* crop flowers during the crop pollination window (Table 3). Most wild bees seen visiting *Cucurbita* crop flowers were hoary squash bees, accounting for 69 ± 2 % of all bee visits to crop flowers (Table 3). The combined relative abundance of bumble bees and other wild bees combined was below 10% (Table 3).

In Ontario, wild bees were the most abundant bee group visiting *Cucurbita* crop flowers (77%), comparable to studies in the northeastern United States (range 52–90%, mean ± SE = 73.9 ± 4.1%: Table 3), but the relative abundance of the constituent taxa of wild bees in Ontario was different. In Ontario, ~69% of bees visiting *Cucurbita* crop flowers were hoary squash bees and 6% were bumble bees, whereas, in studies in the northeastern United States, the relative abundance of hoary squash bees ranged between 12 and 58% (mean ± S.E. = 37.9 ± 7.3%) and the relative abundance of bumble bees was 5–76% (mean ± SE = 27.2 ± 7.9%: Table 3). The relative abundance of other wild bees was below 5% for all studies, except those conducted in Michigan, Indiana, and Pennsylvania, which were close to 20% (range 1–19%, mean ± SE = 8.8 ± 4.0%: Table 3).

Discussion

Characterizing the Crop Pollination Window

The seasonal pollination window described here for Ontario is an estimate because planting dates vary across the province, and *Cucurbita* crop species differ somewhat in both the timing of peak production of pistillate (fruit-producing) flowers and the number of days to produce marketable fruit after pollination (Stapleton *et al.* 2000, Westerfield 2014). However, many *Cucurbita* planting and harvest dates in the province are tied to the calendar dates of holidays, such as Canadian Thanksgiving (early October) or Halloween (October 31), resulting in a fairly consistent seasonal pollination window from year-to-year. Tracking pollen depletion on *Cucurbita* crop flowers provided a means to confirm the presumed daily pollination window (06:00–08:00) from the perspective of pollen supply rather than pollen deposition (Fig. 3). Here, maximum pollen depletion by 08:00 (i.e., the end of the 07:00 hourly interval) corresponded well with the time of maximum pollen deposition on the stigmas reported by multiple previous studies (i.e., by 08:00: Tepedino 1981, Willis 1991, Phillips and Gardiner 2015). However, others have suggested that pollination in *Cucurbita* crops may be occurring within 30 min of flower opening at some sites (Cane *et al.* 2011). Regardless, the pattern of pollen depletion shown here confirms that the effective daily pollination window for *Cucurbita* crops in Ontario does not extend beyond 08:00. Thus, to provide information to crop growers, bee abundance on *Cucurbita* crop flowers should be evaluated between mid-July and mid-August (the seasonal pollination window) and from 06:00 to 08:00 (the daily pollination window).

Bee Census

Variation by Farm

Variation in the relative abundance of bee taxa by the farm was substantial suggesting that both farm management practices and the resources provided by the surrounding landscape play a role.

As ground-nesters, variation in hoary squash bee abundance among farms may be related to soil type (as squash bees prefer sandier- over clay soils for nesting), farm practices such as tillage

Table 3. Comparison of the abundance and relative abundance (%) of bee taxa visiting *Cucurbita* crop flowers in six studies in the northeastern United States and Canada

Study	Counting Method	Location	Years	Total Bees[†]	Abundance (Relative abundance %)				
					Total Wild bees[§]	Squash Bees	Bumble Bees	Other Wild Bees	Honey Bees
Willis Chan & Raine: this study	number of bees per 25 flowers, 4 times per hour, 06:00–08:00	Ontario	2015–2018	4171	3406 (82%)	3148 (76%)	221 (5%)	37 (1%)	765 (18%)
Appenfeller *et al.*, 2020	number of bees in 5 flowers observed for 1 min by citizen scientists, 07:00–12:00	Michigan & Indiana	2017–2019	1715	1408 (82%)	876 (51%)	220 (13%)	312 (18%)	307 (18%)
McGrady *et al.*, 2019	45 sec observation per flower on 80–100 m transects, 6:30–12:00	Pennsylvania	2013–2015	844	697 (83%)	164 (19%)	372 (44%)	161 (19%)	147 (17%)
Phillips & Gardiner, 2015	video recording of 8 flowers, 06:00–12:00	Ohio	2011	2992	1565 (53%)	898 (30%)	606 (20%)	61 (2%)	1427 (48%)
			2012	7900	7074 (90%)	964 (12%)	6023 (76%)	87 (1%)	826 (11%)
Petersen *et al.*, 2013	3 transects of 40 m with 2 rows	New York	2011	2390	1695 (71%)	1382 (58%)	241 (10%)	72 (3%)	695 (29%)
			2012	2709	2037 (75%)	1272 (47%)	628 (23%)	44 (2%)	765 (28%)
Artz *et al.*, 2011	3 × 10 m transects with 2 rows & 20 plants per transect, 06:00–11:00	New York	2008	5670	3923 (69%)	2585 (46%)	1272 (22%)	66 (1%)	1747 (31%)
			2009	7393	3816 (52%)	3344 (45%)	384 (5%)	88 (1%)	3577 (48%)

[†]Total Bees = Squash Bees + Bumble Bees + Other Wild Bees + Honey Bees.
[§]Total Wild bees = Squash bees + Bumble bees + Other wild bees.

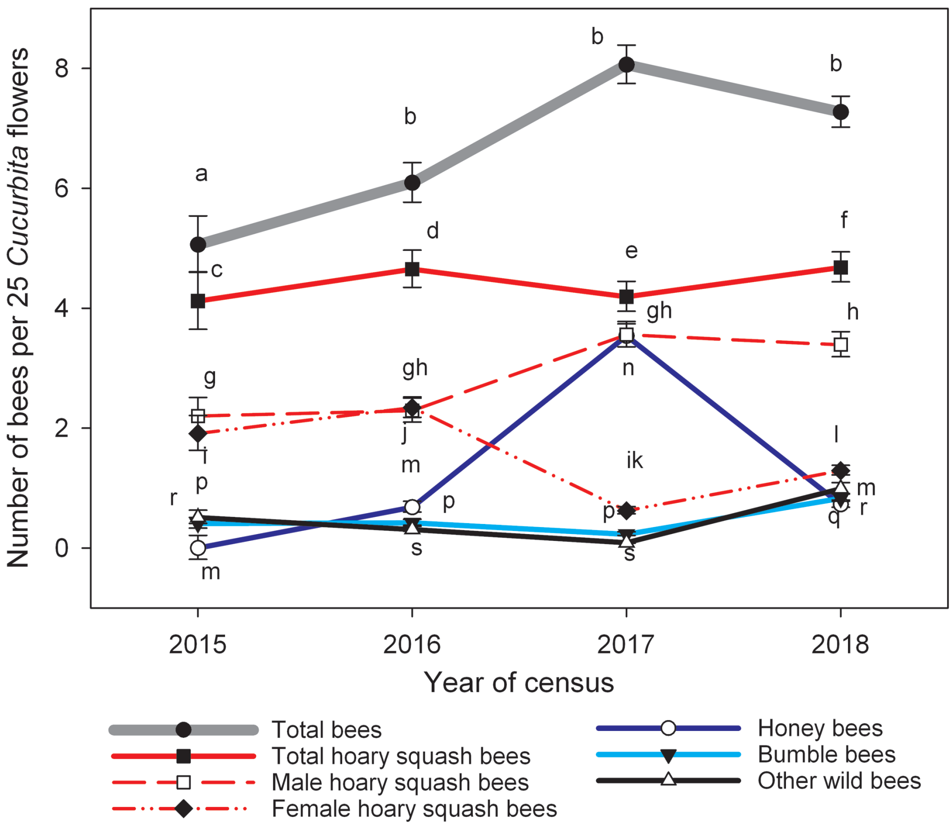

Fig. 6. Bee abundance (mean ± SE) in 25 *Cucurbita* flowers by total bees, bee taxon and by hoary squash bee sex over 4 yrs on 19 farms in Ontario, Canada during the Cucurbita flowering period (July–August; 06:00–12:00). Points within a line labeled with the same letter are not significantly different. No comparison among lines is intended.

(which is attractive to nesting females but can destroy nests), or the use of soil-applied neonicotinoid insecticides that may put hoary squash bees at risk of population decline (Julier and Roulston 2009, Ullmann *et al.* 2016, Skidmore *et al.* 2019, Willis Chan *et al.* 2019, Willis Chan and Raine 2021). Hoary squash bee abundance may also be affected by the length of time *Cucurbita* crops have been grown at a location, allowing nesting aggregations to expand. For example, on farm #17, *Cucurbita* crops have been grown continuously for more than 30 yrs with a protected nesting aggregation of over 3,000 nests in an 8 m^2 area on a lawn adjacent to the production area (S-video 1; see https://www.youtube.com/watch?v=1D_8BzMb6io).

As such, identifying existing hoary squash bee nesting aggregations on farms and subsequently protecting them from tillage or soil-applied insecticide exposure should be as much a priority for *Cucurbita* crop growers, as it is for alfalfa seed growers with nests of the alkali bee (*Nomia melanderi* Cockerell 1906, Vinchesi *et al.* 2018). Indeed, we have observed rapid expansion of protected hoary squash bee nesting aggregations on farms where growers have taken such protective measures.

The causes of low relative abundance and indeed the absence of bumble bees and other wild bees found visiting *Cucurbita* crop flowers on some farms in Ontario was not evaluated here but may be related to the inadequate or overly fragmented habitat to support the nesting, foraging, or overwintering needs of these wild bee taxa (Kevan *et al.* 1990, Kremen *et al.* 2002, Sheffield *et al.* 2008, Kennedy *et al.* 2013, Pindar *et al.* 2020). For *Cucurbita* crop flowers, bumble bee visitation rates appear to be highest in landscapes surrounded by lawns and seminatural habitats, which correspond well to the nesting habitat requirements of the common eastern bumble bee (*B. impatiens*) (Colla *et al.* 2011, Phillips and Gardiner 2015, Lanterman *et al.* 2019).

Such habitat deficits for wild bees could be remedied by creating intentional bee habitat on farms that is protected from pesticide exposure (Bótias et al. 2015, Willis Chan *et al.* 2019, Wintermantel *et al.* 2020). Indeed, reported slowing in the rates of bee decline in northwestern Europe may be related to increased efforts to create habitat that supports bees via agri-environmental schemes (Carvalheiro *et al.* 2013, Scheper *et al.* 2013). Alternatively, protecting wetlands and tall grass woodlands and increasing the complexity of the landscape surrounding farms may also provide solutions for generalist wild bee species (Kleijn *et al.* 2006, Rundlöf *et al.* 2008, Isaacs *et al.* 2009, Lanterman *et al.* 2019, Vickruck *et al.* 2019, Pindar *et al.* 2020).

Annual Variation

Hoary squash bees, honey bees, and bumble bees can each provide more than adequate pollination services to *Cucurbita* crops (McGrady *et al.* 2019). However, fluctuations in total bee abundance and the relative abundance of specific taxa from year-to-year may have an impact on crop pollination and yield that may not be well understood or could be mis-attributed to other factors (Kremen *et al.* 2002).

The annual fluctuations in hoary squash bee abundance observed here were mostly attributable to fluctuations in the abundance of females as males did not fluctuate significantly between consecutive years. Solitary bees (such as hoary squash bees) often have male-biased sex ratios and may preferentially produce male offspring because they are smaller and require fewer resources for development when pollen supplies are limited or increased pressure from nest parasites prevents females from maximizing their foraging opportunities in favor of guarding their nests (Torchio and Tepedino 1980, Seidelmann 2006, Seidelmann *et al.* 2010, Cane 2016). Male hoary squash bees may be more important for *Cucurbita* crop pollination than females because they are more abundant, pick up pollen on their bodies passively, move quickly between flowers, and tend to land on the synandria or gynecia of *Cucurbita* flowers as they search for mates, whereas females remove pollen from the system to provision their nest cells (Artz and Nault 2011, Cane *et al.* 2011, personal observation). The inter-annual consistency of male hoary squash bee abundance (Fig. 6) means that these wild bees can be relied upon for pollination in these crops from year-to-year.

Annual fluctuations in the abundance of bumble bees and other wild bee taxa are harder to interpret because these taxa are composed of multiple species. However, the fluctuation itself is an important reminder that the wild bee taxa visiting *Cucurbita* crop flowers are not static in abundance from year-to-year, further underlining the importance of hoary squash bees and of having diverse pollinator communities visiting the crop (Fig. 6; Garibaldi *et al.* 2016).

The increase in honey bee abundance in 2017 corresponded to an apparent decline in the hoary squash bee population that year (Fig. 6). However, this is likely an artifact of uneven sampling of farms between years and an unexplained one-year increase in honey bees on two farms (#9 and #12) that were sampled more extensively in 2017. There was no increase in the number of managed honey bee colonies in Ontario from 2016 to 2017 (AAFC 2018), nor was there evidence that the abundance of honey bees affected the abundance of hoary squash bees or vice versa (Table 1c, h) so it is unlikely that these taxa were displacing each other.

Despite the demonstrated importance of wild bees for pollinating *Cucurbita* crops (Hurd *et al.* 1971, Graças Vidal *et al.* 2010, Artz and Nault 2011, McGrady *et al.* 2019, Stoner 2020), honey bees can play a role as back-up or substitute pollinators in this cropping system when wild bee abundance or diversity decreases. Conversely, the presence of honey bees does not eliminate the need to maintain the pollination services of wild bees, and honey bees should not be considered the primary pollinators of *Cucurbita* crops in North America (Garibaldi *et al.* 2013, Mallinger and Gratton 2015, McGrady *et al.* 2019). These results provide more evidence that multiple bee taxa are needed to provide resilient pollination services for *Cucurbita* crops year over year.

Daily Variation

Hoary squash bees typically began to forage on the crop flowers as soon as they opened and were active throughout the daily pollination window, suggesting that their intrinsic daily activity cycle was well matched to the daily pollination window of the crop and that they were not experiencing restrictions on their activity related to light, temperature, humidity, or wind (Mathewson 1968, Hurd *et al.* 1974, Willis 1991, Brittain *et al.* 2013b). Females hoary squash bees may have been less abundant after 11:00 because some individuals are likely to have changed the focus of their activity to nest building rather than foraging (Fig. 3; Kevan *et al.* 1988). Male abundance throughout the daily flowering period did not change (Fig. 3), likely because male activity (foraging, mate-seeking, mating, resting) all happens on *Cucurbita* flowers (Hurd and Linsley 1964, Hurd *et al.* 1974, Willis Chan 2020).

Despite their ability to fly in cool, low light conditions, bumble bees reached peak numbers an hour later than hoary squash bees but remained active throughout the pollination window and beyond (Heinrich 1975, Corbet *et al.* 1993, Kapustjanskij *et al.* 2007, Couvillon *et al.* 2010, Reber *et al.* 2015). This delayed appearance may represent a pollen avoidance strategy by bumble bees as pollen supplies on staminate *Cucurbita* flowers are reduced by about 60% by hoary squash bees in the first hour after flower opening (Fig. 3; Brochu *et al.* 2020).

Honey bee abundance increased as pollen availability decreased, and peak numbers were reached well after the daily pollination window (Fig. 3). Thus, for behavioral reasons, such as their preference for warm temperatures and high light conditions (Corbet *et al.* 1993, Vicens and Bosch 2000, Abou-Shaara *et al.* 2017, Clarke and Robert 2018), honey bees are not likely to be providing pollination services to *Cucurbita* crops in Ontario when hoary squash bees or bumble bees are present, despite being physically able to do so.

The tendency of bumble bees and honey bees to forage on the *Cucurbita* crop flowers in peak numbers after much of the pollen has already been depleted may be explained by the likelihood that honey bees and bumble bees are visiting the flowers primarily to collect nectar (Percival 1947, Artz and Nault 2011, Brochu *et al.* 2020). Both these taxa lack the specialized scopa of hoary squash bees and may experience mechanical difficulty packing the large spiny *Cucurbita* pollen into their corbiculae (Lunau *et al.* 2015). Furthermore, both honey bees and bumble bees have been observed discarding passively collected *Cucurbita* pollen (Michelbacher *et al.* 1964, Tepedino 1981, personal observation for bumble bees), a behavior exhibited by nectar-seeking bees (Parker 1981, Vaissière and Vinson 1994, Thorp 2000).

Other wild bees reached peak abundance after the pollination window (Fig. 3) and likely contributed little to pollination in Ontario *Cucurbita* crops because of their low abundance and the mismatch between the daily crop pollination window and their peak activity.

Although hoary squash bees, bumble bees, and honey bees can each provide pollination services to *Cucurbita* crops (McGrady *et al* 2019), the differences in the overall abundance of these bee taxa (Fig. 4), their relative abundance from farm-to-farm (Fig. 5), annual fluctuations in abundance (Fig. 6), and variation in abundance over the daily flowering period (Fig. 3) provide further evidence that pollinator diversity is important to maintaining the resilience of crop pollination services over time and space (Kremen *et al.* 2002, Winfree *et al.* 2007, Julier and Roulston 2009, Garibaldi *et al.* 2013, Mallinger & Gratton 2015, Delgado-Carrillo *et al.* 2018, McGrady *et al.* 2019, Nicolson and Ricketts 2019).

Inter-taxa Effects

Although honey bees, particularly at high densities, are frequently considered to negatively impact wild bees through exploitative competition (Thomson 2004, Lindström *et al.* 2016, Cane and Tepedino 2017, Mallinger *et al.* 2017), there was no evidence of such impacts on *Cucurbita* crop flowers in other studies or here—likely because honey bees forage on *Cucurbita* flowers later in the morning than other bee taxa (Julier and Roulston 2009, Fig. 3; Supp Table 9 [online only]). However, hoary squash bees had a significant, though the weak negative effect on other wild bees, likely because as specialists on *Cucurbita* they quickly and efficiently depleted resources on the crop. Bumble bee abundance had a weak positive correlation with the abundance of other wild bees, perhaps because they were both responding to the same environmental conditions that affect generalist species, such as the availability of alternative foraging sources and nesting sites. Hoary squash bees are less vulnerable to the availability of alternative foraging and nesting habitat because of their specialization on *Cucurbita* crops and their tendency to nest within or close to those crops (Hurd and Linsley 1964).

Grower Benchmarks

Here, abundance benchmarks of bee taxa visiting *Cucurbita* crop flowers during the crop pollination window suggest that typically hoary squash bees are responsible for the pollination of these crops in Ontario (Table 2). Whether the low abundance benchmarks for bumble bees and other wild bees mean that Ontario's agricultural landscapes are depauperate of bumble bees and other wild bees, that those wild taxa and honey bees prefer to avoid *Cucurbita* pollen, or that other flowering plants are drawing those bees away from the crop is currently unknown. However, both bumble bees and other wild bees visit *Cucurbita* crops in greater numbers in other locations suggesting that landscape structure may be an important factor here (Julier and Roulston 2009, Artz *et al.* 2011, Artz and Nault 2011, Petersen *et al.* 2013, Phillips and Gardiner 2015, McGrady *et al.* 2019, Appenfeller *et al.* 2020, Table 3).

The benchmarks presented in Table 2 raise questions about current *Cucurbita* crop pollination guidelines that recommend supplementing wild pollinators with colonies of managed honey bees (Woodcock 2012, OMAFRA 2019). A better approach would be to use a total bee benchmark that encompasses all the bee taxa that visit the crop flowers. If the total bee counts on a farm fall below the provincial benchmark, a grower could choose to rent honey bee hives for the short term, while making changes to mitigate or eliminate practices that are detrimental to bees, and/or initiating practices that support and enhance wild bees. To ensure the resilience of pollination services from year-to-year, growers may also benefit from comparing the abundance of individual bee taxa to the provincial benchmarks for those taxa (Table 2). With minimal training, growers could learn to identify the major bee taxa (hoary squash bees, bumble bees, other wild bees, and honey bees) and to make more precise management decisions based on the outcome (Appenfeller *et al.* 2020).

Our results showing that wild bees are more abundant than honey bees in the bee communities visiting *Cucurbita* crop flowers in Ontario align with data from other studies conducted in the northeastern United States (Table 3). However, the variation among these studies in the relative abundance of the individual bee taxa within the wild bee communities may be related to the same factors that cause variation among farms, such as soil type, agricultural intensity, farm management practices, or the availability of suitable nesting habitat for wild bees (Cane 1991, Julier and Roulston 2009, Artz and Nault 2011, Ullmann *et al.* 2016, Willis Chan *et al.* 2019, Willis Chan and Raine 2021). Variation in sampling methods may also have contributed to differences among studies (Table 3). Counts of some taxa that spend little time in individual flowers, fly quickly from flower-to-flower, and nest near to the crop may be overestimated in all studies. Further work is needed to provide more insight into the relationship between the relative abundance of certain taxa and these key environmental factors.

Conclusion

The abundance and types of bees visiting *Cucurbita* crop flowers fluctuated spatially among farms and regions and temporally on an annual and daily basis. Having the full diversity of bee taxa visiting *Cucurbita* crop flowers at a farm offers the best assurance of pollination resilience. Although bumble bees are important pollinators of *Cucurbita* crops elsewhere in the northeastern United States, they do not appear to be playing a major role in Ontario. This important difference requires further attention, especially if related to habitat loss or negative impacts of exposure to pesticides. Hoary squash bees play a primary role in pollination of *Cucurbita* crops in Ontario because of their abundance, their ubiquity, and the synchronicity of their diurnal activity patterns with the daily crop pollination window. The importance of wild bees as visitors of *Cucurbita* crop flowers highlights the inadequacy of current pollination recommendations for this crop in Ontario that place sole emphasis on managed honey bee stocking rates. Going forward, pollination recommendations for *Cucurbita* should include benchmarks for all bee taxa that could visit the crop flowers. In concert with this, greater efforts should be made to conserve and protect wild bees in the agricultural contexts where they provide pollination services to growers for free.

Supplementary Data

Supplementary data are available at *Environmental Entomology* online.

Acknowledgments

We would like to thank all 19 Ontario farmers who allowed us access to their land and crops. Beatrice Chan, Katie Fisher, Dillon Muldoon, Lauren Moran, Emma Jane Woods, Leonard Zettler, Matthew Gibson, and especially Elaine Roddy, cucurbit crop specialist for the Ontario Ministry of Agriculture, Food and Rural Affairs (OMAFRA) provided excellent assistance with counting bees in the field. We also thank Peter Kevan for permission to use and modify his figure showing the distribution of hoary squash bees across Ontario. Ann Sanderson has kindly drawn two figures on commission from D.S.W.C. This work was supported by Ontario Ministry of Agriculture, Food and Rural Affairs (OMAFRA) grant UofG2015-2466 (awarded to N.E.R. and D.S.W.C.), Natural Sciences and Engineering Research Council (NSERC) Discovery grant 2015–06783 (awarded to N.E.R.), the Fresh Vegetable Growers of Ontario (FVGO: awarded to N.E.R. and D.S.W.C.) and the Food from Thought: Agricultural Systems for a Healthy Planet Initiative, by the Canada First Research Excellence Fund (grant 000054). D.S.W.C. was supported by the George and Lois Whetham Scholarship in Food Systems, an Ontario Graduate Scholarship, the Keith and June Laver Scholarship in Horticulture, the Fred W. Presant Scholarship, and a Latournelle Travel Scholarship. N.E.R. is supported as the Rebanks Family Chair in Pollinator Conservation by the Weston Family Foundation.

Author Contributions

DSWC and **NER**: conceived and designed the project and wrote the paper. **DSWC**: carried out the experimental work and the statistical analyses.

Data Availability

The data that support the findings of this study are available in the supplementary information as data set 1 and data set 2.

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