

SHARING THE WEALTH: POLLEN PARTITIONING IN A *CUCURBITA PEPO* CROP POLLINATION SYSTEM WITH REFERENCE TO FEMALE WILD HOARY SQUASH BEES (*EUCERA PRUINOSA*)

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Abstract—*Cucurbita pepo* crops (pumpkin, squash) are entirely dependent upon insect pollinators for reproduction. In Ontario, Canada, their most important pollinator is the hoary squash bee (*Eucera pruinosa*), a wild ground-nesting, solitary bee whose only source of pollen in the region is *Cucurbita* crops. As such, in this context, we have a unique opportunity to study pollen partitioning in a cropping system in which a wild bee is the main pollinator. To evaluate pollen partitioning in the system, we measured pollen production by the crop, the pollen lost as waste due to the activities of bees in staminate flowers, pollen loads collected by female squash bees, and the number of pollen grains in fully provisioned hoary squash bee nest cells, and we compared these to the crop's pollination requirements as reported in the literature. From the perspective of both plant and bee reproduction, about 13% of the pollen produced by staminate acorn squash flowers was wasted, but it may be harvested by other organisms like ants. After waste is accounted for, about 9% of the pollen left is needed for plant reproduction leaving the remaining 91% available for hoary squash bee reproduction. We also evaluated the mass of pollen a female hoary squash bee could carry in a single foraging trip relative to her own body mass (~4%). The information contained here is useful for understanding the relationship between a crop and an oligolectic wild bee species or to set up controlled, field realistic experiments involving the hoary squash bee.

Keywords—pollen budget, nest cell provisions, foraging trip, ground-nesting solitary bee, ants

INTRODUCTION

Many organisms are involved in relationships in which the interaction can be understood as a mutualism because the costs are exceeded by the benefits for both organisms (Morris et al. 2010). The mutualistic relationship between entomophilous plants and their insect pollinators often revolves around pollen and nectar produced by the plant in its flowers. From the plant's perspective, pollen is a protective means of transporting male gametes for sexual reproduction. However, much of that pollen is siphoned away from plant reproduction by pollinators to supply their own nutritional needs for amino acids and lipids, resulting in a cost to the plant (Thorp 2000; Barraud et al. 2022). Thus, pollen can be thought of as a transactional

currency in the mutualistic pollination systems of entomophilous plants.

Between 25-35% of the solitary bee species of North America are pollen specialists, preferentially foraging for pollen from a narrow group of plant species with which they have a strong co-evolutionary relationship (Fowler 2020a,b; Fowler & Droege 2020; Cane 2021). A small number of these pollen specialists are known to specialize on crop plants, including the alkali bee (*Nomia melanderi*) on alfalfa (*Medicago sativa*) (Stephen 1959), the southeastern blueberry bee (*Habropoda laboriosa*) on rabbiteye blueberry (*Vaccinium virgatum*) (Cane & Payne 1988), the sunflower chimney bee (*Diadasia enavata*) on sunflower (*Helianthus annuus*) (Parys et al. 2018), and the hoary squash bee (*Eucera (Peponapis)*

pruinosa Say, 1837), on pumpkin and squash (*Cucurbita* spp.) (Hurd & Linsley 1964).

Although other bees, such as honey bees (*Apis mellifera*) and bumble bees (*Bombus* spp.), are commonly found visiting squash crop flowers and are effective pollinators (Willis Chan & Raine 2021a), the specialist bee of focus in this study is the hoary squash bee (*E. pruinosa*), which is a univoltine, ground-nesting, solitary wild bee species with a pan-American distribution (Hurd et al. 1971; Hurd et al. 1974; López Uribe et al. 2016; Willis Chan & Raine 2021a). The characteristics of a squash crop–hoary squash bee pollination system provide a unique opportunity to study how pollen is shared in the system between the reproductive needs of the crop and the closely related dietary and reproductive needs of a wild pollinator, including some losses to both plant and pollinator that may benefit other opportunistic organisms, such as ants. When considering the mutualistic relationship between squash crops and the hoary squash bee, it makes sense to focus on the pollen produced by the plant because pollen is so directly tied to reproductive success in solitary bees (Strickler 1979).

In this system, each squash flower lasts about six hours, opening at dawn and wilting by noon or earlier, depending on temperature (Whitaker & Davis 2012; Willis Chan & Raine 2021b). Squash crops present abundant floral resources as soon as their flowers open, including a high-quality sucrose-dominant, amino acid-rich nectar and large (>100 µm diameter), spiny pollen grains whose exine layer is covered with oil (Lau & Stephenson 1993; Nepi & Pacini 1993; Ashworth & Galetto 2001; Nepi et al. 2001; Graças Vidal et al. 2010). The size and oiliness of the pollen precludes dispersal by wind.

Although flowers can be pollinated by pollen from the same plant (geitonogamy) or other plants (xenogamy) (Whitaker & Davis 2012), the squash crop is entirely dependent upon bees to transport pollen from its staminate (male) flowers to its pistillate (female) flowers. Research has already demonstrated that *Cucurbita* crops require the deposition of between 2300–2500 pollen grains on the stigma of pistillate flowers for good pollination (Winsor et al. 1987; Willis 1991; Nepi & Pacini 1993; Graças Vidal et al. 2010; McGrady et al. 2020; Stoner 2020). Pollen deposition on pistillate

flowers in open field settings with visits from hoary squash bees, bumble bees, and honey bees is maximized by about 2 hours after anthesis (~0800) coinciding with full pollen depletion on staminate flowers (Willis 1991; Willis Chan & Raine 2021a). There is no difference in the time of full pollen depletion among sites with different pollinator community composition in Ontario (Willis Chan, unpublished data). Where they have been measured in the northeastern United States, *Cucurbita* crop pollination deficits appear not to be common in commercial agricultural contexts (McGrady et al. 2020, Stoner 2020).

Across North America, the hoary squash bee commonly visits both pumpkin and squash crops, along with honey bees and bumble bees (Rondeau et al. 2022). In fact, because there are no wild *Cucurbita* species present across most of its range, including Ontario, Canada, where this study was undertaken, the hoary squash bee is entirely dependent for pollen resources upon cultivated *Cucurbita* spp. (Hurd et al. 1974; López Uribe et al. 2016). Hoary squash bees are known to provide efficient and reliable pollination services to pumpkin and squash crops (Tepedino 1981; Cane et al. 2011; Artz & Nault 2011; McGrady et al. 2020; Stoner 2020; Willis Chan & Raine 2021a). Their pollination efficiency is related to the synchrony between crop flowering and bee activity on a daily and seasonal basis and their flower handling behaviour that ensures good contact between the bees and the anthers of staminate flowers and the stigmas of pistillate flowers (Willis & Kevan 1995; Willis Chan & Raine 2021b; for an example of flower handling on a staminate flower see: <https://youtu.be/StDyTk9UKts>).

However, not all the pollen adhering to the body of female hoary squash bees is used for pollination. After leaving a staminate flower, female hoary squash bees groom pollen from their bodies into their scopae (see above video) where the pollen is held by specialized, widely spaced hairs that evolved in this species to handle the large, oily, and spiny pollen characteristic of *Cucurbita* spp. (Michelbacher et al. 1964; Roberts et al. 1978). Thus, pollen harvested into the scopae of hoary squash bees is likely unavailable for pollination and can be considered a removal from the pool of pollen available for plant reproduction to the pool of pollen available for bee reproduction.

Squash flowers are visited by both male and female hoary squash bees, but only females are involved in nest construction, pollen harvesting, and larval provisioning (Mathewson 1968; Hurd et al, 1971). Because they do not harvest pollen and provision nests, males may be superior pollinators of squash (Cane et al. 2011).

Where pollination of squash crops is primarily dependent on hoary squash bees (as is the case in Ontario, Canada), pollen losses from the pool of pollen available for both plant and bee reproduction occur (1) within flowers when pollen is dislodged from the synandrium as bees land on it; (2) in the broader environment as bees travel from flower to flower or back to their nests; and (3) at the entrance to nests as the female hoary squash bees slip underground through the nest entrance.

Thus, pollen presented by squash flowers visited by hoary squash bees ends up in three main pools: (1) pollen deposited by bees on the stigma of the pistillate flowers leading to plant reproduction, (2) pollen harvested by bees as food and which supports bee reproduction, and (3) pollen wasted as a result of bee activities, characterized by Harder (2000) as bee “sloppiness”, and is therefore not available to support either plant or bee reproduction (though this “waste” pollen is often gathered by ants - see Fig. 4). The sum of all these pools could be considered the pollen budget of the whole pollination system.

Our main objective in this study is to improve understanding of the hoary squash bee-squash crop pollination system using acorn squash to track how much pollen ends up in each of the above pollen pools (plant reproduction, bee reproduction, waste) and to use this information to calculate how many squash flowers a female hoary squash bee needs to support the production of five offspring. This is important because it provides foundational knowledge about a ground nesting bee species that is important in agricultural systems across North America. Furthermore, this paper provides benchmarks for researchers who wish to set up controlled systems that mimic a field realistic situation to study hoary squash bees for a wide variety of reasons.

MATERIALS AND METHODS

STUDY SITES

This study incorporates work done on 5 commercial farms in southern Ontario, Canada (Peterborough County-3 farms, City of Kawartha Lakes-1 farm, Wellington County-1 farm) all of which are similar in size (25-50 ha) with similar average maximum/minimum temperatures in July/August of 26°C/17°C). Data were collected in 3 different years (pollen waste counts and counts of pollen loads on bees: 2017; pollen in nest cells: 2019; pollen counts on staminate flowers: 2022) because of time constraints of other projects undertaken in the short three-week period during which hoary squash bees are active in Ontario. All measurements presented here were taken in the field under normal growing, foraging, or nesting conditions except for measurements of wasted pollen which were undertaken in three large mesh-covered enclosures (6.1 x 4.9 x 3.0 m, area of each enclosure = ~30 m²) on a farm in Peterborough County. The mesh used was a 50% shade cloth (mesh size = 2 mm x 2 mm) that effectively excluded bumble bees, male hoary squash bees, and honey bees and contained female hoary squash bees. Within those enclosures, we grew 28 acorn squash plants (*Cucurbita pepo* var. Table Star), introducing eight mated female bees into each enclosure once flowering commenced in the crop. In a previous study, we demonstrated that the system was well below carrying capacity (Willis Chan & Raine 2021b,c). Field realistic conditions were closely mimicked within the enclosures, and introduced bees established well, foraged normally, and produced about five offspring each (Willis Chan & Raine 2021c). Studying the amount of waste pollen produced by the activities of female hoary squash bees in the squash pollination system within screened enclosures allowed us to eliminate the contributions to waste made by male hoary squash bees, honey bees (*A. mellifera*) and bumble bees (*Bombus* spp.), all of which commonly visit this crop under field conditions (Willis Chan & Raine 2021a).

POLLEN PARTITIONING

We tracked pollen in the acorn squash-hoary squash bee system by measuring the amount of pollen that was: (a) presented on staminate flowers

at anthesis ($N = 30$ flowers), (b) knocked off the synandria of staminate flowers by the activities of female hoary squash bees and subsequently wasted ($N = 30$ flowers), (c) carried by female hoary squash bees in a single foraging trip ($N = 87$ bees), and (d) amassed within a completely provisioned hoary squash bee nest cell ($N = 13$ nest cells).

POLLEN PRESENTATION

To determine the maximum amount of pollen available we collected synandria from 30 staminate acorn squash flowers grown on three farms in Peterborough County (Fig. 1). The flowers were collected from 10 different, haphazardly selected, plants within a field of acorn squash on each farm on August 10, 2022, which is about midseason for acorn squash flowering in Ontario. To choose a plant, a wire flag was thrown over the collector's shoulder and the plant nearest to it was selected. If that plant had no available unopened flowers, the process was repeated. The day before each collection, unopened flowers were taped closed such that synandria could dehisce but access by bees was prevented (Fig. S1). Early the following morning, the tip of the corolla was cut away below the tape, a 2 mL microcentrifuge tube was inverted carefully over the synandrium which was then cut from the flower with a razor blade. Ethanol (70%, 0.5 mL) was added to the tube, which was spun in a microcentrifuge for 3 minutes at 2500 rpm to dislodge the pollen from the synandrium. Each synandrium was then removed from the tube and checked by eye to ensure that all pollen had been dislodged. Subsequently 1.5 mL of 50% glycerin solution was added to the tube. After thorough mixing with a mini vortex, pollen counts were made by taking five 5- μ L aliquots from each tube

(i.e., five aliquots per synandrium), placing the aliquot onto a gridded sheet, and counting all the pollen grains on the grid under 25X magnification using a dissection microscope. The number of pollen grains per aliquot was averaged across the five 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 \times 2 mL \times 1000 μ LmL⁻¹ / 5 μ L). Following work done by Willis Chan (2020), a conversion factor of 609 pollen grains per mg of pollen was applied throughout this study to convert all pollen counts to pollen mass.

POLLEN WASTAGE

The activity of hoary squash bees on staminate acorn squash flowers often dislodges pollen that then falls to the base of the corolla where it collects over the day and is wasted (i.e., it is neither harvested by bees nor available for pollination) (Fig. 1). We collected waste pollen from wilted staminate flowers on August 17 and 23, 2017 ($N = 30$ flowers). By this point, the synandria of the flowers had been fully stripped of pollen. All waste pollen in the flowers was attributable only to the activities of female hoary squash bees because no bumble or honey bees were present. After carefully removing the stripped synandrium from each flower, the pollen remaining in the base of the corolla was tapped into a small disposable plastic cup and transferred into a 2 mL microcentrifuge tube. Subsequently, 0.5 mL of 70% ethanol and 1.5 mL of 50% glycerin solution were added to the tube. The resulting suspension was mixed and counted using the method described above for synandria of staminate flowers.



Figure 1. Pollen apportioning in the hoary squash bee-acorn squash pollination system. **A:** pollen presentation on the synandrium of a staminate flower (available pollen), **B:** pollen dislodged from the synandrium by the activities of hoary squash bees and wasted at the base of the corolla (waste pollen), **C:** pollen load on a female hoary squash bee returning to their nest, **D:** pollen deposited by bees on the stigma of an acorn squash pistillate flower (pollination), and **E:** pollen deposited into a subterranean nest cell for hoary squash bee larvae (provisions).

POLLEN LOAD SIZE

At 0600 at a large nesting aggregation on a farm near Guelph, Ontario, we collected 90 female hoary squash bees returning to their nests with full pollen loads by grasping them around the thorax with finger and thumb as they walked towards their nest entrances (Fig. 1). Upon capture, we introduced each bee to an aerated 2 mL microcentrifuge tube, placed it in a cooler with ice packs, and stored all the bees overnight in a refrigerator. While in the tubes, the bees groomed the pollen off themselves, leaving it in the base of the tube. Three bees did not groom pollen off themselves thus were removed from the data set. The next morning, all bees were released into acorn squash flowers and 0.5 mL of 70% ethanol plus 1.5 mL of 50% glycerin solution was added to the pollen left in the tubes. The resulting suspension was mixed and counted using the method described above for synandria of staminate flowers.

We measured the mass of 82 live female hoary squash bees collected on five farms across Ontario by placing the bees on ice in a cooler to immobilize them and then weighing them to obtain an average body mass for a female bee. We discarded data for two of these bees, one of which was tiny (10 mg) and the other was mistakenly recorded as 930 mg. We then compared the mean mass of pollen loads collected to the mean mass of live female hoary squash bees to calculate the average percentage of live body mass that a female hoary squash bee carries in a foraging trip. This method is reasonable in this case because hoary squash bees only collect the pollen of *Cucurbita* spp. (Neff 2008).

POLLEN PROVISIONING A NEST CELL

We excavated 30 subterranean hoary squash bee nests from an aggregation on a farm near Peterborough, Ontario to obtain nest cells that contained both provisions and an egg ($N = 13$ nest cells). Each cell corresponded to a different nest and therefore a different female hoary squash bee. The selected nest cells were used for the pollen provision counts as they represented fully provisioned nest cells whose contents had not yet been eaten by larvae (Fig. 1). Because sampling was destructive, we had a small sample size and were unable to determine the sex of the egg. In the lab, the contents of each nest cell were scraped into

a 2-mL microcentrifuge tube. As described earlier (see pollen assays for synandria of staminate flowers), we added a mixture of 70% ethanol and 50% glycerin and processed and counted pollen to estimate the number of grains per nest cell.

STATISTICAL ANALYSIS

Data were analysed using SAS Studio in SAS OnDemand for Academics, Copyright © 2021 SAS Institute Inc. All means are reported with their associated standard error.

RESULTS AND DISCUSSION

The pollen budget of the acorn squash-hoary squash bee pollination system is summarized in Fig. 2. Here we present the results for each part of the system:

POLLEN PRESENTATION

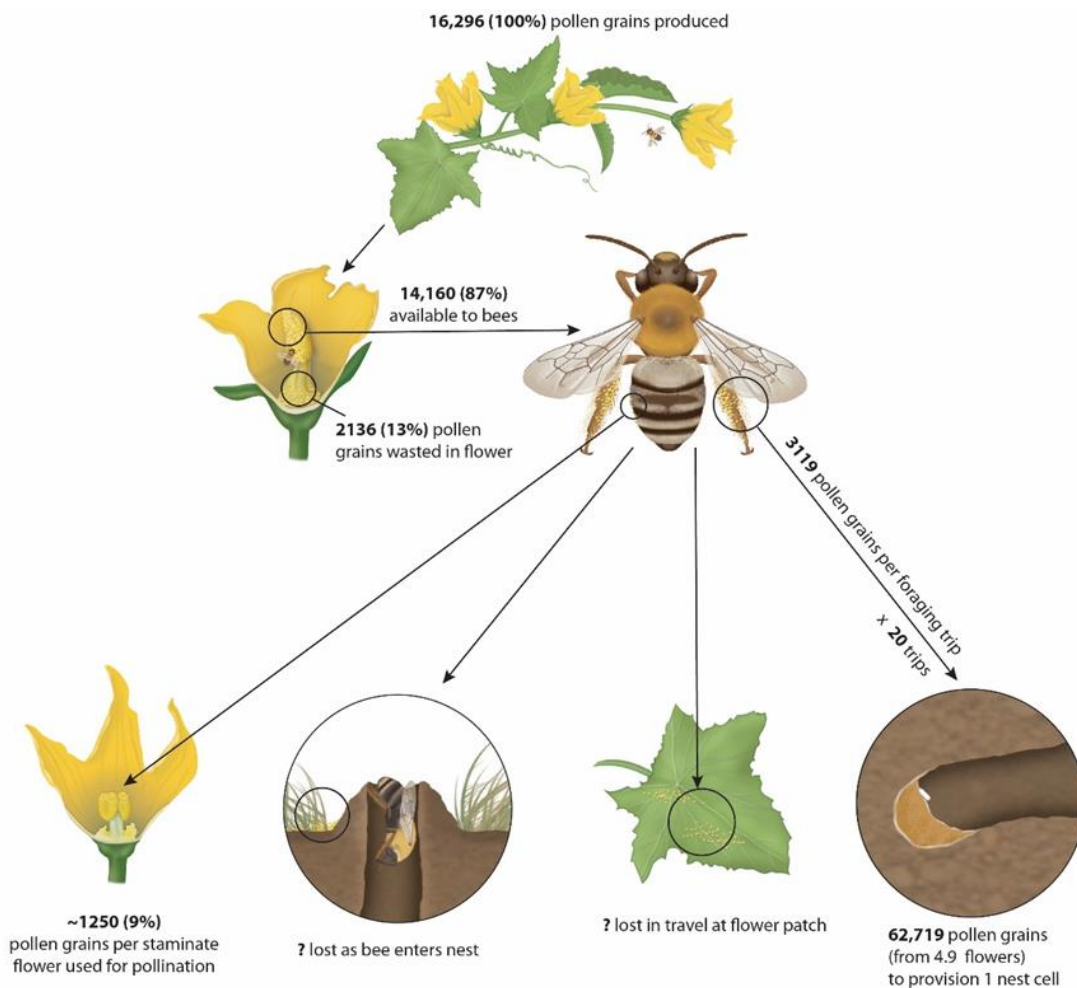
The mean amount \pm SE of available pollen presented by dehisced staminate acorn squash crop flowers was $16,296 \pm 2,989$ pollen grains per synandrium (26.7 mg; $N = 30$ synandria; Table S1), which represents 100% of the average available pollen per staminate flower in the system.

POLLEN WASTAGE

The mean amount \pm SE of waste pollen found in the base of staminate acorn squash flowers was $2,136 \pm 267$ pollen grains/flower (4.54 ± 0.39 mg; $N = 30$ staminate flowers; Table S2), which represents 13.1% of the average amount of pollen initially available on each synandrium at anthesis. Excluding this wastage from the maximum available pollen on the synandria of *Cucurbita* flowers, there was an average usable supply of 14,160 pollen grains per flower (~87% of the original supply) available for the reproductive needs of the plant and the dietary needs of the bees.

POLLEN DEPOSITION

We did not directly measure pollen deposition but used published information to characterize the amount of pollen needed per pistillate flower for full pollination. Based on data from the literature, pollination is complete when pistillate *Cucurbita* spp. flowers have a pollen load of about 2,300–2,500 pollen grains (Fig. 1; Willis, 1991; Nepi & Pacini 1993; McGrady et al. 2020; Stoner 2020). Here, we have assumed the value of 2,500 pollen



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Figure 2. The pollen budget of the whole *Cucurbita*-hoary squash bee pollination system including the source of pollen resources (the synandrium of the staminate flower), the pollen harvester and pollination vector (the female hoary squash bee) and endpoints of plant reproduction represented by pollination, bee reproduction represented by a fully provisioned nest cell, and pollen that is wasted within staminate flowers and at other unquantified places in the system. Diagram designed by D. Susan Willis Chan and drawn by Ann Sanderson and used with permission.

grains per stigma as the average number of pollen grains deposited per pistillate flower following the activities of bees. This does not consider variability in pollen deposition due to flower attractiveness, differences among pollinator taxa, or stochastic variation during dispersal by individual bees (Richards et al. 2009) and assumes that pollen deposited comes from either the same plant or other conspecific plants. In acorn squash, the sex ratio of staminate to pistillate flowers is 2:1 (33% of flowers are pistillate; Rodrigues Peirera 1968). As such, on average, about one half of the 2,500 pollen grains needed for full pollination of a pistillate flower in this crop can be supplied by each staminate flower (1,250 pollen grains for

pollination from each staminate flower). After accounting for wastage within each staminate flower (2,136 pollen grains), 8.8% of the remaining 14,160 pollen grains would be needed for plant reproduction if each pistillate flowers received an average of 2,500 pollen grains. The remaining 91.2% is available for production of bee offspring (Table 1). In practice, female squash bees remove pollen presented in staminate flowers, lose some of it within the flower and elsewhere (pollen waste), and accidentally deposit some of it on the stigmas of pistillate flowers as they forage for nectar. The amount of pollen that remains in their scopae is taken back to the nest to provision nest cells.

Table 1. Pollen accounting for an acorn squash (*Cucurbita pepo*)-hoary squash bee (*Eucera pruinosa*) pollination system showing the average amounts of pollen produced by staminate flowers, lost as waste in staminate flowers, and available for plant reproduction and bee offspring production purposes. Amount of pollen needed for plant reproduction is taken from Winsor et al. 1987; Willis 1991; Nepi & Pacini 1993; Graças Vidal et al. 2010; McGrady et al. 2020; Stoner 2020.

Category	Number of pollen grains (\pm SE)	Percent of total pollen production	Percent of available pollen after wastage
Pollen presentation by a staminate flower (A)	16,296 \pm 2,989	100.0%	-
Pollen wastage in a staminate flower (B)	2,136 \pm 267	13.1%	-
Pollen available after wastage (C = A-B)	14,160	86.9%	
Pollen from each staminate flower needed for maximum pollination (D, from literature and sex ratio of flowers)	1,250	7.7%	8.8%
Pollen available for bee offspring production (C-D)	12,910	79.2%	91.2%

POLLEN LOAD SIZE

The mean number of pollen grains harvested from staminate acorn squash flowers in a single foraging trip by female hoary squash bees was 3,119 \pm 374 ($N = 87$ female bees; 5.1 mg of pollen; Table S3). Based on her average live body mass of 111 \pm 0.2 mg ($N = 80$; Table S4), a female hoary squash bee carries about 4.2% of its mass in pollen per foraging trip.

POLLEN PROVISIONING A NEST CELL

The mean number of pollen grains in a fully provisioned hoary squash bee nest cell was 62,719 \pm 7,900 ($N = 13$; 102.96 mg; Table S5), equivalent to the entire pollen supply of 4.9 acorn squash flowers after waste pollen in the flowers and pollination needs are subtracted. This represents the average across both male and female offspring as we were unable to differentiate between cells with male or female eggs in them.

SUMMARY

Compared to other cucurbit crops, pollen production in the acorn squash crop studied here is slightly higher than cucumber (*Cucumis sativus*; 10,739 pollen grains/synandrium), and muskmelon (*Cucumis melo*; 11,176 pollen grains per synandrium) but is much lower than watermelon (*Citrullus lanatus*; 30,739 pollen grains/synandrium) or pumpkin (*Cucurbita pepo*; 49,028 pollen grains/synandrium) (Stanghellini et al. 2002; Willis Chan 2020).

Pollen losses to waste alone represented about 13% of the pollen production in an acorn squash staminate flower, almost twice the amount of pollen needed for pollination (7.7% of total pollen produced by the plant). In our study system, waste was caused exclusively by the activities of mated female hoary squash bees on staminate flowers. It should be noted that not all pollen wastage could be quantified. Pollen was also lost to the system as bees flew from flower to flower and as they entered their nests (Fig. 2). The amount of waste pollen in the system may increase if other bees, including male hoary squash bees, bumble bees, or honey bees, were also present. In open systems where corbiculate bees, such as honey bees and bumble bees are commonly present, pollen may also be lost as those bees often groom unwanted *Cucurbita* spp. pollen off themselves, likely because the pollen does not pack well into their corbiculae or because it does not meet their dietary requirements (Fig. 3; Percival 1947; Parker 1981; Tepedino 1981; Vaissière & Vinson 1994; Lunau et al. 2015; Brochu et al. 2020;).

Although we have never observed any bee species collecting waste pollen, we have observed ants (*Prenolepis imparis* and *Lasius neoniger*) collecting it (Fig. 4). Further work might consider how the waste pollen is used by other organisms including pests, such as aphids (e.g., *Myzus persicae*) or striped cucumber beetles (*Acalymma vittatum*), within squash pollination systems.



Figure 3. *Cucurbita* crop pollen discarded by a honey bee (*Apis mellifera*) on a leaf (left) and a bumble bee (*Bombus impatiens*) in the process of discarding *Cucurbita* crop pollen (right). Left photo: D. Susan Willis Chan, Right photo: Nigel E. Raine



Figure 4. Ants collecting waste pollen grains from a staminate pumpkin flower. Photo credit: Patrícia Nunes Silva, used with permission.

Female hoary squash bees can carry about 4% of their body weight in pollen (about 3,119 pollen grains) per foraging trip. Compared to other bees, this is quite low. Neff (2008) reports pollen load masses of foraging female solitary bees of 7–64% of their live mass but suggests that these data are skewed towards smaller bee taxa that would be able to carry proportionately more pollen per load than larger bees like the hoary squash bee.

A fully provisioned nest cell contains about 62,719 pollen grains, requiring about 20 foraging trips by a female hoary squash bee. If all pollen in the pollination system is taken by just female hoary squash bees, each bee will need to harvest the pollen supplies of 4.9 acorn squash flowers (after waste and losses to pollination are removed) to fully provision a single nest cell. However, under field conditions, male hoary squash bees and other bee taxa, especially bumble bees and honey bees, also remove pollen from the system (e.g., Fig. 3), and where density of bees is high, competition for pollen may increase causing the number of flowers needed for a hoary squash bee to provision each nest cell to increase.

Going forward, this information will be useful for researchers wishing to design controlled studies in enclosures with hoary squash bees as models. In those systems, for each bee in an enclosure, researchers should budget about 25 staminate flowers or more over the season (assuming reproductive output of ~5 offspring/female: Mathewson 1968; Willis Chan & Raine 2021b).

The information provided here also contributes to the discussion about competing costs for plants and pollinators in mutualistic pollination systems by providing an example of a concrete pollen budget for a crop-wild pollinator system.

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AUTHOR CONTRIBUTION

D.S.W.C. conceived and designed the project, carried out the experimental work and analysis. D.S.W.C. wrote the paper with input from N.E.R. Both authors declare no competing interests. Data sets are provided in the supplementary material.

DISCLOSURE STATEMENT

No potential conflict of interest was reported by the authors.

DATA AVAILABILITY STATEMENT

The data used to write this article are available in the appendices of the article.

APPENDICES

Additional supporting information may be found in the online version of this article:

Figure S1. Acorn squash flowers showing the taping method to prevent bees from entering flowers and accessing pollen supplies.

Table S1. Pollen count per staminate acorn squash flower.

Table S2. Counts of pollen waste collected from staminate acorn squash flowers.

Table S3. Pollen counts from female hoary squash bees returning to their nests with a pollen load.

Table S4. Live weight of female hoary squash bees captured on *Cucurbita* crop flowers.

Table S5. Amount of pollen in fully provisioned hoary squash bee subterranean nest cells.

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