

**EFFICACY OF HONEY BEES AND NATIVE BEES AS POLLEN VECTORS FOR  
WATERMELON (*CITRULLUS LANATUS*) AND SOME ECOLOGIC PREDICTORS OF  
POLLINATOR ABUNDANCE**

by

ELEANOR KATHARINE SPICER

(Under the Direction of Keith S. Delaplane)

**ABSTRACT**

This study compares pollen carrying and deposition capabilities of honey bees and native pollinators such as the squash bee (*Peponapis pruinosa*), the sweat bee (*Halictidae* sp.), and the bumble bee (*Bombus* sp.), using crimson sweet watermelon (*Citrullus lanatus*) as the target crop. This study also measured various ecological predictors of pollinator abundance, such as distance to bee nest site, distance to wooded margins, number of field sides facing wooded margins, distance to undisturbed land, and percent nesting ground exposed nearby. The best ecologic predictors of native bee presence were distance to nest site and percent of ground exposed in nest site. All taxa observed exhibited a capacity to fully pollinate watermelon plants. While *Apis mellifera* carry the most target pollen in their bodies, *Bombus* sp. deposit the most target pollen on the stigma in a single visit.

**INDEX WORDS:** native pollinators, honey bee, *Peponapis pruinosa*, *Apis mellifera*, *Bombus* spp., *Xylocopa* spp., *Citrullus lanatus*, pollinator diversity, ecological predictor

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Eleanor Katharine Spicer

B.S., North Carolina State University, 2003

A Thesis Submitted to the Graduate Faculty of The University of Georgia in Partial Fulfillment  
of the Requirements for the Degree

MASTER OF SCIENCE

ATHENS, GEORGIA

2007

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ELEANOR KATHARINE SPICER

Major Professor: Keith S. Delaplane

Committee: Darold P. Batzer

Dan L. Horton

Electronic Version Approved:

Maureen Grasso

Dean of the Graduate School

The University of Georgia

December 2007

## ACKNOWLEDGEMENTS

I would like to thank my family, especially my parents Kathryn and Jamesie, brother Will, Aunt Ann, and Gregory Rice for all of their love, encouragement, and support. I would also like to thank my friends in the UGA entomology department, both students and staff. Thank you to Herb Yeomans, Carl Hall, and the people at the UGA Plant Sciences Farm for going beyond their jobs to help me. Dan Harris, I appreciate your kindness and technical assistance and thank you to the employees at the UGA Bee Lab and the Horticulture Farm. Thank you also to Consuello Arellano for all that you have contributed. Finally, I would like to thank my committee, Dr. Batzer and Dr. Horton for all of your help. Dr. Delaplane, I would like to thank you for your patient guidance and for the opportunities you have given me.

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## CHAPTER 1

### INTRODUCTION

Honey bees are purported to pollinate \$ 1.8-8.3 billion of produce in the US annually (Southwick and Southwick 1992, Sanford 1992). However, factors such as pesticide misuse, introduced diseases, and loss of government subsidies are contributing to the decline of beekeeping as a profession in the United States (Kremen 2001). A majority of global crops could display production loss owing to this pollinator limitation (Klein et al. 2006). While the demand for pollination remains constant or increases and the supply of commercial and wild honey bees decreases, native pollinators are being considered as viable options for mass crop pollination. Honey bees are relatively dependable generalist pollinators that are easily managed and transported. However, although honey bees are placed in target crops like watermelon for pollination, they often prefer other crops or wild plant species (Delaplane and Mayer 2000). Many native pollinators are present on farms and their value as pollinators often underestimated or overlooked by farmers (Greer 1999). Although these pollinators occur naturally on farms, many factors, such as habitat fragmentation, agricultural destruction of habitat, grazing by livestock, and pesticides are decreasing the numbers of these beneficial Hymenopterans (Kearns and Inouye 1997). Generalist pollinators like honey bees and native halictids pollinate many species of plants, whereas specialists like the cucurbit bee *Peponapis pruinosa* may pollinate only a few. The generalist-specialist trade-off is that, while generalists are capable of pollinating

many species of plants, specialists are more effective pollinator on their target crop. For example, *Peponapis* sp. are shown to deposit four times as much *Cucurbit* pollen as *A. mellifera* and both males and females of *Peponapis* make significantly more visits to the *Cucurbit* plants, requiring fewer of these specialist insects to pollinate more plants (Canto-Aguilar and Parra-Tabla 2000). To compensate for a loss in pollination efficacy by generalists, some plants produce more flowers. An increase in flower production at a local (conspecific) scale results in a linear increase in the number of pollinators (Morgan 2000). However, if that increase in local flowers is interspecific (i.e., a case of habitat diversity) is the efficacy of pollinators affected, however abundant they may be? Under the conditions of a more natural habitat, in which there is greater floral diversity, it is reasonable to expect that the relative abundance of target pollen on the body of the generalist bee would be affected. Are specialist bees and generalists similarly responsive to such conditions? Understanding the plant-pollinator interactions of these species is useful for conservation. Furthermore, the recent declines in honey bee numbers in the United States and Europe incite a need to further develop and understand native bees as crop pollinators (Kearns et al. 1998). In this study, the pollen vectoring efficacy of native pollinators and honey bees was compared to better understand the potential benefits of natural pollinators.

As production costs increase in traditional agriculture and the negative ecologic effects of some of its practices become more apparent, sustainable agriculture is becoming increasingly popular in today's rapidly changing agro-economy (Feenstra 1997). One component of sustainable agriculture is cultivating a species diverse agro-ecosystem. A diversified agro-ecosystem is usually more economically and ecologically resilient than a traditional monoculture and has many agricultural benefits, such as robust pollen crop and higher crop yield (Feenstra 1997, Francis and Decoteau 1993). However, in the context of crop pollination, a diverse

ecosystem raises questions about pollinator viability if those pollinators are being diverted to non-target plants. Does a diversified agro-ecology necessarily lead to an environment more conducive to improved pollinator diversity, abundance, and efficacy? A proportion of wildlands, important markers of a diversified ecosystem, around a farm field is shown to have a positive correlation with visitation rates by native bees (Kremen 2001). This has been attributed to the preservation of the native bee habitat around the fields. Habitat evaluations have long been considered when examining the quantity and efficacy of bee populations (Klein et al. 2006; Klein et al. 2004; Krauss et al. 2004; Kremen et al. 2002; Jennersten 1998). For example, increased squash bee density has been correlated with no-tillage agricultural practices and semi-natural agro ecosystem habitats are found to be richer in pollinator species abundance than traditional agro ecosystems, which can result in greater seed production (Shuler et al. 2005; Steffan-Dewenter et al. 2002; Morandin and Winston 2004). The present study evaluated such aspects of landscape as distance to nest site, distance to wooded margins, number of sides facing wooded margins, distance to undisturbed land, and percent ground exposed nearby, ideal for ground-nesting bees as predictors of pollinator abundance.

Another aspect of this ecological diversity can be accomplished by intercropping. Numerous plant species have similar bloom periods and require the same animals to pollinate them. This occurrence of flowering species vying for the services of the same pollinators is floral competition (Levin and Anderson 1970). While intercropping increases the level of biodiversity within the field, it also increases the level of floral competition, which can detract from the fitness of either plant. It has been suggested that in nature, staggered flowering of sympatric plants aids in reducing floral competition for pollinators (Ishii and Higashi 2001). However, in agricultural plantations this cannot always be achieved. In one observation year of the study, I

compared the pollen vectoring efficacy of the exotic honey bee (*Apis mellifera*) and native pollinators such as Halictidae, *Bombus* spp., *Xylocopa virginica*, and *Peponapis* spp. under varying levels of floral competition. However, competition as a main effect was never significant in the results of this study. Even so, this design did allow for measuring variation in pollen vectoring capability among the various bee taxa present.

Crimson sweet watermelons (*Citrullus lanatus*) were the model plants for measuring pollinator efficacy in seasons one and two with sunflowers (*Helianthus annuus*) as model competitors in season one.

This study treated the following null statements as testable hypotheses:

- (1) Honey bees and native Hymenopteran pollinators, both generalists and specialists, do not differ in their ability to vector watermelon pollen.
- (2) The proportion and number of wild (non-*Apis*) bees visiting watermelon are not responsive to measurable differences in habitat features suspected of affecting wild bee density.

## CHAPTER 2

### MATERIALS AND METHODS

#### Planting Conditions and Design

This research was conducted during March through August of 2006 and 2007 at the Plant Sciences Farm of the University of Georgia, Oconee County, GA, USA (33°50'N, 83°26'W).

In spring of each year, approximately 500 crimson sweet watermelon seeds were germinated in a greenhouse. Each watermelon flower is open for pollination for only one day, so they are ideal for single-visit observations. Watermelon flowers are also imperfect and so cannot self-pollinate, and they have large, sticky pollen grains that are readily identifiable in comparison with other pollen grains. For these reasons, watermelon plants were chosen as the target crop for this study. After 5 weeks, seedlings were transplanted to each of twelve plots at the University of Georgia Plant Sciences Farm. Half of the plots were managed in an attempt to provide floral competition and the other half to provide minimal competition. Each plot contained four rows of watermelons, ten plants per row. For each competition plot, eight rows of sunflowers were planted 45 cm apart between two rows of watermelons (Fig. 1). To create conditions of floral competition or no floral competition, six of the twelve plots were chosen at random to be competition plots; the other six were designated non-competition plots. The non-competition plots had sunflower heads cut off before they bloomed. Plots were planted across the farm in locations showing unique combinations of the habitat metrics studied. Nine or 20 honey bee

colonies (years one and two, respectively) were placed at one end of the farm to ensure the presence of honey bees in the study. Distance from apiary for each plot was determined by using the eTrex Vista GPS system (Garmin 2002). Sampling for bee taxonomic diversity and vectoring capabilities was measured across an 8-13 day period.

### Habitat Appraisal

Each year, each of the 12 plots was measured with the following metrics of bee habitat quality: nearest wooded margin (m), nearest non-managed land (m), number of plot sides (#4) facing a forested margin within 200 m, nearest likely bee nesting site (m), and percentage of ground cover within nesting site exposed.

All distances were measured with a meter wheel or a measuring tape. The nearest soil-nesting bee nesting site was determined by the observer's walking around the perimeter of each plot and locating the nearest patch of exposed, uncultivated earth ideal for native bee nesting. The percent of exposed ground within the nesting site was determined by placing a 1 dm x 1 dm grid randomly over the nesting site and estimating the percent of exposed ground within the dm square, with ten replications performed for each plot.

The response variable for each plot was the number of bee flowers visitors each day other than *A. mellifera*. Different bee taxa are active at different times of the day. For example, *Peponapis* sp. are active pre-dawn until flower closure in the afternoon, whereas halictids show little activity before 0900 hours (Shuler et al. 2005). Therefore, taxonomic diversity surveys were confined to a period of 0800-1145 hours (EST) to ensure as many species as possible were observed. At the beginning of each season, plot numbers were drawn in a random sequence for observation times, ensuring that each plot was observed once a day, and each plot was observed

at every observation time over the course of the field season. During each survey day, four observers measured the twelve plots, three plots per observer. Plots were measured at one of three observation times (0800, 0915, and 1030 AM EST) and observations were synchronized to eliminate variation from time. Each observer received training in bee identification prior to the survey. While observing the insects for the survey, he or she walked slowly between watermelon aisles recording by sight the number and taxon of every bee visiting an open watermelon flower, for a total of 8 min observation time per plot (2 min x 4 aisles). These surveys were taken on each observation day.

### Pollen Vectoring Capacity

Observations were recorded in 3 one-hour episodes beginning at 0800h and ending at 1145h, allowing for 15 minutes between episodes. This occurred over a 13-day span in year one or an 8-day span in year two. Pollen vectoring capability of different bee taxa was appraised with single bee flower visits. On each day, 10-15 individual virgin female flowers were bagged with light-permitting pollinator-excluding organza drawstring bags and numbered consecutively by plot the day before anthesis. At the beginning of each sampling episode, a bag was removed from an opened flower and the taxon of bee pollinator subsequently visiting it recorded. When possible, the individual bee was captured and labeled. Any other floral visitors attempting to visit the single-visit observation flower were prevented from touching the flowers by waving them away before they landed on the flower. Flowers were harvested immediately after one bee visit. The number of watermelon pollen grains per stigma was measured using a hemacytometer after the methods of Dafni (1992). Each stigma was washed in 0.9 ml of 70% ethanol, 4 drops of detergent, and 3 drops of 0.5% basic fuchsin. Each pollen-covered stigma was then shaken in solution for 90 seconds using a Thermolyne MaxiMix II Type 37600 Mixer to remove pollen

from its surface. The pollen solution was then placed on a hemacytometer (Fisher Scientific), and numbers of watermelon and other pollen grains counted. Numbers of pollen grains in each of two categories (watermelon, non-watermelon) for each stigma were derived by using the extrapolation formula provided by the manufacturer (Glover and Barrett 1986).

Voucher specimens of each pollinator taxon were collected and their relative abundance of target pollen on their bodies determined by using a hemacytometer as above. The relative proportion of watermelon pollen, sunflower pollen, and “other” pollen (neither target species) was derived for each bee.

### Statistical Analyses

The linear relationship of (1) percent non-*Apis* and (2) number of non-*Apis* per plot per day were each tested with the independent environmental variables percent ground exposed, distance to wooded margin, distance to nest site, number of sides facing wooded margin within 200 m, and nearest non-managed land with regression analyses (SAS 2002-2003). The SAS Mixed Procedure (SAS 2002-2003) was used to test a hypothesis of no difference for effects of pollinator taxon and time of day on number of watermelon pollen grains and non-watermelon pollen grains carried on the bee’s body. Random effects were year and day, and least square means were reported and separated by Tukey’s test. When main effects taxon and time interacted, analyses were run by time. The effects of pollinator taxon on number of watermelon pollen grains and non-watermelon pollen grains deposited on watermelon stigma after one bee visit were analyzed as a split plot design with year as main plot and day repeated. Main effects time and taxon were tested with the error term replication (year\*time\*taxon) and means separated by Tukey’s test (Proc GLM, SAS 2002-2003).

## CHAPTER 3

### RESULTS AND DISCUSSION

#### Habitat Appraisal

Of the metrics studied for habitat quality, only distance to nearest nesting site and percent of ground exposed varied in a linear fashion with the percentage of non-*Apis* bee visitors (Figs 2 and 3) in years 2006-2007, and percent of ground exposed in 2006 was the only metric observed that varied in a linear fashion with number non-*Apis* bee visitors per day (Fig 4). Percent non-*Apis* appeared to vary with distance to nest site in a significantly negative linear fashion ( $p= 0.05$   $R^2= 0.14$ ) (Fig 2). Percent non-*Apis* appeared to vary with percent ground exposed within that nest site in a significantly positive linear fashion ( $p= 0.05$   $R^2= 0.13$ ) (Fig 3). Percent non-*Apis* was examined in addition to number of non-*Apis* per plot per day, because observing this percent is a close metric to observing how many wild indigenous bees are in an area in comparison to imported bees, a good indicator of habitat quality. Furthermore, number non-*Apis* bee visitors per day in 2006 also appeared to vary with percent ground exposed within the nest site in a significantly positive linear fashion ( $p= 0.03$   $R^2= 0.39$ ) (Fig 4). The percent ground exposed data in 2007 did not show any statistical significance for number of native pollinators present per day. However, severe drought conditions may have negatively impacted pollinator abundance in field sites.

While it has been purported that proximity to an apiary or a wooded margin provides an abundance of beneficial pollinators for crops, this study detected no relationship. Many native pollinators, such as *Peponapis*, halictids, and to some extent *Bombus* are ground-nesting bees (Appendix I). *Apis mellifera*, on the other hand, prefer to nest in tree holes and are more likely found in wooded areas (Winston 1987). It is therefore reasonable that, while the percent of non-*Apis* present each day exhibits a negative relationship with an increasing distance to nest site (Fig 2), the percent of *A. mellifera* present per day in relation to nest site was not statistically significant. Close proximity to natural habitat has been shown to have a positive effect on bee abundance and diversity (Kim et al. 2006). The results of this study confirm that effect and also show a positive relationship between percent nesting site ground exposed and amount of native pollinators present (Fig 4).

While the need for maintenance of natural upland habitats and the practice of no-till agriculture to foster a large native pollinator community has been established (Kremen et al. 2004, Morandin and Winston 2006), this is the first study to show a positive relationship between the percent of compacted ground exposed in the nesting site and the amount and percent of native pollinators present. Increased amounts of exposed, compacted, undisturbed earth provide these native pollinators with more nesting sites per  $\text{dm}^2$ , which increases the number of available pollinators for crops in a given location.

When considering how to increase natural populations of bees, a landscape approach to pollinator habitat diversity is key to improving both native pollinator populations and crop yields. In the case of ground nesting bees such as *Peponapis*, halictids, and to some extent members of *Bombus*, these data suggest it is important to encourage and maintain nesting sites consisting of undisturbed compacted earth near agricultural fields.

### Pollen Vectoring Capacity

Average number of pollen grains carried on the body of each bee was significantly affected by the main effects bee taxon ( $F=14.36$ ;  $df=3,105$ ;  $P=0.0001$ ) and time of day ( $F=4.43$ ;  $df=2,105$ ;  $P=0.0143$ ). Lsmeans are presented in Table 1. Average number of non-watermelon pollen grains carried on the body of each bee was subject to an interaction between main effects, so it was analyzed separately by time. There was a significant effect of bee taxon at 10:15 and 11:30 ( $F=9.43$ ;  $df=3,39$ ;  $P=0.0052$ ). Mean separations are presented in Table 2.

Honey bees carried significantly more target pollen than *Bombus* spp. and Halictidae (Table 1). Target pollen loads of *Peponapis*, *Apis* and *Bombus* were statistically similar. Species carried diminishing amounts of target pollen as the day progressed. All species observed in this study carried, on average, more than the 500-1000 watermelon pollen grains on their bodies required to adequately pollinate a watermelon stigma (Adlerz 1966). *Apis mellifera* and *Peponapis* sp. both carry more target pollen on their bodies on average than halictids, suggesting that the foraging behavior and morphology of the squash and honey bee are comparatively well-suited for pollinating watermelons. Squash bees are dependent on *Cucurbit* pollen and tend to forage more or less exclusively on this group while it is in bloom (Michener 2000) (Appendix I). Although its surface area is much smaller than the surface area of the average member of *Bombus* sp., the average halictid carried comparable amounts of target pollen on its body overall, suggesting that halictids are comparable pollen vectors in open pollination environments. Halictids also exhibit less variation in numbers of pollen grains carried than members of *Bombus* at any given observation period, suggesting they may forage more exclusively on the target crop and so are better-suited for watermelon pollination than members of *Bombus*. Furthermore,

members of *Bombus* carry much more non-target pollen on their bodies than any other species of bee, which is an indicator of the generalist nature of the bumble bee (Table 2).

While the amounts of target pollen carried on each bee diminished throughout the day, the amounts of non-target pollen on the bodies of the bees increased as the day progressed. As the watermelon flowers are exploited over the course of the day and their resources wane, bees foraging on the target crop will turn to other plants to gather resources.

### Pollen Deposition

Average number of pollen grains deposited in one bee visit was significantly affected by the main effect bee taxon ( $F=6.81$ ;  $df=5,63$ ;  $P=0.0001$ ). Mean separations are presented in Table 3.

Average number of non-watermelon pollen gains deposited in one bee visit was marginally significantly affected by taxon ( $F=2.23$ ;  $df=5, 63$ ;  $P=0.0618$ ). Mean separations are presented in Table 4.

Each taxon of pollinator deposited in one visit, on average, more than the required 500-1000 pollen grains necessary for fruit set (Adlerz 1966) (Table 3). Members of *Bombus* deposited the most pollen grains in a single visit, but also had the greatest amount of variability and the least individual representation in the field, making them more unreliable as pollinators of watermelon than other species observed. Despite the fact that they are modest pollen carriers, *Bombus* deposited a greater amount of target pollen and a greater proportion the target pollen carried on its body than any of the other species observed. In this way, *Bombus* is a more effective pollinator (Stanghellini et al. 2002). *Peponapis* and *Apis* deposited comparable amounts of pollen on stigmas in a single bee visit, although *Peponapis* did so with the least amount of variability. Halictids deposited the least amount of target pollen in each visit, but their large

numbers evident in the field (Appendix I) may compensate for their small single visit deposition as shown by Dedej and Delaplane (2003) for *A. mellifera*. A single visit from *A. mellifera*, *P. pruinosa*, or *Bombus* provides a stigma with a statistically comparable amount of pollen to a flower that has been openly pollinated.

Because reducing pollen competition on a stigma results in greater plant fitness, bees that deposit greater amounts of target pollen and less amounts of other pollen would better pollinate the target crop (Sedgley and Blesing 1982). Although they carry less non-target pollen on their bodies than *Peponapis* at any given time, *Apis mellifera* deposit a much larger proportion of non-target grains-to-target grains on the watermelon stigma than *Peponapis* (Table 4). This result could be a function of morphology, as the comparatively large, sticky watermelon pollen grains may be more easily combed into a honey bee's pollen basket for storage than the smaller other pollen grains. Once in the pollen basket, this pollen is excluded from deposition (Thorp 1979). *Peponapis* sp., on the other hand, store pollen between hairs on their legs and abdomen, making more pollen available for deposition at any given visit (Appendix I).

While the amount of watermelon pollen carried at the 11:30 observation period significantly decreased overall, the amount of watermelon pollen deposited at that time period exhibited a steady increase from the other two observation periods. The amount of non-target pollen carried increases throughout the day, being highest at the 11:30 observation period, but the amount of non-target pollen deposited at that observation period remains statistically similar to the amounts at the other two observation periods. This increase in target pollen and decrease in non-target pollen deposited later in the day suggests that flowers opening later in the morning or those being pollinated later in the morning will be more adequately pollinated in single visits

than those open for pollination earlier in the morning. For flowers opening later in the day, this greater pollen deposition could compensate for a reduced bloom time.

With a mean range of 403-9500 (Table 3), the average number of deposited pollen grains reported here is conspicuously higher than the mean range of 55-152 reported previously for watermelon (Stanghellini et al. 2002). Aside from technical differences in our methods, another explanation may be that our study used a smaller density of supplemental pollinators. Because of this, a greater ratio of available pollen per pollinator is suggested. Our data are more congruent with values published for non-watermelon cucurbits. Winsor et al. (2000) reported that 29% of the flowers of *Curcubita foetidissima* receiving a single pollinator visit have  $\geq 900$  pollen grains on the stigma. Quesada et al. 1993 classified as “small” a single bee visit deposition of 460 pollen grains on *C. pepo* and *C. texana* and “large” a deposition  $>10,000$  pollen grains.

In conclusion, it is important to maintain a habitat for the native pollinators to promote pollination of the target crop. In the case of this study, that optimal habitat would be undisturbed, compacted earth with a large percentage of exposed ground within a 0 and 6m distance from the target crop. All taxon observed exhibited a capacity to fully pollinate watermelon plants. While *Apis mellifera* carry the most target pollen in their bodies, *Bombus* sp. deposit the most target pollen on the stigma in a single visit.

Table 1. Effects of bee taxon and time of day on average (lsmeans± sd) watermelon pollen grains on body of bee flower visitor. There were no interactions between taxon and time, so analyses were run with both terms and mean separations (paired *t*; ±#0.05) performed on overall taxon means and time means.

Taxon	9:00	10:15	11:30	Taxon means
<i>Apis mellifera</i>	19445±5672	30374±4912	16666±4631	22162±2939 a
<i>Peponapis pruinosa</i>	23384±4393	29027±4189	2667±8021	18359±3353 ab
<i>Bombus</i> spp.	25833±9823	2890±8021	1998±8021	10240±5002 bc
Halictidae	3045±3032	1606±2962	1649±3187	2100±1768 c
Time means	17927±3134 a	15974±2678 a	5745±3165 b	

Table 2. Effects of bee taxon and time of day on average (lsmeans± sd) non-watermelon pollen grains on body of bee flower visitor. There were interactions between taxon and time, so analyses were run by time. Column means with different letters (paired *t*) are significantly different ( $\neq 0.05$ ).

Taxon	9:00	10:15*	11:30
<i>Apis mellifera</i>	2889±2079 a	4334±1601 b	4630±48132 b
<i>Peponapis pruinosa</i>	4667±1611 a	7061±3567 b	12667±83366 b
Halictidae	2094±1112 a	2383±1583 b	5666±33126 b
<i>Bombus</i> spp.	5167±3602 a	151667±127674 a	350443±83366 a

\* for 10:15 Proc Mixed calculated all lsmeans as negative values, so for this column reported values are non-adjusted.

Table 3. Effects of bee taxon and time of day on mean ( $\pm$  sd,  $n$ ) watermelon pollen grains deposited on watermelon stigma by one bee visit. There were no interactions between taxon and time, so analyses were run with a whole model and mean separations (paired  $t$ ;  $\pm$ #0.05) performed on overall taxon means and time means.

Taxon	9:00	10:15	11:30	Taxon means
<i>Bombus</i> spp.	.	4000 $\pm$ 4000, 2	9500 $\pm$ 9500, 2	6750 $\pm$ 4498, 4 a
<i>Apis mellifera</i>	1333, 1	466 $\pm$ 368, 7	3105 $\pm$ 1834, 6	1659 $\pm$ 842, 14 b
Halictidae	710 $\pm$ 276, 15	403 $\pm$ 139, 19	1043 $\pm$ 354, 15	693 $\pm$ 149, 49 b
<i>Peponapis pruinosa</i>	1183 $\pm$ 475, 9	925 $\pm$ 372, 9	2500 $\pm$ 2500, 2	1199 $\pm$ 335, 20 b
Open pollination	1353 $\pm$ 246, 47	2899 $\pm$ 486, 51	2643 $\pm$ 454, 31	2274 $\pm$ 245, 129 b
Virgin flower	137 $\pm$ 70, 17	409 $\pm$ 273, 22	132 $\pm$ 132, 5	272 $\pm$ 140, 44 b
Time means	995 $\pm$ 154, 89 a	1673 $\pm$ 268, 110 a	2309 $\pm$ 428, 61 a	

Table 4. Effects of bee taxon and time of day on mean ( $\pm$  sd,  $n$ ) non-watermelon pollen grains deposited on watermelon stigma by one bee visit. There were no interactions between taxon and time, so analyses were with a whole model and mean separations (paired  $t$ ;  $\neq 0.06$ ) performed on overall taxon means and time means.

Taxon	9:00	10:15	11:30	Taxon means
<i>Apis mellifera</i>	6000, 1	904 $\pm$ 904, 7	1500 $\pm$ 806, 6	1524 $\pm$ 649, 14 a
<i>Peponapis pruinosa</i>	148 $\pm$ 113, 9	704 $\pm$ 625, 9	667 $\pm$ 667, 2	450 $\pm$ 287, 20 a,b
Halictidae	400 $\pm$ 201, 15	579 $\pm$ 246, 19	649 $\pm$ 328, 15	545 $\pm$ 149, 49 a,b
Open pollination	284 $\pm$ 116, 47	640 $\pm$ 247, 51	193 $\pm$ 119, 31	403 $\pm$ 111, 129 a,b
<i>Bombus</i> spp.	.	500 $\pm$ 500, 2	0 $\pm$ 0, 2	250 $\pm$ 250, 4 b
Virgin flower	98 $\pm$ 80, 17	318 $\pm$ 194, 22	0 $\pm$ 0, 5	197 $\pm$ 102, 44 b
Time means	318 $\pm$ 97, 89 a	585 $\pm$ 147, 110 a	427 $\pm$ 135, 61 a	

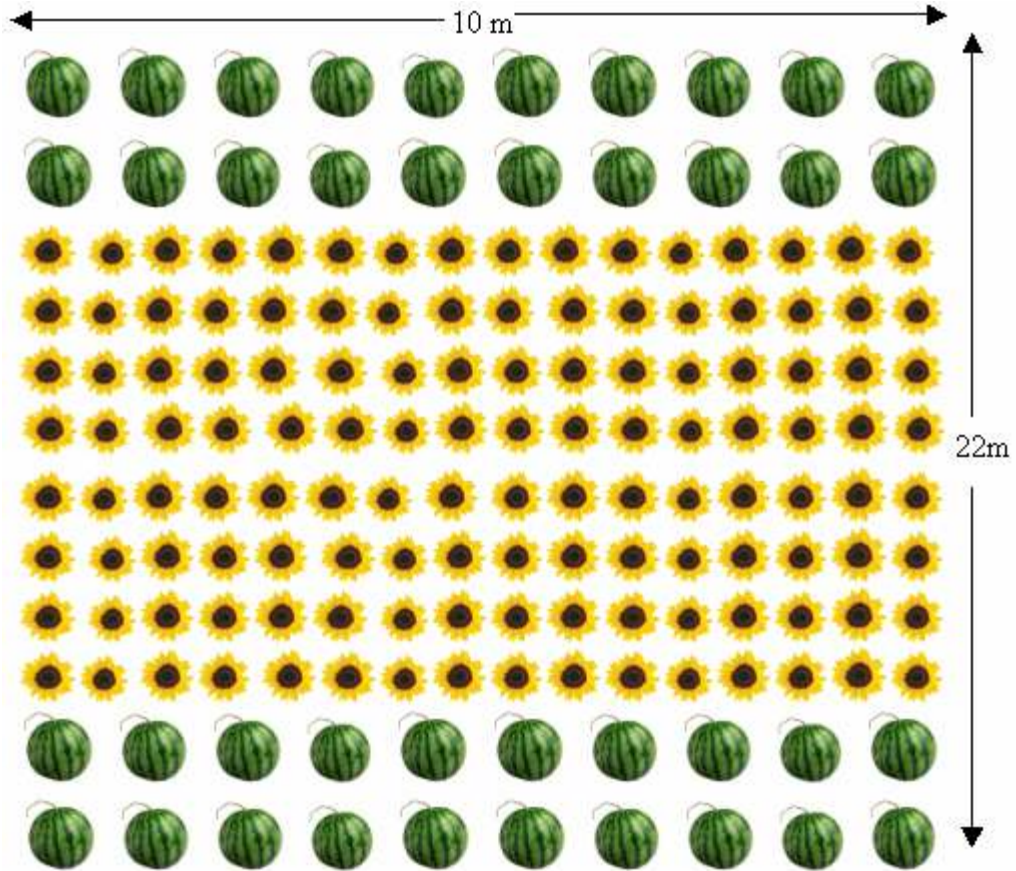


Fig. 1. Experimental plot with 10 x 4 watermelon plants and 8 sunflower rows

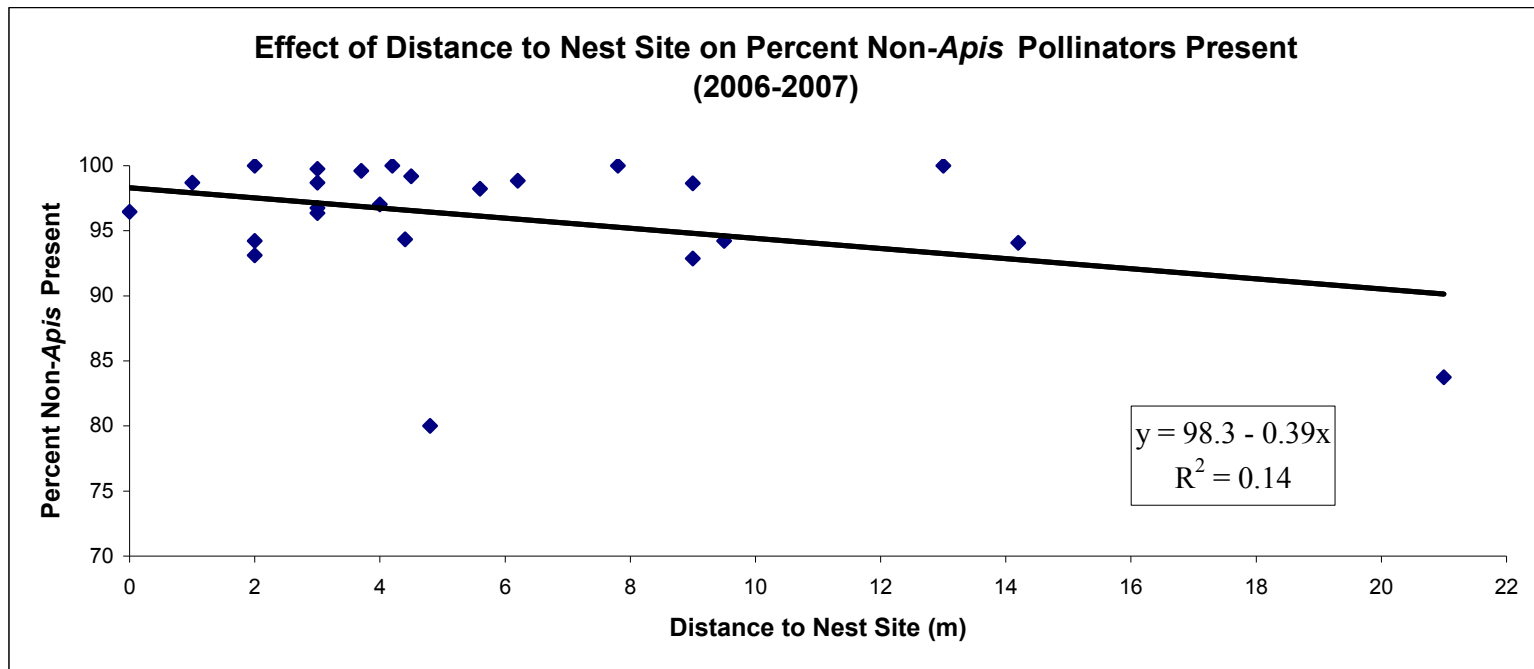


Fig. 2. Effect of distance to nest site on percent non-*Apis* pollinators present in 2006-2007.

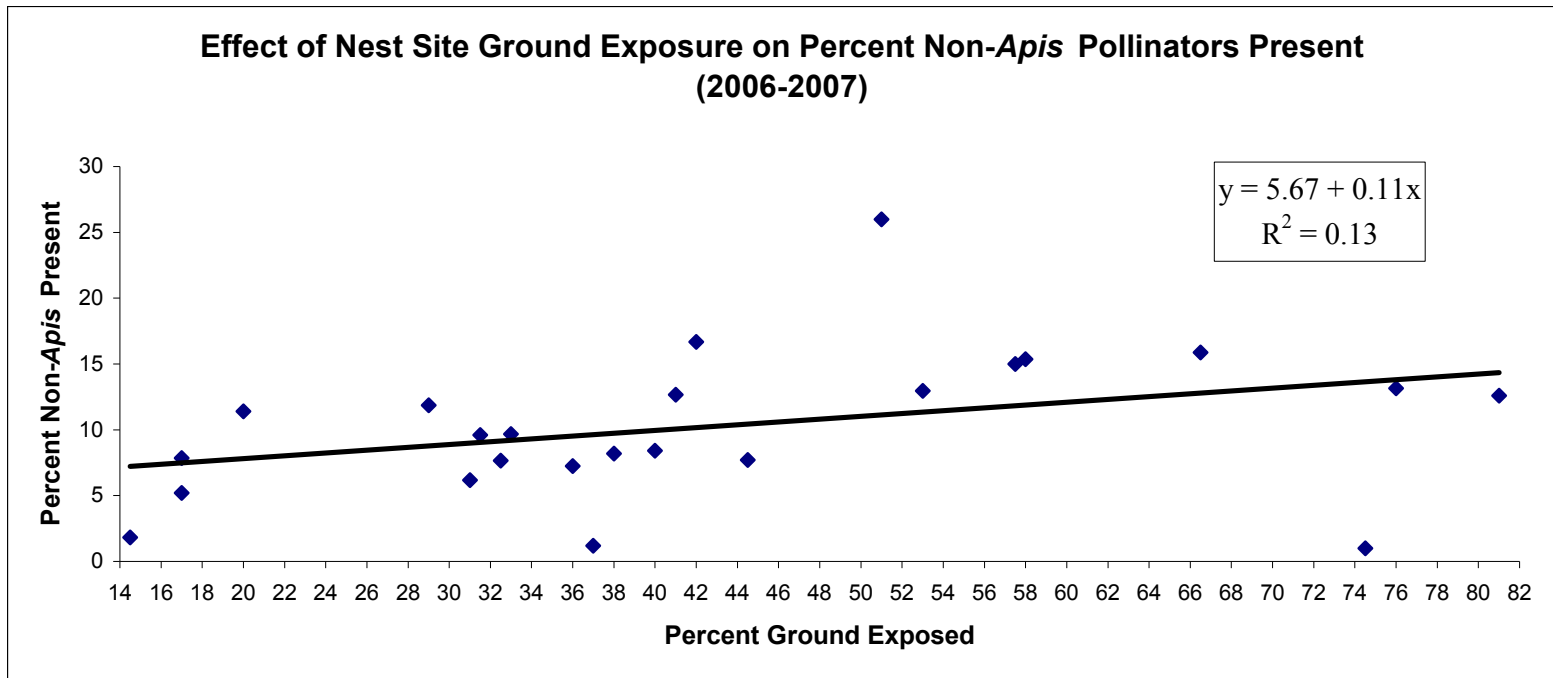


Fig. 3. Effect of percent ground exposed on percent non-*Apis* pollinators present in 2006-2007.

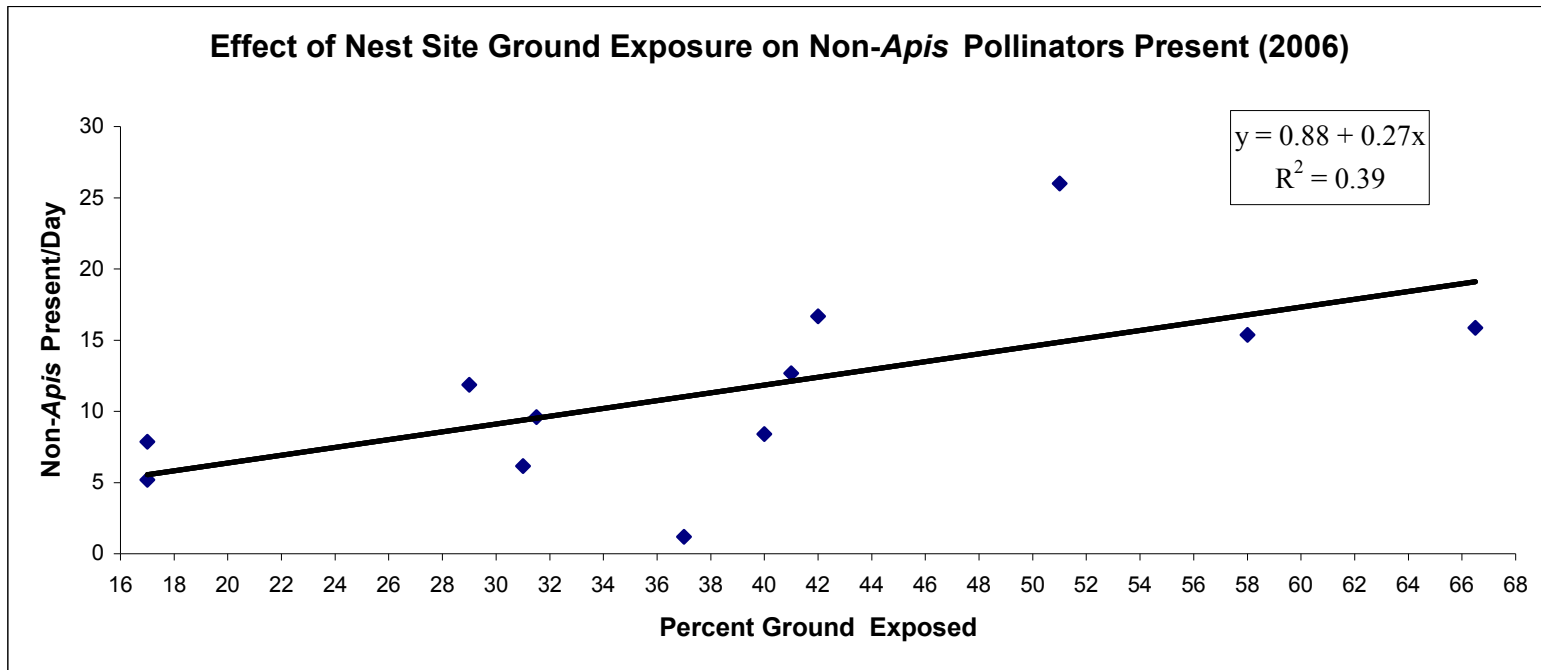


Fig. 4. Effect of percent ground exposed on the number of non-*Apis* pollinators present in each plot per day in 2006.

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## APPENDIX I

The following are descriptions of the bee taxa observed pollinating crimson sweet watermelon flowers throughout our study.

*Peponapis pruinosa pruinosa* (Say)

12.5-14 mm (♀) and 11-13 mm (♂) in length, *Peponapis pruinosa pruinosa* (common name: squash bee) is distributed from Utah and Arizona, and eastward to the New England states and Georgia from June to September. The subspecific designation of *pruinosa* is needed to distinguish from another subspecies in southern Texas (Mitchell 1962).

Like other species of the genus *Peponapis* Robertson, *Peponapis pruinosa pruinosa* has a strongly protuberant clypeus, and the anterior articulation of the mandible is twice as far from the eye margin as the posterior articulation (Michener 2000). They have sparse scopa, which is denser on their hind legs and is used for pollen collection. Due to their size and color, many farmers recognize squash bees on their crops but often mistake them for honey bees. The flight pattern of the squash bees on watermelons in this study was observed as more rapid and direct from flower to flower than honey bees, which tended to wander about the plants, and often landed on leaves.

*Peponapis* is dependent on *Cucurbit* pollen, and its presence in Georgia is posited to be after the advent of squash and pumpkin cultivation, as Georgia is outside the native range of this plant (Michener 2000).

*Xylocopa (Xylocopides) virginica virginica* (Linnaeus)

19-23 mm (♀) and 17-21 mm (♂) in length, *Xylocopa virginica virginica* (common name: carpenter bee) is distributed from Kansas to the New England States and south to Florida and Texas throughout spring and mid- to late-summer (Mitchell 1962).

Females of this subgenus differ from others in having a broad pygidial plate indicated by rows of teeth diverging from the base of the apical spine (Michener 2000). Males differ from other subgenera excepting *Xylocopa* s. str. by the two spines on the outer apex of the hind tibia (Michener 2000).

Often confused by farmers and lay observers with the relatively large and hairy bumble bee, the carpenter bee was an infrequent visitor to the watermelon flowers in this study. Members of this species could more often be seen visiting the competition flower sunflowers.

*Bombus impatiens* (Cresson)

17-21 mm (queen ♀), 8.5-16 mm (worker ♀), and 12-17 mm (♂) in length, *Bombus impatiens* (common name: bumble bee) is widely distributed in North America—from Ontario to Maine, and south to Florida from early spring to late fall (Mitchell 1962).

*Bombus impatiens* were a regular visitor to all plants in this study, owing to their generalist nature and their lack of worker recruitment ability in the nest. While female members

of *Bombus* spp. have polished and bare hind tibiae with a marginal fringe of hairs constituting a corbiculum, the considerably large surface area of these bees is covered in dense, pollen-grabbing hairs, which account for the large pollen-carrying and pollen-depositing numbers reported in this study (Mitchell 1962).

*Apis mellifera* (Linnaeus)

12 mm (worker ♀) in length, the *Apis mellifera* worker (common name: western honey bee) is the form of this species that was collected in the field for this study, as the female worker bee is the form of this bee that forages for nectar and pollen for the hive. *A. mellifera* exhibit a recruitment behavior, in which a scout bee finds a nectar and pollen source and recruits foragers to that source at the exclusion of other nectar and pollen sources (Seeley 1995). For this reason, honey bees tend to stay on an energy source until a richer source is found or the energy is depleted from the source.

The *A. mellifera* worker possesses a corbiculum on her hind tibia for pollen collection and storage. In contrast to the dense hairs on the bodies of *Peponapis* spp. and *Bombus* spp., the body of the female worker bee is covered in less dense hairs (Mitchell 1962, Thorp 1979, Free and Williams 1972).

*A. mellifera* is not native to the United States, with existing members displaying genotypes from colonies imported to the U.S. between the year 1620 and the 1860s (Schiff et al. 1994). Recent studies have debated whether the honey bee is an invasive pest or a beneficial insect (Butzhurny and Moller 1995; Roubik and Wolda 2004; Kearns et al. 1998; Simberloff and Von Holle 1999; Thompson 2004; Butzhurny 1997; Westerkamp 1991). However, in this study, the presence of honey bees did not noticeably detract from crop pollination, native pollinator

presence, or amount of pollen that all pollinators were able to gather from flowers and deposit on stigmas.

### Halictidae

Members of the family Halictidae (common name: sweat bee) are small to moderate in size, often metallic in color, and generally easily recognized by the strongly arched first segment of the medial vein (Triplehorn and Johnson 2005). Although over 500 species of sweat bees are present in the United States, they are representatives of only three subfamilies: Nomiinae, Halictinae, and Rophitinae (Triplehorn and Johnson 2005). Of these subfamilies, only members of Nomiinae and Halictinae were documented in this study. Halictids are ground-nesting bees, preferring compacted earth in which to burrow. Some farming practices such as tilling can destroy the natural habitat of these important native pollinators. In this study, halictids were observed in numbers much higher than all other species combined on and around the target crop.