Farming Practices Influence Wild Pollinator Populations on Squash and Pumpkin

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ABSTRACT Recent declines in managed honey bee, *Apis mellifera* L., colonies have increased interest in the current and potential contribution of wild bee populations to the pollination of agricultural crops. Because wild bees often live in agricultural fields, their population density and contribution to crop pollination may be influenced by farming practices, especially those used to reduce the populations of other insects. We took a census of pollinators of squash and pumpkin at 25 farms in Virginia, West Virginia, and Maryland to see whether pollinator abundance was related to farming practices. The main pollinators were *Peponapis pruinosa* Say; honey bees, and bumble bees (*Bombus* spp.). The squash bee was the most abundant pollinator on squash and pumpkin, occurring at 23 of 25 farms in population densities that were commonly several times higher than that of other pollinators. Squash bee density was related to tillage practices: no-tillage farms hosted three times as great a density of squash bees as tilled farms. Pollinator density was not related to pesticide use. Honey bee density on squash and pumpkin was not related to the presence of managed honey bee colonies on farms. Farms with colonies did not have more honey bees per flower than farms that did not keep honey bees, probably reflecting the lack of affinity of honey bees for these crops. Future research should examine the economic impacts of managing farms in ways that promote pollinators, particularly pollinators of crops that are not well served by managed honey bee colonies.

KEY WORDS pollination, squash, pumpkin, sustainable agriculture, tillage

INSECTS ARE OFTEN VIEWED as the scourge of agriculture, yet many food crops require insect pollination to set fruit. Thus, farm management practices must attempt to reduce the negative effects of herbivorous or disease-transmitting insects while maintaining an environment conducive to pollinator activity. The honey bee, *Apis mellifera* L., is the predominant managed pollinator in much of the world (Robinson et al. 1989). Because it occurs in very large colonies, visits many different crops, and can be transported into and out of agricultural fields, it has provided agriculture with the ability to take aggressive insect control measures through much of the growing season without suffering substantial losses of insect pollination.

The number of managed honey bee colonies in the United States has recently declined due to difficulties in managing them. These difficulties include the recent establishment of parasitic mites and hybridization with the Africanized honey bee, *Apis mellifera scutellata* (Ruttner), in some regions (Peng and Nasr 1985, Weinberg and Madel 1985, Allen-Wardell et al. 1998). The prospect of future honey bee shortages has led to a recent interest in the role of wild pollinators in agricultural systems (Allen-Wardell et al. 1998, Kremen and Ricketts 2000, Westerkamp and Gottsberger 2000, Kremen et al. 2002). Because wild pollinators generally cannot be introduced suddenly to agricultural systems in adequate numbers to ensure pollination, successful management approaches are likely to focus on managing farm conditions rather than the pollinators themselves.

Pioneering work by Kremen et al. (2002) has shown that wild bee populations vary with farming practices and the distance from farms to natural habitats. Working in a major agricultural area of California, they showed that organic farms near natural habitats hosted sufficient wild bees to provide full pollination services for watermelon (*Citrullus* spp. Shrad.), a lucrative crop with large pollination requirements. Wild bee populations were diminished at all other farms, and full pollination required the addition of honey bees. This work points to the possibility that farm management practices that encourage wild pollinator populations may provide ensurance against pollination losses incurred by further honey bee declines and reduce costs associated with renting or maintaining honey bee colonies when they are unnecessary. Some historical evidence shows that honey bees became

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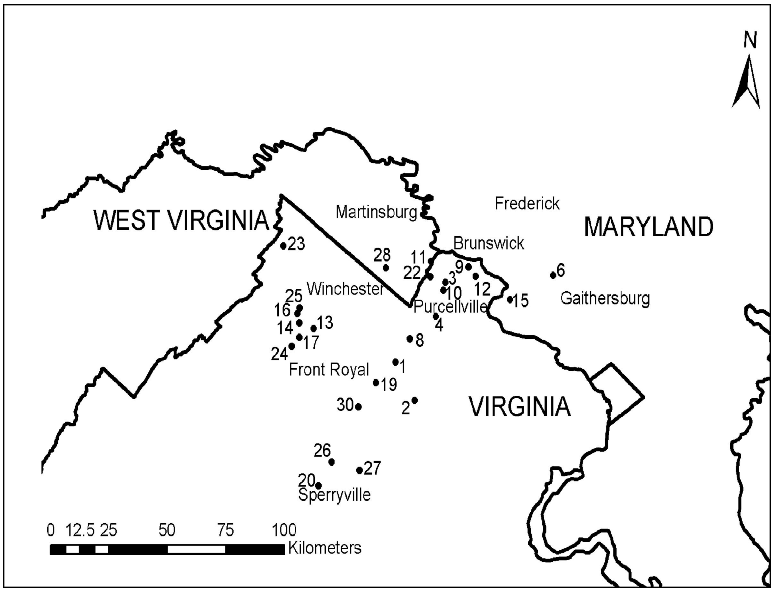

Fig. 1. Distribution of 25 participating farms that grew squash, pumpkin, or both.

increasingly necessary in North American agriculture when intensive farming practices reduced the populations of wild local bee populations (Batra 1995).

To sustain populations, bee species require food resources throughout their active period and undisturbed nesting substrate during their developmental period. Food resources comprise pollen and nectar, which together provide the protein, carbohydrates, and micronutrients required for larval development and adult maintenance (Michener 2000). Nesting substrates vary, but most bee species are either cavity nesters that occupy existing structures such as hollow plant stems (Frankie et al. 1998) or ground nesters that excavate tunnel systems in earthen banks or bare patches of soil (Chapman et al. 1990). Natural cavities are most likely to occur outside the planting area, but bare earth occurs commonly within fields, and many bee species nest alongside crops (Mathewson 1968). The survival of offspring within planting areas depends on nests not being disturbed during development, which takes only a few weeks during the summer in species that have multiple generations (multivoltine) but takes most of the year for univoltine species and for the overwintering generation of multivoltine species.

In the current study, we examine the effect of farming practices on pollinator populations of cultivated squash and pumpkin in the tristate border area of Virginia, West Virginia, and Maryland. Squash and pumpkin (both in genus *Cucurbita*) are valuable, commonly grown crops that require insects for pollination. Although honey bee colonies are often placed in squash and pumpkin fields for pollination, honey bees prefer other crops, weeds, and wild plant species and often fail to visit the target plants if other options are available (Delaplane and Mayer 2000). One of the most effective and persistent pollinators of squash and pumpkin is the bee *Peponapis pruinosa* Say, a specialized, widespread pollinator that collects pollen only from the genus *Cucurbita* (Hurd et al. 1974). Because there are no wild *Cucurbita* in this region, the *P. pruinosa* population is entirely dependent on cultivated *Cucurbita* and cannot maintain refuge populations far from agricultural areas. Our work provides an indication of which bees are primarily responsible for pollination of squash and pumpkin in this region and which farming practices may have the greatest influence on their pollinator populations. We focus on farming practices that seem most directly related to the life cycle of wild bees: tillage (survival of immature bees), crop diversity (continual food supply), and pesticide use (direct impact on adults). This study has implications both for the economics of agriculture and the conservation of biodiversity in agroecosystems.

Materials and Methods

Participating Farms. We compiled a study group of 25 farms within an ≈100 by 130-km area of Virginia, West Virginia, and Maryland (Fig. 1). Participating farmers were initially contacted at regional farmers' markets or at their own farms by driving through the countryside looking for large plantings of squash and pumpkin. Farmers were interviewed concerning their management practices, including pesticide use, tillage, diversity of crops grown, use of managed honey bee colonies, and the number of consecutive years that squash or pumpkin had been grown on the site. Twelve of the participating farms did not use pesticides, whereas 13 applied one or more types of pesticides. Planting area of the target crops ranged from <0.5 to 40 ha (median 0.8). Total farm area ranged from <0.5 to 400 ha (median 80.9).

Insect Surveys. Each farm was surveyed for insect visitation during 1 d between 7 July and 5 August 2003. Surveys were limited to sunny-to-moderately cloudy days in the morning. Squash and pumpkin flowers are open from predawn until ≈1000 hours in this part of the United States, and individual flowers last a single day only. Although squash bees fly from predawn until flower closure, other potentially important pollinators such as honey bees and bumble bees (*Bombus* spp.) were not active until well after dawn. Thus, we confined insect surveys to a period from 0730 to 0900 hours (EST) to make sure that we would encounter all the main pollinator species if they were present on the target plant species at the study site. Pollinator species that may show little activity before 0900 hours, such as sweat bees (Halictidae), are likely underestimated by our methodology. Unless there is a shortage of pollinators, however, most of the pollinating activity has already been carried out by that time of day. Surveys were carried out by one to three researchers trained to recognize the main pollinators without collection. Training was done through field experience with an experienced entomologist (T.H.R.) and through use of a local reference collection at Blandy Experimental Farm. Bumble bees were identified only to genus.

At each farm, we recorded bee abundance and identity by using methods based on those of previous researchers studying pumpkin pollination (Willis and Kevan 1995). During each survey, researchers slowly walked along farm rows counting the number of open flowers and the number and type of bee species seen in flowers. On farms with small plantings, all open flowers were surveyed once, but on larger plantings, fields were divided into regions and subsampled.

Analysis. Many participating farms were clustered geographically and any regional environmental factors influencing pollinator populations could influence our results independent of farming practices. Therefore, we tested for spatial autocorrelation as a prerequisite to the use of parametric statistics for presenting our results. Following Sokal and Rohlf (1995), we conducted a Mantel test of association between corresponding elements of two matrices. One of these matrices held the intersite distances for all 25 participating farms based on latitude and longitude; the other matrix held intersite differences in pollinator population density for all 25 farms. Separate matrices were generated for squash bee, bumble bee, and honey bee intersite differences in population size. We calculated the Mantel Z statistic as the sum of the cross products of corresponding elements of the two matrices. The significance of the Z-statistic was tested by a Monte Carlo algorithm that randomly shuffled the elements of one matrix then calculated a Z-statistic based on shuffled data. Because we were concerned with a positive association between pollinator population size and spatial proximity, we looked for associations in the randomized data that showed as much of a positive association between these factors as the association in the actual data. We carried out 4,999 permutations for each test and calculated the test statistic as the number of permutations with as high a Z-statistic as the original data + 1 divided by the total number of permutations + 1. The algorithm was written in VisualBasic by T.H.R.

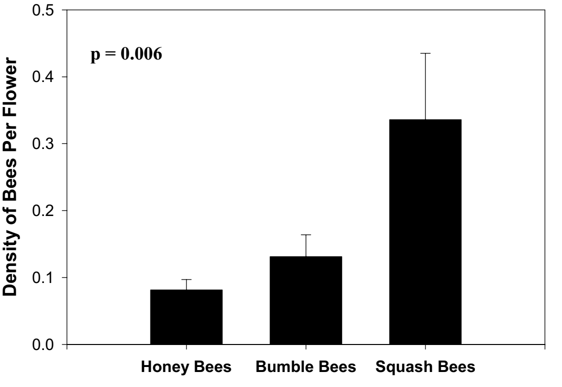

Fig. 2. Density of three main squash and pumpkin pollinators across 25 farms. Mean and SE given for each taxon across all sites at which the taxon occurred (i.e., excluding zero values).

We compared pollinator density (per flower surveyed) of honey bees, *P. pruinosa*, and bumble bees by using a general linear model analysis of variance (ANOVA) with farm and pollinator type as factors, pollinator density as the response variable, and the adjusted sum of squares as the error term. We tested the significance of farming practices on pollinator density through a general linear model by using the categorical variables of tillage/no-tillage and pesticide/no pesticide as factors. The general linear model was carried out using Minitab, version 13.1 (Minitab, Inc. 2000) statistical software. The density of honey bees on squash and pumpkin on farms with and without managed honey bee colonies was examined using a *t*-test.

Results

The specialist bee *P. pruinosa* occurred at 23 of 25 sites and was the most common squash and pumpkin pollinator at 15 of those sites. Bumble bees visited the target plant at 16 sites, predominating at six, whereas honey bees were observed at 13 sites and predominated at four. In addition to visiting squash and pumpkin at more sites, *P. pruinosa* occurred at greater densities within sites (Fig. 2). Other sporadically encountered bees that generally occurred in low abundance were various halictid species (*Lasioglossum* spp., *Agapostemon* spp., and Augochlorinae), and *Melissodes bimaculata* Lepeletier.

There was no evidence of spatial autocorrelation on pollinator population size for the main pollinators. Of 4,999 permutations of the pollinator intersite similarity matrix, 1,355 showed as great an association between intersite distance and intersite population size as the original data for *P. pruinosa* ($P = 0.27$). There also was no association between intersite distance and intersite population size for honey bees ($P = 0.47$) or bumble bees ($P = 0.86$).

Table 1. Effect of pesticide use and tillage on *P. pruinosa* density on squash and pumpkin flowers

Source	df	Seq SS	Adj SS	Adj MS	*F*	*P*
Tillage or no-tillage	1	1.0382	1.0382	1.0382	6.09	0.022
Pesticide use	1	0.0602	0.1063	0.1063	0.62	0.438
Error	22	3.7485	3.7485	0.1704		
Total	24	4.8468				

General Linear Model ANOVA with tillage and pesticide use (yes/no) as factors.

Table 2. Effect of pesticide use and tillage on bumble bee density on squash and pumpkin flowers

Source	df	Seq SS	Adj SS	Adj MS	*F*	*P*
Tillage or no-tillage	1	0.0001	0.0001	0.0001	0.01	0.941
Pesticide use	1	0.0001	0.0001	0.0001	0.00	0.960
Error	22	0.3547	0.3547	0.0161		
Total	24	0.3548				

General Linear Model ANOVA with tilling and pesticide use (yes/no) as factors.

Squash bee population density was influenced by tillage practice but not by pesticide use (Table 1). Farms that practiced no-tillage agriculture had almost a three-fold increase in squash bee density (Fig. 3). Neither honey bee nor bumble bee population size was associated with either of these variables (Table 2).

Honey bee population size on squash and pumpkin was not associated with any measured variable, including the practice of keeping honey bee colonies on the farm. Eight farms kept honey bees on the property, but these farms did not have a greater density of honey bees on squash and pumpkin than did farms that did not keep honey bees (Fig. 4). This was true whether honey bee management was considered a categorical variable or a continuous variable weighted by the number of hives and size of the farm. There were examples of farms that kept honey bees but received no squash or pumpkin visitation by them, and examples of farms that did not keep honey bees but did receive visitation, either through feral colonies or managed colonies at other locations.

Discussion

All of the farmers that we spoke with were aware of the need for insect pollination in their squash and pumpkin fields, but most assumed that they were dependent on managed honey bee colonies or wild bumble bee populations for successful pollination. Several had heard of *P. pruinosa*, but none knew that they occurred in their fields. The biology of *P. pruinosa* is well known, and their value to agriculture has long been recognized by pollination biologists (Hurd et al. 1971, 1974; Willis and Kevan 1995). Squash bees and honey bees seem to be equivalent pollinators of cucurbits in terms of initiating fruit production, but squash bees visit flowers more quickly (Tepedino 1981), more reliably, and disperse pollen over greater distance to conspecific stigmas than honey bees (Ordway et al. 1987). Female squash bees collect nectar and pollen from *Cucurbita*, and males search for mates in the flowers during the morning and then crawl into a flower as it closes and remain there all afternoon and night. Squash bees have expanded their geographic range northward by expanding their host range from wild *Cucurbita* to cultivated *Cucurbita* and now occupy most of the continental United States into eastern Canada (Kevan et al. 1988). Attempts to introduce squash bees to Hawaii to improve yields (Michelbacher et al. 1971) were unsuccessful.

The biology of *P. pruinosa* makes it difficult to manage them in agricultural settings. The bee is a solitary species that excavates nests in the ground near its host plant. Nests are up to 46 cm in depth (Kevan et al. 1988), but most offspring are placed between 12 and 22 cm in depth (Mathewson 1968). The immature offspring lay dormant in the nest from late summer until the following summer, when they complete development and emerge. Thus, they are difficult to acquire as immatures, susceptible to ground perturbations, and difficult to introduce in large numbers to an agricultural setting. Still, there has been some success in initiating and promoting the populations of another ground-nesting bee species, the alkali bee, *Nomia melanderi* Cockerell, which pollinates alfalfa

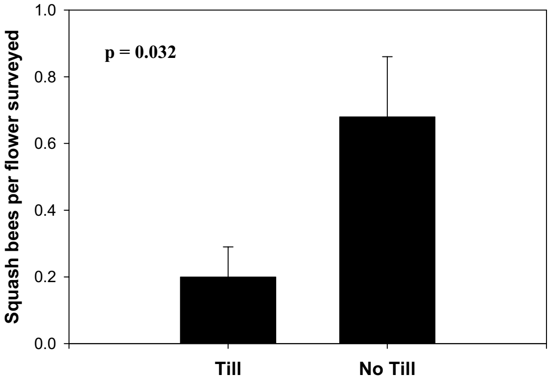

Fig. 3. Effect of tilling practice on *P. pruinosa* density.

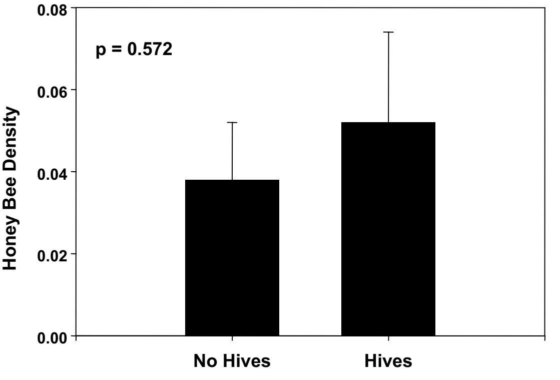

Fig. 4. Honey bee density on squash and pumpkin at farms with and without hives.

(*Medicago* spp.) (Mayer and Johansen 2003) in the northwestern United States.

Although *P. pruinosa* is widespread and common, few studies have attempted to examine its distribution at a relatively local scale. Our finding them at 23 of 25 farms suggests that they are very abundant in this region and either persist on most farms or disperse well from other source populations. Our research suggests that tillage influences *P. pruinosa* population size. Because the bees commonly nest in the fields, it seems likely that tillage could harm their offspring. The exact mechanism, however, is not clear. Some offspring may occur within tillage depth (10–20 cm in this study) and could be destroyed. Many offspring, however, are placed below tillage depth and would not be directly injured. It could be that the collapsing of the tunnels above the nest is sufficient to interfere with offspring emergence the following year. Evidence that tillage is a causative and not merely a correlative mechanism is that the population density of pollinators that do not commonly nest in agricultural fields (bumble bees and honey bees) was not affected by tillage practices.

Bumble bees are excellent pollinators of many agricultural plants, including some, such as tomatoes and solanaceous peppers, that are poorly pollinated by honey bees. Because of their long active season, they require a continuous supply of flowering plants across the year to build up their colonies. Thus, farms with a diversity of crops flowering continuously might be expected to develop larger or more colonies of bumble bees. Although there was a tendency for bumble bee abundance on squash and pumpkin to be greater on more diverse farms, this relationship was not statistically significant. This could reflect our sampling regime (we measured bumble bee density on only one crop, not the whole farm) or a problem with geographic scale. Bumble bees can forage well beyond the edges of most farms (Osborne et al. 1999, Kreyer et al. 2004) and thus the diversity of crops within a farm could represent only a small portion of the foraging options within their range. A study that incorporates relative size and type of surrounding habitats (Kremen et al. 2002, Steffan-Dewenter et al. 2002) as well as crop diversity and farm size simultaneously will likely be a stronger analytical tool for examining the factors that control bumble bee population size.

In contrast to Kremen et al. (2002), we did not find an association between pesticide use and native bee population size. There are several possible reasons for this discrepancy. First, Kremen et al. (2002) found a strong combined effect of pesticide use and isolation from natural habitat, with isolation from natural habitat being the strongest effect. Most farms in our study were located near natural habitat. Most farmers that did use pesticides in our study used them at times when pollinators were not active. Because squash and pumpkin flowers last only 1 d, there is unlikely to be a residual effect of pesticides sprayed on flowers with the next day's floral visitors. Second, farmers used many different pesticides of varying toxicity to bees, and we were unable to quantify their application. Thus, our study design was weak for detecting an effect from any particular pesticide. Other studies examining the broad use of particular pesticides have documented local population declines in bee species (Kevan and LaBerge 1979, Kevan et al. 1997).

Honey bees are commonly used for squash and pumpkin pollination, but it is well known among beekeepers that they prefer many other plants over these crops. Our study suggests that keeping honey bees may often make a minor, if any, contribution to squash and pumpkin pollination. Four participating farms kept 10 or more colonies of honey bees. On all four of these farms, squash bees occurred in greater density than honey bees, averaging 7 times their population density. Honey bees may have been making an important contribution to the pollination of other crops, but even those farms with the greatest investment in pollinator management were relying primarily on wild pollinators on squash and pumpkin.

The decline of honey bees has increased attention on alternative pollinators. Although much research has focused on the development of pollinators to replace the honey bee should it decline further (Strickler and Cane 2003), it has led to an increasing realization that native bees already make substantial contributions to agriculture. As future studies further examine the effect of agricultural practices on pollinator populations, it will be easier to examine both the ecological and economic trade-offs of those practices.

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