Solitary Bees as Alternative Pollinators of Pennsylvania Fruit Crops

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Introduction

Pollination is a pivotal, keystone process in almost all terrestrial ecosystem food webs: it supports global and sustainable productivity in agriculture and forestry, and maintains the biodiversity of plant and animal life. Bees are the most important pollinators, but bee declines in abundance and species richness have been documented on 4 continents. Almost 100 crop species in the US rely to some extent on honey bee pollination and the value of honey bees to U.S. agriculture is estimated to be $15 billion annually. Collectively these 100 crops make up about 1/3 of the US diet and consist mainly of high-value specialty crops (i.e. fruit, vegetable and nut crops) that provide the bulk of vitamins and other nutrients that contribute to healthy diets.

Honey bees are the most valuable pollinators in agriculture currently, because they are well understood, relatively easy to maintain, movable, and able to communicate rapidly the locations of new food sources. Honey bee populations, however, have declined for the past several years to the point that total reliance on them is increasingly risky. From 2006-07, N. American beekeepers lost approximately 1/3 of the honey bee colonies mostly due to Colony Collapse Disorder (CCD). These losses were in addition to declines caused by: 1) the introduction of two parasitic mite species; 2) viral, fungal, and bacterial diseases; 3) insecticide poisoning; 4) hybridization with the African subspecies of honey bee; and 5) economic threats from loss of honey bee price supports and global honey competition. Despite increased need for pollination services for crops such as the $2 billion almond industry, honey bee colonies had already declined by over 40% in the US since 1947, even before CCD. Importation of bees from outside the U.S. to meet the demand for pollination began in 2005, but is a very risky solution because it greatly increases the chances of introducing new pests and pathogens to all of our bee species.

The economic impacts of pollinator shortages on US specialty crops such as fruits, vegetables and nuts could be considerable. Inadequate pollination can reduce crop quality as well as yield in these crops. In apple or pear, pollination efficiency affects seed set which in turn affects size and quality and hence the profitability to growers. The most conspicuous consequence of honey bee declines since CCD, has been a dramatic increase in the costs of producing bees which translates into rising costs for bee rentals for specialty crop growers – from $35/hive for Pennsylvania apple growers in 2006 to $75/hive in 2008. Rising costs combined with declining yields would lead to higher prices of US nuts, fruits and vegetables which would reduce exports of major commodities during a record US trade deficit and lead to increased imports of cheaper commodities from foreign markets where CCD is not a problem (Berenbaum 2007).

There are, however, another 3,500 non-*Apis* bee species in the US which are also important pollinators of most specialty crops. These include the many species of bumble bees and what are often referred to as solitary bees. We will refer to both groups henceforth be referred to as "pollen bees" because their main value, in relation to people, is not the production of honey, but the collection and transfer of pollen for the fertilization of plants. It is obvious that pollen bees are critical components of food webs associated with wildlife habitats of all types in North America because almost all of them were here long before honey bees were introduced by Europeans. The value of pollen bees as pollinators in agriculture is conservatively estimated at $3 billion annually in US agriculture. Because of the popular focus on honey bees, the services of pollen bees most often go unrecognized and their value for agriculture and especially for unmanaged ecosystems is probably much higher. For most bee species, the paucity of long-term population data and our incomplete knowledge of even basic taxonomy, life history and ecology make assessing their value and possible declines in some regions very difficult. It is well-known that honey bees are not the best pollinators for all crops. They are generalist foragers easily distracted from target crops like cucurbits, pears, and apples by other species such as dandelions and other nectar sources. Wild and managed species of pollen bees in many cases can and do supplement honey bees for pollination in specialty crops, but in some situations can replace them.

Many research projects are dealing with the various threats to the honey bee industry in the U.S., but to truly address the threats to pollination there should be contingency plans that include the development of alternative pollinators. The folly of relying on a single pesticide, tactic or cultivar has been seen repeatedly in the development of IPM programs for specialty crops. In the case of pollinators, a similar reliance on one pollinator such as the honey bee is also not wise. As Kevan (2003) has said, “the age of IPM and ecology has come to apiculture”. Developing multiple tactics with multiple pollinator species represents the most robust management approach for a future of uncertain climate, environmental disruptions, and invasive species introductions. We do know, however, that: a) the supply of honey bees in the U.S. will not be able to meet the demand for pollination services in the near future; b) that production costs for apiculturists will go up; and c) that the cost to growers to rent honey bee hives will continue to increase.

<u>Tree Fruit Pollination in Pennsylvania</u>

Agriculture in the Mid-Atlantic uniquely consists of a diverse landscape mosaic of diversified farms, urban areas, and small patches of suitable bee habitat such as field edges with flowering weeds, hedgerows, farm ponds, riparian zones, and drainage ditches. The strong elevation relief in hilly and mountainous areas and the wetlands in the coastal plain region, coupled with land-use patterns of high-value agriculture embedded with urbanizing regions, have resulted in smaller size fields and orchards with higher adoption of no-till, conservation tillage and contour farming than in many other regions. The resulting mix of diverse habitat types in close proximity to the crops may provide native bees with the floral and nesting resources they need, even when the overall proportion of natural habitat in the landscape is low (Vaughn et al. 2007). Our unique landscape ecology of agricultural and non-agricultural lands and a mosaic of diversified fruit and vegetable farms in the Northeast and Mid-Atlantic likely impart unique advantages in pollinator conservation and utilization compared to the monocultures of the Midwest or dry areas of the West. A recent study by Winfree et al. (2007) demonstrated a guild of 46 species of native bees provided full pollination of watermelon on >90% of 23 farms in Pennsylvania and New Jersey. Some of the largest fruit growers in Pennsylvania have relied completely on feral honey bees and wild pollinators for their pollination needs for over 5 years now, with no noticeable loss in fruit quality or yields. These growers still have to pay to chemically or manually thin their crop every year, but with a recommended rate of 1-2 hives/acre for apples, are saving $75-$150/acre in rental fees. It is much more common recently for growers to use only 1 honey bee hive to every 5 to 10 acres rental costs have gone up.

USDA-ARS and European researchers have found that mason bees of the genus *Osmia* are particularly good pollinators of early spring orchard crops. The blue orchard bee, *Osmia lignaria*, is native to North America, and wild populations were found in our 2008 survey of pollen bees in Adams County apple orchards. Populations appear erratic, however, since it was not found in the 2007 surveys of the same orchards. The blue orchard bee is popularly used by small organic growers, but generally will not aggregate in adequate numbers for pollination of large orchards. *O. ribifloris,* a species is widely used as a pollinator of blueberries in the eastern US. The European mason bee, *O. cornuta,* is used extensively to pollinate pears in Europe because honey bees are not attracted to the low sugar nectar of their flowers. *O. cornuta* is also used for the pollination of many other fruit crops in urban areas where keeping of honey bees is not allowed for safety reasons.

The Japanese Orchard Bee (JOB), *O. cornifrons*, used for most of the apple pollination in Japan was introduced into the US in 1977. It was found to be more amenable to pollination of larger scale fruit orchards and to the weather conditions in the mid-Atlantic region than *O. lignaria*. JOB is widely available commercially and has been used extensively for the pollination of cherries in Michigan and Utah because of it is ability to pollinate in temperatures 10^{o}F cooler than the honey bee and because it is not affected by cloudy weather or light rain. It is widely used in smaller-scale organic fruit production throughout the US. Several fruit growers in Adams county have experience with JOB from these early research interactions with ARS (Scott Slaybaugh & Tom Garretson) and one (Barry Rice) still maintains numbers of JOB to pollinate his nursery trees. In 2007, the Penn State Fruit Research & Extension Lab at Biglerville started enough colonies to pollinate 20-30 acres of fruit on the lab for the 2008 season and assisted Tom Garretson in starting new colonies on his farm. JOB has been used successfully for several years to pollinate small plantings of fruit trees at the PSU Rock Spring Research Station at State College.

Successful pollination with *Osmia* bees does not require a large populations. JOB and the European Orchard Bee are 80 times more effective in pollinating apple than the honey bee, which spends most of its time collecting nectar for honey rather than pollen. Only 250-500 JOB are required per acre for pollination compared to 40,000 to 80,000 honey bees. A single JOB can visit 15 flowers/min, setting 2,450 apples/day compared to 50 flowers set by a honey bee (Greer 1999). This high level of pollination efficiency occurs because mason bees land directly upon the reproductive structures of the fruit tree blossom. The abdomens of foraging female bees are loaded with pollen, and the repeated and direct contact with the anthers and stamens results in higher levels of pollen transfer. Female bees collect pollen while constructing nests to provide food for bee larvae. Therefore, the key to heavy pollination in the orchard is to promote maximum nesting activity in the orchard bee population. With each female will lay approximately 30 eggs if provided adequate pollen and nesting sites, populations can increase greatly in a single season to be used in additional sites. Promoting alternative pollinators may be seen by some as a threat to the honey bee industry, but lower numbers of managed or feral JOB can be used to supplement honey bee pollination under adverse weather conditions. Many beekeepers in the western US now offer the services of both honey and orchard bees.

In the Mid-Atlantic region where introduced parasitic mites have almost completely eliminated feral bee colonies (Stanghellini & Raybold 2004), native bees alone have served to provide pollination in non-managed systems. Native bees play important roles in crop pollination as long as the landscapes in and around farms supply forage and nest sites and harmful effects from pesticides are reduced. In Pennsylvania and New Jersey, a diverse fauna of almost 50 species of native bees are key crop pollinators of several vegetable crops and were fully able to pollinate some of these crops without aid of honey bees on the majority of farms evaluated (Winfree et al. 2007, 2008). The Mid-Atlantic region thus appears ideal for native bee conservation and as a potential model for sustainable crop pollination. The following are some of the steps we have undertaken with support from the State Horticultural Association of Pennsylvania do so with wild populations of feral pollen bees and to develop the management of the Japanese Orchard Bee.

Document bee fauna available for the pollination of specialty crops

Native bee diversity and pollination has been little studied in the Mid-Atlantic and what little we know comes from almost 50 years ago. We don't know what bee fauna we have to conserve or their importance in agricultural production. We have no historical data on species abundance to determine if rare species today may have declined and should be considered endangered. Without a baseline of pollinator biodiversity and abundance, we also cannot determine if human changes to the environment (i.e. agricultural intensification, urbanization, pesticide use, invasive species etc.) are affecting pollinator populations. In conjunction an ongoing statewide pollen bee survey by the Pennsylvania Department of Agriculture, we began surveys of bees in fruit orchards in 2007 to give us a baseline of available pollinator species. We are also using this biodiversity and abundance data in an ongoing USDA-Risk Assessment and Mitigation Project (RAMP) to determine if the switch to reduced risk insecticides in fruit orchards dictated by FQPA are conserving beneficial and non-target insects, including bees.

Materials and Methods – We surveyed 12 Pennsylvania apple orchards in 2007 (6 growers) & and 14 in 2008 (7 growers) for pollen bee diversity and abundance during bloom. We only used orchards (5-10 acres in size) where we had detailed records of pesticide applications and some control over what insecticides were used. Two orchards were in Centre County near Penn State University and the rest were in Adams County. Twelve of the orchards are part of the ongoing RAMP Grant to develop tree fruit IPM programs using only reduced risk insecticides and pheromone mating disruption. Each RAMP orchard is paired with contiguous conventionally managed grower blocks of equal size for comparison over time (i.e. 6 RAMP and 6 conventionally managed orchards). The program started in 2002 and the RAMP blocks have not had applications of broadspectrum organophosphate, pyrethroids or carbamate insecticides for 7 seasons. The other two orchards, surveyed only in 2008, were part of the Areawide Mating Disruption Project funded for the last 3 years by the Pennsylvania Department of Agriculture and these blocks were specifically managed during this period using only reduced risk pesticides and tactics through a grower contract with the USDA-NRCS conservation program.

During peak apple bloom, two to 4 separate, two minute counts were made of the general types and abundance of bees visiting the flowers. Maryann Frazier had used this same protocol for counts in some of the same orchards in 1997-8 and we used this data for historical comparison of bee abundance and types before CCD and the shift to reduced risk insecticides was instituted by the Food Quality Protection Act (FQPA). A total of 9 orchards were counted in 1997-8 and twelve orchards in both 2007 and 2008. In addition, after the timed counts were made in 2007-8, bees were net collected from the apple blossoms for a total of 2 man hours/orchard.

Starting at bloom in 2007 and earlier at half inch green stage in 2008, colored pan traps (Solo brand plastic picnic bowls – yellow, white, and dark blue) were placed in all survey orchards to determine seasonal bee diversity and abundance in and around the apple orchards. All three pan colors were placed within six inches of each other to present a visual choice test and two locations near the center of each orchard were sub-sampled. Pans were filled with soapy water, which caused bees attracted to the color to sink to the bottom and drown. Pans were placed in the orchards for 24 hours once a week for a total of 22 weeks in 2007 (May through September) and 29 weeks in 2008 (April through October). The two pan traps of the same color (i.e. yellow, white, or blue) in the same orchard were pooled together for analysis. Bees were stored in 70% ethyl alcohol for later pin mounting and identification and labeled with the grower, treatment, date, bowl color and GPS coordinates. In 2007 at total of 1,584 samples were taken and in 2008 a total of 2,610 samples.

Results & Discussion - A complex of 30 bee species collected on apple blossoms and 96 species were collected in the bowl traps during the 2007-8seasons (Table 1). Some bees seem to have strong preferences for specific colors with the greatest diversity and abundance found in the yellow traps. Multivariate analysis of all the bee data using ordination techniques is ongoing, but from the 2007 season, it appears that there is slightly higher abundance and bee diversity in orchards managed with reduced risk IPM pesticides and tactics. It appears, however, that the landscape surrounding orchards which provide alternative pollen sources and nesting sites are more important to bee diversity and abundance than the pesticide programs.

Looking at the historical data comparing the timed bee bloom counts from 1997-8 with those conducted in many of the same orchards in 2007-8, there has been up to a 6-fold decline in honey bee numbers, even though almost all orchards counted were provided with honey bee colonies (Fig. 1). This probably reflects the current lack of feral bees in most of Pennsylvania, and the weaker strength of many new colonies that growers are forced to use to replace hives killed during the winter by CCD. The numbers of honey bees counted in RAMP orchards were numerically, but not statistically, higher than those in the conventional IPM orchards, but the prebloom insecticide programs in both types of blocks were very similar (i.e. Assail or Calypso at pink). Solitary bee abundance at apple bloom, however, did not decline (Fig. 2) and did not differ significantly between RAMP and conventionally managed orchards, again probably due to the similarity of pre-bloom insecticide programs. In general, however, there appears to be a decline of many pollinator species throughout the world with four species of bumble bees being of most concern in the U.S. http://www.xerces.org/bumblebees/index.html#collaborators.

Examine Biological Threats to Pollen Bees

RNA viruses are emerging as suspected contributors to Colony Collapse Disorder (CCD). At least 18 viruses have been identified from honey bees from different parts of the globe (Allen and Ball 1996, Ellis and Munn 2005). Most of the insect-infecting RNA viruses frequently persist within the host as unapparent, asymptomatic infections but are capable of replicating rapidly under certain stress conditions, resulting in observable symptoms often leading to heavy losses (Christian and Scotti 1998). Singh et al (unpublished 2008) has shown that several of these viruses are found in other bee and wasp species, including some of the pollen bees (bumble bees and some wild solitary bees). These viruses were found not only in the bodies of bees, but also in their pollen loads. These results demonstrate that bee diseases can be freely exchanged among species, and may not even require bee to bee contact. A bee visiting a flower that has been visited by an infected bee may be all that is required for interspecies infections. They have detected these viruses in eleven species of non-honey bee pollinator species ranging from solitary bees, to several bumble bee species, and even wasps. Thus, there is a need to determine if exotic pathogens are affecting native pollinators, and if so how prevalent the problem is. During peach and apple bloom of 2008, we collected and identified several samples of solitary bees in Adams county fruit orchards. These were frozen and later analyzed for IAPV and other RNA viruses, but none were found from our bees. More bees will be collected and analyzed in 2009.

Mites and parasitoids (including cleptoparasitic bees, flies and beetles) can also cause rapid decline in some pollen bees. Efforts in 2008 to manage JOB for orchard pollination met with many difficulties because local colonies suffered over 50% mortality from mites and parasitoids. Barry Rice, a Pennsylvanian fruit grower who has managed the Japanese Orchard Bee for over 10 years to pollinate much of his 300 acre fruit farm, had a population of JOB, which at its peak, measured in the tens of thousands, was reduced to only a few hundred individuals in 2008. This decline apparently occurred over a three year period by heavy mite infestation which the lead author determined to be from the genus *Chaetodactylus* (http://crawford.tardigrade.net/bugs/BugofMonth35.html) and samples are now being identified to species by USDA-APHIS through the Pennsylvania Department of Agriculture. Prior to the discovery of the mites, the decline was thought to be due to pesticides. Control methods are now known and sanitation of the nesting materials will play a key role in developing future JOB colonies.

The mite species is important because there remains the possibility that this is a new mite species/threat brought in by another exotic species of bee introduced accidentally into the area like the accidental introductions of *Varroa* and tracheal mites in honey bees. Biddinger and the survey efforts of the Pennsylvania Department of Agriculture have found several species of bees in our survey efforts that are new records for the state including the another exotic Japanese species, *Osmia taurus*. It was first found in the Washington DC area in 2000 http://www.nbii.gov/images/uploaded/152986_1217253816461_NAm_Introduced_and_Alien_Bee_Species_Jul2008.pdf and has apparently spread and become naturalized around Pennsylvania fruit orchards where populations exist in several counties. JOB was purposefully introduced and screened for pathogens and parasitioids by USDA in the 1990s, but the origins of the newly discovered *O. taurus* are unknown and it is doubtful they were screened for pathogens or parasites. *O. taurus* adults are easily mistaken for those of JOB, which are sold commercially throughout the US and British Columbia. Pictures of JOB and O. taurus can be found at: http://bugguide.net/node/view/173454/bgimage . Currently, nothing is known of the nesting habits of *O. taurus*, but they are probably similar to those of the Japanese Orchard Bee. The big concern with exotic bee introductions like this are that they could easily be moved around the country with commercial sales of sister species like JOB and the Blue Orchard Bees and carry along whatever pathogens or diseases may have been introduced with them.

While exotic threats are a critical and irreversible concern, native natural enemies of pollen bees are also of concern. Many species of pollen bees are also known under the generic name of solitary bees for a reason: they don't naturally nest in large aggregations like honey bees. Living at low densities is a survival trait to minimize the impact of parasitic mites and wasps. In developing the European Orchard Bee in Spain, Bosch (1992), found that parasitic mite, *Chaetodactylus osmiae*, increased from an infestation rate of 10% in isolated wild colonies to over 60% when managed in higher densities for commercial pollination. Cane et al. (1996)

found that management of *Megachile addenda* for cranberry pollination in New Jersey necessitated control of its cleptoparasite *Coelioxys immaculata*, which could otherwise parasitize over 90% of nest cells. A similar possibility of higher natural mortality occurring at higher densities found with managed populations of JOB exists. Not only are mites more of a problem in managed colonies, but we also found torymid wasps of the genus *Monodontomerus* to be very detrimental in maintaining colonies of both JOB and the native Blue Orchard Bee. Three native species are known from the US and Canada, but other species may have become established with exotic introductions like *O. taurus*, so we are sending samples for identification through the Pennsylvania Department of Agriculture. We found 10-25% mortality in managed JOB colonies that use cardboard tubes for nesting materials if they were used more than one season.

Parasitic wasp populations can also be excluded and greatly reduced by placing JOB nesting materials in fine mesh screen just before the end of adult JOB activity in the spring (See the Blue Orchard Bee manual at: http://www.scribd.com/doc/1448269/USDA-blue-orchard-bee). Mortality can be also be significantly reduced by using wooden nesting blocks or thicker-walled tubes of bamboo or marsh reeds that are difficult for the small parasitic wasps to penetrate with their ovipositors. In replicated choice tests in 2008, we found that JOB prefer nesting materials in the following order: bamboo> phragmites marsh reeds > cardboard tubes > Binderboard® wooden blocks (http://pollinatorparadise.com/Binderboards/Osmiabb.htm). Bamboo and wooden blocks give the best protection from parasitic wasps. Cardboard tubes and marsh reeds are the easiest to handle and less bulky while reeds and Binderboard blocks are easier to sanitize. Monitoring and identifying parasitoids and parasites attacking managed populations of *Osmia* orchard bees is essential in developing sustainable managed populations. This must be coupled with prevention of future problems with importation of non-*Apis* bees by establishing a USDA-APHIS certification requirement for disease and parasite/parasitoid shipments, as recommended in the National Academy of Science report.

Examine Pesticide Threats to Pollen Bees

Pollinator exposure to chemical pesticides has long been a concern for beekeepers and growers alike. In response to CCD in honey bees, Penn State faculty have been investigating pesticides as a potential cause or factor contributing to the malady. In a total of 108 pollen samples analyzed, 46 different pesticides including six of their metabolites were identified. Up to 17 different pesticides were found in a single sample. Samples contained an average of 5 different pesticide residues each. Only three of the 108 pollen samples had no detectable pesticides (Frazier et al., 2008). A summary can be found at: http://www.ento.psu.edu/MAAREC/CCDPpt/WhatPesticidesToDoWithItJune08ABJ.pdf. To date, little work has been done to document pesticide exposure to alternative and native pollinators. Since they often nest in crops and other nearby habitats, pollen bees are subject to pesticide applications as well as exposure through flower visitation. Unlike honey bees, they generally cannot be moved out of treated habitats to protect against pesticide treatments. *Osmia* Orchard bees are an exception because their nesting tubes or blocks containing eggs and larvae can be moved to safer locations after the 6 week foraging period of the adults is completed, but during that period, however, the adults are very susceptible.

Honey bees are know to forage distances of up to several miles led to difficulties in relating pesticide residues found in honey bee hives placed in specific apple orchards where the spray programs were well documented. Pollen bees are much more local with foraging ranges, generally of only a couple hundred yards, so are better indicators of the pesticide impacts within specific orchards on bees. Neonicotinoid insecticides are of particular concern as a causal agent of CCD, so in 2008, we placed nesting tubes of JOB along the edges of apple orchards sprayed with pink stage applications of neonicotinoid insecticides (Calypso and Assail). Analysis of pollen samples for these and 150+ other pesticides are currently being conducted, but results have not yet been summarized.

We hope to continue efforts in 2009 to identify the native pollen bee species important for fruit pollination in Pennsylvania and to establish baseline diversity and abundance data. We need to better understand which species are important and how management practices such as providing additional nesting sites, modifying the surrounding landscape with alternative pollen sources, or reducing the use of harmful pesticides at critical times can conserve or augment the native populations we currently have. The need to develop alternative managed pollinators such as the JOB is even more important with the recent discovery of honey bee viruses moving into wild native bee species and in anticipation of continued shortages of honey bees in the future.

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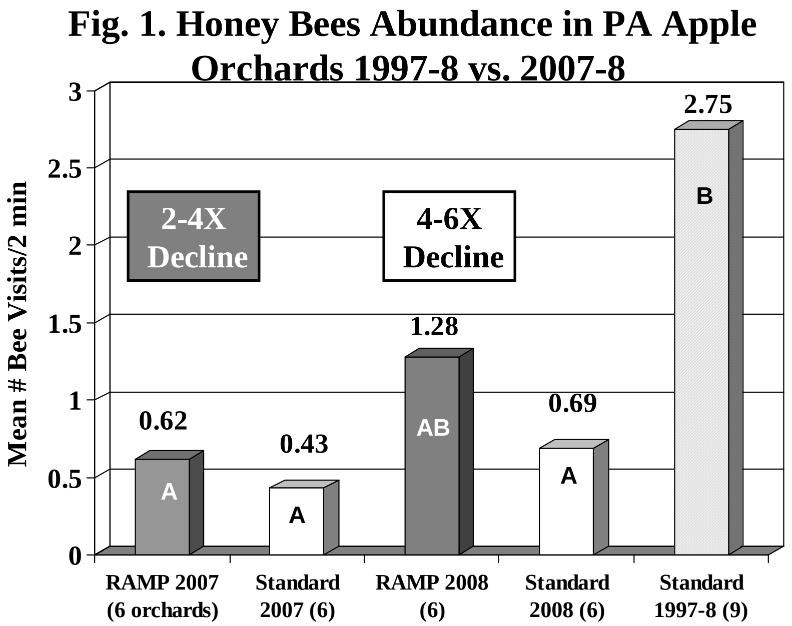
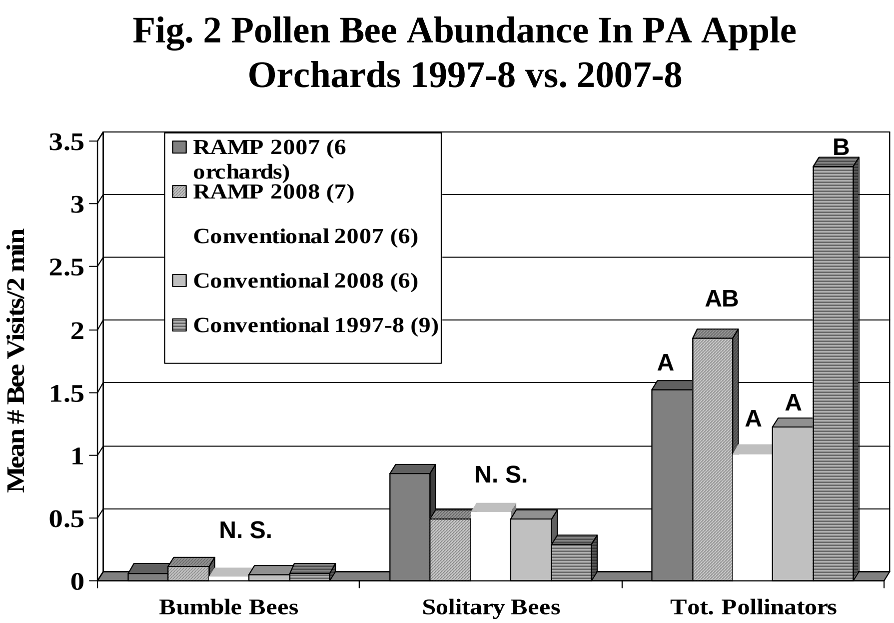
Table 1. List of Bee Species Collected In Pan and Net Samples from Apple Orchards 2007-8.

Bee Name	Family	Net Sample During Bloom	Pan Trap	Bee Name	Family	Net Sample During Bloom	Pan Trap
Agapostemon sericeus	Halictidae	N	Y	*Lasioglossum cinctipes*	Halictidae	N	Y
Agapostemon splendens	Halictidae	N	Y	*Lasioglossum fuscipennae*	Halictidae	N	Y
Agapostemon texanus	Halictidae	N	Y	*Lasioglossum leucozonium*	Halictidae	N	Y
Agapostemon virescens	Halictidae	N	Y	*Lasioglossum pectorale*	Halictidae	N	Y
Andrena arabis	Andrenidae	N	Y	*Lasioglossum pilosum*	Halictidae	N	Y
Andrena barbara	Andrenidae	N	Y	*Lasioglossum quebecensis*	Halictidae	Y	Y
Andrena bisalicis	Andrenidae	Y	Y	*Lasioglossum rohweri*	Halictidae	N	Y
Andrena bradleyi	Andrenidae	Y	N	*Megachile addenda*	Megachilidae	N	Y
Andrena carlini	Andrenidae	Y	Y	*Megachile brevis*	Megachilidae	N	Y
Andrena ceanothi	Andrenidae	N	Y	*Megachile gemula*	Megachilidae	N	N
Andrena crataegi	Andrenidae	N	Y	*Megachile inimica*	Megachilidae	N	N
Andrena cressonii	Andrenidae	N	Y	*Megachile melanophea*	Megachilidae	N	Y
Andrena daeckie	Andrenidae	Y	Y	*Megachile mendica*	Megachilidae	N	Y
Andrena dunningi	Andrenidae	Y	Y	*Megachile sculpturalis*	Megachilidae	N	N
Andrena erythronii	Andrenidae	Y	Y	*Melissodes agilis*	Apidae	N	N
Andrena heraclei	Andrenidae	Y	N	*Melissodes bimaculata*	Apidae	N	Y
Andrena hilaris	Andrenidae	Y	Y	*Melissodes dendiculata*	Apidae	N	N
Andrena kalmiae	Andrenidae	N	Y	*Melissodes desponsa*	Apidae	N	Y
Andrena nasonii	Andrenidae	Y	Y	*Melissodes subillata*	Apidae	N	Y
Andrena nuda	Andrenidae	Y	N	*Melitoma taurea*	Apidae	N	Y
Andrena pruneri	Andrenidae	Y	Y	*Nomada affibilis*	Apidae	N	N
Andrena rugosa	Andrenidae	Y	Y	*Nomada articulata*	Apidae	N	Y
Anthophora bomboides	Apidae	N	Y	*Nomada australis*	Apidae	N	Y
Anthophora ursina	Apidae	N	Y	*Nomada composita*	Apidae	N	N
Apis mellifera	Apidae	Y	Y	*Nomada cvessonii*	Apidae	N	Y
Audrena commoda	Andrenidae	Y	Y	*Nomada depressa*	Apidae	N	N
Augochlorella aurata	Halictidae	N	Y	*Nomada fervida*	Apidae	N	N
Augochlorella pura	Halictidae	Y	Y	*Nomada illoensis*	Apidae	N	Y
Bombus bimaculatus	Apidae	Y	Y	*Nomada inepta*	Apidae	N	Y
Bombus fervidus	Apidae	N	Y	*Nomada lehighensis*	Apidae	Y	N
Bombus impaticus	Apidae	Y	Y	*Nomada lepida*	Apidae	N	N
Bombus perplexus	Apidae	Y	Y	*Nomada luteoloides*	Apidae	N	Y
Bombus vagans	Apidae	Y	Y	*Nomada maculata*	Apidae	N	Y
Calliopsis andreniformis	Andrenidae	N	Y	*Nomada ovata*	Apidae	N	Y
Ceratina calcarata	Apidae	N	Y	*Osmia atriventris*	Megachilidae	N	Y
Ceratina dupla	Apidae	Y	Y	*Osmia bucephala*	Megachilidae	N	Y
Ceratina strenua	Apidae	N	Y	*Osmia cornifrons*	Megachilidae	Y	Y
Chelostoma philidelphi	Megachilidae	N	N	*Osmia georgica*	Megachilidae	N	Y
Coletes inequalis	Colletidae	Y	N	*Osmia lignaria*	Megachilidae	Y	N
Eucera hamata	Apidae	N	N	*Osmia pumila*	Megachilidae	Y	Y
Halictus confusus	Halictidae	N	Y	*Osmia taurus*	Megachilidae	Y	Y
Halictus ligatus	Halictidae	N	Y	*Peponapis pruinusa*	Apidae	N	Y
Halictus rubicundus	Halictidae	Y	Y	*Spchodes antennariae*	Halictidae	N	Y
Heriades carinatus	Megachilidae	N	Y	*Spechodes atlantis*	Halictidae	N	Y
Hylaeus affinis	Colletidae	N	Y	*Spechodes banksii*	Halictidae	N	Y
Hylaeus mesillae	Colletidae	N	Y	*Spechodes carolinus*	Halictidae	N	Y
Hylaeus modestus	Colletidae	N	Y	*Stelis coaretatus*	Apidae	N	Y
Lasioglossum acuminatum	Halictidae	Y	Y	*Xylocopa virginica*	Apidae	Y	Y
Lasioglossum athabascense	Halictidae	N	Y				



*Means followed by the same letter were not statistically significant, Fisher's Protected LSD, P=0.05.



*Means followed by the same letter were not statistically significant, Fisher's Protected LSD, P=0.05.