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Native Pollinators and the Food Supply:

Can Wild Bees Bridge the Gap Left by *Apis mellifera*?

INTRODUCTION

Farmers throughout the world depend on animal pollinators to produce an estimated 35% of the global food supply (Klein et al. 2007). Pollinators come in many forms, including bats, butterflies, birds, beetles, frogs, flies, and wasps, but it's the bee that carries most of the load, accounting for about 75% of all crop pollination services worldwide (Buchmann and Nabhan 1996, Kremen 2002). But of the approximately 20,000 known bee species, only a handful are managed for crop production, and of those, the European honey bee (*Apis mellifera*) is by far the most valuable (Kremen 2002).

During the last century, however, the honey bee has undergone a host of assaults so severe that its future as the primary pollinator of the world's food supply is being called into question. The purpose of this paper is to review the literature on alternative bee species as agronomic and horticultural pollinators, and to access the possibility of substituting wild, native bees for the languishing honey bee.

BEE BIOLOGY AND TERMINOLOGY

Bees are flying insects within the order Hymenoptera, closely related to wasps, ants and sawflies (Shepherd et al. 2003). All 20,000 species fall into just nine families within the superfamily Apoidea. Bees are found on all continents except Antarctica and encompass a wide range of sizes, life histories, and ecological niches (Wcislo and Cane 1996).

The term "wild" usually refers to native, non-managed bees living in a habitat of their choosing. However, "wild" is often used in the literature to refer to non-native bees that escaped managed stock and now live on their own, or to quasi-managed native or non-native bees that are difficult to control. For the sake of clarity, this paper will use “wild” to mean never-managed bees living on their own, “feral” to mean once-managed bees that have escaped into the wild, and “managed” for any bees currently being manipulated by humans.

Bees fall into two organizational types: social and solitary. Social bees are of several different types, depending on whether there is a division of labor among individuals and, if so, if the division of labor is due to morphological difference or simply job description. Groups of cohabiting females are referred to as “semisocial,” while groups consisting of a mother and nearly-identical daughters are called “primitively eusocial.” Species such as the European honey bee, in which all the castes (queen, workers, and drones) are morphologically quite distinct, are known as “highly eusocial.” Wild bees may be either social or solitary, however the large majority is solitary, including nearly all of the four thousand wild bee species found in North America (Shepherd et al. 2006).

Characteristics of Social Bees

Large colonies of highly eusocial bees such as honey bees reach peak populations in the spring and may contain 30,000 to 200,000 individuals, although the average is around 50,000 (Ellis 2004). During this time, a colony typically has only one fertile female called a *queen* and a small percentage of fertile males called *drones*. All the rest of the bees are sterile females known as *workers*. The queen is attended to by a retinue of workers while she lays up to 2000 eggs per day, each in an individual cell constructed and prepared by the workers (Tautz 2008). An over-wintering colony of highly eusocial bees retains the queen, kills all the drones, and drops the worker population to a small fraction of the springtime highs. Such a reduced colony has a better chance of survival, since the requirements for food are greatly reduced.

Besides honey bees, many of the stingless bees (tribe Meliponini) are highly eusocial as well, with hives that can vary from 300 to 80,000 individuals (Buchmann and Nabhan 1996). Most of the eusocial bees have much smaller nests, however. Bumble bees (*Bombus spp.*), although considered eusocial (Kearns and Thompson 2001), build nests that peak at approximately 50 to 200 individuals in the mid to late summer. North America is home to more than fifty species of native bees that are social nesters to one degree or another (Shepherd et al. 2003).

Characteristics of Solitary Bees

Although highly eusocial bees are the most familiar, the large majority of species are solitary; that is, a single fertile female lives alone in a nest she builds herself. Nests may be built in the ground, in hollow twigs or reeds, or in wooden material such as trees, debris piles, or screen doors (Kearns and Thompson 2001). Depending on the species, the nest may be shallow and contain just one egg, or it may be long and contain several eggs arranged in a row or column. In long nests, the female excavates a hole, lays an egg at the furthest end, provisions it with nectar and pollen, and seals it up before laying a second egg adjacent to the first. She repeats the process until the space is full, with the exception that the very last egg will be male. This egg will be the first to hatch, a process known as protandry, which assures that males will be available to mate as soon as females begin to emerge.

Depending on the species, the female prepares one or several nests before she dies. Unlike social bees, solitary bees do not care for their young. The eggs are provisioned and sealed with no further attendance from another bee. In contrast to highly eusocial queens that may lay hundreds of thousands of eggs in a lifetime, a solitary queen may lay a total of 25 or fewer (Buchmann and Nabhan 1996). With very few exceptions, nearly all wild bees are solitary (Kearns and Thompson 2001).

THE ROLE OF BEES IN POLLINATION

Pollination occurs when pollen is transferred from the anther (male part) of a flower to the stigma (female part). The transfer of pollen within the same flower, or to another flower on the same plant, is known as self-pollination. Lima beans and soybeans are examples of self-pollinated plants. Cross-pollination (or outcrossing) occurs when pollen moves from plant to plant, whether by wind, rain, gravity, mammals, birds, or insects. Bees co-evolved with the flowering plants and have a mutualistic relationship with them. As the bees travel from flower to flower in search of nectar and pollen to provision their nests, the flowers are outcrossed to other plants, thus increasing their genetic variability. Even self-pollinated plants benefit from outcrossing, often showing better rates of seed set and larger fruit (Sammataro and Avitabile 1998).

Nearly all bees, both social and solitary, collect pollen as a protein source for their young. Many bees also collect nectar as an energy source, both for themselves and for the next generation. Eusocial bees, especially those who overwinter in colonies, are much more prone to seek out rich sources of nectar than solitary bees that have no such need. Of the species that collect both, such as the honey bee, an individual bee gathers just nectar or just pollen on any one trip, depending on the needs back home. Although occasionally a bee will collect both in one trip, pollen collection is usually an incidental activity to a nectar-collecting bee. Nectar is swallowed into a “honey stomach” to be regurgitated later, whereas pollen is stuffed into sacks on the hind legs. It also sticks to the hairy surface of the bee which carries an electrostatic charge. Bees that are deliberately collecting pollen are much more efficient pollinators than those collecting nectar, although some incidental pollination occurs even with those bees.

Foraging Habits

Bees may also be grouped into three categories based on their foraging habits. Bees that prefer only a small number of flowering species are known as oligolectic. The advantage to the plant kingdom from this behavior is enormous, since it assures cross-pollination within a single species. A few species of bee are known to pollinate one—and only one—species of flower. Bee-flower mutualisms of this type, known as monolectic, are rare but extremely important from an evolutionary perspective. Neither species will survive without the other, so a loss of one means the loss of both (Buchmann and Nabhan 1996). Most bees, however, are opportunistic foragers that gather pollen from a vast number of species. These bees, known as polylectic, are valuable to farmers who often grow more than one crop at a time, or more than one crop in sequence. Both honey bees and bumble bees are polylectic.

Even bees that are polylectic tend to visit only one type of flower per foraging trip, a trait known as "floral consistency." Nature's way of ensuring good pollination, floral consistency prevents a bee from going from a clover to a vinca to a cucumber to a bean, for example. Such random flower visits would not yield the pollination necessary to set seed and maintain plant populations from year to year (Kremen 2009).

Although polylectic bees have eclectic tastes, they still have preferences. Nectar-collecting bees such as honey bees and stingless bees prefer flowers that have high sugar content. Honey bees will readily visit apple, cherry, and plum, for example, but avoid pear unless there is nothing else to eat. On the other hand, most wild bees, because they collect only pollen, readily visit the low-sugar flowers of pear and other similar plants (Tepedino et al 2007).

Pollination Limitations

Crops vary in their need for pollinators. Some crops, notably almonds and squash, are virtually 100% bee pollinated, while others such as apples are only about 50% bee pollinated (Delaplane and Mayer 2000). The grains, the largest human food group in the world, require no bee pollination at all. Not all bees can pollinate all pollination-requiring plants. Both the bees and the plants have certain limitations that restrict, reduce, or prevent pollination. Following are a few examples of species-specific pollination limitations.

Color Limitations: Honey bees don't see red, so red flowers simply don't get pollinated by them. Honey bees pollinate flowers that are blue, yellow, green, and ultraviolet. Other bees see other colors, so a diversity of pollinators has a better chance of pollinating all the species that require it (Sammataro and Avitabile 1998).

Foraging range: Small bees tend to have short foraging ranges compared to large bees (Greenleaf et al 2007), and eusocial bees tend to have larger ranges than solitary bees (Gathmann and Tscharntke 2002). Since most wild bees are small and solitary, they tend to have short foraging ranges (Greenleaf et al 2007).

Structural Features of Flowers: The tripping mechanisms of some flowers tend to ward off certain bees. For example, the pollen-carrying part of the alfalfa flower, known as the keel, trips from the weight of the bee and strikes the bee on the head. Some bees, after being repeatedly stuck, avoid alfalfa altogether, while the members of other bee species don't seem to mind. Other flowers, notably tomato, eggplant, blueberries and cranberries, require sonication or "buzz pollination" to shake the pollen out of the flower. This resonant vibration is performed when the bee grabs on to the flower and beats its wings rapidly, causing the pollen-carrying anthers to vibrate and the pollen to dislodge. Only certain bees—usually large species of bumble bee—can perform sonication (Goulson 2003). According to Stephen Buchmann of the Tucson Bee Lab (2009), "A buzzing bumble bee can extract pollen from nightshade or tomato flowers hundreds of times faster than honey bees." Unfortunately the most important greenhouse pollinator of tomatoes is nearly extinct due to an imported fungal disease (Watanabe 2008). Because of the loss of these bees, greenhouse tomatoes are now often pollinated using hand-held electric vibrators (USDA Bee Lab 2009).

Structural Features of the Bee: Honey bees, for example, have short tongues. While they can easily and efficiently pollinate white clover, alsike clover, yellow clover and crimson clover, they cannot reach into the longer corolla of red clover (Goulson 2002).

Temporal Limitations: Another type of limitation has to do with time of flowering. Bumble bees, for example, haven't yet hatched when the early-flowering orchard trees such as apple and cherry are in full bloom (Greer 1999).

Visitation Efficiency: Although honey bees store large amounts of pollen and nectar (in the form of honey) in the hive for both brood rearing and overwintering, they are not particularly efficient pollinators because they do not move quickly from flower to flower. Many solitary wild bees visit more flowers per unit time and so do a better job of distributing pollen. What honey bees lack in efficiency, however, they make up for in sheer numbers. Ultimately, it is the number of bees in conjunction with their efficiency that determines the total pollination value of a population (Greenleaf and Kremen 2006b).

Weather: Wet or especially cold weather can curtail pollination. A string of warm days may cause the flowers to open, but if rain follows, the honey bees will not be able to fly. Bumble bees, on the other hand, will forage even in the rain (Goulson 2002, Isaacs and Tuell 2007).

THE IMPORTANCE OF BEE POLLINATION TO AGRICULTURAL CROPS

In North America today more than 90 commercial crops are pollinated, at least in part, by bees (NRC 2007). Food crops such as squash, pumpkins, apples, oranges, cucumbers, cherries, blueberries, cranberries, melons, turnips, sunflower, carrots and canola are all substantially pollinated by bees (Sammataro and Avitabile 1998). In 2007 the U.S. almond crop alone was valued at upwards of $1.5 billion—every last nut pollinated by a bee, usually a honey bee (Schacker 2008). Forage crops such as clover, alfalfa, and lespedeza, which make their way into the human food chain via the mouths of livestock, are largely pollinated by bees, as well as most specialty crops such as herbs, nursery stock, and flower crops. In 2007 the estimated value of all bee-pollinated crops was approximately 30% of the $132 billion US field crop total (USDA 2007).

Outside the United States, bees pollinate crops such as coffee, kiwi, cacao, Brazil nut, vanilla, mangos, cherimoya, tangerine, coconut and guava, as well as industrial crops such as cotton, flax, kapok, pyrethrum, and opium poppy (Sammataro and Avitabile 1998). Absent from this list are the approximately 250,000 species of non-commercial flowering plants, 60-80% of which are also bee pollinated (Vaughan and Black 2008, Kremen et al. 2007). Plant pollination is essential to biodiversity, food production on many trophic levels, as well as seed production for food, forage, industrial, horticultural, and ornamental crops, not to mention wildland survival.

THE "POLLINATION CRISIS"

Before the advent of modern agriculture in the United States, crop pollination was performed by local populations of wild bees (Ricketts et al. 2004; Morandin and Winston 2005). Honey bees were often kept by farmers as a source of honey and beeswax, with little or no thought to their benefit as pollinators (Ellis 2004). But after World War II the United States became a crop exporting nation (Horn 2005), and as the crops became intensely managed the pollinators became intensely managed as well (Kremen 2008). Large fields, high-density planting, and the use of monocultures require tremendous numbers of pollinators to be available for a short time. This need gave rise to migratory beekeeping, the practice of moving hundreds or even thousands of beehives into the fields where they are needed, and moving them elsewhere in time for the next crop (Mapes 2007).

In the United States, migratory beekeeping was first attempted in the 1870s by an investor named C.O. Perrine who purchased a fleet of barges and hundreds of bee hives. He headed down the Mississippi River, stopping whenever he encountered vast fields of flowers, planning to export honey to Europe. The experiment failed, however, mostly because Perrine didn’t have a clear understanding of blooming seasons and nectar flows (Horn 2005). Other experiments were tried during the ensuing decades wherein bees were moved by horse-drawn wagon, streamers, and trains, but these endeavors were too slow, too expensive, and too hard on the bees (Horn 2005). It wasn’t until the 1950s that a number of events converged which jumpstarted large-scale migratory beekeeping. Those events included the successful grafting of almond scions onto peach rootstocks in central California, the rise of mechanized agriculture, and the construction of the US Interstate Highway System (Root 2007, Horn 2005, Buchmann and Repplier 2005). Suddenly there was both an urgent need for bees and a way to move them around.

Wild bees were ignored once the pollination problem was “solved” by migratory beekeepers, and much of wild bee habitat was destroyed or degraded as farms got larger and more dependent on heavy machinery and chemical inputs (Delaplane and Mayer 2000). The gradual loss of wild pollinators went largely unnoticed until honey bee populations began to plummet. With wild bee habitat in short supply and managed honey bees increasingly difficult to find, crop yields in many parts of the world began to drop (Ricketts et al 2004). While the cause of lower yields is often difficult to pinpoint, incomplete pollination reveals itself in obvious ways. Lopsided fruit such as apples and pears, deflated cucumbers and squash, distorted raspberries, and shriveled cotton bolls are all indicators of incomplete pollination (Martin and Leonard 1967). In other words, there was enough pollination to initiate fruit set, but not enough to pollinate every ovule within the carpel (fig. 1). A carpel without seeds does not develop fully, thus lowering both the weight and the volume of the yield. The market value is lowered as well because a perfectly symmetrical fruit commands a higher price than a distorted one (Martin and Leonard 1967).

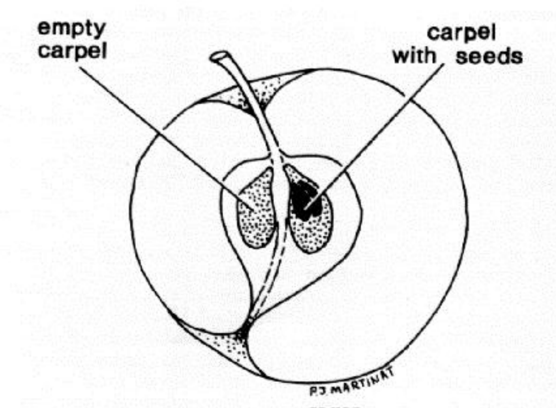

Figure 1 Incomplete pollination in apples causes lop-sided fruit.

An interest in the conservation of "pollination systems" began to rise as honey bee colonies began to fail (Shuler et al. 2005, Ricketts 2004). Since the late 1990s the term "pollination crisis" has been used to describe the decline of native and managed bee populations, as well as the damage to the web of plant-pollinator interactions resulting from agricultural intensification (Kearns et al. 1998).

Agricultural Intensification

Agricultural intensification damages plant-pollinator interactions in a number of ways. Habitat is lost when fields become larger, when hedgerows and adjacent lands are cleared in order to facilitate weed control, and when monocultures replace diverse crops (Kremen et al. 2002). Practices such as heavy tilling and flood irrigation are used in addition to high levels of chemical fertilizer. Poisons of many varieties including fungicides, rodenticides, herbicides, and insecticides can turn large-scale farms into "biological deserts" where nothing lives but the target crop and the migratory bees brought in to pollinate its (Klein et al.). The following consequences of intensive agriculture are particular damaging to populations of wild bees.

Habitat fragmentation: Wild bees have shorter foraging distances than larger managed bees so they cannot travel to distant fragments (Gathmann and Tscharntke 2002). One result of fragmentation is known as the Allee effect. The Allee affect occurs when plant density and population size is so low that pollinators no longer visit certain flowers (Kearns et al. 1998). Bees are biologically programmed to visit many flowers of the same type on any one foraging trip, an adaptation that assures a given species of plant will be adequately cross-pollinated. But if any given flower population is too low to yield much in the way of pollen or nectar, the bees tend to ignore it, which causes a cycle that follows the pattern of an extinction vortex: fewer flowers attract fewer bees which means less pollination and fewer viable seeds. In the subsequent year, there are even fewer flowers, fewer bees, and fewer viable seeds. The cycle proceeds until a local extinction of valuable forage flowers occurs (Groom et al. 2006).

The Allee affect is responsible for the disappearance of many wildflowers and wild bees in agricultural settings. Because the habitats are fragmented and small, they produce few species and small populations. Small flowering plant populations eventually cause the bees to die out or move elsewhere (Groom et al. 2006).

Seasonal shortage of nectar: Monocultures flower all at once for a short time, but wild bees need a continuous supply of food throughout their lifetime. Intensive agriculture destroys the plants that could have provided food before and after the main crop. Because nearly all land in an intensively-managed farm is planted to crops, there is very little land that is fallowed or left in borders and hedgerows. This practice leaves little for the bees to eat. An inviting landscape for wild bees will contain a diversity of wildland plants or weeds that the bees can use between crops (Kremen et al. 2002).

Pesticides: While insecticides kill bees outright, herbicides destroy not only food sources, but nesting sites, nest-building materials, breeding areas, and hiding places as well (Vaughan and Black 2008).

Tilling: Aggressive soil tilling disrupts nesting sites of ground-nesting bees (James and Pitts-Singer 2008). It also disrupts the flowering of annual plants that are one of the main food sources for wild bees (Holzschuh et al. 2007).

Evidence of Pollination Deficits

The decline of wild bees is hard to quantify simply because we don't know much about them, and because we have few or no records of previous population levels (Buchmann and Nabhan 1996). However, case studies from around the world are showing evidence of wild bee shortages (Allen-Wardell et al. 1998). According to Nabhan and Buchmann (1996) these studies, although regional or crop-specific, are nevertheless highly indicative of general problems and should not be considered "merely anecdotal." Declines in cherries in Ontario, pumpkins in New York, cashews in North Borneo, and blueberries in New Brunswick, Canada have all been blamed on a lack of wild pollinators (Allen-Wardell et al. 1998).

More recently, Chinese orchardists have begun hand-pollinating many of their fruit trees because the wild pollinators have been killed by pesticides. Similarly, British botanists are hand-pollinating certain rare orchids because the wild pollinators' habitat has been destroyed (Shepherd et al. 2003). In addition, Alexandra-Maria Klein (2007) reported that, "Passion fruits in Brazil are hand-pollinated through expensive day-laborers as the natural pollinators, carpenter bees, are hardly available because of high insecticide use in the agricultural fields and the destruction of the natural habitats."

Cranberry growers in northeastern United States are renting honey bees to pollinate cranberry—even though honey bees are not efficient pollinators of cranberry—because native bumble bee populations have seriously declined (Goulson 2002). Some crops, such as red clover, have fallen out of favor with growers because there aren't enough pollinators to bring the crop to seed (Goulson 2003). In fact, available statistics show that wild pollinators are declining throughout England, Europe, and North America (Buchmann and Nabhan 1996), and some researches think we may soon have serious worldwide shortages of pollinators, both wild and managed.

In the foreword to *The Forgotten Pollinators* by Buchmann and Nabhan (1996), Edward O. Wilson, the American ecologist writes, “The evidence is overwhelming that wild pollinators are declining. . . . Their ranks are being thinned not just by habitat reduction and other familiar agents of impoverishment, but also by the disruption of the delicate “biofabric” of interactions that bind ecosystems together. Humanity, for its own sake, must attend to the forgotten pollinators and their countless dependent plant species.”

THE PLIGHT OF THE HONEY BEE

Because it is difficult to replace something without understanding the thing to be replaced, it is helpful to review what went wrong with the honey bee.

Regardless of modern agricultural dependence on honey bees, mankind’s close association with them predates agrarian society. A petroglyph of honey hunters found near Valencia, Spain is estimated to be over 8000 years old (Bishop 2005). Other honey hunters are pictured in early drawings from Zimbabwe and South Africa (Ellis 2004). The first depictions of humans actually tending man-made hives are found in three Egyptian tombs ranging from about 3450 to 4400 years ago (Root 2006). Mankind’s persistent interest in honey bees is not difficult to understand. Bees not only pollinate the flowers and crops but produce both food and fuel, a concept made famous by a quote from the work of Jonathan Swift (1667–1745): *We have chosen to fill our hives with honey and wax; thus furnishing mankind with the two noblest of things, which are sweetness and light*. Later in history other products of the hive became valuable as well, including pollen, royal jelly, and propolis (Root 2006).

The honey bee moved from continent to continent, first spreading north into Europe, then traveling with European settlers as they colonized the New World (Horn 2005). Although the history of mankind’s involvement with the honey bee is long and convoluted, honey bees remained easy to raise, easy to handle, and easy to move. Most important of all, they were essentially disease-free. Disease free, that is, until they collided with modern farming techniques and the iconic monoculture.

Before the mid-1800s a honey bee hive could survive in the Americas, unattended, year after year (Ellis 2004). Because they were an introduced species, they had no natural enemies in the New World. Feral swarms that split from managed hives thrived in the forests and could be found living in recognized "bee trees" (Horn 2005). In *Notes on the State of Virginia* (1784), Thomas Jefferson commented, "The Indians . . . call them the white man's fly, and consider their approach as indicating the approach of the settlements." These feral colonies became significant pollinators of both natural landscapes and cultivated crops (Delaplane and Mayer 2000), and both native tribes and settlers collected honey from forest hives "where they are free from anybody" (Ellis 2004). When honey bee diseases began showing up in Europe, the United States enacted the Honey Bee Act of 1922, which prohibited the importation of honey bees from outside North America (NRC 2007).

Meanwhile, back in Europe, honey bee colonies nearly disappeared from a malady called Isle of Wight disease (Horn 2005), which we now know to be caused by tracheal mites. The resultant die-off of colonies caused a shortage of honey across the continent. Europeans kept bees to provide honey for their families, not for pollination of crops, and as sugar became more available to householders after World War I, it gradually replaced the need for honey (Horn 2005). And Europeans, known for their quaint villages with grassy verges, farms lined with hedgerows, cottage gardens, and flower-lined footpaths were never short of wild bees to pollinate their crops: unlike Americans, they never destroyed the habitats were wild bees thrived.

Decline of Honey Bee Populations

In spite of Congress and the Honey Bee Act of 1922 and the subsequent Honey Bee Restriction Act of 1923, which decreed how honey bees could be housed, problems began to plague American honey bees. Feral hives began disappearing (Kearns et al. 1998) and beekeepers began losing vast numbers of managed hives. The losses began just after World War II, commensurate with the rise in intensive agriculture (Horn 2005). In the United States alone, managed colonies dropped from over six million colonies in 1944 (Schacker 2008) to about four million in the 1970s to about 2.4 million colonies in 2005 (USDA National Agricultural Statistics Service 1977, 2006). In the meantime feral hives almost completely disappeared: by 1994 over 98% of the feral colonies were eliminated (Watanabe 1994). The shortage of bees, especially for almond pollination, became so severe that in 2005 the Honeybee Act of 1922 was altered to allow importation of bees from outside of North America (NRC 2007). Since that time, bees have routinely been shipped from Australia into the United States.

The various assaults that precipitated the loss of honey bees can be divided into two types: those caused naturally by diseases or pests, and those arising as the result of intensive agricultural practices.

Naturally Occurring Diseases and Pests: Two major bacterial diseases were the first problems to arise. Although both European foulbrood (*Melissococcus pluton*) and American foulbrood (*Paenibacillus larvae*) were already present during the 1800s, they were successfully controlled by burning infected hives and, much later, by the use of antibiotics (Root 2006). Since migratory beekeeping had not begun, hives were generally further apart and disease did not spread easily between them (National Sustainable Agricultural Information Service).

Slowly, other diseases began to appear. Chalkbrood (*Ascosphaera apis*), a fungal disease of the larva first described in 1916, was discovered in California in 1968; by 1975 it was widespread and common within the United States (James 2008). It was not until 1984 that parasitic Acarine mites (*Acarapis woodi*) were first discovered in North America (NRC 2007). Known as tracheal mites, they live and reproduce in the trachea of young bees.

Nosema apis, a microsporidian that lives in the gut of honey bees, began to be a significant problem in the 1980s, but it was largely controlled by a drug and not considered an insurmountable problem (Watanabe 2008). The real devastation began in 1987 with the introduction of *Varroa destructor*, another parasitic mite (Kearns et al. 1998). This ectoparasite not only sucks the fluid (hemolymph) from the bodies of its host, but disperses a panoply of viral diseases including Israeli acute paralysis virus, deformed wing virus, sacbrood virus, Kashmir bee virus and others (Watanabe 2008). According to Rowan Jacobsen (2008), "Viruses . . . have accompanied honey bees throughout their two-million-year history, yet they normally play a quiet, background roll." As the mites weakened the bees' resistance, however, the viruses were able to thrive. Researchers believe the spread of parasitic mites, and their concomitant viruses, into the wildlands of North America is primarily responsible for the loss of feral colonies (Allen-Wardell et al. 1998, Delaplane and Mayer 2000).

Following on the heels of *Varroa destructor* was another *Nosema* introduced in 1996, *Nosema ceranae*. This one, much more virulent than the first, also lives in the gut and prevents the bee from absorbing nutrients (Watanabe 2008). Other diseases, once only obscure, began to flourish as honey bees became weakened from the onslaught of mites. Chalkbrood disease (*Ascophaera apis*), small hive beetles (*Aethina tumida*), bee lice (*Braula coeca*), wax moths (*Galleria melonella*), stone brood (*Aspergillus flavus*), and the viral infections began to increase and hives began to die.

While breeding disease resistance into plant or animal species is often a viable answer to health problems, a quirk in honey bee genetics makes this avenue extremely difficult. When the honey bee genome was first mapped in 2006, it was discovered that, in comparison to fruit flies (*Drosophila*) and mosquitoes (*Anopheles*), honey bees have only one third as many genes related to immune response (Schacker 2008, James 2008). Even though honey bees seem to rely heavily on hygienic hive behaviors to guard against disease, the lack of immunity-related genes lowers their resistance to new pathogens (James 2008). Similarly, in comparison to other insects, honey bees have only one tenth the number of genes involved in detoxification of environmental poisons (Schacker 2008). Thus, while fruit flies and mosquitoes rapidly develop resistance to new pathogens and industrial toxins such as pesticides, honey bees do not. Bee breeders, hampered by this lack of genetic material, continue to be largely unsuccessful at developing disease-resistant honey bee strains (Schacker 2008). A notable exception to this rule occurred in the 1980s when Brother Adam, working at Buckfast Abbey in England, produced a bee from survivor stock that was largely resistant to the tracheal mite (Ellis 2004).

A completely different type of problem to hit American shores was the accidental introduction of an African subspecies of honey bee, *Apis mellifera scutellata*. Released in Brazil in 1956 these bees soon hybridized with local honey bees resulting in "Africanized" or killer bees, which spread across South and Central America before moving north into the United States in 1990 (Kearns et al. 1998). Although the outcrossing with European honey bees has diluted their aggressive tendencies somewhat, they are still feared by laymen and beekeepers alike (Jacobsen 2008).

In spite of being efficient pollinators, Africanized bees swarm more frequently than their European counterparts, and the swarms travel further distances from the parent hive (NRC 2007). The loss of a swarm—which is generally 50-90% of the total hive population—causes a significant loss of productivity for the beekeeper with respect to both pollinating capacity and honey-making ability (Dadant & Sons 1975, NRC 2007). In addition, beekeepers in areas of known Africanized honey bee infestation have to deal with increased liability and enhanced regulation that often prohibits the movement of hives into or through certain areas (NRC 2007). The complications due to Africanized honey bees have caused many beekeepers in the southern United States (fig. 2) to leave the business, a situation which has further decreased the total number of hives available for commercial pollination (Goulson 2003, Delaplane and Mayer 2000, Kearns et al. 1998).

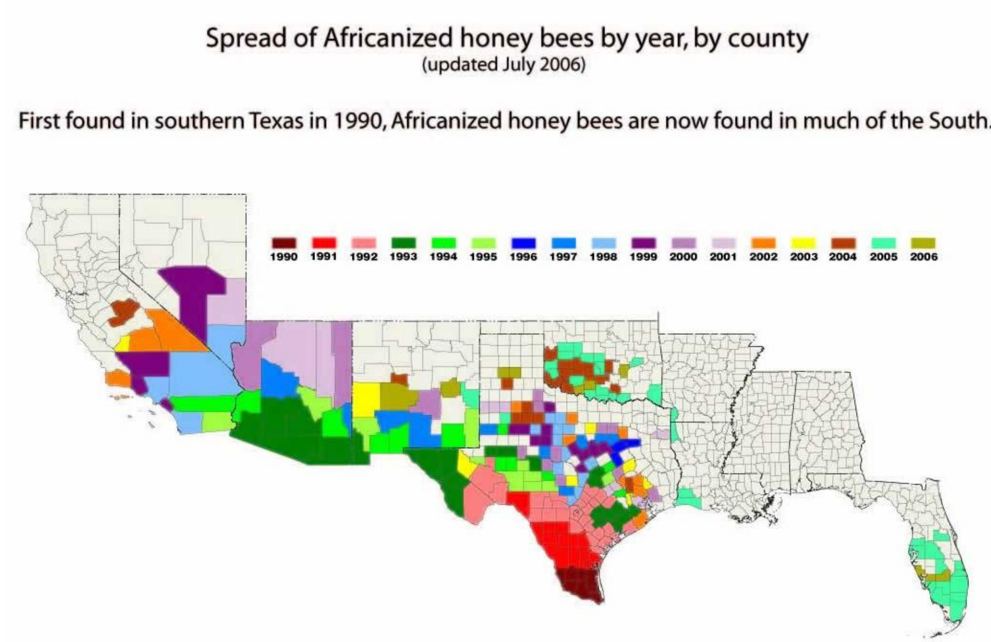

Figure 2 US counties harboring Africanized honey bees in 2006.

Effects of intensive agriculture on honey bee health: Honey bees have been used and abused to a greater and greater extent as agricultural systems have received more intensive management and monocultures have become the norm (Jacobsen 2008). As agricultural intensity has increased, so has the number of maladies affecting honey bees (Schacker 2008). Although some of these maladies resemble naturally occurring pathogens, in many cases researchers believe that modern management methods weaken colonies to the point where they succumb to a disease that would otherwise have had only a minor impact on colony health (Watanabe 2008).

For example, in 2006 an unidentified malady now known as colony collapse disorder (CCD) appeared in North America (fig.3). By spring of 2007, 25% of all managed hives in the United States may have been lost, and some individual beekeepers reported losses of 75-100% of their hives (James 2008). Several theories have arisen to explain CCD. Some scientists believe it is caused by one of the viruses carried by *Varroa* mites, some believe it is the result of the synergistic effects of a combination of pesticides, and others believe it is caused by sub-lethal doses of the agricultural insecticides imidacloprid or clothianidan, which can cause bees to become disoriented and lose their way home (Yang et al. 2008). Still others believe colony collapse is caused by unknown pathogens, parasites, or immune system disruptions (Winfree et al. 2007, Yang et al. 2008).

In addition to the proximal cause of the collapsing colonies, honey bees are losing vitality and disease resistance due to build up of chemicals in the hive (Schacker 2008, Jacobsen 2008). Some of the chemicals are brought in by the bees themselves in the form of contaminated pollen and nectar (Watanabe 2008). Other chemicals are introduced into the hive by the beekeeper in the form of drugs to combat the litany of diseases (Watanabe 2008). In either case, because honey bees reuse their comb from generation to generation and from year to year, the chemicals build up in the wax until they begin to interfere with the health of the bees (Jacobsen 2008, Schacker 2008). Toxicologists at Penn State are currently investigating 171 pesticides and their metabolites found in beeswax, pollen, nectar, and bee tissues that could possibly be causes of colony collapse disorder (Watanabe 2008).

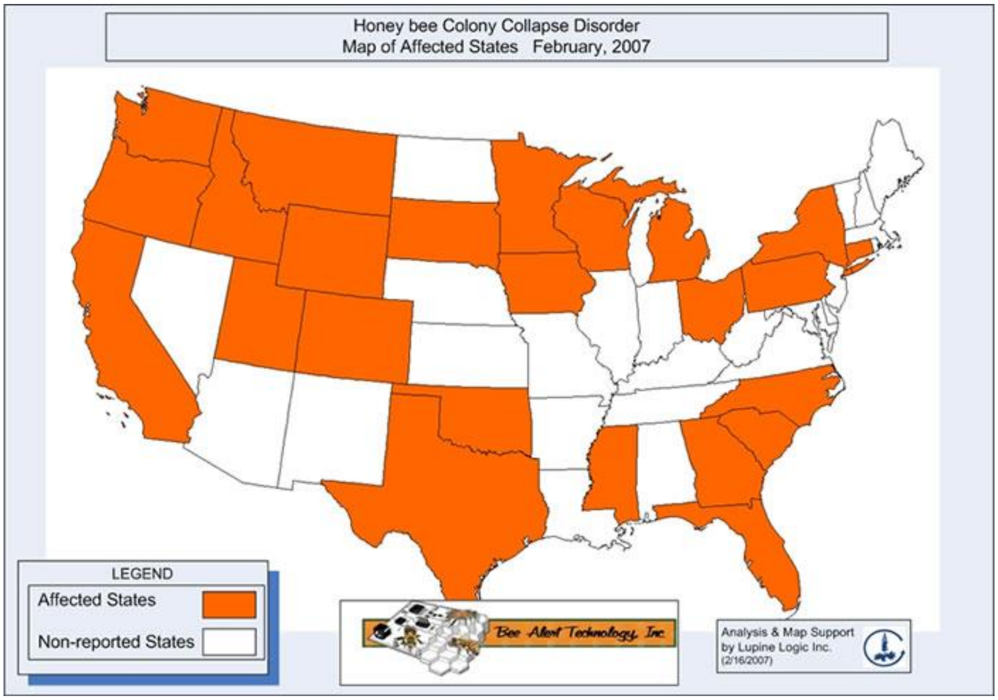

Figure 3 States Reporting Colony Collapse Disorder in 2007.

The huge demand for pollination services required for intensive agriculture poses other problems for honey bee health. Besides using chemicals in the hive, other widespread management practices stress the bees. For example, bees in North American are true migrant laborers. Beekeepers rent out their hives to growers, usually charging a flat fee per hive for a certain length of time. Each year nearly one-half of all managed hives in the continental United States make their way to the almond orchards of California during the crucial month of February, some arriving from as far away as Florida (Kearns et al 1998).

But the trek to California is just the beginning. In what is a fairly typical year for a migrant beekeeper, Eric Olson of Yakima drives his 13,000 hives to Waterford, California for almonds in February, then travels north to Yakima for cherries, apples, peaches, pears and apricots in March, then on to Mossyrock for blueberries and Mount Vernon for raspberries, both in May (Mapes 2007). In June they travel to the cranberry bogs of Long Beach, then to the blackberries and fireweed in Kapowsin, Buckley, and Enumclaw. In June they make the long haul to the clover pastures of North Dakota before returning home to "overwinter" a short two months before the cycle begins again (Mapes 2007).

All the travel is harmful to bees in a number of ways. They often become overheated during the long road trips (Jacobsen 2008). Once they arrive in their new temporary quarters they are exposed to acre upon acre of monoculture that often has been treated with one or a number of pesticides (Schacker 2008). Their diets lack the nutrient diversity found in the varied floral assortment of a natural landscape (Jacobsen 2008). There are high levels of competition for food with so many bees in intensive landscapes, and the transmission of disease from hive to hive is virtually guaranteed (Root 2006). When the crop is exhausted, they are locked inside an overpopulated hive and trucked again, only to repeat the process on another crops in another place (Jacobsen 2008).

To supplement their income, these beekeepers often sell whatever honey they collect and then feed the bees sugar-syrup or high-fructose corn syrup to make up the deficit. While these products provide the calories needed for the bees to survive, they do not contain the phytochemicals and nutrients they would have received from honey (Jacobsen 2008). The bees tend to be nutritionally bankrupt and often are unable to make it through the winter months (Schacker 2008).

In spite of all these problems, managed honey bees continue to be the most popular form of pollination service. But if losses of colonies continue at the present rate, the number of colonies will simply not be sufficient to cover all the pollination requirements of modern farming.

FULL CIRCLE: BACK INTO THE WILD

So without a cure—or even an identification of the cause—of Colony Collapse Disorder, and lacking quick answers from the geneticists, growers worldwide have responded by looking at alternatives for the European honey bee among the wild bee populations. But how can vast numbers of extremely populous colonies of honey bees be replaced by wild bees, most of which are solitary, do not live from year to year, have very specific habitat requirements, and are declining as well?

Two Approaches to Using Wild Bees

Researchers are looking at two alternative ways of using wild bees in place of honey bees (James and Pitts-Singer 2008). The first alternative entails finding additional species that can be managed or "domesticated" much like the honey bee (James 2008b). The second alternative centers on providing habitat in or near agricultural areas that will attract and nourish wild bees to the extent that they will pollinate crops within their range. After a very brief summary of the problems surrounding the domestication of wild bees, the remainder of this paper will focus on the second alternative: the conservation and enhancement of wild bee habitat in agricultural areas.

Management of Additional Species. Although some progress has been made in raising "wild" bees, most of the available species are solitary and extremely difficult to manage, especially in the numbers needed to pollinate expansive monocultures (James 2008b). In some part of the country, especially in the Midwest, the alfalfa leafcutting bee (*Megachile rotundata*) is being used to pollinate alfalfa for seed production, as is the alkali bee (*Nomia melanderi*). Bumble bees (*Bombus spp*.) are raised for some greenhouse crops, *Osmia aglaia* for bramble fruits, and blue orchard bees (*Osmia spp.*) for almonds and some tree fruits (Isaacs and Tuell 2007).

Managing wild bees is not easy, mostly because they do not live in hives, nor do they live in large groups. Providing attractive nesting space is one of the best options for accumulating bees. Bare patches of undisturbed ground or persistent embankments are good for attracting aggregations of ground-nesting bees such as alkali bees and sweat bees (Isaacs and Tuell 2007). Old wooden structures, loose debris piles, and thick underbrush are appropriate for attracting carpenter bees and bumble bees. Old pithy plant stems, hollow reeds, or boards with drilled holes are good for cavity-nesting bees such as leafcutting and mason bees (Pitts-Singer and James 2008).

Trap nests are often used to collect larva for the next growing season. These are usually wooden blocks with a series of parallel holes drilled into them in which the bees can lay eggs. These are then collected and refrigerated until they are needed. Once warmed to ambient temperature, the bees continue their development and release themselves into the field. Although some eggs and/or larva are commercially available, this is not a widespread practice (Pitts-Singer and James 2008).

One of the primary concerns with managed bees is the control of disease. As with any single species, high densities of individuals living in close quarters are bound to transmit disease faster than a variety of species in an open space. Disease is often transmitted with pollen after the pollen has become infected from another bee. When the alfalfa leafcutting bee was first introduced into the United States in the early 1950s, no known pathogens were associated with it. During the 1960s, the leafcutting bee was propagated heavily for the production of alfalfa seed, especially in the western United States. Within ten years severe outbreaks of chalkbrood disease (*Ascosphaera aggregata*) devastated large numbers of the managed stock (James 2008).

Other infections are found in managed stocks of wild bees including *Nosema*, acute bee paralysis, spiroplasmosis, and at least two protozoan bee diseases in bumble bees; iridescent viral disease in Asian honey bees; and chalkbrood in the blue orchard bee. Although wild bees appear to be immune to the various mites that attack honey bees, wild bees reared artificially in great numbers may someday attract their own form of predatory mite (James 2008). Bee diseases among wild managed bees are difficult to control because the larva are sequestered inside drilled holes or hollow reeds and so cannot be easily treated. The adults don't eat from troughs or feeders, so they are not easily treated either (James 2008).

The raising of wild bees bears little resemblance to traditional apiculture, and management practices developed over hundreds of years for honey bees simply will not work for domesticating wild bees that are mostly solitary. Research is just beginning into the new field of wild bee management (Pitts-Singer and James 2008).

Conservation of Wild Pollinators: Provided they have enough of the right type of habitat, wild bees will contribute to the overall health of an ecosystem by simultaneously pollinating native as well as cultivated flowers (Shepherd et al. 2003). But wild bees require a number of things that managed bees do not, the most important and costly of which is acreage.

In order to assure enough wild bees to pollinate a crop, a grower must provide habitat for a vast number of species. Unlike managed honey bees, who themselves are a monoculture, wild bees in sufficient numbers to pollinate a crop will be a diverse community of many species—at least dozens, and perhaps hundreds (Tepedino et al. 2007). They work in concert, each species pollinating those flowers it favors, each occupying the microhabitat it prefers, and most living only a month or less (Sheffield 2008b). The species-area relationship applies to this arrangement. A greater area of land will produce a greater number of species, and a greater number of species will provide a broader range of pollination services to the grower (Groom et al. 2006)

Researcher Claire Kremen (2008), who has studied the role of wild bees in California agriculture, is convinced that wild bees could become "a valuable insurance policy if honey bees become more scarce or fail altogether." She concluded that wild pollinators can serve the needs of crops in four distinct but related ways:

First, wild pollinators can *substitute for managed bees in full or in part.* For example, in a New Jersey study Winfree et al. (2008) found that native pollinators provided 100% of the pollination required in watermelon, and Morandin and Winston (2005) got similar results in organic fields of canola in Alberta, Canada. Nearly all pollination was provided by wild bees in a squash and pumpkin study in Virginia, West Virginia, and Maryland (Shuler et al. 2005), and a large percentage of blueberries were pollinated by wild bees in a Grand Haven, Michigan study (Vaughan et al. 2008b).

Second, wild pollinators can *enhance the activities of managed pollinators*. Greenleaf and Kremen (2006) found that wild bees increased the number of flower visits by managed bees in fields of hybrid sunflower in central California by repeatedly attacking the slower-moving honey bees.

Third, wild pollinators *visit flowers that are not effectively pollinated by honey bees*, such as alfalfa, blueberry, and cranberry (Kremen 2008), and often choose flowers not preferred by honey bees, such as pears and squash (Tepedino et al. 2007).

And finally, wild pollinators *enhance fruit set and fruit size* of normally self-pollinating species such as tomato (Greenleaf and Kremen 2006, Klein et al 2007).

Advantages of wild bees

Although the costs in acreage are substantial, the advantages of wild bees are many. Most obviously, they provide a “free” ecosystem service that exists in the environment for which they are best suited. Since they are in their native habitat, they manage themselves. They don’t have to be fed or moved or medicated. In addition, since each community of wild bees contains a variety of species, the community as a whole can pollinate a number of different crops. A good example of extended crop coverage occurred in the orchards of Capitol Reef National Park: while honey bees ignored the pear trees, the wild bees were frequent visitors (Trepedino et al. 2006). Another example occurs in alfalfa. The structure of alfalfa flowers causes them to snap down on the head of the pollinator—something honey bees dislike and wild alkali bees easily tolerate (Greer 1999).

Because wild bees are adapted to local conditions, many wild bees become active at the first sign of spring, long before managed colonies of honey bees begin to stir (Goulson 2003). This makes wild bees an excellent choice for some of the very early fruit trees. Some bees are early risers as well. The oxaeid bee (*Ptiloglossa arizonensis*), a solitary ground-dweller, will begin pollination at 5 a.m., while the honey bee may sleep in until 7 a.m. (Greer 1999). Weather also affects bees in different ways. Most stay under cover during a drizzle, but the shaggy fuzzyfoot (*Anthophora pilipes villosula*) will work in the rain.

Farmers using wild bees are less likely to suffer a catastrophic loss of all pollinators. While whole colonies of honey bees may disappear at once, it is unlikely that all the wild pollinators will do the same (Allen-Wardell et al. 1997). Although wild bees have short life spans—often less than a month (Sheffield 2008b)—the different species are all hatched at different times, in different places, and under different conditions, so it is unlikely that a disease, pesticide, or temperature anomaly would affect all the species in exactly the same way. Simply stated, “diversifying pollinators spreads the risk” (Isaacs and Tuell 2007).

Wild bees are more efficient than honey bees. It is estimated that 250 blue orchard bees can pollinate one acre of apples, a job that would require 15-20,000 foraging honey bees (Vaughan et al. 2008b).

Wild bees have shorter forages distances than manages bees which means they tend to stay within a particular field rather than flying back and forth between fields. This characteristic assures good pollination coverage of that field. And although they don’t fly far, they tend to fly faster than honey bees, which means more flowers are pollinated per unit time per bee. The hornfaced bee (*Osmia cornifrons*) can easily visit 15 flowers per minute, while a honey bee may spend a minute or more on a single flower (Greer 1999). Also, unlike honey bee drones, male wild bees pollinate just as the females do.

Disease resistance, too, is an advantage. Although wild bees are affected by habitat degradation and pesticide use, most wild bees are completely immune to Varroa and Acarine mites, and are not affected by the genes from the Africanized honey bees (Greer 1999).

Wild bees contribute to the overall health of the ecosystem by pollinating the natural habitat as well as the cultivated landscape. While managed bees are capable of doing that as well, migratory bees are never given a chance to pollinate anything but the target crop. As soon as the crop flowers are exhausted, the bees are shipped out to their next location (Mapes 2007).

Disadvantages of Wild Bees

Unlike managed bees, however, wild bees are few in number, have short life spans, and are often very specific in the flowers they pollinate (Buchmann and Nabhan 1996). So in order for wild bees to accomplish a job normally performed by tens of thousands of honey bees, habitat must be created that supports many species of bees over large spatial and temporal scales. Wild bees do not live in monocultures anymore than wild plants do. A grower or land manager wishing to use wild bees for pollination must prepare his site for dozens of different species, not one or two. Although this commitment of resources seems unwieldy, there are many advantages in providing habitat for wild bees.

To encourage a sufficient number of wild bees to pollinate a crop, enough natural habitat must be provided, such that the wild bees have nesting sites, nesting material, safe harbor, and a continual source of nectar and pollen (Sheffield et al. 2008a).

Floral resources must be available both before and after the main crop or the bees will not remain on site. Therefore, some level of planning must be made to assure that flowers are always present and not treated with insecticide. Hornfaced bees (*Osmia cornifrons*), for example, are excellent pollinators of apple, but since they hatch before the apple bloom is ready, some other flower must be available as forage in the interim (Greer 1999). In addition, most solitary wild bees have very brief life spans—some as short as two or three weeks (Sheffield et al. 2008b). If adequate floral resources are not available during that time, the bees will not be able to provision their young for the next year, thus lowering both fecundity and population recovery (Williams and Kremen 2007).

Wild bees have shorter forages distances than eusocial bees, so the spatial arrangement of the crop with respect to the natural habitat must fall within the bees' flight patterns. Very large fields show more pollination on the edges than they do in the center (Hole et al. 2004). Furthermore, since solitary bees forage within 120-600 meters of their nesting sites, the floral sources must be close by (Gathmann and Tscharntke 2002). In Nova Scotia, Sheffield et al. (2008b) studied *Osmia lignaria* in apple orchards that were bordered with stands of bigleaf lupine (*Lupinus polyphyllus*), a plant that flowers immediately after the apples. The *Osmia* nests closest to the lupines showed greater fecundity than those further away, suggesting that placement of floral sources is important to population maintenance.

The year-to-year population densities of wild bees are extremely variable. For that reason, a large enough area of natural habitat must be available to provide for multiple species of bees.

MANAGEMENT METHODS: HOW TO ATTRACT AND MAINTAIN WILD BEES

Multiple approaches are needed to maintain a wild bee community equal to the task of pollinating large horticultural and agronomic crops (Greenleaf and Kremen, 2005). These approaches can be divide into two major areas of concern: habitat conservation and farm management practices. Both of these areas need to be addressed from the point of view of the bee.

The Bees Needs

To provide for wild bees, it is necessary to know their habitat requirements. For wild bees these fall under several major headings including nutrition, nesting sites, nesting materials, water, and safety (Isaacs and Tuell 2007).

Nutrition*:* Bees need a continuous food supply in the form of diverse flowering plants throughout their free-flying (adult) life stage. Nectar is necessary for adult energy requirements, and pollen provides protein and micronutrients for the young (Gathmann and Tscharntke 2002). Different species prefer different flowers, so a diversity of flowering plants will attract a diversity of bees (Black et al. 2007). To keep the bees on site, flowers must be available both before and after the main crop.

Safety*:* Bees need cover in the form of leafy plants to protect them from birds and other invertebrates, and from extremes in temperature and rainfall.

Nesting Sites*:* A variety of species-specific nesting sites are needed to attract a variety of bees

(Gathmann and Tscharntke 2002). Wood-nesting bees use hollow reeds, the tunnels left behind by wood-boring beetles, or some, like carpenter bees, excavate holes in any wood they find. Ground-nesting bees prefer bare soil that is sloped and well-drained.

According to Shuler et al. (2005) natural nesting cavities are most likely to be found outside the planting area, but since bare earth often occurs in cropland, many of the ground-dwelling species will nest alongside the crop. Nesting substrate needs to remain undisturbed during the bee's developmental period, which is only a few weeks in most species.

Nesting Materials: Depending on the species, wild bees need a supply of mud, green leaves, dead reeds, downed trees or bare areas of land.

Water: If a source of water is nearby, the bees will find it. In particularly dry areas, a small pool or several buckets of water may be put out for them.

Habitat Conservation

Research in North America indicates that natural areas within one-half mile of cropped land produce the greatest number of wild bees (Vaughan 2008b). Many natural areas may already exist in and around a farm, and these areas should be protected from development. Stream banks, verges, powerline easements, hedgerows, drainage ditches, fence rows, and road embankments can provide all the basic bee requirements for forage, nesting, safety, and water.

Size: Since each bee species has different requirements and since wild bee populations fluctuate widely from year to year (Greenleaf and Kremen, 2006), the landscape available to bees must be large enough to accommodate a variety of species. Using a series of plots containing various amounts (1.4-28%) of semi-natural habitat, Steffen-Dewenter et al. (2002) found that the local abundance and diversity of wild bees increased in proportion to the proportion of semi-natural habitat within their foraging range.

Kremen et al. (2004) found that the amount of pollination received by crops on a farm increased as the amount of habitat area increased, up to about 30%. Similar results were found in canola fields in Alberta. When no honey bees were on site, the maximum pollination of canola was obtained when about 30% of the farm was turned into bee habitat. (Morandin and Wilson 2005). While this is a substantial cost, it is not all or nothing: a smaller area could be set aside for wild bees, which would provide a smaller percentage of the total pollination needed (Vaughan et al. 2008).

Distance: Gathmann and Tscharntke (2002) have shown that solitary bees have short foraging distances in comparison to social bees. They selected several species of solitary bees nesting in natural areas, marked the individuals, and transported them various distances from their nests in darkened cages. The distances ranged from 50 to 2000 meters, and the direction of release point was chosen at random. Results from 17 species indicated that wild solitary bees have a maximum foraging range between 150 and 600 meters. Although Gathmann and Tscharntke expected oligolectic species to have a greater foraging range than polylectic bees (since they need to find specific food sources) the results did not bear this out. Instead, they found that body length was positively correlated with foraging distance. They concluded that body length was a better predictor of foraging distance than food specialization. These results suggest that small bees (i.e. short body length) would not thrive in an environment in which the food source is a great distance from the nesting site. Highly fragmented agricultural landscapes would most probably select against small bees, and this reduction of species richness would impact both pollination and seed set.

Ricketts et al. (2008) found that pollinator richness and visitation rates declined exponentially with increased distance from natural habitats, so from a practical point of view, the closer the habit is to the field crop, the more pollination will be received (Vaughan et al. 2008b).

Spatial arrangement: Gathmann and Tscharntke (2002) concluded that habitat patches needed to be closely arranged within cropped areas in order to minimize foraging distances from nesting sites to crop flowers. Farms should strive to have as many patches as possible, and they should be as large as possible. Patches connected by habitat corridors are ideal. Corridors can be planted along fencerows, streambeds, roadways, and drainage ditches, providing connectivity between the habitat patches (Vaughan et al. 2008).

Temporal Considerations: Floral resources must be available throughout the bee's active (adult) stage, and undisturbed nesting substrate must be available throughout the developmental (egg, larval, pupal) stages (Shuler et al. 2005). Areas of natural habitat contain weeds, wildflowers, trees and grasses—all of which can provision wild bees with the resources they need.

Incidental open spaces: Russell et al. (2005) compared unmowed powerline easements and nearby mowed grassy fields for bee species richness. They found more diversity, both spatially and numerically, in the unmowed strips, especially more cavity-nesting bees. The researchers estimated that unmowed powerline easements could provide up to five million acres of bee habitat in the United States if US utilities would adopt bee-friendly management practices.

Farm Management Practices

In nearly all relevant studies, organic farming methods produced greater wild bee diversity and abundance than conventional farms (Holzschuh et al). Although it is not the intent of this paper to compare and contrast these farming methods, many of the studies cited in this paper suggest that any of the following practices can be used to enhance the wild bee biodiversity in even a conventional agricultural setting (Vaughan et al. 2008b, Winfree et al. 2008, Klein et al. 2007, Ricketts et al. 2004, James-Pitt-Singer 2008, Greer 1999, Hole et al. 2004, Black et al. 2007, Delaplane and Mayer 2000, Kearn et al 1998,Gathmann and Tscharntke 2002, Isaacs and Tuell 2007, Goulson 2003, Greenleaf and Kremen 2006b).

Cover cropping: Cover cropping is the planting of a crop in the off-season to reduce infestations of weeds, add organic matter to the soil, and enhance soil structure. If the crop is a nitrogen-fixer such as alfalfa, clover, or vetch, it can also increase soil fertility (Martin and Leonard 1967). For the wild bees, cover crops provide floral resources, protection from predators, nesting habitat, nesting materials, and temperature mediation (Hole et al. 2005)

Crop rotation: Rather than planting the same crop in the same plot every year, organic farmers rotate crops between plots, sometimes not repeating a crop for three or four years. Crops that are hard on the soil, such as corn, are rotated with nitrogen-fixers such as alfalfa, and crops that provide little organic matter to the soil (like carrots) are rotated with those who that amend the soil (like buckwheat.) Rotations are an excellent way to control disease and destructive insects because these organisms tend to accumulate in the soil when the same crops are grown year after year in the same soil (Martin and Leonard 1967). Crop rotations are good for wild bees because growers who rotate crops use fewer pesticides overall (Hole et al 2005).

Hedgerow management: Maintaining hedgerows or other wooded or natural corridors at the perimeters of fields provides habitat and nesting sites for wild bees as well as other pollinators (Sheffield et al. 2008a). Trees that attract wild bees such as dogwood, red maple and willow can be combined with herbaceous border plants such as aster, borage, mint, tickseed, wild buckwheat, and nasturtium (Greer 1999). Another study found that uncropped field margins (6 meters wide and not sown with crops or treated with chemicals) yielded about 6 times as many flowering plant species and ten times as many bumble bees as cropped margins (Goulson 2002).

Intercropping: Intercropping is a practice in which a different crop is planted between the rows of the main crop in order to suppress weeds. Often the intercropped species is a nitrogen fixer such as clover or alfalfa, but any flowering plant can be used to provide wild bees with additional foraging and nesting sites. The increased heterogeneity of intercropped fields increases wild bee diversity (Hole et al. 2005).

Mechanical weeding: Mechanical weeding involves dragging hoes or tines across the soil surface to remove young weeds. Since it is less efficient than chemical weeding, mechanical weeding allows some non-crop flora to live in arable fields, thus providing habitat and a more diverse floral selections for wild bees (Hole et al. 2005).

Minimum tillage: Minimum-till and no-till practices are used to enhance soil structure and aid in weed suppression, erosion control, and water retention with very little or no reduction in yields per acre. In no-till fields a cover crop is sown and then the main crop is planted using a grain drill that forces the seed down through the cover foliage and into the soil. In minimum-till fields, a cover crop is sown in the same way, but a very narrow strip is tilled to receive the crop seed. In either case, wild bees benefit because fewer nesting sites are destroyed, more habitat is preserved, and an increased variety of floral species are available in the cropped fields.

Some species, such as the squash bee (*Peponapis pruinosa*) digs its nest in the ground near its food source. Such species are extremely vulnerable to soil disturbance. Minimum-till or no-till farming practices will greatly increase their numbers. However, moderate shallow tilling in appropriate seasons controls many of the perennial weeds, leaves some annual weeds for bee forage, and doesn't poison the soil the way pesticides do. Moderate tilling in the appropriate season (in the spring or fall before and after bee-nesting season) it can actually enhance rather than detract from wild bee populations.

Multiple cropping: Multiple cropping involves planting a second crop as soon as the first is harvested. It is used not only to enhance revenues, but to control weeds, soil erosion, and water loss. Because wild bees need a continuous supply of flowers, it is good for the bees as well as the grower. Even crops such as organically grown wheat have been found to be valuable foraging habitats for wild bees. Nestled among the wheat are abundant floral sources that can be used by a number of different wild bee species (Holzschuh et al. 2006).

Nesting sites: Natural nesting sites can be augmented with manmade nesting sites close to or within the agricultural fields. Patches of bare earth attract ground-nesting species such as bumble bees and sweat bees (Isaacs and Tuell 2007) . Bee boxes (wooden boxes filled with cotton fiber) and trap nests (wooden blocks drilled with holes)—even piles of scrap lumber and downed trees—will attract the cavity nesting species such as leafcutting bees and carpenter bees (Isaacs and Tuell 2007).

Reduced use of pesticides: While the use of insecticides has the direct affect of killing bees, herbicides have the indirect effect of killing flowering plants that provide food for pollinators, especially during those times when agronomic crops are not in bloom (Sheffield et al. 2008a). In addition, they alter the microclimate, especially the temperature and humidity, due to removal of ground cover (Hole et al. 2005). Avoidance of pesticides whenever possible should be a primary objective of growers wishing to enhance wild bee populations. In cases where pesticides absolutely must be applied, they should be applied in the evenings after the bees have stopped flying (Buchmann and Nabhan 1996).

Small field size: Because wild bees have short foraging ranges, small fields will ensure more uniform pollination. Hole et al. (2005) found that smaller field sizes supported greater biodiversity per unit area, primarily because of the higher percentage of non-crop habitat separating individual fields.

Spatial arrangement of crops: Based on a 2002 study, Gathmann and Tscharntke concluded that habitat patch density was important to minimize foraging distances between patches. Likewise, Ricketts et al. (2000) found that pollinator richness and visitation rate declined exponentially with increased distance from natural habitat (Steffen-Dewenter and Tscharntke 1999). Small fields surrounded by habitat strips or connected with habitat corridors are ideal arrangement for wild bees.

Temporal Considerations: Floral resources including both nectar and pollen must be available throughout the active (adult) period, and nesting substrate must be available throughout the developmental (egg-larval-pupal) stages (Shuler et al. 2005)

Undersowing: Undersowing is the practice of planting one crop beneath another, such as cucumbers under corn or forages under fruit trees (Martin and Leonard 1967). Undersowing provides weed suppression and prevents moisture loss for the farmer and provides more floral choices and, thus, enhances biodiversity of wild bee pollinators (Hole et al 2005).

Windbreaks: Windbreaks in the form of trees or hedgerows buffer pesticide drift, raise the temperature in fields thus extending pollination times, and decrease wind disturbance of flying bees (Vaughan and Black, 2008).

ACCEPTANCE OF WILD BEE POLLINATORS BY THE FARMING COMMUNITY

Many misconceptions about bees and pollinators exist among the nation's growers—perceptions that will make the transition from managed honey bees to wild bee pollinators a difficult one. Most important, growers feel dependent on managed bees, and are afraid to "let go" of their hives (James and Pitts-Singer 2008). This is a natural concern, especially since the practice of using managed honey bees has been accepted for generations. Many pollination deficits occur even when managed bees are on site, but bad weather or disease outbreaks usually get blamed for the low yields and crop failures (Greer 1999). Most growers don't blame the honey bees because they don't understand the complex bee-plant interactions involved in pollination, and because they've been taught that if you rent enough honey bees you won't have a problem (James and Pitts-Singer 2008). Growers need to be educated about how much pollination the honey bees are actually doing, especially in non-favored crops, and how much the wild bee pollinators can do to increase yields.

Using the ecosystem service of wild bees requires maintenance of native environment and trust that the system will succeed. Many modern farming practice cause displacement of wild bees, so a grower not only has to accept the idea that wild bees can help, but has to take an active role in encouraging them. This is a large and expensive commitment for something that "might" work, and resistance to change will be high (Vaughan 2008b).

Economic incentives do exist, however. Relief from the ever-spiraling cost of beehive rental is the most obvious. For example, rental prices for beehives during the five-week season of California almond pollination jumped from $19/per hive in 1992 to $180/hive in 2008. At the recommended rate of two hives per acre, California almond growers require approximately 1.2 million beehives every February—about $216 million for 35 days (Almond Board of California 2008).

Studies Highlight Advantages of Wild Bees

In spite of the various efficiencies and benefits inherent in wild bee populations, farmers who for decades have rented honey bees for pollination will be wary of changing agricultural methods. In order to encourage farmers to make the switch—a move that will require not only the expense of providing suitable habitat, but changing a number of farming practices—it will be helpful to demonstrate the wide range of advantages wild bees can offer.

The most obvious and immediate benefit to the grower is the cost savings associated with hive rental. Also important is the time saved from not having to locate and contract with migrant beekeepers, and the relief from the uncertainty that comes from being dependent on a contract beekeeper for your next crop. A number of recent studies have shown a range of advantages that can accrue from using wild bees for all, or at least part, of the required crop pollination services. The important point here, however, is that *each of the following studies was performed on a farm where suitable wild bee habitat was available adjacent to the cropped fields.*

The studies supply important data points, not only because they show the possible benefits associated with wild bees, but because researchers have found that wild bees are already providing significant amounts of pollination in fields where natural habitat has been available to the bees. A farmer who understands that wild bees are already contributing to his crop production may be more inclined to encourage their propagation than a farmer who doesn't realize their importance—or even their existence. Each of the following examples demonstrates an economic benefit to provide habitat to nurturing wild bees.

Wild Bees Produce More and Larger Tomatoes: A California study by Greenleaf and Kremen (2005) showed that field tomatoes *(Solanum lycopersicum)*, a crop that is generally considered self-pollinating, produced substantially more and larger tomatoes when exposed to wild bee populations. Although the tomatoes used in the experiment (SunGold) were F1 hybrids and, therefore, genetically very similar to each other, the authors believe that cross-pollination by wild bees assures that each flower receives at least some fertile pollen—something not assured with self-pollination. They further noted that of the five genera of bees visiting the tomatoes, none were honey bees. Because tomatoes do not produce nectar, few honey bees are attracted to them. The possibility of more and larger tomatoes is a compelling reason to nurture wild bees.

Wild Bees Increase Efficiency of Honey Bees: A study of hybrid sunflowers by Greenleaf and Kremen (2006) found that wild bees increased the pollination efficiency of honey bees up to five-fold. The increase in pollination occurred because wild bees, both male and female, repeatedly flew into honey bees that were foraging on the sunflowers. Honey bees ambushed in this matter immediately flew to another flower where they were ambushed again, greatly increasing the number of flower visits per foraging trip. The authors concluded that the presence of wild bees could significantly raise the efficiency of honey bees, and thus lower the number of honey bee rentals needed for pollination of sunflower seeds.

Wild Bees Lower Pollination Deficits: Morandin and Winston (2005) studied seed production in organic, conventional, and genetically-modified canola fields in Alberta. They compared pollination deficit (the difference between potential and actual pollination) in the three types of fields with wild bee abundance in those fields. They found no pollination deficit in organic fields, a moderate deficit in the conventional fields, and a large deficit in the genetically modified fields. The pollination deficits increased as the number of wild bees decreased, and the wild bee populations were greatest in the organic fields, followed by the conventional fields, and then the genetically-modified fields, even though all three types of field were adjacent to similar wild bee habitat that included hedgerows with trees and understory vegetation. These results strongly suggest that cropping methods have an effect on the number of wild bees present in the field, and that the number of wild bees affects the amount of pollination.

Wild Bees Can Completely Eliminate the Need for Honey Bee Rentals: In an experiment designed to assess the value of wild bee pollination in squash and pumpkin, Shuler et al. (2005) found that while honey bees are often kept for pollination, it was wild bees that did most of the work. They found the squash bee (*Peponapis pruinosa*) present on 23 of the 25 farms studied in densities several times higher than other pollinators. It was the predominate pollinator at 15 of the 25 sites. The bumble bee was present at 16 sites, predominating at six, and the honey was present at 13 sites, predominating at four. In this case the farmers could have saved themselves the price of the honey bee rentals, because wild bees were already doing the majority of the pollinating.

Wild Bees Pollinate Crops Not Favored by Honey Bees: Researches Tepedino et al. (2007) studied 22 orchards inside Capitol Reef National Park. The orchard managers import honey bees every spring for pollination of pear, apple, apricot, and sweet cherry even though the local area contains over 700 species of wild bees. Tepedino et al. found that although 30 wild bee species visited the trees, in all cases except for pear, the visits were primarily by honey bees. Although they could not prove adverse affects from competition, the authors believe that it exists: if a solitary bee is forced to visit a greater number of flowers because the nectar supply of each has been depleted by honey bees, she will not have the time or stamina to properly nourish her brood. The sheer number of honey bees visiting the flowers makes this likely. Hence, the authors believe that a gradual phase-out of managed honey bee colonies will enhance the local populations of wild bees to the point where the importation of managed honey bees will become unnecessary.

Wild Bees Pollinate an Agriculturally Intensive Crop: Winfree et al (2008) measured watermelon pollination at 23 farms in New Jersey and Pennsylvania. They found that total pollen deposition was greater with wild bees than with managed honey bees, and that the vast numbers of rented honey bees in the area were completely superfluous. According to their research, this was the first documented example of wild bees providing adequate pollination of agriculturally intensive crops in the

United States.

Wild Bees Can Provide more Compete Pollination: Ricketts (2003), studying coffee plantations in Costa Rica, found that tropical rainforest remnants were a rich source of wild bee pollinators. A later study (Ricketts et al. 2004) found that rainforest-based pollinators increased coffee yields by about 20% when those remnants were within approximately one km of the plants. Furthermore, he found coffee quality was improved because pollination by the forest-based pollinators resulted in fewer peaberries (small misshapen seeds). These two factors resulted in a $60,000/year (US) increase to the producer. Ricketts et al. (2004) believe that wild bees provide higher rates of outcrossing among plants than honey bees, which tend to linger on one branch. Moreover, a diverse group of pollinators probably has complementary foraging patterns and behaviors.

CONCLUSIONS

Loss of pollinators through habitat degradation and agricultural intensification may threaten not only the yield and diversity of our food supply, but the very stability of the production system itself (Ricketts et al. 2008). The future of managed honey bees is questionable (NRC 2007) and wild bees are suffering unprecedented declines (Allen-Wardell 1998).

For a variety of reasons managed bees are becoming more difficult to handle and more expensive to rent. Their increasing scarcity and the escalating difficulty of keeping them alive is driving the price of rental ever higher. Yet, in spite of all the warning signs and endless headlines about the disappearance of the honey bee, farms, especially the large corporate type, continue to pray for a miracle.

For many of the same reasons, wild bees are disappearing as well. Habitat loss, habitat fragmentation, increased grazing, loss of hedgerows and grasslands, more monocultures, and greater urbanization all lead to loss of wild bee populations.

What growers often do not realize is how much pollination is performed by wild bees. They frequently blame poor weather or disease for low crop yields when, in fact, the problem is poor quality or incomplete pollination (Klein et al. 2007). Many growers have never considered any pollinator other than managed bees and have no knowledge of their inherent value (Greer 1999). So the question remains: *Can wild bees bridge the gap left by Apis mellifera?*

The short answer: it depends. Clare Kremen, a prominent researcher in crop pollination at UC Berkeley, has compiled a large number of studies of pollination performed at a variety of different farms. She has found that, on average, 80% of organic farms near natural bee habitat receive sufficient pollination from wild bees alone. Of the conventional farms near natural bee habitat, a full 50% received sufficient pollination from wild bees alone, with the amount of pollination varying according to the number of organic practices used in the conventional agricultural setting. On conventional farms with barren intercrop areas, 0% received sufficient pollination from wild bees alone (Kremen 2009). She concludes that, "Yes, on the right kind of farm, one with organic management and nearby natural habitat," wild bees alone can take over the immense job of crop pollination. On the other hand, she says, "No, wild bees cannot pollinate modern conventional agriculture," because there are too few nesting sites, too few floral resources, and too many crop flowers to pollinate all at once (Kremen 2009).

To those farmers looking for a miracle, the miracle is out there in the form of wild pollinators. But we can't just ignore them. We have to invite them into our farms by changing the landscape of arable lands to incorporate native environments and bee-friendly farming practices. While it will cost money to convert strips of agricultural land back into native-type environments, many of the researchers cited in this paper believe it will pay back in the long run (Vaughan et al. 2008b, Winfree et al. 2008, Klein et al. 2007, Ricketts et al. 2004, James-Pitt-Singer 2008, Greer 1999, Hole et al. 2004, Black et al. 2007, Delaplane and Mayer 2000, Kearn et al 1998,Gathmann and Tscharntke 2002, Isaacs and Tuell 2007, Goulson 2003, Greenleaf and Kremen 2006b.). In many cases a local population of native pollinators could offset the cost of renting hives (Vaughan et al. 2008b). But should the honey bee industry collapse altogether, as some have predicted, the payback would come in very short order (Winfree et al. 2007).

Kremen (2009) says that for a grower to succeed at weaning his farm from managed bees, he must possess, above all, a stoic tolerance for weeds. The farm management can then be adjusted by allowing weeds and cover crops to flower, planting a variety of crops with different blooming times, planting flowering vegetative strips between fields, and restoring patches of habitat around the farm. After that, nesting sites should be created by protecting undisturbed soil, leaving dead trees in place, and installing nesting blocks.

It is reasonable to be cautious with change, and it would be imprudent to leave a billion-dollar almond crop in the pollen sacks of a bee that has never encountered such a mind-bending sight. But there is no reason not to begin a program of gradual shift from 100% dependence on honey bees to something less. Fields could be measured for optimal pollinator size, ribbons of habitat could be planted, and tilling practices could be altered over the course of several years while the number of managed hives is gradually decreased.

Like most of the environmental changes needed in the world today, this one needs a starting point. For any given farmer, that place could be a single field, a single habitat strip, or one fewer managed hive. Perhaps, over time, entomologists will find a cure for colony collapse, parasitic mites, fungal and bacterial diseases. That would be great. But the story of monoculture collapse is not new. The Philippines lost 25% of its rice crop in the 1970s, and the U.S. lost much of its corn crop in the 1980s (Heal 2000). Dependence on any one monoculture is bad enough, but to be dependent on a monoculture that is, itself, dependent on another monoculture is irresponsible.

In the immediate future, managed bees will remain the workhorses of the giant monoculture (Klein et al. 2007). Small farms, however, in which local landowners have some say in how things are managed, have a good opportunity to convert in the short run. As reported by Ricketts et al. (2004), providing natural habitat near economically important crops can have large monetary benefits. Just as organic farming gained a foothold after years of guffaws, farming for wild bees can become a viable agronomic practice as well.

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