Apis mellifera: The Domestication and Spread of European Honey Bees for Agriculture in North America

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Throughout history, honey bees have benefited man both for food and their ability to increase crop yield via pollination. This paper will discuss the complex manner in which beekeeping became a part of societies across the globe, and how individuals have altered the natural evolution of honey bees by manipulating location, hive building, and tendency to swarm. Additionally, it will address the recent issue of colony collapse disorder, and the ways in which human disruption of Apis mellifera is leading to mass colony death, which is adversely affecting the agricultural community that has become so dependent on their pollination practices.

Introduction

Roughly 10,000 years ago, receding glaciers and the development of a more stable climate on Earth helped shape the emergence of agriculture-based societies out of communities previously focused on nomadic hunting and gathering practices (Wenke et al. 2007). Social insects, however, had already been collaborating long before humans were even around. Roughly 100 million years ago during the Cretaceous period, angiosperms, or flowering plants, became the dominant foliage type on Earth (Crane 1999). Because many of these plants require intra-species pollination, scientists hypothesize that the emergence of angiosperms is directly correlated to the evolution of honey-storing insects. According to the fossil record, existence of some of the oldest flowering plants requiring insect pollination coincided with the earliest evidence of social bees (Crane 1999).

While *Aculeate Hymenoptera*, honey-storing insects primarily pertaining to bees, existed before the dominance of angiosperms, they were primarily solitary and lived in single units. Anatomical comparisons of prehistoric insects point toward social bees evolving from wasps, slowly adapting to a diet of nectar and pollen rather than preying on other insects (Winston 1987).This change is distinctly marked by the development of pollen carrying appendages, most notably the development of plumose hairs and broadened hind legs that increased their ability to gather and transport pollen back to the nest (Winston 1987). Although researchers cannot be certain when the shift to hive behavior began, the oldest evidence points to the subfamily Miliponinae, a type of stingless bee found exclusively in tropical regions (Crane 1999). Earliest fossils indicate a tendency toward highly social behavior dating to around 80 million years ago, displaying physical characteristics of modern bees (Crane 1999). Roughly 35 million years after the evolution of Miliponinae, the first organized honeybees (*Apis*) began to populate areas with moderate climates and high angiosperm densities (Crane 1999).

Among the genus *Apis*, evolutionary divergences occurred to create the large variety of honey bee species found in the present day. The first of these branches led to *Apis dorsata* and *A. florea*, both of which built rudimentary single-comb nests, often open and poorly protected from predators (Crane 1999). Despite their ineffective building strategy, these were the only two species directly related to modern honeybee, and they existed on the Earth for over 30 million years. Eventually, a more organized method of nest building evolved, leading to the emergence of *A. cerana* and the species most commonly found in Europe and North America, *A. mellifera*. Forming advanced cavity-nesting spaces containing multiple parallel combs, these species initially managed to spread locally because of their unique ability to survive cold winters by forming clusters within their hive (Crane 1999).

Scientists speculate that the spread of honey bees prior to extensive human involvement can most likely be attributed to climate changes during the Pleistocene. During the ice age, glacial formations caused the sea level to fall, often creating land bridges that allowed honey bees to travel between continents in the northern hemisphere. As global temperatures began to rise roughly 10,000 years ago, bridges were submerged and islands formed, leading to divergent evolution and a wide distribution of honey bees (Crane 1999). The recent finding of Hymenoptera fossils in Nevada point to some evidence that early honeybees may have traveled across Beringia, the land bridge thought to connect modern-day Russia to Alaska (Engel et al. 2009). According to this theory, honey bees expanded into western North America from Asia, where they were most likely confined to a small, ecologically supportive environment (Engel et al. 2009). When temperatures increased, fauna and habitat changed drastically, causing the extinction of *Apis* in the New World until they were reintroduced by European settlers in 1622 (Engel et al. 2009). Although the evidence supporting this is limited, similarities between this and the introduction of gingko trees and horses to North America increase the validity of this claim.

Early Domestication

Despite arguments over the introduction of honey bees to North America, scientists do agree that the domestication of *A. mellifera* began much earlier, most likely somewhere in Egypt, although the earliest representations of bees are illustrated in rock art in southern France and northern Spain (Crane 1999). The earliest record of man eating honey can be dated to roughly 3 million years ago, with extensive exploitation of honey bees dating around 10,000 years ago (Crane 1984). Societies originally scavenged for honey in trees and along rocky overhangs where bees often built hives; however, as populations became larger and more sedentary, the demand for honey outgrew its natural availability (Harissis et al. 2009). Honey was used not only as a food source but also as a part of religious rituals and as a medicinal ingredient, which meant that it needed to be readily accessible for collection. The practice of controlled honey production was also not confined to a single area. Tomb paintings in Egypt display beekeeping, and evidence has been found dating as early as the Minoan Civilization indicating large beekeeping practices and extensive honey trade (Engel et al. 2009). Further evidence exists in Jewish laws dating around 597 B.C., in which questions are raised about collecting honey on the Sabbath and how close hives should be in relation to people's homes (Engel et al. 2009). These populations all sought a similar approach to attracting honey bees by housing collected combs in wooden boxes or cylinders made of clay or mud (Engel et al. 2009). By creating these artificial homes, ancient civilizations began the earliest and most crude methods of beekeeping. They laid the groundwork not only for a honey market trade, but alsothe encouragement for later civilizations to perfect beekeeping methods. Simultaneously, these practices altered the evolution of honey bees and increased the importance of honey bees in an agricultural society.

As honey bee domestication spread into Europe, selective pressures from beekeepers drastically changed the development of the once uniform species. These differences primarily stemmed from specific characteristics desired by beekeepers. Generally, this list is confined to six main factors: colony survival during dearth periods, colony survival when honey flow is poor, resistance to disease, maximum amount of honey storage, tendency to sting, and ease of pacification by smoke (Crane 1999). While these characteristics benefitted honey-gatherers, they also acted to remove some natural defenses of bees, detracting from their ability to survive without human interference. Differences in selection arose depending on the degree of desirability in each location. For example, in African societies, honey-hunters were in direct competition with native animals, and therefore beesthat showed increased aggression to deter such competitors were selected (Crane 1999). In areas with a more temperate climate, beekeepers were often less concerned with temperament and focused more on selecting bees that could survive cold winter periods (Crane 1999). Additionally, the removal of honey bees from the tropical regions of African into the temperate zones of Europe most likely affected natural selection of bees. Bees more suitable for changing temperatures would have shown greater fitness in Europe, whereas bees more capable of migration and surviving drought, heat, and excessive rain would have been artificially selected for in tropical regions.

Increasing Alterations and Domestication

A. mellifera is the only species of honey bee native to Europe, and has been the focus of most beekeepers since the time of the Roman Empire. Early European beekeepers focused primarily on ease of access, evolving from large clay hives in Greece to coiled wicker skeps in Romania and Great Britain that were sealed with mud or cow dung to create a more weather-tight hive (Crane 1984). These advances in the stability of honey bee hives increased the longevity of colonies beyond that of wild bees while simultaneously increasing the ease of collection for beekeepers. European beekeepers also affected the natural spread of honey bees by altering their swarming habits. Honeybees generally swarm due to a food shortage, preparing to relocate to an area with higher flower density. To minimize colony loss, beekeepers in Greece and England would often use wine, flute music, and a great number of other tactics to direct bees into a new, local hive and maintain their population (Harissis et al. 2009). This promoted the cultivation of *A. mellifera* with a low tendency to swarm, which is a deviation from the lifestyle of wild bees. Although this was not problematic at the time, recent researchers speculate that removing this characteristic from modern bees is increasing their exposure to disease.

In 1622, honey-deprived British colonists brought the first *A. mellifera* with them to North America, where the Native American population dubbed them "the white man's fly," and used them to mark the westward expansion of the new settlers (Engel et al. 2009). Although controlled mating between races of bees has occurred since their introduction and selective pressures have been applied by queen breeders, *A. mellifera* is one of the best studied domesticated bees because the European racial lines have been fairly well maintained (Winston 1987). Honey bees in the colonies were originally confined to wild hives in hollow trees, with a 1641 court case in Massachusetts providing the first documented practice of controlled bee keeping in the colonies. Honey hunting – that is, following a bee back to its hive or opportunistic honey gathering–remained the most popular way of obtaining honey up until the end of the 18th century, one of the reasons honey bees in North America relate closely to their English ancestors, whereas English honey bees differ greatly from their African relations. This can also be attributed to the fact that many North American bee keepers selected for color and striping, characteristics that have been shown to have no impact on honey production or any other behavioral traits (Crane 1999).

Advances in the domestication of honey bees in the United States at the turn of the 19th century can largely be attributed to coincidence. The accidental introduction of the greater wax moth destroyed roughly 80% of all domesticated hives within two years, leading beekeepers to experiment with hive design (Crane 1999). Creating an artificial hive with a sloped bottom to discharge the

moth larvae, beekeepers increased the fitness of their more docile, weather resistant, domesticated bees, while wild honey bees continued to see substantial hive collapse. The further development of moveable-comb hives encouraged honey bees to change their normal comb building patterns to make them easily extractable from the hive, incorporated gradually by mimicking the natural spacing of wild bee combs (Crane 1999). This revolutionized beekeeping possibilities, making it more profitable for a beekeeper to operate a large number of hives, eventually leading to the large-scale hive management seen in the United States today (Crane 1999).

Large-Scale Agricultural Use and Economic Importance

Since the creation of improved hives, beekeepers in North America have been altering the natural practices of *A. mellifera* to better suit both honey production and crop pollination. For instance, modern colonies have become increasingly resistant to cold winters as farmers now either ship hives to warmer areas in the off-season or wrap hives in insulating material (Crane 1999). This has changed honey bees' tendency to swarm and nest in natural cavities in the wild. Queen excluders have also been used to increase the productivity of honey bees. These hive additions feature a hole just big enough for drones to fit through, allowing hives to include more than one queen as well as directing where combs can be built, forcing bees to use space more efficiently, and thus creating a higher yield than wild bees (Crane 1999). Controlled mating has also been used to direct the evolution of North American honey bees. Early beekeepers attempted to isolate queens with those working drones they found to be more desirable, and artificial insemination has been attempted since 1790 (Crane 1999). While beekeepers were not always selecting for characteristics conducive to productivity, this nonetheless altered the natural evolution of *A. mellifera* in the United States.

In recent decades, crop pollination has replaced the importance of hive maintenance for honey production. Originally used in New Jersey for apple pollination in 1909, this practice has expanded to roughly 2.9 million colonies transported for agricultural purposes annually (Morse et al. 2000). Coupled with increased resistance to cold weather, farmers around the United States have created a complex system of shipping bees in accordance to crop season which has led to a wider variety of angiosperms selected for pollination by bee colonies. In one of her presentations, entomologist Julianna Tuell described how bees on the east coast, where they pollinate orange trees in Florida, are shipped to mid-range states for squash pollination, and finally sent north to Maine during the blueberry bloom before repeating the cycle. While wild bees would normally only visit plants in a specific climate region, this new practice has radically altered the preferences and uses of domesticated *A. mellifera*. This high use of honey bees for pollination has also led to increased dependency by farmers, which could have devastating results if bee colonies continue to decline.

Negative Influences of Domestication

Recently, rapid decline has been noted in colony numbers, which is widely attributed to the stress that forced migration is placing on colonies due to poor nutrition and increased exposure to diseases and harmful pesticides, according to Tuell (2011). These factors, among others, are thought to be the leading causes of colony collapse disorder, an affliction scientists know little about that causes the sudden death of entire hives. Researchers and farmers alike are concerned that this marks the beginning of a severe decline and loss of progress in agricultural honey bee use. Many researchers are afraid that a large amount of blame for colony collapse disorder is actually due to pesticides sprayed on hives to kill pests. These have been proposed as compromising honey bees' immune systems and leading to the evolution of pesticide resistant pests (VanEngelsdorp et al. 2008). In this way, attempts of domesticating honey bees further has actually proved to be a step backwards, creating hives that are less beneficial to agriculturalists with lower individual fitness. Additionally, the recently introduced varroa mite can destroy entire colonies and is expensive to eradicate (Morse et al. 2000). Similar to the wax moth crisis, farmers' methods of treatment have varied effects on their colonies, altering natural defenses that may arise and increasing the spread of bees that have been selected for by infestation resistance.

Conclusion

Since their development into social communities thousands of years ago, honey bees have made a long voyage between continents, cultures, and human exploitation. While early civilizations interacted with bee colonies out of reverence and convenience, beekeeping has since grown into a full-scale occupation for many. Initial modifications to hives for ease of honey collection evolved into safeguards against disease, and sexual selection reshaped the natural evolution of *A. mellifera*. All these disruptions in the normal patterns of honey bees led to a more-or-less accidental development of workers more suitable for human use, creating the domesticated honey bee present in North America today. Farmers benefit from the transportation of colonies reared to pollinate a wide variety of angiosperms, and the bees themselves benefit from safe hive locations and a guaranteed food source. Although domestication efforts have recently been suspected of having a negative impact on *A. mellifera*, pollination remains an integral part of agriculture in the United States, and the evolution of this species will undoubtedly continue to be marked by human interference as long as humans and bees remain interdependent.

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