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Title: Assessing the impacts of European honeybees (*Apis mellifera*) on native bees in prairie ecosystems

Abstract

The reproductive success of European honeybees is dependent on their foraging abilities and competitive abilities against other foragers. Experimental population manipulations were conducted to assess the impacts of honeybee foraging strategy on their biggest competitors, native bee species. In a prairie ecosystem rich with floral resources and native bees, artificially increasing the population of honeybees through hive introduction significantly decreased the population of native bees. Interestingly, while evidence would suggest that honeybees displace native bees to areas farther away from the introduced hive, we found the opposite trend – native bees remained abundant nearest the source of honeybee competitors. Although incidences of aggressive interactions between honeybees and native bees were rare, we believe that colony size, communication tactics, and partitioning of labor give honeybees a competitive edge over native bees that can potentially limit the reproductive success of natives.

Introduction and Significance

The European honeybee, *Apis mellifera*, (Linnaeus) is well known for the ecosystem services it provides, including honey, wax, and commercial pollination of many important cash crops grown within the United States. Since the introduction of the European honeybee to the United States some 375 years ago, it has become the single most prolific and economically important pollinator to managed ecosystems in North America because of its ability to locate even the most ephemeral of pollen and nectar sources (Buchmann and Nabhan, 1997). As pollinators, honeybees provide ecosystem services with an estimated annual value of \$14.6 billion in the United States (Morse and Calderone, 2000). Despite this impressive statistic, North America is also home to more than 4000 native bee species, many of which serve as pollinators in managed and unmanaged landscapes (Mader et al., 2011).

The diversity and ecological importance of native bees as pollinators is of climbing concern, especially in the face of declining honeybee populations that result from diseases, pathogens and pesticides, all of which are implicated in recent outbreaks of colony collapse disorder (Oldroyd, 2007; Winfree et al., 2007; Moron et al. 2008; Tuell et al. 2009). Native bees have also been predicted to buffer the negative effects that global climate change may have on honeybee activity. For example, using modeling, Rader et al. (2013) predicted a 14.5% decline in honeybee pollination of watermelon crops with increased ambient temperatures, but an increase in native bee activity that would result in a net gain in pollination services. This example of ecological resilience being strengthened through biodiversity underscores the importance of conserving native bee populations.

Ecologists generally agree that when a food source like nectar or pollen, on which bees forage, is used by more than one species, that resource becomes limited in supply. Because food resources used by honeybees and native bees overlap considerably, there is potential for honeybees and native bees to compete for these resources. Competition for resources can take two basic forms: exploitative competition and interference competition (Cain *et al.* 2011). Exploitative competition would involve depletion of the food resource by one pollinator before the other could use the resource, without any direct interaction between the two parties. Interference competition involves direct physical interactions, aggression for example. Both mechanisms of competition could influence the foraging patterns, survival, and fitness of involved parties. Either form of competition could therefore result in reduced diversity or abundance of native bee species, or altered foraging patterns when honeybees are present in the area.

In theory the propensity for introduced honeybees to outcompete native bees for resources is undeniable. Unlike honeybees, which store honey in copious quantities, native bees can hardly forage quickly enough to meet the energetic requirements of foraging, let alone collect a surplus of pollen and nectar for raising a brood (Buchmann and Nabhan, 1997). Native bees also differ from honeybees in that they preferentially harvest nectar and pollen from native plants, whereas honeybees show no preference – typically foraging on flowering weeds or agricultural crops (Heinrich, 1975). The energetics of pollination favor honeybees over native bees; a single honeybee colony is capable of producing over 400 pounds of honey annually (Heinrich, 1975), about a quarter of which is surplus and is collected by beekeepers and sold. That quantity of honey exceeds the energetic requirements of 100 bumblebee colonies (Heinrich, 1975). Hence, in an area where floral resources are limited in supply and native bees are capable of fulfilling pollination requirements for plants, the introduction of a honeybee hive could drastically reduce the population of native bees by limiting the energy supply required for their reproductive success.

The extent to which honeybee presence impacts native bee diversity, abundance or activity is largely uninvestigated. In upstate New York, Ginsberg (1983) found evidence of exploitative competition between honeybees and native species during spring months, but no clear pattern later in the season. Other research indicates that interference competition between bees may influence foraging behavior. Roubik (1978, 1980) has shown that exotic Africanized honeybees exclude several species of native stingless bees from floral resources in Panama. Additionally, in North Carolina, Rogers *et al.* (2013) found that when a foraging bee encounters another bee, it is more likely to move away from a shared resource than if it hadn't encountered another bee. Still other studies have found no evidence of competition between honeybees and native bees (Horskins and Turner, 1999; Paton, 1999; Winfree *et al.*, 2007). Nevertheless, the potential impact of honeybees on native bees in natural ecosystems is an unclear and understudied ecological topic and therefore deserves closer investigation.

Before the arrival of honeybees, native bees were the primary source of pollinators in North America, and natives continue to provide essential pollination services. For native crops, such as blueberries, native bees are important contributors to pollen deposition, which increases crop yields (Tuell *et al.* 2009). The pollinating proficiency of native bees in regards to blueberries is not only a national economic concern – the United States is the world's foremost producer of blueberries – but also a statewide concern for Michigan, the state that yields more blueberries than any other in the United States (USDA-NASS). Pollination services from native bees are significantly and positively correlated with the area of upland habitats neighboring foraging sites, like farms (Kremen *et al.*, 2004). Michigan farms are frequently ensconced in forest and upland areas, providing myriad suitable habitats for native bees. At the same time, rising public concern over honeybee population declines has led to increased interest in beekeeping by hobby apiarists (A. Fraser, personal communication). Placement of a honeybee hive to an area where native bees typically provide the bulk of pollination services would likely increase interspecific pollinator competition. Hence, the acquisition of honeybees and the conservation of native bees are important concerns for Michigan.

In this study, the impact of honeybees on native bees was assessed by artificially manipulating the abundance of honeybees in a prairie ecosystem, and subsequently monitoring the population of native bees. Based on the findings of previous research (Ginsberg, 1983; Roubik, 1978, 1980; Rogers *et al.*, 2013) we predicted that if honeybees are more effective foragers than native bees, honeybee presence might displace native bee species due to inferred resource depletion. To test this prediction, changes in bee abundance were categorized over time, before and after the introduction of a honeybee hive to a prairie where honeybee incidence was originally low. The extent to which honeybees physically alter the presence of native bees (interference competition) was addressed by a sister study (Bayha, 2014 Senior Thesis).

Specific Research Question: *Do honeybees alter the foraging, abundance and biodiversity of native bee species through exploitative and/ or interference competition?*

Materials and Methods

Study Site

This study was conducted on the property of Pierce Cedar Creek Institute (PCCI), located in Hastings, Barry Co., Michigan. Encompassing 661 acres, the biological field station at PCCI is situated atop a recessional moraine, allowing a plethora of different ecosystems to persist including fens, swamps, meadows, forests, prairies, fields, and open

water. Surrounding the rural field station are many agricultural fields, and a low density of residential inhabitants. Approximately 17% of total acreage at PCCI is open field, providing a breadth of sampling sites for this study.

Establishment of Transects

Two sampling plots were established where native bee and honeybee abundance could be measured periodically. We chose prairies for these sampling sites because of the abundance of native flora and the dearth of nearby agricultural fields. One plot was designed to monitor pollinator interactions where honeybee presence is constant. We selected a plot at the intersection of the Orange and Blue trails at PCCI, adjacent to a feral hive of honeybees (Honeybee Tree Prairie). Four transects were established at increasing radial distances of 50, 100, 200, 300 m from the feral hive. The second plot was established in the larger North Prairie (adjacent to the Red Trail) where we expected feral honeybee abundance to be low in comparison to the Honey bee tree (HBT) Prairie. We established transects 50, 100, 200, 300 and 400 m to the north and 50, 100, 200, 300 m to the south of the center point of the North Prairie (for a total of nine transects). All established transects were 30 m in length and oriented perpendicular to the axis from which radial distances were measured (Figure 1).

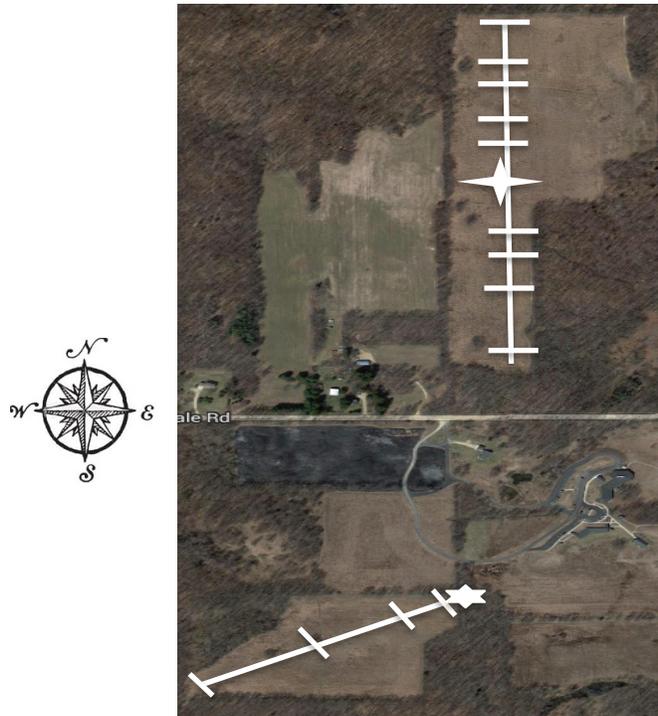


Figure 1. Study site and demarcation of transects. All transects were 30 m in length. The 4-point star in the North Prairie signifies the site of hive introduction. The 6-point star in the control plot signifies the Honeybee Tree. This figure is not drawn to scale.

Sampling Bee Abundance & Biodiversity

Two methods were used to sample bee abundance and biodiversity along transects: bee bowls (pan traps) and hand netting. A bee bowl consists of a 3.25 oz plastic soufflé cup

(Gordon Food Services inc.), painted fluorescent blue, fluorescent yellow (Krylon brand paint), or left white. To make bee bowls more visible to bees, bowls were elevated on 100 cm lengths of 1.25 cm diameter polyvinyl chloride (PVC) tubing. On days when a bee bowl survey was conducted, each bowl was 2/3 filled with soapy water, a mixture of 1-gallon water with 2 tablespoons of blue Dawn[®] dish detergent. Bee bowls were placed in the early morning (between 0800 and 1000 h) and collected in late evening (between 2000 and 2200 h), but always left in place for 12 hours. Bees captured by this method were collected into 70 % ethanol, then dried, pinned and identified using taxonomic keys (discoverlife.org). Bee bowl surveys were conducted only on warm and sunny days when bees were most likely to be active.

Hand netting surveys were also conducted on warm, sunny days, although not necessarily on the same day as a bee bowl survey, and with less frequency. Each hand netting survey was conducted for 30 minutes by a single person, or for 15 minutes if two researchers surveyed together. By this method, researchers walked with uniform speed back and forth along each 30 m transect and netted any bees visible within a 2 m radius of the researcher. Bees collected in hand nets were stored in vials, frozen and then pinned and identified later in the lab. Bees were identified to genus, and species when possible, using the interactive keys at discoverlife.org. In instances where species identification was too difficult, individuals were identified to morphospecies.

Focal Plant Observations and Abundance Surveys

To document the foraging patterns of bees and assess whether the introduction of a honeybee hive to the study site altered the foraging behavior of native bees, we conducted observations of floral visitors. This method did not involve collecting bees. During these 15 minute observations, we walked along our transects and recorded the identity of foraging bees according to the following bee categories that were easily distinguished in the field: honeybee (*Apis mellifera*), green bee (e.g. *Augochlorella*, *Agapostemon* spp.), bumble bee (*Bombus* spp.), small black bee (e.g. *Ceratina*, *Lasioglossum* spp.), medium black bee (e.g. *Megachile*, *Halictus* spp.), carpenter bee (*Xylocopa* spp.). Additionally, the identity and abundance of the flowering plant species along each transect was recorded. Plant abundance was categorized broadly, on a three-point scale: rare (less than 30% of flowering flora on a transect), common (between 30% to 70%), or dominant (more than 70%). Focal observations were conducted at different times of day and under different conditions than aerial netting or bee bowl surveys.

Foraging Observations

To assess the potential for aggressive interactions between honeybees and native bees, we chose to observe bees at food sources, where they are most likely to be aggressive (Roubik, 1978). While we observed foraging activity on a plot of *Monarda fistulosa* (bergamot) in the North Prairie, we primarily observed at nectar feeders. The feeders consisted of a 4x8 array of 1 oz. plastic condiment cups filled with honey solution diluted to 25 brix. A cotton dental wick was inserted into each cup as a substrate for bees to drink from, then each cup was capped with a painted lid, either white or fluorescent yellow Krylon brand paint, to lure bees. Two arrays were made, one for observation in the North Prairie and the other for the HBT prairie. Both arrays were mounted on adjustable platforms, so that the height of the array matched the surrounding vegetation. We trained bees to feeder sites by placing a gravity feeder filled with 25 brix honey solution in each observation site for 3 days prior to placement of the array. Due to the concentration of honey in feeders, these resources were

more profitable for bees than surrounding floral resources. Initially, feeders were placed at 300 m from either the feral or the introduced hive. Later in the season, we moved feeders to 50 m from these hives to assess the impact distance from the hive had on foraging patterns.

Observation periods were 30 mins in duration, and these observations were conducted at various times of the day and under varying weather conditions. Identities of foragers were categorized broadly e.g. honey bee, bumble bee, carpenter bee, green sweat bee, small black bee, medium black bee or other insect. The foraging behavior of the visitor was also noted (e.g. pollen collecting, probing, hovering). In instances where bees interacted directly, via physical contact or close proximity (<5 cm), the behavior of the initiator and the response of the recipient were recorded.

Enclosures

To increase the likelihood of inter- or intra-specific bee encounters, we utilized 75 x 75 x 115 cm enclosure tents constructed from nylon and fine mesh. Two tents were used, each with a different food source. One tent contained a bouquet of *Mondura fistulosa*, while the other contained a triangular arrangement of nectar feeder cups filled with 50 brix honey solution. To each tent, 10 captured *A. mellifera* individuals and 10 captured *B. impatiens* individuals were added and allowed to acclimate for 4-10 hours before observations were conducted. Observation periods were 30 mins in duration – all interactions were noted, as they were in foraging observation surveys.

Manipulation of a Commercial Honeybee Hive

To assess the impacts of introducing a hive of honeybees to a prairie, we obtained a large honeybee colony, consisting of two honey supers and one brood box (approx. 20,000 honeybees), from a local beekeeper and relocated it to the middle of the North Prairie plot following 3 weeks of pre-introduction sampling for bee abundance and diversity. From these surveys we noted that pre-introduction incidence of honeybees was low in this plot. Sampling for bee abundance and biodiversity continued for another 3 weeks after the addition of the honeybee hive.

Data Analysis

Bee abundances were log transformed: $\log(\text{bee count} + 1)$. The effect of distance from the introduced honeybee hive and changes in abundance were assessed for native bees and honeybees using logistic regression. Similarly, the effect of hive introduction on bee abundance was compared to bee abundance in the control plot by logistic regression. Because a dearth of bees was collected on some sampling days, while a plethora was collected on others, the proportions of honeybees to native bees ($\#HB/\#NB$) were analyzed separately to reduce variation. Proportions were analyzed using the Logit function: $\ln(P/(1-P))$. To conduct all of the above analyses, we used the statistical programming software JMP.

Results

Assessment of Abundance and Biodiversity

Using a total of 9 bee sampling events utilizing both bee bowl and aerial netting methods, we collected 618 bees including 86 honeybees and 532 native bees belonging to 22 different genera (Table I). All bees collected i) pre hive introduction, ii) post hive introduction, or iii) in the control plot, were summed and proportions of native bees or

honeybees to total bees collected were compared (Figure 2). Native bees were collected in significantly higher proportions than honeybees were ($F=128.0$, $df=1$, $p<0.0001$; Figure 2). After the introduction of a honeybee hive to the North Prairie, the proportion of native bees to total bees collected significantly declined while the proportion of honeybees to total bees significantly increased ($F=20.4$, $df=1$, $p=0.0007$; Figure 2). Proportions of bees collected before hive introduction did not differ from control ($F=1.80$, $df=1$, $p=0.21$; Figure 2).

Table I. Abundance and diversity of bees at PCCI. The total number of individuals collected from 6/25/14 – 8/7/14 are reported.

Family	Genus	Native?	No. Individuals
Andrenidae	<i>Andrena</i>	Yes	17
Apidae	<i>Apis</i> (spp. <i>mellifera</i>)	No	86
Apidae	<i>Bombus</i>	Yes	48
Apidae	<i>Ceratina</i>	Yes	26
Apidae	<i>Eucera</i>	Yes	1
Apidae	<i>Epeolus</i>	Yes	1
Apidae	<i>Melissodes</i>	Yes	27
Apidae	<i>Xylocopa</i>	Yes	4
Colletidae	<i>Hylaeus</i>	Yes	5
Halictidae	<i>Agapostemon</i>	Yes	32
Halictidae	<i>Augochlora</i>	Yes	11
Halictidae	<i>Augochlorella</i>	Yes	41
Halictidae	<i>Augochloropsis</i>	Yes	2
Halictidae	<i>Dieunomia</i>	Yes	1
Halictidae	<i>Dufourea</i>	Yes	2
Halictidae	<i>Halictus</i>	Yes	52
Halictidae	<i>Sphecodes</i>	Yes	3
Halictidae	<i>Lasioglossum</i>	Yes	225
Megachilidae	<i>Hoplitis</i>	Yes	4
Megachilidae	<i>Megachile</i>	~Yes	28
Megachilidae	<i>Osmia</i>	Yes	1
Megachilidae	<i>Stelis</i>	Yes	1
Grand Total			618

As expected, the total abundance of honeybees collected after hive introduction was significantly higher than pre-introduction abundances ($F=5.65$, $df=2$, $p=0.0125$; Figure 3A). Native bee abundance on the other hand, significantly declined following honeybee hive introduction ($F=5.14$, $df=2$, $p=0.0172$; Figure 3B). Although honeybee abundance decreased with increased sampling distance from the introduced hive, this relationship was not significant ($F=1.93$, $df=1$, $p=0.18$; Figure 3A). Interestingly, native bee abundance on transects closest to the introduced honeybee hive remained higher than abundances on

transects farther from the source of honeybees, but not significantly so ($F=0.34$, $df=1$, $p=0.56$; Figure 3B).

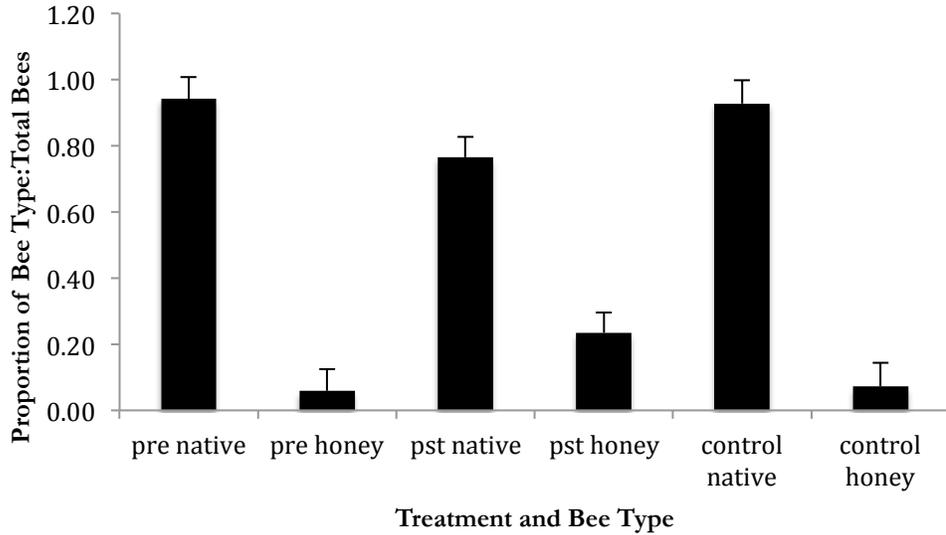


Figure 2. Honeybee hive introduction decreases proportions of native bees. Logit function: $\ln(P/(1-P))$ was used to derive proportions from total abundances. Native bee proportions are significantly lowered after hive introduction compared to pre-hive introduction and control plot proportions. Error bars are set to standard deviation between sampling dates for each treatment and bee type.

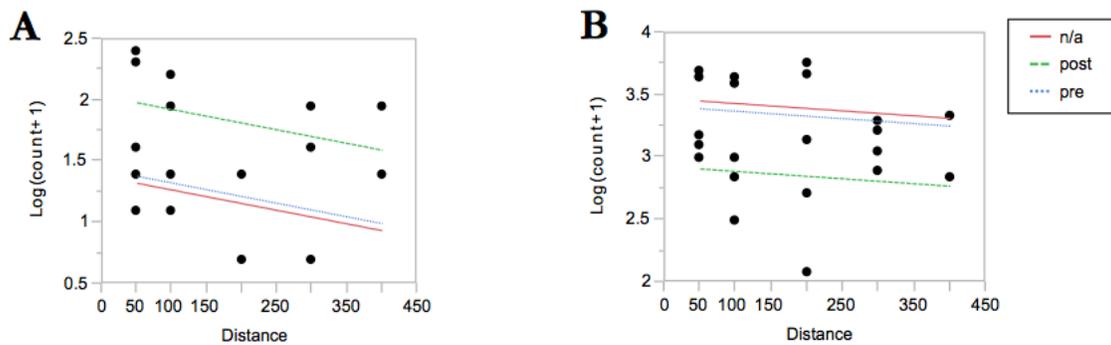


Figure 3. Honeybee hive introduction significantly impacts bee populations, but does not cause a distance effect. **(A)** Introduction of a honeybee hive to the north prairie increases honeybee abundance, as expected. **(B)** Honeybee introduction significantly decreases the population of native bees. **(A, B)** Distance from the honeybee hive (zero point) did not significantly impact bee abundance. N/A describes the control plot, where hive treatment was never conducted and is hence, not applicable.

Foraging Observations

A total of twelve observation periods were conducted throughout the summer in the Honeybee Tree Prairie (HBTP), four before the introduction of the honeybee hive and eight after introduction. In the North Prairie (RTP), a total of nine observations periods were conducted, three pre-introduction and six post-introduction. While the feeders attracted honeybees, a dearth of native bees was attracted. Only one inter-specific encounter between a honeybee and small black bee was recorded in either study site. However, many interspecific interactions between honeybees were recorded. The number of honeybee observations recorded increased in both fields after the introduction of the hive. In the HBTP 38 honeybees were recorded pre-introduction and 42 post-introduction. More notably, before the introduction of the hive there were no honeybee visits to the feeder in the North Prairie and 25 visits post-introduction.

At the focal plant observation plot (located in the RTP) a total of five observation periods were conducted, three pre-introduction and two post-introduction. The focal plant plot attracted more native bees than artificial feeders. Honeybee visits to the plot nearly doubled after the introduction of the hive (8-pre & 14-post). Native bee visitation also increased after hive introduction rising from 35 pre-introduction to 52 post-introduction. Unlike the artificial feeders, a few interactions between honeybees and native bees were observed in this plot (2-pre & 3-post). In all of these instances of interaction, honeybees were the initiators and displaced both small black bees and bumblebees from flower heads either by direct physical contact or by hovering within close proximity (<5cm approx.). The native bee would quickly move away after the interaction while the honeybee would remain in close proximity to the same flower head that the native bee had originally been feeding on or hovering over in four of the interactions, and in a single interaction both parties left the area.

Enclosures

Enclosure observations were conducted on two separate dates, each enclosure had its own food source. Only four interactions at the food source between honeybees and bumblebees were observed. However, bees were more interested in attempting to escape the enclosure than foraging – the majority clung to the walls of the enclosure tents during observations. These few interactions consisted of a bee from each group hovering over the same food source in close proximity to each other (<5cm); this typically resulted in the honeybee staying and the bumblebee moving away (3 of the 4 interactions).

Since the bees were kept in exceptionally close proximity to each other, numerous other interactions away from the food source were observed. These resulted from two different bees from each group haphazardly coming into contact with each other as they explored their new, unfamiliar environment. The initiator of these interactions varied between the two groups, honeybees approached bumblebees and bumblebees approached honeybees in relatively equal proportions. Although, honeybees appeared to be more aggressive towards bumblebees when they came into contact with each other. The honeybees would nearly always try to push away bumblebees and the bumblebees were more submissive and quickly moved away after these interactions as the honeybees remained. However, sometimes the outcome of these interactions would be for both parties to flee the area. A typical bumblebee within the enclosure seemed unconcerned with the presence of a honeybee nearby and even let honeybees crawl over them with no aggressive response and remained docile. In contrast, the honeybees asserted their dominance by quickly pushing

away any bumblebees that ended up within close proximity and in a couple instances appeared to try and sting their bumblebee co-inhabitants.

Discussion

Our results show that increasing the abundance of honeybees in a prairie may decrease the abundance of native bees there. However, the extent to which the decreased abundance of native bee species is related to increased competitive pressure from honeybees remains equivocal. Interference competition probably doesn't contribute to the reduced numbers of native bees in our experimental plot – no evidence of behavioral aggression was noted within or between species of bees at PCCI (Bayha, 2014 Senior Thesis). Furthermore, honeybees are rarely aggressive towards heterospecific bee species (reviewed in Goulson, 2003; Rogers *et al.*, 2013; but see Pinkus-Rendon *et al.*, 2005). Exploitative competition may help explain the drop in native bee numbers after honeybee hive introduction. However, because bee abundance varies considerably between and within seasons, this study should be replicated and continued for several years in order to unequivocally conclude floral resource depletion. To our knowledge, no well-replicated, long-term study has been conducted to conclude exploitative competition between honeybees and native bees.

Our results are congruent with the findings of others. For example, Goulson *et al.* (2002) found that the abundance of native Tasmanian bees was not impacted by the presence of the exotic species *Bombus terrestris*, yet native bee abundance was significantly higher where honeybees were absent. One study conducted in islands of the Pacific Northwest found that native bees were absent or present at low abundances on islands where honeybee numbers were high (Kato *et al.*, 1999 reviewed in Goulson, 2003). Neither of these studies manipulated the numbers of honeybees in the study site. In studies where bee abundance is manipulated experimentally, it is usually done without replication and for a shorter-than-optimal time span. For example, Wenner & Thorp (1994) noted significant increases in native bee numbers where feral and commercial honeybee nests were removed. Additionally, Roubik (1978) found that introduction of Africanized honeybees in the Neotropics significantly reduced the abundance of native insects. Both of these studies were conducted without controls and are un-replicated, so it remains difficult to draw firm conclusions from their findings.

Studies that do focus on bee competition can often be criticized for focusing on generalist native bees, for generalists (*Bombus terrestris*, for example) are the species least likely to be affected by competition (Goulson, 2003). Hudewenz & Klein (2013) however, found that specialist and native bee *Andrena fuscipes* visits its main food source *Calluna vulgaris* (common heather) less frequently in sites where honeybee hives were introduced, compared to sites without honeybee hives. To make stronger conclusions regarding exploitative competition between native and exotic bees, future long-term studies targeting specialist bees may prove insightful – especially when the majority of native bees are specialists (Minckley & Roulston, 2006). Given the difficulty in conducting such a study however, it is impossible to rule out exploitative competition as a potential mechanism driving the reduced abundances of native bees that often follow increases in honeybee numbers.

Honeybee abundance is a good indicator of floral resource availability because honeybees are extremely adept in locating pollen and nectar sources (Buchmann and Nabhan, 1997). The foraging success of honeybees is probably due in part to their foraging strategy. Honeybees forage in groups (Donaldson-Matasci *et al.*, 2013), communicate with each other about forage (Seeley, 1986), and mark flowers with pheromones that usually repel

native bees and honeybees from recently visited, and hence less profitable, flowers (Giurfa & Núñez, 1992; but see Goodale & Nieh, 2012). Before introducing a honeybee hive to the North Prairie, we noted low honeybee abundance on transects farthest from the hive-introduction point compared to the closer transects. After hive introduction, honeybee abundance remained comparatively low on those transects, but not significantly so. This finding suggests that floral resources farthest from the site of hive placement in the North Prairie may have been less profitable for bees, or less abundant.

Although we noted decreased native bee abundance post hive-introduction to the North Prairie, native bee abundance remained high on transects closest to the introduced hive. This finding seemingly contradicts the original hypothesis, that resource depletion by managed honeybees may displace native bees to those transects farthest away from the introduced hive. One explanation for this result is that, as suggested by pre-introduction honeybee abundances, floral resources were more abundant on transects closest to the introduced hive. Hence, native bee abundance may have been reduced because of increased competitive pressure from honeybees, yet native bee abundance remained highest where resources were most plentiful. While our findings may be skewed by the clumped dispersal of floral resources, it is also possible that shifting abundances would have been more noticeable if our study plot were larger than 400 m. For example, Evertz (1995) showed that managed honeybee hives could displace solitary bees native to Germany by over 1 kilometer. Another plausible explanation is that floral resources were so abundant in our study sites that they were never limiting – we rarely observed multiple bees foraging on a single plant simultaneously (Bayha, 2014 Senior Thesis). Hence, reduced native bee numbers could be explained by natural seasonal fluctuation, rather than competition via resource exploitation.

We conclude that honeybee management can affect the abundance of native bees. Although there is little evidence for interference competition between honeybees and native bees at PCCI (Bayha, 2014 unpublished data), some evidence suggests that honeybees may be aggressive towards native bee species (Roubik, 1978; Pinkus-Rendon *et al.*, 2005). And, while exploitative competition has been inferred by many researchers, (Ginsberg, 1983; Goulson, 2003; Hudewenz & Klein, 2013) we cannot conclude that honeybees and native bees are competing at PCCI, because floral resources are clumped in space and there aren't enough bees to exhaust these resources. Nevertheless we show that honeybee management should be a concern for nature preserves – our findings suggest that artificially high honeybee abundance, due to commercial or hobby beekeeping, could affect the conservation of native bee species, although causal evidence is lacking. This study raises some important questions for future study: (1) at what point does bee abundance exhaust floral resources? (2) are honeybees better equipped than native bees to exploit floral resources if those resources are limited in supply? (3) if honeybees do exploit floral resources, how do native bees respond to the competition? If these questions can be elucidated through long-term and well-replicated studies, community ecologists and entomologists will have a much firmer understanding of a currently equivocal topic: competitive impacts of honeybees on native bees.

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End Notes

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