

Quantifying Hedgerow Effects on Native Bee Movement

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ABSTRACT

Pollination is an essential ecosystem service that can be met in a variety of ways. Though honey bees represent the most common agricultural pollinators, native bees offer an alternative pollination option that could address concerns about threats to commercially managed honey bee colonies and their pollination service. The presence of native bees in agriculture represents a type of biological insurance for honey bee pollination, in the event of population decline. The extent of this insurance is predicated on native bees' pollination potential, which has not yet been quantified. The economic benefits of native bees are difficult to determine without greater knowledge of their movement patterns in agricultural fields. I found that in hybrid sunflower fields, native bees foraged further into fields bordered by hedgerows of native vegetation than in similar fields without these enhancements. Though both site types exhibited greater abundances of bees along the edge of the field than inside, native bees were observed moving greater distances at sites with nearby native habitat. Hedgerows seemed to buffer the natural declines in bee visitation that occurred with increasing distance into fields, resulting in a greater observed movement of bees in hedgerow fields. Native vegetation could be essential for promoting the presence of native pollinators in agriculture, a goal that could have dramatic effects on stabilizing pollination services and ensuring agricultural yields to feed a growing global population.

KEYWORDS

pollination, hybrid sunflower, honey bee, biodiversity, generalized linear mixed model

INTRODUCTION

Pollination is a key component of agriculture, with 35% of global food crops dependent upon some degree of animal pollination (Klein et al. 2007). The value of worldwide pollination services is estimated at \$200 billion annually (Gallai et al. 2009), and among animal pollinators, bees are most widely credited for their pollination services. Imported European honey bees represent the most widely used agricultural pollinators, due to their versatile pollination abilities and the convenience of utilizing managed non-native honey bee colonies rather than relying upon more variable wild pollination sources (Klein et al. 2007). However, honey bee populations have experienced widely-publicized declines in recent decades due to phenomena such as Colony Collapse Disorder (vanEngelsdorp et al. 2009), encouraging researchers to explore alternative pollination options.

Research into native bee populations that exist alongside managed honey bee colonies has highlighted the potential for native species to provide “biological insurance” for the pollination services lost by honey bee population declines (Winfrey et al. 2007). This insurance effect, in which native bee pollination could fulfill the same ecosystem services as honey bees, could mitigate the economic losses of honey bee disappearances in commercial agriculture. The potential for native bee populations to augment, insure, and perhaps completely replace honey bee pollination has highlighted the importance of these species in agricultural ecosystems. In organic systems, native bees alone have been shown to provide sufficient pollination services to some crops (Kremen et al. 2002). However, with intensive management, such as that typified by commercial monocultures, native pollination services have experienced widespread declines, primarily due to habitat isolation and degradation (Grunewald 2010). Due to the challenges of conventional, intensive agriculture, the full extent of native pollination is currently untapped in most commercially managed farms.

In light of declines in both honey bee and native bee richness, research efforts have focused on methods of bolstering native bee populations and encouraging their presence in agricultural communities. Habitat restoration increases biodiversity and optimizes native bee pollination on farms (Williams & Kremen 2007). Proximity to natural habitat can aid native bee presence and pollination activities, mitigating the negative effects of intensive commercial agriculture (Winfrey et al. 2007). Hedgerows of native vegetation bordering agricultural lands

are one effective method of habitat restoration that can successfully increase native bee species richness by increasing the proximity of natural habitat to agricultural fields (Hannon and Sisk 2009). However, studies have not yet proven whether hedgerows increase native bee presence and pollination throughout fields, or merely along the edges that they border. The true value of hedgerows to agriculture cannot be determined until data is collected showing whether the presence of hedgerows results in a greater presence of native bees throughout agricultural fields, thus optimizing these species' pollination services for the entire field.

Studies examining native bee foraging patterns have focused primarily on the maximum distance that such species can travel to access floral resources. Current estimations of native bee foraging distances are about 1275m for medium-sized bee, which represents a significant increase from the previous expected distance of about 300-400m (Zurbuchen et al. 2010). However, there is a lack of literature examining how bees move within that maximum distance. It is uncertain whether bees are evenly distributed across the entire foraging range or if distance from their origin plays a role in affecting foraging patterns. In the latter case, the majority of bees would likely take preferential advantage of resources close to their nest and only a small number would achieve that stated maximum distance. The distance between a crop and natural habitat has a negative effect on biodiversity, with both species abundance and richness of flying pollinators dropping by 80% over 500m in studies (Carvalho et al. 2010). Agricultural systems enhanced with natural habitat such as hedgerows could offer a solution to this negative trend by reducing the distance between agricultural fields and natural habitat. Studies have proven the success of hedgerows at attracting beneficial insects, validating their use as a management tool in agriculture (Morandin et al. 2011). However, the effects of these hedgerows on bee movement within the fields that they border is uncertain. Further research to prove how hedgerows affect native bee distribution within agricultural fields is necessary to form a fully informed understanding of the utility of such enhancements.

This study used fluorescent powders to observe the effects of hedgerows on native bee movement within adjacent crops, ultimately asking whether hedgerows improve bees' penetration into fields. I hypothesize that traces of bee movement would be observable up to 50 meters away from the row at which marking occurred (Lavigne et al. 1998). However, I expected to observe a decline in the amount of powder present with increasing distance from the marked row due to the abundance of floral resources. When comparing sites with and without

hedgerows, I predicted that hedgerow sites would have higher native bee populations, due to the presence of non-crop floral resources to sustain populations throughout the year. I therefore anticipated that native bees would move farther into enhanced fields than in fields without hedgerows, as competition for floral resources among a larger native bee population would encourage individuals to forage further into the field (Figure 1). These observations were expected to prove that hedgerows are effective at both maintaining native bee populations and increasing their penetration into fields. This quantifiable data regarding the distance over which the effects of native habitat can be observed in agriculture, will allow farmers to make more informed decisions when designing and maintaining agricultural matrices to promote wild pollination services.

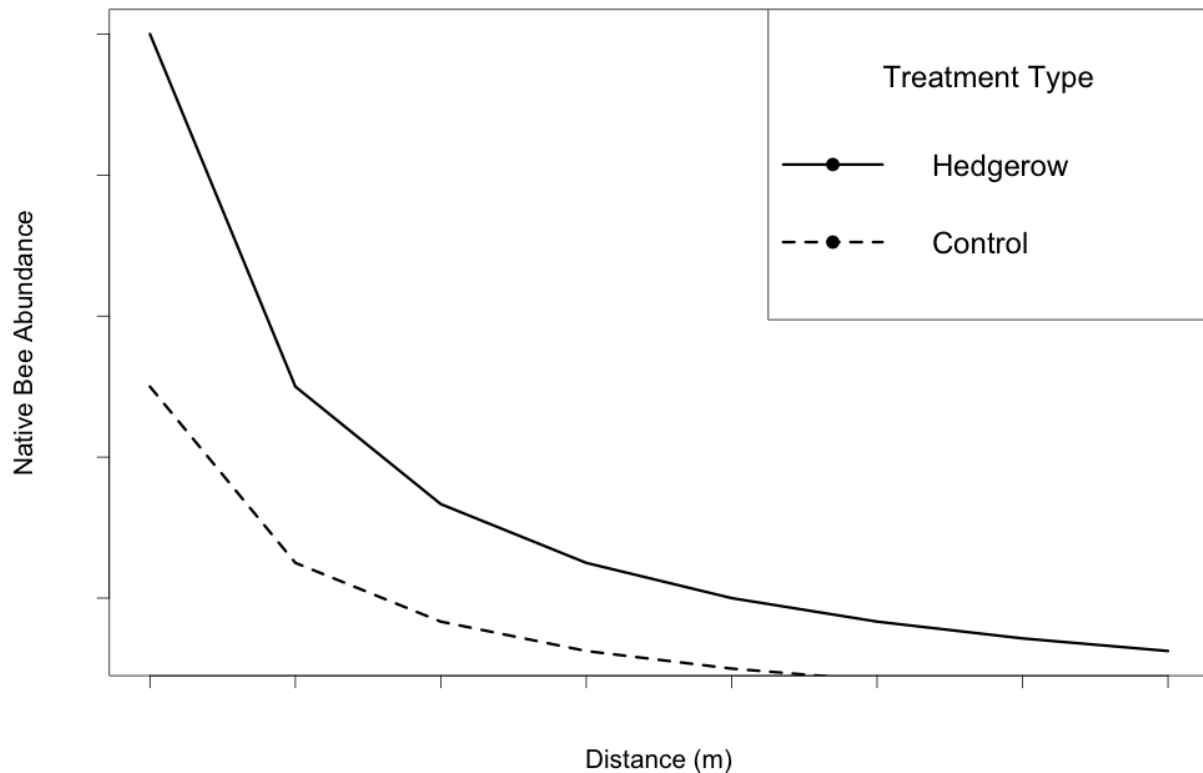


Figure 1. Expected native bee distribution. I anticipated a decline in native bee abundance with increasing distance into the field. Due to the effects of native habitat, I expected sites bordered by a hedgerow to harbor larger native bee populations and exhibit less dramatic declines than control sites.

METHODS

Study site

This study took place in eight hybrid sunflower fields in Yolo County, CA in June and July 2012. Sampling took place during peak sunflower bloom, which occurs for about four to six weeks during the summer. Four fields were bordered by hedgerows, which consist of native trees, grasses, and shrubs planted to bring the benefits of native vegetation closer to agriculture (Morandin et al. 2011). A control field with unenhanced field margins consisting of bare dirt or weedy patches was paired with each hedgerow field to allow comparison of trends between enhanced and non-enhanced fields.

Hybrid sunflowers are dioecious, and the sunflower fields in this system were planted with alternating rows of male and female plants, such that single rows of male (pollen- and nectar-producing) flowers were separated by several consecutive rows of female (nectar-producing) flowers (Figure 2). I numbered the rows of male sunflowers starting with Row 1 at the edge and continuing for about six to seven rows until I had sampled 50 meters from the edge.

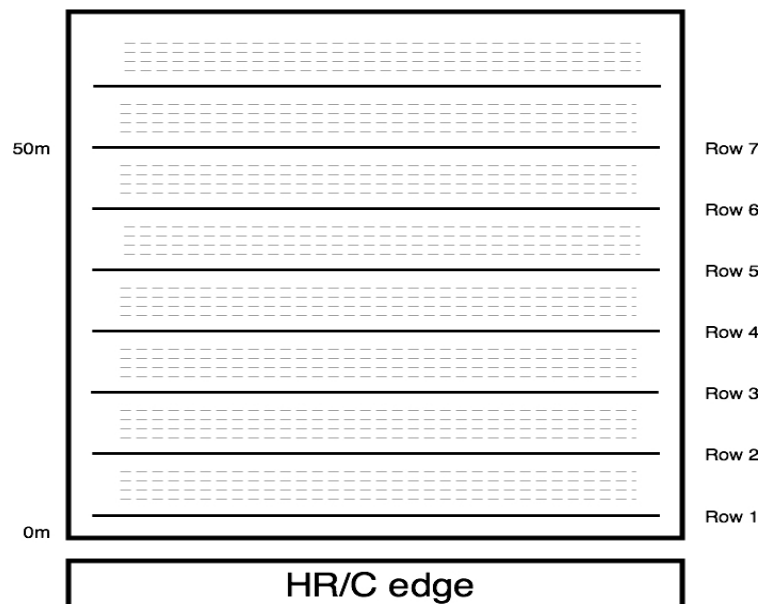


Figure 2. Site design. Numbered solid lines represent rows of male sunflowers, with dashed lines representing several rows of female flowers separating each male row. The first male row is the row at which bee marking occurred. Observation occurred along every male row going 50m into the field. The hedgerow/control edge is pictured as well across a dirt road from the field. Image not drawn to scale.

Powder marking

I measured native bee pollination patterns using fluorescent powders as indicators of bee movement (Frankie 1973, Stockhouse 1976). This type of powder has been reported to act as a pollen analogue (Van Geert et al. 2010), which allowed powder deposition by native bees to mimic the movement of pollen through a field by these insects. At each site I caught and marked 70-120 medium-sized native bees and as many large-sized bees as were present along a 100-meter transect on the first row of male sunflowers. Medium-sized bees included the genera *Melissodes*, *Diadasia*, *Peponapis*, *Megachile*, and *Triepeolus*, which are all roughly the size of an average European honey bee. Large-sized bees included various species of bumble bees (*Bombus vosnesenskii* and *Bombus californicus*), *Xylocopa* (carpenter bees), and *Svastra*. I focused on only medium and large bees because small bees, such as *Halictus* and *Lasioglossum*, did not retain enough powder on their bodies to make their movements observable.

I collected bees with aerial nets, vials, blue vane traps, and bug vacuums (Backyard Safari™). Once caught, the bees were transferred to a collecting vial containing a small amount of fluorescent powder and released after being sufficiently coated with powder, which took about five seconds. Pink powder was used to mark medium-sized bees and blue powder was used for large-sized bees, in order to differentiate marks made by these two distinct sizes of bees. Bees were not recaptured or re-marked so that their pollination activity was undisturbed and data remained unbiased. Natural foraging behavior resulted in the deposition of powder onto sunflowers as if it was pollen, allowing us to track the distance that bees traveled from the marked row. This pollen-like deposition was the key to this method of observing bee movement: bees were marked at the first male row as if they had gathered pollen at that row, and any observed powder traces represented the ability of a bee to move pollen that far from the origin row.

Powder observation

After dusk, I observed traces of fluorescent dye on sunflowers using an ultraviolet flashlight. Observation occurred along parallel 100 m transects on each male row going 50 m into the field. The use of a UV light made traces of powder on the sunflowers very evident and

was effective enough to illuminate individual grains of powder. Observation of powder within the field indicated the movement of a bee from the row in which it was marked, and the color of the powder indicated its size. The patterns of powder distribution at each site suggested the frequency with which bees move from the edges of the fields inward, giving insight into the patterns of native bee movement. Differences between these patterns at hedgerow and control sites indicated if hedgerows exerted any effect on native bee movement.

Generalized linear mixed model

I used a generalized linear mixed model in the statistical software R with a poisson distribution to assess the effect of distance from the marked row and treatment (hedgerow or control) on the number of powder observations in the field (R Development Core Team 2009, Bates et al. 2012). Other variables were collected and included in a second, more complex iteration of this model. These included the sex and species of marked bees, total number of bees marked at each site, and percent bloom – a measure of the number of blooms on each stalk at a site. The use of a generalized linear mixed model allowed my analysis to take into account the random effects of site (McCulloch & Neuhaus 2005). This addition of a random variable to my model allowed me to consider the variation that was inherent in the different sites that could play a role in the number of bees that I was able to mark or the number of powder traces that I was able to observe.

RESULTS

Powder marking

I marked native bees at eight sites in order to observe their movement through sunflower fields. In total, I marked 789 native bees across the eight sites. 759 of the bees were marked pink, designating medium-sized bees, and 30 were marked blue, designating large-sized bees (Table 1). Due to the low occurrence of large-sized bees, I did not use the data from the bees that I marked blue in any analysis, focusing only on the pink, medium-sized bees.

Table 1. Number of bees marked at each site. Sites were subset using the following functions for each site and color: `mark.Rom <- mark [mark$Site=="Rominger",] (site)` and `mark.Rom.P <- mark.Rom [mark$Color=="P",] (color)`

Site	Number Marked	Pink (Medium)	Blue (Large)
HR1	107	102	5
C1	102	101	1
HR2	70	65	5
C2	98	93	5
HR3	73	71	2
C3	108	104	4
HR4	108	101	7
C4	123	122	1

The mean number of medium-sized bees marked pink per site was 94.875, the median was 101, and the standard deviation was 18.558. The median value of 101 bees marked is very close to my goal value of 100 bees, despite the wide range of bees caught among the eight sites. The smallest number of medium-sized bees caught at a single site was 65 at HR2, and the largest was 122 at C4 (Figure 3).

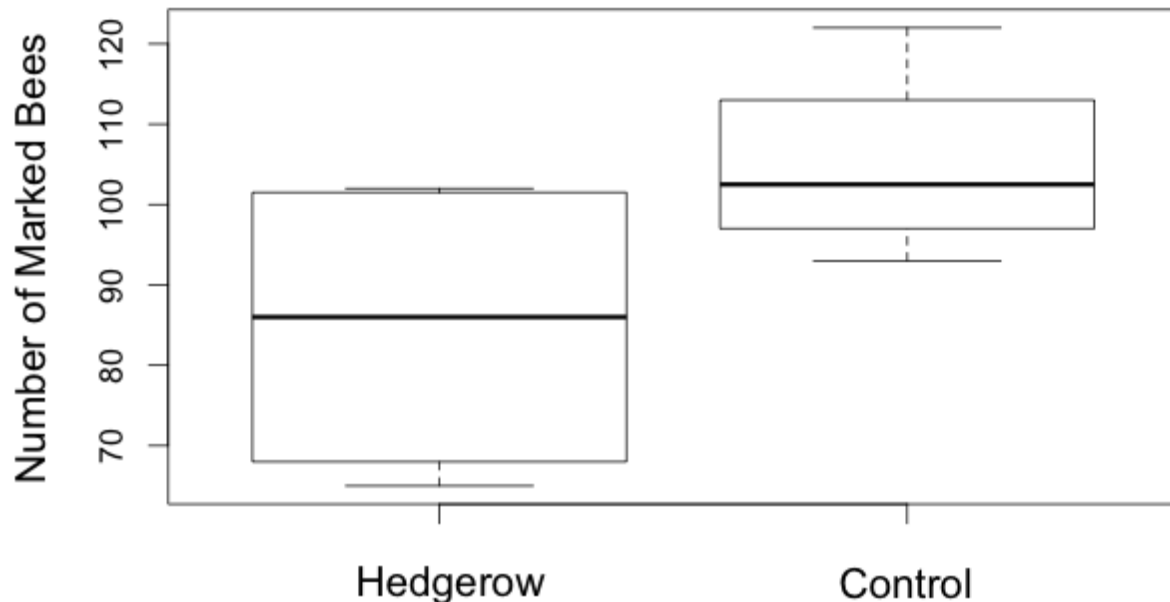


Figure 3. Summary of marked bees by site. Though the number of marked bees ranged from 65 – 122, none of the data are considered outliers, indicating that it can be analyzed normally. Control sites generally had a higher number of bees marked than hedgerow sites, demonstrating higher median, minimum, and maximum values.

There were no differences in sampling efforts among the sites – each had the same number of samplers who stayed in the field for approximately three hours, excluding C4, at which the abundance of bees made it only necessary to mark for 30 minutes. At one site (HR4), the first

row of male sunflowers was too sparse (less than 25% bloom) to successfully mark bees, so I marked along the second row of male sunflowers instead.

Powder observation

After sunset, I observed traces of powder deposited on plants during daytime visitation by marked bees. I observed 464 traces of dye in the male rows up to 50 meters away from the edge of the sunflower fields over the eight sites in my study system, with 431 of those observations being pink and 33 blue (Table 2). No traces of powder were found in the hedgerows of any enhanced sites or field margin of any control sites, indicating that native bees were not directly using the hedgerow as a resource during sampling periods of peak bloom.

Table 2. Number of powder observations by site. Observations of powder dye on sunflowers indicated a visit by a marked bee to that plant. Pink powder indicated visitation by a medium-sized bee, while blue-powder indicated visitation by a large-sized bee.

Site	Number Observed	Pink (Medium)	Blue (Large)
HR1	77	57	20
C1	53	50	3
HR2	41	38	3
C2	24	21	3
HR3	39	39	0
C3	42	41	1
HR4	79	76	3
C4	109	109	0

An average of 80.7% of observed traces of powder were found in the first row of male sunflowers (the same row in which marking occurred). Observations declined with increasing distance from this origin (Figure 4), with an average of 12.5% of observations occurring on the second male row, 2.0% on the third, 1.2% on the fourth, 0.9% on the fifth, 0.5% on the sixth, and 0.2% on the seventh (Appendix A).

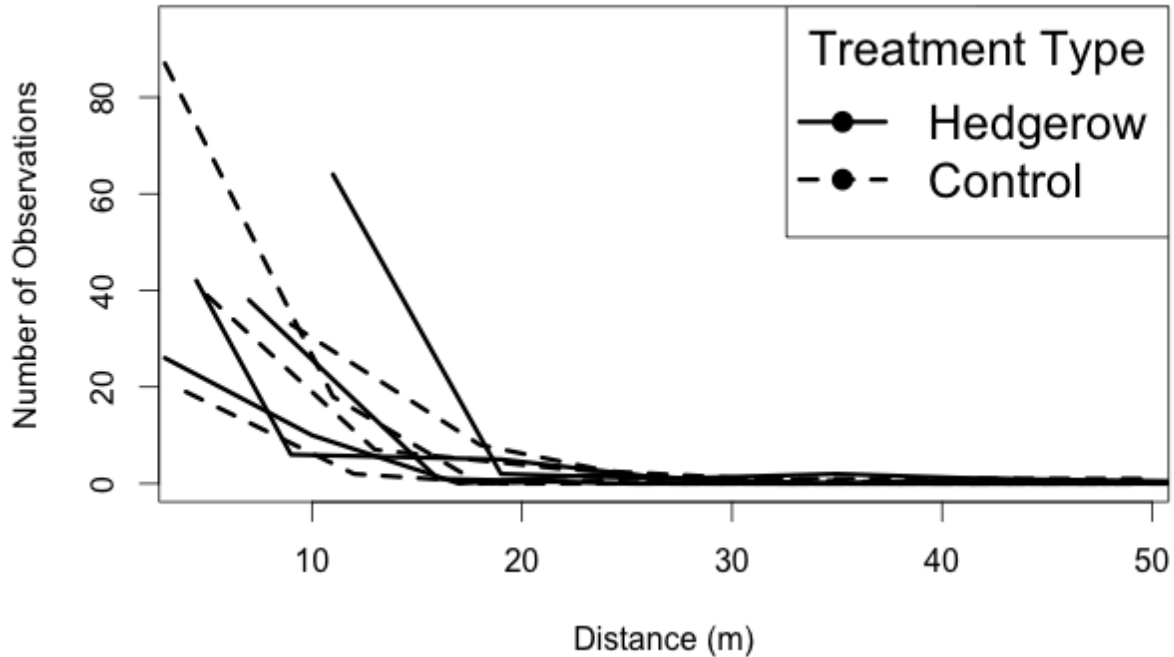


Figure 4. Powder observations by distance. Powder observation declined with increasing distance into the field from the initial row of male sunflowers.

Modeling treatment and distance

I used a generalized linear mixed model to demonstrate the effects of distance, treatment, and the interaction of these two variables (distance:treatment) on the number of powder observations that I observed in the field (Appendix B, Figure B1). The model showed that distance ($p < 0.001$) and the interaction of distance and treatment ($p < 0.001$) were both statistically significant in predicting the number of powder observations found at each site, but treatment alone was not significant ($p = 0.124$) (Table 3a). A similar model relating area and treatment, rather than distance and treatment, to the number of powder observations, failed to run.

I collected data related to site conditions and bee population that I then included in a second generalized linear mixed model (Appendix B, Figure B2) to determine whether these variables had any additional effect on the previous model. Variables included number of distinct species sampled, total number of bees marked, ratio of female to male bees in the sampled population, and percent of the field blooming at each site (how many blooms exist on each plant stem). With these variables, the number of bees marked at each site was found to be statistically significant ($p = 0.011886$) as well as distance ($p < 0.001$) and distance:treatment ($p < 0.001$) (Table 3b).

Table 3. Summary tables – generalized linear mixed models. GLMER analysis was utilized to determine what variables influenced the amount of powder observed in the field. The first analysis (a) was carried out using only the variables of distance and treatment, while the second analysis (b) included variables related to site conditions.

a)	Variable	P-Value	b)	Variable	P-Value
	Distance	<2e-16		Distance	<2e-16
	Treatment	0.12429		Treatment	0.176075
	Distance:Treatment	0.00066		Species Number	0.421976
				Number Marked	0.011886
				Sex Ratio	0.58538
				Percent Bloom	0.541882
				Distance:Treatment	0.000691

DISCUSSION

With both domesticated and wild pollinator communities experiencing population declines, greater understanding of pollinator behavior and movement is important to develop management plans to protect biodiversity and preserve ecosystem services (Brittain et al. 2013). Many studies exist showing positive effects of natural vegetation on wild bee communities: proximity to native habitat has been shown to increase pollinator abundance, and hedgerows of native vegetation in particular have proven successful at encouraging wild pollinator presence in agriculture (Greenleaf & Kremen 2005, Carvalheiro et al. 2010). Hedgerows have been widely studied for their potential utility during non-bloom seasons in adjacent crops as a supplemental resource (Hannon & Sisk 2009, Morandin et al. 2011). This is consistent with findings in this study that wild bees appear not to forage within the hedgerow during peak bloom, though they could utilize hedgerow resources during non-peak seasons. Some of my findings are not consistent with the idea that hedgerows enhance wild bee presence – I collected higher numbers of bees at control sites than at sites bordered by hedgerows, likely reflecting differences in the actual bee populations since sampling efforts remained the same across fields. However despite this population difference, the interaction of hedgerows and distance proved to have a statistically significant effect on the number of powder observations in fields. Bees seemed to travel farther into fields bordered by a hedgerow than a control edge, although both sites showed a decline in the number of observations found with increasing distance. Hedgerows may be

effective at enhancing crop pollination further into a field than at a non-enhanced site, somewhat buffering the decline that is observed with greater foraging distances.

Powder marking

The use of fluorescent powder was a very successful method of marking insects and observing their patterns of movement (Stockhouse 1976, Rademaker et al. 1997). The powder did not noticeably affect insect behavior and was very sticky, remaining on both insects and flowers for four to six days after the initial marking, consistent with other studies using similar powder markers (Frankie 1973, Crumpacker 1974). At two sites, I was unable to conduct powder observation on the same day that marking occurred. At HR1, an insufficient number of bees were marked on the first day, which was remediated by a second day of marking and observation on that subsequent evening, two days after the initial marking date. At C2, a five-day gap separated the marking and observation portions of the study. This was due to irrigation that occurred in the field after the initial marking activity occurred, making it impossible to reenter the field after nightfall due to flooded conditions. Despite these delays, powder remained visible on plants at both sites, warranting confidence that the time variation did not impact the success of this study.

Research has shown a relationship between the amount of offspring produced by nesting bees such as *Melissodes* and *Megachile* species and the distance of these nests from native habitat, with those bees nesting further from native habitat exhibiting a significant decrease in offspring production (Williams & Kremen 2007). These findings suggest that native habitat could be crucial for maintaining wild bee populations. However, I observed the opposite trend: I collected more medium-sized bees at nearly every control site when compared to the paired hedgerow site and the mean over the entire study system was also higher for control sites (99.75) than hedgerow sites (90.00). The standard deviation for the number of medium-sized bees caught over all eight sites was 18.56, proving that the difference between the means for hedgerow and control sites does not indicate any significant difference in marking capabilities between hedgerow and control sites during periods of peak bloom. These results indicate that differences between pollinator populations in enhanced versus non-enhanced agricultural systems might be more prevalent during non-peak seasons, as individuals react to a relative dearth of resources.

During peak bloom in the agricultural field, the resource abundance likely minimizes any hedgerow effects and results in similar pollination activity between the different site types.

Powder observation

Observation of the powder deposited on plants during bee visitation showed a decline in deposition with increasing distance from the row at which the initial marking occurred. Initially, this trend seems to indicate a preference for bees to visit flowers within a limited range, centered on the row at which marking occurred. This would be consistent with literature citing nearest-neighbor rules for foraging behavior such that bees would preferentially visit flowers close to each other rather than forgoing these resources to fly further into the field (Walters & Schultheis 2009). However, this nearest-neighbor approach to understanding of insect foraging has been contradicted by some studies, forcing researchers to consider floral resources as a complex rather than linear system (Lihoreau et al. 2012). The observed decline in powder depositions, though present both at sites with and without hedgerows, was less dramatic at hedgerow sites, suggesting that hedgerows promote the penetration of bees into fields. This trend is especially interesting when coupled with the fact that more bees were marked at nearly all control sites versus their paired hedgerow site. The ability for hedgerows to enhance crop pollination further into a field seems to exist regardless of sample size, further validating the effectiveness of hedgerows in promoting both native bee presence and penetration into fields.

The effects of area must be considered when discussing any instance of powder observation in my study system. While distance was measured in a linear fashion in the study system, an observation at any distance actually represents a much larger area of potential visitation, as a bee can fly that distance in any direction. Because area increases as a square of distance, a trace of powder 35 meters away from the edge, for example, represents a much larger area of potential visitation than a mark 8 meters away (Figures 4a,b).

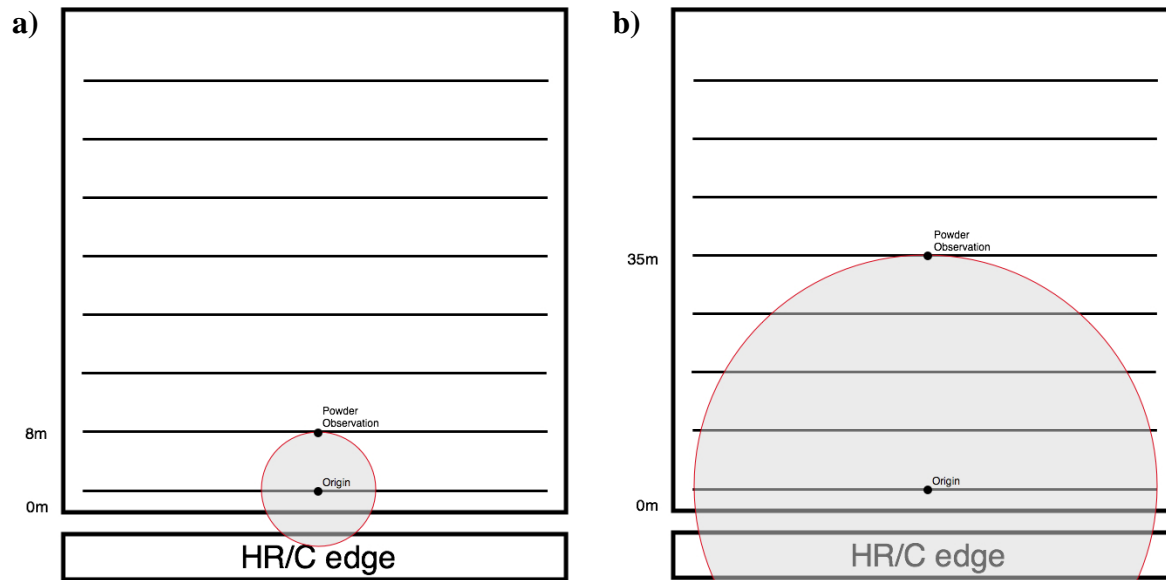


Figure 4. Effects of area on powder observation. A powder observation on a row close to the origin row (a) represents a lower area of potential flight by that bee than an observation on a row further from the origin (b).

This understanding of distance as was measured in this study and the actual area of potential visitation that is represented by such a visit is essential to consider the true implications of the powder observations that were made. Although only 11 observations occurred at distances greater than 25 meters from the edge, those observations represent the greatest penetration potential of bees into fields as well as the largest area of potential native bee visitation and pollination.

No powder was observed outside any of the fields in the adjacent hedgerows or field margins. Any hedgerow effects are likely indirect during periods of peak bloom. Hedgerows are hypothesized to serve a function in attracting bees to the field to nest and are likely essential in maintaining pollinator populations during non-peak bloom seasons (Hannon & Sisk 2009, Morandin et al. 2011). Despite the human error inherent in these observations, it is unlikely that a level of powder marks were missed that would challenge this understanding of hedgerow utility. Bees did not appear to be using the hedgerows as a resource during my sampling period, and were interacting with this enhanced edge in the same way that they do with the field margin. This finding supports the body of literature proving that hedgerows have beneficial properties for pollinator populations.

Dye observation had a very high detection confidence (Stockhouse et al. 1976, Hagler et al. 2011). The use of an ultraviolet flashlight made the fluorescent powder very easily visible at

night, and I frequently observed marks as small as an individual grain of powder with the UV light (227 individual grains), encouraging confidence that very few instances of powder were undetected.

Pressing experiment

In order to ensure that the amount of powder observed was not affected by the physical loss of powder from the marked bee, an experiment was performed evaluating the number of powder depositions that a single marked bee can make. By marking and pressing dead *Melissodes* specimens on sunflowers in the lab, an estimate of the maximum number of powder depositions that a marked bee could make was determined (Rademaker et al. 1997). Due to the success of the bees in depositing powder and tendency for these brittle specimens to deteriorate as they were pressed on the sunflower inflorescence, pressing was abandoned after about 20 marks, or when the specimen was destroyed. Much fewer than 20 powder observations per marked bee were found in the field, indicating that declines in observation with distance into the field were not a result of unrelated powder loss. Some normal bee behavior that could result in powder loss, such as grooming and flight, were impossible to simulate with a dead specimen in the lab. Studies have determined that bees lose approximately 6.1% of the pollen (or powder) that is collected on their body in ways unrelated to pollination, such as flight, grooming, or landing on other parts of the plant (Rademaker et al. 1997). This fraction is small enough to be disregarded in my pressing experiment, and the estimation of 20 powder observations per marked bee can be trusted to prove that powder loss is not a confounding factor in the observation declines observed in this study.

Site as a random variable

The benefit of a field-based experiment, versus one in a laboratory or greenhouse setting, is that in the field, species interactions more closely simulate those in nature. Unnatural conditions in a lab setting, which allow for the control of random variables, also result in non-normal species behavior. However, a major shortcoming of a field-based experiment is that the study system is limited to pre-established sites – fields that are scheduled to be planted with

sunflowers and are bordered by hedgerows. Farmers, rather than a research team, have control over the type of sunflower planted, method of planting, irrigation regime, and schedule. Variation between these sites can have unanticipated effects on data and analysis. For instance, sites had different distances between rows, ranging from three to fifteen meters between rows of male sunflowers, and different irrigation regimes, with drip irrigation at two sites (C1 and C4) and flood irrigation at the rest. Sampling occurred at different points within these irrigation cycles as well, which could have unintended consequences on bee sampling efforts. Sites varied in sunflower type, with the same type between each hedgerow/control pairing, but different types among pairs of sites. Additionally, the hedgerows consisted of different species of native vegetation, and because they were not planted at the same time, they varied in maturity among sites. All of these factors could have unintended consequences, the degree of which is difficult or even impossible to definitively determine. Therefore, site was included as a random variable in statistical analysis to account for these unpredictable qualities.

Limitations

The biggest limitation in this study was a limited supply of labor. Each day in the field consisted of four samplers working for approximately 5 hours. With a larger supply of field workers, more sites could be sampled and numbers of marked bees could be increased and more strictly regulated, allowing for more accurate and robust analysis. With increased labor, observation could take place further than 50 meters into the field, allowing greater confidence in whether powder declines are due to dilution by distance or a true effect of hedgerows. An increase in the distance sampled to about 150-200 meters from the edge would be consistent with research that has extended the maximum range of insect pollination (Chifflet et al. 2011). Additionally, a limited supply of field labor resulted in an inconsistent number of bees marked at each site, which complicated analysis. It was necessary to include the number of bees marked in analysis due to the variation that occurred between sites. Greater effort to standardize the number of bees marked among sites would reduce the effect of this variable on observation and eliminate it from analysis.

The scope of this study is limited to community-level behavior. The movement of individual bees cannot be observed using the simple two-color powder system described here;

only the movement patterns of the entire community of marked bees, and differences between broad size categories, were observable. A mark-release-recapture experiment would allow researchers to study individual bees' movement, putting a finer filter on the analysis of pollination trends in wild bee communities. However, with a highly limited supply of field labor, insect recapture rates in a mark-release-recapture experiment would be impractically low, resulting in unreliable analysis. While the data obtained from studying the movement of individual bees would be highly informative in understanding wild bee pollination and behavior, such a study is highly constrained by available time and labor, making it impossible to include in my study.

Future directions

This study offers preliminary results on the movement of wild bees in agricultural communities. However, there are many ways in which this research could be improved and enhanced if carried out on a larger scale. Sampling a greater number of sites would allow for more robust analysis regarding bee movement, as well as more complex analysis comparing hedgerow and control sites. This would permit observation of more subtle trends between hedgerow and control sites that are otherwise classified as random variation when only four pairs exist. Additionally, with only four hedgerow/control pairs, unrelated variables could easily obscure the true effects of these enhancements. With a greater number of hedgerow/control pairings, these random variables would become less prominent in analysis, allowing the more subtle effects of hedgerows to become evident.

This basic method of fluorescent powder as a marker for pollination study could be adapted to allow greater understanding of insect movement within agricultural fields. In order to more precisely simulate true pollen movement, powder could be applied on flower heads in the field rather than by catching and marking bees directly (Ordoway et al. 1987). As insects visit these marked flowers, they would pick up the powder like pollen and move it as they would move pollen from that flower. This would allow pollen dispersal, rather than community movement, to be studied using fluorescent powder, and potentially reduce erroneous marks such as those from spilled dye or bee grooming behavior. However, pollination behavior from insects

such as imported European honey bees would be included as well, eliminating the ability to isolate the study to native pollinators.

Bee movement and agricultural pollination

This study is highly unique in directly measuring bee movement into fields. Most analyses of insect movement rely upon simulation studies in a greenhouse or other lab setting, and by using a fluorescent marker, bees' natural movement patterns can be observed. The majority of studies related to pollinator movement focus on the maximum distance that can be traveled by the insect, without much discussion of the distribution of bees within that maximum distance. Though the maximum foraging distance is certainly an interesting consideration to determine the possibility of pollination at a given distance, it is difficult to estimate a bee's pollination potential without an understanding of the probability of that maximum being achieved. Very few studies have directly measured native bee movement into agricultural fields, despite the relationship between pollinator movement and pollen movement. Ultimately when studying pollination, researchers need to determine whether pollen is moving in all directions and how pollen movement can be affected by variables such as distance and off-farm vegetation.

Additionally, in agricultural systems such as the sunflowers in this study, plants are grown in methodical rows, which does not occur in nature. There is a potential for bee movement to be influenced by this non-natural row structure in the field. Bees often forage at plants that are close spatially, potentially resulting in a "highway effect" along rows of flowers in which the row acts as a highway of resources and foraging bees simply move along the row, visiting each flower along the so-called highway (Walters & Schultheis 2009). This potential directionality in foraging could have drastic effects for pollination, and though pollen might move long distances, there could be significant barriers to movement in directions opposing these corridors (Van Geert et al. 2010). Understanding wild bee movement is important to enable researchers and farmers alike to predict pollination patterns and determine whether resource distributions are adequate to maintain pollinator diversity and function.

This study was able to directly observe patterns of wild bee movement through the use of fluorescent dye as a pollen analogue to determine that hedgerows are not statistically significant in determining bee movement. Instead, the interaction of distance and treatment were most

important in affecting bee movement and the likelihood of a bee traveling a given distance. Further studies using a greater number of sites and standardizing data more carefully could yield more conclusive and accurate results; however, this study highlights the necessity of observing bees' movement patterns within the confines of their maximum foraging distance. Studies have proved that wild bees have vastly greater maximum foraging ranges than those distances observed in this study (Zurbuchen et al. 2010a-b, Chifflet et al. 2011). However, an understanding of bees' average foraging activity, rather than just the maximum, gives better insight to bees' pollination function. Wild bees' effectiveness as pollinators is important to analyze in light of declining honey bee populations (Allan-Wardell et al. 1998). Even with honey bee availability, some crops have been shown to be more successful with greater pollinator diversity (Williams & Kremen 2007). Wild bees play an important role in agricultural pollination, and proper management steps must be taken to understand and maintain their populations to continue benefiting from this ecosystem service.

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APPENDIX A: Powder Observation Data

Table A1. Powder observation by row. Each male row for 50 meters from the edge was examined for traces of powder dye. Due to sampling along the second row of male sunflowers rather than the first at Site CR101, Row 0 exists to signify the male row between the marked row (Row 1) and the edge.

Site	Treatment	Row	Distance	Observations
HR1	HR	1	4.5	42
HR1	HR	2	9	6
HR1	HR	3	19	5
HR1	HR	4	27	1
HR1	HR	5	35	2
HR1	HR	6	42	1
HR1	HR	7	49	0
C1	C	1	5	39
C1	C	2	13	7
C1	C	3	22	3
C1	C	4	31	1
C1	C	5	40	0
C1	C	6	49	0
HR2	HR	1	3	26
HR2	HR	2	10	10
HR2	HR	3	17	0
HR2	HR	4	24	2
HR2	HR	5	32	0
HR2	HR	6	40	0
HR2	HR	7	48	0
C2	C	1	4	19
C2	C	2	12	2
C2	C	3	19	0
C2	C	4	26	0
C2	C	5	34	0
C2	C	6	42	0
C2	C	7	49	0
HR3	HR	1	7	38
HR3	HR	2	16	1
HR3	HR	3	25	0
HR3	HR	4	35	0
HR3	HR	5	45	0
HR3	HR	6	55	0
C3	C	1	9	33
C3	C	2	18	8
C3	C	3	27	0
C3	C	4	36	0

C3	C	5	45	0
C3	C	6	54	0
HR4	HR	0	4	8
HR4	HR	1	11	64
HR4	HR	2	19	2
HR4	HR	3	27	1
HR4	HR	4	35	0
HR4	HR	5	42	1
HR4	HR	6	59	0
C4	C	1	3	87
C4	C	2	11	18
C4	C	3	18	0
C4	C	4	26	1
C4	C	5	33	1
C4	C	6	41	1
C4	C	7	50	1

APPENDIX B: Statistical Models

Generalized linear mixed model fit by the Laplace approximation
Formula: Number ~ Distance + Treatment + Distance:Treatment +
(1|Site)
Data: obs.P

Figure B1. Generalized linear mixed model. I used the statistical software R to create a model that determined the effects of distance, treatment, and the interaction of distance and treatment on the number of powder observations. Site is included as a random variable to account for random variation between sites.

Generalized linear mixed model fit by the Laplace approximation
Formula: Number ~ Distance + Treatment + Species.Num +
Mark.Count + Female.Prop + Bloom + Distance:Treatment + (1|Site)
Data: obs.P

Figure B2. Generalized linear mixed model with additional variables. Variables of number of distinct species market, total number of bees marked, proportion of female bees to male bees, and percent bloom at the site were included in the model.