A Hive Mind: Bounded Rationality and Bees

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ACADEMIC ABSTRACT

Bees (Anthophila) are experiencing global decline as part of what is being called the Anthropocene extinction. In addition to the drivers of this event, such as climate change, bees are experiencing synergistic challenges from pesticides, poor nutrition, pathogens, and parasites. Bees play a crucial role in our world because they help to pollinate flowers, allowing plants in both agricultural and ecological settings to reproduce, and our reliance on them is projected to increase, even as their numbers decline. Therefore, there is a critical need to identify and understand how the behavior of bees, and human behavior towards bees, function under settings of imperfect information, where we act as boundedly rational actors. Therefore, in our studies, we focus on the impacts of changing landscapes on bees – whether those are environmental or political. In our investigations, we utilized bees, measuring their behaviors and community health, in multiple contexts to evaluate the interface of the human - bee world. In Chapter 2, we investigated the impact of human land use changes on honey bee foraging dynamics. We decoded, mapped, and analyzed the waggle dances of hives in Blacksburg, Virginia before (2018-19) and after (2022) the conversion of some of their prime habitat through construction. We found that bees increased their foraging nearly four-fold on the microhabitat which were untouched by the construction, but they are forced to nearly double their average foraging distance (0.69 to 1.28km) after the land development. In Chapter 3, we deployed dancing honey bees as potential predictors for native bee abundance and diversity. We used an existing dataset of decoded honey bee waggle dances (n = 11,050 from 2018-2019) to map three Virginian locations (Blacksburg, Winchester, and Suffolk) and the places preferred and avoided by bees within. Then we sampled (2021-2022) at 10 sites within each location using hand nets, bee bowls, and blue vane traps to determine the relationship between honey bee predicted landscapes and native bee abundance and diversity. We found a parabolic relationship between honey bee foraging and native bee abundance ($p < 0.001$), a relationship that remains robust when we stratify our capture by family (Apidae and non-Apidae) or sociality (solitary and social). In Chapter 4, we quantified bee community health metrics (abundance, richness, and diversity) in soybean plots in Columbia, Missouri, which were either treated with grower standard pyrethroid spray or attract-and-kill insecticidal netting treatments for the control of Japanese Beetle. These bee community health metrics were based on 1473 captured bees. We found a significant decrease in bee abundance in attract-and kill-plots compared to grower standard plots for all application periods ($p < 0.002$), a trend driven solely by the most common species, *Melissodes bimaculatus*. In Chapter 5, we directly examined human behavior concerning bees by analyzing the location, policy subsystem, and partisan control in which recent state level bee statutes were passed in the United States, following the 2022 midterm elections. We report on a robustly significant relationship between partisan control over states and the category of bee legislation enacted ($p = 0.004$). Our spatial analysis revealed a contiguous bloc of central states, along the Mississippi-Missouri Rivers, which did not enact bee legislation. We speculate this may be because soybean, a self-pollinating crop, is one of their largest agricultural exports. Finally, we conclude this thesis with a brief discussion of how these chapters have advanced our understanding of how bees react to human modified landscapes, and how human assumptions about bees shape our behaviors, from the level of individual farms to entire regions of the country.

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GENERAL AUDIENCE ABSTRACT

Insects, and thus bees, are experiencing widespread population decline. In addition to the global factors like climate change, bees face increased pressure from pesticides, poor nutrition, pathogens, and parasites. Bees play a crucial role in our world because they help to pollinate flowers, allowing plants in both farms and our backyards to reproduce. Our reliance on bees is set to increase, even as their numbers continue to decline. As we continue to lose time and press into unchartered territory, there is a critical need to identify and understand how the behavior of bees, and human behavior towards bees, functions under settings of imperfect information. Therefore, in our studies, we focus on the impacts of changing landscapes on bees – whether those are environmental or political. In our investigations, we measure their behaviors and community health of bees in multiple ways to explore their interactions with people. In Chapter 2, we investigated the impact of land use changes on honey bee food gathering behavior. We mapped and analyzed where bees went to feed in Blacksburg, Virginia before (2018-19) and after (2022) construction appeared in their habitat. We found that bees feed nearly four times as much on what little habitat remained, but the bees are also forced to nearly double the distance flown per foraging flight, after construction removed habitat. In Chapter 3, we used honey bee communication as potential predictors for native bee community health. We used an existing dataset of information on where bees went to gather food from 2018-2019 to map three Virginian locations (Blacksburg, Winchester, and Suffolk) and the places preferred and avoided by bees within. Then we sampled (2021-2022) at 10 sites within each location using hand nets, bee bowls, and blue vane traps to determine the relationship between where honey bees gathered resources, and the number of native bee individuals and species found. We found honey bee foraging predicted for the numbers of native bees found, a relationship which stayed strong regardless of how closely native bees were related to honey bees, and whether they lived in hives or not. In Chapter 4, we measured bee community health in soybean plots in Columbia, Missouri, which either used pesticide spray or chemically treated netting treatments to control Japanese Beetle. We found the number of native bees decreased in plots that used the netting, before during and after the other plots were sprayed with pesticides. This trend was driven by the most common bee, *Melissodes bimaculatus*. In Chapter 5, we explored human behavior on bees by analyzing the location, content, and political party control in which state level bee laws were passed in the U.S., following the 2022 midterm elections. We report that party control over states has a large influence on the type of bee laws enacted. When we mapped the states that passed bee laws, we saw a group of central states along the Mississippi-Missouri Rivers did not pass any. This may be because soybean, a crop that doesn't need bees to pollinate, is one of their largest agricultural exports. Finally, we conclude this thesis with a brief discussion of how these chapters have advanced our understanding of how bees react to human modified landscapes, and how human assumptions about bees shape our behaviors, from the level of individual farms to entire regions of the country.

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"hotter" spot on heat maps, and a better landscape assessment by honey bee waggle dances, as explained in materials & methods section. We see a strongly significant quadratic relationship between residual honey bee foraging score and native bee abundance, but no significant relationship for native bee diversity or species richness.

Figure 3.3. Apidae and non-Apidae abundance plotted against residual honey bee foraging scores. In these graphs, black data points indicate sites from Blacksburg, orange data points indicate sites from Winchester, and blue data points indicate sites from Suffolk. A higher residual honey bee foraging score indicates a "hotter" spot on heat maps, and a better landscape assessment by honey bee waggle dances, as explained in the materials & methods section. Here we can see strongly significant relationships between residual honey bee foraging scores and both Apidae and non-Apidae abundance.

Figure 3.4. Social and solitary bee abundance plotted against residual honey bee foraging scores. In these graphs, black data points indicate sites from Blacksburg, orange data points indicate sites from Winchester, and blue data points indicate sites from Suffolk. A higher residual honey bee foraging score indicates a "hotter" spot on heat maps, or a better landscape assessment by honey bee waggle dances than what we would expect given the distance to the forage. Here we see strongly significant relationships between residual honey bee foraging scores and both social and solitary bee abundance.

Figure 3.5. Pie chart showing percentage of total catch by the four most abundant species, as compared to all others combined. *Melissodes bimaculatus* makes up a large proportion of total catch.

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Chapter 1: Introduction

The social sciences have a concept of bounded rationality (Wheeler, 2020). Boundedly rational actors don't always make optimal decisions, they are limited by their attention span, knowledge, time to dedicate to the decision, etc. (Wheeler, 2020). Instead of making optimal or perfect decisions, they *satisfice*, or make decisions which are agreeable to them given the knowledge they have. It explains why we go to the same coffee shop we have been for ages, even if another one may be having a sale, or a closer one may have opened up since we started our routine, for example. This can be applied to individuals or to groups, such as voters in a state or a beehive. This dissertation presents four chapters on boundedly rational actors.

Bees (Anthophila) are one of many taxa groups experiencing the contemporary global biodiversity decline (Jaureguiberry, Titeux, Wiemers, et al., 2022). Bees face both specific challenges like pesticides, pathogens, poor nutrition, and parasites (Goulson, Nicholls, Botias, & Rotheray, 2015), as well as more generalized threats such as climate change (Soroye, Newbold, & Kerr, 2020) and habitat loss (Naug, 2009). The resulting population decline is challenging to address due to this combination of drivers, and yet extremely important to address because of the free ecosystem services that bees provide (Klein, Boreux, Fornoff, Mupepele, & Pufal, 2018).

Modern agriculture, and thus society, is built on expansive monoculture fields (Crews, Carton, & Olsson, 2018). Many of these resulting crops incur a pollination debt which, in this country, is resolved by a yearly migration of over 90% of the hives of the United States to supply crops with pollination services (Stein, 2024). Pollination from these bees, of which tens of thousands can reside in one hive, is given freely. Within the past decade we have seen certain regions in the world reach a point where there are not enough pollinators to fulfill agricultural demand, resulting in farmers resorting to – and having to pay for – hand pollination, such as with vanilla in Madagascar (Wurz, Grass, & Tscharntke, 2021). As the human population grows, so does this problem, even before considering that many of the pesticides, pathogens, poor nutrition, or parasites can make bees more susceptible to yet another stressor decreasing its health.

At the same time, most bee species are solitary and not actively maintained for agricultural purposes (Danforth, Minckley, & Neff, 2019). They still pollinate our world and keep it green, and there are hundreds of species in each state. These bees are in a similar plight, and one that might be aggravated by the general public's attention on their hive dwelling sister species. Some literature suggests that honey bees can outcompete native bees for resources and transmit parasites and pathogens to the native bee community (Colla & MacIvor, 2017). While we know the broad strokes of what ails the bees, our knowledge is still woefully limited, and so when humans make decision on how to help them, we are boundedly rational.

Humans have worked with the honey bee for thousands of years (evidenced by cave paintings in Coves de l'Aranya), and have become quite familiar with them. As our forefathers studied the bees, they discovered a fascinating honey bee behavior called the waggle dance (von Frisch, 1967). This dance is used by one honey bee to communicate to another where a certain resource (water, nectar, etc.) is. It conveys both how far away the resource is, and what direction it is in (von Frisch, 1967). Remarkably, we have not only deciphered what this dance means, but we have learned how to interpret it for ourselves, and 'decode' where the bees are telling one another to go (von Frisch, 1967). We can consequently study the decision-making in honey bees, which in turn can better inform our conservation or agriculture initiatives, for example (Couvillon, Schürch, & Ratnieks, 2014a; Couvillon, Schürch, & Ratnieks, 2014b; Couvillon & Ratnieks, 2015).

In the second chapter, we explore bee decision-making in the face of human construction. The waggle dances of several hives over two years are recorded and decoded, and then mapped. This way, we see where the bees are going for food and other resources (Ohlinger, Couvillon, & Schürch, 2024). A few years later, large construction projects began where the bees would go for food. We record, decode, and map the waggle dances afterwards, to see how their behavior changes in light of this obstacle. This study highlights how boundedly rational actors—whether bees navigating changing landscapes (and having to satisfice their changing foraging behaviors) or humans reshaping them (without knowledge of the true cost of construction)—make decisions within the constraints of their environment and available information

In the third chapter, we set out to see if the honey bee waggle dance can be used as a proxy for landscape/floral quality, and predict where other bee communities might be more populous and diverse. If honey bees could tell us where the landscape is great for themselves and unmanaged bees, we could again make better policies to help them. We used maps created by previous researchers in Winchester, Suffolk, and Blacksburg, Virginia, who decoded waggle dances into a "heat map", showing where the honey bees preferred to go and which areas they avoided (Ohlinger, Couvillon, & Schürch, 2024; Silliman, Schürch, Malone, Taylor, & Couvillon, 2022; Steele, Schürch, Ohlinger, & Couvillon, 2022). We caught as many bees as we could in plots picked from these maps and measured the health (abundance, richness, and diversity) of each bee community. We could then relate the honey bee indication to the native bee community health. Currently, measuring bee community health metrics entails lengthy, often lethal sampling methods, the results of which come with a significant temporal delay due to curation and processing of specimen. Using the honey bee waggle dance as a bioindicator of bee community health may allow us to make more optimal decisions as researchers, farmers, and conservationists, reducing the need to satisfice.

In our fourth chapter, we begin our research in soybean fields. Soybean is a self-pollinating crop, so until the past decade or two, bees weren't seen as very important in soy agricultural systems (Erickson, 1975). Recently, we're discovering not only are there bees in soybean fields, but we can harvest more soybean with the help of pollinators (Gill & O'Neal, 2015). Concurrently, there is a growing movement to find more sustainable ways to farm (Dessart, Barreiro-Hurlé, & van Bavel, 2019). Foliar application of spray pesticides can leech into the ground (Pérez-Lucas, Vela, El Aatik, & Navarro, 2019), drift through the air (Maybank, Yoshida, & Grover, 1978) and impact both people and animals they are not intended to. The attract and kill control method we study, on the other hand, treats a net with pesticides, and then attaches a soybean pest lure to it (Benthall, 2023). These have shown to be effective against Japanese beetle in soybean and have the benefit of decreasing the amount of pesticide applied to the system (Benthall, 2023). We collected bees from soybean fields which either used attract and kill treatments or the grower standard spray pesticide treatments (Benthall, 2023), thereby investigating assumptions that alternative pest control methods are inherently beneficial for bees.

In our fifth chapter, we take a look at state-level bee statutes passed from January 2023 to August 2024. We wanted to see if there were spatial, economic, or partisan patterns in the bee legislation produced. We suspected that "bee policy" really contained unique policy subsystems hiding behind the same taxa group. For example, conservation and agricultural policies may both be colloquially referred to as "bee policy". We hypothesized that by analyzing statutes based on these variables (spatial, economic, and partisan), the constituent policy subsystems may be able to be distinguished. Here we see the effects of our bounded rationality manifest through legislation, group decision-making akin to aggregate waggle dances representing the decisions of thousands of bees in a hive.

We draw generalized conclusions in our sixth chapter. All in all, we posit throughout each chapter that humans try to make the best decisions we can for pollinators, but often suffer from a lack of good data to base those decisions on. The bees, by choosing to nest in more favorable environments or through the waggle dance, are able to communicate to us their decisions and preferences. While humans satisfice on behalf of the bees, our studies indicate that we may be able to rid ourselves of some guesswork, and let the bees choose what is best for themselves.

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Chapter 2: Concrete Consequences: Construction on Prime Honey Bee Habitat Doubles Foraging Distances

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Abstract

Human-induced land-use change is a well-documented driver of species decline, including bees, but its true cost may be underestimated. The effects of habitat conversion on honey bee foraging metabolic costs are not well documented. Here we quantify the impact of land use change on the foraging of freely flying honey bees (*Apis mellifera*) before (2018-2019) and after (2022) their historical foraging habitat is developed. We decoded and analyzed honey bee waggle dances, through which returning foragers communicate the vector of forage. We found that bees increased (from 2.4% to 8.4%) their use of undisturbed microhabitat within the development. These small-scale developments, covering just 1% of the foraging range, nearly doubled flight distance and energy expenditure. Average distance increased from 0.69 to 1.28 kilometers (from 7 to 13 Joules). Our study updates our understanding of land development costs on local bees, revealing concrete consequences to changing land upon which pollinators depend.

Summary Statement

Construction on 1% of honey bee foraging range nearly doubles foraging distance and energy expenditure, reveals waggle dance analysis.

Introduction

Habitat loss and degradation, largely caused or accelerated by human activities, is a pernicious driver in the decline of the abundance and diversity of species, a loss so severe that it has been labelled the "Sixth Great Mass Extinction" [1]. Affected taxa groups include insects, and bees in particular [2, 3, 4], which is alarming because they provide ecosystem services in natural and agricultural settings [5]. Although previous investigations have established strong correlations between land use changes and bee declines [2-4], these studies may be underestimating the overall cost. For example, little is known about the real-time effect of land use changes on bee community energy expenditure, if they now must forage within developed areas.

Honey bees (*Apis mellifera*) are a tractable study organism that forage at long distances [6, 7] and, importantly, exhibit the waggle dance, a unique behavior where a returning forager communicates the distance and direction to a good resource [6], usually nectar or pollen. Because we can observe and analyze these communications in aggregate to determine where the landscape is good for forage, honey bees may serve as bioindicators of habitat quality for themselves and other bees [8].

Here we decoded from video, mapped, and analyzed [8-10] honey bee waggle dances from nine observation hives in Blacksburg, Virginia, to investigate natural foraging over a mixed-use landscape that experienced land conversion: these dances occurred before (August, 2018 and 2019, n = 382 dances) and after (August, 2022, n = 502 dances) the implementation of several large construction projects in November 2019 within the bees' foraging range [6, 7, 11]. We hypothesized a priori to our study that honey bees may have increased their average foraging distance due to this construction, when we observed the bare soil it was creating. In particular, the construction plowed and paved over areas previously indicated by dancing bees (2018-2019) as prime habitat [11] to create houses, neighborhoods with roads, a large church, and parking lots (developments: grey polygons, Figure 2.1A). The conversions retained some small, isolated patches of microhabitat (orange areas within grey polygons, Figure 2.1A). As previously done, we used flight distance, encoded by the waggle run duration, as a proxy for energy expenditure [8, 11].

Materials and Methods

Observation Hives

Using a methodology developed by our team [8-11], we recorded, decoded, and mapped the waggle dances of honey bee (*Apis mellifera* Linnaeus) colonies in August of 2018 and 2019 and again in August 2022. Three colonies were studied each year in 2018-19 (6 total) as part of another project [11, 15], and three more were studied in 2022. Importantly, sample size is number of waggle dances decoded (382 before construction & 502 after), not colony number. Further, the amount of between-bee variation is so high that any between-hive variation is negligible [9, 10, 21, 25, 26]. All colonies were housed in glass-walled observation hives in our bee lab, a building at Prices Fork Research Center, Blacksburg, Virginia, USA (37.21148º N, 80.48935º W). We installed plumb lines, which were used as a vertical reference for dance decoding, consisting of fishing line weighted at the bottom for vertical alignment. The plumb lines were hung 5 cm apart horizontally and extended vertically down the hive. Each observation hive consisted of three full depth frames, placed vertically on top of one another, with a PVC tube (5 x 30 cm) connecting the hive through the building wall to the outside entrance. This allowed honey bees to forage freely in the landscape. Distinctly colored shapes were painted on the exterior wall of the building near each hive tube to minimize bee drift to different hives.

Throughout the project, we practiced standard beekeeping to prevent swarming and to maintain a consistent population size across colonies.

Recording & Decoding Dances

For both the previous project, which provided the August 2018-2019 data, and again in August 2022, we video recorded waggle dances from all colonies simultaneously for one hour per day between 10:00-11:00am EST, 3–5 times a week (weather permitting) at 30 fps using a Canon Vixia HF R82. We focused our camera on an area of the bottom frame, approximately 25 cm by 20 cm, where most of the dances occurred [7]. We saved videos to SD cards and then uploaded to Google Team Drive (GTD) for dance decoding.

Dances from 2018-2019 were already decoded as part of another project [11, 15], with published waggle dance datasets [16]. We decoded August 2022 dances using a modified methodology developed by our team [10] and used in previously published studies [8, 11, 15, 17-19]. Briefly, we imported videos into ImageJ (version 1.52i). We determined the angle off-set at the start of each video and then played the video until we saw the first dancing bee, which usually occurred within a few minutes. We worked through the video by decoding cohorts of simultaneous dancers. To decrease the likelihood of resampling from the same dance, we skipped ahead six minutes in the video after each decoded cohort [8, 11, 17, 18]. For each dance, we extracted the waggle phase duration, which encodes the distance to the food, and the angle relative to vertical, which encodes the direction to the food [6, 10, 20]. This was done on a subset of four non-first, non-last waggle runs per dance, which has been shown to provide information consistent with averages from entire dances [10]. Then we averaged these four runs to obtain a single duration and angle per dance [9, 21]. As done previously, we treat each dance as an independent sample

[8, 11, 15, 17-19]. In all, we decoded 502 waggle dances from August 2022. The previously published dataset provided 382 dances from August 2018 and August 2019 [16].

Study Location and Time

Blacksburg is a mixed landscape, and within our honey bee foraging range [11], a circle with a radius of 3.25 kilometers, our study site prior to construction was comprised of croplands, developed lands, agricultural grasslands, and forests. A foraging radius of 3.25 kilometers was chosen because over 99% of waggle dances from 2018-2019 occurred within this zone [11]. Land development and construction, notably a large church, parking lots, several neighborhoods with roads, and houses, began in November 2019 and was mostly completed by November 2022. We obtained satellite imagery from June and October of 2022, which were the nearest temporally to our video recording in August 2022. Using ArcGIS, we outlined developed land within a 3.25 kilometers radius of our observation hives (grey polygons, Figure 2.1A) in an area which totaled 0.93 km^2. We then created further shapes within these grey polygons to represent the remaining patches of vegetation (orange within grey, Figure 2.1A). These patches totaled 0.14 km^2. Only one year of post-construction data was analyzed because construction was underway in 2022, and the following year cleared flora may have regrown if it wasn't paved over. August of 2022 proved to be middling in terms of weather as compared to 2018 and 2019. August of 2022 had 675 degree growing days (base 50) as compared to 2018' 657 and 2019's 681, an average temperature of 22ºC compared to 2018's 21.61ºC and 2019's 22.11ºC, and accrued 16.79 cm of rain compared to 2018's 14.35 cm and 2019's 7.24 cm [27].

Statistical Analyses

Because waggle dances are inherently imprecise, we plot advertised foraging locations as probability distributions that reflect our uncertainty about the communicated locations [8-11, 15, 17-19, 21, 22] using Monte Carlo sampling from the universal calibration dataset that performs well across different landscapes and experimental contexts [9, 23]. We simulated the angular component of the dance by sampling from a von Mises distribution with a concentration parameter (κ) of 24.5, which is a circular analogue to a normal distribution [9]. Each averaged dance, consisting of the four decoded waggle phases, was then simulated 1000 times. All statistical analysis was conducted in R version 4.4.0 [24]. Significance was tested for using a linear mixed effect model.

AI (Chat GPT) was used in the creation of the manuscript for this chapter, suggesting synonyms and alternate phrases for original writing.[1]

Results

We found that honey bees foraging in the post-developed landscape experienced a dramatic and significant increase in foraging distance before (average waggle run duration = 0.9 seconds (0.7 seconds to 1.1 seconds) versus after = 1.6 seconds (1.4 seconds to 1.7 seconds) land conversion, with a mean difference: 0.6 seconds (0.4 seconds to 9 seconds); likelihood ratio test: $\chi^2 = 11.007$; $p < 0.001$; Figure 2.1B). As duration of the waggle run (the component of the waggle dance which encodes distance to indicated resource) linearly translates to distance, this corresponds [9] to an increase in communicated distance from approximately 0.69 km to 1.28 km. In other words, honey bees needed to fly twice as far to collect food in 2022 compared to 2018-2019.

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[1] The academic journal this chapter was submitted to for publication requires an AI generated content declaration in the methods section, and as this chapter is presented in the format in which it was submitted, we include this declaration and contextualize why it appears in the dissertation.

When we mapped the dances, we saw two interesting and interconnected shifts. In 2018-2019, the August bees largely advertised to two nearby, highly profitable, conjoined clusters (blue overlaid dances, Figure 2.1C), with the first cluster surrounding the hives, and the second, more diffuse, cluster approximately 500 m to the east and southeast in agricultural grasslands [11]. After development, the land under the second foraging cluster to the east/southeast was converted almost completely to a large church, its parking lots, and some housing developments. The resulting bare soil removed the opportunity for the bees to forage there. The bees correspondingly shifted their resource exploitation towards the back of the housing developments, about 1km away from the hive (red overlaid dances, Figure 2.1C). Particularly, the bees significantly increased their exploitation of what little small patches of habitat remained amid the cleared land: recruitment to orange areas within grey polygons increased by 3.5-fold (2018-2019 = 2.4% (1.0% to 3.9%); 2022 = 8.4% (6.2% to 10.8%); mean difference: 6.0% (3.2% to 8.8%)). Considering how small these patches are in relation to their overall foraging range, 8.4% represents an intense usage, most likely because other options were now limited. We can estimate from published calculations that the doubling corresponds to an increased individual forager energy demand from 7.0 Joules to 13.0 Joules [12].

Discussion

The cost of the observed foraging pattern shifts was a primary driver of the doubled flight distance (Figure 2.1B). While the near doubling of energetic costs is impressive singly, scaling to colony-level underscores the impact's extent. Approximately 1/3 of the tens of thousands of workers are, at any point in the day, foraging [7]. These bees will now be unable to complete as many trips and will experience diminished returns from successful trips, as more energy is consumed en-route, all of which negatively impacts the colony's winter food stores and, ultimately, its fitness [7].

In our study, the land developments (grey polygons), accounting for <1% of the honey bee foraging range, generated a considerable impact on food-collecting behaviors, nearly doubling their average foraging distance by shifting and consolidating their preferred sites to the remaining, undisturbed patches within the larger developments. It is important to remember that honey bees might actually be more resilient than other bees to land use changes because they are eusocial, capable of long-distance foraging, and utilize waggle dances [2, 6]. Therefore, they can scout, discover, and recruit over large areas, allowing them to exploit remaining patches of undisturbed microhabitat, as we have seen here. Other bees from solitary nests that may only forage within tens or maximally hundreds of meters [13], or bees that depend on localized habitat for both food and housing, might experience more severe impacts. Additionally, the land conversion was only 0.9 km^2 in total area, but it nevertheless exerted an influence on bees housed half a kilometer away. One might predict a buffer of neglect, with diminished ecosystem services on and around developments. As habitat loss can lead to biodiversity loss, which cyclically feeds back to more habitat loss [14], we can additionally anticipate synergistic and cascading consequences of land development up the trophic pyramid and throughout the ecosystem.

Next Steps

We do not measure the size of, or the foraging percentage contained within the observed clusters, because it necessitates arbitrary decisions on where exactly they begin or end. Instead, we offer hard data on increased waggle run duration as a proxy of foraging distance. Likewise, we cannot quantitatively measure any potential increased foraging "spillover effect" that remaining microhabitat may have created outside of their measured plots, because it would entail guesswork about how far away from microhabitat is appropriate to measure. Further studies may be able to develop appropriate methods for such questions, using mapped waggle dances in plots with controlled and measured plots of forage.

In the past, August in Blacksburg was a time when bees could forage relatively close on average, at 500m [15]. Post construction, they travelled 1000m. Other months were found to have longer waggle runs [15], which may suggest average distance to forage at these times may be less impacted by this construction.

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Competing Interests

No competing interests declared.

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Data Availability

All data and code will be published in a static dataset after final acceptance of the manuscript. The development version of WagglR, the R package used to map decoded waggle dance data, will be made available upon request.

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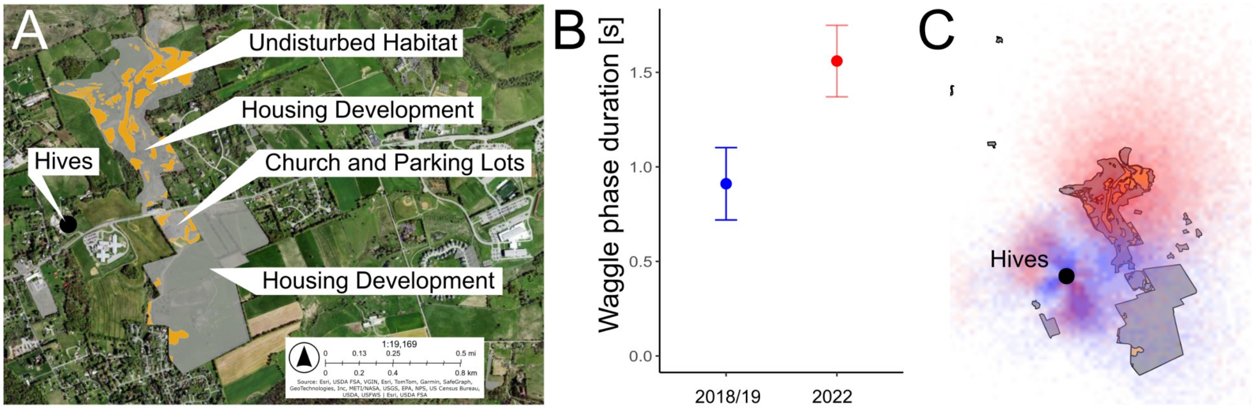
Figure Legends



Source: Esri, USDA FSA, VGIN, Esri, TomTom, Garmin, SafeGraph, GeoTechnologies, Inc, METI/NASA, USGS, EPA, NPS, US Census Bureau, USDA, USFWS | Esri, USDA FSA

Figure 2.1. Honey bees nearly double their foraging distance by shifting and consolidating their preferred sites to remaining, isolated habitat patches within the larger land use changes. (A) Aerial imagery in 2022 of the study area in Blacksburg, VA. Gray polygons represent all the lands converted in 2020-2021. Orange represents small patches of undisturbed microhabitat left within the developments. Black circle denotes the location of the hives. (B) Honey bees nearly double their communicated foraging distance in 2022 compared to 2018-2019. (C) Honey bee foraging, as determined by dance decoding before (2018-2019, blue) and after (2022, red) the land use change, demonstrated that the bees shifted recruitment to the more distant, remaining orange patches within the grey, especially in the northern corner of the new housing development.

Chapter 3: Honey bee foraging predicts native bee abundance, but not species diversity

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Key Words
Waggle dance, landscape ecology, biogeography, predictive abundance, population survey

Abstract

Human induced global change such as international trade ferrying invasive species from one continent to another, warming global temperatures, rapid urbanization and habitat loss are all implicated in the ongoing decline of insects. Wild bees, as a part of this overall insect decline, are of particular concern because they provide pollination services freely and, along with managed bees, underpin modern agriculture practices. The magnitude of these deleterious effects on bees is unknown, as research to quantify the wild populations involves long hours of fieldwork, conducting lethal capture surveys, and then lengthy curation of collected insects before specimens can be identified and data analyzed. This leads to delays in availability of survey data relative to the changes they are meant to study. It was previously suggested that honey bees, a managed pollinator, might serve as bioindicators for monitoring of overall bee habitat quality, and consequently, native bee community health. Here we validate this new method by estimating the relationship between honey bee indicated foraging habitat quality and native bee community health metrics. For this validation, we used decoded, simulated, and mapped honey bee waggle dances in three locations in Virginia, each with a different dominant land cover type, from an earlier study: Winchester (orchards), Blacksburg (mixed-use landscape), and Suffolk (row crops). These maps provided probabilities of honey bee foraging based on observed waggle dances. Because honey bees are economical foragers, we then corrected these probability maps for distance and cumulative elevation change from the hive and took the resulting residuals of the foraging probability as our measure for how honey bees

preferred or avoided foraging locations. We then sampled ten sites in each of the three locations, ranging from low to high honey bee foraging preference, using bee bowls, hand nets, and blue vane traps to measure native bee abundance, diversity, and species richness. We found a parabolic relationship between residual honey bee foraging and native bee abundance ($p < 0.001$), so that native bees are abundant both where honey bees do not forage, as well as where they heavily forage. Where honey bee foraging is intermediate, native bee abundance is lower. In an exploratory analysis, this parabolic significant predictor for abundance remained regardless of whether we stratified by family (Apidae and non-Apidae) or social behavior (social and solitary) of native bees. In contrast, the residual honey bee foraging probability was unrelated to diversity measures richness and Shannon diversity index. In summary, our results support the possibility of bees-as-bioindicators, where researchers may be able to estimate native bee abundance from honey bee waggle dances rather than from lethal capture surveys, which would generate novel and critical data to help inform policy and management decisions.

Introduction

Insects have experienced declines in the past decade (Hallmann et al., 2017), which includes bees (Zattara & Aizen, 2021). The introduction of non-native or invasive species, climate change, habitat degradation and loss, the use of emergent and current insecticides, the spread of pathogens and pests, and agricultural intensification all pose threats to existing insect communities and their critical plant-insect relationships. We can see evidence of bee declines in both wild (Cameron et al., 2011; Potts et al., 2010) and managed honey bees (Seitz et al., 2015). Additionally, although wild honey bee colonies are under-surveyed, the existing European surveys demonstrate that the populations are likewise struggling (Jaffé et al., 2010). The causes of the widespread bee decline are multifaceted and compounded (Goulson, Nicholls, Botías, & Rotheray, 2015; McMenamin & Genersch, 2015; Naug, 2009) and hence intractable.

An additional challenge is that the methods through which we assess the impact of stressors are often time-intensive, bottlenecking our speed and ability to identify potential solutions. For example, gold standard native bee population surveys involve trekking into the field and catching bees by hand, or setting out multiple passive collection traps, then curating and pinning specimens before identification (Olynyk, Westwood, & Koper, 2021; Ostrom & Grayson, 2021). Although meta-barcoding is emerging as a potential method to establish community composition from bulk samples, which reduces labor (Petsopoulos et al., 2024; Remmel et al., 2024; Strutzenberger et al., 2023), the results unfortunately are biased towards larger species (Remmel et al., 2024; Strutzenberger et al., 2023) and do not yet replace the gold standard.

Recently, it was suggested that we may use honey bees' waggle dances to study where the landscape can support pollinators (Couvillon et al., 2012; Couvillon & Ratnieks, 2015; Couvillon, Schürch, & Ratnieks, 2014a; Ohlinger, Schürch, Silliman, Steele, & Couvillon, 2022; Schürch et al., 2013; Silliman, Schürch, Malone, Taylor, & Couvillon, 2022; Steele, Schürch, Ohlinger, & Couvillon, 2022). In such studies, the honey bees, communicating via their waggle dances, act as a bioindicator of the foraging landscape quality, a potential coal-mine-canary to measure the impact of poor nutrition or pesticide exposure on native bees. Honey bees are central place foragers, which means that specialized worker bees, the foragers, leave the hive to collect resources and bring them back to the hive where the resources are stored or consumed (Robinson, Hoover, Pernal, Cartar, & Snell-Rood, 2022; Seeley, 1982). When honey bees find a high-quality resource (e.g., high sucrose nectar, pollen, water, or propolis), they perform a waggle dance that signals the direction and distance of that resource to other bees in the hive (Abbott & Dukas, 2009; von Frisch, 1967), which can crucially be decoded by researchers. Thus, we too can understand, at a landscape level, where the dancing bee is signaling as a high-quality forage location (Dyer, 2002; Schürch et al., 2013; Schürch et al., 2019; Steffan-Dewenter & Kuhn, 2003).

Honey bees are also generalist foragers (Waser, Chittka, Price, Williams, & Ollerton, 1996): they consume the pollen and nectar of a variety of plants, which change seasonally as they begin or finish blooming (Lau et al., 2019). Because honey bees are generalist pollinators, a positive assessment of the landscape through their waggle dances may indicate better floral resources in general, which in turn may indicate that advertised locations should be better for other flower-visiting insects as well. For example, an area that honey bees indicated as valuable foraging spot in the South of England was an area managed generally for pollinators, and butterflies in particular (Balfour, Fensome, Samuelson, & Ratnieks, 2015; Couvillon et al., 2014a).

Although waggle dance studies have now been used in a variety of settings to understand honey bee foraging ecology (Beekman & Ratnieks, 2000; Carr-Markell, Demler, Couvillon, Schürch, & Spivak, 2020; Couvillon, Schürch, & Ratnieks, 2014b; Samuelson, Schürch, & Leadbeater, 2021; Silliman et al., 2022; Sponsler, Matcham, Lin, Lanterman, & Johnson, 2017; Steele et al., 2022; Steffan-Dewenter & Kuhn, 2003), the basic tenet of the validity of bees-as-bioindicators for native bees has not yet been scientifically investigated. That is, currently, we do not know to what extent honey bees can also serve as bio-indicators for habitat quality of other insect pollinators, or for what species honey bee foraging may indicate good habitat overall.

Here, we validated the bioindication of dancing honey bees for native bees by sampling native bee populations in three locations in Virginia (Blacksburg, Winchester, and Suffolk), with 10 collecting sites for each of these locations, with hand nets, blue vane traps, and bee bowls to determine if their population health metrics align with honey bee landscape assessments, which were previously performed across the same locations (Ohlinger et al., 2022; Silliman et al., 2022; Steele et al., 2022). Using the waggle dance data, we created heat maps of indicated resource quality and then sampled sites ranging from high to low honey bee foraging preference. We analyzed the effect of honey bee landscape quality, as communicated by waggle dances, on native bee abundance, species richness, and diversity using the Shannon diversity index (Shannon, 1948). Furthermore, to account for the diversity of native bee life histories, we also conducted exploratory analyses to test if honey bee forage preferences better predict for bees like themselves (i.e., social Apidae species).

Materials and Methods

Study locations

The study was conducted at three locations in Virginia, United States. Our study location in Blacksburg, which is situated in the Appalachian mountains, was centered around the Prices Fork Research Center (PFRC, 37.21148, −80.48935), and the surrounding area consists of a mosaic of suburban, agricultural, forested, and unmanaged grasslands (Ohlinger, Couvillon, & Schürch, 2024). Our study location in Winchester, which is situated in the Shenandoah Valley, was centered around the Alson H. Smith Jr. Agricultural Research and Extension Center (AHS-AREC, 39.11349, −78.28449), and the surrounding area consists of fruit orchards, mostly apples, and forested areas, with sharp rock breaks throughout (Steele et al., 2022). Our study location in Suffolk, which is situated in the Coastal Plain or Tidewater region, was centered around the Tidewater Agricultural Research and Extension Center (TAREC, 36.66447, −76.73278), and the surrounding area consists in part by the Great Dismal Swamp and row crops, growing in sandy soil.

Creation of Honey Bee Foraging Maps and Calculation of Residual Foraging Probabilities

In spring 2018, we installed three observation hives at each of the three locations (PFRC, AHS-AREC, and TAREC). From each of the three hives, we video recorded naturally occurring waggle dances from freely flying bees for two entire foraging seasons (April – October, 2018 – 2019). Waggle dances were decoded from video and mapped as described in Silliman et al.

(2022), Steele et al. (2022), and Ohlinger et al. (2024). We chose the full two years as the basis of our maps, as the abundance or diversity might reflect the integrated forage availability as well. In all, the team decoded 11,050 dances (PFRC = 3881, AHS-AREC = 3710; TAREC = 3459), which were analyzed and mapped (Ohlinger et al., 2024; Ohlinger et al., 2022; Silliman et al., 2022; Steele et al., 2022).This composite dataset forms the foundation from which we built our testable hypotheses.

Honey bees are very sensitive to the energetics of their foraging trips (Schmid-Hempel, 1987), and to understand where bees indicate good habitat, we implemented a distance correction, as was previously done (Ohlinger et al., 2024; Silliman et al., 2022; Steele et al., 2022). Additionally, and new with this study, because two of our field sites were nested in the Appalachian mountains with hilly terrain, we also included a correction for changes in elevation. We selected elevation data of 1/3 arc resolution (approx. 10 m) using the National Map tool (v 2.0) at https://apps.nationalmap.gov/downloader/#/ on October 4, 2024. We bulk downloaded the GeoTIFFs using the resulting input file (data.txt; see code online) provided by the National Map tool with the following command: `wget -i ./data.txt -P ./`. We then re-projected and re-sampled these raw elevation files in R to match the extent and the resolution of our raw foraging probability maps from previous work (Ohlinger et al., 2024; Silliman et al., 2022; Steele et al., 2022).

We then calculated, from hive locations to all grid squares, the elevation profiles that a bee would need to fly if she foraged on that grid square (see code for implementation details). We are assuming that bees fly to and from the food source in a straight line, as they typically do to a familiar foraging location, which is the circumstance that usually generates a waggle dance, and thus considered the absolute changes in elevation. To finally arrive at the residual foraging, we built a mixed-model with the logit of the probability of foraging as the response, and the distance to grid square and the cumulative elevation as predictors. Zero and one foraging probabilities were assigned 0.00001 and 0.99999, respectively, to avoid negative and positive infinity values because of our logit-transform. We allowed for individual study location intercepts in the model. We then extracted DHARMa residuals (Hartig, 2022) from the resulting model to arrive at a foraging map that shows both distance and cumulative elevation corrected foraging probability.

Native Bee Sampling Site Selection at Each Location

Sampling sites for native bee surveys were a function of convenience (land owner permission, road access) and forage quality as indicated by honey bees. We chose 10 native bee sampling sites within each of the three locations of Blacksburg, Winchester and Suffolk, ranging from high to low foraging probability as indicated by the honey bees (Figure 3.1; Ohlinger et al. 2024; Silliman et al 2022; Steele et al 2022). In 2020, when we were selecting our survey sites at each location, we used earlier versions of the foraging maps that only contained a distance correction, as we had not yet recognized the importance of elevation. At each location, we chose sites that were at least 100 m apart from one another to avoid site interference.

Specimen Collection and Processing

We collected insects using hand nets, BioQuip blue vane traps, and three store brand plastic bowls (bee bowl traps) at each of the ten sites within the three locations. Sampling dates were determined by weather and site accessibility. Each collection method (hand netting, blue vane trap, yellow, blue, and white bee bowl traps) in each of the ten sites was sampled twice a month, across each of the three locations (PFRC, AHS-AREC, and TAREC). Sampling occurred in June and July of 2021 and in June, July, and August of 2022. We hand netted at each location for 30 minutes. Blue vane traps were acquired clear and painted fluorescent yellow. Blue, white, and red bowls were acquired, of which the red bowls were primed with white and then painted fluorescent yellow. One of each color (blue, white, and yellow) were deployed at each location. Blue vane traps and bowl traps had a label for the date, location, collection method, and collector inside each trap written in pencil to ensure the specimens were able to be cataloged afterwards. Bowl traps were prepared with water, one information label, and dish soap to break water tension. They were serviced after being out one day. Blue vane traps were prepared with an information label, water, and dish soap, and were likewise serviced after one day. We recorded all information (trap type, site, date, and location) for each catch.

After specimen collection, we sorted out the by-catch of non-bee species from bees. We placed bees from each collection instance in an ethanol vial with the collection label to be processed. In processing, we washed and dried bees according to the Very Handy Bee Manual (https://bee-health.extension.org/wp-content/uploads/2019/08/TheVeryHandyBeeManual.pdf). We pinned, labelled with metadata, and morpho-sorted the bees. We transported the specimens to Sam Droege at the Patuxent Wildlife Research Center for species identification using the Discoverlife database (https://www.discoverlife.org/).

For our exploratory analyses, bee catch identified to species was tagged as either social or solitary. Each species was further tagged by taxonomic group to family level. Namely, abundance data for bees in Apidae (the family of *Apis mellifera*) were analyzed separately from and compared to non-Apidae bees (see below).

Data analysis

To characterize the bee communities at each of the three locations, we calculated total abundance over all sampling events. We then ranked the species ordered by abundance, and we present the top five most abundant species.

From the bee survey data, we calculated total abundance of all bees (primary response variable), the abundance of non-*Apis* and *Apis* species (secondary response variables), and the abundance of non-social (solitary) and social species (secondary response variables) per sampling date and site. For our measures of diversity, we also calculated species richness and Shannon diversity index (Shannon, 1948) calculated using the vegan package; (Jari Oksanen, 2024) for each site and sample date. All abundance outcomes were analyzed using a generalized linear mixed effect model (glmm) of the Poisson family. Richness was analyzed using a Poisson glmm. Shannon diversity index was assumed to be normally distributed, and we used a linear mixed effect model with Normal error to model this outcome. Our fixed effect predictor of interest for our three outcomes was landscape quality as indicated by waggle dancing honey bees. In other words, the predictor was the calculated residual foraging probability (i.e., foraging probability corrected for distance and cumulative elevation) for each site within each location. Because visual inspection of the data set suggested a parabolic relationship, we added the term both as linear and as quadratic. Our random effects were the year, study location (Blacksburg, Winchester, Suffolk), and sample. All mixed-effect models were run using the lme4 package (Douglas Bates, 2015).

We used likelihood ratio tests with two-sided α = 0.05 to test for significance of our main predictor (honey bee foraging probability). We extracted point estimates and confidence intervals using the emmeans package (Russell V. Lenth, 2024). All analyses were conducted in R version 4.3.1 (R Core Team, 2023).

Data Records/Management

Initially, we entered all data into Excel, and all files were stored and backed up from google drive. When we began this analysis, these data were moved to VT’s git repository (http://code.vt.edu) where it was version controlled along with our code, figures, and manuscript drafts. After completion of the project, data will be published on VT's data repository as per the stipulations of the FFAR grant.

Results

Native Bee Community Composition in Blacksburg, Winchester, and Suffolk

We collected 373 bees in Blacksburg (PFRC), 620 bees in Winchester (AHS-AREC), and 960 bees in Suffolk (TAREC; Table 3.1). Each study location in Virginia contained a unique, differently distributed community of bee species. In Blacksburg, the two most abundant bees were two generalist, social Apidae species *Apis mellifera* (n = 82) and *Bombus impatiens* (n = 78). There was then a marked drop in abundance for the next three most common species *Melissodes bimaculatus* (n = 27), *Halictus ligatus/poeyi* (n = 22), and *Ceratina calcarata* (n = 20). In Winchester, we found a more even distribution among the top five species, with *Ceratina* *calcarata* (n = 100), *Augochlora pura* (n = 53), *Halictus ligatus/poeyi* (n = 52), *Agapostemon virescens* (n = 51), and *Melissodes bimaculatus* (n = 50). In Suffolk, the bee community was heavily biased towards *Melissodes bimaculatus* (n = 435). *Lasioglossum bruneri* (n = 185), *Bombus impatiens* (n = 65), *Lasioglossum oblongum* (n = 52), and *Lasioglossum weemsi* (n = 41) made up the remaining four of the five most common bees there.

Table 3.1 Total bees caught by location, followed by the top five most abundant species, and the quantity of each caught.

Location	**PFRC = 373 bees**	**AHS-AREC = 620 bees**	**TAREC = 960 bees**
Top five most abundant species per location	*Apis mellifera*, n = 82	*Ceratina calcarata*, n = 100	*Melissodes bimaculatus*, n = 435
	Bombus impatiens, n = 78	*Augochlora pura*, n = 53	*Lasioglossum bruneri*, n = 185
	Melissodes bimaculatus, n = 27	*Halictus ligatus/poeyi*, n = 52	*Bombus impatiens*, n = 65
	Halictus ligatus/poeyi, n = 22	*Agapostemon virescens*, n = 51	*Lasioglossum oblongum*, n = 52
	Ceratina calcarata, n = 20	*Melissodes bimaculatus*, n = 50	*Lasioglossum weemsi*, n = 41

Native bee abundance in relation to honey bee foraging

We found that honey bee waggle dances significantly predict native bee abundance (log-likelihood ratio test: $\chi^2 = 42.242$; $p < 0.001$). This relationship is parabolic, with high native bee abundance when honey bee residual foraging score is both low and high (Figure 3.2). When honey bee residual foraging score is intermediate, native bee abundance is depressed. Accordingly, the marginal mean counts for residual foraging of 0 are 7.03 bees (3.55 to 13.93), for residual foraging of 0.5 are 4.42 bees (2.24 to 8.71), and for residual foraging of 1 we see 7.40 bees (3.74 to 14.63).

Additionally, we found that honey bee waggle dances significantly predict for both non-Apidae (log-likelihood ratio test: 7.6537; $p = 0.006$) and Apidae (log-likelihood ratio test: 37.155; $p < 0.001$) abundance (Figure 3.3). Both relationships are parabolic as well. For non-Apidae bees, the abundance for intermediate residuals (i.e., residuals around 0.5) decreases from both low and high residuals, but low residuals have a much smaller abundance increase than when analyzing our catch overall. At honey bee foraging residuals of 0, we see 1.5 non-Apidae bees (0.578 to 3.88), at a residual of 0.5, we see 1.4 non-Apidae bees (0.545 to 3.58), and at a residual of 1.0, we see 2.64 non-Apidae bees (1.026 to 6.78, SE: 1.271). In other words, for non-Apidae bees, the parabola seems more centered towards the 0 residuals, and then increases from there. For bees in the Apidae family, a more familiar horseshoe shape returns, where at a residual of 0.0, we see 4.65 bees (2.43 to 8.91, SE: 1.542), at a residual of 0.5 we see 2.41 bees (1.27 to 4.59, SE: 0.791), and at a residual of 1.0 we see 4.18 bees (2.19 to 7.99, SE: 1.381).

When we analyze our data by whether a species is social or solitary, we see similar results. Social bees (log-likelihood ratio test: 8.2426; p = 0.004) still have a non-linear, parabolic, relationship (Figure 3.4). Once more, the parabola seems centered closer to 0 residual honey bee foraging. At a residual of 0.0, we see 1.63 bees (0.837 to 3.18), at a residual of 0.5 we see 1.82 bees (0.950 to 3.48), and at a residual of 1.0 we see 3.87 bees (2.015 to 7.42). Solitary bees follow the parabolic pattern (log-likelihood ratio test: 26.596; p < 0.001), with the parabola minimum centered at intermediate honey bee foraging residuals. At a residual of 0.0 we see 4.24 bees (1.842 to 9.76), at a residual of 0.5 we see 1.89 bees (0.825 to 4.33), and at a residual of 1.0 we see 2.67 bees (1.156 to 6.15).

Native bee diversity in relation to honey bee foraging

In contrast to bee abundance, honey bee waggle dances do not predict diversity of native bee communities, neither for species richness (log-likelihood ratio test: 1.74; p = 0.187), nor Shannon diversity index (log-likelihood ratio test: 1.13; p = 0.287). In the case of Shannon diversity index, a linear fit is actually more descriptive of the data (p = 0.252 as opposed to 0.287), yet both are far from significant relationships. These results are visualized in Figure 3.1.

Discussion

Here we used honey bee foraging preference maps, created from decoded honey bee waggle dances from earlier studies (Ohlinger et al., 2024; Ohlinger et al., 2022; Silliman et al., 2022; Steele et al., 2022), to validate honey bee waggle dances as bio-indicators for native bee community health in three representative landscapes in Virginia, United States. In accordance with the differences in the dominant land type for these three locations, we found differences in the species composition of the bee communities. Crucially, we found that honey bees significantly predict native bee abundance in a parabolic relationship. This significance was maintained throughout exploratory analyses, where we found the parabolic relationship for both Apidae and non-Apidae, as well as social and solitary species. In contrast to these clear relationships, we did not find a relationship between honey bee foraging preferences and native bee diversity / species richness.

The relationship between honey bee foraging and native bee abundance potentially describes a situation where, at high honey bee foraging scores, indicating that honey bees preferentially forage in that area, the landscape is at very high-quality and supportive of both foraging honey bees and native bee abundance. At low honey bee foraging scores, indicating that honey bees rarely forage in that area, there is also high native bee abundance. Although we do not know why this might be, one could speculate that a landscape dominated by just a few plant species, which might be beneficial to some native bees that crucially depend on them, would lead to high native bee abundance but general neglect by generalist foraging honey bees, who do not find sufficient breadth or diversity of plants for the area to show up as a foraging hot spot, especially across the long foraging season experienced by honey bees. One might also speculate, given the documented negative relationship between honey bees and native bees (Angelella, McCullough, & O'Rourke, 2021; MacInnis, Normandin, & Ziter, 2023), that a landscape devoid, for whatever reason, of foraging honey bees might over time have the opportunity to develop a native bee population. In the middle range of the parabola, where honey bees indicate an intermediate preference, we find the lowest abundance of native bees. Perhaps these areas possess just enough honey bees to deplete the intermediary amount of floral resources, such that no native bee populations might flourish.

We found the robust, parabolic, relationship between honey bee residual foraging probability and native bee abundance to be surprising and contrary to our *a priori* expectations: we originally hypothesized that native bee abundance would increase with increasing honey bee foraging scores. As honey bees are generalist foragers (Biesmeijer & Slaa, 2006), we predicted good pollinator habitat with high native bee abundance where the honey bees indicate good forage. This was clearly not the case, or was not the complete story, as native bees were also abundant in places where honey bees indicated poor foraging. Our exploratory analysis shows that the parabola may largely be driven by the solitary and Apidae bees, as these subgroups showed high foraging in areas where honey bee foraging was low and high foraging where the honey bee foraging was high. On the other hand, the social and non-Apidae bees had the predicted minima largely centered towards the lower end of honey bee foraging preferences, suggesting that for these groups, we indeed have a monotonous increase of abundance with honey bee foraging preferences, as we predicted.

It should be stressed here, though, that the direct competition between native bees and our foraging honey bees was not relevant because we deployed honey bees at each location in 2018 – 2019, whereas the native bee surveys took place 2021 – 2022. Of course, there might still be indirect competition, where the presence / absence of honey bees in the earlier years might impact the native bee communities in ways that persist for several years. Additionally, it is not likely that honey bees from other hives (i.e., not our observation hives) played a role in our landscapes, as there were few honey bees in our catch, with Blacksburg, where the university maintains large, permanent apiaries, as the exception (Table 3.1). This indicates that, especially at Winchester and Suffolk, our locations did not possess a strong honey bee presence during our native bee sampling years.

Our data demonstrate a monotonous increase in native bee abundance for non-Apidae native bees across honey bee foraging. This means that waggle dance maps may be used to predict native, non-Apidae, bee abundance. More broadly, when we additionally consider the parabolic relationships, our data support the idea that where the landscape is good for honey bees, we can expect a high abundance of native bees. In other words, the positive predictive value of waggle dance maps is high.

Our study data set possesses some limitations. For example, although we collected data from three landscape types, our study area was limited to the state of Virginia, United States. Furthermore, our data are largely made up of just a few species (Figure 3.5). Accordingly, our finding that honey bee residual foraging scores are predictive for abundance of native bees must be viewed in that light, and follow-up studies should replicate these results, especially in new locations, before these methods are broadly used as a bio-indicator in new environments.

Future studies may be able to collect additional data to make honey bee bioindication even more robust. Here, we did not collect location-level floral diversity. Pesticide use and spray schedules were also not recorded for our locations, which may have influenced collection in and around our agricultural field sites. Lastly, although the sampling of native bees occurred only a few years after our honey bees surveyed and danced in our locations, the length of time in which these bio-indicated maps remain predictive is unknown.

Importantly, though, our results presented here are robust and were upheld as we dissected our capture by family and social organization. This is one of the first predictive tools to reveal where native bee populations are, in stark contrast to the fieldwork required to reveal the same information. Honey bees can continuously survey areas of up to 100 km^2 (Couvillon et al., 2014a), something that is impossible to achieve with traditional transects and surveys. This is particularly important, as recent progress has been made to decode waggle dances automatically from video (Wario, Wild, Rojas, & Landgraf, 2017; Okubo et al., 2019). Currently, the greatest barrier to using dancing honey bees as bioindicators is the manual labor required for dance decoding, which is needed to create the maps of residual foraging probabilities. If that process were automated, it would decrease the temporal mismatch between honey bee foraging data and native bee surveys.

Additionally, using honey bees as native bee bioindicators might relieve our current reliance on native bee lethal sampling, which is debated amongst bee scholars (Gezon et al., 2015; Portman, Bruninga-Socolar, Cariveau, & Morrison, 2020). While dancing bees cannot completely replace lethal capture, as it won't tell you *what* species are in any given area, they may help to restrict its use for a subset of research that is interested in diversity

In short, the data and analyses presented here are extremely encouraging and indicate that the honey bee waggle dances may be used as bio-indicators for native bee abundance. What is not known is how sensitive this predictor is to many of the common challenges of fieldwork, and whether it is more powerful for predicting the habits of certain bees over others. Overall, this study represents an important step forward in our understanding of the complex, multi-species interactions that characterize a landscape. More importantly, these data may help create a tool, where dancing bees bio-indicate a landscape for native bee abundance, to inform future conservation policies.

Figures

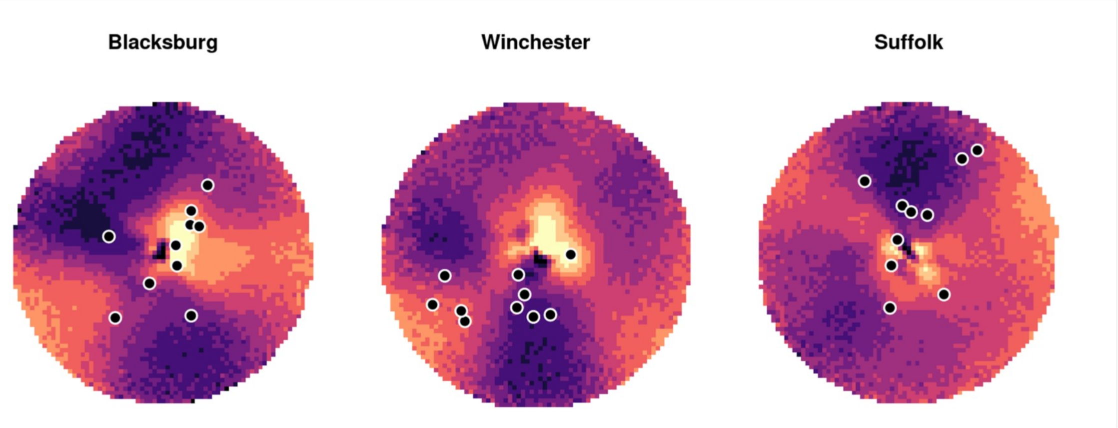

Figure 3.1. Native bee survey site placement (n = 10) at each of the three locations (Blacksburg, Winchester, and Suffolk), with distance and elevation corrected honey bee residual foraging score indicated underneath. Bright/warm colors indicate "hot spots" with higher quality forage, and dark/cool colors indicate "cold spots" with poorer quality forage, as determined from honey bee waggle dance decoding. Both hot spots and cold spots are areas that over or underperform expectations, given that we corrected for distance from the hive and cumulative elevation changes in the flight path.

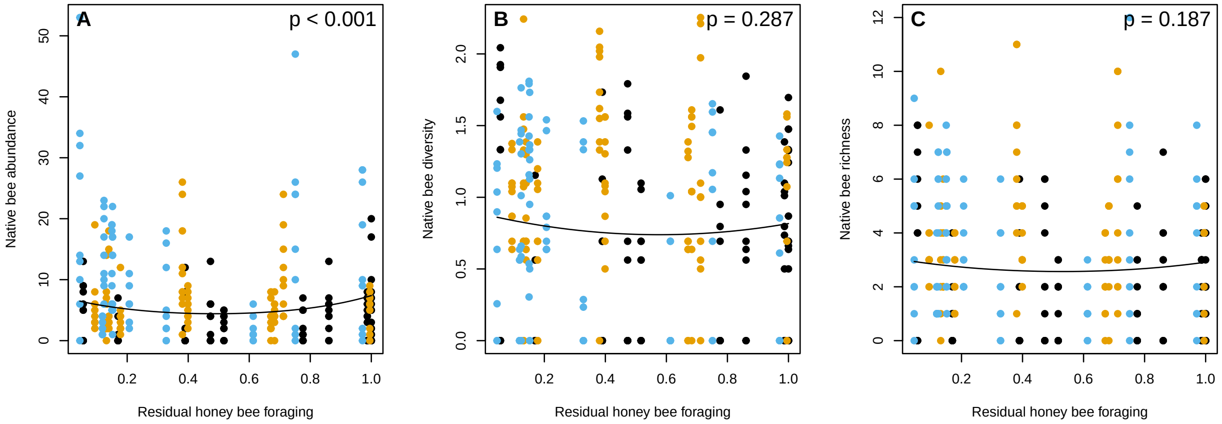

Figure 3.2. Native bee abundance, diversity, and richness measured against residual honey bee foraging scores. In these graphs, black data points indicate sites from Blacksburg, orange data points indicate sites from Winchester, and blue data points indicate sites from Suffolk. A higher residual honey bee foraging score indicates a “hotter” spot on heat maps, and a better landscape assessment by honey bee waggle dances, as explained in materials & methods section. We see a strongly significant quadratic relationship between residual honey bee foraging score and native bee abundance, but no significant relationship for native bee diversity or species richness.

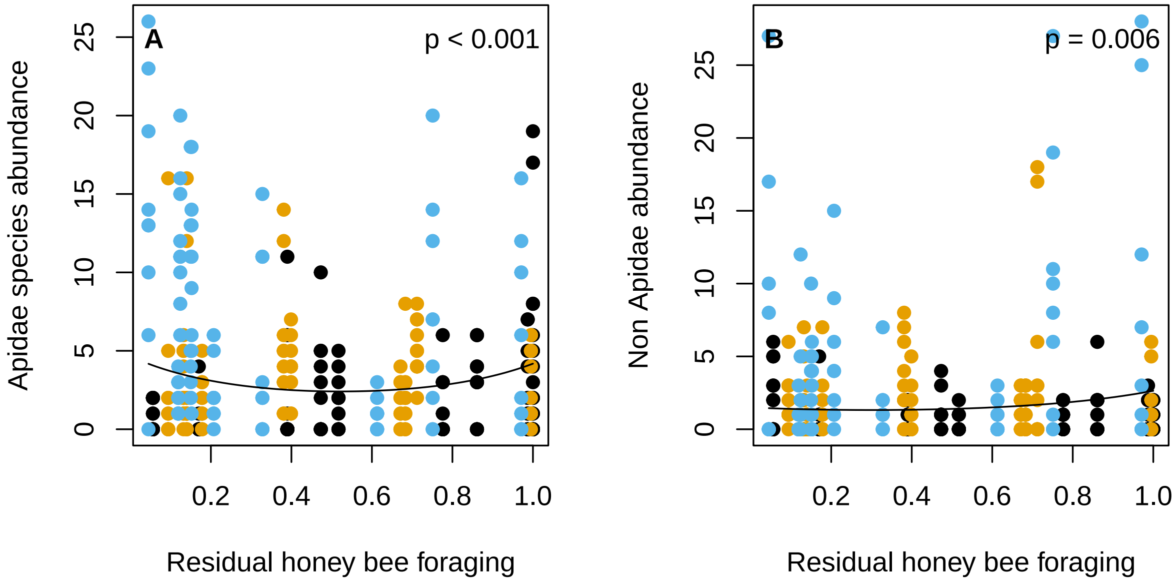

Figure 3.3. Apidae and non-Apidae abundance plotted against residual honey bee foraging scores. In these graphs, black data points indicate sites from Blacksburg, orange data points indicate sites from Winchester, and blue data points indicate sites from Suffolk. A higher residual honey bee foraging score indicates a “hotter” spot on heat maps, and a better landscape assessment by honey bee waggle dances, as explained in the materials & methods section. Here we can see strongly significant relationships between residual honey bee foraging scores and both Apidae and non-Apidae abundance.

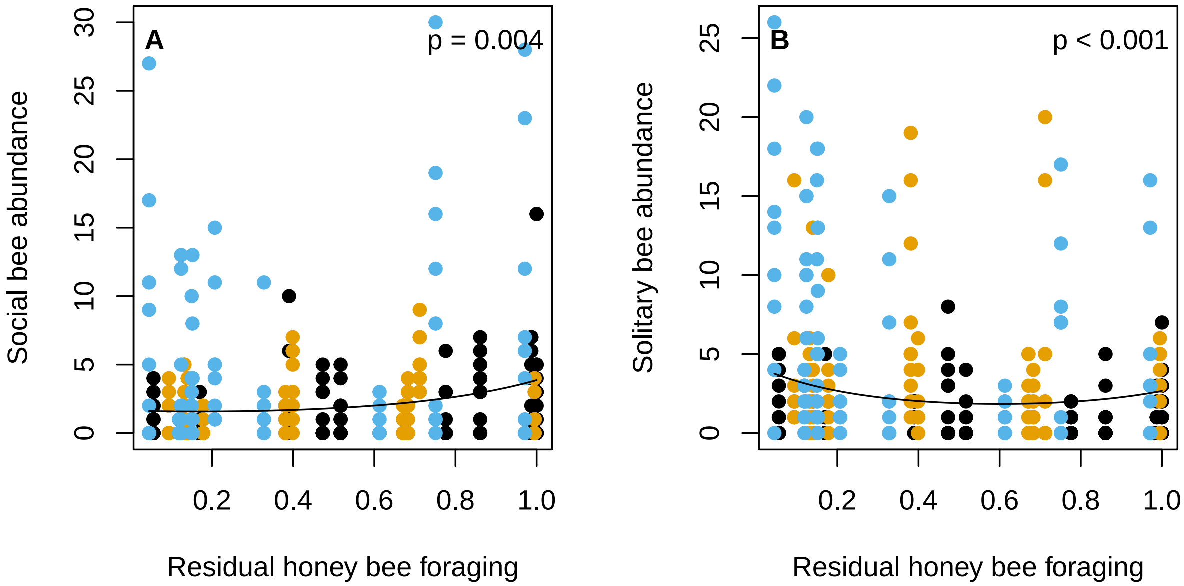

Figure 3.4. Social and solitary bee abundance plotted against residual honey bee foraging scores. In these graphs, black data points indicate sites from Blacksburg, orange data points indicate sites from Winchester, and blue data points indicate sites from Suffolk. A higher residual honey bee foraging score indicates a "hotter" spot on heat maps, or a better landscape assessment by honey bee waggle dances than what we would expect given the distance to the forage. Here we see strongly significant relationships between residual honey bee foraging scores and both social and solitary bee abundance.

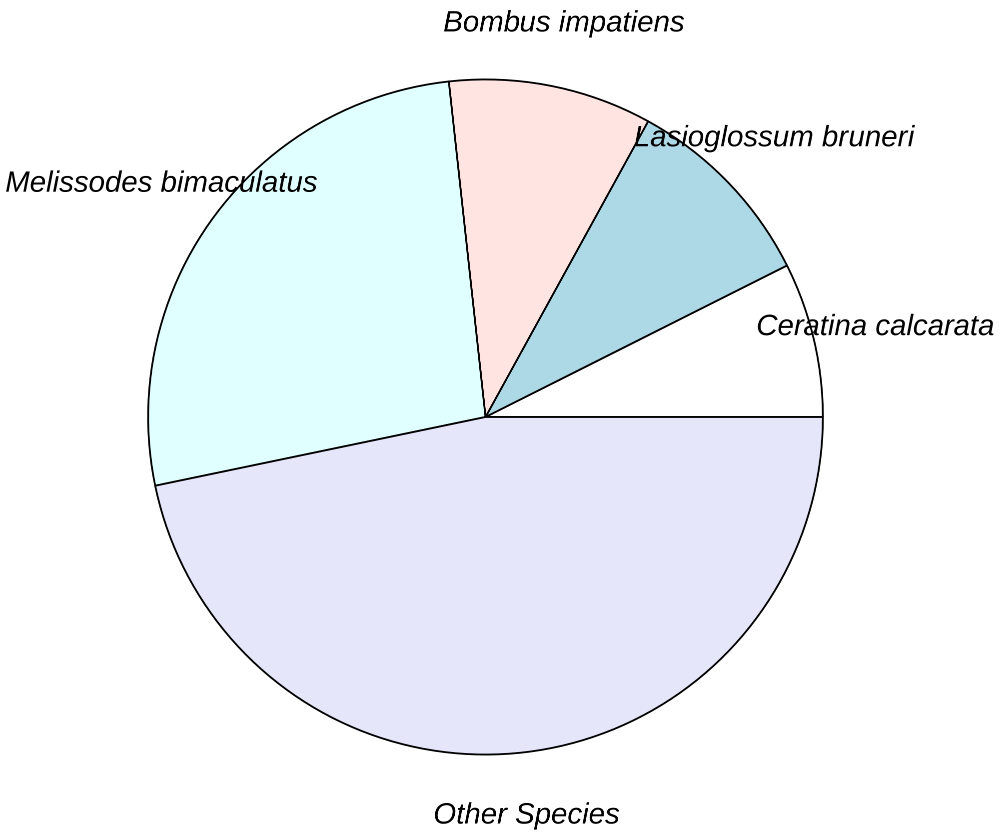

Figure 3.5. Pie chart showing percentage of total catch by the four most abundant species, as compared to all others combined. *Melissodes bimaculatus* makes up a large proportion of total catch.

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Chapter 4: Attract-And-Kill Treatment Reduces Abundance of the Most Common Bee in Soybean

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Abstract

Insecticides are used to manage insect pest species in agricultural systems, including soybean, and often produce lethal and sublethal nontarget effects on the beneficial insects, including natural enemies and pollinators. Soybeans are self-pollinating, yet recent studies have shown bee communities improve yield, and bees visit soybean while it is in bloom. Here we measured bee health metrics (abundance, species richness, and Shannon diversity index) in soybean plots in Columbia, Missouri, in 2019 and 2020 that were treated with either grower standard foliar application pyrethroid spray insecticide or attract-and-kill pheromonal lures on insecticidal nets. We first tested if these treatments and insecticide application periods (before, during, and after applications, each staggered one week to account for spray interval) interacted. There was no interaction between the two (likelihood-ratio test: $\chi^2 = 2.23$, $p = 0.33$). We then simplified the model to only include application period as an additive term and tested if there was a treatment effect on our bee health metrics. We first saw a significant decrease in overall bee abundance in attract-and-kill plots compared to grower standard across all application periods (attract-and-kill = 11.7 (6.44 to 21.4), grower standard: 13.8 (7.61 to 25.2); ratio: 0.85 (0.76 to 0.94); $p < 0.002$). Exploratory analyses of the most common species revealed that of the top five most abundant species, only *Melissodes bimaculatus* experienced a decrease of abundance in attract-and-kill settings compared to grower standard. When excluding this species from the rest of the capture, the significant difference in abundance between treatments disappeared (attract-and-kill: 10.9 (5.02 to 23.5); grower standard: 11.9 (5.48 to 25.7); ratio: 0.916 (0.79 to 1.06); p = 0.228). Additionally, we found no significant difference between the two treatments for richness (attract-and-kill: 8.6 (7.5 to 9.8); grower standard: 9.2 (8.0 to 10.5); ratio: 0.93 (.77 to 1.1); p = 0.470) or diversity (attract-and-kill: 0.10 (0.08 to 0.11); Grower Standard: 0.109 (0.09 to 0.13); treatment difference: -0.01 (-0.03 to 0.01); p = 0.326). Overall, our results suggest *Melissodes bimaculatus* alone drives the abundance decrease in attract-and-kill treatments and that diversity overall is not affected. *Melissodes bimaculatus* is one of the most prevalent species in soybean, and it is a ground nesting species. Thus, it may be disproportionately affected by attract-and-kill insecticidal nets as it moves from nest to crop. Our study underlines the importance of understanding plant-pollinator networks and shows that even alternatives to grower standard treatments possess drawbacks.

Keywords

Agricultural pest control, *Melissodes bimaculatus*, population survey, pyrethroids, Two-spotted Longhorn bee

Introduction

Agricultural pests are a major challenge for farmers: estimated arthropod crop damage worldwide has been valued at $470 billion (Smirti, Rubaljot, & Ramesh, 2017). In soybean, pest pressure, which varies by region, may impact 11-20% of attainable production (Oerke, 2005). As invasive species are increasingly spread to new areas through international trade and global warming (Pyšek et al., 2010), growers are likewise experiencing rising pressure to control pests on their crops.

Insecticides are one common way for growers to protect agricultural crops from insect pests. The industry is globally ubiquitous and economically impactful, estimated to total over $53.7 billion in 2017 (Shattuck, 2021), an amount predicted to increase with human population growth and the arrival of new crop challenges. For example, insecticide usage in soybean (*Glycine max*) experienced a marked expansion from 2000-2010 to combat the spread of the soybean aphid in the Midwestern US (Coupe & Capel, 2015; Osteen & Fernandez-Cornejo, 2013). Interestingly, recent USDA records indicate that pesticide use on soybean remains at this heightened level (USDA, 2020a). In fact, approximately 49% of current US soybean farmers use multiple pesticides in their fields to diversify modes of action and manage pests more effectively (USDA, 2020b). However, insecticide usage is not without consequences, and increasingly, there are studies revealing they may have unintended, detrimental effects on bees (Gandara et al., 2024; Goulson, Nicholls, Botias, & Rotheray, 2015; Henry et al., 2012; R. M. Johnson, 2015; Rundlof et al., 2015; Sanchez-Bayo & Goka, 2016; Whitehorn, O'Connor, Wackers, & Goulson, 2012).

Many crops rely on pollination to set fruit and be fit for harvest and consumption (Aizen et al., 2019), and bees provide this crucial ecosystem service freely (Porto et al., 2020). Increased pollination can improve crop yield, quality, shelf life, and marketability of produce (Garibaldi et al., 2013; Klatt et al., 2014; Klein et al., 2007). Soybean is a self-pollinating crop (Erickson, 1975), so it was previously believed that insecticide treatments in soy would not impact bees. However, soybean can be a source of pollen and even nectar for bees (Gill & O'Neal, 2015), and soybean can support a thriving bee community that in turn may increase crop yield (de O. Milfont, Rocha, Lima, & Freitas, 2013; Erickson, 1975; Gill & O'Neal, 2015; Silliman, Schürch, Malone, Taylor, & Couvillon, 2022; Wheelock, Rey, & O'Neal, 2016)

Bees living and foraging on soybean may be exposed to residual traces of agrochemicals through several different methods, such as direct contact and dietary contamination (F. Sanchez-Bayo & Goka, 2014), and these exposures can cause both fatal and sublethal impacts (Benthall, 2023; Desneux, Decourtye, & Delpuech, 2007; Ingram, Augustin, Ellis, & Siegfried, 2015; Reed M. Johnson, Wen, Schuler, & Berenbaum, 2006). Attract-and-kill treatments, which lure a specific (pest) species to a specific area where they come in contact with insecticides, have been shown to improve abundance of nontarget organisms in other studies when compared to grower standard treatments (Benthall, 2023; Hafsi, Abbes, Harbi, Duyck, & Chermiti, 2015) and can be used to reduce the number of needed insecticide applications (Huang, Gut, & Grieshop, 2014; Morrison, Lee, Short, Khrimian, & Leskey, 2015; Rice, Short, & Leskey, 2017). This raises the question, is there a way to deploy alternative insecticide treatments, such as attract-and-kill, to protect crops while minimizing the exposure of bee populations in soybean?

Here we compare the non-target effects of an attract-and-kill strategy insecticidal nets used to manage Japanese beetle with grower standard foliar application pyrethroid spray insecticide (hereafter, grower standard or spray treatments). Previous studies suggest insecticidal nets baited with Japanese beetle pheromone lures provided equivalent protection from insect defoliators and seed predators as grower standard insecticide applications. Furthermore attract-and kill treatments had higher abundance of natural enemies (Benthal in press). We compared the non-target effects of this attract-and kill methods and grower standard insecticide applications on pollinator abundance from bee bowl captures (number of specimen), species richness (number of unique species caught), and the Shannon diversity index, which takes into account species richness and their proportionality (Shannon, 1948). We measure abundance of capture before, during, and after spray pesticide application, to see if there is an interaction between application period and treatment. Additionally, we further evaluated the five most common bee species captured, in particular the most abundant, *Melissodes bimaculatus*, to determine their roles in the dataset.

Materials and Methods

Study Site

Soybean fields were situated at University of Missouri Research Farms, located in Turkey Farm Lake Dam, 9761 E St Charles Rd, Columbia, MO 65202 and Bradford Research Farm, 4968 S Rangeline Rd, Columbia, MO 65201. We divided soybean fields into 76.2 m by 7.6 m (0.06 ha) treatments, 25 soybean rows deep, of attract-and-kill and grower standard with a 50 m buffer between treatments. During 2019, we had four replicates for each treatment at University of Missouri Research Farms (North, South, East, and West plots), while in 2020 the North Plot was dropped and substituted with a plot on Bradford Research Farm, 4968 South Rangeline Road Columbia, MO 65201-8973.

Treatments

Attract-and-kill treatments consist of 76.2 x 1 m of ZeroFly® insecticidal nets (3.85mg AI/g fiber deltamethrin; VestergaardTM Groups S.A, Vietnam) stapled to wood posts (1”x1”x4’ Redwood Stake #434) spaced 1 m apart and hammered into the ground approximately 0.5 m from the field edge for the length of the treatment. We fixed three Japanese beetle dual lures (GL/TR-9003-25; Trécé Inc., Adair, OK, USA) to the net with binder clips spaced 20 m apart from one another. Japanese beetle lures consist of two components: (1) the synthetic sex pheromone that attracts males ((R,Z)-5-(1-decenyl) dihydro-2(3H)-furanone) and (2) a floral lure of phenethyl propionate, eugenol, and geraniol (3:7:3) that attracts both males and females. We deployed lures in mid-June prior to Japanese beetle emergence and replaced them every six weeks.

Grower standard treatments consist of 25 soybean rows sprayed with pyrethroid insecticide applications of Asana XL Insecticide (Porto et al.) (Item No. 9760425, Purchased from MFA Incorporated, Jefferson City) applied at a rate of 187.1 L/ha with Turbo TeeJets spaced 76 cm apart with 04 orifices spraying at 40 psi. During 2019, we applied two insecticide applications on 16 July and 31 July. During 2020, we applied three insecticide applications on 16 July, 24 July, and 28 July.

During 2019, fields were planted with P37T09 soybean seeds on 31 May at 140,000 seeds/0.4 ha. An herbicide treatment of 0.3 L/ha Fierce XLT, 2.3 L/ha Roundup PowerMax, and 2.3 L/ha Interline was applied on 1 June. During 2020, P38A49L soybean seeds were planted on 1 June at 140,000 seeds/0.4 ha. An herbicide treatment of 0.3 L/ha of Fierce XLT, 2.3 L/ha of Roundup PowerMax, and 2.3 L/ha of Liberty was applied on 2 June. A second herbicide treatment comprised of 2.3 L/ha of Liberty and 1.2 L/ha of Dual II Magnum was applied on 24 June.

Bee Bowl Construction

Bee bowls were supported by a wooden rod (½ in x 48 in Poplar Dowel Rod, Lowe's #19382) and 2 clothespins, which held in place PVC pipes cut to fit 3 paint cups (Solo 9 oz plastic clear cups). The paint cups themselves served as bee bowls, and were colored yellow, white, and blue. For white bee bowls, we used Homefront Decorator Color: Satin Finish (17201 White Interior Acrylic Paint-ACE Hardware #1020890). We colored blue and yellow bee bowls with Guerra & Paint Pigment Corp Silica Flat: Matte Acrylic Polymer Emulsion, Fluorescent Blue and Fluorescent Yellow, respectively.

We deployed 3 bee bowls per treatment at canopy height between soybean rows 5 and 6 from the field edge, in the center of each plot lengthwise. The second bee bowl was placed in the center of the treatment plot's length (38.1m), with the first and third bee bowl 5m away on either side. We filled the bee bowls with soapy water (Dawn Dish Soap Ultra – Original Scent) and then left them to sit for 24 hours before collection.

Bee bowls were deployed in treatments from soybean stage R1 to R6. In 2019, bee bowls were placed in the field on July 8th and first filled on July 11, 2019. The first collection date was July 12, 2019. The last collection date was August 27, 2019. In 2020, bee bowls were placed in the field on July 17th and first filled on July 17, 2020. The first collection date was July 18, 2020. The last collection date was August 23, 2020. Bee bowl heights were adjusted each week to remain slightly above the soybean canopy.

Specimen Processing

We collected specimens from bee bowls every 24 hours. To collect specimens, we poured bee bowl contents into a larger plastic cup with a lid. We placed this into a box for transportation to University of Missouri's campus, where specimens were drained and put into bags, which were then placed into a freezer until they could be processed. We then strained and rinsed out the soapy water contents, placing each insect into a plastic bag and labeling the bag with the collection data (collector, collection date, location of collection, treatment, and bee bowl) from the plastic cup. Finally, we froze all specimens until they were ready to be cold transported to Virginia Tech, where they were processed and identified.

Once at Virginia Tech, the samples were processed by moving all frozen specimens from their plastic bags into ethanol filled scintillation vials, with collection data written on a piece of paper that was placed in the vials.

The specimens were washed and dried according to The Very Handy Manual's (https://bee-health.extension.org/wp-content/uploads/2019/08/TheVeryHandyBeeManual.pdf) Methods for Processing Bees that Have Been Stored in Alcohol, and fluffing bees according to the same document's methods for a Bee Washer and Dryer. The bee washer/dryer was used as a strainer in lieu of a coffee strainer. Bees were pinned and labelled with their collection data (collector, collection date, location of collection, treatment, and bee bowl), then morpho-sorted and brought to the FWS/USGS Native Bee Inventory and Monitoring Lab in Beltsville, MD for species-level identification with the aid of Sam Droege.

Data Analysis

We analyzed the abundance, richness, and diversity of bee communities captured in soybean fields under different insecticide treatments. Abundance is the number of individuals caught and richness is the number of unique species caught; we used the Shannon diversity index to measure diversity (Shannon, 1948). Throughout our analyses, the fixed effects are application period and treatment groups, either grower standard or attract-and-kill insecticide treatments, or the interaction thereof.

First, we analyzed whether treatment (grower standard spray insecticide or attract and kill insecticidal netting) interacted with pesticide application period, because *a priori* we expected a negative effect of spray treatment on bee abundance for grower standard, but not attract-and-kill. As mentioned earlier, we applied two insecticide applications on 16 July and 31 July 2019. In 2020, we applied three insecticide applications on 16 July, 24 July, and 28 July. We categorized our capture temporally into three groups: before application, any date before one week after the first application (July 23 in 2019, and July 23 in 2020); during application, one week after the first application to one week after the final application (July 23 to August 7 in 2019, and July 23 to August 4 in 2020); after application, any date after the last date in the "during" application period. We employed a week-long lag in our categorization because the insecticides used have a 7-10 day spray interval.

We utilized a Poisson generalized linear mixed effect model to test if the interaction between treatment and insecticide application period had an effect on abundance, with plot (north, south, east, west for 2019, dropping north and including Bradford Farm for 2020), year, and month as random effects. In all further analyses, application period is used as an additive fixed effect. We further analyzed abundance of each treatment for the top five most abundant species collectively and individually using Poisson generalized linear mixed effect models with plot as a random effect. Finally, we analyzed the entire capture without the most abundant species using a Poisson generalized linear mixed effect model with plot, year, and month as random effects.

We analyzed richness of each treatment through a Poisson generalized linear model. We analyzed for the Shannon diversity index of each treatment using a Gaussian generalized linear model, assuming Normal distribution of the index (Hutcheson, 1970). The richness and diversity necessitated a generalized linear model because they returned singular fit errors with generalized linear mixed effect models with random effects added.

We tested the significance of terms using single term deletions and likelihood ratio test. All analyses were conducted in R version 4.3.1.

Results

Bee Capture

We caught a total of 1473 specimen. Specifically, we caught 670 in attract and kill insecticidal netting treatments, and 803 in grower standard treatments. 13 of these (<1% of total catch) were removed from analysis, either because they were wasps or they were unable to be identified to species, and thus would skew species richness and Shannon diversity index analysis. All 13 were from grower standard treatments.

Effect of Application Period on Bee Capture

We found no interaction between the treatment (attract and kill vs. grower standard) and insecticide application period (before, during, and after) (likelihood-ratio test: $\chi^2 = 2.23$, $p = 0.33$) for bee abundance. We then simplified the model to only include insecticide application period as an additive term for the following overall treatment effect analyses.

When combining treatment with application period in our model as an additive term, both were significant (application period likelihood-ratio test: $\chi^2 = 11.03$, $p = 0.004$; treatment likelihood-ratio test: $\chi^2 = 9.99$, $p = 0.002$; Figure 4.1). In other words, any differences between the treatments are maintained across all application periods.

Bee Abundance

Our data estimates that attract-and-kill treatments reduce total bee abundance by 15%, corresponding to a 1.18-fold reduction (95%-CI: 1.07 to 1.31; $p < 0.002$; Figure 4.2A) relative to the grower standard treatments. We found this significant decrease in bee abundance in attract-and-kill treatments compared to grower standard treatments averaged across all application periods (attract-and-kill = 11.7 (6.44 to 21.4), grower standard: 13.8 (7.61 to 25.2); Figures 4.1 and 4.2A)[2].

We also found differences in abundance across the application periods of the experiment, with a notable decline in bee abundance after the spray treatments had concluded (during / before: 0.84 (2.66 to 0.26), $p = 0.93$; after / before: 0.26 (0.79 to 0.09), $p = 0.013$; after / during: 0.31 (0.76 to 0.13), $p = 0.006$; Figure 4.1).

Role of *Melissodes bimaculatus*

Next, to further elucidate the effect of treatment on bee abundance, we conducted exploratory analysis on the five most abundant species (*Melissodes bimaculatus, Melissodes comptoides, Halictus ligatus, Halictus parallelsus,* and *Augochlora pura*) as a group to see if they were disproportionately affected. We found the significant decrease in abundance in attract-and-kill treatments was upheld when analyzing just the most abundant species (attract-and-kill: 16.6 (13.2 to 20.9); grower standard: 19.8 (15.7 to 24.9); ratio: 0.84 (0.75 to 0.94); $p = 0.004$). Lastly, to determine which, if any, of these abundant species were driving the overall trend, we further

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[2] These statistics for abundance, as with the statistics following, are presented in abundance per capture. For example, 11.7 bees were captured on average in our bee bowls in attract and kill plots as opposed to 13.8 in grower standard. This is drawn from our total capture of 1460 bees.

analyzed abundance individually for each. There were no significant differences in abundance in four of the five species (Table 4.1). However, we found a significant decrease in the abundance of our most common species, *Melissodes bimaculatus*, in the attract-and-kill treatments as compared to grower standard (Table 4.1, Figure 4.2B).

Table 4.1. The five most common bee species found in our soybean surveys, their abundance in attract-and-kill and grower standard plots, the ratio between them, and *p*-value for each. Note that four of these species saw no significant difference. In *Melissodes bimaculatus*, we see a significant decrease in abundance in attract-and-kill as compared to grower standard treatments.

Bee Species	**Attract-and-Kill Abundance**	**Grower Standard Abundance**	**Ratio attract-and-kill / grower standard**	***p***
Melissodes bimaculatus	9.8 (6.92 to 13.8)	12.7 (9.02 to 17.9)	0.77 (0.66 to 0.89)	< 0.001
Melissodes comptoides	3.07 (2.35 to 4.01)	3.02 (2.40 to 3.79)	1.02 (0.73 to 1.41)	0.916
Halictus ligatus	2.94 (2.03 to 4.24)	2.60 (1.74 to 3.89)	1.13 (0.76 to 1.7)	0.556
Halictus parallelsus	2.45 (1.74 to 3.44)	1.99 (1.40 to 2.84)	1.23 (0.80 to 1.88)	0.348
Augochlora pura	1.66 (1.10 to 2.51)	2.37 (1.61 to 3.49)	0.7 (0.43 to 1.14)	0.149

Based on the results from the individual analysis of the five most abundant species, we then wanted to know if *Melissodes bimaculatus* itself drove the overall trend. We therefore analyzed abundance for the entire capture excluding *Melissodes bimaculatus*. There was no significant difference between treatments (attract-and-kill: 10.9 (5.02 to 23.5); grower standard: 11.9 (5.48

to 25.7); ratio: 0.916 (0.79 to 1.06); p = 0.228; Figure 4.2C) when excluding this species. In other words, the overall decrease in bee abundance in the attract-and-kill treatment is solely driven by a decrease in *Melissodes bimaculatus* abundance.

Bee Diversity

We found no significant difference between the two treatments for species richness (attract-and-kill: 8.6 (7.5 to 9.8); grower standard: 9.2 (8.0 to 10.5); ratio: 0.93 (.77 to 1.1); p = 0.470) or Shannon diversity index (attract-and-kill: 0.10 (0.08 to 0.11); Grower Standard: 0.109 (0.09 to 0.13); treatment difference: -0.01 (-0.03 to 0.01); p = 0.326; data not shown).

Discussion

Here we present results of an experimental study comparing the impact of two pest management options, attract-and-kill insecticidal nets and grower standard pyrethroid spray treatments (used to control Japanese beetle) on bees in soybean. We found that attract-and-kill insecticidal net treatments in soybean reduced bee abundance as compared to grower standard spray pesticides, regardless of grower standard application period. However, neither species richness nor bee diversity, as measured by Shannon diversity index, were affected by the treatments. Exploratory analysis confirmed that the overall reduction in abundance was driven by one species, *Melissodes bimaculatus*. Therefore, our results demonstrate that attract-and-kill insecticidal net treatments can impact native bees, but that the impact may vary from species to species.

Other bee community surveys have also found that *Melissodes bimaculatus* is one of the most common species in soybean (Cunningham-Minnick, Peters, & Crist, 2019; Dennis, 2018; Gill &

O'Neal, 2015; Main, Webb, Goyne, Abney, & Mengel, 2021; Rust, Mason, & Erickson, 1980; Wheelock et al., 2016), regardless of trap type and color used for the survey (Joshi et al., 2015). Even when it is not one of the most common species, it is still present (Bennett & Isaacs, 2014; Torrez, Beauzay, St. Clair, & Knodel, 2023).

Perhaps more importantly, several studies have also shown *Melissodes bimaculatus* with soybean pollen on them, confirming that these bees were not just passing by, but are actively visiting the soybean crop (Gill & O'Neal, 2015; Rust et al., 1980). Interestingly, the bee was found in higher presence in monoculture soybean fields rather than in mixed fruit/vegetable fields (St Clair, Zhang, Dolezal, O'Neal, & Toth, 2020). Altogether, it seems that even though *Melissodes bimaculatus* is a generalist species (Trimm, 2024), it is an common flower visitor for soybean. Together with the circumstantial evidence of its abundance in soybean, collection of soybean pollen, and preference for soybean monoculture over mixed fruit/vegetable fields, it is likely an important pollinator for the crop.

Why then, would we see it in higher abundance in plots treated with spray insecticide, potentially exposing it to toxicants, compared to the attract-and-kill insecticidal net treatment plots? Although we did not test for this specifically here, the answer may lie in its life history. *Melissodes bimaculatus* is a ground-nesting bee that can nest gregariously (Giulian, Danforth, & Kueneman, 2024). Because of this, their nests are more affected by ground tillage (Williams et al., 2010) than above-ground nesters. It may be the case that they nest outside of soybean fields proper, opting for non-turbulent soil on the outside edges, or unmanaged dirt. If this is the case, attract-and-kill insecticidal nets may be constructing a wall between the soybean crop and the bee.

Of course, this is speculation, and there may be alternate reasons. Our treatment of attract and kill insecticidal treated netting created a physical barrier at the edge of the soybean field. It may be possible that flying insects such as bees rest on this barrier, which is treated with contact insecticides. If bees can perceive the insecticidal treatment (such as smelling it), there may be excito-repellency effects. As *M. bimaculatus* is particularly effected, this species may simply be more vulnerable to pyrethroid insecticides than other bees, or have a lower tolerance to insecticides generally. If it is an edge nesting species as we speculated earlier, perhaps our collection methods biased our data. The attract and kill insecticidal netting may have created a barrier between them and the crop, blocking their line-of-sight to the bee bowls. Bee bowls are painted to simulate the colors of flowers, but are not treated with any additional attractants. Blocking line of sight would neutralize their ability to capture bees.

Our study is not without limitations. There were no control plots, capturing bees without either grower standard or attract and kill insecticidal netting treatments applied. Likewise, to quantify the effect of the active ingredient in our attract and kill insecticidal netting, future research should replicate this study with plots containing identical netting, sans insecticidal treatment.

Our results underscore the need to increase our knowledge of plant-pollinator systems in soybean. On average, *Melissodes bimaculatus* populations in attract-and-kill insecticidal netting plots are approximately three quarters (0.771, Table 4.1) that of grower standard plots.

Confirming that this species pollinates soybean, the efficiency of its pollination, and whether this difference in abundance between treatments is large enough to have an economic impact, is not understood and warrants further investigations, especially given that the crop is normally self-pollinating (although see de O. Milfont et al., 2013; Erickson, 1975; Gill & O'Neal, 2015; Silliman et al., 2022; Wheelock et al., 2016). Likewise, we saw no difference in the diversity of the bee communities between our treatments. Further research into soybean systems could explore whether bee diversity, rather than top pollinator abundance, drives the economic benefits of insect pollinator presence (Garibaldi, 2016; Brittain et al., 2013). Future research may compare soybean self-pollination yield to that of soybean exposed to *Melissodes bimaculatus* in exclusion experiments.

Attract-and-kill insecticidal netting control methods have some clear benefits to grower standard spray insecticide. There is no risk of spray drift, reduced concern for active ingredients leeching into the soil, and insect predators are less impacted by attract-and-kill treatments (Gregg, Del Socorro, & Binns, 2016). In soybean fields in particular, attract-and-kill plots with insecticidal netting saw a higher abundance of natural enemies to Japanese Beetle, a pest, than grower standard treated plots (Benthall, 2023). With this information, our results need to be taken in context when growers decide whether to use spray or attract-and-kill insecticidal netting treatments. Additional research in soybean is needed to quantify whether the increase in pest predators negates the loss of pollinators, if either is economically significant, or if something can be done to optimize the gains/losses of these non-target effects for attract-and-kill insecticidal netting treatments.

Attract-and-kill studies using sugar baits in mosquitoes found that the placement of treatments can impact the amount of non-target insects affected (Fiorenzano, Koehler, & Xue, 2017), which raises questions about whether insecticidal treated nets in soybean can be placed differently to reduce non-target effects on pollinators. In our study, the nets were placed 0.5 m from the field edge, and our bee bowls were placed between rows 5 and 6 from the field edge. Perhaps a larger buffer of bare soil (suitable for ground nesting bees) between the insecticidal nets and the field would help to minimize non-target pollinator effects. Research is needed to quantify the foraging range of *Melissodes bimaculatus*, for which our 50m buffer between treatments may be found to be inadequate. Likewise, future research can sample for pollinators in different places within soybean fields to locate where they are most abundant or where there might be a nesting congregation. This information might then be used to minimize the amount of chemicals exposed to those areas. A follow up study may attempt to determine whether most pollinators fly into soybean fields from outside or nest within the rows of the crop.

Our study suggests that the use of attract-and-kill insecticidal netting alternatives could introduce some drawbacks in soybean systems, even if they are effective and increase natural pest predators. This adds complexity to discussions about alternative agricultural pest control methods in context of pollinators, which normally focus on efficacy, and often assume that non-spray treatments are better for bee communities generally. As our body of knowledge grows, it may be time to consider the role of each pollinator within a community, as treatments might impart effects that are species-specific. Further, data demonstrating that individual bee species react differently to the same treatment, while knowing that certain bees are more efficient pollinators of specific plants than others, highlight a need for nuance in EPA pollinator risk assessments, where the honey bee is often used as a model organism for all insect pollinators.

Figures

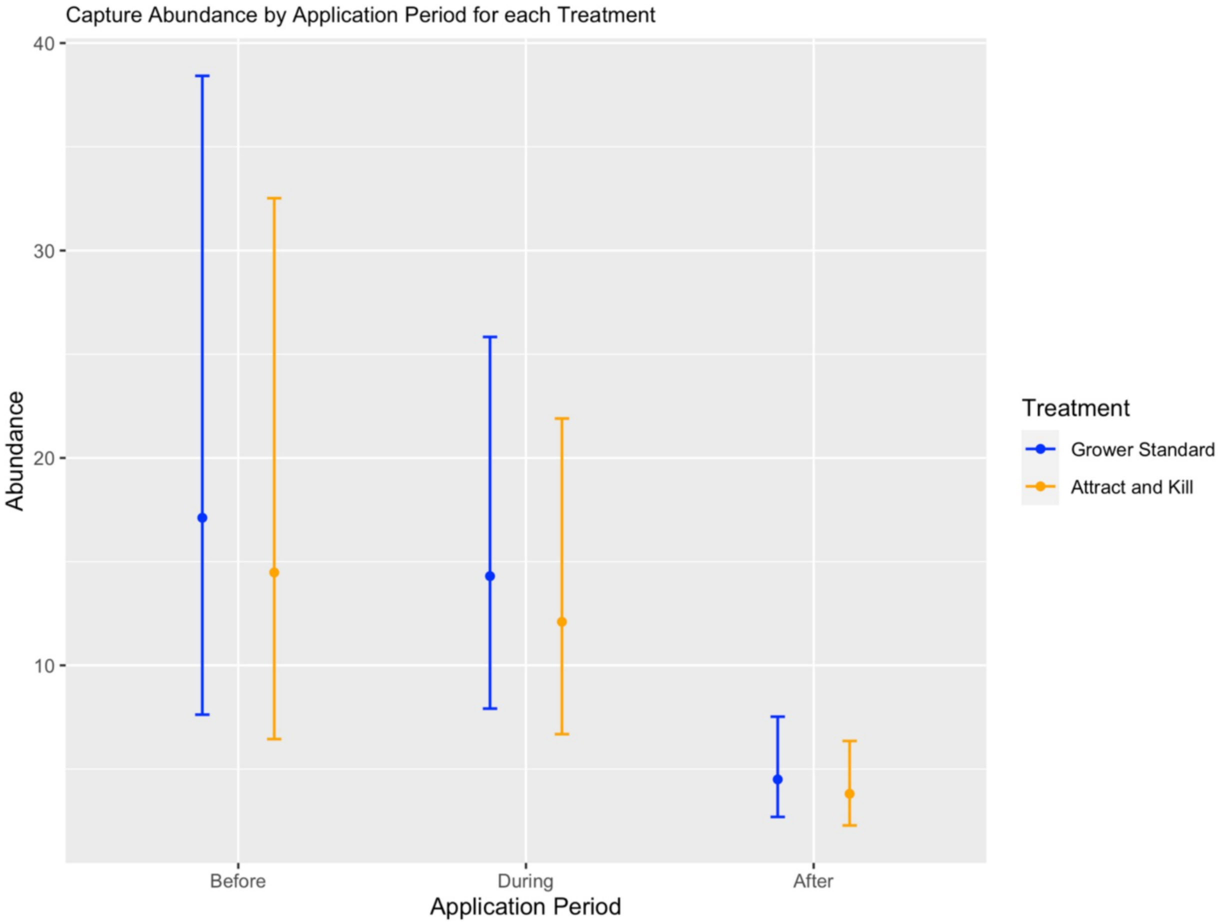

Figure 4.1. Bee abundance against application period and stratified by treatment. There is a notable decline in bee abundance across both treatment types after pesticide application. We found no interaction between application period and treatment type, but both were significant terms in an additive model. The attract and kill treatment abundance was lower regardless of application period (see text for statistical details). This represents average abundance per capture, drawn from our dataset of 1460 bees.

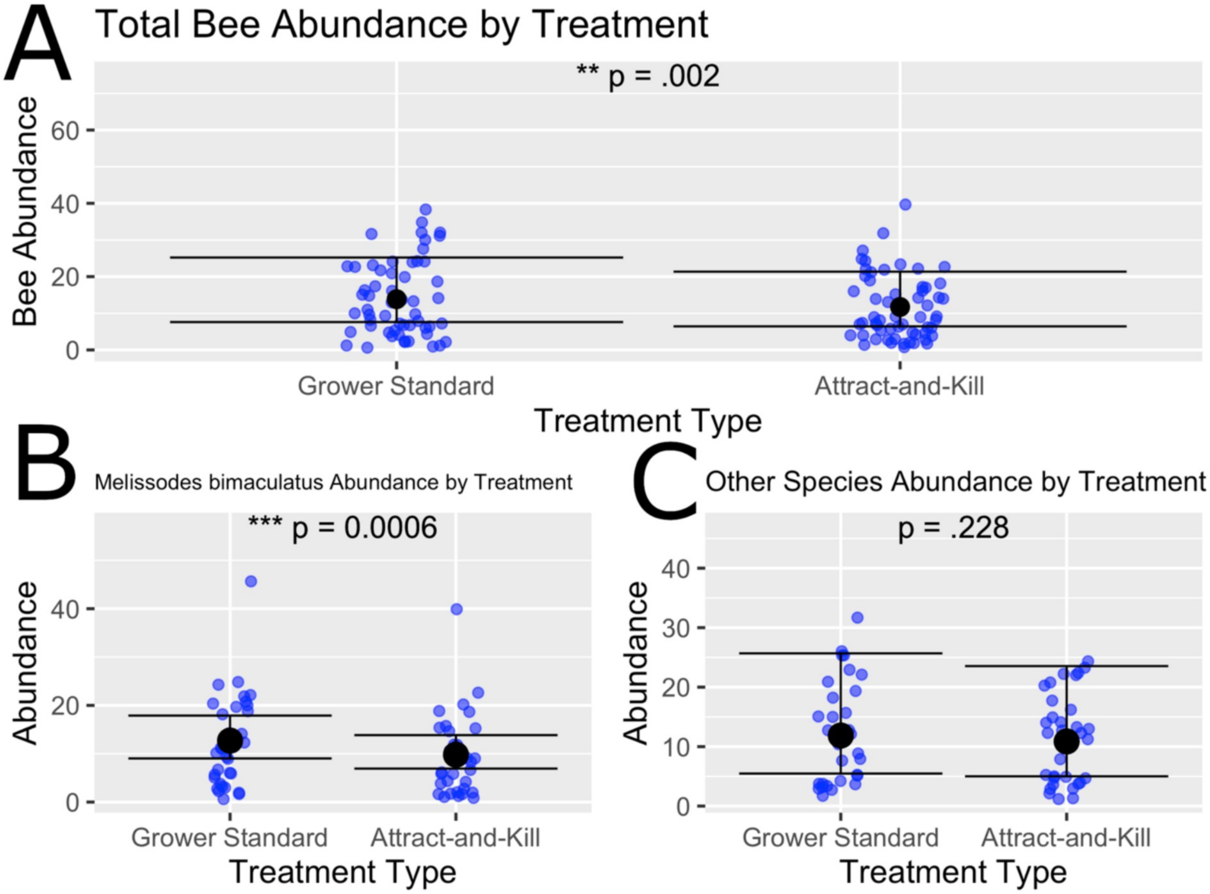

Figure 4.2. Treatment type affects bee abundance through a decrease of *Melissodes bimaculatus* in the attract-and-kill plots. (A) Total bee abundance by treatment, demonstrating a significant decrease in abundance in the attract-and-kill treatments compared to grower standard treatments. (B) *M. bimaculatus* abundance by treatment. The abundance of *M. bimaculatus*, the most common bee in our experiment, was significantly less in attract-and-kill treatments compared to grower standard treatments. (C) Other species abundance by treatment. The exclusion of *Melissodes bimaculatus* from our overall abundance analysis rendered the effect of treatment

non-significant (see text for statistical details). All panels represents average abundance per capture, drawn from our dataset of 1460 bees.

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Chapter 5: Partisan Control of a State Impacts the Number and Subsystem of Bee Statutes Enacted In the United States

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Abstract

Bees underpin modern agriculture and are facing steep declines in number and species diversity. In recent years, agricultural and climate policy have included specific language for bees and pollinators. Despite this, “bee policy” conflates several different policy concerns. To reveal the policy subsystems subsumed by this label, we analyze state level bee statutes in the United States from January 1, 2023 through August 31, 2024. We analyzed where these statutes were passed; whether the relative economic importance of bees to the state, as measured by the ranked peak number of honey bee colonies in 2023, was associated with the volume of legislation enacted, and whether and how partisan control was related to the type of legislation enacted. We found no correlation between relative economic importance and number of bee statutes enacted ($p = 0.643$). However, we saw a statistically significant relationship between state partisan control and the nature of bee statutes passed, ($p = 0.004$). Finally, we found a large contiguous group of states along the Missouri-Mississippi Rivers that did not enact bee statutes, which we speculate

may be due to one of their most important agricultural exports being soybean, a self-pollinating crop.

Introduction

Global insect populations have been steeply declining since at least 1990 (Goulson, 2019; Hallmann et al., 2017), leading to proclamations of an "Insect Apocalypse" (Jarvis, 2018). Of particular concern are bees because of their role in pollination. Over 80% of the flowering plants in the world rely on insect pollination (Ollerton, Winfree, & Tarrant, 2011), and the global agriculture industry is built on the back of this free ecosystem service. Globally, pollination of agricultural systems has been valued between $127-152 billion (Bauer & Sue Wing, 2016).

Public outcry over the plight of the bees, and the potential of a world without them, eventually caught the attention of policymakers (B. E. Erickson, 2023). Within the past few years, bees under the umbrella of agriculture and climate policy have taken the spotlight. At the highest level, the UN's Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services held an interagency workshop with the Intergovernmental Panel on Climate Change to explore the connection between biodiversity loss and climate change (IPBES, 2021). At a national level in the United States, the Biden administration's 2023 extension of the Farm Bill, 30x30 Initiative, and Inflation Reduction Act all earmark significant capital towards habitat restoration and conservation, including language specifically for pollinators (IPBES, 2021; NRCS, 2024; USDA, 2024b).

"Bee policy" is not a simple concept. It has numerous dimensions and foci; having a shared taxa group can conflate what otherwise would be separate concerns (Colla, 2022; D. M. Hall &

Martins, 2020). A range of national and international initiatives beneficial to bees suggests that bees as a policy focus straddle several policy streams. By examining the content of bee legislation, we can potentially reveal distinct policy subsystems, such as agricultural, environmental, and economic, each driven and supported by varied political coalitions.

In 2022 the California Supreme Court ended a prolonged legal battle and let a decision stand that allowed the California Endangered Species Act to list bees and other invertebrates as endangered species (Jepsen, 2022). The expansion of statutory applicability made us wonder about the role of the state legislatures in this policy sphere. Concurrently, focusing on state level legislation allows us to gather a number of bee statutes in the United States sufficient for quantitative analysis. We focus on enacted legislation following the 2022 elections, when 88 of the 99 state legislative chambers held elections, with 85% of state legislative seats contested (Ballotpedia, 2024). With new legislators and this issue reaching the decision agenda in many jurisdictions, this period offers an initial opportunity to analyze patterns in state bee legislation.

Here we conduct a content analysis of state statutes enacted from January 2023 to August 2024. In our analysis, for each state in which bee legislation was proposed, we noted the dates bills were enacted, and the partisan control of the legislative chambers and governorship. We further categorized these statutes by policy subsystems (that is, type of policy) and recorded the peak number of managed honey bee hives in each state in 2023. These rankings served as proxies for the economic importance of bees. Then we analyzed the statutes to examine whether and how enacted legislation varied geographically, whether the relative importance of bees to the state economy was associated with more statutes being passed, and if the partisan control of state legislatures and governorships was related to category or volume of legislation enacted.

Materials and Methods

Content Analysis

To choose search terms for use in examining the corpus of state statutes, we first turned to a study (Damon M. Hall & Steiner, 2019) that conducted a systematic review of subnational bee legislation in the United States from 2000 – 2017. We then modified their keywords, omitting "policy," "neonicotinoids," and "pesticides." This permitted refining the search to include only enacted legislation; since we were interested in neonicotinoid/pesticide legislation only if the text of the statute directly addressed bees. We added "apiary" and "*Varroa*" to our search terms because legislation regarding either would be inherently bee related; we substituted pollina* for pollinate. We did not follow up our search with state names.

With these modifications, we used the following search string to look for state bee legislation:

advanced: (bee beekeeping "colony collapse disorder" honeybee "honey bee" pollinate pollinator pollination apiary varroa)

in which any statute that contained any of these phrases would appear in our results.

We used Thomson Reuter's Westlaw Edge to search for relevant statutes, searching the "Proposed and Enacted Legislation" content type and filtering out proposed legislation. This yielded 139 initial results[3].

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[3] Thomson Reuter's Westlaw Edge claims "full coverage of statutes and regulations covering all 50 states.," However, scholars more frequently rely on other options like the National

Data Collection

We recorded the jurisdiction (state or territory), reference (Chapter/Act/Bill number), date of approval (e.g. by the governor, following legislative override of a veto), and web address for each result. We then added partisan control of the upper and lower legislative chambers and of the governorship for each statute at the time of its approval[4]. We then analyzed the text of each statute by hand, letting subcategories emerge from the text itself. We assigned subcategories that tapped on the statute's effect on its relation to bees, based on new text (i.e., for amendments, only the new language being added or stricken was considered). The subcategories were *economic*, *conservation*, *apiary regulation*, *unrelated*, *redundant*, *pesticide regulation*, *symbolic*, *administrative*, *general administrative*, *criminal*, and *awareness*[5].

The *economic* category involved statutes that either classified bees and their products/equipment/land designations differently for the purposes of business and taxes or directed funding to be spent in a new way towards bees or pollinators. An example is Alabama

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Conference of State Legislatures (NCSL) and state legislative websites.

[4] For Nebraska, a unicameral state, following the state's practice partisan control of its legislature is in the upper body (whose members are "senators"), but all Nebraska statutes were later filtered out and thus it did not affect the analysis.

[5] One additional category, "-" was applied to statutes of Puerto Rico, because the partisan control (PPD or PNP) could not be analyzed with the Democratic or Republican control in other jurisdictions.

Act 2024-448 S.B. No. 94, which exempts honey bee products from sales and use tax. The *conservation* category either expanded protections for bees/pollinators, regulated certain acts/spaces for the protection of bees/pollinators, or created explicit conservation initiatives, responsibilities, and goals. The *apiary regulation* category involved statutes that change how apiaries are viewed or must be maintained to be considered up to code. Alternatively, they defined to what extent governmental authorities can regulate apiaries. For example, one statute changed the scope of regulation from only those with over six hives to anyone in the state that possessed any hives, regardless of number. Another statute limited the authority of homeowner associations to regulate beekeeping. The *pesticide regulation* category regulated who can use what type of pesticides in the state, when, and with what permissions, licenses, or training. The *symbolic* category involved states creating beekeeping license plates, designating the honey bee as the state pollinator, or proclaiming a month to be “Native Plant Month” and the like. The *criminal* and *awareness* categories were among the least populous. Statutes categorized *criminal* designated crimes and legal penalties for certain acts affecting bees. For example, West Virginia Ch. 81 S.B. 164 states that trespassing on a premises with a managed bee colony is an “animal or crop facility trespass,” which is treated differently than other types of trespass. The *awareness* category was only used once, for New York Ch. 280 A. 1528-A. This statute establishes a youth development agriculture technology challenge competition for the state fair, in which the Department of Agriculture is to encourage, among other things, solutions to be found for pollinator loss on farms.

We excluded from analysis the categories of *unrelated*, *general administrative*, *redundant*”, and “-“[3]. The *unrelated* category applied to statutes that did not impact bees. For example, California

Ch. 668 A.B. 1850 designated the banana slug as the state slug. This statute appeared in the search because the preamble notes that it is a pollinator. Other statutes amended existing legislation, but the changes were unrelated to the bee or pollinator effects that appeared elsewhere in the document. The *redundant* category was given to statutes whose effect appeared in duplicate. For example, both the senate and house bill of a statute appeared in our search, but we only counted the version that passed the legislature. The *general administrative* category was applied to statutes that involved routine or repeated legislative activities, but did not otherwise impact, change, or create something new regarding bees (e.g., renewing annual funding for maintenance of apiaries as a line item in a state agricultural department budget with no other changes). These appeared in our search but were excluded from further analysis unless they created new funding or designations specifically regarding bees or pollinators. In the latter instance, the statute was classified "*administrative*", and not "*general administrative*". For example, Washington Ch. 310 S.H.B. 2134 amends the state budget generally, but also specifically charges the Department of Transportation to use funds for the new purpose of creating roadside pollinator habitat. Because this is a change in duties and not just an update in numbers, it is categorized *administrative* and not *general administrative*.

To create a proxy for the statewide economic impact of bees, we used USDA's National Agriculture Statistics Service (https://quickstats.nass.usda.gov/#70C15599-95F2-3DBD-82EA-175C08A46C36) to determine the maximum number of honey bee colonies in each jurisdiction in 2023 (commodity: honey, data item: honey, bee colonies – inventory, max, measured in colonies).[6] The National Agriculture Statistics Service provides data at four points in the year, January – March, April – June, July – September, and October – December. We chose the highest of the four values for the year and ranked each jurisdiction using this number. We focus on the peak of 2023, because it is based on a full year of data, and the peak number represents when the state may be importing hives from elsewhere during bloom (and thus, is representative of the size/importance of bees to the state agricultural industry). Using the median, mean, or other measures would include months out of the state's agricultural season, and skew data towards the number of hives that overwinter in the state, not tapping their relative economic importance.

Data Analysis

After this process of filtering and paring down, we analyzed 48 state statutes enacted between January 2023 through August 2024. We utilized Rstudio version 4.3.1 for the preparation and analysis of data and the creation of figures. We used a gitlab repository (https://code.vt.edu/) for version control to check in data and code.

Table 5.1 2023 Peak Hive Rankings and Numbers of Enacted Statutes by State

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[6] We compiled this number for all jurisdictions with the exception of Puerto Rico, even if they were excluded from analysis due to statute category assignment. Hawaii was the only jurisdiction that did not have 2023 data, so we used data from the most recent full year, 2021, instead.

State	Statutes Enacted	Peak Hive Rank (2023)
AL	1	16
CA	2	1
CO	3	10
CT	1	26
HI	1	14
ID	2	3
IL	3	19
IN	2	17
KS	2	25
LA	1	9
MD	1	24
ME	2	17
MN	3	7
MT	1	6

NJ	**1**	**13**
NM	**1**	**22**
NY	**3**	**8**
OR	**1**	**5**
PA	**2**	**11**
PR	**1**	**-**
SC	**1**	**15**
TN	**2**	**18**
TX	**1**	**2**
UT	**2**	**12**
VA	**1**	**20**
VT	**4**	**21**
WA	**3**	**4**
WV	**1**	**23**

Spatial Patterns

To examine whether spatial patterns appear in where bee statutes are passed, we mapped the statutes by state in Figure 5.1.

Economic

To see if the relative economic importance of hives in a state is associated with the number of statutes it enacted, we first ranked each state by its peak number of honey bee colonies during 2023. This enabled us to measure the relative importance of bees to the state's economy, while also mitigating outliers. Most importantly, we do not expect statutes to be passed proportionally with colony numbers, just monotonically. We then counted the number of statutes passed for each jurisdiction.

We utilized Spearman's rank correlation to examine whether the existence and the strength of a relationship between the state's rank in peak honey bee colonies and the number of bee statutes enacted in a state. We hypothesized that states with higher rankings would be more likely to pass bee legislation due to this economic importance. Because our data set is small and we found a tie, we utilized the approximate version of the correlation test, rather than exact, ensuring that the test remains robust and interpretable (Hollander & Wolfe, 1973).

Partisan Control

To see if there is a relationship between partisan control of the state legislature and governorship and the category of bee statutes enacted, we collected partisan control of a state's upper legislative body, lower legislative body, and governorship separately.

In our analysis, we treat the three as interchangeable and count how many of the bodies are controlled by each party. This results in four possibilities for partisan control of the senate/house/governorship: DDD, DDR, RRD, and RRR; the first and last categories are commonly referred to as state "trifectas". We do this to allow analysis on our small dataset, which would otherwise be divided across categories too sparsely if we were to analyze by all possible permutations.

We conducted a Fisher's exact test with a two-sided alternative hypothesis to examine whether these categories of partisan control are associated with the subcategories and the total number of bee statutes enacted. We hypothesized that certain categories of legislation may be more or less likely to be enacted under different partisan alignments.

Results

Spatial

Our map of where bee statutes were passed in 2023-204 seems to indicate that certain regions enact less bee legislation than others. In particular, a notable group of contiguous states along the Missouri-Mississippi rivers did not pass any bee statutes.

Economic

The Spearman's rank correlation did not indicate that there was a relationship between economic importance (tapped by ranked 2023 peak honey bee colonies) and number of bee statutes enacted (rho = -0.069, p = 0.643).

Partisan

When examining partisan control of state government, we see a strong statistically significant association between partisan control and the category of bee statute passed (p = 0.004).

Figure 5.3 displays the number of enacted bee statutes by partisan control for all policy categories. States with unified Democratic governments passed more bee statutes (n = 25) than those under unified Republican control (n = 14). Meanwhile states with unified party government passed more statutes than states with a divided party government; states in which Democrats controlled both chambers of the legislature but not the governorship or the governorship and one of the legislative houses passed 7, while states with the same pattern for Republicans passed 2.

Discussion

Here we present the results of an analysis of U.S. state bee policy between January 2023 and August 2024. We found no statistical relationship between the relative economic importance of bees, measured as ranked peak colony numbers for 2023, and the number of bee statutes passed. At the same time, state party control and the type of enacted legislation was associated. These data suggest the impact of party control and pollinator protection, taking into account the policy subsystems present in bee policy.

We saw evidence of spatial patterns in where bee statutes were enacted (Figure 5.1). Nearly all the Mid-Atlantic states passed bee statutes as did many of the Western states. Interestingly, the largest contiguous group of states that did not pass bee legislation fall along the Mississippi to Missouri rivers.

Among these 13 states, soybean was the most valuable agricultural export in 2022 in seven. For 11 of the thirteen, soybean was at least their second most valuable agricultural export (USDA, 2024a). This is telling, because soybean is a self-pollinating crop (E. H. Erickson, 1975), and bees traditionally have not been viewed as important for soybean systems. The 2019 Hall and Steiner study of bee legislation from 2000 – 2017 reported that among these thirteen states, six passed no bee statutes during this time period, six passed only one or two statutes, and Wyoming passed nine. Although the search terms we used are slightly different from this systematic review, the review is mostly consistent with our spatial pattern observation.

In recent years, we are beginning to understand not only that bees visit soybean for pollen but also that soybean supports a diverse bee community, which increases crop yield and plant resilience (de O. Milfont, Rocha, Lima, & Freitas, 2013; Gill & O'Neal, 2015; Silliman, Schürch, Malone, Taylor, & Couvillon, 2022; Wheelock, Rey, & O’Neal, 2016). It may be the case that as we begin to better understand the importance of pollinators within soybean systems, and communicate this to stakeholders and policy makers, these states may begin passing similar statutes as nearby states, exemplifying horizontal policy diffusion (Walker, 1969).

The study here also identified a clear example of horizontal policy diffusion in Vermont’s No. 182 H. 706 and New York Ch. 107 S. 8031. Not only did these statutes both ban the use of neonicotinoids, but Vermont’s statute states that is to be contingently repealed if New York’s statute is repealed. This spread of policies between jurisdictions is not just a hope for soybean states in the future; it also may be another vehicle for addressing the collective action problem of global biodiversity decline and climate change in the absence of national and international action.

We see two interesting patterns in the number of statutes passed by different configurations of partisan control regardless of statute category. First, bee statutes were passed more often in states with unified Democratic governments than in those under unified Republican control; bee statutes also were enacted more often in Democratic-leaning states than in Republican leaning states (Figure 5.3). Yet, states controlled by either party passed at least double the legislation as the states where partisan control was split. This reaffirms a pattern seen across many contemporary policy areas, suggesting that a split in partisan control may make it more difficult to pass bee legislation, regardless of which party is in power. At the same time, the figure does not account for the number of states with particular partisan configurations. For example, there may just be more states with partisan trifectas than with split partisan control, leading to an increase in total statutes passed, but not an increase in statutes enacted per state.

We organized statutes by category to identify the policy subsystems in state "bee" policy. As noted earlier, we analyzed *economic*, *conservation*, *apiary regulation*, *pesticide regulation*, *symbolic*, *administrative*, *criminal*, and *awareness* policies. State party control was associated with the category of bee statute passed. Statutes in the categories *apiary regulation*, *economic*, *conservation*, *pesticide regulation*, and *symbolic* were passed at least five times in our timeframe, and we visualized how many of each were passed by various levels of partisan control in Figure 5.2. We can see that states controlled by a Democratic trifecta were much more likely to enact *conservation* statutes than states with other types of partisan control. In contrast, *Apiary regulation* statutes were passed four out of six times in states under unified Republican control. The most evenly divided statutory category was *economic*, where nine statutes were passed in Democratic-leaning or Democratic trifecta states and four in Republican-leaning or Republican trifecta states. *Pesticide regulation* was passed four out of five times by Democratic-leaning or trifecta states, and *symbolic* legislation was passed three out of five times by Republican trifecta state.

Although this study analyzed initial patterns in state bee statutes, it is not without limitations. This dataset, while comprehensive for the defined period, can be likened to a convenience sample due to the limited timeframe chosen. Consequently, findings may not generalize to legislation from earlier or subsequent time periods. Nonetheless, the data provide a snapshot of subnational legislative trends during a critical period of attention to pollinators. Future research could build on this base, analyzing longer time periods, pivoting to focus on federal or local legislation, or examining departmental and agency regulations at the national or state levels. Deeper content analyses may look into complexity of statutes such as word count in order to glean more information

In addition, our method of developing relative economic importance of bees for each state will likely underestimate the value of bees as the survey data are voluntary. It may well serve as a valid proxy for commercial scale beekeeping, however states like VA are likely underrepresented here because the majority of beekeepers are hobbyists and unlikely to report their numbers. There may be better metrics of the economic importance of bees to a state than cumulative hive numbers altogether.

Bees are distinctive creatures. Despite being “creepy crawlies,” the public generally views them favorably (Stanisavljević & Stanisavljević, 2017). Their importance to modern agriculture means they are vital to humanity’s way of life (Porto et al., 2020), and the recognition of this crosses partisan and ideological boundaries, as a liberal conservationist and a conservative farmer might well agree. Despite this agreement on their importance, or perhaps because of it, “bee policy” often confounds several distinct policy subsystems. Although some recent literature analyzes bee legislation (Damon M. Hall & Steiner, 2019; Damon M. Hall & Steiner, 2020), in general bee policies remain understudied relative to the importance of the taxa group and pervasiveness of bees in our lives. Before we can understand global, intractable problems like bee biodiversity decline, we may benefit from better understanding our own attitudes and the policy processes through which we address such problems.

Figures

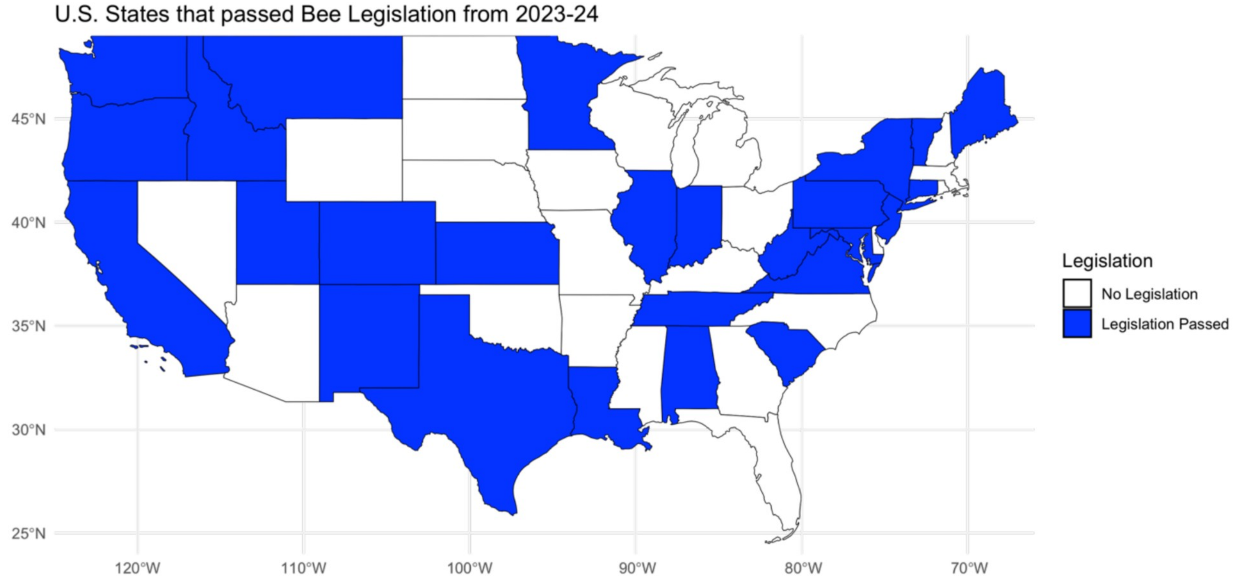

Figure 5.1. States that passed bee statutes between January 2023 and August 2024. One contiguous group of states along the Missouri-Mississippi rivers did not pass any bee statutes. Hawaii also passed one statute, which we include in our analysis. Cartographic shapefile from (https://www.census.gov/geographies/mapping-files/time-series/geo/carto-boundary-file.html)

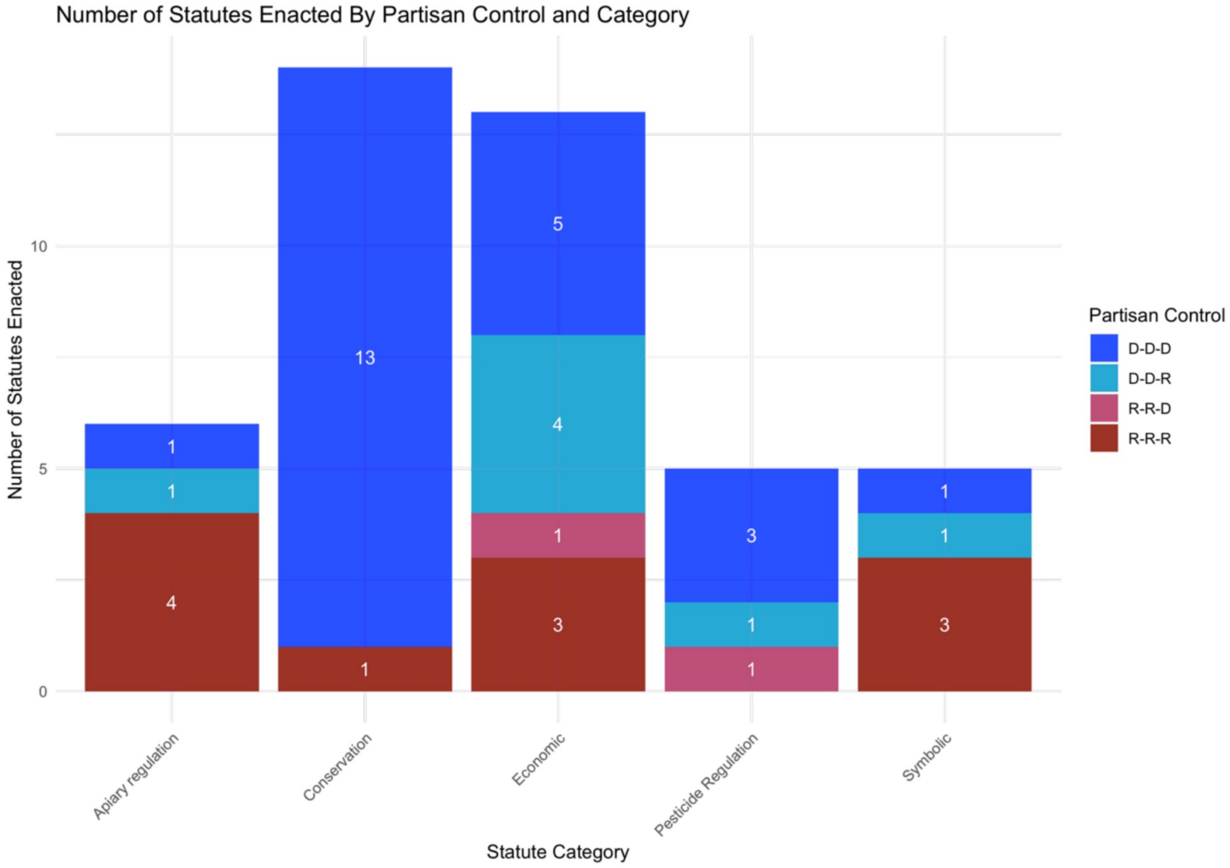

Figure 5.2. Number of statutes enacted by category varies by state partisan control. The X axis lists our statute subcategory, and the Y axis is the number of statutes enacted within each category. Here we visualize the five most common categories for legislation, those with more than five statutes.

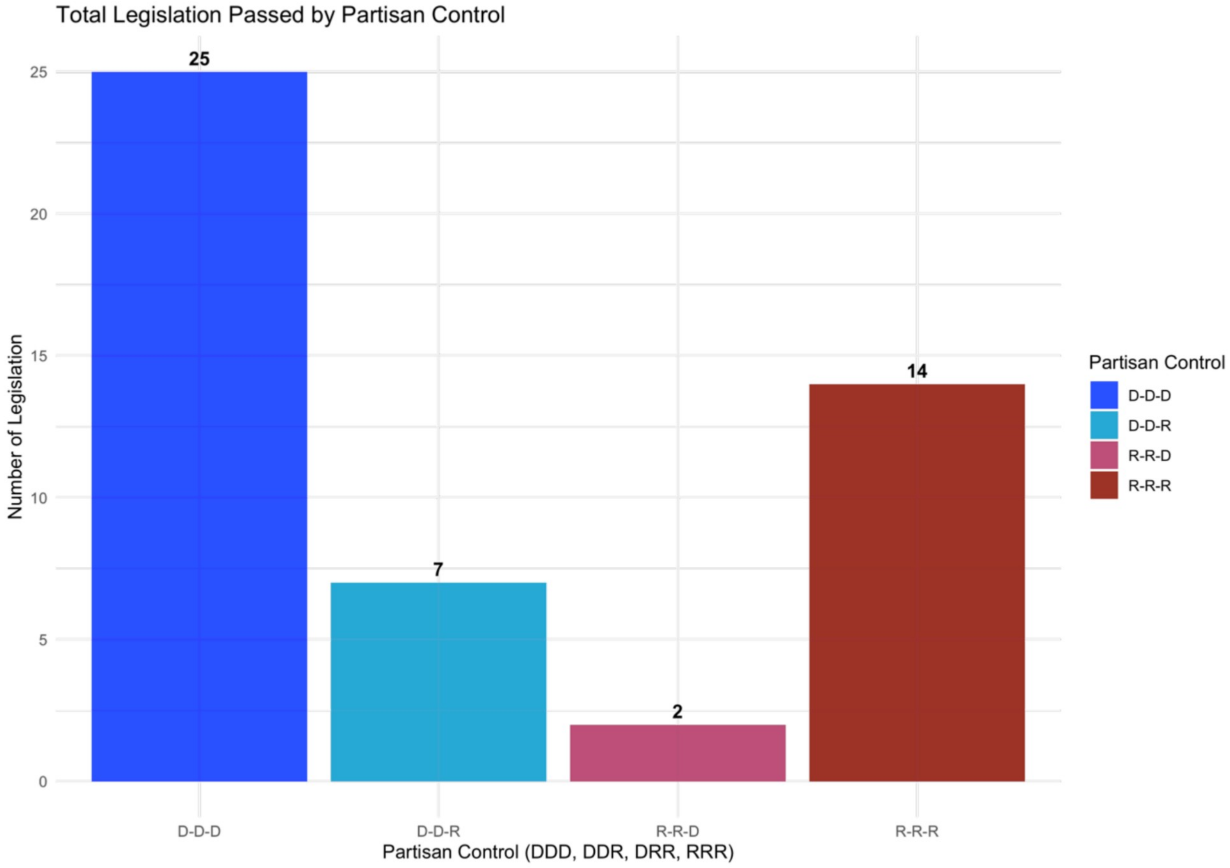

Figure 5.3. Number of total statutes enacted by partisan control of state. The X axis denotes partisan control, and the Y axis the number of passed statutes.

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A Hive Mind: Bounded Rationality and Bees

Robert Benjamin Joel Ostrom

Chapter 6: Generalized Conclusions

This dissertation research has focused on the decision-making of humans and bees in situations of imperfect knowledge, and therefore acting as boundedly rational actors. We started with the honey bee waggle dance, a unique behavior which can be used to measure colony-level decision-making (von Frisch, 1967). Specifically, we created one of the first quantifications of habitat loss on honey bee foraging, validated the honey bee waggle dance as a bioindicator for wild bee abundance, investigated the assumption that alternatives to spray pesticides are always beneficial to bees, and conducted a content analysis of state level bee statutes from 2023 to August 2024.

By quantifying the costs of habitat destruction on honey bee foraging, we demonstrated how the waggle dance could be used as a tool to assess the impact of future construction on pristine foraging land. Such assessments could be used in environmental impact surveys, state and federal infrastructure projects, housing developments in rural areas, models of future biodiversity trends, ecological restoration work, and habitat conservation initiatives. Putting a number on the effect that construction will incur on bees will allow stakeholders to make better informed and more purposeful decisions when they want to consider the welfare of the bees.

By demonstrating that the waggle dance has predictive value for native bees as well, we are able to now generalize the finding from the second chapter and the value of the bee dance for environmental assessments. Where honey bees find good forage, native bees are abundant as well. In our conservation efforts, we could therefore target good honey bee foraging areas and potentially help native bees.

Such assessments are dearly needed, as assistance for bee communities is often given in broad strokes; (The Bee Conservancy, 2024) planting more flowering plants to create a pollinator garden, reducing spray pesticide or finding alternative treatments to help bee health, etc. We demonstrate such behavior in an agricultural setting in Chapter 4, where we tested the effect of a treatment that is better for beneficials overall compared to current pesticide treatments, but has a negative impact on one likely important flower visiting bee species in particular.

Lastly, our work shows the capacity that we, the people, can help the bees. In recent years, many laws were enacted that allow us to better protect bees. Our work will give policy makers additional tools in hand to assess bee health, and to tailor laws more specifically to the needs of both managed and native bees.

Unexpectedly, in addition to the broad relevance of the work regarding bee health assessment and policy, we see a strong throughline between chapters three, four, and five in soybean. In chapter three, we see *Melissodes bimaculatus* as a dominant species in Suffolk's bee community, whose landscape happened to be made up of row crops including soybean. In chapter four, our follow up research on *Melissodes bimaculatus* in soy systems revealed that they are an important and perhaps underrecognized flower visitor (and likely pollinator) for the crop. Not only is it one of the most abundant species in soybean systems, but it was uniquely impacted by the attract and kill insecticidal netting (as compared to the other most abundant species in our capture). This indicates that plant-pollinator networks may need to be studied at an increasingly granular level, as individual life history traits of species may make them react differently than the rest of the bee community.

The under recognition of *Melissodes bimaculatus* in soybean is mirrored by the history of bees as a whole in the system. This has cascading effects, which we can see on a multi-state level. The largest contiguous bloc of states which did not pass bee statutes in 2023 to August 2024 were those whose most (or second most) important agricultural export is soybean. Even as we continue to research increasingly specific minutiae about bees, we have been caught out as boundedly rational actors. Our treatment of bees in soybean, an incredibly economically important export to these states, has been satisficing all along. The potential for future researchers to quantify the economic effect of *Melissodes bimaculatus* on soybean, perhaps utilizing a honey bee waggle dance "bee radar," can lead to the development of pest control methods suited to the crop's beneficial insects, which may then provide a measurable boost to the economy of several states. Much like how we found habitat loss can have an outsized effect on honey bee foraging behavior, introspective studies on our own behavior can yield impressive results.

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