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RESEARCH ARTICLE

Floral resource selection by wild bees and honey bees in the Midwest United States: implications for designing pollinator habitat

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Many seed mix recommendations for creating pollinator habitat are in part based on anecdotal evidence or field observations of bees visiting forbs (i.e. use). However, there is limited information on what forbs are preferred by bees, particularly in working landscapes where bee forage may be limited. We examined floral resource selection by wild bees and honey bees on grasslands in the Midwest using a 5-year dataset containing over 8,000 plant-bee interactions. We observed wild bees visiting 83 forb species, but only 14 species were significantly selected (i.e. bees visited a plant more than expected based on availability). Approximately 70% of all wild bee visitations were on native flowers, whereas only 20% of all honey bee visitations were on natives. Honey bees visited 70 forb species, but only four forbs were significantly selected. The selection ratio for each forb species was not correlated with proportion of use by wild bees or honey bees, suggesting that bee visitation data alone do not elucidate patterns of forb selection or avoidance. We then compared our resource selection results to forbs recommended by U.S. Department of Agriculture (USDA) for regional pollinator habitat plantings. Many forbs that were selected by bees in our study were also recommended by USDA; however, some USDA-recommended forbs were selected against by bees. A greater understanding of which floral resources are selected by bees can assist land managers in assessing conservation seed mixes and ultimately provide diverse, season-long pollinator forage in working landscapes.

Key words: bloom period, conservation, plant-bee interactions, seed mix, selection ratio

Implications for Practice

- Wild bees and honey bees only showed selection for two of the same forb species, suggesting land managers may need to consider separate seed mixes for wild bees and honey bees because these pollinator groups are attracted to different forbs.
- Floral selection changed throughout the growing season, particularly for wild bees. Seed mix design should account for changes in preference throughout the growing season.
- Although our results generally support U.S. Department of Agriculture-recommended forbs, we identified several forbs with limited value to either wild bees or honey bees that are currently recommended for pollinator plantings. Including unattractive forbs in conservation seed mixes may reduce the cost-effectiveness of pollinator habitat.

Introduction

Global bee declines (Potts et al. 2010) have led to a concerted effort among government agencies, private sectors, and the general public to improve habitat for bees (Wratten et al. 2012). One key habitat element for both honey bees (*Apis mellifera* L.) and wild bees (i.e. non-*Apis* bees) is flowering plants, where a lack of floral resources has been cited as a major driver of pollinator declines in agricultural regions (Williams et al. 2012; Durant & Otto 2019). The recent awareness of bee declines coupled with decreasing floral resources has led to heightened efforts to develop pollinator habitat in agro-ecosystems (Decourtye et al. 2010). In 2015, the United States created a federal strategy with goals of enhancing 7 million acres of land for pollinators, bolstering monarch butterfly (*Danaus plexippus*) populations, and decreasing honey bee annual losses (Pollinator Health Task Force 2015). To achieve these goals, multiple federal, state, and local government organizations have developed conservation programs that provide technical and financial assistance to landowners to establish pollinator-friendly conservation covers (USDA-NRCS 2015).

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With an increasing focus on providing pollinator habitat, it is important to understand which flowering species, particularly forbs, are preferred by bees so that cost-effective pollinator seed mixes can be developed. Many seed mix recommendations are based on anecdotal evidence of bee visits, but forbs may simply be highly visited because they are also highly abundant on the landscape. Such heavily utilized and very abundant forbs represent easy-to-access bee forage and can be important for generalist bees, like honey bees (Otto et al. 2017). However, abundant plant species may not always be highly visited by certain pollinator groups (Kells et al. 2001) and other less abundant forbs may be preferred by wild bees or honey bees. The idea of combining resource availability and utilization data to understand resource "preference" or "selection" has been previously emphasized in the wildlife biology literature (Johnson 1980; Alldredge et al. 1998). The concept of selection enables inferences on whether resources are used relative to their availability (Manly et al. 2002). In the case of pollinators, forb species are selected for when they are visited by bees more than expected given the forb's abundance and selected against when the forb is underused relative to its abundance (Bartomeus et al. 2016). Pollinator seed mix recommendations that take into account floral selection by bees may result in more cost-effective mixes that benefit pollinator habitat.

Few studies have examined forb selection by bees in the Midwest United States, even though agro-ecosystems in this region are critical habitat for honey bees and wild bees (see Williams et al. 2011, Morandin & Kremen 2013, and Cole et al. 2020 for studies from the Eastern United States and California). Furthermore, no studies compared bee preference data to seeding lists developed by natural resource managers that are often tasked with creating pollinator habitat. The Midwest is a crucial area for wild bees (Koh et al. 2016) and beekeepers (Hellerstein et al. 2017), and is an area targeted by government and nongovernment organizations for creating pollinator habitat. There is significant wild bee diversity in this region with well over 100 bee species (Evans et al. 2018; Vickruck et al. 2019) along with documented declines of bumble bee species in the Midwest (Grixti et al. 2009). Parts of the upper Midwest (i.e. Minnesota, North Dakota, and South Dakota) represent key summer foraging grounds for honey bees and these three states alone support approximately 33% of all honey-producing colonies in the United States (USDA-NASS 2020). The upper Midwest has also undergone significant land use change, with increasing conversion of grasslands to croplands resulting in a loss of suitable bee forage (Koh et al. 2016; Hellerstein et al. 2017). Understanding floral use and selection by bees is crucial to scientifically guide seed mixes used by many conservation organizations and to provide suitable bee forage on remaining grasslands within the upper Midwest.

One key aspect of providing high quality bee forage is understanding seasonal changes in forb utilization and selection by bees. Depending on plant phenology and bee activity across the growing season, plant-pollinator interactions and floral resource use may shift seasonally (Wood et al. 2018; Bendel et al. 2019). For example, both social and solitary wild bees collected more pollen from non-native plants in July in agricultural landscapes, whereas solitary bees collected more pollen from native plants at the beginning and end of summer (Wood et al. 2018). Seeding recommendations should account for phenology of species by considering the bloom period of forbs and bee activity to provide season-long floral resources that are critical for bee health (Vaudo et al. 2015; Williams & Lonsdorf 2018). A deeper examination into the temporal differences of forb use and selection by bees will further advise natural resource managers on how to provide season-long bee forage and ultimately improve pollinator forage options on the landscape.

We used a 5-year dataset on plant-bee interactions to quantify floral use and selection by wild bees and honey bees across a variety of land categories in the upper Midwest. We asked the following questions: (1) What forb species are highly utilized versus selected by wild bees and honey bees, and how do these change temporally across the growing season? (2) Do wild bees or honey bees visit more introduced forbs than native forbs? (3) Is there a positive association between forb utilization and selection by bees? and (4) How do seed mix recommendations for pollinator habitat developed by the U.S. Department of Agriculture (hereafter, USDA) compare to our results of forb species selected by bees? To address these questions, we calculated the proportion of use and selection ratios of bee-visited forbs. We expected that not all highly visited forbs would be selected, and that wild bees would use and preferentially select a different suite of forb species than honey bees. Across the growing season, we expected that floral selection would shift accordingly with the changing abundance of forb species and their bloom periods.

Methods

Site Selection and Sampling

This study was part of a larger research effort to quantify honey bee colony response to land use change in the Northern Great Plains (Smart et al. 2018). As part of our site selection process, we randomly selected honey bee apiary locations across a land use gradient (described in Smart et al. 2018) and randomly selected grassland sites within 4.8 km of selected apiaries to quantify bee forage availability. Whereas the results of the honey bee land use research have been previously reported (Smart et al. 2018, 2019; Simanonok et al. 2020), we have not reported on the results of our grassland surveys.

We surveyed bees and forbs from June through September 2015–2019 across 244 sites within the upper Midwest in Minnesota, North Dakota, and South Dakota (Fig. 1). Our sites were located across a variety of grassland cover types; 42% were private lands enrolled in Federal programs (i.e. Conservation Reserve Program, Conservation Stewardship Program, Environmental Quality Incentives Program, Grassland Reserve Program, or Wetlands Reserve Program), 32% were roadsides, 15% were privately-owned pastures and grasslands, 7% were on state and federal lands (i.e. National Wildlife Refuge, Wildlife Management Areas, Waterfowl Production Areas), and 4% were private lands enrolled in the Bee & Butterfly Habitat Fund

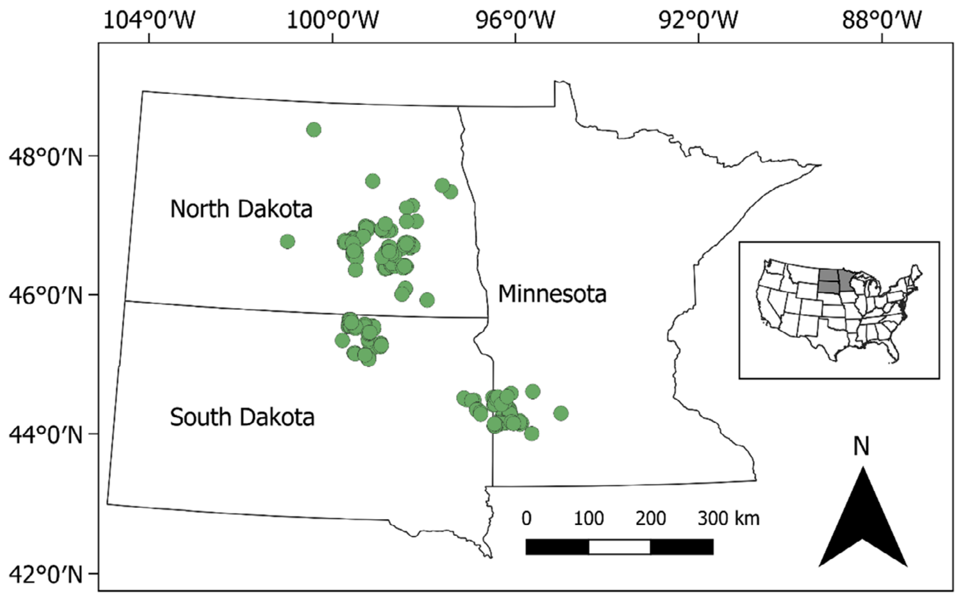

Figure 1. Locations of 244 sites within Minnesota, North Dakota, and South Dakota where bees and forb species were surveyed from 2015 to 2019. Map created using the Free and Open Source QGIS.

(https://www.beeandbutterflyfund.org). We focused much of our sampling on private lands because they constitute more than 80% of the total area in the region. At each site, 2–26 transects were randomly placed depending on site size. The 20 × 2–m transects were, on average, 66 m apart from one another within a site with at least 10 m between each other.

On each sampling day between 06:45 and 19:40 hours (97% of surveys were between 09:00 and 18:00 hours), we recorded the number of flowering stems (i.e. a stem supporting one or more inflorescences) and number of bees (wild bee vs. honey bee) observed visiting specific flowers at each transect. All stems of forbs containing open flowers were counted within each transect; we did not count non-forb species such as grasses or trees. Forbs were identified to species when possible and classified following the PLANTS Database (USDA-NRCS 2020*a*). We defined the indigenous status (native or introduced) as the status of the species in one or more of the lower 48 States (USDA-NRCS 2020*a*). Furthermore, any species referred to as a "noxious weed" are defined as a State-listed noxious weed in either Minnesota, North Dakota, or South Dakota (USDA-NRCS 2020*a*). The total number of wild bees and honey bees observed visiting specific flowers within each transect was recorded. The duration of each observation per transect varied depending on the number of flowering stems but ranged from 1 to 120 minutes (median = 3 minutes; mean = 5.9 minutes). Finally, after completing the counts of flowering stems and bees, we performed a 5-minute bee netting period while walking the transect length, where bees observed contacting the reproductive parts of a flower were hand netted, processed in a kill jar, and placed into a collection vial. Honey bees were not collected. Data collection involving wild bees (observations or netted) was not conducted in 2015.

We aimed to sample sites during three periods each year with visits separated by approximately 4 weeks in order to capture variation in forb and bee phenology across the growing season. This sampling scheme resulted in early (8 June–15 July), mid (16 July–15 August), and late (16 August–28 September) bloom periods. Due to workload and inadequate weather for sampling, some sites were sampled 1–13 days outside of the anticipated periods. Sampling effort varied from year-to-year due to fluctuating numbers of sites in the study (i.e. new sites were added while others dropped because of land ownership change or grassland conversion to cropland, property being flooded or hayed, etc.). Across all years, sampling resulted in 8,304 unique transect sampling events.

Resource Selection Ratios

Wildlife biologists have developed multiple methods for inferring and analyzing resource selection (Manly 1974; Neu et al. 1974; Johnson 1980). Here, we calculated resource selection ratios to quantify forb selection by wild bees and honey bees (Manly et al. 2002). Although we initially considered other methods that have been used to study bees and resources (e.g. preference ranking used in Williams et al. 2011), we chose selection ratios because of the ability to estimate selection with associated measures of variability for categorical resources (Manly et al. 2002). Our study can be considered "Design I" in which we are making inferences on a population of animals, with used and available resources sampled, but we did not track uniquely identified individuals (Manly et al. 2002). Due to the likelihood of changing floral abundances within a growing season influencing forb selection by bees, we report selection separately for early, mid, and late bloom periods. We calculated selection ratios at the site-level for each forb observed within a site following cluster sampling (e.g. transects) methods

(Cochran 1977; Manly et al. 2002). Within each bloom period, the selection ratio for forb species i at site k was calculated as:

$$\hat{w}_{ik} = \frac{o_{ik}}{\pi_{ik}}$$

where o_{ik} = the proportion of used units in a category (i.e. number of bee visits to a specific forb species/total bee visits to all forb species within that site) and π_{ik} = the proportion of available units in a category (i.e. number of flowering stems of a specific forb species/total flowering stems of all forb species within that site). Selection ratios were calculated separately for wild bees and honey bees. For analyses on wild bees, we summed both observed and netted bee counts. We calculated the standard error of the estimated selection ratio for each forb at each site as:

$$\text{se}(\hat{w}_{ik}) = \hat{w}_{ik}\sqrt{\left[V(\hat{o}_{ik})/\hat{o}_{ik}^2\right] + \left[V(\hat{\pi}_{ik})/\hat{\pi}_{ik}^2\right]}$$

where $V(o_{ik})$ = the variance for proportion of use and $V(\pi_{ik})$ = the variance for proportion of availability (Manly et al. 2002); these variances were computed using cluster sampling methods (Cochran 1977). After calculating selection ratios and associated measures of variability for each forb at the site level, we computed the average selection ratio for each forb within a bloom period as:

$$\bar{\text{SR}}_i = \frac{\sum \hat{w}_{ik}}{N_i}$$

where $\hat{w}_{ik}$ = the selection ratio for species i from field k and N_i = the number of fields with species i. The associated variance of the average selection ratio was computed as:

$$V(\bar{\text{SR}}_i) = \frac{1}{N_i^2}\left(\sum V(\hat{w}_{ik})\right)$$

In the above calculations, we assumed each site by year combination was an independent observation because of annual turnover in floral and bee communities. Because the goal of our study was to recommend forbs selected by bees, we calculated 90% confidence intervals (CIs) for each forb within a bloom period to ensure an inclusive list of forbs. A selection ratio greater than one with a 90% CI not overlapping one indicates the specific forb species was selected by bees whereas a selection ratio less than one with a 90% CI not overlapping one suggests the forb was selected against. If the 90% CI overlaps one, this suggests the forb species was neither selected for nor against (i.e. neutral selection). To determine forbs most utilized by bees in terms of bee visits, we calculated average proportion of use in the same manner as average selection ratios; that is, proportion of use for each observed forb at a site by year combination were averaged within each bloom period.

Data Filtering

Sites with no bees observed during a site visit within a bloom period were not included in analyses due to the inability to calculate resource selection (i.e. no use). This resulted in 55 and 57% of site visits with no honey bees and wild bees, respectively, being dropped from our analysis. We also chose not to interpret selection for forb species with fewer than five bee visits because resource selection methodology specifies that there be at least five observations in categories of used and available units (Manly et al. 2002). However, all forb species were included in analyses to accurately represent total forbs available to bees. We dropped eight roadside sites from South Dakota in 2017 and 2018 because of poor representation of sampling effort—no other sites were sampled in South Dakota in those years. We also excluded 11,845 stems out of 1.27 million total flowering stems (approximately 1% of all stems) that were only identified to genus or family level. All analyses were conducted in program R using "tidyverse" (R Core Team 2019; Wickham et al. 2019) and graphics were produced using "ggplot2" (Wickham 2016).

Correlational Analyses

To test if forb species highly utilized by bees were also highly selected by bees, we calculated Kendall rank correlation coefficients due to non-normality of variables (Quinn & Keough 2002). For wild bees and honey bees separately, we calculated average proportion of use and selection ratios from all sites within a bloom period and then ranked proportion of use and selection ratio to enable a nonparametric correlational analysis. We limited this analysis to forbs with an average proportion of use greater than or equal to 0.1 with at least five bee visits within a bloom period, representing forbs with significant visits. Analyses were conducted in program R using "stats" (R Core Team 2019).

USDA Pollinator Habitat Recommendations

To compare our list of forb species selected by wild bees and honey bees against what is commonly seeded in USDA conservation programs, we obtained documents from USDA offices in Minnesota, North Dakota, and South Dakota on what forbs are recommended as being beneficial for honey bees or general pollinators. For Minnesota, we used tables 6–9 which refer to plant species beneficial for honey bees or general pollinators (USDA-NRCS 2020*b*). For North Dakota, we used table 4 which lists recommended pollinator forbs (USDA-NRCS 2018) and a further 21 annual cover crop species listed in a Conservation Program Application (USDA-NRCS 2019*a*). For South Dakota, we used the Honey Bee Fact Sheet (USDA-NRCS 2017), but we were unable to use the Pollinator Fact Sheet (USDA-NRCS 2016) because it only gave example seed mixes and not concrete lists of recommended plants. We compared the USDA lists to our compiled list of forb selection by either wild bees or honey bees from early, mid, and late bloom periods. Similar to our resource selection ratios and correlational analyses, we did not interpret selection by bees for forbs with less than five bee visits. However, forbs with no bee visits at all and high numbers of flowering stems could be interpreted as having likely minimal to no forage value for bees. Because the selection of some forbs

Table 1. Top five forb species visited by wild bees within each early, mid, and late bloom period based on average proportion of use. Proportion of use for each observed forb at a site by year combination was calculated and then those values were averaged within a bloom period to obtain average proportion of use. The number of sites at which a forb was present could vary and is indicated by the "Total sites" column. Indigenous status in the United States is according to the PLANTS Database (USDA-NRCS 2020*a*).

Bloom period	*Scientific name*	*Common name*	*Indigenous status*	*Total sites*	*Total flowering stems*	*Total wild bees*	*Average proportion of use ± 1 Standard Error*
Early (8 June–15 July)	*Sinapis arvensis*	Charlock mustard	Introduced	2	582	8	0.76 ± 0.17
	Phacelia tanacetifolia	Lacy phacelia	Native	5	521	16	0.37 ± 0.04
	Zizia aurea	Golden zizia	Native	4	147	12	0.35 ± 0.10
	Carduus nutans	Nodding plumeless thistle	Introduced	5	339	8	0.35 ± 0.03
	Monarda fistulosa	Wild bergamot	Native	14	1,592	27	0.31 ± 0.04
Mid (16 July–15 August)	*Phacelia tanacetifolia*	Lacy phacelia	Native	7	2,714	330	0.67 ± 0.02
	Cirsium flodmanii	Flodman's thistle	Native	6	96	7	0.61 ± 0
	Grindelia squarrosa	Curlycup gumweed	Native	6	729	6	0.25 ± 0.05
	Ratibida pinnata	Pinnate prairie coneflower	Native	21	4,844	54	0.24 ± 0.03
	Cirsium vulgare	Bull thistle	Introduced	16	180	16	0.23 ± 0.03
Late (16 August–28 September)	*Helianthus maximiliani*	Maximilian sunflower	Native	38	5,046	139	0.32 ± 0.02
	Symphyotrichum novae-angliae	New England aster	Native	4	10	7	0.29 ± 0.02
	Oligoneuron rigidum	Stiff goldenrod	Native	21	683	46	0.28 ± 0.03
	Echinacea purpurea	Eastern purple coneflower	Native	28	994	30	0.27 ± 0.01
	Gaillardia aristata	Blanketflower	Native	19	1,359	42	0.25 ± 0.02

differed depending on the bloom period, we classified the forb as selected for if it was selected for during at least one bloom period and selected against if it was selected against during at least one bloom period (as opposed to neutral). If a forb species was selected for in one bloom period and selected against in another bloom period, we classified this forb as selected for since it was beneficial to bees in at least one bloom period.

Results

Resource Selection Ratios—Wild Bees

Of 232 unique forb species recorded from 2015 to 2019, we recorded 1,880 wild bees (1,416 observed and 464 netted) visiting 83 forb species from 2016 to 2019 (Table S1). Out of all visits, 71% were to native forbs and 29% were to introduced forbs (Table S1). Within each bloom period, wild bees visited between 36 and 59 forb species (Table S1). The top five most commonly visited forbs varied for each bloom period, except for *Phacelia tanacetifolia* (lacy phacelia) which was one of the most highly used forbs during both early and mid-bloom periods (Table 1). Forb species with the greatest proportion of use typically included native forbs, with the exceptions of *Sinapis arvensis* (charlock mustard), *Carduus nutans* (nodding plumeless thistle), and *Cirsium vulgare* (bull thistle) (Table 1). Out of all wild bee visits for each bloom period, 50%, 20%, and 28% (early, mid, and late, respectively) were to introduced forbs (Table S1).

Within each bloom period, wild bees visited between four and seven forb species more than expected based on the forb's availability, for a total of 14 forbs selected by wild bees (Fig. 2). Five of these forbs were introduced species—*C. nutans*, *Cirsium arvense* (Canada thistle), *C. vulgare*, *Sinapis arvensis*, and *Sonchus arvensis* (field sowthistle). Three forbs were selected during multiple bloom periods—*Gaillardia aristata* (blanketflower), *Helianthus maximiliani* (Maximilian sunflower), and *Ratibida pinnata* (pinnate prairie coneflower). The remaining forbs were visited in proportion to their availability (i.e. neutral selection; $n = 29$ [early], $n = 36$ [mid], $n = 17$ [late]) or were used less than expected based on the forb's availability (i.e. selected against; $n = 9$ [early], $n = 13$ [mid], $n = 10$ [late]; Table S1).

Resource Selection Ratios—Honey Bees

We observed 6,298 honey bees visiting 70 different forb species from 2015 to 2019 (Table S2). Out of all visits, 80% were to introduced forbs (Table S2). Within each bloom period, honey bees visited between 41 and 42 forb species (Table S2). The top five most commonly visited forbs varied less among bloom periods with honey bees (Table 2) than with wild bees (Table 1). *Medicago sativa* (alfalfa) and *Melilotus officinalis* (sweetclover) were highly visited by honey bees in each of the three bloom periods. Similar to wild bees, *Phacelia tanacetifolia* was highly visited in both early and mid-bloom periods. Out of all honey

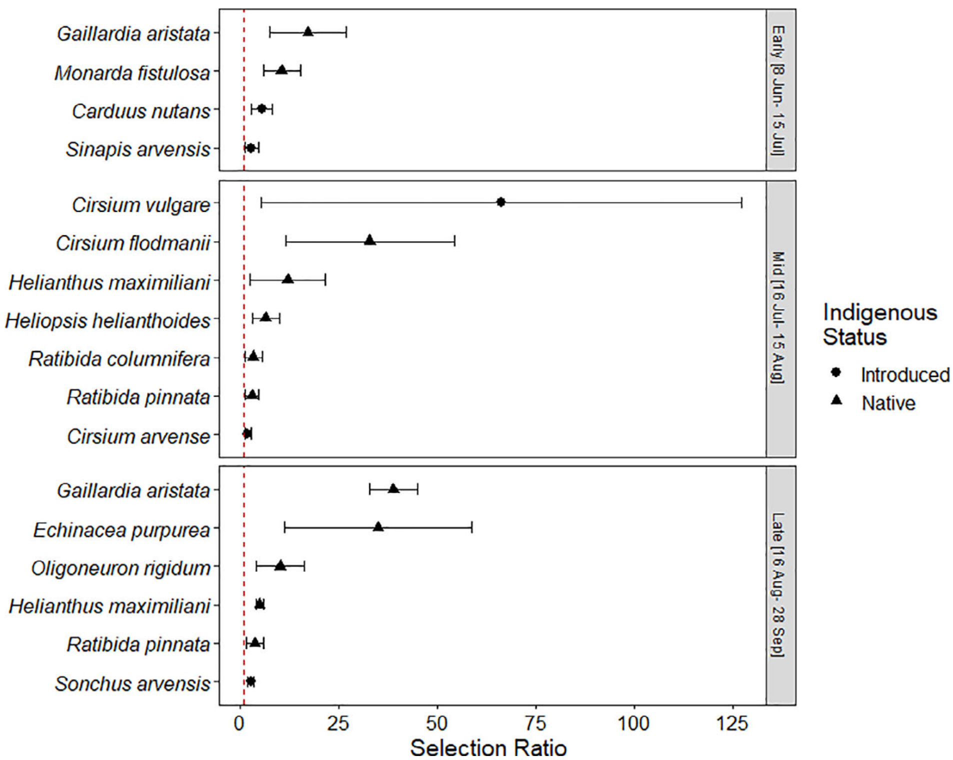

Figure 2. Estimated selection ratio ($\hat{w}_i$) with ± 90% CI for forb species significantly selected by wild bees during early, mid, and late bloom periods. Forb species are selected for when the selection ratio is greater than one (dashed red line) and results are considered significant when the 90% CI does not overlap one. Forb species that were visited as much as or less than expected based on availability are shown in Table S1. Indigenous status in the United States is according to the PLANTS Database (USDA-NRCS 2020*a*).

bee visits for each bloom period, 83%, 73%, and 82% (early, mid, and late, respectively) were to introduced forbs (Table S2).

During each bloom period, honey bees significantly selected between two and four forb species, resulting in selection of four species overall (Fig. 3). Two were native forbs (*Agastache foeniculum* [blue giant hyssop] and *Gaillardia aristata*) and two were introduced forbs (*C. arvense* and *M. officinalis*). All forbs except for *G. aristata* were selected during multiple bloom periods. Many forbs were considered to have neutral selection by honey bees during each bloom period ($n = 18$ [early], $n = 23$ [mid], and $n = 22$ [late]; Table S2). The remainder of forbs were visited less than expected based on their availability (i.e. selected against). The introduced forb, *M. officinalis*, was highly visited as well as significantly selected by honey bees during all three bloom periods (Fig. 3; Table 2). However, the native forb, *A. foeniculum*, had higher selection ratios than *M. officinalis* during early and late bloom periods. For example, *A. foeniculum* was 5.4 times more likely to be selected than *M. officinalis* from 8 June to 15 July (Fig. 3). The only forbs selected by both honey bees and wild bees were *G. aristata* and *C. arvense*.

Correlational Analyses

We found no association between proportion of use and selection ratio in any bloom period for wild bees (early: $\tau = 0.10$, $p = 0.60$; mid: $\tau = 0.26$, $p = 0.15$; late: $\tau = 0.16$, $p = 0.54$) or honey bees (early: $\tau = -0.15$, $p = 0.55$; mid: $\tau = 0.24$, $p = 0.38$; late: $\tau = 0.30$, $p = 0.20$); that is, forb species that were highly visited were not always highly selected by bees. For example, the introduced forb, *Sinapis arvensis*, was highly utilized by wild bees in the early bloom period ($o_{ik} = 0.76 \pm 0.17$), but it had a low selection ratio ($\hat{w}_{ik} = 2.90$ [90% CI: 1.18–4.62]). Other native forbs were less visited but had higher selection ratios, such as *G. aristata* ($\hat{w}_i = 17.19$ [90% CI: 7.55–26.83]), which was approximately six times more likely to be selected by wild bees than *S. arvensis* in the early bloom period (Table 1; Fig. 2). Likewise for honey bees, *Phacelia tanacetifolia* had the highest average proportion of use in early and mid-bloom periods, but we found honey bees used it either in proportion to its availability (early) or significantly less than in proportion to its availability (mid, Tables 2 & S2).

USDA Pollinator Habitat Recommendations

A total of 140 plant species were recommended by USDA for pollinator habitat seeding in Minnesota, North Dakota, or South Dakota. Of those 140 species, we observed 79 blooming within our 5-year dataset. We recorded wild bees and honey bees on 52 and 48 USDA-recommended species, respectively (Table 3). Plant species with no bee visits are noted in

Table 2. Top five forb species visited by honey bees within each early, mid, and late bloom period based on average proportion of use. Proportion of use for each observed forb at a site by year combination was calculated and then those values were averaged within a bloom period to obtain average proportion of use. The number of sites at which a forb was present could vary and is indicated by the "Total sites" column. Indigenous status in the United States is according to the PLANTS Database (USDA-NRCS 2020*a*).

Bloom period	*Scientific name*	*Common name*	*Indigenous status*	*Total sites*	*Total flowering stems*	*Total honey bees*	*Average proportion of use ± 1 Standard Error*
Early (8 June–15 July)	*Phacelia tanacetifolia*	Lacy phacelia	Native	8	809	38	0.5 ± 0
	Melilotus officinalis	Sweetclover	Introduced	153	87,176	1,152	0.46 ± 0.01
	Sinapis arvensis	Charlock mustard	Introduced	3	671	29	0.37 ± 0
	Medicago sativa	Alfalfa	Introduced	156	219,808	697	0.32 ± 0.01
	Agastache foeniculum	Blue giant hyssop	Native	8	1,068	75	0.30 ± 0.03
Mid (16 July–15 August)	*Phacelia tanacetifolia*	Lacy phacelia	Native	7	2,513	228	0.42 ± 0.01
	Melilotus officinalis	Sweetclover	Introduced	149	44,027	627	0.41 ± 0.01
	Medicago sativa	Alfalfa	Introduced	137	167,599	522	0.35 ± 0.01
	Monarda fistulosa	Wild bergamot	Native	49	11,064	137	0.22 ± 0.01
	Cirsium arvense	Canada thistle	Introduced	135	11,821	152	0.21 ± 0.01
Late (16 August–28 September)	*Agastache foeniculum*	Blue giant hyssop	Native	3	264	9	0.67 ± 0
	Linaria vulgaris	Butter and eggs	Introduced	4	2,532	5	0.36 ± 0.05
	Medicago sativa	Alfalfa	Introduced	82	75,784	426	0.35 ± 0.01
	Melilotus officinalis	Sweetclover	Introduced	98	12,624	630	0.28 ± 0.01
	Oligoneuron rigidum	Stiff goldenrod	Native	22	1,664	26	0.27 ± 0.03

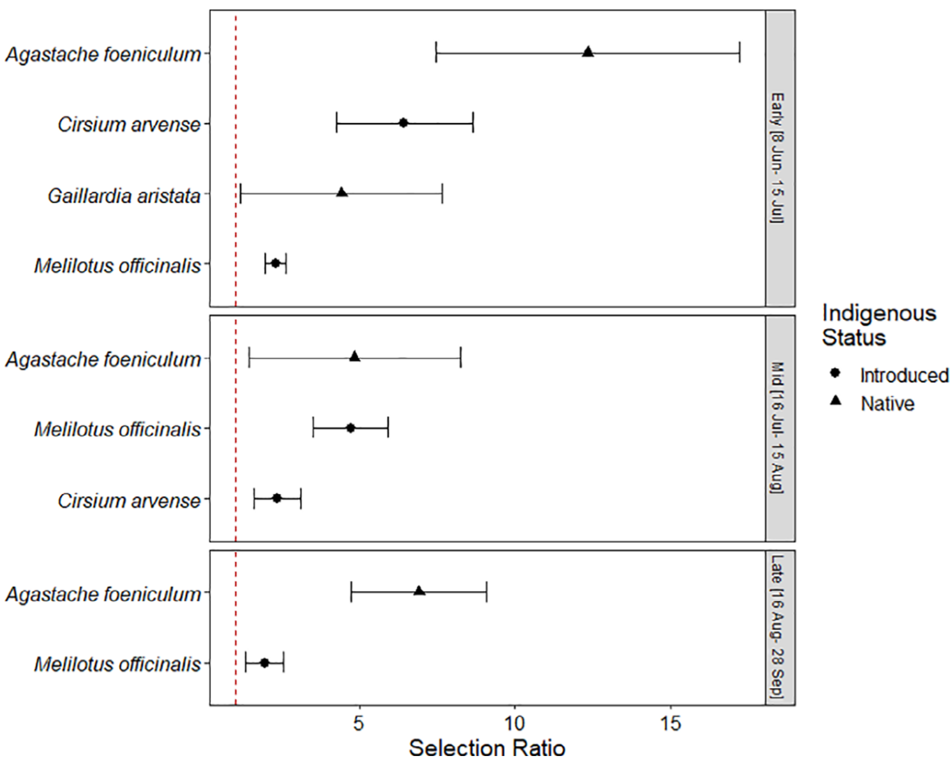

Figure 3. Estimated selection ratio ($\hat{w}_i$) with ± 90% CI for forb species significantly selected by honey bees during early, mid, and late bloom periods. Forb species are selected for when the selection ratio is greater than one (dashed red line) and results are considered significant when the 90% CI does not overlap one. Forb species that were visited as much or less than expected based on availability are shown in Table S2. Indigenous status in the United States is according to the PLANTS Database (USDA-NRCS 2020*a*).

Table 3. The number of USDA-recommended plant species along with their respective selection by wild bees or honey bees within our study, where "Selected for" = visited more than expected given the availability of the plant; "Selected against" = visited less than expected given the availability of the plant; and "Neutral" = visited in proportion to the plant's availability. Some plant species were observed but had fewer than five bee visits (unable to assess selection) or no bees were seen visiting that species ("No bees observed"), whereas some plants were not observed at all ("Plant not observed").

Plant species selection	*Wild bee*	*Honey bee*
Selected for	8	3
Selected against	9	17
Neutral	12	10
Fewer than five bees observed	23	18
No bees observed	22	31
Plant not observed	66	61

Table S3. Out of plant species observed during our study ($n = 79$), wild bees visited 25% of the recommended plants as much or more than expected based on the plant's availability (i.e. neutral or selected for), with only 11% of species considered selected against (Table 3). Honey bees visited 16% of the recommended plants as much or more than expected based on the plant's availability (Table 3). Of all USDA-recommended species, 17 were considered selected against by honey bees. All forb species that we concluded were selected by wild bees or honey bees were listed within one or more of the three-state's USDA recommendations, with the exceptions of *Cirsium flodmanii* (Flodman's thistle; selected by wild bees), *Sinapis arvensis*, and four noxious weed species (*C. arvense*, *C. vulgare*, *C. nutans*, and *Sonchus arvensis*). A complete comparison between our selection ratios and USDA-recommended plants is found in Table S3.

Discussion

Given the global decline of bees (Potts et al. 2010) and the United States goal of enhancing pollinator habitat in working landscapes (Pollinator Health Task Force 2015), it is crucial to understand floral selection by bees to maximize the effectiveness of pollinator habitat. Our research highlights forb species most commonly visited by wild bees and honey bees in the upper Midwest, as well as forbs that are visited in greater proportion than expected based on availability. Our study also revealed the number of visits a forb species receives is not associated with higher selection by either wild bees or honey bees, suggesting there is a need to place greater emphasis on forb preference by bees when developing seed mixes for pollinator habitat. If decision-making for pollinator habitat is solely based on the number of bee visits to a forb species, land managers may be missing a key piece of information on what forbs are preferentially selected by bees. However, highly abundant forbs such as *Medicago sativa* may be important forage plants for honey bees and honey production (Gallant et al. 2014), even if they are not considered selected for by honey bees. The limitation of resource selection functions of highly used and abundant resources has been recognized elsewhere (Garshelis 2000). Demonstrating selection of an abundant resource is more challenging because selection functions assume the more available a habitat or resource is, the more likely an animal should be to use it. However, this assumption may not hold for highly abundant resources (Garshelis 2000), such as *M. sativa*.

The differences we observed in wild bee versus honey bee floral visitation and selection suggest pollinator habitat seed mixes may need to be tailored based on whether the primary objective is providing forage for honey bees, or habitat for wild bees. Whereas our research suggests dense stands of monotypic flowers may be highly advantageous for honey bees, more diverse mixes may be required to support wild bees. For example, *M. sativa* and *Melilotus officinalis* were consistently among the top five most visited forbs within each bloom period for honey bees. These two forbs are also some of the most abundant forbs in our study region (Smart et al. 2021) which corroborates the idea that honey bees may be more likely to use the most abundant floral resources because of their social structure and ability to communicate locations of rewarding floral patches to fellow foragers (Leonhardt & Blüthgen 2012). Likewise, Nürnberger et al. (2019) showed that honey bees foraged on just a few forb species in landscapes with high floral abundance, suggesting honey bees can develop an optimal diet with a mix of fewer plant species. Thus, diverse plantings of native forbs typical of pollinator plantings such as the Conservation Reserve Program's Conservation Practice-42 Pollinator Habitat may not provide maximum benefit for honey bees. Conversely, uniform stands of *M. sativa* do not represent ideal wild bee habitat. Ultimately, land managers will need to consider conservation objectives along with the biological impact, financial cost, regional growing conditions, and soil type when designing seed mixes for conservation programs.

Floral selection by bees can vary depending on the season (Wood et al. 2018), time of day (Vaudo et al. 2014), or specific species of pollinator (Bartomeus et al. 2016). Although we were unable to assess some of these sources of variation, we examined how selection by wild bees and honey bees changed across the growing season. Honey bees did not exhibit much variation in floral selection across bloom periods, with *Agastache foeniculum* and *M. officinalis* being selected in every bloom period. Wild bees, on the other hand, selected completely different forbs in each bloom period except for *Gaillardia aristata*, suggesting temporal effects of floral selection. These seasonal shifts in forb selection by wild bees mirror documented seasonal changes in plant-pollinator networks which are likely driven by temporal turnover of bees and floral resources (Bendel et al. 2019). Our study corroborates the idea of providing season-long, diverse floral resources which has been emphasized in scientific literature (Vaudo et al. 2015; Williams et al. 2015) and regional planting guides (Ley 2008).

We found that both wild bees and honey bees selected introduced forbs in multiple bloom periods, but honey bees selected a greater proportion of introduced forbs than wild bees (50% vs. 35%, respectively). Our finding of bees selecting certain introduced forbs is consistent with other research highlighting the importance of these plants for native and managed bees in working landscapes (Morandin & Kremen 2013). Our study region represents grassland-agriculture gradients within the upper Midwest where non-native forbs are more common than native forbs on conservation grasslands (Smart et al. 2021). Introduced forbs, such as *M. sativa* and *M. officinalis*, are reflective of the agricultural-dominated landscape and lands impacted by anthropogenic influences in our study region. Whereas honey bees exploited these common floral resources throughout all bloom periods, we found that wild bees only visited specific introduced species during certain bloom periods. Additionally, wild bees showed selection for more native forbs than introduced forb species, which emphasizes the need to tailor seed mixes based on whether the primary objective is providing wild bee or honey bee forage. A possible limitation is that we did not adequately sample native prairie remnants that are managed to maintain pre-European settlement conditions and hence we may have missed additional native forbs selected by wild bees but are none-the-less exceptionally rare on the landscape. Some conservation groups would consider including these rare, native species in seed mixes, but these species are unlikely to be included in most conservation seed mixes available to landowners because of cost and seed availability. Thus, we believe our results are generalizable to a vast majority of conservation programs available to landowners in our study region.

With 1.6 million hectares (4 million acres) of private lands enrolled in USDA conservation programs in our three-state study region (USDA-NRCS 2019*b*), our results are relevant to land managers tasked with developing pollinator seed mixes. By comparing our list of selected forbs to recommendations for pollinator habitat on USDA conservation program lands, we found that USDA-recommended forbs were generally consistent with our findings. The only species missing from USDA recommendations were *Cirsium flodmanii*, which was selected by wild bees during the mid-bloom period, and five introduced forbs, four of which were noxious weeds. The Federal Noxious Weed Act was established to control the spread of noxious weeds and prevents any transport or seeding of these species (USFWS 1975). Many publications on pollinator plantings discourage the use of introduced species and instead focus on native species to fulfill ecological goals such as soil conservation and resilience to weed invasion (USDA-NRCS 2015; Havens & Vitt 2016). However, our finding of noxious weeds being highly utilized or selected by bees in our study region highlights a benefit of noxious weeds to bees in disturbance-prone landscapes. Although certain bee groups can prefer invasive thistles (Russo et al. 2019), there is a general stigma against thistles on working landscapes. The potential benefit of native thistles to pollinators warrants further study and consideration in seed mixes especially with our finding of *C. flodmanii*, a native thistle, being highly visited and selected by wild bees.

Although there were 140 USDA-recommended plants within our three-state study region for pollinator habitat, we did not detect approximately 45% of those species across our 5-year study. It is possible some USDA-recommended plants are either failing to become established once seeded or are not being included in USDA conservation seed mixes at all, potentially due to high seed costs. On the other hand, we observed several USDA-recommended plants that were common yet had no bee visits or were selected against by bees, which is suggestive of minimal to no forage value for bees. For example, *Rudbeckia hirta* (blackeyed Susan) and *Symphyotrichum ericoides* (white heath aster) are forbs recommended in North Dakota for pollinators (USDA-NRCS 2018). We observed several thousand flowering stems of each species, yet concluded these forbs were selected against by wild bees or honey bees in at least one bloom period. Forb species with high numbers of flowering stems, yet no bee visits or very low bee visits warrant further investigation of their inclusion on lists of forbs recommended for pollinator plantings. In addition, a promising avenue of future research would be examining what forbs were seeded on USDA conservation program lands, and then comparing seed specifications to forbs that established and were ultimately selected by pollinators.

Our study on floral resource selection had several important strengths and limitations. We quantified selection ratios of forbs separately across all sites for our analysis. This allowed us to account for how differences in plant communities across sites may affect floral selection by bees. Although there are different approaches to calculating selection ratios (Alldredge et al. 1998), this approach is highly conservative because of the inherent differences in flower availability across sites. For a forb species to be considered selected, it needed to exhibit high selection ratios across multiple sites. Thus, our results are spatially robust to grasslands of the upper Midwest. Even though our list of highly visited and selected forbs is comprehensive for our region, we may be masking certain preferences that could be revealed by analyzing wild bees to species. Similar to Urbanowicz et al. (2020), a limitation of our study was that we grouped all wild bees together and may have missed important information on forbs selected by specific bee species or other non-bee floral visitors of conservation concern. This may be of interest for conservation organizations concerned with single-species success, such as pollinator plantings focused on the benefit of the endangered rusty patched bumble bee (*Bombus affinis*) or the monarch butterfly. However, most pollinator plantings are meant to benefit a wide breadth of both native and managed pollinators (USDA-NRCS 2015), and species-specific conservation plantings are seldom implemented in our region. Understanding the overall floral selection by different bee groups is important to inform multi-species habitat conservation, but future research is needed to understand resource selection by specialist bees.

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Supporting Information

The following information may be found in the online version of this article:

Table S1: Average selection ratios with 90% confidence intervals for all forbs with wild bee visits from 2016–2019 analyzed separately by bloom period.
Table S2: Average selection ratios with 90% confidence intervals for all forbs with honey bee visits from 2015–2019 analyzed separately by bloom period.
Table S3: Plants recommended by the U.S. Department of Agriculture for pollinator plantings in Minnesota, North Dakota, or South Dakota.

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