Cavity-nesting Bee Nesting Success Across Gradients of Floral Resources and Land Cover

Michael P. Simanonok[1*], Mary Powley[1], and Clint R.V. Otto[1]

Abstract - Floral resource limitation and habitat loss resulting from land-cover change can influence the reproductive success of solitary cavity-nesting bee species. However, surprisingly scant knowledge exists on the population dynamics and demographics for most bee species, and even less knowledge exists regarding how floral resources or land cover may influence nesting rates and nesting success. We measured nesting rates and nesting success for a community of cavity-nesting bees across gradients of floral abundance, floral richness, and land cover in the Prairie Pothole Region of North Dakota. Specifically, we were interested in studying how nest occupancy and nesting success of cavity-nesting bees were related to nests located near managed grassland, wetlands, and woodlands. Surprisingly, we observed no relationships between bee nesting metrics and nearby land cover. We also observed no significant influence of floral abundance or floral species richness on any recorded bee nesting metrics. While other research has found variability in floral resources across land cover within the Prairie Pothole Region, we were unable to detect strong influences of either floral resources or land cover on nesting of solitary cavity-nesting bee species in our study system.

Introduction

The Prairie Pothole Region (PPR) of the Northern Great Plains is an area typified by wetland "potholes" intermixed among remnant prairie in an agriculturally dominated system. Despite the PPR hosting up to 40% of the United States' managed honey bee apiaries (Otto et al. 2016), the region's native bee communities are noted as being particularly understudied (Evans et al. 2018). Agricultural land use in the region is intensifying, which reduces available floral resources and habitat for pollinators (Otto et al. 2018). Habitat loss is by far the most significant factor contributing to declining native bee abundances across ecosystems (Winfree et al. 2009). Of particular concern are native cavity-nesting bees, a taxonomic guild of bees that nest in standing dead wood, coarse woody debris, large pithy stems, and other substrates. In the agriculturally dominated landscape of the PPR, these nesting resources persist primarily within wooded areas, wetlands, and pastures (Evans et al. 2018). Although we may expect that cavity nesting habitat may naturally be limited in a landscape that is heavily dominated by agriculture (Rashford et al. 2011), even anthropogenic habitats that may be likely cavity-nesting refugia, such as shelterbelts, are being removed from the landscape (Burke et al. 2019).

In addition to potential limitations of available nesting habitats, most cavity-nesting bees are solitary, and, once their nests are established, they are central-place foragers that typically only forage for floral resources within a few hundred meters of their nests (~250–600 m; Gathmann and Tscharnke 2002, Zurbuchen et al. 2010). Thus, the proximity, quality, and quantity of both nesting and floral resources are key for solitary cavity-nesting bees (Westrich 1996). Floral resource limitation from habitat loss can impact the reproductive capacity of solitary cavity-nesting bees of both generalist and specialist species (Roulston and

[1]Northern Prairie Wildlife Research Center, US Geological Survey, 8711 37th St. SE, Jamestown, ND 58401 USA. *Corresponding author: msimanonok@usgs.gov.

Goodell 2011). Despite such concerns for cavity-nesting bees in anthropogenic landscapes, there is surprisingly scant knowledge on the population dynamics and demographics for most bee species, particularly on how nesting and survival can vary with floral resources (Palladini and Maron 2014, Woodard and Jha 2017) or how floral resources can influence nesting rates and nesting success (Persson et al. 2018, Simanonok and Burkle 2019, Westerfelt et al. 2015). One reason for this knowledge gap is that cavity-nesting bees are notoriously difficult to locate in their natural nesting habitats (Roulston and Goodell 2011). Thus, researchers often focus on a single species or use artificial trap nests (e.g., Persson et al. 2018, Staab et al. 2018), limiting our understanding of solitary bee demographics. Many studies focused on individual bee species have found that floral resource availability is positively associated with nest occupancy and other reproductive metrics for a variety of species (Franzén and Nilsson 2013, Minckley et al. 1994, Peterson and Roitberg 2006, Steffan-Dewenter and Schiele 2008). For example, reproductive output of *Osmia lignaria* Say (Blue Orchard Bee), a generalist species of orchard bee native throughout most of North America and reared for agricultural pollination, decreases with greater distance from floral resources (Williams and Kremen 2007). Nest occupancy and reproductive output of *O. lignaria* was also found to increase with increasing native floral abundance and richness but decreased with increasing abundance of non-native flora (Palladini and Maron 2014). Abundant bee-friendly crops can, in some instances, enhance the number of broods produced (Dainese et al. 2018); however, the presence of wild forbs in addition to such pollinator-friendly crops increases reproductive output of solitary bees (Klaus et al. 2021). Furthermore, sex determination in solitary bee species can also depend on available floral resources, with evidence that greater quality and/or quantity of food can result in more female offspring (Fitch et al. 2019, Kim 1999, Seidelmann et al. 2010). This body of work suggests that, although some species may be more likely to be limited by nesting habitat availability (Steffan-Dewenter and Schiele 2008), floral abundance and richness have significant influences on nesting rates and nesting success of solitary cavity-nesting bees.

Our goal was to investigate how nesting rates (i.e., nest occupancy) and success (i.e., adult bee emergence, bee species richness, and sex ratio) of solitary cavity-nesting bees vary with abundance and diversity of floral resources in proximity to artificial nest blocks located in grasslands of the PPR. Furthermore, we were interested in studying how nest occupancy and nesting success of cavity-nesting bees varied in relation to nearby land cover of grassland, wetland, and woodland. Since 2015, the PPR has been the focus of several large-scale studies regarding the distribution of pollinators and floral resources (e.g., Simanonok et al. 2021, Smart et al. 2021). However, no studies to date in this region have investigated how floral or nesting resource availability affects native-bee reproductive output, an important yet understudied component of bee demography. We measured nesting rates and nesting success for a community of cavity-nesting bees across gradients of floral abundance, floral richness, and land cover. Specifically, we wanted to assess (1) how bee nesting occupancy and success related to floral abundance and richness and (2) how bee nesting occupancy and success may change based on areas of pollinator-beneficial land covers nearby (grassland, wetland, and woodland). We expected that greater floral abundance and richness would positively influence nest occupancy, nesting success, and species richness. We also expected that land cover with some floral resources (grassland) may be associated with increased nesting success, while land cover more likely to have cavity-nesting bee nesting resources (woodland and wetland) may be associated with increased nest occupancy and species richness, as cavity-nesting bees may be more likely to disperse to our nest blocks.

Methods

Study Area

   We leveraged existing floral data collected across the PPR (Otto et al. 2020, Smart et. al 2021) to identify areas with a range of floral resources throughout the growing season in North Dakota, USA. These areas span a variety of land uses focused on covers that provide bee forage, such as Bee and Butterfly Habitat Fund plantings (https://www.beeandbutterfly-fund.org/), Conservation Reserve Program fields planted with perennial covers, and prairie restoration fields at Arrowwood National Wildlife Refuge as well as two pollinator plantings on the Northern Prairie Wildlife Research Center (NPWRC) campus in Jamestown, North Dakota. We used previously available data (Otto et al. 2020, Smart et al. 2021) to select study transects that represented a gradient of floral resources to ensure we had a uniform distribution of transects with low, medium, and high flower abundance (Smart et al. 2021) and that were logistically feasible to sample multiple times throughout the season. This design resulted in a total of 48 transects selected for bee nesting and floral data collection. Each transect was 2 × 20 m and was oriented north-to-south. Most transects were located within or near Stutsman County, North Dakota (Fig. 1). Nearest neighbor distance among transects varied widely (minimum = 19.2 m, maximum = 10,399.0 m, mean = 448.5 m, SE = 221.9 m) as a result of fields available for this study.

Data Collection

   Three times over the course of the summer in 2019, we identified flowering plants to species and quantified floral abundance (number of floral stems for each species) for each transect. Sampling windows for floral transects were early season (16 June–15 July), mid-
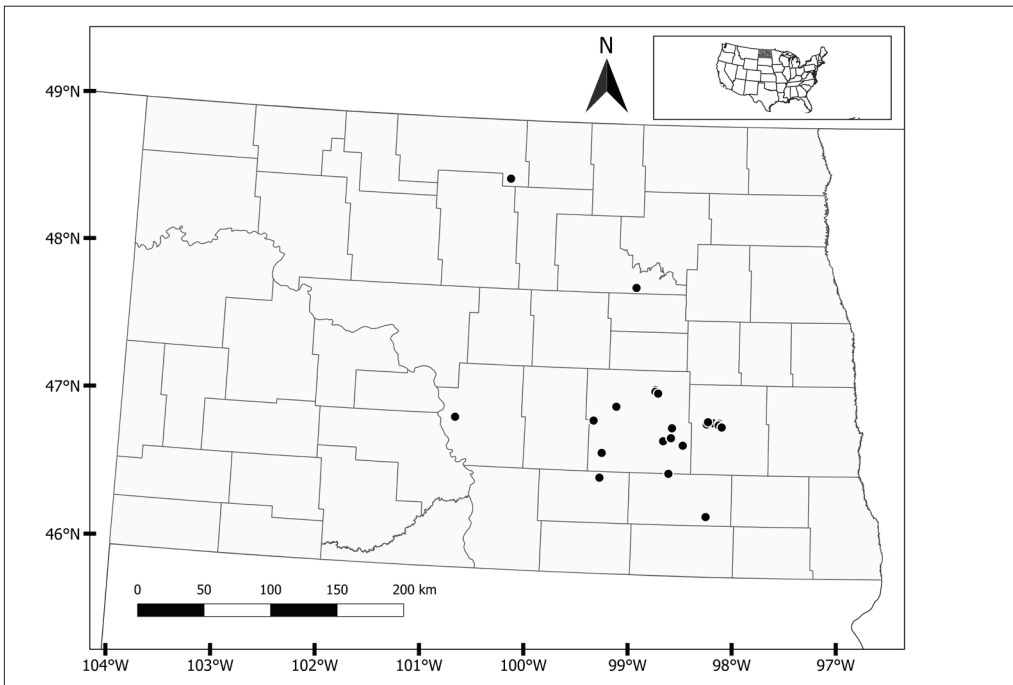

Figure 1. Map of the study area within North Dakota. Each point represents the location of one bee nest block from this study. Lines within state boundary are county borders.

season (16 July–15 August), and late season (16 August–15 September). Because bee nest blocks were present at the transects during multiple sampling periods, our counts of floral stem abundance and richness are totaled per transect for the entire season.

Most work regarding solitary cavity-nesting bees is performed by passive sampling via artificial bee nest blocks (i.e., trap nests), which can act as a proxy for the cavity-nesting bees' natural habitats and provide a variety of data regarding cavity-nesting bees (Staab et al. 2018). We constructed bee nest blocks out of untreated 0.1 m × 0.1 m (4″ × 4″) Douglas-fir cut to a length of 0.3 m (12″). We drilled 21 holes, each 9.5-mm (3/8″) diameter and ~76.2 mm (3″) deep, in one side of each nest block. While cavity size can influence the suite of bee species that occupy trap nests, we selected a single cavity size as a logistical constraint based on available materials and budget. Within each hole, we placed parchment paper, cut to size, to allow for removal of nests at the end of the season. Nest blocks were secured vertically to t-posts with zip ties at a height of ~1 m, with cavity entrances facing southeast. Nest blocks were deployed to each of the 48 transects in early summer 2019 (23 May 2019 to 15 July 2019, Table S1 in Supplemental File 1, available online at https://eaglehill.us/prnaonline/suppl-files/prna-010e-simanonok-s1.pdf) and allowed to remain in place until late summer when they were collected (21 August 2019 to 9 October 2019, Table S1). Date variability in deployment and collection was due to logistical constraints, and all nest blocks remained at transects for a minimum of 2 months.

After the third floral count, nest blocks were removed from the field. Occupied cavities were counted ($n = 214$), removed from nest blocks, and placed into individual, vented, plastic vials where they were overwintered in an uninsulated storage building at NPWRC. Nests not easily removed from their blocks (77 of the total 214) were overwintered in their blocks to preserve the nest and decrease the chance that damage from handling would influence emergence success. Most bee species in temperate regions require seasonal temperature cues for the initiation and/or termination of diapause to complete development (e.g., Forrest and Thomson 2011). Thus, leaving the nests exposed to ambient conditions throughout fall and winter is a common practice in similar studies seeking to approximate natural bee emergence responses (e.g., Simanonok and Burkle 2019). Beginning in April 2020, we periodically checked nests for emerging adult bees. When emergence was first detected, nests were moved indoors to room temperature conditions (~22 °C) where they were checked approximately daily for emergence. Emerged bees were captured, euthanized via cyanide kill-jars, and identified to species by using a combination of appropriate keys (e.g., Michener et al. 1994, Sheffield et al. 2011) and comparison with NPWRC reference collections. Because cavity-nesting bees often provision several individual larval cells end-to-end within a cavity, we continued to observe parchment paper nests and nest blocks for emergence approximately daily until October 2020. All specimens collected from this study were preserved and are maintained in collections at NPWRC. We considered bee metrics at the nest-block level, recording the number of occupied cavities out of 21 possible in each nest block, the number of bees that emerged, the proportion of emerged bees that were female, and bee species richness. We did not consider cavities as occupied if there was any evidence of non-bee invertebrates in the cavity (e.g., wasps, earwigs, spiders).

We extracted land-cover data from the 2019 National Agricultural Statistics Service Cropland Data Layer ([CDL]; USDA NASS 2020) using the 'raster' (Hijmans 2021) and 'rgdal' R packages (Bivand et al. 2021) to quantify land cover within 500 m of each nest block. We selected 500 m as an ecologically relevant distance for solitary cavity-nesting bees because most species typically do not forage beyond a few hundred meters after establishing their nests (Gathmann and Tscharntke 2002) and thus may be more influenced by local, as opposed to landscape-level, factors (Hopfenmüller et al. 2014, Simanonok and

Burkle 2019). We calculated the number of hectares of land cover from the CDL binned together into categories of grassland (Other Hay/Non Alfalfa, Sod/Grass Seed, Fallow/Idle Cropland, and Grassland/Pasture), wetland (Woody Wetlands and Herbaceous Wetlands), and woodland (Deciduous Forest, Evergreen Forest, and Shrubland). We did not explicitly consider cropland in our analyses, as the amount of cropland nearby is generally negatively correlated with the amount of grassland and other beneficial land-cover types. We repeated these analyses using the same methodologies and models for a 1,500-m buffer to account for the possibility of a landscape-scale response.

Data Analysis

We used generalized linear models (GLMs) to test how bee nest occupancy and emergence related to floral abundance and richness and how bee nest occupancy and emergence might change based on the area of pollinator-benefiting land cover. For each of our response variables (nest occupancy, bee species richness, number of emerged bees, and proportion of bees that were female), we built a GLM with the explanatory variables of floral stem abundance, floral species richness, grassland area, wetland area, woodland area, and nest-block deployment date. Nest occupancy was assessed as the proportion of occupied cavities out of 21 possible per block and was tested using a binomial GLM. Likewise, the proportion of emerged bees that were female was tested using a binomial GLM. Bee species richness and the number of emerged bees were tested using a GLM with Poisson error distribution; however, the model for the number of emerged bees showed overdispersion. Thus, we used a quasi-Poisson distribution for the number of emerged bees model. For bee species richness, the number of emerged bees, and the proportion of bees that were female, only nest blocks with occupied cavities (38 of 48 nest blocks) were included in the models. All analyses were conducted in the statistical software R (version 4.0.5; R Project for Statistical Computing, Vienna, Austria).

Results

We had 214 occupied nesting cavities out of the 1,008 cavities available, yet only 152 total bees emerged. The proportion of emerged bees being female was 0.46. Of the 152 bees that emerged, 116 emerged from nests that were stuck in nest blocks. We identified 6 species (*Coelioxys funerarius* Smith [3 individuals], *Megachile brevis* Say [Short Leafcutter] [1 individual], *Megachile centuncularis* [L.] [Patchwork Leafcutter Bee] [12 individuals], *Megachile pugnata* Say [Pugnacious Leafcutter] [3 individuals], *Megachile relativa* Cresson [Golden-tailed Leafcutter] [108 individuals], *Megachile rotundata* [Fabricius] [Alfalfa Leafcutting Bee] [22 individuals]) and 1 morphospecies (*Osmia* sp.) (3 individuals). Cavity occupancy ranged from 0 to 21 of 21 possible cavities per block (mean 4.46 ± 0.76 SE), while emergence ranged from 0 to 39 individual bees per block (mean 3.17 ± 1.14). Overall, at least one adult bee successfully emerged from 14 of our 48 nest blocks (29%); however, 10 of 48 nest blocks had no occupied cavities (21%).

We detected no significant relationships between nest cavity occupancy, emergence, bee species richness, or proportion of emerged bees that were female and floral abundance or floral richness (Table 1; Fig. 2). Similarly, we detected no relationships of nest cavity occupancy, bee species richness, number of emerged bees, or the proportion of emerged bees that were female with area of grassland, wetland, or woodland within 500 m of a nest block (Table 1; Fig. 3). Results at the 1500-m scale were not qualitatively different from those at the 500-m scale, and thus we include them as a supplement (see Table S2 in Supplemental File 1).

Discussion

We sought to assess how nesting rates and emergence of solitary cavity-nesting bees may vary in response to floral resources and local land cover; however, we observed no relationships with floral abundance or floral species richness. Similarly, we also observed no relationships between bee nesting metrics and grassland, wetland, or woodland land cover.

Table 1. Model outputs for generalized linear models testing the proportion of occupied cavities, bee richness, number of emerged bees, and proportion of emerged bees that were female against floral richness, floral abundance, area of grassland (ha), area of wetland (ha), area of woodland (ha), and deployment date of each nest block. Responses of floral abundance and richness were measured at the nest-block level, while areas of grassland, wetland, and woodland were measured within 500 m of each nest block. Bee richness, number of emerged bees, and the proportion of bees that were female only include nest blocks with occupied cavities (38 of 48 blocks).

| Occupied Cavities	Estimate	SE	z	P
Floral Richness	0.02	0.08	0.24	0.81
Floral Abundance	$4.22e^{-5}$	$2.89e^{-4}$	0.15	0.88
Grassland	-0.03	0.03	-0.94	0.35
Wetland	-0.07	0.07	-1.00	0.32
Woodland	0.05	0.48	0.11	0.92
Deployment Date	-0.01	0.03	-0.45	0.65
Bee Richness	**Estimate**	**SE**	**z**	**P**
Floral Richness	0.04	0.06	0.55	0.58
Floral Abundance	$1.22e^{-4}$	$2.11e^{-4}$	0.58	0.56
Grassland	-0.02	0.02	-0.95	0.35
Wetland	-0.03	0.04	-0.77	0.44
Woodland	-0.17	0.37	-0.47	0.64
Deployment Date	0.01	0.02	0.39	0.70
Number Emerged Bees	**Estimate**	**SE**	**t**	**P**
Floral Richness	-0.02	0.09	-0.19	0.85
Floral Abundance	$1.25e^{-4}$	$3.68e^{-4}$	0.34	0.74
Grassland	-0.05	0.03	-1.76	0.09
Wetland	-0.10	0.06	-1.66	0.11
Woodland	-0.38	0.68	-0.55	0.58
Deployment Date	$-3.36e^{-3}$	0.03	-0.11	0.91
Proportion Female Bees	**Estimate**	**SE**	**z**	**P**
Floral Richness	0.14	0.11	1.25	0.21
Floral Abundance	$4.47e^{-5}$	$3.31e^{-4}$	0.14	0.89
Grassland	-0.01	0.03	-0.17	0.87
Wetland	-0.01	0.08	-0.18	0.86
Woodland	0.18	0.58	0.31	0.76
Deployment Date	0.03	0.05	0.74	0.46
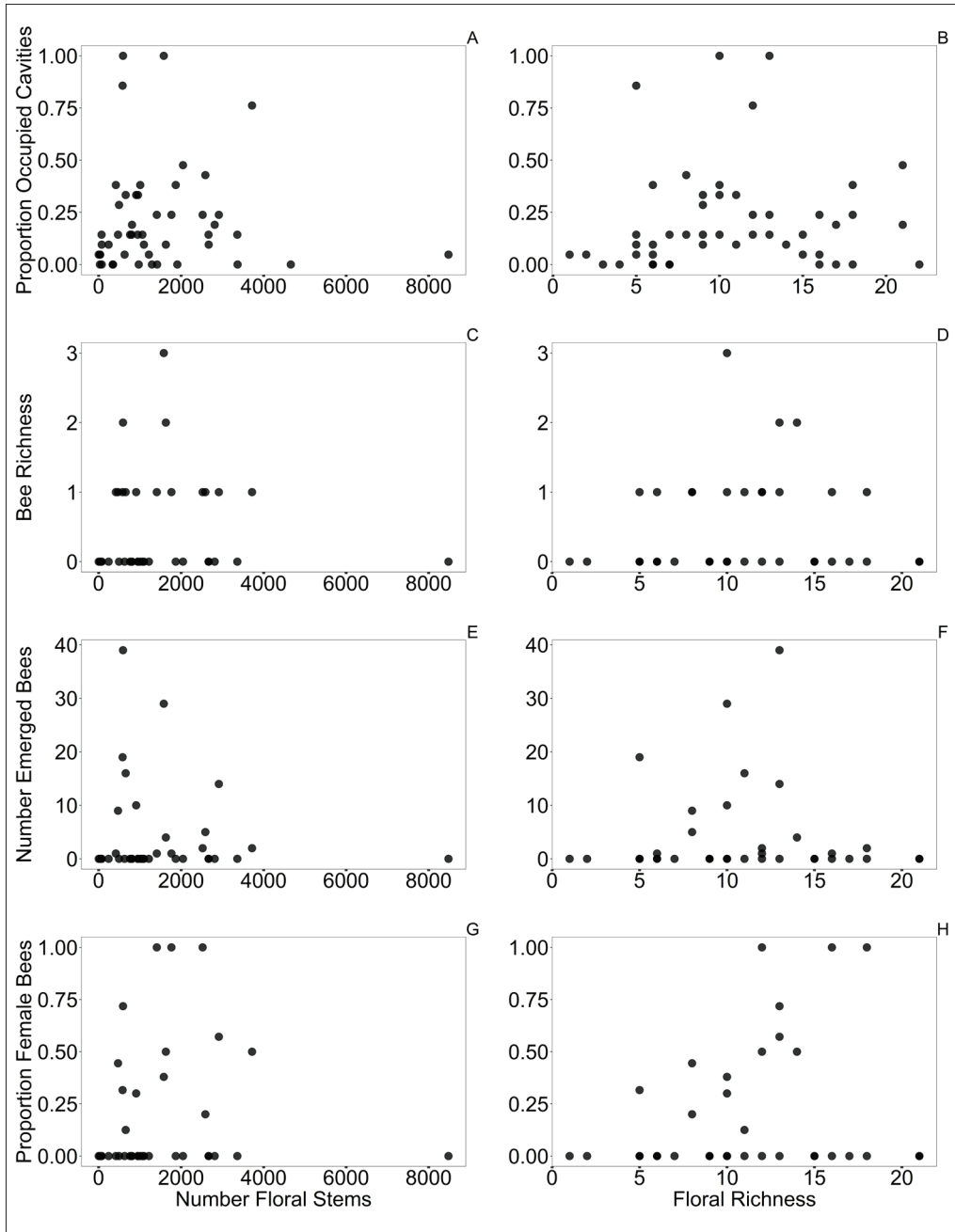
Figure 2. Proportion of 21 cavities in each block occupied by cavity-nesting bees plotted across (A) floral abundance and (B) floral richness; bee richness, i.e., the number of bee species that emerged per nest block, plotted across (C) floral abundance and (D) floral richness; number of bees that emerged after overwintering from each nest block plotted by (E) floral abundance and (F) floral richness; and proportion of emerged bees that were female plotted across (G) floral abundance and (H) floral richness. Note that bee richness, number of emerged bees, and the proportion of bees that were female only include nest blocks with occupied cavities (n = 38 of 48 nest blocks).

While the PPR of North Dakota reportedly has variability in floral resources across land-cover types (Smart et al. 2021) that has subsequent effects on honey bee health (Smart et al. 2018), our research suggests that floral resources and land cover in this system may not be predictive of nesting success for cavity nesting bees.

Contrary to expectations, we observed no relationships among bee nesting metrics and land cover. Although it has been previously suggested that working grassland and wetland habitats may be bee biodiversity hotspots for this region (Evans et al. 2018, Vickruck et al. 2019), it may be the case that these habitats are not reservoirs of cavity-nesting bee habitat in our study system. We hypothesize this might be due to limited nesting resources (e.g., standing dead wood, coarse woody debris) or inconsistent distribution of floral resources across grassland types. Furthermore, our nest-block cavity size limited the potential suite of species that could be detected in our study. The dominance of *M. relativa* in our samples, potentially a result of our single nest-block cavity size (e.g., Medler and Koerber 1958), limits the inferences we can draw regarding other detected bee taxa. Other cavity-nesting bee taxa, such as *Ceratina* spp., are more likely to nest in pithy stems and could be abundant yet unlikely to nest in our nest blocks. Alternatively, or cooperatively, these habitats may be sufficiently degraded in our study region such that they are more depauperate in solitary bees than expected. For example, neonicotinoid pesticides used in agriculturally dominated landscapes like the PPR can reduce the reproductive output of solitary cavity-nesting bees, although these effects can be at least partially offset by diverse (but not abundant) floral resources (Klaus et al. 2021). In an agroecosystem like ours, even mass-flowering fruit crops with abundant floral resources may still be negatively associated with the reproductive output of bee species (Eeraerts et al. 2021). Generally, habitats that support cavity-nesting bees are limited in the PPR of North Dakota, and these findings highlight the importance of woodland-type habitat, including engineered habitat such as shelterbelts (Burke et al. 2019), as cavity-nesting bee refugia in an agriculturally dominated system. Woodland habitat was especially limited near our study area, particularly compared to grasslands, and thus the ability of bees to disperse to our nest blocks may have been limited.

All bees identified in this study belong to the family Megachilidae and are commonly referred to as leaf-cutting bees (*Megachile*) and mason bees (*Osmia*), as they seal their nest cavities with leaves and plant material or with mud, dirt, and other debris. Except for parasitic members of this family, the presence of pollen-collecting hairs on the underside of the abdomen of females is an indicator that the species belongs to the family Megachilidae (Mitchell 1962). The genera *Osmia* and *Megachile* contain species with a diverse range of nesting habits between and within species, with various species using cavities in wood, cavities in pithy stems, holes in the ground, and other opportunistic habitats (Mitchell 1962). Furthermore, these taxa are particularly efficient pollinators in similar agroecosystems (Eeraerts et al. 2020). *Megachile relativa*, the most abundant bee in our study, has previously shown a strong preference for cavity sizes such as those in our nest blocks and has also been evaluated for agricultural applications (Medler and Koerber 1958). Since its introduction to the United States, *M. rotundata* has been used extensively for pollination of the introduced forage crop Alfalfa (*Medicago sativa* L., Pitts-Singer et al. 2011) that is common in our study area (Smart et al. 2021). Meanwhile, the Asteraceae pollen-specialist *M. pugnata*, a species native to the United States, has been investigated as a potential candidate for commercial sunflower pollination (Parker and Frohlich 1983, Tepedino and Frohlich 1982). In contrast to the *Megachile* spp. and *Osmia* spp., which used our nest blocks, parasitic bees avoid the task of foraging for nest provisions by laying their eggs in the already provisioned nests of host species (Bohart 1970). Bees of the cleptoparasitic genus *Coelioxys*
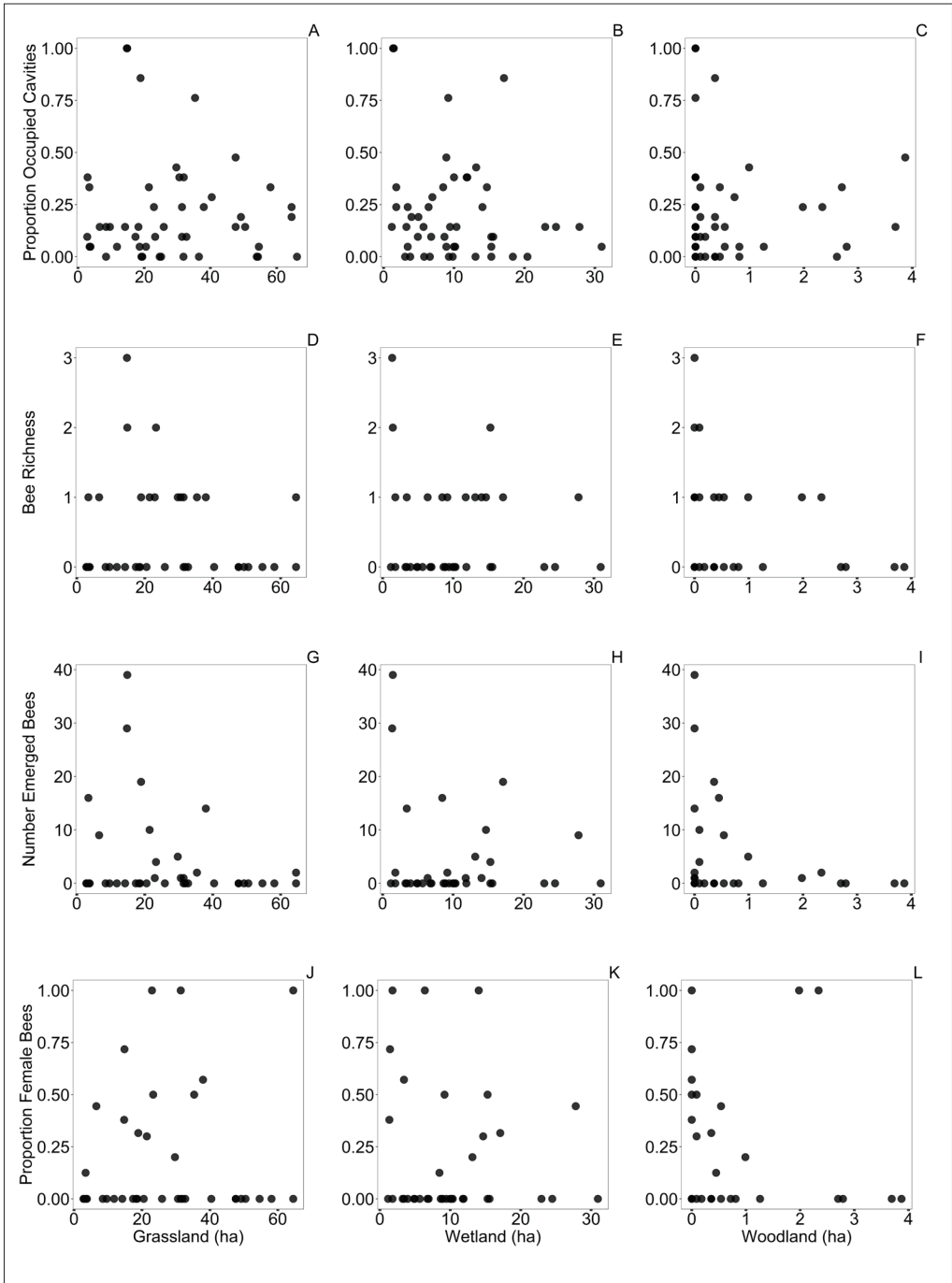
Figure 3. Bee metrics ([A–C] proportion of occupied nest cavities, [D–F] emerged bee species richness, [G–I] number of emerged bees, and [J–L] the proportion of emerged bees that were female) plotted across hectares of land-cover type (grassland, wetland, and woodland) within 500 m of each nest block. Note that bee richness, number of emerged bees, and the proportion of bees that were female only include nest blocks with occupied cavities ($n = 38$ of 48 nest blocks).

primarily parasitize members of the closely related genus *Megachile* (Michener 2000). The sole cleptoparasitic bee species that emerged from our nest blocks, *C. funerarius*, has been documented parasitizing a wide range of host species (as summarized in Baker 1975), including the species *M. relativa* and *M. rotundata* (Hobbs 1968, Medler and Koerber 1958), both of which were captured in our study. Based on our emergence data, it is likely that the *C. funerarius* captured in our study emerged from parasitized *M. relativa* nests.

Published estimates on both solitary-bee nest occupancy and successful adult emergence vary widely (e.g., Persson et al. 2018, Simanonok and Burkle 2019, Westerfelt et al. 2015), and we found similar variability in our study with a range of 0 to 100% occupancy of different nest blocks and an overall successful emergence rate of ~29%. There are many possible explanations for reported nest occupancy variability, and there are no clear ecological explanations provided by our explanatory variables. For example, our floral transects might not have reflected the scale at which these bees foraged, i.e., the bees nesting in each block had access to resources beyond our transects that we did not quantify. In some systems, and certainly with some bee species (particularly specialists), the suitability of different pollens can enhance reproductive output of solitary bees (Klaus et al. 2021). The PPR has become increasingly agriculturally dominated (Lark et al. 2015), and it may simply be the case that the surrounding lands are sufficiently degraded or relatively homogeneous in their distribution of floral and nesting resources such that we observed no nesting response. Much of the floral landscape of the PPR is dominated by non-native species (Smart et al. 2021) that may not be preferred by native bee species (Simanonok et al. 2021). For these reasons, we may not be able to discern an influence of land cover, either at a local or landscape scale, on cavity-nesting bees because their resources may not be abundant or high quality. Low nesting success can also result because of greater distances between solitary bee nesting and foraging habitats (Westrich 1996), highlighting the possibility that nesting habitat might be limited or simply too distant from preferred floral resources. Our ability to make broad inferences to such specialist species and to the bee community as a whole is fairly limited, however, because the majority of our observed specimens were of a single species, *M. relativa*. Furthermore, this single-species dominance in our data also limited our ability to infer relationships regarding bee richness for our study area. Our study was also limited in temporal scale. Nest blocks could not be deployed simultaneously, thus introducing possible unresolved seasonal influence. A final important caveat is that our sample size was relatively small, and the spatial scale of our study was limited. Future work in this region that considers a greater spatial scale would help clarify observed patterns.

Together, our results provided little evidence of any influence of local floral resources or land cover on the nest occupancy and nesting success of solitary cavity-nesting bee species in our study area. However, our use of artificial nest blocks likely limited our ability to detect differences. Future work, particularly in the PPR, focusing on the use of natural nesting substrates and investigating connectivity among habitat patches may help to illuminate how different habitats and nearby land cover influence solitary bee nest occupancy.

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