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Research Article

Floral Resources Used by the Endangered Rusty Patched Bumble Bee (*Bombus affinis*) in the Midwestern United States

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ABSTRACT

The once-common rusty patched bumble bee (RPBB, *Bombus affinis*) has disappeared from most of its original range in eastern North America. As a result of this dramatic population decline, RPBB was listed as federally endangered in 2017. Unlike many endangered species, remnant populations of the RPBB often occur in urban/suburban parks and natural areas. This paper summarizes photographic records of RPBB floral use collected largely by volunteer community scientists in the midwestern United States, with a focus on Wisconsin, one of the species' remaining strongholds. RPBB were documented in 37 of Wisconsin's 72 counties. We identified flowers to genus in 772 of 803 digital images (some bees were not on flowers). Although 87 plant genera were identified, 76% of the flowers represented just 13 genera. Over half of the flower records (54.6%) were from *Monarda*, *Eutrochium*, *Veronicastrum*, *Agastache*, or *Solidago*. Incidental surveys from other states show a similar pattern, although additional genera have been shown to be used by RPBB. Our results support existing recommendations for plantings and habitat management favoring specific plant species, generally associated with native grasslands and savannas. Because the active period of RPBB covers a large part of the growing season, however, we also provide evidence for the importance of spring ephemeral woodland wildflowers (e.g., *Dicentra*, *Anemone*, *Hydrophyllum*) and late-flowering species of wetlands and wet meadows (e.g., *Eutrochium*, *Eupatorium*). A landscape that includes woodland, native grassland, and wet meadows provides floral resources that support all RPBB life history stages, including early-season queens, late-season gynes, and males.

Index terms: Bombus affinis; community science; conservation; Rusty patched bumble bee

INTRODUCTION

Most insect pollinators and flowering plants in temperate regions are generalists; pollinators visit multiple species of flowers, and most flowering plants are visited by multiple insect species (Waser et al. 1996 and others). If adult pollinating insects are active through much of the growing season (even though individuals themselves might be active during a short time interval), the species necessarily must depend on nectar and pollen from seasonally changing flower arrays. The generalist nature of most insect pollinators does not mean that these pollinators are indiscriminate, however. In fact, some degree of preference and even specialization is common in bees (Fründ et al. 2010; Avargues-Weber and Chittka 2014; MacIvor et al. 2014; Rasmussen et al. 2020). Fowler and Droege (2020) estimated that ~25% of the ~770 species of bees native to the eastern United States are pollen specialists. Shimizu et al. (2014) have demonstrated that specializations of insects and flowering plants may be hidden within multispecies pollination networks. Vázquez et al. (2009) reviewed the complex nature of plant–animal mutualisms, suggesting that networks of interacting species invariably include asymmetric interactions with different (although mostly weak) intensities of links among species. In other words, even generalists forage nonrandomly and exhibit adaptations for exploiting a subset of available plant resources. The nature of pollinator preferences, whether weak or strong, may be complicated by many factors including interspecific competition, varying relative abundances, and unrelated physiological constraints affecting both pollinator and plant species. Vaudo et al. (2020) described differences in nutritional quality among potential pollen resources, a factor that surely influences flower preferences among bees and other pollinators.

Jones (1997) outlined a framework for quantifying preferential foraging behavior in pollinators, a task that is more challenging than it first appears. For example, a pollinator species might forage mainly on one plant species because competitors have depleted pollen or nectar in a different, otherwise preferred flower species. Even without complications, nonrandom foraging behavior might be expressed as differences in constancy (nonrandom sequences of flower visits during individual foraging bouts), preference (nonrandom use of flower species by a local population of pollinators), or some other dimension of individual decision-making. Also, most individual bees are active for only a short time during the growing season, while the species itself might be present for months or a large portion of the growing season. At a coarse scale, however, some flowering species are completely or largely ignored by certain pollinator species, while other species are visited often, likely reflecting a suite of factors guiding individual selectivity (e.g., Fussell and Corbet 1992; Harmon-Threatt et al. 2017). Even if the underlying behavioral mechanisms are not completely understood, the outcome of these complex decisions can yield meaningful patterns of floral use that are relevant for conservation.

Pollinator foraging preferences have important implications for pollinator and wildflower conservation. Preservation and restoration of high-quality habitat, for example, clearly will be most effective when preferred plant species are selected and included in restorations and habitat augmentations. In this paper we provide a first step in identifying foraging preferences of the rusty patched bumble bee (*Bombus affinis,* RPBB), one of North America's most imperiled insect species. We are unable to clearly document preferences, but we provide a list of flower species most used by the RPBB in Wisconsin and other midwestern states, setting the stage for more systematic studies of foraging preferences and seasonal patterns of foraging in this generalist, but not indiscriminate, bee species.

The RPBB has experienced severe declines and range constriction across its historical distribution in eastern North America (Colla and Packer 2008; Grixti et al. 2009; Cameron et al. 2011; Colla et al. 2012; Bartomeus et al. 2013). Today, the species appears to be nearly absent in New England states (Conservation Unit 5; Bushmann and Drummond 2015; Goldstein and Ascher 2016; Jacobson et al. 2018), Michigan, most of Indiana (Conservation Unit 3), and all of Canada, even after extensive searches by entomologists. Since 2010 isolated populations have been documented near the Virginia–West Virginia border and in northern Ohio (Bumble Bee Watch 2022), but the primary range today occurs in southern Minnesota, Iowa, northern Illinois, and the southern two-thirds of Wisconsin. The RPBB was designated as federally endangered in 2017 (Federal Register 82 FR 10285), the first bee species outside of Hawaii listed under the U.S. Endangered Species Act.

In Wisconsin, records from the 1960s indicate that RPBB was present historically throughout the state (Medler and Carney 1963). This is no longer the case, but currently Wisconsin appears to be a stronghold, one of only ten states and one Canadian province where RPBB has been documented in the past 10 years. Recent records of the RPBB in Wisconsin occur mainly south of the "tension zone" defined by Curtis (1959) and along eastern counties from Green Bay to the Illinois border.

Data on the floral associations of the RPBB are vital for developing effective conservation actions. Accurate foraging information for regional populations will allow a better understanding of overall trends and drivers of decline, in addition to insights for developing and implementing effective conservation measures. This study summarizes a large body of recent natural history observations, primarily collected using community science programs. Specifically, we aim to:

1) describe regional variations in RPBB abundance within Wisconsin;
2) identify seasonal patterns of floral resource use;
3) discuss historical changes in floral use, including a comparison of today's flower usage with data published by Medler and Carney (1963); and
4) discuss the implications of flower associations for conserving RPBB populations in the midwestern United States.

METHODS

We evaluated 803 digital images (records) of *Bombus affinis* contributed by observers over a 4-year period (2018 to early 2022) in Wisconsin. All records were part of the community-based monitoring program, Bumble Bee Brigade (B3, Wisconsin Department of Natural Resources, https://wiatri.net/inventory/bbb/). B3 was initiated in 2018 and today engages more than 380 contributors throughout Wisconsin in almost every county. Identifications of both bees and flowers from B3 digital images were conducted by professional biologists, and associated metadata on location and date were linked in a computerized database. Using submitted photos, floral hosts were then identified to species when possible. When plant species identification was not possible from the image, flowers were identified to genus.

To minimize bias, only one record from a given site (defined as a geographic location and ~100 m buffer), date, and flower taxon was included in the analysis. In other words, if more than one flower species was documented at a given site and date, each flower type was included as a separate record, but multiple images of the same species were treated as just a single record for that site and date.

Floral visitation data for RPBB from Indiana ($n = 49$ from 1956–2005), Iowa ($n = 37$ from 2018–2019), Illinois ($n = 7$ from 2021), Virginia ($n = 32$ from 2019), and West Virginia ($n = 2$ from 2019), plus 12 records from Columbia and Marquette counties, Wisconsin in 2021, were compiled by RJ from personal observations to provide a very general comparison of B3 Wisconsin data (Conservation Unit 1) to other conservation units as defined in the RPBB draft recovery plan (see https://www.federalregister.gov/documents/2020/01/24/2020-01203/endangered-and-threatened-wildlife-and-plants-draft-recovery-plan-for-the-rusty-patched-bumble-bee). Indiana data include 49 RPBB collected 1956–2005, representing Conservation Unit 3. These results provide some analysis of historical change in flower use but inferences from these data are limited, as the collections were either haphazard or focused on a single habitat type (black oak savanna) with restricted geographic distribution. We also reviewed records from the online image repository iNaturalist (https://www.inaturalist.org/) to identify additional flowers used by RPBB in its midwestern range. Because many of these records overlap with those in the B3 database, we only provide a qualitative summary of these records and do not include them in our quantitative analyses and tables.

Medler and Carney (1963) provided an important historical summary of the distribution and natural history of 18 bumble bee species in Wisconsin nearly 60 years ago. They provided a table of floral hosts of Wisconsin bumble bees as well as state distribution maps and natural history information. We used descriptions from this landmark publication to compare current distributions and flower use of RPBB based on data from B3 and our own observations (e.g., Wolf and Ascher 2008).

If pollen loads were visible on corbicula, we documented the bee as collecting pollen. These same bees might also have collected nectar during their foraging bout, but we use this terminology to distinguish records from observations where only nectaring was observed. In some cases, a foraging bout may include a combination of collecting pollen and nectar. Bees were recorded as nectaring when the individual contained no visible pollen on the corbicula(e) but was foraging on a flowering plant. Pollen loads did not necessarily come from the plant on which the bee was photographed; the bee could have collected pollen from a previous visit to a different flower species. We frequently observed "nectar robbing," where the bee was piercing the corolla to gain access to nectar resources; we counted this behavior as nectaring for purposes of analysis.

To illustrate the distribution of *Bombus* surveys across Wisconsin, B3 visits were grouped by date and geographic coordinates rounded to 3 decimal points, equivalent to a buffer of approximately 75–110 m. This approach ignores the duration or intensity of individual daily visits but avoids multiple counting of locations visited more than once in a day by the same or different observers. Surveys where bumble bees were not detected were included in the map, even when the local survey was short in duration or conducted in a small area. We compiled 10,388 B3 visits at 2445 grouped sites; RPBB were detected during only 711 of these visits (yielding 803 RPBB floral use records, since some visits showed use of multiple flower species) representing 431 grouped sites. Over 75% of B3 sites were visited one time by a single observer or team of observers. Each plant species used by and photographed with a RPBB during a visit was included in the analysis. The sample size in our calculations ($N = 803$ images) is much lower than the total number of RPBB images reviewed because multiple images at a site were often submitted of RPBB on the same flower species, and because visits were grouped by date and rounded GPS coordinates. In other words, we included only one record of a given flower species at the same site and date to minimize pseudoreplication (Hurlbert 1984).

RESULTS

Contributors to the B3 project documented RPBB in more than half (51%) of Wisconsin's 72 counties. Flowers were identified to at least the level of genus on 772 RPBB B3 images (Tables 1 and 2), representing 29 plant families, 87 plant genera, and at least 122 identified flower species. Pollen loads were visible on bees in 18.7% ($N = 151$) of the images. Most of the RPBB records were acquired from mid-July through early September (Figure 1), although individuals were found as early as 6 April. The importance of the late summer period (15 July–1 September) was evident during all four full years of our analysis (2018, 2019, 2020, and 2021). The increase in numbers of foraging RPBBs was particularly dramatic from early to late July (Figure 1). More than twice as many records were acquired during 2020 than during either 2018 or 2019, and the number of contributions nearly doubled again in 2021, likely reflecting the increasing popularity of the B3 program, not a difference in abundance of RPBB.

The distribution of RPBB records among flower species resembled the widely observed negative exponential distribution of species (Figure 2); most visits occurred on relatively few plant species, with many other species visited infrequently. By far the largest number of documented visits occurred on native bee balm (*Monarda fistulosa*) or closely related *Monarda* cultivars. Most of the bees observed on *Monarda* lacked pollen loads, suggesting that this plant provides mainly nectar. Other frequently visited plant taxa included Joe Pye weed (*Eutrochium purpureum* and *E. maculatum*), Culver's root (*Veronicastrum virginicum*), hyssops (*Agastache scrophulariifolia* and *A. foeniculum*), goldenrods (*Solidago* spp.), purple coneflower (*Echinacea purpurea*), mountain mint (*Pycnanthemum virginianum*), knapweeds (*Centaurea* spp.), St. John's wort (*Hypericum* spp., especially shrubby St. John's wort, *H. prolificum*), and thistles (*Cirsium* spp.). Not surprisingly, these species were available during the peak activity period for RPBB. Bees with pollen were observed most frequently on *Veronicastrum*, *Hypericum*, *Monarda*, *Eutrochium*, *Agastache*, and *Pycnanthemum* (mountain-mint) (Figure 2), although RPBB with pollen were observed on 47 flower species overall.

Despite low numbers of early season records, several species, notably *Dicentra* spp. (Dutchman's breeches, *D. cucullaria*; and squirrel corn, *D. canadensis*), were important during spring or early summer (Figure 2b) when the other floral resources were unavailable to queens. Other spring floral resources included a horticultural relative of *Dicentra* (bleeding heart, *Lamprocapnos spectabilis*), native and introduced species of St. John's wort (*Hypericum* spp.), eastern bluebells (*Mertensia virginica*), meadowsweet (*Spirea* spp.), Virginia waterleaf (*Hydrophyllum virginianum*), clovers (*Trifolium* spp.), purplestem angelica (*Angelica atropurpurea*), and lupine (*Lupinus* sp.).

Differences in floral use by males vs. females reflected the appearance of males later during the season (the first males were not recorded until July) and the fact that males do not collect pollen (Figures 2c and 2d). St. John's wort, for example, one of the most important RPBB pollen sources in Wisconsin, was not recorded at all for RPBB males. Joe Pye weed was the most common flower taxon used by males, followed by hyssops, Culver's root, goldenrods, bee balm, purple coneflower, and mountain-mint. Females were seldom recorded on sunflowers (*Helianthus*), the ninth-most frequently visited genus by males (Figure 2d).

The geographic distribution of records (Figure 3) was biased toward urban areas, where observers were most active. Inevitably, multiple observations were recorded from the same sites (on different dates in our database) given the rarity of established populations today. Geographic bias does not fully account for the observed floral associations, however. RPBB records were obtained from 37 of Wisconsin's 72 counties (Figure 3). *Monarda*, the most frequently observed plant genus, was recorded in association with RPBB in 24 counties, followed by *Veronicastrum* (17 counties), *Eutrochium* (16 counties), *Solidago* (13 counties), *Pycnanthemum* (12 counties), *Echinacea* (12 counties), and *Agastache* (9 counties). Only 8 of the 43 plant genera observed two or more times were recorded from just a single county.

Although the methods of data collection were different and the range of coverage (both seasonally and geographically) much more restricted, RJ's records of plants used by RPBB in other states (Table 2) show some agreement with results from the Wisconsin Bumble Bee Brigade project. Like in Wisconsin, *Monarda* was an important floral resource in Iowa and Virginia, while *Eutrochium* also was well-represented in RJ's Wisconsin and Illinois surveys. Several important differences include the

Table 1.—List of 98 plant genera used by rusty patched bumble bees (RPBB) during 2018–2022 in Wisconsin and 11 additional localities visited by Robert Jean in nearby states. Genera marked with an asterisk were reported as RPBB host plants by Medler and Carney (1963). Seasonal records are based on Great Lakes states (WI, IL, MI, IN, OH) phenology. Sp=spring (March–April), Su=summer (May–August), F=fall (September–October).

Genus	Season	Family	Most frequent species
Actaea	Sp, Su	Ranunculaceae	*Actaea racemosa*
Agastache	Su	Lamiaceae	*Agastache foeniculum, A. scrophulariifolia*
Allium	Sp, Su	Amaryllidaceae	*Allium cernuum*
Amorpha	Su	Fabaceae	*Amorpha canescens*
Anemone[a]	Sp, Su	Ranunculaceae	*Anemone tomentosa*
Angelica	Su	Apiaceae	*Angelica atropurpurea*
Aquilegia	Su	Ranunculaceae	*Aquilegia canadensis, Aquilegia vulgaris*
Arnoglossum	Su, F	Asteraceae	*Arnoglossum atriplicifolium*
Asclepias	Su	Apocynaceae	*Asclepias incarnata, Asclepias purpurascens*
Aster[a]	Su, F	Asteraceae	*Aster furcatus*
Aureolaria	Su, F	Orobanchaceae	*Aureolaria grandiflora*
Barbarea[b]	Sp, Su	Brassicaceae	
Blephilia[b]	Sp, Su	Lamiaceae	
Brassica	Su, F	Brassicaceae	
Buddleja	Su	Scrophulariaceae	*Buddleja davidii*
Campanula[b]	Su, F	Campanuloideae	
Carduus	Su, F	Asteraceae	*Carduus nutans*
Centaurea	Su, F	Asteraceae	*Centaurea stoebe*
Chamaecrista	Su, F	Fabaceae	
Chelone	Su, F	Plantaginaceae	*Chelone lyonii*
Cichorium[b]	Su, F	Asteraceae	
Cirsium[a]	Su, F	Asteraceae	*Cirsium discolor, Cirsium altissimum*
Claytonia[b]	Sp	Montiaceae	
Coreopsis	Sp, Su	Asteraceae	
Coriandrum	Su	Apiaceae	*Coriandrum sativum*
Dalea	Su	Fabaceae	*Dalea purpurea*
Daucus	Su, F	Apiaceae	*Daucus carota*
Desmodium	Su	Fabaceae	*Desmodium canadense*
Dicentra	Sp	Papaveraceae	*Dicentra cucullaria*
Echinacea	Su	Asteraceae	*Echinacea purpurea*
Echinops	Su, F	Asteraceae	*Echinops* cultivar
Eryngium	Su	Apiaceae	*Eryngium yuccifolium*
Eupatorium	Su, F	Asteraceae	*Eupatorium perfoliatum*
Eurybia	Su, F	Asteraceae	*Eurybia furcata*
Euthamia	Su, F	Asteraceae	*Euthamia graminifolia*
Eutrochium	Su, F	Asteraceae	*Eutrochium maculatum*
Gaillardia	Su, F	Asteraceae	*Gaillardia × grandiflora*
Hasteola	Su	Asteraceae	*Hasteola suaveolens*
Helianthus[a]	Su, F	Asteraceae	*Helianthus strumosus*
Hibiscus[b]	Su, F	Malvaceae	
Hydrangea	Su, F	Hydrangeaceae	*Hydrangea arborescens*
Hydrophyllum	Sp, Su	Boraginaceae	*Hydrophyllum virginianum*
Hylotelephium	Su, F	Crassulaceae	*Hylotelephium telephium*
Hypericum	Su	Hyperiaceae	*Hypericum perforatum*
Impatiens	Su	Balsaminaceae	*Impatiens capensis*
Lamprocapnos	Sp	Papaveraceae	*Lamprocapnos spectabilis*
Lespedeza	Su	Fabaceae	*Lespedeza capitata*
Liatris	Su	Asteraceae	*Liatris spicata*
Lonicera[a]	Sp, Su	Caprifoliaceae	*Lonicera dioica*
Lotus[a]	Su, F	Fabaceae	*Lotus corniculatus*
Lupinus	Sp, Su	Fabaceae	
Medicago[a]	Su, F	Fabaceae	
Melilotus[a]	Su	Fabaceae	*Melilotus albus*
Mentha[a]	Su, F	Lamiaceae	*Mentha spicata*
Mertensia	Sp, Su	Boraginaceae	*Mertensia virginica*
Monarda	Su	Lamiaceae	*Monarda fistulosa, Monarda* cultivars
Napaea	Su	Malvaceae	*Napaea dioica*
Nepeta[b]	Su	Lamiaceae	
Origanum	Su, F	Lamiaceae	*Origanum vulgare*
Pastinaca[b]	Su	Apiaceae	
Pedicularis	Sp, Su	Orobanchaceae	*Pedicularis canadensis*
Phlox	Sp, Su	Polemoniaceae	
Physostegia	Su, F	Lamiaceae	*Physostegia virginiana*
Platycodon	Su	Campanulaceae	*Platycodon grandiflorus*
Polymnia	Su, F	Asteraceae	*Polymnia canadensis*
Primula	Sp, Su	Primulaceae	*Primula meadia*
Prunus	Sp, Su	Rosaceae	*Prunus avium*
Pycnanthemum	Su	Lamiaceae	*Pycnanthemum virginianum*
Rhododendron[b]	Sp, Su	Ericaceae	
Pyrus	Su	Rosaceae	*Pyrus* cultivars
Ratibida	Su	Asteraceae	*Ratibida pinnata*
Ribes	Sp	Grossulariaceae	*Ribes missouriense*
Rosa	Su	Rosaceae	*Rosa rugosa*
Rubus[a]	Sp, Su	Rosaceae	*Rubus odoratus*
Rudbeckia[a,b]	Su, F	Asteraceae	
Salvia	Su	Lamiaceae	
Scilla	Sp	Asparagaceae	*Scilla siberica*
Scrophularia[b]	Su, F	Scrophulariaceae	
Securigera	Su, F	Fabaceae	*Securigera varia*
Senecio	Sp, Su, F	Asteraceae	*Senecio suaveolens*
Silphium	Su, F	Asteraceae	*Silphium perfoliatum*
Solanum	Su, F	Solanaceae	*Solanum dulcamara*
Solidago[a]	Su, F	Asteraceae	*Solidago canadensis*
Sonchus	Su, F	Asteraceae	*Sonchus arvensis*
Spiraea	Su, F	Rosaceae	*Spiraea alba*
Symphyotrichum	Su, F	Asteraceae	*Symphyotrichum novae-angliae*
Symphytum	Su	Boraginaceae	*Symphytum officinale*
Taraxacum	Sp, Su, F	Asteraceae	*Taraxacum officinale*
Thalictrum	Sp, Su	Ranunculaceae	*Thalictrum dasycarpum*
Thymus	Su	Lamiaceae	*Thymus vulgaris*
Tradescantia	Sp, Su	Commelinaceae	*Tradescantia ohiensis*
Trifolium[a]	Sp, Su, F	Fabaceae	*Trifolium repens*
Verbena	Su, F	Verbenaceae	*Verbena hastata*
Vernonia	Su, F	Asteraceae	*Vernonia fasciculata*
Veronica	Sp, Su, F	Plantaginaceae	*Veronica austriaca*
Veronicastrum	Su	Plantaginaceae	*Veronicastrum virginicum*
Vicia	Su	Fabaceae	*Vicia villosa*
Weigela	Sp, Su	Caprifoliaceae	*Weigela* cultivar

[a] Reported by Medler and Carney (1963).
[b] Not reported in Wisconsin.

high frequency of asters, in this case *Silphium* (cup plant, *Silphium perfoliatum*) and *Rudbeckia laciniata* (green-headed coneflower) in Iowa and the importance of *Aureolaria* (false foxgloves) in Indiana. RJ's surveys identified 11 genera not photographed by the Wisconsin Bumble Bee Brigade, although only *Rudbeckia laciniata* (Iowa), *Nepeta* (Virginia), and *Cichorium intybus* (Virginia) were recorded more than once.

Using the same criteria applied to the B3 database (a single record counted per day per site per flowering species), we reviewed midwestern images submitted to iNaturalist (https://www.inaturalist.org/). Results were consistent with our findings

Table 2.—Number of records of rusty patched bumble bees (RPBB) on plant genera (Table 1) reported by Wisconsin Bumble Bee Brigade Project (B3) and by Robert Jean (RJ) in other states. Numbers in parentheses identify the Conservation Unit defined by the RPBB draft recovery plan (U.S. Fish and Wildlife Service 2021a).

Flower genus	WI^{B3} (1)	WI^{RJ} (1)	IA (2)	IL (2)	IN (3)	VA (4)	WV (4)
Actaea	2					6	2
Agastache	62		1				
Allium	3						
Amorpha	5						
Anemone	1						
Angelica	2						
Aquilegia	2						
Arnoglossum	4	1					
Asclepias	8				1		
Aster	2						
Aureolaria	1				16		
Barbarea					1		
Blephilia					1		
Brassica	1						
Buddleja	1						
Campanula					1		
Carduus	2						
Centaurea	23					1	
Chamaecrista	1						
Chelone	1						
Cichorium						2	
Cirsium	22					5	
Claytonia					1		
Coreopsis	1						
Coriandrum	1						
Dalea	3						
Daucus	3						
Desmodium	1	1	1				
Dicentra	8						
Echinacea	28						
Echinops	5						
Eryngium	1						
Eupatorium	8				4		
Eurybia	1						
Euthamia	2						
Eutrochium	77	2		3			
Gaillardia	1						
Hasteola	1						
Helianthus	8						
Hibiscus						1	
Hydrangea	1						
Hydrophyllum	3						
Hylotelephium	3						
Hypericum	23					2	
Impatiens	3						
Lamprocapnos	6						
Lespedeza	1						
Liatris	15			1	2		
Lonicera	1						
Lotus	1						
Lupinus	2				2		
Medicago	1				1		
Melilotus	5				3		
Mentha	3						
Mertensia	5						
Monarda	169	4	11		1	3	
Napaea	1						
Nepeta						3	
Origanum	7						
Pastinaca					1		
Pedicularis	1						
Phlox	1						
Physostegia	8						
Platycodon	1						
Polymnia	2						
Primula	1						
Prunus	2						
Pycnanthemum	28					5	
Rhododendron						1	
Pyrus	1						
Ratibida	1						
Ribes	1						
Rosa	1				1		
Rubus	4				1		
Rudbeckia			5				
Salvia	2						
Scilla	3						
Scrophularia					1		
Securigera	2				1		
Senecio	1						
Silphium	15	1	16				
Solanum	1						
Solidago	47		3	2	2	1	
Sonchus	1						
Spiraea	5						
Symphyotrichum	11						
Symphytum	1						
Taraxacum	2						
Thalictrum	1						
Thymus	2						
Tradescantia	1				1		
Trifolium	5				2	1	
Verbena	5						
Vernonia	2				3		
Veronica	2						
Veronicastrum	67			1	1		
Vicia	1						
Weigela	1						

from B3. Joe Pye weed (*Eutrochium*), bee-balm (*Monarda*), goldenrods (*Solidago*), thistles (*Cirsium*), hyssops (*Agastache*), Culver's root (*Veronicastrum*), boneset (*Eupatorium*), and cup plant (*Silphium*) were the most frequently photographed flower species, respectively. Records from B3 captured more flowering species than those submitted to iNaturalist; however, several additional taxa were recorded by iNaturalist submissions but not by B3. Notable among these records is an iNaturalist image of a bee on flowers of *Tilia* (basswood), a June-flowering tree that could easily be overlooked or undercounted by observers. Several records of creeping charlie (*Glechoma hederacea*), chickory (*Cichorium intybus*), and forget-me-not (*Myosotis scorpioides*) were also added to the Wisconsin list from iNaturalist observations. iNaturalist images from nearby states contribute additional early flowering species: willow (*Salix* sp.) and Labrador tea (*Rhododendron groenlandicum*), both from Minnesota. Other midwestern iNaturalist records not represented in our Table 2 include hosta (*Hosta* sp.), larkspur (*Delphinium* sp.), foamflower (*Tiarella* sp.), tall bellflower (*Campanula americana*), *Lobelia* spp., yellow flag iris (*Iris*

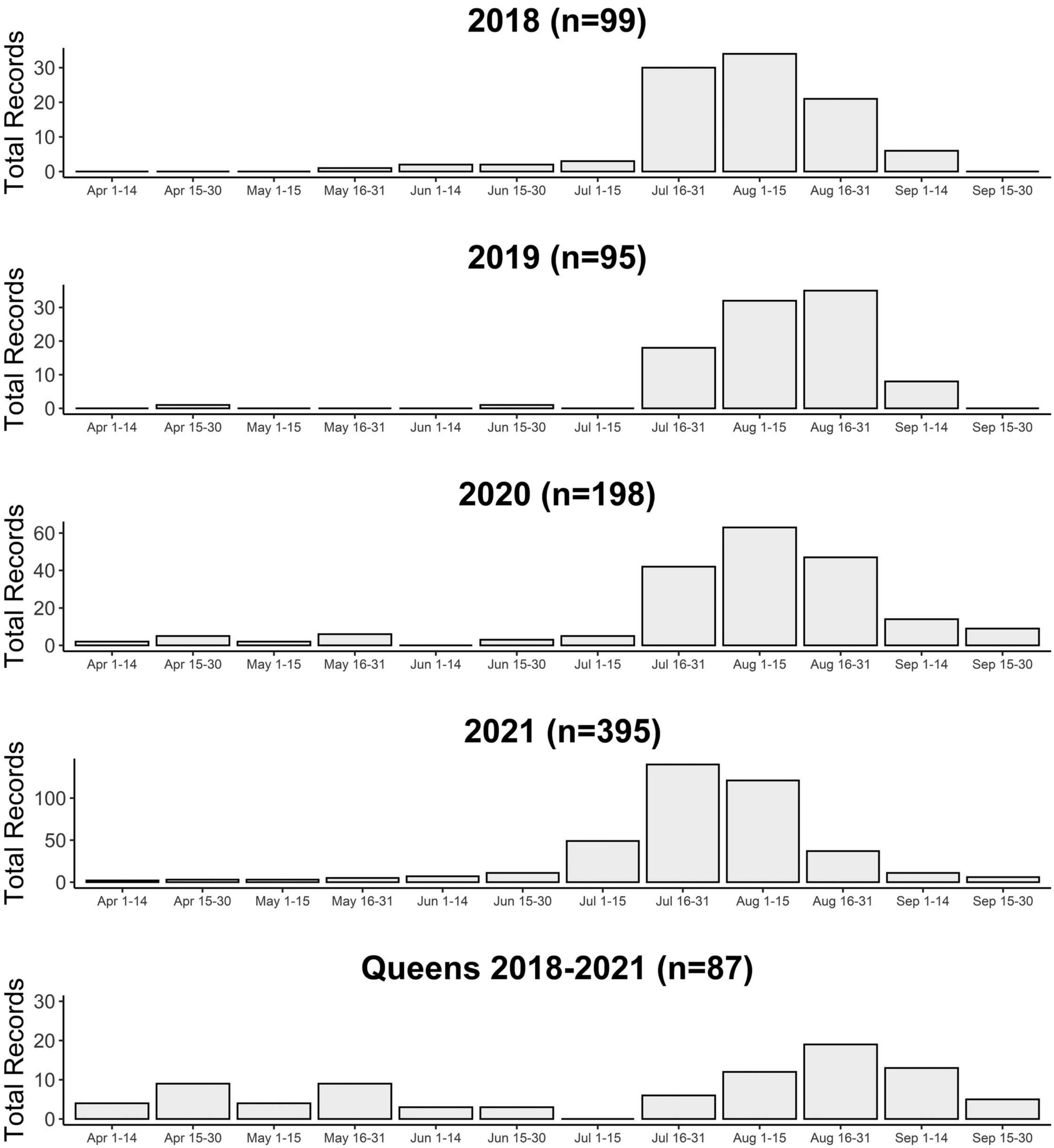

Figure 1.—Seasonal distribution of rusty patched bumble bee photo records reported by Wisconsin Bumble Bee Brigade Project (B3) during 2018–2021.

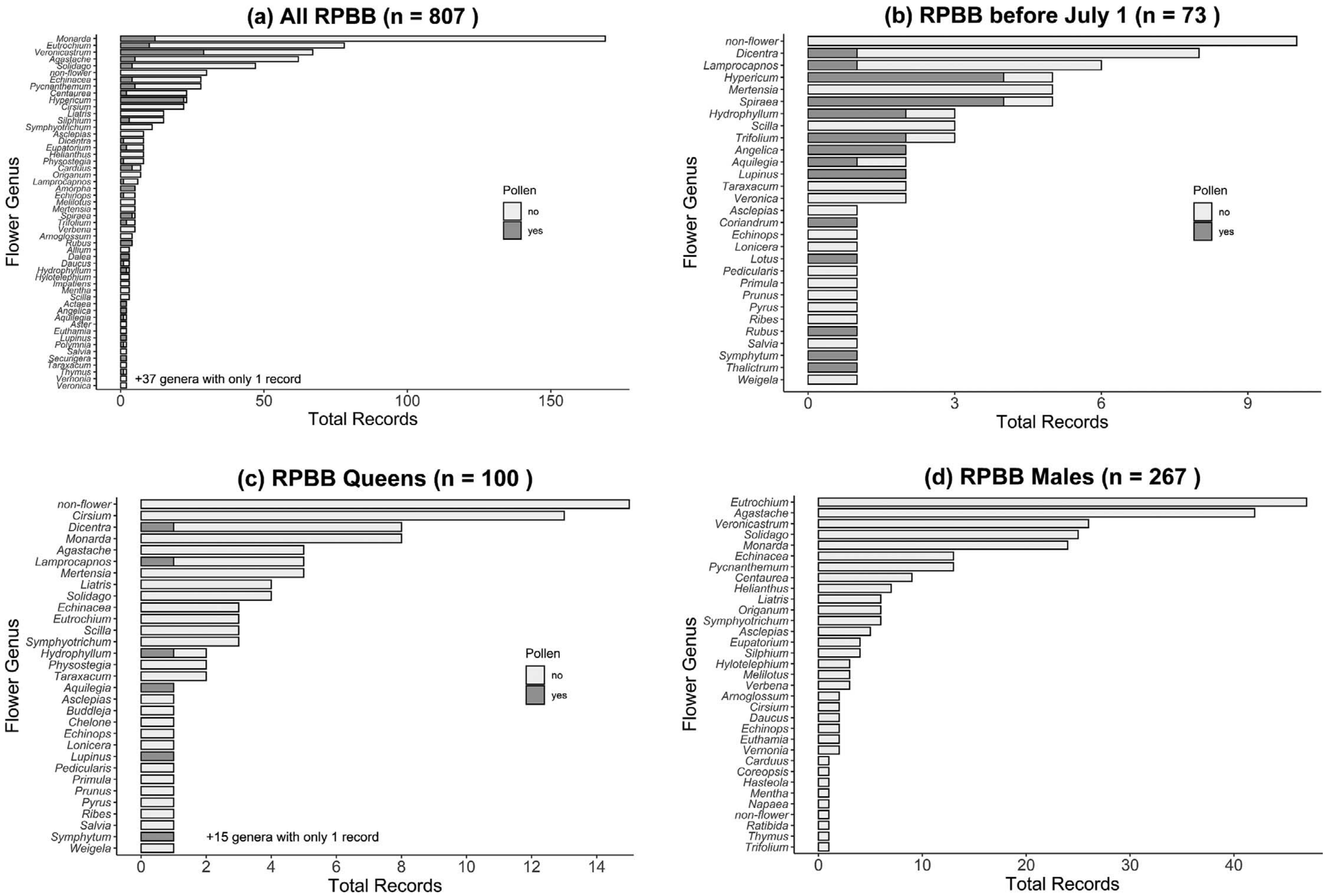

Figure 2.—Frequency of flower genera used by rusty patched bumble bees (RPBB) from the Wisconsin Bumble Bee Brigade Project (B3) in 2018–2022. Dark shading (Pload = yes) represents bees that were carrying pollen on their corbicula.

pseudocorus), motherwort (*Leonurus cardiaca*), wingstem (*Verbesina alternifolia*), and others not easily identified from photo submissions.

DISCUSSION

We recognize the bias inherent in this and most other studies of floral use by pollinators; we have virtually no data available on the relative availability of different flower species at the time of each submitted photograph, and comparisons with other studies are limited because of differences in field effort; the more samples available, the larger will be the number of flower species documented by the study.

Nevertheless, our results provide a substantial list of flower species used by RPBB in a state where the species still occurs relatively widely. An effective habitat conservation strategy for the RPBB in Wisconsin and elsewhere requires knowledge about these resources and their phenology. The U.S. Fish and Wildlife Service's Status Assessment for *B. affinis* (Szymanski et al. 2016) compiled hundreds of historical records of this bee across the species' historical range in the northeastern United States and southeastern Canada. These authors and others concluded that RPBB was previously associated with native grasslands, which have been reduced today by as much as 99% in eastern North America (Colla and Packer 2008). Our observations are consistent with this habitat profile; the most frequently reported plant species used by RPBB in Wisconsin are characteristic of native prairies and savannas. RJ's observations from other states (Iowa, Illinois, Indiana, Virginia, and West Virginia as well as Wisconsin) further support this assertion. These patterns do not tell the complete story, however. An exclusive emphasis on prairie wildflowers obscures critical features of productive RPBB landscapes and ignores the possibility that absence of RPBB today might be at least partly due to factors unrelated to floral resources, such as pathogens or proximity to agricultural fields where neonicotinoid pesticides are used (Whitehorn et al. 2012; Tsvetkov et al. 2021). During spring, native prairie flowers are mostly unavailable, so queens require alternative pollen and nectar sources during their critical colony-establishment period (Mola et al. 2021a, 2021b). Spring floral resources often can be found in woodlands adjacent to native grassland remnants or plantings (Hines and Hendrix 2005; Watson et al. 2011; Szymanski et al. 2016). Woodland wildflowers (e.g., *Claytonia virginica*, *Actaea racemosa*, *Dicentra cucullaria*, *Hydrophyllum virginica*, and *Mertensia virginica*) are not among the most visited plant species overall but they are disproportionately

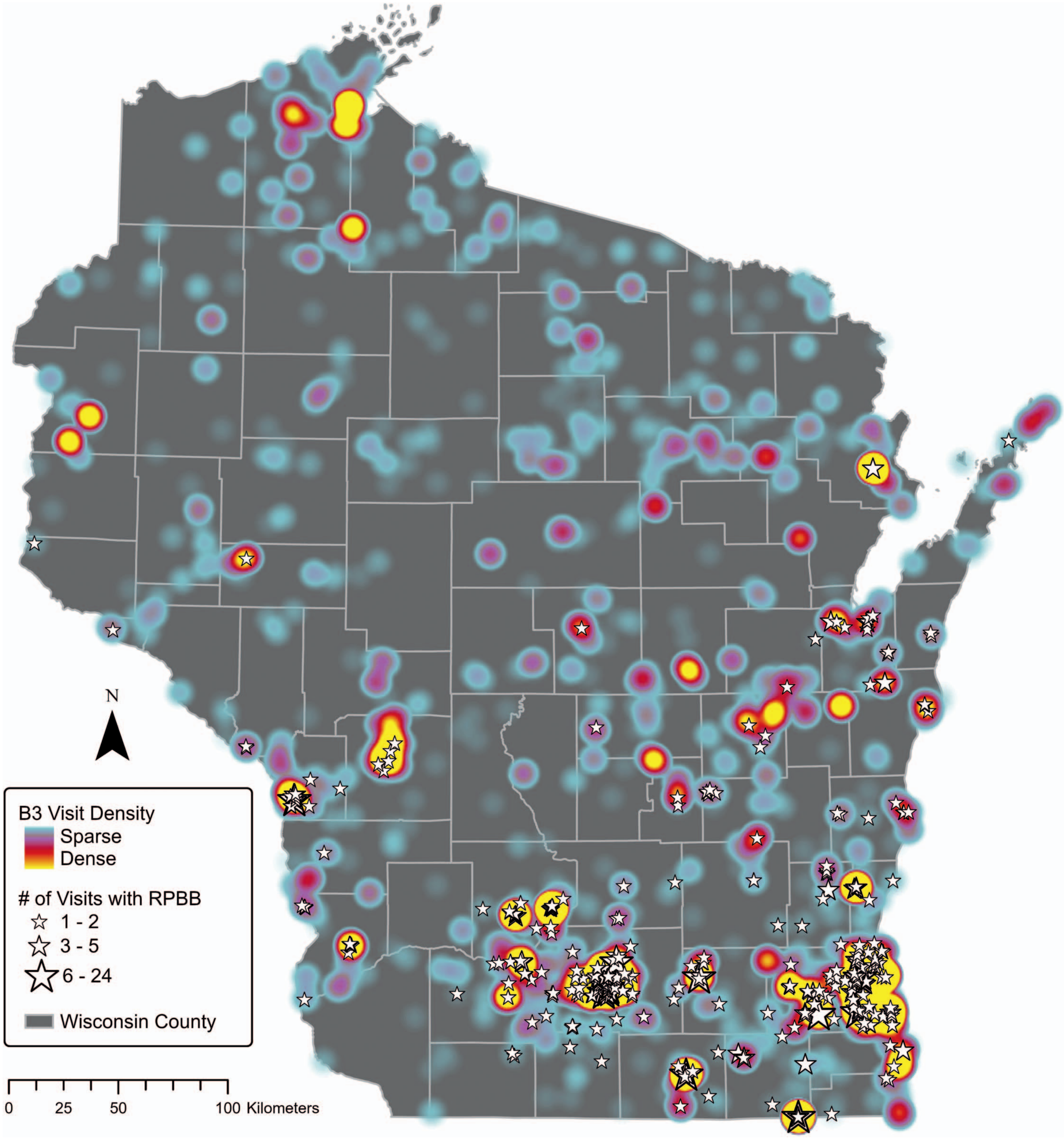

Figure 3.—Map of all sites visited by contributors to the Wisconsin Bumble Bee Brigade (B3) Project during 2018–2022. Colors represent the relative density of records, ranging from light blue (sparse density) to yellow (high density). Visits where rusty patched bumble bee was photographed are indicated by stars.

represented during spring and early summer, suggesting that woodland habitats are important, likely necessary, landscape elements of viable RPBB habitat. Fewer RPBB (mostly queens) are foraging in the spring (Figure 1), and fewer observers are actively reporting records during this period. These restrictions and the scarcity of RPBB queens in general contribute to low numbers of records on spring flowers.

Likewise, spotted Joe Pye weed (*Eutrochium maculatum*), a species of wet meadows and marshes, was frequently used by RPBB in late summer, suggesting that moist habitats might be an important landscape element during the latter part of the RPBB's seasonal activity period. We note that many recent records of RPBB have been associated with riparian corridors, which include wetlands and other moist habitats. Our findings support the view that a mosaic of flower-rich grasslands, woodlands, and wet meadows or riparian floodplains forms a desirable landscape objective for RPBB habitat management. Mola et al. (2021a, 2021b) provided evidence that spring-flowering forest wildflowers have declined during the past two decades, coinciding with declines in bumble bee populations in Illinois. Plant communities in a suitable landscape must provide flowers during the entire duration of a RPBB colony, which may extend five months or more from March (in the most southern populations) to early October.

The RPBB is a short-tongued *Bombus* (Williams et al. 2014), so some flower types are at least temporarily inaccessible without "nectar robbing" (Irwin et al. 2010), a behavior known to occur in RPBB (Rust 1977; Zimmerman and Cook 1985) and observed frequently by us on *Monarda* and by RJ on false foxgloves in Indiana. Dohzono et al. (2011) demonstrated that morphological constraints may significantly affect floral preference in bumble bees. Short-tongued species tend to prefer flowers with relatively short corollas, as expected, but flower species with long corollas are not avoided entirely. A short-tongued bee can exploit nectar directly in a long-corolla flower like *Monarda*, for example, until nectar levels are depleted below the accessible depth; once the nectar falls below this depth, nectar robbing (perforating the corolla near the base) provides a secondary option. We found that flowers most widely used by RPBB for pollen collection have exposed anthers and short corollas, except *Monarda*. Pollen was most frequently observed on RPBBs visiting species like Culver's root (*Veronicastrum virginicum*), St. John's wort (*Hypericum*), and Joe Pye weed (*Eutrochium maculatum*), all exhibiting exposed anthers.

Simanonok et al. (2021) recently analyzed floral use of RPBB by applying DNA bar-coding analysis of pollen on museum specimens collected between 1913 and 2013. They found no temporal change in the diversity of plant species or the proportion of native vs. introduced plant species during this 100-year period. Plant species represented by pollen samples varied regionally and these differences were inconsistent with patterns of RPBB decline. They detected pollen of 83 flower taxa, expanding the known range of potential pollen resources, yet supporting the conclusion that RPBB is a generalized and opportunistic forager. Wood et al. (2019), however, noted that RPBB and other declining *Bombus* species in Michigan (*B. auricomus* [black and gold bumble bee], *B. borealis* [northern amber], *B. fervidus* [golden northern], *B. pensylvanicus* [American], and *B. terricola* [yellow banded]) exhibited lower dietary breadth than congeners that showed little or no decline in range since the year 2000, a result that is similar to the findings of Kleijn and Raemakers (2008) in Europe. Simanonok et al. (2021) and Wood et al. (2019) both found that *B. affinis* and other declining species used a rather wide variety of pollen resources, even though this breadth was less than that of *Bombus* species with more stable geographic ranges. Indeed, Simanonok et al. (2021) documented pollen from 70 genera representing 25 plant families. This breadth covered a wide temporal window and broad geographic scale; within a given region, a narrower assemblage of pollen resources would be expected.

Unlike recent pollen studies based on museum specimens (Wood et al. 2019; Simanonok et al. 2021), the data presented here reflect RPBB exploitation of both pollen and nectar resources. Not surprisingly, our findings yielded a wide diversity of plant genera (87) despite a much narrower period of study ($\sim$4 years) and a rather limited geographic area. We also present data from many more samples, which inherently will result in a higher number of flower species and genera, all else being equal.

Medler and Carney (1963) described floral hosts of Wisconsin bumble bees at a time when RPBB was common. They included 23 genera of host plants for RPBB, 13 of which overlap with our list (Table 1). Five woody genera (*Salix*, *Creteagus*, *Cercis*, *Rhus*, *Syringa*) and one herbaceous genus (*Hieracium*) visited by queen RPBBs were recorded by Medler and Carney (1963) but did not appear in our list. Willows (*Salix*) and lilacs (*Syringa*) bloom in spring and early summer when RPBBs are scarce and difficult to photograph. The majority of B3 observations are reported from grassland/shrubland and urban/suburban/rural sites, leading to a bias in our flower data. Medler and Carney's records also came from a time when RPBB were widespread, whereas today populations are much more local in occurrence. This inevitably would lead to a wider variety of flowers available to RPBB foragers when Medler and Carney recorded their observations. Among the 10 most frequently documented plant genera in the Wisconsin B3 project, only *Solidago* (goldenrods) and *Cirsium* (thistles) also were reported by Medler and Carney (1963). These differences may reflect Medler and Carney's focus on agricultural habitats (especially alfalfa fields), places where RPBB may no longer be abundant today. Their surveys also were conducted before the widespread use of neonicotinoid pesticides and Roundup-ready crops. In short, both our study and the study by Medler and Carney (1963) include unmeasured (and perhaps unmeasurable) sources of bias, so comparisons between the lists of flowers used by RPBB need to be interpreted very cautiously. This does not mean that comparisons are without value, however, especially if they lead to future, more controlled studies aimed at improving land management for RPBB populations.

Interestingly, the higher frequencies of woody plants in Medler and Carney (1963) and the museum analysis by Simanonok et al. (2021) infer that our B3 samples might be biased against trees and shrubs, or perhaps early-season RPBB foraging hosts in general. A better representation of RPBB floral hosts might be obtained by recommending more B3 surveys early in the season on spring flowering plants, including woody species. We also recommend additional training or educational materials to help identify RPBB queens.

The wide range of observed RPBB flower hosts reported by both the B3 project and other observers does not necessarily imply indiscriminate foraging. Over half of the RPBB records represented just 5 plant genera, with 35 plant genera documented only once. This uneven distribution is unlikely the result of oversampling bees at a few dates and localities. Our data analyses utilize a single record for each plant taxon at a given site and date. For example, at least 40 RPBB individuals were observed on *Veronicastrum virginicum* at a site in Green Lake County on 16 July 2021. This observation was reduced to just one record in our database according to the screening process described in our methods. Because the number of known RPBB localities is limited, some sites were visited multiple times, but only a single record was included at that locality for each date and flower taxon. This conservative approach may underrepresent the importance of species like *Veronicastrum virginicum* to RPBB colonies.

We were unable to objectively quantify floral preferences in RPBB because the relative abundances of alternative flower species at observation sites are not routinely documented by B3 participants. Nevertheless, the scarcity of B3 records for many of today's widespread and common flowering species like birdsfoot trefoil (*Lotus corniculatus*), sweet clovers (*Melilotus* spp.), purple vetch (*Vicia purpurea*), black-eyed Susan (*Rudbeckia hirta*), red clover (*Trifolium pratense*), and others suggests that RPBB do not forage randomly, a conclusion supported by the analysis of Wood et al. (2019). Native forbs such as *Monarda fistulosa* (bee balm), *Agastache* spp. (hyssops), *Eutrochium maculatum* (Joe Pye weed), *Veronicastrum virginicum* (Culver's root), and *Solidago* spp. (goldenrods) are especially important for Wisconsin's remnant RPBB populations, regardless of the species' innate floral preferences (or lack of preferences). Species like *Spiraea alba* (meadowsweet), *Dalea* spp., and other native wildflowers are reported by others as important floral resources for RPBB and they occur in our database, but they are absent or uncommon at sites where most RPBB occur today in Wisconsin. Consequently, these species are not major floral resources for RPBB in the areas sampled (so far) by B3 field observers but could be added to plantings and managed natural areas. RJ's field observations reveal several other genera (*Aureolaria*, *Rudbeckia*, *Actaea*, and *Silphium*) that seem to be important elsewhere but are not documented extensively by RPBB in Wisconsin. Surveys of all flowering resources in an area (not just those being visited by RPBB) are needed to determine floral preferences of this and other bumble bee species.

Our findings support published recommendations by the U.S. Fish and Wildlife Service (USFWS 2021b) for habitat management aimed at sustaining or restoring local RPBB populations in Wisconsin and nearby states. Most of the key plant species and genera recommended by this source were prominent in both our analysis and in additional observations by RJ (Table 2) and other community science initiatives like iNaturalist.

Like others (e.g., Hines and Hendrix 2005; Watson et al. 2011; Szymanski et al. 2016) we recommend a comprehensive habitat management strategy that provides access to native floral resources (both pollen and nectar sources) across the entire growing season. Spring and early summer wildflowers like *Dicentra cucullaria* (Dutchman's breeches) and *Hydrophyllum virginianum* (Virginia waterleaf) and perhaps woodland shrubs and trees (e.g., *Amelanchier* spp., *Tilia* spp., *Prunus* spp., *Salix* spp., and, outside Wisconsin, *Rhododendron* spp.), provide resources for queens at the critical colony-establishment phase of the RPBB life cycle. During late summer, wet meadow plants like *Eutrochium* spp. (Joe Pye weed) also might be critically important, especially during dry years.

Griffin et al. (2021) suggested that management for favored plant communities is not sufficient for successful conservation or restoration of native bee species. Other targeted habitat measures are needed, including management of bee-favorable grassland disturbance regimes, protection of nearby woodland understory plants and habitat, and conservation of favorable nesting sites like abandoned rodent burrows and other types of underground cavities and overwintering habitat. These recommendations are supported by many recent studies of wild bee communities (Winfree 2010; Roulston and Goodell 2011; Kennedy et al. 2013; and others). Our analysis, therefore, sheds light on just one aspect of RPBB conservation needs. We provide evidence that specific floral resources are frequently used by RPBB in the midwestern United States, particularly a suite of approximately 10–12 flowering plant species (Table 2) that are consistently used in today's highly modified landscapes.

Community science programs engage people in applied research (Van De Gevel et al. 2020) and have become widely recognized as valid contributors to science-based natural resource management (McKinley et al. 2017; Fraisl et al. 2020; McPhail and Colla 2020; Lepczyk et al. 2020). Community science projects and associated outreach efforts promote interest in conservation efforts overall; their potential for building valid data sources, however, is not just a secondary benefit. Our project demonstrates how carefully guided field efforts by community scientists (participants in Wisconsin's Bumble Bee Brigade program) can meaningfully support informed, effective conservation of endangered insects like the RPBB. A disadvantage of data from community science programs, of course, is that analysts have limited control over collection biases and sampling effort on the short term, although protocols can be improved over time. For example, contributors are more likely to collect photographs from gardens, parks, and other easily accessible places, leading to strongly biased spatial distribution maps. In addition, early season observations are often missed, and data from species where flowers are difficult to observe directly (trees), are sparse. Feedback from biologists and project coordinators can provide a basis for modifying protocols and producing educational materials to help minimize these biases. As long as researchers recognize the bias and restrain their interpretations accordingly, community science provides an advantage of large and geographically broad sample sizes that otherwise would be difficult or impossible to achieve by research specialists (Johnston et al. 2020). In our case, the lists of plant species used by RPBB would be very difficult to obtain by a single research team, inevitably limited by a narrower geographic or temporal scope. Community science projects can adapt over time with feedback from a large base of hands-on participants and researchers. Despite its biases, the database compiled by Wisconsin's Bumble Bee Brigade reveals some consistent patterns of floral use by RPBB. These patterns agree with our personal field experience in Wisconsin and reports by U.S. Fish and Wildlife Service biologists (USFWS 2021a) for midwestern states in general. This combination of findings by academic researchers, government agency biologists, and community scientists provides strong inference that RPBBs in the Midwest prefer a suite of grassland/savanna forbs, woodland wildflowers, and late-blooming plant species of wet meadows. Hence, a mosaic of grassland, woodland, and wet meadow habitats is desirable for ecological restoration and maintenance of habitats aimed at preserving this federally endangered bee species in midwestern landscapes.

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