Environmental Entomology, XX(XX), 2020, 1–10
doi: 10.1093/ee/nvz159
Research

Pollinator Ecology and Management

Plant Selection by Bumble Bees (Hymenoptera: Apidae) in Montane Riparian Habitat of California

Jerry S. Cole,[1,4] Rodney B. Siegel,[1] Helen L. Loffland,[1] Erin A. Elsey,[1] Morgan B. Tingley,[2] and Matthew Johnson[3]

[1]The Institute for Bird Populations, PO Box 1346, Point Reyes Station, CA 94956, [2]Ecology and Evolutionary Biology, University of Connecticut, 75 North Eagleville Road, Unit 3043, Storrs, CT 06269, [3]Plumas National Forest, USDA Forest Service, 159 Lawrence Street, Quincy, CA 95971, and [4]Corresponding author, e-mail: jcole@birdpop.org

Subject Editor: Theresa Pitts-Singer

Received 6 September 2019; Editorial decision 11 December 2019

Abstract

Many bumble bee species (*Bombus* Latreille) have declined dramatically across North America and the globe, highlighting the need for a greater understanding of the habitat required to sustain or recover populations. Determining bumble bee species' plant selection is important for retaining and promoting high-quality plant resources that will help populations persist. We used nonlethal methods to sample 413 plots within riparian corridors and meadows in the Sierra Nevada of California for bumble bees during two summers following extremely low and normal precipitation years, respectively. We assessed the five most abundant bumble bee species' plant selection by comparing their floral use to availability. Additionally, we described the shift in plant selection between years for the most abundant species, *Bombus vosnesenskii* Radoszkowski. Bumble bee species richness was constant between years (13 species) but abundance nearly tripled from 2015 to 2016 (from 1243 to 3612 captures), driven largely by a dramatic increase in *B. vosnesenskii*. We captured bumble bees on 104 plant species or complexes, but only 14 were significantly selected by at least one bumble bee species. Each of the five most frequently captured bumble bee species selected at least one unique plant species. Plant blooming phenology, relative availability of flowers of individual plant species, and plant selection by *B. vosnesenkii* remained fairly constant between the two study years, suggesting that maintaining, seeding, or planting with these 'bumble bee plants' may benefit these five bumble bee species.

Key words: *Bombus* spp., floral selection, wild bee, Sierra Nevada, pollinator

Population size and geographic extent of many North American bumble bee (genus *Bombus* Latreille) species have declined in recent decades (Cameron et al. 2011). Declines have been attributed to stress from parasites, pesticides, and a lack of flowers on the landscape (Szabo et al. 2012, Goulson et al. 2015), factors that may interact with one another (Winfree et al. 2009) and might be exacerbated by competition with introduced honey bees (e.g., Mallinger et al. 2017, Wojcik et al. 2018). In montane landscapes of western North America, bumble bees are generally most abundant in meadows and other riparian habitat with diverse floral communities (Hatfield and LeBuhn 2007, Aldridge et al. 2011, Loffland et al. 2017). Determining which plant species are selected by bumble bees in riparian habitats is useful for managing and restoring those habitats to conserve bumble bees.

M'Gonigle et al. (2017) provided a tool for selecting the most beneficial plant mix to meet specific management goals for bees, based on knowledge of their plant use. We support this approach, which allows users to select a particular metric to maximize (e.g., pollinator visitation or species richness) and uses number of bumble bees captured using a plant as an index of plant value. We suggest extending this method with information on bumble bee plant selection, i.e., plant use in relation to plant availability on the landscape. Explicitly considering plant availability in addition to use recognizes that bumble bees may visit a plant species frequently because the plant is highly abundant on the landscape, as opposed to visiting that plant because it prefers its pollen or nectar relative to other plants. Selection is often defined as the proportion of times an organism uses a resource relative to how often that resource is available in the environment (Lele et al. 2013) and is useful in describing the relative value of resources to an organism (Johnson 1980). Determining plant selection by individual bumble bee species may be especially important for species with specialized foraging niches, as bumble bees with narrower pollen diet breadths have exhibited greater population declines in both Europe (Kleijn and Raemakers 2008) and North America (Wood et al. 2019).

Research on bumble bee–plant interactions has commonly examined specific bumble bee or plant characteristics that drive bumble bee flower use, such as bumble bee tongue length (Harder 1985), flower symmetry (Møller 1995), color preference (Gumbert 2000), and pollen nutritional value (Vaudo et al. 2016), with the aim of making generalizations that are broadly applicable across different habitats and bee species (Ogilvie and Forrest 2017). Although substantial annual turnover in pollinator (including bumble bees) associations with specific plants has been demonstrated (e.g., Alarcón et al. 2008, Petanidou et al. 2008), few studies have examined bumble bee plant selection or how it may vary within and between years. Pollinator flower use may shift due to within-year changes in plant availability that reflect blooming phenology (Loffland et al. 2017) as well as between-year turnover in the plant or pollinator community (Alarcón et al. 2008, Lázaro et al. 2010), and floral availability can have a strong effect on abundance of bumble bee species (Ogilvie et al. 2017).

Understanding bumble bee plant selection, including how it varies within and between years, aids habitat management and restoration efforts by identifying floral communities capable of supporting bumble bee populations. Here, we report bumble bee community composition, floral availability, and use and selection of flowering plants by bumble bees in montane riparian corridors and meadows over two consecutive years with markedly different precipitation patterns. The first year of study followed a winter that had the lowest snowpack in 120 yr of instrumental records and was the culmination of a multi-year drought (Luo et al. 2017). The second year of study followed a winter with weather conditions much closer to the long-term average. Our objective was to identify flowering plant species selected by bumble bees, while assessing and accounting for between-year variation in the composition of the bumble bee and plant communities during years with contrasting weather patterns.

Methods

Study Area

We surveyed bumble bees from May to August during 2015 and 2016 on Plumas National Forest in the northern Sierra Nevada of California, United States (Fig. 1) at plots ranging in elevation from 1,100 m to 2,168 m a.s.l. The Sierra Nevada region is generally warm and dry during the summer and receives most of its precipitation between October and April. Annual precipitation (which we defined as October of the prior year through September of the study year) across the study area differed sharply between our two study years, with 585 mm of precipitation estimated during the 2015 study year, versus 884 mm during the 2016 study year [mean for the period 1981–2010 = 740.4 mm ± 289.5 (SD); Thornton et al. 2018].

We sampled bumble bees within riparian corridors and meadows that spanned diverse vegetative and physiographic conditions embedded in a matrix of Sierran Mixed Conifer forest and montane chaparral (Mayer and Laudenslayer 1988). Surveyed plots were on National Forest land within the perimeter of the Moonlight fire, which burned 27,370 ha of forested land at mixed severity in 2007 (Micheletty et al. 2014), or outside the fire but within a 6-km buffer of the perimeter (Fig. 1). Heterogeneous physiography and burn severity, and nearly a decade of postfire succession prior to our study, contributed to highly diverse riparian vegetation structure and composition across survey plots (Cole et al. 2019).

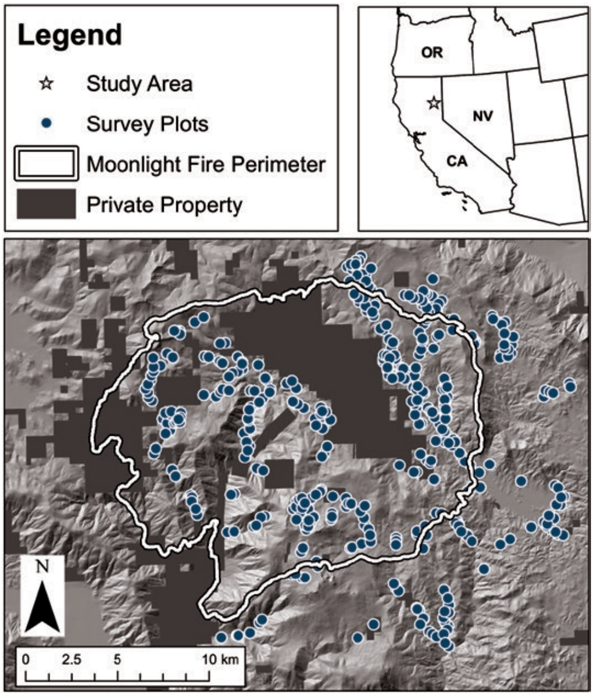

Fig. 1. Riparian and meadow survey plots for bumble bees on Plumas National Forest lands within and near the Moonlight fire perimeter in the northern Sierra Nevada, CA (see inset; state abbreviations are as follows: OR—Oregon, NV—Nevada, CA—California). Gray background texture represents topographic relief.

Study Design

Our study encompassed 413 bumble bee sampling plots, each defined by a 20-m radius around a central point. The plots were aggregated from two distinct sampling efforts that shared a common data collection protocol and were surveyed by the same observers. About half of the plots were generated for a study that assessed habitat covariates of bumble bee and riparian bird species richness in riparian corridors (Cole et al. 2019). To generate this portion of the sample, we used a GIS to place points representing centers of possible plots every 100 m along first, second, and third Strahler order streams (Strahler 1957) on National Forest land within and near the area burned by the Moonlight fire. We used unstratified, unequal probability, generalized random tessellation stratified (GRTS) sampling (Stevens and Olsen 2004) to select sampling plots from this initial set of possible plots with the R package 'spsurvey' (Kincaid and Olsen 2013). This form of GRTS sampling selected plots proportional to stream reach length and Strahler order present within the study area. For each selected point, we established a survey plot centered 25 m from the stream in a randomly chosen (left or right bank) direction, unless one stream bank was inaccessible, in which case we established the plot on the opposite side. This approach yielded 203 plots in riparian corridors.

The riparian corridor sampling scheme yielded relatively few plots within meadows. Many pressing management issues on National Forest land in the Sierra Nevada manifest in montane meadows, where livestock grazing, recreation, and habitat management for wildlife (potentially including bumble bees) often conflict. We therefore supplemented the GRTS-derived plots with 210 additional plots in montane meadows throughout our study area. Plot locations were selected randomly (but at least 100 m apart and ≥20 m from the meadow edge) throughout all previously delineated meadows within our study area (Fryjoff-Hung and Viers 2012), and in additional meadows that were known to the authors but had not been delineated. Most meadows throughout the study area were used historically for livestock grazing, and many were within grazing allotments that remained active during our study. During subsequent plot visits, we found that these two habitat classes (riparian vs meadow) were highly overlapping, with riparian corridors often bisecting meadows, and small stringer meadows often lining streams, in effect constituting the riparian corridor. We therefore pooled all plots, regardless of which selection procedure yielded them, for all analyses.

Data Collection

From early May to mid-August in both 2015 and 2016, we conducted bumble bee surveys between 0900 and 1700, suspending surveys during rain or cold that would suppress bumble bee activity. Most plots were surveyed twice during each season with visits typically separated by 4–6 wk, to accommodate substantial inter-specific variation in phenology of bumble bee colony life cycles (Pyke et al. 2011) and plant blooming periods. We staggered plot visits such that surveys of relatively low- and high-elevation plots were well distributed throughout the overall survey period each year (Supp Fig. 1 [online only]). For each survey visit, we captured bumble bees throughout the 20-m radius circular plot via sweep net during a 16-min period (see Loffland et al. 2017 for detailed survey methods) and recorded the plant species each bee was foraging on when captured. Bumble bees were placed in vials, chilled in a cooler, and then photographed and identified to species immediately after the survey period. Bumble bee species identification followed the key created by Koch et al. (2012).We released bumble bees at the survey plot after they warmed and became active again, except for a small number of voucher specimens of the commonly encountered species that we collected each year. An expert bumble bee biologist (E.A.E.) reviewed photographs to confirm species identification when surveyors were uncertain of bumble bee species identity. Handling and collection of bumble bees was authorized under California Department of Fish and Wildlife Entity Permit SC-008645. During each visit to each survey plot, we described floral resources available to bumble bees by identifying the five plant species (including herbaceous plants and shrubs) with the greatest number of inflorescences within the 20-m radius plot (e.g., flower species A, B, C, D, and E were all included in the top five because they had 50, 40, 30, 20, and 10 inflorescences, respectively, within the plot, but species F was not included because it had five inflorescences). We identified plants using a combination of botanical keys (Jepson 1993, Weeden 1996) and photographs and other resources housed online at CalFlora (https://www.calflora.org) and eJepson (http://ucjeps.berkeley.edu/eflora). In some instances, observers were unable to identify plants to species with adequate confidence (see below), but were nearly always (97% of plant records) able to determine at least the genus with certainty.

Statistical Methods

We indexed individual bumble bee species' floral use as the proportion of captures on each flowering plant species relative to total captures on all plants which that bee species was captured on, across all plots in both years. Following Loffland et al. 2017, we indexed floral availability as the proportion of times each plant species was among the five plant species with the most inflorescences during plot surveys, including only plants which a particular bumble bee species was captured on at least once. The abundance rank of a plant species within a plot (1 through 5) did not factor into the availability calculation. Although some rarer species may have never been included among the top five blooming species during any plot visit, we considered our list of top five plant species a sufficient representation of the floral community because in many instances (38.8 % of plot visits) the number of species recorded was <5. We estimated plant selection via use and availability indices for each of the five most frequently captured bumble bee species: *Bombus vosnesenskii*, *Bombus bifarius* Cresson, *Bombus melanopygus* Nylander, *Bombus vandykei* Frison, and *Bombus flavifrons* Cresson. Each plant species thus had a distinct availability index for each bumble bee species, reflecting the particular set of plant species that each bumble bee species was captured on.

We assessed most plants at the species level. We grouped plants into a genus complex when observers were not able to identify all plants to species within a given genus [e.g., all *Salix* (Linnaeus) (Malpighiales: Salicaceae) species were identified as *Salix* spp.]. We grouped plants to genus if >15% of observations of plant species in a particular genus consisted of genus-only observations [e.g., 30 entries for *Rosa* (Linnaeus) (Rosales: Rosaceae) spp. and 84 for *Rosa woodsii* (Lindley)]. Plant observations were dropped and the associated bumble bee captures excluded from availability and use index calculations in instances where ≤15% of plant identities were to genus only, rather than grouping them into complexes, because we desired to maintain as many species-level assessments as possible. In most cases, complexes included all species within a genus. However, we grouped *Phacelia egena* (Greene ex Brand) Greene ex J.T. Howell (Boraginales: Boraginaceae), *Phacelia hastata* (Douglas ex Lehmann), and *Phacelia heterophylla* (Pursh) into a '*Phacelia* complex' because our surveyors had trouble distinguishing them, but we retained *Phacelia hydrophylloides* (Torrey ex A. Gray) and *Phacelia humilis* (Torrey & A. Gray) as separate species because surveyors could identify them with confidence. We report the species that comprise each plant complex in Supp Table S1 (online only).

We evaluated bumble bee use versus availability of flowering plant species (or plant complex) with a chi-squared goodness-of-fit test to determine whether the distribution of available plant species was proportional to the use of those species (Neu et al. 1974, Loffland et al. 2017) for each of the five most commonly captured bumble species. If the chi-squared test indicated that plant use was significantly different from plant availability, we used a Bonferroni Z-statistic (Alldredge and Ratti 1992) to test which individual plant species were used significantly more (selected) or less (avoided) than expected based on availability.

We estimated bumble bee floral selection (use divided by availability) for each of the five most frequently captured bumble bee species, by dividing the use index by the availability index for plant species i, where

$$\text{if } \frac{use_i}{availability_i} \geq 1 \text{ then } selection\ index_i = \frac{use_i}{availability_i},$$

$$\text{if } \frac{use_i}{availability_i} < 1 \text{ then } selection\ index_i = -1 * \left[\left(\frac{use_i}{availability_i} \right)^{-1} \right].$$

For instance, if use for bumble bee species A on plant B was 0.1 and availability of plant B was 0.01, the selection index would be 10. This indicates bumble bee species A selected plant B 10 times more than it was available at sampled plots. Conversely, if use for bumble bee species A on plant B was 0.01 and availability was 0.1, then the selection index would be −10. This index suggests that plant B was used 10 times less often than it was available. We also summarized the interannual change in plant selection for the most frequently captured bumble bee species (*B. vosnesenskii*) using the same methods outlined above, except limiting use and availability to bee captures and plant observations during each individual year (2015 or 2016). For plants that were significantly selected by at least one of the five most frequently captured bumble bee species, we also plotted weekly indices of bloom phenology along with weekly indices of bumble bee captures, to explore use relative to plant availability in each of the study years. We grouped plant species using phenology data from 2016 into early (maximum bloom before 18 June), mid (maximum bloom after 18 June and up to 15 July), and late blooming (maximum bloom after 15 July) for plotting. These groupings are somewhat arbitrary but facilitate visualizing variation in bloom phenology.

Results

We captured and identified 1243 bumble bees of 13 species during 807 surveys on 413 plots in 2015, and 3,612 bumble bees of 13 species during 818 surveys on 410 plots in 2016 (Table 1). In 2015, the three most frequently captured species were *B. bifarius* (367 captures), *B. flavifrons* (301 captures), and *B. vandykei* (156 captures). In 2016, captures were dominated by *B. vosnesenskii* (2641 captures) followed by *B. flavifrons* (349 captures) and *B. melanopygus* (268 captures). Phenology of captures of individual bumble bee species was relatively consistent across each sampling year (peaking near the same date in each year) for the five species analyzed (Fig. 2). However, captures of *B. vosnesenskii* vastly outnumbered all other species beginning in late June of 2016 and lasting through the remainder of the sampling season (Fig. 2).

Bumble bee and plant data filtering (see criteria in Methods) resulted in 13% (2015) and 7% (2016) of bumble bee captures being removed from the data set (Table 1). Most (76%) of the discarded bumble bee captures were filtered because the bumble bee was captured on an item other than vegetation (e.g., the ground or a log) or captured in flight (324 of 426 filtered captures). The final (filtered) dataset contained 1,078 captures in 2015 and 3,351 in 2016 (Table 1). Pooling data across 2015 and 2016, we captured bumble bees using 86 plant species and 18 plant complexes (Supp Table S2 [online only] and Supp Fig. 2 [online only]). We never captured any bumble bees on 24 plant species that nevertheless were among the top five blooming plant species at one or more plots (Supp Table 3 [online only]). The number of bumble bee species using each plant species or complex was generally positively correlated with the plant's index of availability (Spearman's rho = 0.62) such that more bumble bee species were captured on plants that were more available. However, the most available plant species [*Achillea millefolium* (Linnaeus) (Asterales: Asteraceae): availability index = 0.095] was an outlier with only two bumble bee species captured using it. The greatest number of bumble bee species were captured on *Sidalcea oregana* (Nuttall ex Torrey & A. Gray) A. Gray (Malvales: Malvaceae) (availability index = 0.052; 12 species) and *Monardella odoratissima* (Bentham) (Lamiales: Lamiaceae) (availability index = 0.049; 10 species; Table 2).

Fourteen plant species were used by at least one bumble bee species significantly more than expected based on availability (i.e., selected by bumble bees, Fig. 3). *Agastache urticifolia* (Bentham) Kuntze (Lamiales: Lamiaceae) was the plant species most often used by two of the frequently captured bee species (*B. flavifrons* and *B. vandykei*), and the second most frequently used plant species by *B. vosnesenskii* (Fig. 3). The plant species most frequently used by *B. vosnesenskii* was *Lupinus polyphyllus* (Lindley) (Fabales: Fabaceae); for *B. bifarius* it was *Eurybia integrifolia* (Nuttall) G.L. Nesom (Asterales: Asteraceae); and for *B. melanopygus* it was *Penstemon rydbergii* (A. Nelson) (Lamiales: Plantaginaceae) (Fig. 3). Each of the five individual bumble bee species we evaluated showed significant selection for two to seven plant species or complexes (Fig. 4). One of the 14 selected species, *Cirsium arvense* (Linnaeus) Scopoli (Asterales: Asteraceae) (selected by *B. vosnesesnkii*) is not native to North America. *Agastache urticifolia* was most strongly selected by three of the five individual bumble bee species evaluated (including *B. vosnesenskii*, *B. vandykei,* and *B. flavifrons*). The most frequently captured bumble bee species, *B. vosnesenskii*, used *A. urticifolia* 5.8 times more than expected based on its availability. However, *B. melanopygus* avoided *A. urticifolia*, and *B. bifarius* used this plant approximately in proportion to its availability.

Plant availability and *B. vosnesenskii* usage of several plant species shifted moderately between 2015 and 2016 (Fig. 5). Availability of *S. oregana* declined most substantially from 2015 to 2016 compared with any of the 14 plant species that were selected by at least one bumble bee species (Fig. 5). Usage of *Perideridia* complex, *A. urticifolia*, *M. odoratissima*, and *L. polyphyllus* increased from 2015 to 2016, whereas *S. oregana* and *Chamerion angustifolium* (Linnaeus) Holub (Myrtales: Onagraceae) usage declined (Fig. 5).

Table 1. Bumble bee species captures and percentage of all captures (%) during the 2015 and 2016 sampling seasons

	Total captures				Filtered captures			
	2015		2016		2015		2016	
Bumble bee species	no.	%	no.	%	no.	%	no.	%
B. bifarius	367	30	108	3	305	29	99	3
B. californicus	69	6	33	1	51	5	21	1
B. centralis	9	1	12	0	7	1	11	0
B. fernaldae	1	0	3	0	1	0	3	0
B. flavifrons	301	24	349	10	262	24	326	10
B. insularis	12	1	21	1	5	0	16	0
B. melanopygus	53	4	268	7	51	5	249	8
B. mixtus	36	3	73	2	28	3	68	2
B. nevadensis	3	0	4	0	3	0	3	0
B. occidentalis	5	0	1	0	4	0	1	0
B. rufocinctus	14	1	1	0	10	1	1	0
B. vandykei	156	13	98	3	152	14	94	3
B. vosnesenskii	217	17	2641	73	199	18	2459	73
Grand total	1243		3612		1078		3351	

Total captures denotes the number of bumble bees captured during all visits and filtered captures denotes the total bumble bee captures in the filtered data set (see text for data filtering criteria).

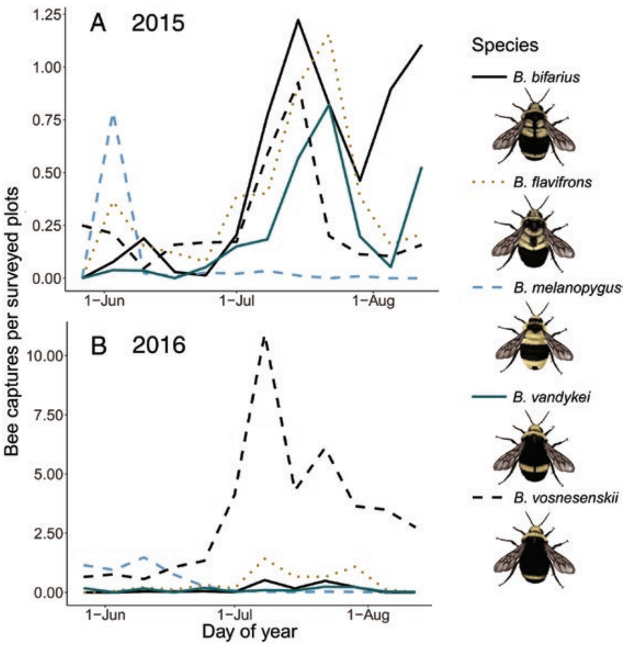

Fig. 2. Weekly capture rate (bumble bees captures/plots surveyed per week) for the five most commonly captured bumble bee species in 2015 (A) and 2016 (B). Note that axis scales differ between years. Illustrations of each bumble bee species are provided below each species name. Artwork was created by Lauren Helton.

Plants that were selected or avoided in 2015 (whether significant or not) tended to continue to be selected or avoided in 2016. *Bombus vosnesenskii* selected three plants in both years, avoided five in both years, and either selected or avoided three in one year but not in the other. Two plant species never visited in 2015 (*P. rydbergii* and *Spiraea douglasii*) were selected by *B. vosnesenskii* in 2016, and *B. vosnesenskii* was never captured on *Aconitum columbianum*.

The 14 plant species selected by at least one bumble bee species varied substantially in bloom phenology (Fig. 6), but plant blooming appeared to peak during the same portion of the summer each year. The number of bumble bee captures on each of the 14 selected plant species roughly tracked the availability of those plants across the season. Assessing relationships for individual bumble bee species, floral selection index values were generally greater for plants with peak bloom occurring when bees were most abundant (Fig. 7). For instance, *B. melanopygus* abundance (inferred from capture rates) peaked in early June, largely in synchrony with floral abundance of its most strongly selected plant species, *P. rydbergii* (Fig. 7). No plant species with peak floral abundances after late-June were selected by *B. melanopygus*, which appeared in substantial numbers earlier than the other common bumble bee species and then became scarce after mid-June. Alternatively, *B. vosnesenskii,* which peaked in abundance in mid to late-July, most strongly selected *A. urticifolia* which also peaked in floral abundance around the same period (Fig. 7).

Table 2. Truncated list of plant species or complexes on which any of 13 observed bumble bee species were ever captured

Plant species or complex	Floral availability index	Bumble bee richness
Sidalcea oregana	0.052	12
Monardella odoratissima	0.049	10
Agastache urticifolia	0.024	9
Mertensia ciliata	0.021	9
Stachys albens	0.013	9
Lupinus polyphyllus	0.038	8
Phacelia complex	0.014	8
Wyethia complex	0.027	7
Chamerion angustifolium	0.022	7
Perideridia complex	0.031	6
Cirsium vulgare	0.018	6
Spiraea douglasii	0.012	6
Eurybia integrifolia	0.010	6
Hydrophyllum occidentale	0.008	6
Mimulus guttatus	0.039	5
Prunella vulgaris	0.014	5
Symphyotrichum ascendens	0.014	5
Phacelia humilis	0.007	5
Epilobium complex	0.026	4
Potentilla gracilis	0.018	4
Trifolium longipes	0.016	4
Penstemon rydbergii	0.012	4
Verbascum thapsus	0.011	4
Veratrum californicum	0.010	4
Polygonum bistortoides	0.008	4
Penstemon procerus	0.007	4
Symphyotrichum spathulatum	0.006	4
Pedicularis groenlandica	0.004	4
Penstemon deustus	0.004	4
Corydalis caseana	0.004	4
Gilia capitata	0.004	4
Lathyrus nevadensis	0.004	4
Camassia quamash	0.002	4

For space considerations, we truncated this list to plant species visited by > 3 bumble bee species. Plants are sorted according to number of bumble bee species captured using them (Bumble bee richness). The proportion of times a plant species was among the five most abundant flowering plants during a plot survey is listed under the floral availability index column and are based on data pooled across 2015 and 2016.

Discussion

We observed identical bumble bee community richness but dramatic changes in the abundance of one species (*B. vosnesenskii*) between 2015 and 2016. Although we captured bumble bees on >100 plant species in our study area, bumble bees positively selected a relatively small subset of these plants, with just 14 plant species yielding statistically significant selection indices by at least one bumble bee species. Each of the five commonly captured bumble bee species selected at least one plant species that was not significantly selected by any of the other five bumble bees. Selection of floral resources by *B. vosnesenskii,* the most frequently captured bee species, was relatively consistent between years, even as floral availability of individual plant species shifted. Blooming periods for selected plants were temporally staggered throughout our study period, providing floral resources throughout the annual cycles of each of the frequently captured bumble bee species.

Interannual Variation in Bumble Bee Assemblage

Bombus vosnesenskii relative abundance varied dramatically between 2015 and 2016. Causes of the more than ten-fold increase in *B. vosnesenskii* captures during 2016 are unclear. Between-year phenology of selected plant species and bumble bee captures were relatively stable, so a phenological shift by either plants or bees seems an unlikely driver of observed changes in bumble bee relative abundance. The increase in *B. vosnesenskii* abundance in 2016 may

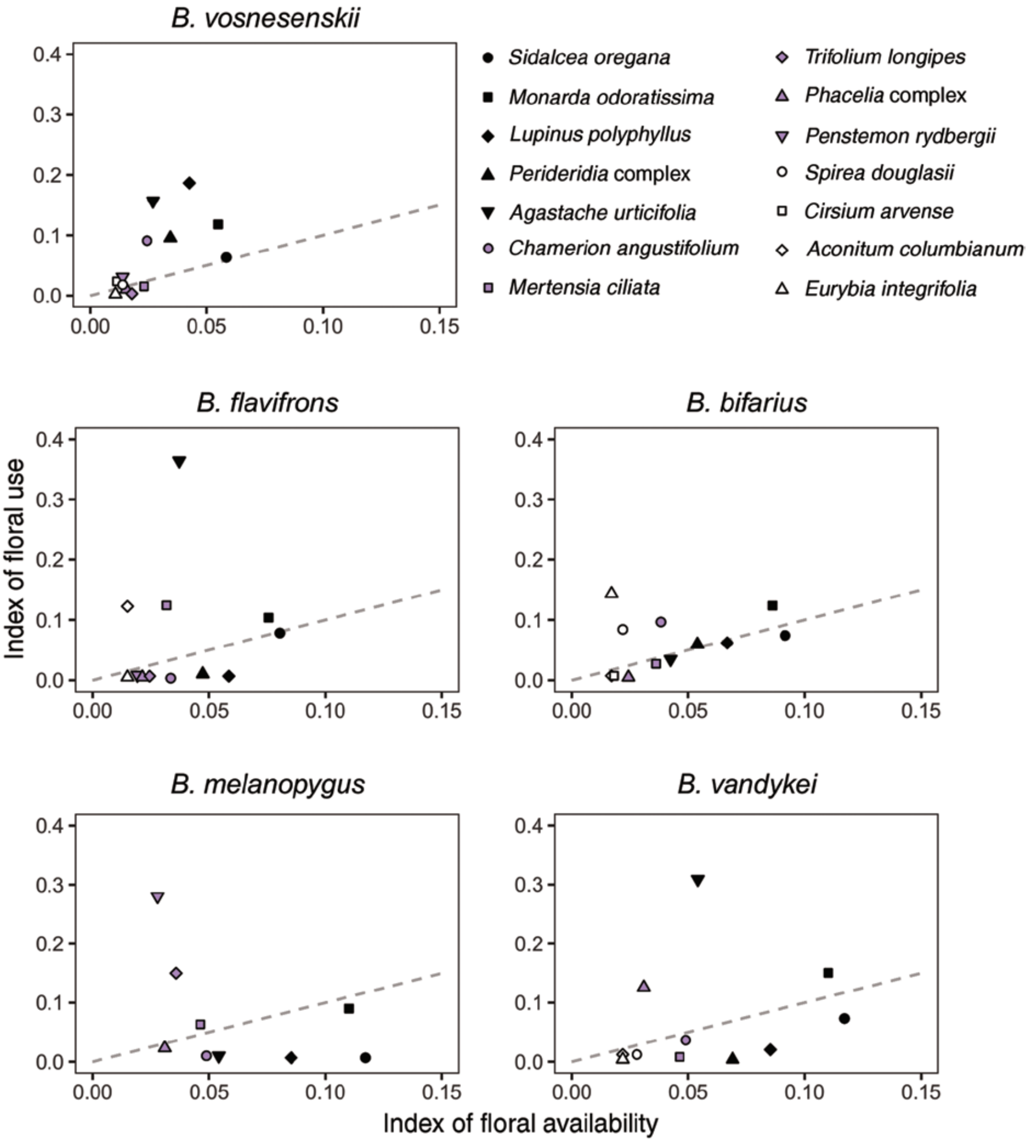

Fig. 3. Availability and usage indices for plant species or complexes significantly selected by at least one of the five most frequently captured bumble bee species (data pooled across 2015–2016). If a bumble bee species was never captured on a plant species, then that symbol was omitted from the panel. Dashed gray line denotes a 1:1 relationship between plant use and availability (neutral selection). Plant species in legend are sorted from most to least available, top to bottom and left to right.

have led to increased competition for resources among the bumble bee assemblage, and potentially the decline in abundance of *B. bifarius*, *B. californicus*, and *B. vandykei* in our study area. However, *B. bifarius* and *B. vandykei* each selected for only a single shared plant species with *B. vosnesenskii,* a different plant species in each instance. We did not assess floral selection for *B. californicus* in this study. In a separate study of urban parks, *B. vosensenskii* abundance was negatively associated with bumble bee species richness, and authors suggested that *B. vosensenskii* may have outcompeted other bumble bee species for nest sites early in the season (McFrederick and LeBuhn 2006). In our study, the abundance of some species was relatively stable (*B. melanopygus, B. flavifrons,* and *B. mixtus*) and others declined (*B. bifarius*, *B. californicus*, and *B. vandykei*) when *B. vosnesenskii* abundance spiked in 2016. *Lupinus polyphyllus*, the plant species most strongly selected by *B. vosnesesnkii*, was available throughout the sampling period (2015–2016), but it was relatively more abundant in mid and late summer 2016, when *B. vosnesenskii* abundance dramatically increased. Factors unrelated to plant availability or interspecific competition (e.g., overwinter survival of queens) may also have driven between-year changes in bumble bee abundance. In a different study in California which shared our survey methodology, *B. vosnesenskii* was 2.62 times more abundant in 2016 relative to 2015 (Loffland et al. 2017) perhaps indicating a larger population-wide phenomena.

Within- and Between-Year Variation in Plant Availability

Blooming phenology of plant species selected by bumble bees varied greatly, with species like *T. longipes* and *M. ciliata* providing abundant food resources in late May through mid June, numerous species exhibiting peak bloom around the middle of our summer sampling season, and species like *C. angustifolium* and *E. integrifolia* providing food resources in late August. Varied blooming phenology of important food plants may support bumble bee

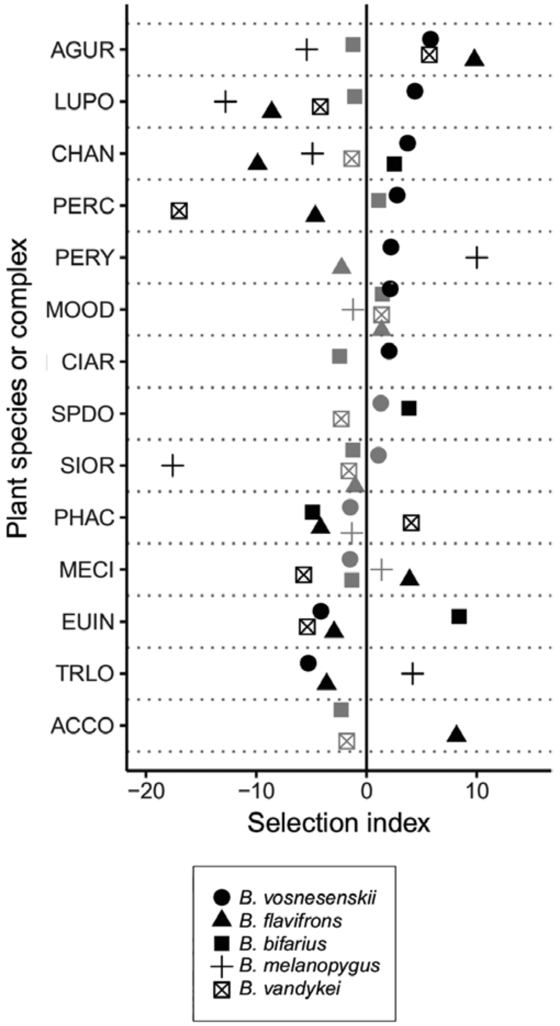

Fig. 4. Plant selection index values for the five most frequently captured bumble bee species. See Methods for plant selection index calculations. Black symbols indicate significant selection or avoidance and gray symbols nonsignificance. Dotted lines group symbols by plant. Bumble bees without symbols for a given plant species or complex were never captured on that plant. Only plant species or complexes that were used significantly more often than expected based on availability by at least one bumble bee species are included. Plants are sorted from highest selection index to lowest for *B. vosnesenskii* and legend is ordered from most frequently to least frequently captured bumble bee species. Codes are as follows: SIOR: *Sidalcea oregana*, MOOD: *Monardella odoratissima*, LUPO: *Lupinus polyphyllus*, PERC: *Perideridia* complex, AGUR: *Agastache urticifolia*, CHAN: *Chamerion angustifolium*, MERC: *Mertensia ciliata*, TRLO: *Trifolium longipes*, PHAC: *Phacelia* complex, PERY: *Penstemon rydbergii*, SPDO: *Spirea douglasii*, CIAR: *Cirsium arvense*, ACCO: *Aconitum columbianum*, and EUIN: *Eurybia integrifolia*.

species with diverse phenology and is important for providing food resources to individual bumble bee species throughout the full nesting cycle (Loffland et al. 2017). Availability indices of most plants declined between years, likely because we observed bumble bees using more plant species in 2016 (88 species or complexes) versus 2015 (67 species or complexes) such that each plant comprised a smaller proportion of the total plant species available. However, the duration and timing of blooming period appeared relatively similar between years for most plant species, despite considerable differences in precipitation (i.e., extreme drought prior to the 2015 sampling season vs precipitation closer to the long-term average prior to the 2016 season).

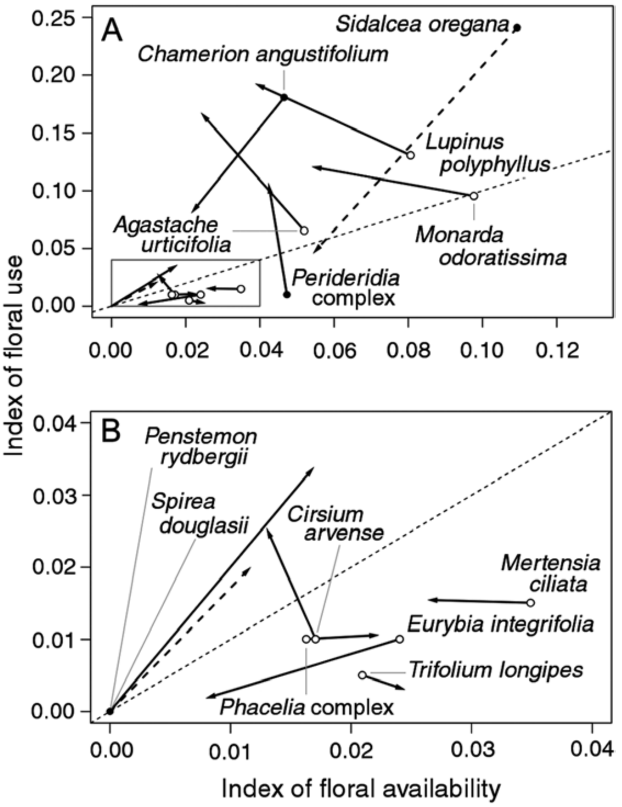

Fig. 5. Changes in floral availability and usage by *Bombus vosnesenskii* from 2015 to 2016. The gray rectangle in A is enlarged in B. Filled black dots represent plant species which were significantly selected or avoided in 2015. Open dots represent nonsignificant selection or avoidance in 2015. Arrows originate from availability and use indices in 2015 and terminate at 2016 indices. Solid lines represent significant selection or avoidance in 2016 and dotted lines represent nonsignificant selection or avoidance in 2016. Plant species not used by *B. vosnesenskii* in 2015 (*Penstemon rydbergii* [the longer, solid arrow] and *Spiraea douglasii* [the shorter, dotted arrow]) have arrows extending from the origin.

Interspecific Variation in Floral Selection by Bumble Bees

Bumble bees select among the most profitable and abundant plant species during a given time period and switch to a new plant as a particular species' floral abundance wanes (Heinrich 1976). Use of plants by pollinators (including bumble bees) can differ between years in response to changes in the composition of the pollinator community and changes in plant blooming period (Lázaro et al. 2010), but little is known about interannual variation in bumble bee plant selection (i.e., explicitly accounting for availability). When bumble bee species' associations with plants are defined as any plants used by a species (i.e., without accounting for availability), a metric frequently applied in plant-pollinator networks, and then associations with particular plants often change dramatically between years (Alarcón et al. 2008, Dupont et al. 2009). We had sufficient captures to assess between-year changes in plant selection by only one species, *B. vosnesenskii*, which significantly selected a greater number of plant species in 2016, likely a product of more captures in that year rather than a wider diet breadth. Plant species that were selected (or avoided) in 1 yr of the study were generally also selected (or avoided) in the other year.

Pooling data between years, we observed a high degree of variability in plant selection among the five most frequently captured

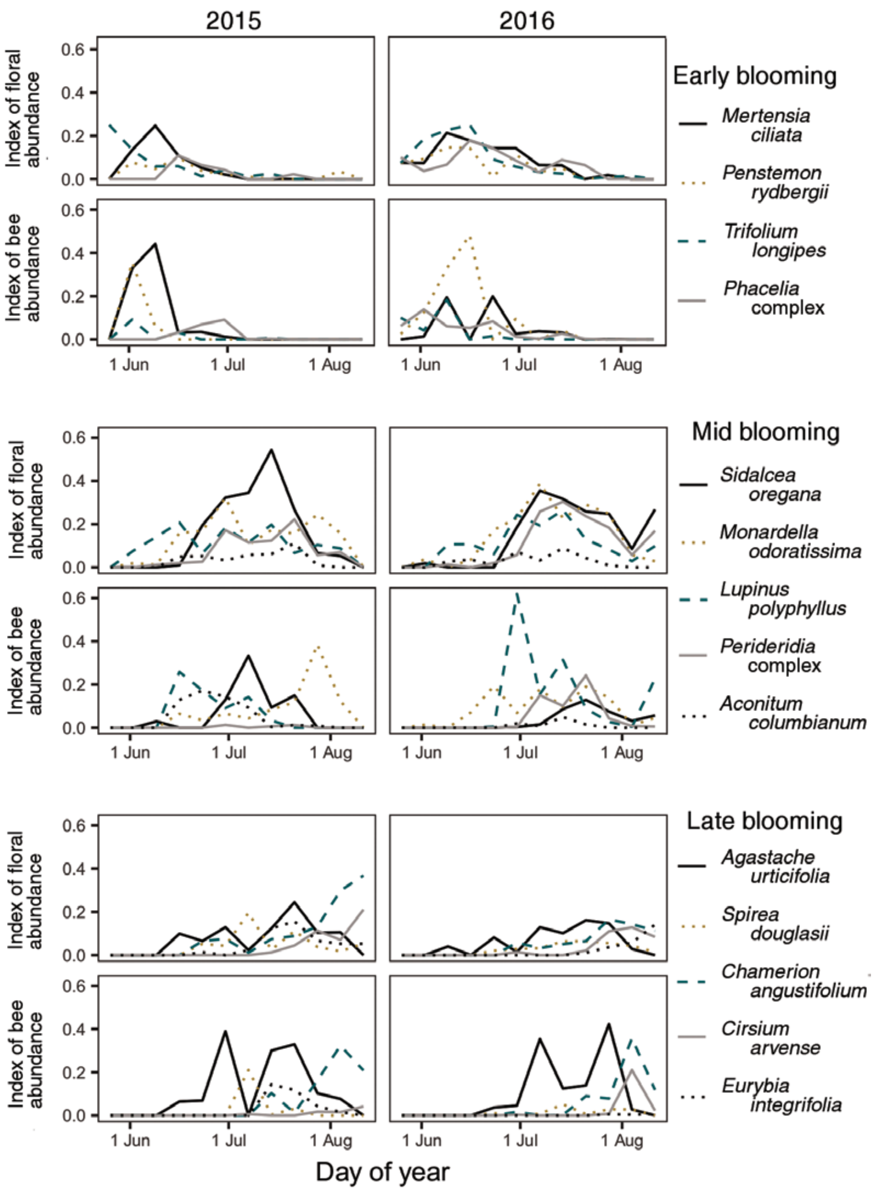

Fig. 6. Phenology of plants and bumble bee abundance (pooling all bumble bee species) during 2015 and 2016. Plants are divided into groups that correspond to early, mid, and late season blooming phenology, based on their peak abundance in 2016 (see Methods). Top row in each grouping displays the number of plant detections in a given week divided by the total plots surveyed in the same week. Bottom row in each grouping displays the number of bumble bee captures on a plant species in a given week divided by the plots surveyed in a week.

bumble bee species, with each having a distinct set of plants that it significantly selected. Some of the bee-plant relationships we report have been documented previously in the context of studies that determined plant selection by dividing number of bee visitors per flower in a patch (e.g., Pleasants et al. [1981] observed *B. flavifrons* heavily using *A. urticofolia*), whereas others (e.g., *B. bifarius* and *B. melanopygus* most strongly selected for *E. integrifolia* and *P. rydbergii*, respectively) are apparently undocumented. Bumble bee species generally selected plants with blooming phenology that matched their own phenology, which may partially explain observed patterns of interspecific variation in plant selection. For example, *B. melanopygus*, which had the highest capture rates earliest in the season of the five common bumble bee species we studied, was the only species to significantly select *Trifolium longipes* (Nuttall) (Fabales: Fabaceae), the earliest blooming of all the 14 plant species that were significantly selected by any bumble bee species. *Bombus melanopygus* exhibited the most distinctive phenology of the five bumble bee species we studied in detail. The other four bumble bee species all had relatively similar phenology, but still selected at least one plant species that was unique.

Some interspecific variation in plant species selection also may have simply reflected varying statistical power, stemming from capture numbers varying across species. *Bombus vosnesenskii,* by far our most frequently captured species (2,658 captures after data filtering), also was observed to significantly select the most plant species (seven species). The other four bumble bee species we studied in detail ranged from 246 (*B. vandykei*) to 588 *(B. flavifrons*) captures after data filtering. However, in most cases, observed selection of any of the 14 focal plant species by any of the five common bumble bee species reached the threshold of statistical significance. We also documented numerous cases of *B. vosnesenskii* or other species significantly selecting a plant while other bumble bee species significantly avoided it.

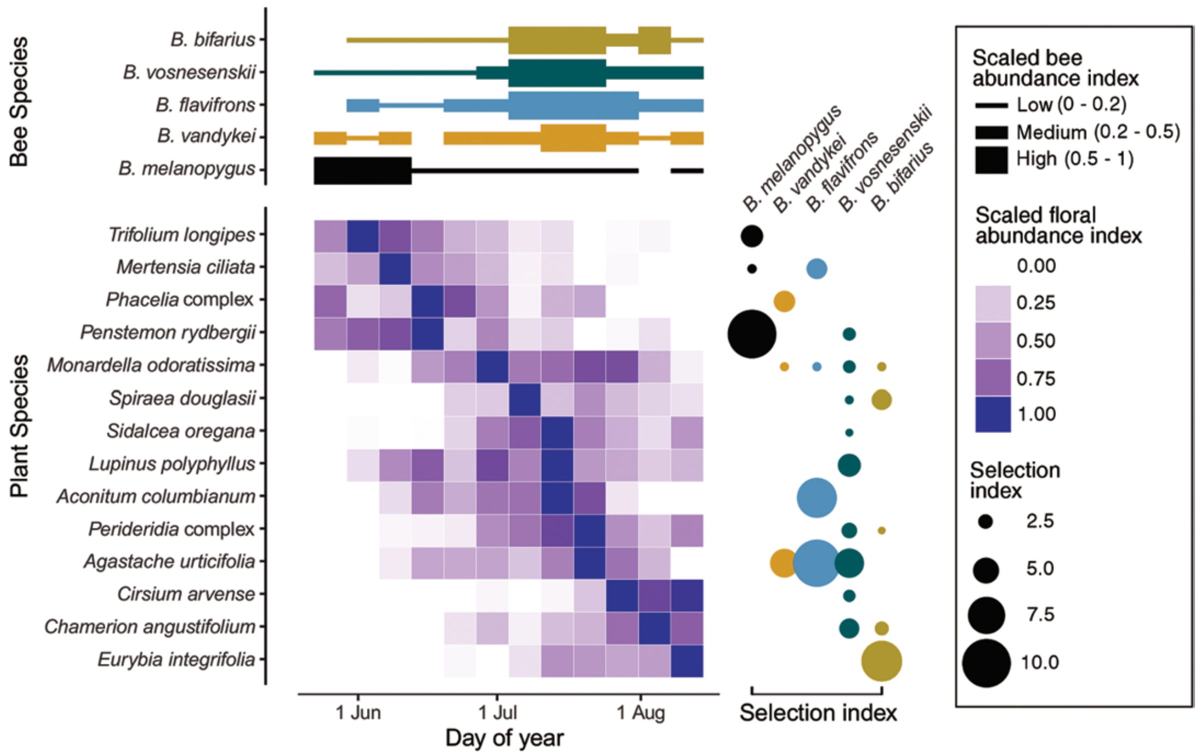

Fig. 7. Phenology of captures of five bumble bee species (variable thickness lines), floral abundance phenology for 14 plant species positively selected by at least one bumble bee species (shaded cells), and selection index for each bumble bee species and plant species combination (variable radius dots), all pooled across 2015 and 2016. Scaled bumble bee abundance index is the number of bumble bee captures divided by the number of plots visited in a week, then scaled from 0 to 1. Line thickness corresponds to category of scaled abundance and the thinnest line only extends through weeks that had ≥ 1 bee capture. Scaled floral abundance index represents the number of times a plant species was recorded among the top five blooming plants divided by the number of plots visited in a week, then values were scaled from 0 to 1. Each cell represents a survey week. Plant selection index symbols correspond to bumble bee plant use divided by plant availability and are also reported in Fig. 4. Selection indexes are only displayed for indexes that were > 0.

Applicability to Habitat Restoration or Enhancement

Our results should be interpreted with caution because we did not record whether plants were being used as pollen sources versus nectar sources. Plants that were preferred only for their pollen or nectar may not have been determined to be significantly selected when in fact they were important to bumble bee diet. A diversity of pollen resources are important in maintaining the health of bees (Filipiak et al. 2017); therefore, the plant species we identified as selected by bumble bees may not provide a full suite of resources required for bumble bee species' health. We also caution that bumble bee plant selection is not fixed, but instead likely depends on factors including presence of other pollinators (Lázaro et al. 2010), abundance of conspecifics (Fontaine et al. 2008), floral abundance (Fowler et al. 2016), and weather variation (Ogilvie et al. 2017). Bumble bees are believed not to have innate preferences for particular plant species per se, but instead sample available plants based on their perceived value (i.e., quantity and quality of nectar or pollen) and the ease with which they can be harvested (Heinrich 1976).

Our results and other related research (e.g., Winfree 2010) suggests that a small subset of plants receive the majority of bumble bee visits. The identification of plants selected by five bumble bee species at our study site provides a good starting point for choosing plants of value to bumble bees when seeding and restoring meadow and riparian habitat in our study region. We found that 13% of available plant species or complexes were positively selected by bumble bees. Maintaining, seeding, or planting with these 'bumble bee plants' while managing the surrounding landscape for heterogeneous vegetation structure supporting a diverse floral community (Cole et al. 2019) is likely to benefit bumble bees, especially if some combination of favored plant species are blooming across the duration of bumble bee activity at a given location (Loffland et al. 2017, Cole et al. 2019). Identifying appropriate areas dominated by plants avoided by most bumble bee species and lacking plants selected by bumble bees may provide target locations for habitat restoration or enhancement.

Supplementary Data

Supplementary data are available at *Environmental Entomology* online.

Acknowledgments

We thank our field crew, T. DuBridge, M. Finley, L. Hansen, S. Hardy, M. Hash, and A. Schrage for collecting the data and J. Polasik and J. Wu for assistance with study design and project management. R. W. Thorp confirmed bumble bee species identification and curated voucher specimens and G. LeBuhn advised on bumble bee sampling methods. We thank Lauren Helton for creating the bumble bee illustrations. We thank two reviewers for their thoughtful review of this manuscript. The study was funded by the U.S. Department of Agriculture, U.S. Forest Service, Plumas National Forest under Challenge Cost Share Agreement 15-CS-11051100-024. This is contribution number 649 of The Institute for Bird Populations.

References Cited

Alarcón, R., N. M. Waser, and J. Ollerton. 2008. Year-to-year variation in the topology of a plant-pollinator interaction network. OIKOS. 117: 1796–1807.

Alldredge, J. R., and J. T. Ratti. 1992. Further comparison of some statistical techniques for analysis of resource selection. J. Wildl. Manage. 56: 1–9.

Aldridge, G., D. W. Inouye, J. R. K. Forrest, W. A. Barr, and A. J. Miller-Rushing. 2011. Emergence of a mid-season period of low floral resources in a montane meadow ecosystem associated with climate change. J. Ecol. 99: 905–913.

Cameron, S. A., J. D. Lozier, J. P. Strange, J. B. Koch, N. Cordes, L. F. Solter, and T. L. Griswold. 2011. Patterns of widespread decline in North American bumble bees. Proc. Natl. Acad. Sci. U. S. A. 108: 662–667.

Cole, J. S., R. B. Siegel, H. L. Loffland, M. W. Tingley, E. A. Elsey, and M. Johnson. 2019. Explaining the birds and the bees: deriving habitat restoration targets from multi-species occupancy models. Ecosphere. 10: e02718.

Dupont, Y. L., B. Padrón, J. M. Olesen, and T. Petanidou. 2009. Spatio-temporal variation in the structure of pollination networks. OIKOS. 118: 1261–1269.

Filipiak, M., K. Kuszewska, M. Asselman, B. Denisow, E. Stawiarz, M. Woyciechowski, and J. Weiner. 2017. Ecological stoichiometry of the honeybee: Pollen diversity and adequate species composition are needed to mitigate limitations imposed on the growth and development of bees by pollen quality. PLoS One. 12: e0183236.

Fontaine, C., C. L. Collin, and I. Dajoz. 2008. Generalist foraging of pollinators: Diet expansion at high density. J. Ecol. 96: 1002–1010.

Fowler, R. E., E. L. Rotheray, and D. Goulson. 2016. Floral abundance and resource quality influence pollinator choice. Insect Conserv. Divers. 9: 481–494.

Fryjoff-Hung, A., and J. Viers. 2012. Sierra Nevada Multi-Source Meadow Polygons Compilation (version 1.0). University of California Center for Watershed Sciences, Davis, CA.

Goulson, D., E. Nicholls, C. Botías, and E. L. Rotheray. 2015. Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. Science. 347: 1255957.

Gumbert, A. 2000. Color choices by bumble bees (Bombus terrestris): innate preferences and generalization after learning. Behav. Ecol. Sociobiol. 48: 36–43.

Harder, L. D. 1985. Morphology as a predictor of flower choice by bumble bees. Ecology. 66: 198–210.

Hatfield, R. G., and G. LeBuhn. 2007. Patch and landscape factors shape community assemblage of bumble bees, Bombus spp. (Hymenoptera: Apidae), in montane meadows. Biol. Conserv. 139: 150–158.

Heinrich, B. 1976. The foraging specializations of individual Bumblebees. Ecol. Monogr. 46: 105–128.

Jepson, W. L. 1993. The Jepson manual: higher plants of California. University of California Press, Berkeley, CA.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology. 61: 65–71.

Kincaid, T. M., and A. R. Olsen. 2013. spsurvey: spatial survey design and analysis. R package version 2.6.

Kleijn, D., and I. Raemakers. 2008. A retrospective analysis of pollen host plant use by stable and declining bumble bee species. Ecology. 89: 1811–1823.

Koch, J., J. Strange, and P. Williams. 2012. Bumble Bees of the Western United States. USDA Forest Service and the Pollinator Partnership, Washington, DC.

Lázaro, A., A. Nielsen, and Ø. Totland. 2010. Factors related to the inter-annual variation in plants' pollination generalization levels within a community. OIKOS. 119: 825–834.

Lele, S. R., E. H. Merrill, J. Keim, and M. S. Boyce. 2013. Selection, use, choice and occupancy: clarifying concepts in resource selection studies. J. Anim. Ecol. 82: 1183–1191.

Loffland, H. L., J. S. Polasik, M. W. Tingley, E. A. Elsey, C. Loffland, G. Lebuhn, and R. B. Siegel. 2017. Bumble bee use of post-fire chaparral in the central Sierra Nevada. J. Wildl. Manage. 81: 1084–1097.

Luo, L., D. Apps, S. Arcand, H. Xu, M. Pan, and M. Hoerling. 2017. Contribution of temperature and precipitation anomalies to the California drought during 2012–2015. Geophys. Res. Lett. 44: 3184–3192.

M'Gonigle, L. K., N. M. Williams, E. Lonsdorf, and C. Kremen. 2017. A tool for selecting plants when restoring habitat for pollinators. Conserv. Lett. 10: 105–111.

Mallinger, R. E., H. R. Gaines-Day, and C. Gratton. 2017. Do managed bees have negative effects on wild bees?: a systematic review of the literature. PLoS One. 12: e0189268.

Mayer, K. E., and W. F. Laudenslayer. 1988. A guide to wildlife habitats of California. California Department of Forestry and Fire Protection, Sacramento, CA.

McFrederick, Q. S., and G. LeBuhn. 2006. Are urban parks refuges for bumble bees Bombus spp. (Hymenoptera: Apidae)? Biol. Conserv. 129: 372–382.

Micheletty, P. D., A. M. Kinoshita, and T. S. Hogue. 2014. Application of MODIS snow cover products: wildfire impacts on snow and melt in the Sierra Nevada. Hydrol. Earth Syst. Sci. 18: 4601–4615.

Møller, A. P. 1995. Bumblebee preference for symmetrical flowers. Proc. Natl. Acad. Sci. 92: 2288–2292.

Neu, C. W., C. R. Byers, and J. M. Peek. 1974. A Technique for Analysis of Utilization-Availability Data. J. Wildl. Manage. 38: 541–545.

Ogilvie, J. E., and J. R. Forrest. 2017. Interactions between bee foraging and floral resource phenology shape bee populations and communities. Curr. Opin. Insect Sci. 21: 75–82.

Ogilvie, J. E., S. R. Griffin, Z. J. Gezon, B. D. Inouye, N. Underwood, D. W. Inouye, and R. E. Irwin. 2017. Interannual bumble bee abundance is driven by indirect climate effects on floral resource phenology. Ecol. Lett. 20: 1507–1515.

Petanidou, T., A. S. Kallimanis, J. Tzanopoulos, S. P. Sgardelis, and J. D. Pantis. 2008. Long-term observation of a pollination network: fluctuation in species and interactions, relative invariance of network structure and implications for estimates of specialization. Ecol. Lett. 11: 564–575.

Pleasants, J. M. 1981. Bumblebee response to variation in nectar availability. Ecology. 62: 1648–1661.

Pyke, G. H., D. W. Inouye, and J. D. Thomson. 2011. Activity and abundance of bumble bees near Crested Butte, Colorado: diel, seasonal, and elevation effects. Ecol. Entomol. 36: 511–521.

Stevens, D. L., and A. R. Olsen. 2004. Spatially balanced sampling of natural resources. J. Am. Stat. Assoc. 99: 262–278.

Strahler, A. N. 1957. Quantitative analysis of watershed geomorphology. Trans. Am. Geophys. Union. 38: 913–920.

Szabo, N. D., S. R. Colla, D. L. Wagner, L. F. Gall, and J. T. Kerr. 2012. Do pathogen spillover, pesticide use, or habitat loss explain recent North American bumblebee declines? Conserv. Lett. 5: 232–239.

Thornton, P. E., M. M. Thornton, B. W. Mayer, Y. Wei, R. Devarakonda, R. S. Vose, and R. B. Cook. 2018. Daymet: Daily Surface Weather Data on a 1-km Grid for North America, Version 3. Oak Ridge, TN.

Vaudo, A. D., H. M. Patch, D. A. Mortensen, J. F. Tooker, and C. M. Grozinger. 2016. Macronutrient ratios in pollen shape bumble bee (Bombus impatiens) foraging strategies and floral preferences. Proc. Natl. Acad. Sci. U. S. A. 113: E4035–E4042.

Weeden, N. F. 1996. A Sierra Nevada flora, fourth. ed. Wilderness Press, Berkeley, CA.

Winfree, R. 2010. The conservation and restoration of wild bees. Ann. N. Y. Acad. Sci. 1195: 169–197.

Winfree, R., R. Aguilar, D. P. Vázquez, G. LeBuhn, and M. A. Aizen. 2009. A meta-analysis of bees' responses to anthropogenic disturbance. Ecology. 90: 2068–2076.

Wojcik, V. A., L. A. Morandin, L. Davies Adams, and K. E. Rourke. 2018. Floral resource competition between honey bees and wild bees: is there clear evidence and can we guide management and conservation? Environ. Entomol. 47: 822–833.

Wood, T. J., J. Gibbs, K. K. Graham, and R. Isaacs. 2019. Narrow pollen diets are associated with declining Midwestern bumble bee species. Ecology. 100: e02697.