



# Variation in foraging patterns as reflected by floral resources used by male vs female bees of selected species at Badlands National Park, SD, USA

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Received: 7 September 2021 / Accepted: 25 December 2021 / Published online: 11 February 2022

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## Abstract

Female and male bees forage for different reasons: females provision nests with pollen appropriate for larval development and consume nectar for energy while males need only fuel their own energetic requirements. The expectation, therefore, is that females should visit fewer floral resource species than males, due to females' focus on host plant species and their tie to the nest location. We used pollen collected from bees' bodies and the flowers they were collected on to infer floral resource use in 2010–2012 at Badlands National Park, SD, USA. We collected bees on 24 1-ha plots centered on particular plant species. We compared number of floral species and families (1) associated with individual female and male bees (via generalized linear mixed models) and (2) accumulated by each sex (using rarefaction); and (3) effect of variation between sexes in plant-bee interactions via modularity analyses. Analyses were restricted to bee species with  $\geq 5$  individuals per sex. Contrary to expectation, female and male bees differed infrequently in the number of floral resources they had visited, both on single foraging bouts and collectively when accumulated across all males and females of a species. When males and females did differ, males visited fewer floral species than females. Generalist and specialist bee species did not differ markedly in floral resource use by females and males. When separated by sex, seven of eleven species occupied different modules than they did when analyzed as a species; most of the bee species were connectors, thus important for stability of the network during perturbations.

**Keywords** Badlands · *Augochlorella* · *Bombus* · *Calliopsis* · Diet breadth · Floral resources · *Halictus* · *Lasioglossum* · *Megachile* · *Melissodes*

## Introduction

Bees are consummate pollinators (Thorp 2000). Reliance on pollen to provision young and, along with nectar, to meet adult energetic requirements, ensure ongoing plant-bee interactions and thus plant sexual reproduction. That said, foraging patterns of female bees can be quite different from those of male bees of the same species (Ne'eman G, et al. 2006; Roswell et al. 2019; Tang et al. 2019; Kishi and Kakutani

2020): females are essentially central-place foragers around their nest location while males may forage more broadly as they search for mates (Jennersten et al. 1991; Smith et al. 2019b), but see Ogilvie and Thomson (2015). Reproductive output can decline considerably as female foraging distances increase (Zurbuchen et al. 2010) with implications for other fitness components such as proportion of daughters produced and larval survival (Peterson and Roitberg 2006). On the other hand, males of some bee species defend territories, which reduces their foraging range (Smith et al. 2019b). Male mating behavior can strongly determine their overall range; oligolectic species may be most likely to encounter mates at the limited appropriate floral resources, while those females that nest in aggregations are most likely to be encountered at their closely-spaced nests (Paxton 2005).

In addition to sex, there are multiple factors that are thought to influence the degree of ecological specialization in bees, including lecticity and body size (Smith et al.

Communicated by Heikki Hokkanen.

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2019a). While it is clear that female and male bees forage for different purposes, bee taxa also vary in their foraging preferences; as many as 9% of bee genera worldwide are oligolectic (i.e. females restrict their pollen foraging to a set of related plants (Linsley and MacSwain 1958)) and such specialists may be found in most lineages (Rasmussen et al. 2020). Again, however, females may have greater likelihood of foraging more narrowly, as the morphology of scopae may limit the sizes of pollen they can carry back to the nest (Roberts and Vallespir 1978; Rasmussen et al. 2020). Body size also has an influence on foraging; larger bees can range over larger areas (Greenleaf et al. 2007; Zurbuchen A, et al. 2010). For example, male *Bombus terrestris* have been found to have much larger flight ranges than the smaller workers (Kraus et al. 2009); in general, however, male solitary bees are smaller than females of the same species (Helms 1994). Depending on landscape heterogeneity, a larger foraging range may result in more pollen species used by an individual generalist forager. However, generalists with smaller ranges may forage on more species, as a population, if individuals sample small, separate portions of the larger landscape. Individual- and species-level diet breadth may therefore differ. Floral constancy, which refers to the tendency of individual bees to restrict their foraging to one or a few plant species within a single foraging bout (Waser 1986), does not imply the same constancy for the species as a whole (Araujo et al. 2011; Latty and Trueblood 2020).

Discussions of foraging behavior in bees can be tricky due to the potential confounding of different definitions of specialization. Specifically, bees can be pollen specialists, or oligolectic (Linsley and MacSwain 1958), as described above. However, most oligolectic bees are still generalist nectar foragers, and will nectar at plants other than their preferred pollen hosts (Robertson 1925). In many ecological and network studies, “specialization” refers to ecological specialization, or the total number of interactions a bee species has with different plant species, regardless of whether it is gathering pollen (Blüthgen et al. 2006). In addition, even bees that are not gathering pollen still passively accumulate pollen on their bodies (Portman et al. 2019). As a result, ecological specialization can be a poor proxy for oligolecty, especially since male visits are often included in calculations of ecological specialization. In this paper we focus on ecological specialization, which includes foraging for the bees’ energetic requirements rather than only for nest provisioning.

Flower-visitor networks are typically constructed without distinguishing or separating the sexes of the flower visitors. When downscaling from species-species pollination networks to individual pollinator-species networks, Tur et al. (2014) found that pollinator species are typically composed of both generalist and specialist individuals; they did not distinguish sexes. Smith et al. (2019b) suggested that networks

constructed with separate sexes of insect visitors might be a way forward without the extreme computational resources necessary for individual scale networks. If females and males forage consistently in a sex-specific manner, network metrics could be much more informative by taking these differences into account. For example, if conspecific female and male bees forage on a sufficiently different suite of plant species to be partitioned into separate modules, this structural characteristic, related to our understanding of network stability (Thébault and Fontaine 2010; Grilli et al. 2016), could be altered.

In this study, we use pollen removed from individual bees, plus the species of flower on which they were captured, to infer floral resource use of male and female bees present in our study sites at Badlands National Park (BNP), South Dakota, USA. With this information we test the hypothesis suggested by Smith et al. (2019b), that female bees should have smaller diet breadth than male bees. We also examine whether oligolectic bees have a higher degree of ecological specialization and whether oligolectic and polylectic bees show different patterns of foraging between the sexes. We expect that generalist species in the Halictidae should show little difference in foraging between the sexes. On the other hand, we anticipate female *Melissodes* species, which often specialize on Asteraceae, will visit fewer plant species and families than males. We also explore the implications of separating male and female bees when calculating network modularity. If females and males forage on different flower species, this could result in their separation into different modules and potentially change our understanding of network stability.

## Methods

The bees used in this study were captured as part of several network analyses conducted at BNP in 2010–2012 (Larson et al. 2014, 2016). Studies in 2010–11 took place on four 1-ha plots surrounding populations of each of three rare plant species in Badlands sparse vegetation complex (Von Loh et al. 1999): *Astragalus barrii* (mid-May–mid-June), *Eriogonum visheri* (late June – mid-August), and *Ericameria parryi* (September–mid-October). The sample periods corresponded to the blooming period of the focal plant. Studies in 2012 took place on 12 1-ha plots in wheatgrass prairie vegetation type (Von Loh et al. 1999), half of which had infestations of *Cirsium arvense* and half of which did not; these were sampled in late June–mid-July. The sample period corresponded to the peak bloom and early senescence of the focal plant. Hereafter, the studies will be referred to by their focal plant species (*A. barrii*, *E. visheri*, *E. parryi*, and *C. arvense*). We analyzed data from each study separately because each had different plant species available to foragers. Flower counts

by species were conducted on the same transects on which we collected insects, but we used variable widths: very abundant flower species were counted within a smaller width, but all were standardized to 2-m for summaries. Flowers were counted approximately weekly on each 1-ha plot for a total of 36, 30, 28, and 58 surveys at *A. barrii*, *E. visheri*, *E. parryi*, and *C. arvense* study sites, respectively.

Insect sampling was done during timed (20 min. per transect) walks on ten 2-m wide by 75-m long transects at each 1-ha plot. Any insect that was observed to be in contact with the reproductive parts of a flower was hand-netted and placed in a vial charged with ethyl acetate until it became quiet. From the vial, the insect was transferred to a labeled glassine envelope and placed into a larger collecting jar, also charged with ethyl acetate. We did insect surveys on the same days as flower counts at *A. barrii*, *E. visheri*, and *E. parryi* sites but at *C. arvense* sites insect surveys were done more often and we completed 89 insect surveys. All captured insects—not only bees—were identified to species or species group. Only those identified to species were used in these analyses. We include the flower species upon which the insect was captured as an indication of resource use, along with pollen on the insect's body, because we only collected those insects contacting reproductive parts of flowers.

Prior to pinning, pollen was removed from the insects' bodies by rubbing a small cube of fuchsin jelly over the entire body, including scopae. The jelly was then carefully melted onto a slide and covered with a cover slip. A thin line of latex paint around the edge of the cover slip helped keep the contents of the slide from evaporating. Pollen was identified and counted using a light microscope at 10–100x; we created a reference collection of pollen from each study site to aid in identification.

## Statistical methods

We used generalized linear models to compare species or family richness of floral resources (pollen species carried plus flower species on which the bee was captured if different from pollen species) between individual male and female bees within species to answer the question, does the average number of floral resources (species or families) used differ between males and females during individual foraging bouts. Each bee species was modeled separately. Only bee species with  $\geq 5$  individuals of each sex were used in these analyses. All models were one-way analysis of variance models assuming a Poisson distribution and run using PROC GLIMMIX in SAS (SAS Institute Inc. 2018).

We estimated species and family richness of floral resources used by bees of a single species (with  $\geq 5$  individuals of each sex) and sex with rarefaction as implemented with the “exact” method in the specaccum function in Vegan 2.5–4 (Oksanen et al. 2020) for R v. 3.4.2 (R Core Team

**Table 1** Number of individuals of each species and sex (F=female, M=male) captured at sites associated with each study, where  $\geq 5$  individuals of each sex were captured

Study	Species	F	M	Total
<i>Ericameria parryi</i>	<i>Bombus huntii</i>	6	15	21
	<i>Lasioglossum packeri</i>	10	5	15
	<i>Melissodes glenwoodensis</i>	5	7	12
<i>Cirsium arvense</i>	<i>Augochlorella aurata</i>	65	40	105
	<i>Halictus confusus</i>	10	7	17
	<i>Lasioglossum albipenne</i>	30	21	51
	<i>Lasioglossum pruinosum</i>	52	15	67
	<i>Lasioglossum semicaeruleum</i>	58	22	80
	<i>Megachile brevis</i>	11	53	64
<i>Eriogonum visheri</i>	<i>Calliopsis andreniformis</i>	34	35	69
	<i>Lasioglossum packeri</i>	100	5	105
Total		381	225	606

2015). Each bee was a sample, grouped according to species, sex and study.

For each bee species used to develop rarefaction curves, we also visualized female and male floral resource use with principal coordinates analysis (McCune and Grace 2002) in the software package PCOrd Version 7.08 (McCune and Mefford 2018). We plotted individual bees in plant species space and enclosed females and males of each bee species in separate envelopes. These plots illustrate overlap between female and male floral resource use, not statistical significance.

To explore potential differences in the sexes in their interactions among species, we compared module affiliations for bees grouped by species with those separated by sex within species. For the modularity analysis we considered all insects captured in each study to be a network, but we report only on bees with  $\geq 5$  of each sex, as in the other analyses in this paper. We used the Netcarto software package (Guimera and Amaral 2005) to calculate modularity and a one-sample t-test to determine whether the mean modularity of 100 randomized networks differed from the point estimate of modularity for the observed network. We assigned roles to species as described by Dupont (2009; 2012) based on participation coefficient (a measure of connections outside a node's module) and within-module relative degree (a measure of connections within a node's module Guimera and Amaral 2005; Guimera et al. 2007)).

## Results

We collected  $\geq 5$  individuals of each sex for only 10 species, one of which occurred at two sites (Table 1). We failed to collect enough individuals of any species at our early season

*A. barrii* sites, so this study was not included in further analyses. In all, we identified > 98% of the pollen grains to species; approximately 1.5% were only identified to morphospecies and likely originated off-site. During flower surveys we detected only 11 flowering species in four families at the late-season *E. parryi* sites, compared to 59 species in 22 families at *E. visleri* and 59 species in 21 families at *C. arvense* sites, which were sampled mid-season. Mean flowers counted per plant family for each study can be found in Table S1. Data used for analyses presented in this paper can be found at Larson et al. (2018). (Note that the site naming convention in Larson et al. (2018) is different from the one used here: *A. barrii* = *sp-early*, *E. visleri* = *sp-mid*, *E. parryi* = *sp-late*, and *C. arvense* = *wg-mid*.)

The mean number of species of floral resources per individual bee (i.e., within a single foraging bout) differed between males and females for three bee species-by-study combinations: *Melissodes glenwoodensis* at *E. parryi* sites, *Lasioglossum semicaeruleum* at *C. arvense* sites and *Calliopsis andreniformis* at *E. visleri* sites (Table 2). In each case, and contrary to our expectation for the two oligolectic species (*M. glenwoodensis* and *C. andreniformis*), individual females were associated with a greater number of floral resource species than individual males. Only *C.*

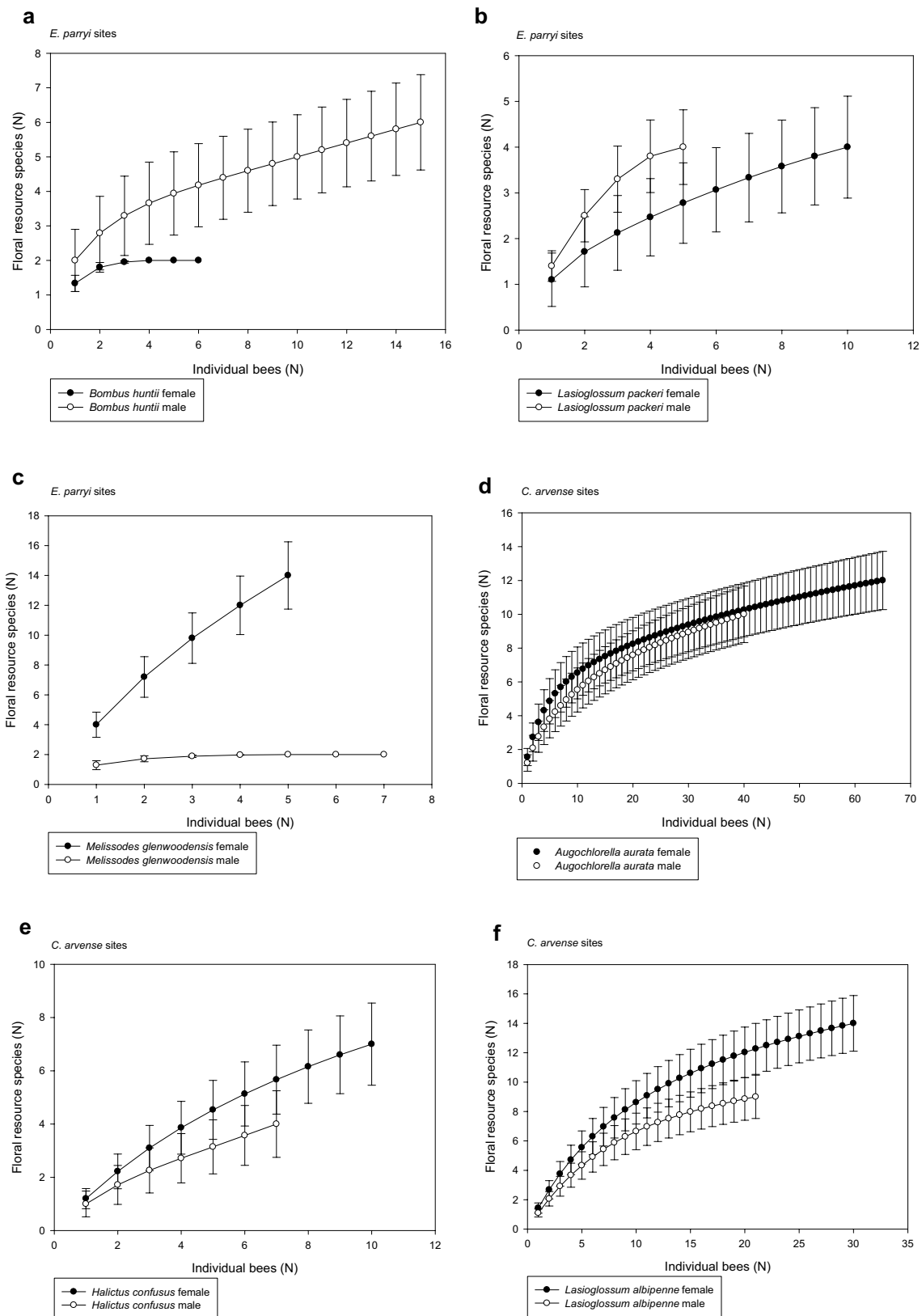
*andreniformis* females and males differed in floral family use: females visited more families than did males, again contradicting our hypothesis (Table 2).

Rarified accumulation curves for males and females by bee species illustrate the differences in total accumulation of floral resource species (Fig. 1) or families (Figure S1) as more individuals of a bee species were sampled. At *E. parryi* sites the polylectic *Bombus huntii* (Fig. 1a) and oligolectic *M. glenwoodensis* (Fig. 1c) floral resource species richness diverged, with male *B. huntii* accumulating more floral species than females but the reverse was true for *M. glenwoodensis*. This trend was also reflected in family floral resources: female *B. huntii* (Figure S1a) and male *M. glenwoodensis* (Figure S1c) only used floral resources in the Asteraceae. *Lasioglossum* spp. males and females accumulated similar numbers of floral resource species (Fig. 1b,f,g,h,k) and families (Figure S1b,f,g,h,k) at all three study areas, although the trajectory of male *L. semicaeruleum* at the *C. arvensis* sites (Figure S1h) suggested a leveling-off with respect to floral resource families. Polylectic *Augochlorella aurata* (Figs. 1d and S1d) and *Megachile brevis* (Figs. 1i and S1i) male and female accumulation curves, for both species and families, overlapped broadly. In contrast, male *C. andreniformis*

**Table 2** Back-transformed least square mean and standard error of number of floral resources (species or families) associated with female or male bees

Study	Bee species	Plant level	Statistic	Female mean (SE)	Male mean (SE)
<i>Ericameria parryi</i>	<i>Bombus huntii</i>	Species	$F_{1,19} = 0.57; p = 0.4584$	1.5 (0.5)	2 (0.37)
	<i>Lasioglossum packeri</i>	Species	$F_{1,13} = 0.56; p = 0.4663$	1.3 (0.36)	1.8 (0.6)
	<i>Melissodes glenwoodensis</i>	Species	$F_{1,10} = 7.88; p = 0.0186$	<b>4.2 (0.92)</b>	<b>1.4 (0.45)</b>
<i>Cirsium arvense</i>	<i>Augochlorella aurata</i>	Species	$F_{1,103} = 2.17; p = 0.1435$	1.55 (0.15)	1.2 (0.17)
	<i>Halictus confusus</i>	Species	$F_{1,15} = 0.78; p = 0.3897$	1.5 (0.39)	1.0 (0.38)
	<i>L. albipenne</i>	Species	$F_{1,49} = 1.81; p = 0.1847$	1.93 (0.25)	1.43 (0.26)
	<i>L. pruinsum</i>	Species	$F_{1,65} = 0.17; p = 0.6774$	1.48 (0.17)	1.33 (0.30)
	<i>L. semicaeruleum</i>	Species	$F_{1,78} = 4.89; p = 0.0299$	<b>1.91 (0.18)</b>	<b>1.18 (0.23)</b>
	<i>Megachile brevis</i>	Species	$F_{1,62} = 0.16; p = 0.6893$	1.45 (0.36)	1.62 (0.17)
	<i>Calliopsis andreniformis</i>	Species	$F_{1,67} = 7.51; p = 0.0079$	<b>2.56 (0.27)</b>	<b>1.6 (0.21)</b>
<i>Eriogonum visleri</i>	<i>L. packeri</i>	Species	$F_{1,103} = 0.16; p = 0.6905$	2.7 (0.16)	2.4 (0.69)
<i>Ericameria parryi</i>	<i>Bombus huntii</i>	Family	$F_{1,19} = 0.07; p = 0.7949$	1 (0.41)	1.13 (0.27)
	<i>Lasioglossum packeri</i>	Family	$F_{1,13} = 0; p = 1.0$	1 (0.32)	1 (0.45)
	<i>Melissodes glenwoodensis</i>	Family	$F_{1,10} = 1.36; p = 0.2705$	1.8 (0.6)	1 (0.38)
<i>Cirsium arvense</i>	<i>Augochlorella aurata</i>	Family	$F_{1,103} = 0.23; p = 0.6307$	1.23 (0.14)	1.12 (0.17)
	<i>Halictus confusus</i>	Family	$F_{1,15} = 0.04; p = 0.8464$	1.1 (0.33)	1.0 (0.38)
	<i>Lasioglossum albipenne</i>	Family	$F_{1,49} = 0.57; p = 0.4558$	1.33 (0.21)	1.1 (0.23)
	<i>Lasioglossum pruinsum</i>	Family	$F_{1,65} = 0.32; p = 0.5718$	1.25 (0.16)	0.17 (0.27)
	<i>Lasioglossum semicaeruleum</i>	Family	$F_{1,78} = 2.55; p = 0.1141$	1.47 (0.16)	1 (0.21)
	<i>Megachile brevis</i>	Family	$F_{1,62} = 0.08; p = 0.7766$	1.27 (0.34)	1.17 (0.15)
	<i>Calliopsis andreniformis</i>	Family	$F_{1,67} = 10.04; p = 0.0023$	<b>2.32 (0.26)</b>	<b>1.29 (0.19)</b>
<i>Eriogonum visleri</i>	<i>Lasioglossum packeri</i>	Family	$F_{1,103} = 0.11; p = 0.7832$	1.38 (0.12)	1.2 (0.49)

Means in bold indicate female and male means were significantly different from each other ( $p \leq 0.05$ )



**Fig. 1** Estimated floral resource species accumulated with each additional female or male bee of species with  $\geq 5$  individuals of each sex at *Ericameria parryi* (a–c), *Cirsium arvense* (d–f), and *Eriogonum*

*visheri* (j–k) sites. Shown are mean  $\pm$  standard deviation for female (closed dots) and male (open dots) bees

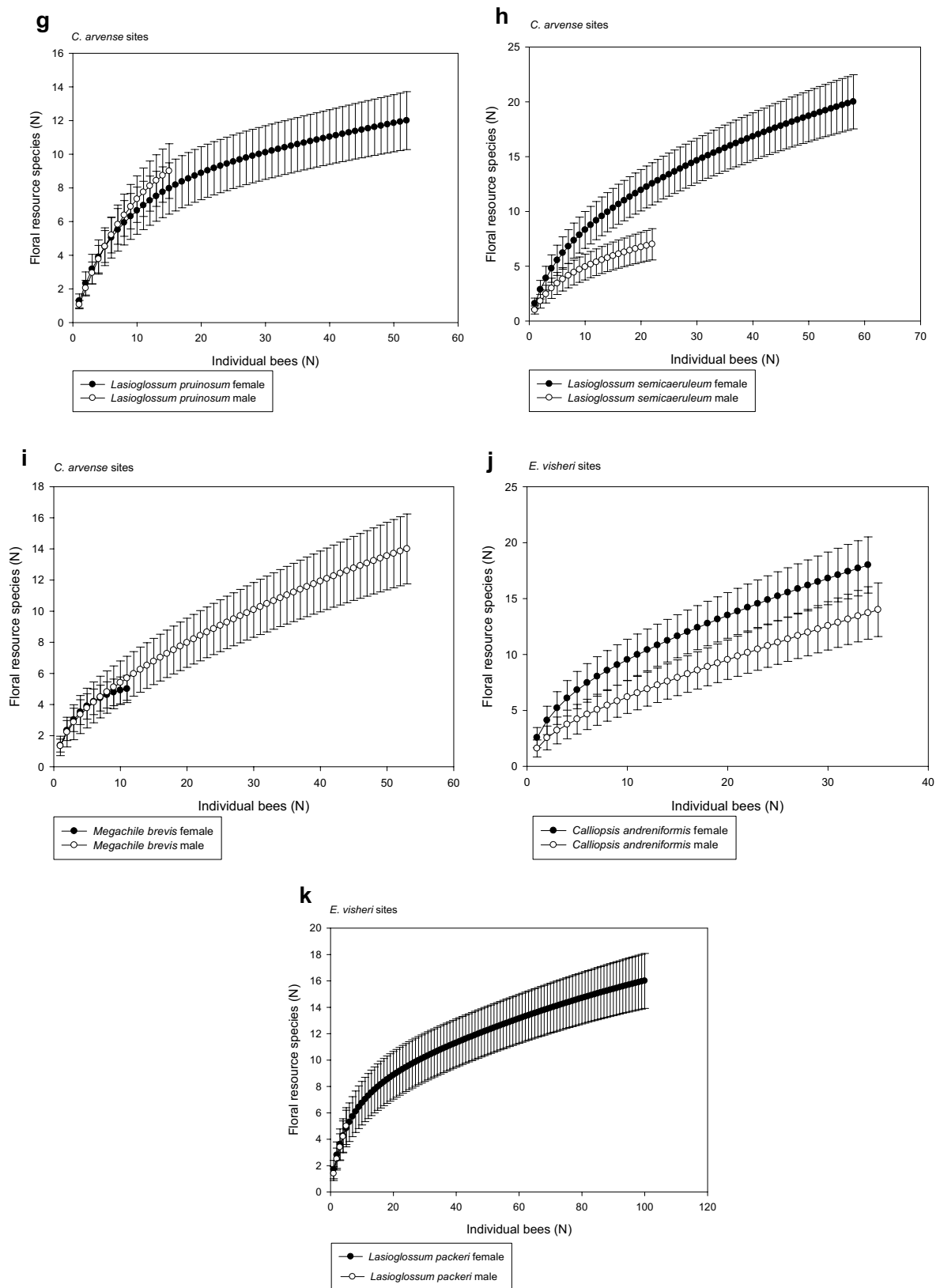
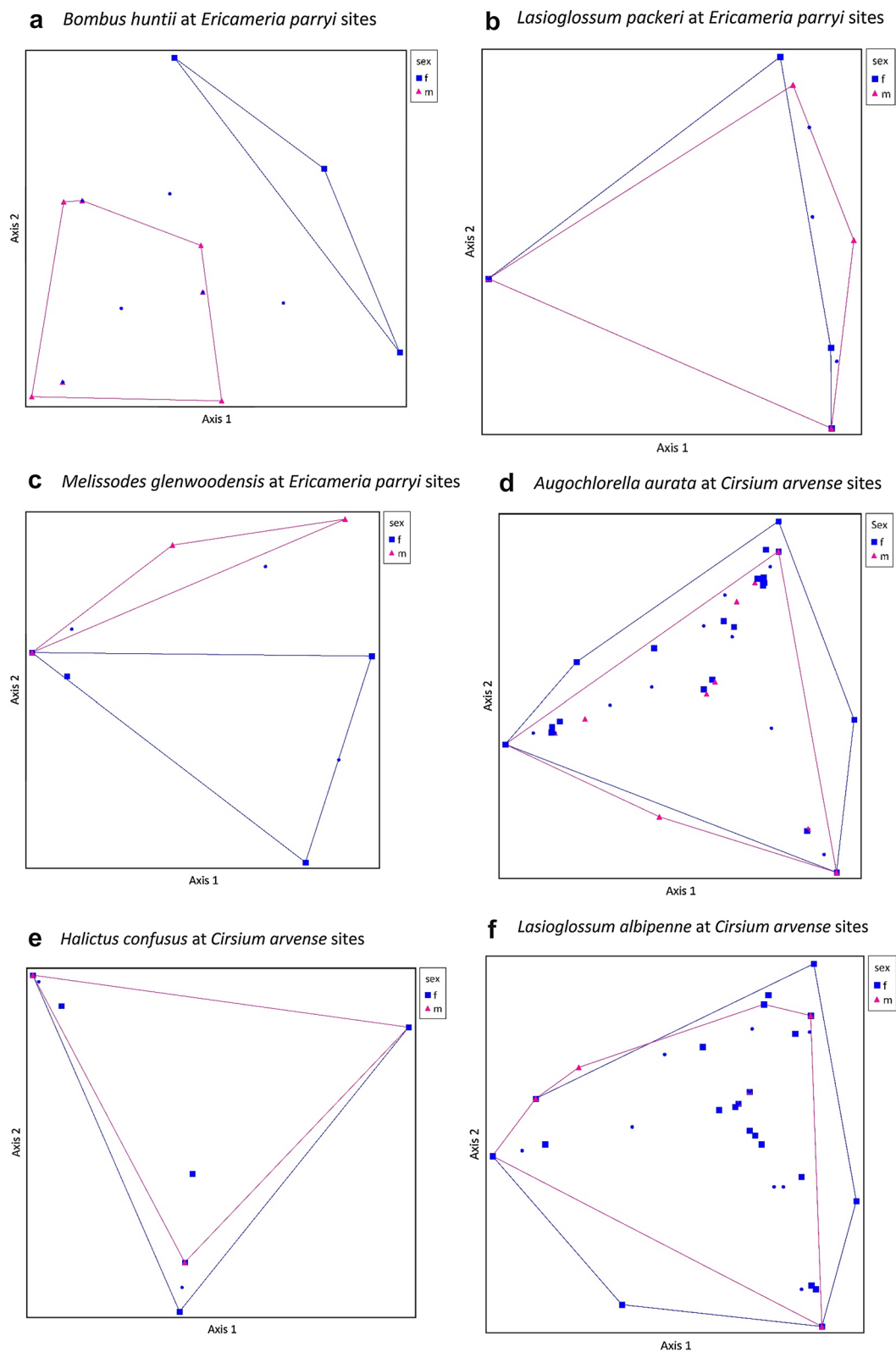


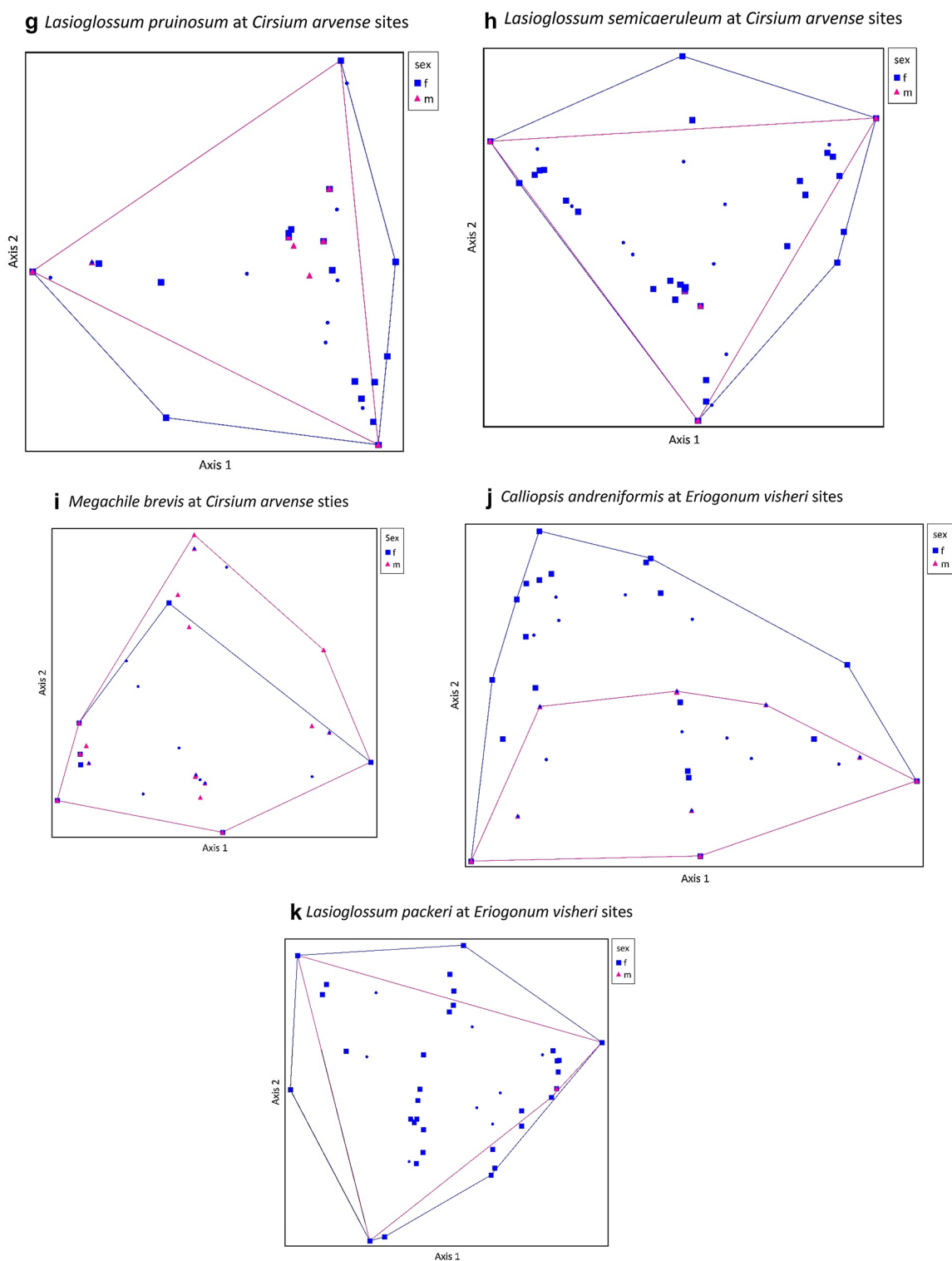
Fig. 1 (continued)



**Fig. 2** Principal coordinates analysis for bee species used in rarefaction graphs. Small blue dots represent floral resource species, blue squares represent female (f) bees and magenta triangles represent male (m) bees. Blue and magenta envelopes enclose all individuals of female and male bees, respectively. **a** *Bombus huntii* at *Ericameria parryi* sites. **b** *Lasioglossum packeri* at *Ericameria parryi* sites. **c** *Melissodes glenwoodensis* at

*Ericameria parryi* sites. **d** *Augochlorella aurata* at *Cirsium arvense* sites. **e** *Halictus confusus* at *Cirsium arvense* sites. **f** *Lasioglossum albipenne* at *Cirsium arvense* sites. **g** *Lasioglossum pruinosum* at *Cirsium arvense* sites. **h** *Lasioglossum semicaeruleum* at *Cirsium arvense* sites. **i** *Megachile brevis* at *Cirsium arvense* sites. **j** *Calliopsis andreniformis* at *Eriogonum visheri* sites. **k** *Lasioglossum packeri* at *Eriogonum visheri* sites





**Fig. 2** (continued)

accumulated fewer floral resource species (Fig. 1j) and families (Figure S1j) than females at *E. visheri* sites.

Principal coordinates analysis illustrated patterns similar to those we found in the rarefaction curves. Most species in

the Halictidae had broadly overlapping diet extents between males and females (Fig. 2). In contrast, *B. huntii*, *M. glenwoodensis*, and *C. andreniformis* plots (Fig. 2a, c, and j, respectively) illustrated less overlap in male and female



**Table 3** Modularity of networks with and without bee species separated by sex

Study	Network type	Modules (N)	Observed modularity	Random modularity	Sigma	<i>p</i>
<i>Ericameria parryi</i>	Separate sexes	7	0.327358	0.334378	0.004393	1.81E-29
	Combined sexes	6	0.317668	0.337359	0.004605	6.18E-66
<i>Cirsium arvense</i>	Separate sexes	6	0.340141	0.340135	0.003849	0.493797
	Combined sexes	7	0.335003	0.325443	0.00473	3.26E-37
<i>Eriogonum visheri</i>	Separate sexes	7	0.415894	0.399936	0.004922	7.89E-55
	Combined sexes	8	0.411118	0.393979	0.004715	2.28E-59

floral use. Even when the floral resource use extents varied little between females and males, male extent was enclosed within female extent, with the exception of *M. brevis* (Fig. 2i), where female extent was a subset of male extent and *L. packeri* at *E. parryi* sites (Fig. 2b), where male extent slightly exceeded female extent.

When sexes were separated, all networks except *C. arvense* sites were significantly more modular than randomly assembled networks (Table 3). When bees were separated by sex, networks at *C. arvense* and *E. visheri* sites had one fewer module than when sexes were combined by species; the opposite was true at *E. parryi* sites (Table 3). In seven of the eleven bee species-study combinations, when sexes were separated, they occupied different modules (Table 4). *Lasioglossum packeri* females and males occupied the same module when analyzed separately at *E. parryi* sites, but different modules at *E. visheri* sites. Roles changed for females twice and for males three times compared to modularity analyses where sexes were not separated (Table 4). Nearly all bee species, whether or not separated by sex, occupied connector roles; only three times were they peripherals, and these happened when sexes were separated. The two specialists, *M. glenwoodensis* and *C. andreniformis*, were hubs when grouped by species; female *M. glenwoodensis* retained the hub role when separated from males, which were peripheral in a different module (Table 4). The proportion of nodes classified as hubs did not change in networks at any of the three sites, but proportion of connectors declined, and peripherals increased when sexes were separated at *E. parryi* and *E. visheri* sites (Table S2).

## Discussion

Of the 11 species-study combinations, individual female- and male-conspecific bees differed in the number of floral resource species they used three times, and in floral families only once. This implies that, on average, females and males of most species we studied had visited a similar number of distinct flower species or families when captured. Of the exceptions, the specialists *M. glenwoodensis* at *E. parryi* sites and *C. andreniformis* at *E. visheri* sites also differed in

floral resource accumulation curves: females of both of these species carried and accumulated more floral resource species than did males. Contrary to our expectations, and the predictions of Smith et al. (2019b), in no cases did individual males visit more plant species or families than females. In general, males and females visited similar numbers of plant species, both as individuals and collectively as a species. We had expected the females of at least some species to be pickier foragers than males because males are primarily seeking nectar for their own energetic needs, whereas we expected females to restrict themselves more to flowers that are their pollen hosts. For example, in the Alkali Bee (*Nomia melanderi*), males visit a wider variety of nectar sources than females, which primarily take nectar from their pollen hosts (Stephen et al. 1969). Only in the generalist *B. huntii* did males accumulate more pollen species than did females. Although Smith et al. (2019b) hypothesized that females would have a smaller diet breadth than males, they also posited reasons the opposite might be true. If females' foraging decisions are based on varying nutritional quality of pollen, they might forage more broadly than males to achieve the desired quality for nest provision. Smith et al. (2019b) also recognized that oviposition sites might influence pollen choice. Locating nests and determining the nutritional value of the provisions therein to evaluate these alternatives were beyond the scope of the current study. There is a great need for such detailed natural history studies.

Our results largely do not align with the findings by Roswell et al. (2019) that males and females commonly have major differences in foraging preferences. Instead, we found that males and females generally aligned in their foraging preferences. However, part of this may be due to differences in study design. Roswell et al. (2019) conducted their study in meadows in New Jersey, whereas the present study was conducted in the badlands of South Dakota, which was less florally diverse. In addition, our practice of reconstructing visitation using pollen on the body rather than just observed visitation captured the resource use history of a given forager and may have provided a better assessment of less commonly used floral hosts that may be otherwise overlooked (e.g. those with flowers that are only open for a brief period in the early morning). Finally, because our methods depend

**Table 4** Module affiliation in networks with and without bee sexes separated

Study	Bee species	Network type	Sex <sup>a</sup>	Role <sup>b</sup>	Module hub(s)
<i>Ericameria parryi</i>	<i>Bombus huntii</i>	Combined sexes		C	<i>Polistes aurifer</i>
		Separated sexes	F	P	<i>Grindelia squarrosa</i> / <i>Gutierrezia sarothrae</i>
			M	C	<i>Polistes aurifer</i>
	<i>Lasioglossum packeri</i>	Combined sexes		C	<i>Gutierrezia sarothrae</i>
		Separated sexes	F	C	<i>Grindelia squarrosa</i> / <i>Gutierrezia sarothrae</i>
			M	C	<i>Grindelia squarrosa</i> / <i>Gutierrezia sarothrae</i>
	<i>Melissodes glenwoodensis</i>	Combined sexes		H	<i>M. glenwoodensis</i> / <i>Ericameria nauseosus</i>
		Separated sexes	F	H	<i>M. glenwoodensis</i> / <i>Ericameria nauseosus</i>
			M	P	<i>E. Parryi</i>
	<i>Cirsium arvense</i>	Combined sexes		C	<i>Cirsium flodmanii</i> / <i>Convolvulus arvensis</i> / <i>Helianthus annuus</i>
		Separated sexes	F	C	<i>Cirsium flodmanii</i> / <i>Convolvulus arvensis</i> / <i>Helianthus annuus</i>
			M	C	<i>Cirsium flodmanii</i> / <i>Convolvulus arvensis</i> / <i>Helianthus annuus</i>
	<i>Halictus confusus</i>	Combined sexes		C	<i>Cirsium flodmanii</i> / <i>Convolvulus arvensis</i> / <i>Helianthus annuus</i>
		Separated sexes	F	C	<i>Melilotus officinalis</i>
			M	C	<i>Melilotus officinalis</i>
	<i>Lasioglossum albipenne</i>	Combined sexes		C	<i>Formica BADL2</i> - <i>Pedimelum argophyllum</i>
		Separated sexes	F	C	<i>Cirsium flodmanii</i> / <i>Convolvulus arvensis</i> / <i>Helianthus annuus</i>
			M	C	<i>Cirsium arvense</i>
	<i>Lasioglossum pruinosum</i>	Combined sexes		C	<i>Cirsium flodmanii</i> / <i>Convolvulus arvensis</i> / <i>Helianthus annuus</i>
		Separated sexes	F	C	<i>Cirsium flodmanii</i> / <i>Convolvulus arvensis</i> / <i>Helianthus annuus</i>
			M	C	<i>Cirsium flodmanii</i> / <i>Convolvulus arvensis</i> / <i>Helianthus annuus</i>
	<i>Lasioglossum semicaeruleum</i>	Combined sexes		C	<i>Cirsium flodmanii</i> / <i>Convolvulus arvensis</i> / <i>Helianthus annuus</i>
		Separated sexes	F	C	<i>Formica obscuripes</i> / <i>Medicago sativa</i>
			M	C	<i>Cirsium arvense</i>
	<i>Megachile brevis</i>	Combined sexes		C	<i>Medicago sativa</i>
		Separated sexes	F	C	<i>Melilotus officinalis</i>
			M	C	<i>Formica obscuripes</i> / <i>Medicago sativa</i>
<i>Eriogonum visherii</i>	<i>Calliopsis andreniformis</i>	Combined sexes		H	<i>Calliopsis andreniformis</i>
		Separated sexes	F	C	<i>Astragalus racemosus</i>
			M	C	<i>Agapostemon angelicus/texanus</i> female
	<i>Lasioglossum packeri</i>	Combined sexes		C	No hub
		Separated sexes	F	C	<i>Grindelia squarrosa</i>
			M	P	<i>Eriogonum pauciflorum</i> / <i>E. visherii</i>

<sup>a</sup>F female, M male<sup>b</sup>H hub, C connector, P peripheral

on visitation history, differences between male and female grooming habits could potentially influence our results. If females are more fastidious groomers due to their provisioning behavior, then males could be retaining pollen for longer periods. However, we do not expect this to be a major effect since females have been found to retain pollen on their

bodies even after depositing pollen in the brood cell (Cane and Love 2019).

Two of the ten species with  $\geq 5$  individuals per sex were pollen specialists (oligolectic) – *C. andreniformis* and *M. glenwoodensis* – who provision their young with pollen from a single plant family. *Calliopsis andreniformis* visits a wide

variety of plants, but analysis of female pollen loads indicates that it is a specialist on pollen from the Fabaceae, particularly from the non-native genera *Trifolium* and *Melilotus* (Shinn 1967; Dyer and Shinn 1978); *C. andreniformis* overwhelmingly visited *M. officinalis* at *C. arvense* sites, as well (38 of 41 Fabaceae floral resources recorded were *M. officinalis*). Nonetheless, host (Fabaceae) resource use was detected on only 15 of 35 females and 23 of 36 males. This is consistent with research by Smith et al. (2019a) that unexpectedly found a high diversity of non-host pollen on some oligolectic bees. *Melissodes glenwoodensis* is specialized on the pollen of Asteraceae, particularly the genus *Eri-cameria* (formerly *Chrysothamnus*; Moldenke 1979; Hurd et al. 1980). Our sample size is small for *M. glenwoodensis*, but we detected host pollen on all captured females and males. In both cases, we found that males visited a subset of the plant species visited by females. Following the predictions of Smith et al. (2019b), we expected that males would visit more plants than females because they would nectar opportunistically whereas females would take nectar primarily from their pollen sources. This was not the case, as both males and females visited a variety of plants unrelated to their pollen hosts. Nutritional quality of the pollen collected by females of these species might shed light on the patterns we observed (Smith et al. 2019b).

Similar to the pollen-specialist bees, patterns of male and female visitation were similar in generalist (polylectic) species, with individual males and females visiting similar numbers of flower species and males typically visiting a subset of flower species that females visited. An interesting exception was *L. semicaeruleum*, the only member of the family Halictidae in which individual females visited more flower species than did males and females accumulated more floral resources than did males. The modularity analysis also separated *L. semicaeruleum* females and males into different modules, though principal coordinate analysis illustrated substantial overlap between floral use extents of males and females. We found no information on foraging or diet of this widespread species with which to compare our results, although Gibbs (2010) provides a list of plant species on which the bee has been recorded. Another generalist bee in which males and females differed substantially was *B. huntii*. In this case, patrolling behavior by males may be instrumental in determining their foraging strategy (Williams et al. 2014).

Availability of floral resource species at the different study sites undoubtedly influenced resource use, but our data were not suitable to formally analyze preference. Of 13 *Lasioglossum* putative species across *C. arvense* and *E. parryi* sites, only three were shared across the two sites and none of these had adequate representation of both females and males for within-species comparison across sites. The limited floral diversity at *E. parryi* sites, which clustered within

only three plant families (Asteraceae, Chenopodiaceae, and Polygonaceae), likely selected for bees that could make use of the floral resources available (Ritchie et al. 2016) and possibly limited our ability to detect differences between sexes. *Lasioglossum packeri* used far fewer floral resources at the *E. parryi* sites than at the *E. visheri* sites, based on floral resource rarefaction curves, likely because of limited diversity (Cullen et al. 2021) as noted above. Despite abundant flowers, floral resources in the Chenopodiaceae were never used by *L. packeri* at *E. parryi* sites but were commonly used at *E. visheri* sites by both sexes. Modularity results for *Lasioglossum* species revealed that for some species, females and males separated into different modules, while others did not. This suggests that, even though the genus is considered to be composed primarily of generalists (Michener 2007), *Lasioglossum* species may still have important differences in foraging strategies. Gibbs (2010) noted that sexual dimorphism in *Lasioglossum* can make taxonomy difficult, but it could as well make it likely that males and females forage differently, despite being generalists.

Our modularity analysis calls attention to potential issues of lumping sexes within species, recognized by Roswell et al. (2019). Even though sexes of most species we studied overlapped in floral resources visited, details of the interactions resulted in separation of sexes into different modules in seven of the eleven species-study combinations we highlighted in the other analyses. Nonetheless, roles changed relatively rarely when sexes were separated, but when they did, the proportion of connectors declined, and the proportion of peripherals increased, which indicates that connections among modules were rewired when module affiliation changed. If separating sexes changes the wiring of a network such that roles and modules are affected, conclusions about stability of pollinator communities, especially regarding propagation of disturbances across modules, may be incorrect (Sheykhalil et al. 2020). Hemprich-Bennett et al. (2021) discussed the importance of species-level node resolution; sex may be another aspect of resolution to be considered.

## Conclusions

We demonstrate, for a small number of bee species in two distinct habitats, that females and males for the most part forage similarly; when they do not, females, with few exceptions, visit more floral taxa than males. Ranges of all of these bees extend well beyond the areas we observed at BNP and we make no claim to species-wide patterns in female versus male diet breadth. Foraging by bee species is known to be contingent on plant community composition (Albrecht et al. 2014; Albrecht 2016), which may explain differential foraging on Chenopodiaceae by *L. packeri* at *E. visheri* and *E. parryi* sites. Nonetheless, our results suggest that

generalization is unwise; differences in foraging between the sexes did not follow predictable patterns based on known life history traits; this picture may change as our understanding of bee life history improves.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s11829-021-09881-x>.

**Acknowledgements** We thank the field assistants, volunteers, and interns who made this study possible. We are grateful to Badlands National Park for permitting us to work there. Sam Droege and Jelle Devalez identified the insects with taxonomic assistance from John Ascher, Jason Gibbs, Terry Griswold, and Karen Wright. Ian Lane and an anonymous reviewer provided helpful advice on an earlier version of this paper. Funding was provided by U.S. Geological Survey Natural Resources Protection Program/Park-oriented Biological Support, U.S. Geological Survey Invasive Species Program, Northern Prairie Wildlife Research Center, and Patuxent Wildlife Research Center. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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