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Native Bees Associated With Isolated Aspen Stands in Pacific Northwest Bunchgrass Prairie

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ABSTRACT: In the western United States, up to 90% of quaking aspen (*Populus tremuloides* Michx.) is estimated to have disappeared since European settlement due to human activities. This loss poses a significant threat to many forms of biodiversity associated with aspen, including plants, birds, and mammals. However, no work has investigated native bee diversity associated with aspen. Our objectives were to: (1) describe the diversity, taxonomic composition, and sex ratios of bees in aspen stands in native bunchgrass prairie of northeastern Oregon, (2) compare bee communities in aspen with those in an adjacent grassland, and (3) document differences in floral resources associated with each habitat. We sampled native bees and quantified blooming non-anemophilous plant richness in four aspen stands and four locations in bunchgrass prairie three times during the summer. Bee abundance increased in both habitats as the summer progressed. Although taxa richness and overall abundance of bees did not differ significantly between habitats, community composition did. Bumble bees (*Bombus*) were more abundant in aspen stands, while sweat bees (*Lasioglossum* and *Halictus*) were more abundant in grassland locations. Four species of bumble bees were significantly associated with aspen stands and sex ratios of bumble bees were significantly more male-biased in aspen stands compared to grassland locations. Floral resources are one potential driver of observed differences between habitats. In late summer, aspen stands had higher blooming plant richness, as well as a distinctive floral community. This study suggests that conserving aspen benefits not only many plants and vertebrates, but also ecologically significant invertebrates, such as native bees.

Index terms: aspen, bumble bees, native bees, pollinators, Zumwalt Prairie Preserve

INTRODUCTION

The decline of quaking aspen (*Populus tremuloides* Michx.) has been a long-standing conservation concern (DeByle and Winokur 1985; Kay 1997; Frey et al. 2004). In the western United States, a loss of 60% – 90% of aspen is estimated to have occurred since European settlement (Lachowski et al. 1996). These deciduous trees, native to cold regions of North America, face a variety of threats, including overgrazing by deer (*Odocoileus*), elk (*Cervus*), and livestock (cattle (*Bos*) and sheep (*Ovis*)) and changes in fire regime that limit reproduction (Kay 1997). Urbanization and agriculture have also contributed to the decline of aspen. Declines in aspen are exacerbated by the fact that many remaining trees are quite old and clones have very low regeneration rates (Kay and Bartos 2000). Concern over aspen conservation has been magnified most recently by “sudden aspen decline,” a disease that results in rapid branch die-back and mortality. In less than a decade, the disease has affected large areas in the western United States and Canada and is predicted to become more severe with climate change (Worrall et al. 2010).

The loss of aspen poses a threat to biodiversity dependent on healthy stands. Aspen stands help minimize runoff and erosion (DeByle 1985) and serve as natural fire

breaks because they do not readily burn (Brown and Simmerman 1986); and, thus, their presence benefits biodiversity in adjacent streams and grasslands. They also provide habitat, refuge, and food for a variety of wildlife. Their high diversity of shrubs, grasses, and forbs makes them optimal grazing locations for ungulates, as well as for birds, beavers (*Castor*), and other vertebrates (DeByle and Winokur 1985; Naiman et al. 1988; Sallabanks et al. 2005). However, little research has examined the importance of aspen stands for supporting invertebrate diversity. Although some work has examined invertebrate pests of aspen (Jones et al. 1985), no studies have focused on the importance of aspen as habitat for beneficial invertebrates. Native bees are of particular interest, not only because of their importance in providing pollination services, but also because evidence suggests that some native bees, particularly bumble bees (*Bombus*), are experiencing declines (NRC 2007). To address the lack of knowledge about the importance of aspen as a habitat for native bees, we conducted a study of native bees in aspen stands found in the largest remnant of the Pacific Northwest Bunchgrass Prairie, the Zumwalt Prairie Preserve.

Owned by The Nature Conservancy, the Zumwalt Prairie Preserve, located in Wallowa County in northeastern Oregon, is a 13,269 ha preserve of the once extensive

(8 million hectares) Pacific Northwest Bunchgrass Prairie (Tisdale 1982). A total of 27 remnant aspen stands are scattered throughout the grasslands of the preserve. Because aspen habitat has been decreasing on the Zumwalt Prairie, with an estimated loss of 18% occurring between 1976 and 2001 alone (Bartuszevige et al. 2012), The Nature Conservancy has established conservation programs in an effort to increase the size and quality of this habitat. Previous work has documented that a diverse and abundant native bee community inhabits the grassland habitat of the prairie (Kimoto et al. 2012, a), but no studies have examined the importance of aspen stands in providing habitat or foraging resources for native bees.

The objectives of our study were to: (1) describe the diversity, taxonomic composition, and sex ratios of native bees in aspen stands in the Zumwalt Prairie of northeastern Oregon, (2) compare bee communities found in aspen with native bees in an adjacent native grassland, and (3) document differences in floral resources associated with each habitat type.

METHODS

Study Area

The Nature Conservancy's 13,269-ha Zumwalt Prairie Preserve (45° 34' N, 116° 58' W) ranges in elevation from 1060 – 1680

m. The grassland portion of the Zumwalt Prairie is dominated by native grass species including Idaho fescue (*Festuca idahoensis* Elmer), Sandberg bluegrass (*Poa secunda* J. Presl), prairie Junegrass (*Koeleria macrantha* (Ledeb.) Schult.), and bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Löve) (Kennedy et al. 2009). Forbs are also common, with over 112 species, most of which are native to the Pacific Northwest Bunchgrass Prairie (<https://www.conservationgateway.org/ConservationByGeography/NorthAmerica/UnitedStates/oregon/grasslands/zumwalt/mapsdata/Pages/default.aspx>). Although the preserve is dominated by grassland habitat, 27 aspen stands occur on north and east facing draws of upland prairie buttes (Figure 1a), where snowdrifts can last into the spring (R.V. Taylor, unpubl. data). Sizes of aspen stands on the Zumwalt Prairie Preserve range from 0.02 – 2.34 ha, with an average size (± 1 SE) of 0.67 ± 0.12 ha; elevation of stands ranges from 1378 – 1590 m. We selected four aspen stands to sample native pollinators based on size, location, and tree species composition. Specifically, we focused on larger stands (with a range of 0.78 – 2.13 ha and an average size (± 1 SE) of 1.46 ± 0.28 ha) that were near grassland sampling sites and that were not invaded by conifers. All aspen stands were elliptical and details of selected aspen sites, including size and perimeter to area ratios, are presented in Table 1. For comparison purposes, we sampled grassland habitat at four nearby

sampling sites of similar elevation that are part of a long-term native bee monitoring program that began in 2007 (Kimoto et al., 2012, a; Rao et al. 2011). The elevation of grassland sites ranged from 1454 to 1467 m and each were separated by approximately 200 m from their nearest neighbor and were located 3 – 5 km from aspen sites.

Field Sampling

Pollinators were sampled from the selected aspen and grassland sites three times in 2010: 22–30 June, 14–21 July, and 3–5 August using UV-reflective blue vane traps, a relatively new method of trapping native bees that has been used successfully in numerous studies of grasslands and agroecosystems in the Pacific Northwest (Stephen and Rao 2005, 2007; Rao and Stephen 2009, 2010; Stephen et al. 2009; Kimoto et al., 2012, a, b). A blue vane trap consists of two 24-cm x 13-cm blue polypropylene cross vanes of 3 mm thickness inserted in a screw funnel attached to a semi-transparent plastic container (15-cm diameter x 15-cm high) (SpringStar™ LLC, Woodinville, WA, USA). Blue vane traps were hung approximately 1.2 m from the ground with wire hangers inserted into aluminum pipes (Figure 1b). No liquids or other killing agents were used in traps. One blue vane trap was used at each site and was left open for 24 hours during each time period. Traps located in aspen stands were placed in the center of the aspen stand to reduce edge effects. Weather data for each

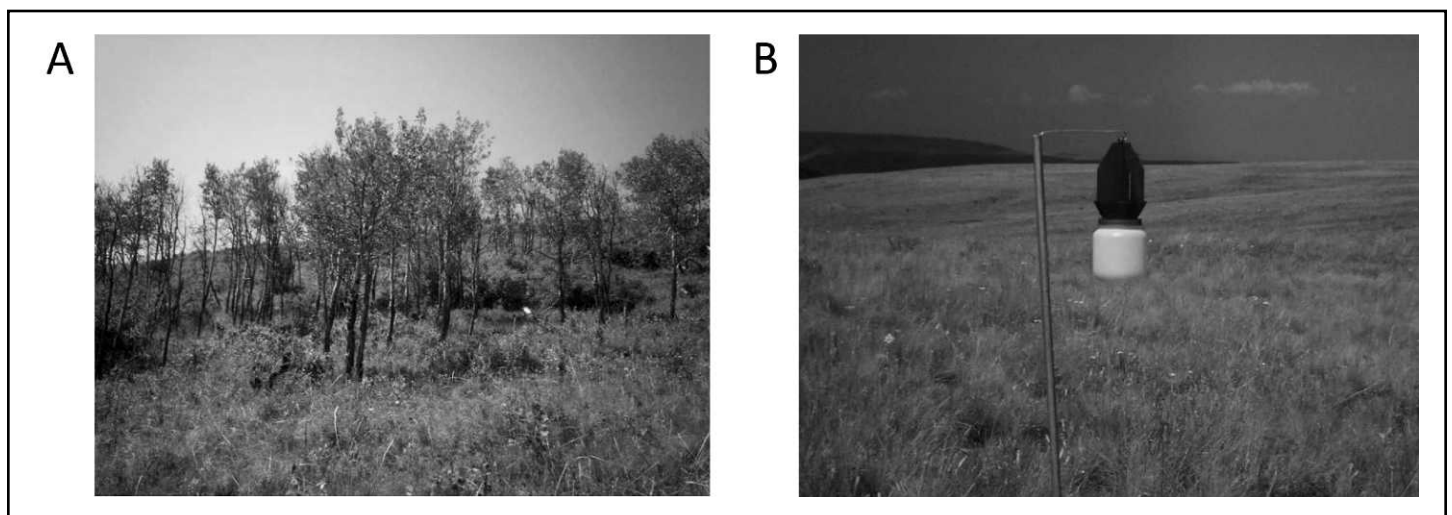


Figure 1. (A) An aspen stand and (B) a blue vane trap in a grassland site at the Zumwalt Prairie in northeastern Oregon.

Table 1. Characteristics of four aspen stands in the Zumwalt Prairie Preserve in northeastern Oregon included in the study.

Site Name	Size (ha)	Perimeter (m)	PAR ¹ (m/ha)	Elevation (m)	Coordinates: ²		Fenced?
					(latitude)	(longitude)	
DCU1	2.13	686.2	322.3	1436	500022.90184	5046015.28893	Yes ³
DCG1	0.78	149.4	191.8	1438	500071.06912	5045816.81259	No
DG1	1.62	490.8	303.2	1540	500995.380707	5043674.58735	No
DG2	1.32	430.1	324.6	1509	501232.238741	5043311.56382	No

¹Perimeter to Area Ratio

²UTM, NAD83, Zone 11N

³Buck-pole enclosure erected in 2002 – excludes both cattle and wild ungulates

trapping date were collected at a weather station located in the center of the Zumwalt Prairie Preserve (lat 45° 34'39.88"N, long 116° 58'18.31' W, elevation 1337 m) and less than 3 km from the nearest blue vane trap; trapping across sites was conducted under similar temperatures, humidity, and wind speeds within each time period. Collected pollinators were frozen in the laboratory until processing, when they were pinned, labeled, sexed, and identified to genus, and—for bumble bees—species. The presence of blooming non-anemophilous plant species was recorded along three parallel 100-m long x 0.3-m wide belt transects at each location during each sampling period. Each transect was separated by approximately 10 m.

Statistical Analyses

We used analysis of variance (ANOVA) to compare means of all univariate variables between aspen and grassland sites, including the abundance of all bees, generic richness, bumble bee species richness, sex ratios, and blooming non-anemophilous plant richness. Because so few bees were collected in the first two sampling periods (Figure 2a), bee data from all three sampling periods were combined before analysis. Because most bumble bee species have three castes (queens, workers, and males) and other genera do not, we examined sex ratios for bumble bees separately from other genera. We used proportion of males to characterize sex ratio for both analyses. Plant richness data were analyzed separately by time period,

given the high number of blooming non-anemophilous species found at all sites in each sampling period.

We used multi-response permutation procedures (MRPP) to determine whether generic composition and bumble bee species composition differed between aspen and grassland sites. We also used MRPP on presence/absence data of blooming non-anemophilous plant species to determine if plant composition differed between aspen and grassland sites. MRPP is a multivariate, non-parametric procedure for testing the hypothesis of no difference between two or more groups. MRPP calculates the mean within-group distance and generates an expected distance through permutation (McCune and Mefford 2006). The p-value generated by the test is the probability of observing a within-group distance smaller than the observed distance due to chance alone. MRPP tests also provide a measure of the effect size (A), which is one minus the ratio of the observed mean within-group distance to the expected within-group distance. An effect size of 1 indicates that all items within each group are identical (i.e., the within-group distances are zero), a value of 0 indicates that the heterogeneity within group is no different from that expected by chance, and a negative effect size indicates there is more heterogeneity within groups than expected by chance (McCune and Grace 2002). In community ecology, effect size values are commonly below 0.1 and values greater than 0.3 are considered indicative of large differences between communities (McCune and Grace

2002). We used Sorensen's as the distance measure in all MRPP analyses.

In addition, we characterized the generic composition of bee communities and species composition of bumble bees using non-metric multidimensional scaling (NMS) ordinations. NMS ordination is a robust technique that is based on ranked distances and performs well with data that are not normally distributed and contain numerous zero values (McCune and Grace 2002). NMS was run on the abundance of taxa using Sorensen's distance measure. The best solution was determined through 250 runs of randomized data and dimensionality was determined by evaluating the relationship between final stress and the number of dimensions. We used Pearson's correlation coefficients to quantify relationships between bee abundance and ordination axes results (McCune and Mefford 2006). Ordinations were run using PC-ORD, version 5.19, set on "autopilot" mode (McCune and Mefford 2006).

To determine which blooming non-anemophilous plant species were most important in separating aspen and grassland sites, indicator species analyses on presence/absence data for each sampling bout were conducted (Dufrene and Legendre 1997). For each species within each group, a value of 0 to 100 is calculated. A value of 100 indicates that the taxon is found exclusively in one group and is found at every site within that group and, thus, is a "perfect" indicator of that group. Values less than 100 occur when a taxon

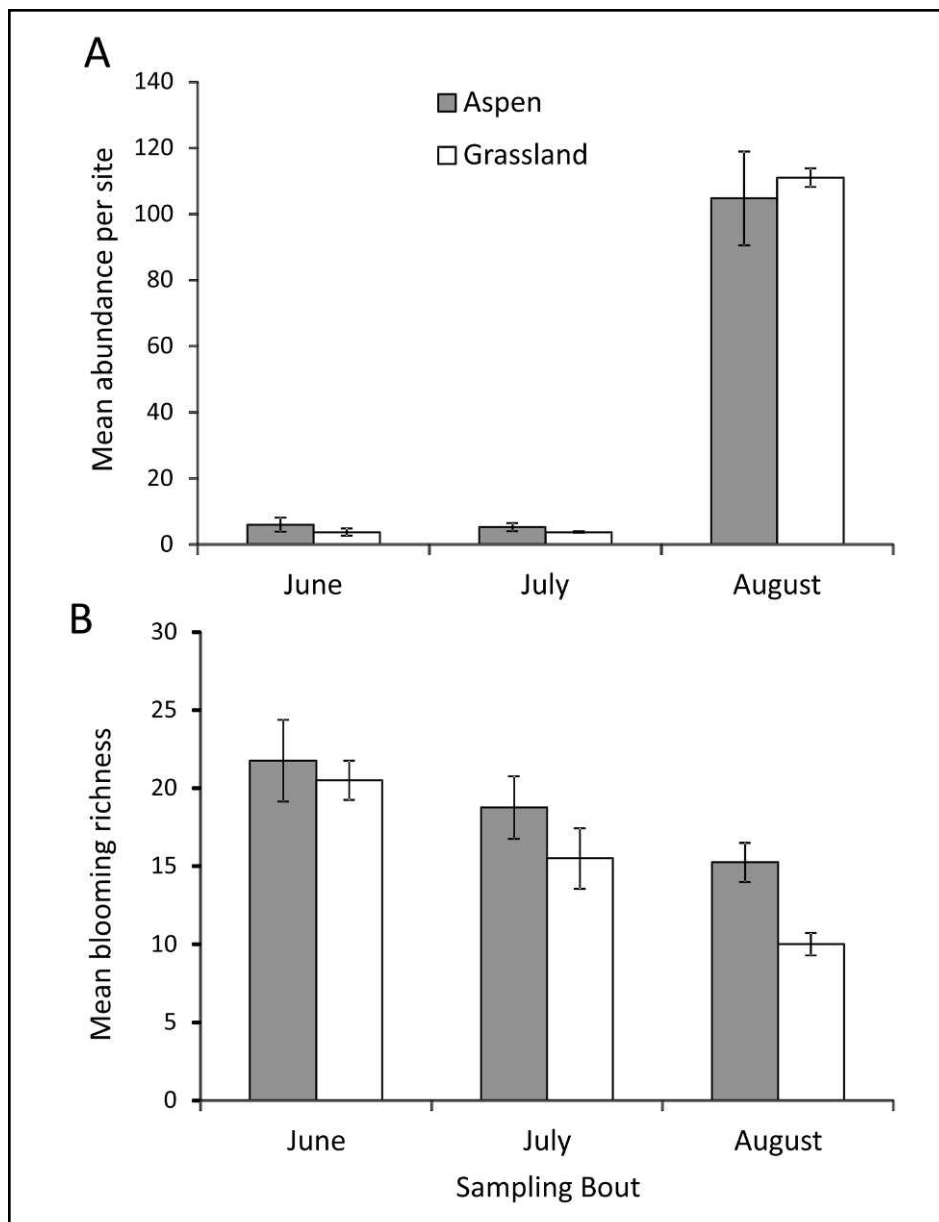


Figure 2. Mean (± 1 SE) (A) number of bees and (B) blooming non-anemophilous plant richness in aspen and grassland sites during three bouts of sampling (June, July, August) in the Zumwalt Prairie Preserve of northeastern Oregon.

is not found at all sites within a group, is not found exclusively in that group, or a combination of the two. To determine the statistical significance of indicator values, a Monte Carlo test was conducted in which the data set was randomized (1000 times) and the indicator value for each taxon was compared to the population of randomized results.

We tested variables for normality using Lilliefors' test and arcsine transformed, if non-normal. Only sex-ratios were non-normal, and transformations normalized

the data. All univariate statistical analyses were conducted with SYSTAT, version 7.0 (1997); and all multivariate analyses were conducted with PC-ORD, version 5.19 (McCune and Mefford 2006). Means in the text are reported \pm one standard error.

RESULTS

A total of 938 bees in 16 genera were collected in blue vane traps through the course of the study, with 464 bees collected in aspen stands and 474 collected in traps

in grasslands. Bumble bees were the most common genus collected, with 579 specimens collected in both types of habitats. Most bees in both habitats were collected in the third sampling period (Figure 2a), while blooming non-anemophilous plant richness decreased at both types of sites from June to August (Figure 2b).

Although samples from aspen and grassland sites did not differ significantly in the cumulative number of bees or genera collected with blue vane traps ($F = 0.03$, $p = 0.87$; $F = 0.0$, $p = 1.00$, respectively), the composition of the two communities differed. Ordination results revealed that generic composition varied between aspen and grassland sites (Figure 3a). A two dimensional solution explained 72% of the variation in community composition at the genus level (Table 2), with Axis 1 explaining 68% of the variation. Three genera (*Anthophora*, *Lasioglossum*, and *Halictus*) were significantly positively correlated with Axis 1 (and, thus, associated with grassland sites), and bumble bees were negatively correlated with Axis 1 (and, thus, associated with aspen sites) (Table 2). Mean number of *Bombus* were almost twice as great in aspen sites compared to grassland sites and mean number of *Halictus* and *Lasioglossum* were three times as great in grassland sites compared to aspen sites (Table 2). In addition, five relatively rare genera were found only in aspen sites, while two relatively rare genera were found only in grassland sites (Table 2). MRPP analysis showed that the difference in generic composition between aspen and grassland sites was statistically significant ($A = 0.37$, $p = 0.006$).

Ordination focused on bumble bees showed that the bumble bee species composition in aspen and grassland sites also varied (Figure 3b). A one-dimensional solution explained 72% of the variation in bumble bee species. Four species were significantly negatively associated with Axis 1 (and, thus, were positively associated with aspen sites) (Table 3). MRPP analysis showed that difference between bumble bee species composition between aspen and grassland sites was significantly different ($A = 0.12$, $p = 0.03$).

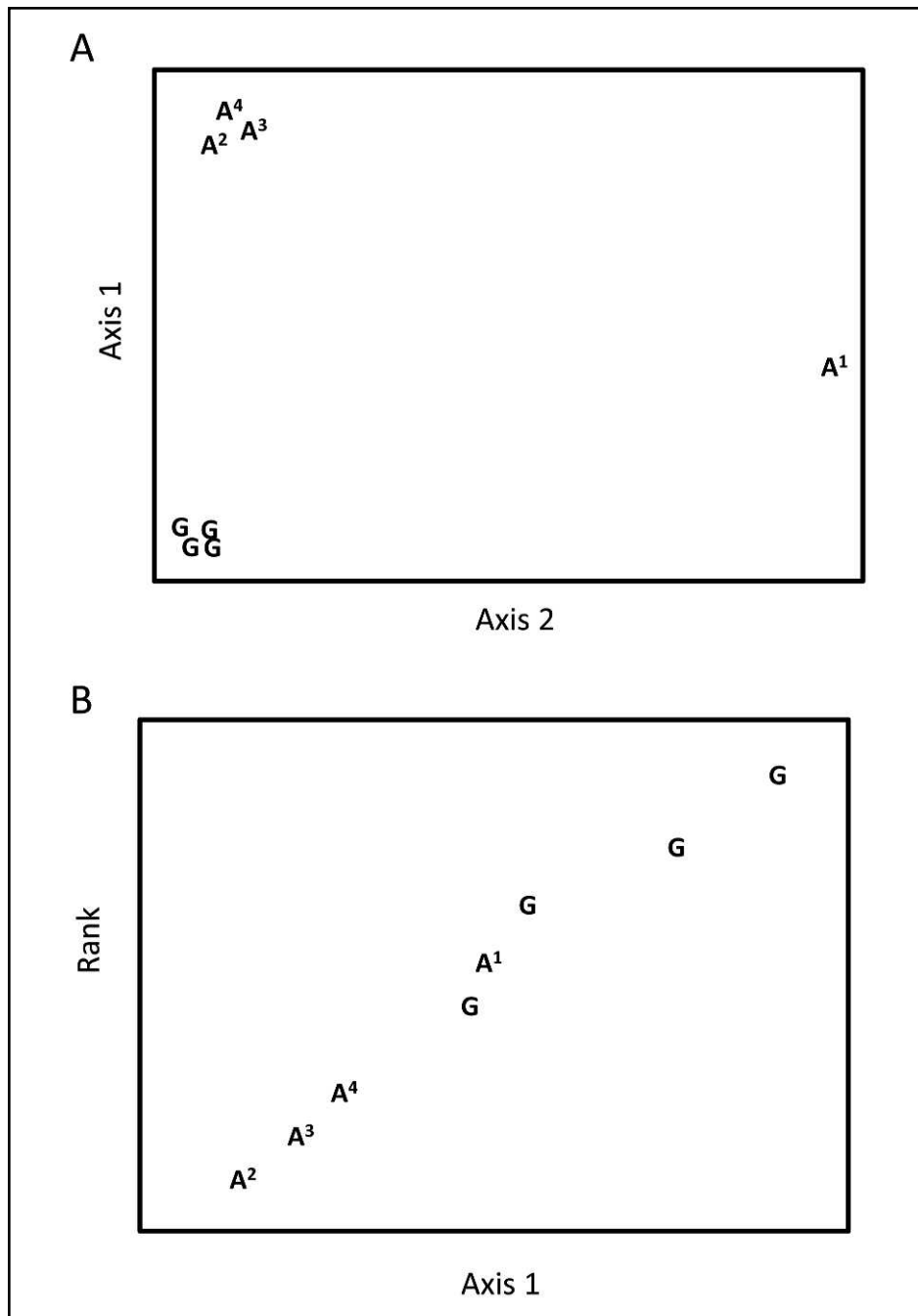


Figure 3. NMS ordinations of aspen (A) and grassland sites (G) in the Zumwalt Prairie Preserve of northeastern Oregon for (A) all bees relative to genus and (B) bumble bee species. A¹=site DCU1, A²=Site DCG1, A³ = Site DG1, A⁴=Site DG2.

Sex ratios between habitats did not differ significantly for non-bumble bees ($F = 2.2$, $p = 0.19$; Figure 4a), but did differ for bumble bees ($F = 6.9$, $p = 0.04$). Aspen sites had significantly higher proportions of male bumble bees than grassland habitats (Figure 4b).

A total of 98 blooming non-anemophilous plant species were observed over the course

of the study in both grassland and aspen sites. Of these, 43 species were found only in aspen sites, and 25 were found only in grassland sites. MRPP analyses on presence/absence data showed that the blooming species composition of the two communities was significantly different each month (June, $A = 0.23$, $p = 0.005$; July, $A = 0.27$, $p = 0.006$; August, $A = 0.34$, $p = 0.006$). Indicator species asso-

ciated with aspen and grassland sites are shown in Table 4. Aspen and grassland sites had a similar number of blooming non-anemophilous plant species in June ($F = 0.18$, $p = 0.68$) and July ($F = 1.35$, $p = 0.29$), but there were significantly more blooming species in aspen stands than in grassland sites in August ($F = 13.0$, $p = 0.01$) (Figure 2b).

DISCUSSION

Although past studies have examined bee communities associated with other forest types (e.g., Liow et al. 2001; Brosi et al. 2008; Williams 2011), no previous work has described the native bee fauna associated with aspen stands at any location. Our study indicates that remnant aspen stands in the Zumwalt Prairie are associated with a diverse and abundant bee fauna that, while similar to the fauna found in grassland habitat, differs in some important respects. Like previous work (Kimoto et al., 2012, a), we found a grassland bee community dominated by bumble bees, sweat bees (*Lasioglossum* and *Halictus*), and long-horned bees (*Melissodes*). In contrast, the aspen stand bee community was dominated much more strongly by bumble bees. Not only was the relative abundance of bumble bees greater in aspen, but the species composition of the bumble bee community differed from grasslands, with four species being significantly associated with aspen. In addition, male bumble bees occurred at higher proportions in aspen compared to grassland sites.

Differences in bee communities between aspen and grassland sites could reflect differential responses of bees to floral resource availability. Aspen stand sites were associated with significantly higher plant richness in August, when bees were more abundant. Although we did not quantify floral resource abundance in this study, previous work in the grasslands of the Zumwalt Prairie has shown that transects with higher non-anemophilous blooming species richness also have higher non-anemophilous bloom abundance (Kimoto et al., 2012, a). If this relationship holds true for aspen habitat as well, then aspen stands in late summer may be associated with a greater availability of pollen and nectar

Table 2. Mean (± 1 SE) abundance of bee genera sampled by blue vane traps in aspen stands and adjacent grasslands sites in the Zumwalt Prairie Preserve of northeastern Oregon and Pearson correlation coefficients with NMS ordination axis 1. Bold-faced correlations are statistically significant, with “*” indicating significance at $p = 0.05$, and “**” indicating significance at $p = 0.01$. Axis 1 explained 68% of the variation in generic composition of bee communities; axis 2, not shown, explained only 4%.

Genus	Aspen	Grassland	NMS Axis 1
<i>Agapostemon</i>	0.25 \pm 0.25	1.75 \pm 0.48	-0.66
<i>Andrena</i>	1.50 \pm 0.50	2.50 \pm 1.04	-0.26
<i>Anthophora</i>	0 \pm 0	0.75 \pm 0.25	-0.72*
<i>Bombus</i>	92.25 \pm 11.47	52.5 \pm 3.88	0.92**
<i>Emphoropsis</i>	0.25 \pm 0.25	0 \pm 0	0.47
<i>Diadasia</i>	0.25 \pm 0.25	0.25 \pm 0.25	-0.27
<i>Halictus</i>	4.50 \pm 1.04	15.25 \pm 2.13	-0.75*
<i>Hoplitis</i>	0.75 \pm 0.96	0 \pm 0	0.67
<i>Hylaeus</i>	0.75 \pm 0.48	0 \pm 0	0.67
<i>Lasioglossum</i>	8.75 \pm 1.80	34.25 \pm 0.50	-0.76*
<i>Megachile</i>	0.50 \pm 0.29	0.50 \pm 0.29	-0.16
<i>Melissodes</i>	1.25 \pm 0.48	8.00 \pm 2.00	-0.70
<i>Osmia</i>	4.00 \pm 2.04	2.00 \pm 0.41	0.40
<i>Perdita</i>	0 \pm 0	0.75 \pm 0.48	-0.50
<i>Protostelis</i>	0.25 \pm 0.25	0 \pm 0	-0.001
<i>Sphecodes</i>	0.75 \pm 0.48	0 \pm 0	0.67

resources than grassland sites. Bumble bees may be more responsive to these changes in floral resource availability compared to other native bees because of their higher energetic needs and/or their ability to fly longer distances. Because of their large body mass, bumble bees have one of the highest metabolic rates of any animal measured, approximately 75% higher than hummingbirds (Goulson 2010). Not only do bumble bees need to maintain their own energy reserves, but females also need to provide energy for colony development (Goulson 2010). Given this high need, bumble bees may be more likely to forage in aspen stands compared to adjacent grasslands and/or queens may prefer nesting in aspen stands due to the fact that a greater richness of floral resources are available for longer periods of time in aspen compared to grassland sites. Bumble bees that do nest in grasslands may be more capable of exploiting late-season floral resources located in aspen stands because of their ability to fly longer distances than other

groups, such as sweat bees (Zurbuchen et. al. 2010); and, thus, are better able to engage in opportunistic foraging (i.e., taking advantage of shifting mosaics of high quality floral resources).

In addition, bumble bees may be more common in aspen stands than nearby grassland sites because the particular flowering plant community associated with aspen stands may be more attractive to at least some species of bumble bees than the flowering plant species found in the adjacent grassland. For example, bumble bee species that have long tongues or proboscises may prefer to forage, and do so more efficiently, on flower species not available to most short-tongued bees (Hobbs 1962; Inouye 1978, 1980). In our study, most species of bumble bees were long-tongued, and all of these, with the exception of one (*B. nevadensis*), were more common in aspen stands (Table 3). The only common short-tongued bumble bee (*B. rufocinctus*) sampled during the

course of our study was more abundant in grassland sites. The blooming species composition of aspen and grassland sites differed, and aspen sites may have provided more flowers suitable for long-tongued bees. Previous work (Hobbs et al. 1961; Hobbs 1962) showed that the species most common in our aspen stands, *B. appositus*, prefers to gather food from flowers with long corollae, such as clover (*Trifolium* sp.). In fact, several species of long-corolla flowers, including clover and nettle leaf giant hyssop (*Agastache urticifolia*), were either exclusively found or were much more common in aspen stands. These results are consistent with other work on the understory composition of aspen stands. Mueggler (1985) discusses the rich forb and flowering shrub understory associated with aspen stands, and most of the indicator species found in our study were identified in his work as members of “aspen associated” species, including *Agastache urticifolia*, *Symphoricarpos albus*, and *Galium boreale*. Although we measured blooming non-anemophilous species richness in this study, we did not quantify floral resource abundance. Future studies measuring the quantity and quality of floral resources available in aspen stands, including both pollen and nectar, and documenting the association of native bees and particular plant species, would be useful in determining the importance of these factors in explaining differences between aspen and grassland habitats.

An alternative explanation for the higher proportion of bumble bees and smaller proportion of sweat bees in aspen stands relative to grasslands relates to thermo-regulation. Larger bees generate more heat and have less surface area (proportionally) to dissipate heat (Goulson 2010), and bumble bees are known to overheat at higher temperatures (Heinrich 1975, 1979). Although we did not measure microhabitat temperatures in grassland and aspen habitats, the shading effect of aspen trees likely decreased air temperatures in those areas. If so, then bumble bees may be more metabolically efficient foragers in aspen stands, and may be less likely to overheat, especially in warm months like August.

Table 3. Mean (\pm 1 SE) abundance and correlations with ordination axes of common bumble bee species (\geq 6 individuals collected) sampled by blue vane traps in aspen stands and adjacent grasslands sites in the Zumwalt Prairie Preserve of northeastern Oregon. Bold-faced correlations are statistically significant, with “*” indicating significance at $p=0.05$, and “” indicating significance at $p=0.01$. Axis 1 explained 72% of the variation in species composition of bumble bees.**

Species (Subgenus)	Aspen Mean (SE)	Grassland Mean (SE)	Axis 1	Tongue Length	Male Mate Locating Behavior
<i>B. appositus</i> (<i>Subterraneobombus</i>)	23.5 (5.05)	12.75 (2.46)	-0.83**	Long	Nest surveillance (Hobbs 1966b)
<i>B. flavifrons</i> (<i>Pyrobombus</i>)	7.5 (1.56)	2.5 (0.64)	-0.85**	Long	Patrolling – scent marking (Hobbs 1967)
<i>B. insularis</i> (<i>Psythirus</i>)	14 (2.94)	3.75 (1.93)	-0.95**	Intermediate	Patrolling – scent marking (Lavery and Harder 1988)
<i>B. vagans</i> (<i>Pyrobombus</i>)	1.5 (0.65)	0	-0.75*	Long	Patrolling – scent marking (Hobbs 1967)
<i>B. fervidus</i> (<i>Fervidobombus</i>)	1.25 (0.48)	0.5 (0.50)	-0.66	Long	Nest surveillance (Hobbs 1966a; Lloyd 1981)
<i>B. bifarius</i> (<i>Pyrobombus</i>)	21.75 (4.73)	10.25 (1.65)	-0.54	Intermediate	Patrolling – scent marking (Foster 1992)
<i>B. californicus</i> (<i>Fervidobombus</i>)	13.5 (4.25)	9.75 (1.60)	-0.49	Long	Nest surveillance (Foster 1992)
<i>B. nevadensis</i> (<i>Bombias</i>)	0.25 (0.25)	1.5 (0.65)	0.27	Long	Territorial (O’Neill et al. 1991)
<i>B. rufocinctus</i> (<i>Cullumanobombus</i>)	8.5 (1.32)	11 (3.34)	0.31	Short	Territorial (O’Neill et al. 1991)

Differences in the bee fauna between aspen and grassland sites could also reflect variation in habitat preferences or life history traits. Hobbs (1966b) found that *B. appositus* was confined to wooded areas in Canadian regions that included both forest and prairie. Although *B. appositus* is common in grassland habitat on the Zumwalt Prairie (Kimoto et al., 2012, a), the species may prefer wooded habitat. Another species, *B. insularis*, is a cuckoo bee (in which the queens take over nests of other bumble bee species and use their host workers to produce their own progeny). This species may benefit by being in aspen stands because several of its main hosts, including *B. appositus*, are more common in aspen. *B. insularis* is known to successfully rear young to maturity in nests of *B. appositus*; in fact, 20% of *B. appositus* nests were parasitized by *B. insularis* in a study in Canada (Hobbs 1966b).

Differences in male mate-locating behavior may also play a role in explaining the differences in both bumble bee species composition and sex ratio of bees between aspen and grassland sites. The bumble bee species found at the Zumwalt Prairie are known to display one of three types of female-locating behavior: territoriality, patrolling and scent marking, and nest surveillance (Table 3). In territorial species, males have large, protuberant eyes and typically perch on vegetation and defend small territories in which they intercept all potential mates (O’Neill et al. 1991). Males of other bumble bee species engage in nest surveillance behavior, in which males congregate around nests from which virgin females emerge. Males of other bumble bee species employ a non-territorial behavior of patrolling and scent-marking to locate female bees (Goulson 2010). Males of these species, including cuckoo bees (subgenus *Psythirus*), mark landmarks with labial

gland secretions and then fly from one landmark to another in circuits, where they encounter females who are presumably attracted by species-specific scent gland secretions (Goulson 2010). Many species that engage in patrolling and scent-marking use landmarks such as trees or hedgerows (Goulson 2010). Different heights on landmarks are selected and, unlike solitary bees, which commonly scent-mark flowers to attract females, bumble bees use non-flowering landmarks (Kullenberg 1956; Haas 1960). Bumble bees may use non-flowering landmarks to avoid non-reproductive workers, which are common at flowers (Goulson 2010). Aspen stands located in the prairie may provide particularly good habitat for bumble bees that use patrolling and scent-marking because of the abundance of physical structure in the form of trees in which to scent-mark. This explanation is consistent with the fact that all bumble bee species that employ

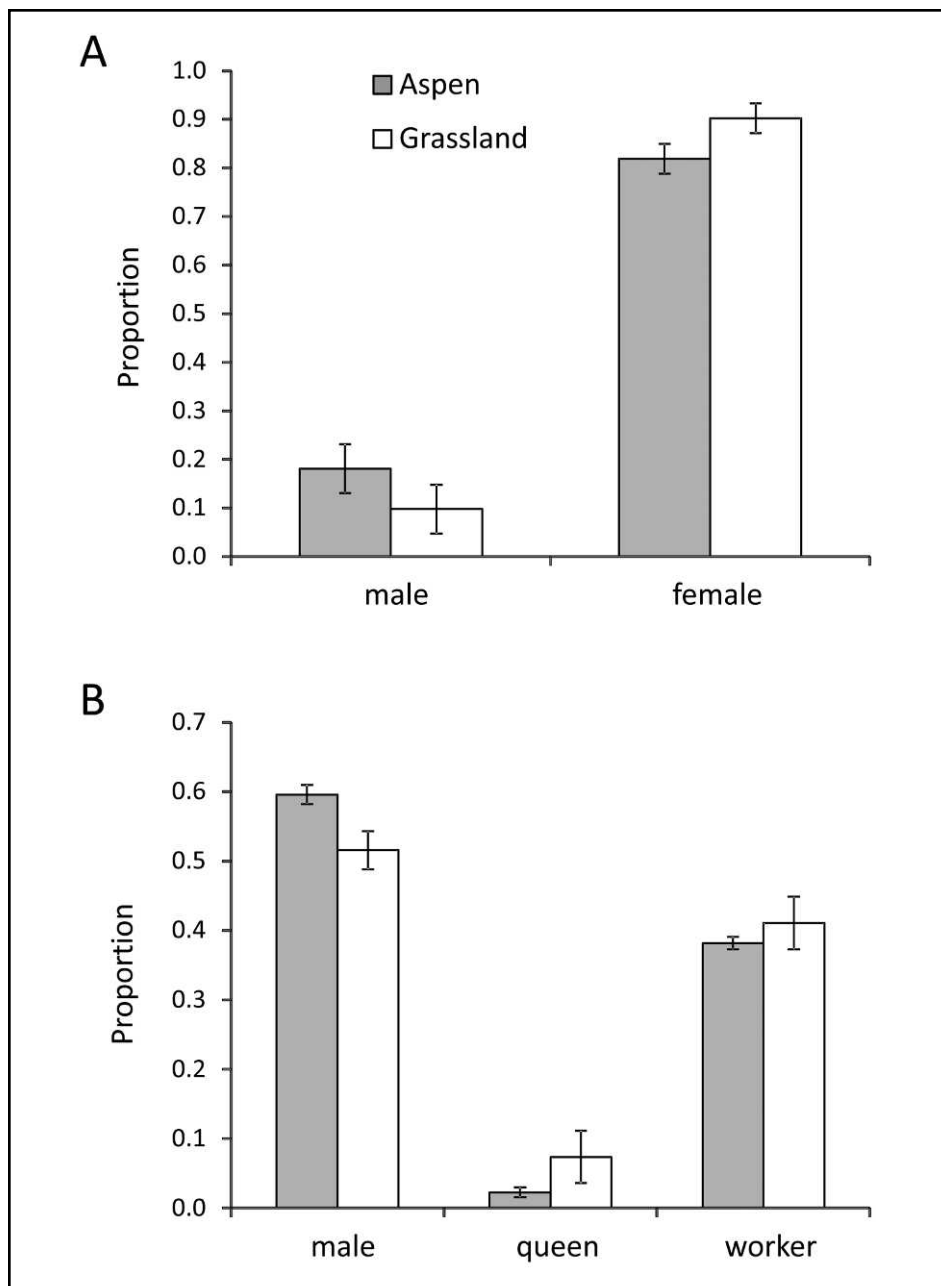


Figure 4. Mean proportion (± 1 SE) of (A) males and females for non-social bees and (B) males, queens, and workers for bumble bees in the Zumwalt Prairie Preserve of northeastern Oregon.

patrolling and scent-marking were more abundant in aspen than in grassland sites on the Zumwalt Prairie (Table 3).

One of the aspen stands we sampled in our study was fenced to prevent herbivory by cattle, elk, and deer. Although not a major focus of our study, we did not find obvious differences in the abundance or community composition of pollinators between this one fenced stand and the unfenced aspen stands. Both contained similarly high numbers of blooming forb

and shrub species, and community composition did not differ strongly. Although understory vegetation in aspen stands can be reduced by ungulate herbivory (Kay and Bartos 2000), unpalatable forbs and native grasses are left to grow and these may provide sufficient food resources for *Bombus*. However, fencing is one management action that can increase the quantity of aspen habitat, which our study suggests is beneficial for some native bees. Future research should be conducted to further

investigate whether fencing aspen stands also improves the quality of aspen stands for native bees.

CONCLUSION

The preservation of remnant aspen stands is crucial not only because of the benefit of this habitat to vertebrates, but also because it appears to sustain a diverse and abundant bee fauna by providing important habitat and floral resources for certain species of bumble bees that are not available in other nearby habitats, at least in late summer. Whether bumble bees are exploiting aspen habitat only during certain times for foraging and mating resources, or whether they are actually nesting at higher densities in these habitats, is unknown. This question, as well as the relative importance of the life history and mating behavior of each species in explaining these observed patterns, deserves further study. In addition, studies of the importance of aspen stands for other functionally important invertebrates are needed. These types of studies are particularly pressing given the precipitous loss of aspen due to sudden aspen decline; a more thorough understanding of the ecological function aspen currently fulfill is necessary to better understand the consequences of losing this function in the face of future declines.

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Table 4. Results of indicator species analyses of non-anemophilous blooming forbs and shrubs associated with aspen and grassland habitats in June, July, and August. All listed species had an indicator value of 100 and $p < 0.04$.

Aspen Indicator Species	June	July	Aug
Nettleleaf giant hyssop - <i>Agastache urticifolia</i> (Benth.) Kuntze	x	x	x
White spirea - <i>Spiraea betulifolia</i> Pall.	x		
Northern bedstraw - <i>Galium boreale</i> L.		x	
Canada goldenrod - <i>Solidago canadensis</i> L.		x	x
Common snowberry - <i>Symphoricarpos albus</i> (L.) S.F. Blake		x	x
Grassland Indicator Species	June	July	Aug
Spring draba - <i>Draba verna</i> L.	x		
Sheldon's milkvetch - <i>Astragalus sheldonii</i> (Rydb.) Barneby	x		
Nineleaf biscuitroot - <i>Lomatium triternatum</i> (Pursh) J.M. Coult. & Rose	x		
Sagebrush mariposa lily - <i>Calochortus macrocarpus</i> Douglas		x	

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