

Short-term responses of native bees to livestock and implications for managing ecosystem services in grasslands

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Abstract. Rangelands are significant providers of ecosystem services in agroecosystems world-wide. Yet few studies have investigated how different intensities of livestock grazing impact one important provider of these ecosystem services—native bees. We conducted the first large-scale manipulative study on the effect of a gradient of livestock grazing intensities on native bees in 16 40-ha pastures in the Pacific Northwest Bunchgrass Prairie. Each pasture was exposed to one of four cattle stocking rates for two years and grazing intensity was quantified by measuring utilization. We measured soil and vegetation characteristics related to floral and nesting resources as well as several metrics of the bee community. Increased grazing intensity significantly reduced vegetation structure, soil stability, and herbaceous litter and significantly increased soil compaction and bare ground. Native bees responded with changes in abundance, richness, diversity, and community composition. Responses varied with taxa and time of season. Bumble bees were sensitive to grazing intensity early in the season, showing reduced abundance, diversity, and/or richness with increased intensity, potentially because of altered foraging behavior. In contrast, sweat bees appeared unaffected by grazing. These results show that native bee taxa vary in their sensitivity to livestock grazing practices and suggest that grazing may potentially be a useful tool for managing pollination services in mosaic agroecosystems that include rangelands.

Key words: bumble bees; floral resources; grazing intensity; livestock grazing; native bees; nesting resources; Pacific Northwest Bunchgrass Prairie; pollinators; soil characteristics; sweat bees; vegetation characteristics.

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INTRODUCTION

Sustainable land management practices in agroecosystems involve balancing multiple eco-

system services, such as provisioning (e.g., food production) and supporting services (e.g., food webs, pollination, decomposition) (MEA 2005). An added complication of managing agroeco-

systems occurs when influences from one habitat affect the availability of ecosystem services in another. This is particularly likely for “mobile agent-based ecosystem services” or MABES, which are ecosystem services provided by organisms that depend on habitats that are spatially or temporally segregated from the location where services are delivered (Kremen et al. 2007). MABES play major roles in most agroecosystems, which are often landscape mosaics of agricultural production areas (e.g., croplands, rangelands) embedded in a matrix of non-cultivated lands (e.g., riparian areas, field margins) (Forman 1995). Currently, little information is available to inform producers and rangeland managers about potential consequences and opportunities of different management practices on MABES.

Pollination represents one of the most significant MABES provided in both agroecosystems and natural habitats (Ollerton et al. 2011). Bees play a particularly crucial role, pollinating over 75% of flowering plant species, including crops that make up 35% of the world’s food supply (NRC 2007). The fitness of many cross-pollinated, non-cultivated plants depends on bee pollination and even plants capable of self-pollination may benefit from pollinators through higher seed set and a reduction in inbreeding depression (Michener 2007). With concerns over a global pollinator crisis (Potts et al. 2010), research in this area is critical. Factors implicated in the decline of native bees include exposure to parasites and pathogens, the overuse of insecticides, the introduction of non-native species, such as the honey bee, *Apis mellifera*, and habitat destruction and degradation associated with human activities, such as agriculture (Thomson 2004, Winfree et al. 2009, Potts et al. 2010).

Although much work has centered on understanding how management of cropped systems affects pollination services provided by bees (Klein et al. 2007, Kremen et al. 2007), relatively little attention has focused on another widespread agricultural production system: rangelands (Black et al. 2011). This is true despite the fact that livestock grazing is the most common use of grasslands world-wide (White et al. 2000). Many of these grasslands, including those in western North America, support a diverse and abundant bee fauna (Kimoto et al. 2012).

Livestock grazing may impact native bees through its effect on plant growth, architecture, diversity, and quality, as well as soil characteristics and microhabitat temperature and relative humidity (Kruess and Tscharntke 2002, DeBano 2006 *a,b*, Black et al. 2011). Several studies of livestock grazing and native bees have found significant effects, some negative (e.g., Kruess and Tscharntke 2002, Hatfield and LeBuhn 2007, Sjödin 2007, Xie et al. 2008, Kearns and Oliveras 2009) and some positive (e.g., Carvell 2002, Vulliamy et al. 2006, Yoshihara et al. 2008). Whether livestock grazing has a positive or negative effect on bee communities may depend upon various factors including the species composition of the community, the intensity of grazing, the types of grazers (e.g., cattle, goat, sheep), how long grazing has occurred, land use history, and habitat type. However, previous work on native bees suffers from some limitations common in many livestock grazing studies. First, most studies have been observational (i.e., they have not experimentally manipulated grazing level), and thus lack the ability to infer a causal relationship (e.g., Sugden 1985, Carvell 2002, Kruess and Tscharntke 2002, Vulliamy et al. 2006, Hatfield and LeBuhn 2007, Sjödin 2007, Sjödin et al. 2008, Xie et al. 2008, Kearns and Oliveras 2009). Second, many studies have compared only the presence or absence of grazing (e.g., Sugden 1985, Xie et al. 2008), rather than a gradient of grazing intensities. Finally, few studies of livestock grazing effects on native bees have been conducted in North America (Sugden 1985, Hatfield and LeBuhn 2007, Kearns and Oliveras 2009). Thus, we have little information on how grazing impacts native pollinators of grassland types that form the majority of U.S. rangelands or how to develop sustainable livestock management plans that are relevant to U.S. producers.

Here, we describe the first large-scale, manipulative study examining how native bees, a significant provider of MABES, respond to short-term exposure to a gradient of cattle grazing intensity in a native grassland of North America. The specific objectives of this study were (1) to document grazing-induced changes in environmental variables hypothesized to influence bee communities and (2) to describe associated responses in native bee abundance,

richness, diversity, and community composition to the grazing gradient.

MATERIALS AND METHODS

Study area

We conducted the study within The Nature Conservancy's (TNC) 13,269 ha Zumwalt Prairie Preserve (latitude 45°34' N, longitude 116°58' W) in Wallowa County of northeastern Oregon, USA (Fig. 1A). Located at an elevation of 1,100–1,700 m, the Preserve receives a mean annual precipitation of 43.3 cm/yr, and has an average maximum temperature of 26.9°C in August and an average minimum temperature of –7.9°C in December (30-year average, 1971–2000, at Joseph, OR, NOAA 2010). Although the Zumwalt Prairie has been used as summer pasture for horse, sheep, and cattle for over 100 years, the majority of the area remains dominated by native species including Idaho fescue (*Festuca idahoensis*), prairie Junegrass (*Koeleria macrantha*), and bluebunch wheatgrass (*Pseudoroegneria spicata*) (Kennedy et al. 2009, Bartuszevige et al. 2012). In addition, a rich forb community (>112 species of forbs) is associated with a diverse bee community (>200 species in 27 genera), with the most common genera being sweat bees of the genus *Lasioglossum* (Halictidae) and bumble bees (*Bombus*: Apidae) (Kimoto et al. 2012).

Study design

The study was designed as a large-scale manipulation of four stocking rates: high (24 cow-calf pairs), medium (16 cow-calf pairs), low (8 cow-calf pairs), and no cattle. The moderate grazing treatment was designed to reflect prevailing stocking rates in the region. Treatments were randomly assigned to 16 40-ha pastures on a plateau in the center of the Preserve in a randomized complete block design (Fig. 1B) and applied for two summers. Cattle grazed from 20 May to 2 July in 2007 and 28 May to 8 July in 2008 (Fig. 2A, B).

Utilization, or the percent of aboveground biomass removed by grazers, was estimated each year within a week after cattle were removed from all 16 pastures to quantify the intensity of grazing resulting from stocking rates. The same stocking rate may result in different grazing pressure because of differences in grassland

condition, cow behavior and physiology, and micro-distribution of resources in a pasture (Allison 1985). Utilization was quantified using ocular estimation in 0.5 m² (1 m × 0.5 m) areas at 36 uniformly spaced subplots in each of the 16 pastures (for a total of 576 subplots; Fig. 1B) (Wyffels 2009). Observers were trained to recognize five utilization categories: (1) 0% use, (2) 1–25% use, (3) 26–50% use, (4) 51–75% use and (5) 76–100% use. Before collecting data in the field, each observer estimated the utilization in ten 0.25 m² test plots that had been clipped at various levels. Then, the remaining vegetation of the test plots was clipped to within 2 cm of ground level and weighed to determine actual utilization values. Regression equations of estimated versus actual utilization values were developed for each observer to correct for observer bias (Wyffels 2009).

Environmental variable measurement

To evaluate changes in vegetation physical structure occurring during the experiment, estimates of visual obstruction were obtained in 2007 and 2008 using the Robel method (detailed in Johnson et al. 2011). Vegetation height was measured at 10 m intervals along eight randomly placed 100 m transects within each pasture within 24 hours after cattle were removed.

Post-treatment soil characteristics, including surface coverage, compaction, and surface soil stability, were measured at each of the 36 uniformly spaced subplots in each of the 16 pastures. Percent bare ground and soil surface coverage of herbaceous litter were measured in July 2009 in 0.5 m² at each subplot (methods detailed in Damiran et al. 2007) and compaction and surface soil stability were measured in August and September 2008. Soil compaction was measured up to a depth of 2 cm with a dynamic cone penetrometer using a 2-kg hammer dropped from a height of 60 cm (Herrick and Jones 2002). Surface soil stability was measured at 0–3 mm depth using a modified slake test (Herrick et al. 2001). Soil stability data are presented on a scale of 1–6, with 6 being the most stable and 1 being the least stable (detailed in Schmalz 2011).

Pollinator sampling

We sampled pollinators during the summers of

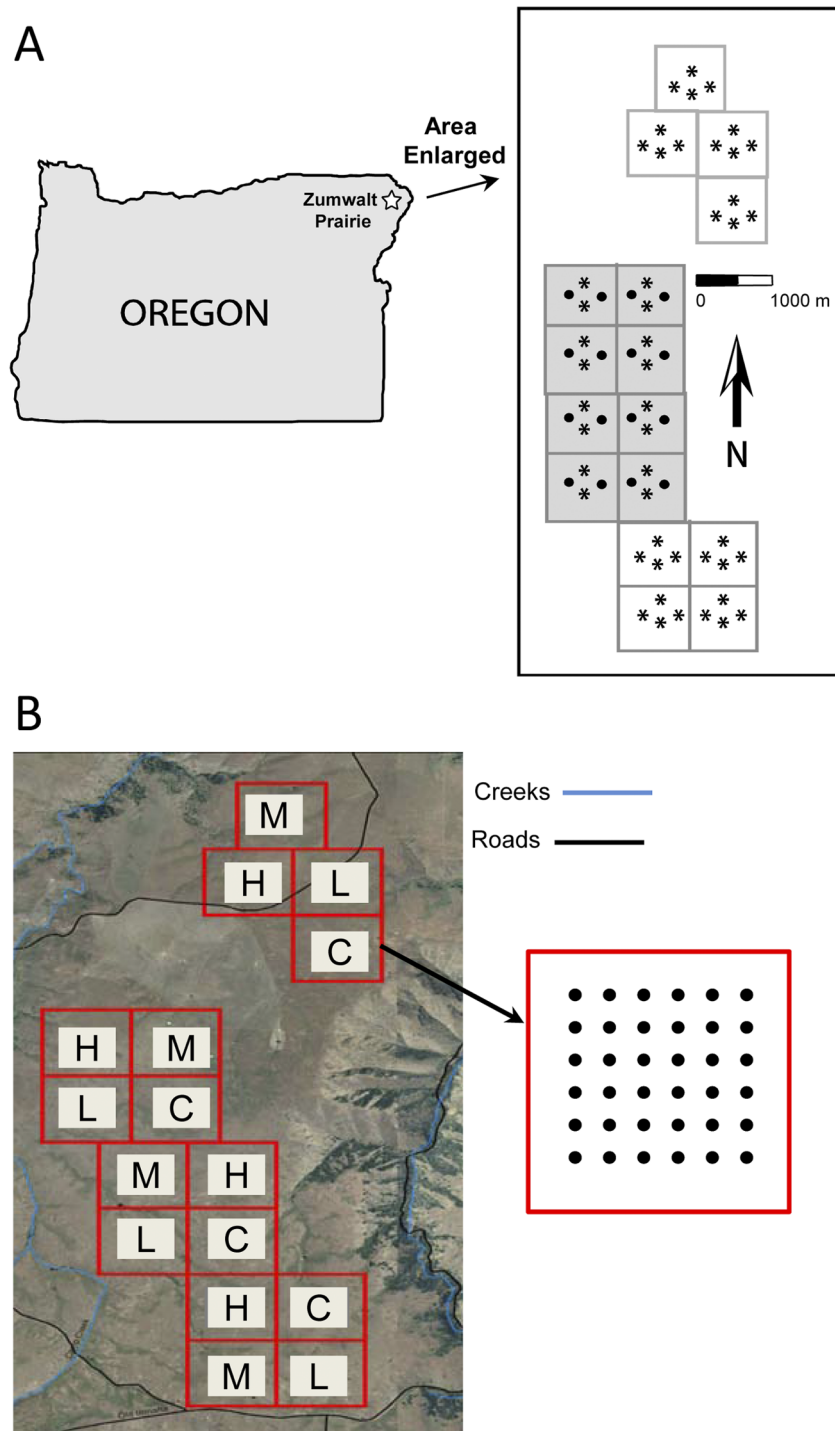


Fig. 1. (A) Location of the Zumwalt Prairie in northeastern Oregon and location of pollinator traps in each pasture (all sites were sampled in each season of each year except that unshaded pastures and traps denoted with “*” were not sampled in June 2007), and (B) map showing stocking levels for each 40 ha pasture (H-high, M-medium, L-low, C-control) and a close-up view of the 36 subplots in each pasture, where vegetation and soil characteristics were sampled.

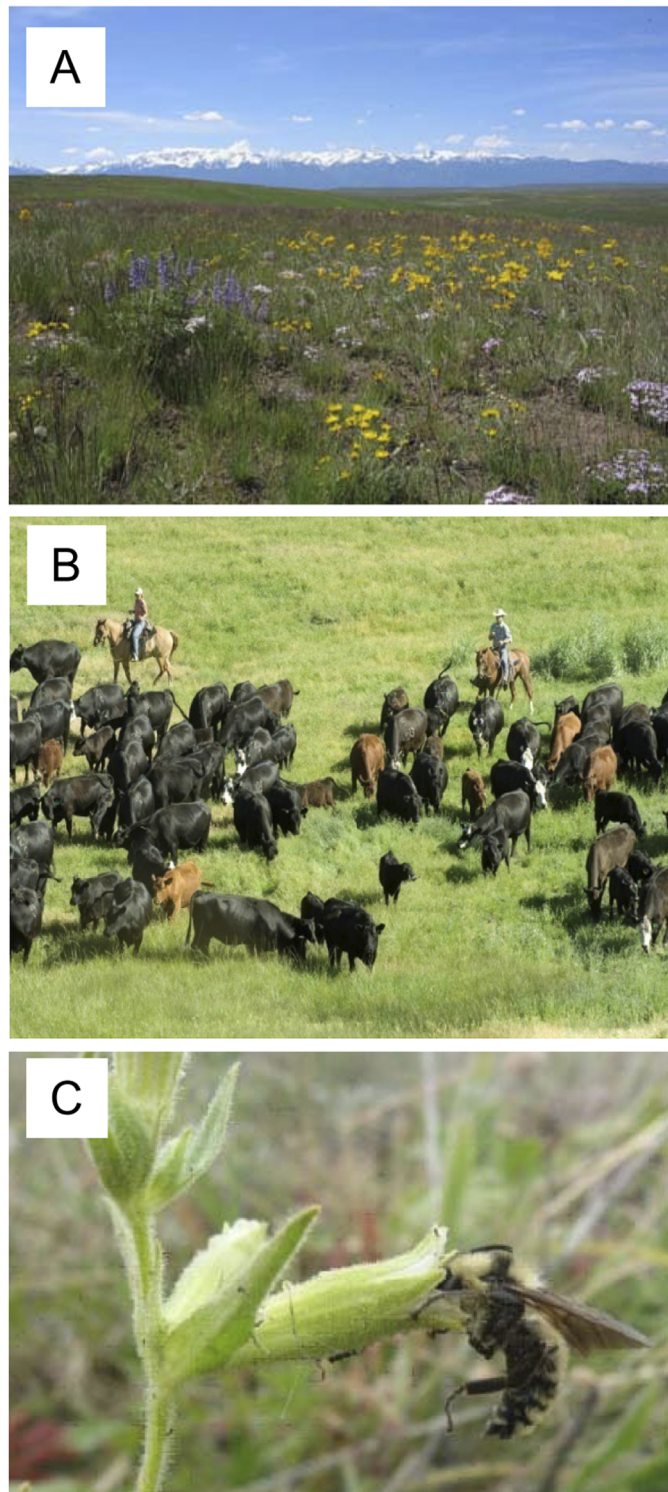


Fig. 2. (A) Study sites in June, (B) application of the grazing treatment (photograph by L. Ketchum), and (C) a bumble bee visiting Spalding's catchfly, a threatened species in the Pacific Northwest Bunchgrass Prairie (photograph by C. Strohm).

2007 and 2008 using ultra-violet reflective blue vane traps (Stephen and Rao 2005). Blue vane traps consist of a plastic container (15 cm diameter \times 15 cm high) with a blue polypropylene screw funnel with two 24 \times 13 cm semi-transparent blue polypropylene cross vanes of 3 mm thickness (SpringStar, Woodinville, WA, USA) (Stephen and Rao 2005). Traps were suspended approximately 1.2 m from the ground with wire hangers inserted into aluminum pipes. No liquids or other killing agents were used in traps. We used blue vane traps because they provided a number of advantages in sampling expansive grassland habitats over other commonly used methods, such as hand-netting and pan-trapping (detailed in Kimoto et al. 2012). Advantages include the fact that relatively few traps are needed to collect large numbers of bees, traps are easy to work with in field conditions and are highly selective for bees, and their effectiveness is not affected by the experience and capabilities of the sampler (Westphal et al. 2008). Traps were placed in each of the cardinal directions halfway between the center of the pasture and the perimeter, resulting in four traps per pasture, except for June 2007, when only two traps were used per pasture. Traps within each pasture were separated by approximately 200 m from their nearest neighbor and were 360 m or more from traps in neighboring pastures (Fig. 1A).

Pollinators were sampled during two bouts in 2007 (18–20 June and 9–21 July) and three bouts in 2008 (7–16 June, 10–18 July, and 25–29 August). In June 2007 we sampled using 16 blue vane traps in 8 pastures; for all other sampling bouts we used 64 traps in 16 pastures (Fig. 1A). Elevation of traps ranged from 1,372 to 1,499 m. In 2007, traps were left open for two consecutive days each bout and, because of high efficiency demonstrated in the first year, in 2008 they were left open for one day each bout. Bees collected in the traps were frozen, then pinned, labeled, sexed, and identified to species or morphospecies. Representative specimens of all species and morphospecies are vouchered at the Oregon State Arthropod Collection at Oregon State University in Corvallis. Abundances are expressed as the number of bees collected per trap per hour of daylight.

Statistical analyses

Although the manipulation was designed as a randomized complete block design, quantification of grazing intensity using utilization showed that treatment effects displayed a continuous distribution rather than a categorical one (Fig. 3). Therefore, we used linear regression analysis to determine how grazing intensity, as measured by utilization, affected (1) environmental variables hypothesized to influence bees and (2) native bee communities. Environmental variables regressed against utilization included vegetation physical structure in 2007 and 2008, percent bare ground and herbaceous litter, compaction, and surface soil stability. For bee communities, we regressed utilization against abundance, species richness, Shannon diversity, and community composition. We examined abundance and species richness of all bees, and the two most common genera, *Bombus* and *Lassioglossum*. Shannon diversity indices were calculated for all bees and *Bombus*. In addition, bee community composition was characterized with non-metric multidimensional scaling (NMS) ordination using the abundance of taxa and Sorenson'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 species abundance and ordination axes results (McCune and Mefford 2006). NMS scores for each pasture were used as dependent variables in regression analyses.

Because pasture was our experimental unit, all variables used in regressions were averaged for each pasture. For all environmental variables and most bee variables, 16 pastures were used. The only exception with regard to bees was June 2007, when 5 pastures were used because traps in 3 of the 8 pastures sampled were disturbed, and June 2008, when 14 pastures were used because traps in 2 pastures were disturbed. We tested variables for normality using Lillefors' test and log transformed, if non-normal. Year-specific utilization was used for all regressions involving bee and vegetation dependent variables, and averaged utilization of 2007 and 2008 was used in regressions for soil characteristics that were measured once at the end of the experiment. Each sampling month of each year was analyzed

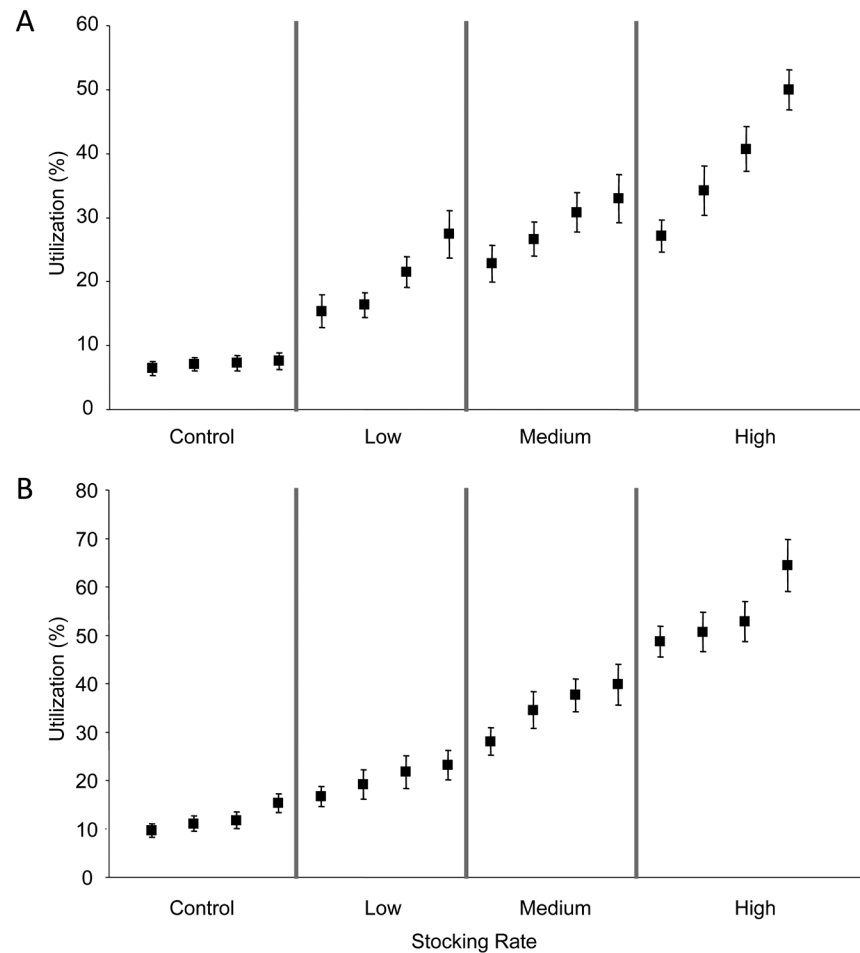


Fig. 3. Average utilization in (A) 2007 and (B) 2008 in each 40 ha pasture exposed to four stocking rates (high, medium, low, and control).

separately because bees in this area show substantial temporal variability in abundance, richness and community composition both among months and between years (Kimoto et al. 2012). SYSTAT (1997) Version 7.0 was used for linear regression analyses and PC-ORD, version 5.19 (McCune and Mefford 2006) was used for calculating diversity indices and for ordinations.

RESULTS

Effect of grazing intensity on environmental variables

Vegetation structure decreased significantly as grazing intensity increased in 2007 and 2008 (Fig. 4A; $r^2 = 0.71$, $P < 0.01$; $r^2 = 0.64$, $P < 0.01$, respectively). After two years exposure to the

treatment, grazing intensity significantly increased soil compaction (Fig. 4B; $r^2 = 0.80$, $P < 0.001$) and significantly decreased surface soil stability (Fig. 4C; $r^2 = 0.34$, $P = 0.01$). Grazing intensity also significantly increased the percent of bare ground (Fig. 4D; $r^2 = 0.40$, $P < 0.01$) and decreased the percent of ground covered by herbaceous litter (Fig. 4E; $r^2 = 0.41$, $P < 0.01$).

Effect of grazing intensity on bee abundance, richness and diversity

A total of 9,158 bees were collected throughout the study. Total bee abundance was not significantly affected by grazing intensity for any season (Table 1). In June, bumble bees (*Bombus*) and sweat bees in the genus *Lasioglossum*, the most common genera, showed similar patterns

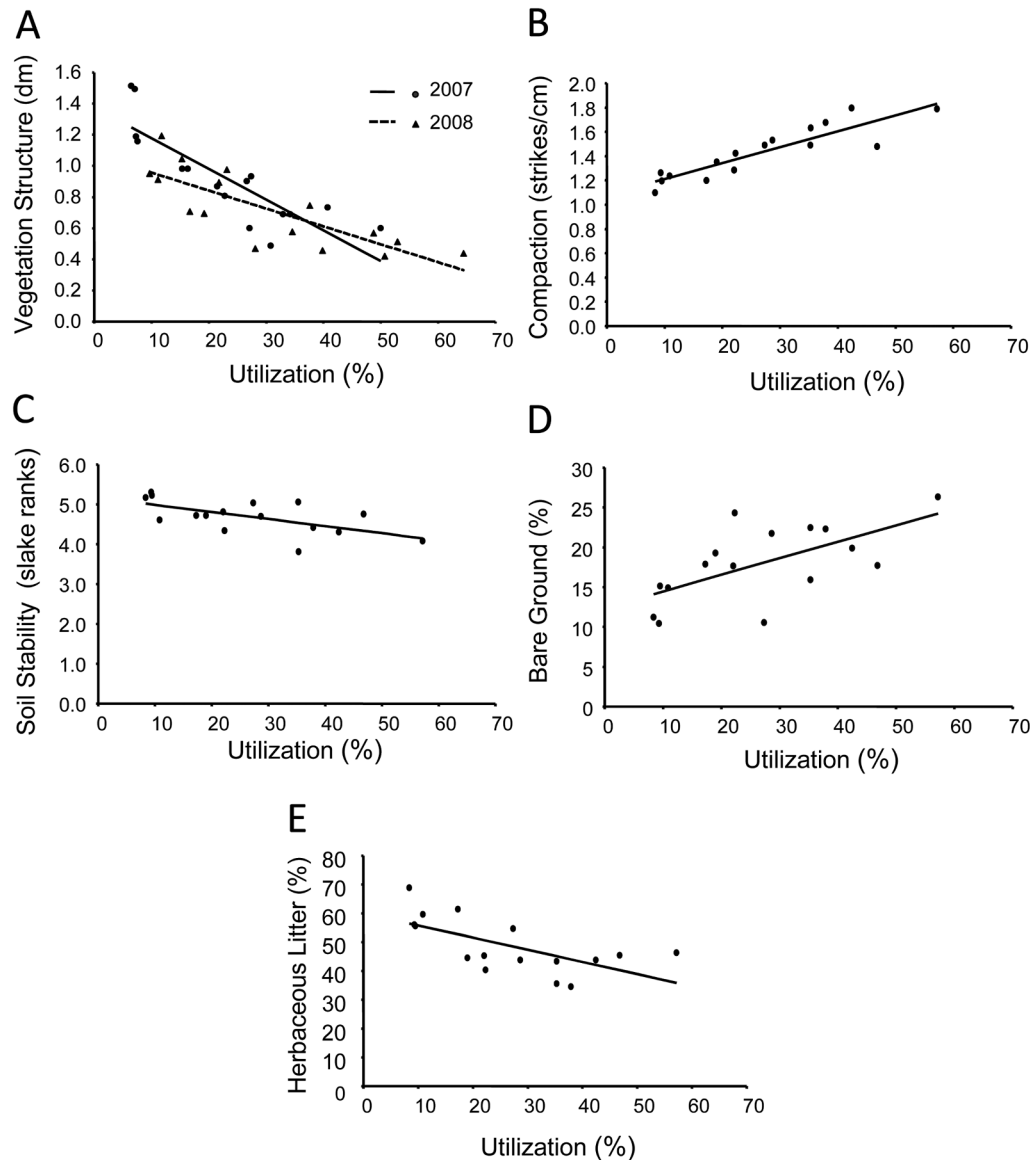


Fig. 4. Effect of grazing intensity on (A) vegetation physical structure in 2007 and 2008, (B) soil compaction, (C) surface soil stability, (D) percent bare ground, and (E) percent herbaceous litter.

both years. Specifically grazing intensity had a significant negative effect on *Bombus* abundance (2007: $r^2 = 0.85$, $P = 0.03$; 2008: $r^2 = 0.40$, $P = 0.02$; Fig. 5 A, B) but no effect on *Lasioglossum* abundance (Table 1). In July of both years and August 2008, there were no statistically significant relationships of abundance of these two common genera with grazing intensity (Table 1).

For both years combined, 91 species and 118 morphospecies in 27 genera were identified

(Appendix). Total species richness did not differ significantly with grazing intensity in any season (Table 1). The patterns in taxa richness of the two most common genera were similar to those shown in abundance of both years, with *Bombus* richness decreasing with increased grazing intensity in June, although this effect was only statistically significant in 2008 (2007: $r^2 = 0.37$, $P = 0.27$, 2008: $r^2 = 0.32$, $P = 0.04$; Fig. 5C). There was no statistically significant effect of grazing

Table 1. Results of linear regression models of abundance and richness with utilization for all bees and the two most common genera for each time period.

Time period	Bee taxa	Abundance (no. bees/trap/h)			Richness		
		Relative abundance (%)†	r^2	P	Total no. species‡	r^2	P
June 2007	All bees	N/A	0.27	0.37	54	0.64	0.10
	<i>Bombus</i>	20	0.85	0.03	9	0.37	0.27
	<i>Lasioglossum</i>	49	0.05	0.72	19	0.21	0.44
July 2007	All bees	N/A	0.22	0.07	183	0.14	0.15
	<i>Bombus</i>	33	0.09	0.26	14	0.13	0.18
	<i>Lasioglossum</i>	34	0.04	0.44	45	0.05	0.43
June 2008	All bees	N/A	0.02	0.65	58	0.02	0.63
	<i>Bombus</i>	15	0.40	0.02	9	0.32	0.04
	<i>Lasioglossum</i>	58	0.003	0.86	18	0.01	0.72
July 2008	All bees	N/A	0.03	0.51	92	0.001	0.93
	<i>Bombus</i>	22	0.06	0.37	10	0.001	0.91
	<i>Lasioglossum</i>	35	0.02	0.61	35	0.03	0.53
August 2008	All bees	N/A	0.01	0.76	51	0.00	0.95
	<i>Bombus</i>	13	0.003	0.83	10	0.00	0.98
	<i>Lasioglossum</i>	43	0.02	0.65	26	0.01	0.68

†Relative abundance is presented for the two most common genera, and is simply the percentage of all bees that belonged to each genus. “N/A” indicates “not applicable.”

‡Total no. species is the number of species detected in all pastures during the sampling period.

intensity on *Lasioglossum* richness (Table 1).

Shannon diversity of all bees decreased in response to increased grazing intensity in June, although only significantly in 2007 (2007: $r^2 = 0.81$, $P = 0.04$; 2008: $r^2 = 0.26$, $P = 0.07$; Fig. 5D). Likewise, for *Bombus*, grazing intensity decreased diversity in June although only significantly in 2008 (2007: $r^2 = 0.34$, $P = 0.30$; 2008: $r^2 = 0.33$, $P = 0.05$; Fig. 5E). Diversity in all bees and bumble bees in other time periods did not show statistically significant responses (July 2007: $r^2 = 0.01$, $P = 0.76$ for all bees and $r^2 = 0.01$, $P = 0.72$ for bumble bees; July 2008: $r^2 = 0.23$, $P = 0.06$ for all bees and $r^2 = 0.12$, $P = 0.19$ for bumble bees; August 2008: $r^2 = 0.00$, $P = 0.97$ for all bees and $r^2 = 0.002$, $P = 0.87$ for bumble bees).

Effect of grazing intensity on community composition

Ordination results revealed that bee community composition during most seasons varied among pastures, with 1–3 dimensional solutions that explained 59–94% of the variation in bee community composition (Table 2). In June 2008, one axis was significantly affected by grazing intensity ($r^2 = 0.43$, $P = 0.02$; Fig. 5F). This axis, which explained 37% of the variation in community composition, was significantly correlated ($P < 0.05$) with four taxa. Two of these taxa were positively associated with the axis and thus negatively impacted by grazing intensity

(*Bombus californicus*, $r = 0.78$ and *Osmia* morphospecies 1, $r = 0.58$) and two were negatively impacted (*Andrena* morphospecies 1, $r = -0.72$ and *Andrena* morphospecies 12, $r = -0.56$). There were no significant effects of grazing intensity on bee community composition in July and August (Table 2).

DISCUSSION

Using a large-scale manipulative experiment we showed that short-term rangeland practices can alter vegetation and soil structure in Pacific Northwest Bunchgrass Prairie, and that these changes can impact a significant group of MABES providers—native bees. Grazing intensity affected a variety of metrics of sampled bee communities including diversity and species composition of the entire community and abundance and species richness of bumble bees. The strength of response varied with taxa and season, with the largest responses associated with bumble bees in June of both years.

Livestock grazing can impact native bees through its effect on food and/or nesting resources (Vázquez and Simberloff 2004, Black et al. 2011). Flowering plants provide nectar and pollen resources to specialist and generalist bees alike, plant material is used in nest construction, and the physical structure of plants plays a role

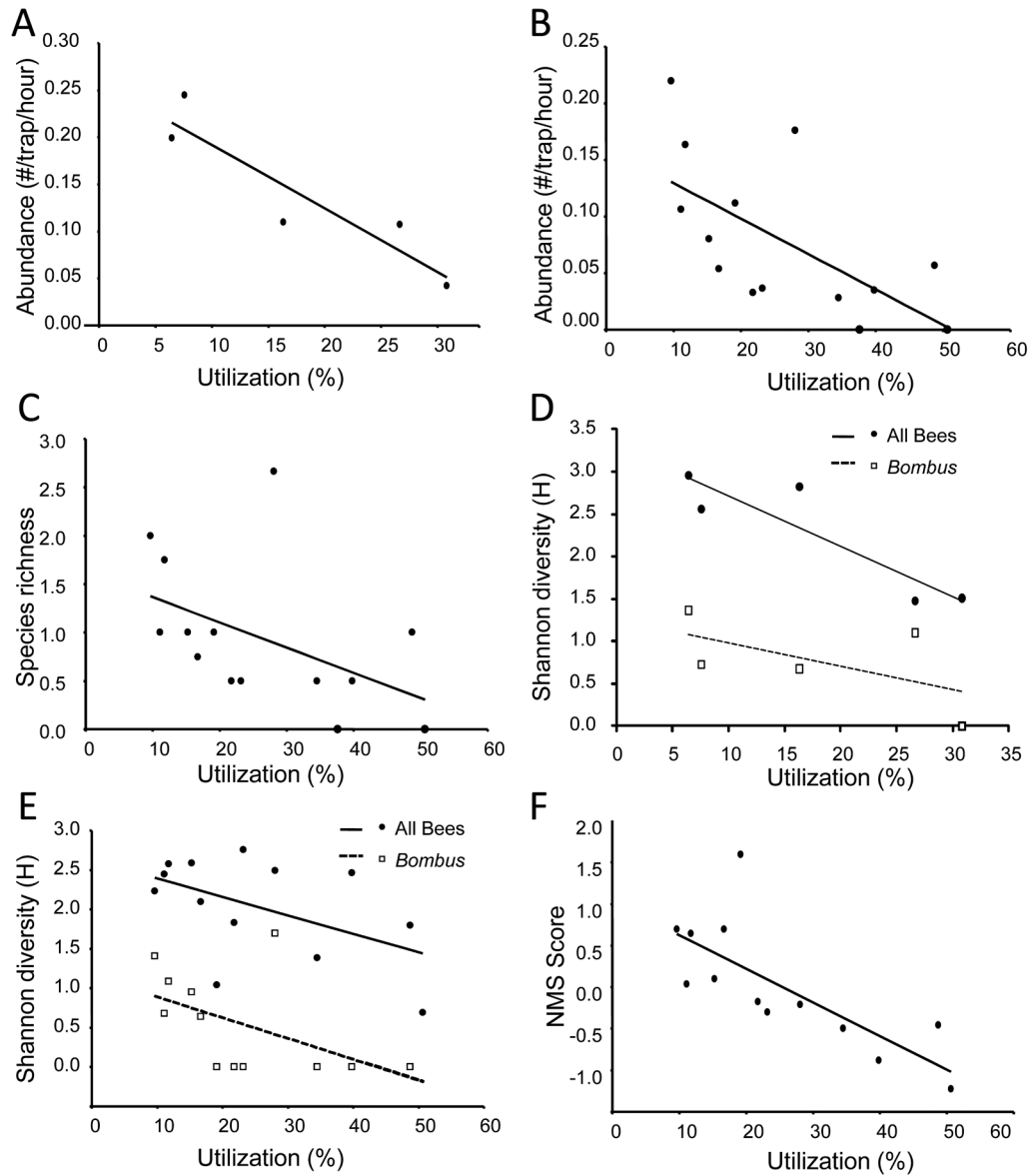


Fig. 5. Effect of grazing intensity on (A) *Bombus* abundance in June 2007, (B) *Bombus* abundance in June 2008, (C) *Bombus* species richness in June 2008, (D) diversity index of all bees and *Bombus* in June 2007, (E) diversity index of all bees and *Bombus* in June 2008, and (F) NMS scores for ordination axis 2 for all bees in June 2008.

for some bees that build above-ground nests (Black et al. 2011). Likewise, soil characteristics affect ground-nesting bees, which may prefer different levels of soil compaction, bare ground, and stability (Cane 1991, Potts and Willmer 1997, 1998). Because grazing intensity had strong and similar effects on all environmental variables measured in this study (i.e., were highly correlated), we were unable to partition out which variable or combination of variables were most

important in driving observed changes in bumble bee abundance and richness. However, the fact that responses were detected in June of the first year (before soil responses likely occurred) suggests that the removal of floral resources by grazing cattle is a major driver.

Several studies have suggested that livestock effects on floral resources should be particularly important to bumble bees (Carvell 2002, Hatfield and LeBuhn 2007, Sjödin 2007, Xie et al. 2008).

Table 2. Results of linear regression models of community composition with utilization. July 2007 and June 2008 had a two axis NMS solution, July 2008 had a one axis solution, and August 2008 had a three axis solution. Percent variation explained by each NMS axis is listed. No solution was found for June 2007.

Time period	Axis 1			Axis 2			Axis 3		
	Variation explained (%)	r^2	P	Variation explained (%)	r^2	P	Variation explained (%)	r^2	P
July 2007	7	0.02	0.58	87	0.02	0.66
June 2008	49	0.15	0.19	37	0.43	0.02
July 2008	59	0.05	0.40
August 2008	23	0.02	0.60	13	0.05	0.39	51	0.002	0.88

Because bumble bees can forage longer distances than smaller bees (Greenleaf et al. 2007) and are able to fly further to access better quality floral resources (Dramstad 1996), the decreased abundance and richness of bumble bees associated with increased grazing intensity in our study may be caused by females shifting their foraging activities to areas with abundant floral resources (i.e., areas with fewer livestock). The importance of floral resources in driving bumble bee responses in this system is further supported by the fact that differences were not observed later in the season, after grazing was discontinued.

In contrast to bumble bees, *Lasioglossum*, a genus with smaller bodied bees with shorter flight distances, did not appear to be sensitive to livestock grazing in this study. This may be because individuals may not be able to fly long distances to take advantage of higher floral resource availability in adjacent ungrazed areas (Gathmann and Tschardt 2002, Sjödin 2007). In addition, this group may be positively affected by changes in soil compaction and stability associated with higher grazing intensity; previous work suggests that sweat bees prefer nesting sites with bare ground and compacted soils (Potts and Willmer 1997, 1998). The only study conducted on the effect of grazing on this group that we are aware of showed a strong positive response to grazing intensity (Vulliamy et al. 2006).

Our study showed that responses to grazing intensity were not only apparent at the genus level. Ordination results showed several species contributed to the overall change in bee community composition in June 2008. Several species were negatively affected by grazing intensity, including one bumble bee species, *B. californicus*,

which made up 5% of the entire native bee fauna. This contrasts with some other common bumble bee species, such as *B. bifarius*, which showed no response to grazing intensity. The few studies that have examined the effect of grazing intensity on the species composition of bumble bees demonstrated that species responses are varied (Carvell 2002, Sjödin 2007, Sjödin et al. 2008). Differences in sensitivity to grazing may be driven by differences in life history, including morphology associated with foraging strategy (e.g., tongue length) and different requirements for nesting (Goulson 2010). Other factors that may play a role include how grazing affects the floral resources a particular species uses, whether the bee is a specialist or generalist, the type of grazing regime, the habitat and its evolutionary history, the season of the year, and the type of grazer.

Like *B. californicus*, one *Osmia* morphospecies also made a significant contribution to differences in bee community composition in June 2008, showing decreased abundance with increased grazing intensity. In general, *Osmia* species are generalist feeders and most nest in cavities in pithy stems and wood, including abandoned beetle burrows, in crevices under or between stones, in the soil, and even in empty snail shells (Cane et al. 2007, Michener 2007). In our study, 62% of the *Osmia* collected are believed to nest in the soil, on the surface of the soil, or on sides of rocks (Cane et al. 2007). These nests may be disturbed by direct trampling, or decreasing soil stability and compacting soils may lead to the filling in of cavities used for nesting. Unfortunately, we are aware of no other studies of livestock grazing intensity on species in this genus.

In contrast to species negatively affected by grazing intensity are two *Andrena* morphospecies that made a significant contribution to bee community composition differences in June 2008 by showing an increased abundance with grazing intensity. The reasons for this response are unclear. Most species of *Andrena* are generalist feeders, although some are specialists, and all are ground nesters (Michener 2007). The few studies that have examined the effect of grazing on this genus have shown variable responses. Vulliamy et al. (2006) found no correlation between abundance of Andrenidae and grazing intensity, while Sjödin et al. (2008) found four species of *Andrena* were more dominant in semi-natural grasslands exposed to low intensity grazing in Sweden and two species were more dominant in grasslands exposed to intensive grazing. More research is needed to understand the factors responsible for the variation in response in this important group of early season bees.

The community level responses found in this study also have implications for basic ecological theory related to the intermediate disturbance hypothesis. The intermediate disturbance hypothesis predicts that moderate grazing will reduce the dominance of competitive plant species, such as some grasses, and result in a higher plant species richness as less competitive plants, like some forbs, increase (Curry 1994). In fact, several studies suggest that plant diversity is highest at intermediate grazing (Bowers 1993, Noy-Meir 1995). This increased plant richness may result in higher bee richness or diversity (e.g., Potts et al. 2003). Thus, the intermediate disturbance hypothesis predicts that the greatest bee diversity should occur at moderate levels of grazing. However, bee diversity did not show “hump-shaped” curves relative to grazing intensity. Instead, the relationship was generally linear, with the slope of the relationship varying by season. Patterns in diversity of bumble bees also did not support the intermediate disturbance hypothesis; moderate grazing intensities were not associated with the highest bumble bee diversity or richness. In June 2008, grazing intensity negatively affected bumble bee diversity.

Our results relative to the intermediate disturbance hypothesis are difficult to compare with

other studies because most do not report diversity indices. Diversity indices that incorporate both richness and evenness, such as the Shannon diversity index used here, provide the best test of the intermediate disturbance hypothesis because both richness and evenness are hypothesized to change under the paradigm. Examining just species richness is less than ideal because as systems move from low to moderate disturbance, strongly competitive species (e.g., *k*-selected species) that dominate the community are predicted to lose their competitive edge and decline in abundance. This may result in the competitive release of other species, which may increase in abundance. Under this scenario, changes in evenness may be more pronounced than changes in species richness.

Only one study on the effect of livestock grazing on native bee communities examined diversity indices. In contrast to our results, Kearns and Oliveras (2009) found some support for the intermediate disturbance hypothesis in grasslands of Colorado, where bee diversity was positively correlated with flowering richness, and flowering richness was highest in plots with intermediate grazing disturbance. Other authors have used species richness to test the intermediate disturbance hypothesis, and like us, did not find support for it (e.g., Vulliamy et al. 2006, Xie et al. 2008). Variation in habitat type (e.g., forest, grasslands) and its evolutionary history with native ungulates may be key in explaining these different findings (Vulliamy et al. 2006). In our case, we may not see responses expected under the intermediate disturbance hypothesis because of the fact the Pacific Northwest Bunchgrass Prairie is not believed to have evolved in the presence of large herds of native ungulates.

Management implications

Grazing is an important component of rural economies, and as such, will continue on both private and public land in the United States (Knight et al. 2002). The management of organisms providing MABES in rangelands is presumably a powerful tool for increasing ecosystem service production within those habitats and in adjacent habitats (Chaplin-Kramer et al. 2011). Our results show that bumble bees are less abundant and species-rich in areas actively grazed by livestock, potentially because these

pollinators forage in other areas with more abundant floral resources. These results have several implications for pollinator management in agroecosystems. First, cattle grazing should be managed carefully in areas where sensitive, bumble bee-pollinated plant species occur, especially during their blooming period (e.g., Spalding's catchfly [*Silene spaldingii*], Fig. 2C). Even if these plants are not fed on by livestock, our study suggests that fewer bumble bees are available for pollination in areas where livestock are actively grazing. This study also supports the assertion that maintaining a heterogeneous landscape, with some areas grazed and other ungrazed, or a rotation of grazing, may be necessary to support native bee diversity (Black et al. 2011). The effect of long-season grazing, especially over multiple years, is less clear. We found increased soil compaction and decreased soil stability with increased grazing intensity over two years, effects that would presumably be magnified with longer season grazing or more years. Although these changes may be detrimental to some bees, such as bumble bees, which often nest in abandoned rodent nests and other soil cavities (Michener 2007), they may be beneficial for other groups that prefer compacted soils (Potts and Willmer 1997, 1998). More research is needed to address this question.

Finally, although our study did not demonstrate that decreases in bumble bee abundance were due to changes in foraging behavior, this possibility suggests the need for research on whether livestock grazing can be a useful tool to enhance pollination services in adjacent lands. For example, if further research verifies that livestock grazing changes bumble bee foraging behavior, rotational grazing at small scales could be used in areas adjacent to known concentrations of sensitive plant species during peak bloom, to increase bumble bee activity in areas containing those species. Similarly, in mosaic agroecosystems, grazing in rangelands adjacent to crop production areas could enhance pollination services for insect-pollinated crops. The potential of enhancing native pollinator efficiency in croplands is particularly important with the decline of honey bees (*A. mellifera*). These possibilities indicate a pressing need to conduct studies that examine pollinator visitation rates and pollination efficiency in areas adjacent to

grazed lands. Finally, this research highlights the need for studies of other MABES provided by rangeland invertebrates, many of which are highly mobile and play significant roles in other ecosystem services, such as decomposition, food web provisioning, and nutrient cycling.

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SUPPLEMENTAL MATERIAL

APPENDIX

Table A1. List of bee taxa found in pastures with four stocking rates: control (no livestock), low (8 cow-calf pairs), medium (16 cow-calf pairs), and high stocking rates (24 cow-calf pairs). Morphospecies are labeled with “sp#” and subgenera are enclosed in parentheses.

Taxa	Control	Low	Medium	High
Family: Colletidae				
Subfamily: Colletinae				
Genus: <i>Colletes</i>				
<i>C. simulans</i>	x	x	x	x
<i>Colletes</i> sp#1		x		
<i>Colletes</i> sp#2		x		
<i>Colletes</i> sp#3	x	x	x	x
Subfamily: Hylaeinae				
Genus: <i>Hylaeus</i>				
<i>Hylaeus</i> sp#1	x	x	x	x
<i>Hylaeus</i> sp#2	x			
<i>Hylaeus</i> sp#3	x	x		x
<i>Hylaeus</i> sp#4		x		
<i>Hylaeus</i> sp#5	x	x	x	x
Family: Andrenidae				
Subfamily: Andreninae				
Genus: <i>Andrena</i>				
<i>Andrena</i> sp#1	x	x	x	x
<i>Andrena</i> sp#2	x	x	x	x
<i>Andrena</i> sp#3	x	x		x
<i>Andrena</i> sp#4		x		
<i>Andrena</i> sp#5	x	x	x	x
<i>Andrena</i> sp#6		x		
<i>Andrena</i> sp#7		x		
<i>Andrena</i> sp#8	x			
<i>Andrena</i> sp#9	x	x		x
<i>Andrena</i> sp#10	x		x	x
<i>Andrena</i> sp#11			x	
<i>Andrena</i> sp#12			x	
Subfamily: Panurginae				
Genus: <i>Perdita</i>				
<i>P. oregonensis</i>	x	x	x	x
Family: Halictidae				
Subfamily: Halictinae				
Genus: <i>Agapostemon</i>				
<i>A. texanus</i>	x	x	x	x
<i>A. virescens</i>	x	x	x	x
Genus: <i>Halictus</i>				
<i>H. confusus</i>	x	x		x
<i>H. farinosus</i>	x	x	x	x
<i>H. ligatus</i>	x	x	x	x
<i>H. rubicundus</i>	x	x	x	x
<i>H. tripartitus</i>	x	x	x	x
<i>Halictus</i> sp#1	x	x	x	
Genus: <i>Lasioglossum</i>				
<i>L. anhypops</i>	x	x	x	x
<i>L. egregium</i>	x	x	x	x
<i>L. olympiae</i>	x	x	x	x
<i>L. pacificum</i>	x	x		
<i>L. rubicundus</i>	x	x		
<i>L. sisymbrii</i>	x	x	x	x
<i>L. titusi</i>	x	x	x	x
<i>Lasioglossum</i> sp#1	x	x		x
<i>Lasioglossum</i> sp#2	x	x	x	x
(<i>Chloralictus</i>) sp#1	x			x
(<i>Chloralictus</i>) sp#2	x		x	x
(<i>Chloralictus</i>) sp#3	x	x	x	x
(<i>Chloralictus</i>) sp#4	x	x	x	x
(<i>Chloralictus</i>) sp#5	x	x	x	x
(<i>Chloralictus</i>) sp#6	x	x	x	x

Table A1. Continued.

Taxa	Control	Low	Medium	High
(<i>Chloralictus</i>) sp#7	x	x	x	x
(<i>Chloralictus</i>) sp#8	x	x	x	x
(<i>Chloralictus</i>) sp#9	x	x	x	x
(<i>Chloralictus</i>) sp#10	x	x	x	x
(<i>Chloralictus</i>) sp#11	x	x	x	x
(<i>Chloralictus</i>) sp#12	x	x	x	x
(<i>Chloralictus</i>) sp#13	x	x	x	x
(<i>Chloralictus</i>) sp#14	x	x	x	x
(<i>Chloralictus</i>) sp#15	x	x	x	x
(<i>Chloralictus</i>) sp#16	x	x	x	x
(<i>Chloralictus</i>) sp#17	x	x	x	x
(<i>Chloralictus</i>) sp#18	x	x	x	x
(<i>Chloralictus</i>) sp#19	x	x	x	x
(<i>Chloralictus</i>) sp#20	x	x	x	x
(<i>Chloralictus</i>) sp#1A	x	x	x	x
(<i>Chloralictus</i>) sp#1B	x	x	x	x
(<i>Chloralictus</i>) sp#3A	x	x	x	x
(<i>Chloralictus</i>) sp#5A	x	x	x	x
(<i>Chloralictus</i>) sp#13A	x	x	x	x
(<i>Chloralictus</i>) sp#11A	x	x	x	x
(<i>Chloralictus</i>) sp#11B	x	x	x	x
(<i>Chloralictus</i>) sp#11C	x	x	x	x
(<i>Chloralictus</i>) sp#7A	x	x	x	x
(<i>Chloralictus</i>) sp#7B	x	x	x	x
(<i>Evylaeus</i>) sp#1	x	x	x	x
(<i>Evylaeus</i>) sp#2	x	x	x	x
(<i>Evylaeus</i>) sp#3	x	x	x	x
(<i>Evylaeus</i>) sp#4	x	x	x	x
(<i>Evylaeus</i>) sp#6	x	x	x	x
(<i>Evylaeus</i>) sp#7	x	x	x	x
Genus: <i>Sphecodes</i>				
<i>Sphecodes</i> sp#1	x	x	x	x
<i>Sphecodes</i> sp#2	x	x	x	x
<i>Sphecodes</i> sp#3	x	x	x	x
<i>Sphecodes</i> sp#4	x	x	x	x
<i>Sphecodes</i> sp#5	x	x	x	x
<i>Sphecodes</i> sp#6	x	x	x	x
<i>Sphecodes</i> sp#7	x	x	x	x
<i>Sphecodes</i> sp#8	x	x	x	x
<i>Sphecodes</i> sp#9	x	x	x	x
<i>Sphecodes</i> sp#10	x	x	x	x
<i>Sphecodes</i> sp#11	x	x	x	x
<i>Sphecodes</i> sp#12	x	x	x	x
<i>Sphecodes</i> sp#13	x	x	x	x
<i>Sphecodes</i> sp#14	x	x	x	x
<i>Sphecodes</i> sp#15	x	x	x	x
Subfamily: Rophitinae				
Genus <i>Dufourea</i>				
<i>D. rufiventris</i>	x	x	x	x
Family: Megachilidae				
Subfamily: Megachilinae				
Genus: <i>Anthidiellum</i>				
<i>A. notatum</i>	x	x	x	x
Genus: <i>Anthidium</i>				
<i>Anthidium</i> sp#1	x	x	x	x
<i>Anthidium</i> sp#2	x	x	x	x
<i>Anthidium</i> sp#3	x	x	x	x
<i>Anthidium</i> sp#4	x	x	x	x
<i>Anthidium</i> sp#5	x	x	x	x
<i>Anthidium</i> sp#6	x	x	x	x
<i>Anthidium</i> sp#7	x	x	x	x
<i>Anthidium</i> sp#8	x	x	x	x
<i>Anthidium</i> sp#9	x	x	x	x
Genus: <i>Ashmeadiella</i>				
<i>A. sculleni</i>	x	x	x	x
<i>Ashmeadiella</i> sp#1	x	x	x	x
<i>Ashmeadiella</i> sp#2	x	x	x	x
<i>Ashmeadiella</i> sp#3	x	x	x	x

Table A1. Continued.

Taxa	Control	Low	Medium	High
<i>Ashmeadiella</i> sp#4	x	x	x	x
Genus: <i>Atoposmia</i>				
<i>Atoposmia</i> sp#1		x		
Genus: <i>Coelioxys</i>				
<i>Coelioxys</i> sp#1			x	
<i>Coelioxys</i> sp#2	x			x
<i>Coelioxys</i> sp#3			x	
<i>Coelioxys</i> sp#4			x	
Genus: <i>Dianthidium</i>				
<i>D. singulare</i>	x			
Genus: <i>Stelis</i>				
<i>Stelis</i> sp#1		x		
<i>Stelis</i> sp#2				x
Genus: <i>Hoplitis</i>				
<i>H. albifrons</i>	x	x	x	x
<i>H. fulgida</i>	x	x	x	x
<i>Hoplitis</i> sp#1	x			
(<i>Anthocopa</i>) sp#1		x		
Genus: <i>Megachile</i>				
<i>M. bradleyi</i>	x		x	
<i>M. dentitarsus</i>	x	x		
<i>M. latimanus</i>	x	x	x	x
<i>M. melanophaea</i>	x			x
<i>M. mellitarsus</i>		x	x	
<i>M. nevadensis</i>	x	x	x	x
<i>M. perihirta</i>	x	x		
<i>M. pugnata</i>	x			
<i>M. relativa</i>		x	x	
<i>M. rivalis</i>	x			
<i>M. wheeleri</i>	x	x	x	x
<i>Megachile</i> sp#1		x		x
<i>Megachile</i> sp#2			x	
Genus: <i>Osmia</i>				
<i>O. albolateralis</i>	x	x	x	x
<i>O. atrocyanea</i>		x		x
<i>O. bella</i>	x	x	x	x
<i>O. brevis</i>	x	x	x	x
<i>O. bruneri</i>	x	x	x	x
<i>O. bucephala</i>	x			
<i>O. californica</i>	x	x	x	
<i>O. calla</i>	x	x	x	x
<i>O. caulicola</i>		x	x	
<i>O. cobaltina</i>	x			
<i>O. coloradensis</i>		x		
<i>O. cyanella</i>	x	x	x	
<i>O. cyaneonitens</i>		x	x	x
<i>O. ednae</i>	x	x	x	x
<i>O. juxta</i>			x	
<i>O. kincaidii</i>	x			x
<i>O. longula</i>	x	x	x	x
<i>O. montana</i>	x			
<i>O. nanula</i>	x		x	x
<i>O. nigrifrons/raritatis</i>	x	x		
<i>O. nifoata</i>	x	x	x	x
<i>O. pellax</i>	x	x	x	x
<i>O. pentstemonis</i>		x	x	x
<i>O. regulina</i>			x	
<i>O. sculleni</i>			x	
<i>O. subaustralis</i>	x	x		
<i>O. trevoris</i>	x	x	x	x
<i>O. tristella</i>	x	x	x	x
<i>O. vandykei</i>	x	x	x	x
<i>Osmia</i> sp#1	x	x		x
<i>Osmia</i> sp#2		x		
<i>Osmia</i> sp#3	x	x	x	
<i>Osmia</i> sp#4		x	x	x
<i>Osmia</i> sp#5			x	x
<i>Osmia</i> sp#6	x	x	x	x

Table A1. Continued.

Taxa	Control	Low	Medium	High
<i>Osmia</i> sp#7	x		x	
<i>Osmia</i> sp#10	x			x
<i>Osmia</i> sp#15	x			x
<i>Osmia</i> sp#16	x			x
<i>Osmia</i> sp#22	x			
Family: Apidae				
Subfamily: Apinae				
Genus: <i>Anthophora</i>				
<i>A. bombooides</i>	x	x	x	x
<i>A. pacifica</i>	x	x		x
<i>A. terminalis</i>	x			
<i>A. urbana</i>	x	x	x	x
<i>A. ursina</i>	x	x	x	
<i>Anthophora</i> #1	x			x
<i>Anthophora</i> #2	x	x	x	x
Genus: <i>Bombus</i>				
<i>B. appositus</i>	x	x	x	x
<i>B. bifarius</i>	x	x	x	x
<i>B. californicus</i>	x	x	x	x
<i>B. fernaldae</i>		x	x	
<i>B. fervidus</i>	x	x	x	x
<i>B. flavifrons</i>	x	x	x	x
<i>B. griseocollis</i>	x	x	x	x
<i>B. huntii</i>	x	x	x	x
<i>B. insularis</i>	x	x	x	x
<i>B. mixtus</i>	x	x	x	x
<i>B. nevadensis</i>	x	x	x	x
<i>B. occidentalis</i>	x	x	x	x
<i>B. rufocinctus</i>	x	x	x	x
<i>B. vagans</i>			x	
Genus: <i>Diadasia</i>				
<i>D. enavata</i>	x	x	x	x
<i>D. nigrifrons</i>	x	x	x	x
Genus: <i>Eucera</i>				
<i>Eucera</i> sp#1				x
<i>Eucera</i> sp#2	x		x	x
Genus: <i>Habropoda</i>				
<i>Habropoda</i> sp#1	x	x	x	x
Genus: <i>Melissodes</i>				
<i>M. agilis</i>	x	x	x	x
<i>M. bicolorata</i>	x			
<i>M. bimatrix</i>			x	
<i>M. confusa</i>	x	x	x	x
<i>M. metenua</i>	x		x	x
<i>M. rivalis</i>	x	x	x	x
<i>M. robustior</i>	x	x	x	x
<i>Melissodes</i> sp#1	x	x	x	x
<i>Melissodes</i> sp#2	x	x	x	x
<i>Melissodes</i> sp#3		x		
Genus: <i>Xeromelecta</i>				
<i>X. californica</i>	x		x	x
Subfamily: Xylocopinae				
Genus: <i>Ceratina</i>				
<i>Ceratina</i> sp#1		x	x	