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Author(s): Carmen Tubbesing , Christopher Strohm , Sandra J. DeBano , Natalie Gonzalez , Chiho Kimoto and Robert V. Taylor

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Insect Visitors and Pollination Ecology of Spalding's Catchfly (*Silene spaldingii*) in the Zumwalt Prairie of Northeastern Oregon

Carmen Tubbesing¹

¹Biology Department
Brown University
Providence, RI 02912

Christopher Strohm²

Sandra J. DeBano^{3,7}

Natalie Gonzalez⁴

Chiho Kimoto⁵

Robert V. Taylor⁶

⁷ Corresponding author: sandy.debano@oregonstate.edu; 541-567-6337 Ext. 116

ABSTRACT: *Silene spaldingii* S. Watson (Spalding's catchfly) is a threatened wildflower that relies on insect-mediated pollination. However, its pollination ecology is not well understood, particularly in the Zumwalt Prairie of northeastern Oregon, which contains the largest known *S. spaldingii* population. Our objectives were to: (1) describe the principal insect visitors to *S. spaldingii* in the Zumwalt Prairie, (2) quantify the available pool of pollinators in the area, and (3) determine whether the visitation rate to individual plants is associated with the density of *S. spaldingii* at the patch scale, as predicted by the resource concentration hypothesis, and/or by the density and composition of non-*S. spaldingii* blooming plants, as predicted by the facilitation and competition hypotheses. We recorded insect visits to *S. spaldingii* during peak bloom at 30 patches and characterized the local bee community using blue vane traps. We quantified the patch-scale density of *S. spaldingii* and the composition and abundance of other blooming species at each patch. Two bumble bee species comprised all observed visits, although they constituted only 20% of the total bees sampled on the prairie. Bumble bees showed a high degree of host fidelity even when other blooming plants were present. Per capita visitation rates increased with catchfly density and blooming plant abundance at the patch scale, supporting the resource concentration and facilitation hypotheses. *Silene spaldingii* in the Zumwalt Prairie appears to rely on a narrow pool of pollinators that may preferentially visit it over other blooming plants, and more dense patches of *S. spaldingii* may increase pollination efficiency.

Index terms: bumble bees, native bees, pollinators, *Silene spaldingii*, Spalding's catchfly, Zumwalt Prairie Preserve

INTRODUCTION

Native plants in the Pacific Northwest face a variety of threats related to habitat destruction (e.g., agricultural/urban/suburban conversion) and degradation (e.g., non-native plant invasions, recreational activities, improper livestock grazing practices) (Parish et al. 1996; Parks et al. 2005). In Oregon alone, 60 plant species are listed as threatened or endangered by the state and federal governments (ODA 2011). Anthropogenic disturbances not only directly impact plants, but can also affect pollinators on which many flowering plants depend (Kearns et al. 1998; Aguilar et al. 2006; Winfree et al. 2009). The risk of pollination failure is highest in systems where plants are pollinated by relatively few species (Wilcock and Neiland 2002), especially those that require specialized pollinators (e.g., Steiner and Whitehead 1996). Therefore, an important step for the protection of threatened plant species that rely on pollinators is identifying significant pollinators and understanding factors that influence plant-pollinator relationships, including the spatial distribution and density of floral resources (Kearns et al. 1998; Kremen et al. 2007).

In this study, we focused on one such threatened plant species, Spalding's catchfly (*Silene spaldingii* S. Watson: Caryophyllaceae), a perennial forb na-

tive to the Pacific Northwest Bunchgrass Prairie, one of the most threatened and understudied grasslands in North America (Tisdale 1982). Historically, this unique grassland type covered over 8 million hectares, but over 90% of it has been converted to agriculture (Tisdale 1982). This habitat loss has limited *S. spaldingii* to small, fragmented populations throughout its original range in Washington, Oregon, Idaho, and Montana. In 2001, the species was listed as “threatened” by the United States Fish and Wildlife Service (U.S. Fish and Wildlife Service 2007).

The importance of insect pollination in *S. spaldingii* reproduction is well established. This perennial forb is a long-lived, sexually reproducing plant with a low reproductive rate. Although it can produce seed through geitonogamous self-pollination, fecundity (i.e., production of viable fruits and seeds) is much greater when insects move pollen from one plant to another (Lesica 1993). Lesica (1993) found an overall reduction in *S. spaldingii* fitness of more than 95% in the absence of insect pollinators due to decreases in the proportion of fruits maturing, the number of seeds per fruit, rates of germination, and seedling growth and survival. Subsequently, Lesica and Heidel (1996) found that the rate of fruit abortion was negatively correlated with the rate of insect visitation. Thus, there is ample evidence that insect-mediated cross-pollination is critical to maintaining viable populations of this species.

However, several significant gaps remain in our understanding of the pollination ecology of *S. spaldingii*, including the identity of its current pollinators. Work by Lesica (1993) and Lesica and Heidel (1996) at five locations in Washington, Oregon, and Idaho between 1988 and 1995 found that over 90% of visitors to *S. spaldingii* were of one bumble bee species, *Bombus fervidus* (Fabricius). Other insects observed on flowers included halictid bees, noctuid moths, and one vespid wasp (Lesica and Heidel 1996). Although these data provide important baseline information about potential pollinators of *S. spaldingii* over 15 years ago, more current data are needed to inform recovery planning, especially given concerns over pollinator declines (Allen-

Wardell et al. 1998; Kearns et al. 1998).

Additionally, we know little about how spatial variability in floral resources affects pollinator visitation of *S. spaldingii*. Plant-pollinator relationships are highly contextual and depend on a number of variables, including the distribution of the target plant species as well as the identity and abundance of proximate plant species with overlapping flowering phenologies (Kunin 1997; Ghazoul 2005; Kremen et al. 2007). For *S. spaldingii*, these factors have not been studied.

Even in areas with relatively large populations (> 50,000 individuals), such as at The Nature Conservancy’s Zumwalt Prairie Preserve in northeastern Oregon (U.S. Fish and Wildlife Service 2007), the local density of flowering *S. spaldingii* plants can vary widely (e.g., 0.01 to 0.3 individuals m⁻² in 2006 – 2008, R.V. Taylor et al. unpubl. data). The resource concentration hypothesis (Root 1973) suggests that herbivores are more likely to find and use dense concentrations of host plants. This work has been extended to pollinators, often in the context of Allee effects in plant populations, where low densities can reduce reproductive rates because of decreased per capita visitation rates by pollinators (Platt et al. 1974; Silander 1978; Thomson 1981; Feinsinger et al. 1986; Sih and Baltus 1987; Klinkhamer et al. 1989; Kunin 1997; Groom 1998). If this phenomenon occurs for *S. spaldingii*, then individual plants in denser patches would garner more visits from pollinators than those in lower density patches, allowing more opportunity for pollination.

The effect of other blooming plant species on *S. spaldingii* pollination is also unknown, although hypothetically, higher densities of blooming heterospecific plants at the patch scale can either increase pollinator availability for *S. spaldingii* via facilitation (Waser and Real 1979; Schemske 1981; Feldman et al. 2004; Moeller 2004) or decrease it through competition (Pleasants 1980; Rathcke 1983; Mitchell et al. 2009; Morales and Traveset 2009). The facilitation hypothesis predicts that, for generalist pollinators, the total density of all blooming plants, regardless of species,

may act as an attractant for pollinators. Generalist pollinators may be more likely to visit *S. spaldingii* where it coexists with other species that bloom at the same time. Alternatively, nearby blooming forbs could compete with *S. spaldingii*, attracting pollinators that would otherwise visit *S. spaldingii*. According to the competition hypothesis (Pleasants 1980; Rathcke 1983; Mitchell et al. 2009), competition for pollinators among plants has resulted in plant species evolving spatially and/or temporally distinct blooming periods. This hypothesis leads to the prediction that *S. spaldingii* would have lower pollinator visitation rates in patches with higher densities of heterospecific plants. In fact, Lesica and Heidel (1996) suggested that non-native plants may compete with *S. spaldingii* for pollinators.

The objectives of this study were to: (1) describe the principal insect visitors to the threatened plant *S. spaldingii* within the Zumwalt Prairie Preserve, (2) quantify the available pool of pollinators in the area, and (3) determine whether the frequency with which a *S. spaldingii* plant is visited is associated with the patch-level density of *S. spaldingii*, or the density and composition of non-*S. spaldingii* blooming forbs and shrubs.

METHODS

Species Description

Silene spaldingii Wats. (Caryophyllaceae) is an iteroparous, tap-rooted, perennial herb having one to several stems 20 – 50 cm in height (Hitchcock et al. 1969; Lesica 1999). Plants reproduce only by seed; no reproduction via rhizomes or other asexual means has ever been observed (Lesica 1993; Lesica and Crone 2007). Within a growing season some plants remain dormant, some lack reproductive structures, and others bear flowers. Flowers (3 – 20 per stem) are hermaphroditic, and borne in a branched, terminal, cymose inflorescence (Lesica 1999; Lesica and Crone 2007). Stems, leaves, and flower bracts are densely covered with sticky, glandular hairs (Hitchcock et al. 1969). Flowers are tubular, bell-shaped, and have a single, one-celled ovary and 2 – 10 anthers (Hitchcock et al.

1969). Five, cream-colored, lobed petals barely extend beyond the calyx, each of which has four appendages. Flowers bloom asynchronously, beginning on the Zumwalt Prairie mid-July and continuing into late August (Taylor et al. 2012). Flowers remain open for two to several days (Lesica 1993). Within a flower, anthers mature and shed pollen before styles expand and stigmas become receptive to pollen, reducing the likelihood of self-pollination (Lesica 1993). Open flowers may be available for two to several days and more than one flower may be in bloom on the same plant, allowing for geitonogamous pollination (Lesica 1993). Fertilized flowers mature vertically into capsules, each of which holds an average of 61 seeds (R.V. Taylor, unpubl. data). Although *S. spaldingii* is self-compatible, seed production, germination rates, and seedling growth are all substantially lower in fruits resulting from self-pollination (Lesica 1993). Seed dispersal studies have not been conducted; however, seeds from ruptured cup-shaped fruit capsules are probably dispersed by wind, passing wildlife, or when the plant is knocked over (U.S. Fish and Wildlife Service 2007).

Study Area

The study was conducted at the Zumwalt Prairie Preserve (lat 45° 34' N, long 116° 58' W) located in Wallowa County in northeastern Oregon (Figure 1a,b). The 13,269-ha preserve is owned and managed by The Nature Conservancy (TNC) and lies in the southwestern portion of the Pacific Northwest Bunchgrass Prairie (Tisdale 1982). At 1060 – 1680 m elevation, the preserve is dominated by native bunchgrasses, 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). It has a diverse assemblage of over 112 forb species; common species include *Aster* L. spp., western yarrow (*Achillea millefolium* L.), lupines (*Lupinus* L. spp.), prairie smoke (*Geum triflorum* Pursh), and cinquefoil (*Potentilla* L. spp.) (Kennedy et al. 2009). The Preserve also supports a diverse native bee community (Kimoto, DeBano, Thorp, Rao, and Stephen 2012a), including the western

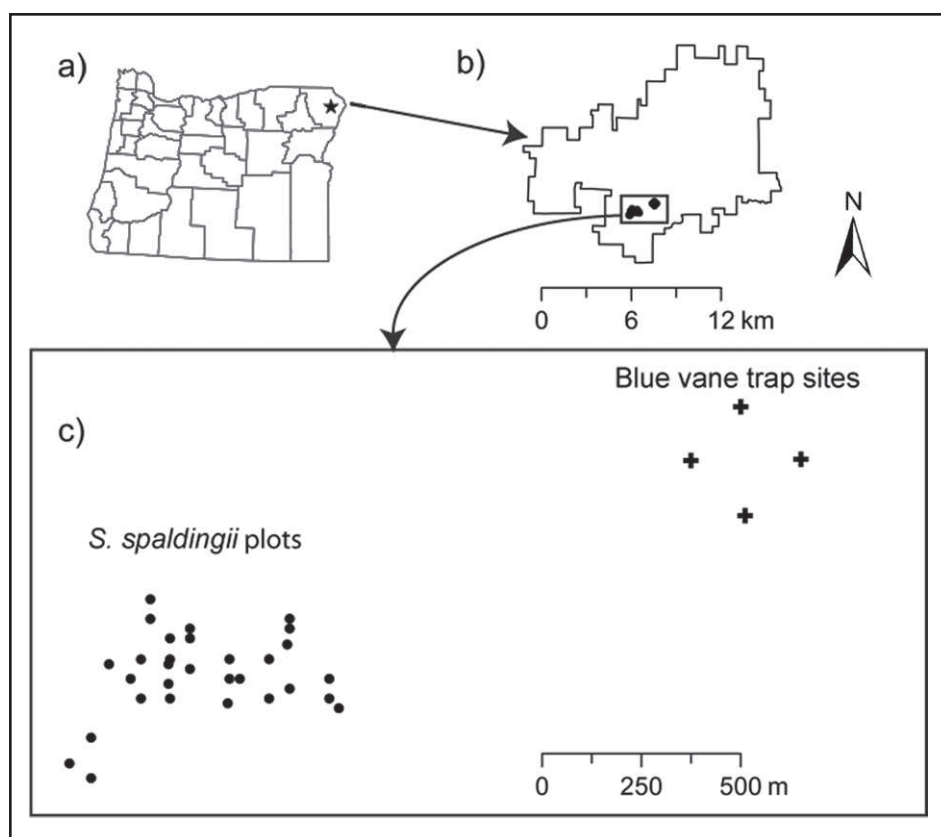


Figure 1. (a) Location of the Zumwalt Prairie in eastern Oregon, (b) boundaries of the Zumwalt Prairie Preserve, and (c) the location of the 30 *S. spaldingii* patches and the four blue vane traps.

bumble bee (*Bombus occidentalis* Greene), which has declined in western Oregon and Washington (Rao et al. 2011).

The preserve has a large population of *S. spaldingii* (estimated at > 50,000 plants across 112 ha) with a patchy distribution (Taylor et al. 2009), including a relatively dense concentration in Harsin Pasture in the southern portion of the preserve (Figure 1c). We attempted to locate all *S. spaldingii* plants that had been documented in Harsin Pasture in a previous study using GPS (R.V. Taylor et al. unpubl. data). When a *S. spaldingii* plant could be found, we used the location as the center of a 15-m radius sampling patch. We were able to locate 30 patches in Harsin Pasture that were separated from each other by at least 30 m.

Observations of Insect Visitors

Observations of insect visits to *S. spaldingii* flowers were conducted between 3 and 12 August 2010 at the 30 Harsin Pasture patch-

es (described above) as well as at one other location on the preserve (Grader Pasture), where blooming catchfly was also known to occur. Our 10-day observation period occurred in the middle (and presumably during the peak) of the 29-day blooming season in 2010 documented by the annual demography and phenology monitoring survey of the preserve by TNC (Taylor et al. 2012). The blooming season extended from 22 July to 19 August 2010, with 85% of all blooms recorded that year before 13 August (Taylor et al. 2012).

We conducted 76.25 person-hours of observations by walking from patch to patch recording all instances of insect visits to *S. spaldingii*, following visitors to multiple plants, and capturing when possible. We collected data on species and caste identification for captured individuals, genus identification for non-captured individuals, and the number and identity of flowering plants visited. These observations were supplemented with observations described

in the “Density and Competition Studies” section below and seven person-hours after dusk between 2000 and 2300 using red-tinted lights (to minimize the likelihood of attracting insects). All three activities resulted in a total of 91.25 person-hours spent by five observers in areas containing catchfly. Most person-hours were spent at Harsin Pasture, but 17 person-hours were spent at Grader Pasture.

Additionally, bees caught on *S. spaldingii* were checked for pollen in the hair covering their bodies. Pollen was photographed using scanning electron microscopy (SEM) at Oregon State University. We collected pollen samples from anthers of the only other species in Caryophyllaceae (*Dianthus armeria*, *S. scouleri*, and *S. douglasii*) that were blooming at that time and examined them with SEM. All pollen was collected at the preserve except for that of *D. armeria*; insufficient collection at the preserve required the use of samples from plants in Corvallis, Oregon. We compared images of pollen on bees’ bodies with pollen from blooming species of Caryophyllaceae.

Available Pollinators

We estimated the pool of native bees, a taxon believed to include major pollinators of *S. spaldingii* (Lesica 1993; Lesica and Heidel 1996), by sampling for 24 hours with four UV-reflective blue vane traps (Stephen and Rao 2005, 2007) in an adjacent area of bunchgrass prairie within the Zumwalt Prairie Preserve on 4 – 5 August 2010. Vegetation in this area was similar to that of Harsin and Grader Pastures. Blue vane traps were separated by approximately 200 m, and were more than 2.5 km away from catchfly patches. Blue vane traps consist of a clear plastic container (15-cm diameter × 15-cm high) with a blue polypropylene screw funnel with two 24-cm × 13-cm semitransparent blue polypropylene cross vanes of 3 mm thickness (SpringStar™ LLC, Woodinville, WA, USA; Figure 2a; 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.

Bees collected during observations and in traps were frozen, pinned, labeled, sexed, and identified to genus, and for bumble bees, species. We treat *B. californicus* and *B. fervidus* as one species (*B. fervidus*) although their taxonomic status remains uncertain (Williams 2010). Representative specimens of all species are vouchered at the Oregon State Arthropod Collection at Oregon State University in Corvallis.

Density and Competition Studies

To determine whether the frequency of insect visitors to *S. spaldingii* flowers was related to the patch density of *S. spaldingii* or other blooming forbs and shrubs, we monitored each of the 30 patches in Harsin Pasture four times, once within each of the following time periods: 0800 – 1000, 1000 – 1200, 1300 – 1530, and 1530 – 1800. During each of these time periods, each patch was observed for two min by two individuals simultaneously, so that two person-hours of observations (30 patches × 2 minutes/patch × 2 people) were conducted in each time period. Although the afternoon time periods were 0.5 hours longer than the morning periods, the number of minutes

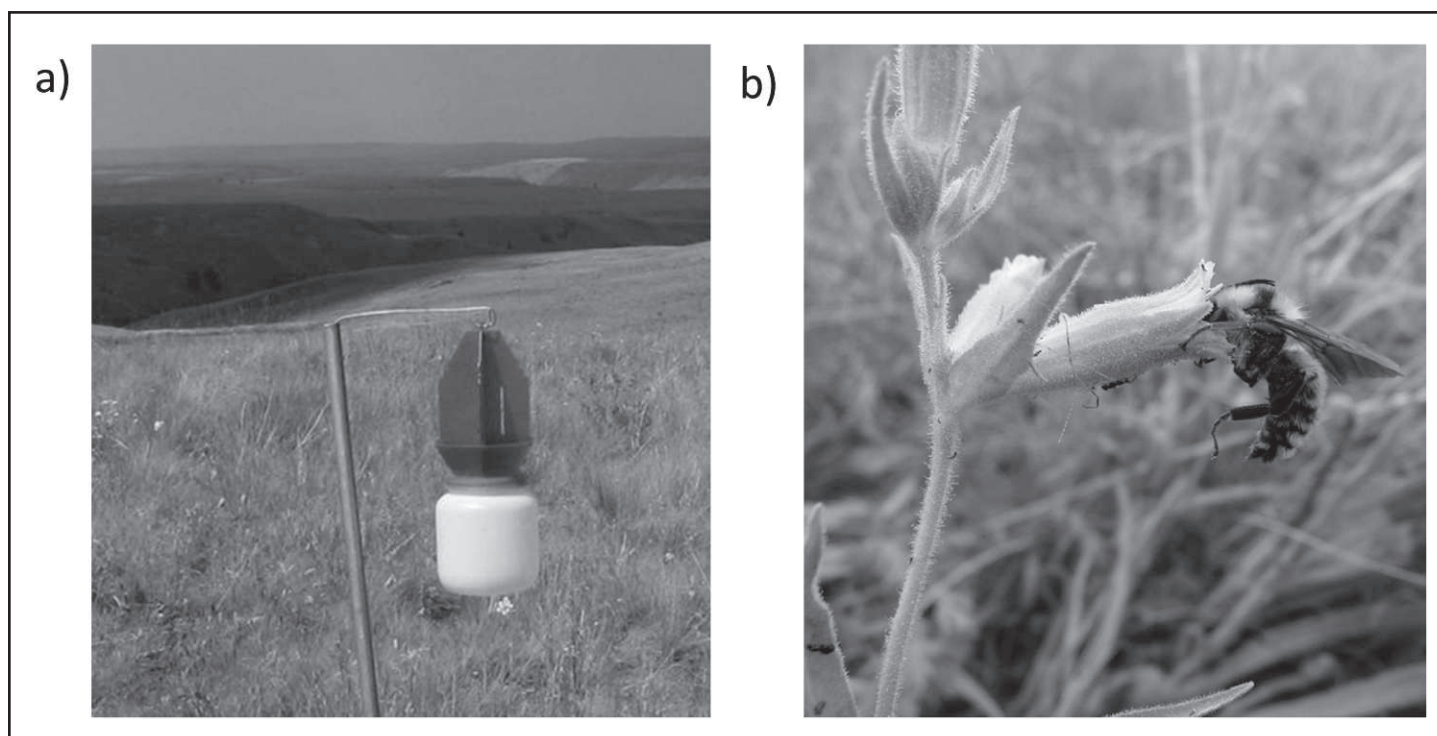


Figure 2. (a) Blue vane trap in grassland adjacent to *S. spaldingii* observation patches, and (b) *B. fervidus* visiting *S. spaldingii*. Photograph taken by C. Strohm using a Canon Powershot A540.

of observations in each time period was equal. During each two minute observation session, the same two people recorded and, if possible, captured, any visitors to flowers of *S. spaldingii* within view of the patch's center (an approximately 15 m radius). Collected specimens were identified to species and caste; individuals not collected were identified to genus.

Silene spaldingii density was recorded by counting the stems of catchfly within a 10-m radius of the "focal" catchfly plant at the center of the patch following the first observation period at each patch. The density of all blooming, non-catchfly plants was estimated by counting stems of all non-catchfly blooming forbs or shrubs within 3 m of the focal plant. A blooming stem was defined as containing visible anthers and/or stigmas on at least one open flower. The total number of blooming forb and shrub species within a 3 m radius was also counted and the identity of each species recorded; however, counts of stem abundance for each species were not made. When an insect visitor was observed at a *S. spaldingii* plant that was not the focal individual but that was within the patch, the non-catchfly blooming density and richness was also estimated within the 3 m radius surrounding that catchfly plant. Because surrounding blooming plant composition may have changed at the first patches we monitored between initial data collection and completion of all observation periods, we repeated stem-counts and species tallies of non-catchfly blooming plants at patches for which observation periods were separated by more than three days. The scale of measurement for intra- and inter-specific densities differed because *S. spaldingii* density was much lower than all non-target blooming forbs and shrubs. Thus, meaningful variation in *S. spaldingii* density occurred at a larger patch size than variation in all non-target bloom density.

Statistical Analyses

To test predictions generated by the resource concentration, facilitation, and competition hypotheses, we summed all

visits to catchfly plants at each patch, and divided this number by the total number of catchfly plants at the patch to calculate a per capita visitation rate for each patch throughout the duration of the study. The resource concentration hypothesis predicts that per capita visitation rate will be positively correlated with catchfly density at the patch. The facilitation hypothesis predicts that per capita visitation rate will be positively correlated with forb and shrub blooming abundance and species richness while the competition hypothesis predicts a negative correlation with these variables. In addition, the possibility exists that only a subset of blooming plants may be key in driving facilitation or competition. In this case, we predict that per capita visitation rate will vary with changes in blooming community composition at a patch. To test this, we used non-metric multidimensional scaling (NMS) ordination to characterize the blooming forb and shrub community at each patch. NMS ordination is a robust technique 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 presence/absence data of plant species using Sorenson's distance measure. We excluded all plant species that occurred at less than 10% of patches from the analyses to reduce noise (McCune and Grace 2002), resulting in a data set reduced from 21 to 13 species. 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. Ordinations were run using PC-ORD, version 5.19, set on "autopilot" mode (McCune and Mefford 2006).

Patch-level variables analyzed included NMS scores, abundance and species richness of blooming forbs and shrubs, and density of catchfly. Because most variables were not normally distributed, Spearman rank correlation was used to test whether each patch-level variable was significantly associated with per capita visitation rate. All univariate analyses were conducted with SYSTAT (1997).

RESULTS

Insect Visitors to Catchfly

Throughout the entire study, we observed 78 visitation bouts in which a flying insect landed on one or more catchfly flowers (the only other insects found on flowers were caterpillars, which were observed feeding on all parts of the plant). All flying visitors were bumble bees (*Bombus*). Data from the density and competition portion of the study allowed us to compare diurnal patterns (because of equal observation effort per time period) and showed that bumble bee visitations were more frequent in the afternoon than the morning. Only 4% of visitors were observed in the 0800 – 1000 period, while 21% were observed between 1000 and 1200, 43% between 1300 and 1530, and 32% between 1530 and 1800. Fifty-five individuals visiting catchfly were collected in all portions of the study, of which 10% were *B. appositus* Cresson and 90% *B. fervidus* (Figures 2b, 3a). Percentages of workers, queens, and males are shown in Figure 4 a,c,e.

We were able to follow 27 visitors to multiple plants, with the average number of plants visited being seven, including both *S. spaldingii* and non-*S. spaldingii*. Fifteen percent of bees visited only one *S. spaldingii* plant within the bout, 52% visited 2 – 5 *S. spaldingii* plants, 11% visited 6 – 10, 19% visited 11 – 15, and 4% visited more than 15 consecutively. Fifty-nine percent of the 27 bees visited only *S. spaldingii* flowers. These visitation bouts occurred in areas with flowers of many other species (listed in Table 1), and bees often flew over other blooming forbs as they traveled from one *S. spaldingii* plant to another.

Attempts to take SEM photographs of pollen on bees that were caught on *S. spaldingii* resulted in one photograph with distinguishable pollen. The pollen was located on the face of one *B. fervidus* worker and its shape and external markings matched *S. spaldingii* pollen and did not match the pollen of the other three Caryophyllaceae species that were blooming at the study site during the study period (Figure 5). This

provides anecdotal evidence that *Bombus* carries pollen of *S. spaldingii*.

Available Pollinators

Blue vane traps in an adjacent grassland yielded 444 bees in 10 genera; 47% of bees collected were *Bombus* and 53% belonged to other genera. A total of nine species of *Bombus* were collected. *B. fervidus* made up 19% of *Bombus* individuals caught in traps and 9% of all bees, while *B. appositus* made up 25% of *Bombus* and 11% of all bees (Figure 3b). Percentages of workers, queens, and males are shown in Figure 4b,d,f.

Density and Competition Studies

Of the 78 visitations described above, 28 occurred during the course of the density and competition studies, during which 440 *S. spaldingii* plants in 30 plots were observed, resulting in a visitation rate of 0.008 visits per catchfly plant per hour. Patches with higher densities of *S. spaldingii* were visited by more potential pollinators than patches characterized by low catchfly densities, and the number of visits per catchfly plant increased with catchfly density ($r_s = 0.51$, $P < 0.005$, $n = 30$). Although patches varied in blooming plant composition (NMS ordination

resulted in a two axis solution, with axis 1 explaining 45% of the variation in plant community composition and axis 2 explaining 29%), the number of visits per catchfly plant was not significantly correlated with axis 1 ($r_s = 0.34$, $P > 0.05$, $n = 30$) or axis 2 ($r_s = 0.13$, $P > 0.05$, $n = 30$). The number of visits per catchfly plant did not significantly increase with blooming forb and shrub species richness ($r_s = 0.34$, $P > 0.05$, $n = 30$). However, patch-scale density of blooming non-catchfly forbs/shrubs showed a positive relationship with per capita pollinator visits ($r_s = 0.42$, $P < 0.05$, $n = 30$). There was a significant positive correlation between the densities of catchfly and blooming plants at each patch ($r_s = 0.39$, $P < 0.05$).

DISCUSSION

Extensive research on *Silene* has shown that most species in this genus are either primarily pollinated by Lepidoptera (especially nocturnal moths) or bumble bees (Kephart et al. 2006). However, the relative roles of pollinators are expected to vary spatially and temporally and with a variety of factors, including patch size and isolation (Kephart 2006). Our study adds to previous work conducted on smaller populations of *S. spaldingii* in other areas, and suggests that the principal pollinators of *S. spaldingii* in

the Zumwalt Prairie Preserve are bumble bees, a conclusion consistent with these other studies (Lesica 1993; Lesica and Heidel 1996). However, although Lesica and Heidel (1996) identified *B. fervidus* as the only species of bumble bee associated with *S. spaldingii* throughout its range, we found that 10% of bees visiting the plant in the Zumwalt Prairie were *B. appositus* (Figure 3a). In addition, they found non-bumble bee visitors; at one location, 17% of *S. spaldingii* visitors were halictid bees, and at two other locations noctuid moths and vespid wasps were rare visitors (2% and 1%, respectively). In contrast, we did not observe any non-bumble bee flower visitors.

Several lines of evidence suggest that these two species of bumble bees are providing pollination services for *S. spaldingii* at the Zumwalt Prairie. First, since recruitment of *S. spaldingii* is pollinator-limited (Lesica 1993) and the size of the Zumwalt population is relatively large, some plants can be assumed to be receiving pollination services. The fact that no other invertebrates were found visiting the plant in over 90 person-hours of observation during the peak blooming season suggests that these two species of bumble bees are the most significant pollinators. Second, we ob-

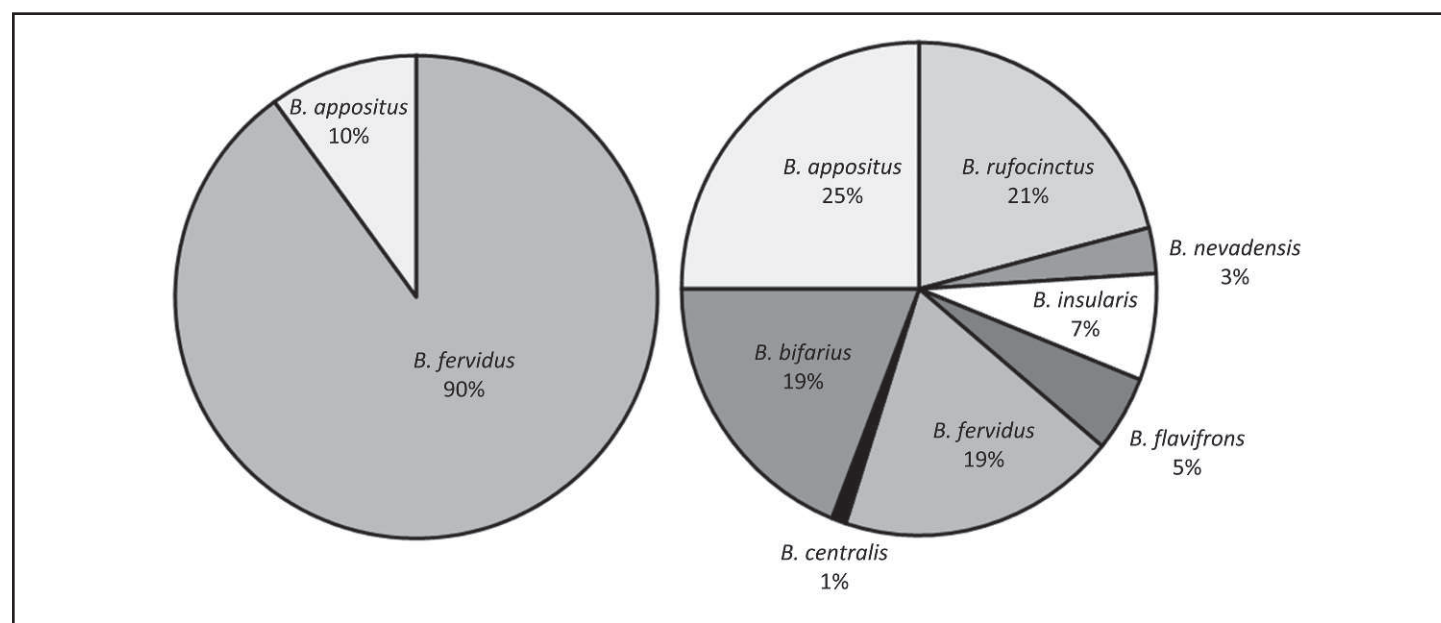


Figure 3. Comparison of (a) *Bombus* species observed visiting *S. spaldingii*, and (b) *Bombus* collected in an adjacent grassland using blue vane traps.

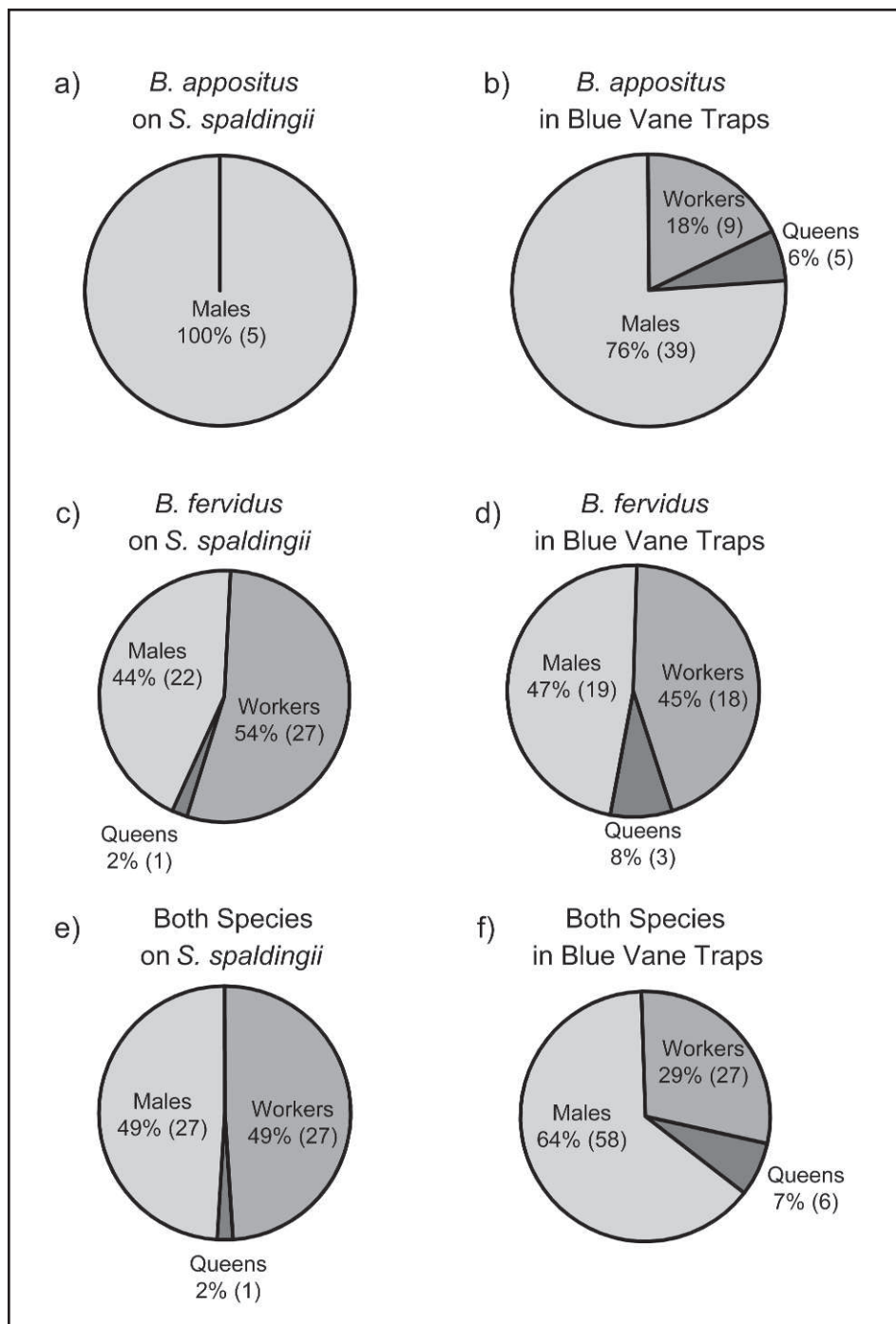


Figure 4. Comparison of percentages of males, workers, and queens collected while visiting *S. spaldingii* and in blue vane traps for *B. appositus* (a, b), *B. fervidus* (c, d), and both species combined (e, f).

served *Bombus* individuals visit multiple catchfly plants consecutively. Only 15% of observed multiple-plant visitation bouts involved only one catchfly plant, while 34% included six or more. Over half of the bouts, in which bees visited an average of seven plants, were exclusively to *S. spaldingii*. Interspecific pollen transfer

caused by pollinators frequently switching between plant species, or interference competition, significantly reduces seed set of plants (Waser 1978; Petit 2011). Therefore, high pollinator constancy is important for providing efficient pollination services. Our observations suggest that *Bombus* provides this necessary pollinator constancy. Third,

our discovery of *S. spaldingii* pollen on the face of a *Bombus* worker caught on a catchfly flower suggests that bumble bees actually transport *S. spaldingii* pollen.

Males accounted for 49% of *Bombus* individuals caught on *S. spaldingii* and 64% of those caught in blue vane traps. These are larger proportions than would be expected for bumble bees in most times of the year, but male bumble bees can reach significant numbers in the late summer (Kearns and Thomson 2001) and sometimes even outnumber workers (Ostevik et al. 2010). Though males generally visit fewer flowers than female workers do, they may be more effective pollinators (Ostevik et al. 2010). Ostevik et al. (2010) found that males transfer more pollen between each flower, potentially because they have denser, longer pile (Kearns and Thomson 2001), spend more time handling each flower (Ostevik et al. 2010), and do not remove pollen into corbiculae (i.e., the pollen baskets found on the hind tibiae of most female bumble bees). Male bumble bee pollination may also reduce inbreeding depression because males are not tied down to a colony and, therefore, have larger foraging ranges (Kraus et al. 2009), and switch between patches of host plants more frequently than female workers (Ostevik et al. 2010). Therefore, the high proportion of male *Bombus* individuals visiting *S. spaldingii* may result in more effective pollination than if flowers were pollinated by females only.

Bombus fervidus and *B. appositus* may visit *S. spaldingii* more frequently than other bumble bees because they are long-tongued. A bumble bee's tongue or proboscis length often corresponds with the corolla depth of the flower it visits (Pleasant 1980), and species with long tongues may prefer and forage more efficiently on flower species not available to most short-tongued bees (Hobbs 1962). Catchfly flowers have long narrow corollas that may require bumble bees with long tongues to reach the nectar and pollen (Figure 2b). The species found visiting catchfly were the two most common long-tongued bees present at the Zumwalt Prairie during the *S. spaldingii* blooming period, making up 19% and 25% of all bumble bees captured

Table 1. Blooming plants observed through the course of the study and the number of patches in which the species was present.

Family Name	Scientific name (common name)	# of patches occurred at:
Apiaceae	<i>Perideridia gairdneri</i> (Hook. & Arn.) Mathias (Gardner's yampah)	10
Asteraceae	<i>Erigeron pumilus</i> Nutt. (shaggy fleabane)	12
	<i>Cirsium brevifolium</i> Nutt. (Palouse thistle)	3
	<i>Pyrrocoma carthamoides</i> Hook var. <i>cusickii</i> (A. Gray) Kartesz & Gandhi (largeflower goldenweed)	2
	<i>Grindelia squarrosa</i> (Pursh) Dunal (curlycup gumweed)	2
	<i>Symphyotrichum campestre</i> (Nutt.) G.L. Nesom var. <i>campestre</i> (western meadow aster)	11
	<i>Solidago missouriensis</i> Nutt. var. <i>missouriensis</i> (Missouri goldenrod)	16
	<i>Hieracium cynoglossoides</i> Arv.-Touv. (houndstongue hawkweed)	8
	<i>Achillea millefolium</i> L. var. <i>occidentalis</i> DC. (western yarrow)	24
Caprifoliaceae	<i>Symphoricarpos albus</i> (L.) S.F. Blake (common snowberry)	1
Caryophyllaceae	<i>Silene scouleri</i> Hook. (simple campion)	2
	<i>Dianthus armeria</i> L. (Deptford pink)	7
Fabaceae	<i>Lupinus leucophyllus</i> Douglas ex Lindl. (velvet lupine)	2

Continued

Table 1. Blooming plants observed through the course of the study and the number of patches in which the species was present.

Table 1 (Continued)

Family Name	Scientific name (common name)	# of patches occurred at:
Gentianaceae	<i>Gentiana affinis</i> Griseb. (pleated gentian)	1
Geraniaceae	<i>Geranium viscosissimum</i> Fisch. & C.A. Mey. ex C.A. Mey. (sticky purple geranium)	1
Liliaceae	<i>Calochortus macrocarpus</i> Douglas (sagebrush mariposa lily)	5
Onagraceae	<i>Clarkia pulchella</i> Pursh (pinkfairies)	6
	<i>Epilobium brachycarpum</i> C. Presl (tall annual willowherb)	9
Polygonaceae	<i>Eriogonum heracleoides</i> Nutt. var. <i>angustifolium</i> (Nutt.) (parsnipflower buckwheat)	3
Scrophulariaceae	<i>Orthocarpus tenuifolius</i> (Pursh) Benth. (thinleaved owl's-clover)	10
	<i>Castilleja oresbia</i> Greenm. (pale Wallowa Indian paintbrush)	1

in blue vane traps, respectively (Figure 3). Other bumble bees abundant in blue vane traps, such as *B. bifarius* Cresson (19%) and *B. rufocinctus* Cresson (21%), have intermediate or short tongues. Other long-tongued bees, such as *B. flavifrons* Cresson, *B. centralis* Cresson, and *B. nevadensis* Cresson, were relatively rare, making up 5% or less of bumble bees in blue vane traps.

Bees visited individual *S. spaldingii* plants more frequently when the plants were in more dense patches. This is consistent with several studies finding higher pollination success and reproduction in more dense patches (Platt et al. 1974; Silander

1978; Thomson 1981; Feinsinger et al. 1986; Klinkhamer et al. 1989) as well as experimental results showing more visitors per plant in patches of plants placed closer together than those placed farther apart (Kunin 1997). According to the resource concentration hypothesis, herbivores concentrate in dense patches of their host plants (Root 1973), with the effect being strongest for highly specialized herbivores that have adapted tolerance to host-specific herbivore resistance. Similarly, pollinators that are specialized to access and benefit from the floral resources of a particular plant may be more likely to disproportionately occupy dense stands of that plant. The bumble bees *B. fervidus* and *B. appositus* both have

long proboscises that aid in accessing *S. spaldingii* floral resources. They also display pollinator constancy, visiting multiple catchfly plants consecutively. These factors imply that these two bumble bee species may be specializing or “majoring” (*sensu*, Heinrich 1976) on *S. spaldingii* in this area during this part of the season, which would account for their preference of dense host patches under the resource concentration hypothesis.

Although previous work (Lesica and Heidel 1996) has suggested that other species of blooming plants may act as competitors of *S. spaldingii* for pollinators, our results do not support this hypothesis. Instead of

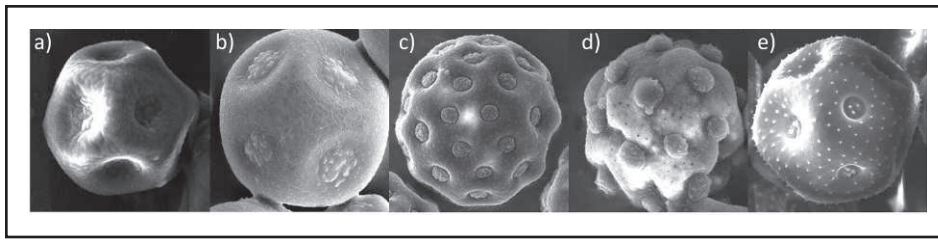


Figure 5. SEM photographs of pollen from (a) the face of a *B. fervidus* worker caught visiting *S. spaldingii*, (b) *S. spaldingii*, (c) *S. scouleri*, (d) *S. douglasii*, and (e) *D. armeria*.

decreased per capita visitation rates to *S. spaldingii* in areas with higher densities of other blooming species, we found higher per capita visitation rates, and no difference in visitation rates at patches with varying richnesses of blooming species or different blooming species compositions. These results are consistent with the facilitation hypothesis; patches with high densities of flowers may attract *B. fervidus* and *B. appositus*, increasing catchfly visitation in those patches. Facilitation is expected to occur with generalist pollinators, which these species are. *B. appositus* has been found on 9 families and 18 genera of flowers and *B. fervidus* has been found on 15 families and 34 genera of flowers (Thorp et al. 1983). However, once at the patch, *B. fervidus* and *B. appositus* may preferentially visit *S. spaldingii* because their proboscis morphology is particularly well suited for taking advantage of its pollen and nectar sources. Thus, these two species may be “facultative specialists,” in the sense that they may be attracted to patches of dense floral resources but are then selective within the patch because of morphological characteristics that may impart more efficient handling of certain flowers (Heinrich 1979). However, more work is needed to examine the relative strength of facilitation and resource concentration effects, because, in our study, there was a weak but significant positive correlation between the densities of catchfly and blooming plants at each patch.

Implications for Conservation

This study supports Lesica (1993) and Lesica and Heidel’s (1996) conclusions concerning the importance of protecting pollinators of *S. spaldingii*. Plants that

require pollination by few species with specialized morphologies are more sensitive to land-use change than plants that can be pollinated by a wide variety of generalist pollinators (Kremen et al. 2007). *Silene spaldingii* appears to have only two major pollinators in the Zumwalt Prairie, of which one (*B. fervidus*) accounts for 90% of visits, and those pollinators appear to preferentially visit catchfly. It is, therefore, vital to prevent *B. fervidus* and *B. appositus* populations from declining. Like most bumble bees, these two species can nest in underground cavities or above ground in grass tussocks (Hobbs 1966a, b; Thorp et al. 1983). Understanding how sensitive these habitats are to a variety of land-use changes, including fire, livestock grazing, and pesticide use, is important for the continued recovery of *S. spaldingii*. In addition, management of grasslands should ensure that floral resources for these long-lived generalist bumble bees are available throughout the season, not just when catchfly is in bloom (Menz et al. 2011). This may include limiting heavy grazing in early and mid summer, which can decrease floral resources available to bumble bees in Pacific Northwest Bunchgrass Prairie (Kimoto, DeBano, Thorp, Taylor, et al. 2012b).

Additionally, this study showed that dense patches of catchfly plants are disproportionately important for conservation, since they are visited more frequently by pollinators and thus probably have greater seed set and recruitment. Other work has found that dense floral patches tend to have higher pollinator constancy, further improving pollination services (Kunin 1997). Because population traits such as patchiness are likely to be affected rapidly by land-use changes and management (Kremen et

al. 2007), conservation strategies should incorporate information about small-scale densities. In portions of the plant’s range that have cattle (*Bos*) or large populations of other herbivores, fencing particularly dense patches of *S. spaldingii* may be an appropriate conservation tool since ungulate herbivory can be substantial (Taylor et al. 2012). In addition, declines in patch-level density of *S. spaldingii* due to other factors could result in a “positive” feedback spiral if these diminished patches fail to attract significant numbers of bees, and plants in these patches begin to suffer from pollen limitation. Likewise, land use or management actions that result in decreased native forb abundance may also negatively impact catchfly populations via decreases in pollinator visitation rates.

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Carmen Tubbesing is a biological technician with Nature’s Capital, an Ecological Assessment Services company based in Boise, Idaho. She recently graduated from Brown University with a B.S. in Biology. Carmen plans to pursue graduate work in forest ecology after exploring a variety of field work.

Christopher (Chris) Strohm is a graduate student in the Department of Entomology at the University of Kentucky. Chris received a B.S. in Biology from Mercyhurst College. His research interests are focused in plant-insect interactions including the impacts

of invasive species on insect communities and the conservation of native plants and insects.

Sandra (Sandy) DeBano is an Associate Professor in the Department of Fisheries and Wildlife at Oregon State University's Hermiston Agricultural Research and Extension Center in northeastern Oregon. Sandy's research interests focus on invertebrate-mediated ecosystem services including pollination, food web provisioning, and decomposition. She works primarily in grasslands, riparian areas, and agroecosystems.

Natalie Gonzalez received a B.S. in Biology at Texas State University. Her interests include wildlife conservation and pollination. She is an accountant for the Revenue Department at Texas Parks and Wildlife Department in Austin, Texas. Natalie is a member of the Sierra Club and volunteers for Austin Wildlife Rescue.

Chiho Kimoto is a Faculty Research Assistant at Oregon State University's Hermiston Agricultural Research and Extension Center in northeastern Oregon. Chiho received a B.S. in Environmental Science and a M.S. in Wildlife at Oregon State University. Her research interests center on the ecology and identification of native bees in natural and managed systems.

Robert V. (Rob) Taylor is the Northeast Oregon Regional Ecologist for The Nature Conservancy. Rob conducts and coordinates inventory, monitoring, and research efforts in support of the Conservancy's conservation and restoration work on the Zumwalt Prairie. Rob completed his undergraduate degree at St. John's University and received a Ph.D. at the University of New Mexico.

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