AN ABSTRACT OF THE THESIS OF

<u>Melissa Broussard</u> for the degree of <u>Master of Science</u> in <u>Entomology</u> presented on 6 December, 2012.

Title: Foraging in disturbed areas: a study of sweat bees (Hymenoptera: Halictidae) in Oregon

Abstract approved:	
	Sujaya U. Rao

Bees provide vital ecosystem services for cropping systems as well as natural landscapes. Declines in both both native bee and managed honey bee (*Apis mellifera* L.) populations has brought attention to the significance of their role as pollinators in managed and native ecosystems. As a result, conservation efforts have been undertaken to preserve them.

While considerable attention has been given to honey bees, relatively little is known about many native bee species. Of particular interest is the family Halictidae, which can comprise the majority of observed individuals in many habitats. These, often small, bees are difficult to identify, and, as a result, relatively little is known about their preferred floral hosts. Because bee species assemblages vary significantly from region to region, it is important to have an understanding of local populations and their floral hosts. It is also important to understand factors which affect the quantity and quality of floral resources, such as anthropogenic disturbance.

The Pacific Northwest is a diverse landscape, with rich agricultural and wildland environments that require pollinators in order to continue to thrive. Two studies examine the interface between these two systems, the first explores how

roadside disturbance, which is prevalent across the world, impacts native pollinators across habitat types, and the second explores the diet of common native species, and how that diet changes across habitat types. In these studies, it was found that roadside disturbance was associated with reduced native bee diversity and abundance in the seasonally wet Willamette Valley of Oregon, but not in the more xeric Central Oregon. Bee abundance was positively correlated with temperature. Bee diet was more diverse in areas of scarce floral resources. In both regions, exotic plants were important floral hosts, representing nearly half of observed floral visitations. This thesis presents results of species analysis, floral richness and density correlations, and comparisons of floral resources used by different bee species. Implications and recommendations for land management are discussed.

Key Words: native bees, roadside disturbance, foraging, pollinators, *Lasioglossum sisymbrii*

Corresponding e-mail address: melissa.a.broussard@gmail.com

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Foraging in disturbed areas: a study of sweat bees (Hymenoptera: Halictidae) in Oregon

by Melissa Broussard

A THESIS

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Master of Science thesis of Melissa Broussard presented on 6 December, 2012.
APPROVED:
Major Professor, Representing Entomology
Director of the Entomology Graduate Program
Dean of the Graduate School
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Dr. Sujaya Rao assisted with study design, writing, and manuscript preparation of chapters 2 and 3. Dr. W.P. Stephen assisted with study design, data interpretation, and writing of Chapter 2.

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Chapter 1: **General Introduction**

Bees are vitally important to cropping systems as well as natural landscapes and have been considered among the most ecologically important arthropods (Engel 2000). As the majority of plant species require insect-vectored pollination, a service principally by bees (Klein *et al.*, 2007), these species are of particular concern when assessing ecosystem health. Concern about the decline of both native bees and managed honey bees (*Apis mellifera* L.) has brought attention to the significance of their role as pollinators in managed and native ecosystems (Winfree *et al.*, 2009).

Over 16,000 species of bees have been described worldwide (Danforth *et al.*, 2006), with about 4,000 species recorded in North America. These species represent a significant amount of biodiversity in and of themselves, ranging from solitary to social, specialist to generalist, and ground to cavity nesting. As the landscape-scale importance of these species is recognized, conservation efforts have been enacted to preserve them. However, without a strong comprehension of the biology and ecology of these species, conservation is difficult.

Much attention in the literature has been given to honey bees and various bumble bee species, but relatively little is known about many of the other thousands of bee species. Of particular interest is the family Halictidae, which can represent 18-70% of observed bees in the United States, South America, Eurasia, and Africa (Rao *et al.*, 2009; Siqueira de Castro 2002; Al–Ghzawi *et al.*, 2006; Gess and Gess 2004) and 14% of bees in Australia (Goulson *et al.*, 2002). These, often small (Fig 1.1), bees are notoriously difficult to identify (Michener, 2000, p.339), and, as a result, relatively

little is known about the resources utilized by theses species.

Two principal resources are required by bees: forage plants and nesting sites. Bees in the family Halictidae are typically ground-nesting (Eickwort, 1969, Wcislo *et al.*, 1993), and thus may be less constrained by nest site availability than twig- and other cavity-nesters. It is likely that the availability and quality of floral resources is the larger influence on halictid populations.

Because bee species assemblages can vary significantly, even within localized areas, it is important to have an understanding of local populations and what resources they require. It is also important to understand factors which affect the quantity and quality of those resources, such as anthropogenic disturbance (Potts *et al.* 2003; Harris and Johnson 2004, Goulson 2008; Hopwood, 2008; Winfree *et al.*, 2009). Bee species in the Pacific Northwest (PNW) have received relatively little attention from the scientific community, with the foraging habits of many species unknown. The PNW is a diverse landscape, with rich human and wildland environments that require pollinators in order to continue to thrive. The region's relatively low population density (US Census Bureau, 2000) and extensive intertwining of wildlands and human habitation provide unique opportunities to examine pollinators at the interface between these two habitat types.

Chapter 2 of this thesis explores this interface by examining how bee foragers respond to roadside disturbance. Twenty-four sites across the state of Oregon were sampled in the first year of this study in order to locate areas suitable to conduct a season-long exploration of how roadside disturbance alters native bee assemblages in the second year of the study. The effect of roadside disturbance was examined across

two habitat types in the second year, key forage resources identified, and bee species which may serve as indicators of roadside disturbance suggested.

Chapter 3 takes a closer look at the forage plants of some common halictid species found in Chapter 2. Host plants for these bees were identified, individual specimens analyzed for pollen, and historical floral records examined. The final chapter reviews the findings of the both studies in context with previous publications and offers future research directions.



Figure 1.1. A halictid female, *Lasioglossum (Dialictus*), foraging on *Raphanus raphanistrum*

Chapter 2:

Impact of Roadside Disturbance on Native Bee Foragers in Oregon

Keywords: verge, pollinator, conservation, invasive weeds, diversity, grassland

Introduction

Anthropogenic disturbance has broad impacts on plant and animal communities. Increasingly, this disturbance is being associated with long-term changes in nutrient cycling, vegetation patterns, and animal diversity (Ellison and Farnsworth, 1996, Dale *et al.*, 2001, Thonicke *et al.*, 2008, Winfree *et al.*, 2009). The biological impact of habitat disturbance is often measured by changes in plant and arthropod communities. Because arthropods, particularly insects, respond rapidly to environmental change (Rosenberg *et al.*, 1986; Kremen *et al.*, 1993) they are often used as bioindicators of ecosystem health.

Insects have long been used as bioindicator organisms in aquatic systems (Rosenberg *et al.*, 1986). In terrestrial systems, bees have become a species group of great interest because of their ecological (Linder, 1998; Klein *et al.* 2007) and agricultural (Klein *et al.* 2007; Chaplin-Kramer *et al.*, 2011) importance as pollinators, as well as their diverse responses to habitat disturbance (Tscharntke *et al.*, 1998; Basset *et al.*, 2008).

A number of different types of disturbance have been examined with respect to bee populations: habitat degradation/fragmentation, conversion to agriculture, pesticide use, fire, grazing, logging, disease, and roadside disturbance (Potts *et al.* 2003; Harris and Johnson 2004, Goulson 2008; Hopwood, 2008; Winfree *et al.*, 2009). By far, the effect of habitat fragmentation has received the most attention (Winfree *et al.*, 2009), with the

effect of roadside disturbance being addressed by a single study (Hopwood, 2008).

Roadsides are pervasive, accounting for over 10 million acres of land in the United States (Forman *et al.*, 2003). The area potentially affected by roadside disturbance is even greater, as roads can significantly affect soil quality over 150 m away from the edge of the road surface through alterations in pH (Auerbach, 1997; Hansen and Clevenger, 2005), heavy metals (Bell *et al.* 2010), and non-native vegetation (Gelbard and Belnap, 2003). These changes can lead to the alteration of the quantity and quality of the two key resources required for bee survivalship, namely foraging and nesting (Gelbard and Belnap, 2003; Steffan-Dewenter and Westphal, 2008; Noordijk *et al.*, 2009).

Despite the prevalence of roadsides, very little is known about their effects on bee diversity and abundance. In the one study that has addressed this issue, Hopwood (2008) compared bee populations at 'weedy' and 'restored' roadsides to remnant Iowa prairie. Bee richness was lower at 'weedy' roadsides than prairie remnants, while 'restored' roadsides had a similar bee composition to prairie remnants, indicating that the prevalence of non-native plants at roadsides could hinder native bee populations. However, the focus of the study was the effect of restoration, not the effect of roadside disturbance, which is known to promote the establishment and spread of non-native vegetation (Gelbard and Belnap, 2003). There is thus a clear need to explore the effect of typical (non-restored) roadsides on native bees.

The objectives of this study were to (1) investigate the effect of roadside disturbance on native bee forager richness and abundance and (2) determine which, if any, native bee species may serve as bioindicators of roadside disturbance.

Methods

This study was conducted over a two year period in Oregon. In the first year, a statewide survey was conducted, focusing on halictids. Using information from the first year's survey, sites were selected for season-long analysis of all bee species in the second year. All sites consisted of a paired roadside and natural area, with roadsides matched for width, depth, aspect, and highway type. In the second year, additional data were collected on season-long floral and temperature trends in order to account for the confounding effects of these variables.

Study area

In year one of this study, twenty-four paired roadside verges and non-roadside natural areas were sampled across the state of Oregon. Sites were selected via a stratified random sampling method; a 0.5 latitude by 0.5 longitude grid was placed over a map of the state, and three quadrants were selected from each of Oregon's eight principal level III ecoregions (Central Pacific coastal forests, Willamette Valley grasslands, Klamath-Siskiyou forests, Central and Southern Cascades forests, Eastern Cascades forests, Snake-Columbia shrub steppe, Blue Mountain forests, and Palouse grasslands; Fig 2.1). Some level of grazing had occurred at all 24 remnant natural areas. All roadside sample sites were adjacent to paved roads with the exception of one in the

southeastern corner of Oregon, as no paved roads were present within the quadrant. At this site, a gravel road was selected instead.

Using the information from the first year's statewide survey, two quadrants were chosen for closer analysis in year two. The Willamette Valley prairie and the Snake-Columbia shrub steppe south of Madras were chosen, as both had high bee richness and abundance in year one, and are open habitat types with similar surrounding land use. In each quadrant, two sites were selected for season-long sampling (Fig 2.2 and 2.3). The roadside verge at each site bordered a paved 2-lane highway. In the Willamette Valley, samples were taken on Finley National Wildlife Refuge (Finley NWR), E. E. Wilson Wildlife Area (EEW). In the Madras area, samples were taken in the Crooked River National Grasslands (CRNG).

To reduce the likelihood of sampling from the same population at different sites, all sample sites in this study were >10 km apart, greater than the maximum observed foraging distance of many bee species (Osborne *et al.*, 1999; Beekman and Ratnieks, 2000; Greenleaf *et al.*, 2007; Zurbuchen, 2010, Rao and Strange, 2012). The paired roadside verge and natural area were 200-500m apart, a distance within the foraging range of many species (Osborne *et al.*, 1999; Zurbuchen, 2010). Surrounding land use within a 5 km radius of each site was determined with the use of satellite imagery (NASA Landsat Program, 2012). Roadsides were all managed by the Oregon Department of Transportation (ODOT) with similar management plans; mowing and strip herbicide sprays did not occur during the sampling period. Two spot-treatments of

a mixture of picloram, aminopyralid, and dicamba for spotted knapweed were made by ODOT during sampling in Central Oregon in the second year of the study. Non-native forbs were common at both roadsides and natural areas.

Estimation of native bee richness and abundance

Bees were sampled primarily using hand-collecting methods. At each roadside and natural area, a ~200m transect was established parallel to the road. Each transect was then traversed at a slow walk (1-5 m per minute) and specimens were collected through a combination of hand-collecting, aspiration and directed sweep-netting. At each site, two ~200m transects were established parallel to the road. Each transect was then traversed at a slow walk (1-5 m per minute) and bees were collected through a combination of hand-collecting and directed sweep-netting. Collections occurred on days without precipitation where the average temperature was above 18°C

During the preliminary statewide survey in year one, each ecoregion was sampled three times (24 samples in total): late spring (May 27-Jun 5), summer (Jun 25-Jul 6), and late summer (Jul 19-Aug 1). Each site was sampled between 8:30 am and 2:00 pm. Collections were focused on halictid bees.

In year two, sampling was expanded temporally, and the species collected broadened. Each of the four sites was sampled 14 times (56 samples in total), once every one to two weeks between May 5 and September 12. Each site was sampled between 8:30 am and 5:00 pm. Bees from all families were collected.

Bees from both years were stored—individually frozen or in ethanol—sorted, and identified. Identifications were made using Stephen (1957), Stephen *et al.* (1969), Roberts (1973a and 1973b), McGinley (1986), Michener (2007), and the Oregon State Arthropod Collection, or, where regional keys and identified specimens were not available (particularly for *Lasioglossum* [*Dialictus*]), specimens were sorted to subgenus or morphospecies. Specimens are vouchered in the Rao Lab Native Bee Collection at Oregon State University.

Estimation of temperature, floral richness and floral abundance

In both years, floral richness was calculated by examining all in-bloom forbs within a 5-m band centered around the transect line. In the first year of the study, this measure was taken once at the roadside and once at the natural area for each of the 24 sites. In the second year of the study, this measure was taken 14 times throughout the season at each natural area and roadside.

In the second year of the study, the quantity of bloom was estimated during each successive visit to Willamette Valley and High Desert sites in order to approximate flowering phenology. A 1x1 m PVC square was tossed every 20-30 m along each transect. The 1x1 m area was photographed and digitally adjusted for distortion, scaled to a standard size and analyzed to estimate percentage cover of open flowers.

Temperature was recorded with a handheld reader (Sper Scientific) at the end of each

roadside and natural area sample.

Data analysis

The effect of roadside disturbance on bee abundance and richness was explored by examining data from both years with multivariate statistical analysis. Non-metric multidimensional scaling (MDS) was used to summarize bee incidence temporally and across site types with an ordination plot generated in R (R Development Core Team, 2010). In an ordination plot, sites with similar species composition are plotted closer together than those with dissimilar species composition. Distribution of bee species across site types were explored with 95% confidence elipses, calculated using bivariate standard deviation (Milligan *et al.*, 2004). Ellipses were generated by the ORDIELLIPSE function in the R-package VEGAN (Oksanen et al., 2012). Interpretation of the MDS plots was checked with an analysis of similarities (ANOSIM) test. Significance was determined at α = 0.05.

Indicator Species Analysis (ISA; Dufrêne & Legendre, 1997) was used to identify indicator species for roadside and natural area site types, both in the Willamette Valley and in central Oregon. This analysis tests species fidelity to site types and assigns each species an indicator value. ISA was conducted in R with the package INDICSPECIES (Caceres and Jansen, 2010). Significance for this analysis was determined at α = 0.10, the level recommended by McCune and Grace (2002) for indicator species analysis. Taxa comprising less than 0.2% of the total species abundance were excluded from this analysis to avoid rare taxa bias.

Results

Estimation of native bee richness and abundance

In year one, 1,226 bees were collected across 22 out of the 24 sites surveyed. Members of the family Halictidae comprised 80.1% of the total catch (Fig 2.4). Five genera of Halictidae were collected, with the subgenus *Dialictus* accounting for more half of all halictids (49.3%; Table 2.1). Ordination of bee populations found at all 24 sites indicated that roadside disturbance was not associated with changes in species composition (p > 0.1; Fig 2.5), or with ecoregion (p = 0.083). Although ordination of data collected from year one did not yield significant results, there was suggestive evidence that the subgenus *Dialictus* may be more abundant at natural areas than at roadsides (p = 0.051).

In year two, 1,686 bees were collected from the four study sites, representing 25 genera and over 90 species (Table 2.2), including the non-native European honey bee (*Apis mellifera* L.). The number of bees caught at roadside sites and natural areas did not differ (p > 0.01), but a larger number of non-*Apis* bees were collected at natural sites (Fig 2.4). Overall, Apidae was the most commonly collected family (731 specimens), but, excluding *A. mellifera* (478 specimens), Halictidae was the most commonly collected family (684 specimens).

Estimation of temperature, floral richness and floral abundance

Floral density changed significantly over time (p = 0.012) in year two, peaking in early July and again in early September in Central Oregon, and in late May through mid-

June in the Willamette Valley. Overall floral richness did not significantly change over time, but highest richness was seen in mid-June through mid-July in the high desert, and late June through early July in the Willamette Valley. A large percentage (42.3%) of specimens were collected off of invasive weeds (Table 2.3). At every site except the East1 natural area (the only site without exotic plant species), exotic plants were the primary blooming resource during the month of June.

There was a strong positive correlation between average temperature and bee abundance and richness (p = 0.005) in year two of the study, but no significant relationship between floral characteristics and bee species composition (p > 0.1, Table 2.4).

Data collected in year two had less sample-to-sample variation in bee richness due to repeated within-season site sampling. Initial ordination of 2012 specimen data revealed several outliers (Fig 2.6). All outlier species originated from the first sample of a single Central Oregon site (East1). These spring species affected the overall significance of roadside versus natural area (p = 0.001 with, p = 0.816, without; ANOSIM, 1000 permutations). As species composition at the Willamette Valley and Central Oregon sites was significantly different (p = 0.001 with or without outliers; ANOSIM, 1000 permutations), eastern and western sites were analyzed separately.

In Willamette Valley natural areas, bee richness ranged from 7 to 26, with an average of 17 species. Bee abundance ranged from 7 to 54, with an average of 23 individuals.

In paired roadside samples, bee richness ranged from 3 to 26, with an average of 14 species. Bee abundance ranged from 3 to 47, with an average of 25 individuals. Ordination of western species revealed a significant difference in species composition between roadsides and natural areas (p = 0.001; ANOSIM, 1000 permutations; Fig 2.7).

In Central Oregon natural areas, bee richness ranged from 1 to 12, with an average of 5 species. Bee abundance ranged from 1 to 39, with an average of 16 individuals. In paired roadside samples, bee richness ranged from 1 to 13, with an average of 5 species. Bee abundance ranged from 1 to 41, with an average of 14 individuals. Ordination of eastern species including outliers did not detect a significant difference in species composition between roadsides and natural areas (p > 0.1; ANOSIM, 1000 permutations; Fig 2.8). In this ordination, *Lasioglossum titusi* was an outlier, with only two specimens collected in Central Oregon sites. Removing initial outliers, but not *L. titusi*, did not change the significance (p > 0.1), nor did removing *L. titusi* alone (p > 0.1), or all four outliers (p > 0.1).

Indicator species

Indicator species were selected at α = 0.10 and IV > 0.35 (Table 2.5). Only one species was selected as a potential indicator of roadside conditions, *A. mellifera*, while five were selected as potential indicators of natural areas: *Bombus appositus*, *B. californicus*, *B. griseocollis* in the Willamette Valley, *Agapostemon femoratus* in Cenral Oregon and *Lasioglossum* (*Dialictus*) in both regions. The subgenus *Dialictus*

was the strongest indicator of natural area conditions (IV = 0.73, p = 0.030).

Discussion

Summary

This is the first study to examine the impacts of roadside disturbance on bee communities in the western United States. Disturbance was found to have a negative impact on native bee abundance and richness in the Willamette Valley, but not in Central Oregon. The findings of this study thus indicate that habitat type has the potential to change the effect of roadside disturbance on bee populations. Hopwood (2008), noted a similar trend within-habitat at sites that had different floral communities. Roadside disturbance may, then, generally, impact bee communities differently in different habitat types. This finding, that habitat type affects bees' response to disturbance, is consistent with previous studies on other types of anthropogenic disturbance (Tylianakis *et al.*, 2005; Winfree *et al.*, 2006; Cane *et al.*, 2006; Aizen, 2007; Frankie *et al.*, 2009; Winfree *et al.*, 2009). Unlike these studies, however, neither floral richness nor abundance was associated with increased bee richness or abundance. This finding may be an artifact of sampling a set transect in connected landscapes where bloom is patchy and dispersed.

While this study did not find a significant relationship between bees and floral findings, roadside disturbance was, interestingly, associated with altered bee communities in Western Oregon, but not Eastern Oregon. It is interesting to note that a large number of kleptoparasitic species were collected at the West1 site—principally in

the natural area—represented by numerous members of the genera *Nomada* and *Sphecodes*. Given the bare ground and management conditions at this site, it is possible that the area is host to high density nesting of native species.

Although *A. mellifera* was selected as a possible bioindicator of roadside disturbance, the species is ubiquitous, and was collected at every site, natural and roadside, it cannot be recommended as an indicator species. One possible cause for this selection was that honey bees in the Willamette Valley were most commonly collected on exotic, mass-flowering plants, such as Himalayan blackberry and pennyroyal, which were principally found at those sites. No equivalent mass-flowering resource was located differentially at roadsides in Central Oregon.

Five possible indicators of natural habitat were found, the strongest being the subgenus *Dialictus*, which was an indicator for both Central Oregon and Willamette Valley sites. However, given the limited scope of this study, more research is necessary before this group could be considered a bioindicator of natural habitat in Oregon.

Effect of temperature and floral characteristics on bee diversity and abundance

Much of the variation in bee populations in the Willamette Valley and Central Oregon

could be explained by temperature alone. Floral characteristics, however, measured in

year two of the study, did not appear to have a significant effect on bee communities. It

is possible that this finding is a result of sparse sampling; sampling once every 1-2

weeks will yield only one or two data points for many short-flowering plant species.

This can result in high seasonal variability and hinder statistical analysis. Future years of surveying have the potential to yield more satisfactory data with regards to bees and their response to floral resources.

This study also highlights the importance of non-native plants as a food resource for pollinators, as 42% of collected specimens were from these plants. The high utilization of exotic plants by native bees found here supports previous findings by Tepedino *et al.* (2008) and Bergh (2011).

Effect of disturbance on bee diversity and abundance

Sites in Central Oregon did not show a strong effect of roadside disturbance on bee populations. Although these roadsides had similar physical characteristics as sites in the Willamette Valley, there was no clear line between Central Oregon verges and the associated natural area. Except for outcroppings of tumblemustard and tansymustard, there was little visual difference between the two site types. In the more lush Willamette Valley, roadside verges are often backed by hedgerows, which may impede travel between the two sites. This is an interesting possibility, as hedgerows are often considered beneficial for bees (Hannon and Sisk, 2009; Le Féon *et al.*, 2011). In addition, western roadside sites had larger populations of attractive exotic plants, such as Himalayan blackberry and pennyroyal.

A growing body of work is examining the possibility of honey bee – native bee competition for floral resources (Schaffer *et al.*, 1983; Buchman *et al.*, 1996; Thomson,

2004; Shavit *et al.*, 2009). Honey bees were abundant at Western Oregon roadside sites and were observed chasing away smaller, native bees throughout the study period. While no data were collected pertaining to competition, the difference in community composition between roadsides and natural areas may be a case of competitive exclusion.

Conclusions

The effect of roadside disturbance on bee populations appears to be more pronounced in the Willamette Valley than in Central Oregon. In the apparently more susceptible western sites, roadside disturbance seems to promote honey bees, and have a negative impact on native bees, particularly the subgenus *Lasioglossum* (*Dialictus*). Hopwood (2008) also observed reduced native bee richness and abundance when examining non-restored roadsides. It is possible that the negative effect of roadsides in the Willamette Valley could be mitigated by roadside restoration, which Hopwood found to increase bee richness and abundance to levels similar to remnant natural areas.

Managing roadsides for native bees has the possibility of creating large, connected thoroughfares, which can become reservoirs for native species. However, care should be taken when creating new management plans. Many current roadside management and conservation practices focus on the control and/or removal of exotic plant species; as this study, along with others (Tepedino *et al.*, 2008; Bergh, 2011) have found, these exotic species may be the principal resource available to native bees at the time of bloom. Small changes in management tactics, such as mowing after attractive exotic

species have passed peak bloom, may help sustain bee populations. By managing plants in roadside areas so that attractive bloom, whether from exotic or native plants, is available season-long, these sites may become valuable resources for native bee populations.

Because bee populations can vary greatly from region to region, local-level sampling is necessary in order to determine which bee species are present, and which flowers are visited by those species. This is important not just for the understanding of roadside disturbance, but any disturbance—anthropogenic or natural.

Bees are vital for the continued functioning of agricultural and ecological systems.

Conservation efforts are necessary in order to maintain current bee populations and prevent future declines. Although roadsides are not often considered habitat for native bees, there is potential for these large corridors to host and even bolster native bee populations. Managing roadsides for native bees is an option which merits further investigation and may supplement existing conservation programs.

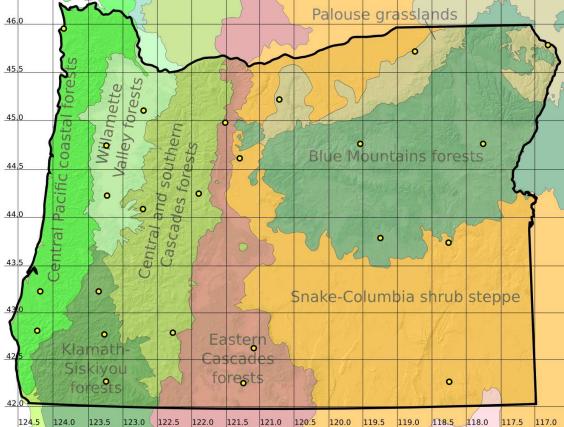


Figure 2.1. Map of sites surveyed in 2011. Three sites were sampled in each of Oregons eight principal ecoregions, as described by Olson and Dinerstein (2002)



Figure 2.2. Map of sites surveyed in 2012. West1 = E.E. Wilson Wildlife Refuge, West2 = Finley National Wildlife Refuge, East1 = Crooked River National Grassland (east), East2 = Crooked River National Grassland (west)



Figure 2.3. Examples of sites sampled in the Willamette Valley (top) and Central Oregon (bottom).

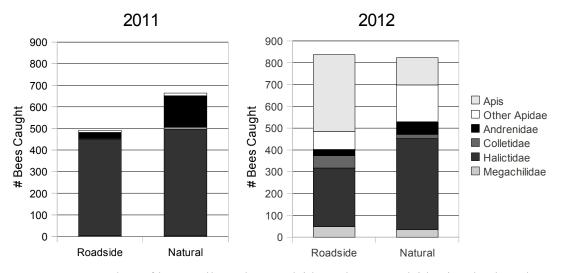


Figure 2.4. Number of bees collected at roadside and non-roadside sites broken down by family. Left: 2011 collections focusing on Halictidae. Right: 2012 collections of all bees.

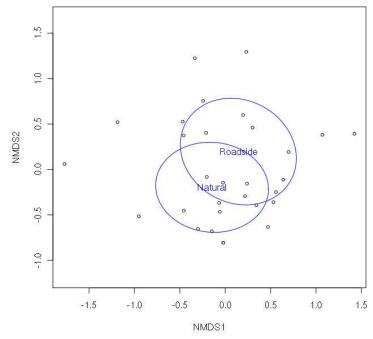


Figure 2.5. Ordination plot of bee populations found at sites in 2011. Circles represent individual sampling events. Ellipses are 95% confidence regions for roadside and natural area species composition.

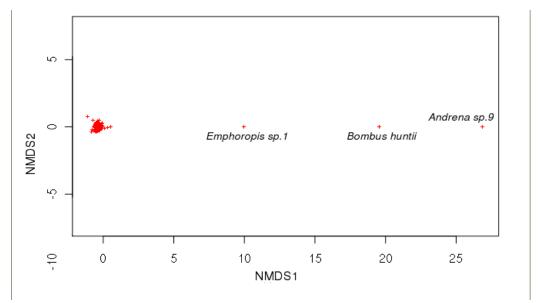


Figure 2.6. Ordination plot of bee species distribution across all roadsides and natural areas in 2012. Crosshairs represent individual bee species. The three labelled outliers all originate from a single sample: the first survey of the East1 site.

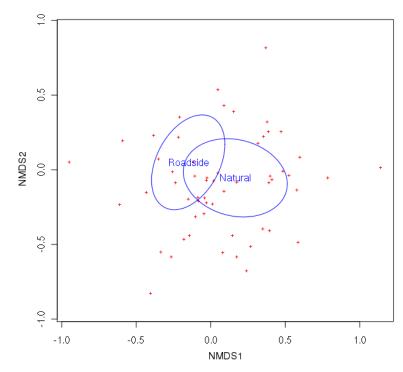


Figure 2.7. Ordination plot of bee species distribution in Willamette Valley roadsides and natural areas. Crosshairs represent individual bee species. Ellipses are 95% confidence regions for roadside and natural area species.

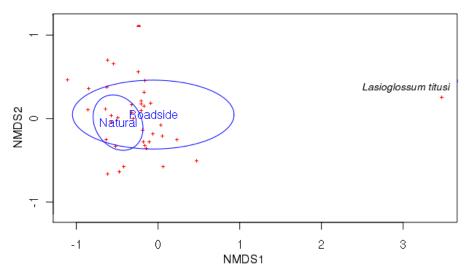


Figure 2.8. Ordination plot of bee species distribution in Central Oregon roadsides and natural areas. Crosshairs represent individual bee species. Ellipses are 95% confidence regions for roadside and natural area species.

Table 2.1. Halictid species collected in 2011 from 24 sites across Oregon

	Site																	
G	BMF		CPCF		CSCF		ECF		KSF		PP		SCSS		WV		Total	
Genus	R	N	R	N	R	N	R	N	R	N	R	N	R	N	R	N	Collected ¹	
Agapostemon	0	0	0	1	1	0	0	0	1	0	0	1	11	14	0	0	29	(2)
Duforea	0	0	0	0	3	0	0	0	0	2	0	0	0	1	0	0	6	(2)
Halictus	4	13	5	22	5	3	36	41	55	3	19	30	52	15	9	16	328	(6)
Lasioglossum (s.s.)	4	1	8	21	3	0	0	1	3	5	3	10	0	6	2	0	67	(6)
Lasioglossum (Dialictus)	38	35	14	45	28	27	12	35	8	19	50	39	57	25	11	8	432 (>	>20)
Sphecodes	0	1	0	0	4	2	1	0	0	1	0	0	2	0	2	0	13	(6)
Total	46	50	27	89	44	32	49	77	65	30	72	80	122	61	24	24		705

Numbers in parentheses represent the number of species collected for each genus

BM = Blue Mountain Forests, CPCF = Central Pacific Coastal Forests, CSCF = Central and Southern

Cascased Forests, ECF = Eastern Cascades Forest, KSF = Klamath-Siskyou Forests, PP = Palouse

Prairie, SCSS = Snake-Columbia Shrub Steppe, WV = Willamette Valley

Table 2.2. Bees collected in 2012 from the Willamette Valley and Central Oregon. EEW = E.E. Wilson Wildlife Refuge, FNWR = Finley National Wildlife Refuge, HWY26 = Crooked River National Grassland (east), HWY97 = Crooked River National Grassland (west)

r (wording)	ssianu (west)	Site							
	Species	EI	EW	FNWR		HWY26		HW	Y97
Family		R	N	R	N	R	N	R	N
Andrenidae	Andrena caerulea		√						
	Andrena sp.1	√			√				
	Andrena sp.2	√			√				
	Andrena sp.3	√	√		√				
	Andrena sp.4					√		√	1
	Andrena sp.5	√							
	Andrena sp.6	√							
	Andrena sp.7							√	
	Andrena sp.8		√						
	Andrena sp.9						√		
	Andrena sp.10		√						
	Perdita sp.1					√	√	√	√
	Perdita sp.2								√
	Perdita sp.3			√					
Apidae	Anthophora urbana		√			√	√	√	√
1	Apis mellifera	√	√	√	√	√	√	√	√
	Bombus appositus		√		√				
	Bombus californicus		√	√	√				
	Bombus caliginosus	√							
	Bombus griseocollis	√	√	√	√				
	Bombus huntii						√		√
	Bombus mixtus	√	√	√	√				
	Bombus nevadensis	√	√		√				
	Bombus vosnesenskii	√	√	√	√			√	
	Ceratina acantha	√	√	1	√	√	√		√
	Ceratina michneri		√			√			√
	Ceratina nanula	√	√	√	√	√	√	√	√
	Emphoropis sp.1						√		
	Melissodes metenua		√						
	Melissodes pulatella			√					
	Melissodes rivalis		√						
	Melissodes robustior							√	
	Melissodes sp.1							√	√
	Nomada sp.1		√						

	Species	Site							
		EEW		FNWR		HWY26		HW	Y97
Family		R	N	R	N	R	N	R	N
	Nomada sp.2	√							
	Nomada sp.3								√
	Nomada sp.4	√							
	Nomada sp.5				√				
	Synhalonia sp.1		√			√			
Colletidae	Colletes sp.1	√							
	Colletes sp.2								√
	Hylaeus sp.1	√		√					
	Hylaeus sp.2	√		√	√				
	Hylaeus sp.3	√		√	√				
	Hylaeus sp.4	√	√	V	√				
	Hylaeus sp.5	√		√	√				
	Hylaeus sp.6				√				
Halictidae	Agapostemon femoratus					V		√	
	Agapostemon texanus/angelicus	√				V		√	
	Agapostemon virescens	√		1					
	Duforea sp.1								√
	Halictus confusus	√							
	Halictus farinosus	√		√	√				
	Halictus ligatus	√	√		√	√	√	√	√
	Halictus rubicundus	√	√	√	√	V			
	Halictus tripartitus	√	√	√		V	√		
	Lasioglossum (Dialictis) ¹	√	√	√	√	√	√	√	√
	Lasioglossum mellipes							√	
	Lasioglossum olympiae	√	√	√	√			√	
	Lasioglossum pacificum	√	√		√				√
	Lasioglossum sisymbrium	√	√	√	√	√	√	√	√
	Lasioglossum titusi		√		√	√			
	Lasioglossum trizonatum		√						
	Sphecodes sp.1		√		√				
	Sphecodes sp.2						√		
	Sphecodes sp.3	√	√						
	Sphecodes sp.4		√						
	Sphecodes sp.5		√						
	Sphecodes sp.6	√	√		√				
	Sphecodes sp.7	√							
	Sphecodes sp.8						√		
	Anthidium sp.1					√			

			Site								
	Species		EEW		FNWR		HWY26		HW	Y97	
Family		R	N	R	N	R	N	R	N		
Megachilidae	Ashmeadiella sp.1		√	√	√	√					
	Ashmeadiella sp.2						√	V			
	Ashmeadiella sp.3						√				
	Callanthidium sp.1							√			
	Dianthidium sp.1						√				
	Hoplitis sp.1						√		√		
	Hoplitis sp.2									√	
	Hoplitis sp.3		√				√				
	Hoplitis sp.4						√	V			
	Megachile brevis		V								
	Megachile pascoensis			√					√		
	Megachile perihirta			√		√	√				
	Osmia lignaria						√	√			
	Osmia sp.1						\checkmark	√		√	
	Osmia sp.2						√				
	Osmia sp.3							√		√	
	Osmia sp.4			√		√					
	Osmia sp.5		V								
	Osmia sp.6						√				
		Total	39	38	23	31	28	48	18	20	

¹ There were more than 10 species within this subgenus

Table 2.3. Common forage plants of bees caught in 2012

Family	Species	Bees Collected
Apiaceae	Daucus carota ^I	62
Asteraceae	Chrysothamnus viscidiflorus N	89
	Eriophyllum lanatum N	129
Brassicaceae	Sisymbrium altissimum ^I	101
Caprifoliaceae	Symphoricarpos albus N	119
Geraniaceae	Geranium spp. I/N	33
Hypericaceae	Hypericum perforatum ^I	57
Lamiaceae	Mentha pulegium ^I	207
Onagraceae	Epilobium spp. ^N	35
Rosaceae	Rubus armeniacus ^I	172

Introduced species

Table 2.4. Non-metric, multidimensional scaling analysis of the effects of date, temperature, floral density and richness on bee populations

temperature, merar density and members on ever populations								
	NMDS1	NMDS2	r^2	Pr(>r)				
Date	0.95836	-0.28556	0.1048	0.015 *				
FloralDensity	-0.98840	-0.15188	0.0066	0.753				
FloralRichness	-0.37485	-0.92708	0.0301	0.272				
AvgTemp	0.83233	0.55429	0.1382	0.005 **				

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' '1 P values based on 999 permutations.

N Native species

Table 2.5. Bee species identified as indicator taxa through Indicator Species Analysis for roadside and natural areas

Site Type	Order	Species	IV*	P-value
Roadside	Apidae	Apis mellifera	0.6905715	0.035
Natural	Apidae	Bombus appositus	0.4131969	0.015
		Bombus californicus	0.4543046	0.005
	Bombus griseocollis		0.4737586	0.010
	Halictidae	Agapostemon femoratus	0.3814531	0.050
		Lasioglossum (Dialictus)	0.7324615	0.030

^{*} Indicator Variable α = 0.10

References

- Aizen, M.A. 2007. Enfoques en el estudio de la reproduccion sexual de las plantas en ambientes alterados: limitaciones y perspectivas. Aust. Ecol. 17:7-19.
- Auerbach, N.A., M.D. Walker, and D.A. Walker. 1997. Effects of roadside disturbance on substrate and vegetation properties in arctic tundra. Ecological Applications 7:218-235.
- Basset, Y., O. Missa, A. Alonso, S.E. Miller, G. Curletti, M. De Meyer, C. Eardley, O.T.
 Lewis, M.W. Mansell, V. Novotny and T. Wagner. 2008. Changes in
 Arthropod Assemblages along a Wide Gradient of Disturbance in Gabon.
 Conservation Biology 6:1552-1563.
- Beekman, M., and F. L. W. Ratnieks. 2000. Long-range foraging by the honey-bee, Apis mellifera L. Functional Ecology 14:490-496.
- Bell, T., S. Campbell, D.G.E. Liverman, D. Allison, and P. Sylvester. 2010.

 Environmental and potential human health legacies of non-industrial sources of lead in a Canadian urban landscape the case study of St John's, Newfoundland. 52:771-800.
- Bergh, J.E. 2011. Native Bee Diversity and Floral Resource Availability in Two Willamette Valley Oregon Ecosystems. Master's thesis. Oregon State University.
- Buchmann, S. L., A. Matheson, C. O'Toole, P. Westrich, and I.H. Williams. 1996.

 Competition between honey bees and native bees in the Sonoran Desert and global bee conservation issues. Academic Press for the Linnean Society of London and the International Bee Research Association. pp. 125-142.

- Caceres, M., and F. Jansen. 2010. indicspecies: Functions to assess the strength and significance of relationship of species site group associations (R package). http://cran.r-project.org/web/packages/indicspecies/index.html
- Cane, J.H., R.L. Minckley, L.J. Kervin, T.H. Roulston, and N.M. Williams. 2006.

 Complex responses within a desert bee guild (Hymenoptera: Apiformes) to urban habitat fragmentation.
- Chaplin-Kramer, R., K. Tuxen-Bettman, C. Kremen. 2011. Value of wildland habitat for supplying pollination services to Californian agriculture. Rangelands 33:33-41.
- Dale, V.H., L.A. Joyce, S. McNulty, R.P. Neilson, M.P. Ayres, M.D Flannigan, P.J.
 Hanson, L.C. Irland, A.E. Lugo, C.J. Peterson, D.S. Simberloff, F.J. Swanson,
 B.J. Stocks and B.M. Wotton. 2001. Climate change and forest disturbances.
 BioScience, 51:723-734.
- Dufrêne, M. and P. Legendre. 1997. Species assemblages and indicator species: The need for a flexible asymetrical approach. Ecological Monographs 67:345-366.
- Ellison, A.M. and E.J. Farnsworth 1996. Anthropogenic disturbance of Caribbean mangrove ecosystems: past impacts, present trends, and future predictions. Biotropica, 549-565.
- Frankie, G.W., M. Rizzardi, S.B. Vinson, and T.L. Griswold. 2009. Decline in Bee Diversity and Abundance from 1972-2004 on a Flowering Leguminous Tree, Andira inermis in Costa Rica at the Interface of Disturbed Dry Forest and the Urban Environment. Journal of the Kansas Entomological Society 82:1-20.
- Forman, R.T.T., D. Sperling, J.A. Bissonette, A.P. Clevenger, C.D. Cutshall, V.H. Dale,

- L. Fahrig, R. France, C.R. Goldman, K. Heanue, J.A. Jones, F.J. Swanson, T. Turrentine, and T.C. Winter. 2003. Road ecology: science and solutions. Island Press, Washington, D.C., USA.
- Frankie, G.W., M. Rizzardi, S.B. Vinson, and T.L. Griswold. 2009. Decline in Bee Diversity and Abundance from 1972-2004 on a Flowering Leguminous Tree, Andira inermis in Costa Rica at the Interface of Disturbed Dry Forest and the Urban Environment. Journal of the Kansas Entomological Society 82:1-20.
- Gelbard, J.L., and J. Belnap. 2003. Roads as Conduits for Exotic Plant Invasions in a Semiarid Landscape. Conservation Biology 17:420-432.
- Goulson, D., G.C. Lyle, and B. Darvill. 2008. Decline and conservation of bumble bees. Annual Review of Entomology 53:191-208.
- Greenleaf S, N. Williams, R. Winfree, and C. Kremen. 2007. Bee foraging ranges and their relationship to body size. Oecologia 153:589-596.
- Hannon, L.E., and T.D. Sisk. 2009. Hedgerows in an agri-natural landscape: Potential habitat value for native bees. Biological Conservation *142*:2140-2154.
- Hansen, M.J. and A.P. Clevenger. 2005. The influence of disturbance and habitat on the presence of non-native plant species along transport corridors. Biological Conservation 125:249-259.
- Harris, L.F. and S.D. Johnson. 2004. The consequences of habitat fragmentation for plant-pollinator mutualisms. International Journal of Tropical Insect Science 24: 29-43.
- Hopwood, J.L. 2008. The contribution of roadside grassland restorations to native bee

- conservation. Biological Conservation. 141:2632-2640.
- Klein, A.-M., B.E. Vaissiére, J.H. Cane, I. Steffan-Dewenter, S.A. Cunningham, C. Kremen, and T. Tscharntke. 2007. Importance of pollinators in changing landscapes for world crops. Proceedings of the Royal Society of London B 274:303-313.
- Kremen, C., R.K. Colwell, T.L. Erwin, D.D. Murphy, R.F. Noss, M.A. Sanjayan. 1993.

 Terrestrial arthropod assemblages: their use in conservation planning.

 Conservation Biology 7:796–808.
- Le Féon, V., F. Burel., R. Chifflet, M. Henry, A. Ricroch, B.E. Vaissière, and J. Baudry. 2011. Solitary bee abundance and species richness in dynamic agricultural landscapes. Agriculture, Ecosystems & Environment. Available online 26 July 2011, ISSN 0167-8809, 10.1016/j.agee.2011.06.020.

 (http://www.sciencedirect.com/science/article/pii/S0167880911002118)
- Linder, H.P. 1998. Morphology and the evolution of wind pollination. pp 123-135 in S.J. Owens and P.J. Rudall, eds. Reproductive biology. Royal Botanic Gardens, Kew, Richmond, UK.
- McCune, B. and J.B. Grace. 2002. Analysis of Ecological Communities. MjM Software Design, Gleneden Beach. 300pp.
- McGinley, R.J. 1986. Studies of Halictinae (Apoidea, Halictidae), I: Revision of New World Lasioglossum Curtis. Smithsonian Institution Press. 294pp.
- Michener, C.D. 2007. The Bees of the World. Second edition. The Johns Hopkins University Press, Baltimore. 992 pp.

- Milligan, A.L., P.D. Putwain, E.S. Cox, J. Ghorbani, M.G. Le Duc, and R.H. Marrs. 2004. Developing an integrated land management strategy for the restoration of moorland vegetation on *Molinia caerulea*-dominated vegetation for conservation purposes in upland Britain. Biological Conservation, 119:371-385.
- NASA Landsat Program. 2012. Landsat ETM+ scene. SLC-Off, USGS, Sioux Falls, 2012.
- Noordijk, J., A.P. Schaffers, K.V. Sýkora. 2008. Diversity of ground beetles (Coleoptera: Carabidae) and spiders (Araneae) in roadside verges with grey hair-grass vegetation. European Journal of Entomology 105:257-265.
- Oksanen, J., F.G. Blanchet, R. Kindt, P. Legendre, P.R. Minchin, R.B. O'Hara, G.L. Simpson, P.Solymos, M. Henry, H. Stevens and H. Wagner. 2011. vegan:

 Community Ecology Package. R package version 2.0-2. http://CRAN.R-project.org/package=vegan
- Olson, D.M., E. Dinerstein. 2002. The Global 200: Priority ecoregions for global conservation. Annals of the Missouri Botanical Garden 89:199-224.
- Osborne, K.E., and B.P. Oldroyd. 1999. Possible causes of reproductive dominance during emergency queen rearing by honeybees. Animal Behaviour 58:267-272.
- Potts, S.G., B. Vulliamy, A. Dafni, G. Ne'eman, and P. Willmer. 2003. Linking bees and flowers: how do floral communities structure pollinator communities? Ecology 84: 2628-2642.
- R Development Core Team (2010). R: A language and environment for statistical

- computing, reference index version 2.x.x. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.
- Rao, S., W. Stephen, L. White. 2009. Native Bee Pollinator Diversity in Oregon Blueberries. Acta Horticulturae (ISHS) 810:539-548.
- Rao, S. and J. Strange. 2012. Bumble Bee (Hymenoptera: Apidae) Foraging Distance and Colony Density Associated With a Late-Season Mass Flowering Crop. Environmental Entomology 41:905-915.
- Roberts, R.B. 1973. Bees of northwestern America: Agapostemon (Hymenoptera: Halictidae). Agricultural Experiment Station, Oregon State University, Corvallis.
- Roberts, R.B. 1973. Bees of northwestern America: Halictus (Hymenoptera: Halictidae). Agricultural Experiment Station, Oregon State University, Corvallis.
- Rosenberg D.M., H.V. Danks, D.M. Lehmkuhl. 1986. Importance of insects in environmental impact assessment. Environmental Management 10:773–783.
- Schaffer, W.M., D.W. Zeh, S.L. Buchmann, S. Kleinhans, M.V. Schaffer and J. Antrim. 1983. Competition for nectar between introduced honey bees and native North American bees and ants. Ecology 564-577.
- Shavit, O., A. Dafni, and G. Ne'eman. 2009. Competition between honeybees (*Apis mellifera*) and native solitary bees in the Mediterranean region of Israel—

 Implications for conservation. Israel Journal of Plant Sciences 57: 171-183.

- Steffan-Dewenter, I. and C. Westphal. 2008. The interplay of pollinator diversity, pollination services and landscape change. Journal of Applied Ecology 45: 737-741.
- Stephen, W.P. 1957. Bumble bees of western America (Hymenoptera: Apoidea).

 Agricultural Experiment Station, Oregon State College.
- Stephen, W.P., G.E. Bohart, and P.F. Torchio. 1969. The biology and external morphology of bees. Oregon State University Agricultural Experiment Station.
- Stephen, W.P. and S. Rao. 2005. Unscented color traps for non-Apis bees (Hymenoptera: Apiformes). Journal of the Kansas Entomological Society. 78: 373-380.
- Tepedino, V.J., B.A. Bradley, and T.L. Griswold. 2008. Might flowers of invasive plants increase native bee carrying capacity? Intimations frm Capitol Reef National Park, Utah. Natural Areas Journal 28: 44-50.
- Thomson, D. 2004. Competitive interactions between the invasive European honey bee and native bumble bees. Ecology, 85:458-470.
- Thonicke, K., S. Venevsky, S. Sitch, and W. Cramer. 2008. The role of fire disturbance for global vegetation dynamics: coupling fire into a Dynamic Global Vegetation Model. Global Ecology and Biogeography, 10:661-677.
- Tscharntke, T., A. Gathmann, and I. Steffan-Dewenter. 1998. Bioindication using trapnesting bees and wasps and their natural enemies: community structure and interactions. Journal of Applied Ecology 35:708-719.

- Tylianakis, J.M., A.M. Klein, T. Tscharntke. 2005. Spatiotemporal variation in the diversity of Hymenoptera across a tropical habitat gradient. Ecology 86:3296-3302.
- Winfree, R., T. Griswold, C. Kremen. 2006. Effect of Human Disturbance on Bee Communities in a Forested Ecosystem. Conservation Biology 21:213-223.
- Winfree, R., R. Aguilar, D.P. Vázquez, G. LeBuhn, and M.A. Aizen. 2009. A metaanalysis of bees' responses to anthropogenic disturbance. Ecology. 90:2068– 2076.
- Zurbuchen, A., L. Landert, J. Klaiber, A. Muller, S. Hein, and S. Dorn. 2010.

 Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances. Biological Conservation. 143:669-676.

Chapter 3

Assessment of floral resources utilized by sweat bees (Hymenoptera: Halictidae): foraging and pollen analysis

for aging and ponen analysis

Keywords: native plants, invasive weeds, high desert, oak savannah, ephemeral

wetland

Introduction

Pollinators are not only essential for agricultural production, but also the continued

health of ecological environments (Bawa, 1990; Buchmann and Nabhan 1997; Aizen

and Feinsinger 2003). Bees, as the principal pollinator group, are of particular

importance (Klein et al., 2007). However, with reports of both honey bee and native

bee declines (Kremen et al., 2002; Cane and Tepidino, 2008; Goulson et al., 2008;

Pettis and Delaplane, 2010), there has arisen a need to investigate methods of bee

conservation.

A number of studies have attempted to address the issue of landscape-scale native bee

conservation (Winfree et al., 2009). In many of these studies, there is a strong focus on

agricultural landsapes and large-scale environmental variables, but relatively little

information on what flowering plants in the landscape are utilized by individual bee

species. Some management plans reflect this lack of plant-pollinator association by

assuming the 'favorite' floral hosts of honey bees and bumble bees are also the primary

food sources for other native bee species (USDA Plants, 2006).

Much research has focused on the ecological requirements of the European honey bee

(*Apis mellifera* L.) and a number of bumble bee species. However, as halictid bees can comprise up to 70% of western North American samples (Rao *et al.*, 2009) and relatively little is known about their foraging habits, this family was selected for further examination.

Bees require two principal resources: nesting sites and forage plants. Because bees in the family Halictidae are primarily ground-nesters (Eickwort, 1969, Wcislo *et al.*, 1993), they may not be as nest-site-limited as twig- and other cavity-nesters. Although the flight distances of most bee species are unknown, the foraging distance of several halictid species has been estimated to be somewhere between 200 and 600m away from the nest (Zurbuchen *et al.*, 2010). With such short foraging distances, local-level forage availability is perhaps the principal factor in individual halictid bee success. This study focuses on the foraging habits of halictid bees.

Halictid bees are broadly considered generalists (Danforth *et al.* 2008). Forage records for these species are often incidental notes in papers examining the pollinators of a particular plant (Cockerell, 1914; Lindsay, 1984; Sih *et al.*, 1987; Cruden et al., 1996; Li *et al.*, 2008; McIver *et al.*, 2010), and rarely are the forage preferences of halictids examined holistically. While generalists may forage on a number of different floral species in an environment, they do not necessarily forage on *every* species in that environment. Although bloom may be present, if it is not suitable—or not abundant—generalist bee species may still be resource-limited. In order to conserve generalist species, it is important to understand their preferred floral hosts.

Conservation plans often assume that the preferred floral host of a native bee must be a native plant. The resulting focus on the removal of non-native plant species overlooks the fact that some exotic plants benefit native bees by filling in temporal gaps between native blooms (Tepedino, 2008). The presence of attractive exotic plants may be especially important for longer-lived generalist species, which would have otherwise been resource-limited.

Because different localities have different plant and bee assemblages, it is important to examine each locality, the bee species present, and the forage they visit for conservation practices to be effective. Many such studies rely on visual counts (Stubbs *et al.*, 1997; Winfree *et al.*, 2007; Broussard *et al.*, 2011), which often leads to misidentification of taxa and/or poor taxonomic resolution (Cane, 2001), but even collecting individuals off of flowering plants may underestimate forage scope, as they may be visiting multiple flowers in a single trip (Tepedino *et al.*, 2008; Broussard, 2011).

Pollen analysis of individual bee specimens has the unique capacity to represent previous floral visits, and may even be used to estimate foraging distance (Zurbuchen *et al.*, 2010). By combining visual observations and pollen analysis, more information can be collected per specimen--information that is of importance for conservation efforts.

The objectives of this study were to: (1) determine which flowering plants are utilized by common halictid species and (2) compare floral resource utilization across habitat types.

Methods

This study was conducted over a single growing season in Oregon. Halictid bees were collected from forage plants and their pollen removed. Data from both the observed forage plant and plants represented in their pollen loads was recorded and analyzed.

Sample sites

Four sites were selected in Oregon. Two sites were located in the Willamette Valley prairie and two in the Snake-Columbia shrub steppe south of Madras, as they are both open habitat types, which may provide more resources for pollinators than forested areas (Moldenke, 1979; Winfree *et al.*, 2006). In the Willamette Valley, samples were taken at E. E. Wilson Wildlife Area (West1), and Finley National Wildlife Refuge (West2). In Central Oregon, samples were taken at two sites in the Crooked River National Grasslands (East1, East2). Western sites had low-lying vegetation with few shrubs; hedges composed primarily of hawthorn, poison oak, and Himalayan blackberry created a barrier between these sites and surrounding farmland. Eastern sites were dominated by cheatgrass, sagebrush and green rabbitbrush, without clear division from surrounding farm and rangeland. Non-native forbs were common at all sites.

Sample sites were >10 km apart, greater than the maximum observed foraging distance of many bee species (Osborne *et al.*, 1999; Beekman and Ratnieks, 2000; Greenleaf *et al.*, 2007; Zurbuchen, 2010, Rao and Strange, 2012), thus reducing the likelihood of sampling from the same bee population at different sites.

Bee sampling method

At each site, two ~200m transects were established. Each transect was then traversed at a slow walk (1-5 m per minute) and specimens were collected through a combination of hand-collecting and directed sweep-netting. Bees from all families were collected, but only those belonging to the family Halictidae examined here. Floral richness was recorded by identifying every blooming plant within 1m of either side of each transect. Each of the four sites was sampled 14 times (56 samples in total), every 5-9 days between May 5 and September 12. Collections occurred on days without precipitation where the average temperature was above 18°C.

Pollen analysis

In order to determine which floral resources bees were utilizing in addition to those they were collected on, pollen carried on the body was analyzed. Bees were submerged in glacial acetic acid, agitated, and then removed; pollen from the whole body was then processed using the acetolysis techniques described in Erdtman (1952). Pollen was stained with 0.01% saffranin O and mounted on slides with silicone oil. Two-hundred grains were visually identified from each slide and the pollen richness of each slide was recorded. Although single pollen grains were recorded, slides with multiple pollen

types usually contained 10% or more of the secondary pollen.

To facilitate pollen identification, anthers were collected from flowers observed in bloom during the study period and their pollen processed as described above to create an extensive, local pollen reference collection. This collection, combined with plant richness data, allowed most pollen grains to be identified to the genus level.

Data analysis

Multidimensional scaling (MDS) ordination plots were generated in R (R Development Core Team, 2010) and used to summarize the proportion of different plant species present in individual bee pollen loads. In an ordination plot, sites with similar species composition are plotted closer together than those with dissimilar species composition. Distribution of plant species in pollen loads were explored with 95% confidence elipses, calculated using bivariate standard deviation (Milligan *et al.*, 2004). Ellipses were generated by the ORDIELLIPSE function in the R-package VEGAN (Oksanen, 2008). Interpretation of the MDS was checked with an analysis of similarities (ANOSIM) test. Linear regression was used to examine trends in floral richness.

Results

Throughout the field season, 684 halictid bees, belonging to 5 genera and over 25 species, were captured (Table 3.1). Collectively, halictids were observed foraging on 55 plant species in 21 families. The most common forage in western sites was *Symhoricarpos albus* (L.), and the most common forage in eastern sites was

Eriophyllum lanatum (Pursh).

Plants utilized by common halictid species

Further analysis was done for species of which more than ten specimens were collected. Species chosen are presented in Table 3.2, along with floral records. Due to uncertainty in *Lasioglossum* (*Dialictus*) species identification, these individuals were not examined. Individuals of *Agapostemon angelicus* and *A. texanus* were combined for data analysis because females of these species are morphologically indistinguishable (Roberts, 1973).

All nine species listed in Table 3.2 are generalists (Danforth *et al.* 2008). All but *A. femoratus* are present in both eastern and western sites, though the distribution between the two site types is not even. The percentage of bees carrying pollen was not significantly different between the nine focal species (p > 0.1; Fig 3.2), and varied from 75% to 92%.

Focal bee species were observed foraging on 35 different plant species, belonging to 18 families (Table 3.2). Richness of taxa visited by bee species ranged from 4 to 12—although this observed (but not significant; p > 0.1) difference is likely due to the variation in the number of specimens collected from each species. The number of individuals caught was positively correlated with plant host richness, but the relationship was not statistically significant (p > 0.1; Fig 3.1)

Although halictid bees were not observed host-switching on the wing, pollen analysis revealed that all examined bees had visited, on average, 2-3 different floral species. Pollen richness ranged from 1-7; multiple individuals from all nine species were observed to carry single-species loads, while only one specimen of each *A. texanus* and *L. titusi* were observed to carry seven different pollen types (Fig 3.2).

Floral utilization across habitat types

Although there was no significant difference in flowering plant richness between the two site types (p > 0.1), focal halictids were collected off of 25 plant species in the Willamette Valley, and only 10 in Central Oregon (Table 3.2). Of the available flowers, *Epilobium* was the only genus present at all locations. Although common, this genus was not observed to have many floral visitors.

Over 30 *Lasioglossum sisymbrii* were collected in both eastern and western sites, permitting examination of species-level differences in preferred forage plants across habitat types. This species ranges across most of western North America and has over 150 recorded plant hosts from more than 45 families (McGinley, 1986). In this study, specimens were found from early June through mid-August, and were present during the blooming time of 81 plant species belonging to 23 families.

Initial ordination indicated that there was a very significant difference between the foraging habits of L. sisymbrii in the Willamette Valley and Central Oregon (p < 0.001, ANOSIM, 1000 permutations; Fig 3.3). To examine within-site trends, eastern and

western sites are analyzed individually.

In western sites, 31 individuals of *L. sisymbrii* were directly captured off of 7 plant species belonging to 6 families. The most common forage in the west was *Rubus* armeniacus. NMDS analysis suggested that forage plant could explain 96% of the variability in pollen load content (p = 0.001, ANOSIM, 1000 permutations; Fig 3.4). None of the observed forage plants were associated with increased pollen load diversity (p > 0.1, ANOSIM, 1000 permutations).

In eastern sites, 53 individuals of L. sisymbrii were directly captured off of 5 plant species belonging to 4 families. In eastern sites, the most common forage plant was Sisymbrium altissimum. Ordination analysis in eastern sites found that forage plant could only explain 69% of the variability in pollen load content (p = 0.001, ANOSIM, 1000 permutations; Fig 3.5). Certain forage plants in these sites are linked to higher richness in pollen load (p = 0.001, ANOSIM, 1000 permutations). In particular, it appears that specimens collected from Achillea mellifolium were more likely to have collected pollen from other sources. Pollen from A. mellifolium could not reliably be separated from that of Eriophyllum Inanatum using light microscopy. However, even if all uncertain pollen was assumed to be Achillea, bees collected from A. mellifolium still had significant proportions of other plant species in their pollen loads (p = 0.001, ANOSIM, 1000 permutations).

Discussion

Summary

This study explored the foraging habits of nine halictid bee species, which are often overlooked due to a general focus on honey bees and bumble bees. Floral resources utilized by each species were identified and differences in foraging across different habitats were examined. Very few studies have taken in-depth examinations of local bee fauna and the floral resources they rely on.

Plants utilized by common halictid species

Based on observations in this study, we estimate that, on average, individual halictid bees forage on 2-3 different floral species. This is less than values reported for bumble bees (Fontaine *et al.*, 2008), which is surprising given that halictids are estimated to have relatively short foraging distances compared to those of bumble bees (Zurbuchen *et al.*, 2010), possibly necessitating a more diverse diet.

Floral utilization across habitat types

Sites in Central Oregon provide a very different set of floral resources than do sites in the Willamette Valley. Although there was no difference in overall plant richness between the two locations, common halictid bees were observed foraging on 25 plant species in western sites, and only 10 in eastern sites, implying that floral richness alone may not be a good indicator of bee forage availability. *Lasioglossum sisymbrii* was the only bee abundant enough at eastern and western locations to further examine the effect of habitat type on diet.

Despite higher plant richness at western sites, pollen within loads was primarily the same as the observed forage plant. At eastern sites, more variability in pollen loads was observed. Fontaine *et al.* (2008) found that bumble bees collected from more plant species when resources were scarce. It is possible that the same trend is being observed here, with bees in flower-poor, but species-rich, xeric diversifying their diets out of necessity.

Conclusions

Generalist bee species have the ability to adapt their diet to different localities. The nine bee species examined in this study foraged on 35 different species of plants, which represented many of the most common in the environment, both in the Willamette Valley and Central Oregon. In flower-rich environments, there is less competition for individual resources. Low competition has been observed to cause bumble bees to forage on fewer types of flowers (Morse, 1977; Fontaine *et al.*, 2008), and the results of these studies are echoed here.

The difference in bee foraging habits of *L. sisymbrii* in the Willamette Valley and Central Oregon underscores the importance of understanding which plant species are valuable for native bees; while the two sites had similar floral richness, fewer species were visited in Central Oregon. Given the sparser availability of forage in the high desert, these plants (particularly *Eriophyllum lanatum* and *Sisymbrium altissimum*) may play a significant role in maintaining current native bee populations. Forage plants

appear to be less limiting for halictids in the Willamette Valley, although only 42.3% of plant species present were observed to have bee visitors. Land management personnel in should consider the plants listed in Table 3.2 potentially valuable resource to bees. Poison oak should be given special consideration, as collections from the plant were limited by the ability of the researcher to collect specimens without sustaining personal injury. With further study, it is possible to elucidate a better understanding of which plants are the most vital to native bee species.

Bees are necessary for the continued health of agricultural and ecological systems. By knowing more about their foraging habits, it is possible to enact sensible management programs which benefit their populations by providing the necessary resources for survival.

Future work should include the development of local-level databases of plant-pollinator correspondences, and long-term studies of areas in and near agricultural systems, to promote native bee pollination of crops.

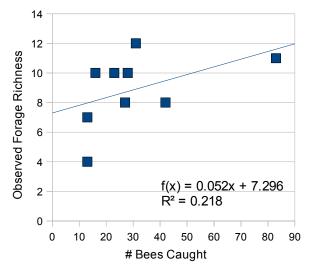


Fig 3.1. Relationship between the number of individuals captured for each focal species and the number of observed floral hosts. The furthest point to the right is *Lasioglossum sisymbrii*.

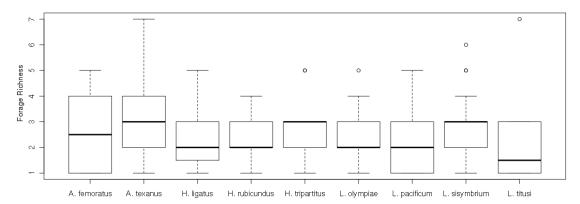


Fig 3.2. Number of floral species represented in the pollen loads of focal halictid species.

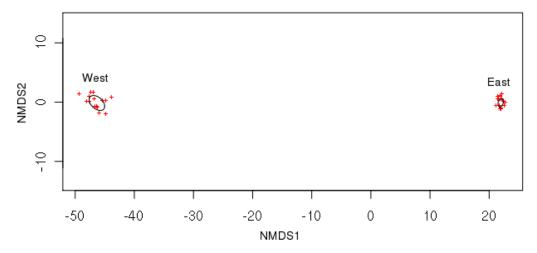


Fig 3.3. Ordination plot of plant composition of pollen loads of individual *L. sisymbrii* specimens in eastern and western sites. Crosshairs are floral species. Ellipses are 95% confidence regions.

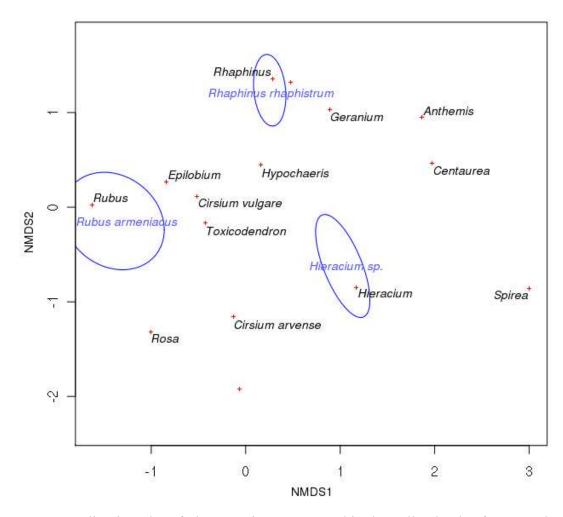


Fig 3.4. Ordination plot of plant species represented in the pollen loads of *L. sisymbrii* in western sites. Crosshairs are floral species. Ellipses are 95% confidence regions of plants on which specimens were collected.

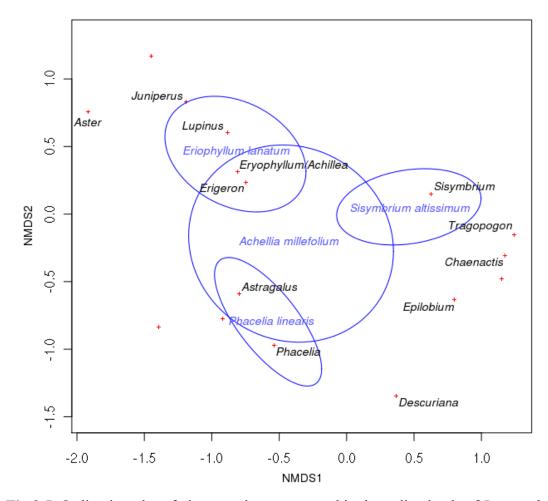


Fig 3.5. Ordination plot of plant species represented in the pollen loads of *L. sisymbrii* in eastern sites. Crosshairs are floral species. Ellipses are 95% confidence regions of plants on which specimens were collected.

Table 3.1. All halictid bees captured in 2012 in Central Oregon and the Willamette Valley

Species	CO*	WV*	# Caught
Agapostemon femoratus	√		13
Agapostemon texanus/angelicus	√	√	42
Agapostemon virescens		√	9
Duforea sp.1	√		4
Halictus confusus		√	1
Halictus farinosus		√	3
Halictus ligatus	√	√	28
Halictus rubicundus	√	√	16
Halictus tripartitus	√	√	23
Lasioglossum (Dialictis) ¹	√	√	352
Lasioglossum mellipes	√		1
Lasioglossum olympiae	√	√	27
Lasioglossum pacificum	√	√	31
Lasioglossum sisymbrium	√	√	83
Lasioglossum titusi	√	√	13
Lasioglossum trizonatum		√	1
Sphecodes sp.1		√	3
Sphecodes sp.2	√		2
Sphecodes sp.3		√	4
Sphecodes sp.4	√	√	2
Sphecodes sp.5		√	5
Sphecodes sp.6		√	20
Sphecodes sp.7		√	1
Sphecodes sp.8	√		1

There were more than 10 species within this subgenus
* CO = Central Oregon, WV = Willamette Valley

Table 3.2. Forage plants of common sweat bee species

1able 5.2. 1 016	age plants of common swe	ai oci	spec	108						
Family	Species	A. angelicus/texanus	A. femoratus	H. ligatus	H. rubicundus	H. tripartitus	L. olympiae	L. pacificum	L. sisymbrii	L. titusi
Apiaceae	Daucus carota				$\sqrt{}$				√	
	Heracleum maximum				$\sqrt{}$		√	√		
	Lomatium sp.						√			
Anacardiaceae	Toxicodendron diversilobum					V				
Apocynaceae	Apocynum sp.					V				
Asteraceae	Achillea millefolium	√		√		√			√	
	Cirsium arvense								√	
	Cirsium vulgare				√					
	Centaurea sp.	√		$\sqrt{}$						
	Eriophyllum lanatum	√	√	$\sqrt{}$		√		√	√	
	Hieracium sp.	√				√		√	√	√
	Hypochoeris radicata									
	Leucanthemum vulgare				√		√	√		
	Senecio jacobaea			$\sqrt{}$						
	Tragopogon sp.	√								V
Brassicaceae	Descuriana sp.			√						V
	Rhaphinus rhaphistrum							√		
	Sisymbrium altissimum		√	√		√	√	√	√	
Boraginaceae	Myosotis discolor									V
Caprifoliaceae	Symphoricarpos albus			√					√	
Fabaceae	Lupinus sp.					√				
Geraniaceae	Geranium spp.							√	√	V
Grossulariaceae	Ribes cereum					√				
Hydrophillaceae	Phacelia linearis	√	√	√				√	√	
	Phacelia sp.		√							
Hypericaceae	Hypericum perforatum				√			√		
Lamiaceae	Mentha pulegium			$\sqrt{}$		V				
Liliaceae	Calochortus sp.	V								
Malvaceae	Sidalcea sp.						√	1		
Onagraceae	Epilobium sp.				√				√	

Phyrmaceae	Mimulus guttatus									
Rosaceae	Potentilla sp.				√		√			
	Rosa sp.						V	V		
	Rubus armeniacus	√		√	√	√	√	√		
	Spirea douglasii				V				√	
	Total	8	4	10	10	10	8	12	11	7

References

- Aizen, M.A. and P. Feinsinger. 2003. Bees not to be? Responses of insect pollinator faunas and flower pollination to habitat fragmentation. En: G.A. Bradshaw and P.A. Marquet (editores). How landscapes change: human disturbance and ecosystem fragmentation in the Americas. pp. 111-129. Springer-Verlag, Berlin.
- Bawa, K.S. 1990. Plant-pollinator interactions in tropical rain forests. Annual Review of Ecology and Systematics, 399-422.
- Beekman, M., and F. L. W. Ratnieks. 2000. Long-range foraging by the honey-bee, Apis mellifera L. Functional Ecology 14:490-496.
- Broussard, M., S. Rao, W.P. Stephen and L. White. 2011. Native bees, honeybees, and pollination in Oregon cranberries. HortScience 46:885-888.
- Buchmann, S.L., G.P. Nabhan, G.P. 1997. The forgotten pollinators. Island Press. p. 199.
- Cane, J.H. 2001. Habitat fragmentation and native bees: a premature verdict? Conservation Ecology 5:3.
- Cane, J.H. and V.J. Tepedino. 2001. Causes and extent of declines among native North American invertebrate pollinators: detection, evidence, and consequences.

 Conservation Ecology 5:1.
- Cockerell, T.D.A. 1914. Bees Visiting Helianthus. The Canadian Entomologist, 46:409-415.
- Cruden, R.W., A.M. McClain, and G.P. Shrivastava. 1996. Pollination biology and

- breeding system of Alliaria petiolata (Brassicaceae). Bulletin of the Torrey Botanical Club, 273-280.
- Danforth, B.N., C. Eardley, L. Packer, K. Walker, A. Pauly, and F.J.

 Randrianambinintsoa. 2008. Phylogeny of Halictidae with an emphasis on endemic African Halictinae. Apidologie 39:86-101.
- Eickwort, G.C. 1969. Tribal positions of Western Hemisphere green sweat bees, with comments on their nest architecture (Hymenoptera: Halictidae). Annals of the Entomological Society of America, 62:652-660.
- Erdtman, G. 1952. Pollen Morphology and Plant Taxonomy: Angiosperms An Introduction to the Study of Pollen Grains and Spores. Almqvist & Wiksell. pp. 6-8.
- Fontaine, C., C.L. Collin, I. Dajoz. 2008. Generalist foraging of pollinators: diet expansion at high density. Journal of Ecology 98:1002-1010.
- Goulson, D., G.C. Lye, and B. Darvill. 2008. Decline and conservation of bumble bees. Annu. Rev. Entomol., 53, 191-208.
- Greenleaf S., N. Williams, R. Winfree, C. Kremen. 2007. Bee foraging ranges and their relationship to body size. Oecologia 153:589-596.
- Hayes, J., R.M. Underwood, and J. Pettis, 2008. A survey of honey bee colony losses in the US, fall 2007 to spring 2008. PLoS One, 3(12), e4071.
- Oksanen, J., F.G. Blanchet, R. Kindt, P. Legendre, P.R. Minchin, R.B. O'Hara, G.L. Simpson, P.Solymos, M. Henry, H. Stevens and H. Wagner. 2011. vegan:

 Community Ecology Package. R package version 2.0-2. http://CRAN.R-

- project.org/package=vegan
- Klein, A.-M., B.E. Vaissiére, J.H. Cane, I. Steffan-Dewenter, S.A. Cunningham, C. Kremen, and T. Tscharntke. 2007. Importance of pollinators in changing landscapes for world crops. Proceedings of the Royal Society of London B 274:303-313.
- Kremen, C., N. Williams, and R. Thorp. 2002. Crop pollination from native bees at risk from agricultural intensification. Proceedings of the National Academy of Science, USA 99:16812-16816.
- Li, P., Y. Luo, P. Bernhardt, Y. Kou, and H. Perner. 2008. Pollination of *Cypripedium plectrochilum* (Orchidaceae) by *Lasioglossum* spp. (Halictidae): the roles of generalist attractants versus restrictive floral architecture. Plant Biology, 10: 220-230.
- Lindsey, A.H. 1984. Reproductive biology of Apiacea. I. Floral vistors to Thaspium and Zizia and their importance in pollination. American Journal of Botany, 375-387.
- McGinley, R.J. 1986. Studies of Halictinae (Apoidea, Halictidae), I: Revision of New World Lasioglossum Curtis. Smithsonian Institution Press. 294pp.
- McIver, J., R. Thorp, and K. Erickson. 2009. Pollinators of the invasive plant, yellow starthistle (*Centaurea solstitialis*), in north-eastern Oregon, USA. Weed Biology and Management, 9:137-145.
- Milligan, A.L., P.D. Putwain, E.S. Cox, J. Ghorbani, M.G. Le Duc, and R.H. Marrs.

 2004. Developing an integrated land management strategy for the restoration of moorland vegetation on *Molinia caerulea*-dominated vegetation for

- conservation purposes in upland Britain. Biological Conservation, 119:371-385.
- Moldenke, A.R. 1979. Host-plant coevolution and the diversity of bees in relation to the flora of North America. Phytologia. Plainfield NJ, 43:357-419.
- Morse, D.H. 1977. Resource partitioning in bumble bees: the role of behavioral factors. Science 197:678–680.
- Osborne, K.E., and B.P. Oldroyd. 1999. Possible causes of reproductive dominance during emergency queen rearing by honeybees. Animal Behaviour 58:267-272.
- Pettis, J.S., and K.S. Delaplane. 2010. Coordinated responses to honey bee decline in the USA. Apidologie, 41:256-263.
- R Development Core Team. 2010. R: A language and environment for statistical computing, reference index version 2.x.x. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.
- Rao, S., W. Stephen, L. White. 2009. Native Bee Pollinator Diversity in Oregon Blueberries. Acta Horticulturae (ISHS) 810:539-548.
- Rao, S. and J. Strange. 2012. Bumble Bee (Hymenoptera: Apidae) Foraging Distance and Colony Density Associated With a Late-Season Mass Flowering Crop. Environmental Entomology 41:905-915.
- Roberts, R.B. 1973. Bees of northwestern America: Agapostemon (Hymenoptera: Halictidae). Agricultural Experiment Station, Oregon State University, Corvallis.

- Sih, A. and M.S. Baltus. 1987. Patch size, pollinator behavior, and pollinator limitation in catnip. Ecology, 1679-1690.
- Stubbs, C.S., F.A. Drummond and S.L. Allard. 1997. Bee Conservation and Increasing Osmia spp. in Maine Lowbush Blueberry Fields. Northeastern Naturalist 4:133-144.
- Tepedino, V.J., B.A. Bradley, and T.L. Griswold. 2008. Might flowers of invasive plants increase native bee carrying capacity? Intimations from Capitol Reef National Park, Utah. Natural Areas Journal 28: 44-50.
- USDA Plants. 2006. Improving forage for native bee crop pollinators. USDA Agroforestry Notes 33:1-4.
- Wcislo, W.T., A. Wille, and E. Orozco. 1993. Nesting biology of tropical solitary and social sweat bees, *Lasioglossum* (*Dialictus*) *figueresi* Wcislo and *L.(D.) aeneiventre* (Friese) (Hymenoptera: Halictidae). Insectes sociaux, 40:21-40.
- Winfree, R., T. Griswold, C. Kremen. 2006. Effect of Human Disturbance on Bee Communities in a Forested Ecosystem. Conservation Biology 21:213-223.
- Winfree, R., N.M. Williams, J. Dushoff, and C. Kremen. 2007. Native bees provide insurance against ongoing honey bee losses. Ecology Letters 10:1105-1113.
- Winfree, R., R. Aguilar, D.P. Vázquez, G. LeBuhn, and M.A. Aizen. 2009. A metaanalysis of bees' responses to anthropogenic disturbance. Ecology 90:2068– 2076.
- Zurbuchen, A., L. Landert, J. Klaiber, A. Muller, S. Hein, and S. Dorn. 2010.

Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances. Biological Conservation 143:669-676.

Chapter 4: Summary

Review of findings

Bees and the pollination services they provide are essential for ecosystem health.

Conservation efforts to preserve these species require an understanding the resources they require. Based on the data collected in this study, there is evidence that habitat type can have impacts on the ways in which bees respond to disturbance and forage in the environment.

Roadside disturbance appeared to affect bee species differentially across the different habitat types studied. Roadside disturbance had no measurable effect on bee communities in xeric Central Oregon, but was associated with reduced native bee diversity and abundance in the seasonally wet Willamette Valley. Halictidae was the most abundant native bee family in both regions, and roadside disturbance was observed to have a particularly strong, negative effect on the halictid subgenus *Lasioglossum* (*Dialictus*). It is of note that this subgenus accounted for over half of all observed halictid bees.

Reduced floral abundance in Central Oregon resulted in concentrated foraging of a small number of productive flowers by halictid species. This trend is exemplified by the diet of *L. sisymbrii*, which was single-plant oriented in the Willamette Valley, but broader in the drier high desert.

Both studies highlight the current importance of exotic plants in the diets of native bees, with just under half of specimens collected on exotic plants. This trend is of particular concern for wildland management, which often elects to remove as many 'weeds' and non-native plants as practical, potentially harming the species that currently rely on them.

One of the valuable outcomes of this study is the identification of the 'top ten' plants bees were collected off of, half of which are introduced species. Management recommendations for local roadside and wildland management would include the preservation of these species until sufficient, desirable, native bloom is established. This is perhaps more important in Central Oregon, where the scarcity of bloom is already causing bees to expand their foraging preferences.

Study limitations

Although study blocks were chosen randomly, local-level site selection was non-random, limiting inference from these studies. In addition, due to the frequency of the sampling, it was difficult to schedule samples around unavoidable circumstances, such as poor weather and wildfires. Frequent sampling of the same populations created problems with sample independence—which may be exacerbated for species with long foraging seasons.

As specimens were collected by hand, there is clear potential for sample bias. To mitigate this effect, the same person collected at all sites, but collector efficacy can

change from sample to sample. However, some bias was unavoidable in hand-collections, particularly the under-representation of bees foraging on poison oak and other injurious plants.

Perhaps the largest limitation of this study is that it only focused on set sites for one season, which is insufficient to discern year-to-year fluctuations in plant and pollinator populations.

Conclusions

Although habitat type has historically not been linked to changes in bee response to disturbance (Winfree *et al.*, 2009), the data collected herein indicate that the effect of roadside disturbance on native bee populations may vary in different ecoregions. It is possible that this observed response is due to indirect effects altering bee communities. In the context of roadside disturbance, habitat type influences how roadsides are managed, the type of vegetation, and how similar roadside vegetation is to vegetation further from the road. Hopwood (2008) found that there was significant variability even between different roadsides within a single habitat type, depending on whether restoration had occurred or not. This raises the interesting question of what the "natural" state of a roadside even is. Hansen and Clevenger (2005) noted that grassland habitats in Alaska allowed the spread of invasive weeds further away from roadside sites, out to over 150m, while forested areas only experienced increased exotics 10m from the road. Data are not available for either of the two habitat types explored here.

The forage choices of non-*Bombus* native generalists are often recorded in studies where plant pollination is the focus, rather than the bee. A recent study by McIver *et al*. (2010) in Oregon looks at the pollinators of yellow starthistle, finding that generalist halictids are among its most common pollinators. Other ecological studies use traps to passively collect bees (Cane *et al.*, 2006; Rao *et al.* 2009), which prevents the elucidation of plant-pollinator associations. It is unfortunate that, although important for ecosystem function, the foraging habits of generalist bees are rarely examined holistically.

Future research

Further investigation into local-level bee populations will be critical for continued bee conservation. Although difficult, the development of a method to identify bees alive in the field would reduce the ecological impact of such studies. Conducting floral choice tests with native bees has proved difficult, but such studies would illuminate true floral preferences for individual species. In the context of long-term studies of local-level bee populations, this information would greatly assist land management personnel in selecting management schemes which are beneficial to bee species. As more is understood about the basic biology and ecology of local bee species, effective conservation methods can be developed for preserving those species.

Bibliography

- Aizen, M.A. 2007. Enfoques en el estudio de la reproduccion sexual de las plantas en ambientes alterados: limitaciones y perspectivas. Aust. Ecol. 17:7-19.
- Aizen, M.A. and P. Feinsinger. 2003. Bees not to be? Responses of insect pollinator faunas and flower pollination to habitat fragmentation. En: G.A. Bradshaw and P.A. Marquet (editores). How landscapes change: human disturbance and ecosystem fragmentation in the Americas. pp. 111-129. Springer-Verlag, Berlin.
- Al-Ghzawi, A., S. Zaitoun, S. Mazary, M. Schindler & D. Wittmann. 2006. Diversity of bees (Hymenoptera, Apiformes) in extensive orchards in the highlands of Jordan. Arxius de Miscel·lània Zoològica, vol. 4: 42–48.
- Auerbach, N.A., M.D. Walker, and D.A. Walker. 1997. Effects of roadside disturbance on substrate and vegetation properties in arctic tundra. Ecological Applications 7:218-235.
- Basset, Y., O. Missa, A. Alonso, S.E. Miller, G. Curletti, M. De Meyer, C. Eardley, O.T. Lewis, M.W. Mansell, V. Novotny and T. Wagner. 2008. Changes in Arthropod Assemblages along a Wide Gradient of Disturbance in Gabon. Conservation Biology 6:1552-1563.
- Bawa, K.S. 1990. Plant-pollinator interactions in tropical rain forests. Annual Review of Ecology and Systematics, 399-422.
- Beekman, M., and F. L. W. Ratnieks. 2000. Long-range foraging by the honey-bee, Apis mellifera L. Functional Ecology 14:490-496.
- Bell, T., S. Campbell, D.G.E. Liverman, D. Allison, and P. Sylvester. 2010.

- Environmental and potential human health legacies of non-industrial sources of lead in a Canadian urban landscape the case study of St John's, Newfoundland. 52:771-800.
- Bergh, J.E. 2011. Native Bee Diversity and Floral Resource Availability in Two Willamette Valley Oregon Ecosystems. Master's thesis. Oregon State University.
- Broussard, M., S. Rao, W.P. Stephen and L. White. 2011. Native bees, honeybees, and pollination in Oregon cranberries. HortScience, 46:885-888.
- Buchmann, S. L., A. Matheson, C. O'Toole, P. Westrich, and I.H. Williams. 1996.

 Competition between honey bees and native bees in the Sonoran Desert and global bee conservation issues. Academic Press for the Linnean Society of London and the International Bee Research Association. pp. 125-142.
- Buchmann, S.L., G.P. Nabhan, G.P. 1997. The forgotten pollinators. Island Press. p. 199.
- Caceres, M., and F. Jansen. 2010. indicspecies: Functions to assess the strength and significance of relationship of species site group associations (R package). http://cran.r-project.org/web/packages/indicspecies/index.html
- Cane, J.H. 2001. Habitat fragmentation and native bees: a premature verdict? Conservation Ecology 5:3.
- Cane, J.H. and V.J. Tepedino. 2001. Causes and extent of declines among native North American invertebrate pollinators: detection, evidence, and consequences.

 Conservation Ecology 5:1.

- Cane, J.H., R.L. Minckley, L.J. Kervin, T.H. Roulston, and N.M. Williams. 2006. Complex responses within a desert bee guild (Hymenoptera: Apiformes) to urban habitat fragmentation.
- Chaplin-Kramer, R., K. Tuxen-Bettman, C. Kremen. 2011. Value of wildland habitat for supplying pollination services to Californian agriculture. Rangelands 33:33-41.
- Cockerell, T.D.A. 1914. Bees Visiting Helianthus. The Canadian Entomologist, 46:409-415.
- Cruden, R.W., A.M. McClain, and G.P. Shrivastava. 1996. Pollination biology and breeding system of Alliaria petiolata (Brassicaceae). Bulletin of the Torrey Botanical Club, 273-280.
- Danforth B.N., J. Fang, S. Sipes. 2006. Analysis of family-level relationships in bees (Hymenoptera: Apiformes) using 28S and two previously unexplored nuclear genes: CAD and RNA polymerase II. Mol. Phylogenet. Evol. 39:358-72.
- Danforth, B.N., C. Eardley, L. Packer, K. Walker, A. Pauly, and F.J.

 Randrianambinintsoa. 2008. Phylogeny of Halictidae with an emphasis on endemic African Halictinae. Apidologie 39:86-101.
- Eickwort, G.C. 1969. Tribal positions of Western Hemisphere green sweat bees, with comments on their nest architecture (Hymenoptera: Halictidae). Annals of the Entomological Society of America, 62:652-660.
- Dale, V.H., L.A. Joyce, S. McNulty, R.P. Neilson, M.P. Ayres, M.D Flannigan, P.J.Hanson, L.C. Irland, A.E. Lugo, C.J. Peterson, D.S. Simberloff, F.J. Swanson,B.J. Stocks and B.M. Wotton. 2001. Climate change and forest disturbances.

- BioScience, 51:723-734.
- Dufrêne, M. and P. Legendre. 1997. Species assemblages and indicator species: The need for a flexible asymetrical approach. Ecological Monographs 67:345-366.
- Ellison, A.M. and E.J. Farnsworth 1996. Anthropogenic disturbance of Caribbean mangrove ecosystems: past impacts, present trends, and future predictions. Biotropica, 549-565.
- Engel, M. 2000. Classification of the Bee Tribe Augochlorini (Hymenoptera: Halictidae). Bulletin of the American Museum of Natural History, 250:1-90.
- Erdtman, G. 1952. Pollen Morphology and Plant Taxonomy: Angiosperms An Introduction to the Study of Pollen Grains and Spores. Almqvist & Wiksell. pp. 6-8.
- Fontaine, C., C.L. Collin, I. Dajoz. 2008. Generalist foraging of pollinators: diet expansion at high density. Journal of Ecology 98:1002-1010.
- Forman, R.T.T., D. Sperling, J.A. Bissonette, A.P. Clevenger, C.D. Cutshall, V.H. Dale, L. Fahrig, R. France, C.R. Goldman, K. Heanue, J.A. Jones, F.J. Swanson, T. Turrentine, and T.C. Winter. 2003. Road ecology: science and solutions. Island Press, Washington, D.C., USA.
- Frankie, G.W., M. Rizzardi, S.B. Vinson, and T.L. Griswold. 2009. Decline in Bee Diversity and Abundance from 1972-2004 on a Flowering Leguminous Tree, Andira inermis in Costa Rica at the Interface of Disturbed Dry Forest and the Urban Environment. Journal of the Kansas Entomological Society 82:1-20.
- Gelbard, J.L., and J. Belnap. 2003. Roads as Conduits for Exotic Plant Invasions in a

- Semiarid Landscape. Conservation Biology 17:420-432.
- Gess, S., and F. Gess. 2004. A Comparative Overview of Flower Visiting by Non-Apis Bees in the Semi-arid to Arid Areas of Southern Africa. Journal of the Kansas Entomolical Society, 77:602-618.
- Goulson, D., J.C. Stout and A.R. Kells. 2002. Do exotic bumblebees and honeybees compete with native flower-visiting insects in Tasmania? Journal of Insect Conservation 6:179-189.
- Goulson, D., G.C. Lyle, and B. Darvill. 2008. Decline and conservation of bumble bees. Annual Review of Entomology 53:191-208.
- Greenleaf S, N. Williams, R. Winfree, and C. Kremen. 2007. Bee foraging ranges and their relationship to body size. Oecologia 153:589-596.
- Hannon, L.E., and T.D. Sisk. 2009. Hedgerows in an agri-natural landscape: Potential habitat value for native bees. Biological Conservation 142:2140-2154.
- Hansen, M.J. and A.P. Clevenger. 2005. The influence of disturbance and habitat on the presence of non-native plant species along transport corridors. Biological Conservation 125:249-259.
- Harris, L.F. and S.D. Johnson. 2004. The consequences of habitat fragmentation for plant-pollinator mutualisms. International Journal of Tropical Insect Science 24: 29-43.
- Hopwood, J.L. 2008. The contribution of roadside grassland restorations to native bee conservation. Biological Conservation. 141:2632-2640.

- Klein, A.-M., B.E. Vaissiére, J.H. Cane, I. Steffan-Dewenter, S.A. Cunningham, C. Kremen, and T. Tscharntke. 2007. Importance of pollinators in changing landscapes for world crops. Proceedings of the Royal Society of London B 274:303-313.
- Kremen, C., N. Williams, and R. Thorp. 2002. Crop pollination from native bees at risk from agricultural intensification. Proc. Natl. Acad. Sci. USA. 99:16812-16816.
- Kremen, C., R.K. Colwell, T.L. Erwin, D.D. Murphy, R.F. Noss, M.A. Sanjayan. 1993. Terrestrial arthropod assemblages: their use in conservation planning. Conservation Biology. 7:796–808.
- Le Féon, V., F. Burel., R. Chifflet, M. Henry, A. Ricroch, B.E. Vaissière, and J. Baudry. 2011. Solitary bee abundance and species richness in dynamic agricultural landscapes. Agriculture, Ecosystems & Environment. Available online 26 July 2011, ISSN 0167-8809, 10.1016/j.agee.2011.06.020. (http://www.sciencedirect.com/science/article/pii/S0167880911002118)
- Linder, H.P. 1998. Morphology and the evolution of wind pollination. pp 123-135 in S.J. Owens and P.J. Rudall, eds. Reproductive biology. Royal Botanic Gardens, Kew, Richmond, UK.
- Li, P., Y. Luo, P. Bernhardt, Y. Kou, and H. Perner. 2008. Pollination of *Cypripedium plectrochilum* (Orchidaceae) by *Lasioglossum* spp. (Halictidae): the roles of generalist attractants versus restrictive floral architecture. Plant Biology, 10: 220-230.
- Lindsey, A.H. 1984. Reproductive biology of Apiacea. I. Floral vistors to Thaspium and Zizia and their importance in pollination. American Journal of Botany, 375-

- McCune, B. and J.B. Grace. 2002. Analysis of Ecological Communities. MjM Software Design, Gleneden Beach. 300pp.
- McGinley, R.J. 1986. Studies of Halictinae (Apoidea, Halictidae), I: Revision of New World Lasioglossum Curtis. Smithsonian Institution Press. 294pp.
- McIver, J., R. Thorp, and K. Erickson. 2009. Pollinators of the invasive plant, yellow starthistle (*Centaurea solstitialis*), in north-eastern Oregon, USA. Weed Biology and Management, 9:137-145.
- Michener, C.D. 2000. The Bees of the World. The Johns Hopkins University Press, Baltimore. p.339.
- Michener, C.D. 2007. The Bees of the World. Second edition. The Johns Hopkins University Press, Baltimore. 992 pp.
- Milligan, A.L., P.D. Putwain, E.S. Cox, J. Ghorbani, M.G. Le Duc, and R.H. Marrs. 2004. Developing an integrated land management strategy for the restoration of moorland vegetation on *Molinia caerulea*-dominated vegetation for conservation purposes in upland Britain. Biological Conservation, 119:371-385.
- Moldenke, A.R. 1979. Host-plant coevolution and the diversity of bees in relation to the flora of North America. Phytologia. Plainfield NJ, 43:357-419.
- Morse, D.H. (1977) Resource partitioning in bumble bees: the role of behavioral factors. Science, 197, 678–680.

- NASA Landsat Program. 2012. Landsat ETM+ scene. SLC-Off, USGS, Sioux Falls, 2012.
- Noordijk, J., A.P. Schaffers, K.V. Sýkora. 2008. Diversity of ground beetles (Coleoptera: Carabidae) and spiders (Araneae) in roadside verges with grey hair-grass vegetation. European Journal of Entomology 105:257-265.
- Oksanen, J., F.G. Blanchet, R. Kindt, P. Legendre, P.R. Minchin, R.B. O'Hara, G.L. Simpson, P.Solymos, M. Henry, H. Stevens and H. Wagner. 2011. vegan:

 Community Ecology Package. R package version 2.0-2. http://CRAN.R-project.org/package=vegan
- Olson, D.M., E. Dinerstein. 2002. The Global 200: Priority ecoregions for global conservation. Annals of the Missouri Botanical Garden 89:199-224.
- Osborne, K.E., and B.P. Oldroyd. 1999. Possible causes of reproductive dominance during emergency queen rearing by honeybees. Animal Behaviour 58:267-272.
- Pettis, J.S., and K.S. Delaplane. 2010. Coordinated responses to honey bee decline in the USA. Apidologie, 41:256-263.
- Potts, S.G., B. Vulliamy, A. Dafni, G. Ne'eman, and P. Willmer. 2003. Linking bees and flowers: how do floral communities structure pollinator communities? Ecology 84: 2628-2642.
- R Development Core Team. 2010. R: A language and environment for statistical computing, reference index version 2.x.x. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

- Rao, S., W. Stephen, L. White. 2009. Native Bee Pollinator Diversity in Oregon Blueberries. Acta Hort. (ISHS) 810:539-548.
- Rao, S. and J. Strange. 2012. Bumble Bee (Hymenoptera: Apidae) Foraging Distance and Colony Density Associated With a Late-Season Mass Flowering Crop. Environmental Entomology 41:905-915.
- Roberts, R.B. 1973. Bees of northwestern America: Agapostemon (Hymenoptera: Halictidae). Agricultural Experiment Station, Oregon State University, Corvallis.
- Roberts, R.B. 1973. Bees of northwestern America: Halictus (Hymenoptera: Halictidae). Agricultural Experiment Station, Oregon State University, Corvallis.
- Rosenberg D.M., H.V. Danks, D.M. Lehmkuhl. 1986. Importance of insects in environmental impact assessment. Environmental Management 10:773–783.
- Schaffer, W.M., D.W. Zeh, S.L. Buchmann, S. Kleinhans, M.V. Schaffer and J. Antrim. 1983. Competition for nectar between introduced honey bees and native North American bees and ants. Ecology 564-577.
- Shavit, O., A. Dafni, and G. Ne'eman. 2009. Competition between honeybees (Apis mellifera) and native solitary bees in the Mediterranean region of Israel—
 Implications for conservation. Israel Journal of Plant Sciences 57: 171-183.
- Sih, A. and M.S. Baltus. 1987. Patch size, pollinator behavior, and pollinator limitation in catnip. Ecology, 1679-1690.
- Siqueira de Castro, M. 2002. Bee Fauna of some tropical and exotic fruits: Potential

- pollinators and their conservation, p.275-288. P.G. Kevan & V. L. Imperatriz-Fonseca (eds.). Pollinating bees the conservation link between agriculture and nature. Brasília, Ministry of Environment, 313p.
- Steffan-Dewenter, I. and C. Westphal. 2008. The interplay of pollinator diversity, pollination services and landscape change. Journal of Applied Ecology 45: 737-741.
- Stephen, W.P. 1957. Bumble bees of western America (Hymenoptera: Apoidea).

 Agricultural Experiment Station, Oregon State College.
- Stephen, W.P., G.E. Bohart, and P.F. Torchio. 1969. The biology and external morphology of bees. Oregon State University Agricultural Experiment Station.
- Stubbs, C.S., F.A. Drummond and S.L. Allard. 1997. Bee Conservation and Increasing Osmia spp. in Maine Lowbush Blueberry Fields. Northeastern Naturalist 4:133-144.
- Tepedino, V.J., B.A. Bradley, and T.L. Griswold. 2008. Might flowers of invasive plants increase native bee carrying capacity? Intimations from Capitol Reef National Park, Utah. Natural Areas Journal 28: 44-50.
- Thonicke, K., S. Venevsky, S. Sitch, and W. Cramer. 2008. The role of fire disturbance for global vegetation dynamics: coupling fire into a Dynamic Global Vegetation Model. Global Ecology and Biogeography, 10:661-677.
- Thomson, D. 2004. Competitive interactions between the invasive European honey bee and native bumble bees. Ecology 85:458-470.
- Tscharntke, T., A. Gathmann, and I. Steffan-Dewenter. 1998. Bioindication using trap-

- nesting bees and wasps and their natural enemies: community structure and interactions. Journal of Applied Ecology 35:708-719.
- Tylianakis, J.M., A.M. Klein, and T. Tscharntke. 2005. Spatiotemporal variation in the diversity of Hymenoptera across a tropical habitat gradient. Ecology 86:3296-3302.
- US Census Bureau. 2004. Total and Federally Owned Land by State: 2004. In The National Data Book: 2008 Statistical Abstract Geography & Environment: Land and Land Use Retrieved November 19, 2012, from http://www.census.gov/compendia/statab/2008/tables/08s0349.pdf
- Wcislo, W.T., A. Wille, and E. Orozco. 1993. Nesting biology of tropical solitary and social sweat bees, *Lasioglossum* (*Dialictus*) *figueresi* Wcislo and *L.(D.) aeneiventre* (Friese) (Hymenoptera: Halictidae). Insectes sociaux, 40:21-40.
- Winfree, R., T. Griswold, and C. Kremen. 2006. Effect of Human Disturbance on Bee Communities in a Forested Ecosystem. Conservation Biology 21:213-223.
- Winfree, R., R. Aguilar, D.P. Vázquez, G. LeBuhn, and M.A. Aizen. 2009. A metaanalysis of bees' responses to anthropogenic disturbance. Ecology 90:2068– 2076.
- Zurbuchen, A., L. Landert, J. Klaiber, A. Muller, S. Hein, and S. Dorn. 2010.
 Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances. Biological Conservation 143:669-676.