IMPACTS OF HABITAT ALTERATIONS AND PREDISPERSAL SEED PREDATION ON THE REPRODUCTIVE SUCCESS OF GREAT BASIN FORBS

By

Robert L. Johnson

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GRADUATE COMMITTEE APPROVAL

of a dissertation submitted by

Robert L. Johnson

This dissertation has been read by each member of the following graduate committee and by majority vote has been found to be satisfactory.

Date	Val Jo Anderson, Chair
Date	Shawn M. Clark
Date	C. Riley Nelson
Date	Russell B. Rader
	Nancy Shaw
Date	Nancy L. Shaw

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____________________	______________________________
Date	Val Jo Anderson Chair, Graduate Committee

Accepted for the Department

____
Loreen A. Woolstenhulme
Graduate Coordinator

Accepted for the College

____
Rodney J. Brown
Dean, College of Life Sciences

ABSTRACT

IMPACTS OF HABITAT ALTERATIONS AND PREDISPERSAL SEED PREDATION ON THE REPRODUCTIVE SUCCESS OF GREAT BASIN FORBS

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Sexual reproductive success in wild plant populations is dependent upon the ability to bank seed for when environmental conditions favor seedling recruitment. Seed production in many plant populations requires the pollination services of local bee populations. A loss in bee diversity as a result of exotic plant invasion or revegetation practices which do not adequately restore the flowering plant resources that support pollinators, contributes to habitat fragmentation. Even after successful pollination, developing ovules and maturing seed are subject to predation by insects. Several species of fruit flies (Tephritidae) are host specific to members of the plant family Asteraceae and can cause significant reductions in total seed yields in wild populations. Such losses in seed yield impact a plant’s annual contribution to the seed bank. Reductions in seed yield can also impact the potential rewards from harvesting wild seed for use in the reclamation industry. With the heightened interest in using native plants for restoring western rangelands, securing a reliable seed source, whether from wild seed collection or agricultural production, has become increasingly important. Restoring native forbs in degraded rangelands will help restore native bee populations, improve population stability for pollinators, and improve wildlife habitat. This dissertation presents three separate manuscripts that address factors affecting the reproductive success of wild plant populations. All three manuscripts are formatted for publication in professional journals and are included as separate chapters. Chapter 1 examines the impact of cheatgrass and crested wheatgrass habitat on bee diversity compared to sagebrush and pinyon/juniper habitat. It was found that bee diversity is highest in pinyon/juniper habitat and lowest in crested wheatgrass. Chapter 2 examines the impact of seed predation on *Wyethia amplexicaulis* (Nutt.) Nutt. by the fruit flies *Neotephritis finalis* (Loew) and *Trupanea nigricornis* (Coquillett) (Diptera: Tephritidae). On average, seed damage was estimated at 38.9%. Chapter 3 examines the impact of seed predation on *Agoseris glauca* (Pursh) Raf. and *Crepis acuminata* Nutt. by the fruit fly *Campiglossa* sp. (Diptera: Tephritidae) and the moth *Phycitodes albatella* subsp. *mucidella* (Ragonot) (Lepidoptera: Pyaralidae). Treatment of plants with the pesticide imidacloprid was also investigated and found to provide significantly increase seed yield.

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CHAPTER 1

IMPACT OF HABITAT ALTERATIONS TO BEE DIVERSITY IN SAGEBRUSH AND PINYON/JUNIPER COMMUNITIES OF THE EASTERN GREAT BASIN

Robert L. Johnson[1,2], Val Jo Anderson[3], and Shawn M. Clark[4]

[1] Department of Plant and Wildlife Sciences, Brigham Young University,
Provo, UT, 84602, U.S.A.

[2] Address correspondence to R. L. Johnson, email Robert_johnson@byu.edu

[3] Department of Plant and Wildlife Sciences, Brigham Young University,
Provo, UT, 84602, U.S.A.

[4] Department of Biology, , Brigham Young University,
Provo, UT, 84602, U.S.A.

Abstract – Habitat alterations due to the expansion of non-native plant species can have serious impacts on native bee populations. We sampled bee diversity across two native and two non-native habitat types common to the arid Great Basin in 2006 and 2007. Sampled habitats include; 1) pinyon/juniper, 2) sagebrush, 3) cheatgrass, and 4) crested wheatgrass. Bee diversity was generally found to be highest in pinyon/juniper habitat and lowest in crested wheatgrass. Bee diversity in cheatgrass and sagebrush habitat was similar but generally higher than in crested wheatgrass. Juniper habitat also supported higher flowering plant diversity even though it had the highest percent bare ground. A significant relationship was found between flowering plant diversity and bee diversity. A total of 161 bee taxa was encountered of which 44 were singletons. Mature stands of pinyon/juniper that support a diverse flowering plant population provide valuable habitat for wild bee populations. Restoration of degraded rangelands should consider the importance of including nectar and pollen rich forbs in seed mixes. Replacing cheatgrass with aggressive wheatgrass can negatively impact bee populations if further restoration or secondary succession is arrested.

Keywords: Bee diversity, restoration, plant diversity, floral visitation, prevalent species, modal species, cheatgrass, crested wheatgrass, sagebrush, juniper, Great Basin.

Introduction:

The arid Great Basin, particularly precipitation zones receiving less than 30 cm annually, has experienced significant habitat alterations due to the encroachment of *Bromus tectorum* L., (cheatgrass) increased fire frequency, and revegetation with non-native perennials grasses. The resulting fragmented habitats within the shrub-steppe of the Great Basin can be defined in four general but ubiquitous types, namely; 1) intact *Artemisia tridentata* Nutt., (sagebrush), 2) intact *Pinus edulis* Engelm. or *P. monophylla* Torr. & Frém. and *Juniperus osteosperma* (Torr.) Little, (pinyon/juniper), 3) cheatgrass, and 4) *Agropyron cristatum* (L.) Gaertn., (crested wheatgrass) or *Agropyron desertorum* (Fisch. ex Link) Schult, (desert wheatgrass). Exotic annual or perennial grassland expansion is pervasive throughout the Great Basin. A survey of cheatgrass invasion in 1994 estimated 3.3 million acres of public land was dominated by cheatgrass, with another 76.1 million acres infested or at risk (Pellant 1994). Wildfires since 1994 have escalated dramatically, encouraging the spread of cheatgrass monocultures as well as enhancing crested wheatgrass expansion through post-fire revegetation. A typical response to revegetating burned areas throughout the Great Basin is to reseed with available, affordable species that have proven establishment and are competitive against cheatgrass. Prior to 1975, over 14.8 million acres of crested wheatgrass had been seeded in arid rangelands of the United States and Canada (Dewey & Asay 1975). The current number of seeded acres is unknown, but expected to greatly exceed pre 1970 estimates (Pellant 2005). Even though a current emphasis exists to incorporate more native plant species, a large part of government seed purchases still include crested wheatgrass, or other similarly effective non-native plant material.

Impacts of large-scale habitat alterations have been documented on many vertebrate species in cheatgrass (Gitzen et al. 2001) and crested wheatgrass (Reynolds & Trost 1980; Wiens & Rotenberry 1985) but effects on invertebrate species, which form important links in food webs and provide important ecological functions, are largely unknown. Bees especially play a critical role in supporting the stability of pollinator-dependent plant communities. Habitat fragmentation has a demonstrated negative impact on plant reproductive success (Aguilar et al. 2006), largely through disruptions of pollination processes. Compartments within the pollination web are recognized as important for conservation consideration in order to maintain high plant diversity (Corbet 2000). The mutualistic relationship between many plants and their bee pollinators is a well known aspect in conservation biology (Kearns & Inouye 1997). The conservation of rare, endangered, or threatened plant species must take into account the conservation of their associated pollinators.

The conservation of flowering plants with very specialized pollinator requirements may necessitate preserving very specific niche requirements of the pollinator. A more prevailing need requires conservation of substantial habitat to ensure the persistence of a diversity of pollinators, including common species. Stable pollinator populations are necessary to help support diverse and stable plant populations and vice-versa. This study investigates the effect of large-scale habitat alterations that dominate much of the western landscape by comparing bee diversity in two natural plant communities (pinyon/juniper and sagebrush) contiguous with two altered/introduced communities (cheatgrass and crested wheatgrass) at multiple sites and their representative bee diversity. We propose that native habitats support higher bee diversity than non-native replacement habitats, and that revegetating a cheatgrass monoculture to a crested wheatgrass monoculture does not improve bee diversity. If regional increases in cheatgrass and crested wheatgrass contribute to a decline in bee diversity, then it becomes increasingly important to conserve those habitats contributing most to bee diversity as well as to restore expanding grasslands to some functional state that maintains adequate pollination processes.

Methods:

Three sites (Tintic Valley, Antelope Valley, Yuba) possessing contiguous stands of pinyon/juniper, sagebrush, cheatgrass, and crested wheatgrass were located in the eastern Great Basin of central Utah. The occurrence of cheatgrass and crested wheatgrass at all sites was the result of wildfire. The selected cheatgrass community at Tintic Valley (Juab Co.) established following a July 1999 wildfire started by railroad track grinders. The crested wheatgrass was likely planted in 1996 subsequent to a wildfire, though it could have been from an earlier fire. The cheatgrass and crested wheatgrass community at Antelope Valley (Sanpete Co.) was the result of a fire started during oil exploration in 1980. The history of the same communities at the Yuba (Juab Co.) site was not discovered though the cheatgrass and crested wheatgrass have existed for at least 11 years.

Sites were sampled continuously from April 1 to October 1 in 2006 and 2007 for bee diversity using Townes (1972) style Malaise traps. In each habitat type three Malaise traps were installed without respect to the presence of flowering plant species. Traps were located well within the habitat polygon and spaced equidistant with respect to each other in a fashion that best fit the polygon or habitat fragment. The orientation of each trap was set 120° opposing each other thus effecting a full 360° sample orientation. Samples were collected biweekly, except during May and June where weekly sample retrieval was occasionally required due to full sample bottles. Study sites and trap locations are as follows:

Tintic Valley; Utah, Juab Co.

pinyon/juniper 1: 39.78396°N, 112.15729°W, 1752 m. elev.
pinyon/juniper 2: 39.78422°N, 112.15594°W, 1753 m. elev.
pinyon/juniper 3: 39.78431°N, 112.15489°W, 1756 m. elev.
sagebrush 1: 39.72314°N, 112.20226°W, 1595 m. elev.
sagebrush 2: 39.72495°N, 112.20297°W, 1595 m. elev.
sagebrush 3: 39.75257°N, 112.20272°W, 1600’ m. elev.
cheatgrass 1: 39.72902°N, 112.20428°W, 1597 m. elev.
cheatgrass 2: 39.73052°N, 112.20581°W, 1596 m. elev.
cheatgrass 3: 39.73276°N, 112.20479°W, 1599 m. elev.
crested wheatgrass 1: 39.71356°N, 112.16980°W, 1626 m. elev.
crested wheatgrass 2: 39.71475°N, 112.16943°W, 1627 m. elev.
crested wheatgrass 3: 39.71565°N, 112.16902°W, 1630 m. elev.

Yuba; Utah, Juab Co.

pinyon/juniper 1: 39.45350°N, 111.96699°W, 1614 m. elev.

pinyon/juniper 2: 39.45380°N, 111.96674°W, 1615 m. elev.

pinyon/juniper 3: 39.45430°N, 111.96667°W, 1613 m. elev.

sagebrush 1: 39.41016°N, 111.99285°W, 1553 m. elev.

sagebrush 2: 39.41016°N, 111.99281°W, 1556 m. elev.

sagebrush 3: 39.41017°N, 111.99333°W, 1556 m. elev.

cheatgrass 1: 39.43857°N, 112.0024°W, 1536 m. elev.

cheatgrass 2: 39.43994°N, 112.0047°W, 1540 m. elev.

cheatgrass 3: 39.44125°N, 112.0010°W, 1538 m. elev.

crested wheatgrass 1: 39.45201°N, 111.99307°W, 1565 m. elev.

crested wheatgrass 2: 39.45618°N, 111.99165°W, 1571 m. elev.

crested wheatgrass 3: 39.45763°N, 111.99073°W, 1565 m. elev.

Antelope Valley; Utah, Sanpete Co.

pinyon/juniper 1: 39.23526°N, 111.75134°W, 1753 m. elev.

pinyon/juniper 2: 39.23594°N, 111.75281°W, 1760 m. elev.

pinyon/juniper 3: 39.23655°N, 111.75351°W, 1765 m. elev.

sagebrush 1: 39.23163°N, 111.74507°W, 1724 m. elev.

sagebrush 2: 39.23323°N, 111.74503°W, 1722 m. elev.

sagebrush 3: 39.23454°N, 111.74355°W, 1731 m. elev.

cheatgrass 1: 39.23733°N, 111.73499°W, 1718 m. elev.

cheatgrass 2: 39.23993°N, 111.73408°W, 1730 m. elev.

cheatgrass 3: 39.24272°N, 111.73335°W, 1743 m. elev.

crested wheatgrass 1: 39.22784°N, 111.75111°W, 1722 m. elev.
crested wheatgrass 2: 39.23237°N, 111.75197°W, 1750 m. elev.
crested wheatgrass 3: 39.23374°N, 111.75343°W, 1762 m. elev.

Malaise traps were used because of their characteristic passive sampling. Bee communities display substantial variation in time and space (Williams et. al. 2001) that is amplified when pollinators are subjected to a diversity of resource options in a given habitat. Malaise traps intercept flight and sample the habitat area independent of pollinator preferences, unlike methods designed to attract. Pan trapping and netting are more common sampling methods and can produce more specimens per sample period (Bartholomew & Prowell 2005), but they do not necessarily gain significant increases in species richness, plus you may introduce sample bias via strong pollinator preference to color (Kirk 1984; Leong & Thorp 1999). Leong and Thorp (1999) erroneously considered pan trapping as passive. It is passive in the sense that it collects independent of direct human capture, but not in the sense of influencing bee flight patterns. Using multiple randomly positioned Malaise traps within a habitat construct helps remove experimental error associated with trap proximity to given plant species. Also, the Malaise traps were operating continuously for the duration of bee activity (April-October), eliminating sample variation that occurs from sequentially sampling different sites.

In all cases the pinyon/juniper and sagebrush stands were the habitat isolates with cheatgrass and/or crested wheatgrass dominating the local region. In Antelope Valley, the study site comprised a grass dominated valley with abundant pinyon/juniper and sagebrush on the adjacent slopes to the West and North. At the other sites, the pinyon/juniper and sagebrush stands were islands in a grassland sea. Overall topography was relatively flat except where dry washes bisected the study site. Because of habitat fragmentation, some tree or shrub stands were small. A stand requirement of 5 hectares was established as the minimum stand size for study. Only the Yuba sagebrush stand was near the minimum size of 5 hectares. All other shrub stands greatly exceeded the minimum stand size.

As the season progressed each year, the condition of the Malaise traps deteriorated due to prolonged ultraviolet light exposure. Continuous repairs kept traps functional until the end each season, but degrading trap quality may have influenced late season trap results to some extent. New traps were installed prior to the 2007 trapping season in the precise location as previous traps.

The abundance of flowering plants (plant providing nectar or pollen rewards) was documented throughout the study period concurrent with Malaise trap sample retrieval. This was accomplished by counting flowering plants by species within a 10-50 meter radius (depending upon plant density) at each Malaise trap. Total species composition and cover estimates were determined using eight $0.25m^2$ nested frequency quadrats placed in each of the cardinal directions at 5-meter intervals radiating from the Malaise trap center.

Captured bees were sorted and grouped to species or morphospecies within identifiable genera. Nomenclature of identified bees primarily follows the Integrated Taxonomic Information System on-line database (ITIS 2008) otherwise as found in the Catalog of Hymenoptera in America North of Mexico, Vol. 2 (Krombein et al. 1979). Analysis of bee and plant composition among sites, years and habitat types was done using Primer-E v6 (2006). Abundance and species richness was also compared using ANOVA for the factors: habitat, site, and year.

Results:

Analysis of bee abundance using ANOVA revealed a significant interaction between site and year (p=0.04). Significantly higher bee abundance was found at the Tintic Valley site in 2007 compared to all other sites in both years except Yuba in 2006 (fig. 1). The main effect "habitat" revealed significant differences (p<0.01) between habitat groups (fig. 2). Juniper habitat had the highest average trap abundance with an average of 89.6 bees compared to: 29.2 in cheatgrass, 20.7 in sagebrush, and10.1 in crested wheatgrass. Only cheatgrass and sagebrush were not significantly different from each other in bee abundance. A total of 2,691 bees were collected during the study period of which 525 bees were sampled from cheatgrass, 182 from crested wheatgrass, 1612 from juniper, and 372 from sagebrush.

An analysis of bee species richness revealed an interaction between habitat-x-site (p=0.06) and site-x-year (p=0.06). Since these interactions did not fall within our 95.0%

confidence limit we examined main effects. Significant differences between habitat ($p<0.01$), site ($p<0.01$), and year ($p=0.05$) were detected. Species richness by habitat followed the same trend as for abundance (fig. 3) with bee richness in juniper habitat significantly higher than any other, and bee richness in crested wheatgrass significantly lower than any other. No difference was found between cheatgrass and sagebrush. Average richness per trap sample in the four different plant habitats was: juniper (29.3), cheatgrass (13.6), sagebrush (10.9), and crested wheatgrass (7.8). Total richness across all factors was 161 species and/or morphospecies (Table 1). 69.8% of taxa were identified to species, the remainder to morphospecies within an identified genus. Total richness across the four communities was: juniper (125), cheatgrass (75), sagebrush (75), and crested wheatgrass (64). The Tintic Valley site supported significantly higher bee richness than the Antelope Valley and Yuba sites ($p<0.01$) (fig. 4), and greater richness was observed in year 2007 ($p=0.05$) (fig. 5).

Pairwise similarity comparisons of bee composition using Bray-Curtis across the four habitat types revealed the least habitat similarity expressed between juniper and cheatgrass followed by juniper and crested wheatgrass (table 2). All other comparisons expressed weak similarities, the most similarity found between cheatgrass and crested wheatgrass. Of the bees sampled, 40 taxa were unique to juniper, 11 to cheatgrass, 9 to crested wheatgrass, and 9 to sagebrush.

The same data were tested for significance using ANOSIM (analysis of similarity) (Primer-E Ltd. 2006. v6). The null hypothesis was stated as no differences in bee composition between groups within the classes habitat, site, and year. Significant differences in bee composition were were found between habitat type ($p<0.01$), site ($p<0.01$), and year ($p<0.01$)

The ANOSIM test for significance across the four habitats revealed that the global R test statistic of 0.52 was much larger than any of the 999 permuted values, thus the null hypothesis was rejected. Pairwise comparisons of bee composition show all habitats are significantly different from each other (table 3), as well as all sites (table 4).

Bee composition was further compared across habitats using non-metric multidimensional scaling (MDS) (Primer-E Ltd. 2006. v6). A three dimensional ordination plot depicted habitat relationships with a stress value $S=0.19$. The model does not show clear habitat delineations (fig. 6) but does reveal a gradient ordered juniper, sagebrush, cheatgrass, and crested wheatgrass. This gradient suggests closer affinities in bee composition between immediatley neighboring habitats. The MDS model is consistent with the Bray-Curtis pairwise tests of bee composition across habitats seen in table 1. The highest degree of clustering and separation was observed in the juniper habitat. Other habitats had poor clustering and separation but did follow a gradient.

Use of MDS to plot bee composition across sites revealed a similar phenomenon as found within habitat, a lack of tight group clustering but still an evident gradient (fig. 7). Bee composition at Antelope Valley was separated more distinctly than at other sites even though within site similarity was the broadest of any site. Bray-Curtis pairwise tests of similarity for bee composition across sites revealed that Antelope Valley and Yuba were most similar (similarity index = 0.64), and Antelope Valley and Tintic Valley least similar (similarity index = 0.56)

As observed with habitat comparisons, strong between site separation and within site clustering was not found even though sites were significantly different. A high percentage of bee species unique to a particular site versus habitat, coupled with some ubiquitous species can dilute resolution even though significanct site differences were found using ANOSIM. Of the 161 bee species, 115 were sampled at Tintic Valley compared to 97 at Antelope Valley, and 89 at Yuba. Of the 2691 total bees trapped, 1191 came from Tintic Valley, 622 from Antelope Valley, and 878 from Yuba. Tintic Valley also had the highest number of singletons (37), followed by Antelope Valley (23), and Yuba (11).

Of the 161 total bee taxa encountered it is interesting to note that 44 taxa were singletons, and 21 doubletons. Together, singletons plus doubletons, accounted for 40.1% of the trapped bee taxa reaffirming the fact a large percentage of bees in a given bee population are rare in numbers (Williams et al. 2001). Of the singletons, 21 came from juniper habitat versus 9 from sagebrush and 7 each from both cheatgrass and crested wheatgrass. It is possible that some bee species counted as singletons may acutally be gender segregates within the morphospecies group. The most commonly trapped bee species was *Eucera actuosa* Cresson, represented by 198 specimens.

One method for nonarbitrarily characterizing common species within a habitat type is the application of the prevalent species concept (Curtis 1959). A prevalent species as modified for bee composition in this report is determined by the average richness per habitat type and ranked according to frequency (tables 5-8). Prevalent species are those species that random sampling will most likely encounter within a given habitat: therefore, it is possible for the same species to be prevalent in more than one habitat. Species which reach their maximum presence within a given habitat are called modal speices (Curtis 1959). Some modal bee species may be specific to a single habitat type, others are ubiquitous but more prevalent in their modal habitat. Singletons, by default, are unique to a single sampled habitat, but listing singletons or very rare species as modal has little value for predicting the functional groups that may influence habitat patterns. A rare species may not occur with enough sample frequency to ascribe reasons for its occurrence. The greater prevalence of a modal species within one habitat versus another implies strong ties to specific habitat attributes. Identifiying modal species can help pinpoint which habitats support those bee species providing the greatest ecological service per given habitat.

It is apparent that juniper habitat had the most prevalent (30) and modal (28) species (table 7). Cheatgrass had the second most prevalent (16) and modal (8) species (table 5). Crested wheatgrass had zero (table 6) modal species and sagebrush only one (table 8). It is also interesting to note that of the 28 modal species found in juniper habitat, 15 were found nowhere else.

A total of 58 plants (table 9) providing nectar or pollen rewards for bee species was discovered within 50 meters of Malaise traps across the entire project and both years. An analysis of variance with the dependent variable “flowering plant density” (plant density defined as the number of plant per unit area) and the dependent variables habitat, site, and year, revealed a significant interaction ($p<0.01$) between habitat and site. Year was not significant. Juniper habitat contributed to the interaction especially at Tintic Valley where flowering plant density greatly exceeded all other sites and habitats (fig. 8). Low densities of flowering plants in cheatgrass and crested wheatgrass communities also contributed to a strong interaction, especially when compared to the cheatgrass at Tintic Valley, the sole cheatgrass community with an appreciable flowering plant density.

Flowering plant richness also had a significant habitat-x-site interaction ($p<0.01$). Year was not significant. Juniper habitat had greater mean species richness at all sites except Antelope Valley where sagebrush had the highest mean species richness (fig. 9). In contrast, the Antelope Valley cheatgrass had the lowest mean species richness. The cheatgrass community at Tintic Valley had higher mean species richness than either crested wheatgrass or sagebrush at that location. Crested wheatgrass richness remained similar across all habitats. A total of 15 flowering plant species was found only in the juniper habitat compared to 9 in sagebrush, 2 in crested wheatgrass, and 2 in

The average abundance of flowering plants per meter^2 was plotted against average bee abundance per sample over the combined 2006-2007 seasons. Data were transformed using log10(x+1) in order to display plant and bee data on a more equivalent scale. Flower phenology was bimodal with a spring flowering surge peaking in May and June and ending in July (fig.10). A second smaller peak occurred in August-September. A corresponding increase in bee abundance occurred with the increase of flowering during the spring flowering peak and again during the fall flowering peak. The spring flowering plants were primarily forbs while the late summer flowering plants were primarily shrubs. Plotting species richness over the same time interval yielded similar results as with abundance (fig. 11). Bee and flowering plant richness followed the same seasonal trend with spring and fall peaks. Correlation between total bee diversity and total plant diversity was tested using the RELATE routine in Primer-E (Primer-E Ltd. 2006. v6). A significant relationship was found ($p<0.01$). Estimates of percent ground cover among the four habitat types found juniper with the highest percent open ground (ground not encumberd with plants or plant litter). Open ground in juniper habitat averaged 57.6% compared to 51.7% in sagebrush, 46.1% in crested wheatgrass, and 13.1% in cheatgrass. Percent bare ground does not appear correlated with bee diversity accross habitat types.

Discussion:

An important outcome of this study was determining the relationship between common habitats within the Great Basin and corresponding bee diversity. Observed low bee diversity in cheatgrass and crested wheatgrass was striking compared to the remarkably high diveristy found in juniper habitat. Surprisingly, bee abundance and richness in sagebrush habitat was not different from cheatgrass, though both were better than crested wheatgrass. Flowering plant abundance and richness was also not different between sagebrush, cheatgrass, and crested wheatgrass at most sites, providing a reasonable explanation for similar results in bee diversity. ANOSIM and MDS did provide some insight to bee diversity beyond parametric analysis. All habitat types were significanlty different from each other based purely on species composition. Accordingly, bee composition in sagebrush habitat had a closer affinity to juniper habitat than with cheatgrass or crested wheatgrass. It was not suprising to find signficant differences between years and sites relative to bee diversity. Population fluctuations across years and between sites are common among terrestrial insects (Herrera 1988; Williams et. al. 2001; Price et al. 2005).

Crested wheatgrass supported the lowest bee abundance and richness. This can be partly explained by its competitive nature. Crested wheatgrass was commonly planted because of its ability to out compete cheatgrass. Even though crested wheatgrass can effectively exclude the less desirable cheatgrass, it also effectively excludes the herbaceous natives necessary for sutaining bee populations. Additionally, a contributing factor to low bee diversity in crested wheatgrass stands may be a prolonged history of grazing disturbance. Crested wheatgrass does have high forage value for domestic cattle, but selective grazing on forb species can contribute to decreased bee diversity by disrupting plant-insect associations (Kearns & Inouye 1997; Kruess & Tscharntke 2002). All crested wheatgrass sites in this study experience regular grazing, the Tintic Valley and Antelope Valley sites by sheep, and the Yuba site by cattle; however, the other contiguous habitats at each site are open range and also have the same potential for grazing impacts. From the perspective of soil stabilization and exotic weed control, crested wheatgrass has a valuable role in restoration. If the restoration objective however, is to retain crested wheatgrass as an alternative stable state, flowering forb and bee diversity will be impacted even more severely than in cheatgrass. The fact that cheatgrass supported 8 modal bee species, 4 of which were habitat exclusive, was likely due to the presence of forb species which achieved greater expression in the annual grassland. *Stephanomeria exigua* Nutt. and *Cirsium* sp. were the only two flowering plants found exclusively in cheatgrass, but *Sphaeralcea munroana* (Douglas) Spach (Munro's globemallow) and *S. grossulariifolia* (Hook. & Arn.) Rydb. (gooseberryleaf globemallow) were common forbs with high insect activity found predominantly in cheatgrass habitat.

Restablishment of native forbs requires reducing the competitive effect of crested wheatgrass and ensuring the establishment and persistence of the native component (Pellant 2005). Reintroducing native grasses and shrubs into crested wheatgrass following chemical or mechanical disturbance has been accomplished and may be easier to achieve in crested wheatgrass than cheatgrass (Cox & Anderson 2004). This has led to the concept of “assisted succession” as a model for first restoring cheatgrass to crested wheatgrass, and then restoring the desired native species into crested wheatgrass (Cox & Anderson 2004).

Dense stands of pinyon/juniper have typically been considered less desirable than open stands or other vegetation types where decreased tree density favors increased herbaceous cover and water infiltration. In this study, the pinyon/juniper stands consisted of mature trees of similar physiognomy and a functional stage expressed with little herbaceous understory and bare interstitial space. Although herabaceous cover was extremely low, flowering plant richness was relatively high, comprised primarily of diminutive species adapted to utilize the mostly bare interstitial space between trees. From a perspective of herbaceous cover, dense pinyon/juniper is considered to have low forage value, but it possesses considerable value for bees. The open ground found in juniper habitat may contribute to bee diversity, especially for ground nesting bees; however, the sagebrush and crested wheatgrass site had similar (within 11.5%) open ground. Open ground in cheatgrass was the lowest though it had a singinificantly higher bee diversity than crested wheatgrass. The effect of plant stratigraphy and physiognomy between habitats is an unresolved variable. The architecture of trees in juniper habitat may enhance bee capture in Malaise traps as a funneling affect; however, the rarifaction of samples in ANOSIM ensured reliable analysis results.

The pinyon/juniper and sagebrush communities in this study represent fragments of a once dominant brushland and woodland, now surrounded by grassland. It would be interesting to compare the bee diversity found in pinyon/juniper isolates against larger extensive stands. A study on carrion beetle abundance and diversity found decreases in forest fragments compared to continuous stands in New York (Gibbs & Stanton 2001). As demonstrated with butterflies, specialized species are much more senstitive to proportionally diminishing fragment size (Tscharntke et. al. 2002). The affect of fragmentation can also disrupt gene flow between fragment isolates.

It has been thought that bee specialists forage further than generalists due to potentially fewer plant resources (Rathcke & Jules 1993); however, foraging distances of oligolectic bees were found to be the same as those by polylectic bees (Gathmann & Tscharntke 2002). Gathmann & Tscharntke (2002) also found a maximum flight range of 150-600 meters for food and nesting for 16 solitary bees species, with large bees traveling further than small bees. This supports the possibility of genetic isolation between plant populations separated by distances larger than the flight range of the largest bees in the local population. Conserving rare plant species in the Great Basin would of necessity require conserving large continous tracts of pollinator rich habitat types and ensuring continuity of habitat fragments within the flight range of bee populations. This is especially relavent considering the floristically depauperate and large extents of cheatgrass and crested wheatgrass.

Singletons and rare bees made up a significant proportion of the bee diversity found in this study. Pinyon/juniper harbored 47.7% of all singletons, and 24.7% of all species exclusively. Not only did the pinyon/juniper habitat have the most rare species, it also had the greatest numbers of prevalent and modal species. The preference of modal species for juniper habitat was likely a factor of higher flowering plant diversity. A signficant relationship between flowering plant diversity and bee diversity supports this assumption. If plant diversity is causal to bee diversity, then increasing flowering plant diversity in any habitat can yield positive outcomes for bee populations. Overall, the Tintic Valley site had both the highest plant diversity and bee diversity. The exception perhaps was at the Antelope Valley-sagbrush site where the highest plant richness was observed without a correspondnig increase in bee richness. Flowering plant abundance is likely more important than flowering plant richness for bee diversity.

Conserving pinyon/juniper may seem extrodinary within the context of published literature documenting the pinyon/juniper expansion across the western United States (Miller & Wigand 1994; Miller et al. 2000), but care should be taken to note that pinyon/juniper within the low precipitation zones (<30 cm annually) of the Great Basin exhibits poor recruitment and is transforming to the alternative stable states of fire maintained or reclaimed grasslands. Weisberg et al. (2007) documented the expansion of pinyon/juniper to be largely influenced by factors such as slope and aspect of which mesic slopes and aspects are much more prone to expansion. Similarly, north slopes and increasing elevation favor juniper establishment (Johnson & Miller 2006). Juniper encroachment in harsh, arid sites remains minimal, and if encroachment is a factor of available moisture, then loss of juniper habitat from relict sites of suboptimal moisture may preclude successful reestablishment.

Conclusion:

We recommend maintaining mature stands of pinyon/juniper for their inherent benefit for wild bee populations. This can be accomplished using a mosaic model for habitat heterogeneity in managed wildlands. Because some species are unique among the different habitats, habitat heterogeneity would be necessary to maximize gamma diversity of plants and bees. Because of the mutualistic relationship between bees and the plants they pollinate, successful restoration of either group requires stable populations for both groups. Because bees are mobile and forage for resources, the reestablishment of flowering plant resources is the requisite first step to improve bee diversity in low diversity habitats.

Implications for Practice

- Pinyon/juniper habitat can harbor a diverse flowering plant population that supports a diverse bee population.
- Due to the relationship between flowering plant diversity and bee diversity, management practices that enhance flowering plant diversity should be encouraged.
- Historic crested wheatgrass seedings require additional inputs to restore pollinator structure.
- Sagebrush habitats with impoverished flowering forb diversity should be evaluated for methods to restore diversity.

Acknowledgments:

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Figure legend:

Figure 1: Site x year interaction for average bee abundance per trap ($p=0.04$).

Figure 2: Average bee abundance per trap between habitats ($p<0.01$).

Figure 3: Average bee richness per trap between habitats ($p<0.01$).

Figure 4: Average bee richness per trap between sites ($p<0.01$).

Figure 5: Average bee richness per trap between years ($p=0.05$).

Figure 6: Three dimensional MDS plot of bee composition across habitats.

Figure 7: Three dimensional MDS plot of bee composition across sites.

Figure 8: Site x habitat interaction for average flowering plant density ($p<0.01$).

Figure 9: Site x habitat interaction for average flowering plant richness ($p<0.01$).

Figure 10: Seasonal response of bee abundance and flowering plant abundance.

Figure 11: Seasonal response of bee richness and flowering plant richness.

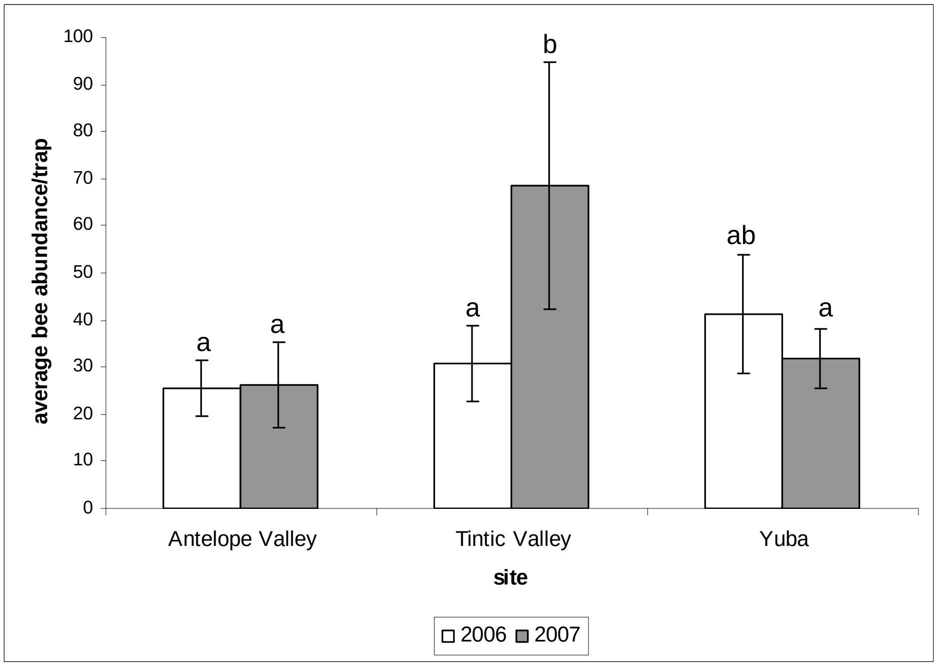
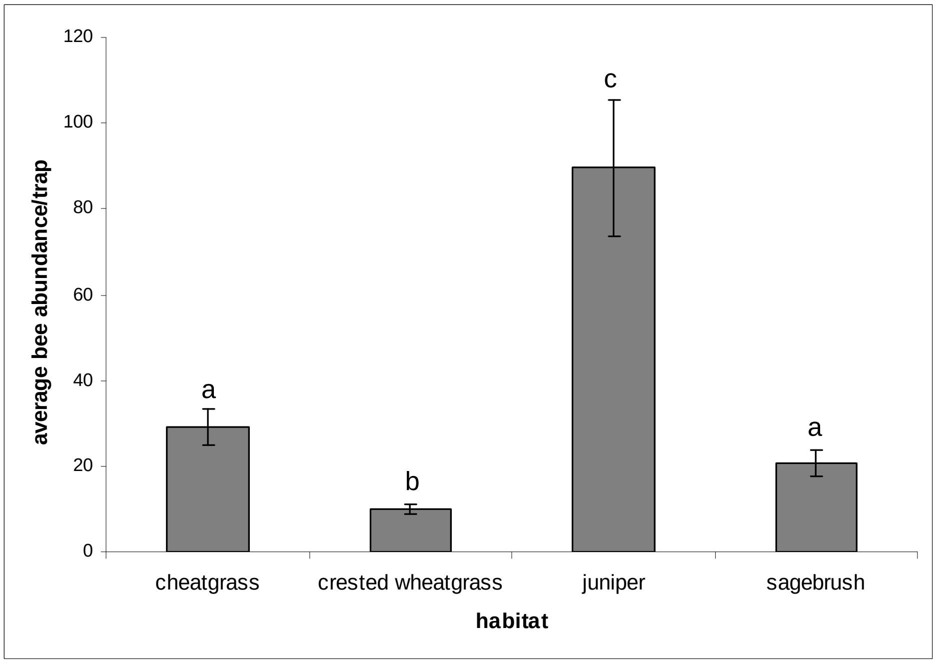


Figure 1



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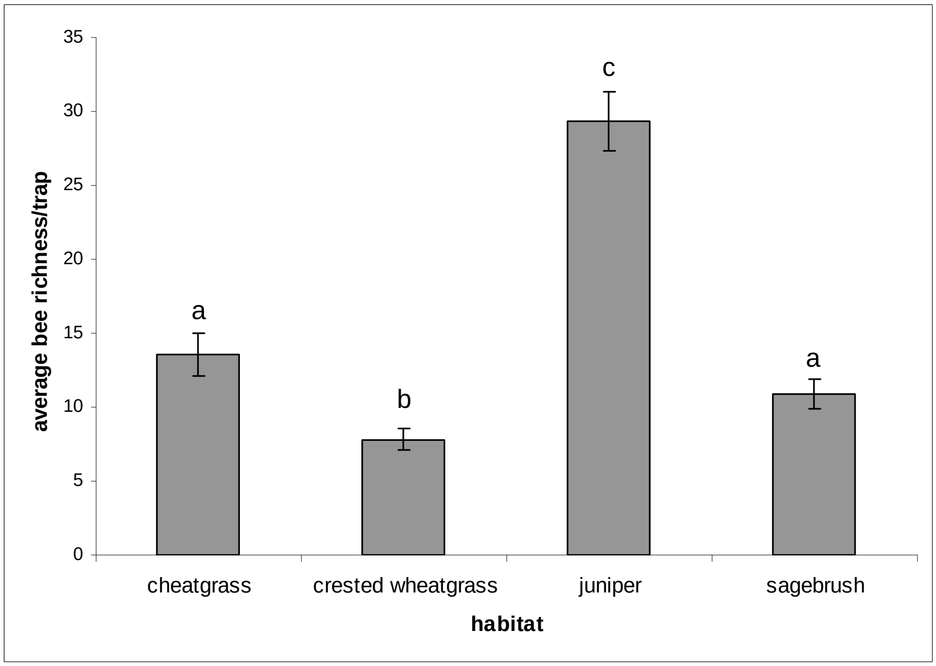

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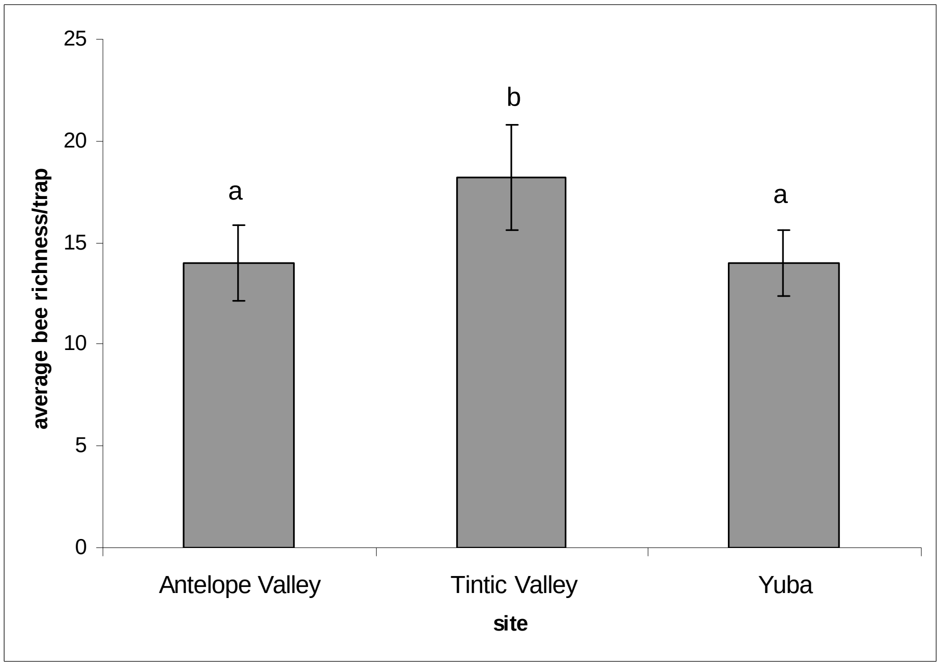

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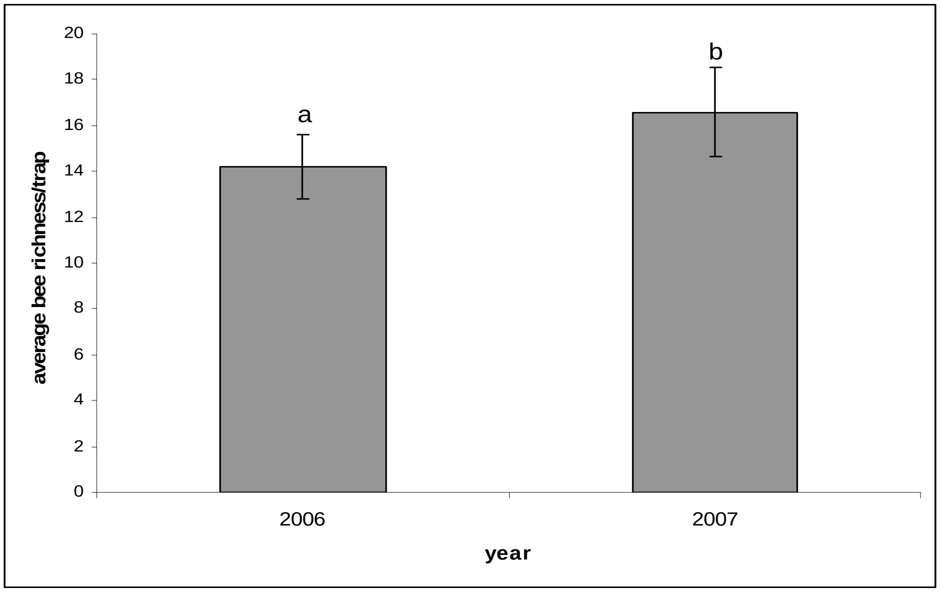

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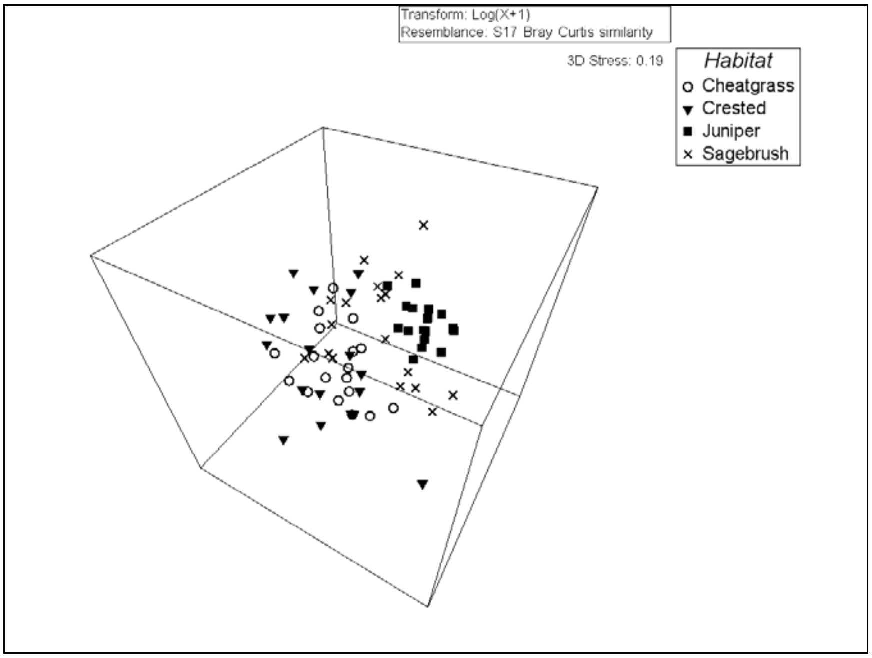

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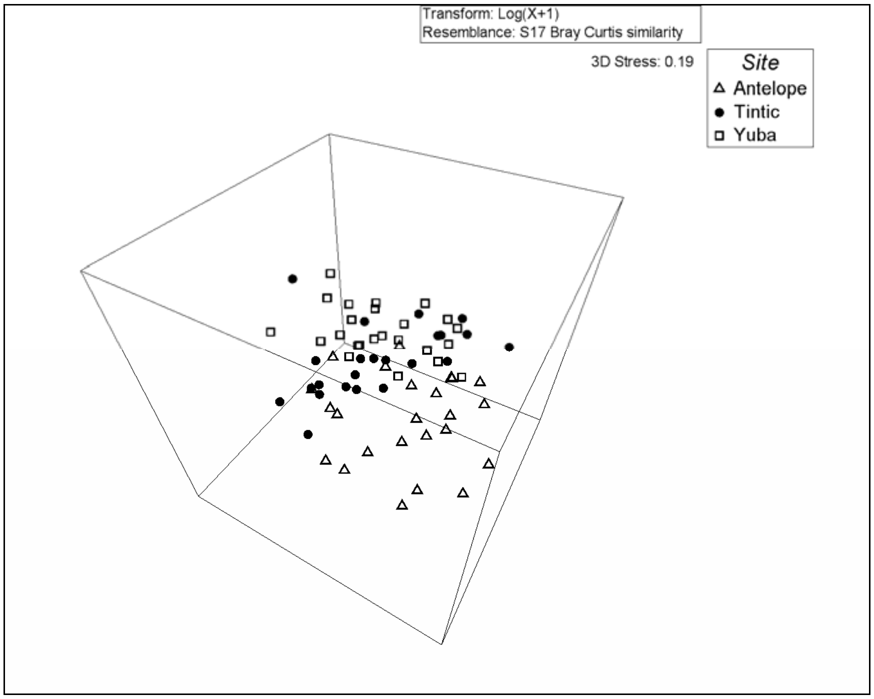

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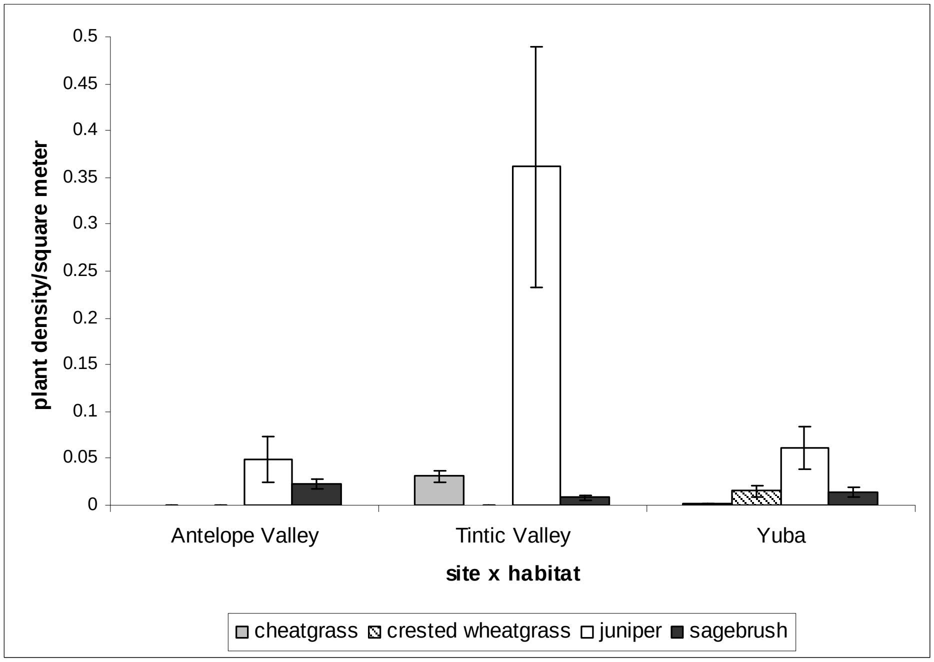

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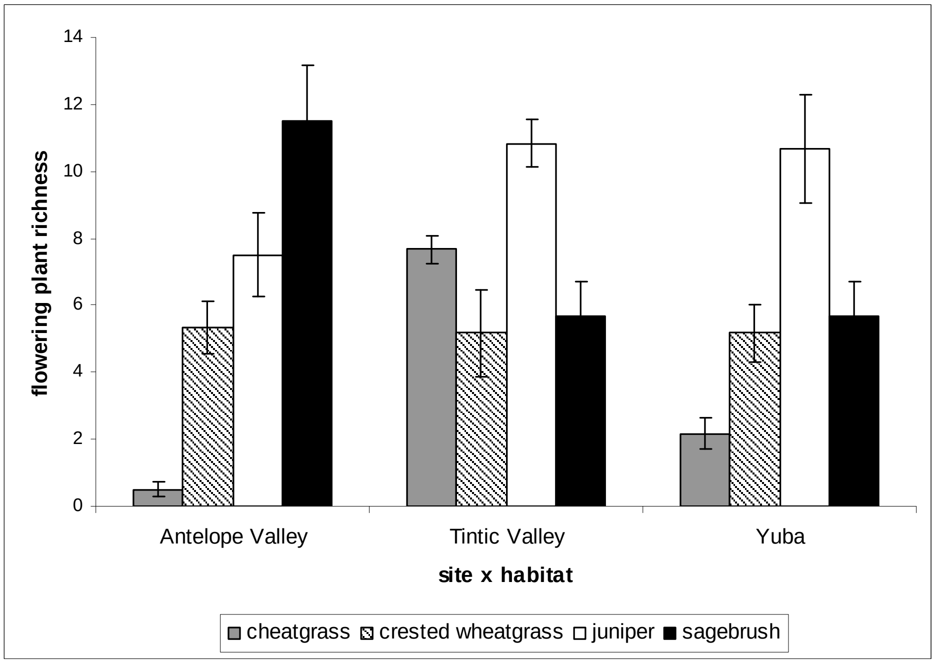

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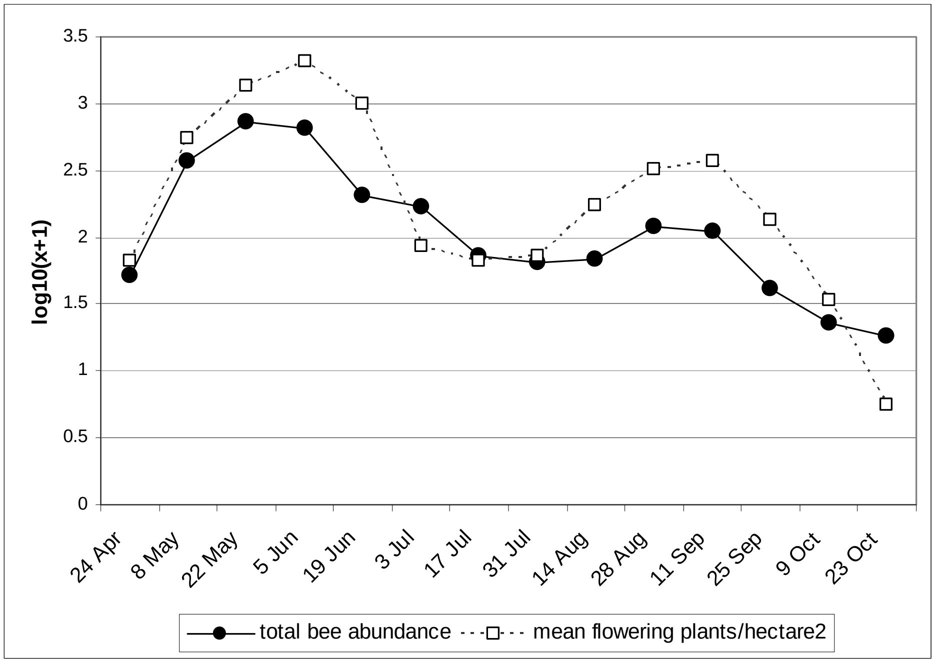
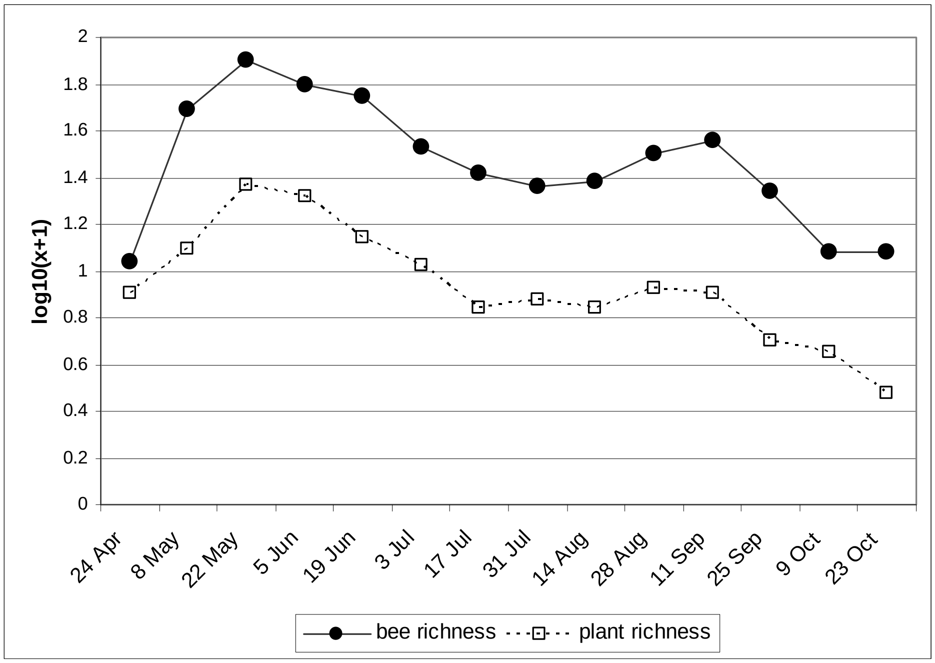


Figure 10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24 Apr
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22 May
5 Jun
19 Jun
3 Jul
17 Jul
31 Jul
14 Aug
28 Aug
11 Sep
25 Sep
9 Oct
23 Oct
bee richness
plant richness

Figure 11

Table legend:

Table 1: Bee species sampled using Malaise traps within habitats and sites. Lower case (x) indicates a singleton.

Table 2: Bray-Curtis pairwise test of similarity for bee composition by habitat.

Table 3: Pairwise comparisons of bee composition between habitats generated using ANOSIM.

Table 4: Pairwise comparisons of bee composition between sites generated using ANOSIM.

Table 5: Prevalent and modal species found in cheatgrass habitat.

Table 6: Prevalent and modal species found in crested wheatgrass habitat.

Table 7: Prevalent and modal species found in crested pinyon/juniper habitat

Table 8: Prevalent and modal species found in sagebrush habitat

Table 9: Plant species sampled within a 30 meter radius of Malaise traps within habitats and sites.

		Habitat				Site		
Species	Family	Cheatgrass	Crested wheatgrass	Juniper	Sagebrush	Antelope Valley	Tintic Valley	Yuba
Agapostemon angelicus Cockerell 1924	Halictidae	X	X	X	X	X	X	X
Agapostemon coloradinus (Vachal 1903)	Halictidae	x					x	
Agapostemon femoratus Crawford 1901	Halictidae		X					X
Andrena anograe Cockerell 1901	Andrenidae			x				x
Andrena astragali Viereck & Cockerell 1914	Andrenidae			X		X		
Andrena auricoma Smith 1879	Andrenidae	X		X		X		
Andrena chapmanae Viereck 1904	Andrenidae			X		X		X
Andrena lupinorum Cockerell 1906	Andrenidae	X	X	X		X		X
Andrena piperi Viereck 1904	Andrenidae	X	X	X	X	X	X	X
Andrena pruinosa Erichson 1835	Andrenidae	X		X	X	X	X	X
Andrena scurra Viereck 1904	Andrenidae	X	X	X	X	X	X	X
Andrena sp. 1	Andrenidae			x			x	
Andrena sp. 2	Andrenidae	X						X
Andrena sp. 3	Andrenidae	X			X			X
Andrena sp. 4	Andrenidae				x	x		
Andrena sp. 5	Andrenidae	X		X			X	
Andrena transnigra Viereck 1904	Andrenidae	X		X				X

Anthidium atripes Cresson 1879	Megachilidae			X		X	X	
Anthidium clypeodentatum Swenk 1914	Megachilidae		x			x		
Anthidium emarginatum (Say 1824)	Megachilidae	X	X	X	X	X	X	X
Anthidium formosum Cresson 1878	Megachilidae			x			x	
Anthidium mormonum Cresson 1878	Megachilidae		X	X		X	X	
Anthophora affabilis Cresson 1878	Apidae	X	X		X	X	X	
Anthophora edwardsii Cresson 1878	Apidae	X	X	X		X	X	X
Anthophora lesquerellae (Cokerell 1896)	Apidae	X	X	X	X	X	X	X
Anthophora neglecta Timberlake & Cockerell 1936	Apidae			X	X	X	X	X
Anthophora porterae Cockerell 1900	Apidae	X	X	X	X	X	X	X
Anthophora sp.1	Apidae			x		x		
Anthophora urbana Cresson 1878	Apidae	X	X	X	X	X	X	X
Anthophora ursina Cresson 1869	Apidae	X		X	X	X	X	X
Apis mellifera Linnaeus 1758	Apidae			X			X	
Ashmeadiella aridula Cockerell 1910	Megachilidae				x	x		
Ashmeadiella bucconis (Say 1837)	Megachilidae			X	X		X	X
Ashmeadiella opuntiae (Cockerell 1897)	Megachilidae				x		x	
Bombus griseocollis (DeGeer 1773)	Apidae	X	X			X		
Bombus huntii Greene 1860	Apidae	X		X	X	X	X	
Bombus morrisoni Cresson 1878	Apidae		x					x

Bombus nevadensis Cresson 1874	Apidae	X	X	X		X	X	
Calliopsis coloratipes Cockrell 1898	Andrenidae			x		x		
Calliopsis puellae (Cockerell 1933)	Andrenidae			X	X		X	
Ceratina pacifica H.S. Smith 1907	Apidae			X		X	X	X
Colletes phaceliae Cockerell 1906	Colletidae	X		X	X		X	X
Colletes sp. 1	Colletidae	X					X	
Colletes sp. 2	Colletidae	X					X	
Colletes sp. 3	Colletidae	X	X	X		X	X	X
Colletes sp. 4	Colletidae	X		X		X	X	X
Diadasia australis (Cresson 1878)	Apidae			X	X	X	X	X
Diadasia diminuta (Cresson 1878)	Apidae	X					X	
Diadasia enavata (Cresson 1872)	Apidae	X					X	
Dianthidium subparvum Swenk 1914	Megachilidae			X	X	X	X	X
Dianthidium ulkei (Cresson 1878)	Megachilidae				x	x		
Dioxys pomonae Cockerell 1910	Megachilidae			x			x	
Eucera actuosa (Cresson 1878)	Apidae	X	X	X	X	X	X	X
Eucera delphinii (Timberlake 1969)	Apidae		X		X	X		X
Eucera edwardsii (Cresson 1878)	Apidae	X	X	X	X	X	X	X
Eucera frater (Cresson 1878)	Apidae			X		X	X	X
Eucera fulvitarsis (Cresson 1878)	Apidae	X	X	X	X	X	X	X

Eucera lutziana (Cockerell 1933)	Apidae	X	X	X	X	X	X	X
Eucera sp. 1	Apidae	X		X		X	X	
Eucerini sp. 1	Apidae				x	x		
Habropoda cineraria (Smith 1879)	Apidae	X	X		X	X	X	X
Habropoda morrisoni (Cresson 1878)	Apidae			X	X	X	X	X
Habropoda sp. 1	Apidae		x			x		
Halictus confusus Smith 1953	Halictidae		x					x
Halictus farinosus Smith 1853	Halictidae		X	X		X		X
Halictus ligatus Say 1837	Halictidae	x					x	
Halictus rubicundus (Christ 1791)	Halictidae	X	X	X	X	X		X
Halictus tripartitus Cockerell 1895	Halictidae	X	X	X	X	X	X	X
Heriades cressoni Michener,1938	Megachilidae			x		x		
Heriades timberlakei Michener 1938	Megachilidae			X		X		
Hoplitis albifrons (Kirby 1837)	Megachilidae		X	X	X	X		
Hoplitis incanescens (Cockerell 1922)	Megachilidae			x				x
Hoplitis producta (Cresson, 1864)	Megachilidae			X	X	X		
Hoplitis zuni (Parker 1977)	Megachilidae			x				x
Hylaeus granulatus (Metz 1911)	Colletidae			x		x		
Lasioglossum albohirtum (Crawford 1907)	Halictidae	X	X	X		X	X	X
Lasioglossum hyalinum (Crawford 1907)	Halictidae	X	X	X	X	X	X	X

Lasioglossum impavidum (Sandhouse 1924)	Halictidae	X	X	X	X	X	X	X
Lasioglossum incompletum (Crawford 1907)	Halictidae	X	X	X	X	X	X	X
Lasioglossum lampronutum McGinley 1986	Halictidae			X		X	X	
Lasioglossum lusorium (Cresson 1872)	Halictidae		x				x	
Lasioglossum nevadense (Crawford 1907)	Halictidae	X		X	X	X	X	X
Lasioglossum pectoraloides (Cockerell 1895)	Halictidae	X		X				X
Lasioglossum perdifficile (Cockerell 1895)	Halictidae			X			X	X
Lasioglossum pruinosiforme (Crawford 1906)	Halictidae	X	X	X	X	X	X	X
Lasioglossum pruinosum (Robertson 1892)	Halictidae	X	X	X			X	X
Lasioglossum pulveris (Cockerell 1930)	Halictidae	X	X	X	X	X	X	X
Lasioglossum sedi (Sandhouse 1924)	Halictidae	X	X	X	X	X	X	X
Lasioglossum sisymbrii (Cockerell 1895)	Halictidae	X	X	X	X	X	X	X
Lasioglossum sp. 1	Halictidae	X	X	X	X	X	X	X
Lasioglossum sp. 2	Halictidae			X	X	X	X	X
Lasioglossum sp. 3	Halictidae	X					X	
Lasioglossum sp. 4	Halictidae		X	X			X	X
Lasioglossum sp. 5	Halictidae	x					x	
Lasioglossum sp. 6	Halictidae	X	X	X	X	X	X	X
Lasioglossum sp. 7	Halictidae			X		X	X	X
Lasioglossum sp. 8	Halictidae	X	X	X		X	X	X

Lasioglossum sp. 9	Halictidae	X	X	X	X	X	X	X
Lasioglossum sp. 10	Halictidae	X	X	X	X	X	X	X
Megachile **aff.** revis Say 1837	Megachilidae	X		X	X	X	X	X
Megachile anograe Cockerell 1908	Megachilidae			x		x		
Megachile inimica Cresson 1872	Megachilidae			x			x	
Megachile laurita Mitchell 1927	Megachilidae		X	X		X		
Megachile parallela Smith 1853	Megachilidae	X		X			X	
Megachile sp. 1	Megachilidae	x					x	
Megachile subnigra Cresson 1879	Megachilidae			X	X	X	X	X
Melecta pacifica Cresson 1878	Apidae			X	X	X	X	X
Melissodes agilis Cresson 1878	Apidae	X	X	X	X	X	X	
Melissodes bimatris LaBerge 1961	Apidae	X			X		X	X
Melissodes dagosa Cockerell 1909	Apidae		X	X	X	X	X	X
Melissodes semilupina Cockerell 1905	Apidae	X	X				X	X
Melissodes sp. 1	Apidae	X	X	X	X	X	X	X
Melissodes tristis Cockerell 1894	Apidae	X	X	X	X	X	X	
Nomada elegantula Cockerell 1903	Apidae				x			x
Nomada hesperia Cockerell 1903	Apidae	X	X	X	X	X		X
Osmia bakeri Sandhouse 1924	Megachilidae		x				x	
Osmia brevis Cresson 1864	Megachilidae			X	X	X	X	X

Osmia bruneri Cockerell 1897	Megachilidae			X	X	X	X	X
Osmia coloradensis Cresson 1878	Megachilidae			x			x	
Osmia gaudiosa Cockerell 1907	Megachilidae			X			X	
Osmia grinnelli Cockerell 1910	Megachilidae			X			X	
Osmia integra Cresson 1878	Megachilidae			X	X	X	X	X
Osmia iridis Cockerell and Titus 1902	Megachilidae		X	X	X	X		X
Osmia latisulcata Michener 1936	Megachilidae	X		X			X	X
Osmia lignaria Say 1837	Megachilidae		X	X			X	X
Osmia sp. 1	Megachilidae			X	X	X	X	
Osmia sp. 2	Megachilidae			X			X	
Osmia sp. 3	Megachilidae			x		x		
Osmia sp. 4	Megachilidae			X	X		X	
Osmia sp. 5	Megachilidae			X			X	X
Osmia sp. 6	Megachilidae			x			x	
Osmia sp. 7	Megachilidae			X	X		X	
Osmia sp. 8	Megachilidae			X			X	
Osmia sp. 9	Megachilidae			x			x	
Osmia sp. 10	Megachilidae	X	X	X	X	X	X	X
Osmia sp. 11	Megachilidae			X			X	
Osmia trevoris Cockerell 1897	Megachilidae			X	X		X	X

Osmia unca Michener 1937	Megachilidae			X			X	
Perdita **aff.** *aridella* Timberlake 1960	Andrenidae	X	X	X	X	X	X	X
Perdita **aff**. *mesillensis* Timberlake 1968	Andrenidae		X	X		X		
Perdita **aff.** *munda* Timberlake 1958	Andrenidae		X	X	X	X	X	X
Perdita albonotata Timberlake 1954	Andrenidae	X		X	X		X	X
Perdita aridella Timberlake 1960	Andrenidae	X		X	X		X	X
Perdita dilecta Timberlake 1960	Andrenidae	X		X			X	
Perdita dubia Cockerell 1896	Andrenidae		X	X		X		X
Perdita mormonica Timberlake 1956	Andrenidae			X		X		
Perdita sp. 1	Andrenidae	X	X	X	X	X	X	X
Protandrena sp.1	Andrenidae			x		x		
Sphecodes sp. 1	Halictidae	x					x	
Sphecodes sp. 2	Halictidae				x		x	
Sphecodes sp. 3	Halictidae	X	X	X	X	X	X	X
Svastra obliqua (Say 1837)	Apidae		x				x	
Svastra sp. 1	Apidae				x			x
Svastra sp. 2	Apidae			x		x		
Triepeolus sp. 1	Apidae			x			x	
Triepeolus sp. 2	Apidae				x			x
Triepeolus sp. 3	Apidae			x			x	

Triepeolus sp. 4	Apidae			X	X		X
Triepeolus sp. 5	Apidae		x		x		
Triepeolus sp. 6	Apidae			x		x	
Triepeolus sp. 7	Apidae	x				x	

Table 1

	cheatgrass	crested wheatgrass	juniper	sagebrush
cheatgrass				
crested wheatgrass	0.56			
juniper	0.46	0.41		
sagebrush	0.55	0.55	0.52	

Table 2

```
TESTS FOR DIFFERENCES BETWEEN Habitat GROUPS
(across all Site groups)
Global Test
Sample statistic (Global R): 0.523
Significance level of sample statistic: 0.1%
Number of permutations: 999 (Random sample from a large number)
Number of permuted statistics greater than or equal to Global R: 0

Pairwise Tests
                             R Significance     Possible      Actual Number >=
Groups               Statistic      Level % Permutations Permutations  Observed
Cheatgrass, Crested      0.331          0.1     98611128         999         0
Cheatgrass, Juniper      0.864          0.1     98611128         999         0
Cheatgrass, Sagebrush    0.435          0.1     98611128         999         0
Crested, Juniper         0.632          0.1     98611128         999         0
Crested, Sagebrush       0.327          0.2     98611128         999         1
Juniper, Sagebrush       0.614          0.1     98611128         999         0
```

Table 3

```
TESTS FOR DIFFERENCES BETWEEN Site GROUPS
(across all Habitat groups)
Global Test
Sample statistic (Global R): 0.456
Significance level of sample statistic: 0.1%
Number of permutations: 999 (Random sample from a large number)
Number of permuted statistics greater than or equal to Global R: 0

Pairwise Tests
                          R Significance      Possible       Actual  Number >=
Groups            Statistic      Level %  Permutations Permutations   Observed
Antelope, Tintic      0.533          0.1    Very large          999          0
Antelope, Yuba        0.425          0.1    Very large          999          0
Tintic, Yuba          0.428          0.1    Very large          999          0
```

Table 4

RANK	BEE SPECIES	% FREQUENCY	MODAL SPECIES	HABITAT SPECIFIC
1	*Lasioglossum hyalinum* (Crawford 1907)	88.9	x	
2	*Lasioglossum sisymbrii* (Cockerell 1895)	83.3	x	
3	*Lasioglossum incompletum* (Crawford 1907)	77.8	x	
4	*Eucera actuosa* (Cresson 1878)	50.0		
5	*Lasioglossum albohirtum* (Crawford 1907)	50.0	x	x
6	*Lasioglossum sedi* (Sandhouse 1924)	50.0		
7	*Eucera lutziana* (Cockerell 1933)	44.4		
8	*Agapostemon angelicus* Cockerell 1924	38.9	x	x
9	*Lasioglossum pruinosiforme* (Crawford 1906)	38.9	x	x
10	*Lasioglossum pulveris* (Cockerell 1930)	38.9	x	
11	*Lasioglossum* sp. 10	33.3		
12	*Melissodes* sp. 1	33.3		
13	*Anthophora urbana* Cresson 1878	27.8		
14	*Lasioglossum (Dialictus)* sp. 19	27.8		
15	*Lasioglossum incompletum* (Crawford 1907)	27.8		
16	*Perdita albonotata* Timberlake 1954	27.8	x	x

Table 5

RANK	BEE SPECIES	% FREQUENCY	MODAL SPECIES	HABITAT SPECIFIC
1	*Lasioglossum sisymbrii* (Cockerell 1895)	66.7		
2	*Lasioglossum hyalinum* (Crawford 1907)	50.0		
3	*Lasioglossum pulveris* (Cockerell 1930)	33.3		
4	*Eucera actuosa* (Cresson 1878)	27.8		
5	*Halictus tripartitus* Cockerell 1895	27.8		

6	*Lasioglossum incompletum* (Crawford 1907)	27.8
7	*Lasioglossum sedi* (Sandhouse 1924)	27.8
8	*Lasioglossum* sp. 10	27.8
9	*Melissodes* sp. 1	27.8

Table 6

RANK	BEE SPECIES	% FREQUENCY	MODAL SPECIES	HABITAT SPECIFIC
1	*Eucera fulvitarsis* (Cresson 1878)	100.0	x	
2	*Lasioglossum* sp. 10	94.4	x	
3	*Eucera lutziana* (Cockerell 1933)	83.3	x	
4	*Eucera edwardsii* (Cresson 1878)	77.8	x	x
5	*Lasioglossum* sp. 1	77.8	x	
6	*Halictus tripartitus* Cockerell 1895	72.2	x	
7	*Lasioglossum impavidum* (Sandhouse 1924)	72.2	x	x
8	*Lasioglossum nevadense* (Crawford 1907)	72.2	x	x
9	*Eucera actuosa* (Cresson 1878)	66.7	x	
10	*Anthophora lesquerellae* (Cokerell 1896)	61.1	x	x
11	*Lasioglossum hyalinum* (Crawford 1907)	61.1		
12	*Lasioglossum sedi* (Sandhouse 1924)	61.1	x	
13	*Lasioglossum (Dialictus)* sp. 19	61.1	x	
14	*Osmia* sp. 10	61.1	x	
15	*Lasioglossum incompletum* (Crawford 1907)	55.6	x	
16	*Andrena pruinosa* Erichson 1835	50.0	x	x
17	*Ceratina pacifica* H.S. Smith 1907	50.0	x	x
18	*Lasioglossum* sp. 7	50.0	x	x
19	*Lasioglossum sisymbrii* (Cockerell 1895)	50.0		
20	*Anthophora porterae* Cockerell 1900	44.4	x	x

21	*Anthophora ursina* Cresson 1869	44.4	x	
22	*Dianthidium subparvum* Swenk 1914	44.4	x	x
23	*Melissodes* sp. 1	44.4	x	
24	*Anthophora urbana* Cresson 1878	38.9	x	
25	*Eucera* sp. 1	38.9	x	x
26	*Habropoda morrisoni* (Cresson 1878)	38.9	x	x
27	*Lasioglossum* sp. 2	38.9	x	x
28	*Osmia bruneri* Cockerell 1897	38.9	x	x
29	*Osmia latisulcata* Michener 1936	38.9	x	x
30	*Perdita* **aff.** *aridella*	38.9	x	x

Table 7

RANK	BEE SPECIES	% FREQUENCY	MODAL SPECIES	HABITAT SPECIFIC
1	*Eucera actuosa* (Cresson 1878)	55.6		
2	*Eucera lutziana* (Cockerell 1933)	55.6		
3	*Osmia* sp. 10	55.6		
4	*Lasioglossum* sp. 1	44.4		
5	*Lasioglossum hyalinum* (Crawford 1907)	38.9		
6	*Lasioglossum sisymbrii* (Cockerell 1895)	38.9		
7	*Eucera fulvitarsis* (Cresson 1878)	33.3		
8	*Lasioglossum* sp. 10	33.3		
9	*Andrena piperi* Viereck 1904	27.8	x	x
10	*Anthophora ursina* Cresson 1869	27.8		
11	*Lasioglossum sedi* (Sandhouse 1924)	27.8		

Table 8

	Habitat				Site		
		Crested			Antelope	Tintic	
Plant species	Cheatgrass	Wheatgrass	Juniper	Sagebrush	Valley	Valley	Yuba
Androstephium breviflorum S. Watson	X	X	X	X		X	X
Arenaria fendleri A. Gray			X	X	X		X
Argemone munita Durand & Hilg.		X				X	
Astragalus beckwithii Torr. & A. Gray		X	X		X	X	
Astragalus calycosus Torr. ex S. Watson			X			X	X
Astragalus lentiginosus Douglas ex Hook.	X	X	X	X	X	X	
Astragalus sp. 1			X		X	X	
Astragalus sp. 2			X		X		X
Calochortus nuttallii Torr. & A. Gray	X	X	X	X	X	X	X
Castilleja angustifolia (Nutt.) G. Don var. dubia A. Nelson		X	X	X	X	X	X
Caulanthus crassicaulis (Torr.) S. Watson				X	X		
Chaenactis douglasii (Hook.) Hook. & Arn.	X		X	X	X	X	X
Chaetopappa ericoides (Torr.) G.L. Nesom		X	X	X	X		X
Chrysothamnus viscidiflorus (Hook.) Nutt.		X	X	X	X	X	X
Cirsium sp.	X				X	X	
Cryptantha humilis (A. Gray) Payson			X		X	X	X
Cymopterus purpurascens (A. Gray) M.E. Jones	X		X	X	X	X	X

Delphinium nuttallianum Pritz. ex Walp.				X			X
Ephedra nevadensis S. Watson				X			X
Ericameria nauseosa (Pall. ex Pursh) G.L. Nesom & Baird	X	X			X	X	
Ericameria nauseosa ssp. *consimilis* var. *turbinata* (M.E. Jones) G.L. Nesom & Baird				X		x	
Erigeron aphanactis (A. Gray) Greene		X	X	X	X	X	X
Erigeron concinnus (Hook. & Arn.) Torr. & A. Gray	X			X	X	X	X
Eriogonum brevicaule Nutt. var. *laxifolium* (Torr. & A. Gray) Reveal			X	X			X
Eriogonum ovalifolium Nutt.			X	X	X		X
Eriogonum villiflorum A. Gray			X				X
Gutierrezia sarothrae (Pursh) Britton & Rusby		X	X	X	X		X
Helianthus annuus L.	X	X				X	
Lactuca serriola L.	X	X				X	
Linum lewisii Pursh			X				X
Lithospermum incisum Lehm.			X				X
Machaeranthera canescens (Pursh) A. Gray	X	X		X	X	X	
Oenothera caespitosa Nutt.	X	X		X	X	X	
Opuntia polyacantha Haw.		X	X	X	X	X	X
Packera multilobata (Torr. & A. Gray ex A. Gray) W.A. Weber & A. Löve			X			X	

Penstemon confusus M.E. Jones			X	X	X		X
Petradoria pumila (Nutt.) Greene			X				X
Phlox hoodii Richardson			X	X	X	X	X
Phlox longifolia Nutt.	X	X	X	X	X	X	X
Physaria chambersii Rollins			X			X	
Polygala subspinosa S. Watson			X	X	X		
Purshia stansburiana (Torr.) Henrickson				X		X	
Salsola tragus L.		X				X	
Sisymbrium altissimum L.	X	X	X	X	X	X	X
Sphaeralcea coccinea (Nutt.) Rydb.	X	X		X	X		X
Sphaeralcea grossulariifolia (Hook. & Arn.) Rydb.	X	X	X	X	X	X	X
Sphaeralcea munroana (Douglas) Spach	X			X	X	X	X
Stanleya pinnata (Pursh) Britton			X				X
*Stenotus acauli*s (Nutt.) Nutt.			X		X		
Stephanomeria exigua Nutt.	X					X	
Streptanthus cordatus Nutt.			X	X	X	X	X
Tetradymia glabrata Torr. & A. Gray				X		X	
Tetradymia nuttallii Torr. & A. Gray				X	X		
Tetradymia spinosa Hook. & Arn.				X		X	
Thelypodiopsis vermicularis (S.L. Welsh & Reveal) Rollins				X	X		

Townsendia jonesii (Beaman) Reveal			X		X		X
Tragopogon dubius Scop.	X	X		X	X	X	X
Zigadenus paniculatus (Nutt.) S. Watson			X		X	X	

Table 9

CHAPTER 2

PREDISPERSAL SEED PREDATION IN WILD POPULATIONS OF *WYETHIA AMPLEXICAULIS* (NUTT.) NUTT. (ASTERACEAE) BY *NEOTEPHRITIS FINALIS* (LOEW) AND *TRUPANEA NIGRICORNIS* (COQUILLETT) (DIPTERA: TEPHRITIDAE)

Robert L. Johnson and Val Jo Anderson

(RLJ) Department of Plant and Wildlife Science, Brigham Young University, UT 84602 U.S.A. (E-mail: robert_johnson@byu.edu), (VJA) Department of Plant and Wildlife Science, Brigham Young University, UT 84602 U.S.A. (E-mail: val_anderson@byu.edu)

Abstract - We harvested capitula of *Wyethia amplexicaulis* (Nuttall) Nuttall from three sites in central Utah in 2006 and 2007 for rearing trials. Average seed production per capitulum was 76.7. Nearly all capitula (95.9%) and all plants in the population were infested with seed predators. Damage by seed predators averaged 38.9% per capitulum with a high of 46.9%. The dominant seed predator reared was the capitivorous (capitulum feeder) fruit fly *Neotephritis finalis* (Loew). An average of 9.3 seeds was consumed per *N. finalis* larva per capitulum. *Trupanea nigricornis* (Coquillett) occurred less frequently. A positive correlation existed between capitulum diameter and the number of flies reared per capitulum. Even though fly abundance increased with increasing capitulum diameter, percent seed damage did not increase. Parasitoidism of *N. finalis* by *Pteromalus* sp. averaged 11.5% and 3.7% by *Zaglyptonotus mississippiensis* Breland. This is the first recorded occurrence of *Z. mississippiensis* west of the Rocky Mountains.

Key Words: Capitivorous, host plant, parasitoids, Torymidae, *Pteromalus*, *Zaglyptonotus,* Utah.

Introduction

Non-frugivorous fruit flies (Tephritidae) are common seed predators of plants in the family Asteraceae (Goeden et al. 1987, Foote et al. 1993). I prefer to use the term “capitivorous” to distinguish the tephritid taxa that feed on flowerheads of the family Asteraceae from those that feed on fruit or are gall-makers. Capitivorous fruit flies feed on parts of the flower head, or capitulum. Capitivorous is derived from; capit = “Latin, diminutive of *caput*, *capit-*, head,” and vorous = “Latin *-vorus*, from *vorāre*, to swallow, devour” (Anonymous 2000). Capitivorous fruit flies are known to feed on receptacle tissue, ovules, seed, flowers, or any combination of these; however, developing seed are the primary tissue targeted by tephritid species discussed in this paper.

This study examines the occurrence of *Neotephritis finalis* (Loew) and *Trupanea nigricornis* (Coquillett), two capitivorous fruit flies found on *Wyethia amplexicaulis* (Nuttall) Nuttall (Mule’s ear). Their parasitoids are also examined. *Neotephritis finalis* is considered the most commonly encountered fruit fly in North American (Foote et al. 1993) and has been reared from flower heads of many members of the family Asteraceae, including other species in the genus *Wyethia*: *W. arizonica* A. Gray (Wasbauer 1972) *W. ovata* Torrey and Gray, *W. mollis* Gray, and *W. helenioides* (deCandolle) Nuttall (Goeden et al. 1987). *N. finalis* larvae begin feeding on immature achenes and tunnel into adjacent achenes during development (Goeden et al. 1987).

Like *N. finalis*, *T. nigricornis* is a common polyphage that has been documented previously as a pest of *W. amplexicaulis* (Kazuo 1993). Females of *T. nigricornis* are known to insert eggs into developing achenes or corolla tissue (Khousama et al. 2007a, 2007b). Larvae then feed on developing achenes, proximal corolla tissue, and occasionally on receptacle tissue. As the larvae mature, they continue to feed on maturing achenes. *T. nigricornis* has been reared on 71 species and 33 genera in the family Asteraceae (Goeden 1985, 1992, Khousama et al. 2007a).

W. amplexicaulis, is a large seeded species in the tribe Heliantheae, subtribe Engelmanniinae (Clevinger and Panero 2000, Moore and Bohs 2003). It is common in the Rocky Mountains, often forming large, floristically dominant herbaceous meadows, or as a dominant understory species in aspen (*Populus tremuloides* Michx.) or Gambel's oak (*Quercus gambelii* Nutt.) It is found at elevations from 1525-2900 meters throughout the north-central counties of Utah (Welsh et al. 2003) and occurs elsewhere in Colorado, Wyoming, Montana, Idaho, Nevada, Washington, and Oregon (USDA, NRCS. 2008)

Within the last several decades, the understanding of capitivorous fruit fly host plant associations in North America and their biology has increased dramatically, largely through the work of R. D. Goeden (Department of Entomology, University of California Riverside). Predispersal seed predation in wild plant populations can have considerable impact on the total annual seed production of a population. A decrease in seed production by flower or seed predation can limit seedling recruitment (Louda 1982). The degree to which these flies impact the host population's reproductive capacity remains an intriguing and valuable subject for research. This study investigates the impact of seed damage by capitivorous fruit flies in wild populations of *W. amplexicaulis*.

Materials and Methods

We studied three separate sites (Manti Ridge, Payson Canyon, and Squaw Peak) in 2006 and 2007 from central Utah, each possessing a large population of *W. amplexicaulis*. Manti Ridge (39.27092°N 111.51873°W) is situated at 2792 m. elevation on the Wasatch Plateau between Ephraim and Manti Canyon in Sanpete County, Utah. The site supports a monoculture of *W. amplexicualis* surrounding a cluster of aspen with a mixed herbaceous understory. A hard frost in 2007 caused some damage to emerging buds of *Wyethia*. The Payson Canyon (39.90569°N, 11.63626°W) site is located at 2502 m. elevation in southern Utah county. At this site *W. amplexicaulis* is a prevalent species in aspen understory, especially in open areas with more abundant sunlight. Squaw Peak (40.3027°N, 111.6251°W) is the lowest elevation site at 2015 m., also in Utah county but approximately 43 km. north of the previous site. At this site *W. amplexicaulis* occupies the open areas between *Quercus gambelii* Nutt. (Gambel oak) and *Acer grandidentatum* Nutt. (bigtooth maple).

Within each population 20 random plants were selected along a transect line that bisected the center of the population. Plants were selected as the nearest plant-to-transect point, with the 20 transect points spaced equidistant across the plant population. A selection criterion was imposed to ensure that plants were mature, producing at least 4 flowering stalks per plant. If the nearest plant-to-transect point did not meet this selection criterion, then the next nearest appropriate neighbor was selected.

Immediately following flower anthesis, capitula from all sample plants were collected, stored in plastic bags, and transported to the laboratory. In the laboratory up to 10 random capitula were subsampled from each of the 20 plants. If there were less than 10 capitula, all were used to make up the sample. Capitula were placed individually in 4.5 oz portion cups with perforated lids for ventilation. The extra capitula from each plant were bulked and sealed in paper bags to rear out additional insects that could shed light on the total composition of emergents.

Rearing containers were maintained at room temperature (~24 °C daytime, and ~16 °C nighttime) for the duration of the rearing trial. Emergence of fruit flies began within several days of capitula harvest and peaked approximately 2 weeks thereafter. Fruit fly emergence ended within one month though some wasp parasitoids emerged up to 4 months later.

After 3 months of rearing, most (>99%) insects had emerged and died. At this time we assessed the abundance and composition of emerged fruit flies and parasitoids as well as the percent seed damage in each capitulum. Because of the large capitulum size, each flowerhead was halved and quartered across the receptacle yielding four portions to dissect under a 10-40 x stereomicroscope. Each seed was independently removed from the chaffy receptacle and inspected for damage. Damage was counted as any breach through the seed coat from feeding larvae. In case where damage was so excessive that little evidence of the seed remained except frass, damaged seed was counted by the number of suspended florets or receptacle seed scars. Emerged insects were identified to species (where possible) and abundance, composition, and damaged seed calculated for each sampled capitulum. Fruit fly abundance was based on reared adults and their puparium. All emerged flies were correlated with puparia to ensure that abundance counts included flies that emerged prior to capitula harvest or pupae that died prior to emergence. Puparia of *N. finalis* and *T. nigricornis* could be distinguished based on size and color.

Percentage seed damage was determined by dividing the damaged seed by the total seed count. Average seed consumption per fruit fly and average fly emergence per capitulum was calculated. Capitula that yielded more than one fruit fly species or unknown parasitoids were not used to calculate average seed consumption since it was impossible to attribute seed damage to a specific seed predator species. In 2007, 175 random capitula were sampled for basal diameter measurements in order correlate seed damage and *N. finalis* abundance with capitulum size. Capitula were grouped into 7 size classes based on capitulum diameters of 7-10 mm, 11-12 mm, 13-14 mm, 15-16 mm, 17-18 mm, 19-20 mm, and >20 mm. *N. finalis* abundance was based on emerged flies and known parasitoids.

Rate of parasitoidism was determined for *N. finalis* (Table 2) as follows: (parasitoid emergence)/(fly emergence + parasitoid emergence). Because the contribution to total parasitoidism by *T. nigricornis* was not always apparent due to its low occurrence and by not segregating the pupae found within each flowering head prior to emergence, parasitism rates were only calculated for *N. finalis*.

Results and Discussion

Seed production. From a sample of 644 flower heads across all sites and both years, average seed production per capitulum was 73.4 (SEM = 5.9) seeds with a range of 20 to 184 and mode of 40 (Fig. 1). Only 25 capitula samples make up the mode, and capitula represented by more than 10 samples all fell within the range of 40 and 90 seeds. The extreme range in seed abundance per capitulum is explained by inflorescence morphology. A typical *W. amplexicaulis* inflorescence is composed of a flower stalk with a single, large, terminal capitulum and multiple, smaller subtending capitula which elongate on pedicels and open following terminal flower anthesis. The terminal capitulum produces more seed than the subtending lateral capitula. Lateral capitula were found with a dry basal diameter as small as 7.7 mm but ranged into the same size class found in lower range of terminal capitulum sizes. The largest terminal capitulum had a dry basal diameter of 24.7 mm.

Seed predators. Two fruit fly species were reared from *W. amplexicaulis* capitula. Over two years and from all sites a total of 2,256 *N. finalis* (average per site = 376.2, SEM = 49.8) emerged compared to only 186 (average per site = 31.0, SEM = 12.0) *T. nigricornis*. The consistent dominance of *N. finalis* over *T. nigricornis* is similar to results found in the south-western Rocky Mountains of Colorado (Kazuo 1993), but in stark contrast to the dominance of *T. nigricornis* over *N. finalis* reared from capitula of *Encelia* spp. in southern California (Khouzama et al 2001). A two factor (site and year) analysis of variance (ANOVA) for emerged abundance of both *N. finalis* (p=0.01) and *T. nigricornis* (p=0.03) differed significantly across years but not across sites. Additionally, a *Melanagromyza* sp. (Agromyzidae) fly emerged consistently but at a very low frequency (see Table 1). Seed damage by moth larvae was also observed; the larvae did not survive rearing through adulthood, often expiring well before pupation.

The occurrence of *N. finalis* per seed head ranged from 1 to 27 with an average of 4.7 (se = 0.24). Even though 27 emergents is extraordinarily high, it is consistent with a reported high of 28 emergent *N. finalis* from *W. amplexicaulis* (Kazuo 1993). High numbers of flies per capitulum however, is not the norm. The majority of capitula had only one or two flies (Fig 2). Decreased intraspecific competition may contribute to increased individual fitness.

Parasitoids. Insect emergence also included parasitoids of the seed predators. Rearing trials revealed at least two parasitoid wasps of *N. finalis*. The most common parasitoid was a presumably unidentified species belonging to the genus *Pteromalus* Swederus (Pteromalidae) followed by *Zaglyptonotus mississippiensis* Breland (Torymidae) (Fig. 3). *Pteromalus* spp. are a common parasitoid encountered with both *Trupanea* (Khouzama et al. 2007b) and *Neotephritis* (Goeden et al. 1987). Several other species of wasps emerged but their association with either fruit fly remains uncertain especially considering the presence of the *Melanagromyza* sp. and a lepidopteran. They could represent hyperparasitoids of recognized wasps but their identity could not be verified.

Over the 2-year study 399 *Pteromalus* sp. were reared with a range of 8-174 emergents per site (average = 66.5/site). A total of 86 specimens of *Z. mississippiensis* were reared with a range of 5-28 emergents per site (average = 14.3/site). A significant difference was found in the abundance of *Pteromalus* sp. across both sites and years ($p<0.01$). There existed no significant difference in *Z. mississippiensis* abundance across sites. A difference was found across years at $p=0.09$. *Pteromalus* sp. emerged from both *N. finalis* and *T. nigricornis* pupae, whereas *Z. mississippiensis* emerged only from *N. finalis* pupae.

The parasitoidism rate of *N. finalis* by *Pteromalus* sp. averaged 11.5% and 3.7% by *Z. mississippiensis*. Year 2007 revealed a marked decrease in parasitoidism rates compared to 2006 except at Manti Ridge (Table 2). The other two sites (Payson Canyon and Squaw Peak) decreased from an average 22.5% to only a 2.0% parasitoidism rate. This annual fluctuation was not observed in *Z. mississippiensis*. Population densities across years are obviously dynamic but the exact cause is unknown. Possible reasons could be climatic differences, disease, natural cycles, or even hyperparasitoidism effects. Because of the relative scarcity of *T. nigricornis* in the sample, *Pteromalus* emergence was not quantified for the *Trupanea* even though it was observed as an occasional host.

Mention of *Z. mississippiensis* has been relatively rare in the literature over the past five decades; it has been referenced only in various broad taxonomic works or catalogs (Grissell 1979, 1995, 1997). *Z. mississippiensis* is one of two species representing the genus in the family Torymidae in North America. Breland (1938) described this species after rearing specimens from sunflower heads. He was able to determine the host relationship with *N. finalis* Loew (reported as *Tephritis finalis*) after observing ovipositing females, killed in situ on the flower heads, with ovipositors still inserted and positioned above fly puparia. Additionally, *N. finalis* emerged from some of the living puparia to clearly establish the host relationship. Breland was, however, not able to determine the parasitism rate due to the abundant emergence of different host-parasitoid species. *Z. mississippiensis* was apparently rare relative to the great quantity of other reared species. Despite apparent scarcity, its only known host, *N. finalis,* is one of the most common fruit flies in North America, occurring in 26 states and in parts of Canada and Mexico (Foote et al. 1993). Considering the large host range, you would expect a comparable range for the wasp, but published records only list occurrences in Alabama and Mississippi (Breland 1938, Grissell 1979). This paper expands the known range of *Z. mississippiensis* and sheds doubt on its presumed scarcity.

The only other *Zaglyptonotus* species, *Z. schwarzi,* appears to occupy a niche different than *Z. mississippiensis*, both in terms of other parasitized hosts and associated plant species. While *N. finalis* is known to prey upon members of the tribe Heliantheae (family Asteraceae) (Goeden et al.1987), recorded host plants for tephritids preyed upon by *Z. schwarzi* have different tribal affinities. One known hostplant, *Vernonia baldwini,* (Brandhorst 1943) resides in the tribe Vernonieae (subfamily Cichorioideae), and another host plant, *Bidens pilosa*, (Needham 1948) is from the tribe Coreopsideae (Seung-Chul 1999) a distinct tribe separate from Heliantheae (Ryding and Bremer 1992).

Seed damage. Percent seed damage varied significantly by site and year ($p<0.01$). In 2006, the Manti Ridge site revealed the greatest seed damage (46.9%) and Payson Canyon (40.4%) in 2007. A severe late frost at the Manti Ridge site may have negatively affected fruit fly populations, resulting in less seed damage in 2007, though temporal fluctuations among parasitoid populations are expected in spatially heterogeneous environments (Comins et al. 1992, Wilson and Hassell. 1997). Percent seed damage ranged from 30.6% to 46.9% overall with an overall average of 39.0% (SEM = 2.6) (Fig. 4). Seed damage per sampled capitulum ranged from 0.0% to 100.0% indicating the potential for total seed loss if all flower-heads of a plant and all plants in a population are infected (Table 1). Considering an average potential seed production per capitulum of 76.7 seed, an average of 46.9 undamaged seeds per capitulum could still contribute to the annual seed bank given a lack of post-dispersal seed predation by vertebrates. Of the total 666 reared capitula, only 28 (4.0%) were free of seed predation. The greatest percent difference across two years was observed in the Squaw Peak population at 14.2%. The average number of seeds damaged per *N. finalis* ranged from 1.1 - 46.0 with an average of 9.3 (se = 0.5). A histogram (Fig. 5) of seed damage shows that most *N. finalis* damaged between 4 and 8 seeds. Seed consumption of 4-8 seed is a reasonable quantity whereas the higher numbers in the range of seed damage is likely a factor of seed damage from undocumented Lepidoptera or flies that emerged prior to harvesting capitula.

Seed damage by *T. nigricornis* averaged 8.9 seeds/fly (SE = 2.0). This number is high considering the much smaller size of *T. nigricornis* compared to *N. finalis* and is likely an artifact of the small sample size (n=9) of capitula with only *T. nigricornis* emergents. Seed damage estimates were only based on samples where *T. nigricornis* emerged independent of *N. finalis* and/or parasitoids.

Average flower head and plant infestation rates by seed predators was 95.9% and 100% respectively indicating high pest prevalence across the sampled population. The incidence of plant infestation is remarkably high, but high infestation rates are more common in plant species with large capitula compared to species bearing small capitula (Fenner et al. 2002). We found a higher infestation rate in larger diameter capitula (Fig. 6) of *W. amplexicaulis* (p = 0.09). This is consistent with documented higher infestation rates in larger capitula of the same species by Fenner et al. 2002; however, the greater infestation rate did not affect an increase in the percent seed damage per capitulum (Fig. 7). Rather, it was observed that as *N. finalis* density increased in a single flower head, the number of seeds damaged per fly decreased (Fig. 8). The highest number of damaged seed occurred when a single larvae was present. Evidently, as more larvae compete for a limited resource, their individual consumption of seed is more complete but less extensive. Comparatively, a single larva can selectively sample more of the immediate food base, leaving more damaged, and partially consumed seed. Because larvae can not migrate from their resident capitulum, ovipositioning females control the number of eggs laid per flower-head.

Management implications. Seed yield losses due to pre-dispersal seed predation can have a profound effect on annual seed production for *W. amplexicaulis.* Since the seed of most species in the tribe Heliantheae are relatively short lived in-situ, they require a steady input of seed into the seed bank to effectuate seedling recruitment. Because *W. amplexicaulis* is a long-lived perennial with a life expectancy of 28 years (Treshow and Harper 1974), it has multiple chances across multiple years to contribute seed to the seed bank. Given the fluctuations apparent in seed predator densities across multiple years, it is advantageous to be a long-lived perennial to ensure high seed production in some years. Even with high insect predation rates, some seed persist and disperses. Pre-dispersal seed predation is not limited, however, to insects. Domestic cattle (personal observation), sheep and horses are known to feed on flowers and seed-heads of *W. amplexicaulis* (Young and Evans 1979). Birds would likely feed on flower heads to take advantage of the large carbohydrate and fat reward in mature seed prior to dispersal. The fate of the seed post-dispersal is unknown, however, it is expected that small rodents would also utilize the rich food stores post shattering.

W. amplexicaulis has value to wildlife for foragers, seed consumers, and pollinators and merits use in reseeding mixes by land management agencies. Seed has primarily been obtained by wild collecting, though interest to produce seed agriculturally has been increasing for many wildflowers. In either scenario, managing wild stands for maximum seed production or as a row crop, the presence of seed predators can cause significant reductions in yields. In this study up to 46.9% of the seed was damaged. Kazuo (1993) reported seed predation rates on *W. amplexicaulis* often exceeding 50% at lower elevations. The use of appropriate insecticides alone can potentially help increase yields up to 50% in areas of high pest infestation. The parasitoids discovered in this paper do not kill fly larvae prior to seed damage, therefore; their effect can only be looked at over the long-term in moderating fruit fly populations.

In summary, seed loss in *W. amplexicaulis* from *N. finalis* and *T. nigricornis* can have a significant effect on total yield. The extent of seed damage by seed predators varies both spatially and temporally due the fluctuating population dynamics of the seed predator and its parasitoids. In this case a *Pteromalus* sp. wasp parasitoidized up to 23% of its host population, but parasitoidism rates across years can be dramatically different. The occurrence of *Z. mississipiensis* as a secondary parasitoid illustrates that even seemingly rare species can contribute to the population dynamics of host pests and ultimately the fate of seed production in wild plant populations.

Acknowledgments

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Figure legend:

Fig. 1 Histogram: the number of seed per capitulum for *W. amplexicualis.* Mean = 76.7 seed, n = 644.

Fig. 2 Histogram: the number of reared *N. finalis* per capitulum.

Fig. 3 Average percent parasitoidism of *N. finalis* at each site (2006 – 2007).

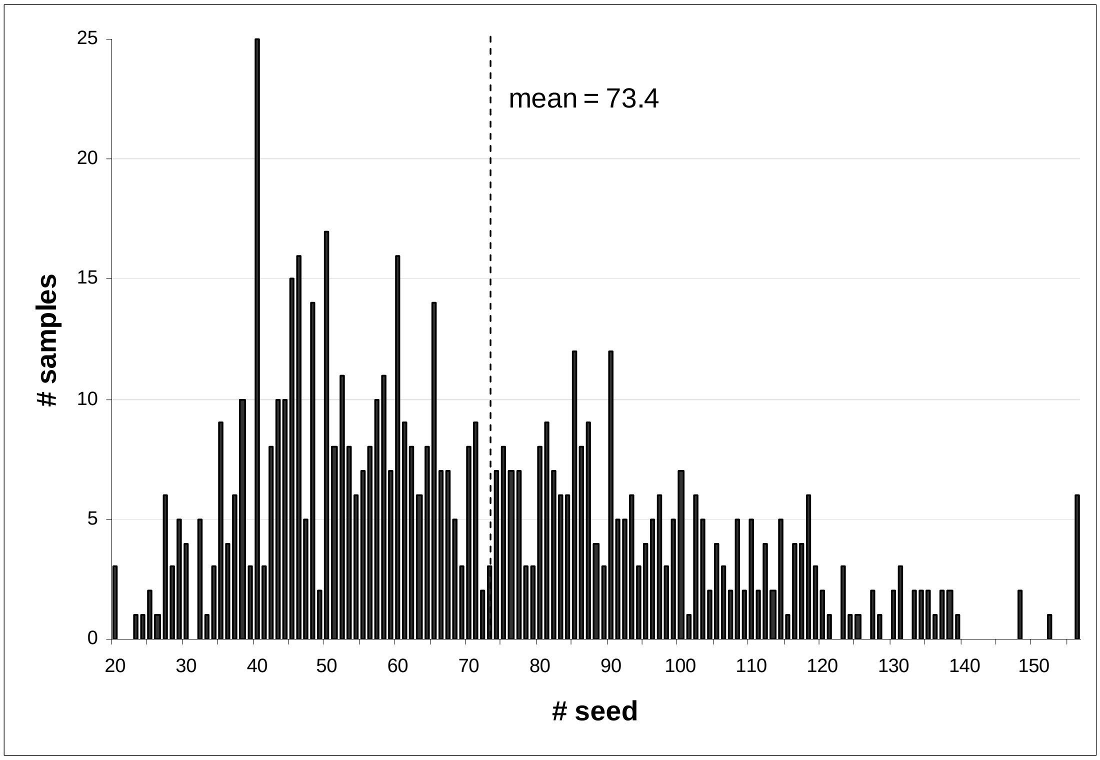
Fig. 4 Histogram: percent seed damage in *W. amplexicaulis* by seed predators. Mean = 39.0%, n = 644.

Fig. 5 Histogram: number of damaged seed per capitulum by *N. finalis*.

Fig. 6 Correlation between average numbers of reared fruit flies per capitulum and capitulum basal diameter.

Fig. 7 Correlation between the numbers of damaged seed per capitulum and capitulum basal diameter.

Fig. 8 Relationship between the average number of damaged seed per capitulum and the number flies per capitulum.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# samples
0
5
10
15
20
25
20
30
40
50
60
70
80
90
100
110
120
130
140
150
seed

Fig. 1

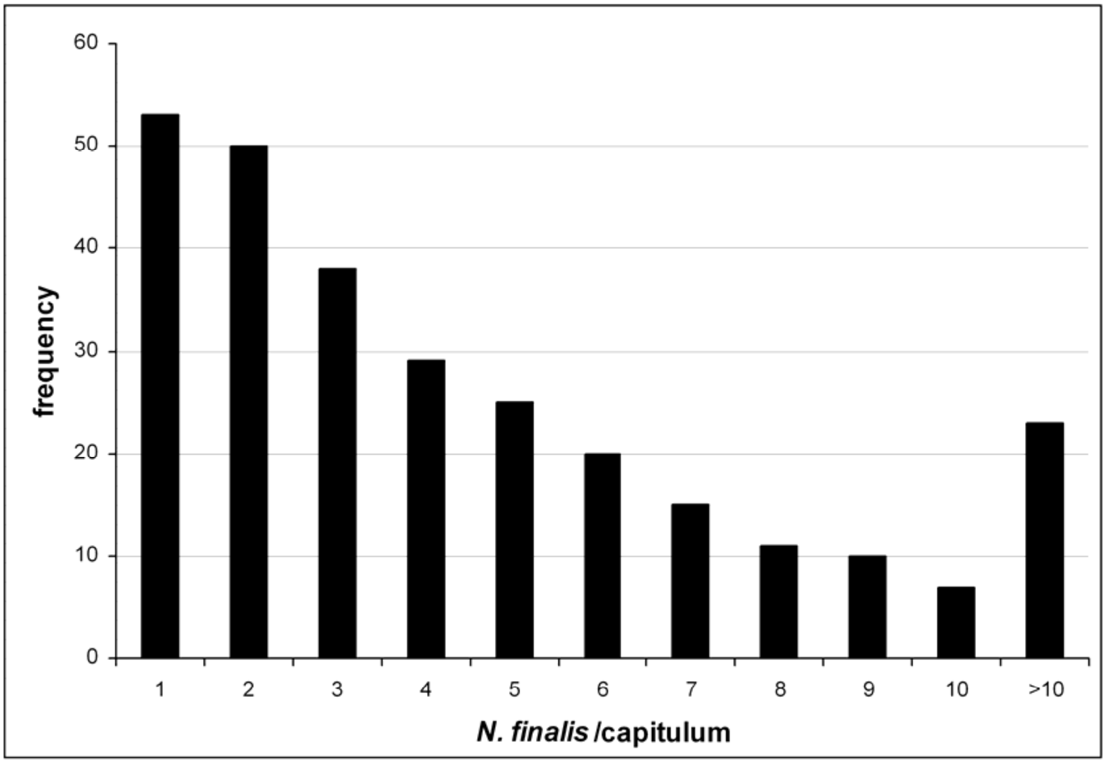

frequency
0
10
20
30
40
50
60
1
2
3
4
5
6
7
8
9
10
>10
N. finalis /capitulum

Fig. 2

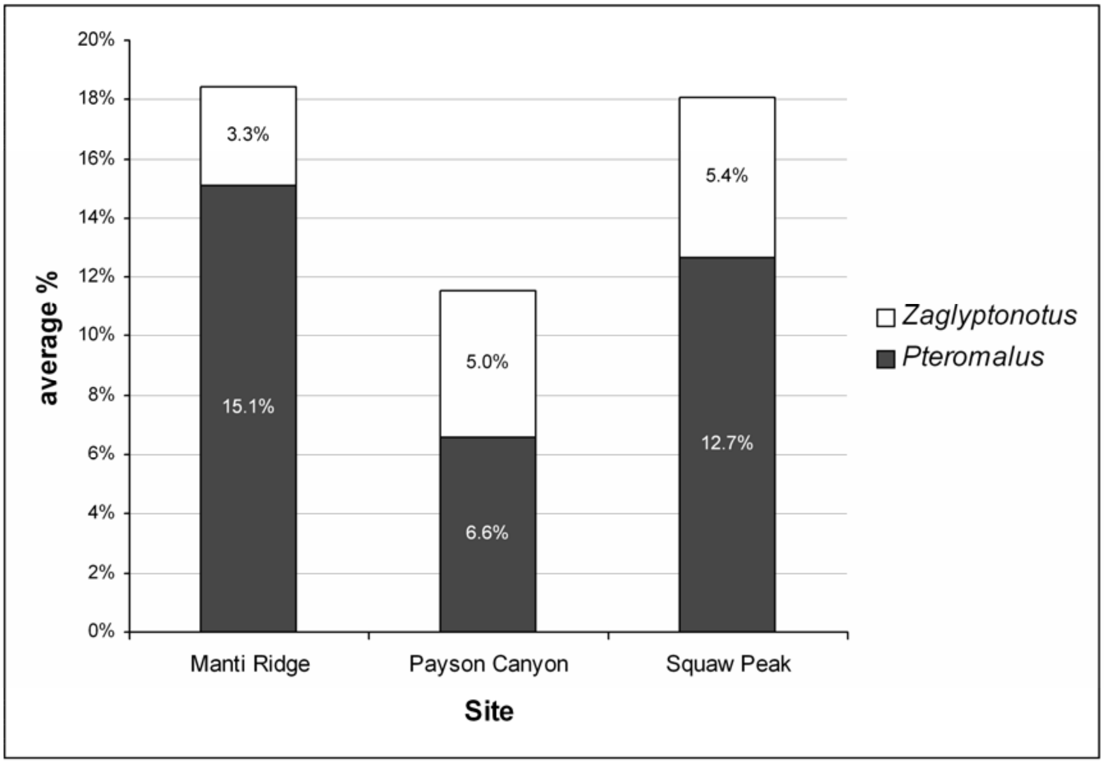
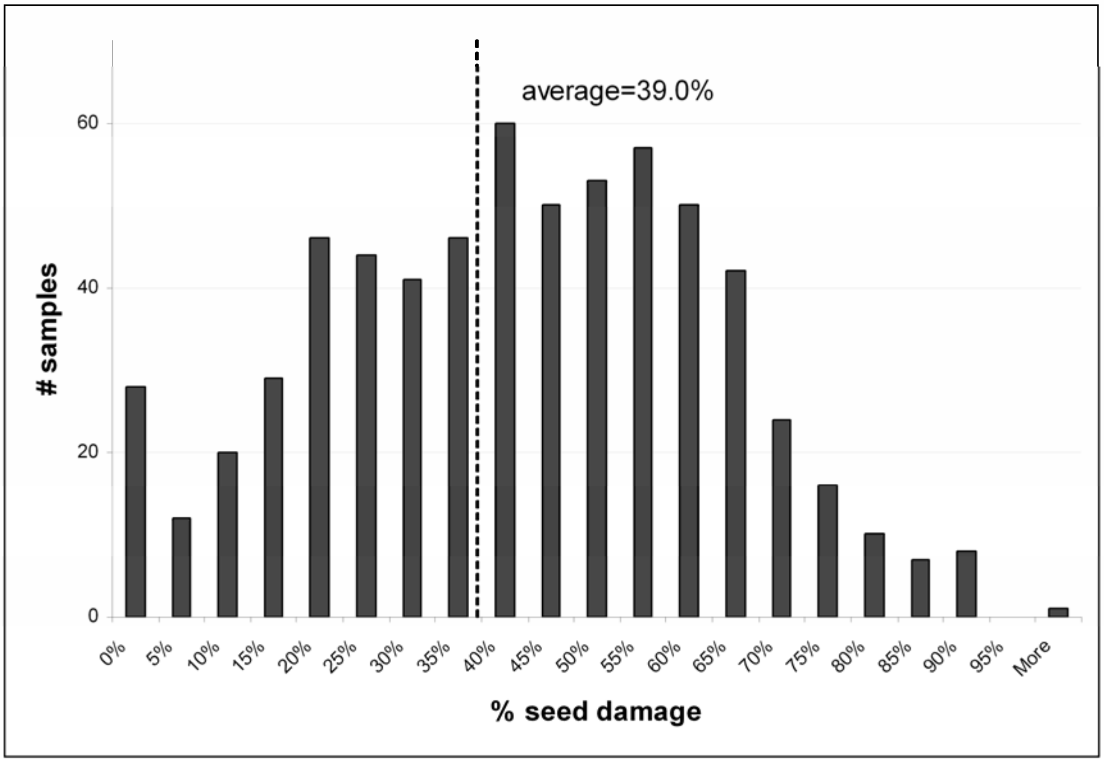

20%
18%
16%
14%
12%
10%
8%
6%
4%
2%
0%
average %
3.3%
15.1%
5.0%
6.6%
5.4%
12.7%
Manti Ridge
Payson Canyon
Squaw Peak
Site
☐ Zaglyptonotus
■ Pteromalus

Fig. 3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60
40
20
0
samples
0%
5%
10%
15%
20%
25%
30%
35%
40%
45%
50%
55%
60%
65%
70%
75%
80%
85%
90%
95%
More
% seed damage

Fig. 4

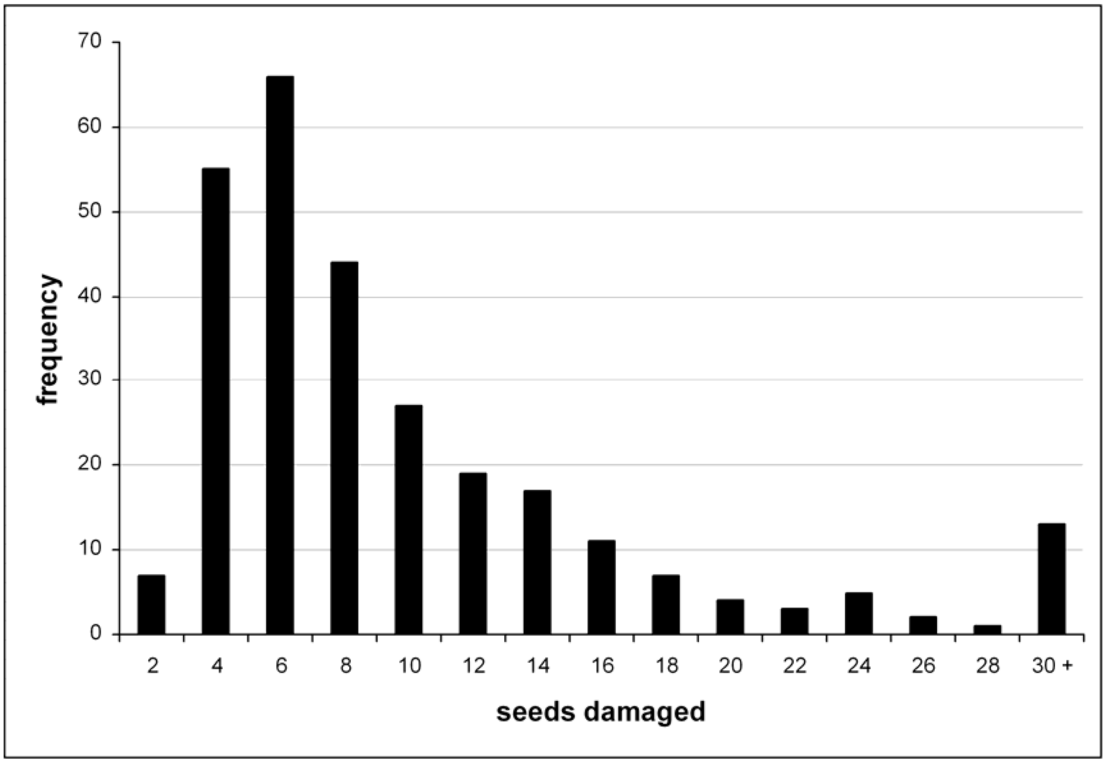
70
60
50
40
30
20
10
0
frequency
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30 +
seeds damaged

Fig. 5

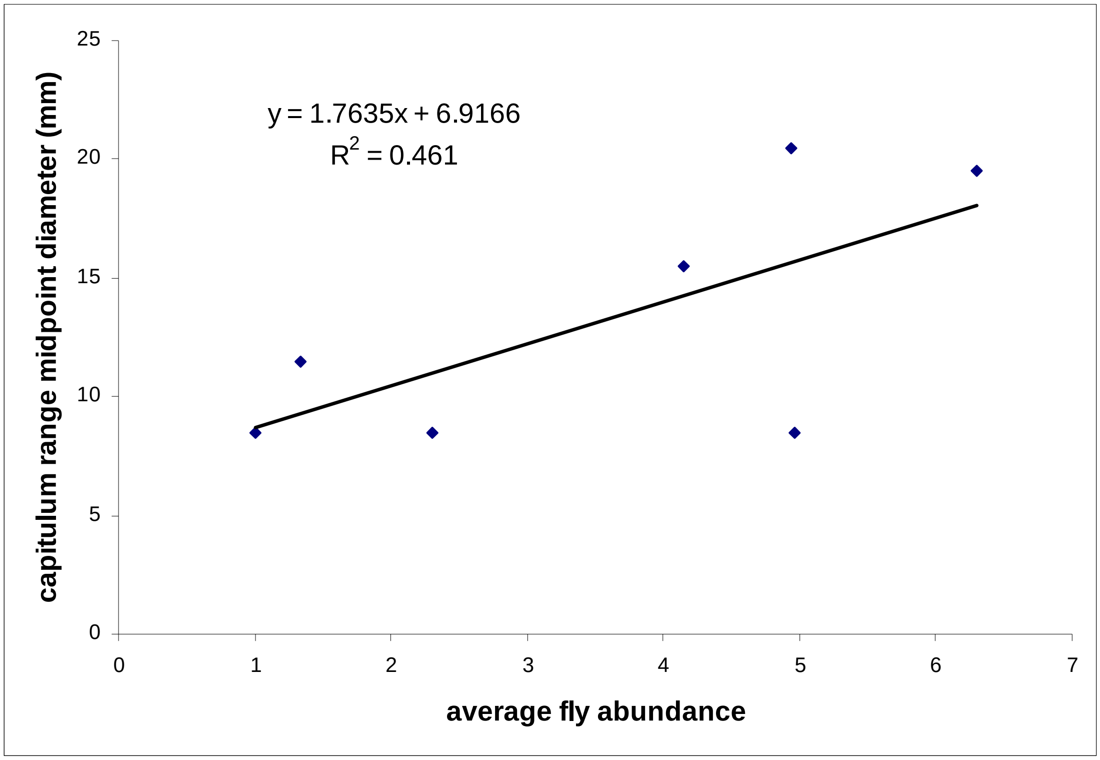
25
20
15
10
5
0
capitulum range midpoint diameter (mm)
y = 1.7635x + 6.9166
R2 = 0.461
0
1
2
3
4
5
6
7
average fly abundance

Fig.6

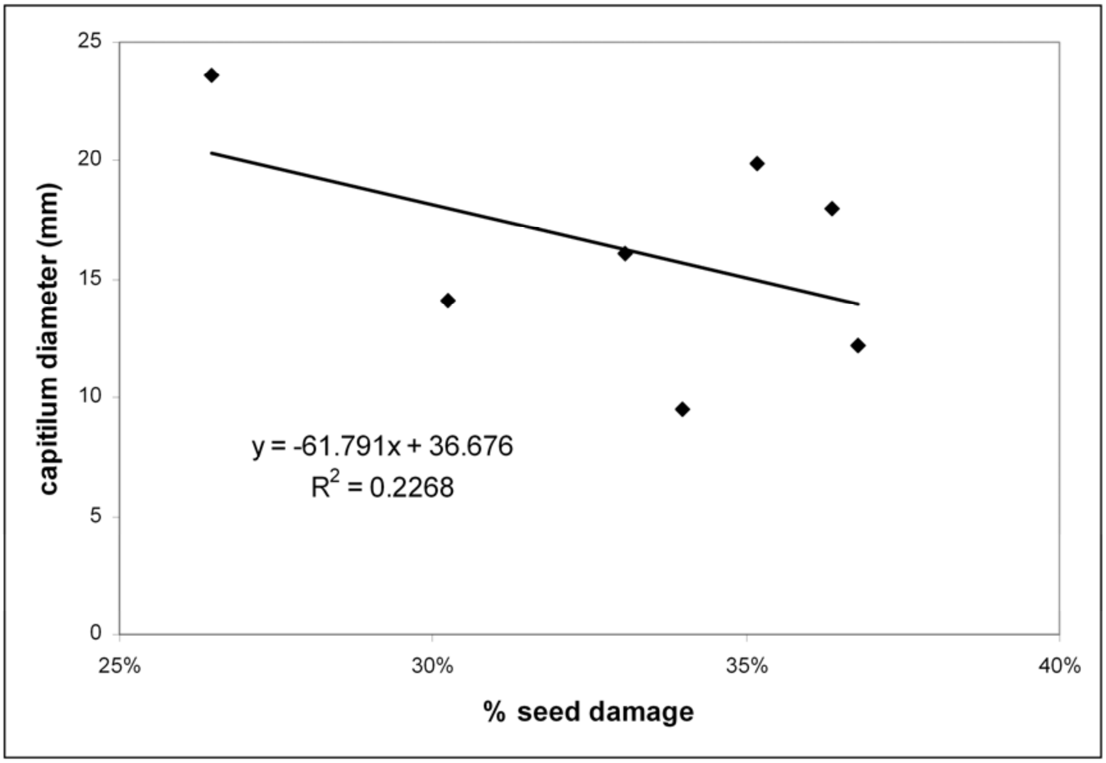
25
20
15
10
5
0
25%
30%
35%
40%
capitulum diameter (mm)
% seed damage
y = -61.791x + 36.676
R2 = 0.2268

Fig. 7

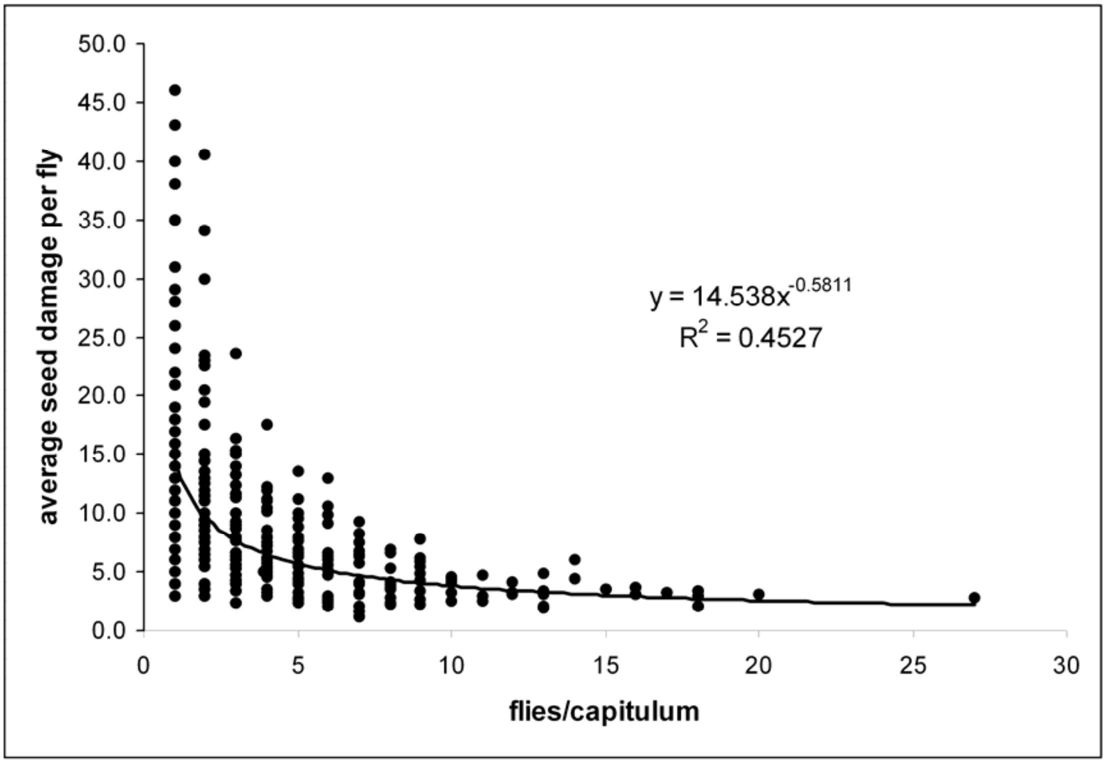
50.0
45.0
40.0
35.0
30.0
25.0
20.0
15.0
10.0
5.0
0.0
0
5
10
15
20
25
30
average seed damage per fly
flies/capitulum
y = 14.538x-0.5811
R2 = 0.4527

Fig. 8

Table legend:

Table 1. Seed production, seed damage, and infestation rates by seed predators in *W. amplexicaulis* per site 2006-2007.

Table 2. Parasitoidism rates in *N. finalis* by *Pteromalus* sp. and *Z. mississippiensis.*

2006

	site	plants *n*	reared capitula *n*	total seed *n*	seed/ capitula mean, min, max	% seed damaged	% flower head infestation	% plant infestation	reared seed predators	#
Agoseris glauca	Manti Ridge	80	80	2823	35, 19, 62	4.6%	5.0%	5.0%	*Campiglossa* sp.	11
	Teat Mountain	80	88	3371	38, 12, 64	20.9%	38.6%	39.8%	*Campiglossa* sp. Diptera unkown	25 14
	Willow Creek	80	80	3372	42, 30, 66	5.2%	10.0%	10.0%	*Campiglossa* sp.	12
Crepis acuminata	Sheep Creek	20	345	2669	8, 5, 10	10.7%	50.0%	78.9%	*Campiglossa* sp. *Phycitodes albatella*	4 13
	Rock Canyon Overlook	19	357	3441	10, 5, 13	8.5%	37.3%	68.4%	*Campiglossa* sp. *Phycitodes albatella*	2 4
	West Mountain	20	380	3395	9, 6, 12	22.2%	80.3%	100.0%	*Campiglossa* sp. *Phycitodes albatella*	14 30

2007

	site	plants *n*	reared capitula *n*	total seed *n*	seed/ capitula mean, min, max	% seed damaged	% flower head infestation	% plant infestation	reared seed predators	#
Agoseris glauca	Manti Ridge	76	94	3035	32,14,53	6.1%	6.4%	7.9%	*Campiglossa* sp.	20
	Teat Mountain	84	108	4291	40,22,70	11.3%	20.4%	23.8%	*Campiglossa* sp. Diptera unkown	43 4
	Willow Creek	80	125	5170	41,18,73	0.5%	0.8%	1.3%	*Campiglossa* sp.	4
Crepis acuminata	Sheep Creek	20	594	4339	8,4,13	12.0%	11.3%	85.0%	*Campiglossa* sp. *Phycitodes albatella*	5 48
	Rock Canyon Overlook	20	519	5365	10,7,14	20.4%	20.2%	95.0%	*Campiglossa* sp.	25
	West Mountain	20	664	6112	9,3,11	0.7%	0.9%	25.0%	*Campiglossa* sp. *Phycitodes albatella*	1 3

Table 1

2006

site	*Pteromalus* sp.			*Z. mississippiensis*		
	reared	% SUM frequency	% parasitoidism	reared	% SUM frequency	% parasitoidism
Manti Ridge	45	88.0%	12.6%	6	12.0%	1.7%
Payson Canyon	25	63.0%	11.2%	15	38.0%	6.7%
Squaw Peak	174	97.0%	23.0%	5	3.0%	1.0%

2007

site	*Pteromalus* sp.			*Z. mississippiensis*		
	reared	% SUM frequency	% parasitoidism	reared	% SUM frequency	% parasitoidism
Manti Ridge	99	78.0%	17.5%	28	22.0%	5.0%
Payson Canyon	8	38.0%	2.0%	13	62.0%	3.2%
Squaw Peak	10	34.0%	2.3%	19	66.0%	4.4%

Table 2

CHAPTER 3

PREDISPERSAL SEED PREDATION IN *AGOSERIS GLAUCA* (PURSH) RAF. AND *CREPIS ACUMINATA* NUTT. (ASTERACEAE: CICHORIEAE) AND CONTROL WITH IMIDACLOPRID

Robert L. Johnson and Val Jo Anderson

(RLJ) Department of Plant and Wildlife Science, Brigham Young University, UT 84602 U.S.A. (E-mail: robert_johnson@byu.edu), (VJA) Department of Plant and Wildlife Science, Brigham Young University, UT 84602 U.S.A. (E-mail: val_anderson@byu.edu)

Abstract – Pre-dispersal seed predation can significantly reduce annual seed production in plant populations. Wild plant populations are often targeted for seed collecting to meet supply deficits in the restoration seed industry. *Agoseris glauca* and *Crepis acuminata* are native plants in the Great Basin that have priority for developing technologies to increase seed supplies. An important aspect of seed production requires an understanding of decreased yields due to pre-dispersal seed predation by insects. We investigated seed predation in wild populations of *A. glauca* and *C. acuminata* in central Utah in order to determine a baseline for potential seed yield losses. We also compared the effectiveness of imidacloprid applied as a foliar spray and soil drench for controlling seed pests. *A. glauca* averaged 8.1% seed damage across all sites in 2006 and 2007. Average seed damage in *C. acuminata* was 12.4%. Both plant species had at least one site with seed damage above 20.0%, indicating that seed predators can significantly reduce seed yields in some plant populations. *Campiglossa* sp. (Diptera: Tephritidae), a capitivorous (capitulum feeder) fruit fly, was found preying on capitula of both plant species. *Phycitodes albatella* subsp. *mucidella* (Lepidoptera: Pyaralidae) was the dominant seed predator in *C. acuminata*. This establishes a new host association between the moth and *C. acuminata*. Effective control of seed predators was observed using imidacloprid as either a foliar spray or a soil drench, though site and year variables influenced results.

Key words: seed predator, *Campiglossa*, *Phycitodes*, capitivorous, fruit fly, sage-grouse, pesticide

Introduction

Losses in seed production due to flower or seed predation by insects can limit seedling recruitment (Louda 1982) and thereby impact the stability of plant populations. Annual seedling recruitment is in part a function of existing seeds in the seed bank, and a replete seed bank can help alleviate plant mortality. Losses in seed production can also negatively impact seed collectors who harvest seed from certain native species because of their marketability to the reclamation industry. An understanding of the pests impacting seed yield is also important as native forbs are agriculturally cultivated by farmers who want to realize the financial returns of producing native seeds restoration. The extent of seed damage by seed predators, however, is largely unknown for most non-crop species. Impacts to seed production by seed predators in wild populations of *Agoseris glauca* (Pursh) Raf. (pale agoseris) and *Crepis acuminata* Nutt. (tapertip hawksbeard) were investigated in 2006 and 2007.

A. glauca and *C. acuminata* are common forbs of mid to high elevations in the Intermountain West. They occupy a variety of habitat types including sagebrush, pinyon-juniper, mountain brush, aspen, spruce-fir (Welsh et al. 2003) and herbaceous mountain meadows. Because of their broad distribution across many habitats, they have broad application for a variety of seed mixes targeted for restoration across the Intermountain West and Great Basin. Plant nomenclature follows “The PLANTS Database” (USDA, NRCS 2008) except when citing older names from published literature in which cases the current nomenclature follows the cited name. Tribal affiliations in Asteraceae follow Barkley et al. (2006).

This study was in part a response to the recognition that *A. glauca* and *C. acuminata* have important wildlife value and that revegetation seed mixes would be enhanced by the addition of these species. Both species are preferred food items of sage-grouse *(Centrocercus urophasianus)* (Klebenow and Gray 1968, Barnett and Crawford 1994, Huwer 2004). While sagebrush *(Artemisia tridentata)* formed the major dietary constituent by dry weight of pre-laying hens, *Crepis* formed the second most preferred plant in many plant communities in an Oregon study, and *Agoseris* was among the top five (Barnett and Crawford 1994). In the same study, *Crepis* had the highest average percent crude protein in plants comprising >1% of the diet for pre-laying hens (Barnett and Crawford 1994). Klebenow and Gray (1968) found that among juvenile sage-grouse in Idaho, *C. acuminata* was either a dominant or codominant dietary component of 2- and 3-week old chicks. They also recorded *A. glauca* in crops of 6-week old chicks. Juvenile sage-grouse have a preference for forbs in the tribe Cichorieae, foraging on species as they emerge and remain green. Human imprinted chicks were found to feed on the leaves of both *A. glauca* and *C. acuminata* and also the flower buds of the latter (Huwer 2004). Juveniles also extensively utilized other forbs by from the tribe Cichorieae including: *Lactuca serriola*, *Taraxacum officinalis*, and *Tragapogon dubius* (Klebenow and Gray 1968, Peterson 1970).

Both *C. acuminata* and *A. glauca* belong to the tribe Cichorieae and characterized by liguliforous flowers and milky sap (Barkley et al. 2006). While *A. glauca* is scapose, producing a single flower per stem, C*. acuminata* produces numerous flowers on a branching corymb. Both species bloom over a 3-4 week period from late spring through summer. Despite their broad distribution, availability of seed for purchase is both limited and cost prohibitive. Retail cost per pound of pure live seed (PLS) can exceed $100 due to its limited availability. Even though a revegetation study in Oregon demonstrated the high potential of *C. modocensis* as a valuable restoration species for improving sage grouse habitat, the investigators identified the limitation of commercially available seed (Wirth and Pyke 2003).

Addressing the need for a reliable seed supply for many native forbs, the Great Basin Native Plant Selection and Increase Project was implemented and funded under the United States Department of Interior (USDI), Bureau of Land Management (BLM), Great Basin Restoration Initiative to support research into the development of native seed production technology (Shaw et al. 2005). Both *A. glauca* and *C. acuminata* were identified in the as priority species for plant material development (Walker and Shaw 2005).

Recognizing the seed value of *A. glauca* and *C. acuminata*, we were interested in evaluating a pesticide treatment to assess seed predator control and potential increases in seed yield in wild plant populations. We chose to investigate treatment effects using the pesticide imidacloprid (1-(6-chloro-3-pyridylmethyl)-N-nitroimidazolidin-2-ylideneamine), a readily available chemical at most plant nurseries and garden centers.

Imidacloprid is a systemic pesticide that can provide pest protection for an entire growing season. The value of using a systemic in a wild plant population is to provide continual protection against immigrant pests. Also, it only requires a single application which has practical value for treating remote plant populations. Imidacloprid is most effectively taken up by roots and translocated throughout the plant's tissues, therefore; application as a soil drench is a recommended method. Soil drenching has little practical value for wildland seed production, so a foliar spray application was investigated as a possible alternative. Imidacloprid was selected because of its low risk to bee populations. In treated agricultural fields, imidacloprid concentrations in pollen and nectar are negligible, nor does it accumulate in successive crops (Schmuck et al. 2001).

Materials and Methods

Three different populations of *A. glauca* and *C. acuminata* in central Utah were sampled for seed predator composition and associated seed damage in 2006 and 2007. Populations of *A. glauca* were located at three sites; Manti Ridge (39.27092°N 111.51873°W, 2792 m. elev.), Teat Mountain (40.02682°N 111.36567°W, 2543 m. elev.), and Willow Creek (39.28961°N 111.52839°W, 2481 m. elev.). Manti Ridge and Willow Creek populations are located on the Wasatch Plateau in Sanpete County. The Teat Mountain population occurs in Utah County. All three populations are ay similar elevations and in similar habitat types. Vegetation is characterized as a montane meadow of mixed grasses with sparse shrubs.

Populations of *C. acuminata* were located at; Sheep Creek (40.0140°N, 111.3133°W, 7426 ft. elev.), Rock Canyon Overlook (40.27576°N 111.60004°W, 7551 ft. elev.), and West Mountain (40.0996°N 111.8275°W, 6326 ft. elev.). The sites are on three different mountain ranges in Utah County. They occur on steep, west facing slopes that are sparsely vegetated with bunchgrasses and occasional shrubs.

Within each of these populations, 20 plants were randomly flagged using the nearest plant to point method along a transect that bisected the population. At the end of anthesis but before seed maturation, the entire inflorescence of each *C. acuminata* sample was harvested. The inflorescence of each *A. glauca* plus its nearest three neighbors were also harvested. Harvested inflorescences were placed individually in plastic bags and transported the laboratory.

Individual capitula were randomly sub-sampled for placement 4.5 oz portion cups with perforated lids for rearing. Rearing containers were maintained at room temperature (~24 °C daytime, and ~16 °C nighttime) for the duration of the rearing trial. Most larvae had already pupated at capitula harvest, and any remaining larvae pupated within a few days of placement into rearing containers. Emergence of fruit flies began within 1 week of capitula harvest and peaked by week 2 or 3. Cessation of insect emergence occurred within 2 months, but approximately six months were allowed before examination. All samples were examined for emerged insect composition as well as the quantity of damaged verses undamaged seed.

Individual seeds from each capitulum were examined under a 10-40x stereomicroscope. Damaged seed was counted as mandibular penetration through the seed coat. In many cases the entire seed was consumed leaving only the remnant ligulate flowers or the seed indentation in the receptacle as a marker for counting the number of damaged seed. Counts of undamaged seeds were also taken.

Emerged insects, puparia, and dead larvae were counted and identified as far as possible to species. It was apparent that many of the emerged insects were parasitoids of the seed predators. In many instances, a single parasitoid emerged independent of another species in a rearing cup. In such cases it was possible to determine which parasitoid belonged to which seed predator based on the single extant puparium that could be matched against other puparia and their emerged seed predators.

Within each plant population, ten random plants were also selected for pesticide application. Half the plants received a soil drench treatment, the other half a foliar spray treatment. The pesticide imidacloprid was applied as a solution made from 85 grams of the liquid concentrate Bayer Advanced ™ Tree and Shrub Insect Control per 1.9 L of water. The soil drench treatment was applied approximately one month prior to flowering at a rate of 1.9 L solution per plant or cluster of plants. A total of 1.2 grams active ingredient was applied per plant or plant cluster. Soil drenching consisted of watering the plant with the pesticide solution from a watering can. Water was delivered at the base of the plant at a rate that allowed the solution to soak into the soil and not run off. The spray treatment consisted of spraying the foliage approximately two weeks prior to flowering. This allowed us to spray the budding inflorescence as well as the basal leaves. The same solution was used as for the soil drench but dispensed through a backpack sprayer. Plants were sprayed until the foliage was completely wetted and began to drip off the leaves. The amount of dispensed active ingredient was less than for the drench treatment, but more concentrated on the plant tissue. Mature seedheads from treated samples were harvested and examined for seed damage and compared against a control group. Data was analyzed as a three-way ANOVA in SigmaPlot using the General Linear Model (GLM). The dependent variable was percent seed damage, and the independent variables were imidacloprid treatment, site, and year. Pairwise comparisons used the Holm-Sidak method.

Results and Discussion

Seed predators. During years 2006 and 2007 a total of 575 capitula of *A. glauca* yielded 155 specimens of an apparently undescribed species of *Campiglossa* (Diptera: Tephritidae) and 18 pupae of an unknown dipteran. From 2,859 capitula of *C. acuminata* were reared 52 specimens of *Campiglossa* sp. (same undescribed species) and 133 of *Phycitodes albatella* subsp. *mucidella* (Ragonot)*,* (Lepidoptera: Pyaralidae). While investigating seed predators from other wildflowers in the Asteraceae we successfully reared the same undescribed fruit fly from *Crepis intermedia* A. Gray (limestone hawksbeard), *C. modocensis* Greene (Modoc hawksbeard) and *Microseris nutans* (Hook.) Sch. Bip. (nodding microseris) *Crepis*, *Agoseris* and *Microseris* all belong the tribe Cichoreae (Barkley et al. 2006). Within that tribe, *Microseris* and *Agoseris* occur within same phylogenetic clade (Joongku et al. 2003), suggesting an oliophagous host specificity for this *Campiglossa* sp. surrounding that clade within the tribe Cichorieae.

The identity of the 18 puparia represented as "unknown dipteran," remains uncertain since no adults were recovered. The unknown fly species was not a fruit fly and likely requires pupation in soil to complete its lifecycle. This fly was not a major seed predator and only occurred at the Teat Mountain site.

The seed predator *P. albatella* Ragonot is found throughout the United States (Heinrich 1956) as well as in South America and Western Europe (Opheim 1963). The subspecies *P. a. mucidella* seems confined to the western United States with documented occurrences in the states of California, Colorado, Utah, Wyoming, and Oregon as well as British Columbia, Canada (Heinrich 1956). Mention of this moth in published literature has been sparse. The moth was listed under its current taxonomic name in the Check List of the Lepidoptera of America North of Mexico (Hodges et al. 1983), but subsequent research continued to use *Rotruda mucidella* Ragonot, a junior synonym. A report on Lepidoptera trapping efforts at Marine Corps Air Station (MCAS), Miramar, San Diego County, California yielded *P. a. mucidella* (Brown & Bash 1997), and Headrick and Goeden (1998) discuss resource partitioning between this moth with fruit flies in thistle flowers.

Since *C. acuminata* is a new host record for *P. a. mucidella*, it is worth updating known host associations. Heinrich (1956) mentioned *Aster* as a host plant. Headrick and Goeden (1998) describe it as feeding on thistle (*Cirsium*), but do not mention which species. The greatest contribution of host association was made by Frick and Hawkes (1970) who reared *P. a. mucidella* from *Senecio jacobaea* L., *S. integerrimus* Nutt., *Cirsium andersonii* (A. Gray) Petr., *C. brevistylum* Cronquist, C. *cymosum* (Greene) J.T. Howell, *C. occidentale* (Nutt.) Jeps., *C. pastoris* J.T. Howell = *Cirsium occidentale* (Nutt.) Jeps. var. *candidissimum* (Greene) J.F. Macbr., *C. proteanum* J.T. Howell = *Cirsium occidentale* (Nutt.) Jeps. var. *venustum* (Greene) Jeps., *C. vulgare* (Savi) Ten., and *Centaurea virgata* Lam. ssp. *squarrosa* (Willd.) Gugler. There is an apparent prevalence of host-plant associations within the genera *Cirsium*, *Senecio,* and *Centaurea. Crepis acuminata* also represents a new host tribe (Cichorieae) adding to the tribes Cynareae, Senecioneae, and Astereae .

Seed production and seed damage. On average, *A. glauca* produced 38.3 seeds per capitulum, with a range of 12 to 73 seeds (Fig. 1). Seed production differed significantly by site (p<0.01) but not by year. Average seed production was lowest at Manti Ridge (33.6 seeds per capitulum) and highest at Willow Creek (41.8 seeds per capitulum). These differences are likely explained by environmental factors such as rainfall, soil fertility, and resource competition.

Overall seed damage for *A. glauca* was relatively low with an average of only 8.1% and a range of 0.0% to 100.0%. A histogram of the percent seed damage revealed the absence of a normal distribution (fig. 2) due largely to the abundant capitula lacking seed damage. Teat Mountain had the highest degree of seed damage both years with a high of 20% in 2006. That is in sharp contrast to an overall low of 0.5% seed damage at Willow Creek in 2007. Percent seed damaged differed significantly by site ($p<0.01$) but not by year. The presence of the unknown dipteran at Teat Mountain in part contributes to higher seed damage. The unknown fly on average consumes 16.6 seeds per fly verses *Campiglossa* sp. which consumes 10.6 seeds per fly. It was observed that the larvae of this fly foraged haphazardly throughout the capitulum, unlike the *Campiglossa* sp. whose forage range in the capitulum was relatively small.

Seed production for *C. acuminata* averaged 9.0 seeds per capitulum with a range of 4 to 14 (fig 3). Production was significantly different by site and by year ($p<0.01$). The Rock Canyon Overlook averaged 10.0 seed per capitula compared to a low of 8.2 for the Sheep Creek site. Also in 2006, seed production only averaged 8.8 seed per capitula compared to 9.3 in 2007.

Percent seed damage by seed predators in *C. acuminata* averaged 12.4% across all site and both years with a range of 0.0% to 100.0%. A histogram (Fig. 4) shows the majority of capitula had zero or little damage. A significant interaction existed between years and sites ($p<0.01$). The site with the highest average seed damage in 2006 (West Mountain, seed damage = 22.2%) was the lowest in 2007 (seed damage = 0.7%) (Table 1). At this site both the fruit fly, *Campiglossa*, and the moth, *P. albatella* had a substantial decrease in abundance the second year. The lowest site for seed damage in 2006 (Rock Canyon, seed damage = 8.5%) was the highest in 2007 (seed damage = 20.2%). The Rock Canyon Overlook only had 4 moths sampled in 2006 compared to 48 in 2007.

While no parasitoids were reared from *A. glauca* capitula, 9 *Pteromalus* sp. (Hymenoptera: Pteromalidae) were reared from *Campiglossa* sp. in *C. acuminata* capitula. Similarly, 14 braconid (Hymenoptera: Braconidae) specimens representing two different species, and 6 tachinid flies (Diptera: Tachinidae) were reared after parasitoidizing *P. a. mucidella*.

Imidacloprid treatment. A significant interaction was found between treatment, site and year for *C. acuminata* ($p<0.01$). Overall, greater seed damage occurred in the control verses either imidacloprid treatment except at West Mountain in 2007 (Fig. 5). During that year seed predation was so low that pesticide benefits were negligible. In all cases, the drench treatment gave superior results, often zero seed damage, but because of high sample variability, it was not significantly different from the spray treatment. Even though seed damage was low overall, imidacloprid did reduce seed damage substantially

Test results of imidacloprid treatment on *A. glauca* found no significant difference between years, but a significant interaction between site and treatment. Teat Mountain results (Fig. 6) followed the similar pattern as seen for *C. acuminata* with a strong pesticide response compared to the control, the spray treatment intermediate in effectiveness, and the drench treatment with the best results. Both Manti Ridge, and Willow Creek lacked significant difference between the control and the spray treatment, even though the drench treatment yielded 100.0% seed predator control.

Summary. Differences in weather, habitat and natural enemies contribute to expected differences in population numbers of insects (Wallner 1987) across years and sites. The low overall seed damage found in wild populations of *A. glauca* and *C. acuminata* in this study may not persist indefinitely, but merely reflect a cyclic low in seed predator numbers. Large differences in seed predator abundance between sites and years suggest asynchronous populations. Asynchronous population dynamics contributes to spatial and temporal persistence of a species (Liebhold et al. 2004), which in this case would allow localized seed predator extinctions while maintaining adequate population densities among metapopulations. This was the case at two sites where only one capitulum in the sample reared a seed predator. Plant populations with low seed predator populations may have years of high seed productivity until immigrant seed predators from outlying population recolonize in the absence of parasitoids. Even though the examined seed predators are widespread, they are localized around suitable host patches. Polyphagous seed predators would be expected to demonstrate asynchronous patterns compared to monophagous species which are synchronized to the local host. In this case, *Campiglossa* sp. is at least oligophagous to the tribe Cichorieae whereas *P. a. mucidella* is a polyphage.

Seed damage in wild populations of *A. glauca* and *C. acuminata* while not substantial at some sites during some years did cause considerable damage in some instances. Low seed yields due to seed predation are common obstacles faced by wild seed collectors, and methods to enhance seed yields would be valuable. In this case, some sites had seed losses greater than 20.0%. Such losses in seed yield could significantly impact the profitability of private seed collectors. With ongoing efforts to develop methods for agricultural production of these plant species it is important to realize the existing impact seed predators have in wild plant populations. The risk of pest damage under agricultural production, especially in the establishment of native forbs as crop monocultures, can potentially greatly exceed that found in the wild. The agricultural landscape is usually lacking the ecological components that provide natural biological control mechanisms found in wild plant populations. The use of imidacloprid can provide good control of seed predators and help improve seed yields. Though foliar application was never superior to the soil drench, it did provide reasonable decreases in percent seed damage at most sites. Sites where seed damage was not significantly different than the control were also sites where seed damage in the control population was also low. Because spray can be applied with a spray boom on a tractor, it has real potential for wildland or agricultural application. Increasing the concentration of active ingredient in the spray treatment could potentially provide results equal to the soil drench. Because of the potential impact of imidacloprid to non-target organisms, care should be taken in wildland applications. In order to implement an integrated pest management program, other control possibilities such as with cultural practices or biological control agents should be investigated.

Acknowledgments

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Figure legend:

Fig. 1 Distribution of seed production per capitulum for *A. glauca* (n=576, mean=38.3, mode=40).

Fig. 2 Distribution of percent seed damage by seed predators for *A. glauca* (n=576, mean=8.1, mode=0.0).

Fig. 3 Distribution of seed production per capitulum for *C. acuminata* (n=412, mean=9.0, mode=9).

Fig. 4 Distribution of percent seed damage by seed predators for *C. acuminata* (n=412, mean=12.4%, mode=0.0%)

Fig. 5 Three-way interaction (imidacloprid treatment x site x and year) ($p<0.01$) on percent seed damage of *C. acuminata.*

Fig 6. Two-way interaction (imidacloprid treatment x site) ($p<0.01$) on percent seed damage of *A. glauca*.

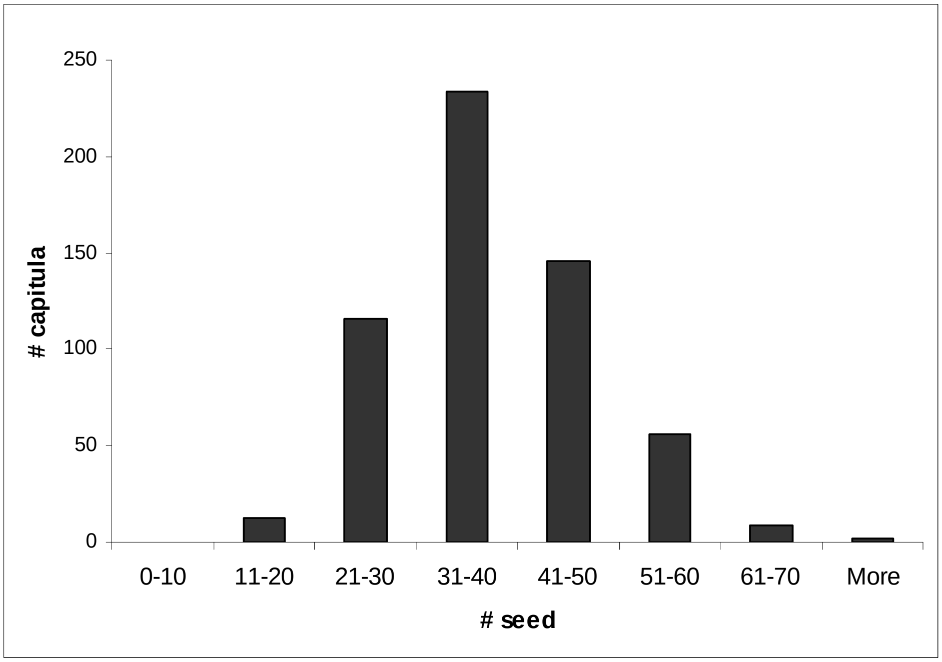


Figure 1

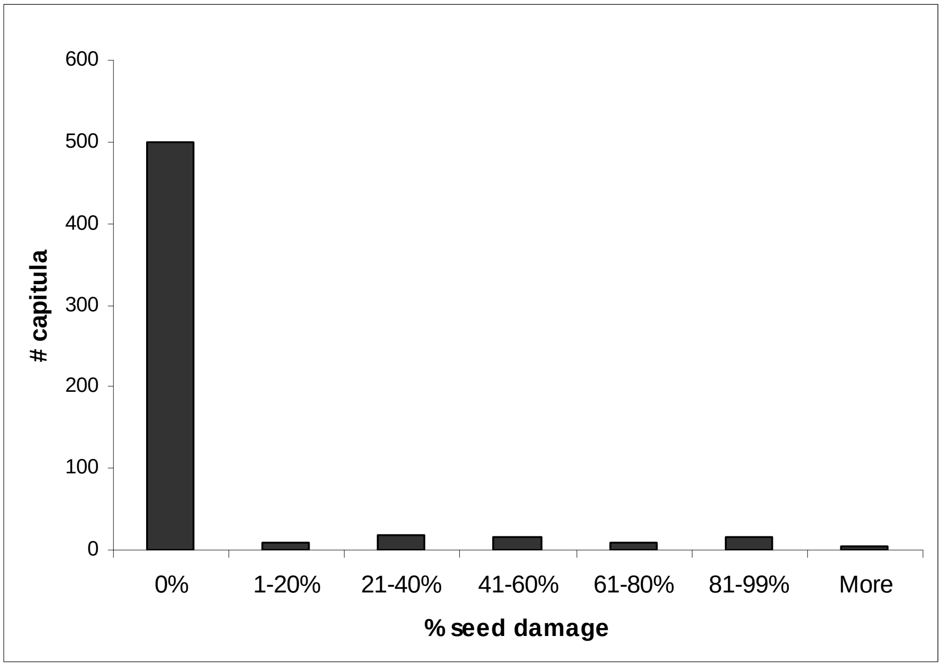


Figure 2

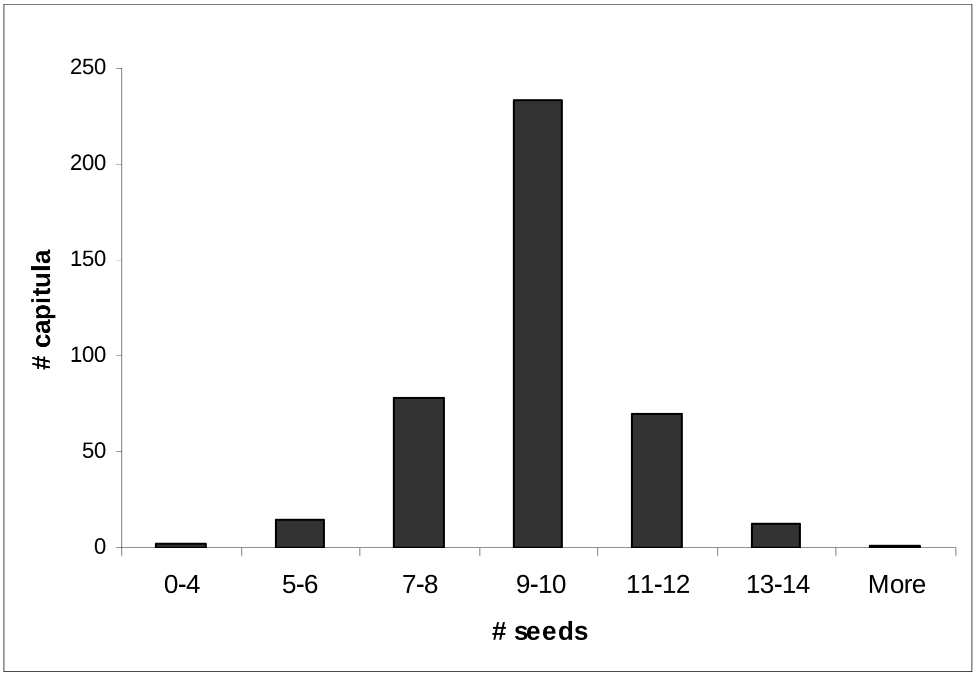


Figure 3

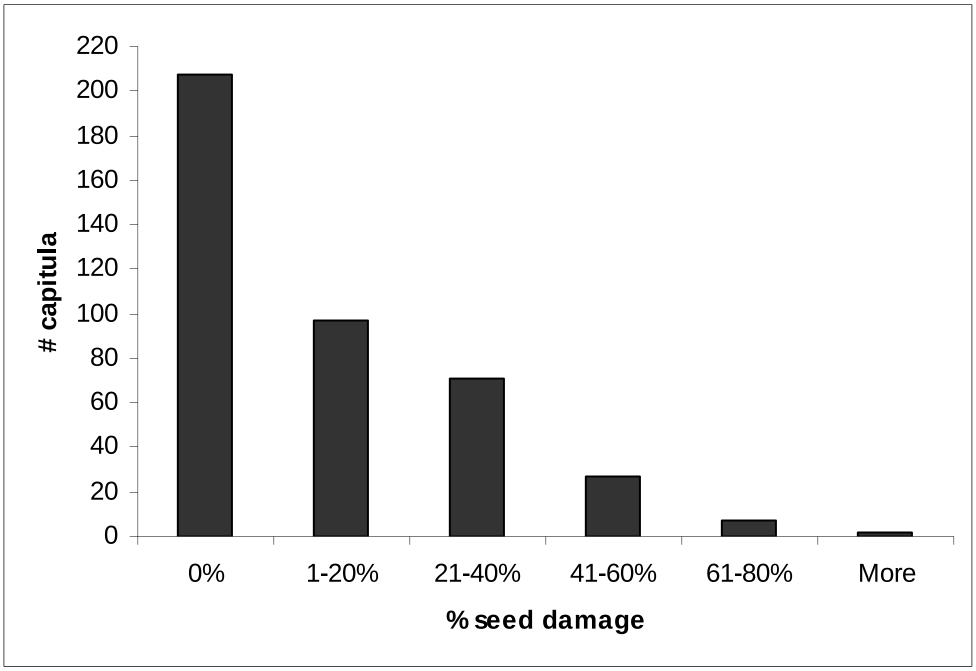


Figure 4

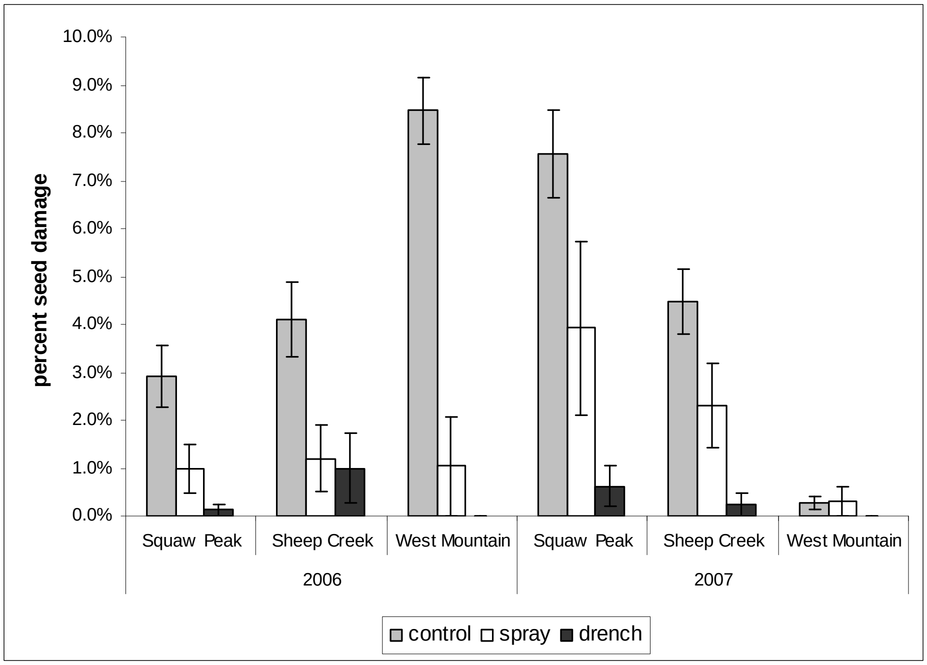


Figure 5

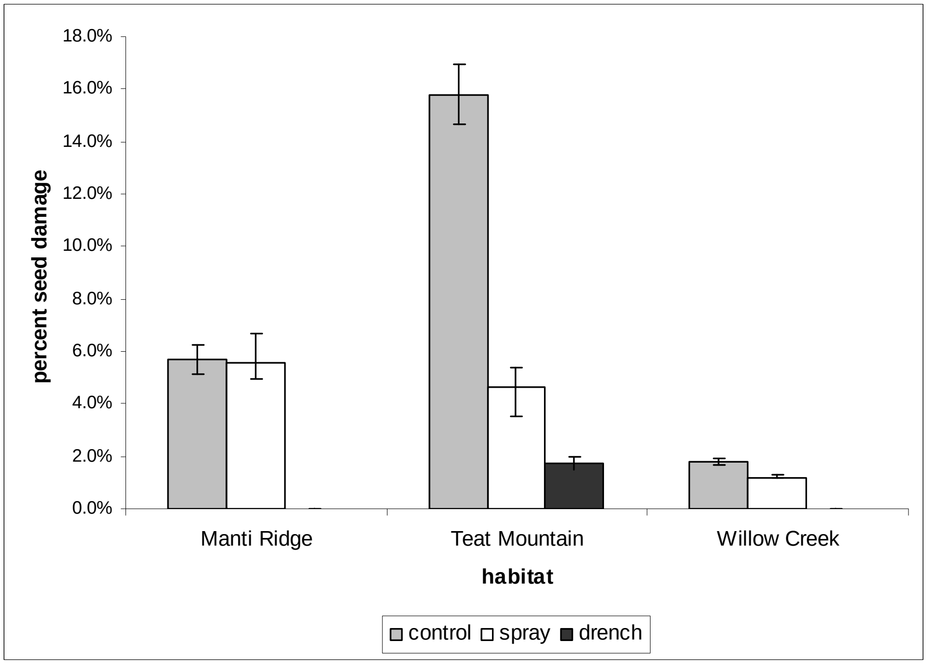
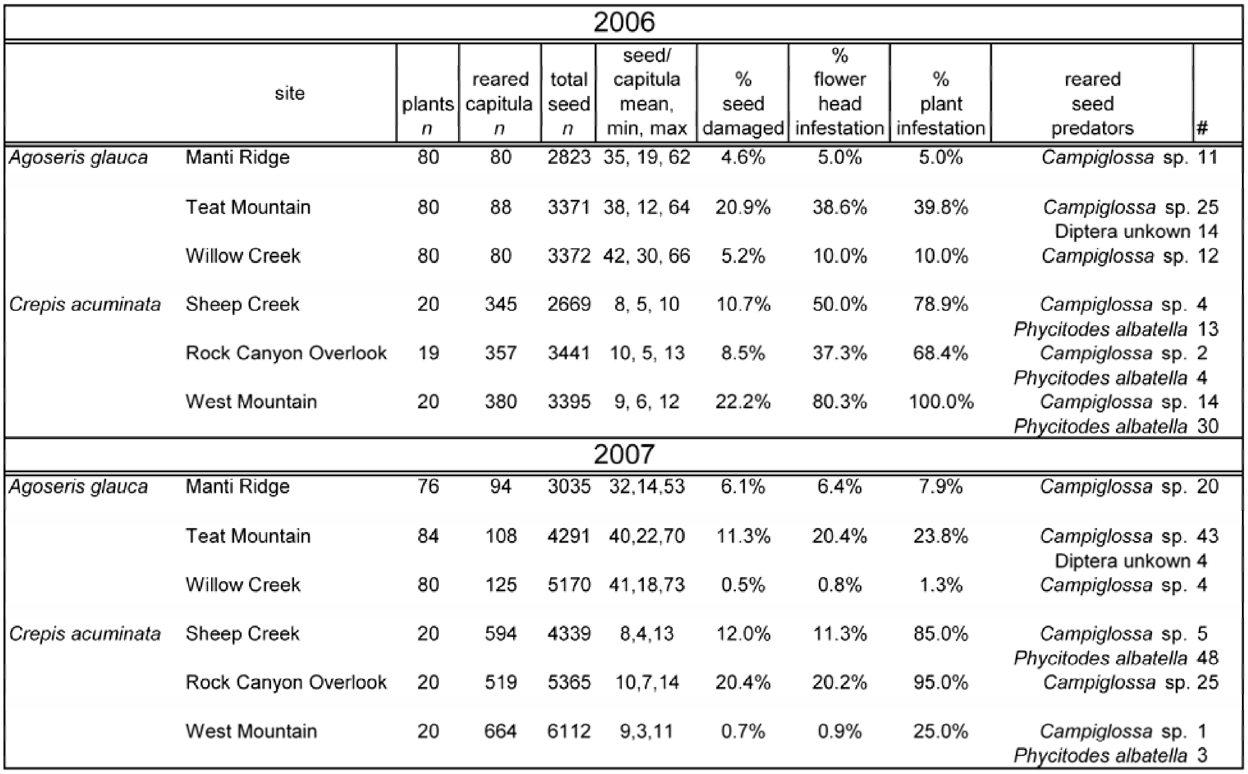


Figure 6

Table legend

Table 1 Descriptive statistics of seed damage, infestation levels, and reared seed predators from *C. acuminata* and *A. glauca.*

Table 1



	site	plants *n*	reared capitula *n*	total seed *n*	seed/ capitula mean, min, max	% seed damaged	% flower head infestation	% plant infestation	reared seed predators	#
2006										
Agoseris glauca	Manti Ridge	80	80	2823	35, 19, 62	4.6%	5.0%	5.0%	*Campiglossa* sp.	11
	Teat Mountain	80	88	3371	38, 12, 64	20.9%	38.6%	39.8%	*Campiglossa* sp. Diptera unkown	25 14
	Willow Creek	80	80	3372	42, 30, 66	5.2%	10.0%	10.0%	*Campiglossa* sp.	12
Crepis acuminata	Sheep Creek	20	345	2669	8, 5, 10	10.7%	50.0%	78.9%	*Campiglossa* sp. *Phycitodes albatella*	4 13
	Rock Canyon Overlook	19	357	3441	10, 5, 13	8.5%	37.3%	68.4%	*Campiglossa* sp. *Phycitodes albatella*	2 4
	West Mountain	20	380	3395	9, 6, 12	22.2%	80.3%	100.0%	*Campiglossa* sp. *Phycitodes albatella*	14 30
2007										
Agoseris glauca	Manti Ridge	76	94	3035	32,14,53	6.1%	6.4%	7.9%	*Campiglossa* sp.	20
	Teat Mountain	84	108	4291	40,22,70	11.3%	20.4%	23.8%	*Campiglossa* sp. Diptera unkown	43 4
	Willow Creek	80	125	5170	41,18,73	0.5%	0.8%	1.3%	*Campiglossa* sp.	4
Crepis acuminata	Sheep Creek	20	594	4339	8,4,13	12.0%	11.3%	85.0%	*Campiglossa* sp. *Phycitodes albatella*	5 48
	Rock Canyon Overlook	20	519	5365	10,7,14	20.4%	20.2%	95.0%	*Campiglossa* sp.	25
	West Mountain	20	664	6112	9,3,11	0.7%	0.9%	25.0%	*Campiglossa* sp. *Phycitodes albatella*	1 3