

AN ABSTRACT OF THE DISSERTATION OF

Michael C. Russell for the degree of Doctor of Philosophy in

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Abstract approved:

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Conservation biological control involves manipulating farm landscapes or management systems to enhance populations of beneficial predators of agricultural pests. Farmscaping is one aspect of conservation biological control where predators of important pests are identified, the availability on the farm landscape of resources and habitat components needed by the beneficials to complete their lifecycles is evaluated, and hedgerows, beetle banks, or other conservation plantings can be added to the landscape to provide the lacking resources. To be able to efficiently survey a farm landscape for the presence of resources that support beneficial predator populations there needs to be information on the resource availability with different habitats. This dissertation describes a series of investigations into determining the amount of resources available in particular habitat types, and how to create conservation plantings which provide these resources with minimal expense and impact on the farming system.

The first investigation is into the floral resource availability to parasitoid wasps in cane berry production landscapes. A meta analysis was performed to estimate the effects of different species on longevity of and attraction to various flowers. This information was then used to evaluate the plant species found on Willamette valley cane berry farms and calculate the total floral resource availability of different habitats during different times of the year. Surveys identified particular habitats on the landscape, and different management regimes as having high floral resource availability relative to other habitats or management regimes.

The second investigation focuses on the biology of a group of ground beetles that are common on Willamette valley vegetable farms. Pitfall trapping and soil core samples were used to determine the seasonal activity patterns of the carabids, and to identify which habitats they were using most. Sentinel prey cards were used to compare pitfall trap counts with the risk of predation of a potential prey item. Laboratory experiments identified differences in the feeding and activity of different species, and the changes over the season.

The third investigation used soil cores to sample the over wintering arthropod predator populations in a variety of habitats on Willamette valley farms, and in plantings of native species on beetle banks in a common garden at the Hyslop research farm in Corvallis, Oregon. Grassy habitats were found to support the highest arthropod populations both on the farms and in the common garden. Some perennial forbs also had high arthropod numbers, while other perennial forbs and annual forbs had low numbers. Differences in the number of over wintering arthropods in different species were related with differences in the structure and composition of the vegetation.

The information presented here can be used to assign value to different habitats based on the provision of specific resources required for beneficial predators to complete their life cycles. This will aid in rapid evaluations of farm landscapes based on aerial imagery interpretation or a quick tour. After initial predictions are made it is easier to conduct more in depth sampling to confirm whether the beneficials are in fact present and thriving. If there are resources that are in too short a supply the information provided here will help in designing conservation plantings to provide those resources.

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Habitat Management for Beneficial Insects on Willamette Valley Vegetable and Berry
Farms

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Michael C. Russell

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APPROVED:

Major Professor, representing Horticulture

Head of the Department of Horticulture

Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Michael C. Russell, Author

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CONTRIBUTION OF AUTHORS

Dr. Mario Ambrosino made a significant contribution to the compilation of articles for the parasitoid wasp floral availability meta analysis. Elizabeth records provided the majority of the labor in the beetle activity trials and dissections.

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Chapter 1 – Introduction

Introduction

Low plant diversity at both the local and regional scale is often associated with increased insect pest problems in agriculture (Altieri and Nichols 2004). One broad potential mechanism underlying this relationship is that greater plant diversity provides enhanced habitat that supports a greater abundance and diversity of natural enemies including predators and parasitoids of pest species (Norris and Kogan 2000). The concept of conservation biocontrol attempts to exploit this mechanism for practical pest management (Jonsson et al. 2008).

A number of recent studies have demonstrated that increasing plant species and habitat diversity in agroecosystems can result in increased natural enemy abundance and diversity. For example, perennial and annual flowering plants grown in rows between crops or as understory vegetation can increase predator abundance and parasite diversity (Jones and Sieving 2006; Steinbauer, Short, and Schmidt 2006). In addition to herbaceous non-crop vegetation, both trees and other crop species can positively impact pest management. For example, diversifying tree composition and the presence of shade trees in agroforestry systems increases the abundance and diversity of predators and parasites (Steinbauer, Short, and Schmidt 2006; Philpott and Armbrrecht 2006). Increasing the number of crop species cultivated in an area can also positively affect pest management. In a meta-analysis of published studies, Langelotto and Denno (2004) found that polycultures (mixtures of crop species cultivated together) resulted in a significant increase in natural enemy abundance relative to monocultures. A number of other studies across scales and taxa also support a clear relationship between plant diversity and the biological control of pests (e.g. Ludy 2007; Olson and Wackers 2007; Pollard and Holland 2006).

Despite considerable evidence supporting the general concept, several factors complicate practical efforts to augment plant diversity for purposes of biocontrol. One important complication is that individual diversity components such as species and landscape elements likely vary considerably in their impact on the specific pest regulation services of most interest to farmers. Because of this, Gurr et al. (2005) argue that we should replace the axiom “diversity helps” with “appropriate diversity helps”.

A study on parasitism rate on sentinel armyworms in Michigan is an example. The study found two important parasitoid species that were common in both simple and complex landscapes, *Glyptapanteles militaris*, and *Meteorus communis* (Menalled et al. 2003). Parasitism rates of *M. communis* were higher in complex landscapes when compared to simple landscapes, but *G. militaris* parasitism rates were similar in both types of landscapes. The researchers note that Cherry trees (*Prunus serotina*) in the forests of the more complex landscape harbor several caterpillars that are alternate hosts for *M. communis*. Alternate hosts for *G. militaris* are found on a variety of herbaceous plants that grow in both simple and complex landscapes. This and other studies reveal that the specific ecological interactions between particular species and their environments determine whether a conservation biological control management activity will be effective.

The first step in developing a conservation biological control management strategy is to identify the pest and predator species and the fluctuation in their populations and activity patterns over the seasons. Many species have distinct periods of maximum activity. For a predator species to be important in agriculture it must have activity patterns that coincide with the presence of the pest (Kovanci, et al. 2007). The predator may focus on a particular life stage of the prey and a generalist predator may need to switch between a variety of prey species as the prey enters and leaves the vulnerable stage (Wearing and Harris 2005). Combining phenological information with an understanding of the feeding habits of different predators is one way to identify potentially important predator species (Rutledge, et al. 2004).

Once important species are identified the next step in developing a conservation biocontrol strategy is to identify the vegetation and landscape components that influence those species populations. A bottom up approach involves identifying specific resources that contribute to the growth, reproduction and survival of the pests and predators in the system. For example, many beneficial predators require floral resources like nectar or pollen, which vary in availability between different plant species (Orr and Pleasants 1996, Idris and Grafius 1995, Ambrosino et al. 2006). In a more holistic, less mechanistic approach important landscape components can be identified by monitoring population levels in and adjacent to different habitats. For instance, the types and abundance of

predatory ground beetles within fields is strongly influenced by the composition of the adjacent landscape (Fournier and Loreau 2001).

When important habitat components are identified, management activities that introduce those resources can be implemented. Cover cropping and conservation tillage have predictable effects on cover, soil structure, biotic communities, and other resources. These practices also contribute to differences in the abundance and activity of beneficial predators (McGrath 2000). With an understanding of the life histories of important predators, resources necessary to maintain high population levels, the distribution of habitat components containing those resources on the landscape, and the effects of management actions on survival and resource provisioning, land managers can actively influence predator populations in order to reduce pest problems.

This level of management requires a detailed understanding of the habitat requirements and seasonal habitat choice behavior for the species of interest. These relationships are likely highly context specific, requiring information developed from field-based studies in specific ecoregions and cropping systems. In addition, the distinct habitat requirements needed by different beneficial insect guilds could create potential management conflicts. For instance, maximizing the amount of perennial grass habitat on farms could inadvertently reduce floral resources for parasitoids. Yet predicting and alleviating these potential conflicts is difficult because we still have only a coarse scale understanding of which habitat components are most critical, and how these specific habitat components are distributed in actual farm landscapes.

This dissertation will provide detailed cropping system and ecoregion specific information to inform more expert management of on farm biodiversity for the purpose of pest control. The study will help identify the elements of habitat quality that are most important in supporting important predators of agricultural pests in the Willamette Valley ecoregion. The two broad beneficial predator guilds I will investigate are ground beetles and parasitoid wasps.

Ground Beetles

Ground beetles are generalist predators that feed on arthropod pests in agricultural systems and contribute to lower pest abundances (Brewer and Elliot 2003, Edwards et al.

1979, Kromp 1999, Sunderland and Vickerman 1980). There are a variety of sampling methods that have been used to describe their role in controlling populations of pests. One study mapped both predator and pest populations through time to demonstrate that the ground beetles were concentrating their activity in areas of high pest populations, and pest populations were decreasing in areas with high predator activity (Winder et al. 2005). Analysis of gut contents of the ground beetle confirmed that their diet was primarily composed of the aphid pest.

Ground beetles belong to an ecological guild of walking generalist predators that can be excluded from particular areas by low plastic fencing buried in the ground. Exclusion experiments have demonstrated that this guild plays a role in reducing pest populations (Edwards et al. 1979, Lang, et al. 1999). However, it is likely that the members of the guild differ in their specific feeding habits, and it may be only a few species that are responsible for the biological control (Sunderland and Vickerman 1980, Prasad and Snyder 2004).

The ecology of specific ground beetles on Pacific Northwest farms has begun to be studied but there is much that remains to be understood. (Green 2011, McGrath 2000, Moulton 2011, Prasad and Snyder 2004, Prasad and Snyder 2006). Previous researchers studied the effects of conservation tillage practices on some of those ground beetles (Green 2011, McGrath 2000). Another study showed that beetle banks could be associated with increased beetle populations (Prasad and Snyder 2006). Unfortunately, information on the long term dynamics of ground beetle populations in response to these sorts of management practices on local farms is scarce. The diets of some ground beetles in the northwest have been studied through laboratory feeding trials and gut analysis of field caught specimens (Prasad and Snyder 2004, Moulton 2011). There are many other species that are common in Willamette Valley agricultural areas, for which little is known about basic life history characteristics like feeding habits, phenology, and habitat affinities. An experiment in Washington demonstrated that interactions between different ground beetle species, and the prey items that are available, can determine whether or not the community as a whole contributes to lower pest numbers (Prasad and Snyder 2006). By collecting more information on the life histories and landscape distribution of these

species we will be better able to manage their populations as a part of a conservation biocontrol program.

A more extensive group of studies from other regions have demonstrated that the activity of some generalist predators is strongly associated with field margins and grassy borders (Thomas et al. 1991, Thomas et al. 2001; Holland et al. 2005). Grassy, 1-2m wide “beetle banks” that run across crop fields are an efficient method to provide this sort of habitat with limited modification to agricultural production systems. Government support of beetle banks in the United Kingdom has resulted in wide acceptance, which has led to important research on both design considerations, and the response of insect communities. Research there has demonstrated that generalist predators, particularly ground beetles, seek out and benefit from the microclimate afforded by grasses on the beetle banks (Denis et al. 1994, Thomas, et al. 1991). In the UK, the highest beetle densities have been found in banks planted with caespitose grass species, particularly *Dactylis glomerata* L. (Collins et al. 2003, Macleod et al. 2004). The soil surface of banks sown to caespitose grasses has been shown to have less variable temperatures than the soil under sod forming grasses (Thomas et al. 1992). Unfortunately, *D. glomerata* has been identified as invasive in natural habitats in the Pacific Northwest (MacDougal et al. 2006, Parendes and Jones 2000, Williamson and Harison 2002). There are numerous caespitose species of Pacific Northwest native grasses that could be used on beetle banks instead. Data on which native plant species perform well as beetle bank species can be used to design beetle banks for the Willamette Valley that are heavily used by beetles, but do not contribute to the spread of invasive species.

Parasitoids

Ground beetle communities do not exist in a vacuum, so any habitat manipulation to enhance their populations needs to consider the other beneficial species that inhabit the area, such as parasitoid wasps. Parasitoid wasps are specialist predators that can be important biological control agents, such as of leaf roller pests in caneberry fields in the Willamette valley (Coop et al. 1989). Although the wasp larvae consume caterpillars as larvae, adult wasps need to eat floral nectar regularly to avoid starvation and maximize their longevity (Baggen and Gurr, 1998, Seikmann, et. al., 2001). Consequently the

seasonal availability of floral resources within and adjacent to fields can have a strong influence on parasitoid abundance and their associated pest control services. There is little information on the availability of floral resources in Willamette Valley cane berry fields, and how availability changes over the season and is affected by management activities.

Research Goals

The specific goals of this research are:

1. Describe the spatial and temporal patterns of floral resource availability for braconid wasps in typical caneberry production landscapes, and understand the ecological and management processes that contribute to the observed variation.
2. Describe the seasonal patterns of activity and feeding behavior of ground beetles of Willamette valley agricultural landscapes.
3. Develop a habitat-based model that predicts the occurrence of beetle species at the farm scale in Pacific Northwest agricultural landscapes.
4. To compare different species of Willamette valley native plants for their utility as beetle bank plantings, and to test different vegetation structure and compositional characteristics that are associated with high generalist predator numbers.

Approach

The availability of floral resources for braconid wasps was evaluated with surveys of floral abundance on cane berry farms. The general farm landscape was surveyed with repeated sampling of the different habitats on a number of farms. The floral abundance within cane berry fields was sampled with fixed area plots and comparisons were made based on the types of management systems fields were under. The floral abundance was compared with reports of the effect of different plant species flowers on the longevity of or attraction to parasitoid wasps found in the literature. Field observations were evaluated based on the literature review findings to estimate the amount of floral resource availability in different habitats and management systems on the cane berry farms.

The seasonal activity of ground beetles was surveyed with pitfall traps on four farms. Beetles were collected and put through a series of trials to determine the voracity and feeding choice, and the changes in those behaviors over the season. The pitfall traps were placed in transects across fields and activity density was compared between habitats. Over wintering distribution was sampled with soil cores taken in the winter.

The winter soil samples were also used to identify the habitats that beetles use for over wintering hibernation sites. This information was combined with common garden experiments comparing the over wintering arthropod populations in soil cores taken from beetle banks sown with a variety of native grasses and forbs. Additionally, a manipulative experiment was conducted to test the effect of removal of vegetation and addition of litter to beetle banks on arthropod predators.

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A meta-analysis of physiological and behavioral responses of parasitoid wasps to flowers
of individual plant species.

Michael Russell

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Abstract

A meta-analysis was conducted to summarize the published information on the relationships between parasitoid wasps and different plant species. Trials can either measure a physiological response such as wasp longevity when only supplied with flowers from a single plant species, or a behavioral response like attraction of wasps to plantings in the field. The log response ratio was the effect size used to make standardized comparisons between plant species and a meta-analysis was conducted to find the mean response for the species included in more than one trial. Physiological response trials have been conducted on 120 different plant species and there is information on 104 plant species included in a behavioral response trial with parasitoid wasps. The effects of different plant species ranged from a log response ratio of zero up to 2.3 for longevity, and 4.1 for attraction. The longevity estimate is equivalent to a nearly 10 to 1 ratio of days longevity with the flower to days longevity in the starvation control. The average increase in longevity was greatest for wasps given flowers from plants in the Polygonaceae, Boraginaceae, Apiaceae, Rosaceae, Solanaceae, Brassicaceae, and Onagraceae. Plant species in the Caryophyllaceae, Scrophulariaceae, Lamiaceae, Fabaceae, and Asteraceae tended to slightly increase wasp life spans, but their effect was lower and less consistent among species. There were a number of families that were represented by a single species which did not increase wasp longevity over the controls at all including Amaranthaceae and Chenopodiaceae. This review can help identify plant species which have been proven to supply nectar for parasitoids for potential use in a conservation biological control program, but plant selection should not be limited to the small list of species that were included in these studies

Introduction

Parasitoid wasps occur worldwide and can be a significant mortality factor in pest populations (Keasar and Steinberg 2008, Wearing, et al. 2012). Most parasitoid species depend on floral nectar to complete part of their lifecycle (Syme 1975, Idris and Grafius

1995). Parasitoid wasps need to eat frequently to avoid starvation, and many species have increased longevity and fecundity when provided with floral resources (Seikmann, et. al. 2001, Baggen and Gurr 1998). A variety of crops, weeds, and wild plants can occur on agricultural landscapes, but not all of these species provide resources for parasitoid wasps. Some of the plant species do not produce nectar, while others may have long or complicated corollas that can limit nectar availability for small wasps and other short mouthed insects (Baggen et. al., 1999, Vatala, et al. 2006, Arévalo, et al.2005). Even plant species with accessible nectar may vary in the quantity and nutritional characteristics of the floral resource such as the sucrose to hexose ratio of the nectar (Koptur 2005).

Agricultural plant communities can be assessed for whether there are plant species that produce nectar available to foraging parasitoid wasp adults. Plants that do not produce any nectar or species which produce nectar inside flowers that hinder access for wasp sized insects generally would not provide available floral resources for parasitoid wasps. Species that produce flowers with accessible nectaries would be the most likely source of nourishment for adult wasps on the landscape. There is a growing body of literature that reports direct tests of the suitability of specific floral resources for parasitoid wasps, but the literature is diverse and scattered making it difficult to use it to comprehensively evaluate the suitable floral resources available in diverse floral landscapes. The goal of this study was to synthesize the body of literature and to provide estimates of the relative parasitoid resource suitability for a range of floral types.

Methods

Literature selection

The objective of the literature search was to compile the results of direct tests on the use of specific plant species by parasitoid wasps. There were two major types of investigations frequently conducted to answer that question, physiological response trials and behavioral response trials. Longevity trials are the most common physiological response trial and involve enclosing individuals or groups of parasitoids with flowers from a single species of plant and measuring the duration of survival of the wasps. In some of the longevity trials the mean number of eggs produced by each female wasp was

also measured providing a more in depth look at the nutritional benefit of the nectar. Behavioral response trials include both observations of wild parasitoids being attracted to plantings of different species in a common garden and studies of insect response to flowers in the lab.

The common goal of the physiological response trials was to estimate the ability of flowers of a plant species to increase the longevity of parasitoid wasps. The trials used a water only control to determine how long the species could live without food and compared that with the survival of insects with access to flowers of a single plant species. A sugar water or honey water positive control is often also included. Either excised flowers were used, or they enclosed the insects with just the flowers of a rooted plant. Previous research suggests that results from either type of study are comparable (Wade and Wratten, 2007).

In the behavioral response studies the goal was to compare how well flowers of a plant species can attract parasitoid wasps in relation to other plant species. Behavioral response studies provide less conclusive evidence than tests of physiological performance because insects may also respond to colors or smells of the flower that do not necessarily indicate that there is available nectar (Slater and Calder 1988). The attraction studies reported the number of parasitoids attracted to plants in the field, or they compared the response of insects to flowers in the lab.

Many of the articles that describe these types of studies that were found in the literature reported results from multiple trials. Each plant species tested was considered a single trial. Additionally, if multiple wasp species were tested each plant species – wasp species combination was considered a separate trial. Multiple trials of the same plant - wasp combination through time were reported in some articles. There were a number of plant species that were tested in more than one article, with more than one wasp species, or multiple times in one article. These species were included in multiple trials so I was able to conduct a meta-analysis to estimate the mean effect size across studies for the plant species. The meta-analysis did not include plant species included in a single trial, but I report the standardized effect size that was calculated for that trial. For genera that included more than one species which was represented in only one study, the unreplicated species were grouped and a meta-analysis was done on those species in the genus. The

species used to calculate the genus groups do not include any species of the genus that had sufficient replication to be meta-analyzed separately.

Data collection and analysis

Longevity trials literature review

For each plant species included in a longevity trial I calculated the mean and standard deviation of the wasp lifespan in days for both the flower and control treatment. The number of replications of each treatment was also recorded. These values were transcribed from tables when possible, but for many studies the values were estimated based on graphical representations.

Two articles (12 trials) only reported the proportion of wasps surviving as the treatments progressed; the proportions were multiplied by the sample size to determine how many died between each sample event. The mean and standard deviation for longevity was calculated based on the reconstructed life spans for all the wasps in the sample.

For each plant species trial I calculated a treatment effect size on longevity using the log response ratio [$\ln(\text{treatment mean} / \text{control mean})$] (Hedges, et al 1999). In the meta-analysis I calculated the mean log response ratio across all trials for the plant species included in multiple trials. The log response ratio is scaled to the value of the control for each wasp species so it takes into account differences in the life histories of the wasp species that are being tested. When there was no difference in response between the flower treatment and the control, the effect size is zero. Positive effect sizes indicate an increase in the treatment response with respect to the control.

Attraction studies

Attraction studies included a greater diversity of methodology than longevity trials. Seventy percent of the articles (67% of the trials) were conducted in the field and reported insect counts on plantings of a single plant species based on direct observation, vacuum sampling, sweep netting, and passive trapping. The lab trials focused on a particular wasp species and either measured the amount of time insects spent on flowers of different species, or the number of times an insect was on a plant during specific

observation instants. The mean, standard deviation, and sample size were transcribed from tables when possible, or estimated from graphs when necessary.

Many of the attraction studies reported the insect response to different plant species, but did not identify a specific control treatment. In some trials a bare area or a stand of grass (with no nectar production) was defined as the control. For consistency in this review however, the control in each trial was defined as the treatment with the lowest attractiveness response among the plant species tested together. When control treatments were defined by the study authors, they generally also had the lowest response values. A few studies only reported ratios between the treatment and the control so the raw values were calculated based on the sample size.

The minimum treatment value in many of the attraction studies was zero. This would produce an undefined log response ratio [$\ln(\text{treatment mean} / \text{control mean})$], so a value of one was added to both the control and treatment values of all the attraction studies before calculating the log response ratios for each trial.

Nectar availability in plant families

Only a few of the vast diversity of flowering plant species have been assessed in direct tests. It is possible that some of the plant species that have not yet been tested may be similar in their ability to provide nectar for parasitoid wasps with the species that have been tested from the same plant family. For the longevity trials I grouped the results by plant families instead of by species and performed a meta-analysis to estimate a mean increase in wasp life span from access to flowers from plants in each family. This information can provide baseline information on taxonomically similar species to aid in the evaluation of untested species as potential nectar sources for parasitoid wasps. The reduced certainty in the results from the attraction studies limited the value of family wide estimates so they were not conducted.

Results

Seventeen articles were found that described studies testing parasitoid longevity. These included 278 distinct trials (Table 2.1). Ten papers were found that compared attraction of parasitoid wasps to different plant species, with 283 distinct trials (Table

2.2). There was a wide variety of responses to flowers. Some species had values similar to the control ($\ln(\text{experimental mean} / \text{control mean}) = 0$), and others had a log response ratio of up to 2.3 for longevity, and 4.1 for attraction (Table 2.1, Table 2.2). The longevity estimate can be back transformed to a 9.97 fold increase in days of wasp life span due to the presence of the flower. Plant species that were used in more than one study were included in a meta-analysis to determine the mean effect size across studies. There were 69 plant species or genus groups that were included in the meta-analysis, and an additional 51 plant species that were only included in a single study (Figure 2.1, 2.2). In attraction studies there were 62 plant species that could be used in the meta-analysis and an additional 42 plant species that were in one study (Figure 2.1, 2.2).

Species tested in longevity trials were from 28 plant families. Fourteen of the families were represented only one species and for six of those species there was only a single distinct trial conducted (Figure 2.3). Five families were represented by more than 10 species and each significantly increased parasitoid longevity, but Apiaceae and Brassicaceae had the highest mean effect sizes while Lamiaceae, Fabaceae, and Asteraceae had lower effect sizes (Figure 2.3).

Discussion

The meta-analysis and calculation of standardized effect sizes for each trial is a useful tool to characterize plant species, but it is important to remember that there are many uncertainties about the individual results. The log response ratio is designed to standardize results, but the wasp species tested may have differed in important ways, and the variability in execution of the experiment may obscure measured effects. Additionally, the meta-analyses and the experiments they are based on are designed to test the hypothesis that there is no difference between the treatment and the control. Rejection of the hypothesis is evidence that the plant does have available nectar. However failure to reject the hypothesis when there is no significant difference between the control and the treatment is not the same as confirming that the plant cannot provide available nectar. This is a particular concern for attraction studies conducted in the field.

Much of the variability in wasp longevity can be explained by floral architecture (Patt, et al. 1997). Corolla length and corolla opening diameter are two floral traits that can be related on whether a wasp can access the nectar (Idris and Grafius 1995).

In a comparison of a group native Iowa species, (Orr and Pleasants 1996) insects kept with eight of the eleven plants tested increased the longevity of a braconid parasitoid *Macrocentrus grandii* Goidanich with respect to the only water treatment. These species all had shallow corollas. *Macrocentrus grandii* has very short mouth parts so it could only access nectar from plants with shallow corollas. The researcher determined it could feed only on those flowers with corolla depths less than 4.5 mm.

Based on this meta-analysis, it is possible to show that there is no significant difference in the effect of longevity between plant species with different plant growth forms (annuals, biennials, perennials, and shrubs). However most of the studies included plant species that were suspected to be nectar source or were readily available cover crops. Random selection of the species is necessary to make a valid analysis of which plant traits are associated with nectar sources for parasitoid wasps.

Floral architecture is not the only factor determining nectar availability on a landscape. There may be nectar available to foraging insects from extra floral nectaries on species with floral nectar hidden within complicated flowers (Baggen et. al., 1999). Actual nectar availability can depend on factors beyond intrinsic species differences. Soil resource limitation can reduce nectar production (Carroll, et al. 2001, Burkle and Irwin 2009). Floral maturation cycles can influence whether a wasp can find food on a plant at a particular time (Idris and Grafius 1995).

Simply evaluating plant community composition and plant biology without considering insect behavior and ecology may lead to erroneous conclusions about the role a plant could play in providing nectar for parasitoid wasps. In one study, wasps were attracted to some of the flowers with long corollas (Idris and Grafius 1995). Those plant species had abundant nectar resources and the wasps were observed to chew holes in the bases of the corollas to access the hidden nectaries. This demonstrates that just looking at floral and insect morphology may lead to wrong conclusions about the utility of various plants if the insect can develop a means to access the nectar.

Conclusion

Wasp longevity can vary greatly based on access to floral resources. Some plant species do not produce nectar and others have nectaries that are difficult or impossible for wasps to access. Floral architecture can be a determinant of whether the wasp can forage from a plant species. Comparing plant species in the same family with similar flowers is one line of evidence that can be used when trying to evaluate whether there is nectar available for wasps in the plant species present in a plant community that have not been tested. There are a variety of additional factors involved in nectar production and accessibility so direct evaluation of the communities in the field are required to make more accurate estimates of available wasp nutrition.

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Table 2.1. The estimates of log response ratio and its standard error for each study included in the meta-analysis on parasitoid longevity when provided with one species of flower. Parasitoid family names are abbreviated (Br. = Braconidae, En. = Encyrtidae). For articles reporting results from multiple studies the studies are differentiated by the study number (#). N is the sample size for the control treatment.

Plant species (family)	Parasitoid (family)	reference	#	ln(RR) (SE)	N
<i>Anethum graveolens</i> (Apiaceae)	<i>Copidosoma koehleri</i> (En.)	Baggen and Gurr 1998	1	1.24 (0.01)	5
<i>Borago officinalis</i> (Boraginaceae)	<i>Copidosoma koehleri</i> (En.)	Baggen and Gurr 1998	1	1.15 (0.012)	5
<i>Coriandrum sativum</i> (Apiaceae)	<i>Copidosoma koehleri</i> (En.)	Baggen and Gurr 1998	1	0.95 (0.013)	5
<i>Vicia faba</i> (Fabaceae)	<i>Copidosoma koehleri</i> (En.)	Baggen and Gurr 1998	1	0.46 (0.013)	5
<i>Fagopyrum esculentum</i> (Polygonaceae)	<i>Copidosoma koehleri</i> (En.)	Baggen, et al. 1999	1	1.2 (0.007)	7
<i>Phacelia tanacetifolia</i> (Hydrophyllaceae)	<i>Copidosoma koehleri</i> (En.)	Baggen, et al. 1999	1	0.89 (0.02)	7
<i>Tropaeolum majus</i> (Tropaeolaceae)	<i>Copidosoma koehleri</i> (En.)	Baggen, et al. 1999	1	1.08 (0.009)	7
<i>Vicia faba</i> (Fabaceae)	<i>Copidosoma koehleri</i> (En.)	Baggen, et al. 1999	1	1.17 (0.01)	7
<i>Agapanthus praecox</i> (Liliaceae)	<i>Coccidoxenoides perminutus</i> (En.)	Davies, et al. 2004	1	2.03 (0.023)	10
<i>Agapanthus praecox</i> (Liliaceae)	<i>Coccidoxenoides perminutus</i> (En.)	Davies, et al. 2004	1	1.79 (0.026)	10
<i>Alpinia zerumbet</i> (Zingiberaceae)	<i>Coccidoxenoides perminutus</i> (En.)	Davies, et al. 2004	1	2.28 (0.025)	10
<i>Brugmansia x candida</i> (Solanaceae)	<i>Coccidoxenoides perminutus</i> (En.)	Davies, et al. 2004	1	1.78 (0.022)	10
<i>Grevillea bipinnatifida</i> (Proteaceae)	<i>Coccidoxenoides perminutus</i> (En.)	Davies, et al. 2004	1	1.32 (0.023)	10
<i>Russelia equisetiformis</i> (Scrophulariaceae)	<i>Coccidoxenoides perminutus</i> (En.)	Davies, et al. 2004	1	1.64 (0.029)	10
<i>Capsella bursa-pastoris</i> (Brassicaceae)	<i>Meteorus rub</i> (Br.)	Foster and Ruesink 1984	2	0.89 (0.064)	7
<i>Pastinaca sativa</i> (Apiaceae)	<i>Meteorus rub</i> (Br.)	Foster and Ruesink 1984	2	0.66 (0.069)	7
<i>Polygonum persicaria</i> (Polygonaceae)	<i>Meteorus rub</i> (Br.)	Foster and Ruesink 1984	2	0.91 (0.064)	7
<i>Sinapis arvensis</i> (Brassicaceae)	<i>Meteorus rub</i> (Br.)	Foster and Ruesink 1984	2	0.6 (0.071)	7
<i>Stellaria media</i> (Caryophyllaceae)	<i>Meteorus rub</i> (Br.)	Foster and Ruesink 1984	2	0.78 (0.066)	7
<i>Calluna vulgaris</i> (Ericaceae)	<i>Coeloides bostrychorum</i> (Br.)	Hougary and Gregoire 2000	1	-0.31 (0.02)	20
<i>Chamerion angustifolium</i> (Onagraceae)	<i>Coeloides bostrychorum</i> (Br.)	Hougary and Gregoire 2000	1	1.2 (0.059)	14
<i>Digitalis purpurea</i> (Scrophulariaceae)	<i>Coeloides bostrychorum</i> (Br.)	Hougary and Gregoire 2000	1	0.03 (0.021)	34
<i>Scrophularia nodosa</i> (Scrophulariaceae)	<i>Coeloides bostrychorum</i> (Br.)	Hougary and Gregoire 2000	1	0.99 (0.041)	30
<i>Senecio vulgaris</i> (Asteraceae)	<i>Coeloides bostrychorum</i> (Br.)	Hougary and Gregoire 2000	1	-0.19 (0.028)	33
<i>Vaccinium myrtillus</i> (Ericaceae)	<i>Coeloides bostrychorum</i> (Br.)	Hougary and Gregoire 2000	1	0.13 (0.072)	54
<i>Chamerion angustifolium</i> (Onagraceae)	<i>Coeloides bostrychorum</i> (Br.)	Hougary and Gregoire 2000	2	1.3 (0.107)	20

Table 2.1 (ctd.). The log response ratio for longevity and its standard error for each study. Br. =Braconidae, Ic. = Ichneumonidae

Plant species (family)	Parasitoid (family)	reference	#	ln(RR) (SE)	N
<i>Digitalis purpurea</i> (Scrophulariaceae)	<i>Coeloides bostrychorum</i> (Br.)	Hougardy and Gregoire 2000	2	0.83 (0.086)	36
<i>Achillea millefolium</i> (Asteraceae)	<i>Orgilus obscurator</i> (Br.)	Ide and Lanfranco 2001	1	0.76 (0.017)	20
<i>Conium maculatum</i> (Apiaceae)	<i>Orgilus obscurator</i> (Br.)	Ide and Lanfranco 2001	1	0.47 (0.02)	20
<i>Daucus carota</i> (Apiaceae)	<i>Orgilus obscurator</i> (Br.)	Ide and Lanfranco 2001	1	0.29 (0.022)	20
<i>Foeniculum vulgare</i> (Apiaceae)	<i>Orgilus obscurator</i> (Br.)	Ide and Lanfranco 2001	1	-0.41 (0.046)	20
<i>Achillea millefolium</i> (Asteraceae)	<i>Orgilus obscurator</i> (Br.)	Ide and Lanfranco 2001	2	1.14 (0.313)	1
<i>Conium maculatum</i> (Apiaceae)	<i>Orgilus obscurator</i> (Br.)	Ide and Lanfranco 2001	2	0.96 (0.327)	1
<i>Daucus carota</i> (Apiaceae)	<i>Orgilus obscurator</i> (Br.)	Ide and Lanfranco 2001	2	0.85 (0.337)	1
<i>Foeniculum vulgare</i> (Apiaceae)	<i>Orgilus obscurator</i> (Br.)	Ide and Lanfranco 2001	2	0.51 (0.387)	1
<i>Iberis amara</i> (Brassicaceae)	<i>Orgilus obscurator</i> (Br.)	Ide and Lanfranco 2001	2	0 (0.569)	1
<i>Lotus pedunculatus</i> (Fabaceae)	<i>Orgilus obscurator</i> (Br.)	Ide and Lanfranco 2001	2	0 (0.569)	1
<i>Prunella vulgaris</i> (Lamiaceae)	<i>Orgilus obscurator</i> (Br.)	Ide and Lanfranco 2001	2	0 (0.569)	1
<i>Achillea millefolium</i> (Asteraceae)	<i>Orgilus obscurator</i> (Br.)	Ide and Lanfranco 2001	3	0.17 (0.016)	20
<i>Conium maculatum</i> (Apiaceae)	<i>Orgilus obscurator</i> (Br.)	Ide and Lanfranco 2001	3	0.98 (0.016)	20
<i>Daucus carota</i> (Apiaceae)	<i>Orgilus obscurator</i> (Br.)	Ide and Lanfranco 2001	3	-0.67 (0.226)	20
<i>Foeniculum vulgare</i> (Apiaceae)	<i>Orgilus obscurator</i> (Br.)	Ide and Lanfranco 2001	3	0.78 (0.016)	20
<i>Achillea millefolium</i> (Asteraceae)	<i>Orgilus obscurator</i> (Br.)	Ide and Lanfranco 2001	4	0.24 (0.006)	20
<i>Conium maculatum</i> (Apiaceae)	<i>Orgilus obscurator</i> (Br.)	Ide and Lanfranco 2001	4	0.46 (0.013)	20
<i>Daucus carota</i> (Apiaceae)	<i>Orgilus obscurator</i> (Br.)	Ide and Lanfranco 2001	4	0.82 (0.01)	20
<i>Foeniculum vulgare</i> (Apiaceae)	<i>Orgilus obscurator</i> (Br.)	Ide and Lanfranco 2001	4	0.33 (0.012)	20
<i>Achillea millefolium</i> (Asteraceae)	<i>Orgilus obscurator</i> (Br.)	Ide and Lanfranco 2001	5	0.31 (0.009)	20
<i>Daucus carota</i> (Apiaceae)	<i>Orgilus obscurator</i> (Br.)	Ide and Lanfranco 2001	5	-0.1 (0.012)	20
<i>Barbarea vulgaris</i> (Brassicaceae)	<i>Diadegma insulare</i> (Ic.)	Idris and Grafius 1995	1	1.89 (0.027)	8
<i>Barbarea vulgaris</i> (Brassicaceae)	<i>Diadegma insulare</i> (Ic.)	Idris and Grafius 1995	1	2.07 (0.021)	8
<i>Capsella bursa-pastoris</i> (Brassicaceae)	<i>Diadegma insulare</i> (Ic.)	Idris and Grafius 1995	1	1 (0.009)	8
<i>Erysimum cheiranthoides</i> (Brassicaceae)	<i>Diadegma insulare</i> (Ic.)	Idris and Grafius 1995	1	0.13 (0.015)	8
<i>Erysimum cheiranthoides</i> (Brassicaceae)	<i>Diadegma insulare</i> (Ic.)	Idris and Grafius 1995	1	-0.1 (0.018)	8
<i>Lepidium campestre</i> (Brassicaceae)	<i>Diadegma insulare</i> (Ic.)	Idris and Grafius 1995	1	0.31 (0.013)	8

Table 2.1 (ctd.). The estimates of log response ratio for longevity and its standard error for each study. Ic. = Ichneumonidae

Plant species (family)	Parasitoid (family)	reference	#	ln(RR) (SE)	N
<i>Thlaspi arvense</i> (Brassicaceae)	<i>Diadegma insulare</i> (Ic.)	Idris and Grafius 1995	1	0.31 (0.063)	8
<i>Thlaspi arvense</i> (Brassicaceae)	<i>Diadegma insulare</i> (Ic.)	Idris and Grafius 1995	1	0.67 (0.01)	8
<i>Barbarea vulgaris</i> (Brassicaceae)	<i>Diadegma insulare</i> (Ic.)	Idris and Grafius 1995	2	1.77 (0.029)	8
<i>Berteroa incana</i> (Brassicaceae)	<i>Diadegma insulare</i> (Ic.)	Idris and Grafius 1995	2	0.94 (0.011)	4
<i>Brassica napus</i> (Brassicaceae)	<i>Diadegma insulare</i> (Ic.)	Idris and Grafius 1995	2	1.44 (0.008)	8
<i>Capsella bursa-pastoris</i> (Brassicaceae)	<i>Diadegma insulare</i> (Ic.)	Idris and Grafius 1995	2	1.25 (0.032)	8
<i>Daucus carota</i> (Apiaceae)	<i>Diadegma insulare</i> (Ic.)	Idris and Grafius 1995	2	1.91 (0.013)	4
<i>Erysimum cheiranthoides</i> (Brassicaceae)	<i>Diadegma insulare</i> (Ic.)	Idris and Grafius 1995	2	-0.05 (0.014)	8
<i>Lepidium campestre</i> (Brassicaceae)	<i>Diadegma insulare</i> (Ic.)	Idris and Grafius 1995	2	0.14 (0.05)	8
<i>Leucanthemum vulgare</i> (Asteraceae)	<i>Diadegma insulare</i> (Ic.)	Idris and Grafius 1995	2	-0.69 (0.043)	8
<i>Rumex crispus</i> (Polygonaceae)	<i>Diadegma insulare</i> (Ic.)	Idris and Grafius 1995	2	0.26 (0.056)	8
<i>Sinapis arvensis</i> (Brassicaceae)	<i>Diadegma insulare</i> (Ic.)	Idris and Grafius 1995	2	1.96 (0.007)	4
<i>Thlaspi arvense</i> (Brassicaceae)	<i>Diadegma insulare</i> (Ic.)	Idris and Grafius 1995	2	0.41 (0.114)	8
<i>Berteroa incana</i> (Brassicaceae)	<i>Diadegma insulare</i> (Ic.)	Idris and Grafius 1995	3	1.21 (0.165)	8
<i>Chenopodium album</i> (Chenopodiaceae)	<i>Diadegma insulare</i> (Ic.)	Idris and Grafius 1995	3	-0.65 (0.184)	8
<i>Daucus carota</i> (Apiaceae)	<i>Diadegma insulare</i> (Ic.)	Idris and Grafius 1995	3	1.72 (0.167)	8
<i>Daucus carota</i> (Apiaceae)	<i>Diadegma insulare</i> (Ic.)	Idris and Grafius 1995	3	1.81 (0.167)	8
<i>Sinapis arvensis</i> (Brassicaceae)	<i>Diadegma insulare</i> (Ic.)	Idris and Grafius 1995	3	1.81 (0.177)	8
<i>Sonchus arvensis</i> (Asteraceae)	<i>Diadegma insulare</i> (Ic.)	Idris and Grafius 1995	3	-0.22 (0.223)	8
<i>Berteroa incana</i> (Brassicaceae)	<i>Diadegma insulare</i> (Ic.)	Idris and Grafius 1995	4	1.48 (1.229)	8
<i>Daucus carota</i> (Apiaceae)	<i>Diadegma insulare</i> (Ic.)	Idris and Grafius 1995	4	1.85 (1.235)	8
<i>Daucus carota</i> (Apiaceae)	<i>Diadegma insulare</i> (Ic.)	Idris and Grafius 1995	4	1.79 (1.213)	8
<i>Daucus carota</i> (Apiaceae)	<i>Diadegma insulare</i> (Ic.)	Idris and Grafius 1995	4	2.01 (1.218)	8
<i>Sinapis arvensis</i> (Brassicaceae)	<i>Diadegma insulare</i> (Ic.)	Idris and Grafius 1995	4	2.19 (1.223)	8
<i>Berteroa incana</i> (Brassicaceae)	<i>Diadegma insulare</i> (Ic.)	Idris and Grafius 1995	5	1.23 (0.278)	4
<i>Chenopodium album</i> (Chenopodiaceae)	<i>Diadegma insulare</i> (Ic.)	Idris and Grafius 1995	5	-0.29 (0.254)	8
<i>Daucus carota</i> (Apiaceae)	<i>Diadegma insulare</i> (Ic.)	Idris and Grafius 1995	5	1.68 (0.261)	4
Honeydew <i>A.fabae</i> <i>C.album</i> (honeydew)	<i>Diadegma insulare</i> (Ic.)	Idris and Grafius 1995	5	1.68 (0.318)	8

Table 2.1 (ctd.).The log response ratio for longevity and its standard error for each study. Ic. = Ichneumonidae, My. = Mymaridae

Plant species (family)	Parasitoid (family)	reference	#	ln(RR) (SE)	N
Honeydew <i>A.fabae</i> <i>Sonchus</i> (honeydew)	<i>Diadegma insulare</i> (Ic.)	Idris and Grafius 1995	5	1.53 (0.343)	8
<i>Sinapis arvensis</i> (Brassicaceae)	<i>Diadegma insulare</i> (Ic.)	Idris and Grafius 1995	5	2.2 (0.255)	4
<i>Sonchus arvensis</i> (Asteraceae)	<i>Diadegma insulare</i> (Ic.)	Idris and Grafius 1995	5	0.34 (0.282)	8
<i>Anethum graveolens</i> (Apiaceae)	<i>Gonatocerus ashineadi</i> (My.)	Irvin, et al. 2007	1	1.37 (0.044)	15
Eliminate food (Eliminate)	<i>Gonatocerus ashineadi</i> (My.)	Irvin, et al. 2007	1	1.33 (0.068)	15
excreta Citrus Planthopper (excreta)	<i>Gonatocerus ashineadi</i> (My.)	Irvin, et al. 2007	1	0.14 (0.031)	15
<i>Fagopyrum esculentum</i> (Polygonaceae)	<i>Gonatocerus ashineadi</i> (My.)	Irvin, et al. 2007	1	1.67 (0.028)	15
Honeydew Citrus Scale (honeydew)	<i>Gonatocerus ashineadi</i> (My.)	Irvin, et al. 2007	1	1.9 (0.036)	15
<i>Lobularia maritima</i> (Brassicaceae)	<i>Gonatocerus ashineadi</i> (My.)	Irvin, et al. 2007	1	1.22 (0.039)	15
<i>Phacelia tanacetifolia</i> (Hydrophyllaceae)	<i>Gonatocerus ashineadi</i> (My.)	Irvin, et al. 2007	1	-0.17 (0.022)	15
<i>Vicia faba</i> (Fabaceae)	<i>Gonatocerus ashineadi</i> (My.)	Irvin, et al. 2007	1	0.55 (0.021)	15
<i>Anethum graveolens</i> (Apiaceae)	<i>Gonatocerus fasciatus</i> (My.)	Irvin, et al. 2007	2	1.06 (0.058)	15
Eliminate food (Eliminate)	<i>Gonatocerus fasciatus</i> (My.)	Irvin, et al. 2007	2	0.91 (0.032)	15
excreta Citrus Planthopper (excreta)	<i>Gonatocerus fasciatus</i> (My.)	Irvin, et al. 2007	2	-0.17 (0.041)	15
<i>Fagopyrum esculentum</i> (Polygonaceae)	<i>Gonatocerus fasciatus</i> (My.)	Irvin, et al. 2007	2	1.71 (0.091)	15
Honeydew Citrus Scale (honeydew)	<i>Gonatocerus fasciatus</i> (My.)	Irvin, et al. 2007	2	1.86 (0.089)	15
<i>Lobularia maritima</i> (Brassicaceae)	<i>Gonatocerus fasciatus</i> (My.)	Irvin, et al. 2007	2	1.1 (0.069)	15
<i>Phacelia tanacetifolia</i> (Hydrophyllaceae)	<i>Gonatocerus fasciatus</i> (My.)	Irvin, et al. 2007	2	0.23 (0.053)	15
<i>Vicia faba</i> (Fabaceae)	<i>Gonatocerus fasciatus</i> (My.)	Irvin, et al. 2007	2	1.45 (0.051)	15
<i>Anethum graveolens</i> (Apiaceae)	<i>Gonatocerus triguttatus</i> (My.)	Irvin, et al. 2007	3	1.67 (0.021)	15
Eliminate food (Eliminate)	<i>Gonatocerus triguttatus</i> (My.)	Irvin, et al. 2007	3	1.17 (0.042)	15
excreta Citrus Planthopper (excreta)	<i>Gonatocerus triguttatus</i> (My.)	Irvin, et al. 2007	3	0.15 (0.033)	15
<i>Fagopyrum esculentum</i> (Polygonaceae)	<i>Gonatocerus triguttatus</i> (My.)	Irvin, et al. 2007	3	2.01 (0.042)	15
Honeydew Citrus Scale (honeydew)	<i>Gonatocerus triguttatus</i> (My.)	Irvin, et al. 2007	3	1.6 (0.023)	15
<i>Lobularia maritima</i> (Brassicaceae)	<i>Gonatocerus triguttatus</i> (My.)	Irvin, et al. 2007	3	1.45 (0.073)	15
<i>Phacelia tanacetifolia</i> (Hydrophyllaceae)	<i>Gonatocerus triguttatus</i> (My.)	Irvin, et al. 2007	3	0.2 (0.031)	15
<i>Vicia faba</i> (Fabaceae)	<i>Gonatocerus triguttatus</i> (My.)	Irvin, et al. 2007	3	0.98 (0.065)	15
<i>Medicago sativa</i> (Fabaceae)	<i>Bathyplectes curculionis</i> (Ic.)	Jacob and Evans 2000	1	0 (0.001)	60

Table 2.1 (ctd.). The log response ratios for longevity studies. Br.=Braconidae , Eu. = Eulophidae , Ic. = Ichneumonidae

Plant species (family)	Parasitoid (family)	reference	#	ln(RR) (SE)	N
<i>Phacelia tanacetifolia</i> (Hydrophyllaceae)	<i>Bathyplectes curculionis</i> (Ic.)	Jacob and Evans 2000	1	-0.03 (0.001)	60
<i>Taraxacum officinale</i> (Asteraceae)	<i>Bathyplectes curculionis</i> (Ic.)	Jacob and Evans 2000	1	0.15 (0.003)	60
<i>Agastache foeniculum</i> (Lamiaceae)	<i>Microplitis croceipes</i> (Br.)	Nafziger and Fadamiro 2011	1	1.02 (0.015)	5
<i>Fagopyrum esculentum</i> (Polygonaceae)	<i>Microplitis croceipes</i> (Br.)	Nafziger and Fadamiro 2011	1	1.01 (0.022)	5
<i>Lobularia maritima</i> (Brassicaceae)	<i>Microplitis croceipes</i> (Br.)	Nafziger and Fadamiro 2011	1	0.15 (0.008)	5
<i>Asclepias syriaca</i> (Asclepiadaceae)	<i>Macrocentrus grandii</i> (Br.)	Orr and Pleasants 1996	1	1.32 (0.013)	12
<i>Cicuta maculata</i> (Apiaceae)	<i>Macrocentrus grandii</i> (Br.)	Orr and Pleasants 1996	1	0.39 (0.032)	4
<i>Echinacea pallida</i> (Asteraceae)	<i>Macrocentrus grandii</i> (Br.)	Orr and Pleasants 1996	1	0.57 (0.011)	17
<i>Erigeron strigosus</i> (Asteraceae)	<i>Macrocentrus grandii</i> (Br.)	Orr and Pleasants 1996	1	0.02 (0.02)	9
<i>Liatris pycnostachya</i> (Asteraceae)	<i>Macrocentrus grandii</i> (Br.)	Orr and Pleasants 1996	1	-0.09 (0.02)	9
<i>Monarda fistulosa</i> (Lamiaceae)	<i>Macrocentrus grandii</i> (Br.)	Orr and Pleasants 1996	1	0.11 (0.021)	9
<i>Pycnanthemum virginianum</i> (Lamiaceae)	<i>Macrocentrus grandii</i> (Br.)	Orr and Pleasants 1996	1	0.25 (0.021)	9
<i>Rosa carolina</i> (Rosaceae)	<i>Macrocentrus grandii</i> (Br.)	Orr and Pleasants 1996	1	0.84 (0.009)	24
<i>Rudbeckia hirta</i> (Asteraceae)	<i>Macrocentrus grandii</i> (Br.)	Orr and Pleasants 1996	1	0.75 (0.01)	21
<i>Solidago canadensis</i> (Asteraceae)	<i>Macrocentrus grandii</i> (Br.)	Orr and Pleasants 1996	1	0.24 (0.019)	10
<i>Vernonia fasciculata</i> (Scrophulariaceae)	<i>Macrocentrus grandii</i> (Br.)	Orr and Pleasants 1996	1	0.6 (0.022)	8
<i>Amaranthus retroflexus</i> (Amaranthaceae)	<i>Peristenus pseudopallipes</i> (Br.)	Shahjahan 1974	1	0.07 (0.283)	12
<i>Conyza canadensis</i> (Asteraceae)	<i>Peristenus pseudopallipes</i> (Br.)	Shahjahan 1974	1	1.35 (0.162)	12
<i>Daucus carota</i> (Apiaceae)	<i>Peristenus pseudopallipes</i> (Br.)	Shahjahan 1974	1	0.99 (0.173)	12
<i>Erigeron strigosus</i> (Asteraceae)	<i>Peristenus pseudopallipes</i> (Br.)	Shahjahan 1974	1	1.39 (0.161)	12
<i>Alyssum alyssoides</i> (Brassicaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	2	1.52 (0.027)	8
<i>Arctium minus</i> (Asteraceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	2	1.07 (0.027)	6
<i>Cirsium vulgare</i> (Asteraceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	2	1.02 (0.021)	3
<i>Daucus carota</i> (Apiaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	2	1.15 (0.032)	9
<i>Fagopyrum esculentum</i> (Polygonaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	2	1.17 (0.06)	6
<i>Leonurus cardiaca</i> (Lamiaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	2	1.23 (0.046)	8
<i>Malus sylvestris</i> (Rosaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	2	1.66 (0.045)	2
<i>Medicago lupulina</i> (Fabaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	2	1.47 (0.03)	6

Table 2.1 (ctd.). The log response ratio for longevity and its standard error for each study. Ic. = Ichneumonidae , Eu. = Eulophidae

Plant species (family)	Parasitoid (family)	reference	#	ln(RR) (SE)	N
<i>Medicago sativa</i> (Fabaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	2	1.08 (0.046)	6
<i>Melilotus officinalis</i> (Fabaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	2	0.92 (0.023)	5
<i>Physalis heterophylla</i> (Solanaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	2	1.1 (0.064)	7
<i>Rumex acetosella</i> (Polygonaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	2	1.33 (0.042)	6
<i>Solanum dulcamara</i> (Solanaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	2	1.29 (0.027)	6
<i>Stellaria media</i> (Caryophyllaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	2	1.28 (0.051)	8
<i>Trifolium repens</i> (Fabaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	2	1.18 (0.026)	6
<i>Vicia sativa</i> (Fabaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	2	1.18 (0.044)	6
<i>Asclepias syriaca</i> (Asclepiadaceae)	<i>Exeristes comstockii</i> (Ic.)	Syme 1975	15	1.26 (0.711)	11
<i>Cynoglossum officinale</i> (Boraginaceae)	<i>Exeristes comstockii</i> (Ic.)	Syme 1975	15	1.96 (0.147)	2
<i>Daucus carota</i> (Apiaceae)	<i>Exeristes comstockii</i> (Ic.)	Syme 1975	15	0.91 (1.567)	13
<i>Echium vulgare</i> (Boraginaceae)	<i>Exeristes comstockii</i> (Ic.)	Syme 1975	15	0.32 (0.272)	14
<i>Hypericum perforatum</i> (Hypericaceae)	<i>Exeristes comstockii</i> (Ic.)	Syme 1975	15	0.95 (2.098)	7
<i>Medicago sativa</i> (Fabaceae)	<i>Exeristes comstockii</i> (Ic.)	Syme 1975	15	0.1 (0.528)	12
<i>Melilotus officinalis</i> (Fabaceae)	<i>Exeristes comstockii</i> (Ic.)	Syme 1975	15	0.39 (0.258)	9
<i>Silene vulgaris</i> (Caryophyllaceae)	<i>Exeristes comstockii</i> (Ic.)	Syme 1975	15	0.26 (0.152)	5
<i>Verbascum thapsus</i> (Scrophulariaceae)	<i>Exeristes comstockii</i> (Ic.)	Syme 1975	15	0.24 (0.887)	7
<i>Achillea millefolium</i> (Asteraceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	0.17 (0.178)	3
<i>Antennaria neglecta</i> (Asteraceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	0.54 (0.042)	1
<i>Asclepias syriaca</i> (Asclepiadaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	1.08 (0.057)	9
<i>Chamerion angustifolium</i> (Onagraceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	0.41 (0.042)	7
<i>Cichorium intybus</i> (Asteraceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	0.83 (0.037)	1
<i>Cirsium arvense</i> (Asteraceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	-0.34 (0.093)	1
<i>Cirsium vulgare</i> (Asteraceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	-0.15 (0.074)	1
<i>Clinopodium vulgare</i> (Lamiaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	0.25 (0.05)	1
<i>Convolvulus arvensis</i> (Convolvulaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	0.93 (0.083)	11
<i>Cynoglossum officinale</i> (Boraginaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	1.27 (0.056)	4
<i>Daucus carota</i> (Apiaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	-0.61 (0.112)	6

Table 2.1 (ctd.). The estimates of log response ratio for longevity and its standard error for each study. Eu. = Eulophidae

Plant species (family)	Parasitoid (family)	reference	#	ln(RR) (SE)	N
<i>Echium vulgare</i> (Boraginaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	0.63 (0.057)	7
<i>Erigeron annuus</i> (Asteraceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	0.25 (0.05)	1
<i>Erigeron philadelphicus</i> (Asteraceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	-0.85 (0.142)	2
<i>Fragaria vesca</i> (Rosaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	0.19 (0.312)	2
<i>Geranium robertianum</i> (Geraniaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	-0.24 (0.064)	2
<i>Hesperis matronalis</i> (Brassicaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	0.21 (0.079)	7
<i>Hieracium aurantiacum</i> (Asteraceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	-0.07 (0.055)	5
<i>Hieracium L.</i> (Asteraceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	-0.11 (0.087)	4
<i>Hypericum perforatum</i> (Hypericaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	-0.09 (0.057)	5
<i>Leonurus cardiaca</i> (Lamiaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	0.39 (0.093)	8
<i>Lepidium campestre</i> (Brassicaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	-0.44 (0.34)	2
<i>Leucanthemum vulgare</i> (Asteraceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	0.45 (0.106)	2
<i>Malus sylvestris</i> (Rosaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	1.57 (0.058)	2
<i>Medicago lupulina</i> (Fabaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	0.04 (0.139)	4
<i>Medicago sativa</i> (Fabaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	0.36 (0.047)	1
<i>Medicago sativa</i> (Fabaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	0.06 (0.082)	5
<i>Melilotus officinalis</i> (Fabaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	1 (0.036)	1
<i>Melilotus officinalis</i> (Fabaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	0.06 (0.159)	5
<i>Nepeta cataria</i> (Lamiaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	0.36 (0.047)	1
<i>Oenothera biennis</i> (Onagraceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	-0.85 (0.202)	1
<i>Oxalis stricta</i> (Oxalidaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	0 (0.159)	2
<i>Physalis heterophylla</i> (Solanaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	-0.28 (0.236)	3
<i>Potentilla intermedia</i> (Rosaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	0.76 (0.038)	1
<i>Potentilla recta</i> (Rosaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	0.19 (0.035)	2
<i>Rumex acetosella</i> (Polygonaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	0 (0.052)	2
<i>Salix nigra</i> (Salicaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	-0.56 (0.094)	2
<i>Sambucus racemosa</i> (Caprifoliaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	0.04 (0.121)	3
<i>Saponaria officinalis</i> (Caryophyllaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	1.01 (0.088)	6

Table 2.1 (ctd.). The estimates of log response ratio for longevity and its standard error for each study. Eu. = Eulophidae

Plant species (family)	Parasitoid (family)	reference	#	ln(RR) (SE)	N
<i>Silene latifolia</i> (Caryophyllaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	0 (0.063)	1
<i>Silene noctiflora</i> (Caryophyllaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	0 (0.12)	3
<i>Silene vulgaris</i> (Caryophyllaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	1.1 (0.089)	4
<i>Sinapis arvensis</i> (Brassicaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	0.54 (0.042)	1
<i>Sisymbrium altissimum</i> (Brassicaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	0.25 (0.05)	1
<i>Solanum dulcamara</i> (Solanaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	-0.15 (0.059)	2
<i>Taraxacum officinale</i> (Asteraceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	0.58 (0.033)	2
<i>Tragopogon lamottei</i> (Asteraceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	-1.25 (0.281)	2
<i>Trifolium pratense</i> (Fabaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	0.66 (0.059)	4
<i>Trifolium repens</i> (Fabaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	-0.04 (0.175)	6
<i>Verbascum thapsus</i> (Scrophulariaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	0 (0.063)	1
<i>Veronica officinalis</i> (Scrophulariaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	-0.15 (0.074)	1
<i>Vicia L.</i> (Fabaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	16	0.04 (0.13)	4
<i>Chamerion angustifolium</i> (Onagraceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	17	1.19 (0.045)	4
<i>Echium vulgare</i> (Boraginaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	17	0.7 (0.087)	7
<i>Fagopyrum esculentum</i> (Polygonaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	17	1.61 (0.028)	5
<i>Leucanthemum vulgare</i> (Asteraceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	17	1.18 (0.034)	9
<i>Achillea millefolium</i> (Asteraceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	18	0.63 (0.057)	7
<i>Centaurea solstitialis</i> (Asteraceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	18	0.99 (0.036)	7
<i>Hypericum perforatum</i> (Hypericaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	18	0.9 (0.096)	6
<i>Leonurus cardiaca</i> (Lamiaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	18	0.74 (0.084)	7
<i>Medicago sativa</i> (Fabaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	18	0.47 (0.068)	6
<i>Melilotus officinalis</i> (Fabaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	18	1.44 (0.116)	4
<i>Nepeta cataria</i> (Lamiaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	18	1.02 (0.099)	6
<i>Oenothera biennis</i> (Onagraceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	18	0.52 (0.148)	5
<i>Chamerion angustifolium</i> (Onagraceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	19	1.01 (0.038)	9
<i>Fragaria vesca</i> (Rosaceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	19	0.88 (0.043)	12
<i>Taraxacum officinale</i> (Asteraceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	19	1.01 (0.038)	9

Table 2.1 (ctd.). The log response ratios for longevity studies. Eu. = Eulophidae, Br. = Braconidae, My. = Mymaridae

Plant species (family)	Parasitoid (family)	reference	#	ln(RR) (SE)	N
<i>Tragopogon L.</i> (Asteraceae)	<i>Hyssopus thymus</i> (Eu.)	Syme 1975	19	1.02 (0.022)	13
<i>Coriandrum sativum</i> (Apiaceae)	<i>Microctonus hyperodae</i> (Br.)	Vattala, et al. 2006	1	0.46 (0.004)	6
<i>Fagopyrum esculentum</i> (Polygonaceae)	<i>Microctonus hyperodae</i> (Br.)	Vattala, et al. 2006	1	0.94 (0.018)	6
<i>Lobularia maritima</i> (Brassicaceae)	<i>Microctonus hyperodae</i> (Br.)	Vattala, et al. 2006	1	-0.05 (0.012)	6
<i>Phacelia tanacetifolia</i> (Hydrophyllaceae)	<i>Microctonus hyperodae</i> (Br.)	Vattala, et al. 2006	1	-0.39 (0.018)	6
<i>Sinapis alba</i> (Brassicaceae)	<i>Microctonus hyperodae</i> (Br.)	Vattala, et al. 2006	1	0.16 (0.004)	6
<i>Trifolium pratense</i> (Fabaceae)	<i>Microctonus hyperodae</i> (Br.)	Vattala, et al. 2006	1	-0.09 (0.004)	6
<i>Trifolium repens</i> (Fabaceae)	<i>Microctonus hyperodae</i> (Br.)	Vattala, et al. 2006	1	-0.13 (0.005)	6
<i>Ammi majus</i> (Apiaceae)	<i>Aphidius ervi</i> (Br.)	Wade and Wratten 2007	1	-0.47 (0.003)	18
<i>Anethum graveolens</i> (Apiaceae)	<i>Aphidius ervi</i> (Br.)	Wade and Wratten 2007	1	0.58 (0.006)	18
<i>Coriandrum sativum</i> (Apiaceae)	<i>Aphidius ervi</i> (Br.)	Wade and Wratten 2007	1	0.35 (0.007)	18
<i>Fagopyrum esculentum</i> (Polygonaceae)	<i>Aphidius ervi</i> (Br.)	Wade and Wratten 2007	1	0.63 (0.005)	18
<i>Linum usitatissimum</i> (Linaceae)	<i>Aphidius ervi</i> (Br.)	Wade and Wratten 2007	1	0.03 (0.007)	18
<i>Lobularia maritima</i> (Brassicaceae)	<i>Aphidius ervi</i> (Br.)	Wade and Wratten 2007	1	0.35 (0.005)	18
<i>Phacelia tanacetifolia</i> (Hydrophyllaceae)	<i>Aphidius ervi</i> (Br.)	Wade and Wratten 2007	1	-0.27 (0.012)	18
<i>Raphanus sativus</i> (Brassicaceae)	<i>Aphidius ervi</i> (Br.)	Wade and Wratten 2007	1	0.36 (0.005)	18
<i>Tropaeolum majus</i> (Tropaeolaceae)	<i>Aphidius ervi</i> (Br.)	Wade and Wratten 2007	1	0.12 (0.013)	18
<i>Agastache nepetoides</i> (Lamiaceae)	<i>Aphidius colemani</i> (Br.)	Walton and Isaacs 2011	1	0.09 (0.036)	6
<i>Daucus carota</i> (Apiaceae)	<i>Aphidius colemani</i> (Br.)	Walton and Isaacs 2011	1	0.72 (0.016)	6
<i>Lobelia siphilitica</i> (Campanulaceae)	<i>Aphidius colemani</i> (Br.)	Walton and Isaacs 2011	1	0.52 (0.027)	6
<i>Monarda fistulosa</i> (Lamiaceae)	<i>Aphidius colemani</i> (Br.)	Walton and Isaacs 2011	1	1.99 (0.457)	6
<i>Penstemon hirsutus</i> (Scrophulariaceae)	<i>Aphidius colemani</i> (Br.)	Walton and Isaacs 2011	1	0 (0.069)	6
<i>Silphium terebinthinaceum</i> (Asteraceae)	<i>Aphidius colemani</i> (Br.)	Walton and Isaacs 2011	1	0.51 (0.41)	6
<i>Solidago juncea</i> (Asteraceae)	<i>Aphidius colemani</i> (Br.)	Walton and Isaacs 2011	1	1.58 (0.269)	6
<i>Trifolium pratense</i> (Fabaceae)	<i>Aphidius colemani</i> (Br.)	Walton and Isaacs 2011	1	0.17 (0.032)	6
<i>Veronicastrum virginicum</i> (Scrophulariaceae)	<i>Aphidius colemani</i> (Br.)	Walton and Isaacs 2011	1	1.61 (0.472)	6
<i>Oenothera speciosa</i> (Onagraceae)	<i>Anaphes iole</i> (My.)	Williams and Hendrix 2008	1	0.23 (0.498)	10
<i>Erigeron annuus</i> (Asteraceae)	<i>Anaphes iole</i> (My.)	Williams and Hendrix 2008	2	0.42 (1.302)	10

Table 2.2. The estimates of log response ratio and its standard error for each study included in the meta analysis on parasitoid attraction when provided with one species of flower. 1 was added to both the treatment and control values to prevent undefined response ratios. Parasitoid family names are abbreviated (Ap. = Aphidiidae, Br. = Braconidae, Ch. = Chalcidae, Ca. = Chalcidoidea, Cy. = Cynipoidea, Eu. = Eulophidae, Ic. = Ichneumonidae, Sc. = Scelionidae, Sp. = Sphecidae, Ta. = Tachinidae, Tr. = Trichogrammatidae, un. = unspecified). For articles reporting results from multiple studies, the studies are differentiated by the study number (#). N is the sample size for the control treatment.

Plant species (family)	Parasitoid (family)	reference	#	ln(RR) (SE)	N
<i>Conoclinium coelestinum</i> (Asteraceae)	<i>Larra bicolor</i> (Sp.)	Arévalo and Frank 2005	1	0.11 (0.003)	12
<i>Elephantopus elatus</i> (Asteraceae)	<i>Larra bicolor</i> (Sp.)	Arévalo and Frank 2005	1	0 (0.001)	12
<i>Passiflora coccinea</i> (Passifloraceae)	<i>Larra bicolor</i> (Sp.)	Arévalo and Frank 2005	1	0.05 (0.002)	12
<i>Solidago fistulosa</i> (Asteraceae)	<i>Larra bicolor</i> (Sp.)	Arévalo and Frank 2005	1	0.05 (0.002)	12
<i>Spermacoce verticillata</i> (Rubiaceae)	<i>Larra bicolor</i> (Sp.)	Arévalo and Frank 2005	1	0.42 (0.015)	12
<i>Carum carvi</i> (Apiaceae)	several species (Ic.)	Coruh and Coruh 2008	3	2.4 (16.641)	1
<i>Daucus carota</i> (Apiaceae)	several species (Ic.)	Coruh and Coruh 2008	3	0 (33.012)	1
<i>Ferula communis</i> (Apiaceae)	several species (Ic.)	Coruh and Coruh 2008	3	0.83 (19.626)	1
<i>Pimpinella tragiium</i> (Apiaceae)	several species (Ic.)	Coruh and Coruh 2008	3	0.81 (19.766)	1
<i>Seseli libanotis</i> (Apiaceae)	several species (Ic.)	Coruh and Coruh 2008	3	1.7 (17.051)	1
<i>Asclepias syriaca</i> (Asclepiadaceae)	parasitoid wasp (un.)	Frank et al. 2008	1	0.61 (0.057)	4
<i>Asclepias tuberosa</i> (Asclepidaceae)	parasitoid wasp (un.)	Frank et al. 2008	1	0.25 (0.045)	4
<i>Coreopsis verticillata</i> (Asteraceae)	parasitoid wasp (un.)	Frank et al. 2008	1	0.79 (0.018)	4
<i>Eupatorium hyssopifolium</i> (Asteraceae)	parasitoid wasp (un.)	Frank et al. 2008	1	1.66 (0.131)	4
<i>Monarda punctata</i> (Lamiaceae)	parasitoid wasp (un.)	Frank et al. 2008	1	1.44 (0.012)	4
<i>Panicum virgatum</i> (Poaceae)	parasitoid wasp (un.)	Frank et al. 2008	1	0.59 (0.022)	4
<i>Pycnanthemum tenuifolium</i> (Lamiaceae)	parasitoid wasp (un.)	Frank et al. 2008	1	1.86 (0.05)	4
<i>Schizachyrium scoparium</i> (Poaceae)	parasitoid wasp (un.)	Frank et al. 2008	1	0.79 (0.142)	4
<i>Scutellaria integrifolia</i> (Lamiaceae)	parasitoid wasp (un.)	Frank et al. 2008	1	0.59 (0.059)	4
<i>Sorghastrum nutans</i> (Poaceae)	parasitoid wasp (un.)	Frank et al. 2008	1	0 (0.05)	4
<i>Asclepias syriaca</i> (Asclepiadaceae)	parasitoid wasp (un.)	Frank et al. 2008	2	0.77 (0.028)	4
<i>Asclepias tuberosa</i> (Asclepidaceae)	parasitoid wasp (un.)	Frank et al. 2008	2	0.62 (0.036)	4
<i>Coreopsis verticillata</i> (Asteraceae)	parasitoid wasp (un.)	Frank et al. 2008	2	0.77 (0.028)	4
<i>Eupatorium hyssopifolium</i> (Asteraceae)	parasitoid wasp (un.)	Frank et al. 2008	2	1.43 (0.164)	4
<i>Monarda punctata</i> (Lamiaceae)	parasitoid wasp (un.)	Frank et al. 2008	2	1.76 (0.008)	4
<i>Panicum virgatum</i> (Poaceae)	parasitoid wasp (un.)	Frank et al. 2008	2	0.38 (0.023)	4

Table 2.2 (ctd.). The estimates of log response ratio and its standard error for each attraction study. un. = unspecified, Br. = Braconidae, Ch. = Chalcidae.

Plant species (family)	Parasitoid (family)	reference	#	ln(RR) (SE)	N
<i>Pycnanthemum tenuifolium</i> (Lamiaceae)	parasitoid wasp (un.)	Frank et al. 2008	2	1.3 (0.038)	4
<i>Schizachyrium scoparium</i> (Poaceae)	parasitoid wasp (un.)	Frank et al. 2008	2	1.04 (0.018)	4
<i>Scutellaria integrifolia</i> (Lamiaceae)	parasitoid wasp (un.)	Frank et al. 2008	2	0 (0.022)	4
<i>Sorghastrum nutans</i> (Poaceae)	parasitoid wasp (un.)	Frank et al. 2008	2	0.41 (0.017)	4
<i>Borago officinalis</i> (Boraginaceae)	parasitoid wasp (un.)	Hogg, et al. 2011	1	0.69 (2.212)	5
<i>Brassica oleracea</i> (Brassicaceae)	parasitoid wasp (un.)	Hogg, et al. 2011	1	2.17 (1.793)	5
<i>Brassica sp.</i> (Brassicaceae)	parasitoid wasp (un.)	Hogg, et al. 2011	1	0.69 (2.212)	5
<i>Cosmos sulphureus</i> (Asteraceae)	parasitoid wasp (un.)	Hogg, et al. 2011	1	2.13 (1.795)	5
<i>Diplotaxis muralis</i> (Brassicaceae)	parasitoid wasp (un.)	Hogg, et al. 2011	1	1.04 (1.993)	5
<i>Fagopyrum esculentum</i> (Polygonaceae)	parasitoid wasp (un.)	Hogg, et al. 2011	1	0.09 (3.257)	5
<i>Lobularia maritima</i> (Brassicaceae)	parasitoid wasp (un.)	Hogg, et al. 2011	1	1.32 (1.897)	5
<i>Ocimum basilicum</i> (Lamiaceae)	parasitoid wasp (un.)	Hogg, et al. 2011	1	0 (3.54)	5
<i>Phacelia tanacetifolia</i> (Hydrophyllaceae)	parasitoid wasp (un.)	Hogg, et al. 2011	1	0.09 (3.257)	5
<i>Tropaeolum majus</i> (Tropaeolaceae)	parasitoid wasp (un.)	Hogg, et al. 2011	1	0.09 (3.257)	5
<i>Achillea sp.</i> (Asteraceae)	Braconidae (Br.)	Kaufman, et al. 2000	1	0 (8.964)	1
<i>Anthemis cotula</i> (Asteraceae)	Braconidae (Br.)	Kaufman, et al. 2000	1	0.69 (1.121)	5
<i>Avena sativa</i> (Poaceae)	Braconidae (Br.)	Kaufman, et al. 2000	1	1.72 (0.925)	5
<i>Erysimum xmarshallii</i> (Brassicaceae)	Braconidae (Br.)	Kaufman, et al. 2000	1	1.61 (0.518)	9
<i>Hesperis matronalis</i> (Brassicaceae)	Braconidae (Br.)	Kaufman, et al. 2000	1	1.93 (0.416)	11
<i>Phacelia tanacetifolia</i> (Hydrophyllaceae)	Braconidae (Br.)	Kaufman, et al. 2000	1	1.32 (0.6)	8
<i>Vicia villosa</i> (Fabaceae)	Braconidae (Br.)	Kaufman, et al. 2000	1	1.7 (2.315)	2
<i>Achillea sp.</i> (Asteraceae)	Chalcidae (Ch.)	Kaufman, et al. 2000	2	0 (0.059)	1
<i>Anthemis cotula</i> (Asteraceae)	Chalcidae (Ch.)	Kaufman, et al. 2000	2	0 (0.012)	5
<i>Avena sativa</i> (Poaceae)	Chalcidae (Ch.)	Kaufman, et al. 2000	2	0 (0.012)	5
<i>Erysimum xmarshallii</i> (Brassicaceae)	Chalcidae (Ch.)	Kaufman, et al. 2000	2	0.29 (0.005)	9
<i>Hesperis matronalis</i> (Brassicaceae)	Chalcidae (Ch.)	Kaufman, et al. 2000	2	0.31 (0.004)	11
<i>Phacelia tanacetifolia</i> (Hydrophyllaceae)	Chalcidae (Ch.)	Kaufman, et al. 2000	2	0.22 (0.006)	8

Table 2.2 (ctd.). The estimates of log response ratio and its standard error for each attraction study. Ch. = Chalcidae, Ic. = Ichneumonidae, un. = unspecified, Eu. = Eulophidae.

Plant species (family)	Parasitoid (family)	reference	#	ln(RR) (SE)	N
<i>Vicia villosa</i> (Fabaceae)	Chalcidae (Ch.)	Kaufman, et al. 2000	2	0 (0.03)	2
<i>Achillea</i> sp. (Asteraceae)	Ichneumonidae (Ic.)	Kaufman, et al. 2000	3	0 (5.068)	1
<i>Anthemis cotula</i> (Asteraceae)	Ichneumonidae (Ic.)	Kaufman, et al. 2000	3	1.76 (0.522)	5
<i>Avena sativa</i> (Poaceae)	Ichneumonidae (Ic.)	Kaufman, et al. 2000	3	1.1 (0.563)	5
<i>Erysimum xmarshallii</i> (Brassicaceae)	Ichneumonidae (Ic.)	Kaufman, et al. 2000	3	1.36 (0.3)	9
<i>Hesperis matronalis</i> (Brassicaceae)	Ichneumonidae (Ic.)	Kaufman, et al. 2000	3	1.16 (0.253)	11
<i>Phacelia tanacetifolia</i> (Hydrophyllaceae)	Ichneumonidae (Ic.)	Kaufman, et al. 2000	3	0.56 (0.42)	8
<i>Vicia villosa</i> (Fabaceae)	Ichneumonidae (Ic.)	Kaufman, et al. 2000	3	0.69 (1.584)	2
<i>Achillea</i> sp. (Asteraceae)	other hymenoptera (un.)	Kaufman, et al. 2000	4	0 (0.018)	1
<i>Anthemis cotula</i> (Asteraceae)	other hymenoptera (un.)	Kaufman, et al. 2000	4	0 (0.004)	5
<i>Avena sativa</i> (Poaceae)	other hymenoptera (un.)	Kaufman, et al. 2000	4	0 (0.004)	5
<i>Erysimum xmarshallii</i> (Brassicaceae)	other hymenoptera (un.)	Kaufman, et al. 2000	4	0 (0.002)	9
<i>Hesperis matronalis</i> (Brassicaceae)	other hymenoptera (un.)	Kaufman, et al. 2000	4	0.09 (0.002)	11
<i>Phacelia tanacetifolia</i> (Hydrophyllaceae)	other hymenoptera (un.)	Kaufman, et al. 2000	4	0.22 (0.002)	8
<i>Vicia villosa</i> (Fabaceae)	other hymenoptera (un.)	Kaufman, et al. 2000	4	0 (0.009)	2
<i>Achillea millefolium</i> (Asteraceae)	<i>Edovum puttleri</i> (Eu.)	Patt, et al. 1997	1	1.26 (0.422)	15
<i>Ageratum houstonianum</i> (Asteraceae)	<i>Edovum puttleri</i> (Eu.)	Patt, et al. 1997	1	0 (0.627)	7
<i>Ammi majus</i> (Apiaceae)	<i>Edovum puttleri</i> (Eu.)	Patt, et al. 1997	1	2.83 (0.414)	7
<i>Anethum graveolens</i> (Apiaceae)	<i>Edovum puttleri</i> (Eu.)	Patt, et al. 1997	1	3.13 (0.315)	20
<i>Angelica archangelica</i> (Apiaceae)	<i>Edovum puttleri</i> (Eu.)	Patt, et al. 1997	1	2.99 (0.321)	5
<i>Bupleurum rotundifolium</i> (Apiaceae)	<i>Edovum puttleri</i> (Eu.)	Patt, et al. 1997	1	3.16 (0.382)	8
<i>Capsella bursa-pastoris</i> (Brassicaceae)	<i>Edovum puttleri</i> (Eu.)	Patt, et al. 1997	1	0.34 (0.366)	6
<i>Chamaesyce maculata</i> (Euphorbiaceae)	<i>Edovum puttleri</i> (Eu.)	Patt, et al. 1997	1	3.27 (0.42)	6
<i>Coriandrum sativum</i> (Apiaceae)	<i>Edovum puttleri</i> (Eu.)	Patt, et al. 1997	1	2.87 (0.339)	7
<i>Eryngium foetidum</i> (Apiaceae)	<i>Edovum puttleri</i> (Eu.)	Patt, et al. 1997	1	1.02 (0.529)	15
<i>Euphorbia corollata</i> (Euphorbiaceae)	<i>Edovum puttleri</i> (Eu.)	Patt, et al. 1997	1	3.12 (0.371)	11
<i>Euphorbia cyparissias</i> (Euphorbiaceae)	<i>Edovum puttleri</i> (Eu.)	Patt, et al. 1997	1	2.43 (0.344)	11

Table 2.2 (ctd.). The estimates of log response ratio and its standard error for each attraction study. Eu. = Eulophidae, Cy. = Cynipoidea.

Plant species (family)	Parasitoid (family)	reference	#	ln(RR) (SE)	N
<i>Euphorbia marginata</i> (Euphorbiaceae)	<i>Edovum puttleri</i> (Eu.)	Patt, et al. 1997	1	2.79 (0.321)	17
<i>Foeniculum vulgare</i> (Apiaceae)	<i>Edovum puttleri</i> (Eu.)	Patt, et al. 1997	1	4.06 (0.406)	16
<i>Galinsoga parviflora</i> (Asteraceae)	<i>Edovum puttleri</i> (Eu.)	Patt, et al. 1997	1	0.42 (0.469)	15
<i>Lobularia maritima</i> (Brassicaceae)	<i>Edovum puttleri</i> (Eu.)	Patt, et al. 1997	1	2.06 (0.384)	15
<i>Mentha spicata</i> (Lamiaceae)	<i>Edovum puttleri</i> (Eu.)	Patt, et al. 1997	1	1.82 (0.351)	9
<i>Pastinaca sativa</i> (Apiaceae)	<i>Edovum puttleri</i> (Eu.)	Patt, et al. 1997	1	3.31 (0.323)	15
<i>Petroselinum crispum</i> (Apiaceae)	<i>Edovum puttleri</i> (Eu.)	Patt, et al. 1997	1	3.63 (0.337)	16
<i>Phaseolus vulgaris</i> (Fabaceae)	<i>Edovum puttleri</i> (Eu.)	Patt, et al. 1997	1	2.97 (0.355)	18
<i>Ruta graveolens</i> (Rutaceae)	<i>Edovum puttleri</i> (Eu.)	Patt, et al. 1997	1	2.22 (0.329)	15
<i>Stellaria media</i> (Caryophyllaceae)	<i>Edovum puttleri</i> (Eu.)	Patt, et al. 1997	1	0.52 (0.36)	8
<i>Ageratum houstonianum</i> (Asteraceae)	<i>Pediobius foveolatus</i> (Eu.)	Patt, et al. 1997	2	0 (0.08)	5
<i>Anethum graveolens</i> (Apiaceae)	<i>Pediobius foveolatus</i> (Eu.)	Patt, et al. 1997	2	3.96 (0.101)	20
<i>Coriandrum sativum</i> (Apiaceae)	<i>Pediobius foveolatus</i> (Eu.)	Patt, et al. 1997	2	3.71 (0.063)	10
<i>Euphorbia cyparissias</i> (Euphorbiaceae)	<i>Pediobius foveolatus</i> (Eu.)	Patt, et al. 1997	2	3.19 (0.244)	8
<i>Lobularia maritima</i> (Brassicaceae)	<i>Pediobius foveolatus</i> (Eu.)	Patt, et al. 1997	2	2.35 (0.071)	16
<i>Matricaria recutita</i> (Asteraceae)	<i>Pediobius foveolatus</i> (Eu.)	Patt, et al. 1997	2	1.64 (0.122)	6
<i>Phaseolus vulgaris</i> (Fabaceae)	<i>Pediobius foveolatus</i> (Eu.)	Patt, et al. 1997	2	4.05 (0.044)	23
<i>Anethum graveolens</i> (Apiaceae)	Cynipoidea (Cy.)	Saidov, et al. 2007	2	1.79 (0.972)	9
<i>Calendula officinalis</i> (Asteraceae)	Cynipoidea (Cy.)	Saidov, et al. 2007	2	1.1 (0.946)	10
<i>Celosia argentea</i> (Amaranthaceae)	Cynipoidea (Cy.)	Saidov, et al. 2007	2	0 (1.548)	11
<i>Celosia argentea</i> (Amaranthaceae)	Cynipoidea (Cy.)	Saidov, et al. 2007	2	0 (1.419)	12
<i>Coriandrum sativum</i> (Apiaceae)	Cynipoidea (Cy.)	Saidov, et al. 2007	2	1.95 (0.869)	10
<i>Foeniculum vulgare</i> (Apiaceae)	Cynipoidea (Cy.)	Saidov, et al. 2007	2	1.95 (0.724)	12
<i>Helianthus annuus</i> (Asteraceae)	Cynipoidea (Cy.)	Saidov, et al. 2007	2	0 (2.129)	8
<i>Impatiens balsamina</i> (Balsaminaceae)	Cynipoidea (Cy.)	Saidov, et al. 2007	2	1.1 (0.946)	10
<i>Ocimum basilicum</i> (Lamiaceae)	Cynipoidea (Cy.)	Saidov, et al. 2007	2	2.08 (0.721)	12
<i>Tagetes erecta</i> (Asteraceae)	Cynipoidea (Cy.)	Saidov, et al. 2007	2	2.2 (0.718)	12

Table 2.2 (ctd.). The estimates of log response ratio and its standard error for each attraction study. Cy. = Cynipoidea, Ta. = Tachinidae, Br. = Braconidae, Ap. = Aphidiidae.

Plant species (family)	Parasitoid (family)	reference	#	ln(RR) (SE)	N
<i>Zinnia violacea</i> (Asteraceae)	Cynipoidea (Cy.)	Saidov, et al. 2007	2	1.95 (0.668)	13
<i>Ziziphora interrupta</i> (Lamiaceae)	Cynipoidea (Cy.)	Saidov, et al. 2007	2	1.61 (0.984)	9
<i>Anethum graveolens</i> (Apiaceae)	Tachinidae (Ta.)	Saidov, et al. 2007	16	1.79 (6.218)	9
<i>Calendula officinalis</i> (Asteraceae)	Tachinidae (Ta.)	Saidov, et al. 2007	16	2.2 (5.512)	10
<i>Celosia argentea</i> (Amaranthaceae)	Tachinidae (Ta.)	Saidov, et al. 2007	16	2.4 (4.991)	11
<i>Celosia argentea</i> (Amaranthaceae)	Tachinidae (Ta.)	Saidov, et al. 2007	16	1.1 (5.041)	12
<i>Coriandrum sativum</i> (Apiaceae)	Tachinidae (Ta.)	Saidov, et al. 2007	16	2.2 (5.512)	10
<i>Foeniculum vulgare</i> (Apiaceae)	Tachinidae (Ta.)	Saidov, et al. 2007	16	3.09 (4.547)	12
<i>Helianthus annuus</i> (Asteraceae)	Tachinidae (Ta.)	Saidov, et al. 2007	16	0 (13.612)	8
<i>Impatiens balsamina</i> (Balsaminaceae)	Tachinidae (Ta.)	Saidov, et al. 2007	16	2.2 (5.512)	10
<i>Ocimum basilicum</i> (Lamiaceae)	Tachinidae (Ta.)	Saidov, et al. 2007	16	3 (4.549)	12
<i>Tagetes erecta</i> (Asteraceae)	Tachinidae (Ta.)	Saidov, et al. 2007	16	3.18 (4.545)	12
<i>Zinnia violacea</i> (Asteraceae)	Tachinidae (Ta.)	Saidov, et al. 2007	16	2.77 (4.205)	13
<i>Ziziphora interrupta</i> (Lamiaceae)	Tachinidae (Ta.)	Saidov, et al. 2007	16	2.71 (6.077)	9
<i>Anethum graveolens</i> (Apiaceae)	Braconidae (Br.)	Saidov, et al. 2007	17	2.71 (5.299)	9
<i>Calendula officinalis</i> (Asteraceae)	Braconidae (Br.)	Saidov, et al. 2007	17	2.89 (4.762)	10
<i>Celosia argentea</i> (Amaranthaceae)	Braconidae (Br.)	Saidov, et al. 2007	17	2.08 (4.384)	11
<i>Celosia argentea</i> (Amaranthaceae)	Braconidae (Br.)	Saidov, et al. 2007	17	2.3 (3.996)	12
<i>Coriandrum sativum</i> (Apiaceae)	Braconidae (Br.)	Saidov, et al. 2007	17	3.04 (4.758)	10
<i>Foeniculum vulgare</i> (Apiaceae)	Braconidae (Br.)	Saidov, et al. 2007	17	2.94 (3.967)	12
<i>Helianthus annuus</i> (Asteraceae)	Braconidae (Br.)	Saidov, et al. 2007	17	0 (11.869)	8
<i>Impatiens balsamina</i> (Balsaminaceae)	Braconidae (Br.)	Saidov, et al. 2007	17	3.04 (4.758)	10
<i>Ocimum basilicum</i> (Lamiaceae)	Braconidae (Br.)	Saidov, et al. 2007	17	2.94 (3.967)	12
<i>Tagetes erecta</i> (Asteraceae)	Braconidae (Br.)	Saidov, et al. 2007	17	3.22 (3.963)	12
<i>Zinnia violacea</i> (Asteraceae)	Braconidae (Br.)	Saidov, et al. 2007	17	2.2 (3.697)	13
<i>Ziziphora interrupta</i> (Lamiaceae)	Braconidae (Br.)	Saidov, et al. 2007	17	2.83 (5.294)	9
<i>Anethum graveolens</i> (Apiaceae)	Aphidiidae (Ap.)	Saidov, et al. 2007	18	2.77 (5.527)	9

Table 2.2 (ctd.). The estimates of log response ratio and its standard error for each attraction study. Ap. = Aphidiidae, Ca. = Chalcidoidea, Ic. = Ichneumonidae.

Plant species (family)	Parasitoid (family)	reference	#	ln(RR) (SE)	N
<i>Calendula officinalis</i> (Asteraceae)	Aphidiidae (Ap.)	Saidov, et al. 2007	18	2.2 (5.016)	10
<i>Celosia argentea</i> (Amaranthaceae)	Aphidiidae (Ap.)	Saidov, et al. 2007	18	0 (9.008)	11
<i>Celosia argentea</i> (Amaranthaceae)	Aphidiidae (Ap.)	Saidov, et al. 2007	18	1.61 (4.294)	12
<i>Coriandrum sativum</i> (Apiaceae)	Aphidiidae (Ap.)	Saidov, et al. 2007	18	2.89 (4.97)	10
<i>Foeniculum vulgare</i> (Apiaceae)	Aphidiidae (Ap.)	Saidov, et al. 2007	18	3.04 (4.138)	12
<i>Helianthus annuus</i> (Asteraceae)	Aphidiidae (Ap.)	Saidov, et al. 2007	18	0 (12.386)	8
<i>Impatiens balsamina</i> (Balsaminaceae)	Aphidiidae (Ap.)	Saidov, et al. 2007	18	2.4 (4.995)	10
<i>Ocimum basilicum</i> (Lamiaceae)	Aphidiidae (Ap.)	Saidov, et al. 2007	18	2.08 (4.193)	12
<i>Tagetes erecta</i> (Asteraceae)	Aphidiidae (Ap.)	Saidov, et al. 2007	18	2.83 (4.143)	12
<i>Zinnia violacea</i> (Asteraceae)	Aphidiidae (Ap.)	Saidov, et al. 2007	18	1.1 (4.235)	13
<i>Ziziphora interrupta</i> (Lamiaceae)	Aphidiidae (Ap.)	Saidov, et al. 2007	18	2.77 (5.527)	9
<i>Anethum graveolens</i> (Apiaceae)	Chalcidoidea (Ca.)	Saidov, et al. 2007	19	2.64 (13.205)	9
<i>Calendula officinalis</i> (Asteraceae)	Chalcidoidea (Ca.)	Saidov, et al. 2007	19	2.48 (11.906)	10
<i>Celosia argentea</i> (Amaranthaceae)	Chalcidoidea (Ca.)	Saidov, et al. 2007	19	2.77 (10.791)	11
<i>Celosia argentea</i> (Amaranthaceae)	Chalcidoidea (Ca.)	Saidov, et al. 2007	19	3.22 (9.869)	12
<i>Coriandrum sativum</i> (Apiaceae)	Chalcidoidea (Ca.)	Saidov, et al. 2007	19	2.56 (11.894)	10
<i>Foeniculum vulgare</i> (Apiaceae)	Chalcidoidea (Ca.)	Saidov, et al. 2007	19	3.5 (9.863)	12
<i>Helianthus annuus</i> (Asteraceae)	Chalcidoidea (Ca.)	Saidov, et al. 2007	19	0 (29.561)	8
<i>Impatiens balsamina</i> (Balsaminaceae)	Chalcidoidea (Ca.)	Saidov, et al. 2007	19	3.71 (11.831)	10
<i>Ocimum basilicum</i> (Lamiaceae)	Chalcidoidea (Ca.)	Saidov, et al. 2007	19	3 (9.878)	12
<i>Tagetes erecta</i> (Asteraceae)	Chalcidoidea (Ca.)	Saidov, et al. 2007	19	2.71 (9.897)	12
<i>Zinnia violacea</i> (Asteraceae)	Chalcidoidea (Ca.)	Saidov, et al. 2007	19	2.08 (9.238)	13
<i>Ziziphora interrupta</i> (Lamiaceae)	Chalcidoidea (Ca.)	Saidov, et al. 2007	19	3.09 (13.165)	9
<i>Anethum graveolens</i> (Apiaceae)	Ichneumonidae (Ic.)	Saidov, et al. 2007	21	2.77 (4.959)	9
<i>Calendula officinalis</i> (Asteraceae)	Ichneumonidae (Ic.)	Saidov, et al. 2007	21	2.71 (4.465)	10
<i>Celosia argentea</i> (Amaranthaceae)	Ichneumonidae (Ic.)	Saidov, et al. 2007	21	1.79 (4.154)	11
<i>Celosia argentea</i> (Amaranthaceae)	Ichneumonidae (Ic.)	Saidov, et al. 2007	21	1.95 (3.78)	12

Table 2.2 (ctd.). The estimates of log response ratio and its standard error for each attraction study. Ic. = Ichneumonidae, Sp. = Sphecidae, Br. = Braconidae.

Plant species (family)	Parasitoid (family)	reference	#	ln(RR) (SE)	N
<i>Coriandrum sativum</i> (Apiaceae)	Ichneumonidae (Ic.)	Saidov, et al. 2007	21	2.83 (4.461)	10
<i>Foeniculum vulgare</i> (Apiaceae)	Ichneumonidae (Ic.)	Saidov, et al. 2007	21	2.71 (3.721)	12
<i>Helianthus annuus</i> (Asteraceae)	Ichneumonidae (Ic.)	Saidov, et al. 2007	21	0 (11.114)	8
<i>Impatiens balsamina</i> (Balsaminaceae)	Ichneumonidae (Ic.)	Saidov, et al. 2007	21	2.89 (4.459)	10
<i>Ocimum basilicum</i> (Lamiaceae)	Ichneumonidae (Ic.)	Saidov, et al. 2007	21	3.04 (3.713)	12
<i>Tagetes erecta</i> (Asteraceae)	Ichneumonidae (Ic.)	Saidov, et al. 2007	21	3.04 (3.713)	12
<i>Zinnia violacea</i> (Asteraceae)	Ichneumonidae (Ic.)	Saidov, et al. 2007	21	2.64 (3.437)	13
<i>Ziziphora interrupta</i> (Lamiaceae)	Ichneumonidae (Ic.)	Saidov, et al. 2007	21	3.14 (4.949)	9
<i>Anethum graveolens</i> (Apiaceae)	Sphecidae (Sp.)	Saidov, et al. 2007	22	0 (0.094)	9
<i>Calendula officinalis</i> (Asteraceae)	Sphecidae (Sp.)	Saidov, et al. 2007	22	0.56 (0.056)	10
<i>Celosia argentea</i> (Amaranthaceae)	Sphecidae (Sp.)	Saidov, et al. 2007	22	0.63 (0.049)	11
<i>Celosia argentea</i> (Amaranthaceae)	Sphecidae (Sp.)	Saidov, et al. 2007	22	0.69 (0.044)	12
<i>Coriandrum sativum</i> (Apiaceae)	Sphecidae (Sp.)	Saidov, et al. 2007	22	0.63 (0.054)	10
<i>Foeniculum vulgare</i> (Apiaceae)	Sphecidae (Sp.)	Saidov, et al. 2007	22	0.97 (0.04)	12
<i>Helianthus annuus</i> (Asteraceae)	Sphecidae (Sp.)	Saidov, et al. 2007	22	0.32 (0.081)	8
<i>Impatiens balsamina</i> (Balsaminaceae)	Sphecidae (Sp.)	Saidov, et al. 2007	22	0.75 (0.052)	10
<i>Ocimum basilicum</i> (Lamiaceae)	Sphecidae (Sp.)	Saidov, et al. 2007	22	0.75 (0.043)	12
<i>Tagetes erecta</i> (Asteraceae)	Sphecidae (Sp.)	Saidov, et al. 2007	22	1.06 (0.04)	12
<i>Zinnia violacea</i> (Asteraceae)	Sphecidae (Sp.)	Saidov, et al. 2007	22	0 (0.065)	13
<i>Ziziphora interrupta</i> (Lamiaceae)	Sphecidae (Sp.)	Saidov, et al. 2007	22	1.1 (0.052)	9
<i>Amaranthus retroflexus</i> (Amaranthaceae)	<i>Peristenus pseudopallipes</i> (Br.)	Shahjahan 1974	1	0 (0.027)	175
<i>Conyza canadensis</i> (Asteraceae)	<i>Peristenus pseudopallipes</i> (Br.)	Shahjahan 1974	1	1.39 (0.015)	175
<i>Daucus carota</i> (Apiaceae)	<i>Peristenus pseudopallipes</i> (Br.)	Shahjahan 1974	1	0.93 (0.016)	175
<i>Erigeron strigosus</i> (Asteraceae)	<i>Peristenus pseudopallipes</i> (Br.)	Shahjahan 1974	1	1.48 (0.014)	175
<i>Agastache</i> sp. (Lamiaceae)	Braconid (Br.)	Sivinski, et al. 2011	1	0.13 (0.003)	5
<i>Ageratina aromatica</i> (Asteraceae)	Braconid (Br.)	Sivinski, et al. 2011	1	0.76 (0.156)	5
<i>Aloysia virgata</i> (Verbenaceae)	Braconid (Br.)	Sivinski, et al. 2011	1	0.25 (0.013)	5

Table 2.2 (ctd.). The estimates of log response ratio and its standard error for each attraction study. Br. = Braconidae, un. = unspecified, Ch. = Chalcidae.

Plant species (family)	Parasitoid (family)	reference	#	ln(RR) (SE)	N
<i>Buddleja davidii</i> (Buddlejaceae)	Braconid (Br.)	Sivinski, et al. 2011	1	0.2 (0.009)	5
<i>Calamintha nepeta</i> (Lamiaceae)	Braconid (Br.)	Sivinski, et al. 2011	1	0.9 (0.246)	5
<i>Conoclinium coelestinum</i> (Asteraceae)	Braconid (Br.)	Sivinski, et al. 2011	1	0.33 (0.023)	5
<i>Daucus carota</i> (Apiaceae)	Braconid (Br.)	Sivinski, et al. 2011	1	0.68 (0.12)	5
<i>Galium aparine</i> (Rubiaceae)	Braconid (Br.)	Sivinski, et al. 2011	1	0.09 (0.002)	5
<i>Geranium carolinianum</i> (Geraniaceae)	Braconid (Br.)	Sivinski, et al. 2011	1	1.06 (0.4)	5
<i>Lobularia maritima</i> (Brassicaceae)	Braconid (Br.)	Sivinski, et al. 2011	1	2.01 (4.256)	5
<i>Monarda punctata</i> (Lamiaceae)	Braconid (Br.)	Sivinski, et al. 2011	1	0.4 (0.098)	5
<i>Phyla nodiflora</i> (Verbenaceae)	Braconid (Br.)	Sivinski, et al. 2011	1	0.41 (0.036)	5
<i>Pityopus graminifolia</i> (Asteraceae)	Braconid (Br.)	Sivinski, et al. 2011	1	0.4 (0.035)	5
<i>Raphanus raphanistrum</i> (Brassicaceae)	parasitoid wasp (un.)	Sivinski, et al. 2011	1	-0.29 (0.017)	5
<i>Sisyrinchium angustifolium</i> (Iridaceae)	Braconid (Br.)	Sivinski, et al. 2011	1	0.22 (0.01)	5
<i>Solidago fistulosa</i> (Asteraceae)	Braconid (Br.)	Sivinski, et al. 2011	1	0.1 (0.002)	5
<i>Spermacoce verticillata</i> (Rubiaceae)	Braconid (Br.)	Sivinski, et al. 2011	1	-0.02 (0)	5
<i>Stachys floridana</i> (Lamiaceae)	parasitoid wasp (un.)	Sivinski, et al. 2011	1	0.02 (0)	5
<i>Stellaria media</i> (Caryophyllaceae)	Braconid (Br.)	Sivinski, et al. 2011	1	1.51 (1.309)	5
<i>Agastache sp.</i> (Lamiaceae)	Chalcid (Ch.)	Sivinski, et al. 2011	2	0.73 (0.142)	5
<i>Ageratina aromatica</i> (Asteraceae)	Chalcid (Ch.)	Sivinski, et al. 2011	2	2.27 (7.591)	5
<i>Aloysia virgata</i> (Verbenaceae)	Chalcid (Ch.)	Sivinski, et al. 2011	2	2.04 (4.52)	5
<i>Buddleja davidii</i> (Buddlejaceae)	Chalcid (Ch.)	Sivinski, et al. 2011	2	1.19 (0.571)	5
<i>Calamintha nepeta</i> (Lamiaceae)	Chalcid (Ch.)	Sivinski, et al. 2011	2	0.22 (0.01)	5
<i>Conoclinium coelestinum</i> (Asteraceae)	Chalcid (Ch.)	Sivinski, et al. 2011	2	1.47 (1.179)	5
<i>Daucus carota</i> (Apiaceae)	Chalcid (Ch.)	Sivinski, et al. 2011	2	1.59 (1.603)	5
<i>Galium aparine</i> (Rubiaceae)	Chalcid (Ch.)	Sivinski, et al. 2011	2	-0.07 (0.087)	5
<i>Geranium carolinianum</i> (Geraniaceae)	Chalcid (Ch.)	Sivinski, et al. 2011	2	0 (0.1)	5
<i>Lobularia maritima</i> (Brassicaceae)	Chalcid (Ch.)	Sivinski, et al. 2011	2	0.18 (0.007)	5
<i>Monarda punctata</i> (Lamiaceae)	Chalcid (Ch.)	Sivinski, et al. 2011	2	1.23 (0.669)	5

Table 2.2 (ctd.). The estimates of log response ratio and its standard error for each attraction study. Ch. = Chalcidae, Ic. = Ichneumonidae, Eu. = Eulophidae.

Plant species (family)	Parasitoid (family)	reference	#	ln(RR) (SE)	N
<i>Phyla nodiflora</i> (Verbenaceae)	Chalcid (Ch.)	Sivinski, et al. 2011	2	0.19 (0.007)	5
<i>Pityopus graminifolia</i> (Asteraceae)	Chalcid (Ch.)	Sivinski, et al. 2011	2	0.18 (0.006)	5
<i>Sisyrinchium angustifolium</i> (Iridaceae)	Chalcid (Ch.)	Sivinski, et al. 2011	2	0.02 (0)	5
<i>Solidago fistulosa</i> (Asteraceae)	Chalcid (Ch.)	Sivinski, et al. 2011	2	0.24 (0.012)	5
<i>Spermacoce verticillata</i> (Rubiaceae)	Chalcid (Ch.)	Sivinski, et al. 2011	2	0 (0.1)	5
<i>Stellaria media</i> (Caryophyllaceae)	Chalcid (Ch.)	Sivinski, et al. 2011	2	0.02 (0.014)	5
<i>Agastache sp.</i> (Lamiaceae)	Ichneumonid (Ic.)	Sivinski, et al. 2011	3	0.56 (0.075)	5
<i>Ageratina aromatica</i> (Asteraceae)	Ichneumonid (Ic.)	Sivinski, et al. 2011	3	0.98 (0.317)	5
<i>Aloysia virgata</i> (Verbenaceae)	Ichneumonid (Ic.)	Sivinski, et al. 2011	3	0.61 (0.09)	5
<i>Buddleja davidii</i> (Buddlejaceae)	Ichneumonid (Ic.)	Sivinski, et al. 2011	3	0.38 (0.032)	5
<i>Calamintha nepeta</i> (Lamiaceae)	Ichneumonid (Ic.)	Sivinski, et al. 2011	3	0.53 (0.066)	5
<i>Conoclinium coelestinum</i> (Asteraceae)	Ichneumonid (Ic.)	Sivinski, et al. 2011	3	-0.36 (0.027)	5
<i>Daucus carota</i> (Apiaceae)	Ichneumonid (Ic.)	Sivinski, et al. 2011	3	0.18 (0.007)	5
<i>Galium aparine</i> (Rubiaceae)	Ichneumonid (Ic.)	Sivinski, et al. 2011	3	0.73 (0.144)	5
<i>Geranium carolinianum</i> (Geraniaceae)	Ichneumonid (Ic.)	Sivinski, et al. 2011	3	1.09 (0.433)	5
<i>Lobularia maritima</i> (Brassicaceae)	Ichneumonid (Ic.)	Sivinski, et al. 2011	3	0.4 (0.036)	5
<i>Monarda punctata</i> (Lamiaceae)	Ichneumonid (Ic.)	Sivinski, et al. 2011	3	0.55 (0.073)	5
<i>Phyla nodiflora</i> (Verbenaceae)	Ichneumonid (Ic.)	Sivinski, et al. 2011	3	0.55 (0.072)	5
<i>Pityopus graminifolia</i> (Asteraceae)	Ichneumonid (Ic.)	Sivinski, et al. 2011	3	0.46 (0.048)	5
<i>Sisyrinchium angustifolium</i> (Iridaceae)	Ichneumonid (Ic.)	Sivinski, et al. 2011	3	0.09 (0.002)	5
<i>Solidago fistulosa</i> (Asteraceae)	Ichneumonid (Ic.)	Sivinski, et al. 2011	3	0.26 (0.014)	5
<i>Spermacoce verticillata</i> (Rubiaceae)	Ichneumonid (Ic.)	Sivinski, et al. 2011	3	0.1 (0.002)	5
<i>Stellaria media</i> (Caryophyllaceae)	Ichneumonid (Ic.)	Sivinski, et al. 2011	3	0.68 (0.117)	5
<i>Atriplex semibaccata</i> (Chenopodiaceae)	Eulophidae sp. (Eu.)	Stephens et al. 2006	1	1.55 (1.045)	5
<i>Baeckea behrii</i> (Myrtaceae)	Eulophidae sp. (Eu.)	Stephens et al. 2006	1	0 (2)	5
<i>Brassicaceae (blank)</i> (Brassicaceae)	Eulophidae sp. (Eu.)	Stephens et al. 2006	1	1.87 (1.024)	5
<i>Chenopodium album</i> (Chenopodiaceae)	Eulophidae sp. (Eu.)	Stephens et al. 2006	1	0.74 (1.228)	5

Table 2.2 (ctd.). The estimates of log response ratio and its standard error for each attraction study. Eu. = Eulophidae, un. = unspecified, Sc. = Scelionidae, Tr. = Trichogrammatidae, Ic. = Ichneumonidae.

Plant species (family)	Parasitoid (family)	reference	#	ln(RR) (SE)	N
<i>Maireana brevifolia</i> (Chenopodiaceae)	Eulophidae sp. (Eu.)	Stephens et al. 2006	1	0.17 (1.706)	5
<i>Rhagodia parabolica</i> (Amaranthaceae)	Eulophidae sp. (Eu.)	Stephens et al. 2006	1	0.45 (1.405)	5
<i>Atriplex semibaccata</i> (Chenopodiaceae)	parasitoid wasp (un.)	Stephens et al. 2006	2	2.07 (1.273)	5
<i>Baeckea behrii</i> (Myrtaceae)	parasitoid wasp (un.)	Stephens et al. 2006	2	0.92 (1.45)	5
Brassicaceae (blank) (Brassicaceae)	parasitoid wasp (un.)	Stephens et al. 2006	2	0.82 (1.495)	5
<i>Chenopodium album</i> (Chenopodiaceae)	parasitoid wasp (un.)	Stephens et al. 2006	2	0 (2.506)	5
<i>Maireana brevifolia</i> (Chenopodiaceae)	parasitoid wasp (un.)	Stephens et al. 2006	2	0.8 (1.506)	5
<i>Rhagodia parabolica</i> (Amaranthaceae)	parasitoid wasp (un.)	Stephens et al. 2006	2	0.6 (1.633)	5
<i>Atriplex semibaccata</i> (Chenopodiaceae)	Scelionidae sp. (Sc.)	Stephens et al. 2006	3	3.28 (29.686)	5
<i>Baeckea behrii</i> (Myrtaceae)	Scelionidae sp. (Sc.)	Stephens et al. 2006	3	3.36 (29.68)	5
Brassicaceae (blank) (Brassicaceae)	Scelionidae sp. (Sc.)	Stephens et al. 2006	3	1.92 (30.279)	5
<i>Chenopodium album</i> (Chenopodiaceae)	Scelionidae sp. (Sc.)	Stephens et al. 2006	3	0 (59.287)	5
<i>Maireana brevifolia</i> (Chenopodiaceae)	Scelionidae sp. (Sc.)	Stephens et al. 2006	3	1.79 (30.467)	5
<i>Rhagodia parabolica</i> (Amaranthaceae)	Scelionidae sp. (Sc.)	Stephens et al. 2006	3	1.3 (31.849)	5
<i>Atriplex semibaccata</i> (Chenopodiaceae)	Trichogrammatidae sp. (Tr.)	Stephens et al. 2006	4	3.17 (14.515)	5
<i>Baeckea behrii</i> (Myrtaceae)	Trichogrammatidae sp. (Tr.)	Stephens et al. 2006	4	1.25 (15.672)	5
Brassicaceae sp. (Brassicaceae)	Trichogrammatidae sp. (Tr.)	Stephens et al. 2006	4	0.3 (22.484)	5
<i>Chenopodium album</i> (Chenopodiaceae)	Trichogrammatidae sp. (Tr.)	Stephens et al. 2006	4	0 (28.978)	5
<i>Maireana brevifolia</i> (Chenopodiaceae)	Trichogrammatidae sp. (Tr.)	Stephens et al. 2006	4	1.77 (14.913)	5
<i>Rhagodia parabolica</i> (Amaranthaceae)	Trichogrammatidae sp. (Tr.)	Stephens et al. 2006	4	1.7 (14.968)	5
<i>Achillea millefolium</i> (Asteraceae)	<i>Exeristes comstockii</i> (Ic.)	Syme 1975	11	0.79 (0.019)	497
<i>Antennaria</i> sp. (Asteraceae)	<i>Exeristes comstockii</i> (Ic.)	Syme 1975	11	1.46 (1.035)	8
<i>Asclepias syriaca</i> (Asclepiadaceae)	<i>Exeristes comstockii</i> (Ic.)	Syme 1975	11	2.54 (0.014)	555
<i>Convolvulus arvensis</i> (Convolvulaceae)	<i>Exeristes comstockii</i> (Ic.)	Syme 1975	11	1.77 (0.099)	82
<i>Cornus sericea</i> (Cornaceae)	<i>Exeristes comstockii</i> (Ic.)	Syme 1975	11	1.9 (0.038)	212
<i>Cynoglossum officinale</i> (Boraginaceae)	<i>Exeristes comstockii</i> (Ic.)	Syme 1975	11	1.61 (0.014)	600
<i>Daucus carota</i> (Apiaceae)	<i>Exeristes comstockii</i> (Ic.)	Syme 1975	11	2.41 (0.017)	463

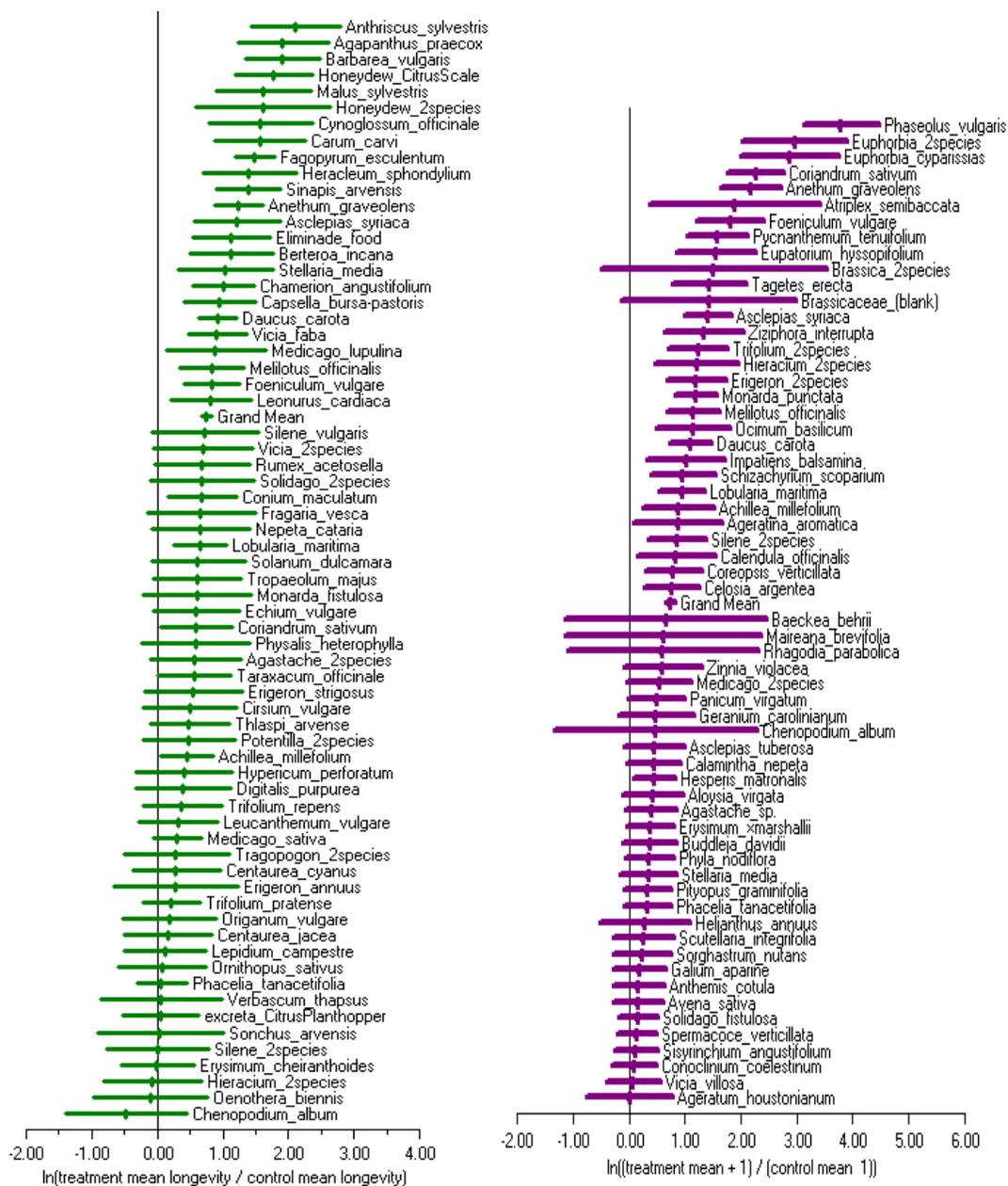


Figure 2.1. The estimated mean effects (log response ratio) of each plant species on longevity (left panel) and attraction (right panel) in parasitoid wasps. Only the species that were included in more than one study were included in the meta-analysis. The error bars are standard errors of the meta-analysis estimate.

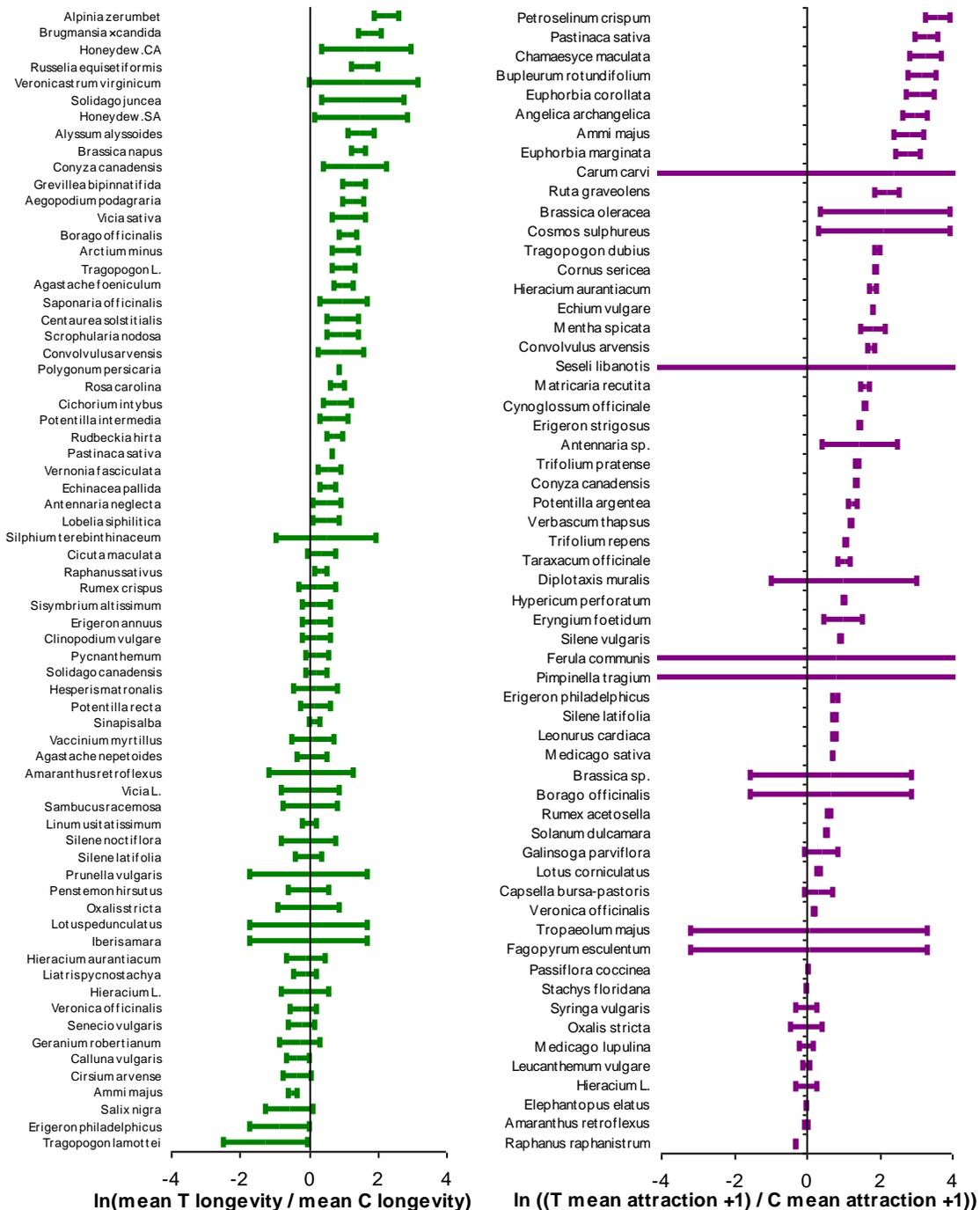


Figure 2.2. The calculated effects (log response ratio = $\ln(\text{treatment mean} / \text{control mean})$) of each plant species that was only included in a single study on parasitoid wasp longevity and attraction. Longevity is in the left panel and attraction is in the right panel. For attraction the data was transformed to avoid undefined ratios. The error bars are standard errors of the log response ratio for both graphs. The estimates are ranked from highest to lowest values. Large standard errors on the attraction graph are cut off to show better detail for the other species.

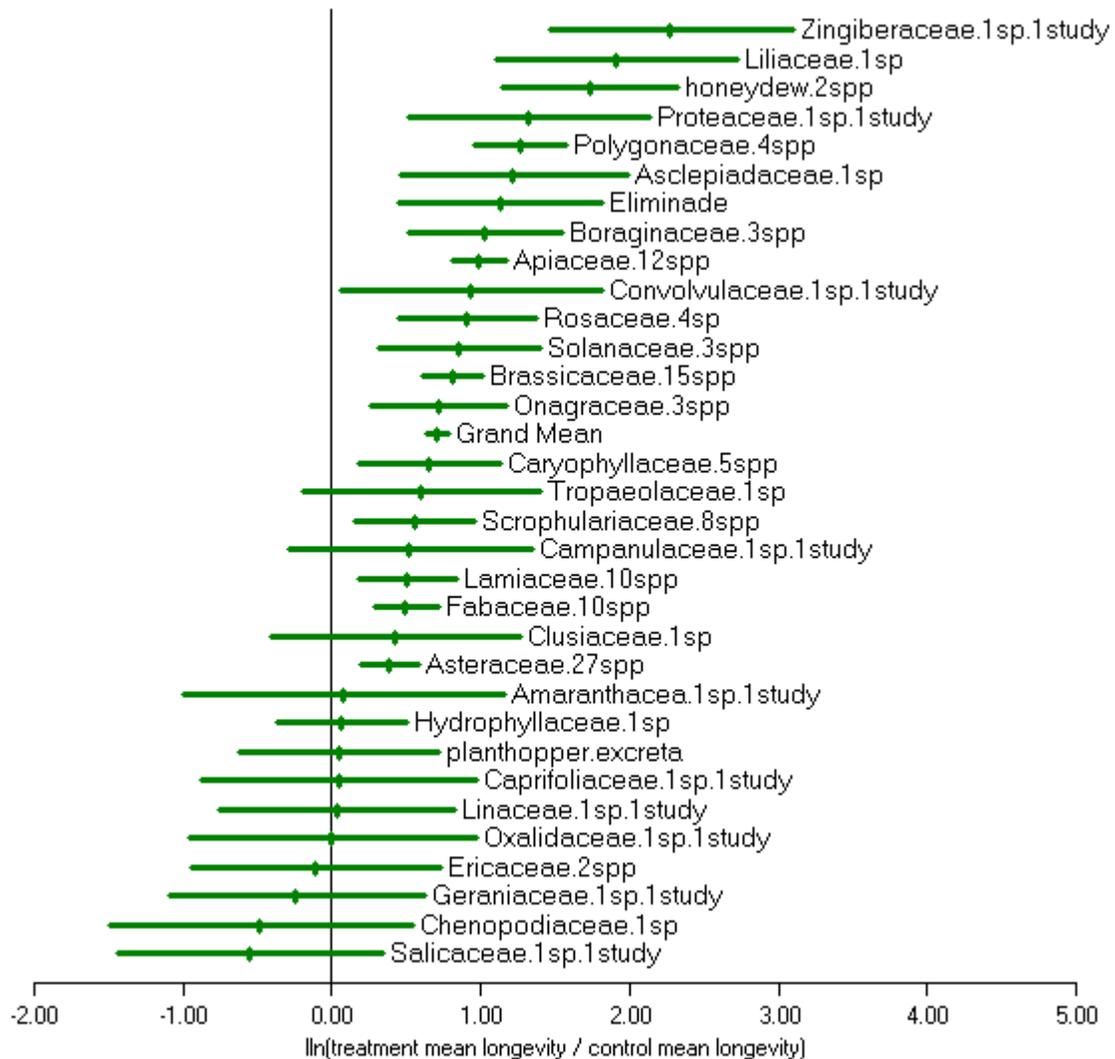


Figure 2.3. The calculated mean effect sizes [log response ratio = $\ln(\text{treatment mean} / \text{control mean})$] of the species within each plant family with tested species. The number of different plant species that were tested in each family is appended to each family name. The error bars indicate the standard errors of the meta-analysis estimates. Some species were only included in one distinct plant test and therefore no formal meta analysis was conducted. These families are labeled as including only 1 study (.1study) and the error bars are the standard error of the effect size estimated. Both types of estimates were included on one graph for ease of comparison.

Patterns of floral nectar availability for parasitoid wasps in cane berry production
landscapes

Michael Russell

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Abstract

Parasitoid wasps that attack pest insects in a variety of agricultural systems require nectar as food for adults. Leafroller caterpillars (Lepidoptera: Tortricidae) are pests of machine harvested cane berries (*Rubus*) in western Oregon that are susceptible to parasitism from a number of parasitoid wasp species. A study of Willamette valley cane berry production farms was conducted to estimate the abundance of flowers on the landscapes that parasitoid wasps can use as a nectar supply. The plant species found in caneberry production landscapes were classified with respect to whether or not they can provide nectar for parasitoid wasps based on information available in the literature. Surveys of habitats across the landscape were conducted to identify the plants species, when and where they bloom, and to quantify the amount of blooming flowers. Fixed area vegetation plots were used to sample the plant communities within cane berry fields under different irrigation regime (overhead or drip) and the inter row management system (tillage or perennial cover crop) and to quantify the floral production. Sampling estimated both the percent cover of each plant species, and the percent of stems that were in bloom at the time of sampling. These numbers were combined to estimate the percent flowering for each species present. The species which were determined to produce available nectar for parasitoids were summed to estimate a potential floral resource availability score for each plot. On the farm landscape, perennial and woody dominated habitats like hedgerows and perennial grassy areas had the highest floral resource availability scores, while annual dominated habitats had fewer resources. Habitats dominated by the invasive blackberry *Rubus armeniacus* Focke. had the highest total potential floral resource availability scores, but low diversity resulted in available resources only during the blackberry bloom. Habitats that were more diverse tended to have more consistent production of floral resources over the season. Within cane berry fields there was higher potential floral resource availability scores in areas with overhead irrigation and perennial cover crops than drip irrigation and inter row tillage management. Appropriate

management of caneberry fields can produce significant amounts of floral resources, which may be sufficient to prevent parasitoid wasps from being limited by adult food.

Introduction

Parasitoid wasps can be a significant cause of mortality for pest insects and have been used in classical and conservation biological control as components of integrated agricultural pest management programs (Legner and Gordh 1992, Hamilton and Lashomb 1996, Wearing, et al. 2012). However, the biological control provided by parasitoid wasps is often limited in agricultural landscapes (Suh, et al. 2000, Bianchi, et al. 2006, Chaplin-Kramer et al. 2011). A number of factors have been proposed to explain this limitation including pesticide use, high rates of disturbance, and habitat fragmentation (Thies, et al. 2005, Tscharntke, et al. 2005). Another commonly proposed mechanism is reduced abundance or diversity of floral resources in agricultural landscapes (Heimpel and Jervis 2005). Wasp adults need to eat nectar frequently to avoid starvation, and both laboratory and field studies have demonstrated that many species have increased longevity, fecundity, and oviposition rates when provided with nectar (Seikmann, et al. 2001, Baggen and Gurr 1998, Lee et al. 2008). The presence of floral resources has also been associated with increased parasitism rates in the field (Lavendero, et al. 2005, Berndt, et al. 2006, Irvin et al. 2006).

The link between floral resources and parasitoid abundance and behavior forms part of the rationale for conservation biocontrol strategies that seek to enhance habitat conditions for natural enemies within agricultural landscapes (Landis et al. 2000). Effectively implementing these strategies requires a detailed understanding of how floral resources vary within particular landscapes, and how these patterns influence the demographic traits and behavior of specific predator-prey species complexes (Landis et al. 2005, Wilkinson and Landis 2005). Yet, few studies have comprehensively documented the spatial and temporal patterns of floral resources available to parasitoids within agricultural landscapes.

Any study of landscape wide measures of floral resources should attempt to distinguish the relative suitability of different floral types to parasitoids. Floral types can vary significantly in their suitability as resources for parasitoids. Some plant species

produce little or no floral nectar, while others have flowers with long or complicated corollas that can limit nectar availability for small wasps and other short mouthed insects (Baggen, et. al., 1999, Vatala, et al. 2006, Arévalo, et al.2005).

Studies that screen for floral suitability typically describe floral resources at limited temporal or spatial scales. However, the phenology and spatial arrangement of floral resources can potentially influence the biocontrol efficacy of parasitoids in farm landscapes that are complex mosaics of intensively managed agricultural fields and minimally managed areas like wetlands, forests, unimproved pastures and other grasslands habitats (Gurr et al.1998, Tschardtke, et al. 2005b, Vollhardt, et al. 2009). A number of studies have documented positive associations between the proportion of semi-natural habitat in a landscape and levels of in-field pest control (Veres et al. 2011). However, few landscape scale studies have explicitly tested the assumption that this relationship is tied to resource levels available to natural enemies, and recent studies have suggested that management factors associated with agricultural intensification such as levels of disturbance and insecticide use may be the main causes of reduced levels of biocontrol in agricultural landscapes (Veres et al. 2011, Jonsson et al. 2012). Disentangling the relative importance of factors influencing the level of biocontrol in particular landscapes is complicated by the fact that many factors associated with agricultural intensification co-vary in space or time (Gabriel et al. 2006, Kremen et al. 2007, Boutin et al. 2008, Fahrig et al. 2011). This could partly reflect direct interactions between resource levels regulated by plant community composition or phenology and management practices such as tillage and irrigation. However, I know of no direct tests of this hypothesis for parasitoid floral resources.

Factors influencing floral resources in Oregon cane berry landscapes

Our limited understanding of parasitoid floral resource dynamics is exemplified by cane berry production landscapes in Oregon. In the Willamette valley of Oregon leafroller moths (Lepidoptera: Tortricidae) are a major pest of machine harvested cane berries. The two primary species, the orange tortrix (*Argyrotaenia franciscana* = *A. citrana*) and the oblique banded leafroller (*Choristoneura rosaceana*) are both parasitized by a variety of hymenopteran parasitoids (Coop, et al. 1989). Some of the parasitoid

species have limited seasons, but the most abundant species, *Apanteles aristoteliae* (Hymenoptera: Braconidae) is present as an adult over much of the year (Coop, et al. 1989). The parasitoid complex plays a significant role in regulating leafroller abundance in these systems (Ambrosino, et al. in review). Conservation biocontrol strategies could be used to maintain and improve floral resources for parasitoids on farms, but little is known about how floral resources vary in space and time in these landscapes or what factors influence these patterns.

Cane berry landscapes include many types of natural and managed habitats that potentially vary in the floral resources they provide parasitoids. Typically, studies describing landscape composition in agricultural systems define habitat patches by broad floristic composition, growth forms or vegetation structure. Habitats can also be defined in relationship to disturbance. Habitats represent a range of successional stages, from recently disturbed sites to areas with mature plants and a relatively stable plant community. Berry production fields themselves can be a significant source of floral resources. Many crops such as wind pollinated grains and vegetables that are harvested before flowering do not generally provide significant floral resources for beneficial insects. In contrast, cane berries and other insect pollinated fruit crops flower prolifically. However, the degree to which the different habitat types composing cane berry landscapes vary in their floral resources or how this variation relates to parasitoid biology is not known. For instance, most berries only flower during specific periods of the year (Black, et al. 2008, Dalton, 2009); this could create significant temporal gaps in floral resources. However, these gaps could be mitigated by adjacent habitat patches with floral bloom earlier or later in the growing season. Cane berry fields also contain non-crop species such as weeds or cover crops that can provide their own significant floral resources for beneficial insects (Norris and Kogan 2000). These species can also have their own distinct floral timing. Evaluating the temporal floral resource abundance associated with broad habitat classifications can provide a practical method for quickly assessing the floral resource condition of a particular farm landscape. It can also provide information to link landscape scale studies with actual estimates of how landscape elements vary in resource abundance.

In-field management practices could also directly and indirectly influence the abundance and timing of floral resources available to parasitoids. In a companion study to this one, experimental field plots under different irrigation and weed management regimes had significantly different understory plant communities (Plant communities appendix). The management systems used in that experimental study are common to cane berry production systems and include either using a perennial cover crop or soil tillage to manage weeds between the berry rows, and either using overhead or drip irrigation systems. It is not known how these management systems influence patterns of floral abundance, or how any effect on in-field patterns relates to broader patterns of floral abundance at the farm landscape scale.

Study goals and approach

The overall goal of this study was to comprehensively quantify patterns of floral resources available to parasitoid wasps within cane berry production systems. This includes three specific objectives: 1) Test the degree to which distinct habitat elements reflecting the dominant plant associations and successional stages in cane berry landscapes differ in their floral resources; 2) test the degree to which floral resource patterns among habitat groups reflect differences in their growth form composition; 3) Test the degree to which weed management and irrigation practices affect patterns of floral resource abundance within cane berry fields.

The study included a literature review to screen floral types for their potential to provide nectar resources for parasitoids and field surveys documenting floral abundance patterns for entire farm landscapes over an entire season. I developed a floral suitability screening protocol by reviewing the extensive literature reporting behavioral or physiological responses of parasitoids to specific floral types (Chapter 2). I then used this screening protocol to filter the results of monthly floral surveys conducted on seven Oregon cane berry farm landscapes. The surveys encompassed both in-field and adjacent habitat that reflected the full range of successional stages and vegetation associations found on the farms. To evaluate the effect of field management on floral resource patterns I conducted more detailed sampling within fields that represented a natural experiment. Sampled fields represented all factorial combinations of two levels of weed

management (inter-row cover crops or tillage) and two levels of irrigation (drip or overhead systems).

Methods

Study region

A cool Mediterranean climate and abundant irrigation water make the Willamette Valley of western Oregon one of the world leaders in blackberry and raspberry production. Historic land use and floodplain geomorphology have resulted in a mosaic consisting of many types of agricultural fields along with riparian forests and other semi-natural areas. Deep silt and clay loams occupy terraces while deep soils with a greater diversity of textures occupy flood plains. Various berry, vegetable, grain, and seed crops are rotated along with hay and pasture on suitable fields in the landscape. Wet sites (like rivers, sloughs and ponds) and steep areas (such as at transitions between higher terraces and the flood plain and from the flood plain to water bodies) are common in the landscape and generally have wild vegetation. This results in a relatively diverse landscape with small to large fields interspersed with wetlands, forests, grasslands, and shrubby areas.

This study was conducted on seven Willamette Valley farms with some commercial blackberry or raspberry fields. They ranged from diverse farms where cane berries were a minor component of a diversified system in a varied landscape, to farms where large berry fields were the dominant land use.

Nectar availability classification

Every plant species encountered during floral surveys was scored for its potential to supply nectar to parasitoid wasps. Plants were assumed to either be a potential source of nectar or not be a potential source of nectar and scored as one or zero. Scores were derived from the extensive literature describing the behavioral and physiological responses of parasitoid wasps to flowers of different plant species. There are two types of direct test that are frequently conducted to document the use of a particular plant species by a parasitoid. The more conclusive studies reported the physiological responses of parasitoids that were given access to flowers of a particular type compared to a control

(usually distilled water or sugar water). Reported physiological responses included how long individuals could live or how many eggs they could lay when only allowed to feed from flowers of a single plant species. Other studies reported the relative attractiveness of flowers to parasitoid wasps. These behavioral response studies provide less conclusive evidence than tests of wasp physiological performance because insects may respond to colors or smells of the flower but this does not necessarily indicate that there is available nectar (Slater and Calder 1988). A recent meta-analysis summarizes many of these results and was used to help classify the species observed on Willamette valley cane berry fields (Chapter 2). Many of the species encountered in the field have not been included in direct tests of the physiological response of parasitoids to flowers of the plant species. However, when the physiological response of congeners or other species in the family or results from behavioral studies are included, around two thirds of the documented species can be classified based information in the literature (Table 3.1). The remainder of the species encountered in the field were classified based on floral architecture.

Landscape and field scale surveys

From May through September 2009, monthly floral surveys were conducted on the nine sample farms. Surveys consisted of two distinct sampling regimes. In the first, the entire landscape was surveyed by directed walks that allowed the surveyor to evaluate the availability of floral resources in different habitat patches on the landscape. The second sampling method involved fixed area vegetation plots installed within the berry fields. These fixed plot samples were used to test the effect of different management regimes on floral resource patterns.

Directed walk floral surveys

Site visits and aerial photo interpretation were used to delineate distinct habitat blocks within 500 m of a cane berry field on each farm landscape. A directed walk survey route was laid out on each farm which allowed a surveyor to observe each habitat patch. The directed walk routes were limited to the farm property so they were concentrated on habitats within 250 m of a cane berry field and some of the habitats toward the margin of the 500 m buffer were not observed. Six of the farms were relatively large so most of the

delineated habitat patches were on the same farm property and fully accessible. The adjacent properties consisted of large, homogenous fields so it was possible to lay out a route on the six farms which allowed a surveyor to observe all of the habitat patches within the 500 m except a few small patches near the edge of the buffer. The other farms were smaller and a larger portion of the 500 m buffer was not on the cooperating farmer's property. Two farms had large fields on adjacent properties that allowed around three quarters of the fields within the buffer to be observed. The final farm was in a rural – residential landscape with smaller habitat patch sizes so the directed walk survey only allowed observation of around three fifths of the fields within the buffer.

There was a diversity of plant communities represented among the habitat patches, but it was possible to group them based on species composition, vegetation structure, and successional stage. In one classification system, each habitat patch observed during the directed walk surveys was classified based on the plant community and management into one of seventeen basic habitat types: annual crop, cultivated berries, weedy brambles, Christmas trees, compost pile, forest, grass field (for hay or seed), grass road, grassy areas, hedgerow, industrial, mint, nursery, orchard, pond, perennial vegetables, and residential. An alternative patch classification was based on vegetation structure. Each habitat patch was classified based on the combination of major plant growth forms present (annuals, perennials, shrubs, and trees). There are sixteen potential combinations of the four growth forms (four types with one growth form, six with two growth forms, four with three growth forms, one type with all four growth forms, and a final type without any plants). Only nine different vegetation structure types were observed on the farms, it is a more objective system but has less thematic resolution than the habitat type classification system with seventeen different groups.

Additionally, patches were classified into one of four successional stage groups based on stand characteristics and typical successional patterns in the Willamette valley. Habitat patches that experienced recent and extensive tillage or other disturbance like heavy vehicle traffic were classified as the earliest successional stage, recently disturbed. This stage includes primarily annual agricultural fields, parking lots, and major roads. Patches where disturbance was less recent or severe and had perennial plants growing there, but generally not as large mature plants, were in the second successional stage,

perennial establishment. This successional stage includes double track roads that experience regular traffic, recently planted berry fields, and heavily disturbed grassy areas. Once perennial plants are established and the role of plant competition becomes ecologically dominant the third successional stage, the mature perennials stage, is reached. Patches assigned to this stage include most of the berry and other perennial crop fields, many grassy areas, and little used grass roads. The fourth successional stage classification, the later seral stage, included primarily mature forest with a shade tolerant understory, but it also included other habitats occupied by competitively dominant grass species.

Surveys were conducted every other week with each farm visited once per month in the same order. This resulted in monthly surveys of each habitat patch, but information on each plant species or habitat type was collected every other week. All of the species that were observed flowering within the habitat patch were recorded along with a visual estimate of the percent of the patch that was covered by that species.

The monthly estimates were compiled, creating a list of all the species that flowered within each habitat patch over the growing season. The monthly coverage estimates for each plant species were combined into a season long means for each habitat patch. The growing season long mean coverage estimates were used to compare plant communities in the habitat patches.

Along with the visual estimate of percent cover for each species observed flowering, the proportion of inflorescences that had open flowers was estimated. Estimates were grouped into four floral abundance classes. Each class included a range of estimates of the percent flowering, and a single value used in the calculations [0–20% = Class 1 (value=0.1); 20–40% = Class 2 (value=0.3); 40–80% = Class 3 (value=0.6); 80–100% = Class 4 (value=0.85)]. The floral abundance score, the abundance of open flowers of each species in each habitat patch during each sample period, was estimated as the product of the percent vegetative cover of each species in the habitat patch and its floral abundance class value (% cover * % flowering). The floral abundance scores were used to both describe the phenology of the plant species on the landscape, and to evaluate the availability of nectar resources for parasitoid wasps.

The weekly sums of the floral abundance scores for each species were relativized to the maximum weekly value for the species over the entire growing season to determine the floral phenology of the species. The peak bloom was defined as the period when the total weekly floral abundance score for the species was more than half of its maximum value. The bloom season was additionally marked by the period when the weekly total was more than 25% of the maximum, and when any open flowers of the species were observed.

Additionally, a potential floral resource availability score for each habitat patch during each sample event was calculated as the sum of all the individual species floral scores in the habitat patch that were classified as having potentially available nectar for parasitoids. This score is an estimate of how many open flowers of species with potentially available nectar a parasitoid wasp could encounter in the habitat patch. The actual nectar availability on a site can also be influenced by site specific differences in nectar production by the plants, competition and facilitation from bees and other nectar feeders, and the presence of aphids or similar insects that produce sugars that some wasps can feed on.

Within field surveys: Vegetation plots

During the directed walks, 25 m² vegetation plots were installed in *Rubus* and other berry fields on the farms. The berry species and management activities in the field were recorded for each plot. The main management activities within cane berry fields were irrigation and weed control. Each activity was performed in one of two ways. Irrigation was either applied with an overhead or drip system while weeds were managed either by mowing a perennial cover crop between the berry rows, or occasional tillage of the inter row spaces. There was some variability in the species make up of the cover crops, and the amount of irrigation applied was not measured, but the fields were assumed to represent typical berry fields in the Willamette valley under each of the four possible irrigation / weed control management regimes.

Berry fields are highly repetitive and the plots were laid out in a standardized way. The berry plants are planted in rows and tied up to trellises. Rows are separated by alleys wide enough for tractor access. The distance between rows was not constant in all

fields, but it was always near 3m. This meant the length of the plots needed to vary slightly (around 8.3 m) to ensure a consistent sample area. Plot boundaries were set along the trellis wires marking the mid-point of each cane berry row and extended across one inter row space to the trellis wire marking the midpoint of the next row of cane berries.

All of the species found in the plot were identified and visual estimates of their percent covers were made. Species were assigned to flowering classes with the same limits in the directed walk sampling. The directed walk sampling focused solely on the species that flowered during the sampling period, while the vegetation plots accounted for all the species present, so a flowering class 0 was included for plants that had no open flowers. A potential floral resource availability score was calculated as described above for each plot.

Statistical analysis of field studies

There were two main questions answered with both the landscape level and the within field plant community data. First, the multivariate plant community data were analyzed to test whether there were differences in plant community composition between samples from different habitat groups or management regimes. Next, the calculated potential nectar availability scores were used to test whether there were differences between habitat groups or management regimes in the abundance of flowers with available nectar for parasitoid wasps.

Comparisons of multivariate community data between habitat and treatment groups were done using multi-response permutation procedures (MRPP). This is a nonparametric statistical method that tests whether placing the samples into groups results in greater similarities in multivariate data among group members than among all the plots together (Mielke and Berry 2001). In the landscape study the habitat patches were the sample unit. The percent cover values were estimated during each monthly visit and season long means were calculated for each plant species in the habitat patch. In the within field study, the vegetation plots were treated as individual samples in the community analysis using the coverage of each species on the plot as the response.

The potential floral availability score is a univariate synthesis of the community data and the literature review based plant classifications. Comparisons of potential floral availability scores between groups were tested with ANOVA. Linear regression was used to test for the effect of the number of plant growth forms present in habitat patches on floral availability score.

Results

Nectar availability classification

There were more than 240 different plant species or groups that were observed on the surveyed cane berry farms. Of those species, 77 had been used in studies directly comparing the response of a parasitoid wasp to the plant species or a congener (Chapter 2). Many of the most common species were among the 77 with specific information, therefore they accounted for approximately 55% of the flowers observed in the landscape study even though they were only 30% of the species. Species that only had information from behavioral response studies or were in the same family of species included in physiological response studies produced most of the rest of the flowers observed in the landscape (Table 3.1). The plant species that had no relationships with any of the tested species tended to be uncommon on the landscape and only contributed around five percent of the observed flowers. All of the species encountered and classified are listed in a supplementary appendix (Table 3.3).

The nectar availability rating was assigned to many species based on results from other species in their family. However, it is likely that nectar availability varies between species in many families. Some families such as Apiaceae, Rosaceae, and Brassicaceae consistently increased wasp longevity in trials. Other families, such as Asteraceae, Lamiaceae, or Scrophulariaceae, had less clear results with only some of the tested species having a positive effect on wasp longevity (Chapter 2). These families tended to have more diverse floral architecture which was taken into account when making the classifications. Additional information, like nectar production studies or evaluation of the use of the flowers by other insect groups, was available in the literature to help corroborate the classification for several species (Andrada, A. C. 2003, Benedek, et al.

1998, Fontaine, et al. 2008, Kaufman, et al. 2000, Raine and Chittka 2007, and Schultz and Dlugosh 1999).

Landscape variation in floral resources

During the directed walk surveys, floral resource availability varied both through time, as different plant species came into and out of their bloom seasons, and across space with different plant communities being found in different parts of the landscape. Over the course of the season, flowers were observed on 33 different crops, more than 31 different types of ornamental plants, and 157 species of wild plants. Flowering plants were found in all habitats including agricultural fields, residential landscaping, heavily disturbed roads and equipment lots, and a variety of minimally managed natural areas. The floral phenology of species differed with some species blooming early in the season, and some blooming later in the season (Figure 3.1).

Floral resource variation across habitat groups

The 316 surveyed habitat patches were assigned to 17 different identifiable habitat types. MRPP confirmed that the patches assigned to different habitat types differed in their floral community composition ($A = 0.09$, $P < 10^{-6}$). Similarly, the season long mean potential floral resource availability score differed between habitat types (ANOVA $F_{16/299} = 4.8$, $P < 10^{-7}$) (Figure 3.2). Habitat patches classified as brambles were dominated by the invasive shrub *Rubus armeniacus* and they had the highest season long floral availability scores. Several other perennial non crop habitat types had relatively high potential floral resource availability scores while habitats associated with the farming system like crop fields, roads and residential landscaping tended to have lower scores (Figure 3.2).

However, the timing of the floral resource availability varies between habitat types and that can influence the relative floral resource abundance. *R. armeniacus* forms dense monoculture thickets so the abundance of available nectar in bramble patches is sharply reduced after the *R. armeniacus* bloom season is over. More diverse perennial habitats, like hedgerows and grassy areas, include species that bloom later in the year and

therefore have high potential floral resource availability scores at the end of the season when the *R. armeniacus* brambles provide few floral resources (Figure 3.3).

Among habitats associated with the farming system, cultivated cane berry fields had a high potential floral resource availability scores throughout the season (Figure 3.3). Cane berry plants tended to bloom during the first few weeks of the sample period although late blooming and primocane fruiting varieties produced flowers later in the season. After the bloom from the berry plants was over, weeds and cover crop plants in the cultivated cane berry fields bloomed and contributed to consistently high potential floral resource availability scores within the berry fields throughout the year (Figure 3.3).

Flower resource variation across plant growth form

Out of the 16 possible vegetation structure types based on combinations of the four plant growth forms (trees, shrubs, perennials, and annuals), only nine were observed on Willamette valley cane berry farms. There were significant differences in plant communities between fields with different vegetation structure types, although the effect was weaker than the difference between habitat group (from MRPP, $A = 0.06$, $P < 10^{-6}$). The potential floral resource availability scores also differed based on the vegetation structure type of the habitat (ANOVA $F_{8/307} = 4$, $P = .0002$).

Habitat patches with a greater number of plant growth forms present had higher potential floral resource availability scores ($F_{1/314} = 10$, $P = 0.001$). When each habitat patch was characterized by the presence or absence of each of the four plant growth forms and analyzed in a linear regression with four main effects, the groups with the strongest positive effect on floral resource availability scores were shrubs ($F_{1/311} = 20$, $P = 10^{-5}$) and perennials ($F_{1/311} = 5$, $P = 0.03$) while trees ($F_{1/311} = 0.04$, $P = 0.8$) and annuals ($F_{1/311} = 1$, $P = 0.27$) did not have a significant effect.

Flower resource variation across successional stages

The flowering plant community composition differed across successional stages (from MRPP, $A = 0.04$, $P < 10^{-6}$). The effect was weaker than when groups were separated based on habitat type, but stronger than when separated by vegetation structural type. Recently disturbed sites had low potential floral resource availability scores

throughout the growing season. Different seral stages differed in the timing of nectar availability. Sites in the perennial establishment and the mature perennials stages had peaks in floral abundance in the middle of the growing season, and in forests and grasslands of later seral habitats had a peak in flowering early in the season (Figure 3.4). These patterns are apparent in the results from ANOVA tests that found significant main effects of successional stage ($F_{3/2039} = 21$, $P = 10^{-13}$) and Julian week ($F_{10/2039} = 10$, $P < 10^{-16}$) when evaluated as factors, as well as the interaction ($F_{30/2039} = 1.7$, $P = 0.008$). Both the peak in availability score in mature perennials stage fields during weeks 29 and 31 ($P = 0.04$), and the decline in availability in old stage fields after week 35 ($P = 0.03$), are supported by significant interaction terms in a linear regression model.

Effect of management on within field floral resources

Weed management and irrigation type had a significant influence on within field patterns of plant species composition and nectar availability. Based on two irrigation methods (drip or overhead), and two inter row management regimes (cover crop or tillage) there are four separate management types. MRPP identified significant differences between the groups ($A = 0.11$, $P = 0$). Pair-wise comparisons found significant differences between all the groups, but the effects were stronger for comparisons between groups with different weed management systems than for groups differing only in irrigation type (Table 3.2).

In a complete ANOVA model testing effects on floral resource availability score of management regime, irrigation type, month (as a factor) and two way interactions between month and either management regime or irrigation type there were significant effects of management regime ($F_{1/304} = 6$, $P = 0.01$) and irrigation type ($F_{1/304} = 7$, $P = 0.007$). The interaction between management regime and month was marginally significant ($P = 0.07$), while neither the main effect of month nor its interaction with irrigation type were significant ($P > 0.4$). In general the potential floral resource availability scores were higher in fields with inter-rows managed with cover crops rather than tillage and higher in fields with overhead irrigation rather than drip (Figure 3.5). In June, the pattern was reversed with the highest floral availability scores in tilled fields irrigated by drip systems. The potential floral resource abundance scores depended on

both the amount of flowers produced and the proportion of those flowers that had potentially available nectar. In the sites with mown cover crops the general floral abundance only declined slightly towards the end of the season, but the species that bloomed later in the year were more likely to have potentially available nectar so the score increased (Figure 6). In tilled fields that used drip irrigation there was a general decline in both the total floral abundance and the potential floral resource availability score later in the season, while in the overhead irrigated tilled fields there was a large bloom of species without available nectar in the mid summer that did not increase the potential floral resource availability score (Figure 3.6).

Synthesis of the results for a farm landscape

In the surveyed cane berry production landscapes, nectar was potentially available for parasitoid wasps from a wide diversity of species including flowers on crops, weeds within the fields, and non-crop areas. During the cane berry bloom season there were abundant floral resources within crop fields. Different crops and varieties included in the production system can create an extended bloom season among other fruits, cover crops and flowering vegetables. A snapshot of floral availability scores from one farm during the last week of July shows some striking patterns (Figure 3.7). This farm has several fields of blackberries with drip irrigation and tilled alley management in three irregular rows across the farm. Native shrubs planted along the property boundaries, and perennial and annual weeds along grassy roads are the primary species in flower at the time of the sample. This can be seen in the high floral availability scores in those habitats (Figure 3.7). The southernmost row of fields has the most crop diversity. The many flowers of zucchini field in full bloom are represented by the high point density in the field on the map (Figure 3.7). Other berry and fruit crops in the south row have different management than the main blackberry fields in the center row, and have higher floral resource availability scores. Two raspberry fields (just west of the center road in the middle row and just east of the center road in the south row) have overhead irrigation and consequently have higher floral availability scores than the drip irrigated blackberry fields (Figure 3.7).

Management intensity was not quantified in this study, but it is a likely explanation for differences in floral resource availability scores within blackberry fields under the same type of management. The large fields across the center of the farm are the primary production areas and receive the most fastidious management (Figure 3.7). The fields in the north and south rows are less intensively managed and some are out of production. The higher densities of flowering weeds and longer periods between mowing in these fields results in higher floral availability scores than the fields in the middle row in which most of the weeds have been controlled.

The habitats with the highest floral resource availability scores on this farm (hedgerows and grassy roads) are dominated by perennials and shrubs (Figure 3.7). Many of the annual weeds in this study were found not to produce nectar. This can be true; however, numerous annuals that do produce nectar are common in farming systems. In the blackberry fields near the east end of the middle row in the example farm, a steady supply of open flowers was available from scattered *Brassica* and other weedy species that grew in low densities throughout the fields (Figure 3.7).

Discussion:

Floral resource availability:

For most plant species, there was some information on the ability of wasps to acquire nectar from the flowers. More than 95% of the flowers observed in the field studies belonged to species that at least were in the same family of species included in direct tests of parasitoids. This result suggests that a group of relatively common species produce most of the floral resources on the landscape and that there may be diminishing marginal returns as total species richness increases. The classification of species into having and not having potentially available nectar for parasitoid wasps was based on a variety of studies in the literature. Some of the tests may have been more rigorous than others, parasitoid species may vary in their response to a flower, and plant species within the same family can vary in significant ways. However, most of the common species had relatively conclusive evidence, so any error this causes should be limited.

The potential floral resource availability score is an estimate of the abundance of flowers that are potential nectar sources for parasitoid wasps. The actual nectar

availability will depend on differences in the quantity and quality of nectar supplied by these flowers and interactions with other nectar feeders in the field (Idris and Graffius 1995, Baggen, et al. 1999). Some species have extra-floral nectaries which can provide an accessible supply of nectar unrelated to the shape of the flower (Baggen, et al 1999). The presence of honeydew producing insects is another potential source of food that parasitoid wasps may exploit in the absence of nectar producing flowers (Idris and Graffius 1995). Confirmation of wasp feeding in the field can improve the classification of the important plant species in a farm landscape and directly relate it to the wasps present in the system. Quantification of nectar production by each flower in the field would allow a more accurate measure of the resources available for the parasitoid wasps.

Around 30% of the observed flowers on the farm landscape were from species which were classified as not having the potential to provide floral resources to parasitoid wasps. In the cane berry fields there were several months that fewer than half of the flowers blooming within fields under the same management regime had potentially available nectar (Figure 3.7). This suggests a significant portion of the floral abundance on the landscape does not in fact provide a food source for adult wasps. It points to the importance of identifying the species present in the farm system and evaluating their ability to provide floral resources. The potential floral resource availability score is an efficient way to characterize the plant communities based on whether the plant species present can provide nectar for parasitoid wasps. However, additional information on the important plant species would improve the accuracy of the model.

This study focused on floral resource availability for parasitoid wasps. Other beneficial insects that depend on floral resources include predators like hoverflies (Diptera : Syrphidae) and ladybeetles (Coleoptera : Coccinellidae) and pollinators like native bees (Hymenoptera) (Ambrosino, et al. 2006, Fussell and Corbett 1992). These groups differ in the floral resources they require and what may limit their access to those resources. If a similar review was conducted on the relationship of plants to these groups, different floral resource availability scores could be generated for each group to evaluate how those species may fare in these landscapes. Moth species, like the adults that develop from the leafroller caterpillars, also can forage from some plant species and not others

and it is possible to find species that have available nectar for wasps but not for moths (Baggen, et al. 1999).

Landscape plant communities

On caneberry landscapes in the Willamette valley, perennial, semi-natural habitat areas produce an abundance of floral resources. The presence of shrubs and perennial forbs was associated with higher potential floral resource availability scores in the habitat patches. The production of an abundance of floral resources for adult wasps may contribute to the association between parasitoid populations and perennial semi-natural habitats that has been found in ecosystems around the world (Theis, et al. 2005, Bianchi, et al. 2008, Letourneau 2012, Thompson and Hoffman 2013). In this study the perennial crop areas also had relatively high potential floral resource availability scores. Cane berry fields had one of the highest mean potential floral resource availability scores during each sample month and other perennial crops had similar patterns. Annual crops tended to have lower and more variable floral availability scores than perennial habitats so the inclusion of a berry field in a farm system may itself be a way to increase the availability of floral resources on the landscape.

Annual plant fitness depends entirely on seed production and annual species are less likely to require insect mediated out crossing than perennial species which can survive if there is a pollination failure (Parrish and Bazzaz 1979). Bee communities often experience succession from species foraging for pollen on annual dominated sites, to species collecting more nectar on sites with more perennials (Steffan-Dewenter and Tschardtke 2001). This suggests that perennial dominated plant communities like cover cropped berry fields or non-crop habitats in later successional stages would be the most important for floral resource availability.

These results suggest that more structural diversity in minimally managed on farm habitats could indicate better nectar resource availability, but it could also be a case of the sampling effect. If a few common shrubs and perennial forbs produce abundant floral resources, the particular species present could be more important than structural diversity in general. In the meta-analysis of direct tests of parasitoid longevity on plant species, there was not a significant difference between species with different plant growth form

(Chapter 2). Many of the species in these studies were chosen because they were suspected of providing available nectar for parasitoids. The inclusion annual species with abundant nectar production, like buckwheat (*Fagopyrum esculentum*), increased the overall mean for annual species to a level similar to the other growth forms.

The low floral resource availability scores in recently disturbed sites in this study are due to the prevalence of species without floral resources like *Chenopodium album* and *Amaranthus retroflexus* which are common in early seral habitats, but do not produce nectar. Some of the first perennials to become established in the next successional stage include species that do provide nectar like *Daucus carota* and *Hypochaeris radicata*. When perennials and shrubs reach maturity in the next stage there is often an addition of more insect pollinated plants like *Rubus armeniacus* and *Senecio jacobaea*. Finally in mature forests many of the early seral species are much reduced in abundance and most of the floral resources are produced by species that flower early in the season, but also have available nectar like *Clematis ligusticifolia* and *Marah oregonense*.

Creating hedgerows or insectary plantings of perennial forbs and grasses creates habitats in the mature perennials stage, and can increase the diversity of plant growth forms on the farm landscape. If the species produce nectar that is available for parasitoid wasps, that hedgerow would function as a source of nutrition for beneficial insects. Mowing, hedging, and coppicing are partial disturbances that can keep perennial insectary habitats in a successional stage that is favorable for the production of floral resources of shrubs and perennial forbs.

Management of perennial, semi-natural habitats can be important for maintaining floral resource availability. If a single species dominates the site, it can decrease the quality of habitat for nectar foraging parasitoids. In dense thickets of invasive blackberries (*R. armeniacus*) the floral availability scores drop to near zero after the season when the blackberry flowers. Hay and grass seed fields (“grass fields” in surveys) receive supplemental nutrients, and regular management to maintain a consistent stand of grass. Weed control and increased fertility remove flowering weeds from the stand, therefore these fields have much lower floral resource availability than minimally managed grasslands (“grassy areas” in surveys). The relationship between increased

management intensity and reduced floral resources has been reported for other regions as well (Weiner, et al. 2010).

Within field floral resources

This study demonstrated that management practices can have a major influence on the within field plant communities and the potential availability of nectar for parasitoid wasps. The weed management system (soil tillage or mowing) had a stronger influence on the plant community than differences in irrigation method (Table 3.2). Tillage is an extreme disturbance that kills and removes live plants while simultaneously redistributing seeds and creating a fertile seed bed. Both of these mechanisms by themselves have been shown to result in different weed communities. No till and conventionally tilled grain fields both kill all of the vegetation each year, the conventional tillage system results in a weed community that includes species that need the tilled seed bed to germinate successfully (Thomas, et al. 2004). In orchards that do not use tillage, but either mow resident vegetation between tree rows or annually kill all the ground cover with herbicides, the presence of the surviving vegetation also results in a different plant community (Mas, et al. 2007). The effect of irrigation was relatively weak in the comparison of potential nectar availability and it tended to cause differences in abundance rather than species composition (Plant communities appendix). Total nectar production was not measured but some of the plant species may be able to produce more nectar per flower when given a greater water supply (Carroll, et al. 2001).

Both management with tillage and drip irrigation were associated with higher potential floral availability scores in June, while during the rest of the year fields with inter row cover crops and overhead irrigation had higher scores. In June there still was soil moisture from spring rains and the fields may not have received their initial tillage treatment of the season, leading to a large number of flowers. Later in the season the inter row spaces in the drip fields dried out. In tilled fields, weeds continued to bloom in overhead irrigated fields, but were significantly reduced in the drip fields. In the cover cropped fields, perennial forbs adapted to the dry conditions, such as *Hypochaeris radicata* and *Leontodon taraxicoides*, continued to produce flowers during the dry

months of late summer in both drip and overhead irrigated fields, although there were more flowers in fields with overhead irrigation.

In grass areas that are managed as a turf with frequent mowing, like the cover cropped caneberry fields and some grassy areas in this study, there are a number of factors that can be adjusted to increase the floral resource availability. The irrigation regime will interact with management practices like mowing height and fertilization to influence the plant competitive relationships to favor either grasses, which lack nectar resources, or forbs, which often produce nectar (Busey 2003). The choice of grass species can be important factor in flowering weed populations as well. In the fields I surveyed, cover cropped berry fields sown with a fine fescue (*Festuca* spp.) mixture had fewer weeds than fields with a perennial rye (*Lolium perenne*) cover crop. Strongly competitive turfgrass species like the fine fescues tend to reduce weedy forb densities in the grass stand (McKernan, et al. 2001).

Parasitoid wasp dispersal across the landscape

Whether there is enough floral resources in the landscape for parasitoid wasp populations depend on the dispersal ability and home range size of the wasps. Identifying actual foraging patterns in the field is difficult, but there have been several attempts to estimate wasp dispersal abilities based on different metrics. Studies have found that wasps can migrate into fields with no apparent decline in density into field interiors, but the transects stopped at less than 100m and do not provide information about longer distances (Freeman Long, et al. 1998, Olson and Wäckers 2007). Some studies have found evidence of dispersal limits of wasps. One study that traced how far Braconid wasps dispersed after feeding from buckwheat (*Fagopyrum esculentum*) that was marked with Rubidium found that most dispersal was within 100 m (Lavandero, et al. 2005). A mass release study found similar results with the probability of recovery of released wasps dropping to near zero at 65m (Paranhos, et al. 2007). These studies can estimate dispersal ability, but the trapping methods are likely to miss many dispersing insects and don't rule out the possibility that the wasps could have moved farther in a different landscape. How far braconid wasps can fly was tested in a wind tunnel experiment where the average flight time was equivalent to a flight of about 6 kilometers while the longest

flight was the equivalent of 18 kilometers (Yu, et al. 2009). This suggests that wasps have the ability to occupy larger individual ranges if necessary. A meta-population model estimated dispersal ability of two wasp species between meta populations of the host over several years. The long term dispersal was estimated as less than two kilometers for one species and less than eight kilometers for the second species (Van Nouhuys and Hanski 2002).

Each of these estimates helps build a general picture of wasp dispersal ability. The directed walk sampling focused on the caneberry fields and habitats within 250m and included fields out to 500m so it was likely to include most of the habitats that are readily accessible for braconid wasps foraging for hosts in the caneberry field. However, the information in the literature is not definitive enough to devise clear recommendations for placement of insectary habitats on the landscape to optimize wasp foraging and host finding. Additionally, peculiarities in landscape features and microclimates on individual farm landscapes and the farm management systems are important factors that determine whether an insectary planting works well.

Management systems that result in floral resource production within the fields avoid this issue by ensuring that there is nectar available for foraging wasps throughout the field. When the floral resources are produced on the crop plants themselves, or on other plants within the field, the wasp can quickly switch between foraging for nectar and searching for hosts. A community dynamics model predicts that for some types of wasps, flowers scattered throughout the crop field will do a better job at increasing wasp longevity and maintaining high parasitism rates at low host densities than flowers that are restricted to field margins or flowering strips (Vollhardt, et al. 2009).

Within field floral resources can be produced by weeds, which may or may not interfere with production practices, or intentionally planted plants as a part of an integrated farming system. Much of the floral abundance in the well managed cane berry fields in the middle row of fields in Figure 7 is produced by scattered, nectar producing weeds and volunteer plants which had few negative effects in the production system. The use of annual cover crop plantings is another way additional floral resources can be produced in this type of system (Berndt, et al. 2006). A perennial cover crop is more commonly used and the cover crop species and weed community will determine how

much effort it takes to manage it. Many flowering species can be easily managed as a part of the inter row cover while they produce floral resources for parasitoid wasps and other beneficial insects. With the appropriate system and species choice, nectar producing plants can be readily accessible to wasps searching for hosts on the crop plants, even for wasp species with poor dispersal ability.

Conclusion

The results of this study add supporting evidence to the hypothesis that floral resource availability for beneficial insects varies through time and across habitats and plant associations in agricultural production landscapes. Identifying the plant communities that are found in different non-production habitat types and within production fields under different management regimes is the first step in evaluating whether there are sufficient floral resources in the landscape. When the species are identified their seasonal bloom patterns can be used to identify periods when there are ample floral resources availability and periods when availability may be low.

On Willamette valley cane berry farms nectar producing flowers can be found throughout the growing season both within the cane berry fields and in other habitats on the farm, although bloom levels do tend to decline later in the summer. Appropriate management of non-production habitats on the farm to encourage nectar producing plant species is one way to help provide bloom throughout the season. Augmenting those habitats by construction of hedgerows or other insectary plantings is another way to increase floral resource availability. Many of the species observed in non-farm habitats in the caneberry landscape bloom in the spring, so including species in conservation plantings that bloom in the late summer can help ensure that there is not reduced nectar availability on the landscape. Beneficial insects may use the entire farm landscape so it is important to consider the system as a whole, including production areas, insectary plantings, and minimally managed non-production areas. Each farm is unique and any of the nectar supplying habitats discussed in this article may be an important resource for parasitoid wasps, depending on the circumstance.

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Table 3.1. The different levels of information used when assigning floral availability scores to each plant species encountered in the field surveys. Each group of species was defined by the taxonomic relationships of each species encountered in the field to any species included in a longevity or attraction study. The percent of species is the number of species in each group divided by the number of species documented in the field surveys. The percent of floral score is the total floral score of all of the species in each group divided by the total floral score of all of the species observed on the landscape.

Longevity	Attraction	Level of information	% of species	% of floral score
Species	Any level	Longevity test for species	17%	45%
Genus	Any level	Longevity test for genus	13%	10%
None or family	Species	Attraction test for species	3%	4%
None or family	Genus	Attraction test for genus	2%	2%
Family	None	Longevity test for family	34%	35%
None	None	Not tested	32%	5%

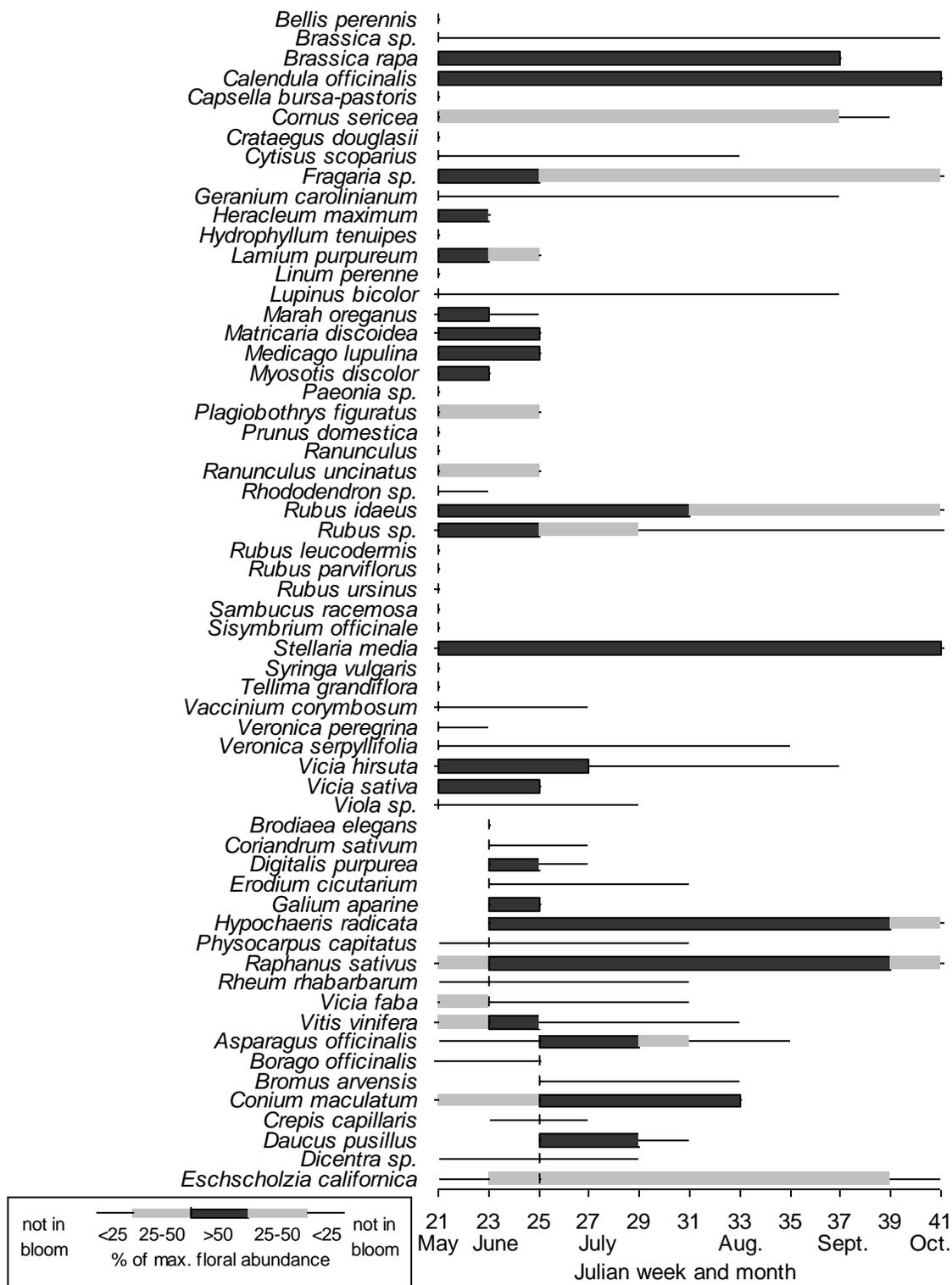


Figure 3.1a. Floral phenology of species on caneberry farm landscapes. The maximum weekly floral abundance score for each species was identified as the peak. The bars indicate weekly floral abundance relative to the peak month (Black > 50%, grey = 25% - 50%, line = in bloom but < 25% of peak, no line = not in bloom) Species are sorted by the beginning of the >50% period with later blooming species on the following panels.

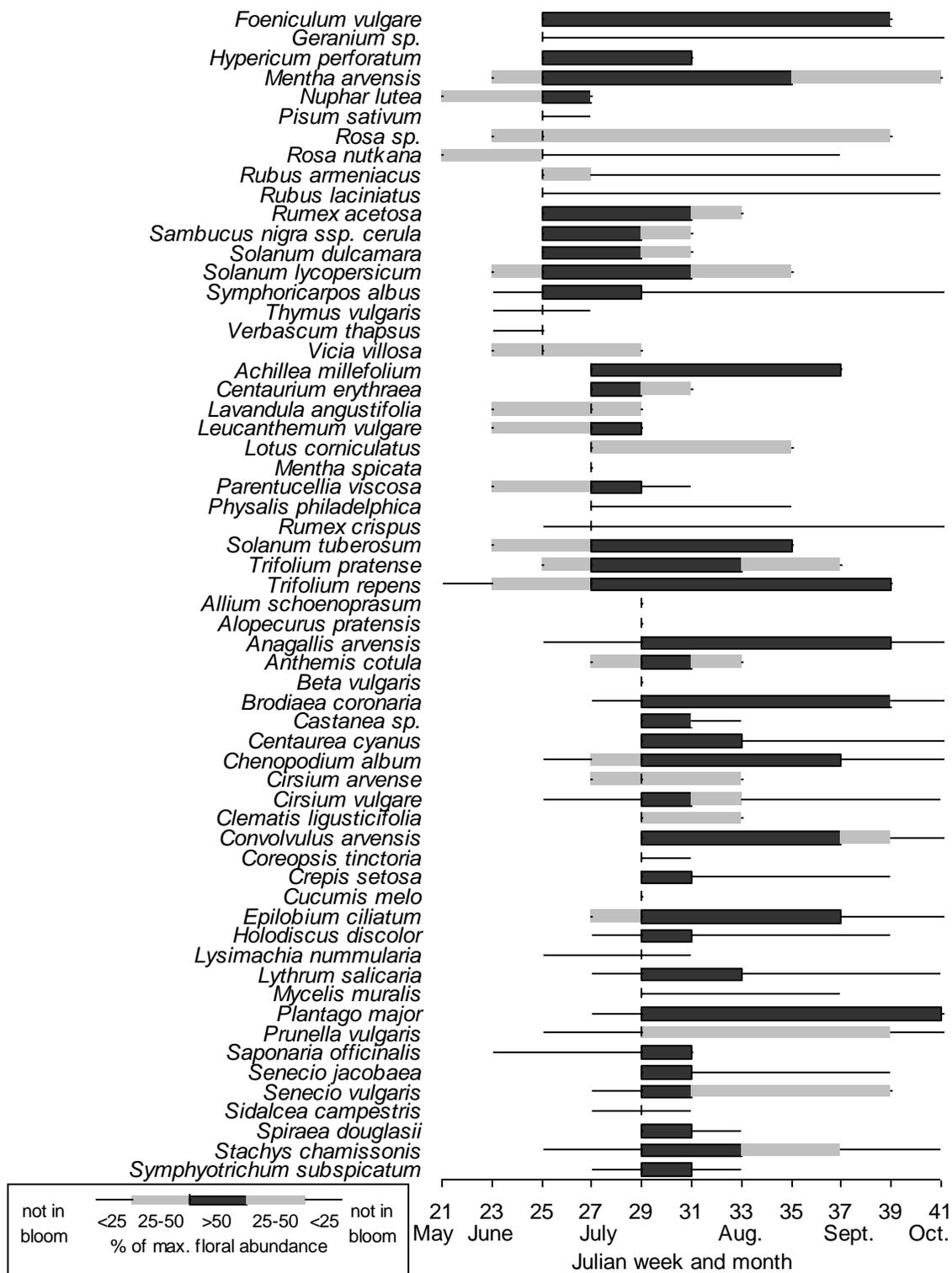


Figure 1b. Floral phenology of species on caneberry farm landscapes. The maximum weekly floral abundance score for each species was identified as the peak. The bars indicate weekly floral abundance relative to the peak month (Black > 50%, grey = 25% - 50%, line = in bloom but < 25% of peak, no line = not in bloom) Species are sorted by the beginning of the >50% period with earlier and later blooming species on other panels.

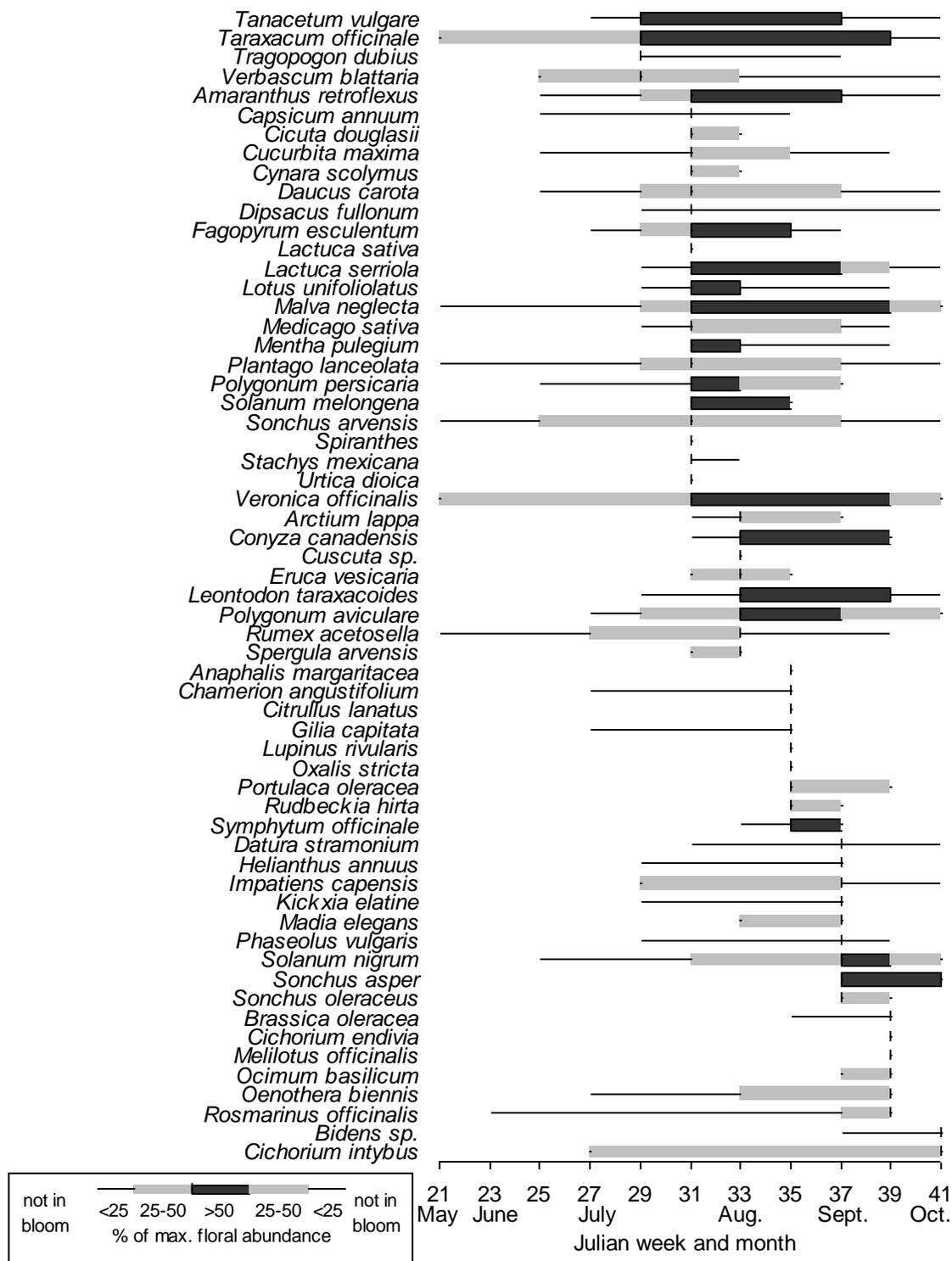


Figure 1c. Floral phenology of species on caneberry farm landscapes. The maximum weekly floral abundance score for each species was identified as the peak. The bars indicate weekly floral abundance relative to the peak month (Black > 50%, grey = 25% - 50%, line = in bloom but < 25% of peak, no line = not in bloom) Species are sorted by the beginning of the >50% period with earlier blooming species on previous panels.

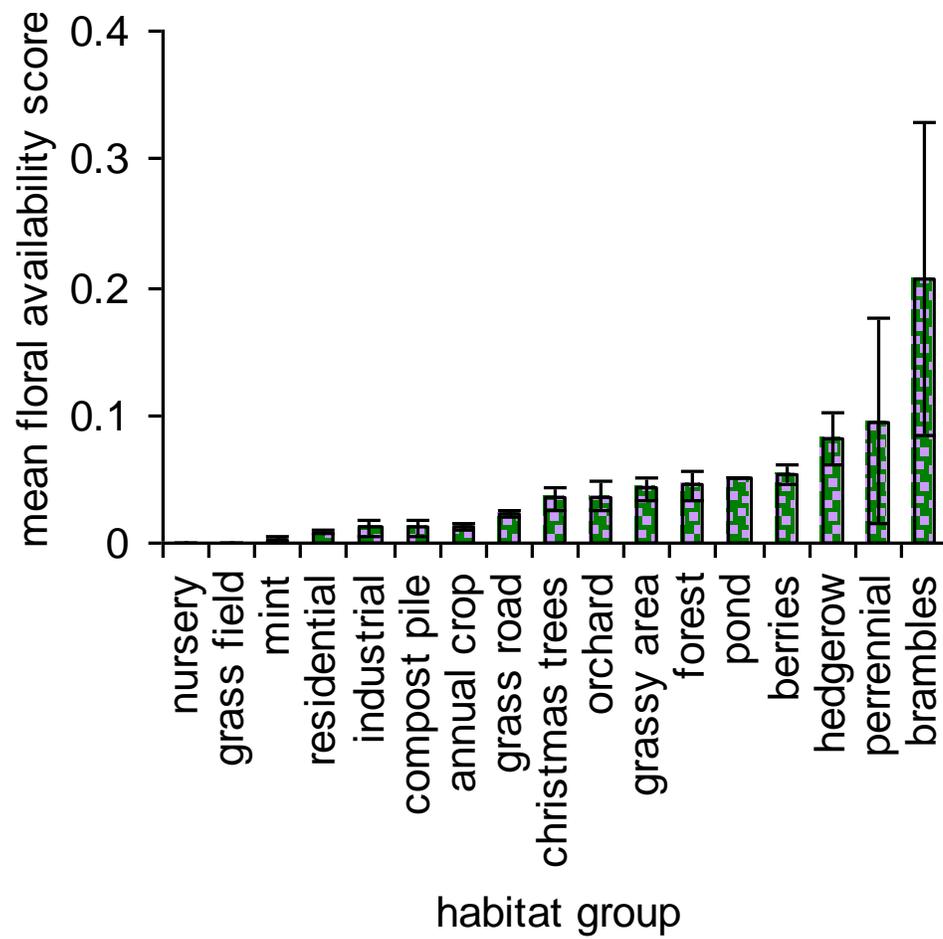


Figure 3.2. Mean season long floral availability scores for fields in different habitat groups. Error bars are the standard errors of the mean.

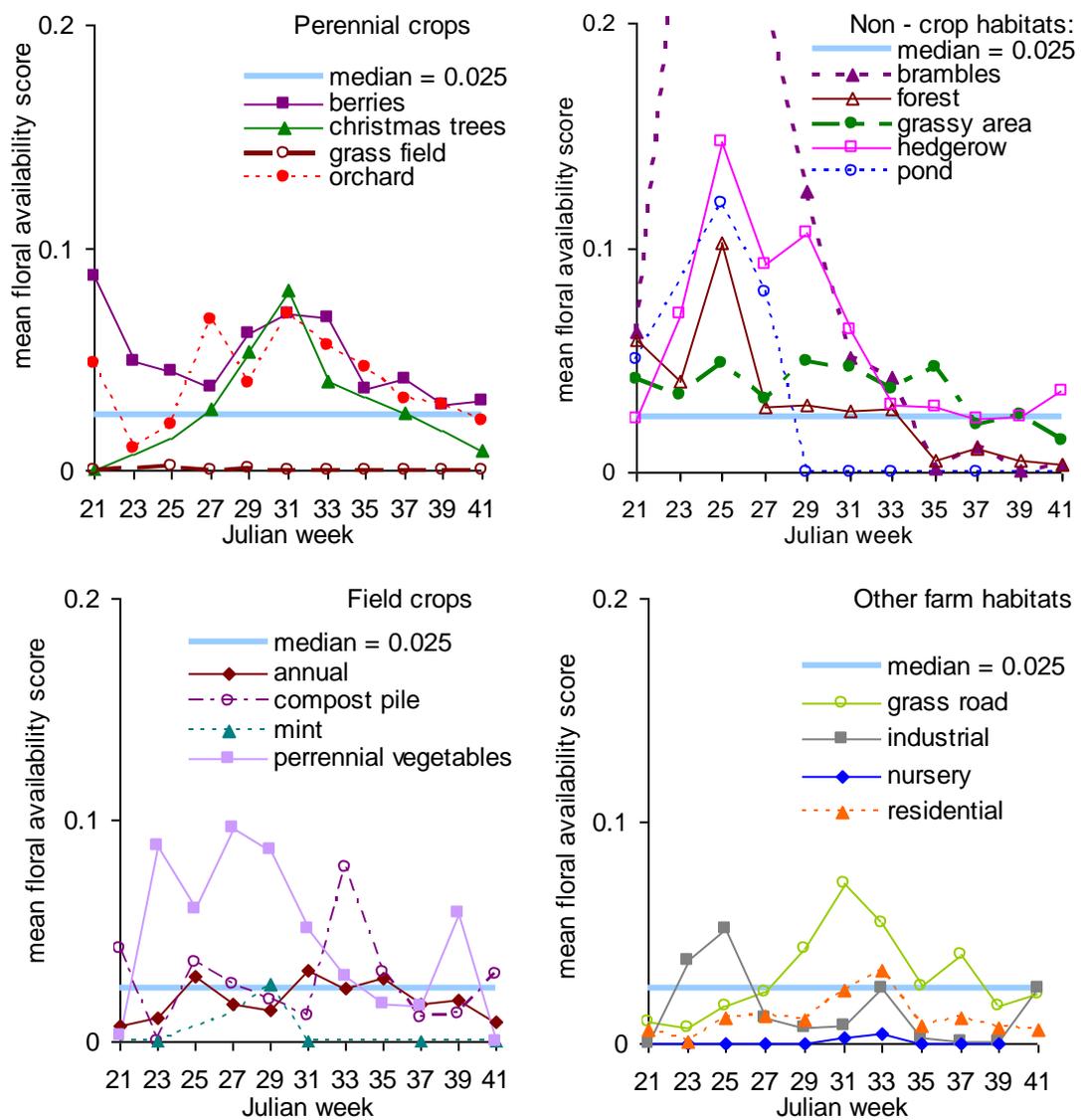


Figure 3.3. The mean potential floral availability score for each habitat during each sample week. The panels each show a different subset of the panels so that the lines are distinguishable, and include a line depicting the median value among monthly means of all of the habitats to help in comparisons between panels. The brambles habitat values of week 23 (= 0.25), week 25 (= 0.45), and week 27 (= 0.21) are greater than the scale of the Y – axis.

Figure 3.4. The mean floral availability score over the season for habitat patches in different successional stages. The solid area represents the floral score of species with available nectar, and the stippled areas represent species without available nectar. Sampling only took place from April to September. It is likely there was a low level of flowers in month before and after, although it is not shown on this graph.

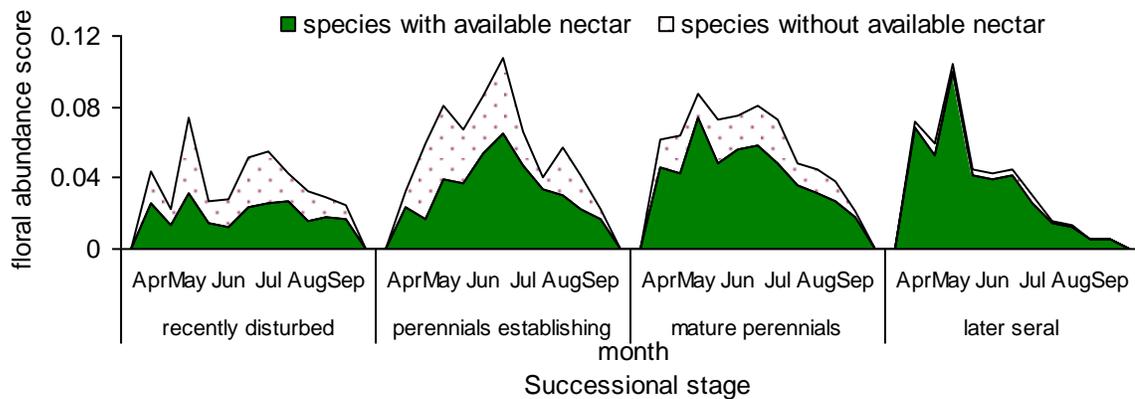


Table 3.2. Results from pair-wise MRPP tests for differences in community composition and abundance between caneberry fields under different irrigation and weed management regimes. The overall test for differences between groups returned an A statistic of 0.11 and a p-value of 0. A-statistics of 1 indicate there are no differences between members of the same group, while values of 0 indicate heterogeneity within groups is equal to what would be expected at random.

management type 1	management type 2	effect size (A)	p-value
tilled, overhead	covercrop, drip	0.09	0
tilled, overhead	tilled, drip	0.05	0
tilled, overhead	covercrop, overhead	0.09	0
covercrop, drip	tilled, drip	0.07	0
covercrop, drip	covercrop, overhead	0.05	0
tilled, drip	covercrop, overhead	0.09	0

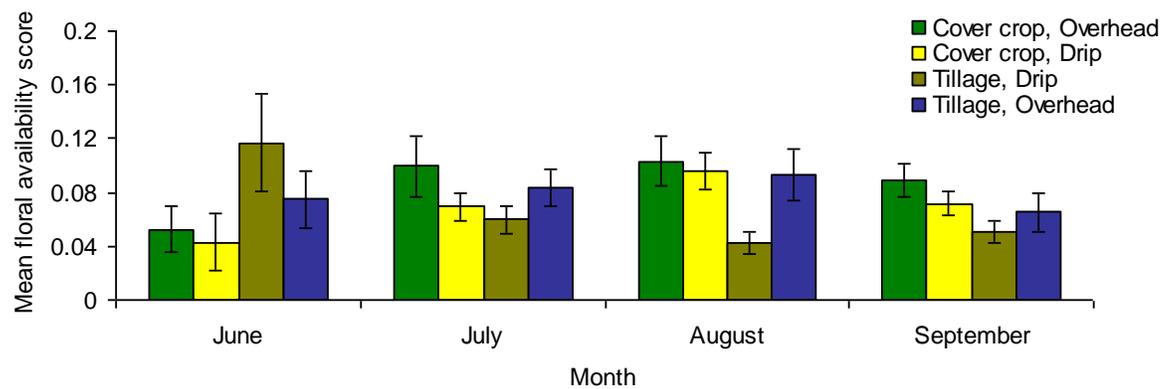


Figure 3.5. Mean floral availability score for fields under different inter row (cover crop or tillage) and irrigation (overhead or drip) management regimes. Error bars are standard errors of the mean.

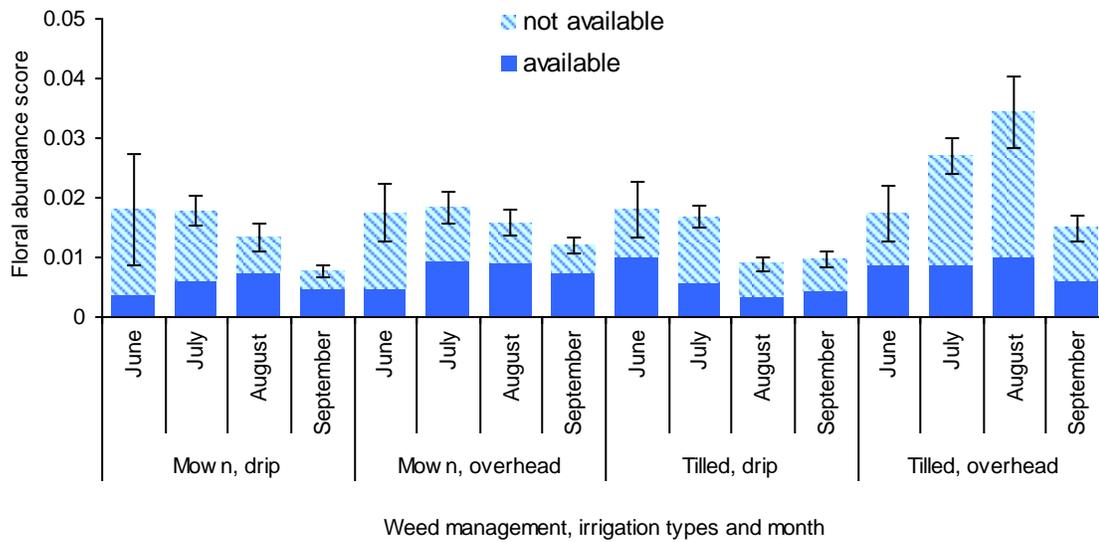


Figure 3.6. Abundance of flowers with and without potentially available nectar in cane berry fields of each management type over the four month growing season. Error bars are the standard error of the mean total floral abundance score.



Legend

1 Brambles	9 Mixed vegetables	17 Annual crop - Zucchini
2 Hedgerow	10 Mown - overhead raspberries	18 Annual crop - Broccoli
3 Grassy area	11 Fallow blackberries	19 Annual crop - Wheat
4 Grassy road	12 Tilled - pear orchard	20 Compost pile
5 Grass field	13 Tilled - drip Kiwis	21 Tilled - bare
6 Nursery	14 Tilled - drip blackberries	22 Paved road
7 Greenhouses	15 Tilled - overhead blackberries	
8 Residential	16 Tilled - overhead raspberries	



Figure 3.7. A map showing the floral availability scores for each habitat patch on farm H during the last week of July. The density of blue dots is proportional to the floral resource availability score for the patch. The different habitat type groups are indicated with polygon color. The highest scores (with dot density so high it obscures the patch color) were in the linear road and hedgerow habitats that separate some of the fields and form the property boundary

Table 3.3. The plant species encountered in the field surveys of caneberry farms. The nomenclature is based on the USDA plants database (USDA 2103). Availability indicator is the value used in floral resource availability score calculations. 1 = plant species predicted to have nectar available to parasitoid wasps, 0 = plant species predicted to not have nectar available to parasitoid wasps. The predictions are based on the meta-analysis results when applicable (Meta-analysis appendix). The information available in the meta-analysis is indicated by the two or three letters in the final column. The first letter indicates whether the species was included in a longevity trial, the second value is for attraction trials, and the third value, when present, indicates whether there is information on nectar production in the literature. The letter indicates whether the species itself or a close relative was tested (S = same species, G = congener, F= a member of the same plant family (longevity only), a dash (-) indicates that no related species were tested.) When no information was found, species were assigned based on general floral architecture.

Scientific name (Common name)	availability indicator	basis
<i>Acer macrophyllum</i> Pursh (bigleaf maple)	1	-, -
<i>Achillea millefolium</i> L. (common yarrow)	1	S, S
<i>Agrostis capillaris</i> L. (colonial bentgrass)	0	-, -
<i>Alcea rosea</i> L. (hollyhock)	1	-, -
<i>Allium schoenoprasum</i> L. (wild chives)	0	F, -
<i>Alnus rubra</i> Bong. (red alder)	0	-, -
<i>Alopecurus geniculatus</i> L. (water foxtail)	0	-, -
<i>Alopecurus pratensis</i> L. (meadow foxtail)	0	-, -
<i>Amaranthus retroflexus</i> L. (redroot amaranth)	0	S, S
<i>Anagallis arvensis</i> L. (scarlet pimpernel)	0	-, -, n
<i>Anaphalis margaritacea</i> (L.) Benth. (western pearly everlasting)	1	F, -
<i>Anthemis cotula</i> L. (stinking chamomile)	0	F, S, n
<i>Arctium lappa</i> L. (greater burdock)	1	S, -
<i>Arrhenatherum elatius</i> (L.) P. Beauv. ex J. Presl & C. Presl (tall oatgrass)	0	-, -
<i>Asparagus officinalis</i> L. (garden asparagus)	1	F, -
<i>Avena sativa</i> L. (common oat)	0	-, -
<i>Bellis perennis</i> L. (lawndaisy)	1	F, -, n
<i>Beta vulgaris</i> L. ssp. <i>cicla</i> (L.) W.D.J. Koch (chard)	1	F, -
<i>Bidens</i> L. (beggarticks)	1	F, -
<i>Borago officinalis</i> L. (common borage)	1	S, S
<i>Brassica</i> L. (mustard)	1	G, G
<i>Brassica oleracea</i> L. (cabbage)	1	G, G
<i>Brassica rapa</i> L. (field mustard)	1	F, -
<i>Brodiaea coronaria</i> (Salisb.) Engl. (crown brodiaea)	1	F, -
<i>Brodiaea elegans</i> Hoover (harvest brodiaea)	1	F, -
<i>Bromus arvensis</i> L. (field brome)	0	F, -
<i>Bromus carinatus</i> Hook. & Arn. (California brome)	0	-, -
<i>Bromus diandrus</i> Roth ssp. <i>rigidus</i> (Roth) Lainz (ripgut brome)	0	-, -
<i>Bromus</i> L. (brome)	0	-, -
<i>Calendula officinalis</i> L. (pot marigold)	1	F, S
<i>Capsella bursa-pastoris</i> (L.) Medik. (shepherd's purse)	1	S, S
<i>Capsicum annuum</i> L. (pepper)	1	F, -
<i>Carex hoodii</i> Boott (Hood's sedge)	0	-, -
<i>Carex</i> L. (sedge)	0	-, -

Table 3.3 (ctd.). The predicted nectar availability of the plant species encountered.

Scientific name (Common name)	availability indicator	basis
<i>Carex obnupta</i> L.H. Bailey (slough sedge)	0	-, -
<i>Castanea</i> Mill. (chestnut)	1	-, -
<i>Centaurea cyanus</i> L. (garden cornflower)	1	S, -
<i>Centaureum erythraea</i> Rafn (European centaury)	1	F, -
<i>Chamerion angustifolium</i> (L.) Holub (fireweed)	1	S, -
<i>Chenopodium album</i> L. (lambsquarters)	0	S, S
<i>Cichorium endivia</i> L. (cultivated endive)	1	G, -
<i>Cichorium intybus</i> L. (chicory)	1	S, -
<i>Cicuta douglasii</i> (DC.) J.M. Coult. & Rose (western water hemlock)	1	G, -
<i>Cirsium arvense</i> (L.) Scop. (Canada thistle)	1	S, -
<i>Cirsium vulgare</i> (Savi) Ten. (bull thistle)	1	S, -
<i>Citrullus lanatus</i> (Thunb.) Matsum. & Nakai (watermelon)	1	-, -
<i>Claytonia perfoliata</i> Donn ex Willd. (miner's lettuce)	1	-, -
<i>Clematis ligusticifolia</i> Nutt. (western white clematis)	1	-, -
<i>Conium maculatum</i> L. (poison hemlock)	1	S, -
<i>Convolvulus arvensis</i> L. (field bindweed)	1	S, S
<i>Conyza canadensis</i> (L.) Cronquist (Canadian horseweed)	1	S, S
<i>Coreopsis tinctoria</i> Nutt. (golden tickseed)	1	F, -
<i>Coriandrum sativum</i> L. (cilantro)	1	S, S
<i>Cornus sericea</i> L. (redosier dogwood)	1	F, S
<i>Corylus cornuta</i> Marshall (beaked hazelnut)	1	-, -
<i>Crataegus douglasii</i> Lindl. (black hawthorn)	1	F, -
<i>Crataegus monogyna</i> Jacq. (oneseed hawthorn)	1	F, -
<i>Crepis capillaris</i> (L.) Wallr. (smooth hawksbeard)	1	F, -
<i>Crepis setosa</i> Haller f. (bristly hawksbeard)	1	F, -
<i>Cucumis melo</i> L. (cantaloupe)	1	-, -
<i>Cucurbita maxima</i> Duchesne (winter squash)	1	-, -
<i>Cuscuta</i> L. (dodder)	0	-, -
<i>Cynara scolymus</i> L. (globe artichoke)	1	F, -
<i>Cyperus esculentus</i> L. (yellow nutsedge)	0	-, -
<i>Cytisus scoparius</i> (L.) Link (Scotch broom)	0	F, -
<i>Dactylis glomerata</i> L. (orchardgrass)	0	-, -
<i>Damasonium californicum</i> Torr. ex Benth. (California damsonium)	1	-, -
<i>Datura stramonium</i> L. (jimsonweed)	1	F, -
<i>Daucus carota</i> L. (Queen Anne's lace)	1	S, S
<i>Daucus pusillus</i> Michx. (American wild carrot)	1	G, G
<i>Dicentra</i> Bernh. (bleeding heart)	1	-, -
<i>Dichanthelium acuminatum</i> (Sw.) Gould & C.A. Clark (western panicgrass)	0	-, -
<i>Digitalis purpurea</i> L. (purple foxglove)	1	S, -
<i>Digitaria sanguinalis</i> (L.) Scop. (hairy crabgrass)	0	-, -
<i>Dipsacus fullonum</i> L. (Fuller's teasel)	0	-, -
<i>Echinochloa crus-galli</i> (L.) P. Beauv. (barnyardgrass)	0	-, -
<i>Elymus glaucus</i> Buckley (blue wildrye)	0	-, -
<i>Elymus repens</i> (L.) Gould (quackgrass)	0	-, -
<i>Epilobium ciliatum</i> Raf. (fringed willowherb)	1	F, -
<i>Equisetum arvense</i> L. (field horsetail)	0	-, -
<i>Erodium cicutarium</i> (L.) L'Hér. ex Aiton (redstem stork's bill)	0	F, -

Table 3.3 (ctd.). The predicted nectar availability of the plant species encountered.

Scientific name (Common name)	availability indicator	basis
<i>Eruca vesicaria</i> (L.) Cav. ssp. <i>sativa</i> (Mill.) Thell. (rocketsalad)	1	F, -
<i>Eschscholzia californica</i> Cham. (California poppy)	1	-, -
<i>Fagopyrum esculentum</i> Moench (buckwheat)	1	S, S
<i>Festuca</i> L. (fine fescue)	0	-, -
<i>Foeniculum vulgare</i> Mill. (sweet fennel)	1	S, S
<i>Fragaria</i> L. (strawberry)	1	G, -
<i>Frangula purshiana</i> (DC.) Cooper (Cascara buckthorn)	1	-, -
<i>Fraxinus latifolia</i> Benth. (Oregon ash)	0	-, -
<i>Galium aparine</i> L. (stickywilly)	1	F, S
<i>Geranium carolinianum</i> L. (Carolina geranium)	1	G, S
<i>Geranium</i> L. (geranium)	1	G, G
<i>Gilia capitata</i> Sims (bluehead gilia)	1	-, -
<i>Helianthus annuus</i> L. (common sunflower)	0	-, S
<i>Heracleum maximum</i> W. Bartram (common cowparsnip)	1	G, -
<i>Holcus lanatus</i> L. (common velvetgrass)	0	-, -
<i>Holodiscus discolor</i> (Pursh) Maxim. (oceanspray)	1	F, -
<i>Hordeum brachyantherum</i> Nevski (meadow barley)	0	-, -
<i>Hydrophyllum tenuipes</i> A. Heller (Pacific waterleaf)	1	F, -
<i>Hypericum perforatum</i> L. (common St. Johnswort)	1	S, S
<i>Hypochaeris radicata</i> L. (hairy cat's ear)	1	F, -, n
<i>Impatiens capensis</i> Meerb. (jewelweed)	1	-, G
<i>Juglans regia</i> L. (English walnut)	0	-, -
<i>Juncus</i> L. (rush)	0	-, -
<i>Kickxia elatine</i> (L.) Dumort. (sharp-leaf cancerwort)	0	F, -
<i>Lactuca sativa</i> L. (garden lettuce)	1	F, -
<i>Lactuca serriola</i> L. (prickly lettuce)	1	F, -
<i>Lamium purpureum</i> L. (purple deadnettle)	0	G, -
<i>Lavandula angustifolia</i> Mill. (English lavender)	0	F, -
<i>Leontodon taraxacoides</i> (Vill.) Mérat (lesser hawkbit)	1	F, -
<i>Leucanthemum vulgare</i> Lam. (oxeye daisy)	1	S, S, n
<i>Levisticum officinale</i> W.D.J. Koch (garden lovage)	1	F, -
<i>Linum perenne</i> L. (blue flax)	0	G, -, n
<i>Logfia arvensis</i> (L.) Holub (field cottonrose)	1	F, -
<i>Lolium perenne</i> L. (perennial ryegrass)	0	-, -
<i>Lotus corniculatus</i> L. (bird's-foot trefoil)	0	G, S
<i>Lotus unifoliolatus</i> (Hook.) Benth. (American bird's-foot trefoil)	0	G, G
<i>Lupinus bicolor</i> Lindl. (miniature lupine)	0	F, -
<i>Lupinus</i> L. (lupine)	0	F, -
<i>Lupinus rivularis</i> Douglas ex Lindl. (riverbank lupine)	0	F, -
<i>Lysimachia nummularia</i> L. (creeping jenny)	0	-, -
<i>Lythrum salicaria</i> L. (purple loosestrife)	1	-, -
<i>Madia elegans</i> D. Don ex Lindl. (common madia)	1	F, -
<i>Maianthemum stellatum</i> (L.) Link (starry false lily of the valley)	1	F, -
<i>Malus pumila</i> Mill. (apple)	1	F, -
<i>Malva neglecta</i> Wallr. (common mallow)	1	-, -

Table 3.3 (ctd.). The predicted nectar availability of the plant species encountered.

Scientific name (Common name)	availability indicator	basiss
<i>Marah oreganus</i> (Torr. ex S. Watson) Howell (coastal manroot)	1	-, -
<i>Matricaria discoidea</i> DC. (disc mayweed)	0	F, G
<i>Medicago lupulina</i> L. (black medick)	0	S, G
<i>Medicago sativa</i> L. (alfalfa)	0	S, G
<i>Melilotus officinalis</i> (L.) Lam. (sweetclover)	0	S, -
<i>Melissa officinalis</i> L. (common balm)	0	F, -
<i>Mentha arvensis</i> L. (wild mint)	0	F, G
<i>Mentha pulegium</i> L. (pennyroyal)	0	F, -
<i>Mentha spicata</i> L. (spearmint)	0	F, -
<i>Mycelis muralis</i> (L.) Dumort. (wall-lettuce)	1	F, -
<i>Myosotis discolor</i> Pers. (changing forget-me-not)	1	F, -, n
<i>Nuphar lutea</i> (L.) Sm. (yellow pond-lily)	1	-, -
<i>Ocimum basilicum</i> L. (sweet basil)	0	F, S
<i>Oemleria cerasiformis</i> (Torr.&A.Gray ex Hook.&Arn.)Landon (Indian plum)	1	F, -
<i>Oenothera biennis</i> L. (common evening primrose)	0	S, -
<i>Oxalis stricta</i> L. (common yellow oxalis)	0	S, S
<i>Paeonia</i> L. (peony)	1	-, -
<i>Panicum capillare</i> L. (witchgrass)	0	-, -
<i>Parentucellia viscosa</i> (L.) Caruel (yellow glandweed)	1	F, -
<i>Phalaris arundinacea</i> L. (reed canarygrass)	0	-, -
<i>Phaseolus vulgaris</i> L. (green bean)	0	F, S
<i>Physalis philadelphica</i> Lam. (tomatillo)	1	G, -
<i>Physocarpus capitatus</i> (Pursh) Kuntze (Pacific ninebark)	1	F, -
<i>Pisum sativum</i> L. (garden pea)	0	F, -
<i>Plagiobothrys figuratus</i> (Piper) I.M. Johnst. ex M. Peck (fragrant popcornflower)	1	F, -
<i>Plantago lanceolata</i> L. (narrowleaf plantain)	0	-, -
<i>Plantago major</i> L. (common plantain)	0	-, -
<i>Poa annua</i> L. (annual bluegrass)	0	-, -
<i>Poa pratensis</i> L. (Kentucky bluegrass)	0	-, -
<i>Polygonum aviculare</i> L. (prostrate knotweed)	1	G, -
<i>Polygonum persicaria</i> L. (spotted ladythumb)	1	S, -
<i>Polystichum munitum</i> (Kaulf.) C. Presl (western swordfern)	0	-, -
<i>Populus balsamifera</i> L. (black cottonwood)	0	-, -
<i>Portulaca oleracea</i> L. (little hogweed)	1	-, -
<i>Prunella vulgaris</i> L. (common selfheal)	0	S, -
<i>Prunus avium</i> (L.) L. (sweet cherry)	1	F, -
<i>Prunus domestica</i> L. (European plum)	1	F, -
<i>Prunus</i> L. (plum)	1	F, -
<i>Prunus persica</i> (L.) Batsch (peach)	1	F, -
<i>Prunus subcordata</i> Benth. (Klamath plum)	1	F, -
<i>Pyrus communis</i> L. (common pear)	1	F, -
<i>Ranunculus orthorhynchus</i> Hook. (straightbeak buttercup)	1	-, -
<i>Ranunculus uncinatus</i> D. Don ex G. Don (woodland buttercup)	1	-, -
<i>Raphanus sativus</i> L. (cultivated radish)	1	S, G

Table 3.3 (ctd.). The predicted nectar availability of the plant species encountered.

Scientific name (Common name)	availability indicator	basis
<i>Rheum rhabarbarum</i> L. (garden rhubarb)	1	F, -
<i>Rhododendron</i> L. (rhododendron)	1	F, -
<i>Ribes nigrum</i> L. (European black currant)	1	-, -
<i>Rosa</i> L. (rose)	1	G, -
<i>Rosa nutkana</i> C. Presl (Nootka rose)	1	G, -
<i>Rosmarinus officinalis</i> L. (rosemary)	0	F, -
<i>Rubus armeniacus</i> Focke (Himalayan blackberry)	1	F, -
<i>Rubus idaeus</i> L. (American red raspberry)	1	F, -
<i>Rubus</i> L. (blackberry)	1	F, -
<i>Rubus laciniatus</i> Willd. (cutleaf blackberry)	1	F, -
<i>Rubus leucodermis</i> Douglas ex Torr. & A. Gray (whitebark raspberry)	1	F, -
<i>Rubus occidentalis</i> L. (black raspberry)	1	F, -
<i>Rubus parviflorus</i> Nutt. (thimbleberry)	1	F, -
<i>Rubus spectabilis</i> Pursh (salmonberry)	1	F, -
<i>Rubus ursinus</i> Cham. & Schtdl. (California blackberry)	1	F, -
<i>Rudbeckia hirta</i> L. (blackeyed Susan)	1	S, -
<i>Rumex acetosa</i> L. (garden sorrel)	1	S, S
<i>Rumex acetosella</i> L. (common sheep sorrel)	1	G, G
<i>Rumex crispus</i> L. (curly dock)	1	S, G
<i>Salix lucida</i> Muhl. ssp. <i>lasiandra</i> (Benth.) A.E. Murray (Pacific willow)	1	F, -
<i>Sambucus nigra</i> L. ssp. <i>cerulea</i> (Raf.) R. Bolli (blue elderberry)	1	G, -
<i>Sambucus racemosa</i> L. var. <i>racemosa</i> (red elderberry)	1	G, -
<i>Saponaria officinalis</i> L. (bouncingbet)	1	S, -
<i>Schedonorus arundinaceus</i> (Schreb.) Dumort., nom. cons. (tall fescue)	0	-, -
<i>Senecio jacobaea</i> L. (stinking willie)	1	F, -
<i>Senecio vulgaris</i> L. (old-man-in-the-Spring)	1	S, -
<i>Sequoiadendron giganteum</i> (Lindl.) J. Buchholz (giant sequoia)	0	-, -
<i>Sidalcea campestris</i> Greene (meadow checkerbloom)	1	-, -
<i>Sisymbrium officinale</i> (L.) Scop. (hedgemustard)	1	F, -
<i>Solanum dulcamara</i> L. (climbing nightshade)	1	S, S
<i>Solanum lycopersicum</i> L. (garden tomato)	1	G, G
<i>Solanum melongena</i> L. (eggplant)	1	G, G
<i>Solanum nigrum</i> L. (black nightshade)	1	G, G
<i>Solanum tuberosum</i> L. (Irish potato)	1	G, G
<i>Sonchus arvensis</i> L. (field sowthistle)	0	S, -
<i>Sonchus asper</i> (L.) Hill (spiny sowthistle)	0	G, -
<i>Sonchus oleraceus</i> L. (common sowthistle)	0	G, -
<i>Spergula arvensis</i> L. (corn spurry)	1	F, -
<i>Spiraea douglasii</i> Hook. var. <i>douglasii</i> (rose spirea)	1	F, -
<i>Spiranthes romanzoffiana</i> Cham. (hooded lady's tresses)	0	-, -
<i>Stachys chamissonis</i> Benth. (coastal hedgenettle)	0	F, -
<i>Stachys mexicana</i> Benth. (Mexican hedgenettle)	0	F, G
<i>Stellaria media</i> (L.) Vill. (common chickweed)	1	S, S
<i>Symphoricarpos albus</i> (L.) S.F. Blake (common snowberry)	1	F, -
<i>Symphyotrichum</i> Nees (aster)	1	F, -

Table 3.3 (ctd.). The predicted nectar availability of the plant species encountered.

Scientific name (Common name)	availability indicator	basis
<i>Symphotrichum subspicatum</i> (Nees) G.L. Nesom (Douglas aster)	1	F, -
<i>Symphytum officinale</i> L. (common comfrey)	1	F, -
<i>Syringa vulgaris</i> L. (common lilac)	1	F, -
<i>Tanacetum vulgare</i> L. (common tansy)	1	F, -
<i>Taraxacum officinale</i> F.H. Wigg. (common dandelion)	1	S, S
<i>Tellima grandiflora</i> (Pursh) Douglas ex Lindl. (bigflower tellima)	1	-, -
<i>Thymus vulgaris</i> L. (garden thyme)	0	F, -
<i>Tragopogon dubius</i> Scop. (yellow salsify)	1	G, S
<i>Trifolium pratense</i> L. (red clover)	0	S, S
<i>Trifolium repens</i> L. (white clover)	0	S, G
<i>Trillium ovatum</i> Pursh (Pacific trillium)	1	F, -
<i>Urtica dioica</i> L. (stinging nettle)	0	-, -
<i>Vaccinium corymbosum</i> L. (highbush blueberry)	1	G, -
<i>Verbascum blattaria</i> L. (moth mullein)	1	G, G
<i>Verbascum thapsus</i> L. (common mullein)	0	S, S
<i>Veronica officinalis</i> L. (common gypsyweed)	0	S, S
<i>Veronica peregrina</i> L. (neckweed)	0	G, G
<i>Veronica serpyllifolia</i> L. (thymeleaf speedwell)	0	G, G
<i>Vicia faba</i> L. (fava bean)	0	S, G
<i>Vicia hirsuta</i> (L.) Gray (tiny vetch)	0	G, G, n
<i>Vicia sativa</i> L. (garden vetch)	0	G, G, n
<i>Vicia villosa</i> Roth (winter vetch)	0	G, S, n
<i>Vinca minor</i> L. (common periwinkle)	0	-, -
<i>Viola</i> L. (violet)	1	-, -
<i>Vitis vinifera</i> L. (wine grape)	0	-, -
<i>Vulpia bromoides</i> (L.) Gray (brome fescue)	0	-, -
ornamental annual (1 spp.) (ornamental annual)	1	-, -
ornamental asteraceae (1 spp.) (ornamental asteraceae)	0	F, -
ornamental asteraceae (3 spp.) (ornamental asteraceae)	1	F, -
ornamental flower (3 spp.) (ornamental flower)	1	-, -
ornamental Iris (1 spp.) (ornamental Iris)	0	-, -
ornamental lilly (2 spp.) (ornamental lilly)	1	F, -
ornamental shrub (1 spp.) (ornamental shrub)	1	-, -
culinary herb (culinary herb)	1	-, -
unknown asteraceae (unknown asteraceae)	1	F, -
unknown asteraceae (1 spp.) (unknown asteraceae)	0	F, -
unknown asteraceae (2 spp.) (unknown asteraceae)	1	F, -
unknown grass (2 spp.) (unknown grass)	1	-, -
unknown seedling (unknown seedling)	0	-, -
unknown wildflower (12 spp.) (unknown wildflower)	1	-, -
unknown wildflower (8 spp.) (unknown wildflower)	0	-, -

Seasonal activity and feeding patterns of ground beetles (Carabidae: Coleoptera) in a western Oregon agricultural landscape.

Michael Russell

Seasonal activity and feeding patterns of ground beetles (Carabidae: Coleoptera) in a western Oregon agricultural landscape.

Abstract

Ground Beetles (Carabidae: Coleoptera) are generalist predators that play a role in controlling agricultural pests. The life histories of different carabid species vary in terms of when the adults and larvae are active, what types of food they eat, and their habitat requirements. Farm surveys and laboratory studies were conducted to document the seasonal changes in activity, feeding, fertility state, and habitat choice of a group of ground beetles common on Willamette valley agricultural fields. Pitfall traps were used to determine the activity season and habitat choice of adult beetles during the growing season, and soil cores were used to determine where beetles hibernated over the winter. Along with the pitfall traps, sentinel prey cards were deployed to measure the risk of predation to a potential prey item of a carabid beetle on the landscape. Beetles were collected each month after pitfall trapping to measure the amount of food they would eat. After the feeding trial, the beetles were dissected and the fertility state and egg load were determined. The activity seasons of the beetles encountered here fell into three general groups. The early season beetles emerge from pupa in the late summer, over winter in perennial grassy habitats, and move into the crop fields to breed and forage during the spring and early summer. Late season beetles emerge from pupae in summer or fall and have a breeding and activity season through fall. One species has two activity seasons per year, once when it emerges from pupation in the spring, and then while breeding in the fall. Larval development occurs during the summer for the early season beetles, and over the winter for the late season and two season species. There was a trend for larger beetles to eat more sentinel prey in the feeding trials than smaller species. The large beetles were primarily late season species, while the midsized beetles were primarily the early season species. Sentinel prey removal rates were significantly increased in areas with high activity of midsized beetles during the spring when midsized beetles were the most active on the landscape. In the summer, when large beetles were active in the landscape, sentinel prey removal rates were associated with large beetle activity densities. These results can help identify the ground beetle species that may be important components of a conservation biological control strategy.

Introduction

Ground Beetles

Historically, the practice of manipulating and managing natural enemies for the biological control of pests has focused on the planned introduction of specialist predators and parasitoids (Greathead 1985). However, the introduction of new species to a region has a number of potential risks, risks that increase as the species moves from specialist to generalist along the host range spectrum (Johnson, et al. 2005, Elkinton and Bottner 2012, Havill, et al. 2012, Simberloff 2012). Conservation biological control attempts to maintain and enhance assemblages of predators and parasitoids that are native or naturalized within an agricultural landscape (Landis, et al. 2000). A growing body of evidence has shown that generalist predators with broad host ranges can be valuable components of a conservation biological system. (Symondson, et al. 2002, Stiling and Cornelissen 2005). Assemblages of generalist predators have a number of potential advantages over specialists including the potential for positive interactions among natural enemy species and the potential for enhanced suppression of pest outbreaks through mechanisms such as density dependent prey switching (Riechert 1992, Losey and Denno 1998, Cardinale, et al. 2003, Snyder, et al. 2006). However, natural enemies can also potentially negatively interact with each other through mechanisms such as intraguild predation and other life history characteristics can limit the ability of generalists to suppress pest outbreaks (Rosenheim, et al. 1995, Snyder and Ives 2001, Koss and Snyder 2004). These complications can make it difficult to predict the actual biocontrol efficacy of generalist assemblages (Symondson, et al. 2002, Snyder and Ives 2003).

Ground beetle assemblages illustrate this complexity. Ground beetles are generalist predators that feed on invertebrates and plant seeds in agricultural systems. A number of studies have demonstrated that both individual species and species assemblages contribute to lower pest abundances (Brewer and Elliot 2003, Edwards, et al. 1979, Kromp 1999, Sunderland and Vickerman 1980). Ground beetles can play an important role in limiting pest outbreaks on farms by concentrating their feeding activity in areas of high pest abundance (Winder, et al. 2005, Bell, et al. 2010). Ground beetles

can also synergistically interact with other natural enemy guilds to reduce pest populations (Losey and Denno 1998, Snyder and Ives 2003).

However, a number of factors complicate our ability to predict the extent to which ground beetles limit pest numbers in actual farm landscapes. First, species differ widely in their specific feeding habits, and it may be only a few species that are responsible for the biological control of specific pests (Sunderland and Vickerman 1980, Prasad and Snyder 2004). Second, ground beetle feeding behavior can be affected by factors other than prey abundance such as relative hunger, size, breeding status, and seasonal preferences (Lovei and Sunderland 1996, Honek, et al. 2006). Third, ground beetle species differ in their overall habitat preferences, and habitat use can vary considerably over the course of a season (Holland, et al. 2005, Holland, et al. 2009). Because of these factors it is likely that ground beetle activity patterns as well as the biocontrol potential associated with that activity is strongly influenced by the specific life history traits of the species composing local beetle assemblages. Although the literature on ground beetles is large and diverse, pertinent life history information for many species is still scarce. In addition, there are few studies that comprehensively document how the dynamics of whole beetle assemblages influences pest suppression potential within farm landscapes. This lack of information makes it difficult to assess how regional and local variation in the composition of beetle assemblages influences the nature of the biological control they provide.

In the U.S. Pacific Northwest ground beetles are known to play a potential role in pest suppression, but we lack a full understanding of how variation in life history and habitat use characteristics among individual species contributes to overall pest suppression potential on farms. Several ground beetle species in the northwest are known to include pest invertebrates and weed seeds in their diet based on laboratory feeding trials and gut analyses of field caught specimens (Prasad and Snyder 2004, Moulton 2011). Several species are also known to forage widely within agricultural fields during the summer, but depend on less disturbed grassy areas during the winter (Prasad and Snyder 2006). Pesticide use and tillage practices can affect ground beetle abundance, but the specific effects vary considerably among species (Green 2011, McGrath 2000). Unfortunately, we currently do not have information on the long term habitat use

dynamics of ground beetle assemblages in the region. In addition, species that are common in Pacific Northwest agricultural areas include both introduced species that have been studied in other regions, and local species for which little is known about basic life history characteristics and habitat affinities.

Prasad and Snyder (2006) demonstrated that interactions between specific life history characteristics in the form of intraguild predation and the preference for alternative prey can indeed influence the level of biological control provided by ground beetles in the Pacific Northwest. It is likely that other life history traits as well as the spatial and temporal patterns of habitat use by individual species influence the overall biocontrol provided by beetles in specific landscapes. The risk that a pest is eaten by a ground beetle is a function of both the likelihood that a pest and a beetle encounter each other and the likelihood that the beetle includes the pest in its diet. Estimating the comprehensive risks that pests face from rich ground beetle assemblages requires developing a fuller understanding of how beetle species differ in their habitat use relative to crop fields and pest phenology (encounter risk) and how beetles differ in their life history traits relative to pest feeding behavior (consumption risk).

Objectives

The goal of this study was to describe how patterns of habitat use and pest feeding characteristics among ground beetle species influence the biological control potential of beetle assemblages in farm landscapes in western Oregon. This study focused on a group of Ground Beetles (Carabidae and Cicindelidae) found on vegetable farms of the Willamette Valley in western Oregon. There were three main objectives: 1) identify the most common ground beetle species and determine where and when those species occur on the landscape and through the seasons; 2) document life history characteristics of species relative to feeding and activity syndromes; 3) relate activity levels of ground beetles in the field to the risk that a potential prey item at the site faces from the beetle predators

To achieve the first objective I sampled the ground beetle community on four farms using pitfall traps and berlese extraction. Sampling occurred across a range of habitats and during each month of the year to characterize the seasonal habitat use (based

on the growth form of the dominant plant species) of each beetle species. To achieve the second objective I used laboratory feeding trials to test the per capita feeding voracity and prey preferences of field caught beetles. I then combined the results of those tests with field observations of life cycle phenology and observations of the reproductive state of live and dissected beetles to characterize broad feeding guilds. The information also provides basic context for understanding the observed patterns in the temporal and landscape distributions of the beetles. To achieve the third objective I measured the removal rate of potential ground beetle prey items in the field using sentinel prey cards deployed concordantly with beetle activity sampling using pitfall traps. Data on both beetle activity and sentinel prey removal were collected at each sampling site to test the degree to which the activity of the defined beetle feeding guilds were correlated with prey removal.

Methods

Study areas

The Willamette valley has deep alluvial soils and a mild climate that is favorable for vegetable production. Vegetables are both grown on diverse smaller farms for the local fresh market and on larger mechanized farms for processing. Habitats surrounding the vegetable fields included other crops like fruit, berries, and seed production. The crops and residential areas are in a landscape mosaic along with roads and wild habitats found in riparian corridors and other areas where steep slopes, wet soils, or other circumstances have prevented cultivation. Wild habitats are often dominated by mixed forests, but grassy areas and shrubby thickets are also common. A diverse community of ground beetles can be found on most types of farms, and they likely play a role in the control of weeds and insect pests.

Ground beetle communities were sampled on four Willamette valley vegetable farms. Three of the farms (G, H, and P) grew a wide variety of vegetables, rotated through smaller fields that are hand harvested for the fresh market. The fourth farm (K) was a larger farm that grew mostly machine harvested sweet corn and green beans for canning. Two of the organic farms (G and P) were sampled over 4 years. These farms had intentionally created grassy habitat to provide shelter for over wintering ground beetles

(beetle banks) in some of their fields. The other two farms (H and K) were sampled for only the last two years. Two methods were used to sample beetles on the farm, pitfall trapping to catch active beetles and soil cores to find inactive beetles.

Pitfall traps

Sampling design

Beetle activity density peaks in the summer and drops to almost nothing during the winter. Pitfall sampling was conducted monthly during all four growing seasons (spring 2008 – fall 2011), but monthly winter pitfall sampling was done only on the two farms sampled during the second winter. All four farms were sampled during the third winter, but samples were only taken every other month on each farm.

The sampling intensity varied over the years of the experiment on three of the farms. In the first year of sampling on farms G and P (2008), traps were evenly spaced along several transects extending across four fields. Pitfall trapping can produce variable results and a single trap at each site lacks the power to distinguish between the effect of the conditions immediately around the trap and the activity density in the general area. Putting more than one trap in each area provides a better measurement of the local activity density and allows for more robust comparisons based on the vegetation around each trap. In subsequent trapping seasons the traps were placed in clusters of four traps on transects across four fields in 2009 and across seven fields in 2010 and 2011. Farms H and K were sampled in 2010 and 2011. Pairs of traps were arrayed along transects extending across fields. There were 26 transects in 2010, but three transects were dropped from farm K in the last year due to low overall beetle numbers. Clusters were laid out so that traps were evenly divided among the different habitat types when there was more than one type of habitat in the area. Putting adjacent traps in different habitats allows comparisons to be made between habitats, while holding the landscape position constant. Trap clusters at the ends of transects included a trap in both the annually tilled crop field, and the perennial field margin. Trap clusters within fields, but on the boundary between crop types, included traps in both crops.

Pitfall trapping method

Non lethal pitfall traps were used to minimize the effects of repeated sampling on the farms and to provide live beetles for laboratory trials. Pitfall traps consisted of a plastic pint (473 ml) cups with a 100 mm diameter at the top. A funnel was fitted in the rim of the main cup to prevent insects from escaping by climbing back up the side of the cup. A smaller cup in the bottom of the main cup had a hole in it to allow the smaller species to escape to an area within the trap that is safe from predation by any of the larger species. The rim of the main cup was buried flush with the soil surface and an aluminum lid was placed over the set up to keep out rain and irrigation water.

Pitfall traps were set out in as close to the same place each month as possible. The habitat type, dominant plant functional group, and recent management activities were assessed at each trap location during each sampling event. Traps were opened for 2 nights before they were checked and the occupants identified and tallied. Most of the collections were released immediately, but some beetles were collected for lab experiments, and vouchers were collected for each ground beetle species identified.

Beetles that have recently emerged from their pupae are called teneral. They are paler and have softer exoskeletons than older beetles. The occurrence of teneral beetles was noted on the sampling days that they were caught. The ground beetles were identified to species based on Lindroth (1969). Rare species are unlikely to exhibit clear patterns in the analysis due to small sample size. All species were characterized based on their size (less than 7 mm = small, 7 – 12 mm = mid-sized, and > 12 mm = large) to allow for analysis of groups made up of all of the carabid species and not limit analysis to only the most common species.

Occasionally, field cultivation or flooding would prevent the opening of a trap, or would destroy it, making data collection impossible. Therefore during some of the months not all of the trap sites were sampled. This only occurred on 315 of the 6175 potential pitfall trap samples (5.1%).

Sentinel prey cards

The risk to predation was estimated with the use of sentinel prey cards placed adjacent to each pitfall trap. *Drosophila melonagaster* pupae were chosen as the sentinel prey item because of their availability and reports that they are an acceptable food choice

for a variety of carabids (Carcamo and Spence 1994). Pupae were freeze killed and 20 were attached to cards with a flour and water paste. The cards were suspended slightly off the ground by a hat pin. A cylinder of 1 cm wire mesh created the walls of an enclosure with a small plastic food tub creating a roof to shed rain and irrigation water. The enclosures allowed entry of ground beetles and smaller organisms, but prevented small mammals from accessing the sentinel prey cards. After the two nights the number of pupae eaten was tallied.

Sentinel prey cards were not used during the second year of sampling, and during a few other months when the fly pupae supply ran out. This reduced the number of samples with both trap and prey card data to 4551. Slugs were attracted to the flour paste, and could damage the cards. It was noted whenever prey cards were clearly destroyed by slugs and those samples were excluded from analysis. This reduced the number of samples to 2557, a 44% reduction in sample size. Pooling the monthly samples into three four-month seasons per year helped to ensure more of the trap sites were included in the analysis. There were 1748 potential seasonally pooled estimates for each site during each four month interval over the four years that had a prey card deployed, in 399 instances (23%) the prey card was destroyed by slugs during each sample month in the season and there was therefore no estimate for the site.

Soil cores

During December, soil cores were taken in several different habitats on the vegetable farms. Plots were haphazardly located in representative patches in each of the main habitat types on the farm. In the first year a single sample was taken in each plot, but in subsequent years paired cores were taken at each plot to make a better estimate of the invertebrate community.

The habitat type and the dominant plant species and growth form were recorded at each sample location. Soil cores were taken with a 15 by 20 cm steel frame that was pounded 15 cm into the ground. Each pair of soil cores was transported to a lab where the cores were broken up by hand while being placed as pairs into Berlese funnels. An incandescent light was used to dry the soil and drive the inhabitants out of the cores and into collecting jars filled with ethanol. The soil was checked for dryness frequently and it

generally took between two to four weeks for the soil to become completely dry. When the soil was dry, the invertebrates, soil, and other debris that had fallen in the sampling jar were strained from the alcohol. The invertebrates were sorted from the other material and tallied. This study focuses on the ground beetles, which were identified to species based on Lindroth (1969).

Feeding trial 1: Voracity

During the last 2 years of pitfall trapping, up to 15 beetles per sampling period from each of the common, large and midsized species were brought back to the lab to determine how much of the sentinel prey (fly pupae) each species would consume. Feeding arenas were created by filling large plastic tubs (approximately 50 by 35 cm by 25 cm deep) with about 2 cm of moistened sand. The tubs were placed on the ground on gravel in a shady area.

Five individuals of a single species were placed in each tub along with five sentinel prey cards (100 fly pupae total). After 2 days the number of pupae eaten from each card was counted. The sum of the pupae eaten from all five cards was divided by the five beetles in the box to calculate the mean number of pupae eaten per beetle over the two days in the arena (Maximum 20 per beetle). There were up to three arenas created for each species each sampling period, but many species had fewer than 15 collections during some sample periods and therefore filled fewer arenas.

Feeding trial 2: Fly pupae versus pigweed seed choice

After the first feeding trial, the beetles were removed from the arenas and brought inside the lab for a feeding choice trial. These trials were conducted in a smaller (15 cm by 30 cm base) box with only a moist paper towel for bedding so it would be possible to distinguish true seed predation from caching behavior that ground beetles sometimes exhibit (Manley 1971, Hartke, et al. 1998). Three beetles of one species were placed in each box. One sentinel prey card with 20 fly pupae on it and a moistened piece of filter paper with 20 imbibed *Amaranthus retroflexus* (pigweed) seeds were placed in the box with the beetles. *Amaranthus* seeds have been seen to be readily consumed by ground

beetles in other studies (Lund and Turpin 1977). The boxes were left in the lab overnight and the numbers of items eaten were checked after 24 hours.

Dissections

The beetles were put through three or four more days of feeding and activity tests before they were freeze killed and stored frozen (Beetle activity appendix). At the end of the field season, the frozen beetles were dissected to determine their fertility state. Male ground beetles of many species can be identified by the presence of special pads on the protarsi, while females lack the pads. Up to five females of each species from each sample period were dissected. Each beetle was measured in millimeters, checked for the presence of developed flight wings, and then dissected to check for the presence of eggs. The eggs, which are clearly visible as they accumulate in female oviducts, were tallied to document beetle fertility state (Luff 1973).

Analysis

Beetle inventory, seasonal activity, and habitat use

The mean number of beetles caught in any of the traps was estimated for each species during each month. The monthly activity patterns of each species were examined to look for qualitative differences between species.

The overall annual mean activity density was calculated for each species at each pitfall trap site. These means were used to estimate the beetle presence within different habitat types during the activity season of the beetle. Analysis of variance and Tukey's Honestly Significant Difference multiple comparison tests were used to test for differences in the number of beetles from each species that were pitfall trapped within different habitat types. The pair of soil cores from each habitat patch was placed together in Berlese funnels to sample inactive season beetles. The beetle collections from each funnel were used to estimate their densities within the habitat patch. Analysis of variance and Tukey's Honestly Significant Difference multiple comparison tests were used to test for differences in the total number of all ground beetles collected from soil cores in each habitat type.

Habitat types were characterized by the growth form of the dominant plant species growing around the trap or soil cores. Plant growth forms were defined as annuals, perennials, and woody species. Additionally, some of the pitfall traps were deployed soon after tillage of the field and were bare of vegetation.

Feeding trials

For the voracity feeding trial, analysis of variance and Tukey's Honestly Significant Difference multiple comparison tests were used to test for differences between the mean number of pupae eaten by each species. Linear regression was used to test whether fly pupae consumption was correlated with beetle size. In the choice feeding trial, the response variable was the ratio of the number of seeds consumed to the total number of items consumed including both seeds and the fly pupae. This is a preference measurement with values falling closer to zero representing a preference for insect prey, and values close to one representing a preference for seeds. Analysis of variance and Tukey's Honestly Significant Difference multiple comparison tests were used to test for differences between the species in the mean seed to total consumption ratio.

Breeding activity, pupal emergence, and guild membership

Dissections documented changes in the breeding state of each beetle species, with the month with the most eggs found in each female being designated the peak of the breeding season. The months that recently emerged teneral individuals of each species were observed during sampling was noted. It marked the completion of the larval and pupal stages that began during the previous egg laying season.

Grouping the species into predator guilds involved identifying species whose similar life history characteristics indicate they should have similar predation habitats. If their activities are similar, field populations of the beetles would have the potential to consume a similar group of pests and other prey items in the area. When a number of these species occur in the area, and the species do not interfere with each other, they would likely create a higher overall risk to a potential prey item in combination than each species would individually.

Measurement of predation risk in the field

Comparing activity density and sentinel prey removal rates requires two sets of data. When either the traps or the prey cards were damaged or not deployed there was a missing data point. The results were pooled for each season so it was possible to have data for more sites. Linear regression was used to test for the relationship between the activity density of each predator group on the sentinel prey removal rate during each season.

Results

Temporal activity pattern

Each beetle species had its own pattern of activity and habitat use over the course of the year. The greatest mean monthly activity density for a single species was more than five beetles per trap during the August peak in activity of *Pterostichus melanarius*. None of the other species had a monthly mean activity density of more than one beetle per trap. Among the large species, only *Omus audounii* was active in the spring and early summer. The other large species were active later in the year with *P. melanarius* and *Harpalus pensylvanicus* most active in the late summer and *Pterostichus algidus* and *Scaphinotus marginatus* in the fall (Figure 4.1).

All the midsized beetles were active in the spring and early summer. The *Amara* and *Agonum* species had peak activity earlier in the season than *Harpalus affinis* and the *Anisodactylus* species. *Nebria brevicaulis* had both the earliest activity of any midsized beetles and a second activity season in the fall (Figure 4.1).

The most abundant small species, *Trechus obtusus*, was active in the fall. Small species also had maximum activity during the spring and summer. The *Bradycellus* species had peak activity in August while *Microlestes linearis* and the *Bembidion* and *Stenolophus* species had peak activity in July (Figure 4.1). *Acupalpus meridianus*, with peak activity in June, and *Clivina fossor*, with peak activity in May, were the most common small species with spring to early summer activity seasons. *Loricera foveata* is the only species that was very active during the winter, with a peak activity in February.

In this beetle community there is a general separation in activity season between large and mid-sized beetles. Overall, the beetle community was numerically dominated

by the large species *P. melanarius* which is active along with a few other large beetles in the late summer to fall. In the spring and early summer midsized beetles are active and the most large beetles are not, therefore mid-sized beetles had the highest activity density early in the growing season (Figure 4.2). A variety of small beetles were active over the growing season, but in relatively lower activity densities than the larger species. Only in January and February when *L. foveata* was the only active species were there more small beetles than other species in the traps.

Spatial activity patterns

The beetle use of different habitats on the landscape varied over the seasons. During the growing season the highest activity density was in annual fields, while over the winter the largest populations of beetles were found in perennial margins.

For all of the common species, there were significant differences in the pitfall trap catch of beetles in habitats dominated by different plant functional groups (Table 4.1). For most species, the greatest activity was seen in recently tilled crop fields dominated by annual plants, or with no established vegetation. Habitats dominated by perennial herbaceous plants had sharply lower activity, while numbers caught were lower still in habitats dominated by woody perennials (Figure 4.3). A few large species, including *Pterostichus algidus*, *Omus audouini*, and *Scaphinotus marginatus*, had maximum activity in habitats dominated by perennial vegetation and only limited activity within crop fields.

Not all of the species collected in the summer were present as adults in the winter soil cores. For the species that were present, the majority were collected from areas dominated by dense perennial grasses and forbs. The number of overwintering adult carabids collected from cores was significantly ($F_{2/167} = 3.9$, $P = 0.02$) higher in areas dominated by perennial herbaceous vegetation and very low in annually tilled fields or areas dominated by woody vegetation (Figure 4.4). This is a striking difference from the summer distribution where these species were primarily active in the annual crop fields.

Feeding trial 1: Voracity

The voracity of each beetle species, measured as the mean number of fly pupae eaten over each two day trial by the five beetles in the box, differed significantly between species ($F_{16/356} = 31$, $P < 10^{-15}$). Some species ate almost all of the offered prey items, while other species ate few items (Figure 4.5). There was a general trend for larger species to eat more than smaller species with the largest species eating nearly all (20 per beetle) of the pupae, and smaller beetles eating fewer than 10 pupae per beetle (Figure 4.6). *S. marginatus* and *O. audouini* are two large beetles that ate very few pupae, suggesting that the items presented were not an acceptable food for those species.

The trend for larger beetles to eat more fly pupae is best seen in the midsized beetles. The large beetles often ate all of the available fly pupae so the results from the trial are likely to be underestimates of prey consumption capacity. Looking at the midsized species in isolation there is a relationship between beetle length and the number of pupae they ate. If mean values are calculated for each midsized species during each sampling week there are 52 discrete sampling events among the eight species. There is a significant effect of beetle length on the number of pupae eaten when the weekly mean values for each species are compared ($F_{1/51} = 6.6$, $P = 0.01$, $R^2 = 0.12$). The fact that *N. brevicaulis* tends to be longer than the other beetles that ate the same number of sentinel prey suggests fly pupae may not be a favored food item for this species as well (Figure 4.6). When *N. brevicaulis* is removed from the data set there are 46 sample events and the effect of length on voracity increases ($F_{1/45} = 12.6$, $P = 0.0001$, $R^2 = 0.22$).

The number of fly pupae a species would eat was not constant over the season for many species and tended to be high during periods when their activity was greatest and low when their activity was reduced (Table 4.2). *Amara littoralis*, *Harpalus affinis*, and the spring season of *N. brevicaulis* are examples of where both voracity and activity density increases in the early part of the activity season and decline during the end of the activity season (Figure 4.7). During the fall activity season of *N. brevicaulis* the voracity is consistent between each month. *H. affinis* beetles continued to have relatively high voracity levels later in the season than the activity density peak (Figure 4.7). *P. melanarius* is a large species which ate all of the pupae offered so it is impossible to determine if it would have eaten more during the months with greatest activity on the landscape. There were differences in the specific pattern among other species as well, but

the tendency for voracity and activity to rise or fall in tandem was observed in several species (Beetle activity appendix).

Feeding trial 2: Fly pupae or pigweed seed choice

All of the ground beetle species were found to eat at least a few seeds, but there was significant variability among the species ($F_{13/382} = 20$, $P < 10^{-15}$). A few species like *Nebria brevicaulis* and *S. marginatus* ate very few seeds, and may have only tested the edibility of the ones that were eaten. Other species, including the two species of *Harpalus* and *Anisodactylus binotatus*, ate almost all of the seeds that were presented (Figure 4.8). However, even for the species that ate the highest number of seeds the proportion eaten was never much more than 0.5 indicating an equal preference for seeds and pupae. Within each beetle species the proportion of their diet that was seeds did not generally vary over the season (Table 4.2).

Life history timing

Larval development for each species must occur between the production of eggs by adult beetles, and the emergence of the next generation of adults from pupae. During the pitfall trapping there were two general peaks in ground beetle larvae activity. One peak was in the early summer and the other was in the winter (Figure 4.9). Ground beetle larvae were assigned to three morphological groups. The size based groups (small larvae and large larvae) included larvae of multiple ground beetle species so there were activity peaks in both the winter and the summer. The third group was a distinctive morphospecies that was caught in large numbers within the annual crop fields throughout the winter (winter larvae).

The appearance of teneral beetles marks the emergence of adults from pupae at the end of pupation. Teneral beetles were observed in nine species, but only at one time of year for each species (Table 4.3). Recently emerged teneral beetles were observed in three of the large species and in each case it was early in the activity season of the species. Among many of the mid-sized beetle species, recently emerged adults join the rest of the population near the end of the activity season. *N. brevicaulis* is the exception

among the midsized beetles because teneral beetles were observed during the initial activity period during the spring and not during the fall activity season (Figure 4.7).

The number of eggs in the females of each species varied over the season with many species having a distinct period of egg production followed by a period of decline in the egg load. The peak in egg load coincided with the peak in activity for some species, but for others it was earlier or later in the season (Table 4.3).

The eggs begin the development process that continues as the larvae hatch and grow through larval and pupal stages until emergence as teneral beetles. The season of larval development can be deduced based on the peak in egg load marking the larval hatch and the observation of teneral beetles marking the end of the immature stages (Figure 4.7). The large beetles lay their eggs during their late summer and fall activity seasons and the larvae develop over the winter before finishing pupation at the beginning of the next activity season. Based on the abundance and timing of the “winter larvae” group, it is likely that they are larvae of the large species, *P. melanarius* (Figure 4.9). Overwintering larvae of other large beetles could be represented among the large larvae or may be small larvae if they were in an early instar.

For most of the midsize beetle species, the highest egg loads were observed early in the activity season. The observation of tenerals later in the activity season suggests that larval development of these species occurs in the summer (Figure 4.7). The collections of small and large larvae from the pitfall traps during the summer likely include these species (Figure 4.9). The midsized beetle with two activity seasons, *N. brevicaulis*, was only found with eggs during its fall activity season. The larvae must develop over the winter in this species before the emergence of adults during the spring activity season (Table 4.3).

Wing development

The three native beetles most closely associated with perennial habitat types, *O. audouini*, *S. marginatus*, and *P. algidus*, did not have fully developed wings, while the other species did (Table 4.3). Only around one third of the dissected *Pterostichus melanarius* individuals had full wings. There was a single female of each species of

Anisodactylus without full wings, while the rest of the winged species had full wings in all individuals (Table 4.3).

Ground beetles and sentinel prey removal rate

After excluding samples that were damaged by slugs, a regression identified significant effects of the abundance of certain beetle predator guilds on the number of pupae removed (Table 4.4). In the March through June activity period there were a large number of mid-sized beetles active in the landscape, and fewer large or small beetles compared to late summer. There were greater numbers of pupae eaten at trap sites as the number of mid-sized beetles caught in the pitfall trap increased (Figure 4.10). For small and large beetles there also was a significant association with the number of pupae eaten, but the number decreased with more beetles. During the July to October activity season the relationships were different. The large carabids, which were by far the most abundant group during the later season, were associated with an increase in the number of pupae eaten, but there was no relationship between the other beetle size classes and the number of sentinel prey eaten (Table 4.4, Figure 4.10). Even though the beetle species associated with the fly pupae consumption changed over the year the seasonally pooled mean number of pupae eaten per card was relatively constant during both the spring to early summer (9.5 pupae removed) and the late summer to fall seasons (10.8 pupae removed). During the winter season when the activity of almost all of the beetle species was very low there were 2.8 pupae removed per card.

Discussion

Carabid beetle life histories

The seasonal phenology and habitat use of some of the species encountered on Oregon farms in this study have been documented from other regions, additionally there are congeners of species studied in other regions. (Lys and Nentwig, 1992, Niemelä, et al. 1993, Lövei and Sunderland 1996, Carmona and Landis 1999, Larsen, et al. 2003). While the activity and habitat patterns of ground beetle species are influenced by relatively fixed life history characteristics, they are also behavioral responses that

potentially respond to differences in climate and ecological conditions present in particular regions.

Carabid life histories are distinguished by three main traits: the time necessary for development from egg to breeding adults, the time of year when adults are active or inactive, and the maximum lifespan of a typical beetle (Matalin 2007). There are many permutations possible in these characteristics, but most species fall into one of a few main groups. With the seasonal activity information and the timing of developmental transitions as determined by the egg load and teneral beetle data I was able to assign the common beetle species of Willamette valley farm landscapes to general life history groups. Overall, the general life history groups observed in Oregon broadly correspond with those that have been observed in other regions; however there are some notable specific differences.

Spring active beetles

Harpalus affinis and the species of *Anisodactylus*, *Agonum*, and *Amara* identified on Willamette valley farms are midsized beetles that have a maximum activity and egg laying season in the spring and early summer. In spring active beetles the egg develops through larval and pupal stages over the growing season (Matalin 2007, Saska and Honek 2008). Adults emerge near the end of summer and have a diapause or similar inactive stage before the activity and breeding season the following spring. Many individuals can live for more than one breeding season as well (Kirk 1977). This means over winter mortality of adults can have a drastic effect on population fitness and points to the importance of suitable over winter habitat for these species.

Late summer active beetles

P. melanarius is the most abundant species in Willamette valley farm fields in the late summer. It is a large European species that has become established in much of the United States and Canada. In Europe, the species has been observed to have two different life histories with some beetles having a peak of activity in early summer and others having a peak in late summer (Matalin 2007). In the Willamette valley, the maximum activity is during August and September and peak egg load is during September. It

appears that the larvae over winter, grow the following spring and summer, and the new adults emerge again near the end of summer. *Harpalus pensylvanicus* is widespread north American late summer active beetle that in some systems exhibits a peak in activity earlier in the year when over wintered adults emerge and another peak when the over wintered larvae finish pupation and emerge (Barney and Pass 1986). Other large beetles, including the Pacific Northwest natives *P. algidus* and *S. marginatus*, have eggs in the late summer and fall and larval development over the winter and spring. These species breed soon after emerging from pupae, but they can live a multiple years so a number of adults of these species are likely to need over wintering habitat.

Other life history groups

Among the beetles encountered in this study the seasonal activity groups largely correspond with the size class groups, with mid sized beetles active in the spring and large beetles active in the late summer and fall. However, a few of the beetle species had life history characteristics that differed from other species within their size group. *N. brevicaulis* is a midsized beetle that produces eggs in the fall, while *Omus audouini* is large beetle that is active in the spring.

Nebria brevicaulis has an activity season in the spring, slightly earlier than the other midsized species, when adults emerge from pupae. During the activity season in the fall females produce eggs. Their life history is similar to spring active beetles in that there is a period of aestivation between when adults emerge from pupae and when the breeding season begins except for *N. brevicaulis* the inactive period is in the summer while in the other midsized beetles it is in the winter. The inactive beetles have been shown to congregate in hedgerows during the summer aestivation, similar to how the spring active beetles shelter in grassy habitats for the winter (Fernandez-Garcia 2000). The bi-modal activity season has been observed in *N. brevicaulis* populations in its native range (Penney 1969). Lab experiments have identified the seasonal changes in photoperiod as being a driver of sexual maturation in *N. brevicaulis* and another species of *Nebria* (Penney 1969, Telfer and Butterfield 2004). Photoperiod may influence the maturation of the spring breeding beetles too, but it could also be signaled by cold winter temperatures, or higher temperatures may simply allow development to proceed (Theile 1977).

Omus audouini is a large, Northwest native species which is active from April to July. This is much earlier than the other large beetles in this study. Although it is included as a ground beetle here, it is not taxonomically in the ground beetle family (Carabidae), but rather in the closely related tiger beetle family (Cicindellidae). Teneral individuals were not observed so the larval development season cannot be fully delimited. The taxonomic differences between tiger beetles and carabids mean this species may belong to its own life history group. The fact that it did not eat many fly pupae suggest that it may not have the same effect on risk to a potential prey items as the other large beetles in the predator guild.

Habitat use

Beetle activity was highest within the crop fields for most of the species described here. This result is similar to results from other regions for *P. melanarius*, which has been shown to have reduced activity in habitats dominated with perennial grass and near field edges (Carcamo and Spence 1994, Tuovinen, et al. 2006, Hajek, et al. 2007). *An. sanctaecrucis* also has been associated with tilled crop fields in other studies as have both *Ag. muelleri*, and other species of *Agonum* from other regions (Esau and Peters 1975, Hatten, et al. 2007, Anjum-Zubair, et al. 2010). *H. pensylvanicus* was collected in higher numbers in mown than unmown sites suggesting that the attraction to more disturbed sites may be associated with the amount of vegetative cover (Crist and Ahern 1999).

Other studies have shown different results with some of these species being less abundant in crop fields than other habitats. In a comparison of trap catches of seven species of *Anisodactylus* in Iowa cornfields, fencerows, and prairie, around 80 percent were caught in the fence row, while the prairie had around 15 percent and the corn had only a few collections (Esau and Peters 1975). *An. californicus* from Idaho was caught in no till fields, but not in conventionally tilled fields, although there were few collections overall (Hatten, et al. 2007). Several species of *Amara* from Iowa were most abundant in the fence row, while one species was most abundant in the corn and another species was most abundant in the prairie (Esau and Peters 1975). *Am. californica* from Idaho showed no differences in activity between tilled and untilled dry land grains, although there were few collections overall (Hatten, et al. 2007). In Oklahoma, *H. pensylvanicus* was most

abundant in the riparian areas adjacent to wheat fields, and least abundant within the wheat fields (French and Elliott 1999). In other studies, *P. melanarius* was found to not be associated with tilled agricultural fields (Clark, et al. 1997, Hatten, et al. 2007).

Ground beetle activity may be driven by many factors. The discrepancies between studies may be influenced by the difference in moisture levels within fields and in field margin habitats depending on the local rainfall pattern and irrigation regime. Midwestern farms receive a significant amount of rain over the growing season that is distributed to all the habitats on the farm. On farms in the Northwest, the soil moisture levels get very low during the late summer except in crop fields where supplemental irrigation keeps the soil moist throughout the season. If beetle activity patterns are limited by soil moisture levels, beetles would be more likely to be found in field margins of farms in areas with summer rain than in areas dependant on irrigation. Pesticides can be another factor if their application influences beetle activity.

Beetles with inactive periods such as winter hibernation or summer aestivation will move between the crop fields and other habitats that provide better shelter. This is clearly shown in the greater number of soil core collections from perennial than annual vegetation patches. Extensive trapping regimes can also document populations as they move into and out of their aestivation sites (Fernandez-Garcia 2000). The soil core samples contained primarily immature beetles belonging to the spring activity group that emerge from pupae at the end of summer. There were also mature adults that were experiencing an additional winter.

There were three common species which were primarily associated with perennial habitats during their activity seasons: *P. algidus*, *S. marginatus*, and *O. audouini*. A study of different habitats on a tree farm in southwest Washington found similar results (Johnson, et al. 1966). In that study, *P. algidus* and a different species of *Omus* (*O. dejeani*) were caught in higher numbers in an open forest of Douglas fir and perennial grass than in a recently clear cut site with bare soil and pioneer vegetation (Johnson, et al. 1966). This differed from a species of *Scaphinotus* (*S. angusticollis* Fisch.), which had high numbers in the young forest and the recent clear cut, and low numbers in the grassy open forest (Johnson, et al. 1966). This suggests that the *S. angusticollis* is not simply

responding to the forest cover, but perhaps the woody debris that remains after the harvest.

Three additional large beetle species were only rarely caught, and when they were caught they were in the same or adjacent traps each time. *Metrius contractus* Esch. was caught in the same forested area where *S. marginatus* was caught. *Blethesia multipunctata* Fisch. was only caught on the margin of seasonal pond with shrubs and emergent aquatic plants. A single collection of *O. dejeani* was made from a wide grassy road between the field and a mature forest. These species also are likely to be associated with particular habitats on the landscape, but were too rare to draw any strong conclusions.

Feeding trials

Most of the beetle species observed in this study readily ate the freeze killed fly pupae and the *A. retroflexus* seeds, but a few species did not. These species likely have prey preferences that were not well represented by the fly pupae or seeds used in the study. *Scaphinotus marginatus* has a unique head morphology that suggests it is a specialist on snails and mollusks. In one instance an individual of the tiger beetle, *O. audouini*, was presented with a leafroller (Lepidoptera: Tortricidae) caterpillar which was live and moving around. The beetle immediately attacked and began consuming the caterpillar, suggesting it may prefer active or larger prey to the freeze killed fly pupae used as sentinel prey in this study. The putative diet of *N. brevicaulis* is Collembolans and other small arthropods, and that may explain why individuals ate fewer pupae than other midsized beetles (Penney 1969, Warner, et al. 2008).

The per capita pupae consumption rate was correlated with the mean length of females of the beetle species. Smaller species, like beetles in the *Amara* genus, tended to eat fewer pupae than the larger species. The largest species tended to eat all of the prey items presented, making it likely that their calculated mean per capita pupae consumption rate is an underestimate. Per capita pupae consumption rate tended to rise and fall along with the seasonal activity patterns of the beetles. The activity density estimate provided by pitfall trapping is insufficient by itself to estimate population density (Topping and Sunderland 1992, Lang 2000, Thomas, et al. 2006). If greater activity is associated with

increased food consumption it supports the notion that the pitfall traps can be a good measure of the amount of foraging that beetles are doing in the field.

Species of *Harpalus* and *Anisodactylus* from the Willamette valley consumed a high number of seeds in this study, species from other regions have been shown to consume seeds as well (Johnson and Cameron 1969, Lund and Turpin 1977, Honek, et al. 2006, White, et al 2007, Sasakawa 2009, Sasakawa 2010). In this study the two species of *Amara* consumed seeds. Species of *Amara* from other regions have varied in the types and amounts of seeds eaten (Klimes and Saska 2010, Saska 2005, White, et al 2007, Sasakawa, et al. 2010). *P. melanarius* and three species of *Agonum* from New York State were observed feeding on seeds in the lab (Johnson and Cameron 1969). *P. melanarius* from the Willamette valley ate a large number of seeds, while the species of *Agonum* were found to eat some seeds, but relatively fewer than other tested species. Although most species did eat seeds, no species ate many more seeds than pupae. This suggests that these species may be foraging on both weed seeds and insect pests when they are active in the agricultural fields. Any estimate of the effect of ground beetles on a single pest species would undervalue their overall importance as these generalist predators may play a role in mortality for multiple agricultural weeds and pests.

Predator guild groupings

Ground beetles were assigned to three predator guilds based on body size (small, midsized, and large beetles). Beetles can easily be grouped into a size class just by observation in the field so all of the species encountered could be classified. Among the species collected here, size is also an effective proxy for a number of other beetle characteristics that influence their predation activity. Larger beetles tend to eat more sentinel prey items than the medium sized beetles and small beetles are likely to eat even less. If the sentinel prey is widely acceptable among other ground beetle species, size class should be a good way to classify species based on how much prey they consume. Size can also group the species encountered in this study based on when they are likely to be actively searching for prey in the field. Large beetle populations were dominated by species that were active in the late summer or fall and had larvae that developed over the winter. Mid-sized beetles were dominated by species that were active in the spring and

early summer and had larvae that developed over the summer (Table3). This means that for the species in this study, grouping by size class identifies guilds of generalist predators that have a similar response to the environment and a similar effect on prey communities. Species within each guild act together to increase the overall predation risk that a potential prey item faces in the field.

Sentinel prey consumption

The field pest predation risk as measured by the sentinel prey was related to the activity of the common beetles in this study. The two strongest correlations between sentinel prey consumption and beetle activity density were with medium sized beetles in the spring and large beetles in the summer. These are the periods that these groups are most active in the field and when they will eat the most food in the lab. There is no direct evidence that the reduction in sentinel prey was caused by the beetles that were sampled with the pitfall traps. The slug damage points to a number of possible fates for the sentinel prey items. This is reflected in the relatively low correlation coefficients of the regression models (adjusted $r^2 = 0.01$ for both equations). Despite the low explanatory power, the fact that the significant positive relationships were identified between the most abundant carabid group of the season and sentinel prey removal rate suggests that these species are consuming a significant number of potential crop pests during the seasons that they are the most active. Also the data suggest that prey consumption is relatively equal throughout the season even though the beetle species doing the consumption change.

Implications for conservation biological control

The value of carabids in conservation biological control depends on the extent to which they increase the risk of predation for a pest organism. Both the phenology of potential pest vulnerability to carabid predation, and the activity season of the carabid will determine if a species can play a role in controlling the pest (Warner, et al. 2008). In this study, the overall predation risk faced by potential prey items was maintained at a relatively constant level throughout the season by a diverse range of beetle species with distinct life histories. Seasonal activity cycles and habitat use are driven by the biology of each species. Knowledge of insect life histories makes it possible to identify the species

present on a farm and make predictions about which carabid species may be important predators of specific pests. Information about habitat use may also make it possible to predict which species from the local pool may be rare or missing from a site, and to evaluate the potential impact on biological control. Appropriate modifications can be made to the landscape or management practices to encourage population growth of the target species.

An example of this approach is illustrated by considering the potential for ground beetle assemblages to control the Cabbage looper (*Trichoplusia ni* Hübner). The Cabbage looper is a pest of cabbage and related crops. The larvae move between the vegetation and the soil at the base of the plant, where they are vulnerable to predation by carabids. In the Pacific Northwest there are two generations per year (Berry 1998). When mean daily temperatures for Corvallis, Oregon are used to calculate degree day accumulation, a phenology model for Cabbage looper predicts larvae will be present in June and August. The August caterpillars are at risk from the late summer active beetles group, particularly *P. melanarius*, the most abundant species on each farm (Figure 4.11). *Pterostichus melanarius* is adapted to the conditions of annual crop fields and is common even on heavily managed farms. The spring active species vary in the relative activity density between farms. On farms with lower relative numbers of spring active beetles (farms P and K), the number of potential predators and the associated risk for predation on the June caterpillars is low relative to the number of predators in August (Figure 4.11). Enhancing the populations of the spring active beetle species through conservation biological control is one potential pest management strategy.

There needs to be further research to identify the critical factors that drive the observed differences in populations, but an understanding of the life histories of these beetles points to some possible ways to encourage their populations. The spring active species emerge at the end of summer, and must find a place to hibernate for the winter. The beetles are primarily found hibernating in perennial grassy areas. If these types of hibernation sites are limiting populations, including more grassy areas in the landscape could result in larger beetle populations (Griffiths et al. 2008). Other factors such as the availability of weed seeds as a larval food supply, or refuge from tillage or pesticides may also be important (Hartke, et al. 1998, Sasakawa 2009). When necessary resources are

identified, simple methods for providing those resources can be devised and communicated to farm managers who wish to benefit from the services of these species.

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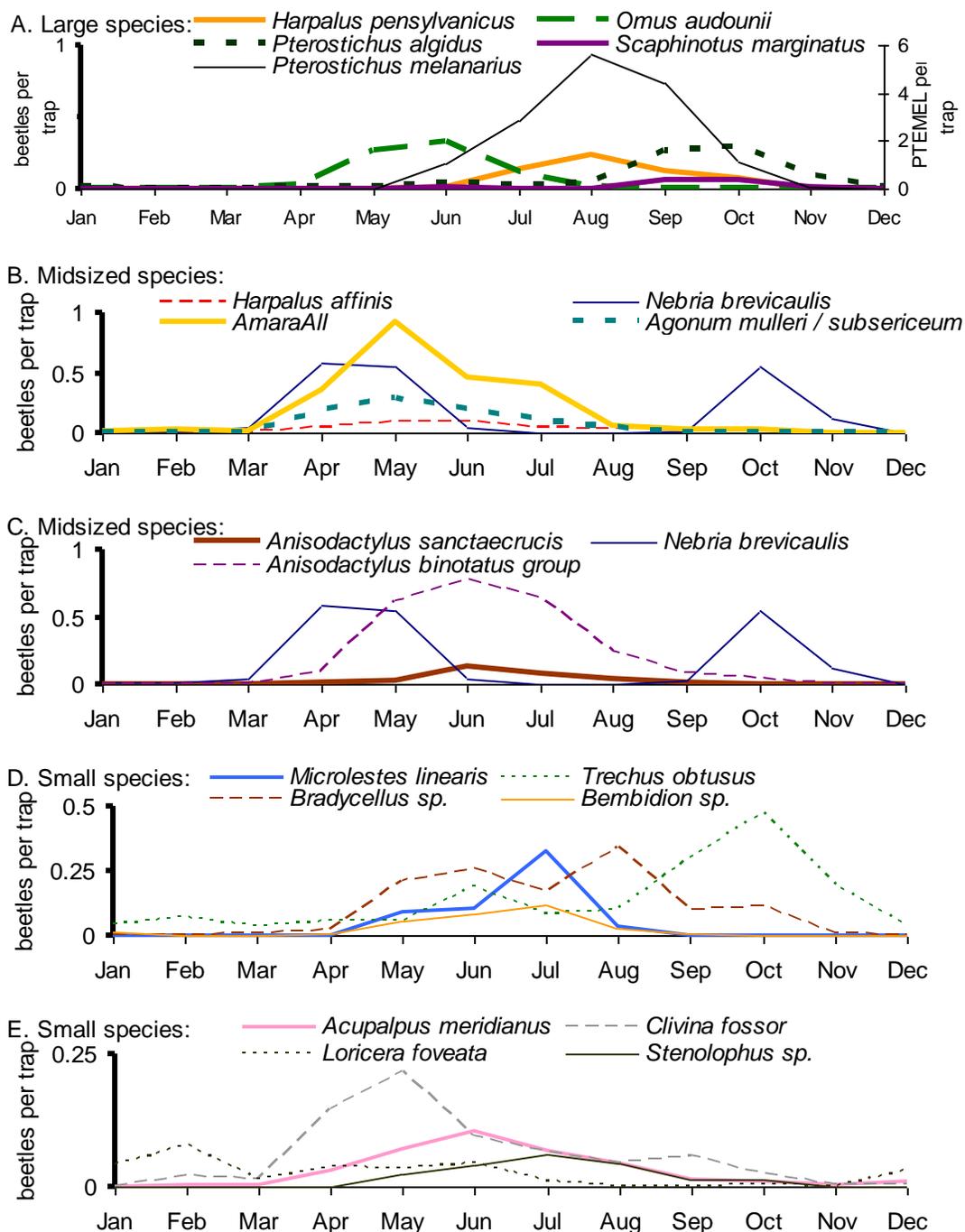


Figure 4.1. The mean number of beetles of each species caught per pitfall trap during each sampling month. The 19 most common species or species groups are indicated by different lines displayed in five panels. A. The secondary axis in the large beetle panel is used to display the extremely high catch counts of *Pterostichus melanarius*. The early midsized beetles are displayed on panels B while the three midsize species with the latest season are on panel C. Panel D displays the four small species with the highest activity density. Panel E displays small beetles with lower mean activity densities. In panels D and E the scale of the Y axis was reduced to more closely match the values.

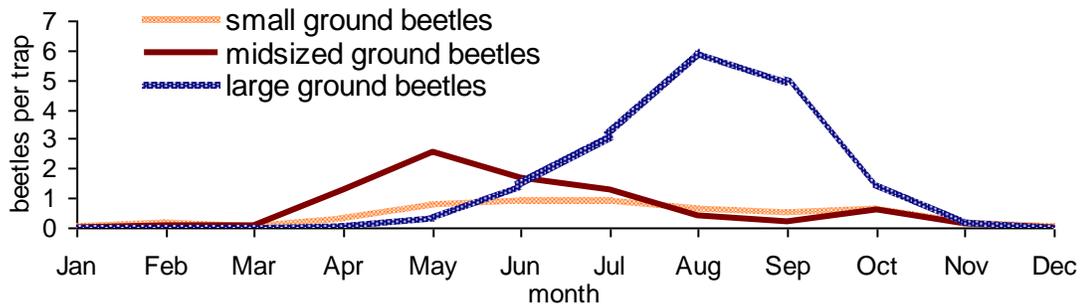


Figure 4.2. The mean number of beetles of each size class caught per trap during each sample month. The beetles are grouped into predator guilds based on their length. Small beetles are less than 7 mm, mid-sized beetles are between 7mm and 12 mm, and large beetles are more than 12 mm.

Table 4.1. F- statistics from anova analyses of the effect of dominant plant functional group on the number of each species caught in pitfall traps. See figure 3 for graphs of the mean counts. Asterisks indicate the significance level (***) < 0.001, ** < 0.01, * < 0.05, < 0.10, otherwise = n.s.). Taxonomy is based on Lindroth 1969.

Species	F - stat and significance code
<i>Agonum muelleri</i> Hbst.	9.7***
<i>Amara littoralis</i> Mnh.	11.7***
<i>Amara californica</i> Dej.	2.1.
<i>Anisodactylus binotatus</i> F., <i>An. californicus</i> Dej. group	9.4***
<i>Anisodactylus sanctaecrucis</i> F.	1.4
<i>Harpalus affinis</i> Schrk.	4.2**
<i>Harpalus pensylvanicus</i> DeG.	10.7***
<i>Agonum subsericum</i> Lec.	1.3
<i>Nebria brevicaulis</i> F.	10.1***
<i>Omus audouini</i> Reiche	29.3***
<i>Pterostichus algidus</i> Lec.	22.6***
<i>Pterostichus melanarius</i> Ill.	57***
<i>Scaphinotus marginatus</i> Fisch.	29.1***
All carabids (and <i>Omus</i>)	70.6***

Figure 4.3. The mean number of ground beetles caught per trap in habitats dominated by different plant functional groups for each carabid species and for all carabids as a group (including *Omus*). The error bars are the standard error of the mean. Bars with different letters were significantly different based on Tukey's HSD multiple comparison test. Table one lists the F-statistics of ANOVA tests for differences in trap counts between dominant plant functional groups.

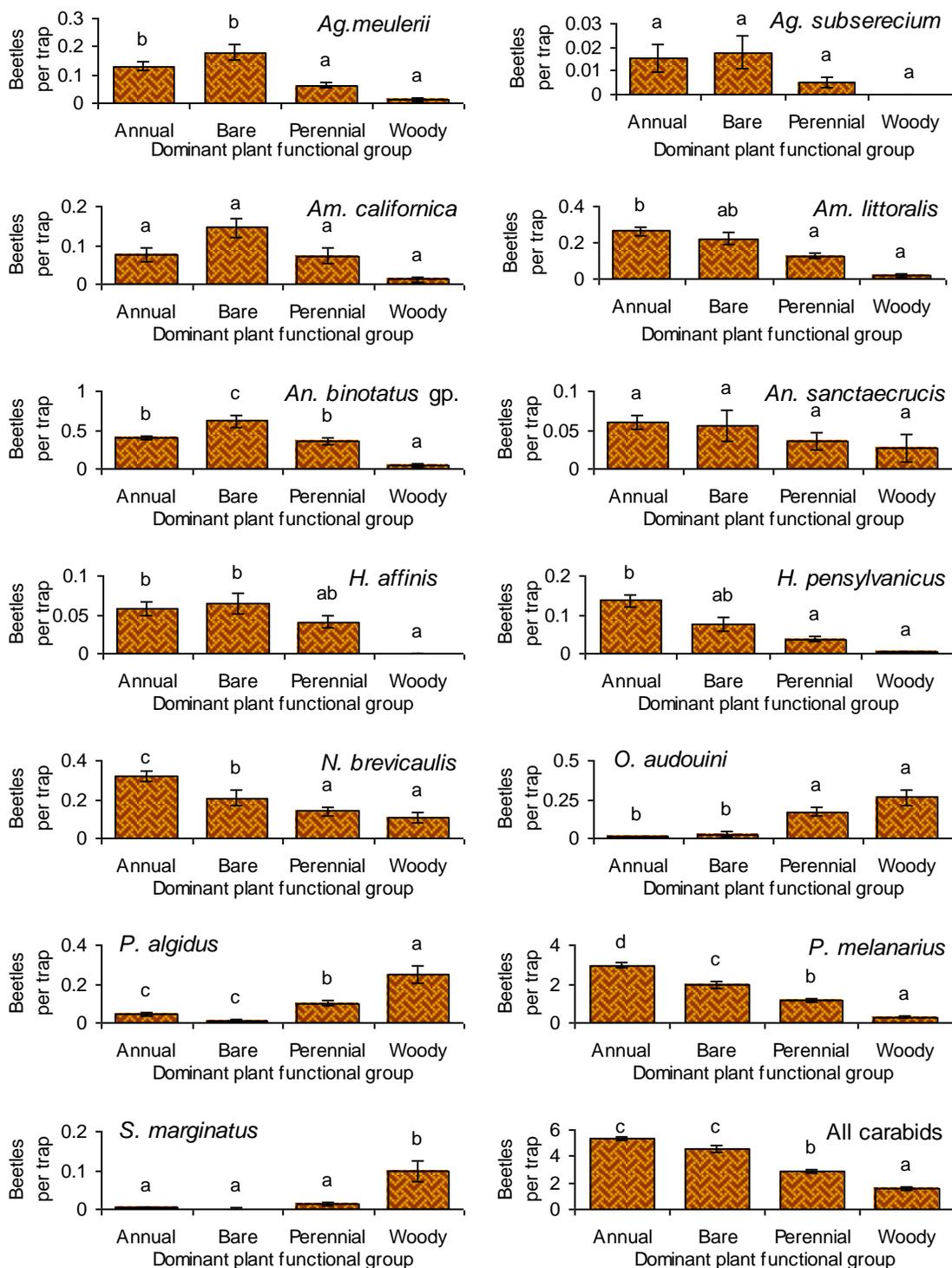
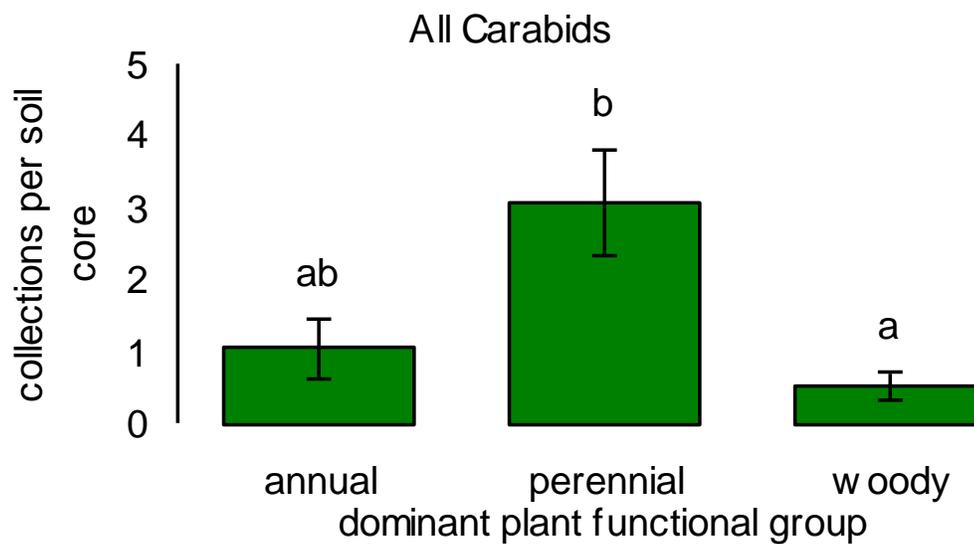


Figure 4.4. The number of ground beetle adults collected from winter soil cores from habitats dominated by different plant growth forms. Error bars are the standard errors of the mean, and different letters indicate significant differences based on Tukey's HSD multiple comparison test.



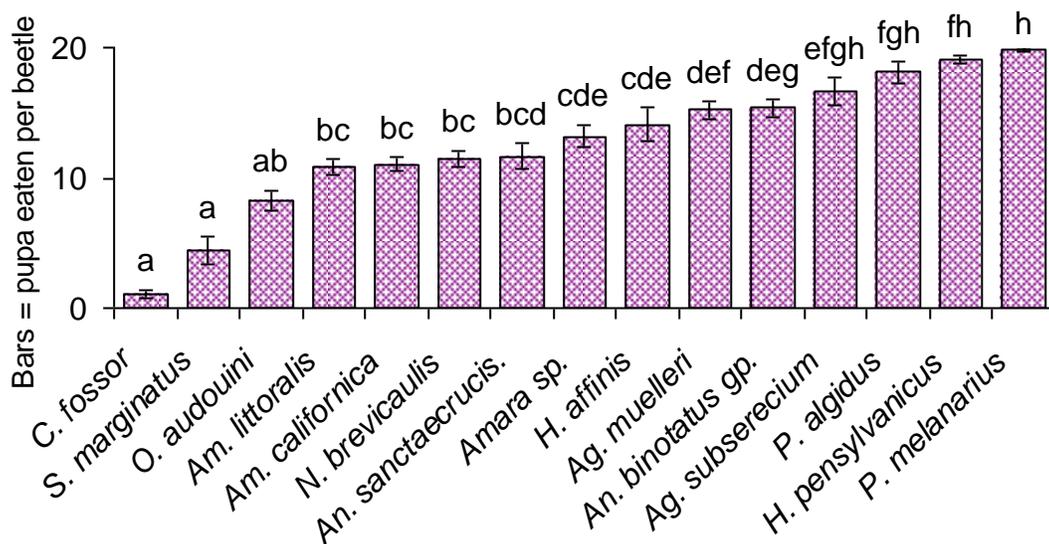


Figure 4.5. The mean number of fly pupae eaten per beetle over two days for species included in the feeding trial. Error bars are the standard error of the mean. Species labeled with different letters were significantly different based on Tukey's HSD multiple comparison test. The points indicate the mean length of female individuals of each species. Species that ate fewer fly pupae than would be expected based on their length are indicated with triangles, diamonds represent the rest of the species.

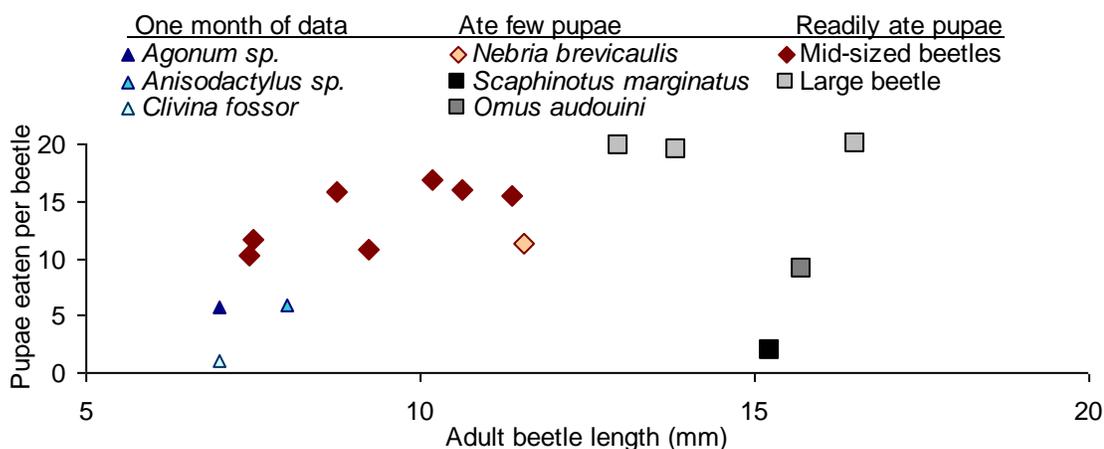


Figure 4.6. The relationship between mean voracity and mean adult length for the common large and mid-sized beetles. Diamonds are mid-sized beetle species and squares are large species. Triangles represent three of the smaller mid-sized species that were only collected during one sample month.

Table 4.2. F statistics, significance, and degrees of freedom from anova models testing for differences between monthly means in the response variables in each feeding trial for each species. Asterisks indicate the significance level (*** < 0.001, ** < 0.01, * < 0.05, < 0.10, otherwise = n.s.).

Trial Response species	Voracity trial pupae per beetle		Feeding choice trial seed to all ratio	
	F - statistic	d.f.	F - statistic	d.f.
<i>Agonum muelleri</i>	7.7**	3/14	3.1.	2/11
<i>Agonum subsericum</i>	9**	3/13	2.2	3/17
<i>Amara californica</i>	3.1.	2/21	3.4*	3/23
<i>Amara littoralis</i>	4.6**	4/39	1.9	5/38
<i>Amara sp.</i>	6*	5/6	1.4	4/9
<i>Anisodactylus binotatus</i>	4.5**	6/48	1.2	6/54
<i>Anisodactylus sanctaecrucis</i>	0.6	4/7	2	5/12
<i>Harpalus affinis</i>	13.9***	4/10	0.2	5/12
<i>Harpalus pensylvanicus</i>	3.6*	4/22	0.5	4/22
<i>Nebria brevicaulis</i>	3.9**	5/29	1	6/31
<i>Omus audouini</i>	4.8*	5/20	1.4	2/16
<i>Pterostichus algidus</i>	0.6	4/16	1.3	4/21
<i>Pterostichus melanarius</i>	1.4	5/51	2.2.	5/51
<i>Scaphinotus marginatus</i>	0.5	1/7	1	2/9

Figure 4.7. The relative activity density, voracity, and egg load of four ground beetle species over the year. The height of the shaded background represents the monthly mean activity density for each species. The line represents the mean number of eggs observed in the dissected females during each month. The values are plotted on the graph relative to the monthly maximum, which is listed in the legend. The bar graph represents the number of fly pupae eaten in each month as a proportion of 20, the maximum value possible. Months when teneral beetles were observed is marked both with a large circle at the top of the graph panel and an asterisk next to the month along the x-axis.

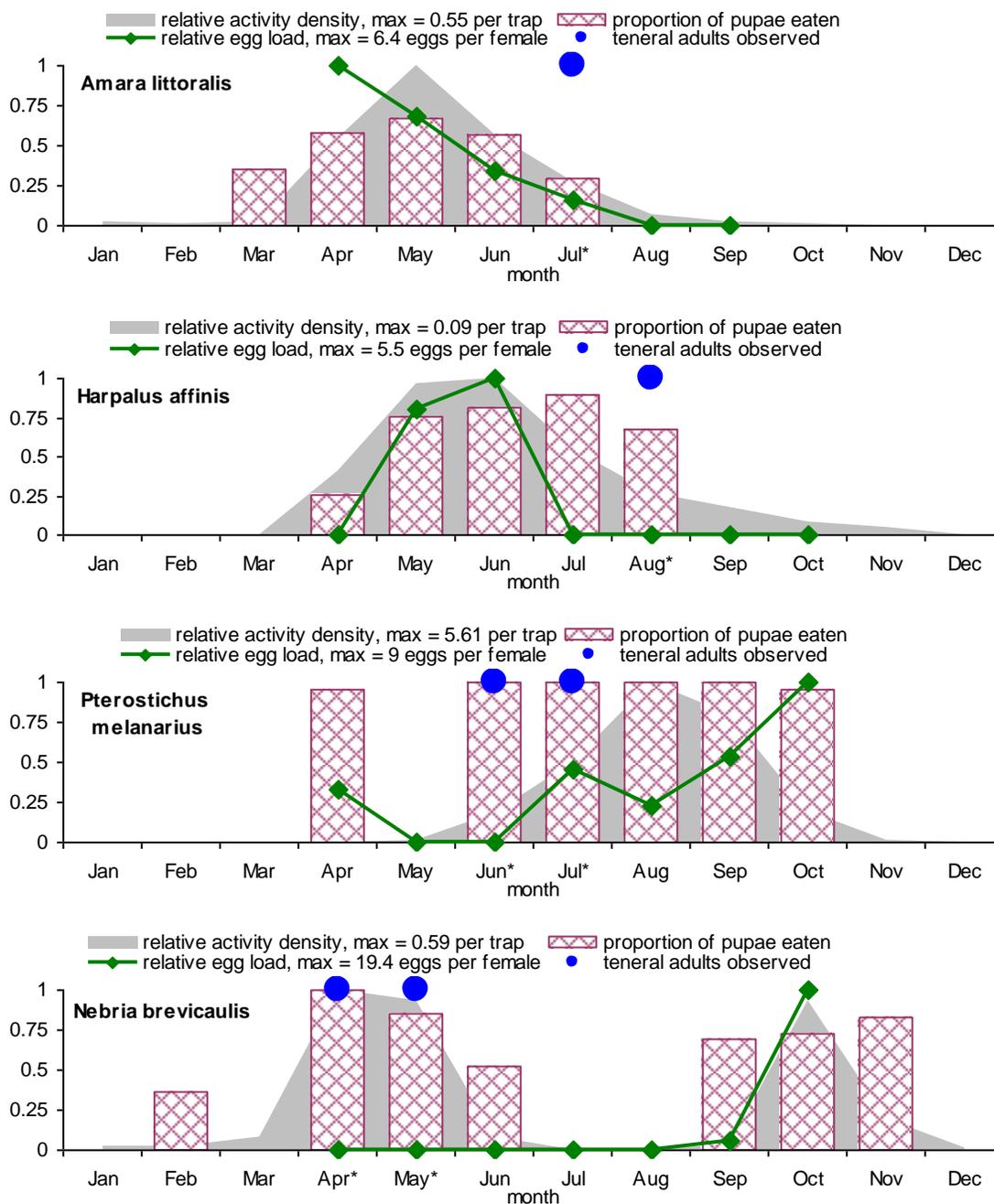


Figure 4.8. The number of pigweed seeds eaten as a proportion of all items eaten for each ground beetle species. Error bars are the standard error of the mean. Species labeled with different letters were significantly different based on Tukey's HSD multiple comparison test.

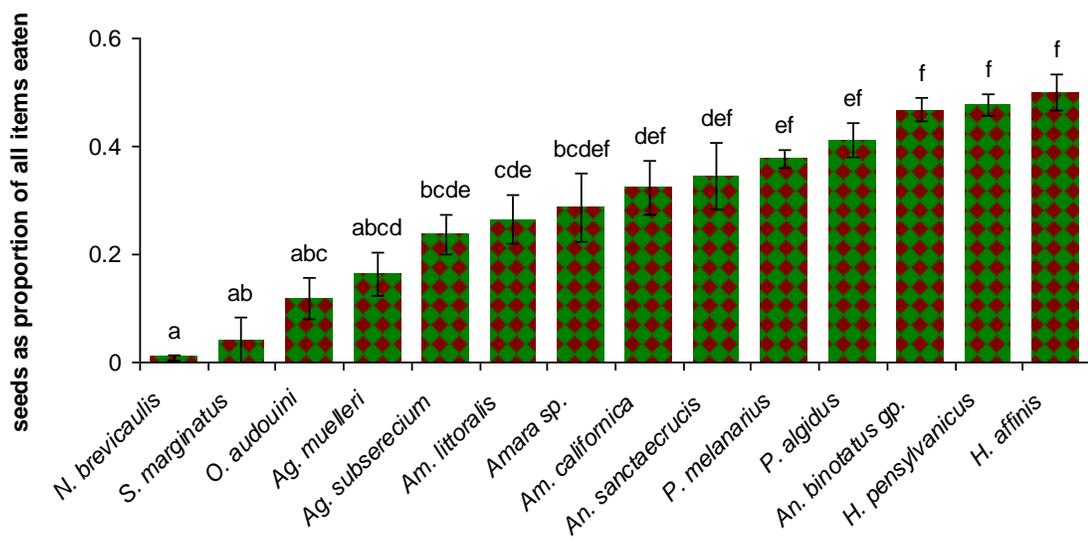


Figure 4.9. The mean number of ground beetle larvae caught per pitfall trap. Beetle larvae were separated into three morphological groups when they were counted. The winter larvae group was the most abundant and the line is drawn with respect to the right side ordinate. Small and large larvae groups are drawn with respect to the left ordinate.

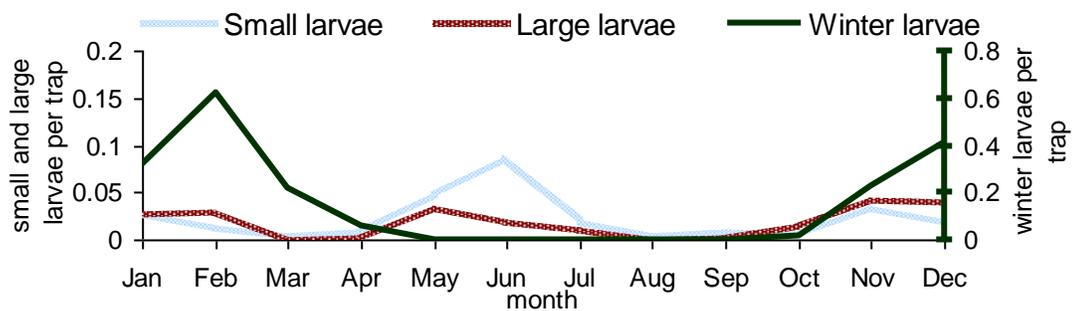


Table 4.3. Life history characteristics of common ground beetle species. Species with a mean length of greater than 12 mm are considered large. Medium sized beetles had mean lengths between 7 mm and 12 mm. The egg load is the number of eggs counted in dissected beetles. The peak is the month with the highest mean egg load. The season range included the months that a significant number of eggs were observed in females of that species. Teneral beetles have recently emerged from their pupa and were only observed at one time of year for each species. The proportion of dissected beetles with full wings is also listed. The active period indicates whether the species are more prevalent near the beginning of the growing season (spring), the end of the growing season (fall) or both in the spring and fall (both).

beetle species	Size class	Egg load of females		tenerals observed	full wings	active period
		peak	season range			
<i>Harpalus pennsylvanicus</i>	Large	Sept.	Aug. - Oct.	Jul-Aug	1	Fall
<i>Omus audouini</i>	Large	July	Apr. - Aug.	NA	0	spring
<i>Pterostichus algidus</i>	Large	Sept.	Sep. / Oct.	August	0	Fall
<i>Pterostichus melanarius</i>	Large	Oct.	Jul. - Oct.	Jun/Jul	0.34	Fall
<i>Scaphanotus marginatus</i>	Large	Oct.	Sep. / Oct.	NA	0	Fall
<i>Agonum muelerii</i>	Midsized	May	Apr. - Jul.	NA	1	spring
<i>Agonum subsericum</i>	Midsized	June	Apr. - Jul.	July	1	spring
<i>Amara californicus</i>	Midsized	June	May / Jun.	NA	1	spring
<i>Amara littoralis</i>	Midsized	April	Apr. - Jul.	July	1	spring
<i>Anisodactylus binotatus</i> gp.	Midsized	July	May - Aug.	Sep	0.99	spring
<i>Anisodactylus sanctaecrucis</i>	Midsized	June	May - Jul.	August	0.98	spring
<i>Harpalus affinus</i>	Midsized	June	May / Jun.	August	1	spring
<i>Nebria brevicaulis</i>	Midsized	Oct.	Sep. / Oct.	Apr/May	1	both

Table 4.4. F statistics from linear regression models testing for the effects of the trap counts of small, medium, and large carabid beetles on removal of sentinel prey items in the field. Asterisks indicate the significance level (***) < 0.001, ** < 0.01, * < 0.05, < 0.10, otherwise = n.s.)

Carabid group	March – June			July - October		
	Estimate	F value	Df	Estimate	F value	Df
Small (< 7 mm)	-0.38	7.3**	1/1181	0.17	2.7	1/1781
Mid-sized (7–12 mm)	0.27	20.4***	1/1181	0.08	2.3	1/1781
Large (> 12 mm)	-0.33	10**	1/1181	0.18	47.7***	1/1781

Figure 4.10. Bar graphs showing the trend for more sentinel prey items eaten when there are more ground beetles present. A.) The mean number of sentinel prey items eaten for each level of medium sized ground beetle trap counts during March through June. The dominant carabid group in the early season is the medium sized beetles and they have the strongest relationship with prey removal rate. B.) The mean number of sentinel prey items eaten for each level of large ground beetle trap counts during July through October. Large beetles are the most abundant group during the late season and also have the strongest relationship with sentinel prey removal.

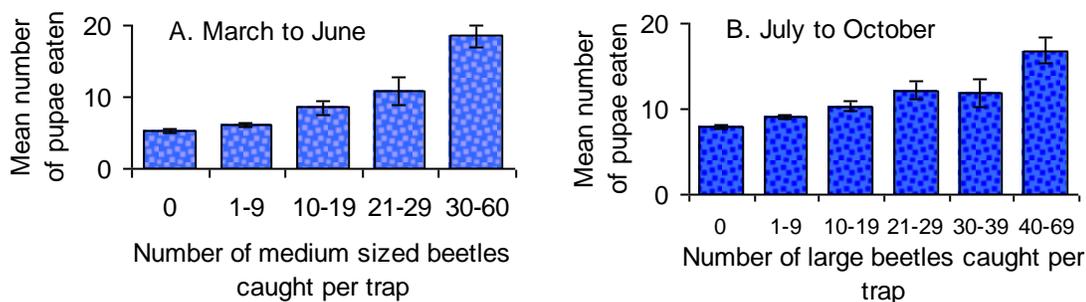
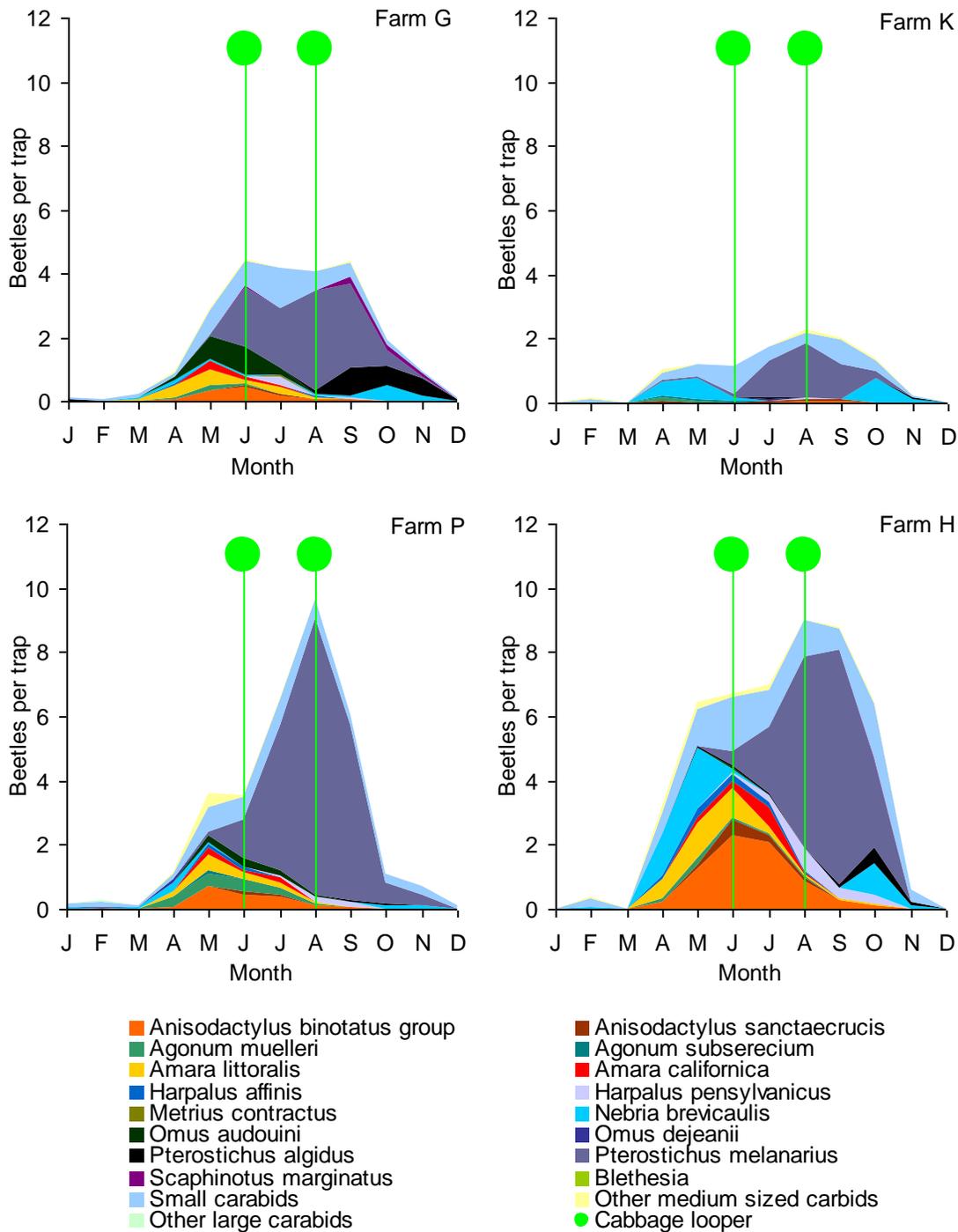


Figure 4.11. The mean number of beetles caught per trap on the four farms. The circles indicate the time of the season that cabbage loopers are in the larval stage in Willamette valley farm fields as predicted by phenology loopers models. The line drawn to the abscissa intercepts the areas whose thickness represents the activity density of all of the carabids mentioned in this study, and other species grouped by size class.



Vegetation characteristics associated with high densities of over wintering predatory
beetles and spiders in western Oregon vegetable farm landscapes

Michael Russell

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Abstract

Carabids (Coleoptera: Carabidae), rove beetles (Coleoptera: Staphylinidae), and spiders (Araneae) are generalist predators of agricultural pests which can overwinter as adults in habitats where dense grass provides protection from cold winter temperatures. These types of habitats are often rare in annual agricultural systems. Beetle banks, raised ridges of soil sown with perennial grasses that run across agricultural fields, are a conservation biological control technique to increase the availability of overwintering habitat for predatory beetles and spiders within annual cropping systems. Ideally, the beetle bank designs would use regionally native species and include a diverse range of species that provide other functional benefits such as floral resources for pollinators. However, the habitat characteristics that influence habitat choice in ground beetles and other generalist ground predators are not well understood. As a consequence it is difficult to predict how variation in the plant species composition of beetle banks might influence their effectiveness. In this study I used soil core sampling to describe the overwintering habitat use of ground beetles, rove beetles, and spiders in vegetable production landscapes in the Willamette Valley, OR. I also experimentally constructed beetle banks using several native Oregon grasses and forbs and tested how variation in plant species composition influenced the overwintering abundance of the three arthropod groups over a four year period. I described habitats with respect to several functional characteristics at three distinct spatial scales (the habitat scale, the plant scale, and the arthropod scale) to identify which specific habitat cues best predicted the overwintering associations of the arthropod groups. Additionally, a litter manipulation experiment was conducted to test the degree to which this specific aspect of habitat accounted for differences in arthropod overwintering abundance.

In the field portion of this study, carabids and rove beetles were most commonly found in habitats dominated by perennial grasses. Beetle banks had the highest beetle densities of any of the habitats sampled. Habitats dominated by annuals or woody plants had few beetles. Few spiders were found in annual habitats, but there were high numbers of spiders in habitats dominated by either perennial grasses or woody plants.

Results from the common garden experiments complimented the field results. In general, beetle bank sections planted with grasses had the highest abundance of arthropod predators while banks planted solely in annual forbs had few overwintering arthropods. Banks composed of perennial forb species supported variable densities of arthropods, depending on the plant species. Habitat scale variables including the habitat type or the species or growth form of the dominant plant were the best predictor of arthropod abundance, but plant and arthropod scale variables, such as the coverage of grass and the thickness of the vegetation mat also explained some of the variance in arthropod abundance. In the litter manipulation experiment both spiders and carabids tended to be more abundant in treatments with more litter, while the rove beetles had low abundance in both the addition and removal treatments but were associated with greater total vegetation height. For both grasses and forbs the ratio of basal area to aerial cover was positively correlated with overwintering arthropod abundance. This index can be used to screen plant species for their potential use within beetle bank designs

Introduction

The goal of conservation biological control is to conserve and enhance populations of naturally occurring predators that help control agricultural pests. A number of species of generalist predators including ground beetles (Coleoptera : Carabidae), rove beetles (Coleoptera : Staphylinidae), and spiders (Araneae) can be found in most farm landscapes. These generalist predators are known to feed on arthropod pests in agricultural systems and contribute to lower pest abundances (Kromp 1999, Sunderland 1999, and Symondson, et al. 2002).

The activity of predatory beetles and spiders within crop fields tends to be influenced by field margins and grassy borders (Thomas, et al. 1991, Thomas, et al. 2001, Holland, et al. 2005, Drapella, et al. 2011). This association can be explained by the requirement of shelter for overwintering arthropods in the life histories of the species. Many ground beetle species can live for more than one year and must survive the winters between growing seasons (Matalin 2007). In addition to overwintering mature beetles, a number of both rove and carabid beetle species emerge from pupae in the end of summer and have an inactive hibernation period over the winter as immature adults before

becoming active and breeding in the spring. (Levesque and Levesque 1996, Petersen 1999, Matalin 2007). Many spider species also over winter during immature stages or as mature adults, often in less disturbed habitats such as hedgerows (Shafer 1977, Pywell, et al. 2005).

Agricultural production practices tend to diminish the availability of over wintering refuges for beetles and spiders, and consequently a number of conservation biological control strategies focus on increasing the abundance and quality of over wintering habitat in agricultural landscapes (Landis et al. 2000). One of these strategies is the creation of grassy, 1 - 2 m wide “beetle banks” that run across annual crop fields. Research in the United Kingdom has demonstrated that generalist predators, including ground beetles, rove beetles, and spiders, seek out and benefit from the microclimate afforded by grasses on the beetle banks (Dennis, et al. 1994, Thomas, et al. 1991, Collins, et al. 2003). In comparisons of banks sown to different grass species, the highest generalist predator densities were found in banks planted with cespitose bunchgrass species, particularly *Dactylis glomerata* L. (Collins, et al. 2003, Macleod, et al. 2004). One functional explanation for this relationship is that banks sown to cespitose bunchgrass species have less variable soil surface temperatures than banks with sod forming grasses (Thomas, et al. 1992).

However, beetle bank design criteria developed for one region may not be well suited to other regions. For instance, *Dactylis glomerata* has been identified as an invasive species in the Pacific Northwest (MacDougal, et al. 2006, Parendes and Jones 2000, Williamson and Harison 2002). There are numerous native Pacific Northwest bunchgrass species that may have the same functional advantage as *D. glomerata* and could be used on beetle banks instead, but this hypothesis has not been tested. In addition, an on farm habitat that produces multiple resources for beneficial insects, such as both over wintering shelter for beetles, and floral resources for pollinators and parasitoids may be a more efficient use of space within the field. Perennial forbs, which produce floral resources may also be suitable as over wintering arthropod habitat and could create a multifunctional beetle bank, but again no studies have tested this hypothesis for Pacific Northwest native plants.

Describing and testing the functional habitat of generalist predators is complicated by the fact that it is often not clear at what scale generalist predators perceive and respond to habitat cues. In addition, from a management perspective habitat metrics at some scale may be easier to describe or incorporate into habitat management plans. For instance, if broad habitat classifications based on dominant plant growth form are sufficient to predict generalist predator abundance it may be straight forward to assess the habitat quality at field and farm scales using broad land cover classifications. However, habitat quality could also be strongly influenced by conditions manifest at smaller spatial scales that are tightly linked with the specific plant species characteristics. Three different scales that may be important for determining where a beetle spends the winter are the arthropod scale, the plant scale, and the habitat scale.

Carabids, rove beetles and spiders are relatively small and generally get around by walking through the vegetation, litter and bare soil of their habitat. Their immediate perspective is the ground level. Assessment of habitat condition made at this scale may be the most relevant to some aspects of generalist predator biology. Also, conditions at this scale may not necessarily correlate well with habitat assessments made at the whole plant or habitat scales. For instance, a hibernating arthropod would occupy a fraction of the space that most mature herbaceous plants occupy. At the arthropod scale, generalist predators interact with specific plant structures. For example, a dense cluster of grass shoots may provide high quality sites for finding shelter, or they could inhibit mobility.

Characteristics at the scale of a whole perennial herbaceous plant can also influence habitat conditions for arthropods. Plants shade and shelter an area that is proportional to the size of the individual plant. At the plant scale, the composition and structure of neighboring plants determine how cover relates to other habitat characteristics such as temperature. For example, a single cluster of grass can be a part of a larger stand of grass, or it may be surrounded by other plant species or open areas.

Arthropods may also respond to vegetation at the habitat scale. A mark recapture study found most beetles stayed within about 20 m of the release point over the 2 month sampling period, but some individuals can travel at least as far as 50 m in just a few weeks (McGrath 2000). The beetles can easily range an area of this size and may respond to the general makeup of the habitat patch, rather than the small part of vegetation that

they occupy at any one time. Different types of habitat patches have different collections of plant structures which determine the conditions and resource levels of the site. A patch of grass may be a part of a long grassy beetle bank, or it may be growing with woody plants in hedgerows and forests, or annual plants along roads and in fields.

The differences in amount and architecture of the vegetation ultimately influences the ground beetles through some ecological function. The temperature moderating effect of dense grass clumps is a suggested explanation for the increased beetle numbers that have been observed (Thomas, et al. 1992). Other possible functions may involve vegetation deflecting rain or influencing drainage and soil water levels.

In this study I combine field observation of generalist predator habitat use with experimental manipulations of vegetation to identify the vegetation components that are the best predictors of over wintering habitat in three distinct predator groups: rove beetles, spiders, and carabid beetles. The goal of this study was to identify traits that can be used to select regionally appropriate plant species in beetle bank designs. In the observational portion of this study I used soil core sampling to describe the overwintering habitat use of ground beetles, rove beetles, and spiders in vegetable production landscapes in the Willamette Valley, OR. The experiments included beetle bank common gardens with sections that varied in the composition of native Oregon grasses and forbs to test how plant species composition influenced the over wintering abundance of the three arthropods groups over a four year period. I also described habitats with respect to several functional characteristics at three distinct spatial scales (the habitat scale, the plant scale, and the arthropod scale) to identify which specific habitat cues best predicted the over wintering associations of the arthropod groups. Additionally, a litter manipulation experiment was conducted to test the effects of specific differences in the vegetative cover on over wintering arthropod populations.

This study had three specific objectives. The first was to identify the habitat patches on farm landscapes that are important sites for over wintering predatory beetles and spiders. The second objective was to test a variety of native species for their suitability as beetle bank plants. And the third was to identify the functional traits of native plants and vegetation that are associated with high abundance of predatory beetles and spiders.

Methods

Study site

The Willamette valley has a maritime climate with cool, wet winters with minimal snow cover while summers are warm and dry. A wide variety of vegetables are grown in crop fields on valley flood plains and terraces intermixed with wild and planted forests, tall shrubs, and grassy meadows. Ground beetles and associated arthropods were sampled on four commercial vegetable farms including three organic farms growing mixed vegetables for the fresh market and a larger, conventional farm that grew for vegetable processing plants. The beetle bank farms were sampled for four years, while the other organic farm and the conventional farm were sampled for two years. The beetle bank common garden experiments were conducted at the Oregon State University Hyslop field station near Corvallis, Oregon. Around the common garden there are fields of annual seed and grain crops grown for research and breeding projects separated by grass (*Lolium perenne* L.) covered roads.

On farm habitat sampling

During December on the four working farms, soil cores were taken in several different on-farm habitats. Plots were located in representative patches in each of the main habitat types on the farm. In the first year a single sample was taken in each plot, but in subsequent years paired cores were taken at each plot to make a better estimate of the invertebrate community.

Habitat patches, distinct areas of relatively homogenous vegetation, were identified on each farm landscape, and classified into one of twelve general habitat types based on the plant community and management history (Table 5.1). Sample sites were identified, making sure to have multiple samples from each of the major habitat types present, and to include samples across the landscape. Soil cores were haphazardly located in vegetation patches to sample the insects. Three sets of vegetation structure and composition measurements were taken; documenting differences at the arthropod, plant, and habitat scales. Additionally, a data logger was deployed to measure the functional effect of the vegetation on the environmental conditions at the site.

Insect sampling

Berlese funnels were used to extract the invertebrates from the soil cores. The soil cores covered a 15 by 20 cm rectangle on the soil surface and had a depth of 15 cm. The cores were transported to the lab in plastic boxes and broken up as they were placed in the Berlese funnels. It generally took three to four weeks for the incandescent light bulb to dry out the soil cores. By that time the invertebrates had moved through the funnel and were collected in jars of Ethanol. The arthropods were sorted into morphological groups and tallied for each sample. Ground beetles (Coleoptera:Carabidae) were identified to species based on Lindroth (1969). Rove beetles (Coleoptera:Staphylinidae) and Spiders (Arachnida) were identified to morphological groups of the most common species or size classes.

Arthropod scale vegetation sampling

Vegetation composition at the arthropod scale was sampled by estimating the basal and aerial coverage of the plant species growing directly on the 15 by 20 cm soil core. The litter and aboveground vegetation together create a structure that can moderate conditions for over wintering arthropods. The thickness of the ground layer mat of the vegetation was documented by inserting a 0.5 cm diameter dowel rod into the vegetation at two points on the surface of the soil core site. One site was centered in an individual plant clump and the other was a few centimeters away in a space between plants. The height at which the rod was completely obscured by the vegetation was recorded as the basal vegetation mat thickness. The aerial cover of the vegetation was estimated as the core was extracted from the ground. The vegetation was clipped at ground level and collected along with the litter for weighing. The coverage of the basal parts of the vegetation that remained was estimated before the soil cores were taken to sample the insects.

Plant scale vegetation sampling

Plant scale vegetation composition and coverage was estimated with a 0.25 m² square point intercept grid. Both the uppermost plant and the soil surface coverage were

recorded. The two dowel rods used in measuring the vegetation mat thickness were also used to measure the total vegetation height by recording the maximum height that each rod intercepted any vegetation.

Habitat scale vegetation sampling

On the working farms, habitat patches were identified based on the dominant plant species and management regime. The vegetation patch that the soil core was in was classified into basic habitat types based on the vegetation in the area around the sample (Table 5.1). Habitat types included annual crop fields with old crops, cover crops, or straw mulch. Other patches, like meadows and grassy roads, were dominated by grasses and other herbaceous perennials. There were also habitats dominated by woody plants including forests, hedgerows and areas where the invasive shrub *Rubus armeniacus* Focke (Himalayan blackberry) forms dense brambles.

Vegetation function and environmental conditions

Moderating extreme temperatures has been suggested as the main functional driver of vegetation providing overwintering arthropod habitat. The light reaching the soil surface is another important environmental condition that relates to vegetative cover. A single Hobo pendant was placed on the ground underneath the vegetation at the sample site for the week prior to soil core sampling. The loggers recorded temperature and the amount of light reaching the soil surface at hourly intervals over the week previous to the soil sample collection. The sample was limited to data collected during the five full days (midnight to midnight, 0:00 - 24:00) between placing the logger and taking the core sample. The mean was calculated for both the light and temperature data, and the moderating effect of the vegetation was measured by calculating the standard deviation of the temperature.

Common garden beetle bank plantings

On the Hyslop research farm a common garden was established to test how variation in plant composition influenced the overwintering abundance of the three arthropod groups. The common garden consisted of several 1.7 m wide raised beds

spaced every 5.5 m across a 60 m long field. Several species of grasses and forbs were sown on the banks which were left to develop with annual mowing in the late summer, but received no further soil disturbance. The spaces between the banks were mowed annually at the same time as the experimental banks, and tilled once or twice a year to plant and turn under winter grain cover crops. There were two experiments that used the banks as a common garden, and one experiment testing the effects of specific litter manipulations. The first common garden experiment compared six grass species, while the other compared five grasses, five perennial forbs, and four annual forbs. The species in the experiment included Willamette valley native prairie plants, an exotic grass recommended for English beetle banks (*Dactylis glomerata*) and annual forbs and a perennial grass that are weeds of regional agricultural areas (Table 5.2).

Grass only common garden experiment

In the grass only experiment, each of the six grass species were sown by seed in fall in three single species sections on the beetle bank. The *Elymus glaucus* seeding resulted in poor establishment, so samples were taken from an adjacent bank that was established with transplants. Each 3.3 m section generally consisted of a relatively pure grass monoculture.

Sampling was limited by the number of temperature data loggers so weekly sampling events between January and March were needed to take all of the samples. Not all of the treatment types were sampled each week, but each species was sampled once before any species received an additional sample. The order that the species were sampled was randomized for each round of sampling. Overall there were six samples per species in the first three years of sampling and three samples per species in the fourth year (Table 5.3). The samples were all almost completely dominated by the grass species planted to the section, and only a few sections had other species become a significant component of the vegetation toward the end of the experiment.

In the common garden, only one soil core sample was placed in each Berlese funnel, but insect sampling methods were otherwise identical to the on farm sampling. The vegetation sampling was also mostly identical to the sampling on the commercial farms except that in the grass only common garden experiment the dominant plant

species was considered the habitat type. The temperature sampling in the common garden used a different type of data logger with a different sampling interval than the commercial farm sampling. The loggers used were Hobo V2 data loggers (Onset Corp.) which have five mm diameter soil probes at the end of insulated wires so they could be inserted into the center of a clump of vegetation. Temperature was measured with two probes for each logger which recorded readings at five minute intervals. The probes were placed at the same sites that were used to sample the vegetation height with the dowel rods (one in center of vegetation clump and one a few cm away in a space between vegetation clumps). Samples were taken for the five full (midnight to midnight) days previous to the soil sampling.

Grass and forb common garden experiment

Native perennial and annual forbs and perennial grasses were included in the second common garden experiment. The species were sown alone and in combination to sections of seven beetle banks in an approximately 0.25 Ha field. A planting during the fall when the banks were first created (2007) resulted in inconsistent establishment, so the following fall additional seed was broadcast. The seeding was done in sections sown to each plant species either alone or in combinations with the other species. Several of the sown species had poor establishment or persistence so the intended experimental design was not achieved. After the third year the banks were surveyed and sections with established stands of sown species were identified. There were five perennial grasses and five perennial forbs with good establishment on the banks, and few native annual forbs persisted on some bank sections. Some sections left unseeded had been colonized with annual agricultural weeds. Representative stands of each of the species were identified for sampling. The stands tended to be less homogenous than in the grass only experiment so for most species there were both relatively large single species patches and stands which were mixtures of multiple species. This created stands that varied on a gradient from grass dominated stands, through grass and forb mixtures, to forb dominated stands. During the first year of sampling (2010) only two samples were taken per species, but four samples were taken from each species in the last two years (Table 5.3). Annual forbs were less common on the bank and were considered as a single group during sampling.

There was the same number of samples taken each year from all of the annual forb species as a group than were taken from each perennial species.

The insect, vegetation, and temperature sampling were identical for both the grass only and the grass and forb experiments. However, the habitat scale variables in the grass and forb experiment included differences between plant species and between different plant growth form (annual forb, perennial forb, or perennial grass). Additionally, the vegetation structure of the dominant species was characterized by finding the ratio of basal cover to aerial cover of the species on the soil core. With a common metric describing the vegetation structure it is possible to evaluate the results based on general characteristics that can be measured for any plant species and not be limited to the species tested.

Litter manipulation experiment

In the sixth year after the grass only bank was established, a manipulative experiment was conducted to try to separate the effects of the litter and green vegetative cover. Only two of the species were used in this experiment, *Danthonia californica* Bol. and *Festuca roemerii* (Pavlick) Alexeev. Both are long lived grass species that were still well established on the banks, and had been shown in previous sampling to maintain good populations of over wintering predatory beetles. Both of the species were represented by three bank sections (Table 5.3). Each section was divided into three subsections, each of which was approximately 1 m along the bank. Treatments were randomly assigned to each subsection.

The experimental banks were mown as usual during late summer. There were three treatments in the experiment, which were applied at the beginning of autumn. Subsections receiving the litter removal treatment had all the grass and other vegetation clipped at ground level and removed. The removed litter was spread evenly around the subsection that was assigned to receive the litter addition treatment. The third section was left as a control. A single soil core sample was taken from each treatment in each section.

Management on one of the farms created a natural experiment that provided an additional way to test for the effects of litter. The farm grows a variety of vegetables. Some crops are harvested by fall and fields are subsequently sown with a winter cover

crop. Garlic is also planted in fall, but the fields are covered with a thick straw mulch. Other crops are harvested too late into the fall for tillage, leaving remnants of crops and weeds during sampling. This management was repeated each year of sampling with the different management activities applied to different areas of the farm each year of the rotation. The fields were sampled to compare plots with straw, with cover crop seedlings, or with mature and senescent plants. In this analysis the plots have been tilled within the past year while in the common garden litter manipulation experiment the plots were on established beetle banks that had not been tilled in several years.

Research questions and analysis

The commercial farm sampling data were used to identify important overwintering habitat for predatory beetles and spiders (first study goal) as well as to help identify the vegetation characteristics that are associated with large overwintering predatory beetle and spider populations (third study goal). One specific research question was whether there were differences in predatory beetle and spider populations between on farm habitats with a different habitat type or dominant plant growth form. The arthropod response data from commercial farm sampling was log transformed ($\ln(x+1)$) to mitigate uneven variance among samples. ANOVA and Tukey's honestly significant difference multiple comparisons tests were done to compare the samples from the different habitats on working farms. Tests for differences in the number of each type of arthropod when the samples were grouped by either the habitat type, or the growth form of the dominant plant at the site were performed. A second research question answered with the commercial farm data was which vegetation characteristics were associated with high arthropod predator numbers. Linear regression was used to test for correlations between the vegetation measurements and predatory arthropod numbers.

The grass only common garden was the first test of the suitability of different species as beetle bank plants (second study goal). ANOVA and Tukey's honestly significant difference multiple comparisons tests (using untransformed beetle and spider abundance response data) were used to test for differences in the mean number of arthropods between samples from different plant species. Additional ANOVA tests were performed to check for differences between grass species in each sample year. The

coverage in each year of the target grass and other species were examined to look for changes in the bank sections through time and to try to determine which vegetation characteristics were associated with abundant predatory beetles and spiders (third study goal). Linear regression was used as a quantitative method to test whether the measured environmental variables were associated with arthropod abundance.

The grass and forb common garden experiment was also used to test more native plant species as beetle bank plants (second study goal) and to help identify vegetation characteristics associated high predatory arthropod numbers (third study goal). ANOVA and Tukey's HSD were used to test for differences between plant species in overwintering arthropod abundance in the grass and forb experiment. ANOVA testing was also performed to determine if there were differences in beetle and spider abundance in sections dominated by different plant growth forms. The mean basal to aerial cover was calculated for each plant species in the grass and forb experiment and ANOVA was used to test whether there were differences between plant species or plant growth forms. Linear regression was used to test for associations between predatory arthropod abundances and measured vegetation and environmental characteristics, including the basal to aerial cover of the target plant species. An additional analysis used regression to compare the mean values for each plant species to test whether the predator groups had different responses to vegetation biomass depending on the plant growth form.

The litter manipulation experiment was conducted to help meet the third study goal and to test whether there was an effect of removing vegetative cover or adding litter to a beetle bank on predatory beetle and spider over winter densities. ANOVA was used to test for differences between treatments in the litter manipulation experiment. Linear regression was used to test for associations between the measured environmental variables and arthropod numbers as well. ANOVA was also used to test for differences in arthropod numbers between crop fields from the commercial farm with the straw mulched garlic fields. The straw mulch analysis differs from the litter manipulation experiment in that the treatments were not randomly assigned, so results from this analysis cannot be used to infer causality.

Results

Commercial farm sampling

Of the twelve general habitats sampled on the farms, the highest densities of ground and rove beetles were found in beetle banks (Figure 5.1). Overall, habitats dominated by herbaceous perennials had higher beetle abundance than habitats dominated by annuals or woody vegetation. When the soil core results were grouped by habitat type there were significant differences in the abundance of both carabids ($P(F)_{11/158} = 0.001$) and rove beetles ($P(F)_{11/158} = 10^{-8}$). The differences were even stronger when cores were grouped by the dominant plant growth form ($P(F)_{2/167} = 10^{-5}$ and $P(F)_{2/167} = 10^{-9}$ for carabids and roves respectively). The greatest abundance of spiders occurred in habitats dominated by woody plants or herbaceous perennials while annual habitats had few spiders (Figure 5.1). The differences between cores with different dominant plant growth forms ($P(F)_{11/158} = 0.02$), but differences between habitat types were not ($P(F)_{2/167} = 0.28$).

Among habitats dominated by herbaceous perennials, habitats with more than 15 percent cover of forbs (Mixed meadow and Mixed road) tended to have fewer collections than habitats more completely dominated by grasses. This pattern is evident among all three predator groups, but the difference was only significant for rove beetles (Figure 5.1).

In the samples from the commercial farms, ANOVA models including either the plant growth form or habitat type as categorical variables measured at the habitat scale explained more variability in beetle density than any regression models using quantitative variables measured at other scales (Table 5.4). For spider density there were also differences between habitat variables, but the strength of the effect was much less. At the plant scale there were positive correlations with grass cover and the number of collections of beetles, and negative correlations with forb, litter and bare covers for all predator groups. Woody habitats had the tallest vegetation, and therefore total vegetation height was negatively correlated with carabid density, but positively correlated with spider numbers.

At the arthropod scale there was a positive correlation with grass cover, and a negative correlation with bare cover for all predator groups (Table 5.4). The height of the basal mat of vegetation as measured by the obscured dowel rod was also correlated with

high densities for all predator groups. The biomass of the green cover, particularly of the herbaceous cover was positively correlated with abundance of both beetle groups.

Both mean soil temperature, and the amount of light reaching the soil surface was highest in fields dominated by annual plants. This led to negative correlations between these variables and carabid and rove beetle numbers respectively.

Grass only common garden experiment

Among the grass species tested there were few consistent differences in overwintering ground beetle ($P(F)_{5/121} > 0.46$) and spider ($P(F)_{5/121} > 0.11$) abundances (Figure 5.2). For rove beetles there were significant differences between grass species ($P(F)_{5/121} > 0.02$) with the highest overall densities were in *Festuca roemerii*. The difference was mostly driven by one year's data and did not persist for all four years (Figure 5.3). When the samples were compared by each year the only time there were significant differences between species was for rove beetles in 2008 ($P(F)_{5/31} = 0.01$) and for spiders in 2010 ($P(F)_{5/30} = 0.03$). There were marginally significant differences in carabid numbers in 2011 ($P(F)_{5/12} = 0.07$), but for the other comparisons there were no differences ($P(F) > 0.14$).

One clear difference between the grass species was their persistence on the bank. *Alopecurus geniculatus* grew well the first year, but had largely disappeared by the time sampling ended. *Elymus glaucus* and *E. trachycaulus* had good establishment and cover in the first two years of sampling, but declined in the next two years. *F. roemerii* and *Danthonia californica* were slower to fill up the site, but continued to expand coverage of the bank each year of the experiment (Figure 5.3). They were the only two species that had enough undisturbed cover in the sixth year to be included in the addition removal experiment.

In the grass only common garden experiment there were no annual or woody plant dominated samples, and the herbaceous community was dominated by perennial grasses. The soil core samples were dominated by the target perennial grass species and other vegetation structures were uncommon. Differences in the form of the vegetation structure were slight, but differences in the density and size of the vegetation were more apparent among the samples.

The only variables that were associated with high carabid numbers were measured at the arthropod scale. The basal cover of grass and litter, and the green biomass were associated with high carabid densities in the grass only experiment, and bare soil was associated with low numbers (Table 5.5).

Rove beetles had stronger correlations with variables at both the arthropod and plant scale. In the grass only experiment, high rove beetle densities were associated with large amounts of litter. Litter was important at the arthropod scale where litter biomass had the strongest correlation with rove beetle density. The thickness of the basal vegetation mat also was positively correlated with rove beetle numbers. The plant scale variables, aerial litter cover and total vegetation height, were positively correlated with rove beetle density, while bare cover was negatively correlated (Table 5.5). The variability of the soil surface temperature was negatively correlated with rove beetle numbers, suggesting temperature moderation is the functional link between the vegetation characteristics and the beetle numbers.

Spiders had the fewest significant correlations with vegetation characteristics. Increased green vegetation biomass and reduced basal bare cover (both arthropod scale characteristics) were associated with higher spider numbers. None of the other variables at any of the other scales were correlated with spider numbers.

Grass and forb common garden experiment

In the experiment that included grasses and forbs, the highest ground beetle densities were found in banks dominated by the perennial forb *Achillea millefolium* L. (Figure 5.4). The grass species had generally high numbers of carabid collections, and the annuals had the lowest number. The differences between the beetle abundance between plant species was only not significant by a small amount ($P(F)_{13/92} = 0.07$) while the difference between plant growth forms was right at the significance cutoff ($P(F)_{2/103} = 0.05$). In general the perennial forbs had about the same number of ground beetle collections as grasses, but there was more variability than within the other growth forms. When the perennial forbs were analyzed alone there were significant differences in the number of ground beetle collections between forb species ($P(F)_{4/43} = 0.05$).

For rove beetles, the highest densities were in the perennial grass *Deschampsia cespitosa*. There were not significant differences between species ($P(F)_{13/92} = 0.16$) or plant growth forms ($P(F)_{2/103} = 0.09$), but there tended to be more rove beetles collected from under grasses, and fewer under annual forbs (Figure 5.4). There were no significant differences in the number of spider collections per plot between species ($P(F)_{13/92} = 0.93$) or growth forms ($P(F)_{2/103} = 0.09$).

The presence of forbs in this experiment resulted in a greater diversity of plant structures among the samples than in the grass only experiment. The plant species included in the experiment were from eight plant families and had a variety of leaf types and rooting patterns (Table 5.2). The plant species also varied in size and how much litter they produced.

One notable difference in the vegetation structure of the different plant growth forms is the ratio of the basal and aerial cover of the target species on the soil core. This ratio represents a structural gradient between dense vertical leaves and stems of a large bunchgrass tussock to a rosette of horizontal leaves in a tap rooted annual forb. There were significant differences between the basal to aerial cover ratio between plant species ($P(F)_{13/92} = 0.001$) and between plant growth forms ($P(F)_{2/103} = 0.0001$). The basal to aerial cover ratio is relatively high for grasses and low for annual forbs (figure 5.5). Perennial forbs had a range of values from low to high. The perennial forb with the lowest basal to aerial cover ratio was *Lomatium nudicaule*, which has a basal rosette of leaves subtended by a taproot, similar to the annual forbs (Table 5.2).

Plant species with low basal to aerial cover ratios tended to support the smallest populations of predatory beetles. This trend is made apparent when the grass and forb experimental results are sorted so that the species with the highest basal to aerial cover ratios within each growth form are furthest left (Figure 5.4 and Figure 5.5). There was no clear relationship between the spider populations and basal to aerial cover ratios of the species (Table 5.6).

When the plant species were considered as categories, instead of being evaluated along the basal to aerial coverage ratio gradient, there was not a significant difference between in the number of carabids collected, but there was a significant difference when plots were grouped by plant growth forms (Table 5.6). There were no significant

correlations with any of the plant scale variables for carabids. Only the arthropod scale variables associated with total plant biomass and cover of the target species on the soil core was significantly correlated with beetle populations.

The rove beetles differed from the carabids in that there were stronger associations with grass cover than target species (both grasses and forbs) cover on the soil cores. Other arthropod scale variables were significantly correlated with rove beetle numbers including the biomass of litter on the core, or the thickness of the vegetation mat (Table 5.6). The total height of the vegetation and the total cover of the target species on the plant scale plot were correlated with high rove beetle numbers as well. There were also non-significant trends for greater rove beetle numbers from plots with more grass, and fewer from plots with more forbs (Table 5.6). At the habitat scale there were no significant differences between the plant species, but when species were grouped by growth form there was a marginally significant difference, and when the species were characterized by their basal to aerial cover ratio there was a significant effect.

There were no clear trends when the spider numbers were compared with the vegetation characteristics of either the soil cores or the vegetation plots and the habitat patches they were sampled from (Table 5.6).

The relationships between the responses of different arthropod groups to plants with different growth forms is clearer when the mean values for each plant species are compared (Figure 5.6). There was a strong trend for grass species with greater mean biomass to have more overwintering rove beetles ($P(F)_{1/4} = 0.02$). The trend for annuals was weak ($P(F)_{1/3} = 0.04$) and for forbs there was no trend ($P(F)_{1/4} = 0.7$). There was no trends among any of the growth forms and either carabids or spiders ($P > 0.3$). There was a tendency among all plant growth forms for there to be more carabids on species with greater total biomass ($P(F)_{1/13} = 0.03$), but there was not a trend for spiders ($P(F)_{1/13} = 0.3$).

The three predator groups examined in this study had different habitat responses to plant growth forms and vegetation biomass (Figure 5.6). The carabids have low abundance among annual and perennial forbs with a low total biomass and higher abundance among grasses and forbs with higher total biomass, but within the different plant growth forms the total vegetation biomass is not associated with carabid abundance

(Figure 5.6). It appears that so long as the dominant species produces a sufficient amount of appropriate vegetative cover the site becomes suitable habitat for the carabids. The rove beetles seem to be responding in a similar way to ground beetles in sites dominated by annual or perennial forbs, but grass species with greater biomass support much higher numbers of rove beetles than grass species with less biomass (Figure 5.6). There were no clear trends among the spiders with respect to plant growth forms and vegetation biomass.

Litter manipulation experiment:

In the addition removal experiment, there were very few ground beetles collected from the removal treatment cores. Both the control and the addition treatment had multiple beetles per core, with the addition treatment having slightly more than the control, although due to the small sample size the differences were not significant ($P(F)_{2/15} = 0.33$) (Figure 5.7). Rove beetles had higher densities in the control plots than either the addition or removal treatments, the differences were relatively distinct, but not enough to be deemed statistically significant ($P(F)_{2/15} = 0.06$). There were significant differences in spider densities with the highest numbers in the addition treatment and low numbers in the removal treatment ($P(F)_{2/15} = 0.04$).

The increase of litter in the addition treatment, and the litter decrease in the removal treatment were associated with an increase in both carabid and spider densities. Rove beetles were only associated with greater total vegetation heights (Table 5.6).

The effects on arthropod populations in the litter manipulation experiment differs from the results in the natural experiment on the working farm that used straw mulch of tilled crop fields. Arthropod populations under the straw mulch were very small, and similar to the numbers in the other annual habitat types, annual cover crops and old crops and weeds (ANOVA - $P(F)_{2/21} > 0.3$). This suggests that before the arthropods can respond to the vegetation, tillage disturbances must be ceased to allow appropriate soil conditions to develop.

Discussion

Winter habitat for predatory beetles and spiders on farm landscapes

The carabid and rove beetle populations on Willamette valley farms over winter primarily in habitats dominated by grasses and other perennial herbaceous plants. Fields dominated by annual crops and weeds, and woody vegetation dominated forests and *R. armeniacus* brambles have low populations of predatory beetles. Spiders also have low populations in annual crop fields and high numbers in habitats dominated by herbaceous vegetation. Unlike beetles, spiders had populations in woody habitats that were as high as in the perennial herbaceous habitats. The results are similar to what has been shown in Europe (Thomas, et al. 1991, Thomas and Marshall 1999, Collins, et al. 2003).

Many of the ground beetles collected were from species that concentrate their growing season activity within the annual crop areas and are likely to play a role in biological control of crop pests (see Chapter 2). These ground beetles leave the annual fields at the end of the growing season and seek out patches of perennial grasses and forbs as shelter to survive the winter. Some rove beetle species have a similar life history to the ground beetles and use grassy areas in this way (Petersen 1999). Beetle banks stand out with the highest predatory beetle densities and thus were shown to be an effective method of providing this habitat component on the landscape. Beetle banks are an efficient way to include perennial vegetation among annual crop habitats, minimizing the distance between growing season and over winter beetle habitats.

While spiders were found in high numbers in soil cores dominated by woody vegetation, few beetles were found underneath shrubs and trees. This seems to differ from an English study where woody plant dominated hedgerow habitats were found to have around the same number of carabids and spiders, and more rove beetles than grass dominated field margins (Pywell, et al. 2005). In that study, perennial grass covered almost half of the area of plots that were classified as hedgerows. In this study the samples from woody habitats were centered on distinct patches of woody vegetation and had very little grass on the actual soil core samples. The beetles may be responding to the grassy vegetation structures that make up the base and edges of the English hedgerow habitats. This grassy vegetation structure is largely absent in samples from woody vegetation types in my study.

Plant species performance in the common garden

The beetle bank common gardens were all dominated by herbaceous perennial plants and a large number of beetles were found in the samples. Within the common garden, the grass and forb experiment had more structural diversity than the grass only experiment and it also had fewer differences in the arthropod communities.

In the grass only experiment there was no one species that consistently outperformed the others in terms of abundance of over wintering predatory beetles and spiders. In studies from the United Kingdom cespitose grass species were found to be more suitability as beetle bank plants than other grasses (Thomas, et al. 1991, Collins, et al. 2003). Arthropod populations are variable so this study may not have had sufficient statistical power to detect differences in beetle populations between Willamette valley grass species. However, the practical differences in both vegetation structure and arthropod communities between grass species is small when compared with the differences between grasses and annual forbs that were found in the grass and forb experiment. The differences between grass species were even smaller when compared with the difference between beetle banks and annual crop fields on the working farms. A beetle bank adds a new type of habitat to an annual crop field that will provide a new function to the landscape with any number of grass species chosen.

In addition to the ability of a specific plant species to provide favorable habitat conditions for arthropods another consideration when designing a beetle bank or other insectary habitat is how the life history of the plant species influences how it fits into the farm management system. The long lived grasses, *D. californica*, *D. glomerata*, and *F. romerii*, created a thick mat of vegetation on the bank that excluded weeds and was simple to manage. *Elymus glaucus* and *E. trachycaulus* plants tended to decline after only a few years and bank sections planted with these species were invaded by weeds and ultimately supported fewer beetles. Similarly, *A. geniculatus* was very short lived. During the initial growth season, a year before sampling started, it had relatively high amounts of cover when compared with the other species. That cover quickly died and was replaced by bare areas and weedy forbs. Only in the last year of sampling were there high numbers of beetles captured. By that time, a weedy grass, *Agrostis capillaris* L., began to dominate the *A. geniculatus* sections, creating suitable beetle habitat.

Some forbs in the common garden supported numbers of predatory beetles that were similar to grasses, while few beetles were collected from plots dominated by other forbs. These differences were associated with structural characteristics of the species. This is consistent with observations of English grasses that identified bunch grasses (tussock forming grasses) as providing better habitats than rhizomatous grasses (Thomas, et al. 1991, Thomas, et al. 1992, Thomas, et al. 2002, Collins, et al. 2003, Macleod, et al. 2004). Bunch grasses have shorter distances between tillers than rhizomatous grasses and should have higher ratios of basal to aerial cover, although these studies did not quantify the vegetation in this way. In this study, the ratio between basal and aerial cover of the soil sample cores was identified as a good predictor of beetle abundance. This easily measured descriptor of plant structure could provide a simple screening tool to identify both grass and forb species that may be good habitat for over wintering predatory arthropods.

In a study of woodlands in France, larger numbers of over wintering beetles were found in edges than interiors (Roume, et al. 2011). Edges likely contained areas of perennial grasses which supplied cover for the carabids, but the study also highlights the fact that many species are moving out of crop fields into the forest edges. This suggests another factor to help explain why *A. millefolium* had the highest carabid populations in the grass and forb experiment. One of the stands of *A. millefolium* was in the corner of the common garden and another was near the side. Those plots would be the closest beetle bank to other fields and would be one of the first areas encountered by beetles leaving the fields.

Vegetation characteristics and predatory beetles and spiders

A key component of habitat quality for ground dwelling generalist predators appears to be dense vegetation at or near the soil surface. The thickness of the basal vegetation mat was associated with high arthropod abundance in this study and these results are consistent with results from a comparison of beetle bank plantings from England (Collins, et al. 2003). Another study from England also found higher beetle numbers associated with taller vegetation, but in Norway there was a negative association

with height (Dennis, et al. 1994). One major difference explaining the results is that the vegetation in the Norwegian sites was less dense at the base than English sites.

While the three predator groups in this study were all generally associated with dense grassy cover, the particular differences in responses reflect the fact that each group is made up of a collection of unique species which may respond to different processes associated with the vegetation structure. Many carabid and rove beetle species overwinter as relatively inactive adults and have better survival under thicker vegetation mats (Dennis, et al. 1994). In the Dennis, et al. study, supplemental food did not improve the survival of the beetles. In this case, it appears that the main resource the vegetation provides is protection from harsh winter conditions.

If the arthropod simply uses the vegetation as a place to hide underneath during inactive periods in their life, they may only require a single layer of sufficient thickness. The relationship between the mean plant biomass and carabid beetle abundance suggests that there is a threshold amount of biomass below which samples contain few beetles and above which there is a relatively consistent number of beetles (Figure 5.6). Even though the results of the addition removal experiment were statistically weak, they were also consistent with the threshold effect for carabids. The removal treatment reduced the number of collections of carabids, but the addition treatment did not result in a large increase (Figure 5.7). High carabid numbers in the common garden studies were mostly associated with vegetation characteristics that indicated the threshold was crossed such as the grass cover or green biomass on the soil core, but not measurements associated with total plant size like litter biomass or vegetation thickness and height. The values for cover on the core and vegetation biomass were constrained by the limited area of the soil core relative to the size of the mature plant and the brief period for new growth after the summer dormant period. Low values for these variables indicate bare areas of the core, but when the core is almost completely covered by the target plant the values are near their maximum. Additional thickness of the vegetation on more productive sites does not greatly influence cover measurements. This differs from litter biomass and vegetation height which are influenced by the amount of plant growth in the previous growing seasons and larger values can develop as site productivity increases.

In contrast to the carabids, rove beetle abundance in the common garden experiments were associated with vegetation variables describing both the presence of vegetation as well as the productivity based plant size variables. This can be seen in the trend for grass species with a greater mean biomass to support more rove beetles (Figure 5.6). The cover of litter and vegetation on the 0.25 m² plot is a plant scale variable that rove beetle populations are associated with which also measures the general plant community and not only the presence of a plant structure. Along with the different types of effects on rove beetles than on carabids, rove beetles had stronger associations with vegetation characteristics in general. In other studies rove beetles were more strongly associated with vegetation characteristics as well (Collins, et al. 2003, Pywell, et al. 2005). This may be related with a continuous effect of vegetation on rove beetles and a threshold effect on carabids.

Rove beetles may have a reduced ability to survive over the winter on minimal food (Petersen 1999). Rove beetles also have been shown to respond more to the detrital food chain than carabids (Birkhofer, et al. 2008). Larger and more productive beetle bank plants should support larger detritivore communities, which may account for the stronger association between the productivity based variables and rove beetles. The results in the addition removal experiment may not be consistent with this hypothesis as the addition treatment reduced rove numbers. However, litter was added at the beginning of winter, so if there was not enough heat accumulation for the detritivore community to respond to the litter addition there would not be a population increase due to greater detritivore biomass.

Spiders were collected in relatively small numbers and the only significant associations with vegetation characteristics in the common garden were the cover of bare soil and green biomass in the grass only experiment. In the addition removal experiment there was a clear effect of litter on spider populations. Spiders are attracted to litter and litter bags can be a more effective way to capture many types of spiders than pitfall traps. (Prafiska, et al. 2007). Spiders have been found climbing in the aerial vegetation in other studies and this tendency to use the full volume of the vegetation structure may explain the relationship with vegetation characteristics (Maudsley, et al. 2002). On the commercial farms, spiders were collected in larger numbers from soil cores with both perennial herbaceous vegetation and below woody plants. Spiders include a much

broader taxonomic group than either carabid or rove beetles. The taxonomic diversity may result in more diverse responses of spiders to the vegetation such as their use of woody habitats.

Conclusion

Choosing native species for beetle banks is a wise strategy to ensure the species can survive in the regional environment with little maintenance and to prevent introductions of invasive species. The basal to aerial ratio and thickness of the basal vegetation mat are good characters with which to evaluate the utility of different species as beetle bank plants. Plant species that provided relatively poor overwintering habitat had low basal to aerial cover ratios, formed thin basal vegetation mats, and formed stands that had high amounts of bare soil. These species included annual forbs and the perennial forb *Lomatium nudicaule* that consisted of rosettes of leaves arising from the single root crown of the original seedling (Table 5.2).

Some forb species were associated with high overwintering beetle abundance. These species had dense clusters of vertical leaves produced from short rhizomes, had high basal to aerial cover ratios, and formed relatively thick basal vegetation mats (Table 5.2). *Achillea millefolium* is a good example of this growth form and it supported the highest number of carabids collected in the grass and forb comparison study. Unlike grasses with similar vegetative characteristics, *A. millefolium* produces flowers with pollen and nectar. This helps increase the value of beetle banks as a conservation biological control strategy that provides resources for many groups of beneficial predators. Forbs with less optimal vegetation structure could also be mixed with bunchgrasses to create beetle banks that provide multiple resources. In addition to nectar and pollen, another resource may be required by carabids is seeds for adult and larval development (Sasakawa 2009, Woodcock, et al. 2010). If the beetle bank species produces seeds that are nutritious for beetles that can be another way to support predator populations. Some seeds germinate only in the cold weather or after a cold stratification period (Russell 2011). This could prevent those species from becoming weeds in spring cultivated agricultural fields, even when the seeds are present in the soil. Whichever species are chosen, the longevity of the plants and the ability of the species to dominate

the site and exclude agricultural weeds are also characteristics of good beetle bank species (Collins, et al. 2003).

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Table 5.1. Types of habitats found on four working farms sampled in the field study. The number of plots within each habitat type and the number of farms where the habitat was documented are listed.

Dominant plant growth form	Habitat type	Number of plots	Number of farms with habitat
Perennials	Beetle bank	22	2
	Grass meadow	27	4
	Grass road	22	4
	Mixed Meadow	8	3
	Mixed road	5	4
	Perennial cover crop	6	3
Annuals	Annual cover crop	14	3
	Crop and weeds	30	4
	Straw mulch	3	1
Woody plants	Brambles	15	4
	Forest	14	3
	Hedgerow	4	1

Table 5.2. Species included in the common garden experiment and their growth forms and basic characteristics. The origin is either native (N) or introduced (I) Basal leaf orientation describes the general direction of the main axis of the leaf blade and notes the presence or absence of a petiole. The stem leaves can be smaller and less persistent than the main basal leaves (reduced upwards), the plant can have mainly stem leaves with basal leaves smaller or deciduous (Reduced downwards), or the plant can have both a cluster of basal leaves and a leafy stem (All leaves full).

scientific name	common name and origin	family	Growth form	basal leaf orientation	basal habit	stem leaves
<i>Cardamine oligosperma</i> Nutt.	little western bittercress (N)	Brassicaceae	Annual forb	rosette, sessile	Taproot	Reduced upwards
<i>Collomia grandiflora</i> Douglas ex Lindl.	grand collomia (N)	Polemoniaceae	Annual forb	rosette, sessile	Taproot	Reduced downwards
<i>Geranium carolinianum</i> L.	Carolina geranium (I)	Geraniaceae	Annual forb	rosette, petiolate	Taproot	Reduced downwards
<i>Madia gracilis</i> (Sm.) D.D. Keck	grassy tarweed	Asteraceae	Annual forb	rosette, sessile	Taproot	Reduced downwards
<i>Alopecurus geniculatus</i> L.	Water foxtail (I)	Poaceae	Grass	vertical, sessile	Rhizomatous	All leaves full
<i>Dactylis glomerata</i> L.	Orchardgrass (I)	Poaceae	Grass	vertical, sessile	Bunchgrass	Reduced upwards
<i>Deschampsia cespitosa</i> (L.) P. Beauv	tufted hairgrass (N)	Poaceae	Grass	vertical, sessile	Bunchgrass	Reduced upwards
<i>Danthonia californica</i> Bol.	California oatgrass (N)	Poaceae	Grass	vertical, sessile	Bunchgrass	Reduced upwards
<i>Elymus glaucus</i> Buckley	blue wildrye (N)	Poaceae	Grass	vertical, sessile	Bunchgrass	All leaves full
<i>Elymus trachycaulus</i> (Link) Gould ex Shinners	slender wheatgrass (N)	Poaceae	Grass	vertical, sessile	Bunchgrass	All leaves full
<i>Festuca romerii</i> (Pavlick) Alexeev	Roemer's fescue (N)	Poaceae	Grass	vertical, sessile	Bunchgrass	Reduced upwards
<i>Achillea millefolium</i> L.	common yarrow (N)	Asteraceae	Perennial forb	vertical, sessile	Rhizome	Reduced upwards
<i>Eriophyllum lanatum</i> (Pursh) Forbes	common woolly sunflower (N)	Asteraceae	Perennial forb	leafy shoots	Suffrutescent from rhizome	All leaves full
<i>Lomatium nudicaule</i> (Pursh) J.M. Coult. & Rose	barestem biscuitroot (N)	Apiaceae	Perennial forb	rosette, petiolate	Taproot	Reduced upwards
<i>Prunella vulgaris</i> L.	Common selfheal (N)	Lamiaceae	Perennial forb	vertical, petiolate	Rhizome	All leaves full
<i>Sidalcea campestris</i> Greene	meadow checkerbloom (N)	Malvaceae	Perennial forb	horizontal, petiolate	Caudex	Reduced upwards

Table 5.3. The number of soil core samples taken from each species in each year in the common garden experiment. The banks that the species were planted in are listed along with the year the banks were created and first planted. The annual forbs as a group were sampled as intensively as each perennial grass or forb in the grass and forb experiment. The sums of the count for each annual forb are marked with a double dagger ([‡]) while the individual species counts are offset in the table. In 2012 the grass only banks were only sampled as a part of the litter manipulation experiment. The numbers of control samples taken from both of the species included in the litter manipulation experiment are marked with an asterisk (*).

	Plant species	2008	2009	2010	2011	2012
Grass only experimental banks	<i>Alopecurus geniculatus</i>	6	6	6	3	
	<i>Dactylis glomerata</i>	6	6	6	3	
	<i>Danthonia californica</i>	6	6	6	3	3*
Created fall 2006	<i>Elymus glaucus</i>	7	6	6	3	
	<i>Elymus trachycaulus</i>	6	6	6	3	
	<i>Festuca romerii</i>	6	6	6	3	3*
Grass and forb experimental banks	<i>Achillea millefolium</i>				4	4
	<i>Danthonia californica</i>			1	4	4
	<i>Deschampsia cespitosa</i>			2	4	4
Created fall 2007	<i>Elymus glaucus</i>			2	4	4
	<i>Elymus trachycaulus</i>			1	4	4
Re-sown fall 2008	<i>Eriophyllum lanatum</i>			2	4	4
	<i>Festuca romerii</i>			2	4	4
	<i>Lomatium nudicaule</i>			2	4	4
	<i>Prunella vulgaris</i>			2	4	4
	<i>Sidalcea campestris</i>			2	4	4
	Sum of annual forb species			2 [‡]	4 [‡]	4 [‡]
	Annual forb species in grass and forb Experiment	<i>Cardamine oligosperma</i>				1
<i>Collomia grandiflora</i>				2	1	
<i>Geranium carolinianum</i>					1	2
<i>Madia gracilis</i>					1	1

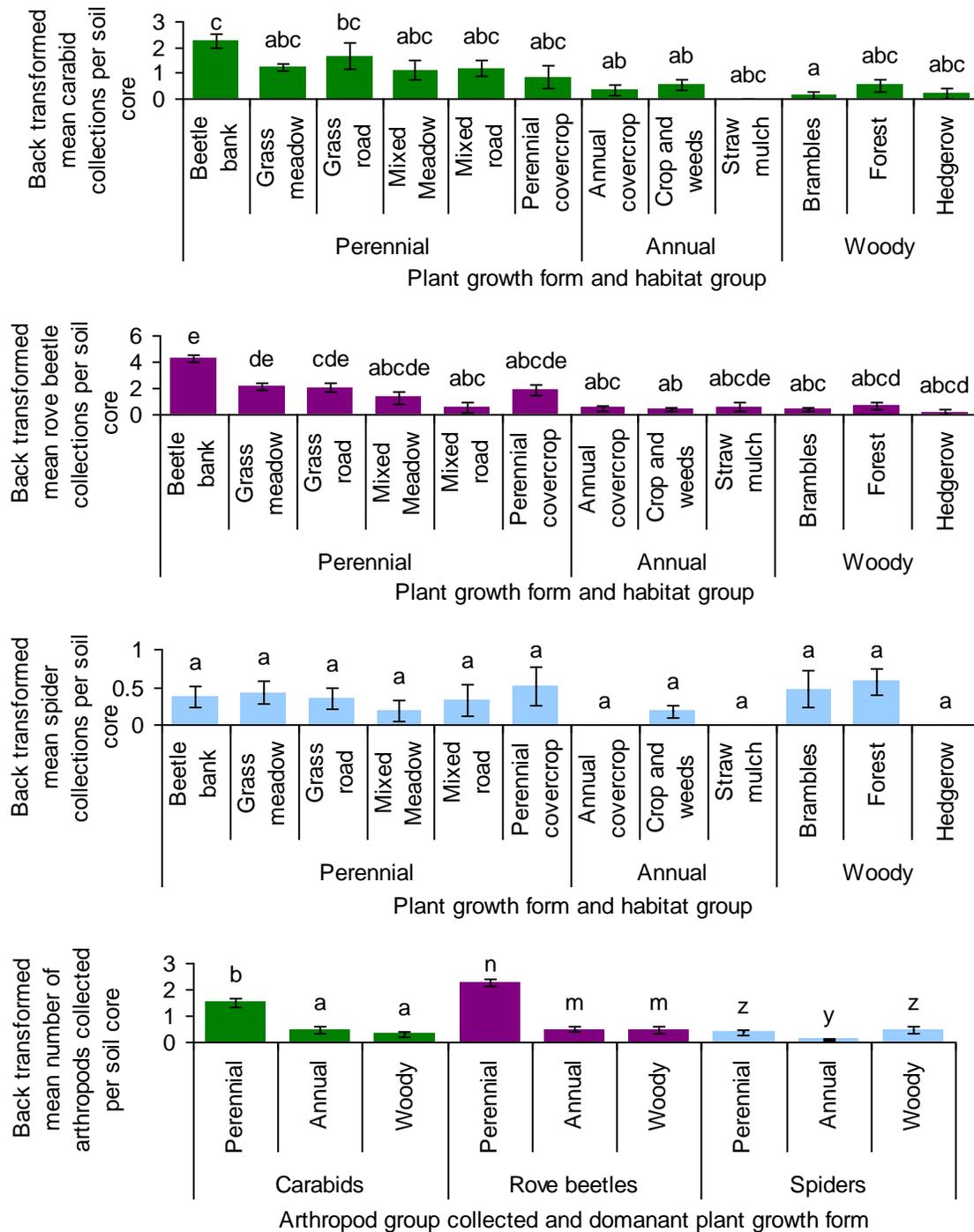


Figure 5.1. The back transformed mean $\log(abundance + 1)$ of three generalist predator groups in soil cores from habitats on the farm landscape. The upper three panels show results for each predator group (carabids, rove beetles, and spiders) in each habitat type while the lowest graph includes all three predator groups and shows the means samples from habitats with each dominant plant growth form. Bars with different letters indicate significant differences based on Tukey's honestly significant difference test. The by habitat group graphs are based on an ANOVA test with 11/158 df while the by dominant plant growth form graph is based on an ANOVA test with 2/167 df.

Table 5.4. The associations between vegetation characteristics at each scale and the log transformed abundance of generalist predators in soil core samples from a variety of habitats on vegetable farms. The first number is the F statistic from an ANOVA test of the effect of each factor. For factors with significant F tests, the T-statistic of the factor in the regression equation, and the adjusted r^2 of the model are listed to show the direction and strength of the effect. Asterisks next to the F statistics represent the significance level of a model with 169 degrees of freedom ($. < 0.1$, $* < 0.05$, $** < 0.01$, $*** < 0.001$)

Scale	Factor	log(carabids+1)	log(roves+1)	log(spiders+1)
Habitat scale	Habitat type	1.3	8.1*** / NA / 0.26	4.2*** / NA / 0.01
	Plant growth form	13*** / NA / 0.13	24*** / NA / 0.22	4* / NA / 0.03
	Mon. since tillage	0.2	0.6	6.1* / 2.5 / 0.03
Plant scale	Total veg. height	4.8* / -2.2 / 0.02	2.2	3.1 / 1.8 / 0.01
	Aer. grass cover	28*** / 5.3 / 0.14	53*** / 7.3 / 0.24	2.1
	Aer. Forb cover	1.7	7.8** / -2.8 / 0.04	4.8* / -2.2 / 0.02
	Aer. shrub cover	7.6** / -2.8 / 0.04	7.6** / -2.8 / 0.04	0.1
	Aer. litter cover	2.9 / -1.7 / 0.01	3.6 / -1.9 / 0.01	0.5
	Aerial bare	13*** / -3.6 / 0.07	21*** / -4.5 / 0.1	1.4
Arthropod scale	Basal veg. thick.	12*** / 3.4 / 0.06	32*** / 5.7 / 0.16	6.7* / 2.6 / 0.03
	Litter biomass	2.1	0.3	1.1
	Tot. green mass	3.4 / 1.8 / 0.01	12*** / 3.5 / 0.06	1.5
	Herb biomass	7.8** / 2.8 / 0.04	23*** / 4.8 / 0.12	1
	Bas. grass cover	34*** / 5.8 / 0.16	57*** / 7.6 / 0.25	7** / 2.7 / 0.03
	Bas. forb cover	0.1	2.5	3.9 / -2 / 0.02
	Bas. litter cover	0	1.1	0
	Bas. bare soil	12*** / -3.4 / 0.06	28*** / -5.3 / 0.14	6.3* / -2.5 / 0.03
Functional variables	Mean soil temp.	7.8** / -2.8** / 0.04	1.3	0.2
	Temp. st. dev.	1.9	1.9	1.1
	Soil surface light	2	4.4* / -2.1* / 0.02	1.2

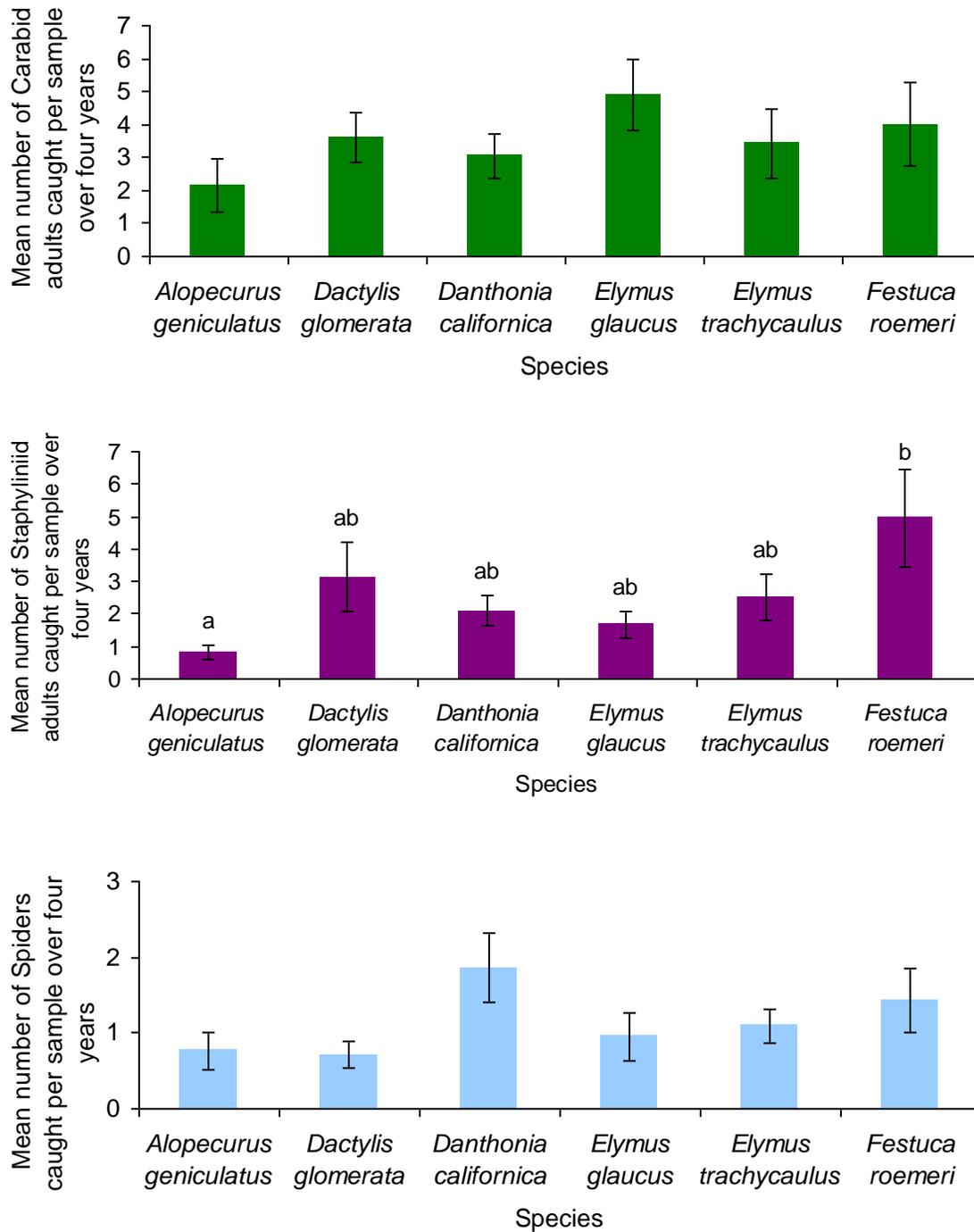


Figure 5.2. Mean number of arthropods collected from soil cores taken from beetle banks sown to only grasses. The p-values are from an anova test for differences between species. Error bars are standard errors of the mean. Bars with different letters indicate significant differences based on Tukey's honestly significant difference test

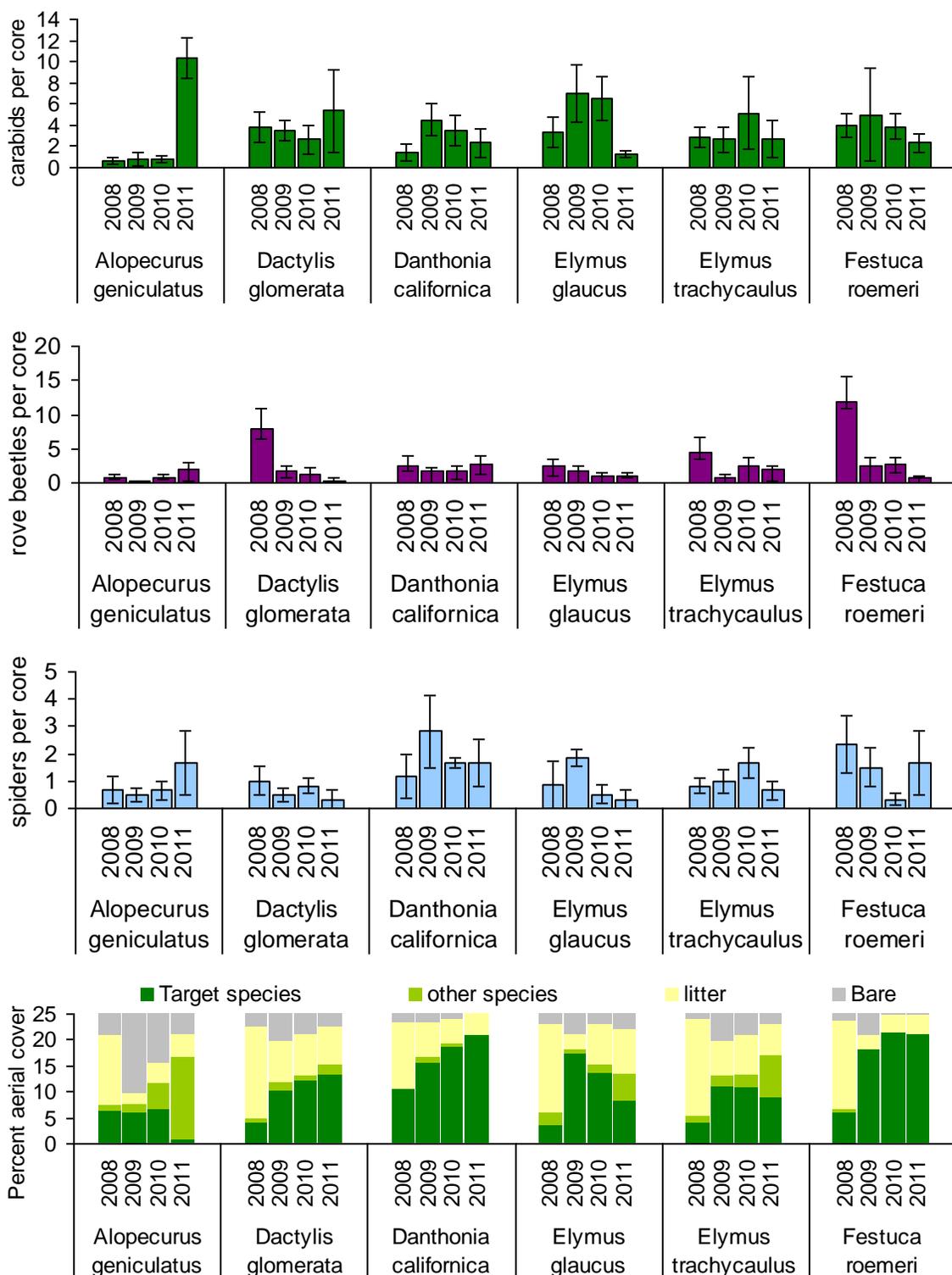


Figure 5.3. Annual changes in arthropod communities and vegetative cover in the grass only common garden experiment. The top three panels show the mean number of collections of each arthropod group over four years of sampling. Error bars are the standard error of the mean. The bottom panel is the percent aerial cover of each cover type on the 0.25 m² vegetation plot around the core site. There were 127 samples in total.

Table 5.5. The associations between vegetation characteristics at each scale and the abundance of generalist predators in soil core samples from the grass only experiment. The first number is the F statistic from an ANOVA test of the effect of each factor. For factors with significant F tests, the T-statistic of the factor in the regression equation, and the adjusted r^2 of the model are listed to show the direction and strength of the effect. Asterisks next to the F statistic represent the significance level based on a model with 126 total degrees of freedom (. < 0.1, * < 0.05, ** < 0.01, *** < 0.001)

Scale	Factor	Carabids	Rove beetles	Spiders
Habitat scale	Plant species (factor)	0.9 / NA / 0	2.8* / NA / 0.07	1.9 / NA / 0.03
	Species B to A ratio	0.7	3.6. / -1.9 / 0.02	5.4* / -2.3 / 0.03
Plant scale	Total veg. height	0	14.5*** / 3.8 / 0.1	0.5
	Aerial grass cover	0.3	3.5. / -1.9 / 0.02	0
	Aerial forb cover	0.6	3.1. / -1.8 / 0.02	0.1
	Aerial target cover	0.1	2.6	0.1
	Aerial litter cover	0.4	16.2*** / 4 / 0.11	0.4
	Aerial bare	0.1	4* / -2 / 0.02	0.9
Arthropod scale	Basal veg. thickness	0.2	5.3* / 2.3 / 0.03	0.1
	Litter biomass	0.5	19*** / 4.4 / 0.13	0
	Total green biomass	6.3* / 2.5 / 0	2.4	8.7** / 3 / 0.06
	Basal target cover	1.6	0.1	1.7
	Basal grass cover	4.8* / 2.2 / 0	0.1	2.7
	Basal forb cover	1	0.1	0
	Basal litter cover	4.1* / 2 / 0.02	3.4. / -1.8 / 0.02	0
	Basal bare soil	5.7* / -2.4 / 0.04	1.2	4.7* / -2.2 / 0.03
Functional variables	Temp. st. dev. clump	0.2	8.8** / -3 / 0.06	1.9
	Temp. st. dev. space	0.1	8.1** / -2.8 / 0.05	0.7

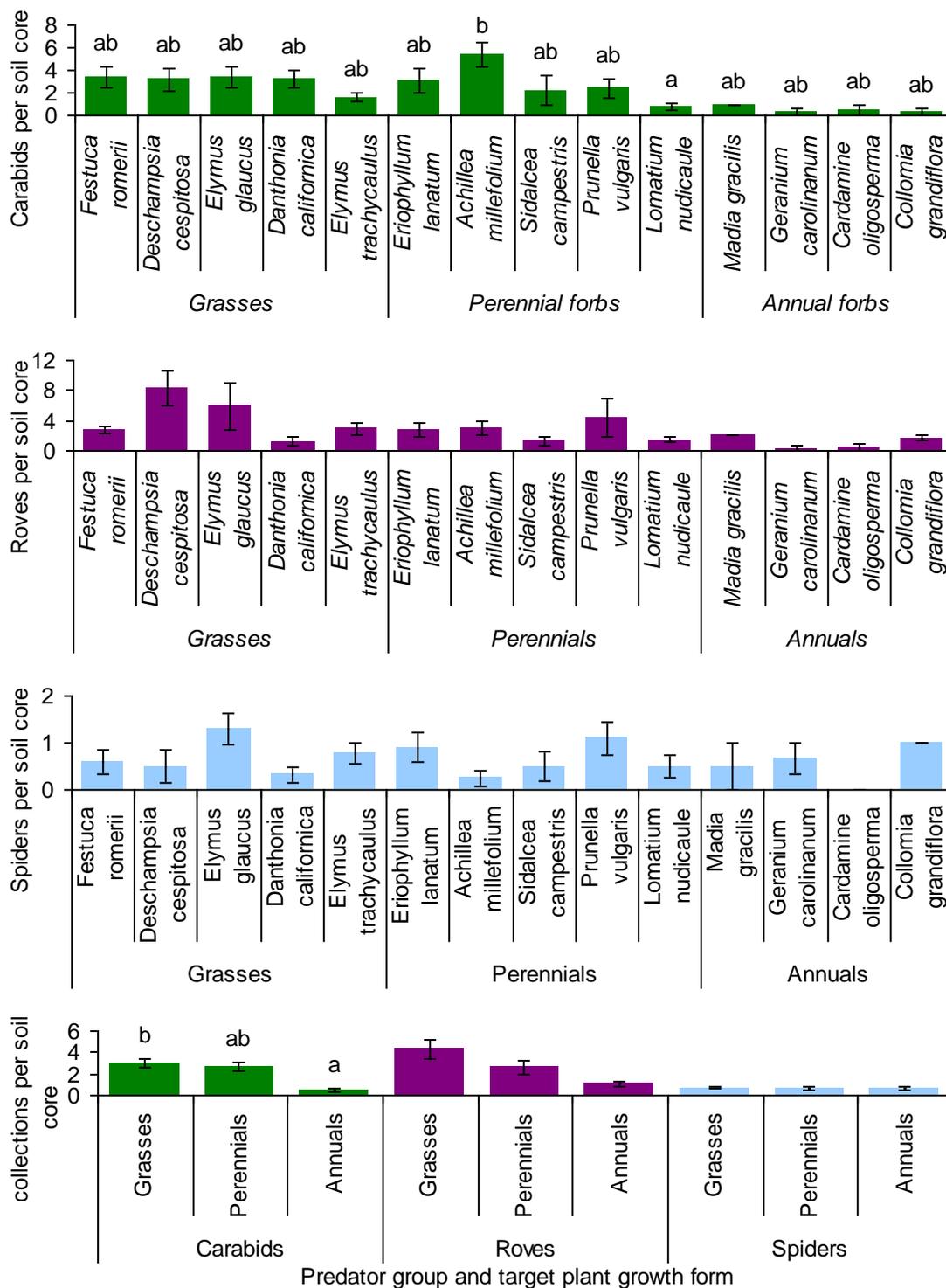


Figure 5.4. Mean number of arthropods collected from soil cores in the common garden experiment with both grasses and forbs. The growth form and then the target species are ordered with the left most having the largest mean ratio between basal and aerial cover on the core. Groups with different letters above the bars had significant differences between them based on Tukey's honestly significant difference tests. Bars without letters had no significant differences from other groups Error bars are standard errors of the mean.

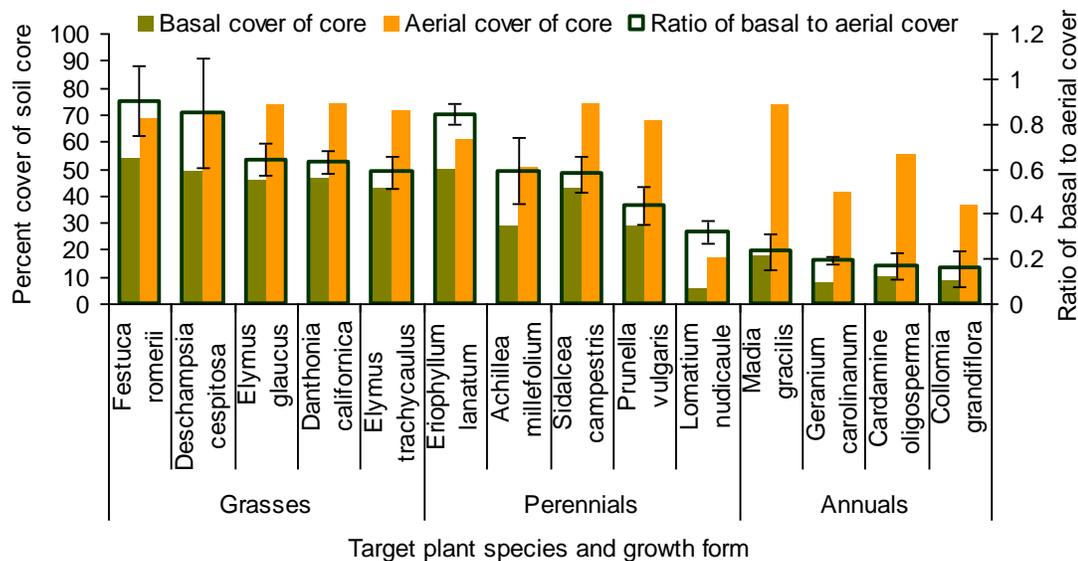


Figure 5.5. The basal and aerial cover of the target grass or forb species on the soil core. The unfilled bars overlaying the filled bars is the ratio of the two values plotted on the second ordinate axis. The error bars are standard errors of the mean of each ratio.

Table 5.6. The associations between vegetation characteristics at each scale and the abundance of generalist predators in soil core samples from the experiment including both grasses and forbs. The first number is the F statistic from an ANOVA test of the effect of each factor. For factors with significant F tests, the T-statistic of the factor in the regression equation, and the adjusted r^2 of the model are listed to show the direction and strength of the effect. Asterisks represent the significance level from a model with 105 total degrees of freedom (. < 0.1, * < 0.05, ** < 0.01, *** < 0.001)

Scale	Factor	Carabids	Rove beetles	Spiders
Habitat scale	Plant functional group	3.1* / NA / 0.04	2.4. / NA / 0.03	0.1
	Plant species (factor)	1.7. / NA / 0.08	1.6	1.2
	Species basal to aerial ratio	10.2** / 3.2 / 0.08	4.2* / 2.1 / 0.03	0
Plant scale	total vegetation height	0.2	15*** / 3.9 / 0.12	0.1
	Aerial grass cover	0.7	3.9. / 2 / 0.03	0.1
	Aerial forb cover	1	3.9. / -2 / 0.03	0
	Aerial target cover	2.5	4.6* / 2.2 / 0.03	0.1
	Aerial litter cover	0.1	0.1	0
	Aerial bare	0.1	3.2. / -1.8 / 0.02	2.4
Arthropod scale	Basal vegetation thickness	2	26.4*** / 5.1 / 0.19	0.7
	Litter biomass	0	8.9** / 3 / 0.07	0.3
	Green vegetation biomass	6.4* / 2.5 / 0.05	21.6*** / 4.6 / 0.16	0.3
	Basal target cover	8.4** / 2.9 / 0.07	10.9** / 3.3 / 0.09	1.1
	Basal grass cover	1.1	11.4** / 3.4 / 0.09	0.2
	Basal forb cover	1.1	0.8	0.1
	Basal litter cover	1.2	0	0.3
	Basal bare soil	1.2	4.9* / -2.2 / 0.04	0.2
Functional variables	Temp. st. dev. clump	0	6.9** / -2.6 / 0.05	0.4
	Temp. st. dev. space	1.3	3.7. / -1.9 / 0.03	0

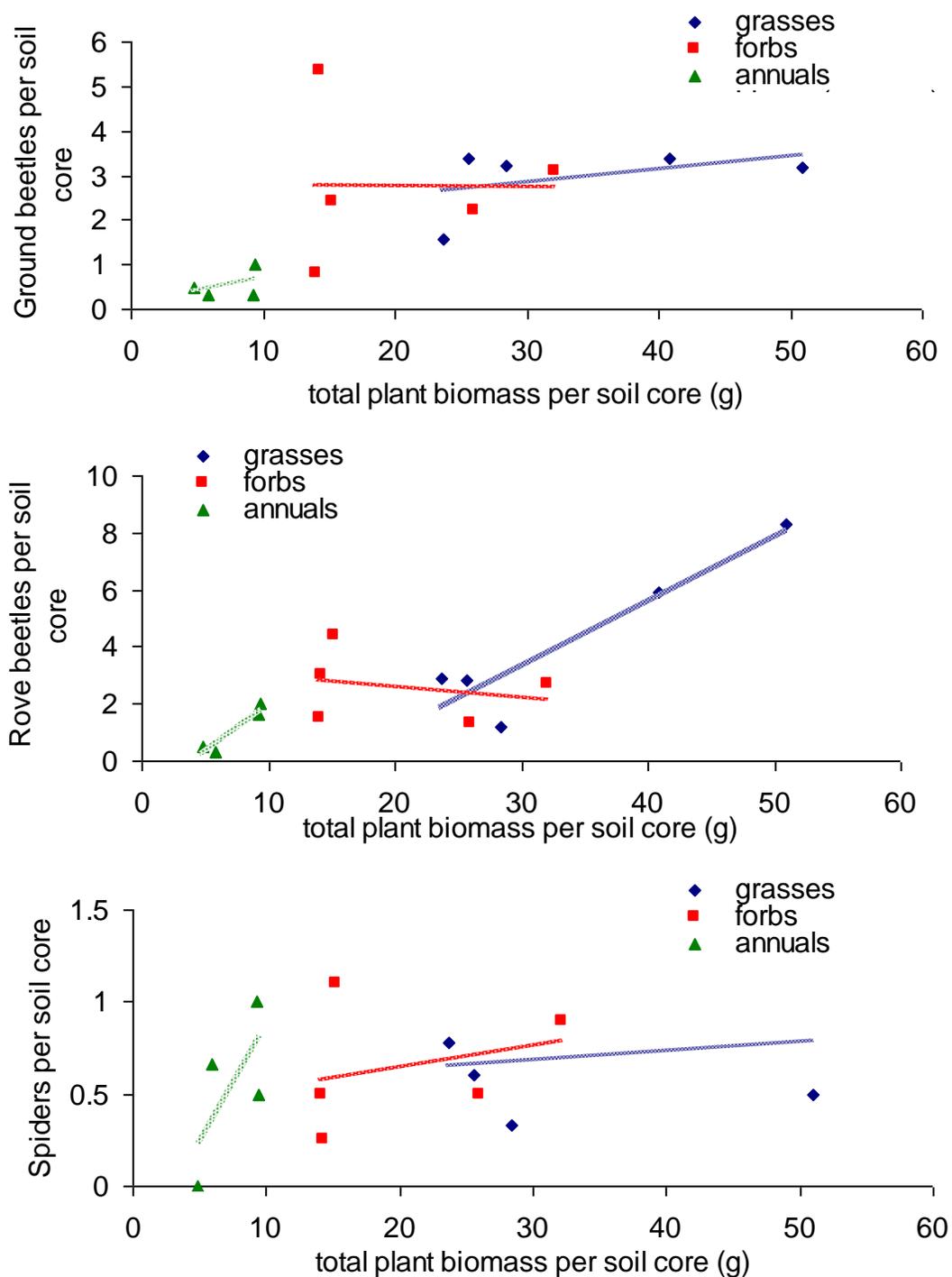


Figure 5.6. The relationship between predatory beetle and spider abundances and total plant biomass for each plant growth form in the grass and forb experiment. Each point represents a single species and the location is based on the mean value for the species. The line shows the trend in the relationship for species with each growth form.

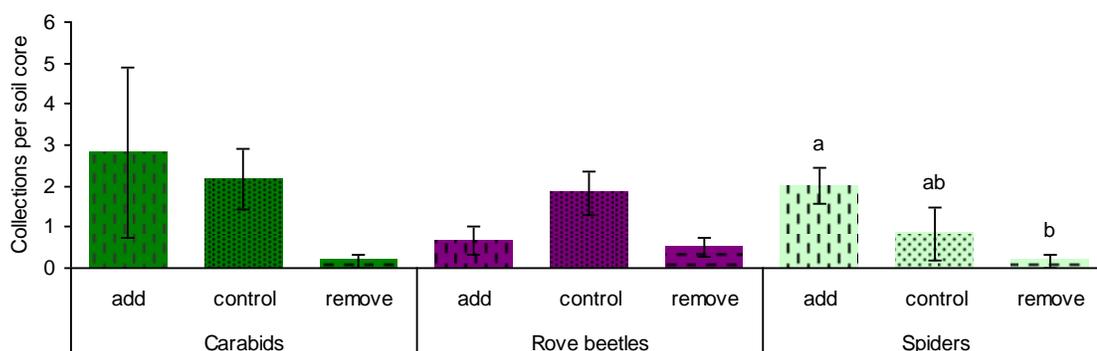


Figure 5.7. Mean number of arthropods collected from soil cores in the addition and removal experiment. Bars with different letters within the same predator group are significantly different based on Tukeys honestly significant difference test. Error bars are standard errors of the mean.

Table 5.7. The associations between vegetation characteristics at each scale and the abundance of generalist predators in soil core samples from the addition and removal experiment. The first number is the F statistic from an ANOVA test of the effect of each factor. For factors with significant F tests, the T-statistic of the factor in the regression equation, and the adjusted r^2 of the model are listed to show the direction and strength of the effect. Asterisks represent the significance level from a model with 17 total degrees of freedom (< 0.1 , * < 0.05 , ** < 0.01 , *** < 0.001).

Scale	Factor	Carabids	Rove beetles	Spiders
Habitat scale	Litter addition ind.	1.1	0.8	6.9* / 1.5 / 0.26
	Litter removal ind.	2.4	2	4.2. / -1.3 / 0.16
Plant scale	total vegetation height	0.8	5.4* / 0.2 / 0.21	2.1
	Aerial target cover	2.5	1	0.5
	Aerial litter cover	0	0	3.5. / 0.2 / 0.13
	Aerial bare	2.3	0.6	3.1. / -0.1 / 0.11
Arthropod scale	Basal veg. thickness	0.2	0.6	1.8
	Litter biomass	14** / 0.1 / 0.43	0.4	6.5* / 0 / 0.24
	Total green biomass	0.2	0.1	0
	Basal target cover	0.2	0	0.2
	Basal litter cover	6.2* / 0.4 / 0.24	0.3	4.6* / 0.1 / 0.17
	Basal bare soil	4.8* / -0.5 / 0.18	0.7	2.9
Functional variables	Mean soil temp.	0	4.3. / -2.6 / 0.16	0.9
	Temperature st. dev.	2.8	0.7	5.5* / -1.3 / 0.21

Conclusion

Farmscaping is a conservation biological control practice where the level of resources and habitats for important beneficial insects is evaluated on a farm landscape. Non-crop habitats are linked with the farming system through a series of interactions between crops, pests, predators, and other plants that provide the predators with cover or supplementary and complementary food supplies. Each farm is unique in terms of what crops are grown, specific pest problems, the suite of beneficial insects present, and the layout and opportunities for beneficial insect habitat. This dissertation both helps define the characteristics of important beneficial predator groups, and describes components of the vegetation that are important contributors to beneficial insect habitat on farm landscapes.

Ground beetles as a family have similar life histories, but the species can be classified into different groups based on their phenology and habitat use. Some species are active within annual agricultural fields during the late summer, while others are active in the spring. Many of the species that are active in the spring over winter in areas dominated by perennial grasses. Beetle banks are an effective way to provide this habitat. There are a variety of native species that would be a good choice on beetle banks in the Willamette valley. Long lived bunch grasses like *Festuca roemerii* and *Danthonia californica* can provide good habitat to over wintering beetles, and with appropriate management can create a dense vegetation mat that prevents invasion by weeds or other species. The bunchgrasses *Elymus glaucus* and *Elymus trachycaulus* can rapidly establish and dominate a site faster than *F. roemerii* and *D. californica*, but they tend to decline in vigor after a few years. Some forbs can provide good over wintering habitat for beetles, but generally forbs are not as good for beetles as grasses. Forbs do contribute floral resources which are required by other beneficial insects including parasitoid wasps. A mixture of long and short lived grasses and forbs may prove to be the best choice for beetle banks, provided the species chosen can be efficiently managed together.

The information in this dissertation can be used in farmscaping to help evaluate the availability of floral resources and over wintering shelter in the landscape. It will also point to plantings and management that can increase habitats that efficiently provide these resources in the farm landscape.

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Appendices

Appendix A Plant communities of cane berry fields under different management systems

Abstract

A survey of vegetation communities within commercial *Rubus* sp. and other berry fields was done to determine if there were differences between the plant communities of fields with different weed management and irrigation systems. Additionally, an experiment was conducted to determine what effect different irrigation treatments had on the weed and cover crop communities of a blueberry field. Fixed area vegetation plots (25 m²) were used to sample the commercial berry fields. There were two main types of weed management on the commercial farms, using tillage to maintain bare soil between the berry rows, and mowing to maintain a perennial grass cover crop. Irrigation was applied either with a drip system or with overhead sprinklers. NMS ordination was used to demonstrate that there were differences in plant communities associated with both different weed management and different irrigation systems. Indicator species analysis was used to identify plant species associated with each of the four possible management regimes. ANOVA was used to test whether there were differences in the cover of each species in fields with different management.

The irrigation experiment included three types of irrigation systems (drip, microspray, and overhead) and three amounts of irrigation (50%, 100%, and 150% of the potential evapotranspiration of the blueberry plants). Point intercept vegetation plots were used to sample both the cover crop communities between the blueberry rows and the weed community in the blueberry row. NMS ordination identified associations between plant community differences and the type of irrigation and MRPP confirmed that there were significant differences between cover crop sections with different irrigation types, but not between sections with different irrigation amounts. There were the fewest weeds in blueberry rows with drip irrigation. The legumes *Trifolium repens* and *Medicago lupulina* had the highest coverage in the drip irrigation treatment and tended to bloom in the early season. The annual grass *Poa annua* and the dandelion like plants, *Taraxicum officinale*, *Hypochaeris radicata*, and *Leontodon tataricoides*, were most abundant in the overhead irrigated sections and tended to bloom later in the summer. The differences species and bloom season are likely to impact populations of beneficial insects that are dependant on floral resources in their life cycle.

Introduction

Caneberry cropping system

In the Willamette valley of Oregon cane berries (*Rubus* spp.) and blueberries (*Vaccinium* sp.) are major horticultural crops (National Agricultural Statistics Service 2012). Within the berry fields there are other plant species growing include a variety of weeds and in some cases cover crops. Berry fields consist of rows of berry plants tied up to trellises and spaced wide enough for tractors to move between the rows. One of the major management activities on Willamette valley berry fields is the control of weeds both within the row underneath the berry plants and between the berries in the inter-row spaces. On organic farms synthetic herbicides can not be used for weed control so managers focus on mechanical or cultural methods. Mechanical control generally means soil tillage is used to maintain bare soil between the berry plants and to destroy any weeds that come up. A commonly used method of cultural control utilizes a perennial cover crop grown in the inter-row spaces between the berry rows that is occasionally mown. In the cover crop system a bare area is still maintained immediately around the berry plants either with mechanical removal of weeds or landscape fabric cover over the soil. Irrigation must be applied in the Mediterranean climate of the Willamette valley where little natural precipitation falls during the summer. Irrigation water can be applied as an overhead spray of the whole field or it can be applied more precisely with drip or other systems that deliver the water directly to the base of the crop plant. Both weed management and irrigation activities influence the ecological conditions of the site and therefore are likely to have profound effects on the non-crop plant species in the berry production field.

Effect of irrigation and tillage on weed communities

The management practices used in Willamette valley Organic berry production create very different disturbance regimes and resource levels for any weeds which may grow in the fields. Tillage removes vegetation cover, kills most live plants, and creates a fresh seed bed of bare soil. Mowing the cover crop only removes a part of the vegetation cover, which can kill some species, but others respond positively to the treatment. Irrigation applies a necessary resource that is limits plant growth in the Willamette valley

throughout the summer. Comparisons of reduced and conventional tillage in annual cropping systems have shown that creating a fresh seed bed can result in different plant communities (Thomas, et al. 2004). A study of orchards in Spain without any differences in soil disturbance found that mowing rather than killing (with herbicides) the resident vegetation between the trees resulted in different weed communities (Mas, et al. 2007). Weed communities have also been shown to be influenced by how precisely the irrigation system delivers water to the crop plant (Karkanis, et al. 2010, Shrestha, et al. 2007). This study is a unique direct comparison within a single crop type between weed communities of systems which use conventional tillage methods and systems which maintain a perennial cover crop to control weeds. Additionally, this study examines how different weed management practices and different irrigation methods interact in their influence on within field plant communities.

Importance of plant communities for pollinators, predators, and parasitoids

In addition to competing with the crop plants weeds and cover crop plants produce biomass and floral resources that may be used by other organisms in the fields. Many insects that are beneficial to agricultural production depend on floral resources like pollen and nectar to complete part of their lifecycle (Syme 1975, Idris and Grafius 1995). Numerous crop plants require or have increased yield when cross-pollinated through the actions of bees and other insect pollinators (Klein, et al. 2007). Often pollinators are active throughout the growing season and need to forage on flowers of other species when crops are not in bloom (Fussell and Corbett 1992). Plants that bloom during periods when the target crop is not flowering can be used by wild bees and resident honey bees to build their populations to levels necessary for pollination. Many predaceous insects use floral resources during part of their life cycle. Parasitoid wasps, syrphid flies, and other insects can have carnivorous larvae that are important predators of agricultural pests, while adults can be dependent on nectar or pollen for survival and fecundity (Ambrosino, et al. 2006). Parasitoid wasps need to eat frequently to avoid starvation, and many species have increased longevity and fecundity when provided with floral resources (Seikmann, et al. 2001, Baggen and Gurr 1998).

Objectives and research questions

The overarching objective for this study was to test for differences in the plant communities of berry fields with different management regimes in western Oregon. There were seven specific research questions that were answered.

Questions:

1. Are there differences in the plant community composition of commercial berry fields under different irrigation and weed management regimes?
2. Do plant species differ in their abundances in commercial berry fields under different management regimes?
3. Are there plant species that are typically found in commercial berry fields with particular management regimes?
4. What are the effects of experimentally applied irrigation methods and amounts on the cover of weeds within the berry crop row?
5. How do different irrigation methods and amounts influence the composition of the plant communities in the perennial cover crop in the inter-row spaces of a berry field?
6. Does the cover of each plant species differ in response to different irrigation treatments on a perennial cover crop between rows of a berry field?
7. What are the effects of different irrigation treatments on the abundance of flowers over the season within perennial cover crops in between rows of a berry field?

Methods

Two separate studies were conducted to document both the plant communities that occur in berry production fields in the Willamette valley, and to experimentally test how plant communities respond to specific management practices. From May through September 2009 field surveys were conducted on nine Willamette Valley farms to describe the non-crop plant communities within berry production fields. There were two main differences in the management regimes of berry fields, the weed management strategy and how irrigation was applied. The spaces between berry rows were either tilled to control weeds or mown to maintain a perennial cover crop, and irrigation was applied with either a drip or overhead system. This creates a natural experiment to test for

differences in the plant communities between management regimes. The manipulative experiment was a factorial comparison of different irrigation methods and irrigation amounts on a blueberry field.

Berry production field surveys - vegetation plots

There were nine farms sampled in total, eight were certified organic commercial farms in the Willamette valley of western Oregon and the ninth was the Lewis- Brown Experimental farm in Corvallis, Oregon. On the experimental station, only berry fields maintained as a part of the breeding program and managed using typical management practices (rather than various experimental treatments) were sampled with vegetation plots. The farm surveys focused on cane berries but other types of berry fields were sampled on some farms. This allowed for more extensive sampling of each farm and increased the power of the study. All of the farms had multiple blackberry or raspberry fields, two farms also had blueberry (*Vaccinium* sp.) fields, two farms had grapes (*Vitis* sp.), and one farm had a currant (*Ribes* sp.) field. While the different berry species need slightly different management, the production systems of the different berry fields were largely similar and resulted in similar non-crop plant communities. Berries fields are highly repetitive. The berry plants are planted in rows and tied up to trellises. Only the berry plants are allowed to grow within the berry rows, all other weeds are controlled in a one to two meter wide strip under the berry plants. Rows are separated by alleys wide enough for tractor access (approximately 3m). The inter-row spaces are either tilled to maintain bare soil between the plants, or a perennial cover crop is grown and managed with mowing.

Fixed area (25 m²) vegetation plots were randomly located in berry fields during monthly surveys. Plot boundaries were set along the trellis wires marking the mid point of each berry row and extended across one inter row space to the trellis wire marking the midpoint of the next row of berries. On the landscape, the plots extended from trellis wire to trellis wire and comprised an entire inter-row space and two halves of the cane berry rows forming opposite edges of the plots. The distance between rows was not constant in all fields, so the length of the plots needed to vary slightly to ensure a fixed area. The percent cover of each species in the vegetation plot was visually estimated. There were

317 vegetation plots installed on the nine commercial farms over the summer, and each plot was considered a sample unit in the analysis.

Irrigation Experiment

A study designed to evaluate blueberry growth and production allowed comparisons in floral resource availability under different, experimentally applied irrigation treatments (Bryla, et al. 2011). In this system the bushes are in trellised rows with the spaces within the rows kept free of other vegetation by occasional removal of weeds and mulching with sawdust. Between the rows are inter-row spaces sown with perennial ryegrass (*Lolium perenne*). Various weedy species have established amongst the ryegrass. See Bryla, et al. (2011) for more complete description of layout and establishment.

The experiment involved three types of irrigation methods, and three levels of irrigation amount. There were four blocks, each consisting of six blueberry rows. Each treatment was applied to a 6.5 m long section of the six adjacent rows which were spaced every 10 feet (3.05 m). Irrigation was applied either as overhead sprays that wet the entire field (including the cover cropped inter-row spaces), micro-sprays that focused the water on the area within the blueberry rows, and drip irrigation along the centers of each blueberry row. Within each irrigation type the amount of irrigation water applied was 50%, 100%, or 150% of the potential evapo-transpiration of blueberry plants. Two of the rows in each treatment section were sampled.

In the bare areas of the blueberry rows weed coverage was sampled on two occasions (July and September), each time a few days before a hand weeding effort was undertaken as part of standard management practices. Weeds were sampled with point intercept plots consisting of one line of 10 points on each side of the inter-row cover crop. The two lines were placed about half way between the cover crop edge and the center of the blueberry row. The number of points that had weeds present was tallied for each section. The 20 point intercept observations were combined to get a section mean. Each section was considered the sample unit and there were 16 segments with each irrigation treatment sampled on both of the sample months (Total = 144 samples).

The perennial cover crop in the inter-row spaces was sampled once a month in April, May, June, July, August, and September with point intercept plots arranged in a 0.25 m² grid of 25 points. The uppermost plant species intercepted was identified and tallied. If there was not a plant at the point, it was tallied as either litter, bare, or moss, depending on the cover of the soil surface. Additionally, for each species the proportion of stems within the plot that had open flowers was estimated. The proportion bloom estimates were grouped into five floral abundance classes. Each class included a range of estimates of the percent flowering, and a single value used in the calculations [not in bloom = 0 (value=0), 0–20% = Class 1 (value=0.1); 20–40% = Class 2 (value=0.3); 40–80% = Class 3 (value=0.6); 80–100% = Class 4 (value=0.85)]. The product of the percent cover of the plot and the flowering class value is an estimate of the floral abundance of the species in the plot. There were two plots in each treatment segment. The segment was considered a single sample unit so the two samples were combined to get the segment mean. There were two segments sampled in each of the four blocks resulting in eight replicates per treatment except for in June when it was only possible to do half of the sampling (four replicates per treatment).

The species observed in the irrigation study were grouped based on their flower type to help understand how the community differences influence the resources available for insects. Plant species and families can have different flower types that may or may not offer floral resources that are available for beneficial insects (Chapter 2). Grasses and other wind pollinated plants formed one group and were assumed to not provide floral resources for beneficial insects. Several species of forbs, shrubs, and trees had exposed nectaries which would provide floral resources for many types of insects including both bees and parasitoid wasps. Another group of flowers included species in the Lamiaceae and Scrophulariaceae with nectaries partially hidden within tubular flowers. Plants in the Chicoreae (Dandelion tribe of the Asteraceae) also have nectar, but it is produced in ligulate flowers which may make it difficult to access for some insect species. There were a few flowers of other species in the Asteraceae and from annual species with small but showy flowers. The Fabaceae are another group of plants which produce floral resources, but a complicated corolla limits access for many insect species. The groups with hidden or partially hidden nectaries generally would provide floral resources to bees and pollen

feeding insects, but some beneficial insects such as parasitoid wasps may only be able to successfully forage nectar from flowers with fully exposed nectaries (Chapter 2).

Analysis

Answering each of the seven research questions required different analytical methods. Non-metric multi-dimensional scaling ordination (NMS) was used to analyze the patterns of plant community composition with respect to the management and environmental variables in both the commercial farm vegetation plots (Question 1) and the irrigation experiment (Question 5). NMS uses similarity between the plots in the species responses to generate scores for the plots along axes indicating a reduced number of synthetic response variables (generally 3 or fewer) (Kruskal 1964, Mather 1976, McCune and Mefford 2009). Environmental variables recorded for each plot can be compared with the ordination scores to see which variables are associated with the strongest differences in plant communities. When there are environmental variables associated with the plant communities they can be aligned so that the ordination axes represent environmental gradients. The mean scores on ordination axes aligned with environmental variables can be used as a measure of how different plant species respond to the environmental gradients. NMS was used to separate the plots based on the plant communities and compare whether the management regime or other environmental variables were correlated with the plant community differences.

The vegetation plots from each study were also grouped by the management regime and ANOVA was used to test for species specific differences in the cover of each common plant species between vegetation plots with different management regimes (Question 2) or irrigation treatments (Question 6). ANOVA was also used to test for differences in the total weed cover within the blueberry rows in sections under each irrigation treatment (Question 4).

Indicator species analysis was used to determine which plant species were associated with each berry production field management regime. Indicator species analysis combines two measures of indication for each species, the relative abundance and the relative frequency. The relative abundance is the percent cover of species in the group divided by the percent cover of the species in all groups. A relative abundance of

100% means the species was always found in that habitat and 0% means the species was never found in the habitat. The relative frequency is the percent of plots in the group with the species, 100% means that the species was found in all the samples in the group and 0% means it was found in none. The indicator value is the product of the two measures, an indicator value of 100% means it was found in every plot in the group and no plots in other groups. Species with significant indicator values were identified for each berry field management regime (Question 3).

The total floral score of each flower type group was calculated for each of the 72 irrigation treatment segments each month. PerMANOVA was used to test for the effect of the three irrigation methods, the three irrigation amounts, and their interaction on the floral abundance scores of the six flower type groups during each month. Additionally, pairwise comparisons were made between each of the three groups in each factor with the variability from the other factor partitioned out to see which group differences were significant (Question 7).

Results

Vegetation plots

Question 1.

The NMS ordination shows clear separation between plots with different management regimes in species space along the first and third axes of a three dimensional ordination (Figure A1). There is very little overlap between the groups of points associated with each management regime. The radial lines are vectors with coordinates set by the correlation between environmental variables of each plot and the plot's ordination scores for each dimension. Environmental variables with strong correlation with the ordination axes are strongly correlated with differences in the plant community composition. Figure A1 shows that the irrigation type indicator variables and inter-row management regime indicator variables were strongly correlated with the ordination axes. Drip (Pearson's $r^2 = 0.35$) and overhead irrigation (Pearson's $r^2 = 0.39$) indicator variables are strongly correlated with axis one. Drip irrigation plots cluster in the left half of the point cloud and overhead irrigation plots cluster in the right side. Mown (cover crop) (Pearson's $r^2 = 0.30$) and tilled management type indicator variables (Pearson's $r^2 =$

0.54) are strongly correlated with axis three. Tilled plots are near the top of the figure and cover cropped plots are near the bottom.

With only 9 farms sampled, and samples taken throughout the growing season, it is important to check for correlations between the ordination scores and the farm indicator variables and the sample week to ensure farm level or seasonal differences are not confounding the effects of the management types. Most of the farm indicator variables were not correlated with any of the axes. Only two farm indicator variables had Pearson correlation coefficients greater than 0.2. One was a farm that had drip irrigation on all the fields and was somewhat correlated with axis one, and the other had cover cropped fields and was weakly correlated with axis three. The correlation coefficients were lower than correlation coefficients with the management regime indicator variables and the plant community composition patterns were consistent with patterns found on other farms with more than one management type. The axis scores were also not correlated (Pearson correlation coefficients < 0.01) with the sample week variable indicating there were not big changes in the plant cover through time within each field.

The full three dimensional ordination accounts for 64.3% of the total variability in the data set. Figure A1 only shows the first and third axes of a three dimensional ordination which together account for 30% of the variability. The second axis accounts for 34% of the variability, but there were no correlations with any of the measured environmental variables. The final stress in the ordination was 21.4.

Question 2.

There were over 140 different species identified on the vegetation plots, and four non-plant cover types (bare soil, litter, moss, and landscape fabric). ANOVA analysis found a significant effect of management type on 51 cover classes. Many species display clear differences in their abundance under different management types. There are clear differences in the 30 most common species between management types (Table A1).

Question 3.

Indicator species analysis identified numerous species that are indicators of each management regime (Table A2). Species with significant indicator values for a management regime are commonly found in that habitat, but they may also be found (with lower cover or less frequency) in other management regimes, particularly in fields with the same weed management system but the other irrigation system.

Irrigation experiment

Question 4.

The point intercept plots measuring weed abundance in the bare areas along the blueberry row showed a clear increase in bare soil (a decrease in grass, forb, or shrub weeds) in drip irrigated plots. This was supported by a significant effect of irrigation type on bare soil in an ANOVA model ($F = 295$, $P < 10^{-16}$, $df = 2/138$). Irrigation amount did not have a significant effect in the ANOVA model, and neither did the interaction ($P > 0.17$). When plots with different irrigation amounts were combined with other plots with the same type of irrigation there were significant differences based on Tukey's honestly significant difference method between microspray and overhead irrigated plots ($P = 0.004$), but the actual difference was minor when compared with the highly significant differences between either overhead or microspray irrigated plots and drip irrigated plots ($P < 10^{-16}$). Total weed cover in drip irrigated plots was less than 2 percent, while in microspray plots it was around 11 percent and in overhead irrigated plots it was slightly more at almost 13 percent (Figure A2).

Question 5.

In the cover crop plant communities subjected to the irrigation treatments there were clear differences in plant communities between irrigation types. On a two dimensional NMS ordination solution with a final stress of 13.8 showing vegetation plots in species space, the sections with drip irrigation (hollow shapes) are clearly separated from the other two irrigation types (filled shapes) (Figure A3). The location of the points is an attempt to summarize the patterns found in the responses of all the plant species encountered in the vegetation plots. The red lines on the biplot show how environmental variables are correlated with the positions of the vegetation plots on the ordination space.

The drip indicator variable is negatively correlated with axis one while the overhead irrigation indicator is positively correlated with axis one.

The differences in community composition are driven by the responses of individual species to the moisture gradient. The correlation between species abundance in each plot and the position of the plot along axis one of the ordination can be used to evaluate which species are strongly affected by the treatments.

In this ordination species with positive correlations (like *Lolium perenne*, *Poa annua*, or *Taraxicum officinale*) will be more abundant on the overhead irrigation plots while negative correlation will be found in species that are more abundant on drip irrigation sites like *Medicago lupulina*, *Trifolium repens*, and *Crepis setosa* (Table A3). The cover types “litter” and “bare” are also negatively correlated with Axis 1 because drip irrigation plots had less vegetative cover than other plots so the ground cover was recorded.

The differences seen on the ordination are confirmed with more specific statistical tests. PermAnova analysis found a significant effect of irrigation type on the covers of the plant species in the plots ($F=29.7$, $P=0.0002$), but no significant effect of water quantity ($F=0.8$, $P=0.56$), nor interaction ($F=0.70$, $P=0.77$). In a blocked MRPP using treatment as the grouping variables significant differences between treatments were found ($A=0.30$, $P=0$). Among pairwise comparisons there were significant differences between drip irrigation and the other two irrigation types (microspray, overhead), and between the driest (50%ET) microspray treatments and overhead treatments (Table A4).

The species with significant effects of irrigation type as measured by ANOVA were generally the same as the species with the most extreme correlations with the first axis of the ordination (Table A3). There were two cover types, *R. armeniacus* and moss cover, which had significant p-values but low correlations with the ordination. Both were rarely encountered and the significant results are likely due to random factors rather than the effect of the experimental treatments.

Question 6.

Total vegetative cover was reduced in the drip irrigated treatments and therefore there were a greater cover of litter, bare soil, or moss on the ground (Figure A4). The

dominant plant species in the cover crop, *L. perenne*, had the lowest cover in the drip irrigated sites, the highest coverage was in microspray irrigated sites. The two legumes, *T. repens* and *M. lupulina*, had the highest abundance in the drip irrigated sites, but were relatively common in the other treatments as well. *Poa annua* and *T. officinale* were very rare in the drip irrigated sites. The overhead irrigated sites had greater coverage of *P. annua* and *T. officinale* than the sites with microspray irrigation. *Poa annua* was the only species with a monotonically increasing cover when the treatments were ordered by the amount of water reaching the cover crop (Figure A4). *Hypocharis radicata* and *L. taraxicoides* both tend to have lower coverage in the drip irrigated sites and greater coverage in the overhead sites than the microspray sites, but they were relatively common in all of the treatment types. The other 26 plant species encountered in the irrigation experiment cover crop were relatively rare and did not have clear patterns with respect to the treatments (Table A4).

Question 7.

PerMANOVA tests found large effects of the irrigation method on the abundance of different types of flowers during each month but the effects of the irrigation amount or the two way interaction were not significant (Table A5). Pairwise comparisons between plots with each irrigation method and each irrigation amount demonstrate that the drip irrigation segments were had different floral abundance than both the microspray and overhead irrigated segments during the whole study, but there were only small differences in floral abundance between the microspray and overhead irrigated segments in July and September (Table A6).

The legume species that are common in the turf of cover crops of drip irrigated sections bloom early in the summer. (Figure A5). Few flowers are available in these sections toward the end of the summer. In the sections with more moisture reaching the cover crop areas, either by direct irrigation with the overhead system, or the light mist that drifts to the inter row spaces during microspray irrigation, there was greater levels of floral abundance later in the season when the flowers from the dandelion tribe (Cichoreae), *T. officinale*, *H. radicata* and *L. taraxicoides*. Differences in the floral communities of the perennial cover crop were mostly driven by differences in community

composition and the abundance of flowers of each species in the different irrigation treatments. Only one species, *T. repens*, had different phenological patterns in cover crop segments with different irrigation treatments. In the drip irrigated segments there is a large *T. repens* bloom in the early summer but few flowers in the late summer. In the microspray and overhead irrigated segments the bloom is more abundant in the late summer than early summer (Figure A6).

Discussion

Both the weed management system used (tilled spaces or mown perennial cover crops) and the irrigation method (drip or overhead) had a strong effect on the plant communities within berry fields in the Willamette valley of Oregon. Numerous perennial species were common in the mown cover crops and many annual species were most abundant in the tilled sites.

The irrigation experiment proved that drip irrigation is a good way to reduce weed pressure within the blueberry rows. Drip irrigation also results differences in the plant communities of the inter-row perennial cover crop. Two species of Fabaceae have high cover in the drip irrigated segments and lower cover in the overhead and microspray segments while three species in the Cichoreae tribe have higher cover in the overhead and microspray treatments than the drip treatments.

Differences in plant community composition will drive differences in the abundance of flowers on the landscape and the availability of resources for foraging insects. The differences in the season long coverage estimates described above translate into a similar pattern in the differences in the abundance of flowers of each flower types. The strong difference in the plant communities in drip irrigated sections from sections with micro spray or overhead irrigation resulted in differences in the availability of floral resources. The drip irrigated sections had abundant bloom by the two species in the Fabaceae and fewer flowers in the late summer when the Cichoreae species were blooming in the overhead and microspray sections. Flowers in the Fabaceae are complicated and restrict access for many species of insects while the Cichoreae have simpler flowers that offer floral resources to a wider variety of foraging insects. Differences in both the floral resource quality and accessibility can influence foraging

insect populations. This information can be used to predict whether beneficial insects in the farm landscape will be able to find the resources they need to thrive on farms with different management systems.

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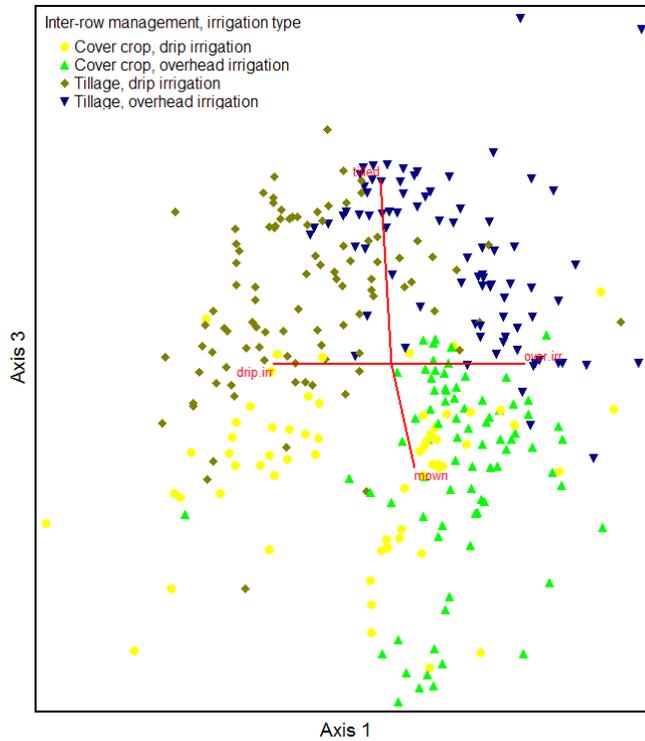


Figure A1 Axes one and three of a three dimensional ordination of vegetation plots in species space. Individual plots are represented by the points in the ordination, and the red lines indicate the correlations of the environmental variables with the ordination scores (position along the axes) of each plot

Table A1. Mean percent covers (standard error) and ANOVA F-statistics from tests of the effect of the management type for the 30 most abundant species in each management group. The number of vegetation plots with each type of management was CC.drip n = 62, CC.over n = 79, Tilled.drip n=95, Tilled.over n=81

	CC.drip	CC.over	Tilled.drip	Tilled.over	f (mgmt.fac)
Rubus sp. (blackberry)	16.05 (2.04)	8.72 (0.98)	16.34 (1.68)	11.4 (1.27)	5.7***
Bare soil	5.23 (0.66)	8.49 (0.96)	29.94 (3.07)	12.65 (1.41)	42***
Rubus sp. (raspberry)	2.52 (0.32)	12.44 (1.4)	9.19 (0.94)	16.05 (1.78)	9.3***
Festuca rubra group	5.97 (0.76)	19.67 (2.21)	0 (0)	0 (0)	22.4***
Lolium perenne	12.45 (1.58)	17.87 (2.01)	1.07 (0.11)	4.62 (0.51)	37.1***
Amaranthus retroflexus	0.1 (0.01)	0.09 (0.01)	5.15 (0.53)	15.64 (1.74)	45.6***
Landscape fabric	9.16 (1.16)	0 (0)	1.84 (0.19)	0 (0)	33.3***
Litter	8.79 (1.12)	5.24 (0.59)	7.77 (0.8)	6.23 (0.69)	3.4*
Agrostis capillaris	3.9 (0.5)	3.35 (0.38)	6.69 (0.69)	0.19 (0.02)	8.4***
Lactuca serriola	0.47 (0.06)	0.54 (0.06)	1.78 (0.18)	6.26 (0.7)	14.6***
Holcus lanatus	8.55 (1.09)	0.38 (0.04)	2.65 (0.27)	0.04 (0)	12***
Hypochaeris radicata	4.58 (0.58)	6.63 (0.75)	0.62 (0.06)	0.1 (0.01)	30.1***
Agropyron repens	5.29 (0.67)	0 (0)	6.08 (0.62)	0.32 (0.04)	15***
Trifolium repens	3.48 (0.44)	5.89 (0.66)	0.27 (0.03)	0.05 (0.01)	25.2***
Digitalis sanguinea	0.65 (0.08)	0.71 (0.08)	0.81 (0.08)	4.6 (0.51)	7.5***
Chenopodium album	0.03 (0)	0.01 (0)	0.53 (0.05)	4.14 (0.46)	30.9***
Cirsium arvense	1.81 (0.23)	2.26 (0.25)	1.05 (0.11)	3.98 (0.44)	7.2***
Taraxicum officinale	1.54 (0.2)	2.32 (0.26)	0.49 (0.05)	1.78 (0.2)	7.3***
Epilobium watsonii	3.68 (0.47)	1.22 (0.14)	1.57 (0.16)	0.43 (0.05)	12.4***
Conium maculatum	0 (0)	0 (0)	0.01 (0)	3.89 (0.43)	26.1***
Sonchus arvense	0.92 (0.12)	0.84 (0.09)	1.48 (0.15)	2.54 (0.28)	6.7***
Daucus carota	1.34 (0.17)	1.92 (0.22)	0.59 (0.06)	0.1 (0.01)	15.3***
Brassica sp. (napus?)	0.26 (0.03)	0 (0)	1.53 (0.16)	0 (0)	7.7***
Leontodon taraxicoides	1.76 (0.22)	1.91 (0.22)	0.22 (0.02)	0.04 (0)	17.6***
Veronica officinale	0 (0)	0.03 (0)	0.59 (0.06)	2.38 (0.26)	16.2***
Convolvulus arvensis	0.76 (0.1)	1.8 (0.2)	0.58 (0.06)	2.3 (0.26)	3*
Solanum nigrum	0.05 (0.01)	0.14 (0.02)	1.44 (0.15)	2.1 (0.23)	10.2***
Plantago lanceolata	0.11 (0.01)	1.82 (0.21)	0.03 (0)	0.02 (0)	23.2***
Avena sativa	0.19 (0.02)	0 (0)	1.28 (0.13)	0 (0)	11.1***
Rumex acetosa	0.66 (0.08)	0.35 (0.04)	0.95 (0.1)	1.82 (0.2)	5.9***
Echinochloa crus-galli	0.63 (0.08)	0.3 (0.03)	1.17 (0.12)	0.36 (0.04)	1.4
Crepis setosa	1.47 (0.19)	0.95 (0.11)	0.83 (0.09)	0.21 (0.02)	4**
Brassica rapa	0.05 (0.01)	0.01 (0)	0.13 (0.01)	1.47 (0.16)	6.3***
Phalaris arundinaceae	0.27 (0.03)	0.18 (0.02)	1.04 (0.11)	0 (0)	2.2.
Cyperus esculentus	0.03 (0)	0.03 (0)	0.93 (0.1)	0.91 (0.1)	1.7
Malva neglecta	0.16 (0.02)	0.19 (0.02)	0.23 (0.02)	0.85 (0.09)	5.1**
Rubus armeniacus	0.5 (0.06)	0.63 (0.07)	0.13 (0.01)	0 (0)	4.4**
Vitis vinifera	0.92 (0.12)	0 (0)	0 (0)	0 (0)	3.9**
Sonchus asperum	0.08 (0.01)	0.62 (0.07)	0.38 (0.04)	0.21 (0.02)	2.1
Hypericum perforatum	0.84 (0.11)	0.49 (0.06)	0.36 (0.04)	0 (0)	3.6*
Portula oleraceae	0.02 (0)	0.18 (0.02)	0 (0)	0.72 (0.08)	2.4.
Poa pratensis	0.06 (0.01)	0.37 (0.04)	0.86 (0.09)	0.01 (0)	1.1
Carex sp.	0.76 (0.1)	0 (0)	0.26 (0.03)	0.01 (0)	4.7**
Stelleria media	0 (0)	0 (0)	0.49 (0.05)	0.69 (0.08)	6.7***
Mentha arvensis	0 (0)	0 (0)	0.34 (0.03)	0.49 (0.05)	5.7***
Conyza canadensis	0.74 (0.09)	0.03 (0)	0.31 (0.03)	0 (0)	4.3**
Equisetum sp.	0.16 (0.02)	0.48 (0.05)	0.09 (0.01)	0 (0)	2.3.
Senecio vulgaris	0.08 (0.01)	0.12 (0.01)	0.1 (0.01)	0.43 (0.05)	1.8
Lotus corniculatus	0.71 (0.09)	0 (0)	0.33 (0.03)	0 (0)	2.6.
Arrhenathera elata	0.16 (0.02)	0.1 (0.01)	0.35 (0.04)	0.37 (0.04)	0.4
Trifolium pratensis	0.65 (0.08)	0.22 (0.02)	0.05 (0.01)	0 (0)	8.2***
Panicum occidentale	0.03 (0)	0 (0)	0.55 (0.06)	0.01 (0)	2.3.
Plantago major	0.02 (0)	0.28 (0.03)	0 (0)	0.03 (0)	3.7*
Geranium cariolanum	0.5 (0.06)	0.26 (0.03)	0.13 (0.01)	0.09 (0.01)	4.6**

Table A2. The plant species with significant indicator values for plots under each management regime. Management regimes were defined by the weed management system in the inter-row spaces (Mowing a cover crop or tillage) and irrigation system (overhead or drip). The indicator value of the species in the management regime is listed in parentheses. The number of stars signifies the significance level (* < 0.05, ** < 0.01, *** < 0.001).

Management regime	Indicator species (indicator value and significance)	
Mown cover crop Drip irrigation	<i>Conyza canadensis</i> (13.4***) <i>Chamerion angustifolium</i> (33.5***) Landscape fabric (33.6***) <i>Holcus lanatus</i> (32***) <i>Senecio jacobaea</i> (12.2***) <i>Trifolium pratense</i> (24***) <i>Hypericum perforatum</i> (16.1***) <i>Carex</i> sp. (8.3**)	<i>Anthemis cotula</i> (12.8**) <i>Crepis setosa</i> (16.4**) <i>Geranium carolinianum</i> (12.4**) <i>Rubus</i> sp. (23.7*) <i>Vitis vinifera</i> (4.8*) Litter (30.9*) <i>Lotus corniculatus</i> (5.5*) <i>Salix lucida</i> ssp. <i>lasiandra</i> (3.2*)
Mown cover crop Overhead irrigation	<i>Daucus carota</i> (25.9***) <i>Festuca</i> sp. (28.2***) <i>Hypochaeris radicata</i> (42.9***) <i>Leontodon taraxacoides</i> (18.5***) <i>Lolium perenne</i> (33.9***) <i>Plantago lanceolata</i> (41.7***) <i>Plantago major</i> (11***) <i>Trifolium repens</i> (36.1***) <i>Taraxacum officinale</i> (23.4**) <i>Allium schoenoprasum</i> (9.8**)	<i>Rubus armeniacus</i> (10.2**) <i>Galium aparine</i> (5.6**) <i>Achillea millefolium</i> (5.1**) <i>Erodium cicutarium</i> (7.3*) <i>Prunella vulgaris</i> (5*) <i>Equisetum arvense</i> (6.6*) <i>Fraxinus latifolia</i> (3.8*) <i>Polygonum aviculare</i> (3.9*) Moss (3.3*)
Inter-row tillage Drip irrigation	<i>Agrostis capillaris</i> (22.9***) <i>Elymus repens</i> (24.6***) <i>Avena sativa</i> (22.9***) Bare (51.5***)	<i>Brassica</i> sp. (21.6***) <i>Bromus arvensis</i> (7.3**) <i>Panicum capillare</i> (4.9*)
Inter-row tillage Overhead irrigation	<i>Amaranthus retroflexus</i> (67.2***) <i>Brassica rapa</i> (16.4***) <i>Chenopodium album</i> (57.5***) <i>Cirsium arvense</i> (30.8***) <i>Conium maculatum</i> (38.2***) <i>Lactuca serriola</i> (30.8***) <i>Malva neglecta</i> (16.8***) <i>Mentha arvensis</i> (16.8***) <i>Rumex acetosa</i> (23.2***)	<i>Solanum nigrum</i> (21.5***) <i>Veronica officinalis</i> (23.5***) <i>Sonchus arvensis</i> (26.6**) <i>Digitaria sanguinalis</i> (16*) <i>Rubus idaeus</i> (18.2*) <i>Stellaria media</i> (8.6*) <i>Hordeum brachyantherum</i> (3.7*) <i>Arctium lappa</i> (3.7*) <i>Portulaca oleracea</i> (4.9*)

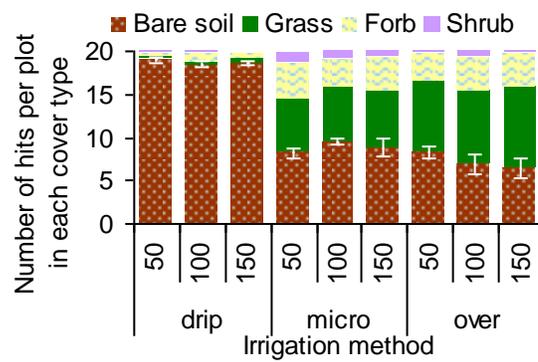


Figure A2. The mean number of hits per point intercept plots of weeds and bare soil underneath the blueberry rows. The error bars are the standard error of the mean number of hits on bare soil.

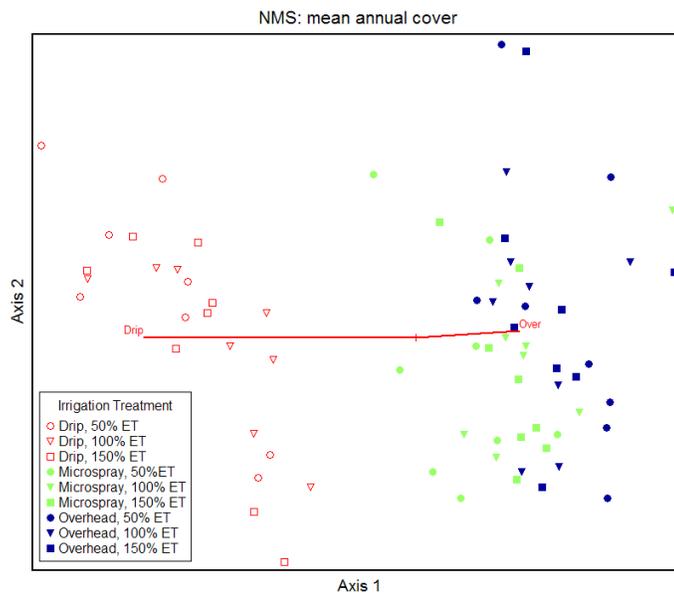


Figure A3. NMS ordination showing both axes of a 2 dimensional solution based on total coverage of each plot over the entire year. Symbols of the same color have the same irrigation type, while similar shapes have the same irrigation amount.

Table A3. Parametric and nonparametric analyses of each species response to the irrigation treatments. The species are sorted by their percent cover among all of the plots which is listed in the second column. The next three columns show correlations between species covers and axis one of the ordination. Non-vegetated cover types (bare soil and litter), the legumes, and *Crepis setosa* are strongly negatively correlated, meaning they have higher values in drip irrigation treatments. The target cover crop grass (*Lolium perenne*), a weedy annual grass (*Poa annua*), and *Taraxicum officinale* are positively correlated with axis one and therefore have higher abundance in microspray and overhead irrigation treatments. The rightmost three columns show F-statistics from ANOVA testing for significant main effects and their interaction. Significance is indicated by stars ($P < 0.001 = ***$, $P < 0.01 = **$, $P < 0.05 = *$, $P < 0.1 = .$). The superscripts after the species name indicate the floral type - = not plant, 0 = no resources, 1 = *Plantago*, 2 = Fabaceae, 3 = Partially hidden nectaries, 4 = Other showy flowers, 5 = Other Asteraceae, 6 = Cichoreae, 7 = Exposed nectaries

Cover group	%cover	R	r-sq	tau	Type	ET	type:ET
<i>Lolium perenne</i> ⁰	55.5	0.48	0.23	0.29	12.4***	0.9	0.1
Litter ⁻	11.8	-0.93	0.87	-0.65	207.1***	0.2	1
<i>Taraxicum officinale</i> ⁶	7.79	0.81	0.65	0.63	48.6***	0.1	1.2
<i>Trifolium repens</i> ²	5.71	-0.27	0.07	-0.19	5.3**	0	0.4
<i>Medicago lupulina</i> ²	3.79	-0.49	0.24	-0.18	11.9***	0.7	1.6
Bare soil ⁻	3.54	-0.72	0.52	-0.51	48.4***	0	0.2
<i>Hypochaeris radicata</i> ⁶	3.06	0.29	0.08	0.17	3.4*	0.7	0.9
<i>Poa annua</i> ⁰	2.91	0.56	0.31	0.56	22.2***	2.9	1
<i>Leontodon taraxicoides</i> ⁶	2.27	0.12	0.01	0.15	1.1	0.3	0.2
Moss ⁻	0.94	-0.09	0.01	-0.07	3.4*	0.3	0.1
<i>Prunella vulgaris</i> ³	0.91	0.25	0.06	0.19	0.9	0.5	0.2
<i>Plantago lanceolata</i> ¹	0.67	0.14	0.02	0.19	0.8	1.2	2.6
<i>Cerastium arvense</i> ⁴	0.33	0.20	0.04	0.25	1.1	0.6	1.7
<i>Bellis perenne</i> ⁵	0.22	0.20	0.04	0.16	1.1	1.5	1.5
<i>Festuca arundinaceae</i> ⁰	0.22	-0.05	0.00	-0.08	0.6	1	0.8
<i>Holcus lanatum</i> ⁰	0.19	-0.08	0.01	-0.15	0.5	0.7	0.2
<i>Geranium carolinianum</i> ⁴	0.057	-0.05	0.00	-0.09	1	0.6	2
<i>Veronica officinale</i> ³	0.029	0.10	0.01	0.12	0.8	1.3	1.3
<i>Rubus armeniacus</i> ⁷	0.027	0.13	0.02	0.09	4.7*	2.5	2.6
<i>Plantago major</i> ¹	0.025	0.09	0.01	0.02	2	0.9	0.9
<i>Stellaria media</i> ⁴	0.015	-0.05	0.00	-0.13	0.4	0.1	0
Dicot seedling ⁰	0.014	-0.14	0.02	-0.08	1.7	0.1	1
<i>Daucus carota</i> ⁷	0.014	-0.13	0.02	-0.11	1.3	1.9	1.9
<i>Sonchus arvensis</i> ⁶	0.009	0.21	0.04	0.19	3.2*	0.3	1.8
<i>Allium schoenoprasum</i> ⁷	0.006	-0.05	0.00	0.00	0.2	0.3	1.2
<i>Crepis setosa</i> ⁶	0.004	-0.19	0.04	-0.15	2	3	3
<i>Sonchus asper</i> ⁶	0.004	0.06	0.00	0.06	0.6	0.3	2.1
<i>Digitaria sanguinea</i> ⁰	0.003	0.01	0.00	-0.04	1	1.5	1.5
<i>Senecio vulgaris</i> ⁵	0.001	-0.14	0.02	-0.11	1	1.5	1.5
<i>Cirsium arvense</i> ⁵	0.001	0.04	0.00	-0.03	1	1.5	1.5

Table A4. Chance corrected within group agreement values (A-statistics) from pairwise comparisons of treatment groups based on blocked MRPP with treatment as the grouping variable. A-statistics of 1 indicate there are no differences between members of the same group, while values of 0 indicate heterogeneity within groups is equal to what would be expected at random. Values greater than 0.1 are considered high. Asterisks indicate significance level ($P < 0.001 = ***$, $P < 0.01 = **$, $P < 0.05 = *$)

	Drip			Microspray			Overhead	
	50%	100%	150%	50%	100%	150%	50%	100%
Drip, 100% ET	0							
Drip, 150% ET	0.02	0						
Microspray, 50% ET	0.36**	0.35**	0.4**					
Microspray, 100% ET	0.4**	0.4**	0.42**	0.08*				
Microspray, 150% ET	0.41**	0.43**	0.44**	0.04	0.01			
Overhead, 50% ET	0.34**	0.36**	0.37**	0.1*	-0.01	0.04		
Overhead, 100% ET	0.43**	0.42**	0.43**	0.15**	0.03	0.08*	-0.03	
Overhead, 150% ET	0.41**	0.4**	0.39**	0.14**	0.01	0.06	-0.02	0.02

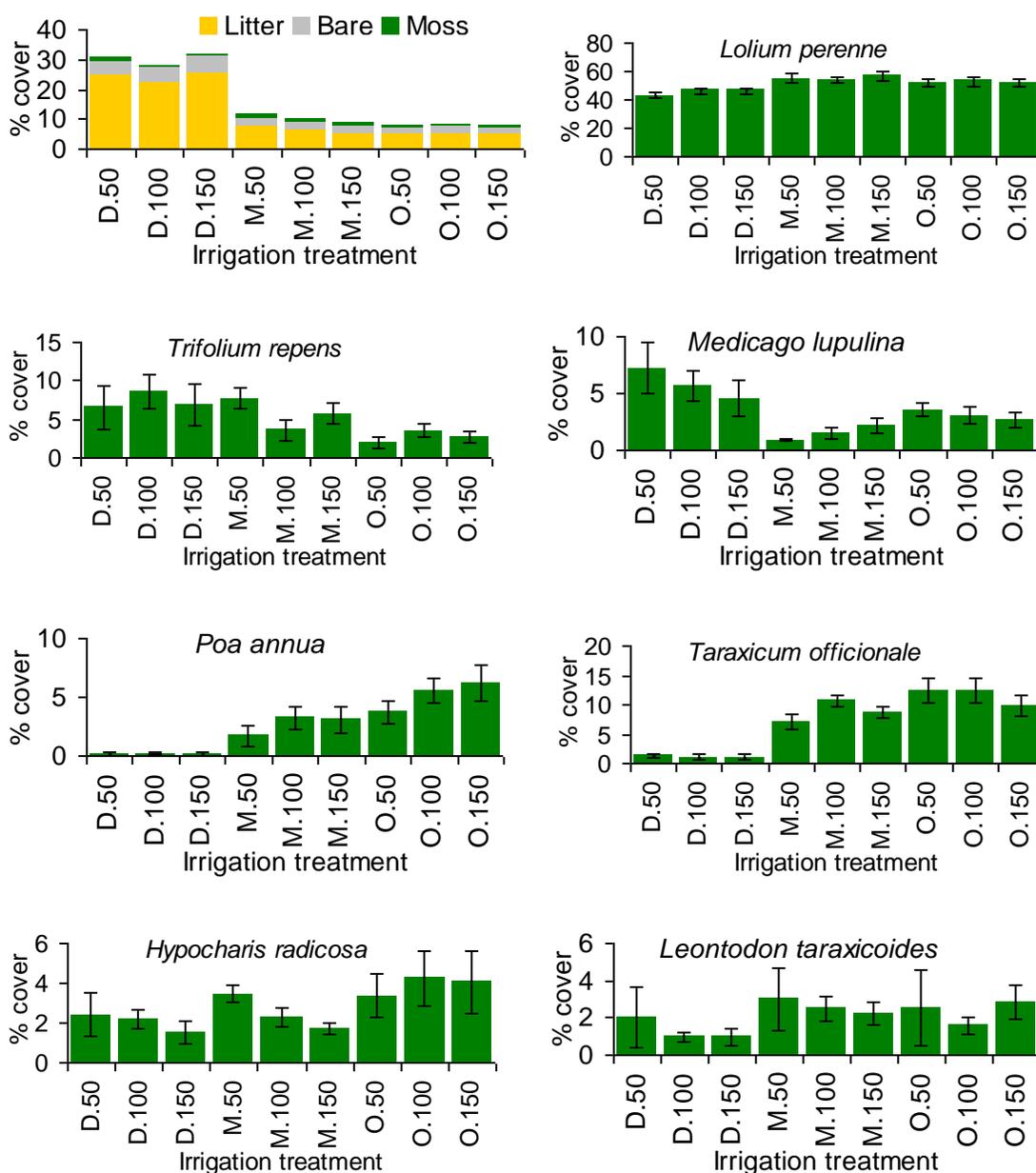


Figure A4. The mean percent cover of the most common species in the different treatments of the irrigation experiment. Irrigation treatments include three methods, Drip, Microspray, and, Overhead and three amounts, 50% of evapotranspiration, 100%ET, and 150%ET, applied in a factorial design with eight replicates taken in two months. Error bars are the Standard error of each treatment mean. The first panel shows the three ground cover types recorded when there was no plant cover and does not include error bars.

Table A5. Pseudo F-statistics from PerMANOVA tests of the effects of irrigation method, Irrigation amount (expressed as the % of the potential evapotranspiration of the blueberry plants), and their interaction. The asterisks indicate the P - values of the tests (< 0.1 , $* < 0.05$, $** < 0.01$, $*** < 0.001$). there were two numerator degrees of freedom for each main effect and four for the interaction. This resulted in 63 degrees of freedom in the denominator for the f tests in the months with 72 segments sampled and 27 denominator degrees of freedom for June samples when there was only 36 segments sampled.

	Irrigation method	Irrigation amount	Interaction
April	20***	0.9	0.5
May	16.6***	0.8	1.6
June	4.9**	0.9	0.8
July	10.2***	0.5	0.8
August	13***	1.2	1.4
September	7.1***	2.2.	1.5

Table A6. T-statistics of pairwise comparisons between treatment factors for each month based on PerMANOVA analysis of the monthly flowering scores of each flower type group (see Figure A6)

Factor	Irrigation Method			% of potential Evapotranspiration		
	Drip vs. Micro	Drip vs. Over	Micro vs. Over	50 vs. 100	50 vs. 150	100 vs. 150
April	5.3***	5.3***	0.4	0.4	1	1.2
May	5.3***	4.3***	1.1	0	1.1	1.1
June	2.9**	2.4**	1.3	0.5	1.3	1.1
July	4.5***	2.3**	3.1***	0.5	0.9	0.5
August	4.2***	4.2***	1.1	1	1.5.	0.4
September	3.1***	2.7**	1.8*	1	1.8*	1.4

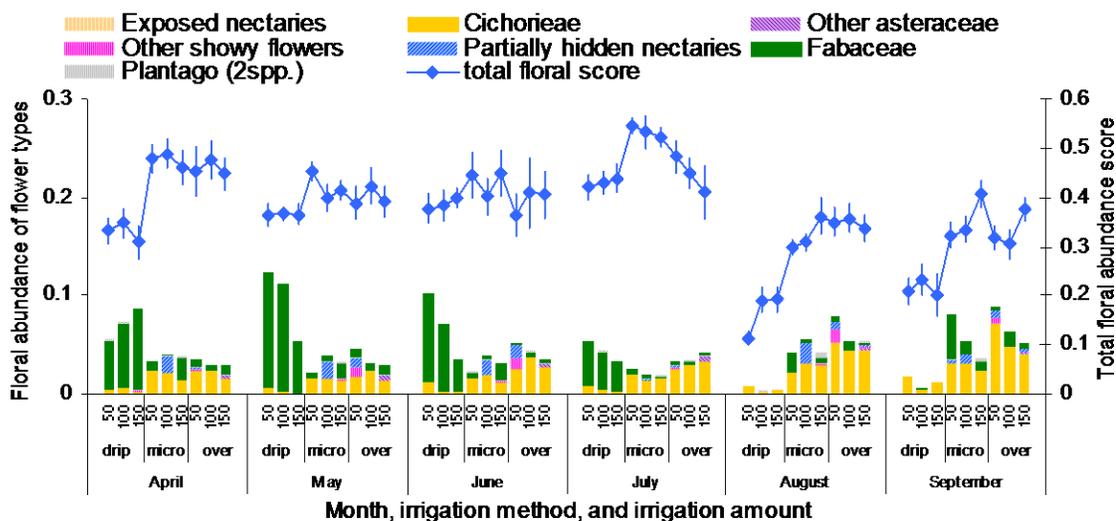


Figure A5. The abundance of each flower type in plots with each irrigation treatment. Treatments include three irrigation method (drip, microspray, or overhead) and three irrigation amounts (50%, 100%, or 150% of the potential evapotranspiration of the blueberries) in each month from April to September. There were eight replicates of each treatment for a total of 72 samples per month except in June when there were only four replicates per treatment (total = 36). Each floral type is depicted as stacked bars scaled to the left Y-axis. The points are the total floral abundance score of the plot (all of the flower types plus the flowers of grass species). The total abundance is scaled to the right axis which is half scale with the left Y-axis. The error bars are the standard error of the mean total floral abundance score of the plot.

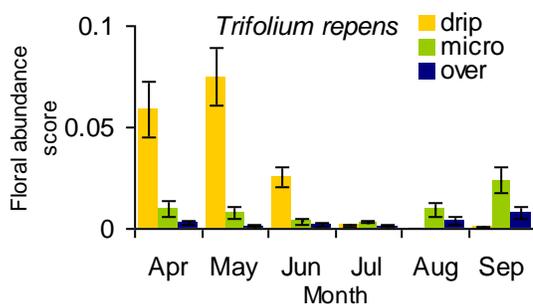


Table A6. The mean floral abundance scores of *Trifolium repens* on plots with each irrigation method during each month. The error bars are standard errors of the mean of each estimate. There were eight replicates of each treatment for a total of 72 samples per month except in June when there were only four replicates per treatment (total = 36).

Appendix B Phenology, feeding habits, activity patterns, and fertility state of common ground beetles (Coleoptera: Carabidae) of agricultural areas in the Willamette valley of western Oregon

Introduction

Ground beetles are a diverse family of beetles that can play an important role in the regulation of pest numbers on farms (Edwards, et al. 1979, Sunderland and Vickerman 1980, Kromp 1999, Brewer and Elliot 2003). The ecology of specific ground beetles on Pacific Northwest farms has begun to be studied but there is much that remains to be understood. (Green 2011, McGrath 2000, Moulton 2011, Prasad and Snyder 2004, Prasad and Snyder 2006). Previous researchers on the ecology of specific ground beetles on Pacific Northwest farms explored the effects of conservation tillage practices on some of those ground beetles (Green 2011, McGrath 2000). Another study showed that beetle banks could be associated with increased beetle populations (Prasad and Snyder 2006). The diet of some ground beetles in the northwest have been studied through laboratory feeding trials and gut analysis of field caught specimens (Prasad and Snyder 2004, Moulton 2011). There are many other species that are common in Willamette Valley agricultural areas, for which little is known about basic life history characteristics like feeding habits, phenology, and habitat affinities. An experiment in Washington demonstrated that interactions between different ground beetle species, and the prey items that are available, can determine whether or not the community as a whole contributes to lower pest numbers (Prasad and Snyder 2006). By collecting more information on the life histories and landscape distribution of these species we will be better able to better understand the adaptations and limitations of the beetle species present in agricultural fields. This information can help managers evaluate the ground beetle communities on their farm and devise strategies to increase their populations as a part of a conservation biological control program.

The objective of this study was to describe the seasonal variation of activity density, feeding rates, activity behaviors, and fertility state among ground beetles

commonly found in vegetable production landscapes. There are six questions I wish to answer with this research.

1. What are the seasonal activity patterns of the most abundant ground beetle species at the sampled farms?
2. Are there differences between ground beetle species in the amount of food consumed and does the consumption activity change over the season?
3. Are there differences in the relative preferences for seeds versus fly pupae of each species and does that preference change over the season?
4. Are there differences in the ability and proclivity of each species for digging and tunneling through soil and do they change over the season?
5. Are there differences in the ability and propensity of each species for climbing on vegetation, and do they change over the season?
6. How does the fertility state of each beetle species change over the course of the species activity season?

Methods

Study areas

The Willamette valley has deep alluvial soils, and a mild climate that is favorable for vegetable production. Vegetables are both grown on diverse smaller farms for the local fresh market and on larger mechanized farms for processing. A diverse community of ground beetles can be found on most types of farms and they likely play a role in the control of weeds and insect pests. Ground beetle communities were sampled on four Willamette valley vegetable farms. Three of the farms (G, H, and P) grew a wide variety of vegetables, rotated through smaller fields that are hand harvested for the fresh market. The fourth farm (K) was a larger farm that grew mostly machine harvested sweet corn and green beans for canning. Two of the organic farms (G and P) had beetle banks in some of the fields and were sampled over 4 years. The other two farms (H and K) were sampled for only two years.

Pitfall traps

Sampling design

The sampling intensity varied over the years of the experiment on three of the farms. Farms H and K were sampled in 2010 and 2011. Pairs of traps were arrayed along transects extending across fields. There were 26 transects in 2010, but three transects were dropped from farm K in the last year because there was a low diversity and abundance of beetles at that farm. In the first year of sampling on farms G and P (2008), traps were evenly spaced along several transects extending across four fields, in subsequent years the traps were placed in clusters of four traps on transects across four fields in 2009 and seven fields in 2010 and 2011. Putting more than one trap in each area is an efficient way to increase the sampling effort and provide a better measurement of the local activity density. The transects extended across fields and included traps in the crop fields and in the adjacent, non-crop habitat at the edges of fields

Pitfall trapping method

Pitfall traps consisted of a plastic pint cup (100 mm diameter), a funnel fitted in the rim of the main cup to prevent insects from escaping, and a smaller cup in the bottom of the main cup. The beetles were captured alive so there was a whole in the inner cup which created a refuge for the smaller species to escape from predation by the larger species. The main cup was buried flush with the soil surface and an aluminum lid was placed over the set up to keep out rain and irrigation water.

Pitfall traps were set out in as close to the same place each month as possible. Traps were opened for 2 nights before the traps were checked and the occupants identified, tallied, and released. Vouchers were collected for each ground beetle species identified. Beetles that are recently emerged from their pupae are called teneral. They are paler and have softer exoskeletons than older beetles. The occurrence of teneral beetles was noted on sampling days that they were caught. Occasionally, field cultivation or flooding would prevent the opening of a trap, or would destroy it, making data collection impossible. Therefore there is not always the same number of samples per month. Beetles were identified based on (Lindroth 1969)

Feeding trial 1: Voracity

During the last 2 years of pitfall trapping, up to 15 beetles per sampling period from each of the common, large species were brought back to the lab for behavior tests. The first test the beetles were exposed to was a feeding test to determine how the quantity of food the beetles would consume changed over the season of activity. Feeding arenas were created by filling large plastic tubs (approximately 50 by 35 cm by 25 cm deep) with about 2 cm of moistened sand. The tubs were placed on the ground on gravel in partial shade.

Five individuals of a single species were placed in each tub along with 5 sentinel prey cards (100 fly pupae total). After 2 days the number of pupae eaten on each card was counted and mean number of pupae eaten per beetle was calculated for the arena. There were up to three arenas created for each species each sampling period, but many species had fewer than 15 collections and therefore filled fewer arenas.

Feeding trial 2: Fly pupae versus pigweed seed choice

After the first feeding trial, the beetles were removed from the arenas and brought inside the lab for a feeding choice trial. These trials were conducted in a smaller box with only a moist paper towel for bedding so it would be possible to distinguish true seed predation from cacheing behavior that ground beetles sometimes exhibit (Manley 1971, Hartke, et al. 1998). Three beetles of one species were placed in each box. One sentinel prey card with 20 fly pupae on it and a moistened piece of filter paper with 20 imbibed *Amaranthus retroflexus* (pigweed) seeds were placed in the box with the beetles. *Amaranthus* seeds have been seen to be readily consumed by ground beetles in other studies (Lund and Turpin 1977). The boxes were left in the lab overnight and the numbers of items eaten were checked after 24 hours.

Activity trial 1: Digging

During the last year of sampling, following feeding trial two, the beetles were taken back outside to the sand filled arenas to test whether the beetles could dig through undisturbed sand. In each arena, five narrow (5 cm by 5 cm by 15 cm deep) seedling pots with open bottoms were pushed into the sand so the rims were at least 1 cm below the

surface of the sand, and 1 cm above the bottom of the box. Up to nine beetles could make it through the second feeding trial so these beetles were put either alone or in pairs into the seedling pots so that their only way to escape into the larger arena would be by digging through the sand.

The arenas were checked the next day. There were three potential outcomes from beetles in the digging trial- not digging, digging, or escaping. When they were checked at the end of the trial, the beetles could be still on the surface in the enclosure pots (not digging). Beetles could have dug into the sand and no longer be visible on the surface, but still be within the rim of the enclosure pot (digging). Finally beetles could have dug into the sand and made their way past the rim of the pot and were out of the enclosure pots, either remaining under the sand or on the surface within the larger arena (escaped). The proportion of beetles exhibiting each type of behavior was recorded.

Activity trial 2: Climbing

Following the digging trials, the beetles were put in another set of boxes to test if they could escape by climbing on plants. The beetles were put in groups of three into one of three 750 ml plastic tubs placed inside a 40 liter plastic box. Several culms of the perennial grass, Meadow fescue (*Schedonorus phoenix*) were put together and their bases were set into the 750 ml tubs with the beetles. The culms extended out of the tubs and their tops were bent down so beetles could climb out into the larger tub. The results of this trial are less definite than the digging trial, because this trial doesn't exclude the possibility that the beetles flew out of the tubs without climbing on the grass, but it is unlikely that they did due to the grass culms blocking a clear flight path out from the bottom of the tub.

Dissections:

After the climbing trial the beetles were freeze killed and stored until the end of the sampling season. The frozen beetles were dissected to determine the fertility state of the beetle. Beetles were sexed based on the large protarsal pads that male beetles have but females lack. For each species up to five male and five female beetles were dissected from each sample month. Most beetle eggs are on the order of two millimeters and are

clearly visible in the female oviducts during the time of year that the beetles are fertile (Luff 1973). The filled seminal vesicles that form large tubes in the abdomens of fertile males are readily distinguished from the immature males that only had small undeveloped structures (Sasakawa 2007). Before the dissection the length of each beetle was measured and the individual was checked for the presence of full flight wings.

Analysis:

Analysis of variance and Tuckey's Honestly Significant Difference multiple comparison test were used to test for differences between beetle species in the response from each experiment. In the voracity feeding trial the mean number of pupae eaten by each species over the whole year was calculated. In the feeding choice trial the number of seeds eaten by the beetle in the trial was divided by the sum of the number of seeds and the number of fly pupae eaten. The means of this proportional preference estimate for each species over the entire year were compared between species. In the digging escape trial, both the proportion of beetles that were found outside the enclosure and the proportion of beetles that were found on the surface within the small enclosures at the end of the trial were compared with ANOVA. In the climbing escape trial species were compared based on the proportion of beetles that were found outside the small enclosure they were placed in. For each of these responses ANOVA was also used to test each species for differences between sample months.

Results

Activity pattern

Each beetle species had its own pattern of activity over the year. In general the species can be separated into three groups based on activity season and when adults emerge from pupae. The first group has maximum activity in the late spring and early summer with teneral beetles observed in late summer, another group has maximum activity in late summer to fall with teneral beetles observed at the beginning of the activity season, and one species has two distinct activity periods – once in early spring and then again in fall with teneral beetles observed during the spring period (Figure B1).

Feeding trial 1: Voracity

Among the species, there were significant differences between the beetle species in the mean number of pupae eaten per beetle ($F_{16/356} = 31$, $P < 10^{-15}$). The mean proportion of freeze killed fly pupae eaten in feeding trial one varied between nearly all (20 per beetle) of the pupae eaten by the largest species, to fewer than 10 pupae eaten per beetle in smaller species (Figure B2). *S. marginatus* and *O. audouini* are two large beetles that ate very few pupae, suggesting that the items presented were not an acceptable food for those species.

Many species exhibited a pattern in the number of fly pupae they eat over the season. Nine of the seventeen tested species had significant differences in voracity in different months (Table B1). The species without significant monthly variation included less common species which had fewer samples during fewer months, large species that ate every pupae offered, and *S. marginatus*, an uncommon species that has morphological adaptations for eating mollusks and which hardly ate any pupae. Often, there were reduced feeding levels in the early and late parts of the species activity season. The peak in feeding rate often occurred during the same part of the season as the maximum activity, and tended to decline later in the season (Figure B1).

Feeding trial 2: Fly pupae versus pigweed seed choice

All of the ground beetle species were found to eat at least a few seeds, but there was significant variability among the species ($F_{13/382} = 20$, $P < 10^{-15}$). A few species like *Nebria brevicaulis* and *S. marginatus* ate very few seeds, and may have only tested the edibility of the ones that were eaten. Other species, including the two species of *Harpalus* and *Anisodactylus binotatus*, ate almost all of the seeds that were presented (Figure B3). *Amara californica* was the only species where there was a significant difference between months in how many seeds it ate as a proportion of total food items chosen, but several other species exhibited a trend in eating a higher proportion of seeds later or earlier in their activity season (Table B1, Figure B1).

Activity trial 1: Digging

Beetle species differed both in the proportion of individuals who did not dig at all and were found on the surface ($F_{13/364} = 22, P < 10^{-16}$), and the proportion of individuals which dug enough to escape from the enclosure ($F_{13/364} = 3.3, P < 10^{-4}$). Species varied from having fewer than five percent of the beetles digging in to the sand to one species which all the individuals had dug into the sand (Figure B4). Relatively few beetles were able to fully escape from the pot enclosures, with only two species having more than 25 percent of the individuals escaping (Figure B4). There were no significant difference in the proportion of beetles of each species that fully escaped from the enclosures between months, but for 4 species there was significant trend of fewer individuals digging at all later in the activity season of the species (Table B1, Figure B1)

Activity trial 2: Climbing

Variation in the proportion of beetles escaping during the climbing trial was less than variation in the digging trial, but there were still significant differences between species ($F_{12/175} = 12, P < 10^{-16}$). One species, *O. audouini*, was unable to escape on the grass stems at all, but the rest of the species had more than 45 percent of the beetles escaping from the enclosures (Figure B5). The proportion of beetles that escaped the enclosure tended to increase in the months later in each species' activity season, but the difference was significant in only four of the thirteen beetle species tested (Table B1, Figure B1)

Dissections:

The maximum number of eggs found within a female beetle was 39, while the species with the fewest eggs per beetle had a maximum egg load of seven (Table B2). The number of eggs in the females of each species varied over the season with many species having a distinct period of egg production followed by a period of decline. The peak in egg load coincided with the peak in activity for some species, but for others it was earlier or later in the season (Figure B1). Male beetles tended to have a more prolonged fertility period either beginning before and / or continuing after the peak in egg load for females of the species.

The three native beetles most closely associated with perennial habitat types, *O. audouini*, *S. marginatus*, and *P. algidus*, did not have fully developed wings, while the other species did (Table B2). Only around one third of the dissected *Pterostichus melanarius* individuals had wings. There was a single female of each species of *Anisodactylus* without wings, while the rest of the winged species had wings in all individuals.

Discussion

Feeding trials

The beetle species observed in this study included species that readily ate the freeze killed fly pupae or the *A. retroflexus* seeds and species that did not. Some species, like the *Amara* species, may have eaten fewer pupae because of their smaller size. Large species that ate few pupae included *S. marginatus*, which is considered to be a specialist on mollusks, or *O. audouini*, which may prefer live or larger prey.

Both *Harpalus* species consumed a high number of seeds. Seed feeding has been observed in both of these species, and other species of *Harpalus* (Sasakawa 2010, Johnson and Cameron 1969, Lund and Turpin 1977, Honek, et al. 2005). However, there have been observations of one species of *Harpalus* where it did not eat many seeds (Johnson and Cameron 1969). *An. sanctaecrucis* from Michigan has been observed eating seeds, and a Japanese species of *Anisodactylus* was shown to have better development and higher fecundity on diets that contained seeds (White, et al 2007, Sasakawa 2009). In this study the two species of *Amara* consumed seeds. This is similar to the observation of *Amara* species from other regions eating seeds, although there has been variability in the types and amounts of seeds eaten by different species of *Amara* (Klimes and Saska 2010, Saska 2005, White, et al 2007, Sasakawa, et al. 2010). *P. melanarius* and three species of *Agonum* from New York State were observed feeding on seeds in the lab (Johnson and Cameron 1969). *P. melanarius* from the Willamette valley ate a large number of seeds, while the species of *Agonum* were found to eat some seeds, but relatively fewer than with other tested species. The putative diet of *N. brevicaulis* is Collembolans and other small arthropods (Penney 1969, Warner, et al. 2008). In the

Willamette valley individuals of *N. brevicaulis* ate very few seeds, and only a moderate amount of pupae.

Activity trials

In the digging trial there were a variety of responses with *O. audouini*, *S. marginatus*, *P. algidus* and *N. brevicaulis* being the least likely to have dug into the soil. In this study almost all of the *An. sanctaecrucis* and the majority of both *Amara* species were found to have dug into the soil. This differs from another lab study where *An. sanctaecrucis* and a species of *Amara* from Michigan failed to find buried seed in a lab experiment, even when they ate a large number of seeds that were left on the soil surface (White, et al 2007). In the Michigan experiment *H. pensylvanicus* dug into the soil up to one centimeter below the soil surface to get at seeds (White, et al 2007). This result concurs with the observation reported here that most of the tested individuals were found to have dug into the soil.

Among Willamette valley species, only *O. audouini* did not escape in the climbing experiment. This is similar to other studies where *Ag. muelleri* and species of *Amara* from multiple regions have been observed climbing on vegetation (Barney and Pass 1986 B, Hajek, et al. 2007, Sasakawa 2010). *H. pensylvanicus* was found to escape in the climbing experiment described here, but the species was not observed climbing on plants in a laboratory study, even though other species were (Barney and Pass 1986 B).

Egg load and fecundity

The maximum number of eggs found in females of each beetle species varied from seven to 39, and the monthly mean egg load during the peak of fertility for each species ranged from 2.3 to 20 eggs per beetle (Table B4). The range of values is similar to what has been reported from carabids in other regions. In a survey of *Pterostichus* species from eastern Canada, the median egg load for *P. melanarius* was 14 and the maximum was 34, while other species had median egg loads between seven and 18 (Barlow 1970). *P. melanarius* from the Willamette valley had fewer eggs than in the Ontario study, but the *P. algidus* egg load was higher than any of the other species. Four *Pterostichus* species from Poland had season long mean egg loads between five and ten,

but that estimate included values from more than just the peak fertility season (Grüm 1984). A species of *Nebria (salina)* from England was found to have means of 10 and 16 eggs per beetle, which is similar to the egg load for *N. brevicaulis* (Telfer and Butterfield 2004). Comparisons with related species may not be informative however. The two species of *Agonum* included in this study are difficult to tell apart based on external characteristics, but in one species the mean egg load during its peak month was five times the mean egg load of the other species (Table B4).

The number of eggs counted during a dissection is an instantaneous measurement. Total fecundity, the number of eggs a beetle produces over the entire season, is a more standardized measure with which to compare species. Total fecundity is related to egg load, but it is ultimately determined by how many eggs are laid per day, and the duration of the egg laying season. In a study of *An. sanctaecrucis* from South Dakota the highest total fecundity was 142 eggs produced by 2 females over 2.5 months, which is a rate of 0.95 eggs per beetle per day for the duration of the period (Kirk 1977). A Japanese species of *Anisodactylus* was observed to lay six eggs per day, but that was only for a 10 day period that could have excluded periods of the breeding season with less productivity (Sasakawa 2009). A carabid from Holland, *Notiophilus biguttatus*, was able to lay on average four eggs per day when given sufficient food, but fewer when the diet was restricted or if the beetle was smaller (De Ruiter and Ernsting 1987). A Swedish beetle, *Pterostichus cupreus*, was shown to lay around 0.5 to 1.1 eggs per day after being collected from the field, depending on the energy reserves at the time of collection (Bommarco 1998). Another European species, *Carabus clatratus*, also was found to lay about one egg per day in a lab experiment (Huk and Kühne 1999).

Beetle activity seasons

The carabid beetles of Willamette valley can be separated into two major groups based on the season when they are most active and when they lay eggs and emerge from pupae – spring active beetles and late summer active beetles. Ground beetles are a diverse family and a number of other life history groups are necessary to account for all of the species that may be found in different habitats or different regions (Matalin 2007).

However, in this study, with a few exceptions, the species that were commonly collected fit within two main groups.

Spring active beetles

Species of *Anisodactylus*, *Agonum*, and *Amara* are a part of a group of beetles that have a maximum activity and egg laying season in the spring and early summer. The egg develops through larval and pupal stages over the growing season (Saska and Honek 2008, Matalin 2007). Adults emerge near the end of summer and have a diapause or similar inactive stage before the activity and breeding season the following spring. Many individuals can live for more than one breeding season, with one study documenting beetles surviving for up to three breeding seasons (four years since egg) (Kirk 1977).

The *An. binotatus* species group also includes *Anisodactylus californicus*, because they could not be consistently distinguished in the field. In the Willamette valley, these species had a combined activity season that extended from April through October with the peak activity in May through July. This was earlier than the peak season of a population in orchards of the Sacramento Delta of California for *An. californicus*, which was at the end of August (Riddick and Mills 1995).

Anisodactylus sanctaecrucis was less common than *An. binotatus* in these surveys, but it is widespread and has been observed in agricultural landscapes throughout the United States and Canada. In the Willamette valley, it is active from April through October with a peak in June. This is similar to results from other regions, although the peak activity is earlier than observed activity peaks in Iowa and South Dakota (Kirk 1977, Los and Allen 1983).

Amara is a large genus of beetles with several species that can be found on Willamette valley agricultural landscapes. The two most abundant species of *Amara* have activity seasons from April through August. Peak activity for *Am. littoralis* was in May, while *Am. californica* had peaks in both May and July. This is similar to the activity season of other species of *Amara* from Europe (Saska and Honek 2008, Warner, et al. 2008).

The two mid sized *Agonum* species commonly caught in the Willamette valley include *Ag. muelleri*, a European introduction, and *Ag. subserecium*, a native species.

Both species are active in the Willamette valley from April through August with peak activity in May. This is similar, but slightly earlier than an *Ag. muelleri* population from New York State (Hajek, et al. 2007).

Harpalus affinis is a European introduction which was most active in May and June. In Europe this species has a similar lifecycle, but in some populations the time between egg and breeding adults can be more than one year (Matalin 2007).

Late summer active beetles

Harpalus pensylvanicus is in the same genus as *H. affinis*, but it belongs to a different life history group. *H. pensylvanicus* is a widespread American species that is abundant in agricultural fields throughout much of the United States and Canada. On vegetable farms of the Willamette valley the activity season is from July through October with a peak of activity in August. Eggs are laid during September, the larvae over winter and grow the following spring and summer, and the new adults emerge again near the end of summer. Adults can live multiple years and in some systems there is a peak in activity earlier in the year when over wintered adults emerge and another peak when the over wintered larvae finish pupation (Barney and Pass 1986 A). The activity pattern reported here was similar to observations from other regions including Virginia, California, and Pennsylvania, (Los and Allen 1983, Riddick and Mills 1995, Barney and Pass 1986 A, Leslie, et al. 2009). Observations from Ohio, Iowa, and southern Ontario showed activity starting earlier in the season (Larsen, et al. 1996, Leslie, et al. 2009, and Brunke, et al. 2009). The discrepancy could be due to variation in the timing of emergence, or the total number of surviving adults beginning their next breeding season (Barney and Pass 1986 A).

P. melanarius has a similar life history to *H. pensylvanicus* but is far more abundant in Willamette valley agricultural fields. *P. melanarius* is a European species that has become established in much of the United States and Canada. In the Willamette valley, the maximum activity is during August and September. In Europe, the species has been observed to have two different life histories with some beetles having a peak of activity in early summer and others having a peak in late summer (Matalin 2007). The

Willamette valley appears to only have the late summer variant, which is similar to reports from New York state and Ontario (Hajek, et al. 2007, Brunke, et al. 2009). Observations of peak activity in June in dry land grain systems of the Palouse region of northern Idaho suggest that some regions of America may have the early summer variant (Hatten, et al. 2007).

Other life history groups

Some of the carabid species collected in Willamette valley agricultural landscapes that have unique characteristics and could not be placed in to a group with any of the other species in this study. One species breeds and lays eggs in the fall but is also active during the spring, while the other is active only in the spring.

N. brevicaulis lays eggs in October. It had activity peaks in the Willamette valley both in the spring when adults emerge from pupae and in the fall during breeding season. Their life history is similar to spring active beetles in that there is a period of aestivation between when adults emerge from pupae and when the breeding season begins. The inactive beetles have been shown to congregate in hedgerows during the summer aestivation, similar to how the spring active beetles shelter in grassy habitats for the winter (Fernandez-Garcia 2000, Russell 2013 - Chapter 4). The bi-modal activity season has been observed in *N. brevicaulis* populations in its native range (Penney 1969). Lab experiments have identified the seasonal changes in photoperiod as being a driver of sexual maturation in *N. brevicaulis* and another species of *Nebria* (Penney 1969, Telfer and Butterfield 2004). Photo period may influence the maturation of the spring breeding beetles too, but it could also be signaled by cold winter temperatures, or higher temperatures may simply allow development to proceed (Theile 1977).

In Europe *N. brevicaulis* has been shown to only live for a single breeding season (Matalin 2007). This is in contrast with other fall active beetles including *P. algidus* and *S. marginatus* which can live for multiple years. These species had peak activity in September and October in the Willamette valley. Similar results were seen in a study from southwest Washington for both *P. algidus* and another *Scaphinotus* sp. (Johnson, et al. 1966).

O. audouini is active from April to July, but although it is included as a ground beetle here it is actually in the closely related tiger beetle family (Cicindellidae). Differences between tiger beetles and carabids mean this species should belong to its own life history group. The related species *Omus dejeanii* Reiche, which was represented by a single collection in this study, was found to have a similar activity season in samples from a forestry research station in southwest Washington (Johnson, et al. 1966). In that case, the activity season was slightly later in sites dominated by dense conifer plantations than sites with open trees in a grassy meadow (Johnson, et al. 1966).

Conclusion

Each of these studies provided a unique bit of information on the life history of the common ground beetles species of Willamette valley agricultural landscapes. Identifying the seasonal activity and feeding habitats can be used to identify which species may be a potential predator of a vulnerable life stage of a specific pest (Russell 2013 – Chapter 4). Beetles that were found to be able to dig through the sand in the digging trial may be better able to survival burial during field tillage than beetles that were not found to dig through the sand or more likely to find buried prey items. Beetles that could not climb are unlikely to be able to access prey items that is on plants while species that did climb may be able to access those prey items. The egg load data not only helps identify the larval development season of the beetle, it also provides some information on the potential fecundity of the species. Currently information about species from different regions are are generally thought to be similar for taxonomically related species. If more species are characterized based on similar physiological tests it may be possible to develop different dimensions of similarity between species in order to more broadly apply lessons learned about ground beetles in one region to ground beetles in other regions.

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Figure B1. Seasonal changes in the activity, feeding, and reproductive state of Ground beetle species included in the studies. The grey solid background indicates the mean number of beetles caught per trap during each month, with the values relativized to the maximum monthly value for the species. The maximum monthly mean catch from each species is listed in the legend. The solid filled bars indicate the mean number of sentinel prey items eaten by each beetle in each month in the first feeding trial. The bars are relativized to the maximum possible, 20 prey items per beetle. The checkered bars indicate the number of seeds that were eaten in the second feeding trial as a proportion of all the food items eaten. The orange hollow bars indicate the proportion of beetles that escaped from the enclosure in the digging trial. The orange error line above the hollow bars indicates the remaining proportion of beetles that had dug below the surface, but did not escape the enclosure. The blue hollow bars indicate the proportion of beetles that escaped by climbing on a grass stem from enclosures in the climbing trial. The round points along the line indicate the mean number of eggs that were found in the female beetles as a relative the maximum monthly mean, which is listed in the legend. The triangles indicate the proportion of males that were fertile when dissected. The month that newly emerged (teneral) beetles were observed is indicated where appropriate with an asterisk after the label along the abscissa, and a star in the graph at the value of one..

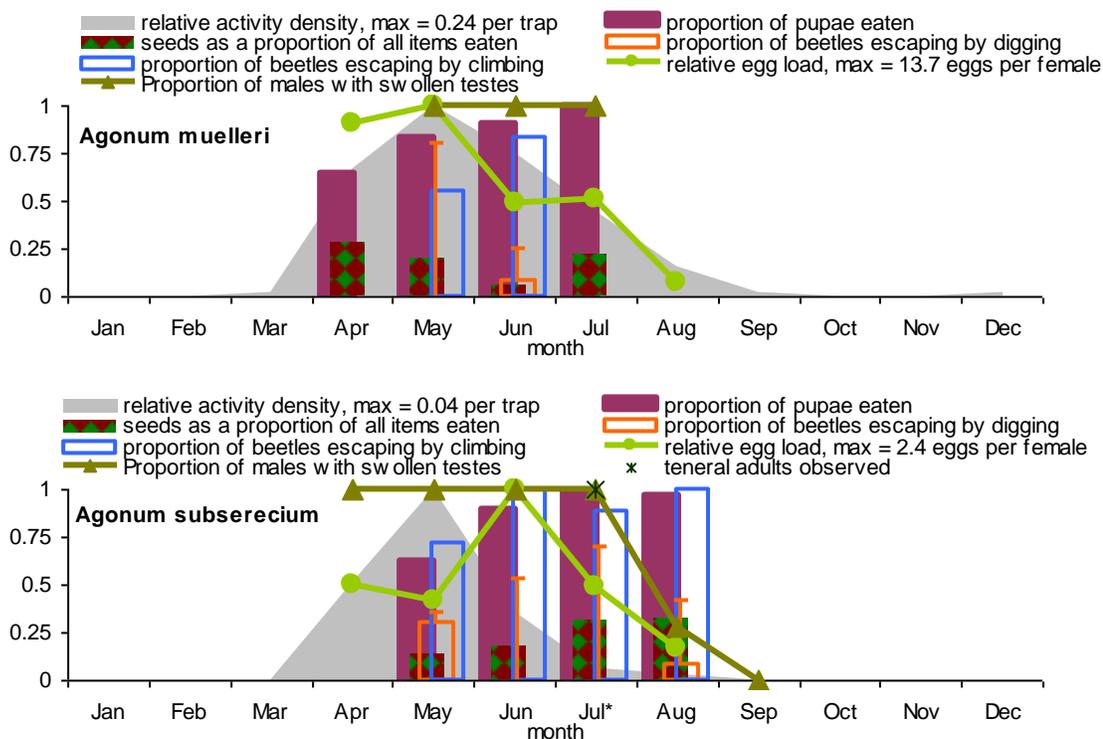


Figure B1 (Ctd.). Seasonal changes in the activity, feeding, and reproductive state of Ground beetle species included in the studies.

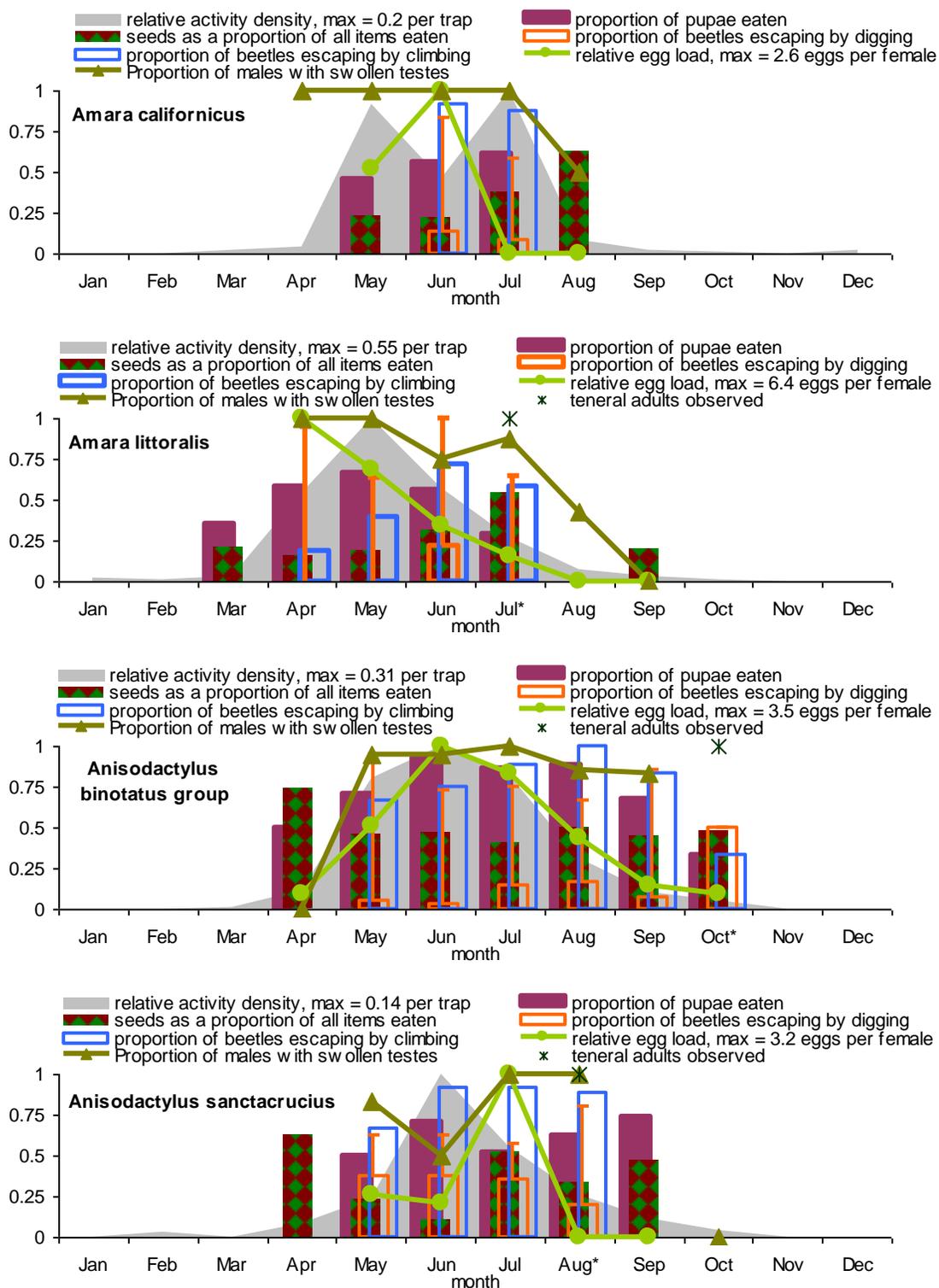


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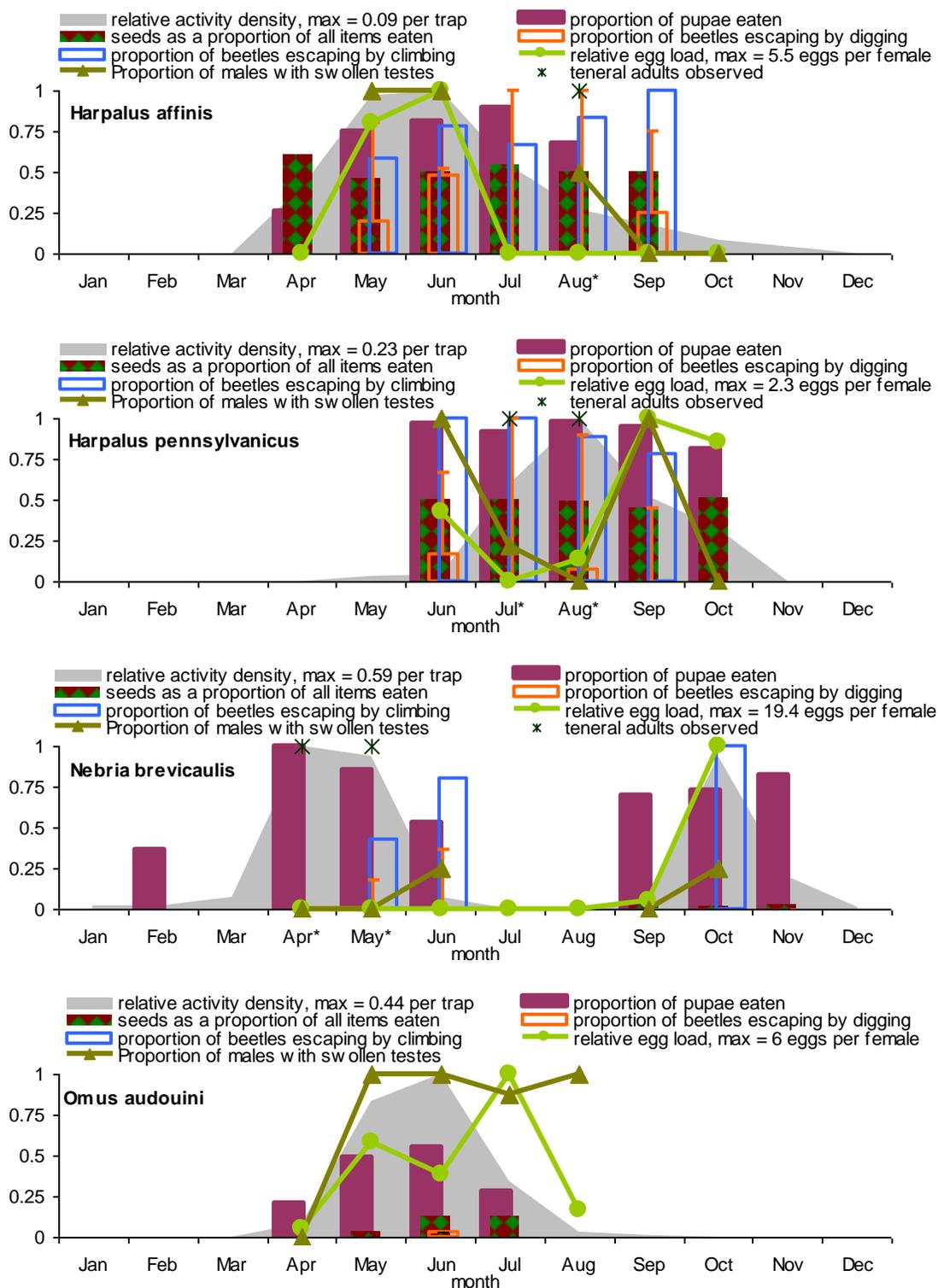


Figure B1 (Ctd.). Seasonal changes in the activity, feeding, and reproductive state of Ground beetle species included in the studies.

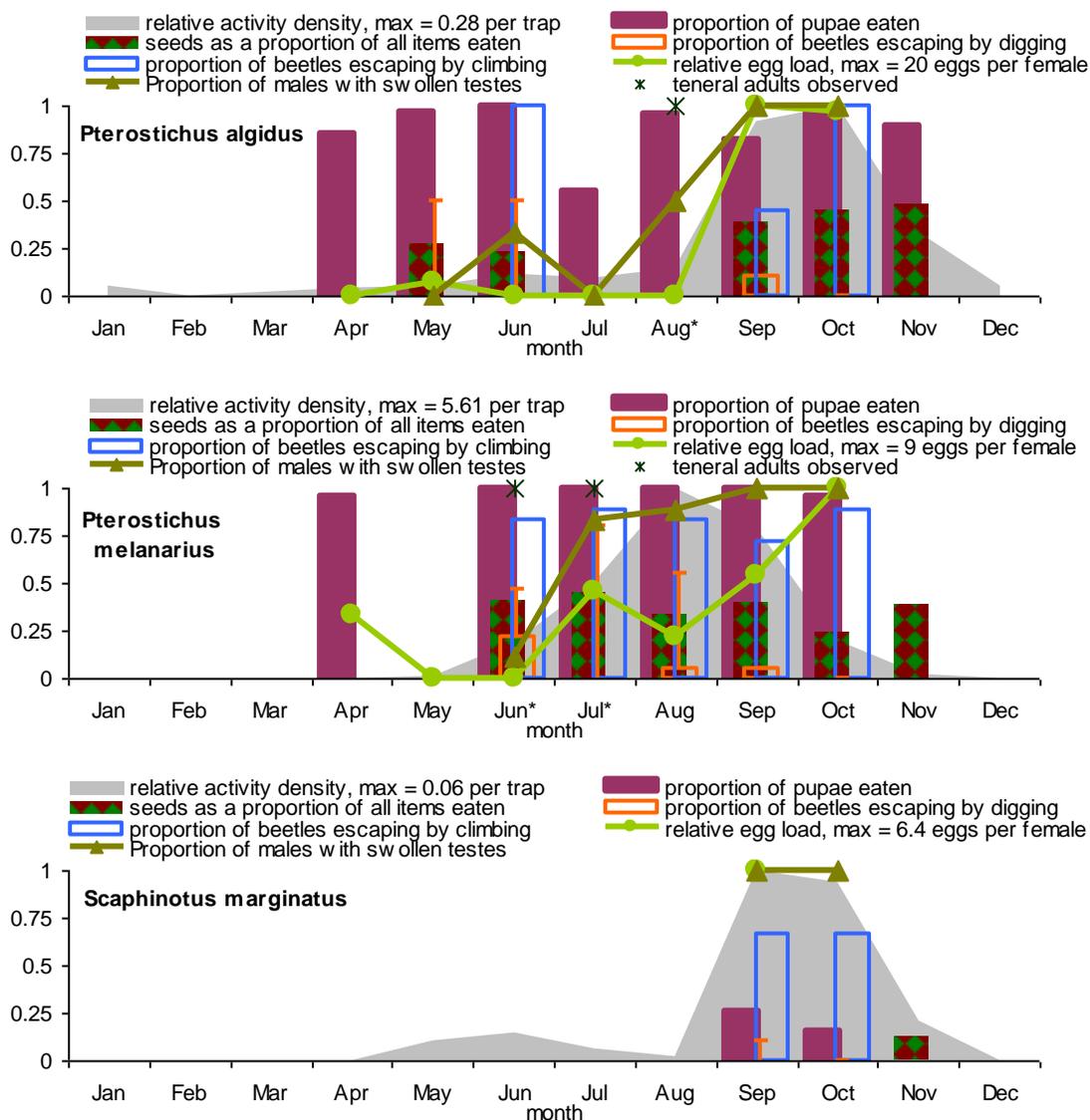


Figure B2. The mean number of fly pupae eaten per beetle over two days for species included in the first feeding trial. Error bars are the standard error of the mean. Species labeled with different letters were significantly different based on Tukey's HSD multiple comparison test.

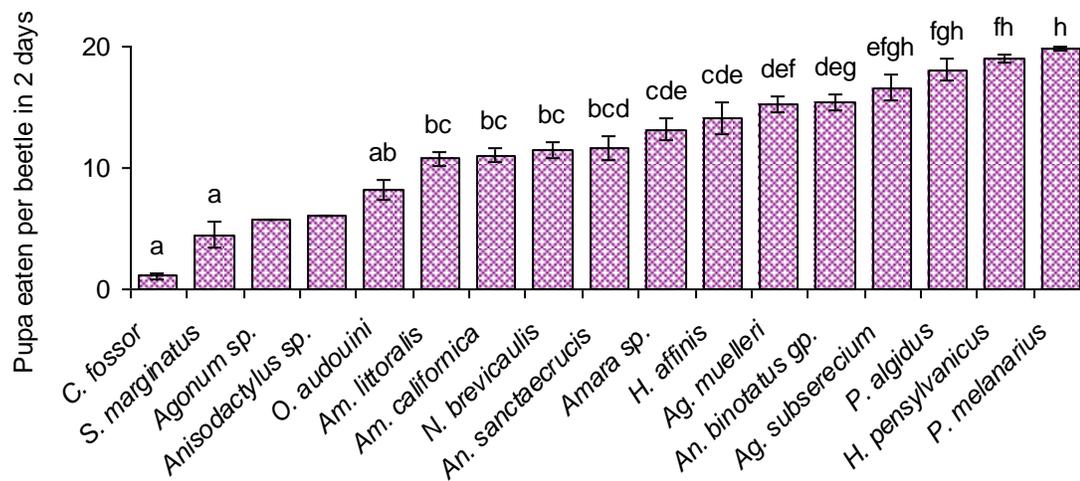


Table B1. F statistics, significance, and degrees of freedom from anova models testing for differences between monthly means in the response variables in each trial for each species. Asterisks indicate the significance level (*** < 0.001, ** < 0.01, * < 0.05, < 0.10, otherwise = n.s.).

Experiment	FT1	FT 2	dig trial	dig trial	dig trial	climb trial
Response	pupae per beetle	seed to all ratio	p.NODIG	p.DIG	p.ESCAPE	climbed out
Factor	month	month	month	month	month	month
<i>Agonum muelleri</i>	7.7** 3/14	3.1. 2/11	4.7. 1/9	6.3* 1/9	0.8 1/9	2.1 1/3
<i>Agonum subsericum</i>	9** 3/13	2.2 3/17	0.3 3/26	0.9 3/26	2 3/26	2.1 3/14
<i>Amara californica</i>	3.1. 2/21	3.4* 3/23	6.9* 1/19	1.7 1/19	0.1 1/19	0.1 1/8
<i>Amara littoralis</i>	4.6** 4/39	1.9 5/38	2.5. 3/39	1.9 3/39	1.4 3/39	5.3** 3/18
<i>Amara sp.</i>	6* 3/6	1.4 4/9	not tested	not tested	not tested	not tested
<i>Anisodactylus binotatus</i>	4.5** 6/48	1.2 6/54	1.1 5/58	0.8 5/58	1.6 5/58	1.5 5/24
<i>Anisodactylus sanctaecrucis</i>	0.6 4/7	2 5/12	0.8 3/20	0.3 3/20	0.2 3/20	1.9 3/10
<i>Harpalus affinis</i>	13.9*** 4/10	0.2 5/12	0 4/18	1.4 4/18	1.4 4/18	4.4** 5/81
<i>Harpalus pennsylvanicus</i>	3.6* 4/22	0.5 4/22	6.9** 3/20	4.1* 3/20	1.4 3/20	0.8 3/13
<i>Nebria brevicaulis</i>	3.9** 5/29	1 6/31	0.7 2/26	0.7 2/26	0 2/26	9.6** 2/12
<i>Omus audouini</i>	4.8* 3/20	1.4 2/16	0.6 2/24	0.3 2/24	0.3 2/24	0 2/8
<i>Pterostichus algidus</i>	0.6 4/16	1.3 4/21	2.2 3/13	3. 3/13	0.8 3/13	18.7** 3/4
<i>Pterostichus melanarius</i>	1.4 5/51	2.2. 5/51	10*** 4/44	9*** 4/44	1.2 4/44	0.6 4/18
<i>Scaphinotus marginatus</i>	0.5 1/7	1 2/9	0.4 1/5	0.4 1/5	0 1/5	0 1/2

Figure B3. The number of pigweed seeds eaten as a proportion of all items eaten for each ground beetle species. Error bars are the standard error of the mean. Species labeled with different letters were significantly different based on Tukey's HSD multiple comparison test.

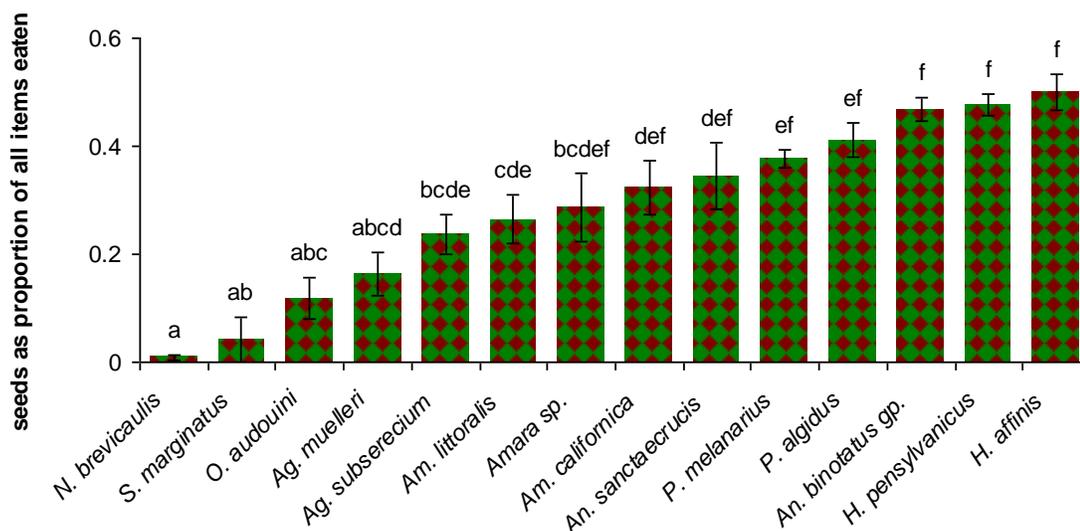


Figure B4. The proportion of beetles that had done each activity in the digging trial. Beetles could be either on the surface within enclosures, they could have dug under the soil but still be within the enclosure, and they could have dug out of the enclosures and into the larger arena.

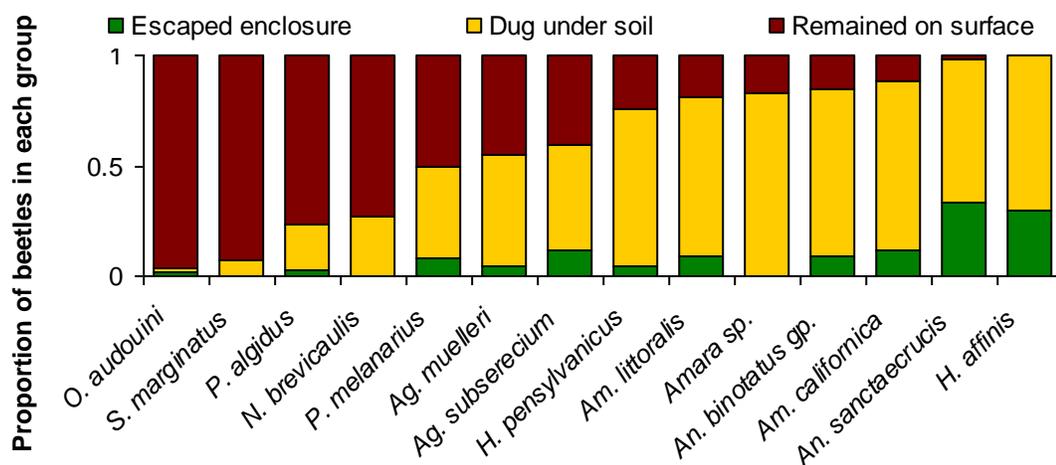


Figure B5. The proportion of beetles escaping enclosures by climbing on grass culms. Error bars are the standard error of the mean. Species labeled with different letters were significantly different based on Tukey's HSD multiple comparison test.

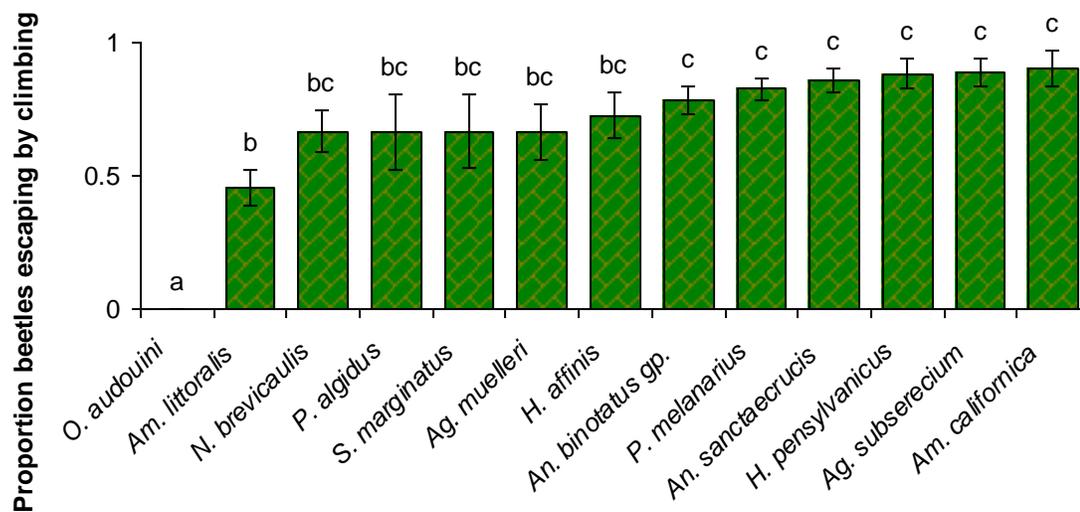


Table B2. The characteristics measured during dissections. Measurements include the mean egg load during the peak month (when egg load was the highest), the sum of all the monthly means, the overall maximum number of eggs found in an individual beetle, the mean body length for females and males, and the proportion of individuals with developed wings.

beetle species	Egg load per beetle			Body length (mm)		P. Wing
	Mean(SE) at peak	mean sum	Indv. max	Mean (SE) Females	Mean (SE) Males	
<i>Harpalus pennsylvanicus</i>	2.3 (1.1)	5.6	7	12.9 (0.1)	13.1 (0.1)	1
<i>Agonum subsericum</i>	2.4 (0.7)	6.2	7	10.3 (0.1)	10.1 (0.1)	1
<i>Harpalus affinus</i>	5.5 (1.7)	9.9	8	10.8 (0.1)	10.4 (0.1)	1
<i>Omus audouini</i>	6 (0.9)	13.1	8	16.5 (0.1)	15 (0.1)	0
<i>Scaphanotus marginatus</i>	9 (n=1)	15.4	9	16.2 (0.2)	14.9 (0.1)	0
<i>Amara littoralis</i>	6.4 (0.9)	14	12	7.3 (0.3)	7.7 (0.3)	1
<i>Anisodactylus binotatus</i> gp.	3.5 (1.1)	10.9	12	11.5 (0.1)	11.4 (0.1)	0.99
<i>Anisodactylus sanctaecrucis</i>	3.2 (2.3)	4.7	12	9.5 (0.1)	9 (0.1)	0.98
<i>Amara californicus</i>	2.6 (2.6)	3.9	18	7.5 (0.2)	7.3 (0.1)	1
<i>Agonum muelerii</i>	13.7 (3.3)	40.7	24	8.8 (0.2)	8.2 (0.1)	1
<i>Pterostichus melanarius</i>	9 (2.9)	23	26	17.1 (0.1)	16 (0.1)	0.34
<i>Nebria brevicaulis</i>	19.4 (3.3)	20.4	37	11.9 (0.3)	11.4 (0.2)	1
<i>Pterostichus algidus</i>	20 (4.5)	40.9	39	13.9 (0.2)	13.8 (0.3)	0