Seasonal Shifts in Ground Beetle (Coleoptera: Carabidae) Species and Functional Composition
Maintain Prey Consumption in western Oregon agricultural landscapes.

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Abstract

Ground Beetles (Carabidae: Coleoptera) are generalist predators that contribute to biological control of agricultural pests. Different ground beetle species vary in terms of size, feeding habits, and season of adult and larval activity. Species with similar biology and feeding habits may form a functional group if they are also similar in their effect on the overall risk to a potential prey item in an area. Farm surveys and laboratory studies were conducted to test whether ground beetle populations on Western Oregon vegetable farms were associated with the predation risk of a sentinel prey item. Pitfall traps were used to measure the activity patterns of adult beetles throughout the year. Along with the monthly pitfall traps, sentinel prey cards were deployed to measure the risk of predation to a potential prey item by a carabid beetle on the landscape. Additionally, beetles were collected after pitfall trapping to measure the amount of the sentinel prey items they would eat. The ground beetle species collected in the sampling were placed into three size based groups. The phenology and feeding habitats of the species within each sized based group tended to be similar. Sentinel prey removal rates in the field were significantly increased in areas with high activity of midsized beetles during the spring, when midsized beetles were the most active on the landscape but the explanatory power was somewhat low. In the summer, when large beetles were active in the landscape, sentinel prey removal rates were similarly associated with large beetle activity densities.

Key Words

generalist predator, biological control, Carabidae, sentinel prey, vegetable farm

1. Introduction

1.1

The goal of conservation biological control is 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 control system. (Symondson, et al. 2002, Stiling and Cornelissen 2005). Assemblages of generalist predators have a number of potential advantages, 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 negatively interact with each other through mechanisms such as intraguild predation. How species in a predator assemblage will interact depends on characteristics of their individual life histories such as the timing of reproduction and feeding, or differences in feeding habits. Life history characteristics can also limit the ability of a generalist species to suppress pest outbreaks (Rosenheim, et al. 1995, Snyder and Ives 2003, 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 can contribute to lower pest abundances (, (Edwards, et al. 1979, Sunderland and Vickerman 1980, Kromp 1999,

Brewer and Elliot 2003). 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).

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 Willamette Valley of Western Oregon, the ground beetle communities of agricultural areas consist of numerous native and non-native species. The species differ in a number of functionally important morphological and life history traits. Size is one important trait. The smallest species are around 4 mm in length, while the largest are up to 20 mm. There

are also several species in the mid-size range that are more than twice as large as the small species and around half as long as the large species. Size differences between the carabid species are likely to influence both intra- and inter- specific trophic relationships (Ball, et al. 2015). For example, large carabid species have been shown to prey upon smaller species and interfere in their effectiveness as biological control agents (Prasad and Snyder 2006).

Phenologically, most species fall in to two main groups. In one group the larvae develop over the winter and the adults breed in the late summer to fall. In the other group the larvae develop during the summer, the adults emerge from pupae in late summer to fall, but remain inactive over winter until their spring to early summer breeding season (Russell 2013). The phenology of each ground beetle species constrains which pest species they may prey upon as they will only be able to consume prey that are in a vulnerable stage during the predator's activity season.

Estimating the comprehensive risks that pests face from rich ground beetle assemblages requires an understanding of how beetle species differ in seasonal activity relative to crop fields and pest phenology, as well as how beetles differ in their life history traits relative to pest feeding behavior. Groups of species with similar life histories may be similar in terms of their ecological functions. Information on the nature of biological control activities of ground beetles in the Northwestern United States is scarce. This study attempts to determine if considering ground beetle species as members of a functional group can help explain their role in pest control in agricultural systems.

1.2 Objectives and research questions.

The objective of this study was to understand how the individual functional traits of species combine to influence the overall biocontrol potential of a beetle assemblage in agricultural landscapes. There were three main parts to meeting this objective. First we used pitfall traps to describe the seasonal phenology and species composition of ground beetle assemblages. Second, we evaluated the species specific and seasonal differences in prey consumption using mesocosms feeding trials. Finally, we tested whether the rate of prey removal in agricultural fields was related to the activity density and potential feeding rate of the ground beetles.

2. Materials and Methods

2.1 Study areas.

The Willamette Valley has deep alluvial soils and a mild climate that is favorable for vegetable production. Vegetables are grown on both 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 fields, along with some residential areas. Wild forests and meadows occur in riparian corridors and other areas where steep slopes, wet soils, or other circumstances have prevented cultivation. 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) were managed organically and 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 conventional 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 strips of 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. Pitfall traps were used to sample beetles while sentinel prey were used to measure the predation risk a potential beetle prey item experienced at each trap site.

2.2 Pitfall traps.

2.2.1 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). Winter activity was assessed using monthly pitfall sampling on two farms during the second winter (2009 – 2010) and every other month on all four farms during the third winter (2010 – 2011).

The spatial sampling intensity varied over the years of the experiment on three of the farms (Figure 1). In the first year of sampling (2008) on farms G and P, traps were evenly spaced in a grid pattern (approximately 25m between traps) along several transects (between 50 and 200 m) 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. In subsequent years we stratified sampling at local nodes and stratified nodes by major vegetation types within the landscape. Putting more than one trap at a specific location provided a better estimate of the local activity density and

161 allowed for more robust comparisons based on the vegetation around each trap. In subsequent
162 trapping seasons the traps were placed in clusters of four traps (at the corners of an
163 approximately 10m square) on transects (between 50 and 300 m) across four fields in 2009 and
164 across seven fields in 2010 and 2011. Farms H and K were sampled in 2010 and 2011. Pairs of
165 traps (approximately 10m apart) were arrayed along transects (between 60 and 350 m long)
166 extending across fields. There were 26 transects in 2010, but three transects were dropped from
167 farm K in the last year due to low overall beetle numbers. Clusters were laid out so that traps
168 were evenly divided among the different habitat types when there was more than one type of
169 habitat in the area. Putting traps within the same cluster in different habitats allows comparisons
170 to be made between habitats, while holding the landscape position constant. Trap clusters at the
171 ends of transects included a trap in both the annually tilled crop field, and the perennial field
172 margin. Trap clusters within fields, but on the boundary between crop types, included traps in
173 both crops.

174 175 *2.2.2 Pitfall trapping method.*

176
177 Non-lethal pitfall traps were used to minimize the effects of repeated sampling on beetle
178 populations and to provide live beetles for laboratory trials. Pitfall traps consisted of plastic pint
179 (473 ml) cups with a 100 mm diameter at the top. A funnel was fitted in the rim of the main cup
180 to prevent insects from escaping by climbing back up the side of the cup. In a pilot study, we
181 found the remains of smaller beetles in several traps indicating they were preyed upon by the
182 larger beetles that were also caught. For this study, we placed a smaller cup in the bottom of the
183 main cup with a hole in it to allow the smaller species to escape to an area within the trap that

was safer from predation by any of the larger species. We almost never found beetle remains in traps with the inner cup, indicating it was effective at preventing predation within the trap. 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 the lab experiments, and vouchers were collected for each ground beetle species identified.

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%).

2.3 Sentinel prey cards.

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

variety of carabids (Carcamo and Spence 1994). They were assumed to be similar to the pupae of two relatively common pests in the system, the carrot rust fly (*Chamaepsila rosae* F.) and the cabbage root maggot (*Delia radicum* L.).

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 4651. 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 2349, a 49% 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 over the four years that had a prey card deployed, in 504 instances (29%) the prey card was destroyed by slugs during each sample month in the season and there was therefore no estimate for the site.

2.4 Voracity feeding trial.

During the last two 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. Small species were tested during only the first sample period. Subsequent tests focused on the larger species to ensure adequate replication of all the important species in the 21 available mesocosms. 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 outside 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 two nights 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 of 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.

2.5 Analysis.

2.5.1 Seasonal activity.

The mean number of beetles caught in any of the traps was estimated for each beetle size class during each month. The monthly activity patterns of each group were examined to look for qualitative differences between species. Anova was also used to test whether any of the fluctuations in beetle activity represented statistically changes in monthly beetle activity.

2.5.2 *Mesocosm 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.

For each of the beetles tested in the feeding trials the mean monthly field activity density and mean number of pupae eaten in the trials were divided by the maximum monthly values (activity density and pupae eaten) for each species to get relative values. This allowed the results for all the species to be analyzed together to test whether there is an association between the relative activity density of beetle species in the field and how many prey items the beetles ate in the feeding trials.

2.5.3 *Calculation of total voracity density for each trap.*

The results from the lab feeding trials were used to estimate the potential number of fly pupae that could be eaten by the beetles caught in the trap (total voracity density). Monthly potential voracity was estimated for every month for each species encountered in the field sampling. For beetle species that were common enough to include in lab trials, the potential voracity was calculated as the mean number of fly pupae eaten per beetle over the two day lab trial during each month. For months when a species was not tested because of low abundance, the potential voracity was calculated by straight line interpolation between two months that were tested. For beetle species that were not abundant enough to be included in lab trials, the potential

voracity was estimated as the overall mean number of pupa eaten pooled over all of the species in the same size class.

The estimates of the monthly potential voracity for each species and species size class were used to calculate a total voracity density for each trap during each sampling event. For each species, the number of individuals caught in the trap was multiplied by the potential voracity of the species during the sample month. The products of the trap count and the potential voracity for each species caught in the trap were summed to calculate a total voracity density for each trap.

$$\text{Total Voracity Density} = \sum (N_i * V_i)$$

Where N_i is the number of individuals of species 'i' caught in the pitfall trap and V_i is the potential voracity of species 'i' during the sample month.

2.5.4 Measurement of predation risk in the field.

Damage to either the pitfall traps or the sentinel prey cards created periodic missing data for individual sample locations. We therefore pooled results into three activity seasons: winter (November-February), spring (March-June), and summer (July-Oct). A mixed effect regression model was used to test for the relationship between the activity density of each predator group and the total voracity density on the sentinel prey removal rate during each season. The trap location was set as the random effect and the analysis was performed with the lmerTest package in R version 3.2.2 (Kuznetsova, A., et al. 2013, R Core Team 2016). To see how much of the

variability in the data the fixed effects explained, the marginal r^2 was calculated using the piecewiseSEM package in R (Lefcheck, J. S. 2015).

3. Results

3.1 Temporal activity pattern.

In this ground 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 *Pterostichus melanarius* Ill. which is active along with a few other large beetles (> 12 mm) in the late summer to fall. In the spring and early summer midsized beetles (7 – 12 mm) are active and most large beetles are not, therefore mid-sized beetles had the highest activity density early in the growing season (Figure 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 *Loricera foveata* Lec. was the only active species were there more small beetles than other species in the traps. The test of whether the activity density of each group of beetles differed between months was significant for mid-sized ($F = 86$; $df = 1, 6173$; $P < 10^{-15}$) and large species ($F = 193$; $df = 1, 6173$; $P < 10^{-15}$), but not significant for small beetles ($F = 0.2$; $df = 1, 6173$; $P = 0.69$).

When the activity densities of all of the carabids are combined into a total voracity density at the trap site, the mean value is more than zero for the entire year, although the value is low during the winter (minimum = 0.74 during December). There is a relatively high total voracity density as indicated by a value greater than the number of sentinel prey deployed at each site (>20) from April to October (Figure 2+). Values during the fall (July to October) months

closely track changes in large beetle abundance, while values from spring months (March through June) are also influenced by mid-sized beetle activity density.

3.2 Mesocosm feeding trial.

The voracity of each beetle species, measured as the mean number of fly pupae eaten over each two day trial by each of the five beetles in the box, differed significantly between species ($F = 31$; $df = 16, 356$; $P < 10^{-15}$). The largest species ate nearly all of the prey items presented to them (20 fly pupae), while the smallest species ate fewer than 10 pupae per beetle (Table 1, Figure 3). Three beetle species were only tested in the feeding trials in one month (*Agonum limbatum* Motsch., *Anisodactylus* sp. Dej., and *Clivina fossor* L.). When mean number of pupae eaten per beetle by each of the species that were tested in more than one month were compared with the mean length of the species in a regression model the trend for larger beetles to eat more fly pupae was not statistically significant ($F = 0.8$; $df = 1, 12$; $P = 0.77$; $MSE = 19.7$; $R^2 = 0.006$). *Scaphinotus marginatus* Fisch. and *Omus audouini* Reiche are two large beetles that ate very few pupae, reducing the significance of the regression and suggesting that the items presented were not an acceptable food for those species. When those species were excluded from the analysis, mean species length was a significant predictor of per capita pupae consumption in the regression model ($F = 21.0$; $df = 1, 10$; $P = 0.001$; $MSE = 3.6$; $R^2 = 0.68$). The mid-sized beetle *Nebria brevicollis* F. is longer than other beetle species that ate the same number of sentinel prey, suggesting fly pupae may not be a favored food item for this species as well. When *N. brevicollis* is removed from the analysis the effect of length on per capita pupa consumption is increased ($F = 39.2$; $df = 1, 9$; $P = 0.0001$; $MSE = 2.1$; $R^2 = 0.81$).

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. The association between monthly activity density in the field and monthly mean voracity in the feeding trials for all species together was highly significant ($F = 14$; $df = 1$, 67 ; $P = 0.0003$; $MSE = 0.06$; $R^2 = 0.16$). There were differences in the specific pattern among species, but the tendency for voracity and activity to rise or fall in tandem was clearly observed in several species (Figure 4).

3.3 Ground beetles and sentinel prey removal rate.

After excluding samples that were damaged by slugs, a mixed effects regression model with trap location as a random effect identified significant fixed effects of the abundance of certain beetle predator size guilds on the number of pupae removed (Table 2). When data from all seasons were pooled for each trap site, there was a significant relationship between sentinel prey removal and beetle activity density. Large beetle activity density had the strongest effect in the regression model, while mid-sized beetle activity densities had a smaller effect and small beetles did not have a significant effect.

An interesting pattern emerged when the data from each season were analyzed separately. In the March through June activity periods there were a large number of mid-sized beetles active in the landscape, and fewer large or small beetles compared to late summer. In the spring season (March through June) there were greater numbers of pupae eaten at trap sites where more mid-sized beetles were caught (Table 2, Figure 5). During the July to October activity season the relationships between pupae removal and beetle activity were driven by large beetles. The large carabids were by far the most abundant group later in the season and were associated with an

increase in the number of pupae eaten (Table 2, Figure 5). There was no relationship between the activity densities of any beetle size classes and the number of sentinel prey eaten during the winter season (November through February).

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 the growing season. During the March through June season the mean (SEM) number of pupae eaten per card was 8.8 (0.30), while during the July through October season it was 8.6 (0.21). During the winter (November to February) season when the activity of almost all of the beetle species was very low there were 3.3 (0.29) pupae removed per card.

4. Discussion

4.1 Temporal size partitioning

Our results suggest that size is an important predictor of adult beetle per capita prey consumption, and that seasonal shifts in the size distribution of beetle species influence the overall predation pressure provided by beetle assemblages in these agricultural landscapes. Theoretical and experimental studies have shown that a suite of functional responses and trophic interactions scale with predator: prey body size ratio (Brose 2010, Vucic-Pestic et al. 2010, Kalinkat et al. 2011). For ground beetles specifically, attack rate has been shown to increase and handling time decrease as a function of the predator:prey size ratio (Ball et al. 2015). Several other studies have used size to predict feeding behavior and to partly define feeding guilds for ground beetles and other generalist predators (Finch 1996, Woodward and Hildrew 2002, Honek et al. 2007). We found similar results in our mesocosm feeding trials where attack rate increased as a function of predator:prey size ratio. However, the strength of this relationship was weak for

the entire tested assemblage, reflecting the fact that three of the tested species had per capita feeding rates that were significantly lower than would be expected given their size. We suspect that these species do not prefer the dead fly pupae used in our feeding trials. *Scaphinotus marginatus* has a unique head morphology and is a known specialist on snails and mollusks (Digweed 1993). The diet preferences of *Omus audouini* and *Nebria brevicollis* have not been specifically described, although species in both genera are known to be active predators of a range of arthropods (Sunderland 1975, Pearson 1988). The *O.audouini* individuals used in this study vigorously attacked live leafroller (Lepidoptera: Tortricidae) caterpillars suggesting that they may prefer active or larger prey. Similarly, the putative diet of *N. brevicaulis* is collembolans and other small arthropods (Penney 1969, Warner, et al. 2008).

We found that sentinel prey consumption in the field was positively correlated with activity density of the size group of ground beetles that was most active at that time of the year (mid-sized beetles during March through June, and large beetles during July through October). However, that relationship explained a relatively low amount of the variation in sentinel prey consumption in the field. Alternate prey preferences may be one factor that contributed to the low explanatory power. Prasad and Snyder (2004) attributed the presence of alternate prey such as aphids as one factor contributing to the lack of a relationship between beetle activity density and consumption rates of fly egg sentinel prey in vegetable fields. Another factor is that while we excluded vertebrate predators, the sentinel prey cards were exposed to a wide range of invertebrate predators in addition to ground beetles, potentially obscuring the signal from beetle consumption. The slug damage observed on the sentinel cards suggests other predators did indeed feed on the sentinel prey. Another contributing factor may be that the activity density estimated by pitfall trapping often does not accurately reflect absolute population density

(Topping and Sunderland 1992, Lang 2000, Thomas, et al. 2006). Despite the low explanatory power of ground beetle activity, we did find a significant positive relationship between beetle activity and sentinel prey consumption in the field. In addition, the relative degree to which small, medium, and large beetles contributed to this relationship tracked the activity density of these size classes over the season. Similarly, Rusch et al. (2015) did not find a significant relationship between the activity density of the ground predator community (spiders, carabids, staphylinids) and the consumption of field placed sentinel aphids. However, they did find a significant relationship between the overall community weighted mean body size of predators and aphid consumption, although the relationship was not significant for the mean weighted size of the carabid assemblage alone.

In our study, combining estimates of per capita attack rate with activity density did not improve the explanatory power of prey consumption in the field, even though the mesocosm measured per capita attack rates exhibited considerable seasonal variation. This could indicate that mesocosm assays do not reflect actual feeding behavior in the field where more preferred prey items may be readily available. In addition, inter- and intra- specific interactions between predators can influence both individual feeding behavior as well as the overall strength of predation provided by predator assemblages, although most evidence for these interactions comes from laboratory experiments (Sih et al. 1998, Symondson et al. 2002, Schmitz 2007, Northfield et al. 2014). Mesocosm studies involving ground beetles have reported conflicting results. Ball et al. (2015) reported that prey consumption when *Pterostichus melanarius* and *P. madidus* foraged together was enhanced relative to the expectation of single species foraging. However, Rouabah et al. (2014) found no synergistic effects of ground beetle size diversity on prey consumption; instead the consumption rate of experimental assemblages was primarily

driven by the presence or absence of large species in the assemblage. Using a field experiment located in similar vegetable systems to our study, Prasad and Snyder (2004) showed that intraguild interference by the large *P. melanarius* on smaller carabids and staphylinids suppressed sentinel prey consumption.

While predator interactions likely occur in our system, the beetle assemblage was also marked by pronounced temporal partitioning among size guilds. Spring and early summer beetle activity was dominated by a rich group of small and medium sized species, while late summer and fall activity was dominated almost entirely by the large non-native *P. melanarius*. This partitioning seems to be driven largely by innate life history differences rather than interference competition (Russell 2013). *Pterostichus melanarius* has an annual, univoltine, summer-autumn, semelparous lifecycle, with a peak adult activity in our system in early August. Most mid-sized (7-12mm) beetles on our system had annual spring iteroparous lifecycles, with peak adult activity in early May. Werner and Raffa (2003) reported a similar temporal partitioning among species within assemblages of ground beetles in Michigan and Wisconsin forests, and speculated that temporal niche partitioning is an important mechanism reducing competition in ground beetles.

Adult medium and large beetles are only likely to encounter each other from May-June in our study system. However, this can be a potentially important phenological window for many pest species. For example, *Trichoplusia ni* Hübner (cabbage looper) larvae are vulnerable to predation by carabids, and in the Pacific Northwest larval abundance peaks in June and August (Berry 1998). Larvae in June are exposed to a species and size rich ground beetle assemblage. Negative interactions between large species such as *P. melanarius* and other species could reduce the biocontrol capacity of the entire beetle assemblage during this period. Overall, the

phenological relationship between carabid and pest activity is a key driver the overall effectiveness of biological control (Warner, et al. 2008).

4.2 Management implications

Larger carabid species are generally more negatively affected by management intensification such as pesticide use and tillage than are smaller species, and larger species tend to be associated with less disturbed habitats (Blake et al. 1994, Ribera et al. 2001, Kotze and O'Hara 2003, Rusch et al. 2013, Winqvist 2014). In addition, functional traits such as body size are the primary influence on prey consumption, not specific species identity (Rouabah et al. 2014, Rusch et al. 2015). This suggests that functional diversity maybe a better indicator of the biocontrol capacity of a particular ground beetle assemblage than broad community descriptors such as species richness. In particular, the size distribution of an assemblage could be a useful field assay to evaluate functional capacity or to plan conservation biological control enhancements. Beetles can easily be grouped into size classes by field observation, reducing the effort and expertise needed to evaluate an assemblage. In our study system, size is also an effective proxy for a number of other beetle life history traits such as seasonal habitat use (Russell 2013). However, universal prescriptions are unlikely to provide useful practical guidance. Prescriptions based on rapid trait assays such as size distribution will need to be tailored to reflect regional and system specific differences. In the vegetable production systems examined here, the potential biocontrol service provided by beetles peaked in mid-August. This peak was driven by the increased activity of a few large summer active species, dominated numerically almost entirely by the non-native *P. melanarius*. Unlike many other large European

carabids, *P. melanarius* has habitat preferences that include disturbed crop production fields, and it has become common on managed farms throughout North America (Hajek, et al. 2007; Hatten, et al. 2007; Brunke, et al. 2009). Prior to the emergence of adult *P. melanarius*, biocontrol capacity is contributed by a diverse array of largely native small and mid-sized beetles. The abundance of these spring active species is more variable between farms than the abundance of the more ubiquitous *P. melanarius*. This variation is partly related to differences in the abundance of suitable overwintering habitat in the form of un-disturbed field margins and conservation biocontrol practices such as beetle banks (Russell 2013). The spring active species emerge at the end of summer, and search for overwintering habitat primarily in the form of perennial grassy vegetation. While factors such as the availability of weed seeds as a larval food supply, or refuge from tillage or pesticides may be important factors influencing the abundance of spring active species (Hartke, et al. 1998, Sasakawa 2009), creating and maintaining suitable overwintering habitat appears to be a critical requirement for maintaining this life history guild of species on farms. Creating and maintaining perennial grass vegetation on farm landscapes has been shown to be an effective approach to enhancing overall beetle abundance (Griffiths 2008), as well as the abundance of the specific life history guild of spring active beetles in the U.S. Pacific Northwest (Prasad and Snyder 2006). Our results suggest that understanding the seasonal shifts in species and functional trait composition that occur within particular predator assemblages can help inform the design of more regionally specific management and conservation strategies.

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Table captions:

Table 1. The mean (SEM) number of fly pupae eaten per beetle over two days and mean (SEM)
length of the ground beetle species included in the feeding trial. Values that are not followed by
the standard errors in parentheses were based on a single observation. Species labeled with
different letters in the voracity column were significantly different based on Tukey's HSD
multiple comparison test.

Table 2. Regression equations testing the effects of beetle group activity densities or total
voracity density on the sentinel prey removal rate. The seasonally pooled data was tested with

two different mixed effect models for each season. The table shows the results for the fixed effects in each model. The full model includes an intercept (β_0) and three factors, the mean activity density of the small (β_1), midsized (β_2), and large (β_3) carabids. The voracity model has one factor, the total voracity density for the trap (β_1). The second column lists the name of each model with the marginal r^2 of the regression included below the model name. For each model, the table lists the estimate and standard error of each term in the regression model in one row. Below each estimate is the F-statistic of the effect of the factor on sentinel prey removal rate. Asterisks indicate the significance level as calculated using the Satterwaithe approximation for degrees of freedom (*** < 0.001, ** < 0.01, * < 0.05, < 0.10, otherwise = n.s.). The final column shows both the total number of observations included in the analysis, and the number of levels in the random effect, trap location.

Beetle species	Mean (SE) voracity	Mean (SE) length
<u>Small species</u>		
<i>Agonum limbatum</i> Motsch.	5.8abcdeg	6.8
<i>Clivina fossor</i> L.	1.1 (0.3)a	6.4 (0.2)
<u>Mid-sized species</u>		
<i>Agonum muelleri</i> Hbst.	15.2 (0.7)def	8.2 (0.3)
<i>Agonum subsericum</i> Lec.	16.6 (1.1)efgh	10.1 (0.1)
<i>Amara</i> sp. Bon.	13.2 (0.9)cde	9.2 (0.3)
<i>Amara californica</i> Dej.	11.1 (0.6)bc	7.4 (0.1)
<i>Amara littoralis</i> Mnh.	10.8 (0.6)bc	7.7 (0.1)
<i>Anisodactylus</i> sp. Dej.	6abcdg	9
<i>Anisodactylus binotatus</i> F. /	15.4 (0.7)deg	11.4 (0.1)
<i>An. californicus</i> Dej. Group		
<i>Anisodactylus sanctaecrucis</i> F.	11.7 (1)bcd	8.9 (0.1)
<i>Harpalus affinis</i> Schrk.	14.1 (1.3)cde	10.4 (0.1)
<i>Nebria brevicollis</i> F.	11.5 (0.6)bc	11.4 (0.1)
<u>Large species</u>		
<i>Harpalus pensylvanicus</i> DeG.	19 (0.3)fh	13.3 (0.3)
<i>Omus audouini</i> Reiche	8.2 (0.8)ab	15 (0.1)
<i>Pterostichus algidus</i> Lec.	18.1 (0.9)fgh	13.8 (0.1)
<i>Pterostichus melanarius</i> Ill.	19.8 (0.1)h	16 (0.1)
<i>Scaphinotus marginatus</i> Fisch.	4.5 (1.1)a	15 (0.2)

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732 Table 2.

Season	model (marginal R ²)	β_0 Est (SE)	β_1 Est (SE)	β_2 Est (SE)	β_3 Est (SE)	N obs. N trap
			f-stat	f-stat	f-stat	
All (Jan - Dec.)	Full 0.04	7.31 (0.22)	0.09 (0.11) 0.7	0.2 (0.06) 12.9***	0.23 (0.04) 40***	1244 486 ⁷³³
	Voracity 0.04	7.44 (0.21)	0.01 (0.001) 47.5***			1244 486 ⁷³⁶
Spring (Mar. - June)	Full 0.03	8.16 (0.36)	0.004 (0.18) 0.001	0.22 (0.07) 8.9**	0.35 (0.25) 1.9	435 ⁷³⁷ 294 ⁷³⁸
	Voracity 0.02	8.3 (0.34)	0.01 (0.003) 10.3**			435 ⁷³⁹ 294
Fall (July - Oct.)	Full 0.05	7.83 (0.29)	0.12 (0.14) 0.8	-0.13 (0.1) 1.6	0.21 (0.04) 31.6***	685 ⁷⁴⁰ 481
	Voracity 0.03	7.91 (0.28)	0.01 (0.001) 20.8***			685 ⁷⁴¹ 481 ⁷⁴²
Winter (Nov. - Feb.)	Full 0.01	2.53 (0.34)	0.71 (0.84) 0.7	0.02 (0.98) 0.0003	-0.53 (1.03) 0.3	124 ⁷⁴³ 114
	Voracity 0.0002	2.64 (0.31)	-0.01 (0.04) 0.04			124 ⁷⁴⁴ 114 ⁷⁴⁵

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Figure legends:

Figure 1. The locations of pitfall traps across the four farms in the study. The first round of sampling used relatively intensive grids on farms G and P (indicated by hollow circles). The second round had more extensive sampling using clustered traps on all four farms (indicated by filled circles). The upper left of the figure shows the locations of the farms relative to Corvallis, Oregon. Note the different scales for each map.

Figure 2. The mean activity densities of three size classes of beetles and the mean monthly total voracity density for each trap. Small beetles are less than 7 mm, midsized beetles are between 7 mm and 12 mm, and large beetles are more than 12 mm. The activity density is the number of beetles caught per trap during a 2 day trapping event and is indicated by the axis on the left side. The voracity density is calculated from the activity density of each beetle species multiplied by the mean number of fly pupae the beetle would eat over 2 days in lab trials. The total voracity density is the mean for all traps of the sum of all of the voracity densities for the species caught in each trap and is indicated by the axis on the right side.

Figure 3. The relationship between mean voracity and mean adult length for ground beetle species included in the feeding trials. Filled squares represent large species that readily ate the sentinel prey (freeze killed *Drosophila melanogaster* pupae) in the voracity trials. These species

frequently consumed all of the sentinel prey (20 per beetle). Hollow squares represent two large beetle species (*Omus audouini* and *Scaphinotus marginatus*) that ate few of the sentinel prey. The filled triangles represent mid-sized ground beetles that readily ate the sentinel prey and the hollow triangle represents *Nebria brevicollis*, a mid-sized species that ate few sentinel prey. The dash indicates a mid-sized beetle species (*Anisodactylus* sp.) that was included in only one, unreplicated, voracity trial. The small beetles were only tested during one month. *Clivina fossor* was included in three trials in the month and is indicated by a hollow diamond. An additional small beetle species (*Agonum limbata*) was included in a single voracity trial and is indicated by a cross.

Figure 4. The relative activity density and voracity of four ground beetle species over the year. The height of the shaded background represents the monthly mean activity density for each species. 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.

Figure 5. The relationship between sentinel prey consumption in the field and carabid beetle activity density. A.) The mean number of pupae removed from sentinel prey cards in the field 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 pupae removed from sentinel prey cards in the field 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

800 relationship with sentinel prey removal. The values defining each activity density group are the
801 number of beetles caught per trap. The number of observations within each activity density
802 group is also listed below the bars.

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