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Plant versus prey resources: Influence on omnivore behavior and herbivore suppression

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ABSTRACT

Conservation biological control tactics, such as beetle banks, that increase habitat complexity generally increase epigeal predator abundance. Habitat complexity also increases alternative food which can attract and sustain predators but may reduce predation of target pests. Our goal was to determine how alternative food from different trophic levels (fly pupae and seeds) affects behavior and biological control efficacy of omnivorous carabid beetles. Seed subsidies increased omnivorous carabid abundance more than pupae by increasing aggregation and reducing emigration. Laboratory experiment demonstrated that both omnivorous carabid species preferred seeds and pupae over cutworms. However, in field cages seeds but not pupae resulted in greater cutworm damage to corn seedlings. Our results indicate that omnivorous carabids have a stronger behavioral response to seeds than prey such that only seeds influence aggregation, emigration, and crop damage. Interestingly, whereas seeds increased omnivorous carabid abundance, pupae had no affect on carnivore abundance. Thus, carabid guild composition is skewed in favor of omnivores when seed density increases. An important finding was that the effect of seeds on behavior, predation, and crop damage was consistent among replicate carabid species suggesting our results pertain to other omnivorous species in resource diverse habitats.

Our results provide insight into the mechanisms underlying the unpredictable benefit of conservation biological control tactics that alter habitat complexity.

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1. Introduction

Agricultural habitats are characterized by low plant species diversity and routine disturbance which have negative effects on natural enemies. The 'enemies hypothesis' posits that increasing plant diversity and structural complexity will increase natural enemy abundance and improve biological control of arthropod pests (Root, 1973). This is the foundation of habitat management as a conservation biological control tactic wherein non-crop vegetation is maintained within crop fields to provide shelter and resources for natural enemies (Landis et al., 2000; Griffiths et al., 2008). There is considerable evidence that habitat management tactics, such as beetle banks (Thomas et al., 1991; Frank and Shrewsbury, 2004), hedgerows (Marshall and Moonen, 2002; Pollard and Holland, 2006), reduced tillage (Brust et al., 1986; Clark et al., 2006), cover crops (Laub and Luna, 1992), or applications of compost (Settle et al., 1996; Bell et al., 2008), increase the abundance of epigeal generalist predators such as carabid beetles (Kromp, 1999; Griffiths et al., 2008). Yet despite increasing predator abundance,

concomitant reductions in pest abundance do not always occur (Griffiths et al., 2008). Therefore, it is essential to understand mechanisms that underlie how habitat complexity affects herbivore suppression by generalist predators.

An important way in which habitat complexity affects the strength of predator–prey interactions is by increasing the abundance of alternative foods such as detritivores (Frank and Shrewsbury, 2004; Bell et al., 2008), seeds (Cardina et al., 2002; Devlaeminck et al., 2005), and other alternative foods (Landis et al., 2000). Alternative foods can support generalist predator populations that are larger and more enduring than could be supported by pests alone by increasing recruitment, residence time, reproduction, and survival (Holt and Kotler, 1987; Cottrell and Yeargan, 1998; Eubanks and Denno, 2000a,b; Lundgren et al., 2004; Shrewsbury and Raupp, 2006; Harwood et al., 2009). However, exploitation of multiple food resources fuels debate about the value of generalist predators for biological control (Symondson et al., 2002).

A unique subset of generalist predators are "true omnivores" that consume plant and prey resources (Coll and Guershon, 2002). True omnivores are common in agricultural ecosystems but their impact on target pests is context dependent. For example, pollen and aphids increase lady beetle density on corn plants but divert predation away from key pests such as *Ostrinia nubilalis*

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Hubner (Lepidoptera: Noctuidae) and *Helicoverpa zea* Boddie (Lepidoptera: Noctuidae) (Cottrell and Yeargan, 1998; Musser and Shelton, 2003). In contrast, Eubanks and Denno (1999, 2000a) found that omnivorous big-eyed bugs, *Geocoris punctipes* Say (Heteroptera: Geocoridae), were more abundant when lima bean pods were available as alternative food. As a consequence, aphid and lepidopteran pest populations were smaller when pods were present compared to when pods were absent (Eubanks and Denno, 1999, 2000a). The impact of alternative food on pest suppression is influenced by predators' numerical response to, or preference for, particular food items present in a habitat (Holt and Kotler, 1987; Symondson et al., 2002). For pest suppression by conservation biological control to be more predictable, research is needed that examines how alternative foods affect predation of crop pests by generalist and omnivorous predators.

Carabid beetles are one of the most abundant predator taxa in agroecosystems (Kromp, 1999). Carabids respond positively to conservation biological control tactics (e.g. Thomas et al., 1991; Marshall and Moonen, 2002; Frank and Shrewsbury, 2004; Shearin et al., 2007) and are important in the biological control of arthropod pests (Brust et al., 1985, 1986; Kromp, 1999; O'Neal et al., 2005; Lundgren et al., 2009). However, many carabid beetle species are true omnivores that consume seeds and prey (Lövei and Sunderland, 1996; Lundgren, 2009). In fact, carabids also contribute to, and their abundance is promoted for, biological control of weed seeds (Menalled et al., 2007; Shearin et al., 2007; Westerman et al., 2008). Therefore, carabid abundance is promoted for two potentially conflicting reasons because consumption of seeds could reduce consumption of pests (Frank et al., 2010). This contradiction may provide insight into the context dependent nature of biological control by carabid beetles and the many cases where increasing carabid abundance by habitat management does not increase predation or reduce abundance of pests (Ramert and Ekbom, 1996; Kromp, 1999; Prasifka et al., 2006).

Our goal was to investigate how alternative food from different trophic levels (grass seeds and fly pupae) affects behavior and pest suppression by carabid beetles that are true omnivores. The first part of this research tests the hypothesis that "…omnivores track resources at the lowest trophic level on which they feed" (Eubanks and Denno, 2000a). To test this hypothesis we conducted field experiments to determine how seeds and pupae affect aggregation and residence time of carabid beetles that are true omnivores. We predicted that carabids would aggregate in plots with seeds more than in plots with fly pupae and will remain in seed plots longer. The second part of our research examines how alternative food resources affect predation of a co-occurring crop pest, black cutworm, *Agrotis ipsilon* Hufnagel (Lepidoptera: Noctuidae), with cascading effects to corn seedling. This was prompted by preliminary research, which demonstrated that omnivorous carabids prefer foods that are captured and consumed most efficiently (Frank, 2007). Therefore, we predicted that carabids would prefer both alternative foods (seeds and fly pupae) over active cutworms. This was expected to reduce consumption of cutworms and increase crop damage. These experiments provide new insight into top-down control of arthropods pests by omnivorous carabid beetles in resource diverse habitats that result from habitat management as a conservation biological control tactic.

2. Methods

2.1. Study system

Two representative carabid species were selected, *Harpalus pensylvanicus* (DeGeer) and *Anisodactylus ovularis* (Casey), that are true omnivores and of similar size. *H. pensylvanicus*, *A. ovularis*, and their relatives are common in agricultural ecosystems and are reported to be important for biological control of *A. ipsilon* and other lepidopteran pests (Brust et al., 1986; Riddick and Mills, 1994). Furthermore, carabids are known to consume seeds and other prey such as fly larvae and pupae (Sunderland, 1975; Kromp, 1999). Beetles were collected in corn fields at the University of Maryland Central Maryland Research and Education Center (CMREC) in College Park, Maryland, USA and maintained in the laboratory in plastic bins with moist peat moss. Black cutworm, the focal herbivore in this study, damages corn seedlings by cutting plants at or below ground level then consuming the fallen plant. Cutworms were reared in the laboratory on artificial diet (Southland Products, Inc., AR, USA).

Alternative food items such as detritivores and seeds are abundant in agroecosystems (Dively, 2005; Cardina et al., 2002). For this research, fruit fly, *Drosophila melanogaster* Meigen (Diptera: Drosophilidae), pupae were used as alternative prey. Fruit fly pupae were selected to represent the many dipterans that occur at high densities in agricultural fields (Frouz, 1999). Carabids encounter and consume dipteran eggs, larvae, and pupae under natural conditions (Coaker, 1965; Sunderland, 1975; Kromp, 1999). In addition, fruit fly pupae were readily consumed by *H. pensylvanicus* and *A. ovularis* in previous experiments (Frank, 2007; Frank unpublished data) and fruit flies have been used as factitious prey in other studies (e.g. Speight and Lawton, 1976; Carcamo and Spence, 1994). Bluegrass, *Poa pratensis* (Cyperales: Poaceae), seeds were used as alternative plant food in this research because they are readily consumed by many species of adult and larval carabids (Frank, 2007; Frank et al., 2010) as are seeds from other grass species (Briggs, 1965; Kirk, 1973; Jørgensen and Toft, 1997). In addition, seeds from *P. pratensis*, other *Poa* species, and many other grass species are common in agricultural fields occurring in the thousands to tens-of-thousands per square meter (Uva et al., 1997; Davis et al., 2005; Swanton et al., 2006).

Our goal was to examine the effect of trophic origin of resources on carabid behavior and efficacy. Therefore we selected plant and prey foods that were as similar as possible. Fly pupae and blue grass seeds are similar in size (3.03 ± 0.04 mm and 2.91 ± 0.04 mm, respectively), and weight (19.9 ± 0.4 mg and 20.0 ± 0.4 mg, respectively). In addition, both food items are immobile. Controlling for these factors allows us to focus on the trophic origin of food without confounding effects of size and mobility which can influence preference (e.g. Eubanks and Denno, 2000b).

2.2. Effect of food subsidies on carabid aggregation

To assess the effects of seeds and fly pupae subsidies on carabid abundance, two levels of seeds (ambient and subsidized) were crossed with two levels of pupae (ambient and subsidized) in a 2×2 factorial design in open field plots as in Frank et al. (2010). Thus, plots received no food subsidy (ambient) or were subsidized with seeds, fly pupae, or both (seeds and pupae mixed). Plots were 4×4 m separated by 8 m. The experiment was replicated 11 times for a total of 44 plots established at CMREC. The experiment was conducted three times (blocks), from 16 to 30 June, 8 to 24 July, and 24 August to 8 September 2007, when 3, 5, and 3 replicates, respectively, were completed.

Six rows of organic corn seed (NC + Organics, hybrid 3448MF-14) with 30 plants per row were planted in each plot. Food supplements were applied to plots the following day by sprinkling seeds, pupae, or both at 1200/m². Additional seeds and pupae were added at the same density every 4–5 days to replace depleted food items. Preliminary surveys in our field in May 2006 indicated that grass seed density in the top 2 cm of soil was 9704 ± 1300 m^{-2} ($n = 10$). Thus for our subsidies to stand out against ambient seed density 50% more seeds and pupae were added to plots in this

experiment than caged experiments (below). However, these are still within realistic seed and alternative food densities that can occur in agricultural fields (Frouz, 1999; Davis et al., 2005; Swanton et al., 2006).

Pitfall traps were used to sample the carabid community on day 10 for 24 h and day 15 for 48 h. All captured carabids were counted, identified to genus, and assigned to a feeding guild (omnivore or carnivore) based on published research (Lundgren et al., 2006; Lundgren, 2009).

Statistical analysis. ANOVA, blocked by time, was used to test the effect of seed subsidies, prey subsidies, and their interaction on the number of omnivorous and carnivorous carabids trapped per plot (pooled sample dates) and the proportion of the carabid community comprised of omnivores (SAS, 2002).

2.3. Effect of alternative food type on carabid residence time

A mark-recapture experiment was conducted in enclosed field plots to determine the effect of alternative food on the residence time of omnivorous carabids. Eight fenced plots (2.5×2.5 m) were established at CMREC. Each plot was surrounded by aluminum flashing to prevent movement of arthropods in and out of the study plots. Soil within the plots was excavated to 6 cm to remove seeds and arthropods and replaced with clean topsoil. Soil around the edge of each plot was packed down resulting in a 0.25 m border of bare soil abutting the flashing, which surrounded the 2×2 m central area of loose soil. To simulate a natural habitat, dead corn stalks and stubble (defaunated by freezing) were scattered over the central area of each plot. A pitfall trap (9 cm plastic cup) was placed in each corner of every plot.

This experiment employed a $2 \times 2 \times 2$ factorial design with two species of carabid (*A. ovularis* and *H. pensylvanicus*), two levels of seed subsidy (absent or present) and two levels of pupal subsidy (absent or present). Pupae or seeds were scattered over the central area of each plot at 800/m^2 (3200/plot). Plots assigned to the pupae and seed combination treatment received 3200 of each food type. This density was based on a review by Frouz (1999) which found the density of dipterans in agricultural fields can range from 400 to 2500/m^2 but the average of 12 studies reviewed was 838/m^2. The eight treatment combinations were randomly assigned to one of eight plots which constituted a single replicate (block). The experiment was replicated in time (3 dates) for a total of three replicates with each beetle species.

Four individuals of one beetle species were released next to a board (10×25 cm) in the center of each plot at 18:00 h. Before release beetles were marked by placing a piece of yellow tape (1 mm $\times 3$ mm) across the elytra. Since both carabid species are nocturnal, beetles quickly crawled under the board. This allowed beetles to come out after dark of their own accord to forage. Beginning at 19:00 h pitfall traps were checked every hour for 12 h to record how many beetles emigrated from the central area containing food subsidies to corner traps. Mean residence time in each treatment plot was calculated by summing individual residence times of the 4 beetles. Releases were conducted in July and August of 2006.

Statistical analysis. ANOVA (blocked by date) was used to test the effect of carabid species, seeds, pupae and their interaction on the mean residence time (mean of the four beetles per plot) of carabids (SAS, 2002). Mean comparisons were made using Tukey's HSD adjustment after a significant ANOVA.

2.4. Effect of alternative food type on carabid preference and consumption of herbivores

Laboratory experiments were conducted using *H. pensylvanicus* and *A. ovularis* to evaluate how carabid species and alternative food

type (seeds or fly pupae) affected preference for and consumption of black cutworms. Choice experiments were conducted in 14-cm diameter Petri dishes, containing one of three food combinations: live cutworms only (no alternative food), cutworms and pupae, or cutworms and seeds. It was determined in advance that the mass (mean ± SEM; $N = 15$) of 15 pupae (19.9 ± 0.4 mg) or 15 moist seeds (20.0 ± 0.4 mg) was equivalent to a single 2nd-instar cutworm (20.4 ± 0.8 mg). Thus, five cutworms and 75 alternative food items were placed in the cutworm-pupae and cutworm-seed treatment dishes. One beetle (starved with water for 24 h) was placed in each dish. Dishes were placed in a dark, 27 °C environmental chamber. The number of food items consumed was recorded after 1 and 4 h. Each of the 3 treatment combinations was replicated 10 times for each beetle species.

Preference was calculated from the number of each food item consumed at the 1-h observation period. Preference was quantified as:

$$\alpha = ln(N_i - R_i)/[ln(N_i - R_i) + ln(N_j - R_j)]$$

where N_i and N_j are the initial numbers of food type 1 and 2 and R_i and R_j are the number of food type 1 and 2 consumed (Chesson, 1978). This yields the same results if mass or number of food items is used. This index ranges from 0 to 1 where an α of 0.5 indicates no preference, α close to 1 indicates a preference for food type 1, and α close to 0 indicates a preference for food type 2.

Statistical analysis. ANOVA was used to test the effect of carabid species, alternative food type, and their interaction on the number of cutworms eaten at hour 4. Mean comparisons were made using Tukey's HSD adjustment after a significant ANOVA (SAS, 2002). Preference (α) of each species for cutworms compared to seeds or pupae at hour 1 was compared using a Kruskal–Wallis test using the NPAR1WAY procedure in SAS (2002) since these data range from 0 to 1 and were not normally distributed.

2.5. Effects of carabid species and alternative food supplements on seedling survival

A 2×3 factorial design was used to test the interactive effects of carabid species (*H. pensylvanicus* and *A. ovularis*) and alternative food (no alternative food, seeds, or pupae) on corn seedling survival. Control cages were set up with cutworms but no carabids. Each of the seven treatment combinations was applied randomly to a field cage ($2 \times 2 \times 2$ m). Seven cages constituted a complete block. Two replicates (blocks) were completed each summer in 2005 and 2006 at CMREC.

To remove ambient arthropods and seeds, soil inside of each cage was excavated to 6 cm. Cages were refilled with seed-free and prey-free topsoil. Corn seedlings were raised in the greenhouse to 8 cm (two-leaf stage). Three rows of ten seedlings were transplanted into each cage. Alternative food treatments were added at 800 seeds or pupae/m^2 as in the residence time experiment. Thirty 2nd instar cutworms were added to each cage. After 1 h, 4 beetles of a single species were released under a board in the center of each cage. Cages were examined after three days to record the number of cut plants. Difficulty recovering cutworms from the soil precluded analysis of cutworm survival.

Statistical analysis. Two-way ANOVA was used to test the effect of carabid species, alternative food type (no alternative food, pupae added, or seeds added), and their interaction on the number of seedlings cut. After finding a significant main effect of alternative food type, the number of seedlings cut in control cages (cutworms but no carabids) was compared to the no alternative food, pupae added, or seeds added cages using one-way ANOVA followed by means comparisons using Tukey's HSD adjustment. The date of

each trial was included as a blocking factor in both analyses (SAS, 2002).

3. Results

3.1. Effect of food subsidies on carabid aggregation

Seed subsidies significantly increased total number (mean ± SEM) of carabid beetles (2.36 ± 0.47; $F_{1,30} = 10.42$; $P = 0.003$) and omnivorous carabids (1.68 ± 0.51; $F_{1,30} = 11.01$; $P = 0.002$) captured in field plots compared to total carabids (1.18 ± 0.28) and omnivores (0.50 ± 0.19) captured in plots without seeds (Fig. 1). The most frequently captured omnivorous carabids were *H. pensylvanicus* which accounted for 33% of all carabids captured. Other omnivorous species in the genera *Harpalus, Anisodactylus, Amara,* and *Stenolophus* accounted for 13% of carabids captured. Pupal subsidies did not affect total number of carabids ($F_{1,30} = 0.99$; $P = 0.329$) or omnivorous carabids ($F_{1,30} = 1.04$; $P = 0.315$) captured nor was there a significant interaction ($F_{1,30} = 0.99$; $P = 0.329$; $F_{1,30} = 0.59$; $P = 0.450$) (Fig. 1). Neither seeds ($F_{1,30} = 0.06$; $P = 0.816$), pupae ($F_{1,30} = 0.06$; $P = 0.816$), or their interaction ($F_{1,30} = 0.06$; $P = 0.816$) affected the abundance of carnivorous carabids (Fig. 1). Carnivorous carabids included *Elaphropus* spp. (36% of carabids captured) as well as species in the genera *Scarites, Chlaenius, Pterosticus, Cicindela* which together accounted for another 10% of carabids captured. As a result the proportion (mean ± SEM) of omnivorous carabids in each plot was significantly greater when plots were subsidized with seeds (0.583 ± 0.12) compared to plots without seeds (0.375 ± 0.12) ($F_{1,18} = 4.53$; $P = 0.047$). Pupal subsidies did not affect the proportion of omnivorous carabids captured ($F_{1,18} = 0.70$; $P = 0.414$) nor was there a significant interaction ($F_{1,18} = 0.01$; $P = 0.941$).

3.2. Effect of alternative food type on carabid residence time

The three-way interaction of carabid species, pupal subsidies, and seed subsidies was not significant which indicates carabid species responded to treatments similarly ($F_{1,12} = 0.92$; $P = 0.355$). There was a significant interactive effect between pupal and seed subsidies wherein pupae and seeds increased residence time by 50% and 100%, respectively, compared to plots with no subsidies but did not have an additive effect ($F_{1,12} = 5.34$; $P = 0.039$) (Fig. 2). Interactions between species and pupae ($F_{1,12} = 2.33$;
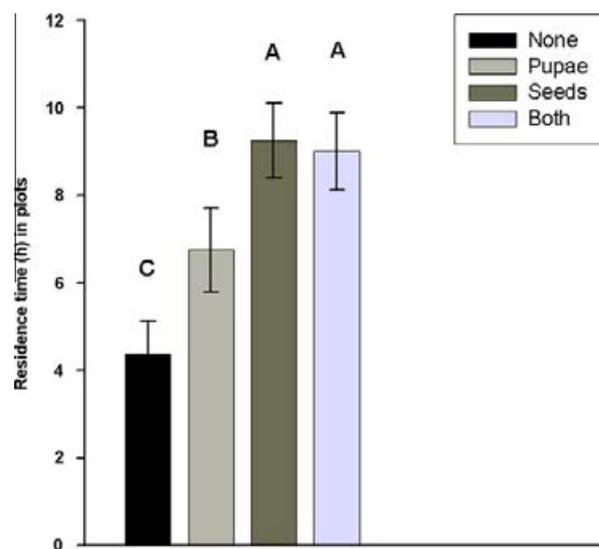
Fig. 2. Mean (SEM) residence time in hours before *H. pensylvanicus* and *A. ovularis* beetles emigrated from plots subsidized with no alternative food, pupae, seeds, or both and were captured on pitfall traps. Bars under different letters are significantly different at $P < 0.05$ using Tukey's HSD adjustment.

$P = 0.153$), species and seed ($F_{1,12} = 0.55$; $P = 0.473$) and main effects of species ($F_{1,12} = 1.45$; $P = 0.253$) and pupae ($F_{1,12} = 3.74$; $P = 0.077$) were not significant although the main effect of seed subsidies was ($F_{1,12} = 31.30$; $P < 0.001$).

3.3. Effect of alternative food type on carabid preference and consumption of herbivores

The number of cutworms consumed was significantly reduced when pupae or seeds were present in Petri dishes ($F_{2,54} = 15.78$; $P < 0.001$) (Fig. 3). After 4 h both carabid species had consumed half as many cutworms when an equal mass of pupae or seeds were present compared to when no alternative food was present (Fig. 3). The main effect of carabid species was significant wherein 45% more cutworms were consumed (mean ± SEM) by *H. pensylvanicus* (2.7 ± 0.3) than *A. ovularis* (1.5 ± 0.3) ($F_{1,54} = 10.36$; $P = 0.002$).
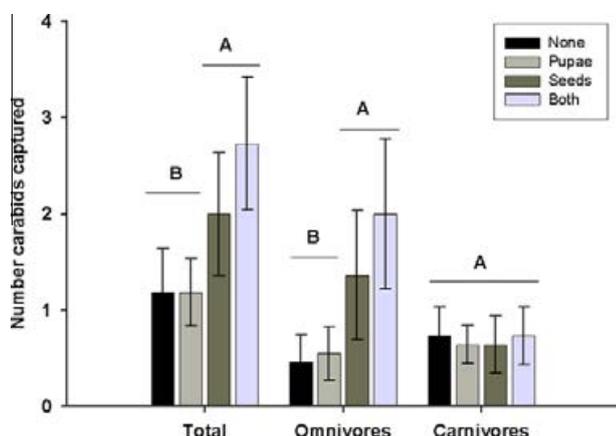
Fig. 1. The total number of carabid beetles, the number of omnivorous carabids, and the number of carnivorous carabids captured in field plots subsidized with no alternative food (none), pupae, seeds, or both pupae and seeds. Bars under different letters indicate a significant main effect of seed subsidies on the total number of carabids and omnivores captured.
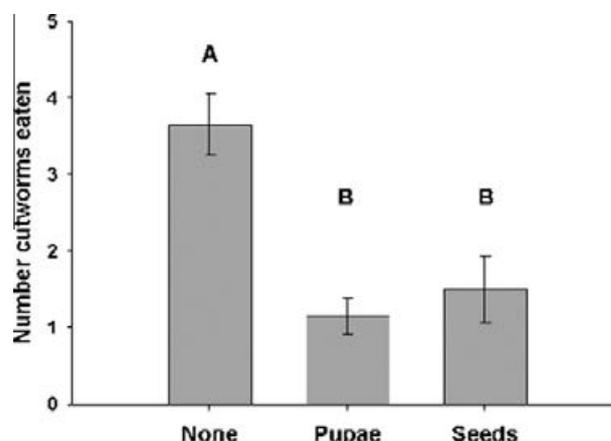
Fig. 3. Number of 2nd instar black cutworms (out of 5) consumed by *H. pensylvanicus* and *A. ovularis* when presented with no alternative food (None), an equal mass of pupae, or an equal mass of seeds in laboratory choice experiments. Data are combined means for both carabid species to represent the significant main effect of alternative food type. Bars under different letters are significantly different at $P < 0.05$ using Tukey's HSD adjustment.

Interaction of alternative food type and carabid species was not significant ($F_{2,54} = 1.43$; $P = 0.249$).

Overall, *A. ovularis* had a strong preference for seeds and pupae over cutworms (0.0 ± 0.0 and 0.06 ± 0.1, respectively; values close to zero), whereas *H. pensylvanicus* showed less preference (0.57 ± 0.1, 0.31 ± 0.1; respectively; values close to 0.5). *H. pensylvanicus* and *A. ovularis* differed in preference (mean $\pm$ SEM) for pupae over cutworms (0.31 ± 0.1, 0.06 ± 0.1, respectively; $X^2_1 = 3.92$; $n = 10$; $P = 0.048$) and in preference for seeds over cutworms (0.57 ± 0.1, 0.0 ± 0.0, respectively; $X^2_1 = 5.73$; $n = 10$; $P = 0.017$). *H. pensylvanicus* had no difference in preference for pupae over cutworms (0.31 ± 0.1) compared to seeds over cutworms (0.57 ± 0.1) ($X^2_1 = 1.5$; $n = 10$; $P = 0.219$). *A. ovularis* also had no difference in preference for pupae over cutworms (0.06 ± 0.1) compared to seeds over cutworms (0.0 ± 0.0) ($X^2_1 = 0.60$; $P = 0.439$).

3.4. Effects of carabid species and alternative food supplements on seedling survival

There was a significant effect of alternative food type on the number of seedlings cut by cutworms such that more seedlings were cut when seeds were available as alternative food than when pupae or no alternative food was present ($F_{2,38} = 14.48$; $P < 0.001$) (Fig. 4). There was not a significant effect of carabid species ($F_{2,38} = 0.26$; $P = 0.612$) or interaction ($F_{2,38} = 2.10$; $P = 0.136$) on the number of seedlings cut indicating *H. pensylvanicus* and *A. ovularis* responded similarly to alternative food treatments. Comparison of control cages with no carabid predators to cages with no alternative food, pupae, or seeds found that control cages and those with seeds had significantly more cut plants than cages with pupae or no alternative food ($F_{3,21} = 9.56$; $P < 0.001$) (Fig. 4).

4. Discussion

Our research demonstrates that omnivorous carabids have strong behavioral responses to seeds in field and laboratory settings. This research was designed, in part, to test the hypothesis that omnivores track resources at the lowest trophic level on which they feed (Eubanks and Denno, 1999). We found clear evidence that omnivorous carabids aggregate and remain in areas of high seed density. Twice as many omnivorous carabids were captured in field plots subsidized with seeds than plots without seeds. Further, subsidizing plots with fly pupae had no affect on the number

Fig. 4. Number of corn seedlings cut down and consumed by cutworms in field cages subsidized with no alternative food (None), pupae, or seeds. Control cages had cutworms but no carabid predators. Data are combined means for both carabid species to represent the significant main effect of alternative food type. Bars under different letters are significantly different at $P < 0.05$ using Tukey's HSD adjustment.

of omnivorous carabids captured suggesting omnivores have a strong response to plant resources rather than alternative food in general. In addition, residence time of omnivorous carabids was twice as long in plots subsidized with seeds than in plots with no resource subsidies. Other research has demonstrated that plant resources promote aggregation by omnivorous arthropods (Eubanks and Denno, 1999, 2000a; Cottrell and Yeargan, 1998) and that seeds are associated with carabid abundance (Honek and Jarosik, 2000; Honek et al., 2005; but see Saska et al., 2008). Prey, particularly aphids, has also been shown to promote carabid aggregation (Bryan and Wratten, 1984; Winder et al., 2005). Our experiment is unique in that we manipulated plant and prey based food to test how trophic origin of alternative food affects carabid aggregation.

Another interesting result of this experiment was that resource subsidies had no effect on capture of carnivorous carabids. Although seeds would not be expected to attract carnivores, even fly pupae, which carnivorous carabids consume (Sunderland, 1975; Kromp, 1999; Frank, 2007) did not elicit aggregation of carnivorous species. Therefore, guild composition of the carabid community shifted from being dominated by carnivores (62.5% carnivores) in plots without seed subsidies to being dominated by omnivores (58% omnivores) in plots with seeds.

Alternative food resources can increase or decrease consumption of target pests by arthropod predators (Symondson et al., 2002). In our experiments, alternative food (pupae or seeds) reduced consumption of cutworms by omnivorous carabids. *A. ovularis*, strongly preferred alternative food to cutworms consuming 79% and 88% fewer cutworms when pupae and seeds, respectively, were present. *H. pensylvanicus* showed less preference but consumed half as many cutworms when alternative food was present. The consequence of this in field cages was twice as many corn seedlings cut down when seeds were present than when seeds were absent. Moreover, when seeds were present crop damage was equal to that of cages with no carabid predators. Seeds effectively nullified the presence of predators and their value for biological control. However, field cages prevent aggregation to seeds that occurred in field experiments. Thus, further research is necessary to determine if a population level numerical response to seeds compensates for reduced per-capita consumption of pests (e.g. Cottrell and Yeargan, 1998; Musser and Shelton, 2003).

Unexpectedly based on laboratory feeding trials, in which pupae reduced cutworm predation, pupae did not increase crop damage in field cages. The number of seedlings cut in cages with carabids and pupae was the same as in cages with carabids and no alternative food. One explanation is that carabids were more active in cages without seeds. This is supported by the mark-recapture experiment wherein carabids emigrated from plots with pupae faster than plots with seeds. Increased activity trying to emigrate from pupae cages may have increased encounter rate with cutworms. In addition, carabids are attracted to prey via olfactory and visual cues (Bauer et al., 1977; Kielty et al., 1996; Thomas et al., 2008). So, another explanation may be that carabids detect or are attracted to cutworms more so than pupae. Research on carabids has documented positive, negative, and neutral effects of alternative prey on predation or abundance of target pests in laboratory and field experiments (Mair and Port, 2001; Symondson et al., 2006; Frank et al., 2010). Future manipulative studies are required to uncover the mechanisms underlying these results though it is clear the type of alternative food affects the outcome.

A particularly interesting result of our research is that throughout our experiments the two omnivore species had similar responses to alternative food treatments. Both species increased residence time in plots with alternative food and consumed fewer cutworms in dishes with alternative food. Particularly noteworthy is the consistently strong interaction with seeds that increased res-
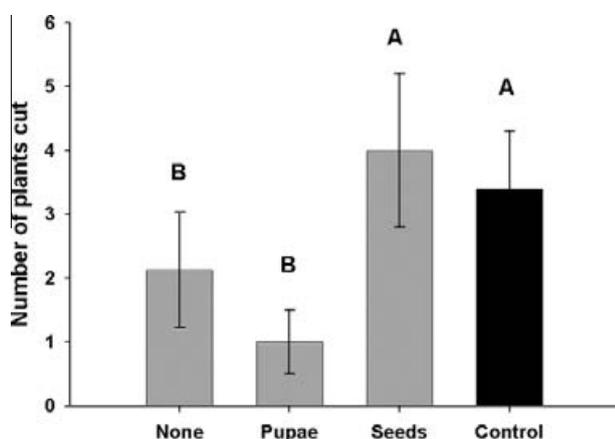
idence time and crop damage more so than pupae. Consistent results among replicate omnivorous species, taken together with results of the aggregation experiment, suggest that the strong influence of seeds on behavior and trophic interactions of omnivorous carabids may be a general phenomenon.

The success of conservation biological control relies on supporting a predator community that is larger and more enduring than could be supported by pests alone. Providing alternative food is a major component of attracting and retaining natural enemies. However, for alternative food to increase pest suppression, natural enemies must either switch to consuming target pests when they are present or exhibit a numerical response large enough to compensate for reduced per-capita predation (Eubanks and Denno, 1999, 2000a). Our goal was to better understand how plant and prey based alternative foods affect the behavior of omnivorous carabids and their efficacy in biological control. The results of our experiments provide conflicting evidence for the value of omnivorous carabid beetles in resource diverse environments that result from habitat management. On one hand we demonstrate that carabids aggregate and remain in areas of high seed density as could result from beetle banks, hedgerows, or no till agriculture (Cardina et al., 2002). On the other hand, preference for seeds reduced predation of cutworm pests resulting in greater crop damage. Our experiments did not test directly whether doubling carabid abundance in the presence of seeds as in our field experiment compensates for a 50% reduction in cutworm predation seen in laboratory experiments and would thus reduce crop damage. However, the strong, consistent behavioral response of omnivorous carabids to seeds in field and laboratory settings suggests that changes in seed abundance and carabid guild composition that could result from habitat management schemes could influence biological control of arthropod pests.

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