Cover crops increase foraging activity of omnivorous predators in seed patches and facilitate
weed biological control

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Abstract

Omnivorous predators are key contributors to biocontrol, but the relative importance and interactive effects of ecological variables (e.g., habitat and prey- or plant-based foods) that impact their colonization, abundance, and/or function in crop fields are poorly understood. Here, we use immuno-marking to examine both activity density and consumption by omnivorous ground beetles in response to experimentally manipulated cover, weed seeds, and invertebrate prey. Vegetative cover increased per-capita seed predation by 73% compared with bare plots, validating existing correlative evidence that cover crops facilitate weed biocontrol. Interestingly, beetles responded differently to the main effects of seeds and prey. In both years, early season seed presence increased activity-density by 77%, while prey availability never influenced beetle activity. These data suggest that within-field habitat manipulation strategies such as cover crops improve biocontrol, not only by promoting increased activity of omnivores, but also by facilitating their function as seed predators on an individual-level.

Keywords: Carabidae, immunomarking, gut content analysis, granivory, omnivory, seed predation, cover crops

1. Introduction

Omnivory is pervasive among generalist predators in agricultural systems where broad diet breadth enables consumers to persist despite seasonal disturbance and food insecurity (Eubanks and Denno 1999). For this reason, omnivores are critical to biocontrol (Ågren et al. 2012), preventing pest outbreaks by consuming pests at low densities before strict carnivores assemble (Eubanks 2005). Plant-based food can support stronger top-down suppression by reducing emigration and supporting higher densities of omnivorous predators, despite reductions in per-capita prey consumption due to plant feeding (Eubanks and Denno 2000, Eubanks and Styrsky 2005, Maselou et al. 2014). In addition to prey- and plant-based foods, structural habitat determines omnivore retention and feeding behavior by providing shelter and refuge from predation (Landis et al. 2000, Kratina et al. 2012). However, the relative importance and interactive effects of food and habitat on omnivore function are mostly unknown because the two resources are co-occurring and difficult to isolate in the field.

Omnivory is prevalent among ground beetles (Coleoptera: Carabidae), and because their feeding ecology is relatively well known at the species-level (Lundgren 2009), carabids make excellent subjects for evaluating how food and habitat drive predator assembly. Although they are important consumers of invertebrate pests (Lundgren and Fergen 2011) and weed seeds (Menalled et al. 2007), most studies report that carabids in the field do not aggregate in response to patches of seeds (Marino et al. 2005, Westerman et al. 2008, Baraibar et al. 2012; but see Frank et al. 2011) or prey (Birkhofer et al. 2008, Frank et al. 2011, Al Hassan et al. 2013). However, carabids commonly aggregate around plants (Brooks et al. 2012, Diehl et al. 2012, Blubaugh and Kaplan 2015), and structural refuge provided by cover may facilitate a numerical response to food patches.

The literature is rich with correlative evidence of omnivorous carabid associations with vegetative cover (Carmona and Landis 1999, Shearin et al. 2008, Diehl et al. 2012), but few studies take a mechanistic approach to understanding how refuge and food availability interactively shape activity patterns of biocontrol agents. Cover supports higher densities of natural enemies by providing a favorable microclimate, and also through provisions of non-pest food associated with vegetated habitats (Diehl et al. 2012), but these may distract biocontrol agents from focal pest suppression (Frank et al. 2010). Without directly measuring pest predation events by omnivores, we cannot confirm that increased natural enemy activity in vegetated habitat confers increased biocontrol.

Most studies are limited by reliance on passive sampling methods, thus direct links between predator activity and pest suppression are rare (Griffiths et al. 2008). However, modern molecular tools make documentation of direct trophic interactions more tractable (Symondson and Harwood 2014), and the development of affordable immuno-marking techniques enable efficient identification of predator gut contents at the field scale (Hagler 2006, 2011, Lundgren et al. 2013, Kelly et al. 2014). PCR-based gut content analysis is also a powerful tool to detect trophic interactions, but requires considerably higher labor investments that often limit the scale of studies (Fournier et al. 2008). Vertebrate immunoglobulin proteins can be easily incorporated in insect food resources, providing a persistent, reliable, specific mark in the guts of insects that consume them (Hagler and Durand 1994; Hagler 2006), detectable with IgG protein-specific ELISAs (enzyme-linked immunosorbent assays).

In this experiment, we manipulate and disentangle three common biological resources: vegetative cover, seeds, and invertebrate prey. We use protein-based marking to link consumption frequencies of both seeds and prey with foraging activity of three numerically

dominant carabid species in agroecosystems. Diet mixing can have a synergistic effect on predator fitness (Eubanks and Styrsky 2005), thus we predicted that availability of both seeds and prey would result in higher carabid activity densities than either food resource alone. We also predicted that cover would provide a favorable foraging microclimate for natural enemies, facilitating predator activity and consumption of both insect prey and weed seeds.

2. Methods

2.1 Study system

This experiment was conducted at the Purdue University Meigs Horticulture Research Farm (40°17'15" N, 86°53'1" W) near Lafayette, Indiana, USA in 2012 and 2013. In March 2012, forty 3x3-m plots were tilled with 2-m buffers between each. Resource manipulation treatments were applied in a 2x2x2 factorial design, in 5 randomized blocks. The combinations of three variables—presence/absence of plant cover, seed subsidy, and prey subsidy—comprised 8 treatment groups. Experimental plots were located in an agronomic crop matrix, surrounded on two sides by a grassy margin, and two sides by conventionally managed soybeans. The cover treatment was established by drill-seeding *Rhizobium*-inoculated red clover (*Trifolium pratense* L.) at a depth of 0.5 cm and a rate of 13 kg/ha. Red clover was used because it is a common cover crop used in annual vegetable systems, and simple to manage as a homogenous stand. Bare plots and the margins were treated with pre- and post-emergent herbicides (a mixture of oryzalin, simazine and glyphosate) in May and August of 2012 and 2013, to maintain a bare-soil environment without tillage. These chemicals are neither toxic nor repellant to adult carabids (Brust 1990). To maintain a homogenous stand of red clover and to ensure that all seed inputs

were those we directly manipulated, clover plots were mowed and weeded as needed to prevent seed production.

Once the cover crop treatment was established, food subsidies were broadcast evenly using a cheese shaker while walking a grid in plots. Common lambsquarters (*Chenopodium album* L.) seed subsidies were applied at a rate of 15,000 seeds/m². *C. album* can produce up to 170,000 seeds/plant (Clements et al 1996), and this subsidy rate approximates natural seed rain densities following senescence, when seed predation services are most critical. However, our subsidy applications were not always timed consistently with natural *C. album* senescence (which occurs in early autumn). Frozen *Drosophila melanogaster* M. pupae (Spider Pharm, Yarnell, Arizona, USA) were initially added to prey resource treatment plots at a density of 10,000 pupae/m², matching the seed treatment by weight. Because this was >10x higher than documented ambient immobile prey densities in this production system, the application rate was reduced to 850 pupae/m² (per Frank et al. 2011) after the first subsidy in June 2012, and for all subsequent applications. *C. album* seeds and *D. melanogaster* pupae were selected as food resources because they are both palatable to ground beetles (Lundgren and Rosentrater 2006, Frank et al. 2010), similar in size, and common in the agricultural environment where the experiment occurred (C. Blubaugh personal observation). *D. melanogaster* is not a pest, but serves as a good model for quantifying natural enemy responses to immobile pests (in egg, larval, or pupal form) on the soil surface, and our application rates simulate natural densities of these immobile prey (Frank et al 2011). *C. album* is a weed of great economic importance, and useful focal species for measuring weed seed biocontrol.

Before deployment in the field, seeds were marked with rabbit IgG and pupae were marked with chicken IgY. The vertebrate proteins were purchased as lyophilized powder

(Equitech Bio, Kerrville, Texas, USA), and dissolved into a 1 mg/mL aqueous solution, which was sprayed on the respective foods at a rate of 3 mL/10 g of food material. Seeds and pupae were fully air-dried before they were broadcast in the designated plots. Food subsidies were applied in 2012 on June 7, August 9, and September 9 and in 2013 on May 23, June 9, July 7, August 20, September 3 and September 19. Subsidies were applied more frequently in 2013 because *C. album* seeds are typically buried and inaccessible to invertebrate granivores within two weeks (Westerman et al. 2006).

2.2 Field sampling

We measured carabid activity density using pitfall traps, which consisted of two 950-mL deli cups in each plot, sunk in the ground flush with the soil surface, connected by a 0.2-m tall barrier made of 1-m aluminum flashing. The two traps were placed on a NE/SW diagonal in the center of the plot. To preserve the internal protein marks in carabid guts, traps were dry with no liquid killing agent, and 1 cm of grass clippings in the bottom provided refuge for trapped animals, reducing the likelihood of cross-contamination of the protein mark due to predation events in the trap (King et al. 2008). Traps were set at dusk on nights without precipitation and collected at 09:00 each morning. Trapped insects were transported to the lab within an hour of collection, immediately transferred to 1.5-mL centrifuge tubes and frozen at -25° C. Daily collections continued for 14 days following deployment of labeled food subsidies, and weekly thereafter. Trapping was suspended for 2-3 weeks each year in mid-summer when carabid activity levels were temporarily depressed due to high nightly temperatures (Lovei and Sunderland 1996).

2.3 Gut content analysis

Protein markers degrade outdoors in 1-2 weeks (Hagler 1997), and our sampling schedule exceeded this window of detectability. Thus, only 3865 out of 6766 beetles captured in the field

experiment were used for gut content analysis. The rest were retained as a reference collection. Rabbit IgG degrades beyond reliable detection levels under field conditions after 14 days, while chicken IgY lasts only 7 days (Hagler 1997), therefore only beetles captured within the reliable window of detection for each protein marker were tested using ELISA. To definitively link the protein mark and an actual predation event (rather than external physical exposure), we dissected guts prior to analysis on all predators greater than 1 cm in length (per Lundgren et al. 2013). Sandwich ELISAs were performed according to Hagler (1997). Briefly, we homogenized samples in tris-buffered saline solution, coated plates with a primary antibody (anti-rabbit IgG from goat or anti-chicken IgY from rabbit; Sigma-Aldrich, St. Louis, Missouri, USA), and incubated them overnight at 4° C. Then we applied a 1% milk blocking agent, followed by aliquots of the macerated predator gut samples. Plates were washed with phosphate-buffered saline with tween, secondary antibodies (anti-rabbit or chicken conjugated with horseradish peroxidase) were applied, and then plates were washed again. Finally, substrate (TMB solution) was added, and after 10 minutes optical density (OD) was measured by a microplate reader at 650 nm. Our positive mark OD threshold was 3 standard deviations above the mean of 8 negative control samples which were included on each plate.

2.4 Protein mark retention trial

We used *Harpalus pensylvanicus* DeGeer, the most common beetle in our system, as a model to determine how long protein labels are detectable in the guts of ground beetles before excretion. Field-collected beetles were starved for 24 hours, then fed *ad libitum* for 24 hours on either marked seeds or pupae, each in a plastic 100-mL Solo™ cup with moistened filter paper. After 24 hours, beetles were removed and either starved or fed unmarked diet. To identify the

amount of time that marked gut contents can be detected, beetles were removed in groups of 8 and frozen for dissection and gut content analysis after 0, 12, 24, 48, 72, and 96 hours.

2.5 Statistical analysis

Because differences in trophic guild are previously described for our focal species (Lundgren 2009), we tested each species separately for responses to experimental treatments. Activity density of carabids was analyzed with mixed-effect, quasi-Poisson generalized linear models (to handle overdispersion) for each of the three most dominant species, using the `glmmPQL` function in the MASS package of R (Ripley et al. 2015). The response variable was nightly pitfall capture, and fixed effects were cover, seed availability, and prey availability. We included a fixed effect of ‘season’ for our analysis of *H. pensylvanicus* activity density, because it exhibits two annual activity peaks. The first occurs during mid-summer after 2nd-year adults emerge from overwintering habitat, and the next occurs after a brief summer aestivation when pupating larvae emerge during breeding season (Kirk 1973). Random effects for activity density models were ‘plot’ nested in ‘block’, and ‘Julian day’ nested in ‘year’.

To identify species-specific consumption patterns, we pooled all individuals across treatments and ran generalized linear models assuming binomial distributions on the incidence of positive marks (per individual) for both seeds and prey, with species as the predictor variable. We tested for changes in consumption rates due to experimental treatments using mixed-effect GLMs for each protein marker (seed or prey), assuming binomial distributions using the `glmmPQL` function in R. The response variable was the binary detection success for each tested beetle. We pooled species and sample dates for this model to produce a robust, overall estimate of biocontrol services performed by the carabid community across resource manipulations. This was necessary because some species were rarely captured in particular habitat types, (i.e. sample

sizes of *P. chalcites* and *A. sanctaecrucis* were inadequate for analysis in several plots) and species-specific models were too unbalanced to converge. Also, for each food marker, we restricted the analysis to plots that contained subsidy treatments of that particular food (seed or prey), assuming that the presence of each focal resource in a plot would greatly increase its rate of detection. This approach enabled us to explicitly examine how alternative food alters foraging behavior on the focal food. Fixed effects were cover and either seed or prey; random effects were ‘year’ and ‘plot’ nested in ‘block.’

3. RESULTS

3.1 Pitfall sampling

We captured 6766 carabids over two years, >85% of which were three numerically dominant species: *Anisodactylus sanctaecrucis* Fab., *Poecilus chalcites* Say, or *H. pensylvanicus*. *A. sanctaecrucis* and *P. chalcites* are both spring-breeding species, which go through larval stadia during the summer and overwinter as adults. *H. pensylvanicus* comprised more than half the annual trap catch, and it is a fall-breeding species, overwintering in the larval stage (Fig 1).

Activity density of *A. sanctaecrucis* was higher in plots with weed seeds in both the cover and bare ground treatments, and cover crops marginally reduced its activity density (Fig. 2a, Table 1). *P. chalcites* showed the opposite response—individuals were nearly twice as active in plots with cover crops (Fig. 2b, Table 1), but did not respond to either of the food subsidies. *H. pensylvanicus*, the most common beetle at our site, had a synergistic response to weed seeds and cover early in the season (significant seed*cover*season interaction; Fig. 2c, Table 1), but this relationship disappeared later in the fall during the second activity peak (Fig. 1), after which only

the cover treatment increased activity density. None of the carabid species responded to fly pupal subsidies (not pictured).

3.2 Gut content analysis

Mark retention of both rabbit IgG and chicken IgY was reliable up to 72 hours after feeding events in *H. pensylvanicus*, and was similar for seeds and prey (>80% of individuals tested positive; Fig. 3). The mark decay rate also did not differ between beetles that were starved after consuming labeled food and those that fed on unmarked diet (pooled data shown).

Among the species examined, *H. pensylvanicus*, a known seed predator (White et al. 2007), was the most frequent consumer of seeds (Fig. 4, $z=12.981$, $df= 2$, 3682, $p<0.001$). *P. chalcites* is often considered a strict predator (Lund and Turpin 1977, O'Rourke et al. 2006), and was the most frequent consumer of pupae ($z=5.063$, $df= 2$, 2282, $p<0.001$), but also tested positive for seeds. *A. sanctaecrucis* had very low positive mark rates in general, and it consumed seeds and prey with similar frequency (Fig. 4).

Across all three carabid species and sample dates, the cover treatment increased the likelihood of testing positive for seeds by 75% compared with bare soil, and fly pupae did not significantly reduce seed predation frequency (Fig. 5a, Table 2). These effects were largely driven by *H. pensylvanicus*, which made up >75% of beetles that tested positive for seeds. Rates of pupal consumption were only half of those observed for seed consumption (Fig. 5b). Proportions of beetles consuming pupae in plots with pupal subsidies were marginally reduced by seed availability, but unaffected by cover (Fig. 5b, Table 2).

4. Discussion

This work demonstrates clear behavioral and trophic links between omnivorous natural enemies and plant-based food (i.e., seeds). Omnivores (*A. sanctaecrucis* and *H. pensylvanicus*) assembled in seed patches (Fig. 2) and *H. pensylvanicus* frequently consumed supplemental seeds (Fig. 4). *A. sanctaecrucis* had a relatively low positive mark rate for seeds, but the probability of positive detection in gut content analysis is likely much lower than that of the other two species examined, given its considerably smaller size. Thus, we expect that our ELISA results strongly underestimate the seed predation services of this species, particularly because its activity increased strongly in response to seed augmentation. Even *P. chalcites*, which is a reluctant seed-feeder in laboratory trials (Lund and Turpin 1977, O'Rourke et al. 2006), frequently tested positive for seeds. Lundgren et al. (2013) found similar rates of seed consumption in a separate marking study, and also discovered many unlikely seed consumers using gut content analysis, suggesting that seed-feeding and omnivory in general are more ubiquitous than previously considered. This and previous evidence of omnivore assembly around seeds and other plant-based foods indicate that omnivores indeed track resources at lower trophic levels in crop environments (Eubanks and Denno 2000, Frank et al. 2011); thus, non-prey food may be critical for predator retention and stability of biocontrol in crop environments.

It is possible that false positives due to secondary predation events occurred in our study, where a predator consumes prey which recently consumed labeled food. Harwood et al. (2001) found that false positives were rare using aphid-specific indirect ELISAs, but rabbit IgG-specific sandwich ELISAs employed here are quite sensitive (Hagler et al. 2015) and may detect secondary predation events more frequently. Error associated with secondary predation is indeed a drawback of this technique, but common to all studies employing molecular tools to document trophic interactions. Using PCR, Sheppard et al. (2005) found that secondary predation was

easily documented immediately following secondary predation event, but only 31 percent of those secondary predation events were detectable after only 2 hours. Because this source of error seems to be limited in duration, we believe that false positives have a relatively low probability of altering our results, however further research must quantify error associated with secondary predation in gut content analysis using protein labels.

In contrast to predictions, none of the omnivores we observed responded to prey availability (Fig. 2), not even the mostly-carnivorous *P. chalcites*, which consumed pupae more often than the other carabids (Fig. 4). This absence of response to prey by carnivores is consistent with Frank et al. (2011), but differs from Brooks et al. (2012), who discovered stronger links between predators and invertebrate prey availability. None of the variables examined had any impact on prey consumption (Fig. 5b). In general, prey consumption by carabids in our system was very low, relative to seed consumption (Fig. 5a), despite strong preferences for fly pupae over seeds in lab preference trials (C. Blubaugh, personal observation). Weak responses to prey subsidies could be related to the lower densities at which they were applied relative to seeds. However, our treatments approximated naturally-occurring densities; thus, plant and prey resources appear not to have synergistic effects on omnivores in this system. Differences in availability of plant and prey food resources common to agricultural environments may explain differences in predator foraging behavior associated with each food resource (Frank et al. 2011). Because plant-based resources are typically more available and persistent in agroecosystems (Moshe and Coll 2002), omnivores may rely on seeds more in the field than they demonstrate in lab preference trials.

While both omnivorous carabid species tracked and consumed weed seeds, they seem to occupy different spatial niches. Specifically, *A. sanctaecrucis* foraged equally in both exposed

and cover crop habitat (Fig. 2a), and *H. pensylvanicus* was more active in cover crop habitat (Fig. 2c). Because *A. sanctaecrucis* is active early in the season, its life history may be linked to winter-annual weeds, which often germinate in exposed environments following fall tillage operations in temperate agronomic systems (Brooks et al. 2012). Being fall-active, *H. pensylvanicus* is linked with summer annual weeds, which senesce in autumn and accumulate more biomass than winter-annuals, thus providing more cover. Niche complementarity that results from contrasting habitat selection among predators reduces the likelihood of predator interference (Gable et al 2012), and may result in more even seedbank depletion across heterogeneous habitat types. This could enhance the ecosystem services of weed seed predators, as agroecosystems are typically a complex matrix of tilled and vegetated habitat patches.

The early-season response of the most common carabid in our system, *H. pensylvanicus*, to seeds and cover was particularly interesting because it suggests that provisions of vegetative cover may have a synergistic effect on beetle assembly around seed resource patches, facilitating their depletion. *Harpalus spp.* are dominant seed predator species in many North American cropping systems (Ward et al. 2014, Blubaugh and Kaplan 2015), and in Europe as well (Westerman et al. 2003), thus these activity patterns may be broadly relevant. By autumn, the synergistic effects of seed and cover resources dissolved (Fig. 2c). At high predator densities, competition and predator interference often promotes dispersal to adjacent food patches (Schmidt et al 2014). High activity densities of *H. pensylvanicus* during the peak activity period late in the season may have caused dispersal to all available vegetated habitats, overwhelming the preference for seed patches observed early in the season.

Our most compelling result was the strong effect of cover on seed foraging behavior. Gut content analysis revealed that cover crops facilitated seed predation by carabids pooled across

the entire season. In plots that contained seeds, a direct consumption event was twice as likely if red clover was present (Fig. 5a). Alternative prey availability (pupae) did not significantly reduce seed consumption frequencies, suggesting that weed seed biocontrol will occur reliably even when diverse food resources are available. While these results are driven by the dominant seed predator in the system, *H. pensylvanicus*, the ubiquity of *Harpalus spp.* in temperate cropping systems (Eitzinger and Traugott 2011, McCravy and Lundgren 2011) suggests that living groundcover may enhance weed seed biological control across a variety of environments. This result validates the utility of cover crops to promote weed seed predation by increasing seed predator activity density (which has been reported numerous times) as well as increasing per-capita predation frequency (which we document here).

These results are important because they confirm correlative evidence of increased seed predator activity and episodic seed removal in cover crops from many studies across a variety of crop landscapes (reviewed in Kulkarni et al. 2015). Indirect sampling methods are limited by uncertainty of seed fate following seed removal (Vander Wall et al. 2005), and without proof that seed predator activity actually leads to biocontrol, growers may be reluctant to implement management strategies that promote their retention and survival. Very few studies evaluate direct links between seed predator activity and predation events in the field via predator observation (Brust and House 1988, Navntoft et al. 2009), or gut content analysis (Lundgren et al. 2013), and our work fills this critical knowledge gap.

5. Conclusions

In summary, our results suggest that omnivorous carabids track weed seeds, but not prey in the field, and that strict predators are unable to identify either type of resource patch. For this

reason, omnivorous carabids seem most competent as biocontrol agents of weed seeds. Weeds are a persistent problem in both horticultural and agronomic systems, even with widespread adoption of herbicide tolerant crops, as many weed species have evolved resistance to multiple modes of herbicide action (Davis et al. 2012). Seed predation is a critical component of a multifaceted approach that can reduce propagule pressure (Westerman et al. 2006), and our research shows that even when alternative prey are available, carabid seed predators can identify and preferentially exploit seed patches. This work provides powerful evidence that vegetative cover not only provides favorable microclimate for natural enemies (Saska et al. 2010), but directly facilitates seed consumption. Thus, provisioning cover (e.g. cover crops and forage crops) may promote ecosystem services by weed seed predators, in addition to the numerous other benefits they provide.

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Figure legend

Figure 1. Seasonal phenology of the three carabid species examined in a) 2012 and b) 2013

Figure 2. Mean (+ SE) nightly pitfall trap capture of a) *Anisodactylus sanctaecrucis* (omnivore), b) *Poecilus chalcites* (predator), and c) *Harpalus pensylvanicus* (omnivore) across cover and seed subsidy treatments. P-values are given for significant effects and interactions.

Figure 3. Proportion of carabids from each species assayed with ELISA which tested positive for a) rabbit IgG on labeled seeds and b) chicken IgY on labeled pupae over time in a protein marker retention trial.

Figure 4. Proportion of carabids from each species which tested positive for seed- and prey-specific protein labels using ELISA.

Figure 5. Mean (+SE) proportions of carabids testing positive for a) seeds in gut content analysis across cover and prey treatments and b) prey across cover and seed treatments. Proportions are pooled across sample dates and species, and calculated only from plots that contained each focal food resource. P-values are given for significant effects.

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	Factor	Coefficient	SE	t	P	
a)	<i>Anisodactylus sanctaecrucis</i>					
	Intercept	-0.286	0.204	-1.403	0.160	
	Seeds	0.498	0.143	3.472	<0.001	**
	Cover	-0.277	0.147	-1.875	0.069	.
b)	<i>Poecilus chalcites</i>					
	Intercept	-1.233	0.370	-3.328	0.001	**
	Cover	0.653	0.208	3.140	0.004	**
c)	<i>Harpalus pensylvanicus</i>					
	Intercept	-1.106	0.217	-5.09	<0.001	**
	Cover	0.286	0.282	1.014	0.310	
	Seeds	0.221	0.287	0.770	0.441	
	Season	1.192	0.217	5.473	<0.001	**
	Cover*seeds	0.589	0.364	1.615	0.106	
	Cover*season	0.352	0.286	1.230	0.218	
	Seeds*season	-0.187	0.294	-0.637	0.523	
	Cover*seeds*season	-0.722	0.371	-1.946	0.051	*

519 Table 1. Results of each decomposed species-specific mixed effect GLM on nightly pitfall trap capture in plots
 520 where cover, seeds and prey were manipulated
 521

	Factor	Coefficient	SE	t	P	
a)	<i>Seeds (rabbit IgG)</i>					
	Intercept	-1.311	0.246	-5.314	<0.001	**
	Cover	0.727	0.190	3.813	0.002	**
	Prey	-0.302	0.1883	-1.605	0.132	
b)	<i>Prey (chicken IgY)</i>					
	Intercept	-1.518	0.206	-7.363	<0.001	**
	Cover	-0.432	0.267	-1.617	0.130	
	Seeds	-0.481	0.268	-1.794	0.096	.

522 Table 2. Results of mixed effect GLMs on seasonal proportions of beetles testing positive for a) seeds and b)
 523 prey, pooled across carabid species
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