Functional Responses to Food Diversity: the Effect of Seed Availability on the Feeding Behavior of Facultative Granivores[1]

Jonathan G. Lundgren[2] and James D. Harwood[3]

J. Entomol. Sci. 47(2): 160-176 (April 2012)

Abstract We examined how diverse communities of carabid beetles and crickets in a perennial hayfield respond to seed availability numerically and in their feeding behavior. Although there were 3 distinct insect communities identified over the diel cycle, these communities were similar in plots supplemented with *Setaria viridis* (L.) P. Beauv. seeds and untreated plots. *Gryllus pennsylvanicus* Burmeister consumed plant material more frequently and ate more food in the fields with greater seed availability. However, they consumed prey with equal frequency in the 2 treatments. *Allonemobius* sp. consumed food less frequently than *G. pennsylvanicus*, and their diet was unaffected by seed availability. Availability of nonprey food resources may not affect soil insect communities in the short term, but some omnivores are quick to alter their diet to exploit nonprey resources.

Key words dietary breadth, granivory, gut content analysis, omnivory, predator

Categorical trophic guilds have been widely used to describe the dynamics within complex food webs (Elton 1927, Hairston et al. 1960, Egerton 2007, Coll 2009), but most animals consume foods at more basal trophic levels (i.e., nonprey foods, nonanimal foods) and are often best described as true omnivores (Pimm and Lawton 1978, Polis 1991, Havens et al. 1996, Coll and Guershon 2002, Thompson et al. 2007, Hunter 2009, Lundgren 2009). Thus, whereas many organisms may frequently be categorized as "predators" or "carnivores", alternative foods can play a crucial role in providing dietary (and nutritional) balance (Jervis and Heimpel 2005, Wäckers 2005, Lundgren 2009) and in the ultimate stability of food chains (McCann and Hastings 1997, Beckerman et al. 2006, Blüthgen et al. 2008). Moreover, relying on biological control for managing insect pests and weed seed banks necessitates that we understand how omnivores balance their foraging efforts between prey (note: hereafter, prey refers to animal-based foods) and nonprey foods. True omnivory is an inherent characteristic in the behavior and physiology of many animals and is a crucial consideration for understanding the functioning of complex food webs. However, omnivory is a dynamic process at the organismal, population, and community levels, and is influenced by the relative availability and nutritional suitability of various classes of food (Eubanks and Styrsky 2005, Lancaster et al. 2005, Sabelis and Van Rijn 2005). Soil arthropod communities offer an excellent study system for examining how animals balance their diet in response to the availability of foods from various trophic

---

[1] Received 19 August, 2011; accepted for publication 19 December 2011.

[2] Address inquiries to USDA-ARS, North Central Agricultural Research Laboratory, 2923 Medary Avenue, Brookings, South Dakota, USA, 57006 (E-mail: Jonathan.Lundgren@ars.usda.gov).
[3] Department of Entomology, University of Kentucky, Lexington, Kentucky, USA, 40546-0091

groups and how the nutritional predisposition of an animal can affect community-level dynamics.

Soil arthropod communities are extreme in their abundance and high levels of diversity, and organisms within such systems, including those that function at the interface between above and below ground food webs (e.g., carabids, crickets), represent broad ranges of dietary specialization. For example, sampling efforts within even the most highly managed systems (e.g., agroecosystems) typically uncover thousands of specimens representing dozens of species (Kirk 1971, Ellsbury et al. 1998, French and Elliott 1999, Lundgren et al. 2006, Gandhi et al. 2008, Lundgren et al. 2009b, Lundgren and Fergen 2010). The mechanisms that permit these complex communities to coexist within a spatially simple (i.e., almost two-dimensional) habitat are varied, but involve activity patterns (Lundgren et al. 2006, Lundgren et al. 2009b, Weber et al. 2009, Romero and Harwood 2010) and dietary niche partitioning (Honèk et al. 2003, Lundgren and Rosentrater 2007) on very fine scales. In temperate regions, carabid beetles (Coleoptera: Carabidae) and crickets (Orthoptera: Ensifera: Gryllidae) often reside in the top trophic tier of these soil communities, and their diversity and relative sensitivity of different species to various habitat qualities make them valuable bioindicators (Doring et al. 2003, Rainio and Niemelä 2003). As is often the case in complex food webs (Thompson et al. 2007), many carabids and crickets also rely on plant material (especially seeds) in addition to consuming prey (Brust and House 1988, O'Rourke et al. 2006, Lundgren 2009), and the degree to which they rely on these 2 different food classes affects their position within soil (and above-ground) food webs.

Post-dispersal granivory (i.e., after the seeds have left the maternal plant) has important implications for plant and insect communities. Seeds are a highly nutritious food source (Bewley and Black 1994), and gross nutrient contents (i.e., calories, protein, carbohydrates, lipids) of seeds are frequently competitive with or superior to that of insect prey (Lundgren 2009). But, seeds are also distinct from insect prey in their defenses and the types of nutrients present, and thus require adaptations in facultatively granivorous insects (e.g., omnivorous insects that consume seeds when they become available) (Forbes 1883, Forsythe 1983, Acorn and Ball 1991, Lundgren 2009). This notwithstanding, numerous facultatively granivorous carabids, crickets, and ants consume seeds when they become available (Brown et al. 1979, MacMahon et al. 2000, Westerman et al. 2003, Azcarate et al. 2005, Honěk et al. 2005, Lundgren et al. 2006, O'Rourke et al. 2006, Lundgren 2009, Frank et al. 2011), thereby providing an important resource in the diet of such species. Additionally, the availability of such food items affects the dynamics of food webs because facultative omnivores may switch to or substitute nonprey foods during times of abundance (Musser and Shelton 2003, Lundgren et al. 2004, Frank et al. 2011). This granivory often shapes the dispersion and densities of the plant communities with which these insects live (Tevis 1958, Harper 1977, Crawley 2000, Hulme 2002), as well as the behaviors of insect communities that occur within a habitat (Johnson and Cameron 1969, Zhavoronkova 1969, Kirk 1973, Brown et al. 1979, Briese and Macauley 1981, Westerman et al. 2003, Heggenstaller et al. 2006). Therefore, although seed availability influences the composition of soil arthropod communities and trophic connectivity within these complex food webs, it is currently poorly understood how facultatively granivorous insects balance their feeding between prey and seeds when the relative availability of the latter is locally increased.

Here, we pair population monitoring techniques with microscopic and prey-specific monoclonal antibody (MAb)-based gut-content analysis to determine how members of a diverse carabid and cricket community of a perennial hayfield respond numerically and behaviorally to the availability of seeds. Specifically, we first investigate the hypothesis that various members of the predator community partition their activity patterns over the diel cycle. Then we test the hypotheses that seeds affect short-term community activity-density and composition initially after seeds become available, and that seed availability affects the diet consumed by 2 abundant facultative granivores in this system- *Gryllus pennsylvanicus* Burmeister and *Allonemobius* sp. (Orthoptera: Ensifera: Gryllidae).

Materials and Methods

Field sites. Research was conducted in a matrix of small perennial alfalfa, *Medicago sativa* L. (Fabales: Fabaceae), fields located on a research farm (44.351° latitude, -96.804° longitude) during 2007 and 2008. In both years, the experimental plots were the same size and separated by similar distances; a major difference between the replicates is that there were alfalfa alleyways between replicates in 2007 and grass alleyways between replicates in 2008. In 2007, two treatments (described below) (9 × 9 m plots) were replicated 3 times, and these plots were separated by at least 6 m to ensure independence between experimental units and minimize plot-to-plot movement by crickets and carabids. In 2008, single pairs of treatments (9 × 9 m plots; 6 m distance between plots; 9 m from field edges) were embedded in 4 areas which were different from 2007 (12 m perennial grass margins between fields).

Treatments consisted of untreated alfalfa and fields augmented with seeds (see below) were initiated on 2 October 2007 and 19 September 2008. In the treatment with augmented seed density, 1-m^2 square sites were established at 10 randomly selected sites per plot. *Setaria viridis* L. (P. Beauv.) (Poaceae) seed (6.74 g per site, locally collected) was applied evenly at each study site. Research indicated that this mean weight corresponded to approx. 250 seeds, which is within the range of seeds produced in managed agroecosystems of this region (Forcella et al. 1992, Kegode et al. 1999). Thus, each site simulated the local seed rain of a *S. viridis* plant.

Insect collection and preparations. Insect sampling was initiated within 24 h of seed deposition in the plots and occurred every 7 - 9 h for 144 h. To collect insects, 2 sets of barrier-linked (1 m long), dry pitfall traps (see Luff 1975, Lundgren et al. 2009b) were placed in each plot, one centralized in the SW and one in the NE quadrants of the plots. Pitfall traps were collected at 0700, 1500, and 2200 h daily, and the number of each taxon collected per hour was calculated for each time period. Carabids and crickets, 2 entomophagous groups with known facultative granivores, were frozen at -20°C until identification.

Gut-content analyses were restricted to the 2 cricket species collected, which were by far the most abundant insects captured in this study. Specifically, the gut contents of a maximum of 5 randomly selected crickets from each plot/time sample were analyzed. Each sampled gut was dissected under sterile conditions, weighed to the nearest 0.1 mg on an AT201 microbalance (Mettler-Toledo, Columbus, OH, USA), and suspended in 1X phosphate-buffered saline (PBS) solution. The guts were macerated using a pestle, vortexed for 10 sec, and each gut solution was divided into 2 subsamples, which were returned to the freezer at -20°C. The contents of one subsample would be analyzed using standard microscopy, and the other subsample would be subjected to indirect enzyme-linked immunosorbent assay (ELISA) to examine predation on dipteran prey using the order-specific *DrosW-VI-B8* monoclonal antibody (Harwood et al. 2007a).

Microscopic gut-content analysis. The contents of one subsample from each cricket were slide mounted and examined under the microscope at 100×. Food remains were categorized as being of plant or insect origin. Thus, each gut was categorized as having no food, plant material only, insect prey only, or both food types.

Monoclonal antibody-based gut-content analysis. The contents of one subsample from each cricket were examined for the presence of dipteran prey using an indirect ELISA involving a monoclonal antibody reactive to the Order Diptera. Diptera was selected because it occurs in high densities near the soil surface in alfalfa systems (Harwood et al. 2007a). Complete protocols are described in detail in Harwood et al. (2007a) and Harwood (2008). Briefly, following homogenization (above), the gut solution was centrifuged at 8,000 rpm for 15 min, and the supernatant was diluted to a working concentration of 1:20,000 tissue:PBS solution by weight. The gut dilution (200 µL) was coated onto the ELISA plate and incubated overnight at room temperature after which time, the sample was ejected and plate washed 3 times with PBS-Tween 20 (0.05% polyoxyethylene-20 sorbitan monolaurate [Sigma-Aldrich, St. Louis, MO, USA]) and 200 µL of antiDiptera primary antibody (*DrosW-VI-B8* from mouse; diluted in 1X PBS-Tween) coated onto the ELISA plate and incubated for 1 h; PBS-Tween was used in the no-antibody control wells. The primary antibody was then ejected, the plate washed 3 further times with PBS-Tween and ImmunoPure goat antimouse IgG horseradish peroxidase enzyme conjugate (Pierce Protein Products, ThermoFisher Scientific, Rockford, IL, USA) was coated onto all wells of the plate and incubated for 1 h. The conjugated antibody was then removed and the plate was washed 3 times with PBS-Tween. A buffered solution containing *o*-phenylenediamine dihydrochloride (Sigma-Aldrich, St Louis, MO, USA; in citric acid solution, phosphate buffer, H_2O, and H_2O_2) was added to each well for 30 min (in the dark). Finally, a 2.5M H_2SO_4 solution was added to each well to stop the reaction, and the absorbance in each well was read at 490 nm (µQuant, BioTek Instruments Inc., Winooski, VT, USA). On each plate, a no-antibody control was run for each sample, as was an 8-well series of *Graminella nigrifrons* (Forbes) (Hemiptera: Cicadellidae) negative controls and an 8-well series of *Drosophila melanogaster* Meigen (Diptera: Drosophilidae) positive controls. Gut samples were considered positive for Diptera if they contained an absorbance above 3 times the standard deviation of the negative control series (after Hagler and Naranjo 2005, Harwood et al. 2007a).

Data analysis. For all analyses, the years were pooled across treatments unless initial exploratory data analyses revealed significant effects of year on the contrast; the experiment was replicated in different fields in 2007 and 2008 to avoid pseudoreplication. The total number of specimens, total number of facultative granivores (all crickets, *Harpalus* spp., *Amara* spp., *Anisodactylus* spp., and *Stenolophus* spp.), and total numbers of the 6 predominant species (each representing >3% of total specimens) captured per plot were compared between the 2 treatments using separate univariate ANOVAs. For significance testing we set $\alpha = 0.05$, and comparisons for which $P < 0.07$ were considered marginally significant. The season-long, total numbers of insects and of granivorous taxa captured per plot per hour during the 3 diel collection times, and at 24, 48, 72, 96, 120, and 144 h after the onset of monitoring were compared using separate univariate ANOVA. Significantly different means were separated using LSD means separations. A forward stepwise (α to enter or remove = 0.15) discriminant function analysis on the total number of each species collected per replicate ($n = 7$) was used to compare the predator communities collected at 0700, 1500, and 2200 h. Reverse stepwise discriminant analyses were used to determine the similarity of communities collected in the 2 diet treatments, and the communities collected at 24, 48, 72, 96, 120, and 144 h after seed deposition. These two approaches to discriminant function analysis were selected by their relative efficiency for describing optimal models to describe the group differences. For each year and cricket species, independent repeated-measures ANOVA was used to compare the effects of diel period (0700, 1500, or 2200 h) and duration until sample collection on mean gut weight (log transformed), and frequencies of consumption of plant, prey, both foods, or no food per plot. A cricket that consumed both plant and prey foods were scored positive for the categories of "plant", "prey", and "both foods". All analyses were conducted using Systat 11 Software (Richmond, CA, USA).

Results

Community structure. A total of 894 and 4,090 carabids and crickets was collected during 2007 and 2008, respectively. Of these total captures in 2007 and 2008, 85.79 and 66.89% (respectively) were specimens of granivorous taxa. A total of 30 species was captured during the observation periods with 23 species being collected in each of 2007 and 2008. In both years, crickets (*Allonemobius* sp. and *G. pennsylvanicus*) dominated the insect community, accounting for over 60% of total specimens captured (Table 1).

Impact of seed density on granivore population parameters. The total number of specimens (and granivores, when considered alone) captured per treatment was not affected by seed availability (total number of species: $F = 0.001$; df = 1, 12; $P = 0.98$; number of granivores: $F < 0.001$; df = 1, 12; $P = 0.99$). Similarly, the 6 most frequently captured species had similar activity densities in the 2 treatments (*Cyclotrachelus alternans*: $F = 0.04$; df = 1, 12; $P = 0.84$; *Abacidus permundus*: $F = 0.03$; df = 1, 12; $P = 0.87$; *Allonemobius* sp. $F < 0.001$; df = 1, 12; $P = 0.99$; *Gryllus pennsylvanicus*: $F = 0.01$; df = 1, 12; $P = 0.95$; *Harpalus pensylvanicus*: $F = 0.01$; df = 1, 12; $P = 0.92$; *Harpalus herbivagus*: $F = 0.08$; df = 1, 12; $P = 0.78$). Discriminant function analysis revealed a single community found within both treatments (Wilk's $\lambda = 0.50$, $F = 0.09$; df = 1, 12; $P > 0.99$). The eigenvalue for the canonical function used to describe this community was 1.02 and described 100% of the data dispersion. Twelve species were used in the model to distinguish the two communities, and these are noted with the symbol α in Table 1.

Predator communities collected at 0700, 1500, and 2200 h displayed distinct diel patterns, based upon their collection time (Fig. 1) and the numbers of total insects and granivores captured varied over the diel cycle, but only marginally so for the total insects captured (total insects: $F = 2.82$; df = 2, 39; $P = 0.07$; granivores: $F = 4.44$; df = 2, 39; $P = 0.01$). Total insects and total granivores were collected significantly less often at the 0700 h collection time than at the 1500 h collection time; the numbers of total insects and granivores collected at 2200 were similar to the numbers collected at 1500, but were marginally greater than those collected at 0700. Discriminant function analysis generated two descriptive canonical functions, eigenvalues for which were 7.88 and 2.49, and cumulatively they accounted for 76 and 100% of the data dispersion (Wilk's $\lambda = 0.03$, $F = 9.49$; df = 26, 54; $P < 0.001$). Thirteen of the species were included in the model to discriminate these three distinct diel communities

Table 1. Number of specimens (carabids and crickets) captured in pitfall traps during 2007 and 2008 (pooled across treatments and replicates).

Group		Species	Granivorous?	2007	2008	Total
Gryllidae	α, *, β	*Allonemobius* sp.	Y	540	2,100	2,640
	α, *, β	*Gryllus pennsylvanicus* Burmeister	Y	48	1,015	1,063
Carabidae	α,*	*Abacidus permundus* (Say)		69	126	195
		Agonum cupreum Dejean		1	0	1
	*, β	*Agonum cupripenne* (Say)		1	0	1
	*, β	*Agonum placidum* (Say)		1	0	1
		Amara angustata (Say)	Y	0	1	1
	β	*Amara carinata* (LeConte)	Y	11	20	31
	*	*Amara exarata* Dejean	Y	2	1	3
		Amara lunicollis Schiødte	Y	1	0	1
		Amara obesa (Say)	Y	0	1	1
	β	*Amara pennsylvanica* Hayward	Y	0	1	1
		Anisodactylus harrisii LeConte	Y	9	0	9
	α	*Anisodactylus sanctaecrucis* (Fabricius)	Y	4	1	5
	β	*Chlaenius purpuricollis* Randall		0	2	2
		Cicindela punctulata Olivier		0	19	19
	α, β	*Cyclotrachelus alternans* (Casey)		32	537	569
	*	*Cymindis pilosus* Say		1	0	1
	*	*Dicaelus sculptilis upioides* Ball		0	1	1

Table 1. Continued

Group	Species	Granivorous?	2007	2008	Total
	Diplocheila obtusa (LeConte)		2	0	2
*	*Galerita janus* (Fabricius)		0	1	1
	Harpalus compar LeConte	Y	0	2	2
β	*Harpalus faunus* Say	Y	0	9	9
β	*Harpalus herbivagus* Say	Y	128	41	169
α, *	*Harpalus pensylvanicus* (DeGeer)	Y	11	190	201
α, β	*Notiophilus aquaticus* (Linné)		9	1	10
α, *, β	*Poecilus chalcites* (Say)		1	4	5
α	*Poecilus lucublandus* (Say)		5	10	15
	Pterostichus femoralis (Kirby)		1	1	2
α	*Pterostichus melanarius* (Illiger)	Y	1	6	7
α, *	*Scarites quadriceps* Chaudoir		4	0	4
α, *, β	*Stenolophus comma* (Fabricius)	Y	12	0	12

Granivorous taxa are identified based on the literature review of Lundgren (2009). The symbols 'α', '*', and 'β' indicate taxa that were included in the step-wise discriminant models to describe communities in the seed/no-seed treatments, three diel sample periods, and over the 144 h after seed placement, respectively.

(species indicated with the symbol * in Table 1). The first function was useful in establishing the communities collected at 0700 h and 1500 h, and the second function helped to delineate the community collected at 1500 h from that collected at 2200 h (Fig. 1a). Each species clearly had a restricted activity pattern over the diel cycle, and examples of these patterns are presented for the 6 most commonly collected species in Fig. 1b.

The numbers of insects and granivores captured over time differed significantly in both treatments (total insects: $F = 2.74$; df = 5, 78; $P = 0.03$; granivores: $F = 2.78$; df = 5, 78; $P = 0.02$). Specifically, there were significantly more insects captured in the intervals of 48 - 72 and 72 - 96 h after seed deposition than there were between

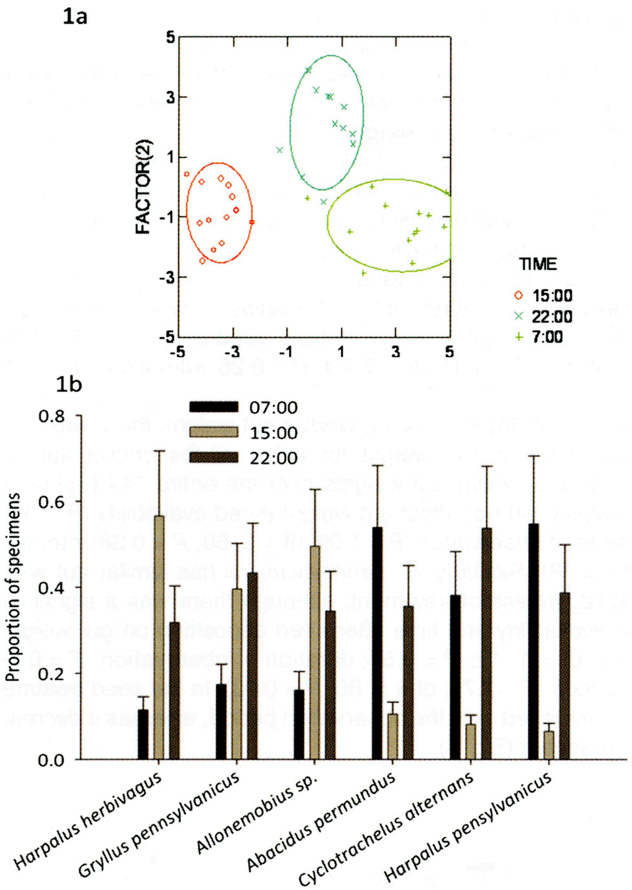

Fig. 1. Insect communities captured during three stages of the diel cycle. (a) Canonical scores plot produced by the Discriminant function analysis of the composition of insect communities captured at 0,700 h, 1500 h, and 2200 h (species included in the model are asterisked in Table 1). 1b) The proportion of each of the 6 most abundant species captured per hour at 0,700 h, 1500 h, and 2200 h that represent the diversity of diel activity patterns observed in this community.

96 - 120 and 120 - 144 h. The total numbers of insects captured during the 0 - 24 and 24 - 48 h observation cycles were intermediate between the other periods. Discriminant function analysis revealed significant changes in the community structure of carabids and crickets over time (Wilk's $\lambda = 0.02$, $F = 1.96$; df = 70, 113; $P < 0.001$). The eigenvalues for the two most descriptive canonical functions used to discriminate these communities were 6.06 and 1.54 and described a cumulative 70 and 88% of the data dispersion, respectively. The first canonical function was used to separate the communities captured 72 and 96 h after seed deposition from the communities

captured at 48, 120, and 144 h. The second canonical function separated the communities captured 24 and 48 h after seed deposition from the communities captured at the remaining times. Fourteen species were used in the model to distinguish the communities, and these are noted with the symbol β in Table 1.

Gut content analyses - gut weight. Time of day had a significant effect on gut weight in *G. pennsylvanicus*, but not *Allonemobius* sp., and seed availability did not affect mean gut weight in either cricket species. These analyses revealed that *G. pennsylvanicus* had significantly heavier guts at the 2200 h collection period, and the lowest in the morning (seed availability: $F = 1.85$; df = 1, 12; $P = 0.20$; time of day: $F = 8.30$; df = 2, 24; $P < 0.01$; interaction: $F = 0.65$; df = 2, 24; $P = 0.53$) (Fig. 2). In contrast, there were no significant relationships between seed availability or time of day and mean gut weight of *Allonemobius* (seed availability: $F = 0.53$; df = 1, 12; $P = 0.48$; time of day: $F = 1.41$; df = 2, 24; $P = 0.26$; interaction: $F = 0.11$; df = 2, 24; $P = 0.89$).

Despite the time of day influencing *Gryllus* gut weight, there was no effect of time after seed deposition on gut weight for either of the cricket species examined. *Allonemobius* sp. had similar gut weights over the entire 144 h observation period, and seed availability did not affect gut weight (seed availability: $F = 0.85$; df = 1, 12; $P = 0.38$; duration of observation: $F = 1.09$; df = 5, 60; $P = 0.38$; interaction: $F = 0.49$; df = 5, 60; $P = 0.78$). Similarly, *G. pennsylvanicus* has similar gut weights over the sample period regardless of treatment, although there was a significant interaction between seed availability and time after seed deposition on gut weight (seed availability: $F = 0.34$; df = 1, 12; $P = 0.58$; duration of observation: $F = 0.64$; df = 5, 60; $P = 0.67$; interaction: $F = 2.79$; df = 5, 60; $P = 0.03$). In the seed treatment, mean gut weight per plot increased over the observation period, whereas it decreased over time in the control treatment (Fig. 3).

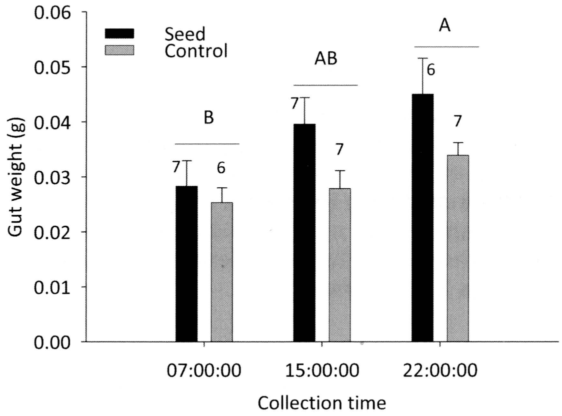

Fig. 2. Cricket gut weights over the diel cycle. Mean (SEM) gut weights of *Gryllus pennsylvanicus* per experimental field at 3 times over the diel cycle. Letters above each group of bars indicate significant differences among the 3 time periods (data pooled across treatments; $\alpha = 0.05$; LSD means separations), and the sample size is noted near the apex of each bar.

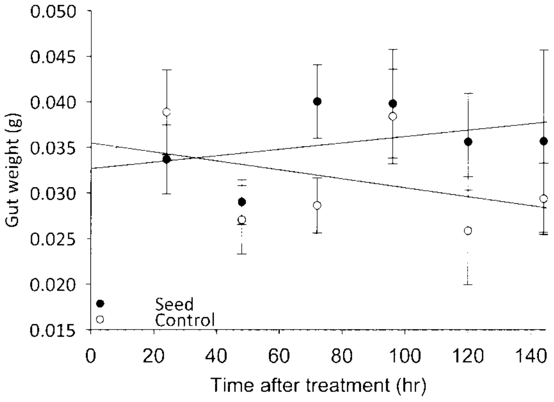

Fig. 3. Cricket gut weights after exposure to seeds. Mean (SEM) gut weights of *Gryllus pennsylvanicus* per experimental field measured at six intervals over a 144-h period following infestation with foxtail seeds.

Footnote: Lines represent linear regressions ($y_{seed} = 0.033 + 3.52x$, $r^2 = 0.15$; $y_{control} = 0.035 - 4.92x$, $r^2 = 0.15$), and there was a significant interaction between treatment and time on mean gut weights.

Gut content analyses - microscopic gut-content analyses. There was no effect of time of day on the types of food found within either cricket species. *Allonemobius* sp. had similar gut contents regardless of time of day or seed availability (ANY FOOD, seed availability: $F = 3.06$; df = 1, 12; $P = 0.11$; time of day: $F = 0.98$; df = 2, 24; $P = 0.39$; interaction: $F = 0.47$; df = 2, 24; $P = 0.63$; PREY ONLY, seed availability: $F = 1.07$; df = 1, 12; $P = 0.32$; time of day: $F = 0.36$; df = 2, 24; $P = 0.32$; interaction: $F = 1.91$; df = 2, 24; $P = 0.17$; PLANT ONLY, seed availability: $F = 0.34$; df = 1, 12; $P = 0.57$; time of day: $F = 1.79$; df = 2, 24; $P = 0.19$; interaction: $F = 1.17$; df = 2, 24; $P = 0.33$; BOTH FOOD CLASSES, seed availability: $F = 1.28$; df = 1, 12; $P = 0.28$; time of day: $F = 2.38$; df = 2, 24; $P = 0.11$; interaction: $F = 0.92$; df = 2, 24; $P = 0.41$). For *Allonemobius* sp. (pooled across treatments), 68.06 ± 2.89% (mean ± SEM) of specimens had food in their guts, 57.77 ± 4.14% had prey only, 31.40 ± 2.14% had only plant material, and 21.09 ± 1.59% had both foods.

Gryllus pennsylvanicus had similar gut contents regardless of time of day, but a greater proportion had plant material (marginally so) and both foods in their guts in the seed treatment than in the untreated control (ANY FOOD, seed availability: $F = 0.04$; df = 1, 10; $P = 0.84$; time of day: $F = 1.64$; df = 2, 20; $P = 0.22$, interaction: $F = 1.93$; df = 2, 20; $P = 0.17$; PREY ONLY, seed availability: $F = 0.76$; df = 1, 10; $P = 0.40$; time of day: $F = 1.75$; df = 2, 20; $P = 0.20$; interaction: $F = 0.56$; df = 2, 20; $P = 0.58$; PLANT ONLY, seed availability: $F = 4.71$; df = 1, 10; $P = 0.055$; time of day: $F = 0.33$; df = 2, 20; $P = 0.73$, interaction: $F = 0.75$; df = 2, 20; $P = 0.49$; BOTH FOODS, seed availability: $F = 5.26$; df = 1, 10; $P = 0.045$; time of day: $F = 0.007$; df = 2, 20; $P = 0.99$, interaction: $F = 1.23$; df = 2, 20; $P = 0.31$) (Fig. 4).

Allonemobius sp. gut contents changed over the 144 h period following seed deposition, but was unaffected by seed availability. The proportion of *Allonemobius* sp. that had either food class in their guts diminished over the observation period

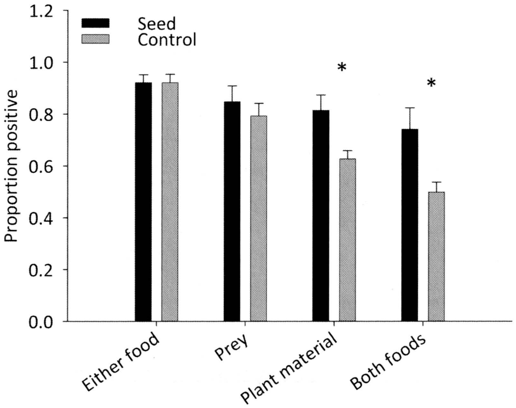

Fig. 4. Frequency of plant and prey consumption by crickets.

Footnote: Mean (SEM) proportion of *Gryllus pennsylvanicus* that consumed various diets in fields where seed densities were augmented (versus untreated fields; determined by microscopic gut content analysis). Asterisks indicate significant differences between treatments ($\alpha = 0.05$).

(they consumed food less often as the experiment progressed) (seed availability: $F = 0.20$; df = 1, 12; $P = 0.66$; duration of observation: $F = 2.57$; df = 5, 60; $P = 0.04$; interaction: $F = 2.14$; df = 5, 60; $P = 0.073$). But, the proportions that had only prey (seed availability: $F = 0.02$; df = 1, 12; $P = 0.89$; duration of observation: $F = 1.20$; df = 5, 60; $P = 0.32$; interaction: $F = 1.67$; df = 5, 60; $P = 0.16$), only plant material (seed availability: $F = 0.77$; df = 1, 12; $P = 0.40$; duration of observation: $F = 1.61$; df = 5, 60; $P = 0.17$; interaction: $F = 0.70$; df = 5, 60; $P = 0.62$), or both foods together (seed availability: $F = 1.48$; df = 1, 12; $P = 0.25$; duration of observation: $F = 1.41$; df = 5, 60; $P = 0.24$; interaction: $F = 0.95$; df = 5, 60; $P = 0.46$) in their guts was unaffected by the time of collection after seed augmentation.

Gryllus pennsylvanicus gut contents were affected by seed availability (Fig. 4), but did not change over the 144 h period after seeds were deposited. Seed availability marginally increased the proportion of *G. pennsylvanicus* that had plant material and both foods together in their guts (PLANTS ONLY, seed availability: $F = 5.62$; df = 1, 60; $P = 0.055$; duration of observation: $F = 0.41$; df = 5, 30; $P = 0.84$; interaction: $F = 0.60$; df = 5, 30; $P = 0.70$; BOTH FOODS, seed availability: $F = 5.50$; df = 1, 6; $P = 0.057$; duration of observation: $F = 0.09$; df = 5, 30; $P = 0.99$; interaction: $F = 0.62$; df = 5, 30; $P = 0.69$). Despite these differences, the proportion of *G. pennsylvanicus* that had neither food, nor prey only, in their guts was unaffected by seed availability (ANY FOOD, seed availability: $F = 1.89$; df = 1, 6; $P = 0.22$; duration of observation: $F = 1.26$; df =5, 30; $P = 0.31$; interaction: $F = 0.98$; df = 5, 30; $P = 0.45$; PREY ONLY, seed availability: $F = 0.88$; df = 1, 6; $P = 0.39$; duration of observation: $F = 1.48$; df = 5, 30; $P = 0.23$; interaction: $F = 1.16$; df = 5, 30; $P = 0.35$).

Gut content analyses - monoclonal antibody-based gut-content analysis. In the 1270 crickets we analyzed, only 13 contained Diptera antigen in their guts. Nine of these positives were *Allonemobius* sp., and 4 were *G. pennsylvanicus*. Only 4 of the positives were found in the plots with augmented seed densities; all but 3 of the positive crickets were collected at 1500 h. Mean absorbance of positive crickets was 0.13 ± 0.05.

Discussion

Although the short-term composition and abundance of this diverse insect community was not affected by local seed availability, at least one prominent facultatively granivorous member of this community shifted their feeding behavior toward plant-based foods when seeds became available. Such patterns of dietary selection, therefore, have implications for the dynamics of these food webs and the relative strength of trophic linkages in complex food webs. Moreover, members of the diverse granivore community displayed distinct diel activity and feeding patterns. Such mechanisms likely contribute to the ability of soil systems to maintain species-rich assemblages within spatially simple habitats.

Individual members of soil arthropod communities, especially those such as carabids and crickets that function at the interface between above- and below-ground systems are well-adapted to living within diverse and complex food webs in part by restricting their activity and feeding behaviors to certain periods in the diel cycle (Brust et al. 1986, Erikstad 1989, Allard and Yeargan 2005, Lundgren et al. 2006, Lundgren et al. 2009b, Romero and Harwood 2010). Not surprisingly, distinct insect communities were captured at 0700, 1500, and 2200 h within our system (Figs. 1a, 2). For *G. pennsylvanicus,* these activity patterns also were correlated with distinct differences in gut contents, such that insects had the heaviest (and presumably fullest) guts when they were most active (Figs. 1b, 2). The activity patterns observed for this cricket were similar to those previously reported (Lundgren et al. 2009b). In contrast, *Allonemobius* sp. gut contents were largely unaffected by diel period, which suggests that this species either digests food more slowly than *G. pennsylvanicus* or that they consume food throughout the diel cycle. This level of partitioning of the diel cycle enables species that use the same habitat and/or food to reduce direct competition for resources within this spatially simple, epigeal habitat. It also leads to a form of community symmetry (sensu Park 1941) throughout a 24 h period that is seldom experienced in more disturbed habitats (e.g., agroecosystems; Brust et al. 1986, Chapman and Armstrong 1997, Lundgren et al. 2006). It is theorized that members of each sympatric but temporally segregated community fulfill key functional roles, such that there is redundancy or symmetry in the ecological services provided by insect communities throughout the diel cycle (Park 1941). Understanding when individual members of diverse soil-dwelling communities feed and are active ultimately provides a clearer understanding of how these complex animal communities have evolved and how food webs function within spatially simple habitats.

Although both cricket species are considered facultatively granivorous, gut-content analysis revealed that the 2 sympatric crickets in this study varied in the frequency that they had prey and plant-based foods in their guts. The gut contents of the most prominent cricket, *Allonemobius* sp., was typically unaffected by seed availability, and this species relied less frequently on plant foods than *G. pennsylvanicus.* Only one-third of *Allonemobius* sp. specimens had plant-based foods in their stomachs, versus approx. 85.00% of *G. pennsylvanicus.* Also, nearly all *G. pennsylvanicus* had prey remnants in their stomachs (often identifiable as ant parts; Fig. 4), versus only 57.77 ± 4.14% (mean ± SEM) of *Allonemobius* sp., which suggests that *G. pennsylvanicus* consumes food more frequently, irrespective of whether it is plant or prey in nature. Thus, based upon these results, it is possible to conclude that *G. pennsylvanicus* is an important granivore and predator of insect prey, and is predisposed to more heavily use seeds as a food resource than *Allonemobius* sp. when such items become available. These results echo those found with carabid beetles by Frank et al. (2011). Previous work has shown that *G. pennsylvanicus* populations are well correlated with seed removal rates under field conditions (Davis and Liebman 2003, O'Rourke et al. 2006), supporting the conclusion presented here pertaining to the importance of granivory to this species life history. A surprising result from our research is that the Diptera immunoassay detected almost no predation on this abundant source of prey in alfalfa systems; whereas, smaller predators (e.g., linyphiids; [Harwood et al. 2004]) frequently rely on small flies as a part of their diet. Dietary specialization of this nature may further allow diverse predator communities to coexist sympatrically. Finally, microscopic gut-content analysis revealed a much higher frequency of feeding detection in field-collected specimens than is often revealed in more directed prey-specific antibody-based (Bohan et al. 2000, Harwood et al. 2004, Hagler and Naranjo 2005, Hagler 2006, Thomas et al. 2009) or PCR-based gut-content analysis (Harwood et al. 2007b, Juen and Traugott 2007, Harwood et al. 2009, Lundgren et al. 2009a). Such information clearly demonstrates the value of this often overlooked tool, and how it can be useful for describing broad (and sometimes specific) dietary patterns in animals, and especially insects (Weber and Lundgren 2009).

Providing nonprey foods to facultatively omnivorous insects may alter their feeding behavior, but does not necessarily cause dietary shifting away from consuming insect prey under natural conditions. A recent study conducted in freshwater aquatic systems showed that ontogenetically increasing levels of true omnivory (with algae as the nonprey food) did not accompany reduced frequencies of predation in trichopterans (Lancaster et al. 2005). Similarly, the microscopic gut-content analysis presented here revealed that *G. pennsylvanicus* ate plant-based foods and mixed meals more frequently when seeds were available (Fig. 4). Moreover, their guts became significantly heavier in the seed treatment over the 144 h after seeds were deposited (Fig. 3). This indicates that these species were eating more food when seeds were available and were, therefore, opportunistically utilizing the sheer abundance of nonprey food items available at this time. Other research also suggests that biodiversity, and the diverse food resources that often accompany it, functions as a source for natural suppression of insect pests, rather than distracting them from consuming prey (McMurtry and Scriven 1966, Eubanks and Denno 1999, 2000, van Rijn et al. 2002, Lundgren 2009). Whereas many predators respond to prey scarcity by actively moving to areas of greater food availability, many other species are adapted to surviving within a suitable habitat when food resources are scarce, and are thus able to quickly exploit spatially and temporally sporadic foods as they are encountered. The importance of understanding how omnivorous animals balance their nutritional needs between prey and nonprey food sources is a complex question that is essential to understanding how food webs function. Our research suggests that at least some omnivorous insects (e.g., *G. pennsylvanicus*) are able to exploit nonprey food resources without consuming prey-based foods less frequently.

Acknowledgments

The authors thank Janet Fergen for supervising this project and conducting the immunoassays; Carson Dinger, Mallory Johnson, and Lucia Pilorget for providing technical assistance;

and Ricardo Bessin and Paula Westerman for reviewing earlier drafts of this manuscript. Mention of any proprietary products does not constitute endorsement by the USDA. James Harwood is supported by the University of Kentucky Agricultural Experiment Station State Project KY008043. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

References Cited

Acorn, J. H. and G. E. Ball. 1991. The mandibles of some adult ground beetles: structure, function, and the evolution of herbivory (Coleoptera: Carabidae). Can. J. Zool. 69: 638-650.

Allard, C. M. and K. V. Yeargan. 2005. Diel activity patterns and microspatial distribution of the harvestman *Phalangium opilio* in soybeans. J. Arachnol. 33: 745-752.

Azcarate, F. M., L. Arqueros, A. M. Sanchez and B. Peco. 2005. Seed and fruit selection by harvester ants, *Messor barbarus*, in Mediterranean grassland and scrubland. Funct. Ecol. 19: 273-283.

Beckerman, A. P., O. L. Petchey and P. H. Warren. 2006. Foraging biology predicts food web complexity. Proc. Natl. Acad. Sci. USA 103: 13745-13749.

Bewley, J. D. and M. Black. 1994. Seeds: Physiology of Development and Germination. Plenum Press, New York, NY.

Blüthgen, N., J. Fründ, D. P. Vazquez and F. Menzel. 2008. What do interaction network metrics tell us about specialization and biological traits? Ecology 89: 3387-3399.

Bohan, D. A., A. C. Bohan, D. M. Glen, W. O. C. Symondson, C. W. Wiltshire and L. Hughes. 2000. Spatial dynamics of predation by carabid beetles on slugs. J. Anim. Ecol. 69: 367-379.

Briese, D. T. and B. J. Macauley. 1981. Food collection within an ant community in semi-arid Australia, with special reference to seed harvesters. Aust. J. Ecol. 6: 1-19.

Brown, J. L., O. J. Reichman and D. W. Davidson. 1979. Granivory in desert systems. Annu. Rev. Ecol. Syst. 10: 201-227.

Brust, G. E. and G. J. House. 1988. Weed seed destruction by arthropods and rodents in low-input soybean agroecosystems. Am. J. Altern. Agric. 3: 19-25.

Brust, G. E., B. R. Stinner and D. A. McCartney. 1986. Predator activity and predation in corn agroecosystems. Environ. Entomol. 15: 1017-1021.

Chapman, P. A. and G. Armstrong. 1997. Design and use of a time-sorting pitfall trap for predatory arthropods. Agric. Ecosyst. Environ. 65: 15-21.

Coll, M. 2009. Foreword: Feeding on Non-prey Resources by Natural Enemies., Pg. ix-xxii. *In* J. G. Lundgren, Relationships of Natural Enemies and Non-prey Foods. Springer Publishing, Heidelberg, Germany.

Coll, M. and M. Guershon. 2002. Omnivory in terrestrial arthropods: mixing plant and prey diets. Annu. Rev. Entomol. 47: 267-297.

Crawley, M. J. 2000. Seed predators and plant population dynamics., Pg. 167-182. *In* M. Fenner [ed.], Seeds: The Ecology of Regeneration in Plant Communities., 2nd ed. CABI Publishing, Oxon, UK.

Davis, A. S. and M. Liebman. 2003. Cropping system effects on giant foxtail (*Setaria faberi*) demography: I. Green manure and tillage timing. Weed Sci. 51: 919-929.

Doring, T. F., A. Hiller, S. Wehke, G. Schulte and G. Broll. 2003. Biotic indicators of carabid species richness on organically and conventionally managed arable fields. Agric. Ecosyst. Environ. 98: 133-139.

Egerton, F. N. 2007. Understanding Food Chains and Food Webs, 1700–1970. Bull. Ecol. Soc. Am. 88: 50-69.

Ellsbury, M. M., J. E. Powell, F. Forcella, W. D. Woodson, S. A. Clay and W. E. Riedell. 1998. Diversity and dominant species of ground beetle assemblages (Coleoptera: Carabidae) in crop rotation and chemical input systems for the northern great plains. Ann. Entomol. Soc. Am. 91: 619-625.

Elton, C. 1927. Animal Ecology. Sidgwick and Jackson, London, UK.

Erikstad, K. E. 1989. The diel activity of carabid beetles (Coleoptera) north of the Arctic circle, with particular reference to *Patrobus assimilis* Chaud. and *Notiophilus aquaticus* L. Polar Biol. 9: 319-323.

Eubanks, M. D. and R. F. Denno. 1999. The ecological consequences of variation in plants and prey for an omnivorous insect. Ecology 80: 1253-1266.

2000. Host plants mediate omnivore-herbivore interactions and influence prey suppression. Ecology 81: 936-947.

Eubanks, M. D. and J. D. Styrsky. 2005. Effects of plant feeding on the performance of omnivorous "predators". Pg. 148-177. *In* F. L. Wäckers, P. C. J. van Rijn and J. Bruin [eds.], Plant Provided Foods for Carnivorous Insects. Cambridge University Press, Cambridge, UK.

Forbes, S. A. 1883. The food relations of the Carabidae and Coccinellidae. Bull. Ill. St. Lab. Nat. Hist. 3: 33-64.

Forcella, F., R. G. Wilson, K. A. Renner, J. Dekker, R. G. Harvey, D. A. Alm, D. D. Buhler and J. Cardina. 1992. Weed seedbanks of the U. S. corn belt: magnitude, variation, emergence, and application. Weed Sci. 40: 636-644.

Forsythe, T. G. 1983. Mouthparts and feeding of certain ground beetles (Coleoptera: Carabidae). Zool. J. Linn. Soc. 79: 319-376.

Frank, S. D., P. M. Shrewsbury and R. F. Denno. 2011. Plant versus prey resources: Influences on omnivore behavior and herbivore suppression. Biol. Control 57: 229-235.

French, B. W. and N. C. Elliott. 1999. Temporal and spatial distribution of ground beetle (Coleoptera:Carabidae) assemblages in grasslands and adjacent wheat fields. Pedobiologia (Jena) 43: 73-84.

Gandhi, K. J. K., D. W. Gilmore, S. A. Katovich, W. J. Mattson, J. C. Zasada and S. J. Seybold. 2008. Catastrophic windstorm and fuel-reduction treatments alter ground beetle (Coleoptera: Carabidae) assemblages in a North American sub-boreal forest. For. Ecol. Manage. 256: 1104-1123.

Hagler, J. R. 2006. Development of an immunological technique for identifying multiple predator-prey interactions in a complex arthropod assemblage. Ann. Appl. Biol. 149: 153-165.

Hagler, J. R. and S. E. Naranjo. 2005. Use of a gut content ELISA to detect whitefly predator feeding activity after Þeld exposure to different insecticide treatments. Biocontrol Sci. Technol. 15: 321-339.

Hairston, N. G., F. E. Smith and L. B. Slobodkin. 1960. Community structure, population control, and competition. Am. Nat. 94: 421-425.

Harper, J. L. 1977. Population Biology of Plants. Academic Press Inc., London, UK.

Harwood, J. D. 2008. Are sweep net sampling and pitfall trapping compatible with molecular analysis of predation? Environ. Entomol. 37: 990-995.

Harwood, J. D., K. D. Sunderland and W. O. C. Symondson. 2004. Prey selection by linyphiid spiders: molecular tracking of the effects of alternative prey on rates of aphid consumption in the field. Mol. Ecol. 13: 3549-3560.

Harwood, J. D., M. R. Bostrom, E. E. Hladilek, D. H. Wise and J. J. Obrycki. 2007a. An order-specific monoclonal antibody to Diptera reveals the impact of alternative prey on spider feeding behavior in a complex food web. Biol. Control 41: 397-407.

Harwood, J. D., H. J. S. Yoo, D. L. Rowley, M. H. Greenstone and R. J. O' Neil. 2009. Differential impact of adults and nymphs of a generalist predator on an exotic invasive pest demonstrated by molecular gut-content analysis. Biol. Invasions 11: 895-903.

Harwood, J. D., N. Desneux, H. J. S. Yoo, D. L. Rowley, M. H. Greenstone, J. J. Obrycki and R. J. O' Neil. 2007b. Tracking the role of alternative prey in soybean aphid predation by *Orius insidiosus*: a molecular approach. Mol. Ecol. 16: 4390-4400.

Havens, K. E., L. A. Bull, G. L. Warren, T. L. Crisman, E. J. Phlips and J. P. Smith. 1996. Food web structure in a subtropical lake ecosystem. Oikos 75: 20-32.

Heggenstaller, A., F. D. Menalled, M. Liebman and P. R. Westerman. 2006. Seasonal patterns in post-dispersal seed predation of *Abutilon theophrasti* and *Setaria faberi* in three cropping systems. J. Appl. Ecol. 43: 999-1010.

Honěk, A., Z. Martinkova and V. Jarosik. 2003. Ground beetles (Carabidae) as seed predators. Eur. J. Entomol. 100: 531-544.

Honěk, A., Z. Martinkova and P. Saska. 2005. Post-dispersal predation of *Taraxacum officinale* (dandelion) seed. J. Ecol. 93: 345-352.

Hulme, P. E. 2002. Seed-eaters: seed dispersal, destruction and demography, Pg. 257-274. *In* D. J. Levey, W. R. Silva and M. Galetti [eds.], Seed Dispersal and Frugivory: Ecology, Evolution, and Conservation. CAB International, Oxon, UK.

Hunter, M. D. 2009. Trophic promiscuity, intraguild predation and the problem of omnivores. Agric. For. Entomol. 11: 125-131.

Jervis, M. A. and G. E. Heimpel. 2005. Phytophagy, Pg. 525-550. *In* M. A. Jervis [ed.], Insects as Natural Enemies. Springer, Heidelberg, Germany.

Johnson, N. E. and R. S. Cameron. 1969. Phytophagous ground beetles. Ann. Entomol. Soc. Am. 62: 909-914.

Juen, A. and M. Traugott. 2007. Revealing species-specific trophic links in soil food webs: molecular identification of scarab predators. Mol. Ecol. 16: 1545-1557.

Kegode, G. O., F. Forcella and S. Clay. 1999. Influence of crop rotation, tillage, and management inputs on weed seed production. Weed Sci. 47: 175-183.

Kirk, V. M. 1971. Ground beetles in cropland in South Dakota. Ann. Entomol. Soc. Am. 64: 238-241.

1973. Biology of a ground beetle, *Harpalus pensylvanicus.* Ann. Entomol. Soc. Am. 66: 513-518.

Lancaster, J., D. C. Bradley, A. Hogan and S. Waldron. 2005. Intraguild omnivory in predatory stream insects. J. Anim. Ecol. 74: 619-629.

Luff, M. L. 1975. Some features influencing the efficiency of pitfall traps. Oecologia 19: 345-357.

Lundgren, J. G. 2009. Relationships of Natural Enemies and Non-prey Foods. Springer Publishers, Heidelberg, Germany.

Lundgren, J. G. and K. A. Rosentrater. 2007. The strength of seeds and their destruction by granivorous insects. Arthropod-Plant Interact. 1: 93-99.

Lundgren, J. G. and J. K. Fergen. 2010. The effects of a winter cover crop on *Diabrotica virgifera* (Coleoptera: Chrysomelidae) populations and beneficial arthropod communities in no-till maize. Environ. Entomol. 39: 1816-1828.

Lundgren, J. G., A. A. Razzak and R. N. Wiedenmann. 2004. Population responses and food consumption by predators *Coleomegilla maculata* and *Harmonia axyridis* (Coleoptera: Coccinellidae) during anthesis in an Illinois cornfield. Environ. Entomol. 33: 958-963.

Lundgren, J. G., D. A. Prischmann and M. M. Ellsbury. 2009a. Analysis of the predator community of a subterranean herbivorous insect based on polymerase chain reaction. Ecol. Appl. 19: 2157-2166.

Lundgren, J. G., J. T. Shaw, E. R. Zaborski and C. E. Eastman. 2006. The influence of organic transition systems on beneficial ground-dwelling arthropods and predation of insects and weed seeds. Renew. Agric. Food Syst. 21: 227-237.

Lundgren, J. G., S. Nichols, D. A. Prischmann and M. M. Ellsbury. 2009b. Seasonal and diel activity patterns of generalist predators associated with *Diabrotica virgifera* immatures (Coleoptera: Chrysomelidae). Biocontrol Sci. Technol. 19: 327-333.

MacMahon, J. A., J. F. Mull and T. O. Crist. 2000. Harvester ants (*Pogonomyrmex* spp.): Their community and ecosystem influences. Annu. Rev. Ecol. Syst. 31: 265-291.

McCann, K. and A. Hastings. 1997. Re-evaluating the omnivory- stability relationship in food webs. Proc. Biol. Sci. 264: 1249-1254.

McMurtry, J. A. and G. T. Scriven. 1966. The influence of pollen and prey density on the number of prey consumed by *Amblyseius hibisci* (Acarina: Phytoseiidae). Ann. Entomol. Soc. Am. 59: 147-149.

Musser, F. R. and A. M. Shelton. 2003. Predation of *Ostrinia nubilalis* (Lepidoptera: Crambidae) eggs in sweet corn by generalist predators and the impact of alternative foods. Environ. Entomol. 32: 1131-1138.

O'Rourke, M. E., A. H. Heggenstaller, M. Liebman and M. E. Rice. 2006. Post-dispersal weed seed predation by invertebrates in conventional and low-external-input crop rotation systems. Agric. Ecosyst. Environ. 116: 280-288.

Park, O. 1941. Concerning community symmetry. Ecology 22: 164-167.

Pimm, S. L. and J. H. Lawton. 1978. On feeding on more than one trophic level. Nature 275: 542-544.

Polis, G. A. 1991. Complex trophic interactions in deserts: an empirical critique of food-web theory. Am. Nat. 138: 123-155.

Rainio, J. and J. Niemelä. 2003. Ground beetles (Coleoptera: Carabidae) as bioindicators. Biodivers. Conserv. 12: 487-506.

Romero, S. A. and J. D. Harwood. 2010. Diel and seasonal patterns of prey available to epigeal predators: Evidence for food limitation in a linyphiid spider community. Biol. Control 52: 84-90.

Sabelis, M. W. and P. C. J. Van Rijn. 2005. When does alternative food promote biological pest control? Pg. 428-437. *In* M. S. Hoddle [ed.], International Symposium on Biological Control of Arthropods. United States Department of Agriculture, Forest Service, Morgantown, WV, Davos, Switzerland.

Tevis, L. J. 1958. Interrelations between the harvestor ant *Veromessor pergandei* (Mayr) and some desert ephemerals. Ecology 39: 695-704.

Thomas, R. S., J. D. Harwood, D. M. Glen and W. O. C. Symondson. 2009. Tracking predator density dependence and subterranean predation by carabid larvae on slugs using monoclonal antibodies. Ecol. Entomol. 34: 569-579.

Thompson, R. M., M. Hemberg, B. M. Starzomski and J. B. Shurin. 2007. Trophic levels and trophic tangles: The prevalence of omnivory in real food webs. Ecology 88: 612-617.

van Rijn, P. C. J., Y. M. van Houten and M. W. Sabelis. 2002. How plants benefit from providing food to predators even when it is also edible to herbivores. Ecology 83: 2664-2679.

Wäckers, F. L. 2005. Suitability of (extra-)floral nectar, pollen, and honeydew as insect food sources., Pg. 17-74. *In* F. L. Wäckers, P. C. J. van Rijn and J. Bruin [eds.], Plant-provided Food for Carnivorous Insects. Cambridge University Press, Cambridge, UK.

Weber, D. C. and J. G. Lundgren. 2009. Assessing the trophic ecology of the Coccinellidae: Their roles as predators and prey. Biol. Control 51: 199-214.

Weber, D. C., R. S. Pfannenstiel and J. G. Lundgren. 2009. Diel predation pattern assessment and exploitation of sentinel prey: new interpretations of community & individual behaviors., Proceedings of the Third ISBCA, Christchurch, New Zealand.

Westerman, P. R., A. Hofman, L. E. M. Vet and W. van der Werf. 2003. Relative importance of vertebrates and invertebrates in epigeaic weed seed predation in organic cereal fields. Agric. Ecosyst. Environ. 95: 417-425.

Zhavoronkova, T. N. 1969. Certain structural peculiarities of the Carabidae (Coleoptera) in relation to their feeding habits. Entomol. Rev. (Engl. Transl.) 48: 462-471.