

ABSTRACT

Title of Dissertation: CONSEQUENCES OF OMNIVORY AND
ALTERNATIVE FOOD RESOURCES ON
THE STRENGTH OF TROPHIC CASCADES

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Omnivorous predators that feed on prey and plant resources are recognized as an important component of food webs but their impact on herbivore populations and trophic dynamics is unpredictable. Feeding on food items from multiple trophic levels increases the reticulate nature of food webs and the labile role of omnivores in promoting trophic cascades. Using carabid beetles in a corn agroecosystem, this research explored the interactive effects of predator guild (omnivore or carnivore) and the trophic origin of alternative food resources (seeds or fly pupae) on the control of herbivores (black cutworms) and plant survival. I demonstrated that the trophic guild and feeding performance of carabids can be predicted from their mandibular morphology. Carnivorous carabids, using mandibles with sharp points and a long

shearing edge, kill and consume caterpillars more efficiently than omnivores that have mandibles with wide molar areas adapted for consuming prey and seeds. Omnivore preference for seeds and pupae further reduced their consumption of cutworms, which resulted in increased plant damage, ultimately dampening trophic cascades.

In open field plots the abundance of omnivorous carabids and ants increased in response to seed but not pupae whereas neither subsidy affected the abundance of carnivorous predators. Pupae subsidies reduced predation of cutworms by carnivores and omnivores, consequently reducing seedling survival. However, in seed subsidized plots omnivorous predators switched from seeds to higher quality cutworm prey. Thus, predation of cutworms increased with cascading positive effects for seedlings.

This research demonstrated that omnivorous carabids interacted more strongly with alternative food resources, particularly seeds, than carnivores. In addition, this difference can be linked to morphological differences that reduced omnivore efficiency as predators suggesting omnivores may be less effective agents of biological control. However, increased tenure time and aggregation to plant resources by omnivores helped restore trophic cascades, and should enhance biological control. Understanding the predacious behavior of omnivores in resource diverse environments is essential to predicting their role in trophic dynamics. I provide evidence that the trophic origin of alternative food drives the strength of this interaction and the extent to which omnivores promote trophic cascades.

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ON THE STRENGTH OF TROPHIC CASCADES

By

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Chapter 1: Mandibular morphology predicts trophic guild and feeding performance in predacious carabid beetles

Abstract

Omnivorous predators, those that feed on prey and plant resources, and carnivores can impose very different dynamics on food-web interactions. Consumers feeding on an array of food items from multiple trophic levels increase the reticulate nature of species interactions and can contribute more to food-web stability than consumers simply feeding from one trophic level. Thus, to predict the trophic position of the dominant players in food webs without conducting a multitude of laborious feeding experiments could be of great interest from both basic and applied perspectives. The morphology of feeding apparatus, because it dictates the efficiency with which food items are captured and handled, could be a useful tool in identifying the trophic position and potential impact of various consumers in complex food webs. This research documents quantifiable differences in the mandibular morphology of omnivorous versus carnivorous carabid beetles, a diverse group of consumers that occur in a multitude of habitats. In general, carnivorous species had mandibles with a sharper-tip and longer shearing edge than omnivorous species. Whereas, omnivores have mandibles with dull tips and wide molars. These differences in mandubular morphology contribute highly to inter-guild differences in the handling time of passive and active herbivorous caterpillars. Thus carnivorous species required fewer attacks to capture, less time to kill, and less time to consume both active and passive

prey than omnivorous carabids adapted to consume seeds and prey. Differences in food preference was directly related to differences in handling efficiency where foods or prey that were easier to capture or consume were preferred in choice arenas. This research identifies functionally significant morphological differences in the mandibles of carnivorous and omnivorous carabids. These differences influence which food resources they efficiently capture and handle and therefore prefer. Due to their reduced efficiency in handling herbivore prey, omnivorous carabids should have relatively less impact on herbivore populations than carnivorous species that capture, kill and handle these prey items more efficiently.

Introduction

Omnivory, feeding at more than one trophic level, is commonplace in natural and managed systems (Polis and Strong 1996; Rosenheim 1995, 1998; Cooper and Vitt 2002; Coll and Guershon 2002; Eubanks 2005). Although, ecologists agree that omnivory is widespread in many systems, its impact on food web dynamics is often unpredictable (Polis et al. 1989; Polis and Strong 1996; Coll and Guershon 2002; Eubanks 2005). Omnivorous consumers that feed from multiple trophic levels often impose less top-down control on herbivores populations, but not always (Chesson 1989; Dennis et al. 1991; Lucas et al. 1998; Cottrel and Yeargan 1998; Eubanks and Denno 1999, 2000a; Musser and Shelton 2003). The variable and context-dependent response of omnivorous predators to multiple resources has spurred debate about their role in suppressing herbivore populations (Agrawal et al. 1999; Agrawal and Klein 2000; Diehl and Feiel 2000; Eubanks 2000a; Snyder and Ives 2001; Snyder and Wise 2001; Finke and Denno 2002, 2005; Bruno and O’Connor 2005).

True omnivory (*sensu* Coll and Guershon 2002; “true omnivores” and “true omnivory” hereafter will be referred to as omnivores and omnivory, respectively), consuming plant and prey resources, represents versatility in resource use. This varied feeding strategy requires adaptations to an organism’s mouth parts, digestive system, and other physiological traits (Cohen 1990, 1996; Coll and Guershon 2000; Cooper and Vitt 2002; Eubanks et al. 2003; Christiansen and Wroe 2007). To the extent that morphological traits increase fitness through improved exploitation of resources, selection should act to improve the form and function of that apparatus (Arnold 1983;

Koehl 1996). Therefore, the phenotypes of organisms reflect both phylogenetic and ecological relationships (Koehl 1996; Losos and Miles 1996; Linde et al. 2004).

The morphology of feeding apparatus has been explored in many organisms as a way to explain observed patterns of resource and habitat use (Lack 1947; Arnold 1983; Mittelbach 1984; Patterson 1984; Wainwright 1994, 1996; Huckins 1997; Verwaijen et al. 2002). The biomechanical function of feeding apparatus establishes the limits of an animal's ability to exploit the array of potentially available resources (Lack 1947; Arnold 1983; Wainwright 1991; Huckins 1997; Verwaijen et al. 2002) and has been shown to differ based on the trophic specialization of consumers (Lauder 1983; Sanderson 1991; Ralston and Wainwright 1997; Horn et al. 2006). These functional limits may predictably influence other behavioral attributes of predators such as attack probability, capture success, and handling time of prey (Verwaijen et al. 2002). Therefore, morphology, as it affects feeding efficiency performance, provides a causal link between observed phenotype and ecological attributes such as resource preference (Arnold 1983; Wainwright 1991). This link often permits predictive power regarding the probable diet, preference, and efficiency of a predator given its specific feeding morphology and the diversity of available food items (Werner 1977; Norton 1991; Osenberg and Mittelbach 1989).

Animals with narrow diets are well adapted to utilize a particular resource. For example, the mandibles of grasshoppers that specialize on tough Graminaeous plants have adaptations that optimize their use of that resource (Patterson 1984; Bernays et al. 1991). Likewise, predacious fish that specialize on mollusks have morphological adaptations that increase the efficiency with which they can crush hard

shells and extract the prey compared to less specialized predators (Lauder 1983; Mittlebach 1984; Huckins 1997). As such, the mandibles of strict carnivores, as more specialized feeders, should be under selection to increase the capture success and handling efficiency of certain prey types.

Adaptations for consumers with broad diets often reflect a trade-off between food availability and foraging efficiency (Futuyma and Moreno 1986; Huckins 1997). This constraint may be particularly true when consumers evolve from a carnivorous to an omnivorous feeding style. For example, plant resources are particularly abundant, which may provide omnivores with a reliable source of food. However, plant feeding entails considerable disadvantages with consequences for individual fitness as plant resources are often tougher and less nutritious than animal prey (Raupp 1986; Bernays et al. 1991; Eubank et al. 2003; Roitberg et al. 2005). Omnivorous predators that feed on a greater diversity of food items than their strictly carnivorous counterparts require morphological adaptations that facilitate feeding on both plant- and prey-based resources (Eubanks et al. 2003; Horn et al. 2006). As such, many omnivores have morphological features that are intermediate to those of strict herbivores and carnivores (Eubanks et al. 2003; Horn et al. 2006; Christiansen and Wroe 2007). This morphology enables the processing of food items from multiple trophic origins that entail multiple behavioral, physical, or chemical challenges (Cohen 1990; Eubanks et al. 2003; Horn et al. 2006).

In this context, the efficiency with which omnivores kill and consume herbivore prey is likely less than that of strict carnivores whose feeding apparatus should be specialized. This difference could affect the impact of omnivores on

trophic dynamics in three ways. First, the less efficient handling of herbivore prey could reduce the functional response of omnivores, and thus reduce the rate at which they reduce herbivore populations (Holling 1966; Chesson 1989). Second, their reduced efficacy as predators could reduce the subset of herbivores that omnivores are capable of capturing (Huckins 1997). If omnivorous predators are able to consume only small herbivores or those that are easy to catch, their impact on herbivores at large would be restricted (Steiner 2001; Duffy 2002; Hillebrand and Cardinale 2004). Third, greater handling time required to consume active, mobile herbivores could shift an omnivore's preference toward immobile plant-based resources such as seeds (Pastorok 1981; Lang and Gsodl 2001). Likewise, this preference would also reduce an omnivore's impact on co-occurring herbivore populations (Murdoch 1969; Pastorok 1981; Lang and Gsodl 2001). However, no empirical comparison exists on how omnivorous and carnivorous predators differ in the efficiency with which they handle herbivore prey. Likewise, no research to my knowledge links differences in the mandibular morphology of arthropod omnivores and carnivores to their feeding preferences and ability to capture and handle a diversity of food resources. The ability to derive predictions of efficacy and feeding preference from morphological characteristics would be useful in forecasting the impact of predators, carnivores versus omnivores, on herbivore populations in the presence of multiple food resources.

Alternative prey or plant resources have variable but significant effects on the ability of omnivorous predators to impact herbivores and on the strength of trophic cascades (McMurtry and Scriven 1966a, b; Eubanks and Denno 1999, 2000a, b). In

many cases, the per-capita consumption of herbivores by omnivorous predators is reduced by the presence of alternative plant food or prey (McMurtry and Scriven 1966a; Eubanks and Denno 2000; Musser and Shelton 2003; Eubanks 2005; Chapter 2). Although understanding the role of feeding preference and efficiency is essential to predicting the influence of omnivorous predators in food-web dynamics, conducting experiments that test multiple combinations of alternative foods and prey is untenable, even for a single predator species. Therefore, investigating the causal relationship between consumer morphology and feeding efficiency on a diversity of food items should provide needed insight into food choice by omnivorous and carnivorous predators (Arnold 1983; Mittelbach 1984; Wainwright 1994, 1996; Huckins 1997; Verwaijen et al. 2002).

Here, I investigate how mandibular morphology (primary feeding apparatus) relates to guild membership, food choice, and handling efficiency in predacious beetles from the family Carabidae. Carabid beetle species are predators ranging from strict carnivores that consume only prey to omnivores that consume both seeds and prey. Omnivory occurs primarily in a single subfamily Harpalinae, a taxon in which strict carnivores also occur. Thus, carabids are ideal for examining the relationship between structure and function because a spectrum of omnivorous behavior is represented by a diversity of species in the same clade. Using laboratory experiments I address five primary objectives, all related to the relationship between mandibular structure and function in carabid beetles. By measuring mandibular characteristics of 13 carabid species, (1) I first test the hypothesis that omnivorous and carnivorous carabid species can be differentiated based solely on their mandibular morphology.

The next two objectives use omnivorous species of carabids to determine (2) the relationship between the handling time of three prey items (mobile prey, immobile prey, and seeds) and preference for those items, and (3) if differences in specific mandibular morphology affect the handling time of each food item. Specifically, this set of experiments identifies mandible characteristics that are associated with the improved handling time of prey. I hypothesize that seeds will require greater handling time than either prey item due to their tough seed coats. A significant interaction between mandibular morphology and the food type consumed would indicate that mandible features differentially affect feeding efficiency on the three food types. I predict that a longer terebral ridge, a knife-like shearing surface, will improve the efficiency of prey feeding, whereas increasing the size of the molar, a crushing region, will improve seed feeding. The last two objectives are addressed using omnivorous and carnivorous carabid species crossed with active and passive herbivore prey to determine (4) if the dimensions of mandible characteristics important in handling prey differ between the carabid guilds (omnivores and carnivores) and (5) how capture success, kill time, and consumption time are affected by carabid guild, prey behavior (active or passive), and their interaction. For these objectives, I hypothesize that the incisor tip will be sharper and the terebral ridge longer in carnivores, whereas the molar region will be larger and more developed in omnivores. Such mandibular differences should promote more efficient prey capture and consumption in carnivores than omnivores. This research aims to provide new insight into how the morphology of feeding apparatus can be used to differentiate

predator guilds, their ability to consume a variety of resources, and thus their functional roles in complex food webs.

Methods

Study system

Carabid beetles are a family of generalist and omnivorous predators that occur abundantly in most managed and natural systems (Lövei and Sunderland 1996). Many carabid species are also true omnivores and regularly consume seeds (Lövei and Sunderland 1996). In fact, carabid species span a spectrum of feeding styles from true omnivory to strictly predacious to specialized seed feeders. Such diversity in feeding behavior is accompanied by morphological diversity of the mandibles and other feeding structures such as the proventriculus (Forbes 1883; Zhavoronkova 1969; Forsythe 1982; Evans and Forsythe 1985). Differences in mandibular morphology have been described and attributed to different feeding guilds within the family Carabidae (Forbes 1883; Zhavoronkova 1969; Forsythe 1982; Evans and Forsythe 1985; Acorn and Ball 1991). Past work has related known guild memberships with very gross morphological features (Forbes 1883; Zhavoronkova 1969; Forsythe 1982; Evans and Forsythe 1985; Acorn and Ball 1991). However, no research has quantified how differences in mandible structure affects feeding efficiency across a diversity of prey items. In addition, no research has quantitatively compared mandubular differences between omnivorous and carnivorous species and associated these differences with feeding efficiency. Therefore, a causal link has not

been established between mandibular morphology, efficiency exploiting different food resources, or efficacy as a predator. As such, there is no basis to make predictions about resource use or feeding preference of carabid species and their role in food-web dynamics under conditions of differing food resources (Werner 1977; Norton 1991; Osenberg and Mittelbach 1989; Wainwright 1994, 1996). Therefore, carabids serve as a unique taxon for addressing questions of omnivory and functional morphology as they relate to resource use and capture efficacy.

Alternative prey species for carabids such as detritivores are abundant in most natural and managed systems. Many carabid species are known to feed on dipteran eggs and pupae (Kromp 1999). For the research proposed here, fruit fly pupae, *Drosophila melanogaster* Meigen (Diptera: Drosophilidae) are used as alternative prey. Seeds from a variety of weeds are also very abundant in carabid habitats (Davis et al. 2005; Swanton et al. 2006). Bluegrass seeds, *Poa pratensis* (Cyperales: Poaceae), are used in this research because they are readily consumed by some carabids and because *Poa* species are common agricultural weeds (Uva et al. 1997). Carabid beetles have been reported to consume all of these food items and they readily encounter them under natural conditions (Lövei and Sunderland 1996; Kromp 1999).

The ability to successfully capture, subdue, and consume prey in vertebrates depends on the ability of a predator to grasp the prey with sufficient force and also how this force translates into piercing and shearing of the prey tissue (Verwaijen et al. 2002; Christiansen and Wroe 2007). In carabids, all of these abilities are expected to depend on morphological features of the mandibles. In this respect, mandibular

characteristics that appear to be functionally significant are the sharpness of the incisor tip used to pierce food items and the length of the terebral ridge used to shear and slice prey into pieces (Evans 1965; Forsythe 1982; Evans and Forsythe 1985; Acorn and Ball 1991).

Foods can be broadly classified as either hard or tough. Hard foods (e.g. seeds) fracture rapidly but the initiation of fractures requires high stress (Lucas 2004). Animals consuming hard foods benefit from broad chewing surfaces that promote fractures but are protected from their own structural failure (e.g. nutcracker) (Lucas 2004). Processing tough foods (e.g. integument of some caterpillar species such as cutworms) require sharp cutting surfaces. Because tough food is pliable, fractures do not propagate readily under stress alone, but require a blade to drive the fracture through the material (Lucas 2004). However, the cutting surface is not in jeopardy of structural failure (e.g. knife). The molar region of the mandibles of carabids aids in the crushing of seeds and mastication of other foods and is predicted to be larger in omnivorous carabids (Evans 1965; Forsythe 1982; Evans and Forsythe 1985; Acorn and Ball 1991).

The herbivorous prey species used in this research were the black cutworm, *Agrotis ipsilon* (Hufnagel) (Lepidoptera: Noctuidae) and the green cloverworm, *Hypena scabra* (F.) (Lepidoptera: Noctuidae), and were selected as focal herbivores in this research because they are phylogenetically related but have very different defensive behaviors. Black cutworm has a relatively passive response to attacks that consists of rolling slowly. Green cloverworms on the other hand thrash violently when disturbed. Based on my morphological predictions, carnivorous carabids are

expected to be more efficient at capturing and consuming both species due to their sharp incisor points and longer terebral ridge (slicing apparatus) relative to omnivores.

Relationship between mandibular morphology and guild membership

Seven characteristics were measured (Figure 1.1) on mandibles of 13 carabid species, 8 omnivores and 5 carnivores (Table 1.1). For each species, 5 individual beetles were measured (Table 1.1). Mandibles were dissected from beetles that were previously preserved in 70% EtOH. The left mandible of each beetle was point mounted. Mandible characteristics were measured using the ocular micrometer of a dissecting scope.

Differences in the mandibular morphology of omnivorous and carnivorous carabid species were examined using principle components analysis (PCA) and redundancy analysis (RDA). These ordination methods construct latent variables (axes) that are linear combinations of the original multiple variables, in this case morphological characteristics. The first axis is constructed to explain the largest part of the total variance and the second is constructed to explain the largest part of what variance is left. More axes are constructed until the total variance is explained. The first two axes typically explain a majority of the variance and are used as the axes in a bi- or tri-plot ordination diagram. PCA is used to visualize the relationships of samples (individual beetles) based on the characteristics (morphological characteristics) of those samples and to determine which morphological variables explain most of the total variance. However, PCA does not statistically test

differences between groups of samples because no explanatory variables (guild assignments) are defined. In RDA the analysis and ordination are constrained by explanatory variables (omnivore or carnivore). Moreover, in RDA a Monte Carlo permutation test can be used to test the significance of the model and thus whether groups defined by explanatory variables are significantly different. Both PCA and RDA provide intra-set correlations or weights of the characteristics on each axis. The absolute value of these weights indicate how correlated a characteristic is with the axis and the sign indicates samples with those characteristics are placed. Performing PCA provides support (or lack there of) for the results of RDA by showing how samples group when not constrained by explanatory variables (Legendre and Legendre 1998).

Statistical analysis: Morphological differences between omnivorous and carnivorous carabids were analyzed using PCA and RDA in CANOCO 4.5 (Ter Braak and šmilauer 2002). Morphological measurements were standardized by beetle length ($x/\text{beetle length}$) prior to analysis to remove the influence of overall length and focus on relative differences in morphology. PCA was used to visualize the relationships of omnivorous and carnivorous species in a bi-plot as defined by morphological characteristics but not constrained by guild assignments and to determine which morphological variables explain most of the total variance. In RDA each individual was designated as an omnivore or carnivore so the analysis and ordination were constrained by guild membership as an explanatory variable. A Monte Carlos permutation test (499 permutations) was used to test the significance of the model and thus whether omnivorous and carnivorous species are significantly

different based on differences in the 7 morphological characteristics (Figure 1.1). In addition, the weights of the morphological characteristics were used to interpret which are most important in separating omnivorous and carnivorous species.

Effect of mandibular morphology and food type on handling time and food preference

Seven omnivorous carabid species were used to determine how mandibular morphology (terebral ridge length, molar width, and tip width) and food type (black cutworm larvae, bluegrass seeds, fly pupae) affected handling time and food preference. The carabid species used in this experiment were *Harpalus pensylvanicus*, *Stenolophus lecontei*, *S. coma*, *S. ochropezus*, *Anisodactylus ovularis*, *Amara familiaris*, and *Am. cupreolata*. The number of individuals tested for each species and food type are presented in Table 1.2. In order to control for the size of the various food items tested, 2nd instar (~4 mm) cutworms were used in this experiment, which are similar in size to the other food items offered (bluegrass seeds and fly pupae). These experiments were conducted in test arenas (6cm diameter petri dishes lined with moistened filter paper) at room temperature in a dimly lit room.

Five individuals of a single food item were placed into a petri dish to determine handling time of each carabid species for each food type. A single beetle was added to the dish at which point a stop watch was started. Beetles were allowed to consume one food item. The time when beetles began and finished consuming a seed or pupa was recorded as the handling time. The experiment was conducted in groups of nine dishes. Beetle species-food type combinations were randomly applied to each dish within each set of nine until 10-12 replicates of each combination were

completed with the exception of a few species. *Stenolophus comma* were difficult to distinguish from *S. lecontei*, and *Am. familiaris* was difficult to distinguish from *Am. cupreolata*. Therefore, it was not until I dissected these beetles that I realized *S. comma* and *Am. cupreolata* had been included and they are thus under represented (Table 1.2). After consuming a food item, beetles were assigned a unique number and preserved in 70% EtOH. Beetles that did not consume a food item within 20 minutes were recorded as having not eaten and were not preserved. To control for possible body size effects, the body length of every beetle for which handling time data were recorded was measured before removing mandibles. Mandibles were prepared and measured as described above.

Five omnivorous carabid species were used to determine the preference of omnivorous carabids for the three food items: *Harpalus pensylvanicus*, *Stenolophus lecontei*, *S. ochropezus*, *Am. santaecrucis*, and *Am. familiaris*. This experiment was conducted in 6 cm petri dishes lined with moistened filter paper. Three combinations of food items were tested for each of the five carabid species. The food combinations were cutworms with pupae, cutworms with seeds, and pupae with seeds. Each species by food combination was replicated 10 times. To prepare each food combination, five individuals of each of the appropriate food items were placed in each petri dish. To start the experiment an individual beetle was placed in each dish. Dishes were placed in a dark growth chamber at 27° C. The number of items remaining in each dish was counted after one hour.

Preference was calculated based on the number of each food item eaten after 1-hour. Preference was quantified as:

$$\alpha = \ln(N_i - R_i) / [\ln(N_i - R_i) + \ln(N_j - R_j)] \quad (\text{eq. 1.1})$$

where N_i and N_j are the number of food type i and j present at the beginning of the experiment and R_i and R_j are the number of food type i and j that were eaten (Chesson 1978, 1983). This index ranges from 0 to 1 where an α of 0.5 indicates no preference, an α close to 1 indicates a preference for food type i , and an α close to 0 indicates a preference for food type j . As such, α values can be compared and analyzed using standard parametric methods (Chesson 1978, 1983).

Statistical analysis. Multiple regression was used to model the effects of the three mandible characteristics (cerebral ridge length, molar width, and tip width), food type, and their interactions on handling time in the MIXED procedure of SAS (SAS 2002). These three characteristics were selected because they were weighted highly in their contribution to inter-guild differences (RDA analysis above), were described by others to have important functions in food processing (Evans 1965; Forsythe 1982; Evans and Forsythe 1985; Acorn and Ball 1991), and were not highly auto-correlated (Table 1.3). The model was reduced in a step-wise manner to remove non-significant ($P > 0.05$) effects. Beetle length remained in the model as a covariate throughout to remove variation due to this variable and better isolate the effect of mandibular morphology.

ANOVA was used to examine the effects of carabid species, alternative food type (pupae or seed), and their interaction on the preference (α) for cutworms (SAS 2002). The preference for pupae compared to seeds did not meet the assumptions of ANOVA so data were analyzed by a Kruskal-Wallis test in the FREQ procedure of SAS (2002).

Correlation analysis was conducted using the CORR procedure of SAS (2002) to examine how preference for food items was related to handling time. The measure of preference (α) describes the preference for one food item relative to a second and is dependent on the arbitrary designation of food types i and j (eq. 1.1). Therefore the difference in mean handling time between food type i and food type j were correlated with the mean preference for food type i of each species x food combination. For example, as the difference in handling time between food type i and j increases (e.g. cutworms and seeds) preference for food type i (e.g. cutworms) becomes stronger.

Handling time of active and passive prey by omnivorous and carnivorous carabids with differing mandibular morphology

Two carabid species from each guild were used to compare the time required for omnivorous and carnivorous carabids to kill and consume both active and passive herbivorous prey. The omnivorous species were *H. pensylvanicus* and *A. sanctaecrusis* and the carnivorous carabids were *Poecilus chalcites* and *Chlaenius tricolor*. This design provided replicate species within each guild to increase the scope of inference with regard to guild comparisons. Carabid guild was crossed with active (green cloverworm) and passive (black cutworm) prey in a 2 x 2 factorial design. The number of replicates for each combination of species or guild and prey is listed in Table 1.4. Experiments were conducted at room temperature in a dimly lit room. Prior to experiments, the mass (g) and length (mm) of beetles and prey were recorded.

The first set of experiments was designed to determine carabid choice as well as the kill and consumption time of prey. To provide choice, one cloverworm and one cutworm of similar weight (± 0.02 g) were placed in 6 cm petri dishes lined with moistened filter paper. A single beetle was placed in each dish at which point a stop watch was started. Beetles were allowed to consume one prey item. The time it took beetles to attack, kill, and finish consuming cutworms was recorded to provide measures of kill time, consumption time and total handling time. Beetles that did not begin to consume a prey item in 20 minutes were recorded as having not eaten.

In the above choice experiment, 91.5% of all beetles consumed cutworms rather than cloverworms so very little data resulted for the kill, consumption, and handling time of cloverworms. Therefore, a set of no-choice experiments was conducted using only cloverworms to achieve the final number of replicates presented in Table 1.4. Otherwise, this experiment was carried out the same as the choice experiment. To compare differences in mandibular morphology between these omnivorous and carnivorous carabids, five individuals of each species were killed in 70% EtOH and their mandibles were prepared and measured as described above.

Statistical analysis. The effect of carabid guild on terebral ridge length, molar width, and incisor tip width were analyzed using ANCOVA, with beetle length as the covariate, in the MIXED procedure of SAS (2002). In addition, the effect of carabid species on terebral ridge length, molar width, and incisor tip width were analyzed using ANCOVA (beetle length the covariate) in the MIXED procedure of SAS (2002) to determine if species within a guild were more similar in morphology than beetles between guilds. The effect of carabid guild, prey type, prey length and their

interactions on the time required to kill and consume prey was analyzed as a 2 x 2 factorial using ANCOVA, with beetle length as the covariate, in the MIXED procedure of SAS (2002). The choice of cutworms or cloverworms was examined using Chi square tests that compared the number of first attacks directed at each prey type and the number of each prey type consumed by carabid species in the two feeding guilds.

Results

Relationship between mandibular morphology and guild membership

The first two axes of the PCA explained 81.6% of the total variance in the data (Table 1.5). The first axis (x) explained 58.1% of the total variance and separated most of the carnivorous (left side) and omnivorous (right side) species. The terebral ridge had a high negative weight on this axis indicating that carnivorous species have longer terebral ridges (Table 1.5; Figure 1.2). In contrast, mandible width and incisor width had high positive weights on the first axis indicating that these species, which are primarily omnivores, have wider mandibles with wider incisor tips (Table 1.5; Figure 1.2). Terebral ridge also had a high negative weight on the end of the second (y) axis resulting in most carnivorous species being clustered in the bottom left quadrant. The second axis also separated species based on overall length of their mandibles which placed species with long mandibles relative to their body size, (having been divided by beetle length) many of which were carnivores (except note Hp) in the bottom two quadrants (Figure 1.2). Molar width had a high positive

weight on the second axis. Therefore, most omnivores are in the upper two quadrants (Table 1.5; Figure 1.2). However, *Agonum punctiforme* (Ap) appears to have a carnivore-like terebral ridge but molar width similar to omnivores which places it far to the left of the upper left quadrant.

The first canonical axis of the RDA (x; Figure 1.3) describes differences between the two guilds and explains 22.8% of the total variation (Table 1.6). Terebral ridge length (Tr) was highly, positively weighted on this axis whereas basal and molar width were highly negatively weighted (Table 1.6; Figure 1.3). Incisor tip width and overall width were also highly negatively weighted on this axis (Table 1.6; Figure 1.3). The morphological variables measured explained 67% of the variance between the two guilds (Table 1.6). Based on Monte-Carlo permutation tests there was a significant difference between omnivorous and carnivorous carabid mandibles based on these seven morphological features (F -ratio = 18.614; P = 0.002) (Figure 1.3). Taken together this provides evidence that carnivores have longer terebral ridges, narrow molars, and narrow (sharp) incisor tips whereas omnivores have wide molars, wide (dull) incisor tips and short terebral ridges. Whereas the first axis (x) describes differences between the guilds, the second axis (y; Figure 1.3) describes differences between species and explains another 42.7% of the total variation. Therefore, having separated omnivores and carnivores on the first axis based on terebral ridge length and molar width, the remaining variation among species is related to mandible length (L), width (w), and molar length (Ml) which are highly weighted on the second axis (Table 1.6; Figure 1.3).

The PCA and RDA are consistent in the morphological features that separate omnivorous and carnivorous species. In particular, both analyses indicate that carnivores have long terebral ridges whereas omnivores have wide molars and wide incisor tips. Agreement between these analyses indicates these highly weighted morphological characteristics are important in separating guilds, even when not constrained in the RDA (Legendre and Legendre 1998). This lends strong support for conclusions drawn from the RDA and Monte Carlo test.

Effect of mandibular morphology and food type on handling time and food preference

After accounting for differences in beetle length (covariate; $F_{1, 144} = 2.09$; $P = 0.151$), there was a significant interactive effect between the omnivorous carabid species and food type on handling time ($F_{8, 144} = 5.12$; $P < 0.001$). The main effects of carabid species ($F_{4, 144} = 5.80$; $P < 0.001$) and food type ($F_{2, 144} = 119.12$; $P < 0.001$) were also significant (Figure 1.4). Handling time was greatest for seeds for all species. However, handling time differed for cutworms and pupae between carabid species. *Amara familiaris* and *H. pensylvanicus* took longer to consume pupae than cutworms whereas the opposite was true for *S. ochropezus*.

Results of multiple regression analysis indicated that increasing molar width (Mw) significantly reduces handling time of cutworms but does not alter the handling time of pupae or seeds (Tables 1.7, 1.8; Figure 1.5). Thus, there was a significant interaction of molar width and food type (Table 1.7). Increasing terebral ridge length (Tr) significantly increased handling time of cutworms but did not significantly affect

handling time of pupae or seeds, as indicated by a significant interaction between the length of the terebral ridge and food type (Tables 1.7, 1.8; Figure 1.5). Increasing incisor tip width significantly increased handling time of all prey types equally (Table 1.7). Food type also significantly affected handling time where handling time of seeds was significantly greater than that of cutworms or pupae (Tables 1.7, 1.8; Figure 1.5).

There was no significant interaction between carabid species and food type on preference for cutworms when either pupae or seeds were present ($F_{4,84} = 1.01, P = 0.408$) (Figure 1.6). However, both carabid species ($F_{4,84} = 3.90, P = 0.006$) and food type ($F_{1,84} = 80.64, P < 0.001$) significantly affected preference for cutworms where preference for cutworms was higher when seeds were present compared to when pupae were present (Figure 1.6). All carabid species preferred pupae over seeds, whereas there was not a significant difference among carabid species in preference for pupae versus seeds ($\chi^2 = 6.40, df = 4, P = 0.171$) (Figure 1.7).

There was a significant, positive correlation between the mean preference for food type i and the difference in mean handling time between food types i and j ($r = 0.627, P = 0.012$) (Figure 1.8). Therefore, as the difference in handling time between food types i and j increases preference for food type i becomes stronger, whereas if handling times are similar preference is weaker. For example, the difference between handling time of cutworms (i) and seeds (j) was great (Figure 1.5) and preference for cutworms was strong when seeds were present (close to 1) (Figure 1.6) whereas the difference in handling time between cutworms and pupae is small (Figure 1.5) and preference for cutworms is weak (close to 0.5) (Figure 1.6).

Morphological and handling time differences between omnivorous and carnivorous carabids

Terebral ridge length was significantly greater in both carnivorous carabid species ($F_{3,15} = 37.78$; $P < 0.001$) than for either omnivore, and was greater for the carnivore guild at large ($F_{1,17} = 127.15$; $P < 0.001$) when adjusted for beetle length as a covariate ($F_{1,15} = 4.23$; $P = 0.058$; $F_{1,17} = 85.32$; $P < 0.001$, respectively) (Figure 1.9a). Width of the molar region was significantly different among carabid species ($F_{3,15} = 22.81$; $P < 0.001$) and was generally greater for the omnivore than carnivore guild ($F_{1,17} = 25.54$; $P < 0.001$) when adjusted for beetle length as a covariate ($F_{1,15} = 0.38$; $P = 0.548$; $F_{1,17} = 11.19$; $P < 0.004$, respectively) (Figure 1.9b). Width of the mandible tip was significantly greater in both omnivorous carabid species ($F_{3,15} = 102.11$; $P < 0.001$) and greater in omnivores as a guild ($F_{1,17} = 109.76$; $P < 0.001$) when adjusted for beetle length as a covariate ($F_{1,15} = 1.82$; $P = 0.197$; $F_{1,17} = 82.39$; $P < 0.001$, respectively) (Figure 1.9c).

There was not significant interactive effect between carabid guild and herbivore prey type (passive vs. active) on the number of attacks, kill time, consumption time, or total handling time (Table 1.9). The number of attacks required to capture active prey was significantly greater than for passive prey (Table 1.9; Figure 1.10a). Overall, omnivores took significantly longer to kill both prey types than carnivores and carnivores required significantly more time to kill cutworms (passive) than cloverworms (active) (Table 1.6; Figure 1.10b). Likewise, omnivores took significantly longer to consume prey overall, and cutworms required significantly more time to consume than cloverworms (Table 1.6; Figure 1.10c). Total

handling time was significantly longer for omnivores than carnivores and for cutworms than cloverworms (Table 1.6; Figure 1.10d).

Significantly more first attacks were directed toward passive prey by both omnivores ($\chi^2 = 14.40$; $df = 1$; $P < 0.001$) and carnivores ($\chi^2 = 8.91$; $df = 1$; $P < 0.001$) (Figure 1.11). Also there was no significant difference between omnivorous and carnivorous carabids in the number of times their first attack was directed toward passive or active prey ($\chi^2 = 0.35$; $df = 1$; $P = 0.553$) (Figure 1.11). There was no difference between omnivorous and carnivorous carabids in the number of passive versus active prey they consumed ($\chi^2 = 1.40$; $df = 1$; $P = 0.238$) (Figure 1.12). However, significantly more passive than active prey were consumed by both omnivores ($\chi^2 = 21.16$; $df = 1$; $P < 0.001$) and by carnivores ($\chi^2 = 11.64$; $df = 1$; $P < 0.001$) (Figure 1.12).

Discussion

Omnivorous and carnivorous carabid species differ in their mandibular morphology and in their efficacy as predators of herbivorous prey. Carnivorous species are characterized by sharp incisor points used to pierce and capture prey and a long terebral ridge used to kill and slice prey into pieces (Figures 1.2, 1.3, 1.9). To the contrary, omnivorous species have features that are advantageous for seed feeding but reduces efficiency with prey. In particular they have a wide molar region for crushing seeds but their incisor tips are dull and their terebral ridge is short (Figures 1.2, 1.3, 1.9). Therefore with mandibles specialized for capturing, killing, and consuming prey carnivores accomplish these tasks more efficiently (Figure 1.10).

Moreover, feeding preference for herbivore species or alternative food items such as seeds is directly related to the efficiency with which predators can capture and consume these items. Based on this research mandibular morphology can now be used to predict the trophic role of carabid beetles reducing the need for elaborate and time consuming feeding trials (e.g. Best and Beegle 1977; Barney and Pass 1986). Further implications of these results are that omnivorous carabids are mechanically restricted in their efficiency as predators, and thus would be less likely to regulate herbivore populations.

Based on descriptions of carabid mandibles by others (Evans 1965; Forsythe 1982; Evans and Forsythe 1985; Acorn and Ball 1991), I predicted that the terebral ridge a knife-like cutting edge, and the molar region used for crushing would be important features for processing prey and seeds respectively. In addition, I predicted that reducing incisor tip width (i.e. increasing sharpness of the mandible tip) used for piercing or grabbing would also reduce the handling time of prey. However, increased molar width in omnivorous carabid species was associated with reduced handling time of cutworms but not seeds or pupae. Also contrary to predictions, increased terebral ridge length of omnivorous carabids was associated with increased handling time of cutworms. However, the importance of particular morphological features can change as food size or other characteristics such as hardness change (Mittelbach 1984; Wainwright 1987, 1988; Huckins 1997). For fish that feed on mollusks and gastropods, the maximum consumable size of easily crushable prey may be limited by mouth gape but as prey hardness increases crushing strength becomes increasingly important (Mittelbach 1984; Wainwright 1987, 1988). In this study, the food items

(seed, pupae, cutworms) fed to the omnivorous carabid species were much smaller than the predators. Therefore, omnivorous beetles likely need to crush and masticate prey, but the slicing function of the terebral ridge may not be necessary. Increasing the portion of the mandible dedicated to terebral ridge rather than the molar area seems to have actually hindered feeding efficiency on these small food items (Figure 1.5). In support of this hypothesis, mandibles of carnivorous carabid species that specialize on relatively small prey such as collembola and mites were found to be shorter (smaller length: width ratio) than typical carnivore mandibles and are thus more like omnivores (Evans and Forsythe 1985). Similar relationships are found among mammals in the order Carnivora. Species that consume small prey or plants have more developed molars, whereas those species that capture and consume prey larger than themselves have sharp canines to grip live animals and highly derived carnassial (fused into a sharp ridge) teeth for shearing flesh (Christiansen and Wroe 2007).

As predicted, seeds required a longer handling time than either of the prey options (cutworms or pupae) for all five of the omnivorous carabid species tested (Figure 1.4). Moreover, seeds are the least nutritious of the food items tested in this experiment (see Mattson 1980; Denno and Fagan 2003; Eubanks 2005; discussion in Chapter 3). However, some omnivorous carabid species benefit from having seeds in their diet in terms of greater fecundity and more rapid development (Jorgenson and Toft 1997; Fawki and Toft 2005). Nevertheless, plant-derived resources also confer mandible damage to herbivorous and omnivorous insects, which often reduces future feeding efficiency and fitness (Bernays 1991; Raupp 1986; Roitberg 2005). In

addition, extended feeding and handling times expose consumers to greater risk of predation by arthropod and vertebrate predators (Price 1980; Heinrich and Collins 1983; Bernays 1991). Therefore, although carabid diet breadth has expanded to include this abundant resource, there may be significant costs associated with its use.

These disadvantages may contribute to my finding that prey, cutworms and fly pupae, were always preferred over seeds by omnivorous carabids in choice experiments. Although prey mobility can also play an important role in preference (Eubanks and Denno 2000b), this was not the case in these experiments. Fly pupae effectively served as a mobility control. Cutworms were preferred significantly more when seeds were present than when pupae were present (Figure 1.6). However, when mobility was equal (seeds and pupae) but handling time differed greatly (seeds > pupae), preference for pupae was very strong over seeds. Taken together these findings support a strong relationship between handling time and food preference in which preference for an efficiently consumed food item increases in the presence of a more difficult-to-handle food item (Figure 1.8). This phenomena has also been found for many other predators where they preferentially forage for the prey they consume most efficiently (Pastorok 1981; Lang and Gsodl 2001). Generalist sunfish selectively forage on soft bodied prey as opposed to hard mollusks, which require extended handling time and specialized jaw morphology (Huckins 1997). However, the reverse is true for specialist molluscivorous sunfish (Huckins 1997) where the proportion of soft or hard bodied prey in their diets differ from the relative frequency of the preferred prey item in the environment (Mittelbach 1981; Osberg and Mittelbach 1989; Huckins 1997). Therefore, resource use by these predators is best

predicted by the morphology that governs feeding efficiency and food choice (Werner 1977; Norton 1991; Osenberg and Mittelbach 1989; Persson et al. 1996), not necessarily food abundance.

Increasing terebral ridge length did not reduce handling time of the omnivorous predators consuming small cutworms and pupae. However, when comparing feeding efficiency between omnivorous and carnivorous carabids, relationships between mandibular morphology and feeding success followed my initial prediction that increased terebral ridge length would reduce handling time of herbivore prey. The relative size of prey compared to carabids may help explain this seeming contradiction. The cutworms and cloverworms fed to the omnivorous and carnivorous carabids in this experiment were of various sizes and most were at least half as long as the carabid predators (mean \pm SE, minimum - maximum: bcw = 10.3 ± 0.5 mm, 5.0 – 18.0 mm; gcw = 14.3 ± 0.6 mm, 7.0 – 25.0 mm) (Table 1.1). Carnivores exhibited greater capture success, and shorter kill and consumption times of both herbivores than omnivorous carabids (Figure 1.10). Carnivores also had mandibles with sharper incisor tips and a longer terebral ridge to more effectively pierce and slice the caterpillars which were rolling (passive) or thrashing (active) to escape (Figure 1.9). Herbivore death was hastened when caterpillars were sliced open to release the fluid and internal pressure which they require to move. Therefore, with larger prey that were more difficult to hold and take longer to kill, the slicing function of the terebral ridge likely plays a more important role in killing prey. In addition, effective prey preparation such as slicing large items into manageable pieces or removing inedible parts reduces consumption time and makes large prey

proportionately less costly to handle (Kaspari 1990). Therefore, sharper mandibles likely enable more efficient processing and consumption of large prey in addition to more efficient killing. With passive and active herbivores, carnivorous carabids have a considerable foraging advantage over omnivores. Thus I have demonstrated that the derived characteristics of omnivore mandibles, such as a reduced terebral ridge and expanded molar region that facilitate feeding on seeds, entails a trade-off for reduced capacity to kill and consume higher quality prey.

When the five omnivorous carabids had small cutworms, pupae, or seeds to choose from, the food type with the lowest handling time was preferred. When omnivores and carnivores had to choose between active and passive caterpillars both guilds preferentially attacked and consumed passive cutworms rather than active cloverworms. However, total handling time with cutworms was greater than that of cloverworms for carnivores and omnivores (Figure 1.10). In this case, capture efficiency played the primary role in explaining the carabids preference for cutworms, as they could be captured with a fewer number of attacks. It is tempting to classify this response as 'passive' selection wherein prey preference is determined not by active predator choice, but rather to their inability to recognize, capture, or consume a particular item (Pastorok 1981; Provost et al. 2006). However, predators in this experiment not only consumed cutworms, but their first attack preferentially targeted cutworms (Figure 1.11, 1.12). Therefore, it appears that the difficulty in capturing cloverworms was recognized by the predator before choosing to attack an individual.

An abundance of research has investigated the role of morphology in the feeding ecology of vertebrate predators such as birds, fish, and reptiles (Lack 1947;

Arnold 1983; Mittelbach 1984; Wainwright 1994, 1996; Huckins 1997; Verwaijen et al. 2002). This work has been successful in documenting how intra- or inter-specific differences in trophic morphology affect individual fitness, habitat use, and competition (Lack 1947; Arnold 1983; Mittelbach 1984; Wainwright 1994, 1996; Huckins 1997; Verwaijen et al. 2002). However, similar research regarding insect predators is minimal except for work that addresses how predator body size affects handling time and prey selection (Cohen and Tang 1997; Cisneros and Rosenheim 1997; Agarwala et al. 2000; Ayre 2001). However, body size is often a surrogate for a multitude of functionally important traits such as mouth gape, bite force, and mobility (Woodward et al. 2005). Predator size therefore does not link specific traits to changes in handling time or ecological role (Cohen et al. 1993; Layman et al. 2005). Work with heteropterans (Cobben 1978; Cohen 1990; Cohen 1996; Boyd et al. 2003), carabids (Forbes 1883; Zhavoronkova 1969; Forsythe 1982; Evans and Forsythe 1985), and coccinellids (Forbes 1883; Samways et al. 1997) has related mandibular morphology to feeding habits or guild membership based on gross morphological relationships and inferred functional differences. Feeding experiments to document how changes in morphology affect efficiency or food preference in insects are almost entirely lacking except for studies that document reduced feeding efficiency due to mandible wear (Raupp 1985; Roitberg et al. 2005). This research demonstrates that insect mandibular morphology, and specific mandible characteristics, is important in food capture and handling efficiency, and ultimately relates to feeding preference. In addition, this research documents differences in mandibular morphology and feeding efficiency between omnivorous and carnivorous

carabids, which has broader implications for the role of omnivores in trophic dynamics.

Omnivory is an important component of ecological food webs. The presence of omnivores increases the reticulate nature of food webs resulting in a complex array of interactions. The impact of these interactions on food web stability and ecosystem function are context dependent and difficult to predict. Eco-morphological research can provide a causal link between the form, function, and ecology of consumers and increases the predictability of ecological interactions (Werner 1977; Norton 1991; Osenberg and Mittelbach 1989; Wainwright 1994). However, no research to my knowledge has compared the trophic morphology and feeding efficiency of omnivorous versus carnivorous species of any animal group. This research links three key concepts that could be used to predict the trophic impact of omnivorous and carnivorous carabids. First, omnivorous and carnivorous carabids have consistent morphological differences in functionally significant mandible characteristics. In particular, carnivores have sharper mandibles and a longer shearing edge than omnivores. As a consequence, carnivorous predators kill and consume herbivores more efficiently than omnivores. Also, preference for alternative food items and herbivores is positively related to capture and handling efficiency. Based on this conceptual framework, and because omnivores consume herbivores less efficiently than carnivores, they are expected to reduce herbivore populations more slowly, particularly when they prefer non-herbivore alternative foods.

Applied implications

Omnivorous predators are frequent players in classical, augmentative, and conservation biological control (Obrycki and Kring 1998; Alomar and Wiedenmann 1996; Symondson et al. 2002). All of these biological control approaches suffer from mixed success influenced by many known and unknown variables (Murdoch et al. 1985; Gurr et al. 2000). This work has identified trophic morphology and guild membership as two variables that could affect the success of biological control.

This research takes a novel approach to understanding and predicting the potential value of carabids as agents of biological control. I have identified terebral ridge length, incisor width, and molar width as mandible characteristics that can be used to distinguish between omnivorous and carnivorous carabid species. In addition, these characteristics play a prominent role in the efficiency that carabids consume herbivores or alternative food such as fly pupae and seeds. Feeding efficiency in turn influences preference for these items. Feeding efficiency and preference are important determinants of the top-down impact that predators can impose on herbivore prey. Much work has been invested in identifying which carabid species are omnivorous versus carnivorous and determining their preference for seeds versus, alternative prey and economically important pests (e.g. Sunderland 1975; Best and Beegle 1977; Barney and Pass 1986). Research of this nature generally entails gut dissection, cafeteria style feeding trials, and, increasingly, molecular techniques all of which are tedious, time consuming, and -particularly molecular methods- expensive. Using mandibular morphology as a predictive tool will increase the efficiency with which the guild, feeding efficiency, and preference can be understood for beetles with

unknown habits. This new approach to understanding predator feeding habits could be applied to other omnivorous predators that play a role in biological control but have an unpredictable impact on pests.

Tables

Table 1.1. Omnivorous and carnivorous carabid species and their average (\pm SE) body and mandible length (mm) included in the PCA and RDA to elucidate the relationship in mandible morphology and food preference among omnivorous and between omnivorous and carnivorous carabids.

Guild	Species	Beetle length	Mandible length	
Omnivores	<i>Harpalus pensylvanicus</i> ^{a, b}	16.40 \pm 0.40	1.98 \pm 0.07	
	<i>Anisodactylus ovularis</i>	12.50 \pm 0.64	1.55 \pm 0.09	
	<i>Anisodactylus sanctaecrusis</i> ^{a, b}	9.10 \pm 0.14	0.97 \pm 0.01	
	<i>Amara cupreolata</i> ^a	7.70 \pm 0.05	0.75 \pm 0.01	
	<i>Amara familiaris</i> ^a	7.22 \pm 0.23	0.72 \pm 0.02	
	<i>Stenolophus lecontei</i> ^a	6.86 \pm 0.26	0.79 \pm 0.03	
	<i>Stenolophus coma</i> ^a	7.00 \pm 0.14	0.79 \pm 0.02	
	<i>Stenolophus ochropezus</i> ^a	6.26 \pm 0.18	0.66 \pm 0.03	
	Carnivores	<i>Poecilus lucublandus</i>	11.46 \pm 0.23	1.21 \pm 0.04
		<i>Chlaenius tricolor</i> ^b	12.70 \pm 0.20	1.28 \pm 0.02
<i>Agonum punctiforme</i>		7.94 \pm 0.19	0.67 \pm 0.03	
<i>Pterosticus melanarius</i>		15.00 \pm 0.17	1.91 \pm 0.04	
<i>Poecilus chalcites</i> ^b		12.60 \pm 0.14	1.27 \pm 0.03	

^a Used in the omnivore only laboratory feeding experiments

^b Used in the omnivore - carnivore laboratory feeding experiments.

Table 1.2. Number of individuals from each carabid species used in laboratory experiments examining the relationship among omnivorous carabids in mandibular morphology and handling time for each food type. Each individual was subsequently killed and dissected to obtain mandible measurements.

Carabid species	Number of individuals tested			Species total
	Cutworm	Pupae	Seeds	
<i>H. pensylvanicus</i>	12	12	11	35
<i>Stenolophus lecontei</i>	9	7	9	25
<i>S. coma</i>	1	3	1	5
<i>S. ochropezus</i>	10	12	11	33
<i>Anisodactylus ovularis</i>	10	10	11	31
<i>Amara familiaris</i>	6	6	7	19
<i>Am. cupreolata</i>	5	4	4	13
Food type total	53	54	54	161

Table 1.3. Results of partial correlation analysis used to examine the relationship between morphological mandibular characteristics of omnivorous carabid species. Values of r (upper) and P (lower) are partial correlations between mandible characteristics while holding beetle length constant. Bold values highlight the relationship between characteristics that were used in multiple regression analysis to identify characteristics that influence handling time of cutworm, pupae, and seed food types. Abbreviations follow those of figure 1.

r	Morphological characteristic						
	L	W	Tr	Ml	Mw	Tw	Bw
L	1.000	0.755	0.722	0.130	-0.212	0.417	0.568
	—	< 0.001	< 0.001	0.101	0.007	< 0.001	< 0.001
W	—	1.000	0.584	0.192	-0.189	0.398	0.648
	—	—	< 0.001	0.015	0.017	< 0.001	< 0.001
Tr	—	—	1.000	0.151	-0.144	0.119	0.487
	—	—	—	0.057	0.070	0.133	< 0.001
Ml	—	—	—	1.000	0.390	-0.020	0.332
	—	—	—	—	< 0.001	0.799	< 0.001
Mw	—	—	—	—	1.000	-0.087	0.170
	—	—	—	—	—	0.270	0.031
Tw	—	—	—	—	—	1.000	0.250
	—	—	—	—	—	—	0.002
Bw	—	—	—	—	—	—	1.000
	—	—	—	—	—	—	—

Table 1.4. Total number of replicates for each species or guild by prey combination used to compare the time required for omnivorous and carnivorous carabid to capture, kill, and consume passive (black cutworm) and active (green cloverworm) prey types.

	Black cutworm	Green cloverworm	Total replicates
<i>H. pensylvanicus</i>	15	5	20
<i>A. sanctaecrusis</i>	9	3	12
Omnivores	24	8	32
<i>C. tricolor</i>	11	3	14
<i>P. chalcites</i>	8	7	15
Carnivores	19	10	29

Table 1.5. Eigenvalues and intraset correlations (weights) of morphological characteristics for the four PCA axes.

Axis	1	2	3	4
Eigenvalues	0.581	0.235	0.098	0.046
Cumulative explained variance	58.1	81.6	91.3	96.0
Intraset correlations				
Length (L)	0.770	-0.610	-0.071	-0.142
Terebral ridge (Tr)	-0.533	-0.808	0.037	0.204
Molar length (Ml)	0.661	0.164	-0.700	0.204
Width (W)	0.914	0.090	0.306	0.251
Molar width (Mw)	0.495	0.446	0.079	-0.229
Basal width (Bw)	0.784	0.011	0.085	-0.323
Incisor width (Iw)	0.837	0.270	0.146	-0.224

Table 1.6. Eigenvalues and intraset correlations (weights) of morphological characteristics and the explanatory variable guild for the four RDA axes.

Axis	1	2	3	4
Eigenvalues	0.228	0.427	0.199	0.079
Morphology-Guild correlations	0.677	0.000	0.000	0.000
Cumulative explained variance				
of morphology	22.8	65.5	85.4	93.3
of morphology - guild relation	100.0	0.0	0.0	0.0
Intraset correlations				
Length (L)	-0.245	0.853	-0.417	-0.127
Terebral ridge (Tr)	0.610	-0.101	-0.744	0.013
Molar length (Ml)	-0.107	0.685	0.510	-0.443
Width (W)	-0.567	0.685	0.155	0.412
Molar width (Mw)	-0.653	0.101	0.311	-0.067
Basal width (Bw)	-0.703	0.482	-0.044	-0.132
Incisor width (Iw)	-0.586	0.553	0.304	0.152

Table 1.7. ANCOVA results for the effect of mandible morphology, food type (cutworms, fly pupae, or seeds), and their interaction on handling time in laboratory no-choice feeding experiments. Beetle length (BL) was included in the model as a covariate to remove the effect of body size on handling time. Iw = Incisor tip width; Tr = terebral ridge length; Mw = molar width.

Effect	ndf, ddf	F	P
BL	1, 149	8.56	0.004
Iw	1, 149	4.20	0.042
Tr	1, 149	1.20	0.275
Mw	1, 149	2.62	0.107
Food type	2, 149	19.06	<0.001
Tr*Food type	2, 149	3.41	0.036
Mw*Food type	2, 149	3.45	0.034

Table 1.8. Intercept and slopes of predicted lines for the interactive effects of mandible characteristics (Tr = terebral ridge length, Mw = molar width) and food type plotted against handling time in laboratory no-choice feeding experiments.

Effect	Factor	Cutworm	Pupae	Seed
		Estimate ± SE		
Food type	Intercept	7.72 ± 0.40 a	7.66 ± 0.40 a	9.45 ± 0.40 b
	$t_{149}; P$	19.42; < 0.001	20.01; < 0.001	22.63; < 0.001
Tr *	Slope	4.21 ± 1.80 a	1.35 ± 1.77 ab	-1.32 ± 1.76 b
	$t_{149}; P$	2.33; 0.021	0.76; 0.448	-0.75; 0.455
Mw *	Slope	-14.24 ± 4.77 a	-3.40 ± 4.99 ab	0.13 ± 5.04 b
	$t_{149}; P$	-2.98; 0.003	-0.68; 0.497	0.03; 0.980

Table 1.9. ANCOVA results for the effect of carabid guild, prey type [cutworms (passive) or cloverworms (active)], and their interaction on handling time in laboratory feeding trials. Beetle length and prey length were included in the model as covariates.

Effect	Number of attacks		Kill time		Consumption time		Total handling time	
	F _{1,47}	P	F _{1,48}	P	F _{1,48}	P	F _{1,48}	P
Beetle length	0.27	0.604	0.92	0.342	2.54	0.118	2.61	0.113
Prey length	16.53	< 0.001	2.88	0.096	42.55	< 0.001	43.27	< 0.001
Guild	2.64	0.111	8.16	0.006	15.86	< 0.001	17.13	< 0.001
Prey	7.75	0.008	6.17	0.017	9.28	0.004	9.76	0.003
Guild*Prey	0.08	0.783	1.15	0.289	0.66	0.422	1.04	0.313

Figures

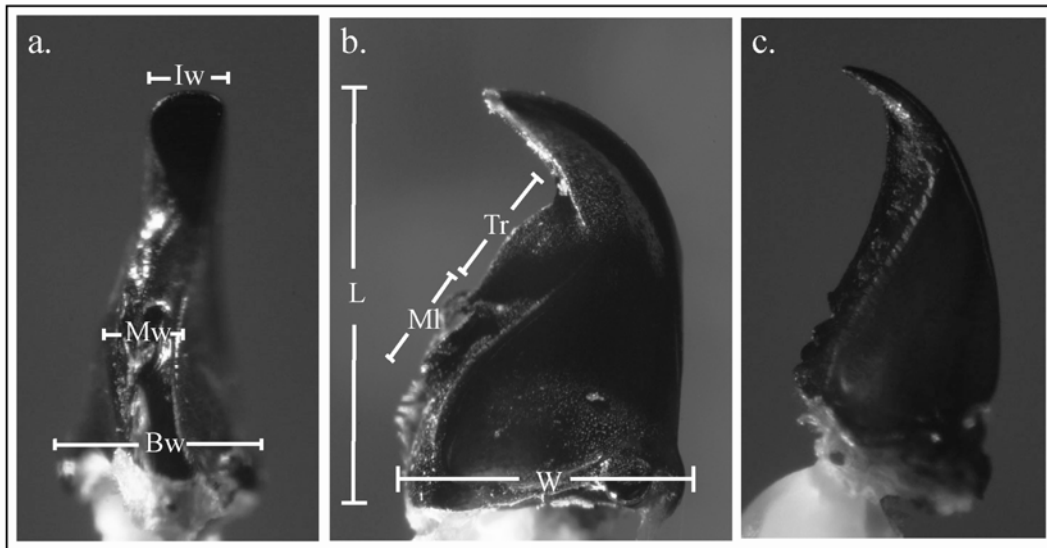


Figure 1.1. Representative carabid mandibles from the omnivorous carabid beetle *Anisodactylus ovularius* (a. lateral, b. ventral perspective) and the carnivore *Chlaenius tricolor* (c. ventral perspective). Measured mandibular characteristics are shown as bracketed lines in a. and b: L = length; W = width; Tr = terebral ridge; Ml = molar length; Mw = molar width; Iw = Incisor width; Bw basal width.

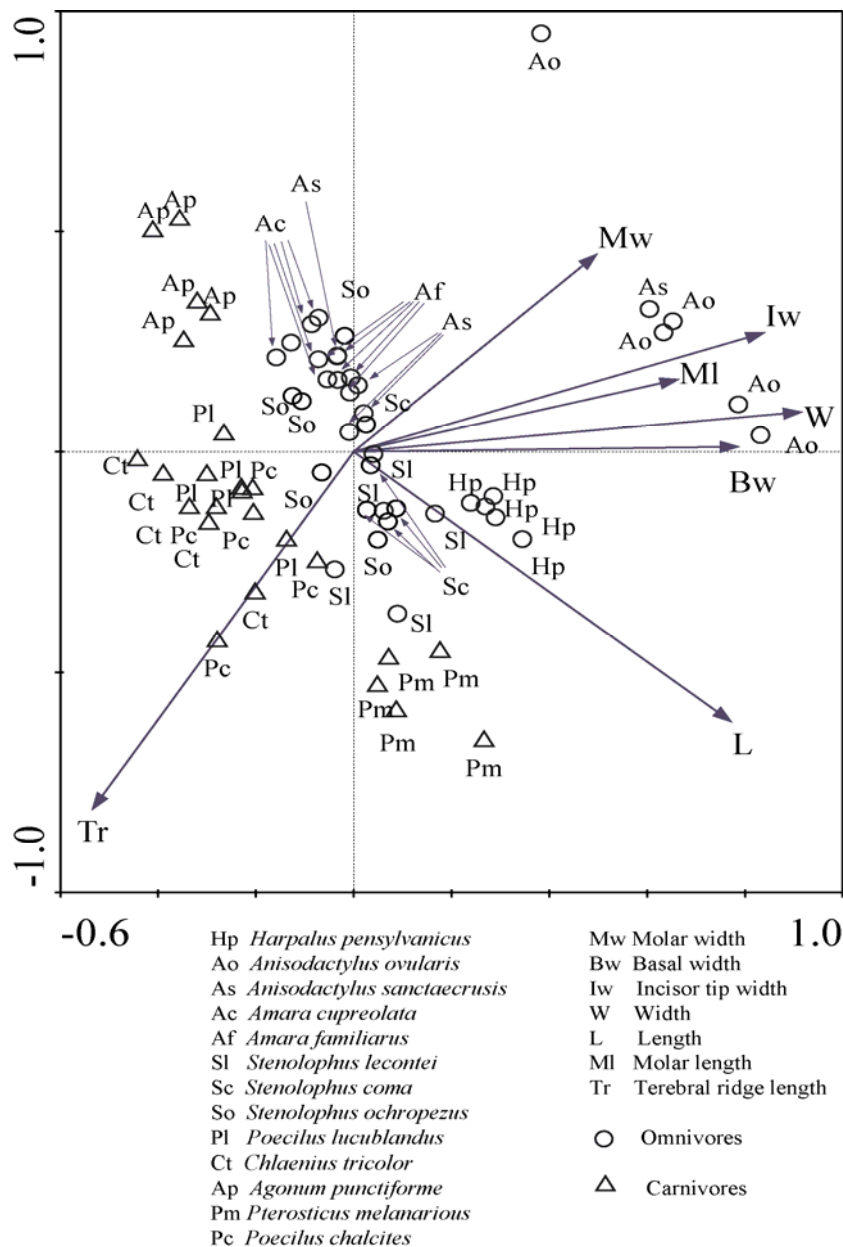


Figure 1.2. Biplot of the PCA that relates mandibular characteristics to omnivorous and carnivorous carabids from 13 species. Measurements from each individual beetle were standardized by body length. Carnivorous species are located primarily in the bottom left quadrant and defined by long terebral ridges which was highly negatively weighted on the first (x) and second (y) axes. In contrast, width, molar width, and incisor width are larger in omnivores placed in positive space on the first and second axes. See table 1.2 for eigenvalues and weights of each characteristic.

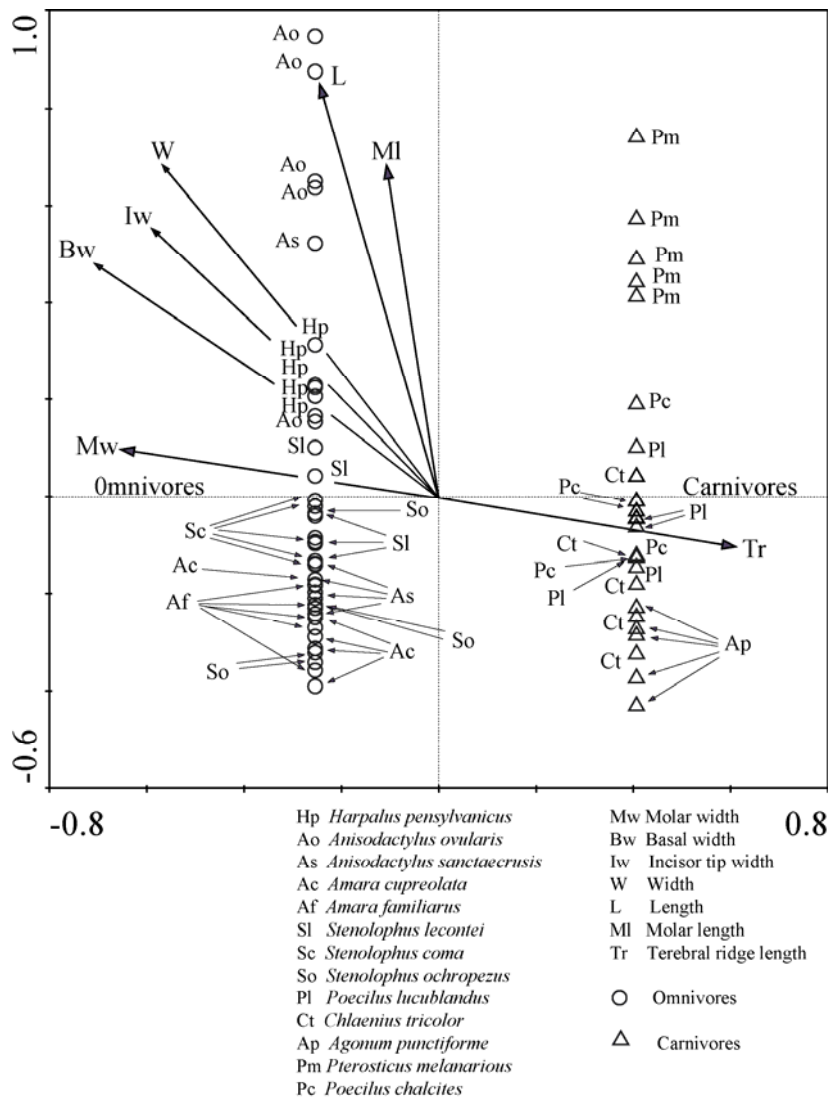


Figure 1.3. Triplot of the RDA that compared mandibular characteristics between omnivorous and carnivorous carabids from 13 species. Measurements from each individual beetle were standardized by body length. Carabid guilds are separated on the first (x) axis primarily by differences in terebral ridge length (longer in carnivores) and molar width (wider in omnivores as indicated by the long Tr and Mw arrows that are nearly parallel to that axis). Guild were significantly different (F -ratio = 18.614; P = 0.002) based on a Monte Carlo permutation test. See table 1.3 for eigenvalues and weights.

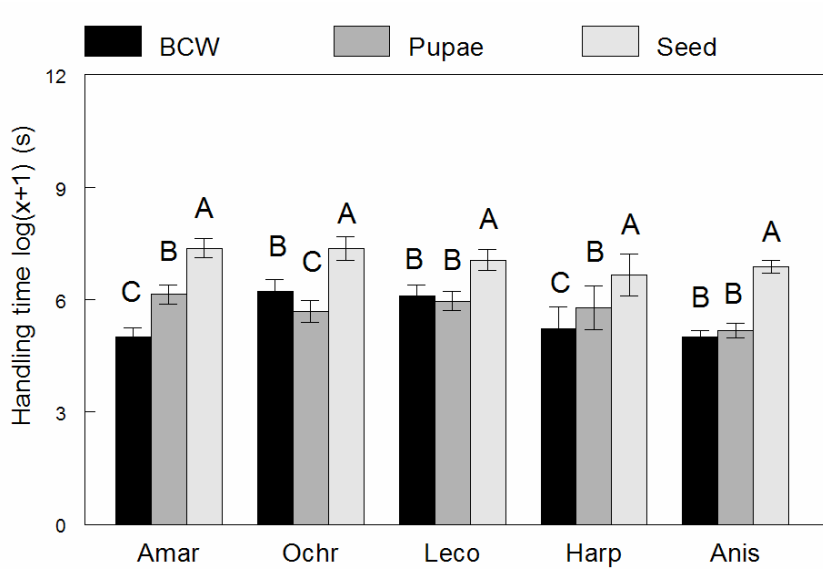


Figure 1.4. Average handling time [$\log(x+1)$ transformed and adjusted for beetle length] required by five species of omnivorous carabid beetles to consume cutworms, fly pupae, or seeds. Amar = *Amara familiaris*; Ochr = *Stenolophus ochropezus*; Leco = *Stenolophus lecontei*; Harp = *Harpalus pensylvanicus*; Anis = *Anisodactylus sanctaecrucis*. Bars within a species that share a letter are not significantly different ($P > 0.05$).

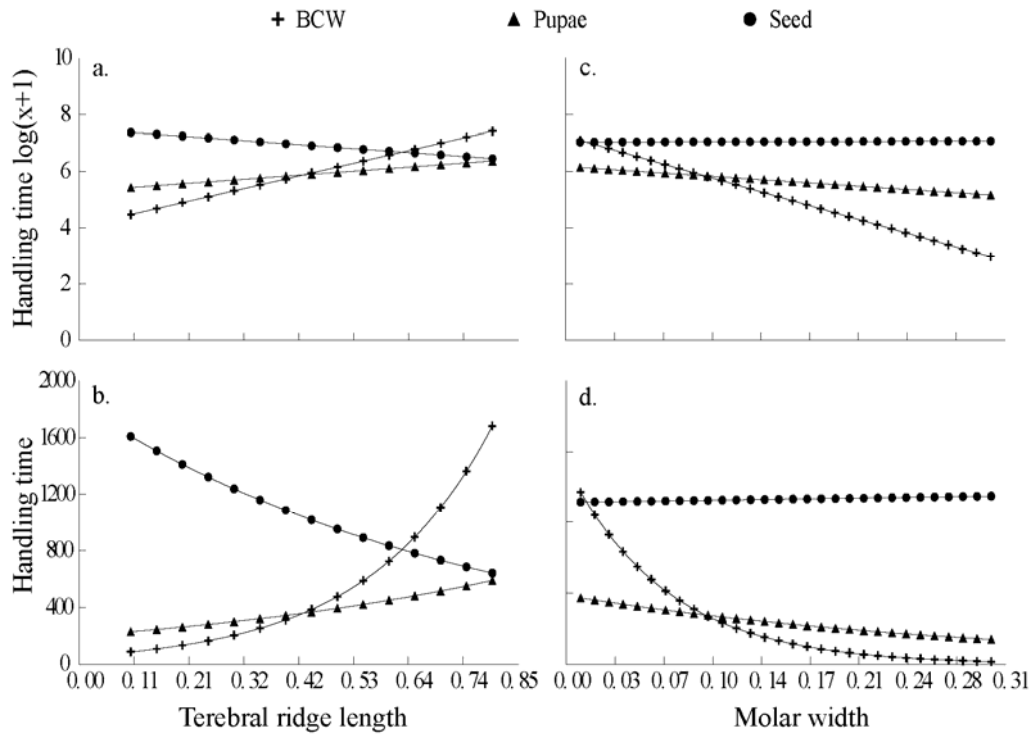


Figure 1.5. Relationship between handling time and the length of the terebral ridge (mm) (a and b) and handling time and the width of the molar area (mm) (c and d) for omnivorous carabid beetles fed three food types: black cutworms (BCW), fly pupae, and seeds. Handling time is presented as $\log(x+1)$ transformed prior to analysis (a and c) and back transformed data (b and d). Figures present predicted lines based on final regression models. Regression models are: $y_{BCW} = 7.7227 - 0.2753*Bl + 4.2080*Tr + 5.2521*Tw - 14.2362*Mw$; $y_{Pupa} = 7.6624 - 0.2753*Bl + 1.3462*Tr + 5.2521*Tw - 3.3874*Mw$; $y_{Seed} = 9.4533 - 0.2753*Bl - 1.3157*Tr + 5.2521*Tw + 0.1263*Mw$; where Bl = beetle length, Tr = terebral ridge length, Tw = tip width and Mw = molar width. See Table 1.7 for statistical results and Table 1.8 for slope and intercept comparisons.

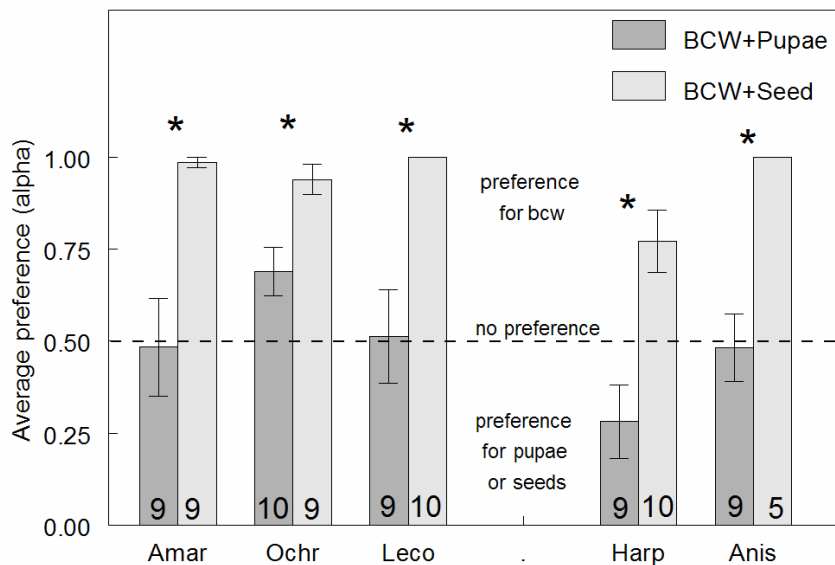


Figure 1.6. Average preference (α) of omnivorous carabid species for cutworms versus fly pupae or seeds. Values of α close to 1 indicate a strong preference for cutworms while values close to 0 indicate a strong preference for seeds or pupae. Individuals that did not eat any food items were excluded from analysis. Numbers within bars indicate the number of individuals (out of 10) that were included in the analysis. Asterisks indicate a significant within-carabid-species difference between preference for cutworms when seeds or pupae are present. Amar = *Amara familiaris*; Ochr = *Stenolophus ochropezus*; Leco = *Stenolophus lecontei*; Harp = *Harpalus pensylvanicus*; Anis = *Anisodactylus sanctaecrucis*.

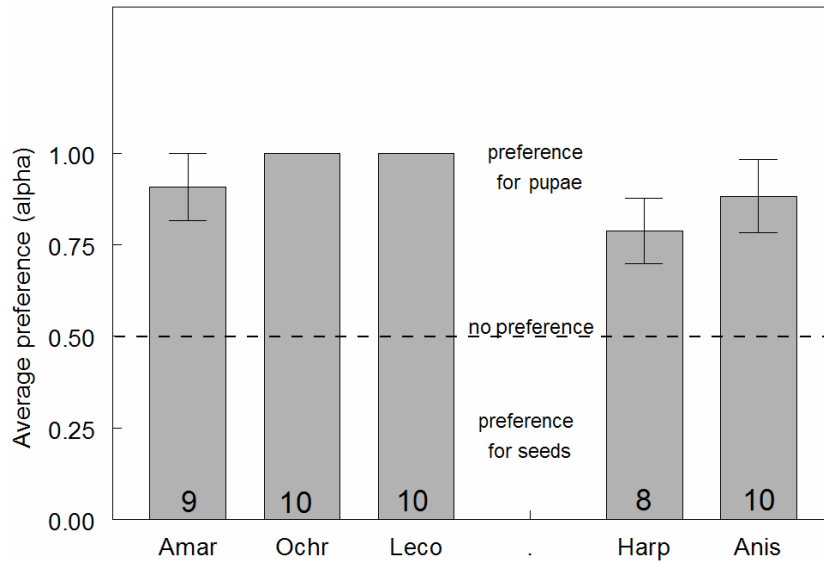


Figure 1.7. Average preference (α) of omnivorous carabid species for fly pupae versus seeds. Preferences among species were not significantly different ($P > 0.05$). Amar = *Amara familiaris*; Ochr = *Stenolophus ochropezus*; Leco = *Stenolophus lecontei*; Harp = *Harpalus pensylvanicus*; Anis = *Anisodactylus sanctaecrucis*. Numbers within bars indicate the number of beetles that consumed at least one food item and could then be included in the analysis.

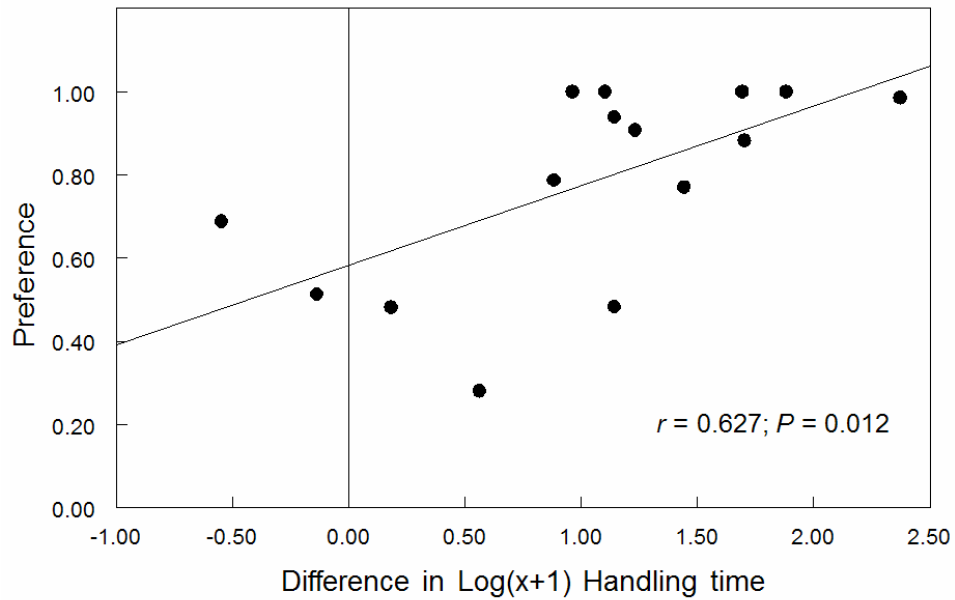


Figure 1.8. Correlation between the difference in mean handling time between food type i and food type j and the mean preference (α) for food type i . In general, as the difference in handling time between food type i and j increases (e.g. cutworms and seeds) preference for food type i (e.g. cutworms) becomes stronger.

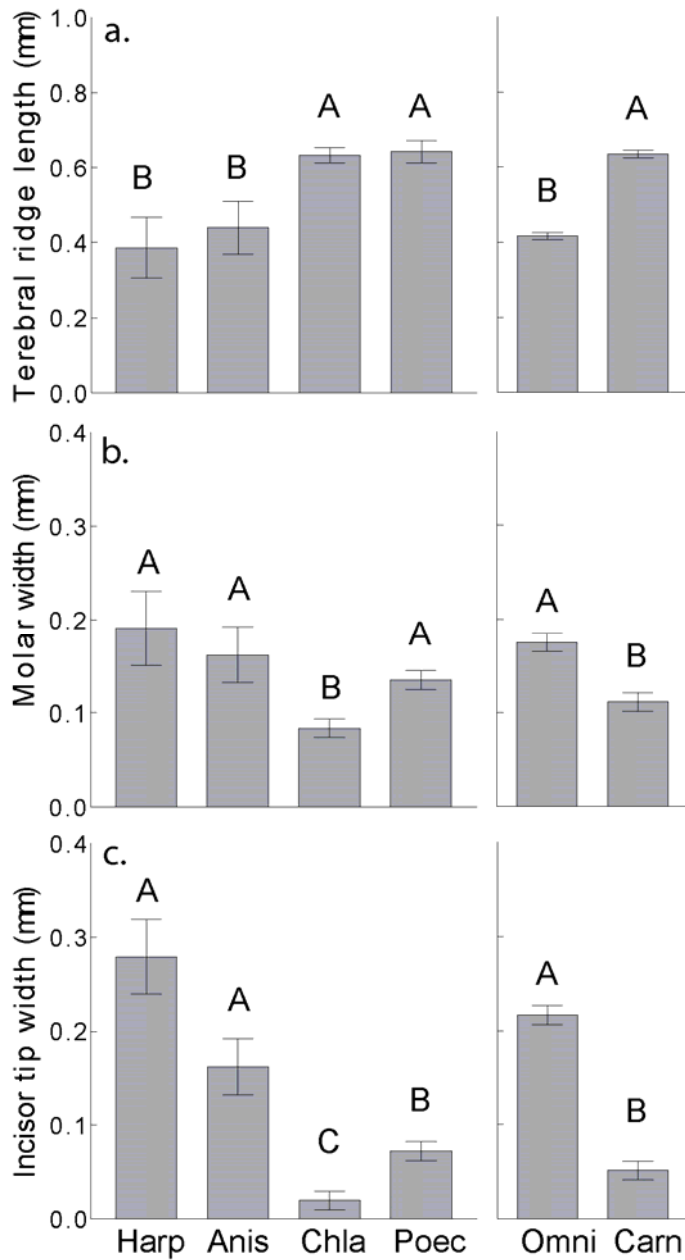


Figure 1.9. Differences in the length of terebral ridge (a), width of molar area (b), and width of incisor tip (c) among omnivorous (Harp and Anis) and carnivorous (Chla and Poec) carabid species and between carabid guilds. These 3 mandibular characteristics serve important functions in handling prey. Harp = *Harpalus pensylvanicus*, Anis = *Anisodactylus sanctaecrucis*, Chla = *Chlaenius tricolor*, Poec = *Poecilus lucublandus*, Omni = combined omnivores, and Carn = combined carnivores. For each characteristic, bars that share the same letter within the species or guild graph are not significantly different ($P > 0.05$).

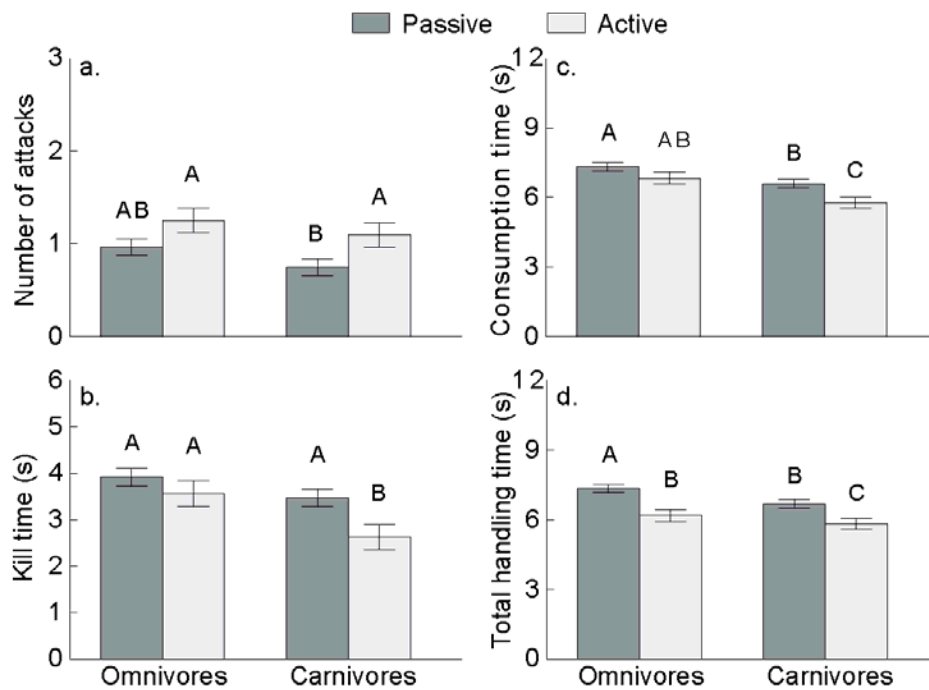


Figure 1.10. (a) Number of attacks required to capture prey, (b) time required to kill prey, (c) time required to consume prey, and (d) total handling time (kill time + consumption time) for omnivorous and carnivorous carabids presented with passive (black cutworms) and active (green cloverworms) prey. Times were $\log(x+1)$ transformed prior to analysis. Bars within a graph that share the same letter are not significantly different ($P > 0.05$).

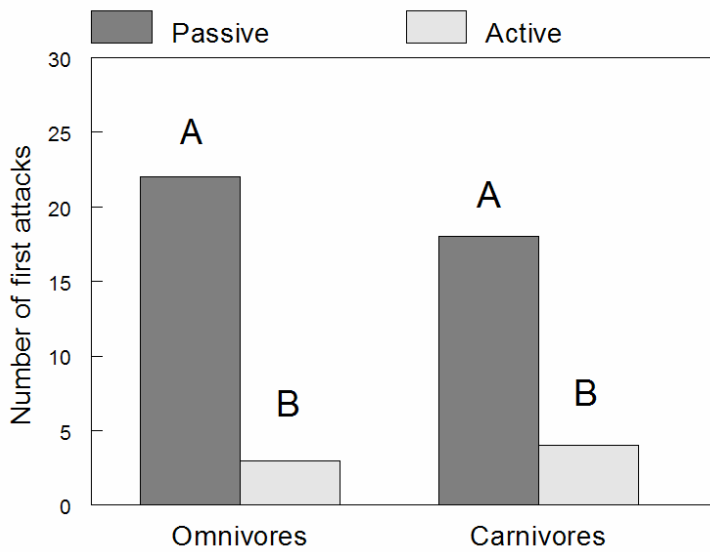


Figure 1.11. The number of first attacks by omnivorous and carnivorous carabids directed toward passive (black cutworm) or active (green cloverworm) prey in laboratory choice tests. Bars that share the same letter are not significantly different ($P > 0.05$).

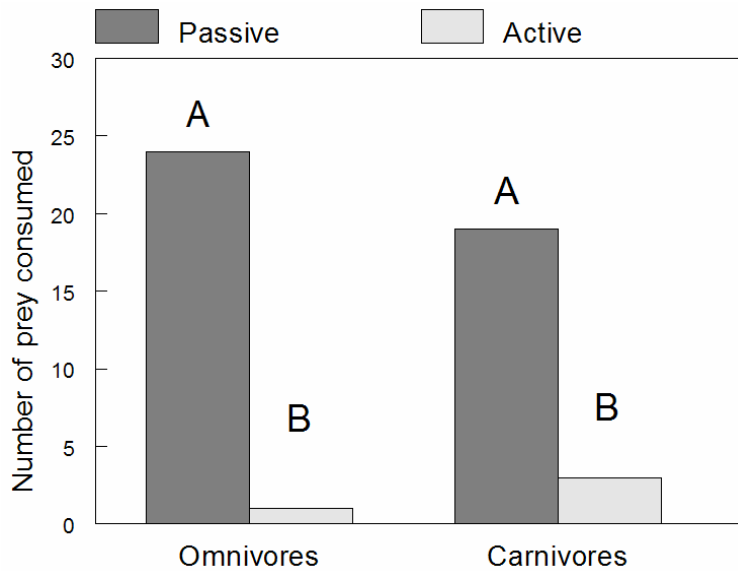


Figure 1.12. The number of passive (black cutworm) or active (green cloverworm) prey consumed by omnivorous and carnivorous carabids in laboratory choice tests. Bars that share the same letter are not significantly different ($P > 0.05$).

Chapter 2: Consequences of omnivory and alternative food resources for herbivore suppression and the strength of trophic cascades

Abstract

Omnivorous predators increase the reticulate nature of food webs and often dampen trophic cascades to basal resources. Although considerable research has investigated the impact of intraguild predators on prey suppression, less work has focused on omnivorous predators that consume both plant and prey resources. Such ‘true omnivores’ are more common in nature than previously thought and they likely play a unique role in trophic dynamics. The way in which alternative resources (plants and prey) affect consumption of herbivores by true omnivores and carnivorous predators will influence the role of each guild in trophic dynamics. In this research I investigate the impact of alternative plant resources (grass seeds) and prey (fly pupae) on the consumption of herbivores (black cutworm) and trophic cascades by omnivorous and carnivorous predators, specifically carabid beetles. In addition, I investigate how plant and prey resources affect carabid tenure time, aggregation, and the guild composition of the carabid community.

In laboratory feeding trials and large field cages, two carabid guilds (carnivore and omnivore) were crossed with three alternative food treatments (no alternative food, pupae added, seeds added) to test their interactive effect on herbivore and plant (corn seedlings) survival. Carnivorous carabids had a strong preference for cutworms

over either alternative food type in laboratory feeding trials. In contrast, omnivores preferred seeds and pupae over cutworms and consumed up to 69% fewer cutworms when alternative food was present. Consequently, in field cages where omnivores were supplied with seeds as alternative food, corn seedlings suffered greater mortality from cutworms than in the other omnivore or carnivore treatment combinations. Thus, alternative plant resources but not prey dampened trophic cascades induced by omnivores.

In field plots subsidized with seeds or fly pupae, I found that seeds increased the tenure time of omnivorous carabids twice as much as did the pupal supplement. Furthermore, omnivores were more abundant in plots subsidized with seeds whereas carnivores did not respond numerically to either food supplement. Altogether, results indicate that true omnivores interact more strongly with plant resources than with alternative prey, a response which promotes their local aggregation, relaxes predation on herbivores, and enhances herbivore effects on basal resources. I provide evidence that the trophic origin of alternative food interacts with predator guild to drive the strength of trophic cascades.

Introduction

Omnivores, including predators that feed on prey as well as plant resources and intraguild predators that feed on herbivores and other predators, are now recognized important components of most ecosystems (Polis and Strong 1996; Rosenheim 1998; Coll and Guershon 2002). As such, research investigating the role of these consumers in trophic dynamics and ecosystem function is becoming increasingly common. Omnivores, by consuming resources across multiple trophic levels, increase the reticulate nature of food webs and thereby contribute to food web stability (Fagan 1997; McCann et al. 1998). Thus, as consumers spread their resource use throughout a food web, their impact on particular herbivore species is often reduced which can dampen trophic cascades (Polis et al. 1989; Rosenheim et al 1993; Polis and Strong 1996; Finke and Denno 2003, 2004, 2005). However, much of the research regarding the impact of omnivorous “predators” on the suppression of herbivores and trophic cascades has investigated “intraguild predators” (Rosenheim 1998). Far less work has focused on omnivorous predators that consume both plant and prey based resources. These so-called “true omnivores” are more common in nature than previously thought and they likely play a unique role in trophic dynamics as they consume herbivorous prey but also compete with herbivores for basal resources (Coll and Guershon 2002; Eubanks 2005). If broad patterns of resource use of omnivorous predators prevail, the traditional and simple linear food chain modules, as conceived by Hairston et al. (1960), are insufficient to predict the impact of

“predators” on basal resources and ecosystem function (Hunter and Price 1992; Polis and Strong 1996).

Plant-based resource subsidies acting as alternative food can affect the impact of omnivorous predators on herbivorous prey if predator survival becomes less dependent on herbivorous prey (Holt and Lawton 1994; Polis et al. 1997). For example, alternative food can result in reduced consumption of herbivores if predators become satiated or switch to feed on such alternative resources that may be either preferred or simply more abundant (McMurtry and Scriven 1966a, b; Chesson 1989; Eubanks and Denno 2000b; Koss and Snyder 2005). By contrast, alternative plant resources can also attract or retain predators in a habitat with dire consequences for herbivores (McMurtry and Scriven 1966a, b; Settle et al. 1996; Eubanks and Denno 2000a; Harmon et al. 2000; Halaj and Wise 2002; Musser and Shelton 2003; Shrewsbury and Raupp 2006). Therefore, in a response analogous to apparent competition between herbivore species, predation of herbivores may increase if alternative food promotes higher-than-usual predator populations over the long term by increasing predator immigration or diminishing their emigration (McMurtry and Scriven 1966a, b; Holt and Lawton 1994; Settle et al. 1996; Eubanks and Denno 2000a; Harmon et al. 2000). In other cases, even when resource subsidies increase predator abundance, there can be no change or a decline in the predation rate of focal prey (Halaj and Wise 2002; Musser and Shelton 2003). A general lack of theoretical and empirical understanding of the consequences of alternative food resources and omnivorous predators for trophic cascades is reflected in the mixed success of biological control efforts (Gurr et al. 2000).

The potential for plant resource subsidies to alter guild composition and the structure of predator communities is a largely unexplored mechanism by which alternative food could affect food-web dynamics. The movement of omnivorous predators in and out of patches in response to plant-resource availability could change the species or guild composition (omnivores versus strict carnivores) of the predator community. As strictly carnivorous predators aggregate in response to herbivores, detritivores or intraguild prey (Polis and Hurd 1995; Chen and Wise 1999; Gratton and Denno 2003), or omnivorous predators respond to plant resources (McMurtry and Scriven 1966a, b; Eubanks and Denno 2000a; Harmon et al. 2000), the proportion and diversity of predator from different feeding guilds could change. If differences exist in the efficacy of each guild at suppressing herbivore populations, such shifts in community composition could have important consequences for the occurrence and strength of trophic cascades (Finke and Denno 2005).

Due to differences in the feeding preferences of predators, food resources from different trophic levels likely differ in their effects on predator behavior, aggregation, and impact on herbivores (Eubanks and Denno 2000a; Finke and Denno 2005). Therefore, interactions between intraguild predators and high-quality prey (herbivores or other predators) may differ in their effects on herbivores from omnivorous predators that include lower-quality plant food in their feeding repertoire. Research comparing the role of omnivorous predators (plant and prey consumers) with that of strict predators (herbivore and intraguild prey consumers) on food-web dynamics is lacking, although it is predicted that the population and trophic dynamics of true omnivores differ from other trophic omnivores (Pimm and Lawton 1978).

Existing research on the interactive effects of omnivorous predators and alternative food on herbivore populations has focused on single species of omnivorous predator (McMurtry and Scriven 1966a, b; Cottrell and Yeargan 1998; Agrawal et al. 1999; Eubanks and Denno 1999, 2000a; Agrawal and Klein 2000). However, the impact of individual predator species on prey can differ dramatically (Chalcraft and Resitarits 2003; Finke and Denno 2005; Wilby et al. 2005; Straub and Snyder 2006). Therefore, research using replicated species within a trophic level or guild is required if generalizations are to be made about the differential impacts of omnivorous and carnivorous predator guilds on herbivore populations and trophic cascades (Finke and Denno 2005).

This research investigates the impact of plant (grass seeds) and prey (fly pupae)-based alternative foods on the consumption of co-occurring herbivores (black cutworms) and trophic cascades by omnivorous and carnivorous predators (carabid beetles). Moreover, in this study replicate species of omnivorous and carnivorous predators were used to isolate the effects of predator species from predator guild. This experimental design yields the ability to test whether species within a guild respond similarly to alternative foods and therefore increases the likelihood that results reflect general phenomena relevant to other predators and systems. Using a blend of laboratory and field experiments, the specific objectives of this research were to determine: (1) the preferences of omnivorous and carnivorous carabids for herbivores when alternative plant and prey resources are available, (2) the effects of alternative plant and prey food resources on the consumption of herbivores by omnivorous and carnivorous carabid beetles, (3) how carabid feeding guild and

alternative food resources interact to affect herbivory with cascading effects to basal resources, (4) if the presence of alternative plant and prey resources affect the tenure time of omnivorous and carnivorous carabids in field plots, and (5) how alternative food supplements affect the abundance and community composition of omnivorous and carnivorous carabid predators in the field. In a companion study I found that omnivores are less efficient at capturing and consuming active herbivorous prey than carnivores (see Chapter 1). Based on this finding, I predict that omnivores will prefer both alternative foods (less active) over herbivores (more active), thus reducing their consumption of herbivores which in turn will adversely affect plant survival. Therefore, it is expected that alternative food will dampen trophic cascades initiated by omnivores to a greater extent than carnivores. In addition, I hypothesize that both alternative food types will increase tenure time and aggregation by omnivores, whereas carnivores will respond numerically only to pupal subsidies. Together, these experiments aim to provide new insight into the interactive effects of resource subsidies and predator feeding guilds on food-web dynamics.

Methods

Study system

Carabid beetles comprise a family of carnivorous and omnivorous predators that abound in most managed and natural systems (Lövei and Sunderland 1996; Kromp 1999). Carabids are of interest to many researchers due to their potential value in controlling populations of economically important herbivorous pests. However, the

ability of carabid beetles to suppress herbivore populations has received mixed support in the ecological and biological control literature, due in part to experimental manipulations that make it difficult to isolate the effect of carabids from other predators (Kromp 1999). For example, manipulations used to enhance conservation biological control such as the establishment of beetle banks (spatial refuges), while often successful in enhancing carabid abundance, also increase the abundance of alternative prey, plant resources, habitat complexity, and other predators such as spiders (Thomas et al. 1991; Kromp 1999; Landis et al. 2000; Frank and Shrewsbury 2004a).

Many carabid species are true omnivores, consuming both plant resources (seeds) and prey whereas other carabids are strict carnivores (Lövei and Sunderland 1996). Little work has investigated how alternative food affects the distribution of carabids or their consumption of herbivores. Moreover, no research to my knowledge has investigated how omnivorous and carnivorous carabids might respond differently to alternative food, or how alternative food type affects their ability to promote trophic cascades. Due to their ubiquity, economic importance, and the co-occurrence of omnivorous and carnivorous species, carabids serve as an ideal trophic group to address questions of omnivory and alternative food as they relate to herbivore suppression and food-web dynamics.

For my experiments, five carabid species, two omnivores and three carnivores, were selected, all similar in size to minimize differences in size-related mobility and prey handling ability. The two omnivorous species, *Harpalus pensylvanicus* and *Anisodactylus ovularis*, are known to consume seeds, lepidopteran

larvae, and other prey (Best and Beegle 1977a; Baines et al. 1990; Frank *unpublished data*). Selected carnivorous species were *Poecilus lucublandus*, *Scarites substriatus*, and *Chlaenius tricolor*, all of which consume lepidopteran larvae, pupae, and other prey, but not seeds (Best and Beegle 1977a, Barney and Pass 1986; Baines et al. 1990; Frank *unpublished data*). Beetles used in experiments were collected in Maryland corn fields using pitfall traps and they were subsequently held in plastic bins with moist peat moss and fed dog food. Corn is attacked by a number of herbivorous insects (Willson and Eisley 2001; Bessin 2003). One of the first pests to damage corn in spring is the black cutworm, *Agrotis ipsilon* (Hufnagel) (Lepidoptera: Noctuidae), which was selected as the focal herbivore in this research (Willson and Eisley 2001). Cutworms damage young corn from seedling emergence to the time it has four to five leaves. Early-instar (1st-3rd) cutworms feed on the leaves of corn. Larger cutworms (4th and 5th instars) cut down corn seedlings by chewing at or below ground level and then consume the entire fallen plant. When seedlings are cut, the meristem is destroyed which leads to plant death and reduced plant biomass and crop yield. Cutworm larvae and pupae are susceptible to carabid predation (Best and Beegle 1977b; Brust et al. 1985, 1986; Frank and Shrewsbury 2004b), and experimentally increasing the abundance of carabid predators in the field can increase predation of cutworms (Brust et al. 1985, 1986, Frank and Shrewsbury 2004a). Because cutworms and carabids co-occur in many other agricultural crops and ornamental plantings (Showers 1997), results from the corn system have broad implications for other managed systems.

Alternative prey species for carabids such as detritivores are abundant in corn ecosystems (Dively 2005). Diptera have been shown to emerge from corn fields at densities of 272/m² every two weeks (G. Dively *personal communication*). Many carabid species are known to feed on dipteran eggs and pupae (Kromp 1999). Thus, for the research proposed here, fruit fly pupae, *Drosophila melanogaster* Meigen (Diptera: Drosophilidae) were used as alternative prey. Seeds from a variety of weeds are also very abundant in corn fields, occurring at densities in the thousands to tens-of-thousands per square meter (Davis et al. 2005; Swanton et al. 2006). Bluegrass, *Poa pratensis* (Cyperales: Poaceae), seeds were used as alternative plant food in this research because they are readily consumed by carabids and because members of the genus *Poa* are common agricultural weeds (Uva et al. 1997). Carabid beetles have been reported to consume all of these food items and they readily encounter them under natural conditions (Lövei and Sunderland 1996; Kromp 1999). Therefore, a corn agro-ecosystem with its complement of omnivorous and carnivorous carabids, alternative prey (detritivorous dipterans), and seeds provides an ideal system to test the interactive effects of predator feeding guild (omnivore versus carnivore) and alternative food resources (*Drosophila* pupae and *Poa* seeds) on beetle aggregation, herbivore suppression, and primary production (corn seedlings).

Effect of carabid feeding guild and alternative food resources on food preference and consumption of herbivores

Laboratory experiments were conducted using each carabid species (2 omnivores and 3 carnivores) to evaluate how carabid guild (omnivore or carnivore)

and alternative food type (grass seeds or fly pupae) affected its preference for herbivores (cutworms), seeds, and pupae (Objective 1) and its consumption of herbivores (Objective 2). Choice experiments were conducted in 14 cm petri dishes, each with one of four combinations of food resources: cutworm only (no alternative food), cutworm and pupae, cutworm and seeds, and seeds and pupae. In order to maintain similar amounts of each food type it was determined 15 pupae or 15 moist seeds were equivalent in mass to a single 2nd-instar cutworm. Therefore, 5 cutworms and 75 alternative food items were placed in the cutworm-pupae and cutworm-seed treatment dishes and 75 of each food item were placed in the seed-pupae treatment dishes. Beetles were starved (water only) for 24 hours prior to the experiment. At the start of the experiment, one beetle was placed in each petri dish and dishes were placed in a dark environmental chamber set at 27° C. All dishes were removed from the chamber and the number of food items eaten was recorded after 1 and 4 hours. Each of the 4 treatment combinations (cutworm-only, cutworm-pupae, cutworm-seed, seed-pupae) was replicated 10 times for each beetle species (20 replicates of omnivores and 30 replicates of carnivores). Data were used in factorial designs to test the effect of carabid guild (omnivore or carnivore) and alternative food type on: (1) carabid preference for cutworms compared to alternative food types (pupae or seeds); (2) the consumption of cutworms in 3 food-type environments (no alternative food, pupae only, seeds only); (3) the consumption of and preference for seeds when prey is available (cutworm or pupae) and the consumption of and preference for pupae when cutworms or seeds are available (cutworm-pupae, seed-pupae). To determine whether individual carabid species within guilds responded to food

treatments similarly, the comparisons described above were also conducted replacing the main effect of guild with carabid species.

Preference is best measured before any of the food items are depleted so that the carabids' first choices are evident (Chesson 1983). Preference was calculated from the number of each food item eaten at the 1-hour 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 number of food type 1 and 2 present at the beginning of the experiment and R_i and R_j are the number of food type 1 and 2 that were eaten (Chesson 1978, 1983). This index ranges from 0 to 1 where an α of 0.5 indicates no preference, an α close to 1 indicates a preference for food type 1, and an α close to 0 indicates a preference for food type 2. As such, α values can be compared and analyzed using standard parametric methods (Chesson 1978, 1983).

Statistical analysis. ANOVA was used to test the effects of carabid guild, alternative food type, and their interaction on the preference (α) for cutworms compared to seeds or pupae at hour 1 of the laboratory feeding trials (SAS 2002). The preference for pupae compared to seeds did not meet the assumptions of ANOVA and were analyzed by a Kruskal-Wallis test in the FREQ procedure of SAS (2002). The analyses of preference were also conducted replacing carabid guild with carabid species as a main effect to evaluate differences in the response of species within the guilds.

ANOVA followed by LSD means comparisons was used to test the effects of carabid guild, alternative food type, and their interaction on the number of cutworms,

seeds, or pupae eaten at hour 4 in the laboratory feeding trials (SAS 2002). The analyses of prey consumption were also conducted replacing carabid guild with carabid species as a main effect to evaluate differences in the response of species within the guilds.

Effects of carabid feeding guild and alternative food on herbivory and seedling survival

A 2 x 3 factorial design was used to test the interactive effects of carabid guild (omnivore or carnivore) and alternative food (no alternative food, seeds, or pupae) on herbivory with cascading effects to corn seedling survival and biomass (Objective 3). Each of the six treatment combinations was applied randomly to a large field cage (2 x 2 x 2 m) and the six cages constituted a complete replicate block. Five and four replicates of each block were completed in the summers of 2005 and 2006, respectively. Within a replicate block, a single omnivorous species was paired with a single carnivorous species. The omnivorous and carnivorous species used for each pair varied among blocks. To complete the nine replicates, the omnivores *H. pensylvanicus* and *A. ovularis* were used in 4 and 5 replicates respectively. The carnivores *P. lucublandus*, *S. substriatus*, and *C. tricolor* were used in 3, 5, and 1 replicate respectively. The experiment was conducted at the University of Maryland Paint Branch Turfgrass Facility, Central Maryland Research and Education Center (CMREC) in College Park, MD.

To remove ambient arthropods and seeds, the soil inside of each cage was excavated to a depth of 6 cm. Cages were then refilled with seed- and prey-free

topsoil. Organic sweet corn seedlings were raised in the greenhouse to a height of 6 cm (two leaf stage). In the morning of the day each cage was set up, three rows of ten corn seedlings were planted in each cage and watered. At 17:00 h alternative food treatments were added at a rate of 800 seeds or pupae / m². Subsequently, thirty 2nd instar cutworms were added to each cage. One cutworm was placed approximately 3 cm from each corn seedling. Cutworms were given one hour to acclimate, after which (18:00 h) 4 beetles of a single species were released under a 6 x 16 cm board in the center of each cage. Cages were monitored daily for five days to record the number of plants (1) cut (cutworm chewing at the base), (2) defoliated (cutworm herbivory on the leaves), and (3) damaged (cut + defoliated). After recording plant damage on day five, all plants were harvested (cut at soil line), dried, and weighed.

Statistical analysis. Repeated measures ANOVA with an unstructured covariance matrix followed by LSD means comparisons was used to test the effect of carabid guild, alternative food type, and their interaction on the number of seedlings damaged and cut in the field cage experiment (SAS 2002). ANOVA followed by LSD comparisons was used to test the effect of carabid guild, alternative food type, and their interaction on seedling dry biomass. The date of each trial was included as a block in both analyses (SAS 2002).

Effect of alternative food type and feeding guild on carabid tenure in food subsidized plots

A mark-recapture experiment was conducted in fenced field plots to determine the effect of alternative food (seeds and dipteran pupae) on the emigration of

omnivorous and carnivorous carabids from the center to the edge of plots (Objective 4). Eight fenced plots (2.5 x 2.5 m) were established in the field at CMREC (Figure 2.1). Each plot was surrounded by aluminum flashing to prevent movement of arthropods in and out of the study plots (Figure 2.1). The bottom edge of the flashing was buried 6 cm below the soil leaving a 24 cm barrier above the soil surface. Soil within the plots was excavated to a depth of 6 cm to remove seeds and arthropods. The original soil was then replaced with clean topsoil that did not contain seeds or arthropods. Soil around the inner edge of each plot was packed down resulting in a 0.25 m border of packed soil abutting the flashing, which surrounded a 2 x 2 m central core of loose soil. To simulate natural habitat, dead corn stalks and stubble were scattered over the 2 x 2 m central core of each plot. Prior to placement, the field-collected litter was frozen for one week at -17°C to kill any ambient arthropods. Just before the release of 4 individuals of a single carabid species at the center of each plot, alternative food items were scattered over the central area of each plot. Thus, plots consisted of a central 2 x 2 m core area of loose soil, corn litter, and alternative food (favorable habitat) surrounded by a 0.25 border of packed soil (unfavorable habitat). A pitfall trap (9 cm plastic cup) was placed in each of the 4 corners of each plot. The effect of food treatment on beetle tenure was measured by its propensity to remain at the center release point and treatment site (central core), and not disperse across the bare-ground border of packed soil to corner traps. The block of 8 plots was reused multiple times to determine the effects of alternative food treatments on carabid emigration

This experiment employed a full 2 x 2 x 2 factorial design with two carabid

guilds (omnivores or carnivores), two levels of seed addition (absent or present) and two levels of pupae addition (absent or present). The eight treatment combinations were randomly assigned to plots. Therefore, the eight plots constituted a single replicate of all treatment combinations. The experiment was replicated in time so each date of the experiment was a block. The experiment was replicated six times. In plots that were assigned to the pupae only and seed only treatments, pupae or seeds were added to the plots at a rate of 800/m² (3200/plot). The plots assigned to the pupae and seed combination treatment received 3200 of each food type. Each of the six replicates used different species of omnivores and carnivores. The omnivores used in this experiment were *A. ovularis* and *H. pensylvanicus* (3 replicated releases of each species), whereas the carnivores were *S. substriatus*, *C. tricolor*, and *P. lucublandus* (3, 2, and 1 replicated releases of each species, respectively).

One replicate consisted of the release of one omnivorous carabid species (4 individuals/plot) in each of the four food-treatment plots (no alternative food, seeds, pupae, and both seeds and pupae) and one carnivorous carabid species (4 individuals/plot) in 4 different plots containing the same four food-treatment combinations. Before release in the center of each plot, beetles were individually marked by placing a small piece of yellow electrical tape (1 mm x 4 mm) across the elytra. This procedure prevented beetles from flying and also allowed the separation of released beetles from any contaminating immigrants. Beetles were released at 18:00 hrs, approximately 2 hours before dark and one hour after food treatments were applied. After release of the beetles, the pitfall traps were checked every hour for twelve hours to record the number of beetles that remained in the plot and those that

‘emigrated’ from the release site to the corner traps. The time from the start of the experiment until an individual beetle was trapped constituted the tenure time for that beetle. In this experiment, the mean tenure time per species in each treatment plot was calculated by summing the individual tenure times of the 4 released beetles. The 6 replicate releases were conducted in July and August of 2006. After each replicate release, plots were prepared for subsequent releases by replacing the existing soil and litter with new clean topsoil and defaunated litter.

Statistical analysis. ANOVA followed by LSD means comparisons was used to test the effect of carabid guild, seeds, pupae and their interaction on the mean carabid tenure time (SAS 2002).

Effect of food subsidies on carabid aggregation and community composition

To assess the effects of plant (seeds) and prey (fly pupae) subsidies on carabid abundance and community composition (omnivores versus carnivores) in open field plots (4 x 4 m), two levels of seeds (ambient and subsidized) were crossed with two levels of pupae (ambient and subsidized) in a 2 x 2 factorial design. Thus, plots either received no food subsidy (ambient) or they were subsidized with seeds, fly pupae, or both (seeds and pupae mixed). The experiment was replicated 11 times for a total of 44 plots established at CMREC in a field where no till corn was grown the previous year. Plots were arranged in rows of four, with each row parallel to the field edge and located at least 10 m from the edge. Each row contained one plot of each treatment and constituted a complete block. Plots within blocks were spaced 6 m apart and

blocks were separated by 10 m from other blocks. The field edge constituted a possible source of carabids (Dennis and Fry 1992). The experiment was conducted three times, from 8 – 30 June, 7 – 24 July, and 22 August to 8 September 2007, when 3, 5, and 3 replicates respectively were completed.

Each experiment ran for approximately 15 days. On day 1, two pitfall traps (9 cm plastic cups) were placed in each plot. Traps could be ‘closed’ to carabids by inserting a cup of soil into the trap or ‘opened’ by inserting a cup of soapy water into the trap. On day 2, 6 rows of organic corn (NC+ Organics, hybrid 3448MF-14) seed with 30 plants per row were planted in each plot, a planting regime that complied with Maryland production specifications (McClurg and Donnelly 1999). Food supplements were applied to plots the following day (day 3) by sprinkling seeds, pupae, or both at a rate of 1200/m². Additional seeds and pupae were added at the same rate every 4-5 days to replace depleted food items.

To allow time for carabids to respond to food treatments, pitfall traps were opened 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).

Statistical analysis. ANOVA followed by LSD pair-wise comparisons 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 and the proportion of the carabid community comprised of omnivores (SAS 2002).

Results

Effect of carabid feeding guild and alternative food resources on food preference and consumption of herbivores

There was no interactive effect of carabid guild and alternative food type on the preference of carabids for cutworms compared to pupae or seeds ($F_{1,83} = 2.05$, $P = 0.156$; Figure 2.2). However, carnivorous carabids preferred cutworms significantly more than did omnivores ($F_{1,83} = 63.15$, $P < 0.001$) and there was an overall greater preference for cutworms in the presence of seeds than when cutworms co-occurred with pupae ($F_{1,83} = 13.93$, $P < 0.001$) (Figure 2.2). There was a significant interaction between carabid species and alternative food type in their preference for cutworms when seeds or pupae were present ($F_{4,77} = 4.74$, $P = 0.002$) as *H. pensylvanicus*, *P. lucublandus*, and *C. tricolor* showed a significantly stronger preference for cutworms over seeds than for cutworms over pupae whereas other species did not (Figure 2.3). The main effects of species ($F_{4,77} = 31.97$, $P < 0.001$) and alternative food on preference for cutworms were also significant ($F_{1,77} = 22.30$, $P < 0.001$). In general, carnivores exhibited a stronger preference for pupae over seeds than did omnivores, although the omnivorous *H. pensylvanicus* was an exception. These patterns are evidenced by a significant effect of carabid guild ($\chi^2 = 36.29$, $df = 1$, $P < 0.001$) and carabid species ($\chi^2 = 42.94$, $df = 4$, $P < 0.001$) on the preference for pupae over seeds (Figures 2.4, 2.5).

There was a significant interactive effect of carabid guild and alternative food type on the average number of cutworms consumed ($F_{2,144} = 5.38$, $P = 0.006$).

Omnivorous carabids consumed significantly fewer cutworms when seeds or pupae were present compared to when food alternatives were absent (Figure 2.6). In contrast, carnivore consumption of cutworms was significantly reduced only when prey (pupae) were present (Figure 2.6). The main effect of guild ($F_{1, 144} = 25.65, P < 0.001$) and of alternative food type were also significant ($F_{2, 144} = 14.63, P < 0.001$). There was also a significant interactive effect of carabid species and alternative food type on cutworm consumption ($F_{8, 135} = 3.46, P = 0.001$). This result reflects significant differences in how omnivores and carnivores respond to the seed and pupae treatments but also indicates significant interspecific differences within each guild in the number of cutworms consumed (Figure 2.7). For example, *C. tricolor* consumed significantly fewer cutworms than either of the other carnivores when alternative food was absent and when pupae were present (Figure 2.7). Likewise, *A. ovularis* consumed significantly fewer cutworms than *H. pensylvanicus* when seeds were present although both omnivores consumed similar numbers of cutworms when alternative prey was absent (Figure 2.7). The main effects of species ($F_{4, 135} = 19.53, P < 0.001$) and alternative food type ($F_{2, 135} = 16.57, P < 0.001$) were also significant.

There was a significant interactive effect of carabid guild and alternative food (cutworms or seeds) on the number of pupae consumed ($F_{1, 96} = 9.00, P = 0.003$; Figure 2.8). For instance, omnivores consumed fewer pupae in the presence of seeds than when cutworms co-occurred with pupae. In contrast, carnivorous carabids consumed more pupae in the presence of seeds than when cutworm prey was present. The main effects of guild ($F_{1, 96} = 1.20, P = 0.276$) and alternative food ($F_{1, 96} = 0.00, P = 1.000$) were not significant. There was a significant interaction of species and

alternative food type on pupal consumption ($F_{4, 90} = 5.18, P < 0.001$) because *A. ovularis* consumed significantly fewer pupae when seeds were present compared to when cutworms were present whereas treatments had the opposite effect on *S. substriatus* (Figure 2.9). The main effect of species ($F_{4, 90} = 3.60, P = 0.009$) but not alternative food ($F_{1, 90} = 0.44, P = 0.508$) was significant.

The analysis of seed consumption includes only omnivores because very few seeds disappeared from experimental arenas when the carnivorous carabids *P. lucublandus*, *C. tricolor* or *S. substriatus* were tested. Omnivorous carabids consumed significantly more seeds when offered in combination with cutworms than when offered in combination with pupae ($F_{1, 36} = 6.93, P = 0.012$) (Figure 2.10). Moreover, there was no effect of omnivore species (*A. ovularis* or *H. pensylvanicus*) on the number of seeds consumed ($F_{1, 36} = 0.34, P = 0.562$) nor was there a significant interactive effect between species and alternative food type ($F_{1, 36} = 2.33, P = 0.136$).

Effects of carabid feeding guild and alternative food on herbivory and seedling survival

There was no main effect of carabid guild or its interaction with alternative food on either the number of corn seedlings damaged (cut and defoliated) by cutworms (Tables 2.1, 2.2) or the number of seedlings cut to the ground by cutworms (Tables 2.3 and 2.4). However, there was a significant effect of alternative food type on both the number of cutworm-damaged seedlings and the number of cut seedlings because seeds but not pupae tended to increase plant damage and decrease seedling survival (Tables 2.2, 2.4; Figures 2.11 and 2.12). Both predator guild ($F_{2, 43} = 2.54; P$

= 0.091) and the type of alternative food ($F_{2, 43} = 3.53$; $P = 0.067$) resulted in marginal but non-significant effects on the dry mass of corn seedlings. In general, the biomass of corn seedlings was lowest when omnivorous carabids were subsidized with seeds (Figure 2.13). The interaction of guild and alternative food did not have a significant effect on the dry mass of seedlings ($F_{2, 43} = 0.16$; $P = 0.850$).

Effect of alternative food type and feeding guild on carabid tenure in subsidized plots

The interactive effect of guild, seed subsidy, and pupal subsidy on the average amount of time spent by beetles in plots was marginal and not significant (Table 2.5). There was a significant interactive effect between carabid guild and seed subsidy on a beetle's tenure time in experimental plots such that adding seeds significantly increased the residence time of omnivores but had no effect on carnivores (Figure 2.14). Pupal subsidies significantly increased the tenure time of beetles in both guilds equally (Table 2.5, Figure 2.14). Moreover, seed subsidies increased an omnivore's tenure time significantly more than did the pupal subsidy, whereas tenure time for carnivorous carabids was extended only in plots subsidized with both seeds and pupae (Figure 2.14).

Effect of food subsidies on carabid aggregation and community composition

Nine omnivorous and seven carnivorous carabid taxa were captured with pitfall traps in the open field plots (Table 2.6). Omnivorous carabids were

significantly more abundant in plots subsidized with seeds ($F_{1,30} = 11.01$; $P = 0.002$), whereas carnivores were not ($F_{1,30} = 0.00$; $P = 1.000$). Pupal subsidies did not affect the abundance of either omnivores ($F_{1,30} = 1.04$; $P = 0.315$) or carnivores ($F_{1,30} = 0.00$; $P = 1.000$; Figure 2.15). Moreover, there was no interactive effect between seed and pupal subsidies on the abundance of either omnivorous or carnivorous carabids ($F_{1,30} = 0.59$; $P = 0.450$; $F_{1,30} = 0.13$; $P = 0.721$). The proportion of omnivores in the carabid community increased from 0.33 ± 0.18 in controls to 0.54 ± 0.17 in plots subsidized with seeds and to 0.62 ± 0.14 in plots supplemented with both seeds and pupae ($F_{1,30} = 4.43$; $P = 0.049$). However, neither adding pupae alone ($F_{1,30} = 0.67$; $P = 0.421$) nor the interactive effect of adding seeds and pupae ($F_{1,30} = 0.01$; $P = 0.942$) significantly affected the proportion of omnivores in the carabid community.

Discussion

This research demonstrates that alternative resources can mediate the impact of omnivorous and carnivorous predators on herbivore and plant survival. Moreover, the presence of alternative plant resources altered the spatial distribution and guild composition of the carabid community. Notably, the presence of alternative resources affected the behavior and distribution of omnivores to a greater extent than that of carnivores. Fly pupae had weak effects on the consumption of cutworms and tenure time of carnivores but did not affect their distribution. For omnivores, grass seeds affected herbivore consumption, tenure time, and beetle distribution to a greater extent than did fly pupal subsidies, a more nutritious alternative.

In support of my hypothesis, omnivorous carabids consumed fewer herbivores (cutworms) in the presence of alternative food resources (seeds or pupae) than did carnivorous carabids (Figure 2.6). The number of cutworms consumed in the absence of alternative resources did not differ between feeding guilds. However, carnivores consumed 26 % fewer cutworms when pupae were present, whereas pupae and seeds reduced cutworm consumption by omnivores by 69% and 59% respectively. Therefore, the indirect effect of alternative plant or prey resources on cutworm survival is determined largely by carabid feeding guild. In comparing replicated predator guilds Finke and Denno (2005) also found that feeding guild was important. Compared to intermediate predators, intra-guild predators (trophic omnivores) had a weaker impact on herbivore populations because their broad resource use included herbivores and other predators.

Differences in herbivore predation are clarified in comparisons of feeding preference whereby carnivores preferred cutworms over pupae and seeds and omnivores preferred alternative food supplements, both seeds and pupae, to cutworms (Figure 2.2). These results may reflect differences in the aggression of carnivorous and omnivorous carabids or an aversion among omnivores to attack large, mobile prey such as cutworms. Prey characteristics such as size (Jiang and Morin 2005; Matlock 2005) and mobility (Eubanks and Denno 2000b) often influence capture success and predator foraging efficiency. Moreover, previous work demonstrated that carnivorous carabids are more efficient than omnivores at capturing and consuming lepidopteran prey based in part on inherent morphological differences between carabid guilds (Chapter 1). Differences in predator foraging ability and efficiency

contribute to food preference and thus mediate the indirect benefit of alternative food on target prey (Chesson 1989; Chapter 1). Based on the preference of carnivores for herbivores, which reduces the influence of alternative plant resources, carnivores are expected to exert stronger effects on herbivores in resource-diverse environments than omnivores (Murdoch 1969; Holt and Kotler 1987; Post et. al. 2000). This expectation is supported by the observation that omnivorous and carnivorous carabids consumed the same number of cutworms when alternative resources were absent but consumption by omnivores dropped considerably when either alternative food was present.

The presence of alternative food resources resulted in decreased corn seedling survival and thus dampened the cascading positive effects of cutworm-inflicted mortality on seedlings. The average number of seedlings cut by cutworms was highest when seeds were supplied to omnivorous carabids and generally lowest when carnivores existed without alternative prey (Table 2.4). This finding is consistent with the results of the laboratory feeding trials and confirms my hypothesis that alternative food has a stronger diversionary effect on omnivores than on carnivores, thus dampening herbivore effects on plants relatively more. Interestingly, neither carabid guild nor alternative food treatments had significant overall effects on seedling biomass. However, the number of plants cut is likely a better measure of a trophic cascade in this system than biomass. Cutworms attack corn seedlings by cutting plants, which effectively removes them from the population. Therefore, changes in seedling biomass were small over the short five-day duration of this experiment, but the impact of seedling mortality on future plant growth, biomass and

reproduction is potentially great since an entire plant is taken out of production.

The impact of arthropod predators can change depending on numerous factors including the type of herbivore or alternative food present (Chesson 1989; Snyder and Wise 2001). For example, carabid beetles and lycosid spiders each imposed top-down control on cucumber beetles resulting in a trophic cascade and increased fruit production (Snyder and Wise 2001). However, later in the season with a different herbivore, the predation impact of carabids increased but that of spiders decreased (Snyder and Wise 2001). Likewise, the impact of notonectid beetles on mosquito larvae depends on the type of alternative food present and how it alters the predator's functional response (Chesson 1989). In my system alternative food items were selected to control for size and mobility effects in order to focus on the effects of their trophic origin. However, if other alternative prey had been used, one that varied in size, mobility, food quality, or that was more preferred by carnivores this would likely alter the relative effect of alternative prey on carnivores compared to omnivores.

Just as alternative food has a strong effect on the consumption of herbivores by omnivores, it also has a strong effect on the tendency of these predators to remain in a habitat. Results of the emigration experiment indicated that the presence of alternative food can increase predator tenure time in the local habitat, an effect that was stronger for omnivorous than carnivorous carabids (Figure 2.14). Fly pupal supplements increased the tenure time of both carabid guilds compared to when this resource was absent. However, the seed supplement alone or in combination with pupae increased the length of time omnivores spent in plots, even more so than plots

augmented with pupae and further demonstrates the strength of omnivore-seed interactions. Although changes in predator density in response to alternative food have been documented (McMurtry and Scriven 1966a, b; Settle et al. 1996; Eubanks and Denno 2000a; Harmon et al. 2000; Halaj and Wise 2002; Musser and Shelton 2003), few studies have demonstrated reductions in emigration or increase in tenure time as the underlying mechanism (Eubanks and Denno 1999; Shrewsbury and Raupp 2006; VanLaerhoven et al. 2006). In addition, no research to my knowledge has demonstrated a differential response of omnivorous and carnivorous members belonging to the same taxon to food supplements.

Alternative plant resources are lower in nitrogen and often considered a lower quality food compared to prey (Mattson 1980; Elser et al. 2000; Fagan et al. 2002). However, alternative plant resources should enable omnivorous predators to survive periods of prey scarcity even if it is of poor quality (Crawley 1975; Eubanks and Denno 1999; Eubanks and Styrsky 2005). Moreover, the survival and development time of many omnivores benefits from mixing plant and animal food (Eubanks and Styrsky 2005). In fact seeds seem to be of higher quality for the performance of larval and adult omnivorous carabids than many animal foods (Jorgenson and Toft 1997). Therefore, for omnivores in general and carabids in particular plant resources may represent a resource that is more predictable and abundant than prey even if not always the most nutritious. Therefore, remaining in habitats with high seed densities may be an adaptive response to ensure a consistent food supply.

In addition to extended tenure time in the local habitat patch, seed supplements encouraged a greater abundance of omnivorous carabid beetles in open

field plots indicating an aggregation response. Omnivorous and carnivorous carabids comprised a similar proportion of the carabid community in the absence of food resource subsidies. It was predicted that carnivores would become more abundant in plots supplemented with pupae, just as omnivores should increase in abundance in plots augmented with seeds. Moreover, omnivores might have responded to both pupal and seed addition, but in these studies they responded positively only to seed additions. This finding supports the suggestion by Eubanks and Denno (1999) that omnivores may track resources at the lowest trophic level at which they feed. In their work, a similar combination of laboratory and field experiments demonstrated that the omnivorous predator, *Geocoris punctipes*, consumed fewer herbivores when seedpods were available, on which they also feed. Seedpods also reduced the emigration of *G. punctipes* from bean plants (Eubanks and Denno 1999). As such, beanpods ultimately resulted in higher populations of the omnivorous predators and lower populations of herbivores (Eubanks and Denno 1999, 2000a). Thus, increased tenure time in local patches enhanced per capita consumption of herbivores as more omnivores took up residence in a patch and spent more time there (Eubanks and Denno 1999, 2000a). Even though the presence of seeds reduced predation of cutworms in the laboratory and had a negative effect on corn seedling survival when omnivores occurred at fixed densities in field cages, increasing carabid abundance has been shown to increase predation of herbivores in field experiments (Kromp 1996; Mennalled et al. 1999; Snyder and Wise 2001). Therefore, similar to Eubanks and Denno (1999, 2000a), increased predator abundance through aggregation and tenure time could counteract lower per-capita predation.

Laboratory and field experiments showed that omnivorous carabids consistently interact more strongly with seeds than pupae, such that in the presence of seeds consumption of herbivores is reduced with adverse cascading effects on seedling survival. Omnivores appear to aggregate and interact most strongly with resources from the lowest trophic level at which they feed. The consistency of this response within replicated carabid species, and in other systems (Eubanks and Denno 1999, 2000a), lends support to the view that this is a general phenomenon. However, this phenomenon appears to be in opposition with emerging literature that documents nitrogen limitation in predators (Fagan et al. 2002; Denno and Fagan 2003). Nitrogen-rich food resources acquired from higher trophic levels better satisfy this stoichiometric mismatch and often increase predator survival and reproduction (Fagan et al. 2002; Denno and Fagan 2003). Although lower in nitrogen, biomass tends to be greater at lower trophic levels (Price 1984; Pauly and Christensen 1995) and foraging costs increase with prey mobility (Provost et al. 2006). Therefore, animal prey may be less common and more costly to capture than plant based resources (Wise 2006). Moreover, low nitrogen plant resources have been shown to support omnivore survival and reproduction in times of low prey abundance (Eubanks 2005). Therefore, the lowest trophic level at which an animal feeds may represent the most reliable food source, regardless of its nutritional content.

In contrast to early theoretical predictions (Pimm and Lawton 1977, 1978) omnivory is currently thought to be a stabilizing feature of food webs as omnivores spread their resource use among different food types thus reducing the amplitude of population oscillations (Fagan 1997; McCann et al. 1998; Polis and Strong 1996). By

comparing explicitly omnivorous and carnivorous predators, my research provides empirical support for these predictions. Through an apparent competition type mechanism alternative food, and seeds in particular, weakens interactions between omnivores and herbivore prey (McCann et al. 1998; Holt and Lawton 1994). Seeds had no influence and pupae only weak influence on the strength of carnivore-herbivore interactions. Although a different type of alternative prey could change the strength of carnivore-herbivore interactions, under this alternative prey regime carnivores imposed top-down control on herbivores which cascaded to increase plant growth and survival. Therefore predator diet breadth influences the strength of top-down control and the co-existence of multiple food items (Jiang and Morin 2005). The interaction between omnivores, seeds, and herbivores in this experiment is more similar to apparent mutualism (Abrams and Matsuda 1996) than apparent competition (Holt and Kotler 1987; Holt and Lawton 1994). However, the aggregation of omnivores to seed subsidies in open field plots suggests that a mechanism similar to true apparent competition would be possible in this situation. If a numerical response to seeds by omnivores resulted in more severe predation of herbivore this could reverse the stabilizing influence of omnivory in this food web (Eubanks and Denno 1999; 2000a).

Essential to understanding the role of omnivores in trophic dynamics is insight into how they interact with the array of alternative food resources present in the environment. I provide further evidence that the trophic origin of alternative food drives the strength of this interaction and the extent to which omnivores promote trophic cascades.

Applied implications

Carabid beetles and other omnivorous predators can be important components of biological control programs in managed agricultural and ornamental ecosystems (Kromp 1996). However, conservation biological control efforts to attract and conserve these beetles has had inconsistent consequences for pest herbivores and plant yield (Kromp 1996; Landis et al. 2000). This research demonstrates two mechanisms by which conservation biological control efforts may fail or yield inconsistent results. First, there has been little regard for the guild of carabids that are being affected by habitat manipulations. Second, is that alternative food, such seeds as (Menalled et. al. 2001), pollen and nectar (White et al. 1995; Hickman and Wratten 1996; Chaney 1998), and detritivores (Settle et al. 1996; Frank and Shrewsbury 2004a), is often increased concomitantly with “predator” populations (Landis et al. 2000). These alternative foods can have a significant impact on the performance of carabid beetles or other predators as agents of biological control (Landis et al. 2000). Based on this research, bolstering alternative prey populations would likely have a minimal effect on the abundance of carabids from either guild. However, seed producing grasses in beetle banks or field margins would be expected to attract and conserve an abundance of omnivorous carabid beetles. Thus, increasing the abundance of omnivorous carabids may compensate for their propensity to consume alternative food resources and provide some level of pest control.

This research has demonstrated that feeding guild has a significant effect on the efficacy of carabids as predators and on how strongly they interact with alternative food to affect herbivore survival. Therefore, conservation biological

control strategies that simultaneously increase predator abundance and the quantity of alternative but preferred food items may have minimal value for crop protection.

Thus, biological control practitioners need to identify the feeding guild to which focal “predators” belong in order to better predict how the predator complex will interact with alternative food resources to influence herbivore suppression and plant yield, and trophic cascades and ecosystem services in general.

Tables

Table 2.1. Repeated measures ANOVA results for the effect of day (Day), carabid guild (omnivore or carnivore), alternative (Alt) food type (no alternative food, seeds or fly pupae), and their interactions on the number of corn seedlings damaged (cut + defoliated) by black cutworms in field cages at CMREC, College Park, MD.

Effect	Ndf, Ddf	F	P
Day	4, 235	47.62	<0.001
Guild	1, 235	0.03	0.865
Alt	2, 235	3.47	0.033
Guild*Day	4, 235	1.56	0.185
Guild*Alt	2, 235	0.58	0.560
Alt*Day	8, 235	1.17	0.316
Guild*Alt*Day	8, 235	0.20	0.991

Table 2.2. Mean (\pm SE) number of corn seedlings damaged (cut + defoliated) by black cutworms on each day of a 5-day field experiment. Treatments were carabid guild (omnivore or carnivore), alternative food type (no alternative food, seeds or fly pupae) in field cages at CMREC, College Park, MD.

Guild	Alternative food	Mean (\pm SE) number of damaged plants				
		Day 1	Day 2	Day 3	Day 4	Day 5
Omnivore	None	6.0 \pm 2.8a	9.0 \pm 3.2a	10.2 \pm 3.6b	10.4 \pm 3.7b	13.2 \pm 4.6b
	Pupae	4.2 \pm 1.6a	8.2 \pm 2.1a	9.2 \pm 1.8b	10.0 \pm 2.0b	11.8 \pm 2.1b
	Seeds	5.4 \pm 1.7a	11.2 \pm 2.7a	14.4 \pm 3.6a	14.6 \pm 3.5a	16.2 \pm 4.1a
Carnivore	None	5.0 \pm 1.2a	10.2 \pm 3.4a	11.0 \pm 3.4ab	12.0 \pm 3.2ab	12.8 \pm 3.3b
	Pupae	3.6 \pm 1.6a	6.0 \pm 2.9a	9.4 \pm 3.7b	10.8 \pm 3.9ab	14.2 \pm 4.5ab
	Seeds	4.6 \pm 1.6a	9.4 \pm 2.6a	12.4 \pm 2.9a	12.6 \pm 2.9a	12.8 \pm 3.0b

Table 2.3. Repeated measures ANOVA results for the effect of day (Day), carabid guild (omnivore or carnivore), alternative (Alt) food type (no alternative food, seeds or fly pupae), and their interactions on the number of corn seedlings cut by black cutworms in field cages at CMREC, College Park, MD.

Effect	Ndf, Ddf	F	P
Day	4, 235	15.79	<0.001
Guild	1, 235	0.19	0.666
Alt	2, 235	3.97	0.020
Guild*Day	4, 235	0.13	0.972
Guild*Alt	2, 235	1.25	0.288
Alt*Day	8, 235	0.68	0.705
Guild*Alt*Day	8, 235	0.89	0.523

Table 2.4. Mean (\pm SE) of corn seedlings cut by black cutworms on each day of a 5-day field experiment. Treatments were carabid guild (omnivore or carnivore), alternative food type (no alternative food, seeds, or fly pupae) in field cages at CMREC, College Park, MD.

Guild	Alternative food	Mean (\pm SE) number of cut plants				
		Day 1	Day 2	Day 3	Day 4	Day 5
Omnivore	None	0.2 \pm 0.1ab	1.2 \pm 0.7ab	1.9 \pm 0.9ab	2.7 \pm 1.1ab	4.2 \pm 1.8ab
	Pupae	0.2 \pm 0.1ab	0.7 \pm 0.4b	0.9 \pm 0.5b	1.7 \pm 0.8ab	2.3 \pm 1.1b
	Seeds	0.9 \pm 0.4a	2.3 \pm 1.0a	3.6 \pm 1.2a	4.0 \pm 1.5a	5.3 \pm 2.2a
Carnivore	None	0.1 \pm 0.1b	1.1 \pm 0.9b	1.4 \pm 0.9b	1.7 \pm 1.0b	2.1 \pm 1.2b
	Pupae	0.3 \pm 0.2ab	1.3 \pm 0.6ab	1.9 \pm 0.9ab	2.6 \pm 1.2ab	3.4 \pm 1.7ab
	Seeds	0.7 \pm 0.3ab	1.6 \pm 0.8ab	2.4 \pm 1.0ab	3.0 \pm 1.0ab	3.7 \pm 1.2ab

Table 2.5. ANOVA results for the effect of carabid guild (omnivore or carnivore), alternative food supplement (no alternative food, seeds, or fly pupae), and their interactions on the average amount of time spent by carabids in manipulated field plots at CMREC, College Park, MD.

Effect	Ndf, Ddf	F	P
Guild	1, 35	3.81	0.059
Seed	1, 35	15.09	<0.001
Pupae	1, 35	10.01	0.003
Guild*Seed	1, 35	6.74	0.014
Guild*Pupae	1, 35	1.52	0.226
Seed*Pupae	1, 35	0.26	0.612
Guild*Seed*Pupae	1, 35	3.52	0.069

Table 2.6. Guild membership, taxa, and number of carabids captured by pitfall traps in open field plots subsidized with no alternative food, seeds, fly pupae or both at CMREC, College Park, MD.

Guild	Species	Number captured
Omnivores	<i>Harpalus pensylvanicus</i>	32
	<i>Anisodactylus</i> sp.	9
	<i>Amphasia</i> sp.	1
	<i>Stenolophus lecontei</i>	1
	<i>Trichotichnus</i> sp.	1
	<i>Acupalpus</i> sp.	1
	<i>Harpalus fulgens</i>	1
	<i>Amara familiaris</i>	1
	<i>Colliuris</i> sp.	1
	Guild total	48
Carnivores	<i>Elaphropus</i> sp.	17
	<i>Cicindela</i> sp.	5
	<i>Bembidion</i> sp.	3
	<i>Chlaenius tricolor</i>	2
	<i>Dyschirius</i> sp.	1
	<i>Scarites substriatus</i>	1
	<i>Clivina</i> sp.	1
	Guild total	30

Figures

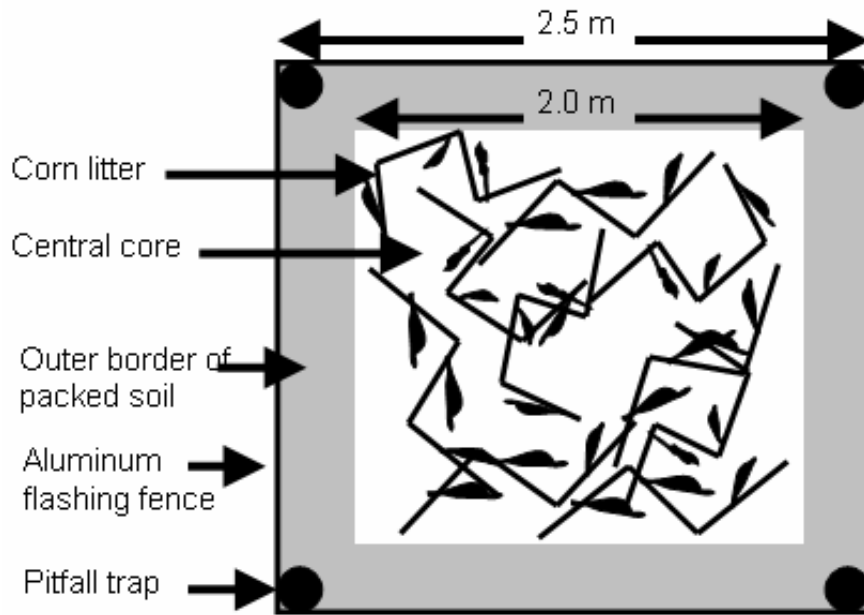


Figure 2.1. Schematic diagram of an experimental field plot used to assess the effects of food resource subsidies (applied in the central core) on the tenure time of omnivorous and carnivorous carabid beetles released in the center of the plot. Tenure time was assessed as the number of hours beetles spent in the central core of the plot before they were captured in peripheral traps.

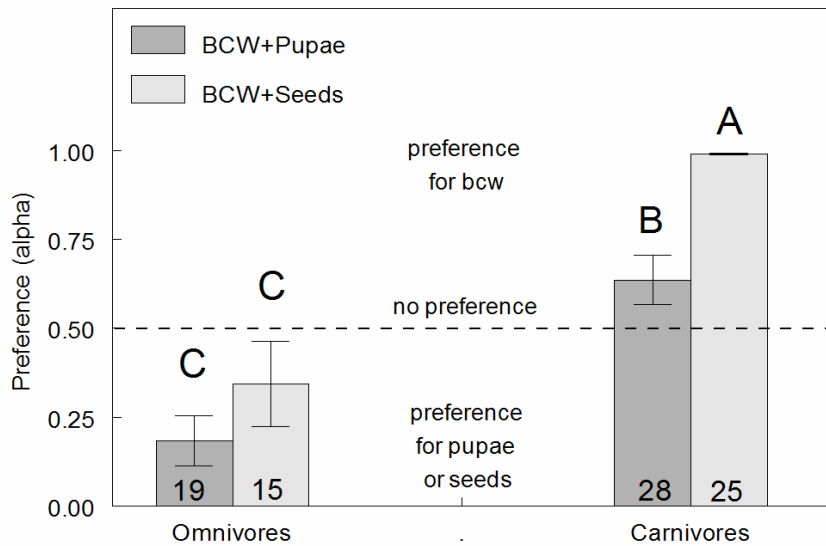


Figure 2.2. Average feeding preference (α) of omnivorous and carnivorous carabids for black cutworm larvae (BCW) when offered in combination with either fly pupae or grass seeds in a laboratory study. Values of α close to 1 indicate a strong preference for cutworms while values close to 0 indicate a strong preference for seeds or pupae. Individuals that did not eat any food items were excluded from the analysis. Numbers within bars indicate the number of individuals (out of 20 or 30 for omnivores and carnivores respectively) that were included in the analysis. Bars with the same letter are not significantly different ($P > 0.05$).

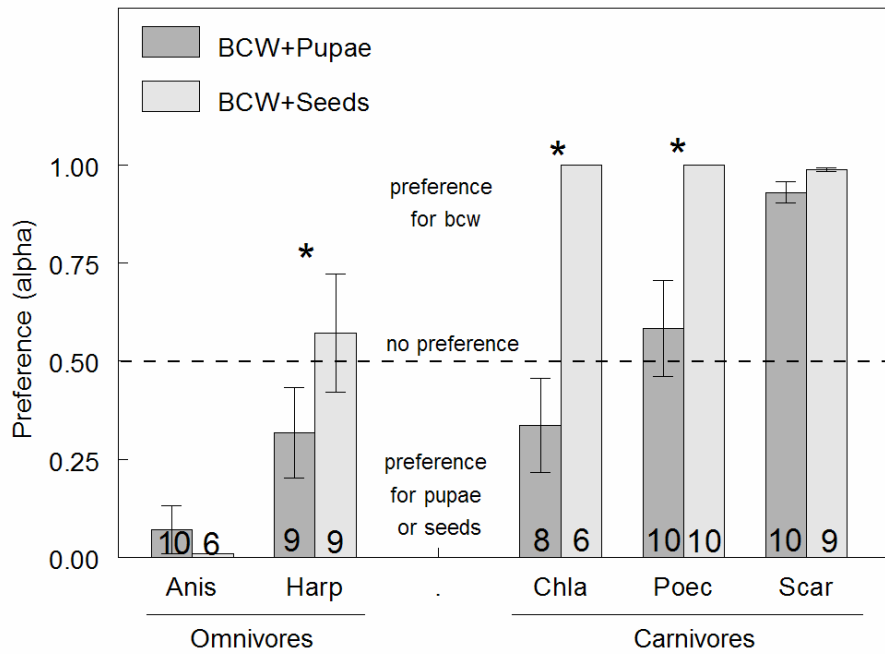


Figure 2.3. Average feeding preference (α) of omnivorous and carnivorous carabid species for black cutworm larvae (BCW) when offered in combination with either fly pupae or grass seeds in a laboratory study. Values of α close to 1 indicate a strong preference for cutworms while values close to 0 indicate a strong preference for seeds or pupae. Individuals that did not eat any food items were excluded from analysis. Numbers within bars indicate the number of individuals (out of 10) that were included in the analysis. Asterisks indicate a significant within-carabid-species difference in preference for cutworms when seeds or pupae are present. Species (abbreviations) included were *Anisodactylus ovularis* (Anis), *Harpalus pensylvanicus* (Harp), *Chlaenius tricolor* (Chla), *Poecilus lucublandus* (Poec), and *Scarites substriatus* (Scar).

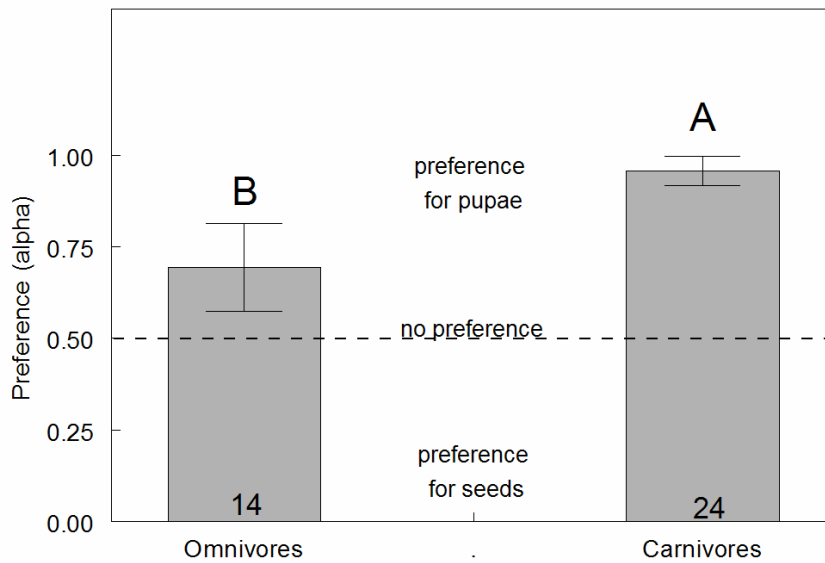


Figure 2.4. Average feeding preference (α) of omnivorous and carnivorous carabids for either fly pupae or grass seeds in a laboratory study. Values of α close to 1 indicate a strong preference for pupae while values close to 0 indicate a strong preference for seeds. Individuals that did not eat any items were excluded from the analysis. Numbers within bars indicate the number of individuals (out of 20 or 30 for omnivores and carnivores respectively) that were included in the analysis. Bars with the same letter are not significantly different ($P > 0.05$).

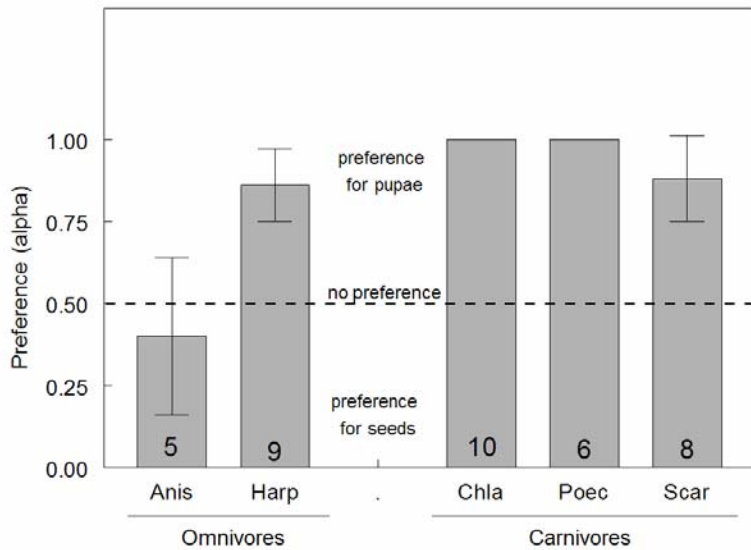


Figure 2.5. Average feeding preference (α) of omnivorous and carnivorous carabid species for either fly pupae or grass seeds in a laboratory study. Values of α close to 1 indicate a strong preference for pupae while values close to 0 indicate a strong preference for seeds. Individuals that did not eat any items were excluded from the analysis. Numbers within bars indicate the number of individuals (out of 10) that were included in the analysis. Species (abbreviations) included were *Anisodactylus ovularis* (Anis), *Harpalus pensylvanicus* (Harp), *Chlaenius tricolor* (Chla), *Poecilus lucublandus* (Poec), and *Scarites substriatus* (Scar).

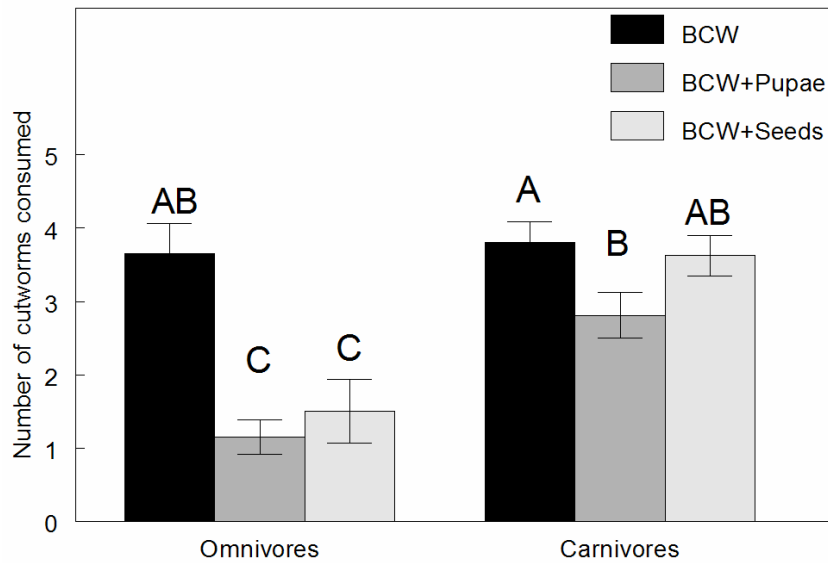


Figure 2.6. Average number of black cutworm larvae consumed by omnivorous and carnivorous carabids when offered alone (BCW) or in combination with either fly pupae or grass seeds in a laboratory study. Bars with the same letter are not significantly different ($P > 0.05$).

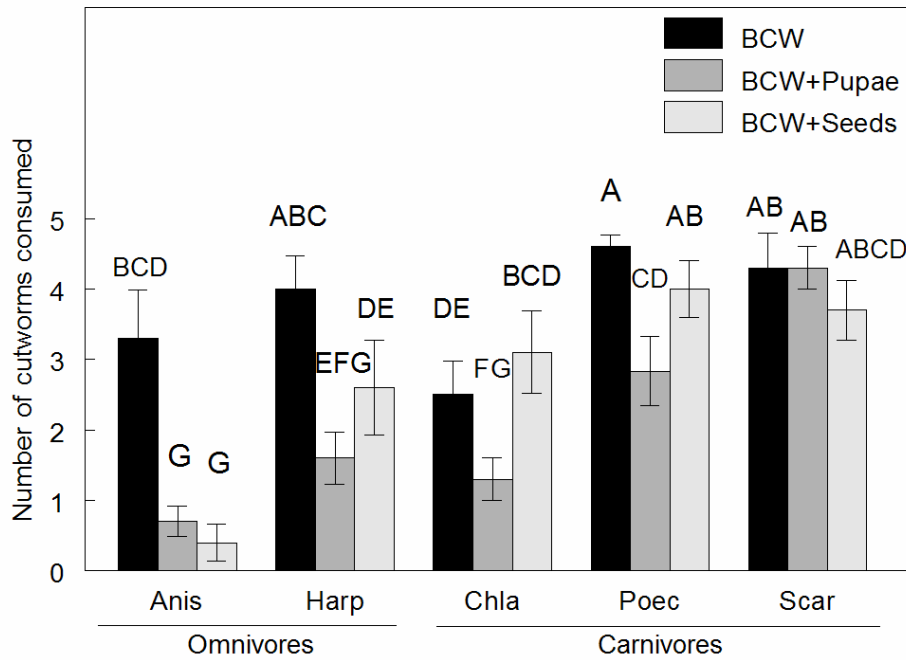


Figure 2.7. Average number of black cutworm larvae consumed by omnivorous and carnivorous carabid species when offered alone (BCW) or in combination with either fly pupae or grass seeds in a laboratory study. Bars with the same letter are not significantly different ($P > 0.05$). Species (abbreviations) included were *Anisodactylus ovularis* (Anis) *Harpalus pensylvanicus* (Harp), *Chlaenius tricolor* (Chla), *Poecilus lucublandus* (Poec), and *Scarites substriatus* (Scar).

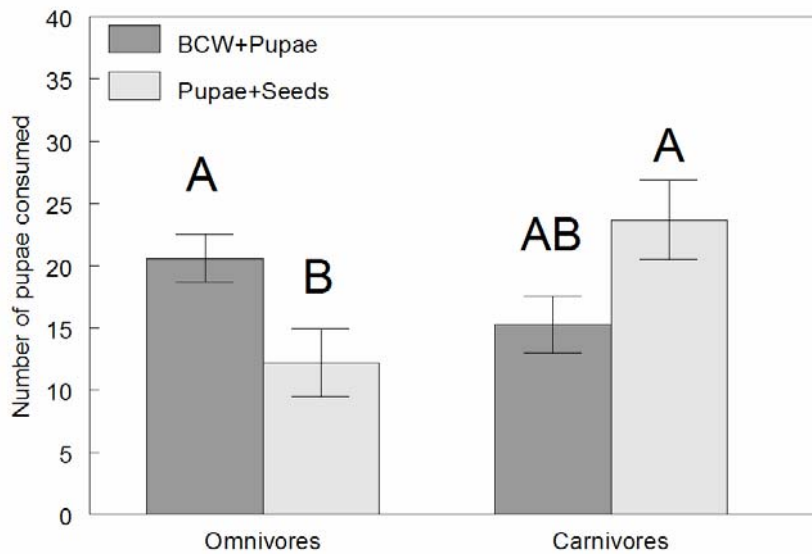


Figure 2.8. Average number of fly pupae consumed by omnivorous and carnivorous carabids when offered in combination with black cutworm larvae (BCW + pupae) or grass seeds (Pupae + seeds) in a laboratory study. Bars with the same letter are not significantly different ($P > 0.05$).

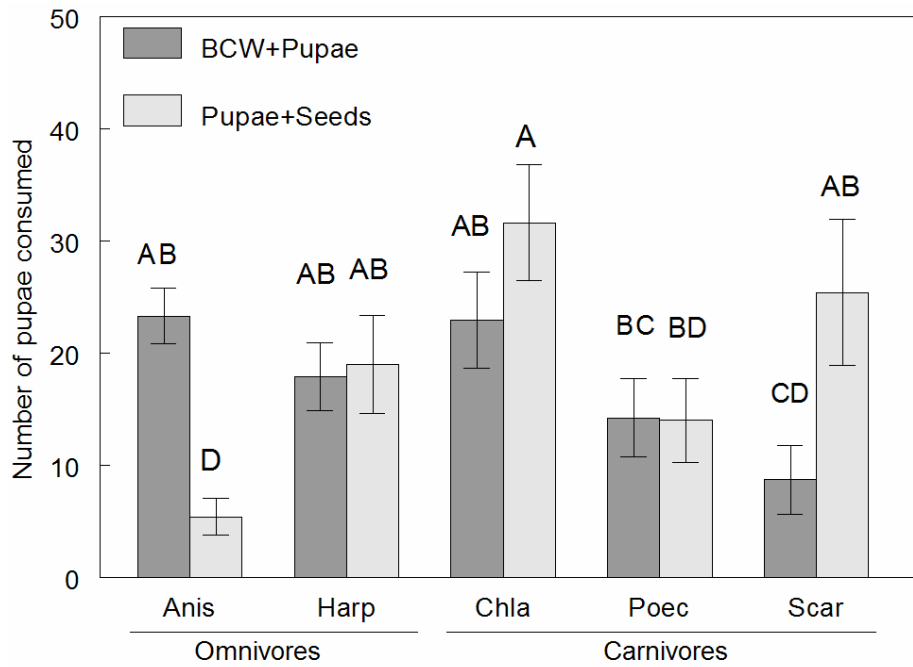


Figure 2.9. Average number of fly pupae consumed by omnivorous and carnivorous carabid species when offered in combination with black cutworm larvae (BCW + pupae) or grass seeds (Pupae + seeds) in a laboratory study. Bars with the same letter are not significantly different ($P > 0.05$). Species (abbreviations) included were *Anisodactylus ovularis* (Anis), *Harpalus pensylvanicus* (Harp), *Chlaenius tricolor* (Chla), *Poecilus lucublandus* (Poec), and *Scarites substriatus* (Scar).

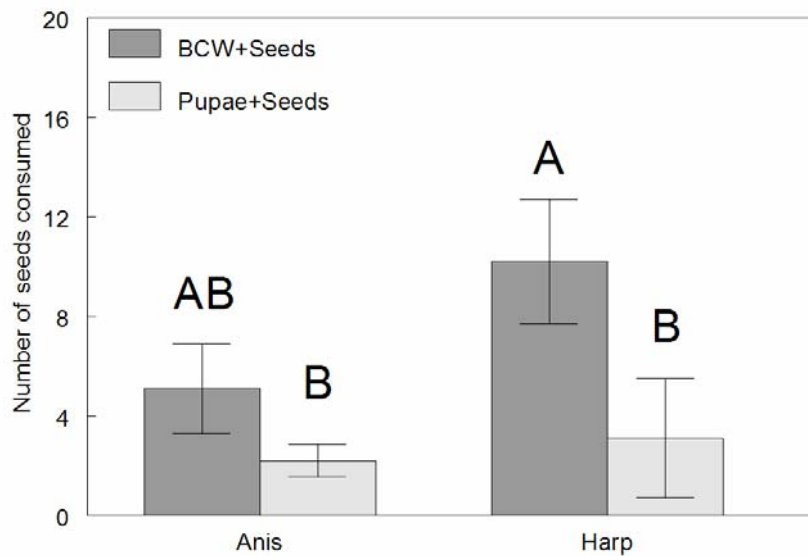


Figure 2.10. Average number of seeds consumed by different species of omnivorous carabids when presented in combination with either black cutworm larvae (BCW+Seeds) or fly pupae (Pupae+Seeds) in a laboratory study. Bars with the same letter are not significantly different ($P > 0.05$). Species (abbreviations) included were *Anisodactylus ovularis* (Anis) and *Harpalus pensylvanicus* (Harp).

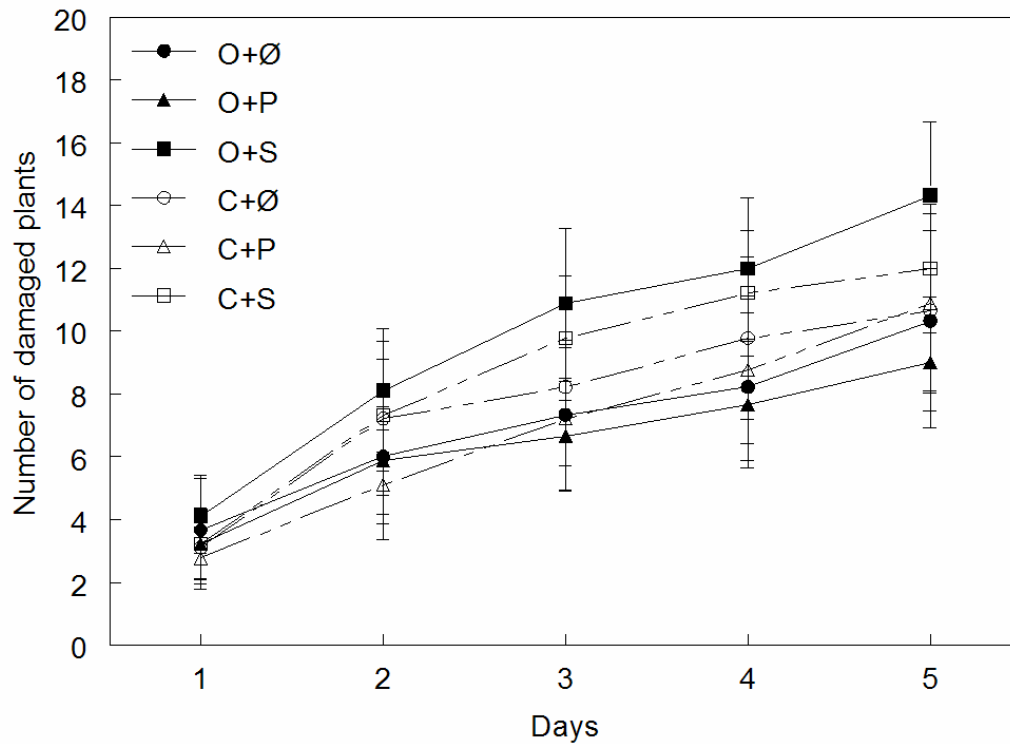


Figure 2.11. Average number of corn seedlings damaged (cut + defoliated) by cutworms over five days in field cages with omnivorous (O) or carnivorous (C) carabids and either no-prey (\emptyset), pupae (P) or seeds (S) present. See table 2.2 for pairwise comparisons of treatments on each day of the experiment.

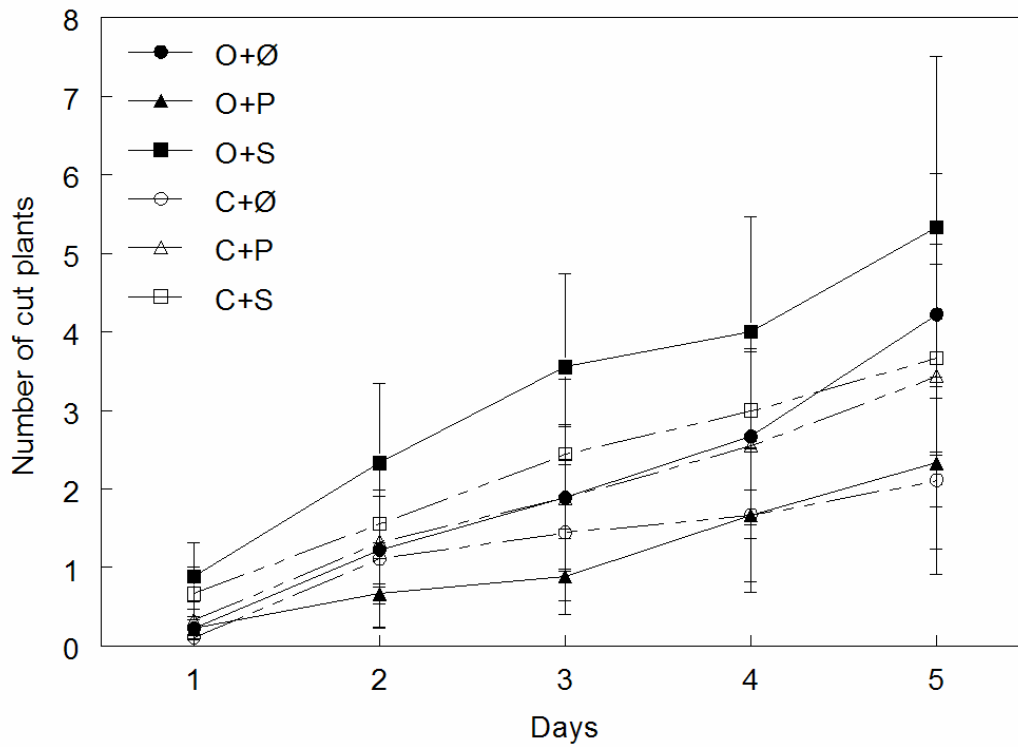


Figure 2.12. Average number of corn seedlings cut by cutworms over five days in field cages with omnivorous (O) or carnivorous (C) carabids and either no-prey (\emptyset), pupae (P) or seeds (S) present. See table 2.4 for pair-wise comparisons of treatments on each day of the experiment.

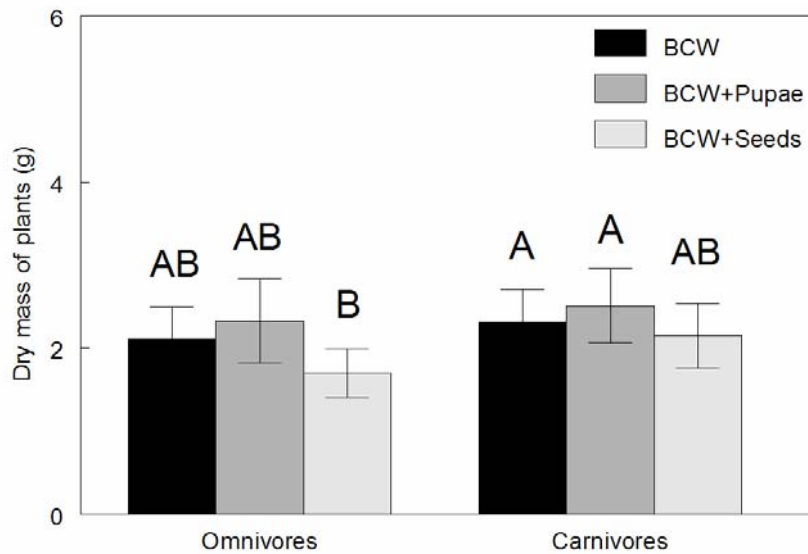


Figure 2.13. Effect of omnivorous and carnivorous carabids on the dry mass (g) of corn seedlings remaining in field cages (as a consequence of cutworm damage) after five days when black cutworm larvae were included alone (BCW), or in combination with either fly pupae (BCW+Pupae) or grass seeds (BCW+Seeds). Bars with the same letter are not significantly different ($P > 0.05$).

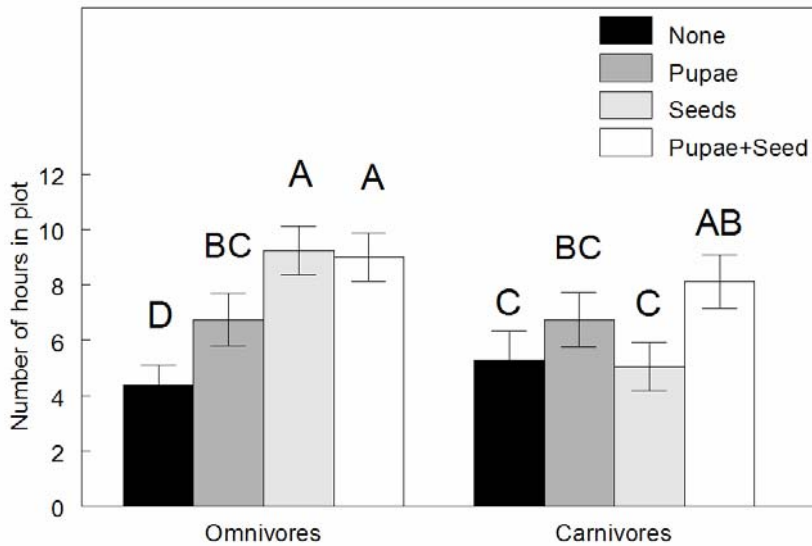


Figure 2.14. Average number of hours spent by omnivorous and carnivorous carabids in field plots containing no alternative food (None), pupae, seeds, or pupae and seeds. Bars with the same letter are not significantly different ($P > 0.05$).

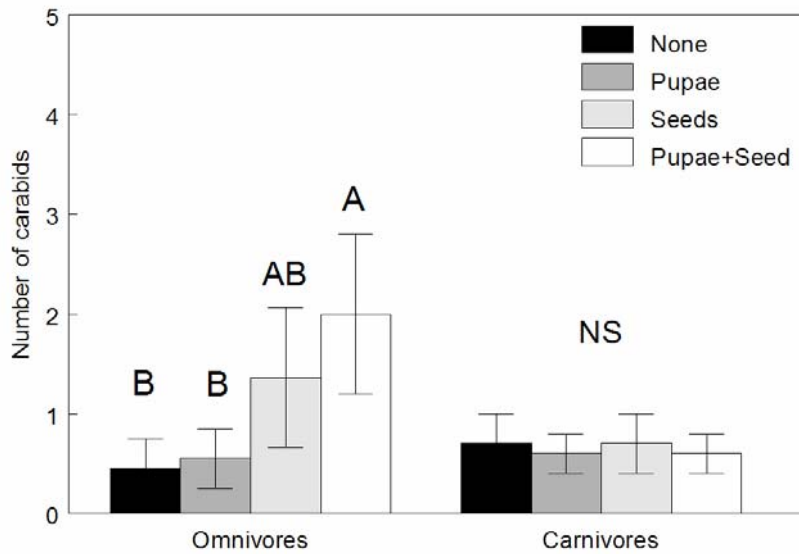


Figure 2.15. Average number of omnivorous and carnivorous carabid beetles colonizing open field plots supplemented with no alternative food (none), pupae, seeds, or pupae and seeds as measured by pitfall traps. Bars with the same letter, within each guild, are not significantly different ($P > 0.05$).

Chapter 3: The effect of plant- and prey-based resources on predator community structure and the strength of trophic cascades

Abstract

Spatial or temporal resource subsidies can affect the predator community present in a habitat, its impact on prey, and its indirect effect on basal resources. The effect of an abundant supplemental resource for predators can propagate through a system to increase (apparent competition) or decrease (apparent mutualism) the impact of predation on herbivores. Further, resource subsidies of different trophic origin (plant versus prey) have the potential to change the proportion of true omnivores or carnivores in the predator community, which can ultimately determine the strength of trophic cascades. However, there is no empirical evidence as to how plant- and prey-based resource subsidies affect the guild composition of predator communities and the resulting trophic dynamics. By subsidizing open field plots of corn with plant resources (grass seeds) and prey (fly pupae), I explored the consequences of resource amendments on the structure of the predator carnivore-omnivore community with cascading effects on herbivores and basal plant resources.

Specifically, I supplemented corn plots with two levels of seeds (seeds added or not) and two levels of prey (fly pupae added or not) in a crossed experimental design and measured the responses of carnivores, omnivores, herbivores and plants. The density of ants (omnivores) increased in additive fashion to both resource

subsidies. In contrast, no carnivore exhibited a numerical response to the resource amendments. Predation of herbivores (cutworms) decreased by half in plots subsidized with fly pupae because predators consumed this alternative prey instead of cutworms. The effect cascaded to corn as evidenced by a concomitant decrease in corn seedling survival. However, in plots subsidized exclusively with seeds, ants avoided seeds, focused their attack on cutworms, and the trophic cascade was restored. These experiments provide empirical support that resource subsidies from different trophic levels have variable effects on food-web dynamics. The variable effect is attributable to the differential aggregative responses and feeding preferences of carnivores and omnivores to the specific resource subsidies, differences which extend to impact herbivore suppression and plant survival.

Introduction

Spatial or temporal resource subsidies can affect the predator community present in a habitat, its impact on prey, and its indirect effect on basal resources (Polis and Hurd 1995; Polis et al. 1997; Ostfeld and Keesing 2000). By alleviating bottom-up limitations, habitats receiving resource subsidies often support larger predator populations than *in situ* resources would allow (Polis and Hurd 1995). The effects of abundant prey resources can propagate through a system because aggregation of predators in response to one prey species often results in increased predation on other co-occurring species (Ostfeld and Keesing 2000; Henschel et al. 2001; Sabo and Power 2002). Such cases of apparent competition (Holt 1987), have been shown to reduce herbivore survival and abundance (Settle et al. 1996; Eubanks and Denno 1999, 2000a). Conversely, because they represent ‘alternative foods’ for generalist predators, prey subsidies can decouple predator-herbivore interactions and reduce predation of herbivores which constitutes apparent mutualism (Polis et al. 1997; Cottrel and Yeargan 1998; Musser and Shelton 2003). Although predator aggregation in response to abundant food resources has been demonstrated in many natural (Ives et al 1993; Polis and Hurd 1995; Ostfeld and Keesing 2000) and managed systems (Evans and England 1996; Settle et al. 1996; Cottrel and Yeargan 1998; Eubanks and Denno 1999; Harmon et al. 2000; Musser and Shelton 2003; Evans and Toler 2007), its impact on focal herbivore prey is variable. Variability in the impact of predators on focal prey can result from a predator’s preference for alternative resources based on prey mobility (Freed 1980; Eubanks and Denno 2000b; Lang and Gsodl 2001),

size (McKemey et al. 2001; Cogni et al. 2002), quality (Greenstone 1979; Janssen et al. 2003), or abundance (Agrawal et al. 1999). In addition, the strength of a top-down instigated trophic cascade is often driven by the guild composition or species identity of the predator complex rather than sheer predator abundance (Finke and Denno 2005; Straub and Snyder 2006). Thus, identifying resources that promote predator aggregation or the increased efficacy of particular predators or predator guilds will increase the predictability of how resource subsidies affect prey suppression and trophic dynamics.

Generalist predator communities consist of several overlapping functional guilds that include varying proportions of plants, herbivores, detritivores, and other predators in their diets. Generalist predators spread their resource use among many available food items, which can reduce their impact on any single prey species (Symondson et al. 2002; Coll and Guershon 2002). The reticulate nature of food webs dominated by generalist predators (carnivores and omnivores) contributes to the context-dependent impact of these predators on herbivores, trophic cascades, and ecosystem function (Polis and Strong 1996; Symondson et al. 2002; Finke and Denno 2003, 2004, 2005). A subset of generalist predators are omnivores that feed at two or more trophic levels. These include intraguild predators that consume prey and other predators (trophic omnivores) as well as “true omnivores” that consume plant and prey resources (Coll and Guershon 2002). True omnivores represent a unique case in that they can have direct negative effects on plants as well as indirect positive effects via consumption of herbivores (Coll and Guershon 2002). Intraguild predators often reduce the strength of trophic cascades as they feed on mesopredators, which relaxes

top-down controls on herbivores (Polis et al. 1989; Rosenheim 1998; Arim and Marquet 2004). However, the response of true omnivores to multiple food resources and their role in trophic dynamics is relatively unexplored (Coll and Guershon 2002). Understanding the factors that influence the abundance and impact of true omnivores in a habitat would fill a considerable gap in our existing knowledge regarding their role in food-web dynamics.

Predator density (Settle et al 1996; Chen and Wise 1999; Eubanks and Denno 2000a; Halaj and Wise 2002), diversity (Settle et al. 1996), and behavior (Chesson 1989; Kaplan and Eubanks 2005) all can be influenced by the presence of abundant food resources. Habitats receiving resource subsidies often exhibit increased quality for predators to the extent that predator competition and intraguild predation are reduced and survival and reproduction are enhanced (Polis et al. 1997). Predators encounter diverse food resources in the environment that vary in their attractiveness and palatability. Some “available” food resources will be rendered unavailable because of their size, quality, or behavior (Steiner 2001; Duffy 2002). Therefore, only a subset of available food resources is palatable and available to a given carnivorous or omnivorous predator. In this way, food type and predator diet breadth can interact to affect the guild-composition of predator communities (Steiner 2001; Duffy 2002). Thus, available resources can have important implications for community assembly and trophic interactions because predator species or guilds interact with different subsets of prey (Hillebrand and Cardinale 2004). Therefore, the same habitat subsidized with different resources could support a different community of predators, which may have very different consequences for resident

herbivores and basal resources. To elucidate the interactive effects of resource subsidies with higher trophic-level players, research is required that simultaneously manipulates multiple resources in the same habitat, while controlling for other habitat variables.

Structurally-complex habitats generally support higher densities of predators than simple ones, due in part to the greater diversity of resources available there (Langellotto and Denno 2004, Shrewsbury et al. 2004, Shrewsbury and Raupp 2006). In contrast to spatial and temporal resource subsidies such as allochthonous detrital inputs (Polis and Holt 1995) or seed masting (Ostfeld and Keesing 2000), predator aggregation in complex habitats is influenced by many non-independent factors. Structurally-complex habitats provide predators with, among other things, refuge from intraguild predation, diverse microclimates, and abundant alternative plant and prey resources (Landis et al. 2000; Tooker and Hanks 2000; Langellotto and Denno 2004; Shrewsbury and Raupp 2000; Langellotto and Denno 2006; Shrewsbury and Raupp 2006). This phenomenon can be exploited in managed crops or ornamental landscapes to enhance pest suppression (Thomas et al 1991; White et al. 1995; Hickman and Wratten 1996; Chaney 1998; Landis et al. 2000; Frank and Shrewsbury 2004a; Shrewsbury et al. 2004, Shrewsbury and Raupp 2006). For example, increasing structural complexity via habitat manipulation can bolster predator populations with the goal of reducing pests and crop damage (Landis et al. 2000). Although predator populations generally increase in structurally-complex habitats, the impact on herbivores and plant growth is often unpredictable (Landis et al. 2000; Gurr et al. 2000). Thus, to understand how resource subsidies *per se* affect food-web

dynamics, it is necessary to consider resource subsidies as a component of habitat complexity. In this context, elucidating factors that promote predator or omnivore aggregation is essential if we are ever able to understand how habitats can be manipulated for enhanced pest management.

For this research, a factorial experiment was conducted to determine how plant-based and prey-based resource subsidies interact to affect predator community composition (omnivore versus carnivore) and impact on herbivore and plant survival. Specifically, plots established in a corn cropping system received no resource subsidies or they were subsidized with animal prey (*Drosophila* fly pupae), or plant resources (*Poa* seeds), or both. The effect of the different resource-subsidy treatments on the composition of the “predator community” was measured as the abundance of specific omnivorous (consume both plant and prey resources) and carnivorous (consume only animal prey) taxa. I hypothesized that omnivorous predators would demonstrate a numerical response to both plant and prey subsidies whereas carnivores would respond only to plots supplemented with animal prey. The survival of herbivores and corn seedlings were used to measure of the impact of the resource-mediated composition of the predator community on food-web dynamics. In this context, I predicted that as the density of carnivorous arthropods increased in plots subsidized with animal prey, herbivore survival would be reduced with extended positive effects on corn seedling growth and survival. However, because the presence of alternative food often reduces predation on herbivores by omnivorous arthropods (Chapter 2), I predict that any aggregative response to resource subsidies by members of this feeding guild will propagate through the food web resulting in enhanced

herbivore density (reduced predation) and reduced plant survival.

Although other research has documented the aggregation of predators to abundant food resources (Polis and Hurd 1995; Ostfeld and Keesing 2000), this study is one of the first to manipulate simultaneously plant and prey resources without altering habitat structure (e.g. by adding mulch or increasing primary productivity via fertilization). It is also the first study to my knowledge that addresses how resource subsidies of different trophic origin affect the composition of the carnivore-omnivore complex. Using open field plots in a corn agroecosystem, the specific objectives of this research were to determine if alternative food resources (grass seeds or fly pupae) affect: 1) predator abundance; 2) predator guild composition (proportion of omnivores to carnivores); 3) herbivore density and survival; and 4) corn seedling survival and biomass.

Higher trophic levels (third and fourth) in natural communities are suffering extinction at an increasing rate due to human activities (Pauley et al. 1998). Moreover, altering the abundance of predators and guild structure of natural communities affects the abundance of consumers and resources at lower trophic levels and the strength of trophic cascades (Estes et al. 1998; Dayton et al. 1998; Pace et al. 1999; Ostfeld and Keesing 2000; Finke and Denno 2005). However, due to the complexity of food-web dynamics, as a consequence of omnivory and intraguild predation, our ability to predict the outcome of changes in the predator complex is limited (Polis and Strong 1996). This gap in understanding impairs our ability to implement appropriate conservation and pest management strategies (Gurr et al. 2000). This study is one of few that have manipulated plant and prey resources to

examine their interactive effect on predator community composition with cascading effects to lower trophic levels. As such, this study provides new insights into how multiple resources affect food-web dynamics via changes in predator community structure.

Methods

Study system

Prey resources for predators are often patchily distributed across agricultural landscapes that include the crop itself and neighboring natural areas such as hedgerows, abandoned fields, and streams (Denys and Tscharnke 2002). Moreover, adjacent natural areas also supply plant resources such as nectar, pollen, and seeds for omnivorous predators (Marshall and Moonen 2002). In addition, the cropping system *per se* can differ in food resources due to changes in weed abundance, organic matter, or soil moisture (Fox et al. 1999; Frampton et al. 2000; Wiles and Brodahl 2004). Thus, it is important to understand how variable food resources influence the spatial dynamics and abundance of carnivores and omnivores across the agricultural landscape.

This research was conducted in a no-till corn agroecosystem, which harbors a suite of generalist and omnivorous predators such as ants (true omnivores), spiders (carnivores), and carabid beetles (both omnivores and carnivores). Corn is susceptible to a number of herbivorous pest insects (Willson and Eislely 2001; Bessin 2003). One of the first pests to damage corn in spring is the black cutworm, *Agrotis*

ipsilon (Hufnagel) (Lepidoptera: Noctuidae) (Willson and Eisley 2001), which serves as the focal herbivore in this research. Cutworms damage young corn plants from seedling emergence to the time it has four to five leaves. Early-instar (1st-3rd) cutworms feed on the leaves of corn. Larger cutworms (4th and 5th instars) cut down corn seedlings at or below ground level and then consume the entire fallen plant. When seedlings are cut, the meristem is destroyed, which leads to plant death and thus reduced plant biomass and yield. Cutworm larvae and pupae are susceptible to predation by a number of predators (Best and Beegle 1977b; Brust et al. 1985, 1986; Frank and Shrewsbury 2004b; Chapter 2), and increasing the abundance of predators in a habitat has been shown to enhance cutworm mortality (Brust et al. 1985, 1986, Frank and Shrewsbury 2004a). Because cutworms are present in many other agricultural crops and ornamental landscapes (Showers 1997) results from the corn system have broad implications for other managed systems.

Alternative prey for predators such as detritivores, are abundant in corn ecosystems (Dively 2005). For example, Diptera have been shown to emerge from corn fields at densities of 272/m² every two weeks (G. Dively *personal communication*). Moreover, many carabid beetle species are known to feed on dipteran eggs and pupae (Kromp 1999). For the research proposed here, fruit fly pupae, *Drosophila melanogaster* Meigen (Diptera: Drosophilidae) were used as an alternative prey subsidy. Seeds from a variety of weeds are also very abundant in corn fields, occurring at densities in the thousands to tens-of-thousands per square meter (Davis et al. 2005; Swanton et al. 2006). For this research, I used bluegrass seeds, *Poa pratensis* (L.) (Cyperales: Poaceae), as a plant-resource subsidy for omnivores.

Members of the genus *Poa* are common agricultural weeds (Uva et al. 1997). In addition, fly pupae and bluegrass seeds are very similar in size and both are immobile which controls for size and mobility affects which would confound inference regarding trophic origin.

Organisms generally increase in nitrogen content and thus in food quality as they occupy higher trophic positions (Mattson 1980; Elser et al. 2000; Fagan et al. 2002) which can influence predator preference (Greenstone 1979). The mean (\pm SE) nitrogen content of ten temperate grass species associated with agricultural fields is 2.84% (\pm 0.44) (range = 1.5-5.6%; n=10) (reviewed by Schroeder et al. 1974). Percent nitrogen of six wild *Drosophila* sp. (adults) averaged 8.0% (\pm 0.3) (range 6.7-9.5%; n=12) (Markow et al. 1999) although laboratory reared *Drosophila* sp. were found to have a nitrogen content of 10% (Burcombe and Hollingsworth 1970). Three species of Noctuid larvae analyzed by Landry et al. (1986) had an average of 8.9% (\pm 0.2) (range = 8.7-9.2%; n=3) nitrogen. Therefore, seeds as a plant resource have lower nitrogen content than either of the animal prey which are very similar and of higher quality as a food source. A corn agro-ecosystem with its complement of omnivorous and carnivorous predators, alternative prey (detritivorous dipterans), and seeds provides an ideal system to test how food-resource subsidies of different trophic origin (*Drosophila* pupae and *Poa* seeds) affect predator aggregation, the guild composition of the predator complex (carnivore versus omnivore), herbivore survival, and primary plant production.

Experimental design and plot establishment

To assess the effects of plant and prey resource subsidies on predator community composition and herbivore suppression with cascading effects to corn plants, two levels of seed addition (ambient and subsidized bluegrass seeds) were crossed with two levels of prey supplementation (ambient and subsidized with fly pupae) in a 2 x 2 factorial design. Thus, plots received either no resource subsidies (ambient) or were subsidized with seeds, fly pupae, or both (seeds and pupae mixed). This experiment was conducted in 44, 4 x 4 m plots in a field where no-till corn was grown the previous year. Plots were located at the University of Maryland Paint Branch Turgrass Facility, Central Maryland Research and Education Center (CMREC) in College Park, MD. The plots were arranged in rows of 4 parallel to the field edge. The field edge represented a potential source of predators (Dennis and Fry 1992) such that each row contained one plot of each treatment and constituted a complete block. Experimental blocks were situated 10 m apart and were located at least 10 m from the field edge. All treatment plots within a block were established 6 m apart. The experiment was conducted three times, from 8 - 30 June, 7 - 24 July, and 22 August to 8 September, 2007, when 3, 5, and 3 replicates respectively were completed (11 replicates total).

For each trial, two pitfall traps, consisting of 473 ml plastic cups, were installed in each plot (day 1). These traps could be 'closed' by inserting a cup full of soil into the cup or 'opened' by inserting a cup with killing solution. On day 2, organic field corn (NC+ Organics, hybrid 3448MF-14) seeds were planted in all plots. As recommended for corn production in Maryland, rows were established 76

cm apart with plants in each row were separated by 20 cm (McClurg and Donnelly 1999). This arrangement resulted in 6 rows of 30 corn plants per treatment plot. Corn seeds were irrigated with sprinklers after planting. The following day (day 3), seeds and/or pupae were hand sprinkled over the soil surface at a rate of 1200/m²; plots assigned to the mixed treatment received 1200 seeds/m² and 1200 pupae/m². Additional seeds and pupae were added at the same rate every 4-5 days throughout the duration of the trial to replace eaten or degraded food items, and maintain treatments. Corn seedlings emerged in 4-6 days. Corn grew too large for cutworms to inflict damage 10 days after emergence (day 15-16), so experiments were terminated at this point.

Predator abundance and community composition

The effect of food subsidies on predator abundance and community composition was assessed using pitfall trapping and vacuum sampling in the established treatment plots (**Objs. 1 and 2**). Pitfall traps were opened on day 10 for 24 h and day 15 for 48 h. Pitfall traps provided a measure of predator activity-density because capture depends both on the abundance and activity of arthropods (Baars 1979; Topping and Sunderland 1992). Pitfall traps also measure activity-density over 24 hour cycles. Vacuum sampling of the arthropod community was conducted on the last day of the experiment and provided an absolute measure of predator density but only measure density in one window of time. A wet/dry shop-vacuum was used to vacuum the entire length of each plot between corn rows 3 and 4. Contents of the vacuum sample were transferred to a Berlese funnel and extracted for 2 weeks.

Arthropods escaping the drying sample were collected in a jar of EtOH. All carabid beetles were identified to genus. Other potential predators were identified to family or order (e.g. ants and spiders). Carabids and other predators were assigned to one of two feeding guilds, either 'carnivore' or 'omnivore' based on published information for each taxon.

Statistical analysis: Analysis of predator abundance focused on groups that were observed to consume cutworms in the field and that were sufficiently abundant to perform a robust analysis. These groups included ants, wolf spiders, adult carabid beetles, and cantharid beetle larvae. Activity-density data for each taxon in each treatment plot was calculated as the sum of the counts collected from the two pitfall-trap sampling sessions on days 10 and 15. The density of each predator taxon was determined from vacuum sampling at the end of each experiment. The effect of seed subsidies, pupae subsidies and their interaction on the mean activity-density (pitfall traps) and density (vacuum sampling) of ants, spiders, carabids, and cantharid larvae was analyzed using ANOVA followed by LSD means comparisons (MIXED Procedure, SAS 2002). "Row" and "month of the experiment" were included as blocking factors.

It was also of interest to determine if the response particular predator taxa were positively or negatively associated with the response of other predator taxa. Therefore, correlation of the activity-density (pitfall) and density (vacuum) of ants, spiders, carabids, and cantharid larvae was investigated using the CORR Procedure in SAS (SAS 2002).

Consumption of free-roaming cutworms, sentinel cutworms, and resource subsidies

The effect of the resource subsidy treatments on the consumption of cutworms was assessed using free-roaming and sentinel (tethered) cutworms placed in each of the experimental plots (**Obj. 3**). In the evening of the day corn emerged (day 4-6), 80 2nd-instar black cutworms were released into each plot and allowed to freely move about the plot (“free-roaming”) for the duration of the experiment. The survival of these and other naturally occurring noctuid caterpillars was established by the vacuum sampling procedure described above.

On four evenings of the experiment and after corn emergence, 5 sentinel cutworms were pinned in each plot for a total of 20 individuals per plot. Third-instar cutworms were pinned to the ground through their penultimate abdominal segment. This procedure secured the cutworms in place but allowed them to remain alive for at least 12 hours (Frank and Shrewsbury 2004a). Sentinel cutworms were pinned in the plots at 19:00 h and visually checked for presence or absence 4 hours later. Cutworms that were being eaten at the time of observation were recorded as absent and the taxon of the culprit predator was recorded. Ants required an average (\pm SE) of 7.55 (\pm 1.4, $n = 6$) hours to remove a cutworm from the pin (S. Frank *unpublished data*). Since I made visual observations after 4 hours it is likely that I witnessed most instances of ant predation in progress. Therefore, when cutworms were consumed or absent and no predator was observed it was attributed to non-ant predators.

To determine if the disappearance of sentinel cutworms was related to the abundance of dominant predator taxa (cantharid larvae, wolf spiders and ants), the

relationship between the number of cutworms consumed per plot was correlated with predator activity-density (pitfall) and density (vacuum).

To confirm that seeds and pupae were consumed, and to determine if shifts in arthropod community structure resulted in the differential consumption of plant and prey resources, sentinel grass seeds and fly pupae were placed in each plot during one night of the experiment. Fifteen seeds and fifteen pupae were affixed to 2.5 x 2.5 cm squares of sand paper with artists spray adhesive (3M). Six of the sand paper squares were then placed in each plot and held in place with tooth picks. The squares were placed in the plots at 19:00 h, and they were collected 12 hours later when the number of remaining seeds and pupae were counted.

Statistical analysis: Data on the number of free-roaming caterpillars recovered did not meet the assumptions of ANOVA and were analyzed by a one-way Chi-square test. The effect of seed subsidy, pupal subsidy and their interaction on the predation of sentinel cutworms (# eaten out of 20, all nights pooled) was compared using ANOVA followed by LSD means comparisons with row and month included as blocking factors (SAS 2002). The effect of seed and pupal subsidies and their interaction on ant predation and non-ant predation (unobserved predators, carabids, spiders, centipedes, opilionids, and cantharid larvae) of cutworms was compared using ANOVA followed by LSD means comparisons with row and month included as blocking factors (SAS 2002). The effect of seed subsidies, pupal subsidies and their interaction on the total number of sentinel seeds and pupae eaten and on the proportion of food items eaten that were seeds (seeds eaten / total seeds + pupae eaten) were compared using ANOVA followed by LSD means comparisons with row

and month included as blocking factors (SAS 2002). Correlation analysis was performed to determine if the activity-density (pitfall trap counts) of each predator group (ants, carabids, spiders, cantharid larvae) was related to the number of sentinel larvae consumed by ants or other predators (SAS 2002).

Growth and survival of seedlings

Survival and biomass of corn seedlings was used as an indication of how the presence of alternative food affected predation on cutworms with cascading effects to corn plants (**Obj. 4**). In all experimental plots, corn seedlings were counted on the day they emerged from the ground and every 3-4 days thereafter, recording the number of plants that were healthy or cut (chewed at soil line). On day 16, the end of the experiment, surviving plants were harvested (removed just above the roots) and dried in an oven for one week (70° C). The total dry biomass of seedlings from each plot was used to assess treatment effects on biomass production (plant growth).

Statistical analysis. The effect of seed subsidies, pupal subsidies and their interaction on the number of cut plants on days 10 and 15 was analyzed by repeated measures ANOVA. The dry weight of harvested seedlings in each plot was compared using ANOVA followed by LSD means comparisons with row and month as blocking factors.

Results

Predator abundance and community composition

Carabids were more abundant in plots subsidized with seeds as assessed by pitfall traps but not as determined by vacuum sampling (Figure 3.1, 3.2; Table 3.1, 3.2). The abundance of wolf spiders (Figure 3.3, 3.4; Table 3.1, 3.2) and cantharid larvae (Figure 3.5, 3.6; Table 3.1, 3.2) were unaffected by alternative resource subsidies when assessed by both sampling methods. Ants, were significantly more abundant when seeds, pupae, or both were added to plots, a response indicated by vacuum sampling but not pitfall trapping (Figure 3.7, 3.8; Table 3.1, 3.2).

There was a negative correlation between spider activity-density and that of carabids and ants (Table 3.3a). A positive correlation was found between ant and carabid abundance, both of which are largely omnivorous (Table 3.3a). As measured by vacuum sampling carabids were positively correlated with spiders and cantharid larvae (Table 3.3b). Vacuum sampling yielded several positive correlations that were different from pitfall traps (Table 3.3b).

Consumption of free-roaming cutworms, sentinel cutworms, and resource subsidies

Predation of sentinel cutworms was significantly reduced when plots were subsidized with fly pupae (main effect of pupae, Figure 3.9; Table 3.4). Moreover, ants accounted for increased cutworm disappearance in plots subsidized with seeds (Figure 3.9). So-called “other predators” (predators other than ants that consumed

cutworms and which went largely unobserved), were responsible for significantly more cutworm predation in plots not receiving food resource subsidies (Figure 3.9; Table 3.4).

The activity-density of cantharid larvae was highly correlated with the number of sentinel cutworms consumed in plots subsidized with seeds and those amended with both seeds and pupae (Figure 3.10 c, d; Table 3.5a). The activity-density of spiders was significantly correlated with the number of cutworms consumed (Table 3.5a), particularly in plots subsidized with seeds (Figure 3.10c; Table 3.5a). Ant activity-density was correlated with the number of cutworms consumed only in plots supplemented with seeds (Figure 3.11 c; Table 3.5a). However, density of cantharid larvae, as sampled by the vacuum, was negatively correlated with the number of sentinel cutworms consumed (Table 3.5b). In addition, the density of other predators was negatively correlated with the number of cutworms consumed (Table 3.5b).

The number of free-roaming noctuid larvae recovered in the treatment plots depended on the alternative food subsidy ($\chi^2 = 12.79$; $df = 3$; $P = 0.005$) (Figure 3.12). More than twice as many caterpillars were recovered from plots subsidized with pupae and seeds than any of the other treatments (Figure 3.12).

The total number of sentinel resources (seeds and pupae combined, and pupae only) consumed did not differ among treatments (Figure 3.13; Table 3.6). However, more sentinel seeds, and proportionally more sentinel seeds, were consumed in plots subsidized with fly pupae (Figure 3.13; Table 3.6).

Growth and survival of seedlings

The number of corn seedlings cut by cutworms was significantly higher in plots subsidized with fly pupae (Figure 3.14; Table 3.7). Neither seed ($F_{1,30} = 1.63$; $P = 0.211$) nor pupal ($F_{1,30} = 0.52$; $P = 0.478$) subsidies or their interaction ($F_{1,30} = 0.78$; $P = 0.383$) affected the biomass of corn seedlings remaining in treatment plots (Figure 3.15).

Discussion

This research demonstrates that the trophic nature of alternative food resources (seeds versus prey) and the guild composition of the predator community interact to produce complex food-web interactions. Whether a predator was omnivorous or carnivorous influenced the strength of its aggregative response to the various food subsidies, and the type of food supplement (plant vs. animal) influenced predator switching behavior, both of which impacted the effect of the predator complex on herbivores and plants. Notably, the relative impact of omnivorous ant predators on herbivores changed depending on whether seed or pupal subsidies were present. Ants switched to consume cutworms when seed were present but not when pupae were present. Because the indirect effects imposed by resource subsidies can shift from apparent mutualism to apparent competition depending on predator guild and alternative food type, this research highlights the limitations of inferring community-wide effects from a specific food resource supplement.

Clearly, omnivorous and carnivorous predators responded differently to food

subsidies. The two omnivorous predator groups, ants and carabid beetles, exhibited a significant numerical response to food resource supplements. Carabids occurred more abundantly in plots subsidized with seeds (either alone or with pupae) (Figure 3.1). Ants, on the other hand, responded positively to seed and pupal supplements when each was provided alone and showed an additive response when both supplements were provided together (Figure 3.8). This finding supports my prediction that omnivores aggregate in response to increases in diverse food subsidies. In contrast to expectation, carnivorous lycosid spiders and cantharid larvae did not aggregate in response to food subsidies (Figures 3.5, 3.6). In general, spiders rely on tactile and vibratory cues to detect and capture prey (Uetz 1992) and the presence of visual or vibratory cues increases patch tenure time (Persons and Uetz 1996). Therefore, it was not surprising that spiders did not aggregate in response to supplements of a sessile prey item such as pupae in the same way they often accumulate in response to the enhanced density of mobile herbivores (Gratton and Denno 2003) and detritivores (Polis and Hurd 1995; Chen and Wise 1999). Alternatively, it has been shown that lycosid spiders reduce their foraging activity in patches with abundant prey (Persons and Uetz 1996; Wagner and Wise 1997). Such altered behavior could reduce the efficiency of pitfall trap sampling, which necessitates predator activity, and may make changes in activity-density difficult to detect (Adis 1979). However, vacuum sampling also failed to reveal changes in spider density in response to food subsidies, but this may be a reflection of very few spiders being captured overall using this technique. Little is known about the spatial dynamics of cantharid larvae, and to my knowledge they have not been documented

as predators of agricultural pests. Although cantharids were present in our plots, food subsidies appeared to have no effect on their abundance.

Seed and prey supplements differentially influenced predation of the focal herbivore, black cutworm. Contrary to my hypothesis, prey subsidies in corn plots relaxed predation on focal herbivores as demonstrated by the increased number of sentinel cutworms, and free roaming caterpillars recovered from vacuum samples (Figure 3.12). This reduction occurred despite the fact that ants, the most abundant predator, increased two- and four-fold in plots subsidized with pupae (mean = 424 ± 105) and both pupae and seeds (mean = 727 ± 247) compared to non-subsidized controls (220 ± 72). Interestingly, ants increased to a similar density in both seed-subsidized and pupal-subsidized plots. However, in seed-subsidized plots ant predation on cutworms was higher than in the other treatment plots (Figure 3.9). This outcome documents a mechanism akin to apparent competition between herbivores (Holt and Kotler 1987; Holt and Lawton 1994) such that an abundance of seeds attracted a large number of omnivorous predators which in turn switched their feeding focus and imposed increased predation on resident herbivores. Similarly, McMurtry and Scriven (1966a, b) found that a strong aggregative response to pollen by omnivorous mites resulted in more intense predation of herbivorous mites. Likewise, a numerical response of omnivorous big-eyed bugs to increased bean-pod abundance resulted in greater predation on aphid prey (Eubanks and Denno 2000a). In this way, the numerical response of omnivores to alternative plant resources can promote greater predator populations and increased predation of focal prey in a habitat than would be possible based on *in situ* or enhanced prey density alone (Holt and Kotler

1987; Holt and Lawton 1994). By supporting a high density of predators when focal herbivores are scarce, alternative food can establish a buffer against herbivore outbreaks (Settle et al. 1996). As herbivore populations increase, the subsidized predator population is already in place to dissuade population growth of herbivores and associated plant damage (McMurty and Scriven 1966 a, b; Settle et al. 1996).

Ants have a propensity for aggregation due to their social life history. For instance, ants frequently aggregate in response to food subsidies such as extra-floral nectaries and hemipteran honeydew, a numerical response that often affects community structure and trophic interactions (Rudgers and Gardner 2004; Kaplan and Eubanks 2005, Strysky and Eubanks 2006). In my seed-subsidized plots, ants switched from an abundant low-quality food (seeds) to a relatively scarce high-quality prey (cutworms) as expected (see Murdoch 1969; Holt and Lawton 1994). The positive correlation between ant activity-density and cutworm predation in seed-subsidized plots supports the assertion that a behavioral shift from seeds to cutworms occurred in seed plots that did not occur when only pupae were present (Figure 3.11). It may be that foraging for fly pupae has a greater per capita return for ants than subduing and dismembering large cutworms. It took hundreds of ants many hours to kill and carry off a single cutworm, whereas an individual ant can carry and quickly handle a fly pupa (S. Frank *personal observation*). Therefore, in plots augmented with pupae, which have a similar nitrogen content as cutworms, worker ants selectively collecting pupae may provide a more efficient use of colony resources and likely represents an optimal foraging choice for ants.

Spiders and other carnivorous predators did not exhibit an aggregative

response in plots subsidized with alternative food resources. However, predation of focal prey by these predators was lowest in plots that received prey subsidies (Figure 3.9). In contrast to apparent competition (negative, indirect prey-prey interaction), such positive prey resource interactions occur when the abundance of one prey item directs predation away from a second prey species in what is termed apparent mutualism (Abrams and Matsuda 1996). The presence of pupae that are nutritionally similar but easier to capture, drew attacks away from cutworms. Alternatively, in plots that received seeds or no prey resource subsidies, carnivorous predators imposed high rates of predation on sentinel and free-roaming caterpillars because no alternative food was “available” (Figures 3.9, 3.12). For example, the activity-density of spiders and cantharid larvae was significantly correlated with the level of sentinel cutworm disappearance in plots that received seed subsidies, suggesting that spiders or cantharids were consuming cutworms. Correlations between predator taxa and predation of sentinel cutworms were different when sampled by pitfall traps or by vacuum sampling. Vacuum samples represent an instantaneous sample taken during the day when many of these predators are likely inactive. However, pitfall traps provide a measure of activity and sample throughout the night when these predators are active. Therefore, pitfall traps data may provide better information regarding the taxa that are actively foraging and consuming cutworms in plots.

Predation by predators other than ants was highest in plots that received no subsidies (Figure 3.9), even though no predator group was positively associated with cutworm predation. Carnivorous spiders, cantharid larvae and carabids were similarly abundant in all treatments despite resource subsidies. Predators such as opilionids

and centipedes were observed to consume sentinel cutworms, but these taxa represented a small percentage of the predators trapped in plots, thus precluding an analysis of treatment effects on their abundance. These and other predators may have contributed to cutworm predation in plots where no alternative food was provided. In addition, these predators may have experienced a refuge from ants, which are known to be agonistic toward other predators (Laakso and Setälä 2000; Kaplan and Eubanks 2005). Antagonistic competitive and predatory interactions are likely responsible for the negative correlation between spiders and ants in this study, a phenomenon that has been demonstrated in other systems (Halaj et al. 1997). For example, ants were observed to consume a cutworm after they drove off the wolf spider that initially captured and killed the cutworm prey (S. Frank *personal observation*). Therefore, it wasn't surprising to find that ant and non-ant predators were negatively correlated.

Organisms generally increase in nitrogen content and thus in food quality as they occupy higher trophic positions (Mattson 1980; Elser et al. 2000; Fagan et al. 2002). As such, nitrogen-rich resources (prey) often support increased survival, growth, and reproduction of predators, which then increase in abundance over the long term (Mayntz and Toft 2001; Denno and Fagan 2003). My experiments took place over 2 – 3 week periods, which were substantially less than the generation time of the dominant predator species in the corn system. Therefore, the numerical response of predators and the resulting indirect prey-prey interactions were a function of predator preference, foraging behavior, and aggregation (Holt and Kotler 1987) rather than increased predator survival and reproduction (e.g. McMurtry and Scriven 1966a, b). The differential impact of ants on herbivores in this experiment supports

theoretical predictions that the short term consequences of resource subsidies on one prey species will depend in part on the abundance and quality of other associated prey species (Holt and Kotler 1987). Seeds in this experiment were of much lower quality (~2.8% N) than the pupae (~8.0% N) and cutworms (~8.9% N) (see methods section). Omnivores will often switch from feeding on plant resources when higher quality prey becomes available (Agrawal et al. 1999; Agrawal and Klein 2000; Coll and Guershon 2002; Janssen et al. 2003) just as ants switched from low quality seeds to cutworms in this experiment.

Differences in resource subsidies and predator guild altered the strength of trophic cascades in this system. Although only omnivores responded aggregatively to food subsidies, predation of cutworms by omnivores and carnivores declined in plots subsidized with pupae (3.9). The reduced predation of cutworms in plots subsidized with pupae resulted in greater survival of free-roaming caterpillars and lower survival of corn seedlings (Figure 3.12, 3.14). The strength of the trophic cascade was not improved by resource subsidies and enhanced predator aggregation as shown in other systems (Polis and Holt 1995; Henschel et al. 2001). To the contrary, the trophic cascade was strongest in plots without resource subsidies and was dampened by the presence of pupal prey (see Nakano et al. 1999). The strength of this trophic cascade was preserved when seeds were present, but only when ant abundance was high. Therefore, reduced per-capita cutworm predation by ants was compensated for by a numerical response by ants and the lack of alternative food for carnivores. Previous investigations have documented the aggregation of predators to abundant alternative food resources (Chen and Wise 1999; Ives et al. 1993; Evans and Toler 2007), and

some studies have demonstrated how aggregation affects herbivore abundance (Evans and England 1996; Harmon et al. 2000; Eubanks and Denno 1999, 2000a; Murakami and Nakano 2002; Ostman and Ives 2003). However, few studies have sought to document the cascading effects of resource subsidies to basal resources (Polis and Holt 1995; Nakano et al. 1999; Henschel et al. 2001) particularly in terrestrial systems (Holt and Lawton 1994). Moreover, the numerical response of predators to abundant food resources is often confounded with habitat structure due to mulching or increased plant growth (e.g. Halaj and Wise 2002; Gratton and Denno 2003).

Omnivores are ubiquitous in natural and managed systems and they impose potentially stabilizing effects on food webs in numerous systems (Polis and Strong 1996; Fagan 1997; Coll and Guershon 2002). My research demonstrates that the type of food resource subsidy can interact with predator guild to affect food-web dynamics. The presence of true omnivores in this system, players that consume both plant and prey resources, complicates trophic dynamics because plant and prey subsidies had different effects on the strength of the trophic cascade. This research demonstrates that as omnivores spread their resource use among animal prey resources, trophic cascades are dampened but that such cascades are restored as true omnivores aggregate in response to plant resources but then switch to feeding on herbivore prey.

Applied implications

Accurately predicting how different resources alter the survival, distribution, and impact of predators on lower trophic levels is essential from both theoretical and

applied perspectives (Holt and Lawton 1994; Ostfeld and Keesing 2000; Gurr et al. 2000; Landis et al. 2000; Symondson et al. 2002). Predators are often the first consumers lost in response to human activities and environmental disturbance, and as a consequence they have been the subject of intense management and preservation efforts (Pauley et al. 1998). Moreover, the influence of spatial and temporal resource subsidies on food web dynamics has implications for the impact of invasive species (King 1983; O'Donnell and Phillipson 1996), the spread of human disease (Elkinton et al. 1996; Ostfeld et al. 1996; Jones et al. 1998), the fate of endangered species (King 1983), and the community-wide repercussions of species declines (Estes et al. 1998; Dayton et al. 1998). Understanding the dynamics of predators and their many food resources will help to improve conservation efforts and mitigate damage as human activities continue to alter the trophic composition of natural communities and disrupt natural processes.

In addition, many arthropod predators contribute to the suppression of economically important pest insects. Attracting and retaining generalist predators with abundant alternative food resources is a primary tenet of conservation biological control (Landis et al. 2000). Increased pest suppression is accomplished either by providing resources directly in the form of floral resources such as pollen and nectar or indirectly by increasing habitat complexity, which in turn often results in increased alternative prey density (Landis et al. 2000; Frank and Shrewsbury 2004a, Shrewsbury and Raupp 2006). Both of these management strategies have returned mixed results in that increasing natural enemy abundance does not always translate into greater pest suppression and reduced plant damage (trophic cascades) (Gurr et al.

2000).

Generalist predators often aggregate and maintain higher densities in areas of increased habitat complexity (Langellotto and Denno 2004, Shrewsbury and Raupp 2006), which offer benefits such as refuge from intraguild predation (Finke and Denno 2002; Langellotto and Denno 2004) a less variable microclimate, and alternative prey and plant resources (Landis et al. 2000, Shrewsbury and Raupp 2006). Due to confounded habitat variables, it is difficult to identify the most important factor influencing predator abundance and impact on pest populations. The natural-enemy taxa that are enhanced by increasing habitat complexity are often generalist carnivores such as lycosid spiders or omnivores such as coccinellids, anthocorids, geocorids, carabids, and parasitoids (Thomas et al 1991; White et al. 1995; Hickman and Wratten 1996; Chaney 1998; Gurr et al. 2000; Landis et al. 2000; Symondson 2002; Frank and Shrewsbury 2004a; Shrewsbury et al. 2004, Shrewsbury and Raupp 2006). The omnivorous and generalist feeding habits of these consumers often increases the reticulate nature of interactions in the food web and thus reduces the predictability of their impact on target herbivores (Polis and Strong 1996; Symondson et al. 2002; Coll and Guershon 2002).

Resource subsidies can alter the composition of a predator community and either reduce or enhance the efficacy of that community at regulating herbivore populations (Evans and England 1996; Gurr et al. 2000). This depends in part on the predators present and the herbivore of interest. For instance, Musser and Shelton (2003) found that the presence of alternative pollen or aphid prey in corn attracted coccinellids but reduced predation of European corn borer eggs in sweet corn.

However, Harmon et al. (2000) demonstrated that the presence of dandelions (pollen resource) attracted coccinellids and increased predation of aphids in corn. Using alternative prey in this experiment that was more preferred by carnivores could have altered the outcome. More mobile or larger prey may have had a stronger effect on spider aggregation which could ultimately increase predation of cutworms. However, if the other prey was more preferred they could also reduce predation of cutworms just as pupae did.

This research demonstrates that independent of habitat complexity, alternative prey, as a high quality resource, can reduce the efficacy of omnivorous and carnivorous predators as agents of biological control. In contrast, alternative plant resources have the potential to increase the abundance of omnivorous predators which may switch to high quality cutworm prey. This in turn can impose top-down regulation of herbivores and restore a trophic cascade which is the goal of biological control. This has been demonstrated by adding floral resources that attracted predators and parasitoids to pest prone systems which then imposed top-down control on resident herbivorous pests (White et al. 1995; Chaney 1998; Stephens et al. 1998; Shrewsbury et al. 2004; Irvin et al. 2006). My study, along with others, provide encouragement that the use of supplemental plant resources may increase the success of conservation biological control, but highlight the possibility that alternative prey has a greater potential to disrupt biological control efforts.

Tables

Table 3.1. ANOVA results for the effect of resource subsidies (no subsidy, seeds, pupae, or both) on the number of carabid beetles, cantharid beetle larvae, wolf spiders, and ants captured in pitfall traps in treatment plots at CMREC in College Park, MD.

Effect	Ants		Wolf spiders		Carabids		Cantharids	
	$F_{1,30}$	P	$F_{1,30}$	P	$F_{1,30}$	P	$F_{1,30}$	P
Seeds	0.11	0.746	0.14	0.709	10.42	0.003	1.43	0.241
Pupae	0.02	0.889	1.99	0.169	0.99	0.329	0.87	0.359
Seeds*Pupae	0.12	0.736	0.07	0.799	0.99	0.329	0.44	0.514

Table 3.2. ANOVA results for the effect of resource subsidies (no subsidy, seeds, pupae, or both) on the number of carabid beetles, cantharid beetle larvae, wolf spiders, and ants captured by vacuum sampling in treatment plots at CMREC in College Park, MD.

Effect	Ants		Wolf spiders		Carabids		Cantharids	
	$F_{1,30}$	P	$F_{1,30}$	P	$F_{1,30}$	P	$F_{1,30}$	P
Seeds	5.31	0.029	0.19	0.665	0.00	0.949	0.11	0.748
Pupae	15.66	< 0.001	0.38	0.540	0.09	0.772	0.86	0.360
Seeds*Pupae	0.00	0.969	0.48	0.493	2.04	0.163	0.30	0.589

Table 3.3. Correlation (*r* value above, *P* value below) between dominant predator groups captured in (a.) pitfall traps and (b.) by vacuum sampling in plots subsidized with no alternative food, seeds, pupae, or seeds and pupae in at CMREC College Park, MD. Bold values highlight significant (*P* < 0.05) correlations.

a. Pitfall traps		Wolf spiders	Carabids	Cantharidae	Ants	Miscellaneous
	Mean±SE					
Wolf spiders	45.11±4.7	-	-0.369	-0.012	-0.525	-0.159
		-	0.014	0.937	<0.001	0.304
Carabids	1.77±0.3	-	-	0.078	0.323	0.022
		-	-	0.614	0.032	0.889
Cantharidae	2.70±0.8	-	-	-	0.055	-0.149
		-	-	-	0.724	0.336
Ants	53.77±7.7	-	-	-	-	0.294
		-	-	-	-	0.053
Miscellaneous	0.41±0.1	-	-	-	-	-
		-	-	-	-	-

b. Vacuum		Wolf spiders	Carabids	Cantharidae	Ants	Miscellaneous
	Mean±SE					
Wolf spiders	0.73±0.2	-	0.387	0.445	0.072	0.238
		-	0.010	0.003	0.644	0.120
Carabids	16.23±1.7	-	-	0.554	0.213	0.374
		-	-	< 0.001	0.164	0.012
Cantharidae	6.05±1.3	-	-	-	0.165	0.481
		-	-	-	0.284	0.001
Ants	521.25±105.5	-	-	-	-	0.305
		-	-	-	-	0.044
Miscellaneous	12.98±2.6	-	-	-	-	-
		-	-	-	-	-

Table 3.4. ANOVA results for the effect of resource subsidies (no subsidy, seeds, pupae, or both) on the number of sentinel cutworms consumed by ants and other invertebrate predators in treatment plots at CMREC in College Park, MD.

Effect	ndf, ddf	Total		Ant predation		Other predation	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Seeds	1, 30	0.49	0.489	1.61	0.214	2.88	0.099
Pupae	1, 30	57.94	< 0.001	10.89	0.003	17.3	< 0.001
Seeds*Pupae	1, 30	0.11	0.746	4.77	0.037	4.5	0.042

Table 3.5. Correlation between dominant predator groups sampled by (a.) pitfall traps or (b.) vacuum sampling and the number of sentinel cutworms observed eaten by ants (ant predation) or for which a predator was not observed (non-ant predation) in all treatment plots combined (overall), plots receiving no alternative food, and plots receiving subsidies of seeds, pupae, or seeds and pupae at CMREC in College Park, MD. Bold values highlight significant ($P < 0.05$) correlations.

a. Pitfall		Overall	No alternative food	Seeds	Pupae	Seeds and Pupae
		r P	r P	r P	r P	r P
Wolf spiders	non-ant	0.322	0.302	0.616	0.258	0.496
	predation	0.033	0.367	0.045	0.444	0.121
Carabids	non-ant	-0.185	-0.089	-0.128	-0.329	-0.115
	predation	0.230	0.795	0.707	0.322	0.735
Cantharids	non-ant	0.187	0.361	0.601	0.099	0.646
	predation	0.224	0.276	0.051	0.771	0.032
Ants	non-ant	-0.258	0.356	-0.474	-0.415	-0.407
	predation	0.091	0.282	0.141	0.205	0.214
Other predators	non-ant	-0.119	-0.390	-0.109	-0.123	0.065
	predation	0.443	0.235	0.749	0.718	0.849
Ants	ant	0.073	-0.406	0.650	-0.111	0.071
	predation	0.638	0.216	0.030	0.745	0.835
Non-ant predation	ant	-0.117	-0.661	-0.489	0.223	0.150
	predation	0.448	0.027	0.127	0.509	0.661

b. Vacuum		Overall	No alternative food	Seeds	Pupae	Seeds and Pupae
		r P	r P	r P	r P	r P
Wolf spiders	non-ant	-0.161	-0.004	-0.572	0.175	-0.217
	predation	0.296	0.990	0.066	0.606	0.522
Carabids	non-ant	-0.223	-0.564	-0.145	-0.414	0.127
	predation	0.146	0.071	0.670	0.206	0.780
Cantharids	non-ant	-0.150	-0.144	-0.594	0.094	-0.245
	predation	0.332	0.672	0.054	0.783	0.469
Ants	non-ant	-0.127	-0.081	-0.110	-0.156	-0.350
	predation	0.450	0.813	0.767	0.646	0.291
Other predators	non-ant	-0.408	-0.422	-0.502	-0.398	-0.549
	predation	0.006	0.196	0.115	0.226	0.081
Ants	ant	-0.106	-0.296	0.450	-0.524	-0.036
	predation	0.493	0.377	0.117	0.098	0.917
Non-ant predation	ant	-0.117	-0.661	-0.489	0.223	0.150
	predation	0.448	0.027	0.127	0.509	0.661

Table 3.6. ANOVA results for the effect of resource subsidies (no subsidy, seeds, pupae, or both) on the number and proportion of sentinel resources (total = seeds + pupae, seeds, and pupae) taken from food stations in treatment plots at CMREC in College Park, MD.

Effect	Total		Pupae		Seeds		Proportion	
	$F_{1,30}$	P	$F_{1,30}$	P	$F_{1,30}$	P	$F_{1,30}$	P
Seeds	0.72	0.403	0.67	0.418	1.51	0.229	0.48	0.496
Pupae	0.16	0.689	1.81	0.188	5.39	0.027	6.07	0.019
Seeds*Pupae	0.19	0.664	0.07	0.787	0.15	0.702	0.52	0.478

Table 3.7. Repeated measures ANOVA results for the effect of resource subsidies (no subsidy, seeds, pupae, or both) on the number of corn seedlings cut by cutworms in treatment plots at CMREC in College Park, MD. Seedlings were counted approximately 5 and 10 days after emergence (= observation).

Effect	ndf,	F	P
	ddf		
Observation	1, 70	11.09	0.001
Seeds	1, 70	0.05	0.819
Pupae	1, 70	8.19	0.006
Obs*Seed	1, 70	0.34	0.561
Obs*Pupae	1, 70	0.03	0.854
Seed*Pupae	1, 70	0.55	0.460
Obs*Seed*Pupae	1, 70	0.83	0.366

Figures

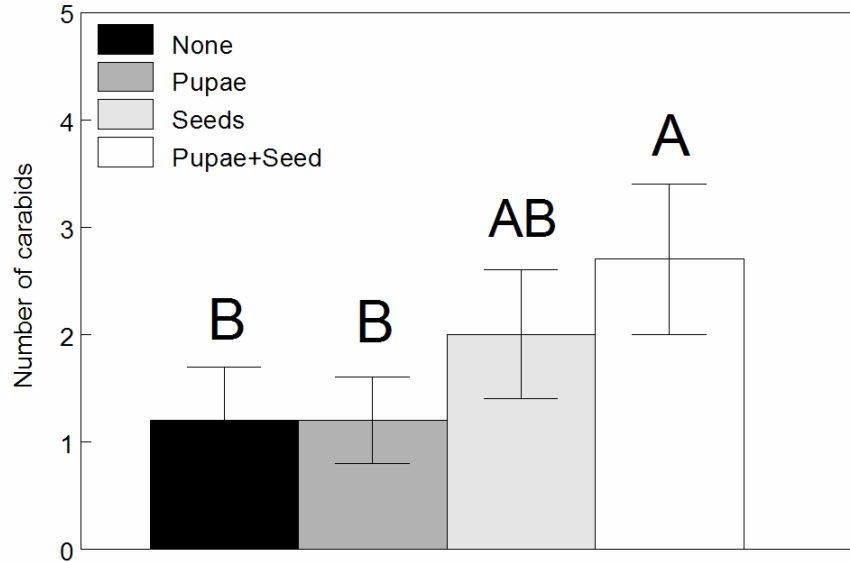


Figure 3.1. Average number of carabid beetles captured by pitfall traps in plots subsidized with no alternative food, seeds, pupae, or seeds and pupae at CMREC in College Park, MD. Bars that share the same letter are not significantly different at $P < 0.05$ level.

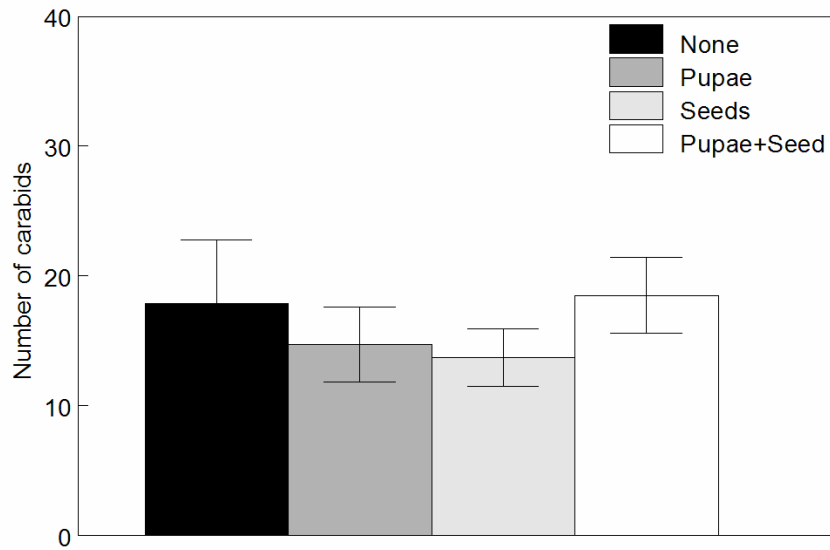


Figure 3.2. Average number of carabid beetles captured by vacuum sampling in plots subsidized with no alternative food, seeds, pupae, or seeds and pupae at CMREC in College Park, MD. Treatments were not significantly different at the $P < 0.05$ level.

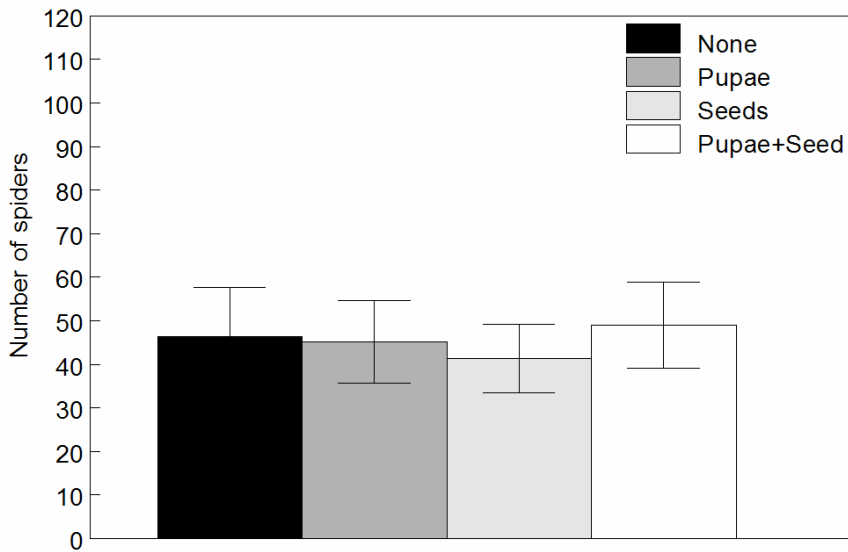


Figure 3.3. Average number of wolf spiders captured by pitfall traps in plots subsidized with no alternative food, seeds, pupae, or seeds and pupae at CMREC in College Park, MD. Treatments were not significantly different at the $P < 0.05$ level.

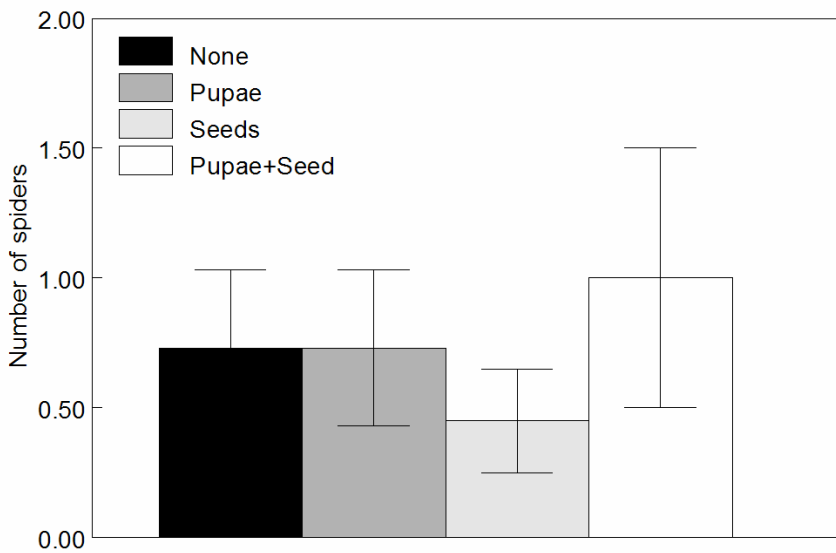


Figure 3.4. Average number of wolf spiders captured by vacuum sampling in plots subsidized with no alternative food, seeds, pupae, or seeds and pupae at CMREC in College Park, MD. Treatments were not significantly different at the $P < 0.05$ level.

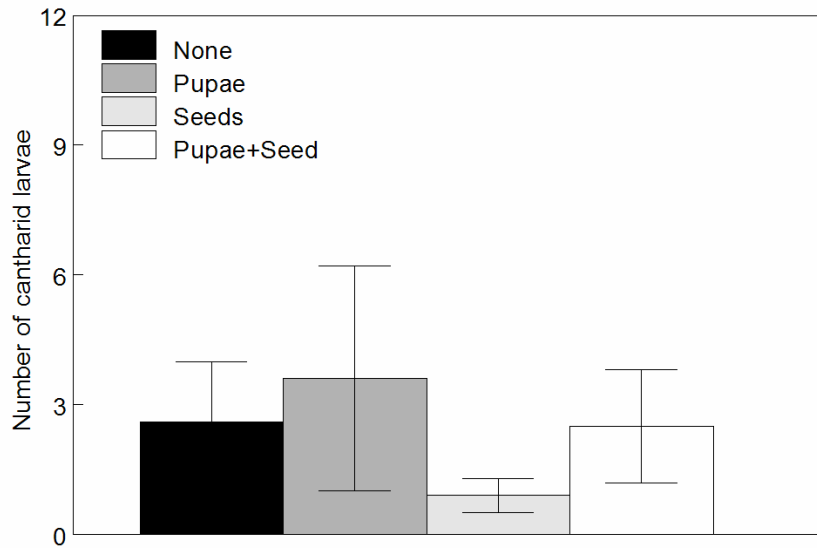


Figure 3.5. Average number of cantharid larvae captured by pitfall traps in plots subsidized with no alternative food, seeds, pupae, or seeds and pupae at CMREC in College Park, MD. Treatments were not significantly different at the $P < 0.05$ level.

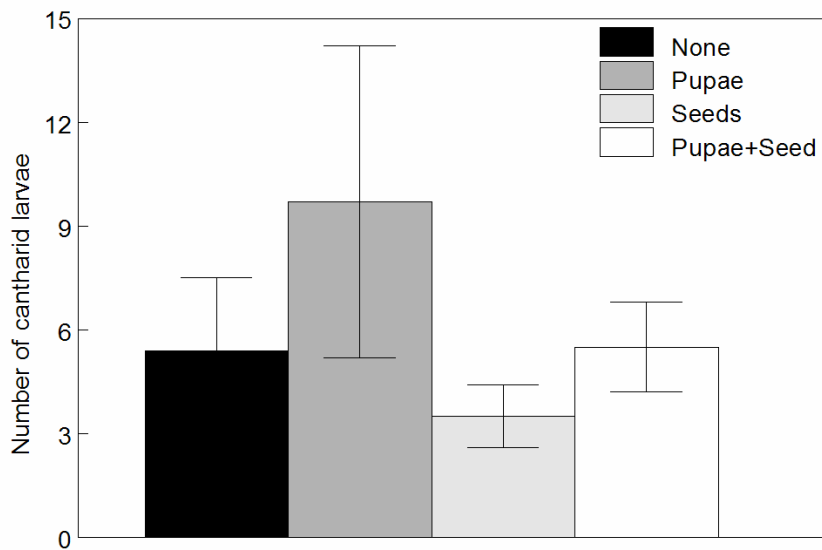


Figure 3.6. Average number of cantharid larvae captured by vacuum sampling in plots subsidized with no alternative food, seeds, pupae, or seeds and pupae at CMREC in College Park, MD. Treatments were not significantly different at the $P < 0.05$ level.

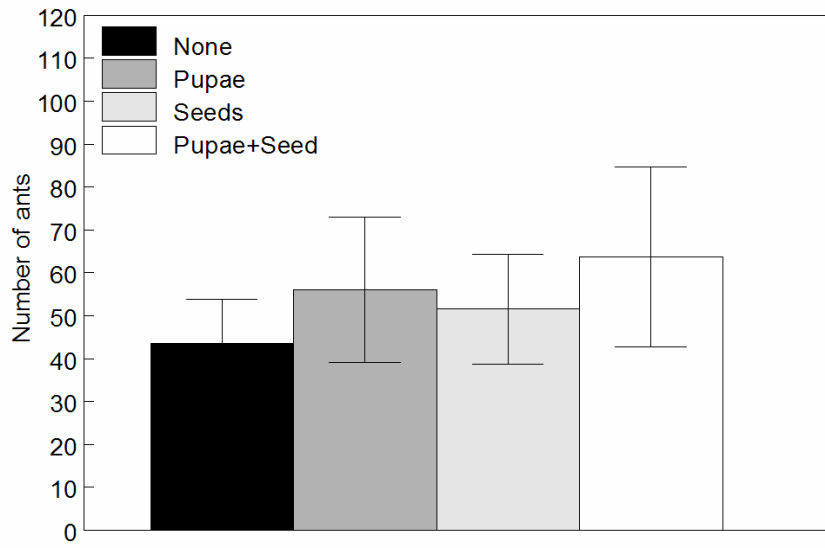


Figure 3.7. Average number of ants captured by pitfall traps in plots subsidized with no alternative food, seeds, pupae, or seeds and pupae at CMREC in College Park, MD. Treatments were not significantly different at the $P < 0.05$ level.

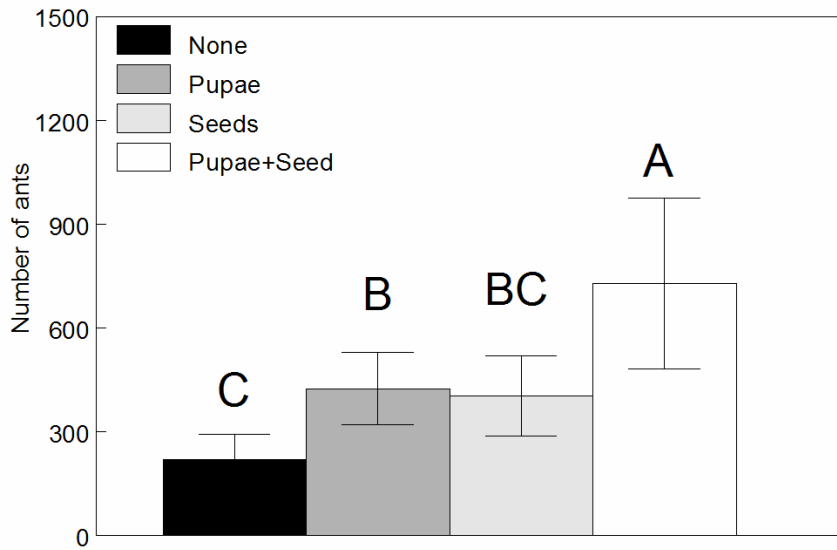


Figure 3.8. Average number of ants captured by vacuum sampling in plots subsidized with no alternative food, seeds, pupae, or seeds and pupae at CMREC in College Park, MD. Bars that share the same letter are not significantly different at $P < 0.05$ level.

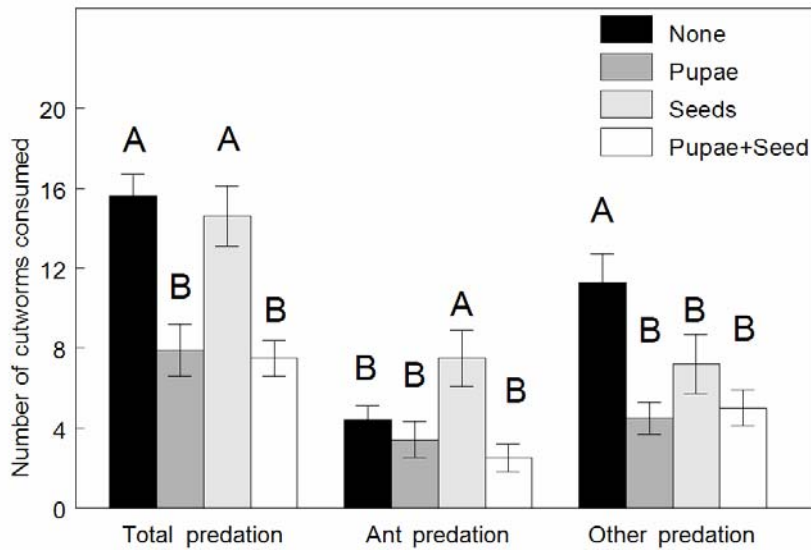


Figure 3.9. Average number of sentinel cutworms consumed (of 20) overall, by ants and by other predators in plots subsidized with no alternative food, seeds, pupae, or seeds and pupae at CMREC in College Park, MD. “Other predation” includes cutworms observed being eaten by spiders (10 observations), opilionids (1), carabids (2), centipedes (1), cantharid larvae (2), and cutworm disappearance when no predation event was observed (292). Bars that share the same letter within a predation category are not significantly different at $P < 0.05$ level.

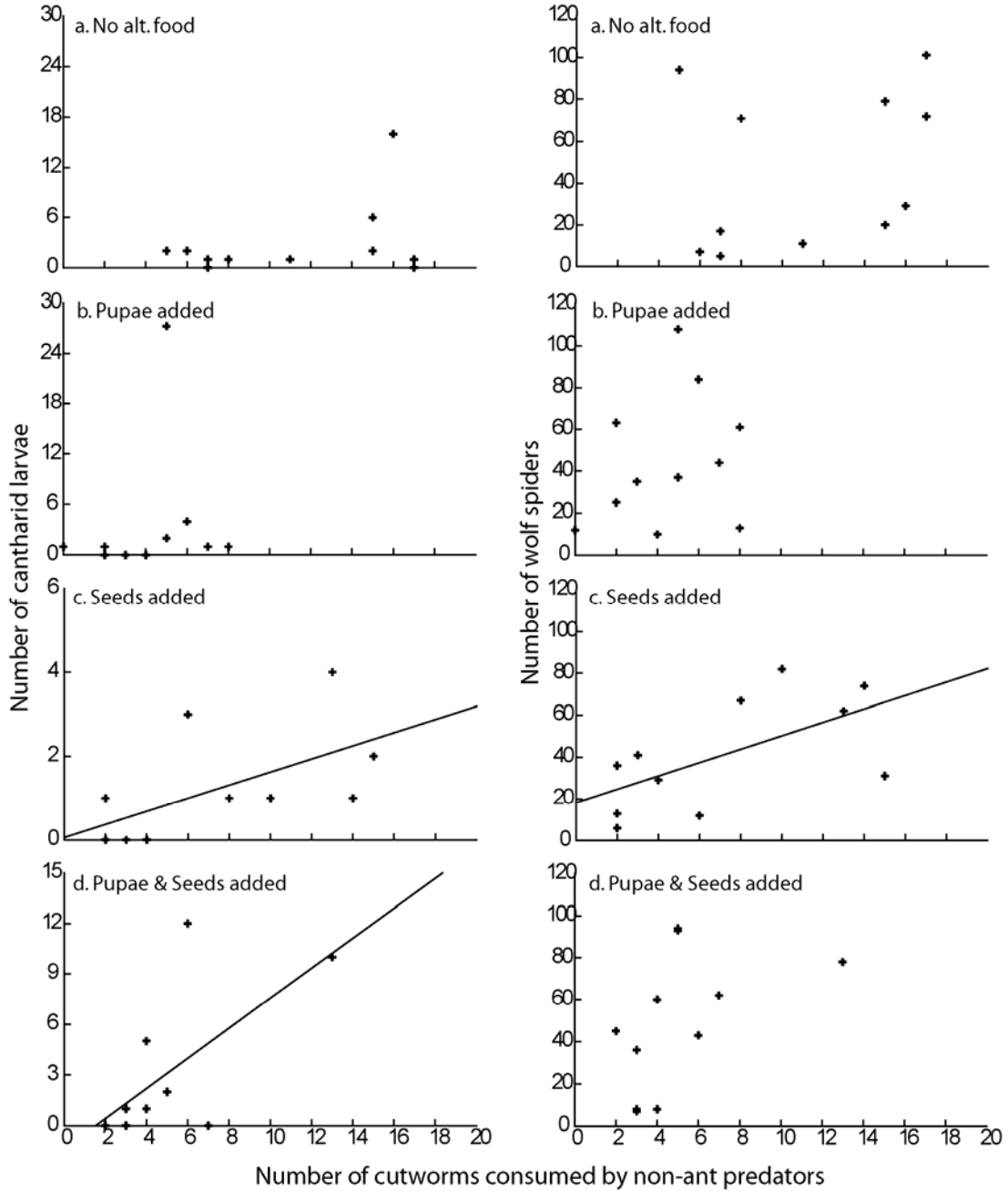


Figure 3.10. Correlation between the abundance of cantharid larvae or wolf spiders captured in pitfall traps and the number of sentinel cutworms consumed in plots subsidized with no alternative food (a), pupae (b), seeds (c), or seeds and pupae (d) at CMREC in College Park, MD. Correlations include only those sentinel cutworms that were not observed eaten by ants. In graphs without a best fit line the variables were not significantly correlated. Statistics are presented in Table 3.5.

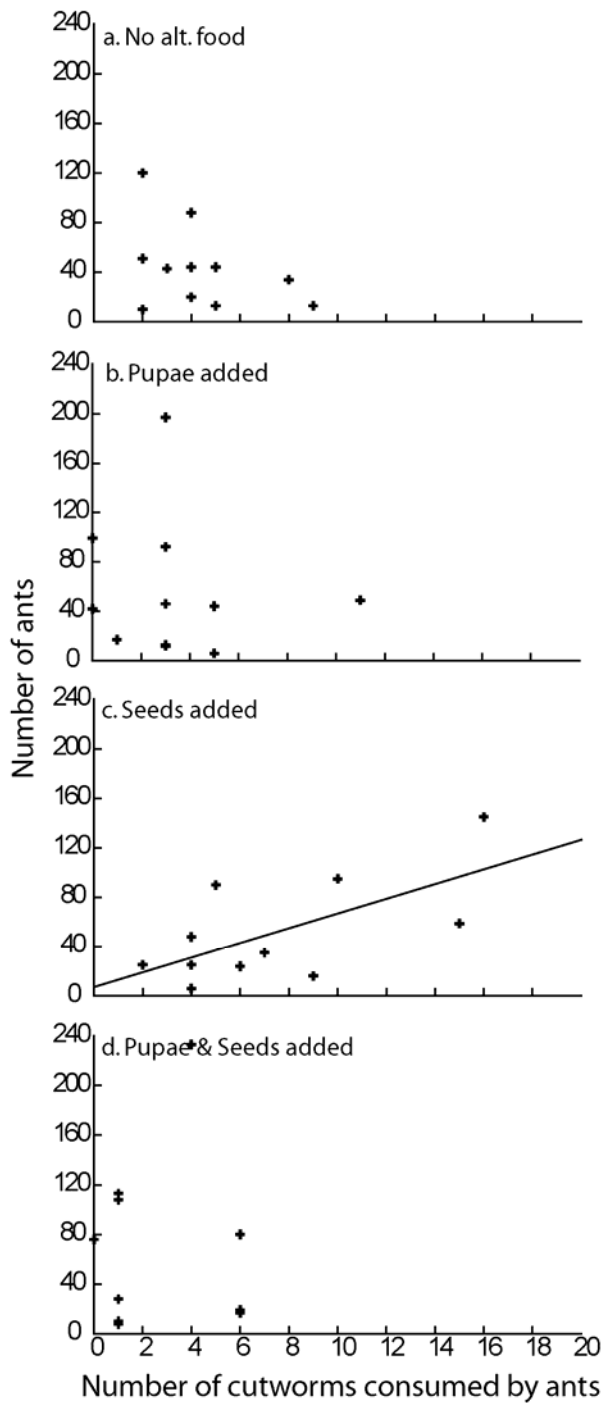


Figure 3.11. Correlation between the abundance of ants captured in pitfall traps and the number of sentinel cutworms consumed by ants in plots subsidized with no alternative food (a), pupae (b), seeds (c), or seeds and pupae (d) at CMREC in College Park, MD. In graphs without a best fit line the variables were not significantly correlated.

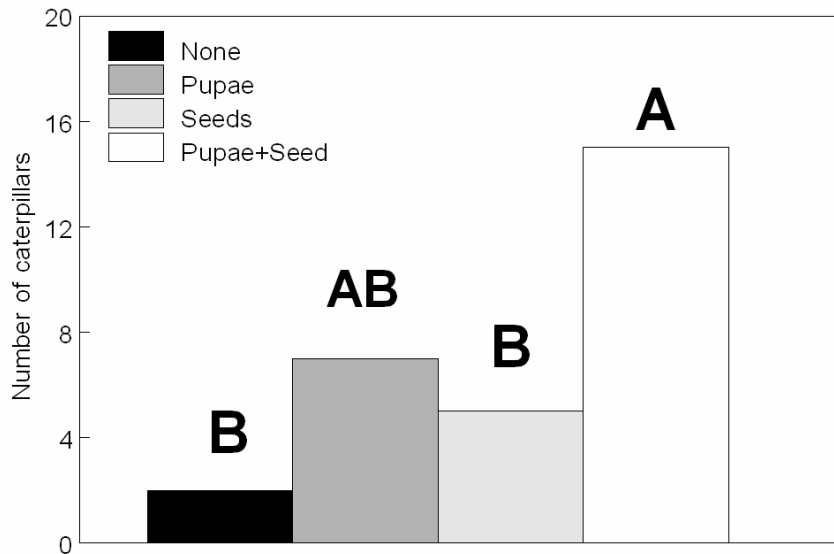


Figure 3.12. Number of free roaming cutworm larvae captured by vacuum sampling in plots subsidized with no alternative food, seeds, pupae, or seeds and pupae at CMREC in College Park, MD. Bars that share the same letter are not significantly different at $P < 0.05$ level.

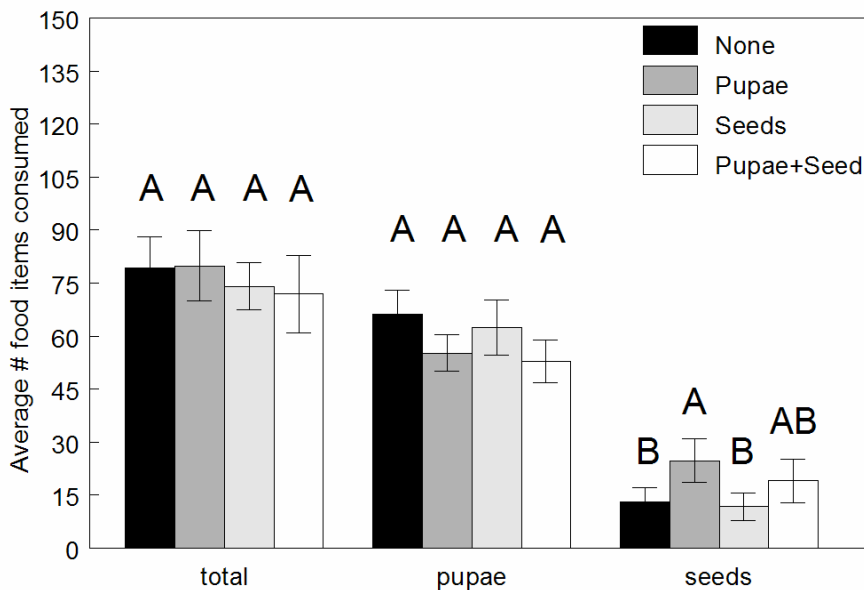


Figure 3.13. Average number of pupae and seeds taken from food stations in plots subsidized with no alternative food, seeds, pupae, or seeds and pupae at CMREC in College Park, MD. Bars that share the same letter are not significantly different at $P < 0.05$ level.

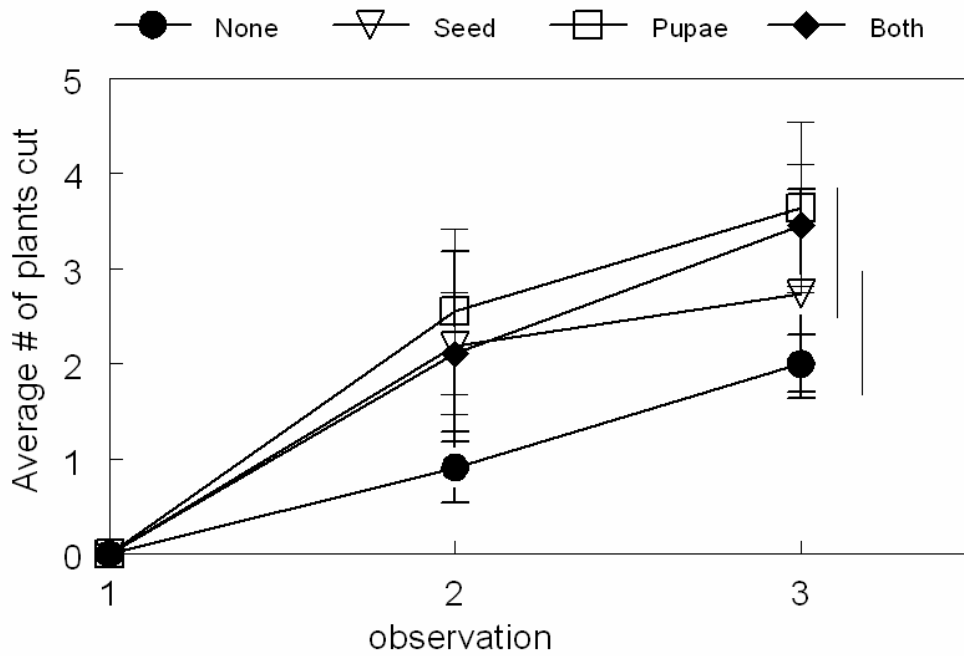


Figure 3.14. Average number of corn plants cut by cutworms during three observation periods in treatment plots subsidized with no alternative food, seeds, pupae, or seeds and pupae at CMREC in College Park, MD. Observation 1 occurred at corn emergence and observation 3 took place just before seedling harvest on day 15 of the experiment. Vertical bars at observation 3 represent the pairwise LSD treatment comparisons. Treatments overlapped by the same vertical bar are not significantly different.

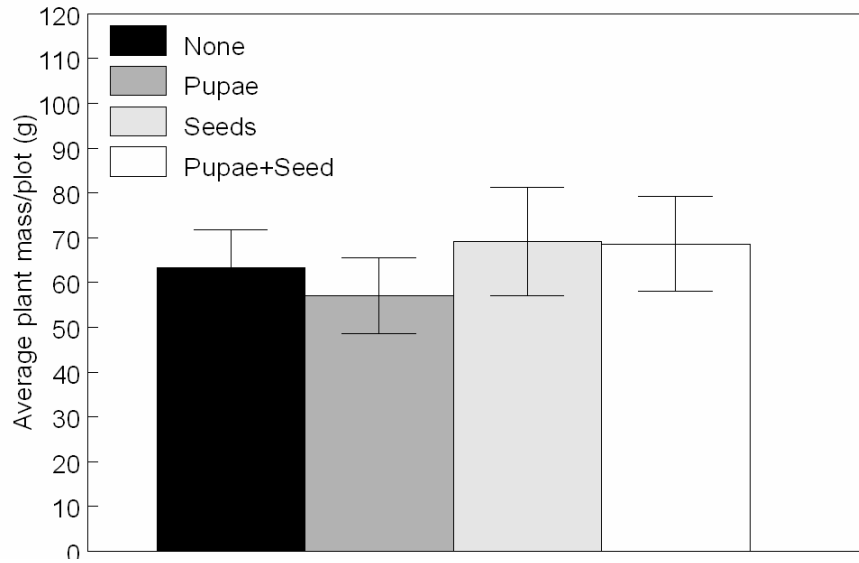


Figure 3.15. Average dry mass of corn seedlings harvested from plots subsidized with no alternative food, seeds, pupae, or seeds and pupae at CMREC in College Park, MD. Treatments were not significantly different at $P < 0.05$.

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