

Effects of alternative food on cannibalism and herbivore suppression by carabid larvae

STEVEN D. FRANK, PAULA M. SHREWSBURY and ROBERT F. DENNO Department of Entomology, University of Maryland, College Park, Maryland, U.S.A.

Abstract. 1. Predator and alternative food density are important factors influencing herbivore suppression by generalist predators. Herbivore suppression can be reduced if predators forage preferentially on alternative foods. Cannibalism can increase at high predator densities, further reducing herbivore suppression. However, complex interactions are possible, as alternative food can increase predator abundance and survival restoring top-down effects on herbivores.

2. In two species of carabid larvae (*Poecilus chalcites* and *Anisodactylus ovularis*), we studied how alternative foods (fly pupae and grass seeds) and predator density affect predation of black cutworm larvae and how alternative foods affect cannibalism among carabid larvae.

3. Adding alternative food to microcosms generally reduced total predation of cutworms. However, the strength of this effect was dependent on carabid species, larval density, and food type.

4. Increasing larval density from one to three per microcosm reduced per-capita predation by both species irrespective of alternative food treatment.

5. Alternative food reduced cannibalism in both carabid species and increased survival of carabid larvae in field plots, such that twice as many were captured in plots subsidised with pupae than plots with no alternative food.

6. These results provide new insight into the complex interactions that influence predator survival and herbivore suppression in resource diverse habitats by demonstrating the primacy of intraguild interactions among carabid larvae.

Key words. Aggregation, alternative food resources, *Anisodactylus ovularis*, apparent competition, biological control, black cutworms (*Agrotis ipsilon*), Carabidae, herbivore suppression, intraguild predation, numerical response, omnivory, *Poecilus chalcites*, predator aggregation.

Introduction

Omnivory, feeding at more than one trophic level, is a common feature of arthropod food-webs in natural and managed ecosystems (Polis & Strong, 1996; Coll & Guershon, 2002). Omnivorous behaviour ranges from ‘true omnivory’ (sensu Coll & Guershon, 2002), in which predators also feed on plants, to intraguild predation and cannibalism in which predators consume other predators (Polis *et al.*, 1989; Rosenheim *et al.*, 1995). In any form, omnivory complicates trophic dynamics as predators feed on alternative foods—plants,

prey, or other predators—in addition to herbivores (Polis & Strong, 1996). Therefore, omnivory can reduce top-down effects on herbivores, weaken trophic cascades, and disrupt biological control (Rosenheim *et al.*, 1995; Denno *et al.*, 2004). Omnivory, including cannibalism, is common among arthropod predators in natural food webs and among predators important in the biological control of herbivorous pests (Rosenheim *et al.*, 1995; Coll & Guershon, 2002; Symondson *et al.*, 2002). Therefore, it is essential to elucidate factors that influence the occurrence and strength of herbivore suppression and intraguild interactions by omnivorous predators.

The presence of alternative food in a habitat has multiple effects on predator behaviour, abundance, and herbivore suppression. By reducing intraguild predation and cannibalism among generalist predators, alternative foods can increase

Correspondence: Steven D. Frank, Department of Entomology, North Carolina State University, Campus Box 7613, Raleigh, NC 27695, U.S.A. E-mail: sdfrank@ncsu.edu

predator survival and abundance in a habitat (Wagner & Wise, 1996, 1997; Cottrell & Yeargan, 1998; N6ia *et al.*, 2008). Alternative foods can also increase predator abundance by reducing emigration from a habitat (Eubanks & Denno, 1999; Shrewsbury & Raupp, 2006). As a result of increasing predator abundance and survival, alternative food can increase predation of herbivores (Holt, 1977). For example, Eubanks and Denno (1999, 2000a) found that omnivorous big-eyed bugs, *Geocoris punctipes* Say (Heteroptera: Geocoridae), were more abundant when lima bean pods were available as alternative food. As a consequence, populations of aphid and lepidopteran pests were smaller when pods were present compared to when pods were absent (Eubanks & Denno, 1999, 2000a).

Omnivory, however, does not always lead to increased prey suppression. If predators preferentially consume alternative food instead of herbivores, predation of target pests can be reduced. Lady beetle density on corn plants is greater when aphids or pollen are available as alternative food, due in part to reduced cannibalism (Cottrell & Yeargan, 1998; Musser & Shelton, 2003; Lundgren *et al.*, 2004). However, these alternative foods divert predation away from key pests such as the European corn borer, *Ostrinia nubilalis* Hubner (Lepidoptera: Noctuidae) and corn earworm, *Helicoverpa zea* Boddie (Lepidoptera: Noctuidae) (Cottrell & Yeargan, 1998; Musser & Shelton, 2003). In these cases, greater predator density does not translate into effective biological control, because pollen and aphids are preferred by lady beetles or are more abundant and easier to find. In addition, aggregation of predators in a habitat can result in intraguild predation, or cannibalism that reduces predator survival and their impact on herbivores (Wagner & Wise, 1996; Finke & Denno, 2003; but see Rosenheim & Harmon, 2006). Therefore, since alternative food and cannibalism can increase or decrease herbivore suppression, it is important to understand how these mechanisms interact in pest prone systems.

Carabid beetles are arthropod predators that are abundant in most agricultural and natural systems and can be important in the biological control of arthropod pests (Brust *et al.*, 1985, 1986; L6vei & Sunderland, 1996; Kromp, 1999; Menalled *et al.*, 1999). Carabid larvae consume small arthropods and some species also consume seeds (Kirk, 1973; J6rgensen & Toft, 1997; Hartke *et al.*, 1998). Carabid larvae occur at a range of densities in habitats such as agricultural fields where such alternative foods are abundant (Briggs, 1965; Luff, 1980; Heessen & Brunsting, 1981; Brust *et al.*, 1986). In addition, cannibalism occurs in most species of carabid larvae and is thought to be a key factor regulating carabid populations (Brunsting, 1981; Brunsting & Heessen, 1984; Currie *et al.*, 1996). Therefore, carabid larvae and their prey make an ideal system in which to explore the impact of alternative food on cannibalism and herbivore suppression in arthropod predators.

In this research we explore how the presence of fly pupae or grass seeds as alternative food affects predation of black cutworms, *Agrotis ipsilon* (Hufnagel) (Lepidoptera: Noctuidae), by carabid larvae. Further, we determine how alternative food affects cannibalism among carabid larvae in laboratory microcosms and carabid larval abundance in field experiments. Alternative food has different effects on herbivore

suppression depending on the predator–herbivore–alternative food complex in question. Therefore, we investigate the effect of fly pupae as alternative prey on herbivore suppression and cannibalism in two different species of carabid larvae, *Poecilus chalcites* (Say) and *Anisodactylus ovularis* (Casey). In addition, we investigate how fly pupae and grass seeds affect predation and cannibalism by the true omnivore *A. ovularis*.

We predict that alternative food will reduce predation of cutworms by carabid larvae. However, we predict that alternative food will reduce cannibalism and lead to a greater abundance of carabid larvae in the field. To address these hypotheses, our specific objectives were to determine (1) how the presence of alternative prey (pupae) and density of carabid larvae affect consumption of cutworms and cannibalism by *P. chalcites* and *A. ovularis*; (2) how the presence and type of alternative food (pupae or seeds) and density of carabid larvae affect consumption of cutworms and cannibalism by the true omnivore *A. ovularis*; and (3) how the presence and type of alternative food affects the abundance of carabid larvae in open field plots.

Materials and methods

Predators, herbivores, and alternative food

Carabid species used in this experiment were *Poecilus chalcites* and *Anisodactylus ovularis*, which are carnivores and true omnivores respectively, as adults (Frank, 2007). Carabid larvae were reared in plastic tubs filled with moist peat moss. Adults of each species were held in the tubs to mate and lay eggs. When larvae began to hatch, adults were removed. Larvae were held in the tubs and fed dog food until used in experiments. The herbivore prey in all experiments were second-instar black cutworms, *A. ipsilon*. Cutworm larvae are susceptible to predation by many species of adult carabids (Best & Beegle, 1977; Frank & Shrewsbury, 2004a). As cutworms and carabids occur together on the ground and in the litter of many other agricultural and natural ecosystems, results have broad implications for many managed systems (Showers, 1997).

The alternative foods in these experiments were bluegrass seeds, *Poa pratensis* L. (Cyperales: Poaceae), or *Drosophila melanogaster* Meigen (Diptera: Drosophilidae) pupae. Fruit fly pupae were selected as alternative prey because dipteran eggs, larvae, and pupae are consumed by many carabid species as adults and larvae (Currie *et al.*, 1996; J6rgensen & Toft, 1997; Kromp, 1999). Further, dipterans occur at high densities in agricultural fields (Frouz, 1999). Bluegrass, *Poa pratensis* (Cyperales: Poaceae), seeds were used as alternative plant food in this research because they are readily consumed by many species of adult and larval carabids (Frank, 2007), as are seeds from other grass species (Briggs, 1965; Kirk, 1973; J6rgensen & Toft, 1997; Lundgren & Rosentrater, 2007). Further, members of the genus *Poa* are common and important agricultural weeds and are thus encountered by carabids in agricultural habitats (Forcella *et al.*, 1992; Uva *et al.*, 1997; Menalled *et al.*, 2001). In addition, fly pupae and bluegrass seeds are very similar in size and both are immobile, which controls for size and mobility effects on predator behaviour and consumption.

Consumption of cutworms, fly pupae, and bluegrass seeds by Poecilus chalcites and Anisodactylus ovularis

We conducted no-choice feeding trials to determine if third-instar *P. chalcites* and *A. ovularis* consume cutworms, fly pupae, and seeds. Feeding trials were conducted in Petri dishes lined with moist filter paper. Five of a single food type and a carabid larva were put in Petri dishes (6 cm diameter). After 6 h, the number of each prey item eaten was counted. Each prey type was replicated 10 times for each carabid species. ANOVA followed by Fisher's protected LSD mean comparisons was used to compare the number of each food item consumed by the two carabid species (SAS, 2002).

Experimental microcosm set-up

Experiments to investigate the effect of alternative food and larval density on predation of cutworms were conducted in laboratory microcosms. Microcosms were constructed of 0.47 l glass jars (Ball® jars with a 6.2 cm opening and 12 cm high, Alltrista Corp., Muncie, Indiana) filled with 2 cm of moist pine bark mulch as substrate. All microcosms contained 15, second-instar cutworms. Microcosms contained one or three larvae of a single carabid species and one of three alternative food treatments: no alternative food, 15 pupae, or 15 seeds. Second and third instars were mixed at random in experimental microcosms. Multiple carabid instars occur naturally in the field, so this made the experiment more realistic but at the expense of increased variation. All treatments with *P. chalcites* were replicated 21 times. The number of replicates that contained *A. ovularis* varied and are presented in Figs 1 and 3. In addition, control microcosms with no predators or alternative food (cutworms only) were conducted to account for cutworm death and recovery from the microcosms. After prey items and predators were added, the jars were covered with mosquito netting and positioned on their sides in a growth chamber at 27°C with a LD 12:12 h setting.

After 48 h the microcosms were hand searched to count cutworms and carabid larvae remaining. Two measures of predation, total and per capita, were used to provide insight to the effect of alternative food and larval density on herbivore suppression. Total predation is the total number of cutworms that were consumed in each microcosm and measures the combined effect of carabid larvae on cutworm abundance. To understand how alternative food and larval density affected individual predation by carabid larvae, we calculated per-capita predation as total predation divided by the initial density of carabid larvae (one or three) in the microcosm. This data set was used to address objectives 1 and 2.

The effect of alternative prey (fly pupae) and carabid larval density on cutworm predation and cannibalism by Poecilus chalcites and Anisodactylus ovularis

This objective was addressed using data from those microcosms containing pupae or no alternative food treatments. The experimental design was a 2 × 2 × 2 factorial of species,

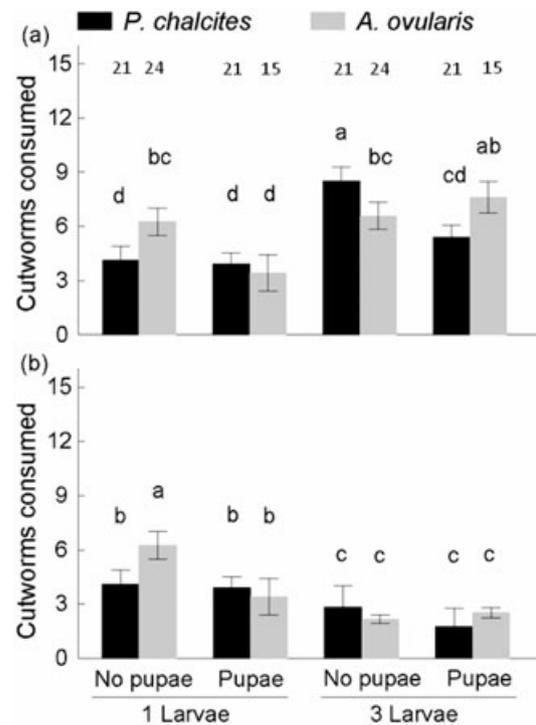


Fig. 1. Total (a) and per-capita (b) consumption of cutworms by one or three carabid larvae of two different species (*Poecilus chalcites* or *Anisodactylus ovularis*) in microcosms with fly pupae as alternative prey present or absent. Numbers above bars indicate the number of replicates per treatment. Bars with different letters are significantly different ($P < 0.05$). Error bars are ± 1 SEM.

larvae density (0, 3) and alternative prey (0, 15 pupae). ANOVA followed by Fisher's protected LSD mean comparisons was used to compare the interactive effects of carabid species, larval density, and alternative prey on total predation and per-capita predation of cutworms (SAS, 2002). Cannibalism was compared as the frequency of replicate microcosms (only microcosms with three larvae were considered) for each species-alternative food combination in which cannibalism occurred. Frequencies were analysed using χ^2 -tests of two way contingency tables.

The effect of alternative prey type (fly pupae or seeds) and carabid larval density on cutworm predation and cannibalism by the true omnivore Anisodactylus ovularis

This objective was addressed using all microcosms that contained *A. ovularis*. The experimental design was a 2 × 3 factorial of larval density (0, 3) and alternative food type (0, 15 pupae, 15 seeds). ANOVA followed by Fisher's protected LSD means comparisons was used to compare the interactive effects of larval density and alternative food type on total and per-capita predation of cutworms by *A. ovularis* (SAS, 2002). Cannibalism was compared as the frequency of replicate microcosms (only microcosms with three larvae were

considered) in which cannibalism occurred. Frequencies were analysed using χ^2 -tests.

The effect of alternative food presence and type on the abundance of carabid larvae in open field plots

To assess the effects of alternative food subsidies (fly pupae and bluegrass seeds) on carabid larvae abundance, two levels of seeds (ambient and subsidised) were crossed with two levels of pupae (ambient and subsidised) in a 2×2 factorial design in open field plots (4×4 m). Thus, plots either received no food subsidy (ambient) or were subsidised with seeds, fly pupae, or both (seeds and pupae mixed). The experiment was replicated 11 times for a total of 44 plots established in a field at the University of Maryland Central Maryland Research and Education Center in College Park, Maryland. The experiment was conducted three times (blocks), from 16 to 30 June, 8 to 24 July, and 24 August to 8 September 2007, when three, five, and three replicates respectively were completed.

Each experiment ran for 15 days. Six rows (76 cm apart) of organic corn seed (NC+ Organics, Lincoln, Nebraska, USA; hybrid 3448 MF-14) with 30 plants per row were planted in each 4×4 m plot (McClurg & Donnelly, 1999). Food supplements were applied to plots the following day by sprinkling seeds, pupae, or both at a density of 1200 m^{-2} . Additional seeds and pupae were added at the same rate every 4–5 days to replace depleted food items. Pitfall traps were used to sample carabid larvae on day 10 for 24 h and day 15 for 48 h. In addition, the ground between the middle two rows of corn was vacuumed and material from the vacuum was placed in a Berlese funnel to extract carabid larvae. Captured carabid larvae from both methods were counted and pooled for each plot for analysis.

Realistic densities of food items were used to subsidise our experimental plots. The ambient density of dipterans in agricultural fields can range from 400 to 2500 m^{-2} (average of 12 studies reviewed by Frouz (1999) = 838 m^{-2}). Within a field the density of alternative prey can vary spatially by twofold or more (i.e. an additional $400\text{--}2500 \text{ m}^{-2}$) in response to tillage (Reeleder *et al.*, 2006), moisture (Frampton *et al.*, 2000), and proximity to non-crop vegetation (Frank & Shrewsbury, 2004b). Therefore, although some patches within a field may contain several hundred dipterans, nearby patches may contain several thousand. Similar densities are seen in detritivores such as collembola (Frampton *et al.*, 2000), and mites (Reeleder *et al.*, 2006). Thus, the *D. melanogaster* pupae in our experiment are a convenient prey item to represent the pool of potential prey in an agricultural habitat that serve as alternative prey for carabid adults and larvae. Seeds from bluegrass and other weeds are also very abundant in agricultural fields, occurring year round in the thousands to tens-of-thousands per square metre (Forcella *et al.*, 1992; Davis *et al.*, 2005; Swanton *et al.*, 2006; S. D. Frank, unpublished). Therefore, subsidies of 1200 m^{-2} also represent a realistic level of variation in grass seed density.

ANOVA, blocked by time and followed by Fisher's protected LSD mean comparisons, was used to test the effect of seed

subsidies, prey subsidies and their interaction on the number of carabid larvae captured per plot (SAS, 2002). Data were $\log(x + 1)$ transformed prior to analysis to correct for non-normal distribution.

Results

Consumption of cutworms, fly pupae, and bluegrass seeds by Poecilus chalcites and Anisodactylus ovularis

There was a significant species by food type interaction ($F_{2,54} = 12.06$; $P < 0.001$) for the number of cutworms, pupae, and seeds consumed. *Poecilus chalcites* and *A. ovularis* consumed similar numbers of cutworms (3.8 ± 0.4 , 3.9 ± 0.4 ; mean \pm SE of *P. chalcites* and *A. ovularis* respectively) and pupae (0.7 ± 0.3 , 1.2 ± 0.2). However, only *A. ovularis* consumed seeds (3.4 ± 0.7), confirming that this species is omnivorous as larvae, just as it is as an adult. The main effects of species ($F_{1,54} = 19.83$; $P \leq 0.001$) and food type ($F_{2,54} = 33.71$; $P \leq 0.001$) were also significant.

The effect of alternative prey (fly pupae) and carabid larval density on cutworm predation and cannibalism by Poecilus chalcites and Anisodactylus ovularis

A mean (\pm SE) of 1.8 ± 0.3 cutworms were not recovered from control (no predator) laboratory microcosms. This was subtracted from the number of cutworms missing from experimental microcosms to adjust for loss of cutworms not attributable to consumption by carabid larvae. There was a significant interactive effect of carabid species, larval density, and alternative prey on total predation of cutworms by *P. chalcites* and *A. ovularis* (Table 1). This is exemplified by pointing out that although total predation was significantly greater at high larval densities in both species, *P. chalcites* consumed significantly fewer cutworms when pupae were present than when they were not (Fig. 1a). There was also a

Table 1. ANOVA results for the effect of carabid species, number or carabid larvae per microcosm (one or three), and alternative prey (pupae present or absent), and their interactions on total cutworm predation and per-capita cutworm predation.

Effect	Total cutworm predation		Per-capita cutworm predation	
	$F_{1,154}$	P	$F_{1,154}$	P
Species	0.72	0.399	1.04	0.310
Predator number	22.20	<0.001	61.03	<0.001
Alternative prey	5.40	0.021	4.97	0.027
Species \times Predator number	0.38	0.537	0.84	0.360
Species \times Alternative prey	0.47	0.495	0.57	0.453
Predator number \times Alternative prey	0.17	0.680	1.93	0.162
Species \times Predator number \times Alternative prey	9.47	0.003	5.81	0.017

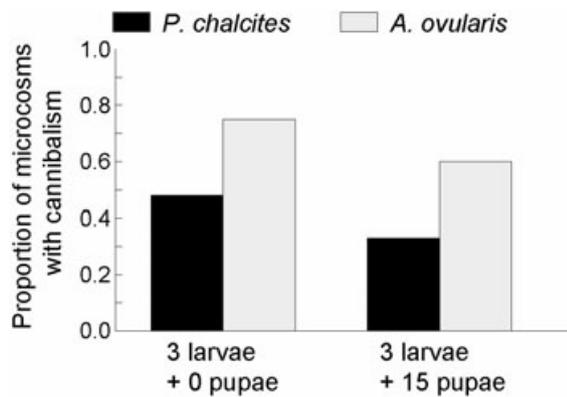


Fig. 2. Proportion of microcosms with three larvae and pupae as alternative prey present or absent in which at least one act of cannibalism occurred. Species \times Pupae ($\chi^2_3 = 10.3$, $P = 0.016$); Species ($\chi^2_1 = 8.03$, $P = 0.005$); Pupae ($\chi^2_1 = 3.24$, $P = 0.072$).

significant interactive effect of carabid species, larval density, and alternative prey on per-capita predation of cutworms, wherein per-capita predation was reduced in both species when three larvae were present, but pupae as alternative prey also reduced per-capita predation by individual *A. ovularis* (Table 1; Fig. 1b).

The number of microcosms in which at least one act of cannibalism occurred was dependent on larval species and alternative prey ($\chi^2_3 = 10.3$, $P = 0.016$) (Fig. 2). The effect of alternative prey (species combined) on cannibalism approached significance ($\chi^2_1 = 3.24$, $P = 0.072$) wherein there was a trend for cannibalism to occur in fewer microcosms when pupae were present as alternative prey. The effect of larval species on cannibalism was significant ($\chi^2_1 = 8.03$, $P = 0.005$) wherein cannibalism was higher among *A. ovularis* (Fig. 2).

The effect of alternative prey type (fly pupae or seeds) and carabid larval density on cutworm predation and cannibalism by the true omnivore *Anisodactylus ovularis*

Larval density and alternative food type (none, pupae, or seeds) had a significant interactive effect on total predation by *A. ovularis* ($F_{2,99} = 3.20$; $P = 0.045$). Pupae reduced consumption by individual larvae, but consumption in all other treatments was similar (Fig. 3a). Main effect of larval density was significant ($F_{1,99} = 7.42$; $P = 0.008$) but alternative food type was not ($F_{2,99} = 1.18$; $P = 0.312$).

Larval density and alternative food type also had a significant interactive effect on per-capita predation by *A. ovularis* ($F_{2,99} = 4.03$; $P = 0.021$) (Fig. 3b). Main effect of larval density was significant ($F_{1,99} = 70.06$; $P < 0.001$), but alternative food type was not ($F_{2,99} = 1.76$; $P = 0.177$).

The number of microcosms in which at least one act of cannibalism occurred among *A. ovularis* was significantly dependent on alternative food type ($\chi^2_2 = 6.13$, $P = 0.047$) wherein cannibalism was less frequent when pupae (cannibalism in nine microcosms) or seeds (cannibalism in eight microcosms) were present compared to when no alternative food was present (cannibalism in 19 microcosms).

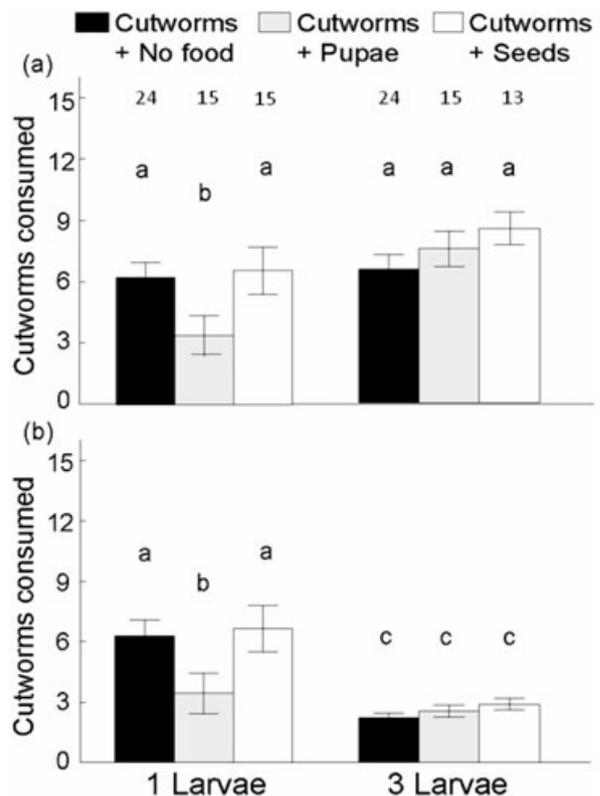


Fig. 3. Total (a) and per-capita (b) consumption of cutworms by one or three *Anisodactylus ovularis* larvae in microcosms with no alternative food, 15 pupae, or 15 seeds. Numbers above bars indicate the number of replicates per treatment. Bars with different letters are significantly different ($P < 0.05$). Error bars are ± 1 SEM.

The effect of alternative food presence and type on the abundance of carabid larvae in open field plots

In field plots, the mean (\pm SE) carabid larvae captured was significantly greater in plots subsidised with pupae (3.73 ± 1.9) or pupae and seeds (3.27 ± 2.0) than in plots with no alternative food (1.91 ± 0.9) or seeds only (1.45 ± 0.7) (main effect pupae; $F_{1,30} = 5.49$; $P = 0.026$). The main effect of seeds ($F_{1,30} = 0.64$; $P = 0.430$) and interaction of seeds and pupae ($F_{1,30} = 0.02$; $P = 0.884$) were not significant.

Discussion

In this research we demonstrate that carabid larvae have the ability to suppress economically important herbivores, a role that has largely been attributed to adults. As predicted, the presence of pupae reduced total predation of cutworms by carabid larvae, although it had a different effect on each carabid species. The presence of pupae reduced total predation by individual *A. ovularis* by 35%, but had no effect on predation when three *A. ovularis* larvae were present. In contrast, the presence of pupae had no effect on total predation of cutworms by individual *P. chalcites*, but reduced consumption of cutworms when three larvae were present. Just as predator

species differ in response to the same prey item, alternative food types can have different effects on predation by a single predator species (Eubanks & Denno, 2000b). Predation by the omnivore *A. ovularis* was reduced by pupae but not by seeds, even though seeds were more readily consumed in no-choice experiments. The influence of alternative foods on predation of herbivores can depend on food quality, mobility (Eubanks & Denno, 2000b), handling time (Frank, 2007), and other factors that ultimately determine predator preference.

The unpredictable influence of alternative food on herbivore predation has led to debate about the role of generalist and omnivorous predators in biological control and trophic dynamics (Symondson *et al.*, 2002). This debate is also stimulated by the tendency of generalist predators to engage in intraguild predation. In our experiments, increasing carabid density from one to three per microcosm—thus introducing the threat of cannibalism—reduced per-capita predation by both species. In the presence of an intraguild predator, intraguild prey (other predators) have adaptive behaviours to avoid or survive an encounter (Lima, 1987; Lima & Dill, 1990). Such behaviours include reducing activity to avoid detection and dispersing from areas where intraguild predators are present (Wagner & Wise, 1996, 1997; Prasad & Snyder, 2006). These behavioural changes can be effective at reducing intraguild predation but also reduce predation of herbivores (Prasad & Snyder, 2006). For example, adult carabids will reduce their foraging activity when larger carabid species are present that function as intraguild predators (Prasad & Snyder, 2006). Reduced foraging by these abundant smaller species reduced predation of herbivorous Dipteran larvae, thus hampering biological control (Prasad & Snyder, 2006). Intraguild predation and cannibalism also disrupt herbivore suppression by reducing the number of predators in a habitat (Rosenheim *et al.*, 1993; Finke & Denno, 2003). In our experiments, changes in survival and behaviour likely both contributed to the reduction in per-capita predation.

Increased immigration and reduced emigration are common mechanisms by which the presence of alternative food results in greater predator density in a habitat (Holt & Kotler, 1987; Eubanks & Denno, 1999, 2000a; Shrewsbury & Raupp, 2006). Both of these play an important role in determining the abundance of adult carabids in a habitat (Frank, 2007; Westerman *et al.*, 2008). However, many carabid larvae have limited mobility due to small size and rapid desiccation (Brunsting, 1983; Lövei & Sunderland, 1996). Thus, although it cannot be fully excluded, it is unlikely that they immigrated to plots with pupae or left plots without pupae.

There are two other explanations for greater carabid larvae density in plots with alternative prey: (1) adult carabids are attracted to and preferentially oviposit in plots with pupae as alternative food; or (2) more carabids that hatched in plots with pupae survived long enough to be captured. Preferential oviposition is not a likely explanation, because previous research has shown that pupae do not increase the abundance of adult carabids in field plots (Frank, 2007). Further, the short duration (15 days) of our experiments did not provide enough time for eggs to be laid, hatch, and reach second and third instars (Ernsting & Isaaks, 1997; Lundgren *et al.*,

2005; Kleinwächter & Bürkel, 2008). As an example, at 28°C, *P. chalcites* requires 4 days to hatch and an additional 34 days to reach pupation (Lundgren *et al.*, 2005). Therefore, greater abundance of carabid larvae in plots with pupal subsidies is best explained by increased larval survival in those plots.

Larvae that hatched during our experiments would benefit from pupal subsidies because first-instar survival is very dependent on quickly locating a suitable first meal (Heessen & Brunsting, 1981). Food subsidies also increase survival of later instar carabid larvae by reducing starvation and increasing development rate (Heessen & Brunsting, 1981; Knisley & Juliano, 1988; Bommarco, 1998). In addition, as demonstrated in our laboratory experiments, cannibalism among carabid larvae is reduced in the presence of pupae or other alternative prey (Heessen & Brunsting, 1981; Currie *et al.*, 1996). Finally survival could have increased because intraguild predators such as adult carabids, spiders, and ants consumed pupae rather than carabid larvae (Frank, 2007). In our field experiment, these mechanisms for carabid larvae survival are impossible to separate. However, as in microcosms, alternative prey promoted survival, resulting in a greater abundance of carabid larvae. Therefore, future research should investigate whether increased survival and abundance in the presence of alternative prey results in greater herbivore suppression under field conditions.

Predator and alternative food density are important factors that influence herbivore suppression and cannibalism by arthropod predators and the success of biological control (Fox, 1975; Rosenheim, 1995; Polis & Strong, 1996). In our research, the presence of alternative food had effects on predation of cutworms that were specific to carabid species and alternative food type. In contrast, increasing larval density reduced per-capita predation of cutworms by both carabid species irrespective of alternative food treatment. These results provide new insight into the complex interactions that influence predator survival and herbivore suppression in resource diverse habitats by demonstrating the primacy of intraguild interactions among carabid larvae. This has implications for understanding how conservation biological control techniques such as beetle banks, which increase carabid abundance and alternative prey abundance, affect herbivore suppression (Frank & Shrewsbury, 2004b). By increasing carabid larval density and subsequent intraguild interactions, beetle banks would be expected to reduce herbivore suppression in the short term. However, alternative prey provided in these habitats could ultimately strengthen herbivore suppression by increasing carabid larval abundance and survival to adulthood.

Acknowledgements

S.D.F. and P.M.S. dedicate this paper to the memory of Robert F. Denno (1945–2008) an irreplaceable ecologist, mentor, and friend. We thank Micky Eubanks and three anonymous reviewers for providing valuable input on previous versions of this manuscript. This work also benefited from discussions with, and comments from, Galen Dively, Pedro Barbosa, Irwin Forseth, and Alan Stephenson. Steph Wyman was invaluable

in the completion of this work. Funding was provided by a Maryland Agricultural Experiment Station Grant to P.M.S. and S.D.F.

References

- Best, R.L. & Beegle, C.C. (1977) Consumption of *Agrotis ipsilon* by several species of carabids found in Iowa. *Environmental Entomology*, **6**, 532–534.
- Bommarco, R. (1998) Reproduction and energy reserves of a predatory carabid beetle relative to agroecosystem complexity. *Ecological Applications*, **8**, 846–853.
- Briggs, J.B. (1965) Biology of some ground beetles (Col., Carabidae) injurious to strawberries. *Bulletin of Entomological Research*, **56**, 79–93.
- Brunsting, A.M.H. (1981) Distribution patterns, life cycles and phenology of *Pterostichus oblongopunctatus* F. (Col., Carabidae) and *Philonthus decorus* Grav. (Col., Staphilinidae). *Netherlands Journal of Zoology*, **31**, 418–452.
- Brunsting, A.M.H. (1983) The locomotor-activity of *Pterostichus oblongopunctatus* F. (Col., Carabidae). *Netherlands Journal of Zoology*, **33**, 189–210.
- Brunsting, A.M.H. & Heessen, H.J.L. (1984) Density regulation in the carabid beetle *Pterostichus oblongopunctatus*. *Journal of Animal Ecology*, **53**, 751–760.
- Brust, G.E., Stinner, B.R. & McCartney, D.A. (1985) Tillage and soil insecticide effects on predator–black cutworm (Lepidoptera: Noctuidae) interactions in corn agroecosystems. *Journal of Economic Entomology*, **78**, 1389–1392.
- Brust, G.E., Stinner, B.R. & McCartney, D.A. (1986) Predator activity and predation in corn agroecosystems. *Environmental Entomology*, **15**, 1017–1021.
- Coll, M. & Guershon, M. (2002) Omnivory in terrestrial arthropods: mixing plant and prey diets. *Annual Review of Entomology*, **47**, 267–297.
- Cottrell, T.E. & Yeargan, K.V. (1998) Effect of pollen on *Coleomegilla maculata* (Coleoptera: Coccinellidae) population density, predation, and cannibalism in sweet corn. *Environmental Entomology*, **27**, 1402–1410.
- Currie, C.R., Spence, J.R. & Niemela, J.K. (1996) Competition, cannibalism and intraguild predation among ground beetles (Coleoptera: Carabidae): a laboratory study. *The Coleopterists Bulletin*, **50**, 135–148.
- Davis, A.S., Renner, K.A. & Gross, K.L. (2005) Weed seedbank and community shifts in a long-term cropping systems experiment. *Weed Science*, **53**, 296–306.
- Denno, R.F., Mitter, M.S., Langellotto, G.A., Gratton, C. & Finke, D.L. (2004) Interactions between a hunting spider and a web-builder: consequences of intraguild predation and cannibalism for prey suppression. *Ecological Entomology*, **29**, 566–577.
- Ernsting, G. & Isaaks, J.A. (1997) Effects of temperature and season on egg size, hatchling size and adult size in *Notiophilus biguttatus*. *Ecological Entomology*, **22**, 32–40.
- Eubanks, M.D. & Denno, R.F. (1999) The ecological consequences of variation in plants and prey for an omnivorous insect. *Ecology*, **80**, 1253–1266.
- Eubanks, M.D. & Denno, R.F. (2000a) Host plants mediate omnivore–herbivore interactions and influence prey suppression. *Ecology*, **81**, 936–947.
- Eubanks, M.D. & Denno, R.F. (2000b) Health food versus fast food: the effects of prey quality and mobility on prey selection by a generalist predator and indirect interactions among prey species. *Ecological Entomology*, **25**, 140–146.
- Finke, D.L. & Denno, R.F. (2003) Intraguild predation relaxes natural enemy impacts on herbivore populations. *Ecological Entomology*, **28**, 67–73.
- Forcella, F., Wilson, R.G., Renner, K.A., Dekker, J., Harvey, R.G., Alm, D.A. *et al.* (1992) Weed seedbanks of the United-States corn belt—magnitude, variation, emergence, and application. *Weed Science*, **40**, 636–644.
- Fox, L.R. (1975) Cannibalism in natural populations. *Annual Review of Ecology and Systematics*, **6**, 87–106.
- Frampton, G.K., van den Brink, P.J. & Gould, P.J.L. (2000) Effects of spring drought and irrigation on farmland arthropods in southern Britain. *Journal of Applied Ecology*, **37**, 865–883.
- Frank, S.D. (2007) *Consequences of omnivory and alternative food resources on the strength of trophic cascades*. Doctoral dissertation, University of Maryland, College Park, Maryland.
- Frank, S.D. & Shrewsbury, P.M. (2004a) Consumption of black cutworms, *Agrotis ipsilon* (Lepidoptera: Noctuidae), and alternative prey by common golf course predators. *Environmental Entomology*, **33**, 1681–1688.
- Frank, S.D. & Shrewsbury, P.M. (2004b) Effect of conservation strips on the abundance and distribution of natural enemies and predation of *Agrotis ipsilon* (Lepidoptera: Noctuidae) on golf course fairways. *Environmental Entomology*, **33**, 1662–1672.
- Frouz, J. (1999) Use of soil dwelling Diptera (Insecta, Diptera) as bioindicators: a review of ecological requirements and response to disturbance. *Agriculture, Ecosystems and Environment*, **74**, 167–186.
- Hartke, A., Drummond, F.A. & Liebman, M. (1998) Seed feeding, seed caching, and burrowing behaviors of *Harpalus rufipes* De Geer larvae (Coleoptera: Carabidae) in the Maine potato agroecosystem. *Biological Control*, **13**, 91–100.
- Heessen, H.J.L. & Brunsting, A.M.H. (1981) Mortality of larvae of *Pterostichus oblongopunctatus* (Fabricius) col., Carabidae and *Philonthus decorus* (Gravenhorst) (col., Staphylinidae). *Netherlands Journal of Zoology*, **31**, 729–745.
- Holt, R.D. (1977) Predation, apparent competition, and structure of prey communities. *Theoretical Population Biology*, **12**, 197–229.
- Holt, R.D. & Kotler, B.P. (1987) Short-term apparent competition. *American Naturalist*, **130**, 412–430.
- Jørgensen, H.B. & Toft, S. (1997) Role of granivory and insectivory in the life cycle of the carabid beetle *Amara similata*. *Ecological Entomology*, **22**, 7–15.
- Kirk, V.M. (1973) Biology of a ground beetle, *Harpalus pensylvanicus*. *Annals of the Entomological Society of America*, **66**, 513–518.
- Kleinwächter, M. & Bürkel, M. (2008) Offspring performance in dynamic habitats: key factors for a riparian carabid beetle. *Ecological Entomology*, **33**, 286–292.
- Knisley, C.B. & Juliano, S.A. (1988) Survival, development, and size of larval tiger beetles—effects of food and water. *Ecology*, **69**, 1983–1992.
- Kromp, B. (1999) Carabid beetles in sustainable agriculture: a review on pest control efficacy, cultivation impacts and enhancement. *Agriculture, Ecosystems and Environment*, **74**, 187–228.
- Lima, S.L. (1987) Vigilance while feeding and its relation to the risk of predation. *Journal of Theoretical Biology*, **124**, 303–316.
- Lima, S.L. & Dill, L.M. (1990) Behavioral decisions made under the risk of predation—a review and prospectus. *Canadian Journal of Zoology*, **68**, 619–640.
- Lövei, G.L. & Sunderland, K.D. (1996) Ecology and behavior of ground beetles (Coleoptera: Carabidae). *Annual Review of Entomology*, **41**, 231–256.
- Luff, M.L. (1980) The biology of the ground beetle *Harpalus rufipes* in a strawberry field in Northumberland. *Annals of Applied Biology*, **94**, 153–164.

- Lundgren, J.G. & Rosentrater, K.A. (2007) The strength of seeds and their destruction by granivorous insects. *Arthropod-Plant Interactions*, **1**, 93–99.
- Lundgren, J.G., Razzak, A.A. & Wiedenmann, R.N. (2004) Population responses and food consumption by predators *Coleomegilla maculata* and *Harmonia axyridis* (Coleoptera: Coccinellidae) during anthesis in an Illinois cornfield. *Environmental Entomology*, **33**, 958–963.
- Lundgren, J.G., Duan, J.J., Paradise, M.S. & Wiedenmann, R.N. (2005) Rearing protocol and life history traits for *Poecilus chalcites* (Coleoptera: Carabidae) in the laboratory. *Journal of Entomological Science*, **40**, 126–135.
- McClurg, C.A. & Donnelly, D.J. (1999) *Growing Sweet Corn*. University of Maryland Cooperative Extension, Fact sheet 458. 8 pp.
- Menalled, F.D., Lee, J.C. & Landis, D.A. (1999) Manipulating carabid beetle abundance alters prey removal rates in corn fields. *BioControl*, **43**, 441–456.
- Menalled, F.D., Gross, K.L. & Hammond, M. (2001) Weed above-ground and seedbank community responses to agricultural management systems. *Ecological Applications*, **11**, 1586–1601.
- Musser, F.R. & Shelton, A.M. (2003) Predation of *Ostrinia nubilalis* (Lepidoptera: Crambidae) eggs in sweet corn by generalist predators and the impact of alternative foods. *Environmental Entomology*, **32**, 1131–1138.
- Nóia, M., Borges, I. & Soares, A.O. (2008) Intraguild predation between the aphidophagous ladybird beetles *Harmonia axyridis* and *Coccinella undecimpunctata* (Coleoptera: Coccinellidae): the role of intra and extraguild prey densities. *Biological Control*, **46**, 140–146.
- Polis, G.A. & Strong, D.R. (1996) Food web complexity and community dynamics. *The American Naturalist*, **147**, 813–846.
- Polis, G.A., Myers, C.A. & Holt, R.D. (1989) The ecology and evolution of intraguild predation—potential competitors that eat each other. *Annual Review of Ecology and Systematics*, **20**, 297–330.
- Prasad, R.P. & Snyder, W.E. (2006) Polyphagy complicates conservation biological control that targets generalist predators. *Journal of Applied Ecology*, **43**, 343–352.
- Reeleder, R.D., Miller, J.J., Coelho, B.R.B. & Roy, R.C. (2006) Impacts of tillage, cover crop, and nitrogen on populations of earthworms, microarthropods, and soil fungi in a cultivated fragile soil. *Applied Soil Ecology*, **33**, 243–257.
- Rosenheim, J.A. & Harmon, J.P. (2006) The influence of intraguild predation on the suppression of a shared prey population: an empirical reassessment. *Trophic and Guild Interactions in Biological Control* (ed. by J. Brodeur and G. Boivin), pp. 1–20. Springer, New York.
- Rosenheim, J.A., Wilhoit, L.R. & Armer, C.A. (1993) Influence of intraguild predation among generalist insect predators on the suppression of an herbivore population. *Oecologia*, **96**, 439–449.
- Rosenheim, J.A., Kaya, H.K., Ehler, L.E., Maros, J.J. & Jaffee, B.A. (1995) Intraguild predation among biological-control agents: theory and evidence. *Biological Control*, **5**, 303–335.
- SAS (2002) *SAS version 9.1*. SAS Institute, Cary, North Carolina.
- Showers, W.B. (1997) Migratory ecology of the black cutworm. *Annual Review of Entomology*, **42**, 393–425.
- Shrewsbury, P.M. & Raupp, M.J. (2006) Do top-down or bottom-up forces determine *Stephanitis pyrioides* abundance in urban landscapes? *Ecological Applications*, **16**, 262–272.
- Swanton, C.J., Booth, B.D., Clements, D.R. & Shrestha, A. (2006) Management in a modified no-tillage corn-soybean-wheat rotation influence weed population and community dynamics. *Weed Science*, **54**, 47–58.
- Symondson, W.O.C., Sunderland, K.D. & Greenstone, M.H. (2002) Can generalist predators be effective biocontrol agents? *Annual Review of Entomology*, **47**, 561–594.
- Uva, R.H., Neal, J.C. & DiTomaso, J.M. (1997) *Weeds of the Northeast*. Cornell University Press, Ithaca, New York.
- Wagner, J.D. & Wise, D.H. (1996) Cannibalism regulates densities of young wolf spiders: evidence from field and laboratory experiments. *Ecology*, **77**, 639–652.
- Wagner, J.D. & Wise, D.H. (1997) Influence of prey availability and conspecifics on patch quality for a cannibalistic forager: laboratory experiments with the wolf spider *Schizocosa*. *Oecologia*, **109**, 474–482.
- Westerman, P.R., Borza, J.K., Andjelkovic, J., Liebman, M. & Danielson, B. (2008) Density-dependent predation of weed seeds in maize fields. *Journal of Applied Ecology*, **45**, 1612–1620.

Accepted 4 October 2009