Biological Control 57 (2011) 229–235

Contents lists available at ScienceDirect

Biological Control

journal homepage: www.elsevier.com/locate/ybcon

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

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ARTICLE INFO

Article history:
Received 3 November 2010
Accepted 9 March 2011
Available online 15 March 2011

Keywords:
Aggregation
Alternative prey
Black cutworms (*Agrotis ipsilon*)
Carabidae
Conservation biological control
Emigration
Habitat management
Harpalus pensylvanicus
Numerical response
Seed predation

ABSTRACT

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

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

1. Introduction

Agricultural habitats are characterized by low plant species diversity and routine disturbance which have negative effects on natural enemies. The ‘enemies hypothesis’ posits that increasing plant diversity and structural complexity will increase natural enemy abundance and improve biological control of arthropod pests (Root, 1973). This is the foundation of habitat management as a conservation biological control tactic wherein non-crop vegetation is maintained within crop fields to provide shelter and resources for natural enemies (Landis et al., 2000; Griffiths et al., 2008). There is considerable evidence that habitat management tactics, such as beetle banks (Thomas et al., 1991; Frank and Shrewsbury, 2004), hedgerows (Marshall and Moonen, 2002; Pollard and Holland, 2006), reduced tillage (Brust et al., 1986; Clark et al., 2006), cover crops (Laub and Luna, 1992), or applications of compost (Settle et al., 1996; Bell et al., 2008), increase the abundance of epigeal generalist predators such as carabid beetles (Kromp, 1999; Griffiths et al., 2008). Yet despite increasing predator abundance, concomitant reductions in pest abundance do not always occur (Griffiths et al., 2008). Therefore, it is essential to understand mechanisms that underlie how habitat complexity affects herbivore suppression by generalist predators.

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

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

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doi:10.1016/j.biocontrol.2011.03.004

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

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

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

2. Methods

2.1. Study system

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

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

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

2.2. Effect of food subsidies on carabid aggregation

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

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