

OVERVIEW OF THE ROLE OF GENERALIST PREDATORS IN BIOLOGICAL CONTROL

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SESSION 9 INTRODUCTION

The subject of generalist predators in biological control is rich, diverse, and stimulating. It is also frustrating, providing ample grounds for enthusiasm for their potential as significant agents of pest population suppression, along with well documented examples of near successes and patent failures. On the basis of ecological theory and extensive meta-analyses of the literature, generalists are apt to be, and have been *found* to be, significant biocontrol agents in many situations (Murdoch *et al.* 1985; Change & Kareiva 1999; Greenstone & Sunderland 1999; Symondson *et al.* 2002). Nevertheless the devil is in the details of habitat, crop phenology, interspecific interactions, and weather, and we are still trying to work out the conditions for success in employing generalist predators for biocontrol.

The broad selection of papers in this session nicely illustrates some of the challenges facing us as we struggle to discover the determinants of such success. Kindelmann and colleagues (this volume), who some might consider to have crashed the party by discussing a group of predators that are more narrowly stenophagous than most of those under discussion, show by means of a removal experiment that two coccinellid species do not reduce the peak numbers of their aphid prey, reinforcing what is becoming a depressing consensus that coccinellids are not effective regulators of pest populations. Furthermore, Harwood & Obrycki (this volume) find that one of those two species, *Harmonia axyridis* (Pallas), is more fit on a pure aphid diet than a mixed lepidopteran one. Being thus averse to using alternate prey as part of a "lying-in-wait" strategy until aphids arrive, coccinellids may be predisposed to avoid crops until aphids are too abundant to control, another blow to their potential effectiveness as pest population regulators.

On the other hand Harwood & Obrycki (this volume) find that the linyphiid spider *Erigone autumnalis* (Emerton) is unable to survive to adulthood on a pure pest (aphid or leaf hopper) diet, requiring a mixed diet including collembolans and flies to reach maturity. It is thus well suited to the lying-in-wait strategy, able to subsist on a variety of other insects until

pests arrive. However, because it prefers non-pest alternate prey to pests, it is probably less effective than it might otherwise be in regulating pest populations. This is exacerbated by the fact that in the alfalfa system studied by Harwood and Obrycki, pests and alternate prey tend to covary in abundance, rising or falling simultaneously. This is different from the verbal model that biocontrol practitioners like to use to describe the lying-in-wait strategy, in which high alternate prey numbers early in the season sustain predators until pest populations build up later.

Spiders are iconic generalists. In their study of the influence of landscape on spider species richness and biocontrol, Schmidt *et al.* (this volume) find that wheat field spider species richness is more strongly affected by the proportion of perennial non-crop habitats in the surrounding landscape than by the presence of directly adjoining non-crop habitats. The proportion of non-crop habitats in the surrounding habitats also influenced spider densities, with the most important spatial scale being smaller (0.19 – 0.53 km) for lycosids, which tend to walk, than for linyphiids (up to 3.0 km), which are more apt to balloon to and from overwintering sites. Knowledge of the influence of the surrounding landscape is important, because spiders may significantly depress aphid densities in this system; unfortunately, since spider densities fluctuate greatly from year to year, they may not be dependable regulators of aphid populations.

But as anyone who has followed coccinellids around a crop field or counted cereal aphids in linyphiid webs knows, even predators that show up too late to an infestation to single-handedly control a pest infestation, or that would rather eat detritivores than pests, can still dispatch phenomenal numbers of pests. They may therefore make significant contributions to pest control despite a few disappointing attributes. Pfannenstiel (this volume) remind us to think about the entire assemblage of generalists rather than focusing on particular groups of predators. He finds that there is strikingly little overlap in the nocturnal and diurnal predator assemblages of lepidopteran eggs in annual crops in the southern USA. He also discovers that spiders are prominent among the nocturnal assemblage, accounting for almost a quarter of egg mortality by a diverse suite of arachnid and insect predators operating at night. Besides showing that generalist arthropod predators impose very high mortality on lepidopteran eggs, Pfannenstiel (this volume) reminds us that there is a great deal that we still do not know about diel periodicity in predators and the relative importance of diurnal vs. nocturnal predation. Greenstone & Roberson (this volume) show that we also know almost nothing about the role of immature predators.

Snyder & Straub (this volume) find that the assemblage of predators attacking *Myzus persicae* (Sulzer) in potatoes is very diverse. In an experiment designed specifically to determine whether there is more or less intraguild complementarity or interference in assemblages made up of different specific predator species, they find that complementarity or interference effects do not affect aphid suppression. However, the identity of predators does, with a coccinellid being more effective than a thomisid spider in suppressing aphids.

Generalist predators are diverse and abundant, and it is critical that we define their role in both agricultural and natural systems. Predation events tend to happen cryptically and infrequently, and there have been significant obstacles to our ability to quantify and characterize predation in usually complex trophic webs. In this necessarily short collection of pa-

pers, we have been unable to highlight any of the exciting work on molecular gut analysis that is transforming our ability to study and understand the role of predators in biological control (Zaidi *et al.* 1999; Chen *et al.* 2000; Hoogendoorn & Heimpel 2001; Harper *et al.* 2005). Molecular techniques, in combination with the kinds of carefully designed experiments (Kindelmann *et al.*; Snyder & Straub) and exhaustive direct observation (Pfannenstiel) illustrated in this session, will facilitate our understanding of predator impact and ecology, and improve our potential for successfully manipulating them for biological control.

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FIELD TEST OF THE EFFECTIVENESS OF LADYBIRDS IN CONTROLLING APHIDS

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ABSTRACT

Some experiments indicate the ability of coccinellids to significantly suppress aphid abundance. Exclusion of predators by caging aphid-infested plants has repeatedly resulted in higher aphid populations and greater aphid population growth rates. However, aphidophagous coccinellids have never proved effective in controlling aphid populations in the field. To resolve this apparent contradiction, a field experiment was used to determine the effectiveness of two coccinellids, *Coccinella septempunctata bruckii* and *Harmonia axyridis* in suppressing populations of the aphid, *Aphis gossypii*, on shrubs of *Hibiscus syriacus* under natural conditions. Instead of caging some of the shrubs, the effect of each species of coccinellid on aphid population dynamics was estimated by direct counts and a manipulative experiment, in which all the eggs of *C. septempunctata bruckii* were removed from 8 shrubs, all those of *H. axyridis* from another 8 shrubs, all those of both species from an additional 12 shrubs, and no eggs were removed from 6 control shrubs. The predators did not have a negative effect on the peak numbers of their prey. This is in full accord with the GTR hypothesis, according to which long-lived predators cannot be effective in controlling a short-lived prey.

INTRODUCTION

Aphidophagous coccinellids are probably the most abundant generalist predators of aphid populations. Some experiments indicate they significantly suppress aphid abundance. Exclusion of predators by caging aphid-infested plants has repeatedly resulted in significantly higher aphid populations (Brown 2004; Chambers *et al.* 1983; Michels *et al.* 2001) and greater aphid population growth rates (Elliott and Kieckhefer 2000), indicating that coccinellids markedly reduce aphid abundance. However, aphidophagous species of ladybirds have never proved effective in controlling aphid populations (e.g., van den Bosch and Messenger 1973).

The apparent contradiction of the results of the exclusion experiments and attempts to use coccinellids in the large-scale biocontrol of aphids may be explained as follows: when access of predators to aphids is excluded by caging the aphid-infested patches, aphids cannot react to their own increasing local density by emigration, which causes large aphid density in caged patches. Thus, there are more aphids in caged patches because they cannot leave the patch, not because predators reduce aphid numbers in non-caged patches. To test this hypothesis, field experiments were used to determine the effectiveness of *Coccinella septempunctata bruckii* Mulsant (Coleoptera: Coccinellidae) and *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) to suppress populations of the aphid *Aphis gossypii* Glover (Homoptera: Aphididae) on small shrubs of *Hibiscus syriacus* L. under natural conditions. Instead of caging infested shrubs, the effect of each species of ladybird on aphid population dynamics was estimated by direct counts on naturally infested shrubs and in a manipulative experiment, in which the eggs of one or both predators were removed from the shrubs.

METHODS

The study site was on the Yamagata University farm (Tsuruoka, Yamagata pref., Japan, 38° 43' N, 139° 49' E). It consisted of about 100 shrubs of *Hibiscus syriacus* L., which is the primary host of the aphid *Aphis gossypii* Glover. This aphid is attacked by two coccinellids: *Coccinella septempunctata bruckii* and *Harmonia axyridis*.

In the years 1993-1996, a total of 30 shrubs naturally infested with aphids and their predators were monitored from mid May to mid July. The numbers of coccinellid eggs, larvae, and of aphids were counted daily. To evaluate the effect of the number of aphids at the beginning of the season, x , the number of egg batches of *C. septempunctata bruckii*, c , and the number of egg batches of *H. axyridis*, h , on the peak number of aphids, Y , a stepwise regression, descending method, was applied to the data from 1993-1996. As aphids multiply exponentially, and therefore linear dependence of the logarithm of the peak on other variables was expected, the same methodology was applied to the data set with $\log(Y+1)$ instead of Y .

It is difficult to identify coccinellids at the egg stage because they are often similar in size, color and number in a batch. In 1993, eggs were identified to species using the larvae that hatched from them. In the following years, a few eggs were removed from each egg mass and placed in Petri dishes at 25 °C and a 14L:10D photoperiod in the laboratory, and identified when the larvae hatched. Eggs reared in the laboratory hatched earlier than those left on the shrubs, which enabled the removal of the eggs before they hatched.

In 2000 and 2001, the effect of the absence of each coccinellid on aphid population dynamics was estimated. For this an additional 34 shrubs were selected for a manipulative experiment. After identification to species but before hatching, all the eggs of *C. septempunctata bruckii* were removed from 8 shrubs, those of *H. axyridis* from another 8 shrubs, eggs of both species from an additional 12 shrubs, and on the remaining 6 control shrubs no eggs were removed. Sticky bands were placed at the bottom of each shrub in order to prevent colonization by larvae from other shrubs. The shrubs were monitored from mid May to mid July. The numbers of coccinellid eggs, larvae and aphids were counted daily.

RESULTS

In the model with the peak number of aphids, Y , as the dependent variable, no independent variable demonstrated a significant effect (Table 1). If $\ln(x + 1)$ was used instead of x and $\ln(Y+1)$ instead of Y , as the aphids are expected to grow exponentially, at least at the beginning of the season, the equation for the reduced model was: $\ln(Y+1) = 4.6 + 0.32 \cdot \ln(x+1) + 0.055 \cdot h$. The selected independent variables explained 33.26% of the variability of $\ln(Y+1)$. There is a 4.82% risk of rejecting the hypothesis that a constant model would be better, so the selected variables make a significant contribution to the model.

The variable that explained the most of the variation was the intercept (Table 1). In neither of the models did the abundance of either predator species significantly affect the peak aphid numbers (Table 1). As there is a lot of unexplained variability in this system, a manipulative experiment was carried out in 2000-2001. On average, 12.9 egg batches of *H. axyridis* and 13.9 of *C. septempunctata bruckii* were laid per shrub during 2000 and 2001. Almost no parasitism was observed. The resulting peak numbers of aphids are shown in Fig. 1. Predators did not significantly affect the peak numbers of aphids (one-way ANOVA gives $F = 3.71$, $P = 0.67$ in 2000 and $F = 3.24$, $P = 0.37$ in 2001).

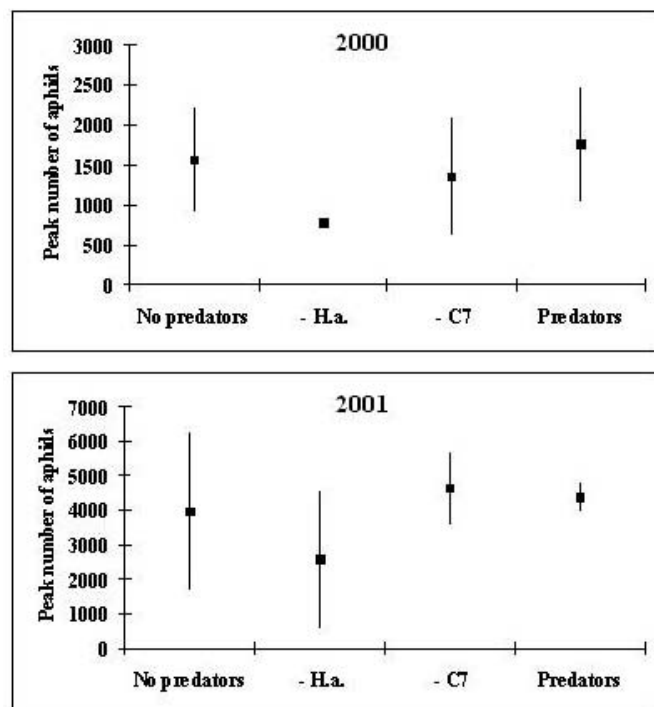
DISCUSSION

There has only been one attempt until recently to account for the low effectiveness of insect predators: Kindlmann and Dixon (1999; 2001) proposed that the ratio of generation time of insect predators to that of their prey (generation time ratio, GTR) determines their effectiveness in suppressing prey. Kindlmann and Dixon (1999) assume that on a large spatial scale, at any instant, herbivore populations exist as patches of prey, associated with patches of good host plant quality. Predators exploit these patches, which vary greatly in number of prey both spatially and temporally (Kareiva 1990). GTR in insect predator-prey systems is often large – the developmental time of insect predators often spans several prey generations and is similar to the duration of a patch of prey (Dixon 2000). Cannibalism is common in insect predators (Agarwala and Dixon 1993; Fox 1975) and is adaptive, as eating conspecific competitors will increase the fitness of their larvae (Dong and Polis 1992). Mortality during larval stages reaches about 99% (Hironori and Katsuhiko 1997; Kindlmann *et al.* 2000; Kirby and Ehler 1977; Matura 1976; Osawa 1993; Wright and Laing 1982). Because of the enormous larval mortality, the life history strategy of these predators is likely to be selected to maximize the probability of survival of their offspring, rather than maximize the number of eggs laid. In major-

Table 1. Results of stepwise regression, descending method, on the effect of the number of aphids at the beginning of a season, x , the number of egg batches of *C. septempunctata bruckii*, c , and the number of egg batches of *H. axyridis*, h , on the peak number of aphids, Y , and on its logarithm, $\log(Y)$. Statistically significant values indicated by asterisks (*means 5%, ** means 1% significance level).

	DF	SS	MS	Fisher's F	Pr > F
Model with Y	2	5753648	2876824	2.83	0.091
Residuals	15	15264871	1017658		
Total	17	21018519			
Model with $\log(Y)$	2	20.38	10.19	3.74	0.048*
Residuals	15	40.90	2.73		
Total	17	61.28	6.00		
		Value	Std dev.	Student's t	Prob.
Model with Y	Intercept	544.3	349.2	1.56	0.14
	Initial # aphids	1.21	0.71	1.70	0.11
	<i>C. septem-punctata bruckii</i>	104.4	86.7	1.20	0.25
Model with $\log(Y)$	Intercept	4.60	0.68	6.75	0.00**
	$\ln(\text{Initial \# aphids}+1)$	0.32	0.19	1.74	0.10
	<i>H. axyridis</i>	0.055	0.043	1.27	0.22

Figure 1. Peak numbers (\pm SD) of aphids on shrubs from which eggs of all predators were removed (no predators), only *C. septempunctata bruckii* eggs were removed (- C7), only *H. axyridis* eggs were removed (- H.a.) and no eggs were removed (predators), in years 2000 and 2001.



ity of cases, the adults are winged and can easily move between patches, whereas the immature stages are confined to one patch throughout their development, and their survival is associated with the quality of the patch of prey in which they were born. Therefore, the fitness of most predators (especially those feeding on highly aggregated and ephemeral prey patches such as aphid colonies, like aphidophagous ladybirds and hoverflies), measured as the number of offspring that survive to reproductive age, is likely to be more closely associated with oviposition strategy (the choice of patch for laying eggs), than the trophic interactions commonly used in models of prey-predator population dynamics.

When GTR is large and cannibalism is common, eggs laid by predators late on in the existence of a patch of prey are highly likely to be eaten by larvae of predators that hatch from the first eggs to be laid. In addition, because of the large GTR, there is insufficient time for the larvae that hatch from late laid eggs to complete their development. Thus cannibalism and the ephemeral existence of patches of prey pose such constraints that females that can assess the age of a patch of prey gain an advantage. As a consequence, females oviposit in young patches (“egg window hypothesis”, Dixon 2000). The short “egg window” during which it is advantageous to lay eggs in a patch of prey in large-GTR systems reduces the number of eggs laid per patch. Incidence of cannibalism is likely to be proportional to the probability of encountering another predator, i.e., to the relative abundance of predators to prey (“meet and eat hypothesis”, Kindlmann and Dixon 2003). If this is true, then even if predators are abundant and therefore many eggs are laid in a patch of prey during the egg window, strong density dependent cannibalism greatly reduces the abundance of the predators (Mills 1982). Therefore, no matter whether abundant or not, insect predators have little impact on prey population dynamics, when GTR is large (“GTR hypothesis”, Kindlmann and Dixon 1999). A simple dynamic model published by Kindlmann and Dixon (1993) demonstrates why the verbal logic presented here is correct.

Laboratory experiments and field observations provided the foundations on which the GTR and egg window hypotheses were built. Several insect predators have evolved mechanisms that enable them to oviposit preferentially early in the development of a patch of prey and avoid patches that are already being attacked by larvae (Hemptinne *et al.* 1992; 1993; 2001). This leads to eggs being laid during the “egg window” and may lead to low effectiveness of these predator species in suppressing the numbers of their prey. However, there has not been a field test of the effectiveness of these predators.

In the coccinellid – aphid system studied here, the GTR is close to 3, and thus the GTR hypothesis would predict a low effect of predators on aphid abundance. In this study the predators did not have a negative effect on the peak numbers of their prey. On the contrary, the peak number of aphids in the control (with both predator species present) was larger, although not significantly so, than on the shrubs from which one or both predator species were removed. These conclusions only apply to predator prey systems with a large GTR and especially to predators feeding on highly aggregated and ephemeral prey patches such as aphid colonies, like aphidophagous coccinellids and syrphids. It does not follow that all insect predators are ineffective in controlling their prey as is well illustrated by the outstanding success of *Rodolia cardinalis*.

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SPIDERS IN SPACE: HOW LANDSCAPE-WIDE MOVEMENT OF GENERALIST PREDATORS INFLUENCES LOCAL DENSITY, SPECIES RICHNESS, AND BIOCONTROL

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ABSTRACT

Arthropods are mobile, and often move beyond the classical bounds of ecological field studies. We have done landscape analyses to explore the influence of the surrounding landscape on spiders in winter wheat fields and on their potential to control cereal aphids. The densities of many spider species were enhanced by high percentages of non-crop habitats at scales ranging from 95 m to 3 km radius, suggesting that complex landscapes with rich populations of natural enemies are favorable for aphid control.

INTRODUCTION

Local arthropod communities can be influenced by the surrounding landscape, either through short-term dispersal events or the dynamics of long-term population establishment and extinction (Kareiva and Wennegren 1995; Ricklefs 1987; Tscharntke and Brandl 2004). Recent studies have demonstrated that ecosystem services such as pollination and biocontrol by arthropods depend on landscape patterns at scales up to several kilometers (Kremen *et al.* 2004; Roland and Taylor 1997; Thies and Tscharntke 1999; Thies *et al.* 2005). Landscape effects on local pest-natural enemy interactions may be particularly strong in arable crops because of the necessity of annual recolonization (Schmidt *et al.* 2004a).

Spiders are important predators of various insect pests (Marc *et al.* 1999; Nyffeler *et al.* 1994). As they overwinter predominately outside of arable fields in Central Europe, the colonization of crops during spring should be related to the availability of perennial non-crop habitats in the surrounding landscape (e.g., Lukzak 1979; Schmidt and Tscharntke 2005a; Topping and Sunderland 1994). The circumference around a field in which the landscape is relevant should further depend on the movement capacity of each species. It may thereby provide a measure for the effective dispersal range of a species, which is otherwise hard to determine.

We studied spider communities in winter wheat in relation to the surrounding landscape and local farming system, and conducted field experiments on the relative importance of spiders and other natural enemies for cereal aphid control.

MATERIALS AND METHODS

The studies started in 2001 in two regions in Germany. Eighteen landscape sectors were selected around the city of Göttingen (Southern Lower Saxony), which had moderate to high percentages of arable land (25-85% at a scale of 1.5 km). In the Lahn-Dill Bergland (Central Hesse), 20 landscapes were selected in which the percentages of arable land were lower (7-61% at a scale of 1.5 km), and percentages of various non-crop habitats correspondingly higher than around Göttingen. In each of the 38 landscape sectors, one or two fields of winter wheat were studied. Landscape composition was calculated for 11 scales between 95 m and 3 km radius around the study fields (Fig. 1). Spiders were sampled with pitfall traps and web abundance with a distance method, and species richness and density were related to local management and to landscape features.

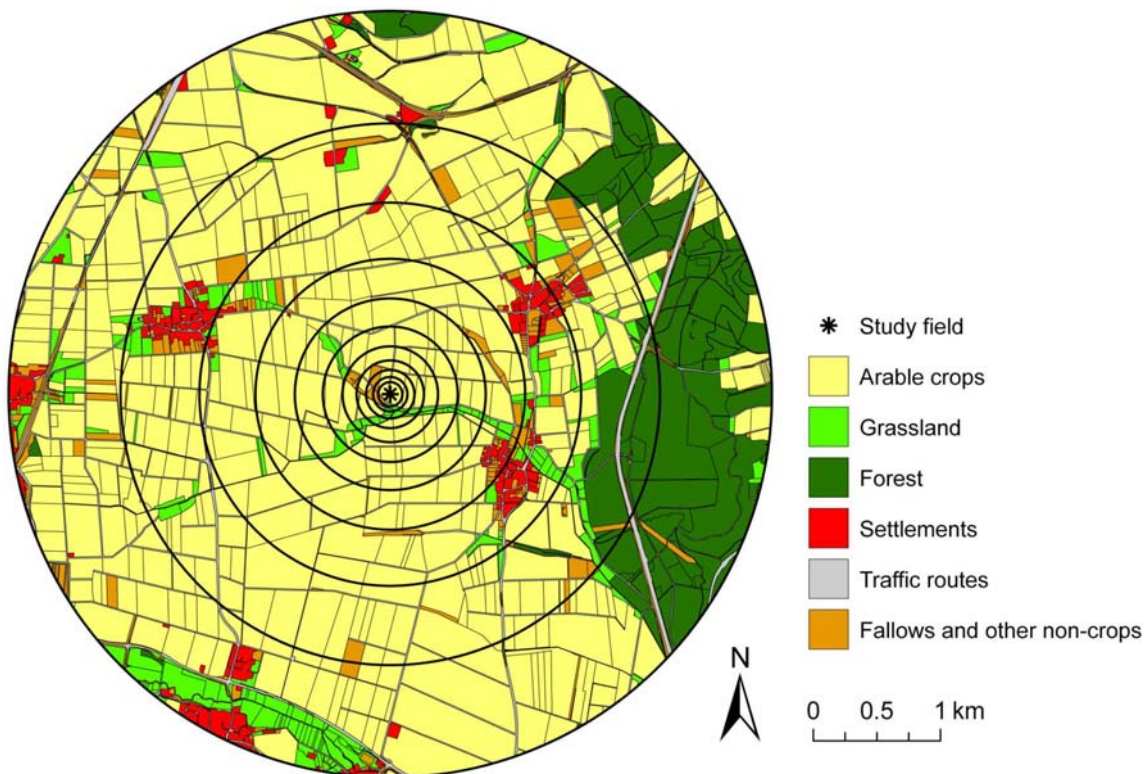


Figure 1. One of the 38 landscape sectors, with a relatively high percentage of arable crops (68.7%), but little grassland (5.6%), forest (12.5%) and other non-crop habitats. The circles represent the eleven spatial scales of 95, 135, 190, 265, 375, 530, 750, 1060, 1500, 2120 and 3000 m radius around the study field, at which landscape composition was calculated.

RESULTS AND DISCUSSION

SPIDER SPECIES RICHNESS

Overall, 37,303 spiders were determined, which belonged to 139 species. Surprisingly, local species richness was influenced more strongly by the composition of the surrounding landscape than by the presence of directly adjoining non-crop habitats, and this relation was consistent across both study regions (Fig. 2). The correlation between species richness and the percentage of non-crop habitats in the surrounding landscape was strongest at 1-1.5 km radius.

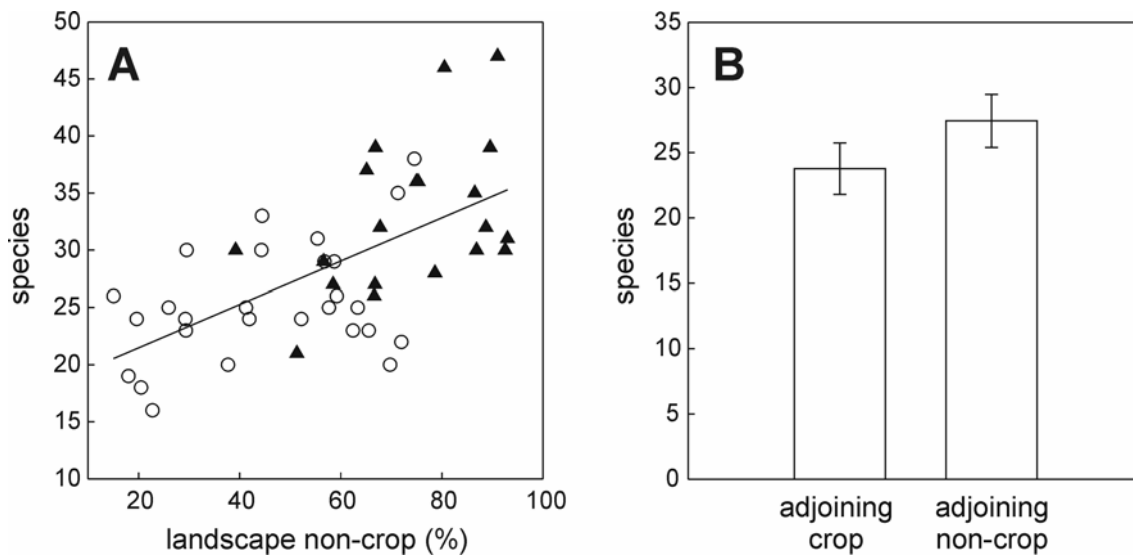


Figure 2. Landscape effects on the species richness of spiders. **A:** Correlation between local species richness and the percentage of non-crop habitats 1.5 km around fields. Open circles: Southern Lower Saxony; Solid triangles: Lahn-Dill Bergland (Hesse). GLM: non-crop: $F_{1,43} = 9.8$, $p < 0.001$; region: $F_{1,43} = 0.1$, $p = 0.8$; non-crop \times region: $F_{1,43} = 0.6$, $p = 0.4$. **B:** Effect of adjoining non-crop habitats. $n = 9$ pairs of fields, each within one landscape sector. t-test for matched pairs: $t_{1,8} = -3.2$, $p = 0.01$.

SPIDER DENSITY

Out of the 64 most common spider species, 34 were locally enhanced by high amounts of non-crop habitats in the surrounding landscape. Wolf spiders (Lycosidae) were influenced by landscape composition at smaller scales (mostly between 190-530 m radius) than the more ballooning Linyphiidae (up to 3 km radius). In contrast, directly adjoining non-crop habitats increased the densities of only two out of 64 spider species, which cannot be considered statistically significant when accounting for the multiple species tested. According to web densities, the abundance of sheetweb spiders (Linyphiinae) rose with the percentage of non-crop habitats in the surrounding landscape, e.g. from 18-130 webs per m^2 in late May 2001 (Schmidt and Tschardtke 2005b). A similar positive relationship between web abundance and landscape composition was also present in other years, and plainest between scales of 1 km and 3 km around the study fields.

In 2002, we compared the effects of landscape to the effects of local organic versus conventional management in twelve pairs of organic and conventional fields along a landscape gradient. Thereby, organic management increased overall density of ground-dwelling spiders by 62%. In contrast, species richness was determined by landscape, only (Schmidt *et al.* 2005). Overall, densities of *Oedothorax apicatus* were affected mostly by management, *Pardosa* species by both landscape and management, and other species mostly by landscape. This shows that enhancement of certain generalist predators can only be effective when the landscape is considered.

BIOLOGICAL CONTROL

In supplementary field experiments, we demonstrated how ground dwelling-predators reduce aphid infestation in winter wheat. Cereal aphid densities increased by 40-55% when ground-dwelling predators were excluded, most likely due to reduced predation by spiders (Schmidt *et al.* 2003; 2004b). The differences in spider density between control and exclusion were in the range of the differences that could be observed between landscapes with high and low percentages of non-crop habitats. Therefore, aphid suppression by spiders can be expected to be stronger in landscapes with high percentages of non-crop habitats. However, sheetweb spider densities in 2002-2004 were less than one third of those in 2001, when the aphid control experiments were carried out. Therefore, an influence of spiders on aphid populations may be inconsistent not only among landscapes, but also among years.

CONCLUSIONS

Spiders in wheat fields are strongly influenced by the surrounding landscape, which could lead to a significant increase of aphid control in landscapes with high amounts of perennial non-crop habitats. This underlines that a purely local orientation of biological control is not always sufficient. Similar effects of landscape-wide dispersal by pests and their natural enemies can be expected in many situations worldwide, offering an exciting field for biocontrol research.

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We thank Christoph Bürger, Jens Dauber, Doreen Gabriel and Tobias Purtauf for collaboration in the field and processing of landscape data. Oliver-David Finch and Theo Blick checked spider identifications. Funding came from the German Ministry for Research and Education BMBF, and from the German Research Foundation DFG. M.H.S. was supported by the German National Academic Foundation (Studienstiftung des deutschen Volkes).

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THE ROLE OF ALTERNATIVE PREY IN SUSTAINING PREDATOR POPULATIONS

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ABSTRACT

Generalist predators are widely acknowledged to contribute valuable levels of biological control in agroecosystems throughout the world. Although their feeding habits can result in the rejection of target pests in favor of preferred and often more nutritious non-pest prey, these natural enemies are capable of colonizing habitats prior to the arrival of pests by subsisting on alternative sources of food. The effect of consuming non-pest species on rates of pest predation by a generalist predator can be twofold; feeding upon these nutritious food items generally enhances fecundity thus improving their population growth, but the presence of alternative prey, especially during times when pest regulation is required, can result in reduced levels of pest consumption per individual predator. However, an increased density of natural enemies can counteract this reduction in pest consumption and exert significant levels of biological control.

The role of alternative prey in sustaining predator populations has been widely reported in laboratory studies and field trials examining the fecundity, feeding behavior and growth rates of species subjected to diets of varying quality. Recently, the application of monoclonal antibody and molecular technology to study predation rates in the field has revealed the extent to which many predator communities rely on alternative prey before, during and after the immigration of pests into crops. In this study we examine the role of key species of alternative prey to generalist predators and discuss their impact in the context of biological control. The importance of these prey items to sustaining linyphiid spider and coccinellid communities will also be examined. Microsite sampling of arthropod populations in alfalfa indicated that the overlap in availability of pests (*Acyrtosiphon pisum* and *Empoasca fabae*) and alternative prey to linyphiid spiders is likely to reduce the ability of these generalist predators to restrict the growth of pest populations.

INTRODUCTION

Generalist predators, as part of a complex community of natural enemies, can make significant contributions to the biological control of many pests (Obrycki and Kring 1998; Sunderland *et al.* 1997; Symondson *et al.*, 2002). Although they readily consume target pests, their polypha-

gous feeding habits can result in alternative non-pest food resources constituting a significant component of their diet. Furthermore, the availability of these alternative food items can affect pest consumption rates in the field (Harper *et al.* 2005; Harwood *et al.* 2004) and reduce their role in integrated pest management. Despite this interference, these arthropods are capable of impacting upon pests once they arrive in the crop, employing a “lying-in-wait” strategy by subsisting on alternative prey (Chang and Kareiva 1999; Murdoch *et al.* 1985) and impacting upon pests with favorable predator:pest ratios when control is required (Settle *et al.* 1996). However, many species of alternative prey are preferred food items (Toft 2005) and increase growth rates (Mayntz and Toft 2001; Toft 1995), while pests may even elicit aversions from some predators after extended exposure (Toft 1997). This diversion away from target pests thus reduces their capacity for effective biological control (Koss and Snyder 2005; Koss *et al.* 2004; Madsen *et al.* 2004) (Fig. 1). However, simply because pests are a poor quality prey item (Toft 2005) does not necessarily translate to little or no biological control in the field where generalist predators are frequently in a state of hunger (e.g., Bilde and Toft 1998) and readily consume these prey (Harwood *et al.* 2004; 2005).

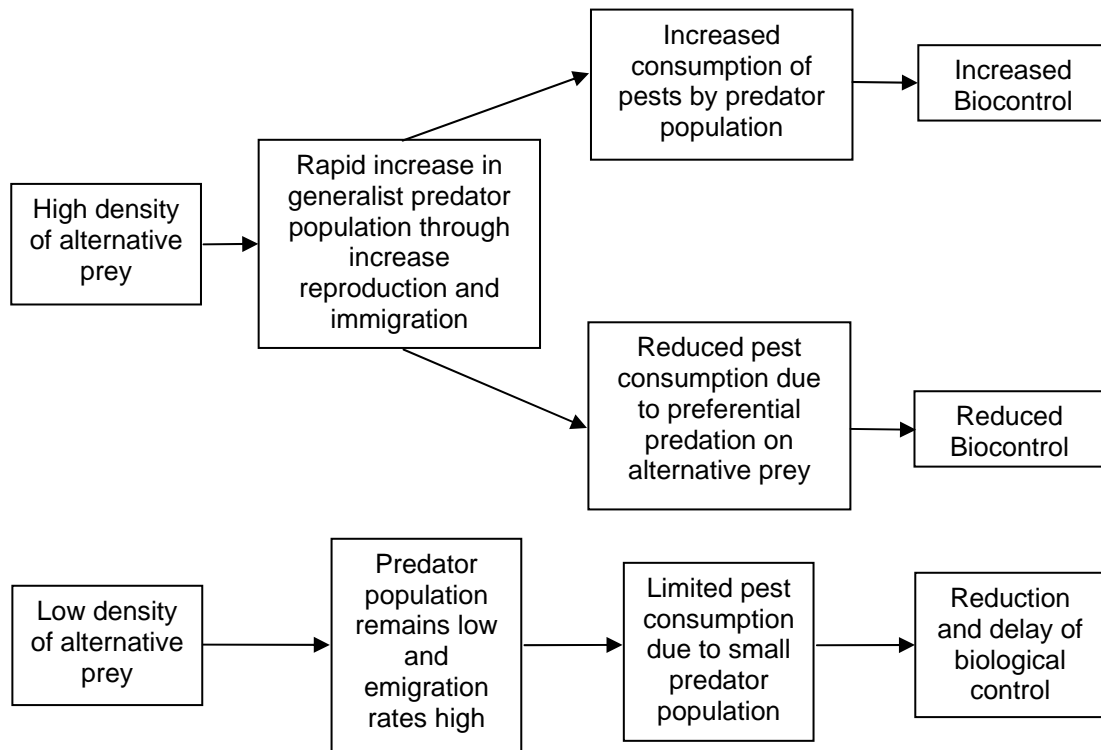


Figure 1. The role of alternative prey in mechanisms of biological control by generalist predator populations.

Many predators build up their populations early in the season by feeding on alternative prey items which are abundant at this time of year (Harwood *et al.* 2001; 2003). This enables them to impact upon pests as soon as they arrive and has been supported by the mathematical modeling of pest populations (Fleming 1980). Murdoch *et al.* (1985) even suggested that generalist predators could be more valuable in biological control than individual specialists acting alone. Early season predation could be extremely important in the control of pests such as the potato leafhopper, *Empoasca fabae* (Harris) (Homoptera: Cicadellidae), since control measures are generally required before injury symptoms first appear (Steffey and Armbrust

1991). The presence of a “lying in wait” predator complex could therefore restrict population growth when their densities are low and before specialist natural enemies colonize the habitat.

This study examines the role of alternative sources of food in sustaining populations of two different groups of predator: spiders (true generalists) and coccinellids (aphidophagous predators that exhibit some generalist habits). Field research will focus on the importance of alternative prey to the diet of linyphiid spiders in alfalfa and form a baseline of ecological data for the subsequent molecular analysis of predator feeding habits in the field.

MATERIALS AND METHODS

Adult coccinellids, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), and spiders, *Erigone autumnalis* (Emerton) (Araneae: Linyphiidae), were collected from the University of Kentucky Spindletop Research Station and maintained in the laboratory at 21°C on a 16:8 L:D cycle. Prior to laboratory experiments (below), all individuals were provided with an *ad libitum* supply of isotomid Collembola and Diptera (for spiders) or aphids (for coccinellids).

EFFECTS OF ALTERNATIVE PREY ON *HARMONIA AXYRIDIS*

Adult male and female *H. axyridis* were paired and provided an *ad libitum* diet of *Acyrtosiphon pisum* (Harris) (Hemiptera: Aphididae) and *Drosophila melanogaster* Meigen (Diptera: Drosophilidae) larvae. Eggs were collected, maintained at 21°C on a 16:8 L:D cycle, and upon hatching equal numbers of larvae were systematically assigned to one of five treatments (Table 1). Three parameters were measured; (a) percentage survival to adult, (b) mean development time, and (c) mean weight of adult females at emergence.

Table 1. Invertebrate prey added to each of five treatments. Food was supplied *ad libitum* to all coccinellid larvae.

Treatment	Prey species
A	<i>Danaus plexippus</i> (L.) (Lepidoptera: Nymphalidae)
B	<i>Papilio polyxenes</i> F. (Lepidoptera: Papilionidae)
C	Mixed diet of <i>Danaus plexippus</i> and <i>Papilio polyxenes</i>
D	<i>Aphis glycines</i> Matsumura (Hemiptera: Aphididae)
E	<i>Aphis glycines</i> , <i>Danaus plexippus</i> and <i>Papilio polyxenes</i>

EFFECTS OF ALTERNATIVE PREY ON *ERIGONE AUTUMNALIS*

Adult male and female *E. autumnalis* were paired and provided with an *ad libitum* diet of alternative and pest prey (Table 2). Eggsacs were collected and upon hatching, spiderlings were separated and placed into individual Petri dishes with a moist Plaster-of-Paris base to maintain high humidity. Equal numbers of individuals were systematically assigned to one of six treatments (Table 2) after the first molt. Prior to this, small isotomid and sminthurid

Table 2. Invertebrate prey added to each of six treatments. Food was supplied *ad libitum* to all spiderlings.

Treatment	Prey species
A	Isotomid Collembola
B	<i>Drosophila melanogaster</i>
C	<i>Acyrtosiphon pisum</i>
D	<i>Empoasca fabae</i>
E	<i>Acyrtosiphon pisum</i> and <i>Empoasca fabae</i>
F	Mixed diet of Isotomid Collembola, <i>Drosophila melanogaster</i> , <i>Acyrtosiphon pisum</i> and <i>Empoasca fabae</i>

Collembola were provided as prey (large food items were not taken by first instar linyphiid spiderlings). Three parameters were measured; (a) percentage survival to adult, (b) mean development time, and (c) mean weight of new adult females.

INTERACTIONS BETWEEN ALTERNATIVE PREY AND PESTS IN ALFALFA

Quantifying the availability of pest and non-pest prey to linyphiid spiders was undertaken in alfalfa fields at the University of Kentucky Spindletop Research Station. Linyphiid spiders were collected weekly from May until August and immediately frozen in separate Eppendorf tubes (for subsequent molecular analysis of gut-content). The availability of prey was monitored by mini-sticky traps following protocols described elsewhere (Harwood *et al.* 2001; 2003). These small (7.5 cm²) sticky traps were left *in situ* for 24 h and were designed to monitor activity-density of all prey entering the web-site over time (total $n = 420$). Thirty web-sites were sampled per week (throughout three cutting cycles of alfalfa).

RESULTS

EFFECTS OF ALTERNATIVE PREY ON *HARMONIA AXYRIDIS*

Larvae of *H. axyridis*, a “generalist” aphidophagous predator, fed with a single-species diet of Lepidoptera had longer development times ($F_{4,27} = 29.02$, $P < 0.001$) and reduced weight at emergence ($F_{4,21} = 13.70$, $P < 0.001$) compared to the mixed Lepidoptera or aphid-containing diets (Table 3). However, these parameters were statistically similar between the mixed lepidopteran diets and those consisting of aphids (either as single species or part of a mixed diet with Lepidoptera) (Table 3). The only parameter reduced in the absence of aphids was survival (<50% survived to adult on Lepidoptera-only treatments).

EFFECTS OF ALTERNATIVE PREY ON *ERIGONE AUTUMNALIS*

No spiderlings survived to adult on single-species diets of *A. pisum* or *E. fabae* although spiderlings consuming *E. fabae* lived significantly longer than those feeding on *A. pisum* ($t_{37} =$

5.37, $P < 0.001$). However, a mixed diet of the two poor quality pests produced a significant increase in survival parameters (20% survived to adult). Alternative prey (Collembola and Diptera) provided as a single-species diet or part of a mixed diet enabled most spiders to survive to adult. Interestingly, development time from hatching to adult did not vary between treatments (aphid-only and leafhopper-only diets excluded from analysis because no individuals survived beyond the third molt) ($F_{3,67} = 3.52$, $P = 0.065$) but adult weight of female spiders was significantly lower in the mixed pest-only diet (Treatment E) compared to those treatments containing alternative prey ($F_{3,31} = 9.45$, $P < 0.001$) (Table 4).

Table 3. Mean (\pm SE) development time and weight at emergence of *Harmonia axyridis* subjected to feeding regimes of different quality.

Treatment	Development (days)	Adult weight (mg)
A (<i>D. plexippus</i>)	31.2 \pm 3.8	21.3 \pm 3.8
B (<i>P. polyxenes</i>)	38.1 \pm 3.4	17.9 \pm 4.8
C (<i>D. plexippus</i> + <i>P. polyxenes</i>)	23.4 \pm 2.9	27.1 \pm 3.1
D (<i>A. glycines</i>)	20.9 \pm 3.1	26.5 \pm 2.8
E (All of above prey)	21.2 \pm 2.1	28.6 \pm 2.4

Table 4. Mean (\pm SE) development time and weight at emergence of *Erigone autumnalis* subjected to feeding regimes of different quality.

Treatment	Development (days)	Adult weight (μ g)
A (Collembola)	34.1 \pm 6.4	68.1 \pm 4.3
B (<i>D. melanogaster</i>)	39.8 \pm 8.0	71.4 \pm 9.1
C (<i>A. pisum</i>)	n/a	n/a
D (<i>E. fabae</i>)	n/a	n/a
E (<i>A. pisum</i> + <i>E. fabae</i>)	41.7 \pm 10.4	39.6 \pm 7.2
F (All of above prey)	38.3 \pm 8.8	66.8 \pm 5.0

INTERACTIONS BETWEEN ALTERNATIVE PREY AND PESTS IN ALFALFA

Spiders captured in alfalfa were dominated by the linyphiid sub-families Erigoninae ($n = 293$) and Linyphiinae ($n = 201$). More spiders were captured than web-sites sampled ($n = 420$) because, occasionally, more than one spider occupied a single web-site. The total number of potential prey captured at web-sites of linyphiid spiders are presented in Fig. 2. Collembola (and other alternative non-pest prey) were an important food resource to these spiders, but pests represented a significant proportion (21%) of their potential diet.

Although alternative prey can improve growth parameters and biological control by spiders (Fig. 1), many of these non-pest food items are preferred by generalist predators (e.g., Bilde and Toft 1994) and can detract biocontrol agents from feeding on pests if populations overlap temporally and spatially. Activity-density of prey in alfalfa indicated a highly significant, and positive, correlation between the availability of *E. fabae* and alternative prey to linyphiid spiders at web-site locations (Fig. 3).

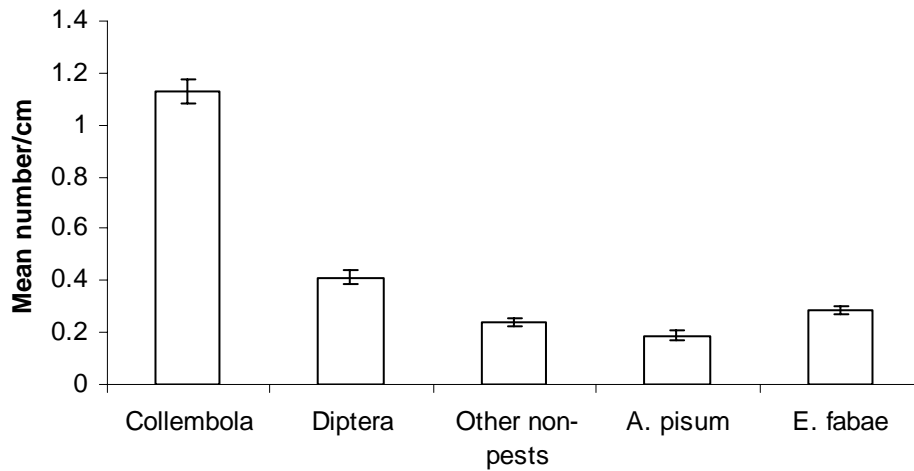


Figure 2. Mean number (\pm SE) of potential prey captured at web-sites of linyphiid spiders in alfalfa.

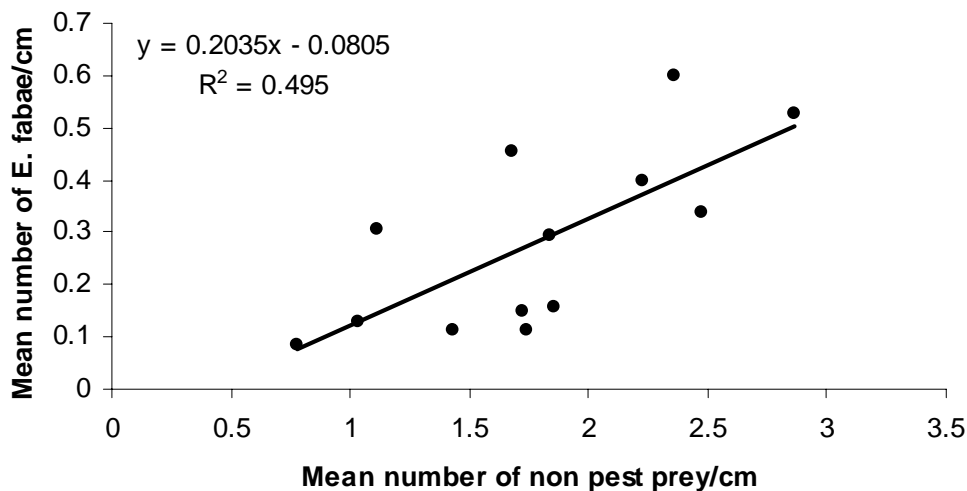


Figure 3. Correlation between availability of *Empoasca fabae* and alternative, non-pest prey in alfalfa.

DISCUSSION

Given the concerns associated with the use of insecticides, it is possible that significant levels of biological control can be provided through the conservation and enhancement of natural enemies. This could be particularly important in crops such as alfalfa which are tolerant to a limited incidence of pests without reducing their yield or quality (Obrycki and Harwood 2005). The aim of this research was to address a key, but poorly understood, component of predator-prey interactions within agroecosystems – the role of alternative prey in sustaining (or disrupting) predator populations from regulation of two pests of alfalfa, *A. pisum* and *E. fabae*. Although conservation biological control may enhance predator growth rates by providing an abundant and nutritionally balanced diet, it is feasible that predators will divert feeding efforts towards non-pest food items, thus reducing biological control. Evidence from manipulative experiments suggests that alternative prey interfere with mechanisms of biological control (Koss *et al.* 2004; Madsen *et al.* 2004). However, molecular evidence and the monitoring of predator population densities are required to accurately quantify the feeding behavior of generalist natural enemies in the field. This may (or may not) implicate alternative prey as a causative factor in the disruption of pest consumption by predator populations. To date, molecular evidence tends to suggest that non-pest prey constitute a significant proportion of diet of many generalist predators (Agustí *et al.* 2003; Harper *et al.* 2005), but even though pest predation rates per individual predator may decline in the presence of these alternative sources of food, feeding activity by the population as a whole may lead to improved levels of control.

Alternative prey has the ability to sustain generalist predators when pest density is low. However, the development of some coccinellids is lengthened and sub-optimal when allowed to feed on such food items (Kalaskar and Evans 2001; Wiebe and Obrycki 2002) and their reproductive output declines on single-species non-aphid diets (Evans *et al.* 2004). Despite these sub-optimal feeding conditions to more specialized aphidophagous predators, true generalists (such as spiders) tend to exhibit increased reproductive output and population growth on alternative non-pest sources of food (Toft 2005). The laboratory studies reported here support these conclusions and indicate that although single-species lepidopteran diets are unlikely to maintain coccinellid populations over significant periods of time, increased diversity of alternative prey could be sufficient to sustain *H. axyridis* (and possibly other coccinellids) until the arrival of favored aphid pests. The ability to employ this lying-in-wait strategy, sustaining themselves on non-pest food resources, would be especially important given that generalist predators are most likely to impact on these pest species early in the year (Chang and Kareiva 1999; Chiverton 1986).

While growth parameters of coccinellids were maximal on aphid diets, the true generalists, spiders, exhibited the opposite effect when fed a diet of alternative prey. Pest-only diets resulted in no hatchling spiders reaching adult, conclusions reported in other spiders (Bilde and Toft 2001). The alternative, non-pest prey items (which consisted of Collembola and Diptera) maximized population growth of these important predators and clearly allowed the juvenile population to be sustained. This ability to subsist (and maximize growth) on alternative prey implicates spiders as particularly valuable biocontrol agents of major pests of agroecosystems. However given that spiders prefer alternative prey, if the availability of non-

pest food overlaps with pests, their potential value in the control target arthropods may be reduced due to diverting their feeding efforts towards alternative prey.

The field-monitoring of arthropod populations in alfalfa supported this hypothesis. There were clear trends indicating that pest and non-pest prey exhibited a strongly positive correlation in their availability to linyphiid spiders. Probably a result of the cyclical nature of cutting, populations of pest and non-pest prey were synchronous such that both occurred in high numbers at the same time. Such synchrony is likely, in the case of true generalists, to compromise their ability to restrict pest population growth given the impact of alternative prey on feeding rates of pest species in the field (Harwood *et al.* 2004). It is clear that while alternative prey items are capable of sustaining generalist predator populations (and in some cases enhancing population growth), the reliance on individual predators in biological control is likely to be ineffective against many agricultural pests. Alternative prey, rather than sustaining predator populations, could reduce the ability of generalists to control crop pests in the field. It is therefore important to maximize the diversity of natural enemies to counteract the interference caused by alternative prey to true generalists such as spiders. This will enable effective levels of control to be exerted by the community as a whole (Sunderland *et al.* 1997; Symondson *et al.* 2002), rather than individual natural enemies acting alone. Ultimately, molecular detection of prey remains (using monoclonal antibodies and/or DNA-based technology) in predator guts and the parallel monitoring of predator population densities will enable the true role of alternative prey in sustaining predator populations to be quantified. Such information can be modeled with prey availability to determine the capacity of different groups of predators in the biological control of arthropod pests and reveal potential interference caused by increased availability of alternative non-pest prey.

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NOCTURNAL PREDATORS AND THEIR IMPACT ON LEPIDOPTERAN EGGS IN ANNUAL CROPS: WHAT WE DON'T SEE DOES HELP US!

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ABSTRACT

Predation is often a key factor maintaining insect populations below pest status in annual crops. However, in many cases, the predators causing significant mortality to particular pests in the field are not well understood. In particular, the complex of nocturnally active predators feeding on pest species is usually unknown.

The predator complexes attacking lepidopteran eggs in cotton, corn and soybean in south Texas, U.S.A., were determined with the goal of characterizing diurnal and nocturnal predator complexes, determining the role of nocturnal predators in lepidopteran pest mortality, and quantifying diel patterns of predation. The evaluations reported here focused on the predator complexes feeding on *Helicoverpa zea* (Boddie) and *Spodoptera exigua* (Hübner), (Lepidoptera: Noctuidae). This work has been conducted using direct observation to accurately measure and identify predation of lepidopteran eggs while removing the bias towards day-active predators.

Egg predation was typically high in all crops in all years, although it ranged from 25 to 99% in any 24 h period. Nocturnal predation was a significant component of this mortality in all crops. The diurnal and nocturnal predator complexes observed feeding on eggs differed between crops. The relative importance of nocturnal predation varied among dates, but on average was similar to diurnal predation in cotton, corn and soybean in 2002 and soybean in 2003. Mortality due to nocturnal predation was >50% higher than diurnal predation in cotton in 2003. Predators observed feeding at night constituted nearly 72% of all observations in south Texas cotton, 52% in corn and 49% in soybean. Nocturnal predators of particular importance included a group of cursorial spiders responsible for nearly 25% of all observations of predation in cotton as well as the formicids (primarily *Solenopsis invicta* Buren). Of the four spider species most frequently observed feeding on eggs, only one had previously been reported as an important predator in agricultural settings (*Cheiracanthium inclusum* [Hentz]). Few predators were commonly active during both day and night. Nocturnal observations revealed both predators that were previously suspected to be important mortality factors as well as those that had not been perceived to be important (e.g., cursorial spiders).

In summary, nocturnal predation was significant in all crops and was usually similar to diurnal predation in relative impact. However, the predators causing mortality were different between day and night with little overlap of dominant predator species. It is likely that there are nocturnally active predators in many crops that are important yet are not perceived as such. Whether nocturnal predation is important in all crops and in all environments is unknown, however these studies demonstrate that there is much to be learned from the study of nocturnal predation. Future research on predation as a component of biological control should incorporate studies of nocturnally active predators.

INTRODUCTION

Predation is often a key factor maintaining populations of lepidopteran pests at a level that prevents injury to annual crops. Studies in cotton (Nuessly and Sterling 1994; Pfannenstiel 2004; Sansone and Smith 2001) and soybean (Anderson and Yeorgan 1998) and soybean and corn (Pfannenstiel and Yeorgan 2002) have demonstrated that predation on lepidopteran eggs can be consistently high. Studies have attempted to identify predators of Lepidoptera using a variety of techniques, including visual observation (e.g., Whitcomb and Bell 1964), autoradiography (e.g., McCarty *et al.* 1980) and molecular techniques (e.g., Ruberson and Greenstone 1998; Sisgaard *et al.* 2002). These studies have produced widely varying results and it is unclear whether the variation is due to regional/yearly variation in predator abundance or variation in methodology. Buschman *et al.* (1977) obtained estimates of the predator complexes feeding on eggs in soybean that varied depending on the use of diurnal visual observations or autoradiography. One possible explanation for the variation between techniques could be the degree to which they sampled predators that are active nocturnally, something that was almost never explicitly controlled for. If some effort was made to evaluate nocturnally active predators, the effort was only a fraction of that expended evaluating diurnal predation. To explicitly address this, Pfannenstiel and Yeorgan (2002) carefully used visual observation to evaluate diel patterns of predation. In almost all circumstances we have no knowledge of the relative contribution of nocturnal mortality, nor much information on the predators that might be causing nocturnal mortality.

During 2001-2004, I evaluated the predator complexes feeding on the lepidopteran pests (*Helicoverpa zea* [Boddie] and *Spodoptera exigua* [Hübner] [Lepidoptera: Noctuidae]) in cotton, corn, and soybean in south Texas, U.S.A. This work has been conducted using carefully conducted direct visual observation to accurately measure and identify predation of lepidopteran eggs, remove biases towards day-active predators, and accurately characterize nocturnal predation. Initial studies indicated that nocturnal predation could be consistently high, predator complexes varied between crops, and that arthropods observed feeding on eggs at night were different from those seen during the day (Pfannenstiel and Yeorgan 2002). In that study, several predators that were important were previously unreported as predators of lepidopteran eggs. Other predators were determined to be primarily nocturnal, whereas they were previously considered diurnal. Here, I will present further research results on predation of lepidopteran eggs in annual crops and directly address the relative importance of nocturnal predation in annual crops.

MATERIALS AND METHODS

Predation on lepidopteran eggs was evaluated in cotton, corn, and soybean in south Texas during 2001-2004. The results presented here come from several different studies and correspondingly plot size and arrangement varied. Egg mortality and the predators responsible were quantified using the methods of Pfannenstiel and Yeorgan (2002) as modified in Pfannenstiel (2004), but will be summarized here. For all studies, stations within each crop planting were established with flags at 3 to 5 m intervals in each of 3 different rows in each plot or field. At each of these stations, fresh sentinel lepidopteran eggs (*H. zea* or *S. exigua*) were placed and monitored over the next 24 h.

Sentinel eggs were obtained by allowing *H. zea* and *S. exigua* moths to oviposit onto green florist paper that was placed as a lining in 3.8 l ice cream cartons. Paper on which eggs had been laid was collected daily and placed into a refrigerator at 4°C to stop development until used or discarded after 4 d. These sheets were cut into small (3 to 20 cm²) sections containing either 10 *H. zea* eggs or one *S. exigua* egg mass each and re-placed into the refrigerator until use. All eggs in each *S. exigua* egg mass (range 20 to 200 eggs/mass) were counted and recorded before placement into the cotton field. *H. zea* eggs were used for studies in all three crops; *S. exigua* eggs were used only in studies in cotton.

Eggs were attached to plants at 3:00 PM by stapling the eggs to the top of a leaf about 55 - 70% of the distance from the ground to the top of the plant and this relative location was maintained as the plants grew during the season. In corn, eggs were attached to the small leaves on the terminal end of the ear. Pests of field crops often deposit their eggs on the foliage of the middle to upper parts of the plant (Terry *et al.* 1987; Sappington *et al.* 2001; R.S.P. pers. obs.) although often on the undersides of leaves. Placing the eggs on the top of leaves was done to facilitate observation. Neussly and Sterling (1994) found no differences in predation on *H. zea* eggs between the upper and lower leaf surfaces in cotton in central Texas. *H. zea* and *S. exigua* eggs typically take 2.5 d or more to develop in the field and would be available to predators throughout this time (R.S.P. pers. obs.).

Egg groups were observed at three-hour intervals (6:00 PM, 9:00 PM, 12:00 Midnight, 3:00 AM, 6:00 AM, 9:00 AM, 12:00 noon, and 3:00 PM CDT) for the following 24 h. This distribution of sampling times results in four day (9:00 AM, 12:00 Noon, 3:00 PM and 6:00 PM) and four night samples (9:00 PM, 12:00 Midnight, 3:00 AM, and 6:00 AM CDT). Sunrise occurred as the 6:00 AM sample was being finished and sunset occurred just before the 9:00 PM sample was initiated, allowing for equal numbers of day and night samples despite a photophase lasting about 14 h. At each observation period, predators observed feeding on the eggs were identified or collected for subsequent identification. All observations of predation could be assigned to day (9:00 AM, 12:00 Noon, 3:00 PM and 6:00 PM) or night (9:00 PM, 12:00 Midnight, 3:00 AM, and 6:00 AM). Eggs of each species were replaced when all eggs on the sheet had been consumed allowing accurate estimation of egg mortality (24 h). *H. zea* eggs were counted at each 3 h period to allow for accurate estimation of mortality for this species at shorter time intervals (3h, or day vs. night). Evaluations of predation were conducted from 8 to 12 times per year from 2001-2004. Observations were initiated in late April/early May and continued at two- to four-week intervals through late August. Not all crops were sampled on each date because of differences in crop development and senescence or the

focus of a particular experiment. Cotton was the focus of several of the studies from which data was obtained therefore sample sizes for cotton are larger than those for corn and soybean. The null hypothesis entering the study was that there would be no difference in the frequency of observed predation events or predator complexes between day and night.

RESULTS

Egg mortality was consistently high, although this varied both within and between seasons with no obvious, consistent pattern. Predation rates on any one date (24h) ranged from 30 to 87% in cotton, 35 to 99% in corn, and 25 to 89% in soybean from 2001 - 2003. On dates where all three crops were evaluated predation was often highest in corn, followed typically by cotton and with soybean having a slightly lower rate of predation. Seasonal mean predation rates were similar between day and night for all crops in 2002 and soybean in 2003. However, mortality due to predation in cotton was significantly higher during the night in 2003 than during the day (Fig. 1).

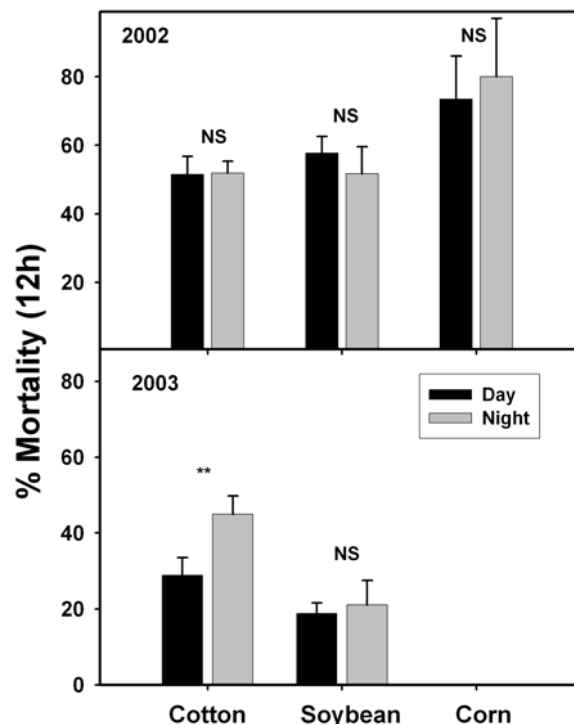


Figure 1. Diel Predation of *H. zea* eggs in cotton, soybean and corn in 2002 and 2003. Data are presented as mean percentage of eggs consumed per 12 h (Day vs. Night) \pm SE. Because eggs were replaced when consumed, summed 12-h predation rates exceed 24-h predation rates. Means are compared using a Paired t-test of arcsin(Square Root[X]) transformed proportion data; significance (**) is $P \leq 0.05$; NS = Not Significant $P > 0.05$.

For all crops except cotton in 2003, there was no apparent pattern to the variation in predation by diel period and it appears that the relative contribution of diurnal vs. nocturnal predation balanced out through the season. In 2003, when nocturnal predation was higher, it was consistently higher throughout the season. In 2002, there was no obvious pattern to the variation in diel predation (Fig. 2.)

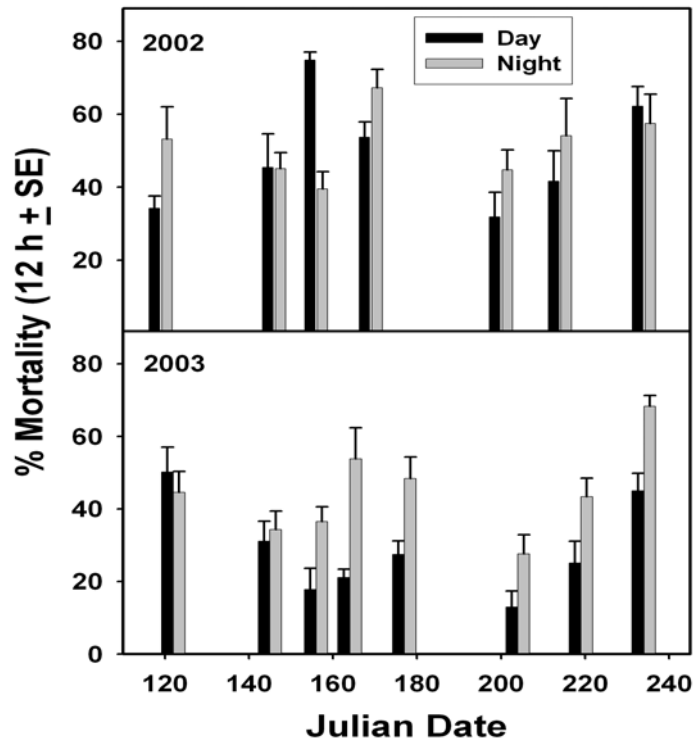


Figure 2. Diel Predation of *H. zea* eggs in cotton by date for 2002 and 2003. Data are presented as mean percentage of eggs consumed per 12 h (Day vs. Night) \pm SE.

Predation on eggs was observed >1500 times during these studies. The percentage of observations of nocturnal predation relative to the total in each crop was 72% in cotton (n=1228), 52% corn (n=142), and 42% in soybean (n=195). The predators responsible for the observed predation varied between crop and between diel period (Table 1). Only two predators made up more than 5% of the predators observed feeding in both the day and night periods in any crop. These were the formicids (predominantly *Solenopsis invicta* Buren) and the omnivorous mirid, *Pseudatomoscelis seriatus* (Reuter), which made up > 5% of the observed predation events in cotton during both day and night. In corn, the formicids were also observed during day and night. Both of these predators are most active at night, but will continue to forage during the day. The 11 other predators that contributed >5% of the observed predation events in either diel period were primarily observed during the day or night, but not both. In soybean, there was no overlap in the predators responsible for >5% of the observed predation in either diel period.

Table 1. Predators most frequently observed feeding on *H. zea* and *S. exigua* eggs in cotton, corn and soybean during 2001-2004. For each crop, the predators are ranked by the most frequently observed during day or night; predators with observations constituting < 5% of the total are not reported. Data are presented as the proportion of observations attributable to a predator taxon during each diel period in each crop.

Crop	Rank	Day		Night	
		Predator Taxa	% of Observed	Predator Taxa	% of Observed
Cotton	1	<i>Geocoris</i> spp.	24.5	Cursorial spiders	23.7
	2	Formicidae	19.9	Mites	12.1
	3	<i>Pseudatomoscelis seriatus</i>	15.0	Formicidae	11.3
	4	<i>Hippodamia convergens</i>	9.5	<i>Pseudatomoscelis seriatus</i>	9.7
	5	<i>Collops</i> sp.	7.8		
Corn	1	<i>Coleomegilla maculata</i>	35.3	Formicidae	50.0
	2	Formicidae	25.0	Elateridae	10.8
	3	<i>Orius</i> spp.	19.1	Cursorial spiders	8.1
	4	<i>Hippodamia convergens</i>	10.3	Dermaptera	5.4
Soybean	1	<i>Geocoris</i> spp.	53.0	Cursorial Spiders	28.4
	2	<i>Collops</i> sp.	21.0	Formicidae	13.7
	3	<i>Coleomegilla maculata</i>	6.0	Nabidae	10.5
	4			Dermaptera	10.5
	5			Elateridae	10.5

Cursorial spiders and ants were consistently among the most important nocturnal predators of lepidopteran eggs in all crops. The cursorial spider complex was dominated by 4 species; the anyphaenids *Hibana futilis* (Banks) and *Hibana arunda* Platnick, the lynphiid *Grammonota texana* (Banks) and the miturgid *Cheiracanthium inclusum* (Hentz). Two species of geocorids, *Geocoris lividipennis* Stål and *Geocoris punctipes* Say, were the most frequently observed diurnal predator of eggs in soybean and cotton. The coccinellid *Coleomegilla maculata* DeGeer was the most frequently observed diurnal predator in corn.

DISCUSSION

Studies of egg predation in annual crops in the southern USA, particularly cotton and soybean, have yielded consistently high estimated predation rates. McDaniel and Sterling (1982) observed an average of 77% daily predation rates of *Heliothis virescens* (F.) eggs in cotton in central Texas. In another, more detailed study, Neussley and Sterling (1994) demonstrated average total (~ 72 h) predation rates > 80% on *H. zea* eggs. Clearly, predation on lepidopteran eggs in these crops can vary, but frequently is quite high. Despite these and other studies that document the impact of predation, we have discovered only a portion of the predators causing this mortality. Although predation of lepidopterans on cotton and soybean in the USA has been relatively well studied in historical terms, very little information exists on the role of nocturnal predation. Recently, a study by Diaz *et al.* (2004) evaluated nocturnal predation of *S. exigua* eggs in relation to *S. invicta* populations, but they did not include diurnal observations.

There were similar levels of predation intensity during the day and night in 2002. Nocturnal predation was essentially equivalent in importance to diurnal predation in cotton, corn and soybean. In 2003, nocturnal predation in cotton was more than 50% greater than was observed during the day. There was no concurrent increase in nocturnal predation in soybean. At the same time, there was little overlap in the predators that are active during the day in comparison with those nocturnally active (2 taxa out of 12). Few studies have directly addressed nocturnal predation and some that may have detected nocturnal predation using molecular techniques did not control sampling intervals in a way that might have accurately identified the diurnal and nocturnal predator complexes. Studies of predation on *H. zea* eggs in corn and soybean in Kentucky (Pfannenstiel and Yeargan 2002), exhibited similar results to those described here. Predation was high during the day and night and most predatory taxa exhibited activity patterns that were primarily diurnal or nocturnal, not both.

Many arthropod species contributed to the high egg mortality rate. However, daylight observations would have correctly identified only a few of the important predators in these crops. The composition of the predator complex observed feeding on lepidopteran eggs at night was different from that observed during the day. Diurnal observations would not have correctly identified other predator groups such as the cursorial spiders, which appear to be particularly important in south Texas cotton. To accurately characterize the predators attacking a particular pest species, it is critical to carefully investigate predation during nighttime as well as daytime hours. Studies using diurnal visual observations alone would not identify a significant proportion of the important predators. In a previous study, Pfannenstiel and Yeargan (2002) also identified unusual taxa such as phalangids (Opiliones) as common predators of lepidopteran eggs. The important predators identified in this study, particularly the cursorial spiders, should be further evaluated to improve our understanding of their role as biological control agents in these crops and to determine if they can be manipulated to increase their impact.

These studies of the predator complexes feeding on lepidopteran eggs in south Texas, as well as the previous studies by Pfannenstiel and Yeargan (2002), demonstrate that nocturnally active predators are important in several annual crop systems in the southeastern USA. Although cotton and soybean have two of the better characterized predator complexes among cropping systems in the USA, evaluation of nocturnal predator activity is reshaping our perception of the predator complexes attacking lepidopteran pests in these crops. It is critical that future research incorporates greater consideration of the role nocturnally active natural enemies play in biological control of crop pests.

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EXPLORING THE RELATIONSHIP AMONG PREDATOR DIVERSITY, INTRAGUILD PREDATION, AND EFFECTIVE BIOLOGICAL CONTROL

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ABSTRACT

In conservation biological control, we seek to make agricultural systems more hospitable to natural enemies, in an attempt to increase enemy abundance and diversity. However, it is unclear whether the effectiveness of biological control actually increases with growing natural enemy diversity, in communities including many species of generalist predators. Studies have shown that suppression of herbivores may be either enhanced or disrupted by adding predator species to a community, but these studies do not distinguish between the effects of predator diversity and the effects of predator abundance, identity, and composition. Here, we first demonstrate that a diverse community of natural enemies, dominated by generalist predators, attacks the green peach aphid, *Myzus persicae*, in potato fields in Washington State. Second, in a large-scale field experiment, we experimentally isolate the effect of predator diversity on aphid biological control. We show that increasing predator diversity does not affect prey exploitation; overall there is no strong, net complementarity or interference among predators that alters the strength of aphid suppression. However, our experiment revealed strong effects of predator species identity, because predators varied dramatically in their per capita consumption rates. Because of these strong species identity effects, green peach aphid biological control will improve with growing predator diversity, because particularly effective aphid predators will be more likely to be included within diverse communities. However, our results do not suggest any benefits to biological control of natural enemy diversity *per se*.

INTRODUCTION

Agricultural systems frequently display explosive herbivore outbreaks, while less-disturbed natural communities rarely do. This has led to the suggestion by agroecologists that restoring some elements of biodiversity to agricultural systems may improve natural pest control (Pimentel 1961). However, much recent work in the predator ecology literature suggests that increasing natural enemy diversity increases the risk of adding intraguild predators, such that herbivore suppression might actually decline as predator diversity increases (Rosenheim *et al.* 1993; Snyder and Ives 2001; Snyder and Wise 2001). But few experimental studies have

explicitly examined the relationship between predator diversity and herbivore suppression, in part due to the lack of logistically manageable experimental designs for examining interactions within complex (> 2 predator species) natural enemy communities (but see Finke and Denno 2004).

The growing body of biodiversity-ecosystem function (“BEF”) literature provides experimental approaches that may be useful to predator ecologists (Ives *et al.* 2005). BEF studies typically have demonstrated that ecosystem function, for example, net productivity for plant communities, improves as species diversity increases (Tilman *et al.* 1996; 1997). However, interactions among multiple trophic levels have almost never been considered in the BEF literature (Duffy 2002; Ives *et al.* 2005; Wilby and Thomas 2002). BEF studies share design traits that are unfamiliar to most predator ecologists: treatment levels are the number of species present, with species drawn from a predetermined pool of possible species, and substitutive rather than additive designs are used, so that the total predator densities are constant across diversity treatments (Ives *et al.* 2005).

We have been studying the community of natural enemies attacking the green peach aphid (*Myzus persicae*) in Washington State potato (*Solanum tuberosum*) fields. Our presentation is in two parts. First, we discuss a compilation of taxonomic surveys within potato fields in Washington, demonstrating this crop’s high natural enemy species diversity. Second, we summarize the results of a large-scale field experiment wherein we experimentally constructed natural enemy communities that varied in their natural enemy diversity, and compared the impacts of these communities on green peach aphid.

MATERIALS AND METHODS

DIVERSITY OF NATURAL ENEMIES IN WASHINGTON POTATO FIELDS

In the northwestern United States, insect pests of potatoes have traditionally been controlled using applications of broad-spectrum insecticides (Ruffle and Miller 2003). However, the specter of loss of these chemicals to changes in federal regulations has led some conventional growers to experiment with newer selective pesticides, and organic potato production is growing rapidly in the region. In the 2001-2003 growing seasons we intensively sampled the arthropods in 15 production potato fields under three pest management regimes: conventional fields treated with broad-spectrum pesticides (Hard), conventional fields treated with selective pesticides (Soft), and certified organic fields (Organic) (Koss *et al.* 2005). All fields were within the Columbia Basin of Washington State, a desert region where crops are typically grown under center-pivot irrigation. We sampled arthropods using three techniques: D-vac suction sampling, pitfall trapping, and visual searching (Koss *et al.* 2005).

EXPERIMENTAL MANIPULATION OF PREDATOR BIODIVERSITY

We have conducted a series of experiments wherein we adopted, and somewhat modified, a BEF experimental approach to examine the role of natural enemy species diversity in modifying the control of the green peach aphid (Straub and Snyder, in review). Here, we use one of these experiments to demonstrate our experimental approach and representative results.

In a large-scale field experiment, we experimentally created communities of natural enemies that varied in diversity (either 1 or 3 natural enemy species present), while keeping total predator density constant, and compared the abilities of these communities to control aphids. Our experimental arenas were large, 2m x 2m x 2m field cages, in the field enclosing 4 large potato plants. Cages were first de-faunated using a D-vac suction sampler followed by extensive hand-removal, after which aphids and then predators (according to diversity treatments as described below) were re-added; we then followed the impact of these predator manipulations on aphid population dynamics through time (Straub and Snyder, in review).

In this experiment our species pool included the following five taxa: the predatory bugs *Nabis* spp. and *Geocoris* spp. bug, *Coccinella* and *Harpalus* spp. beetles, and the spider *Misumenops lepidus*. The diversity of taxa (called species here for simplicity) in this predator community has the potential to enhance or disrupt green peach aphid biological control. The considerable variation in foraging behavior among these predators could lead to complementary resource-use and thus a positive relationship between predator diversity and aphid suppression (Ives *et al.* 2005; Wilby and Thomas 2002). However, intraguild predation is also common among these taxa (Brodeur and Rosenheim 2001; Raymond 2000; Snyder and Wise 2001). Such intraguild predation has the potential to lead to a negative relationship between predator diversity and aphid suppression (Finke and Denno 2004; Polis *et al.* 1989; Rosenheim *et al.* 1995). Thus, we had no *a priori* expectations regarding the value of predator diversity in this system. Each of these natural enemy species was present in monoculture, each replicated four times, together comprising the Low Diversity treatment. The High Diversity treatment included 3 predator species, with each of the ten unique combinations of 3 taxa from the pool of 5 replicated once. Thus, our experiment was designed to minimize any influence of species identity, and to isolate any influence of predator species diversity *per se* upon aphid control (Ives *et al.* 2005; Straub and Snyder in review). Ten No Predator control cages were also included, for a total of 40 cages across the experiment. Aphid densities were recorded at 0, 5, and 10 days following predator release.

RESULTS

DIVERSITY OF NATURAL ENEMIES IN WASHINGTON POTATO FIELDS

Geocoris spp. and *Nabis* spp. bugs, and web building tetragnathid and linyphiid spiders, were the most abundant predators in plant foliage, and ground beetles and linyphiid spiders dominated the community on the ground (Table 1). At least 3 parasitoids were common (Table 1). Determining the total number of species that exist in highly disturbed systems like potato fields is difficult. Many species occurring in these fields are immigrants that move in from surrounding vegetation (Wissinger 1997). Rather than attempting to compile and compare complete species lists for fields under each management regime, we took the approach of comparing predator biodiversity using functional groups of taxonomically related species to examine one component of biodiversity, equitability, in our field samples. Overall, equitability scores did not consistently differ between fields receiving hard or soft pesticides, or those under organic management ($P > 0.5$). However, there was a great deal of variability between individual fields (Fig. 1). Some fields had fairly even species distributions, while others were strongly biased towards certain taxa.

Table 1. Common natural enemy taxon groups in Washington potato fields. Data are presented as overall relative abundance of predators, pooling fields across Soft, Hard and Organic management regimes.

Taxon	Common Name	%*	Notes	Functional Group?
In D-vac samples of the foliage (data from Koss 2003)				
<i>Geocoris</i> spp.	Big-eyed bugs	44	<i>Geocoris</i> spp. are active hunters with good vision. They are primarily insectivores, but also do some plant feeding. Adults ca. 5 mm in length.	Foliar Active
<i>Nabis</i> spp.	Damsel bugs	7	<i>Nabis</i> spp. are also active hunters in the foliage, that like <i>Geocoris</i> will do some plant feeding. Adults can be over 1 cm in length.	Foliar Active
Linyphiidae	Sheet web spiders	20	These are tiny spiders (<5mm in length) that build webs to trap prey on the soil surface and lower in the plant canopy.	Trapping
Tetragnathidae	Long-jawed spiders	11	Larger (> 1 cm adult length) spiders that use webs, constructed in the foliage, to capture prey.	Trapping
Other	NA	Each <5	Predatory flies; Orius bugs; lacewings; coccinellid, staphylinid, and carabid beetles; mantids; other spiders. None > 5% of the total.	
In pitfall trap samples (data from Koss 2003)				
<i>Bembidion</i> spp.	Sm. ground beetle	38.5	<i>Bembidion</i> spp. are smaller ground beetles (< 1 cm adult length) active hunters, often diurnal, and sometimes observed in plant foliage	Ground Active
<i>Harpalus fraternus</i>	Lg. ground beetle	16.0	<i>H. fraternus</i> is a larger ground beetle (> 1.5 cm adult length), and active hunter that is usually nocturnal. Less frequently in foliage?	Ground Active
Linyphiidae	Sheet webspiders	13.1	see above	Trapping
Other	NA	32.4	Other carabid spp., staphylinid beetles; other spiders. No single taxon made up greater than 5% of the total.	
In collections of parasitoids emerging from field-collected <i>M. persicae</i> (Data from Pike 2002)				
<i>Aphidius matricariae</i>	none	61.3	Solitary koinobiont, attacks nymph (pref. 3rd instar), emerges from adult or last instar nymph host	Parasitoid
<i>A. ervi</i>	none	15.3	"	Parasitoid
<i>Diaeretiella rapae</i>	none	12.7	"	Parasitoid
Other parasitoids	NA	10.7	A diverse group of other parasitoids; no single taxon > 5% of the total.	Parasitoid

* percentages are proportion of total predator community that taxon represents, across treatments and fields.

EXPERIMENTAL MANIPULATION OF PREDATOR BIODIVERSITY

We measured predator diversity and abundance at the end of the experiment and found that it had changed little. The High diversity treatment remained more species-rich and more diverse than the Low diversity treatment (richness, $t_{28} = 2.544$, $P < 0.05$; Simpson's diversity index, $t_{28} = 2.735$, $P < 0.05$; Straub and Snyder, in review). There was no difference in predator abundance between diversity treatments ($t_{28} = 0.886$, $P > 0.10$), suggesting that overall rates of predator interference were not different under Low versus High predator diversity (Straub and Snyder, in review). There was no evidence that predator diversity impacted aphid suppression: aphid densities were consistently lower in treatments including predators, compared to No Predator controls [Predator addition (High diversity + Low diversity) vs. Control; Exp 1: $F_{1,38} = 10.442$, $P < 0.01$], but aphid densities were indistinguishable in Low and High diversity cages (treatment x time Wilks' lambda = 0.846, $F_{2,27} = 2.454$, $P > 0.10$; diversity $F_{1,28} = 1.542$, $P > 0.10$) (Straub and Snyder, in review). We then asked if species identity might be a better predictor of herbivore suppression. Using Paine's interaction strength index (Paine 1992) to quantify the per-capita impact of predators, we found that species identity had a strong effect on herbivore suppression ($F_{4,15} = 7.028$, $P < 0.01$), with *Coccinella* beetles provided stronger, and thomisid spiders weaker, suppression than in the High diversity treatment (Straub and Snyder, in review).

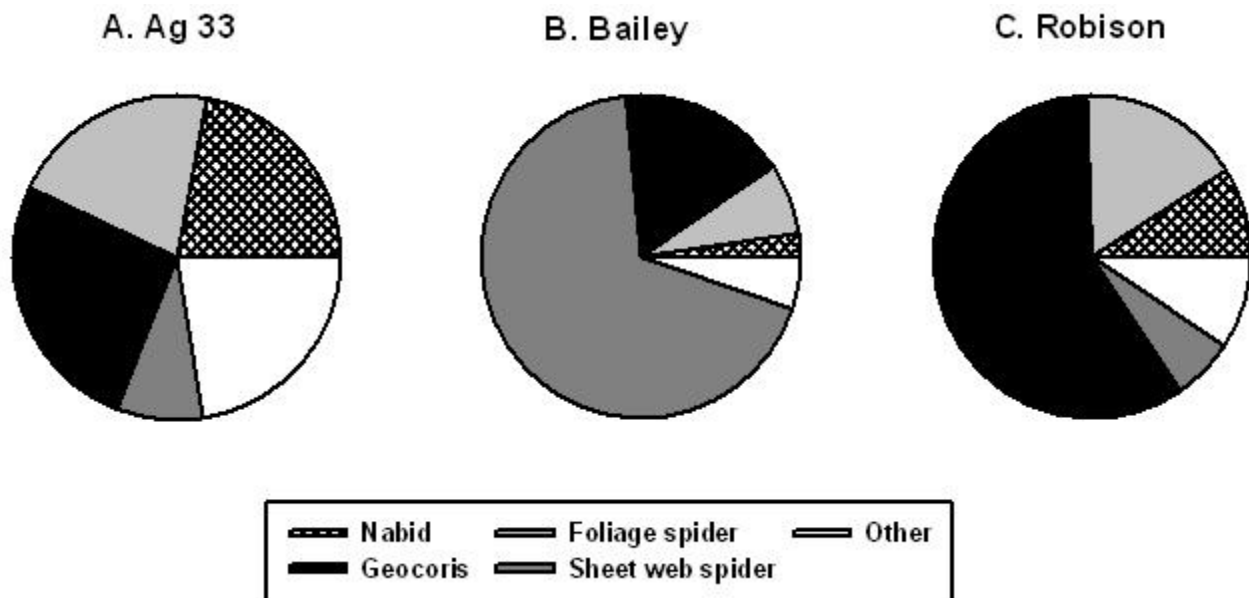


Figure 1. Predator community makeup in three fields in 2001. A) Ag 33 was a Hard field; B) Bailey was a Soft field; and C) Robison was a Hard field. These fields represent the three equitability patterns we saw in the field. Ag 33 has a high equitability score, because the major taxa are similar in abundance. Bailey and Robison have uneven taxa abundances, yielding low equitability scores. However, while their equitability scores are similar, species composition is not – Bailey is dominated by the Trapping functional group, while Robison is dominated by Foliar Active predators.

DISCUSSION

The community of natural enemies attacking green peach aphid locally is diverse, including many species of generalist (and thus likely intraguild) predators. Our predator community includes >20 common species. Therefore, functional diversity of the type necessary for species complementarity, and thus a positive relationship between natural enemy diversity and more complete resource exploitation (Naeem and Wright 2003), likely is present in this community. However, despite our attempts to include representative functional diversity within our field experiment, we found that varying predator diversity *per se* had no effect on the strength of aphid control. It is perhaps surprising that there was no evidence for species complementarity leading to an increase in the strength of herbivore suppression. Our predator species were chosen to span a range of hunting strategies, including active hunters in the foliage, active hunters on the ground, and sit-and-wait hunters in the foliage. Also, we intentionally included one pair of taxa, *Coccinella* and *Harpalus*, which constitute one of the best-documented cases of predator facilitation in a terrestrial system (Losey and Denno 1998). Nonetheless, we recorded no increase in the efficiency of aphid exploitation by more species-diverse natural enemy communities.

Intraguild predation also appeared to be a weak force in our experiment. This result appears in stark contrast to experiments that have shown strong disruptive effects of intraguild predation on herbivore suppression (e.g., Finke and Denno 2004; Rosenheim *et al.* 1993; Snyder and Ives 2001). The lack of intraguild predation in this study is unlikely to be entirely due to an inherent reticence towards intraguild predation within our communities, as many of the included taxa have been shown to feed on one another. For example, *Nabis* and *Geocoris* feed on one another (Raymond 2000), *Harpalus* eats *Nabis* (Snyder and Wise 2001), and most of the predators feed on parasitoids (Brodeur and Rosenheim 2000). One interesting explanation for the difference between the results of this and other studies is that we used a substitutive, rather than an additive, experimental design. Additive designs have often shown strong, disruptive intraguild predation among species (Finke and Denno 2004; Rosenheim *et al.* 1993; Snyder and Ives 2001). However, compared with substitutive designs, additive designs may deflate intraspecific interference and inflate interspecific interference. This is because, in additive designs, predator encounter rates and competition for prey will be higher in treatments including multiple predator species because these treatments also include higher overall predator densities. Regardless, our results suggest that greater predator diversity does not generally weaken pest suppression, as might be surmised from the numerous studies emphasizing the negative effects of predator interference among species (e.g., those reviewed in Polis *et al.* 1989; Rosenheim *et al.* 1995). This is good news given that sustainable agricultural practices such as organic farming often lead to greater on-farm diversity (Hole *et al.* 2005).

The finding that predator identity is a better determinant of pest suppression than predator diversity also has implications for biological control. It implies that, for the biological control of any one pest species, conservation strategies that target particularly effective predator species will be more effective than those targeting predator diversity more broadly. This result supports the common-sense view that conservation biological control practitioners should strive to identify and manage for “the right kind of diversity”, rather than managing for greater biodiversity itself (Landis *et al.* 2000).

In summary, our results suggest that predator diversity *per se* has little effect on the strength of aphid suppression. This result is in contrast with BEF work at other trophic levels, which has consistently revealed a positive relationship between rising consumer biodiversity and the efficiency of resource utilization (Cardinale *et al.* 2002; Naeem and Wright 2003; Tilman *et al.* 2001). Thus, pest suppression may be less sensitive than other ecosystem services to biodiversity loss, provided that key predator species are conserved.

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