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 (*Acyrthosiphon 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 polyphagous 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).

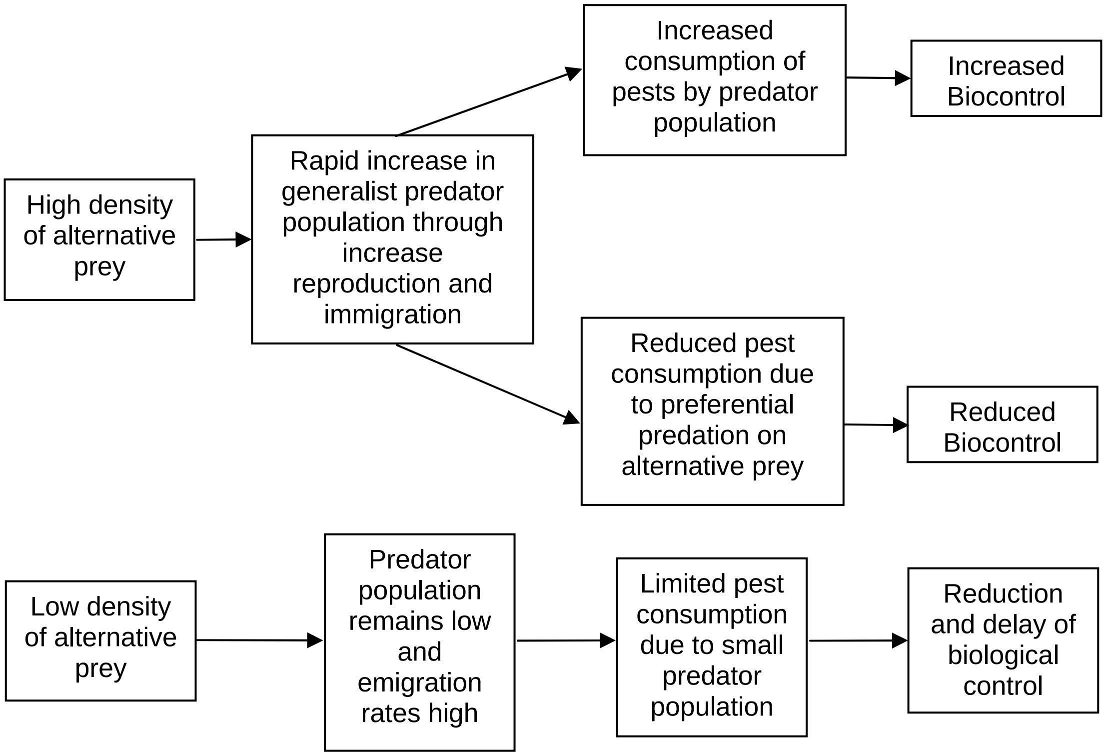

Figure 1. The role of alternative prey in mechanisms of biological control by generalist predator populations.

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 *Acyrthosiphon 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	*Danaus plexippus* (L.) (Lepidoptera: Nymphalidae)
B	*Papilio polyxenes* F. (Lepidoptera: Papilionidae)
C	Mixed diet of *Danaus plexippus* and *Papilio polyxenes*
D	*Aphis glycines Matsumura (Hemiptera: Aphididae)*
E	*Aphis glycines, Danaus plexippus* and *Papilio polyxenes*

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	*Drosophila melanogaster*
C	*Acyrthosiphon pisum*
D	*Empoasca fabae*
E	*Acyrthosiphon pisum and Empoasca fabae*
F	Mixed diet of Isotomid Collembola, *Drosophila melanogaster, Acyrthosiphon pisum* and *Empoasca fabae*

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 cm^2) 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 (± SE) development time and weight at emergence of *Harmonia axyridis* subjected to feeding regimes of different quality.

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

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

Treatment	Development (days)	Adult weight (µg)
A (Collembola)	34.1 ± 6.4	68.1 ± 4.3
B (*D. melanogaster*)	39.8 ± 8.0	71.4 ± 9.1
C (*A. pisum*)	n/a	n/a
D (*E. fabae*)	n/a	n/a
E (*A. pisum* + *E. fabae*)	41.7 ± 10.4	39.6 ± 7.2
F (All of above prey)	38.3 ± 8.8	66.8 ± 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).

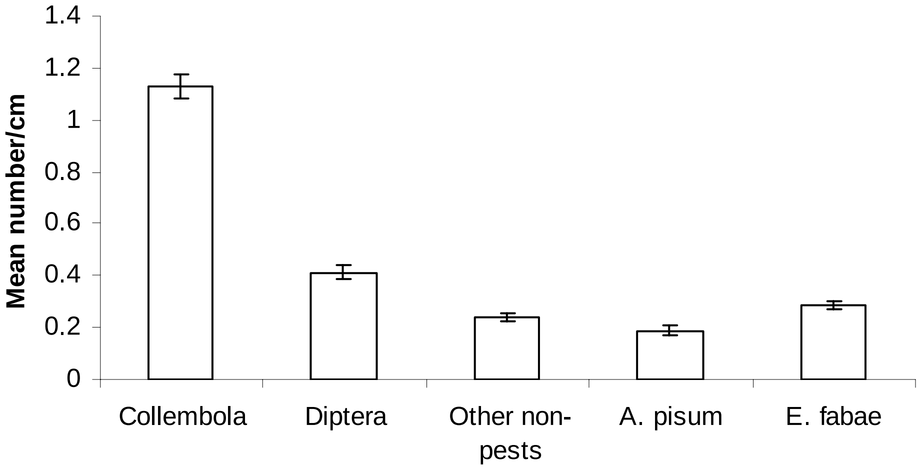

Figure 2. Mean number (± SE) of potential prey captured at web-sites of linyphiid spiders in alfalfa.

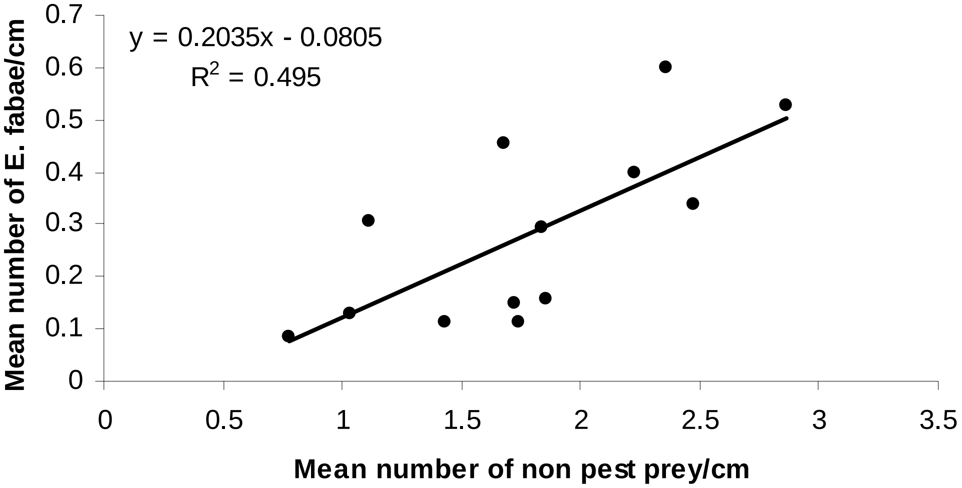

Figure 3. Correlation between availability of *Empoasca fabae* and alternative, non-pest prey in alfalfa.

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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