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thesis entitled

Quantifying the Roles of Competition and Niche Separation in Native and Exotic Coccinellids, and the Changes in the Community in Response to an Exotic Prey Species

presented by

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has been accepted towards fulfillment
of the requirements for

MS degree in **Entomology**

Stuart H Gage
Major professor

Date **5/4/03**

O-7639

MSU is an Affirmative Action/Equal Opportunity Institution

Quantifying the Roles of Competition and Niche Separation in Native and Exotic Coccinellids, and the Changes in the Community in Response to an Exotic Prey Species

By

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A THESIS
Submitted to
Michigan State University
In partial fulfillment of the requirements
For the degree

MASTER OF SCIENCE ENTOMOLOGY

2003

ABSTRACT

Quantifying the Roles of Competition and Niche Separation in Native and Exotic Coccinellids, and the Changes in the Community in Response to an Exotic Prey Species

By

Charles McKeown

Coccinellids are of enormous importance in natural and agricultural systems. Their use as biological control agents has moved different species around the globe. In Michigan two exotic coccinellids are present in the community and their interactions with each other and the native community was examined to provide a more detailed picture of community niche separation. Twelve years of data was used to examine the temporal and spatial dynamics of the exotic species. The dominant members of the community were then analyzed to elucidate the mechanics of niche separation via temporal, spatial, and habitat characteristics using spatial and statistical analysis techniques. The third exotic in the landscape is the recently arrived soybean aphid; the response of the dominant members of the community to this new food resource was examined for possible perturbations in the interactions within the coccinellid community. The exotic species were found not to be in direct competition due to a temporal separation in their niches. The four dominant coccinellids segregated themselves by microhabitat and displayed responses to the soybean aphid ranging from none, to a very strong numerical and spatial response.

Dedicated to my children

Duncan and Devin

and their eccentric but lovable mother,

Kimberly without whom we would all go insane.

ACKNOWLEGEMENTS

I would like to thank my advisor Dr. Stuart Gage for his generous support and willingness to allow me to wander a corn field for two years. Thanks to Dr. Manuel Colunga-Garcia for your help, input, patience and expertise.

I would also like to thank my committee: Drs. Ayers, Whalon and Safir.

A special thank you goes to Dr. Lawrence Besaw, for introducing me to entomology as a science and shepherding me during my undergraduate work.

Partial support for this work was provided by the NSF LTER grant 612560 and the Michigan Agricultural Experiment Station

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Chapter One Introduction

Perspective

The importance of lowering the negative impact of agriculture on the environment has never been higher. The environmental impacts of fertilizers, herbicides, and insecticides on things such as water quality, have forced agriculture into other means of nutrient and pest management. Genetically engineered crops have shown promise in this arena, but the potential collateral effects (such as the potential lethal effects on non-target organisms, gene flow into surrounding organisms, and negative public perception) have reduced this impact (Scriber 2001, Ferber 1999). The modern paradigm in agriculture has been to treat the field as an entity separate from nature and completely controllable by human inputs. This approach has generated perturbations worldwide in ecosystems. The core of the problem is that the field cannot be separated from the surrounding ecosystem. This realization led to the rise of an ecosystem level approach to agriculture that requires ecologists and growers to know the system they work in, understand the communities and abiotic factors that interact within the system, and manage crop production within the confines of nature.

An ecosystem approach to agriculture has inherent advantages (Ramakrishnan 2000):

- Reducing energy inputs by reducing the application of synthetic fertilizers and pesticides
- Reducing the damage caused by weeds and insects
- Reducing the amount of disturbance to the surrounding ecosystem
- Partially restoring a more natural ecosystem energy flow

There are also inherent disadvantages to this approach. The existing paradigm is firmly entrenched, and changing it is a long and arduous task with extensive research and documentation of the system required to make good management decisions. This research is time consuming, expensive, and can be hard to translate into actions for the grower.

A functional ecosystem management approach to landscape also requires a firm definition of the function desired for any management to be successful in the long term. There are many functions a system can be managed for such as:

- Agricultural production
- Recreation
- Aesthetic value
- Hydrological functions such as water retention, groundwater recharge, and in the case of wetlands, water filtration
- Preservation of genetic information
- Preservation of threatened or endangered species

The key to managing for any of these functions is to balance the uses of the landscape with the potential of future degradation. Sustainable management requires that the nutrient, water, and thermodynamic inputs and outputs be balanced.

To analyze the interactions of the agricultural field, with its surrounding ecosystem, the inputs and outputs both floral and faunal, from the surrounding landscape must be identified and quantified, as well as the outputs from the field to the ecosystem. The communities present, both beneficial and harmful, must be managed for maximum positive impact on the crop and minimum negative impact on the ecosystem. To reduce inputs of pesticides to a minimum, ecological management of landscapes requires the heavy use of biological control agents to regulate pest populations.

The overarching goal of this research is to gain a better understanding of the characteristics of the agroecosystems and the communities present therein to develop a means of assessing the overall health of the system. This allows us to use these assessments of ecological health to manage for diversity, increase the overall ecosystem functionality, and to reduce the chemical inputs into agroecosystems to promote long term sustainability.

The Importance of Ladybeetles

Ladybeetles (Coleoptera, Coccinellidae) are a very important family of insects both in natural systems and in agricultural systems as biological control agents. They have been used extensively world wide to control a variety of soft bodied insects in various fruit and row crop systems. The first documented use of a coccinellid as a biological control agent was the importation of an Australian species into California to control cottony cushion scale in 1888 (Gordon 1985). Coccinellids with the exception of a few phytophagous species, notably the mexican bean beetle, which can be a serious pest (Gordon 1985), and a few fungivores in the genus *Psyloibora*, are voracious predators, most as larvae as well as adults. An adult can eat roughly 400 aphids before laying eggs and a single adult may eat 5000 aphids in its lifetime. The larvae can consume up to 350 aphids before pupating (Lyon 2002). This appetite has led to repeated introductions of coccinellids in North America; these introductions have been beneficial to growers. However, there is increasing concern about the impacts of exotic species on endemic communities (Howarth 1991, Miller and Applet 1993, Thomas and Willis 1998).

There are roughly 5,000 coccinellid species worldwide and about 400 in North America (Gordon 1985). The coccinellid community is a member of a larger aphidophagous guild that includes lacewings, dragonflies, and others. The size and distribution of this community is, of course, dependent on the size and distribution of its prey species. Most coccinellids are generalist aphid predators, capable of feeding on aphids that use a wide variety of host plants. In times of especially limiting resources, they will cannibalize the larvae and adults of their own community, even their own species (Cottrell and Yeargan, 1998). Coccinellids are very mobile and continuously move through habitat in search of prey; up to 50% of the adult coccinellids in a field may move to a new field each day and be replaced by beetles from the surrounding fields (Frazer 1988).

Coccinellids are an excellent group to study because they are easily sampled and most are readily identified in the field. The fact that they are present in most habitats and feed on a large variety of pests makes them a good possible indicator of the health of an ecosystem and the system's trophic structure. They are a diverse group, and the number of species of ladybeetles present in a landscape can, with the proper ecological knowledge, be used as an indicator of the landscape diversity and the level of fragmentation. Knowledge of the structure and functional characteristics of the coccinellid community could be an important component of the ecological knowledge necessary to assess the health of an agroecosystem.

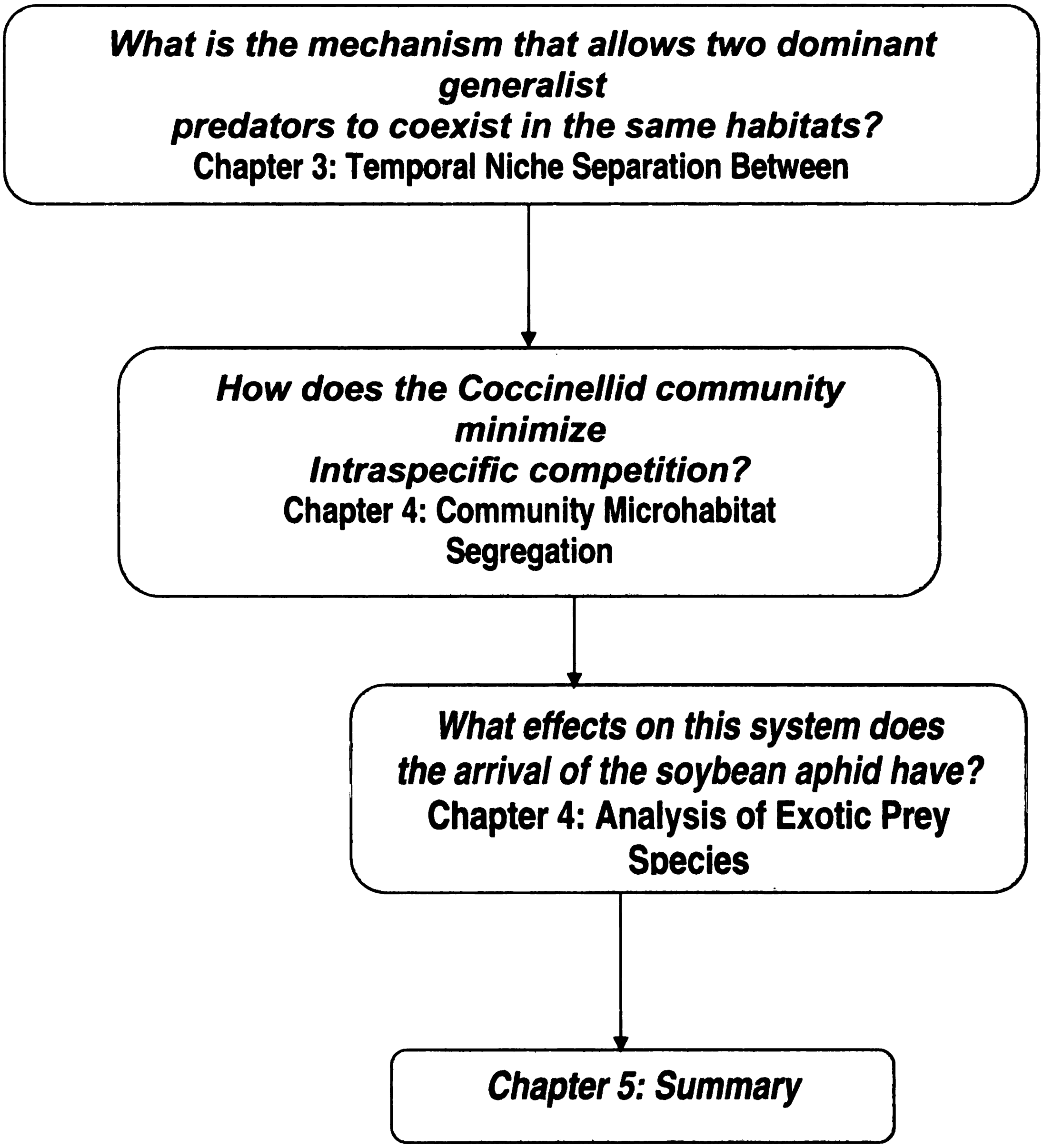
Hypothesis:

Although there is a wealth of knowledge on ladybeetles, the community as a whole has not been studied at a landscape level spatial scale enough to develop reliable indicators of ecosystem function using coccinellid community structure. The recent addition of both an exotic prey species and two exotic Coccinellids further underscores the need for specific knowledge of how this community functions in an agroecosystem. The specific hypotheses tested in this thesis were designed to provide a more complete picture of the ecology of Coccinellids as a group at a large spatial scale. The specific hypotheses were:

- That the separation in the niches of the two exotic coccinellids in this system is temporal.
- The community will avoid direct competition by segregating species according to habitat type and temporal variations.
- The community of coccinellids will respond to the presence of an exotic pest species with changes in their temporal and spatial dynamics.

The direction of the research and the location in this thesis are shown in figure 1.

Research Direction



What is the mechanism that allows two dominant generalist predators to coexist in the same habitats?
Chapter 3: Temporal Niche Separation Between

How does the Coccinellid community minimize Intraspecific competition?
Chapter 4: Community Microhabitat Segregation

What effects on this system does the arrival of the soybean aphid have?
Chapter 4: Analysis of Exotic Prey Species

Chapter 5: Summary

Figure 1. Flowchart representing the direction of research, the questions asked, and the analysis performed. Images in this thesis are presented in color.

Chapter 2: Bionomics of the Species Studied

Coccinella septempunctata

Coccinella septempunctata (L) is a large red ladybird beetle easily recognized by the seven black spots on the elytra. It is a palearctic species that was introduced repeatedly in the United States from 1956 to 1971 (Angelet and Jaques, 1975). The intentional introductions are thought to all have failed to establish a population. In 1973 (Angelet et al) a population was found in New Jersey, this population is thought to by the result of an accidental introduction. The species has since spread and successfully established populations in most of the Eastern United States. The genus Coccinella is primarily aphid predators, feeding on a wide variety of aphids (Gordon 1985). This generalist nature has allowed the rapid spread of *C. septempunctata. Coccinella septempunctata* is commonly found in row crops, old field habitat, and some perennial crops (Maredia et al 1992). The adults overwinter in small groups under the leaf litter and emerge in spring to begin feeding (Gordon, 1985). Mating takes place immediately after emergence, and the eggs are laid in late spring. The larvae are also generalist aphidophagous predators, feeding on the same types of prey as the adults (Gordon, 1985). The population of *C. septempunctata* peaks in mid summer, then slowly declines through late summer and fall (LTER unpublished data).

Figure 2 ***Coccinella septempunctata*** **on a soybean plant, the object on the left is a pupal exuvae. Photo: C. McKeown. Images in this thesis are presented in color.**

Coleomegilla maculata

Coleomegilla maculata Degeer is a medium sized elongate red to yellow ladybird, common throughout the Eastern United States. It is primarily an aphid predator, but up to 50% of its diet can consist of pollen (Gordon, 1985). It overwinters under leaf litter in hedgerows near field edges, generally close to dandelion or other early spring pollen sources (Colunga-Garcia, 1996). It is more common in corn and other row crops than in less disturbed habitat. In Michigan it is the most common coccinellid in corn. Mating occurs in the fall, and the females overwinter mated. In the late spring, after the establishment of prey populations, the eggs are laid in close proximity to aphid colonies (Maredia et al 1992b). This species can have up to five generations per year (Gordon, 1985).

Figure 3 *Coleomegilla maculata* on corn, this specimen has the larvae of a parasitic wasp emerging from its abdomen. Photo: C. McKeown. Images in this thesis are presented in color.

Cycloneda munda

Cycloneda munda Say is a small ladybird with yellow to orange elytra lacking any spots. It is primarily an aphid predator, but it has been known to attack other soft bodied insects (Gordon, 1985). It has been shown to be primarily an arboreal species (Maredia et al, 1992) and is common in woodlot and old field habitat. In late summer it has been shown to move from deciduous habitats to alfalfa and horseweed. It is also found in corn in low numbers (Maredia et al, 1992b).

Harmonia axyridis

Harmonia axyridis Pallas is one of the newest members of the coccinellid community in the United States. As a newer species here, its life history and characteristics in the United States are not familiar. This summary review of *H. axyridis* is longer than the other community members and more thorough to give a larger amount of background information.

Harmonia axyridis is a large red to pale yellow beetle with varying numbers of spots (Lamana and Miller 1995). Eggs are laid midsummer and hatch in three to five days (depending on ambient temperature), and the larvae actively start preying on anything and everything they can catch. The larval stage lasts from 12 to 14 days and pupation from five to six days. The next generation of adults emerges at around 1000 degree-days and feed and mate continuously until just before entering diapause. The females overwinter unmated. Adults have been known to survive for up to three years under optimal conditions (IPM of Alaska, 2003).

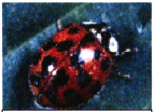


Figure 4 Adult *Harmonia axyridis*. Photo: J.Ogrodnick. Images in this thesis are presented in color.

Figure 5 *Harmonia axyridis* larvae. Photo: M. H. Rhoades Images in this thesis are presented in color.

Harmonia axyridis' establishment in North America was either by intentional introduction or accidentally via commerce (Day et al. 1994). Independent established populations were first documented in 1988 (Chapin and Brou 1991). There is very little documentation of the dispersion and establishment of *H. axyridis* in the United States, so the timeline and rate of spread are not well known. Separate accidental or intentional introductions have established *H. axyridis* in the Pacific Northwest and also in California (Lamana and Miller 1998).

This species has now become a nuisance pest in Michigan due to its drive to aggregate and over winter in buildings. Aggregations of several thousand individuals over wintering in homes and businesses are not uncommon (Tedders, 1994). It feeds on most soft bodied insects including popular aphid, soybean aphid, mealworm, spruce aphid, coccinellid larvae, as well as pollen, nectar, and fruit as alternate energy sources (Lamana and Miller 1998).

Harmonia axyridis has effectively exploited a wider array of habitats than most other coccinellids. When the introductions were being made, it was thought to be a primarily arboreal species (McClure, 1987) but has since proven adept at exploiting various habitats such as:

- Urban and rural development where it can find prey on a large number of horticultural and ornamental plants (Lamana, and Miller 1998).
- Row crop agriculture where it is common in soybean, wheat, alfalfa, and corn (Colunga-Garcia and Gage 1998).

This breadth of suitable habitat shows an expanded ability to find, identify, and successfully capture various prey species (Obata, 1986). This ability includes the ability to determine suitable habitat, find a variety of prey, choose appropriate oviposition sites, and find non-prey food sources when prey is scarce (Obata, 1996).

The overwintering and spring dispersal behavior also gives *H. axyridis* a rapid dispersal mechanism. *Harmonia axyridis,* at around 1400 degree days (personal observations), leaves its summer habitat and flies north. When an individual encounters a substantial vertical surface i.e. a building, bluff, or large tree, then it searches for a crack or crevice and moves insides to overwinter (Nalepa et al, 2000). This is a gregarious phase, and if populations are high, these aggregations can become quite large (Figure 6). The range expansion of *H. axyridis* has been augmented greatly by this tendency. The aggregation can amass in any structure and recreational vehicles, horse and utility trailers, aircraft, and shipping containers (Pecan South, 1993) when moved in the spring the dispersal can be rapid and far-reaching.

Figure 6 Aggregation of *Harmonia axyridis*. Photo: R. Mizell. Images in this thesis are presented in color.

Aphis glycines

Aphis glycines Matsumura is a recent arrival in the United States. It is a small yellow to green aphid with dark cornicles. It was first detected in the Midwest in 2000 and has since been documented from Minnesota to New York. In the summer it feeds primarily on soybean where it could become a major pest . The life cycle of the soybean aphid is complex as is typical for most aphids, according to Takahashi et al (1993). It overwinters on buckthorn, a native weed commonly found in hedgerows, and along the edges of woodlots. In midsummer it moves into soybean and feeds on phloem. Only female that reproduce parthnogenically are present in the summer, primarily in the wingless form. The females reproduce rapidly and mature quickly (seven days), allowing for up to 15 generations annually in soybean. A population doubling can occur in as little as three days on quality soybean. If crowding is detected or the quality of the soybean declined, winged adults appear and reproduce, transferring live nymphs to new sites. In the fall in the soybean dry down phase, winged males and females are produced, and they actively seek out buckthorn to mate and overwinter on. They typically go through three or four generations on buckthorn before moving into soybean in the spring (Ostlie, 2002)

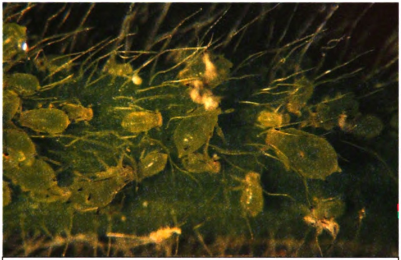


Figure 7 *Aphis glycines* feeding on soybean. Photo: Peter Desborough. Images in this thesis are presented in color.

It has been demonstrated that *A. glycines* is capable of transmitting the soybean mosaic virus, and it is thought that it can transmit other soybean pathogens although no significant crop damage has yet been recorded. The potential economic impact of this species has been estimated at an annual loss of 435 million bushels or $2.2 billion in the North Central Region alone (Ostile, 2002).

Chapter Three: Spatial analysis of landscape dominance by two exotic coccinellids, *Harmonia axyridis* and *Coccinella septempunctata*

Introduction

The role of interspecific competition in ecology has been the subject of a long and continuing debate. Hypotheses on the subject range from placing it as the primary driver of community ecology to disregarding it as a force almost entirely (Connell, 1980). Competition, as defined by Ricklefs (1997), is "any use or defense of a resource by one individual or population that reduces the availability of that resource to other individuals or populations." The resource can be a food source, habitat, mate, or anything else that an individual needs to complete its life cycle and successfully reproduce. Schroener (1997) classified the mechanisms of competition into these categories:

- Consumptive competition, based on the use of some renewable resource
- Preemptive competition, based on the occupation of open space
- Overgrowth competition, which occurs when one individual grows upon or over another, thereby depriving the second of some resource
- Chemical competition, by production of a toxin that acts at a distance after diffusing through the environment
- Territorial competition (defense of space)
- Encounter competition, which involves transient interaction over a resource that may result in physical harm, loss of time or energy, or theft of food

Charles Darwin thought that competition should be most intense among closely related species. "As species of the same genus have usually, though by no means invariably, some similarity in habits and constitution, and always in structure, the struggle will generally be more severe between species of the same genus, when they come into competition with each other, than between species of distinct genera" (Darwin, 1926). As biological control efforts and accidental introductions establish species in new places, the potential for competitive exclusion of native species and conflict between different introduced species increases.

Coccinellid beetles have been introduced repeatedly in the United States as biological control agents. As adults and larvae, they are voracious predators of soft bodied organisms such as mealy worms, aphids, and mites. While these predators are beneficial biological control agents in forest and agricultural settings, there is a growing body of evidence indicating negative impact on native species (Howarth 1991, Miller and Applet 1993, Thomas and Willis 1998). The evidence indicates that some imported predators are driving native species to local extinction due to competitive exclusion (Wheeler and Hobecke 1995, Elliot et al. 1996, Colunga-Garcia and Gage 1998).

Two introduced species *Coccinella septempunctata* (L.) and *Harmonia axyridis* Pallas) are commonly found together in the same habitats (Colunga-Garcia and Gage 1998). As generalist predators with a wide habitat range and a high degree of behavioral plasticity, the two species share many biological traits. Both species were introduced repeatedly into the United States as biological control agents, *C. septempunctata* in the 1970's (Gordon 1985) and *H. axyridis* in the 1980's (Day et al 1994). While these two species are effective biological control agents, their effects on endemic aphidophagous predator populations is unclear.

Once *H. axyridis* was established in the United States it became the dominant coccinellid in the north central region (Upper Great Lakes). Within two years of its detection at the Kellogg Biological Station (KBS) in Hickory Corners Michigan in July of 1994, it quickly became the most abundant coccinellid in the Long Term Ecological Research Site (LTER) (Colunga-Garcia and Gage 1998). Initially thought to be primarily an arboreal species, *H. axyridis* quickly spread to all of the LTER agricultural and old field habitats, exhibiting either a generalist nature or high behavioral plasticity and adaptability (Colunga-Garcia and Gage 1998).

Having arrived more than 30 years ago *C. septempunctata* was well established in the United States before the arrival of *H. axyridis*. Native to Western Europe it was repeatedly introduced as a bio-control agent in North America beginning in the 1970's (Gordon 1985). It has proven able to adapt to and exploit a number of habitats and is quite successful in agricultural systems (Maredia et al 1992, Colunga-Garcia and Gage 1998).

C. septempunctata and *H. axyridis* are aphidophagous predators and both are now common throughout Eastern North America. They are found in the same habitats and feed on the same prey. This niche overlap would seem to result in direct competition between the adults of the two species. Examining the population trends of *C. septempunctata* before and after the arrival of *H.* axyridis revealed neither significant downward population trend nor a shift to marginal habitat or prey (Colunga-Garcia and Gage 1998). The hypothesis of this study was that the lack of observable competition between the adults of these two species was the result of a temporal separation between their niches.

Materials and Methods:

The arrival of *H. axyridis* had little impact on the numbers of *C. septempunctata* present in the LTER (Colunga-Garcia and Gage 1998). The KBS LTER was designed to represent the common landscapes in the North Central Region of The United States. One of the principal components of the LTER research is the long term dispersal and composition of beneficial arthropod predators. The data gathered at the KBS LTER spans 13 years in the same experimental plots. Using this large contiguous dataset allows analysis of patterns of species composition, dispersal, and the specifics of niche separation of these two exotic species.

Study Site:

The site of this study was the Long Term Ecological Research Station (LTER) at Kellogg Biological Station (KBS) in Hickory Corners, Michigan. Southwest Michigan is characterized by a diverse mix of habitat including agricultural, pasture, oldfield, orchard, and woodland landscapes (Burbank et al 1992). Established in 1980 by the National Science Foundation, the KBS LTER was designed to monitor the long term effects of various cropping practices on the environment. One of the primary components of this research has been the long term monitoring of arthropod predators. The resultant data from this monitoring was used for part of this

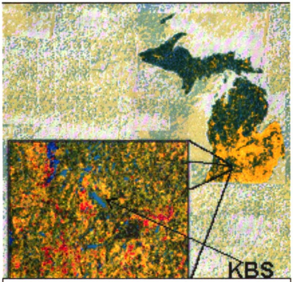


Figure 8. Locator map for the Kellogg Biological Station. Images in this thesis are presented in color.

research and analysis. The coccinellid community structure including an exotic established prior to monitoring is well documented. The dataset covers 13 years both before and after the arrival a second exotic coccinellid, *Harmonia axyridis* and an exotic pest, *Aphis glycines* in Southwest Michigan. This has allowed monitoring of the invasion and establishment of two exotic species and their interactions with a previously established exotic as well as the endemic coccinellids. The main site treatments on the LTER were planted in wheat and soybean during the years analyzed.

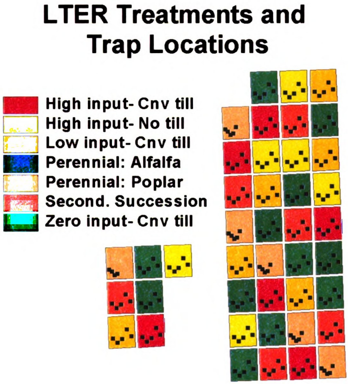


Figure 9. Treatments and Plot Layout at the Kellogg Biological Station's Long Term Ecological Research Site. Images in this thesis are presented in color.

The KBS LTER consists of six repetitions of seven agricultural treatments (Figure 9), including four tilled treatments, sucessional treatments, and two perennial (alfalfa and poplar) treatments. The tilled treatments are subject to an annual rotation of corn, soybean, and wheat. The LTER plots are approximately one hectare each. The plots contain five geo-positioned sampling stations where coccinellid adults were sampled using double-sided, yellow cardboard sticky traps (22.5 x 14.0 cm) attached 1.2 m above the ground to a metal stand as described by Maredia et al. (1992a).

These locations have been sampled weekly from May to August every year since 1987. Coccinellid adults caught on traps were identified, counted, recorded, and removed every week. The sticky cardboards were replaced every second week.

Weekly weather data collected by a permanent weather station on the LTER site was used to determine the degree day progression for each growing season. A 50° (F) base temperature was used to transform the data set from weekly data to degree day intervals. This transformation is necessary to allow direct comparison of data across years at the same points in coccinellid and crop development. The intervals analyzed spatially were 400, 800, and 1200 degree days. These intervals represent early, mid, and late growing season times in Michigan. The interval population numbers represent the average trap catch per location in the field.

The data for each species was then mapped using Arc GIS 3.2. Each trap average was interpolated onto the 12 nearest raster cells using the inverse distance weighted method resulting in raster layers with one square meter resolution. The maps were superimposed on a high resolution aerial black and white photograph to illustrate the surrounding habitat. Each cell in the maps of *C. septempunctata* was then subtracted from each cell of *H. axyridis* resulting in a one meter resolution raster map (18897 cells total) of relative species abundance in the LTER landscape. Positive numbers indicate a preponderance of *H. axyridis* negative *C. septempunctata*. In 1994 and 1997 soybean was planted in the four LTER row crop treatments, and in 1995 and 1998 wheat was the main site cultivar. Corn was planted on 1996 and 1999, and these years were not analyzed due to the very low abundance of *C. septempunctata* in corn as it overwhelmingly prefers soybean or wheat (Maredia et al 1992b). *Harmonia axyridis* is found in corn but not at nearly the numbers in soybean or wheat. The Raster maps were then analyzed using Arc View 3.1's map query functions to assess the total area covered by each species at the three intervals, percent neutral coverage was also calculated.

The relative dominance (*d*) of the species over the rest of the coccinellid community was estimated via the Berger-Parker equation $d = N_{\max} / N_{tot}$ where $N_{\max}$ is the number of insects of the species being examined, and N_{tot} is the number of all insects of all species measured in the sample (Magurran 1988). The entire dataset of 14 coccinellids was used to establish N_{tot}, so the dominance indexes generated are not simply *H. axyridis* vs. *C. septempunctata,* but vs. the entire coccinellid community present in the LTER. This index produces a measure of proportional abundance while having low sensitivity to sample size and it is independent of the number of species (Southwood 1978). Differential attraction between the species to the traps was the largest possible source of error, the attraction and color response was tested during the preliminary LTER design (LTER unpublished data). The relative dominance of *C. septempunctata* and *H. axyridis* was calculated in 100 degree day intervals ending at 1200 degree days. The exception being 1995 where monitoring was stopped at 1100 degree days because the traps had to be removed early due to logistical considerations.

The dataset was tested to see if it met the ANOVA assumptions and then the populations of the two species were then regressed using the model; $y=mx+b$, $y=$ *H. axyridis* population mean, m = slope or the best fit line, x = *C. septempunctata* population mean and b = the x intercept. Least squares linear regression was the best fit, with alpha = .05.

Results:

Comparison of 1994 and 1997 (soybean years):

The actual percent of the LTER area dominated by either species as well as the area that neither had preponderance is shown in table 1. In 1994 before the arrival of *H. axyridis*, *C. septempunctata* coverage peaked mid season and declined later. The same pattern holds true for 1997, the other year where soybean was the main LTER cultivar. The establishment of *H. axyridis* in late 1994 represented a small area of the total area (1.7%). In stark contrast, by the next soybean year in 1997 the proportion of the landscape dominated in the late season by *H. axyridis* had grown to 72%, a 42 fold increase in the same crop in 2 years. Even with this substantial increase in *H. axyridis*, *C. septempunctata* maintained its dominance of the landscape in the midseason dominating 62% of the landscape at the 800 dd interval in 1997.

Year Degree Day interval	*Cells* H. axyridis	*Percent* H. axyridis *Coverage*	*Cells* C. septempunctata	*Percent* C. septempunctata *Coverage*	*Neutral Cells*	*Percent Neutral Cells*
1994						
400	0	0	10742	57	8255	**44**
800	0	0	18505	98	492	**2.6**
1200	322	1.7	12831	68	5844	**31**
1995						
400	1227	6.5	6658	35	11012	**58**
800	100	0.5	16972	89	1925	**10**
1200	11023	58	387	2.0	7407	**39**
1997						
400	11666	61	2669	14	4562	**24**
800	2166	11	11850	62	4981	**26**
1200	13716	72	347	1.8	4934	**26**
1998						
400	2408	13	15286	80	1303	**6.9**
800	1661	8.8	16795	89	541	**2.9**
1200	**18575**	**98**	**51**	**0.27**	**371**	**1.96**

Table 1. The results of the interpolation of the trap data. Each Cell represents 1 square meter with 18897 cells total.

Comparison of 1995 and 1998 (wheat years):

In wheat the early season was dominated by *C. septempunctata* with 35% coverage in 1995 and 80 % in 1998. The midseason was also clearly dominated by *C. septempunctata* with 89 % coverage in both years. However, the late season was characterized by a resurgence of *H. axyridis* in both years with 58% in 1995 and 98% in 1998. In 1995 *H. axyridis* increased its coverage from 0.5 % at 800 degree days to 58% 40 degree days later. The same pattern is present in 1998 where it increased from 8.8% to 98 % habitat coverage over the same interval. The landscape in 1995 was also characterized by comparatively low numbers of both coccinellids and a larger proportion of neutral area across all three time intervals.

The relative dominance index shows clearly that the two species discussed here clearly dominate the system. Of the fourteen species of coccinellid only *Coleomegilla maculata* approached the population of *H. axyridis* and *C. septempunctata.* The spatial representation of species flux, figures 12 and 13, clearly shows that *H. axyridis*, once established in the LTER, is more abundant than *C. septempunctata* in the late season (1200 degree days). *C. septempunctata* is clearly more prevalent mid season (800 degree days). There is no clear pattern of early season (400 degree days) dominance. The pattern of relative

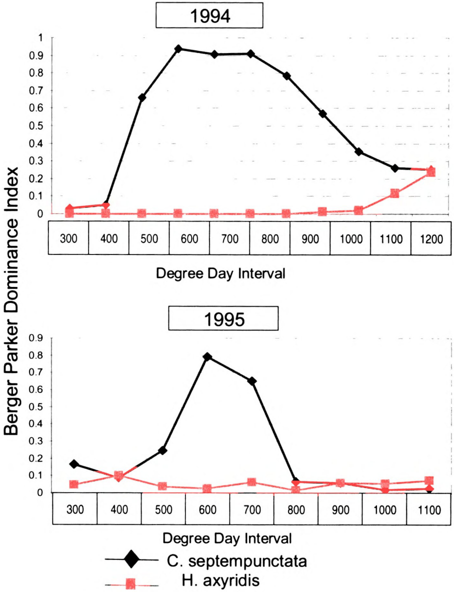


Figure 10. The Berger Parker Dominance Index at 100 degree day intervals for 1994 and 1995. *H. axyridis* makes its first appearance in 1994 in the late season and a year later begins to dominate *C. septempunctata* at the 900 degree day interval. Images in this thesis are presented in color.

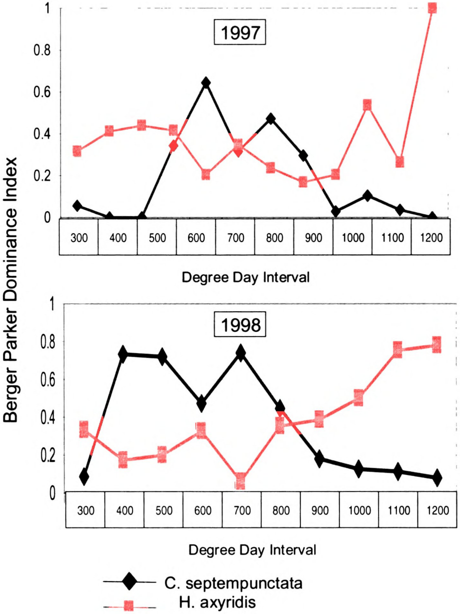


Figure 11. The Berger Parker Dominance Index at 100 degree day intervals for 1997 and 1998. *C. septempunctata* show slight dominance in the early season both years but the crossover to *H axyridis* dominance between 800 and 900 degree days is consistent. Images in this thesis are presented in color.

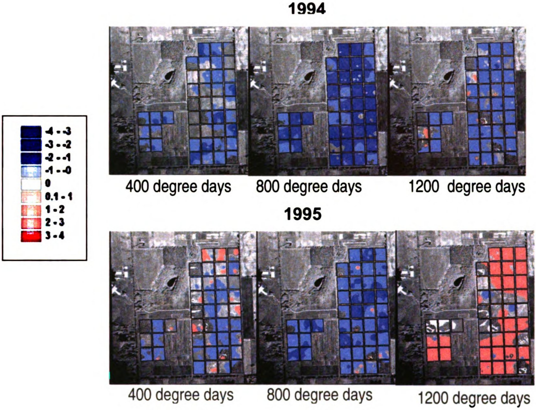


Figure 12. Results of the inverse distance weighted interpolations of the trap averages in 400 degree day intervals for 1994 and 1995. The maps show *C. septempunctata* dominance in blue, and *H. axyridis* dominance in red according t the legend above. Areas where neither species is dominant are transparent revealing the background photograph. The spatial resolution of the interpolations is 1 square meter. Images in this thesis are presented in color.

dominance is consistent and repeats annually, with *C. septempunctata* dominating the mid season of each year and *H. axyridis* dominating the late season. Also apparent is the speed with which *H. axyridis* came to dominate the landscape after its first appearance in late 1994 (table1). The regression analysis of the two populations shows that very little of the variation in the population level of either species is due to the population level of the other, R^2=0.0009 alpha = .05. Also a small amount of habitat preference separates the two species. *H. axyridis* was common in the poplar treatments while *C. septempunctata*

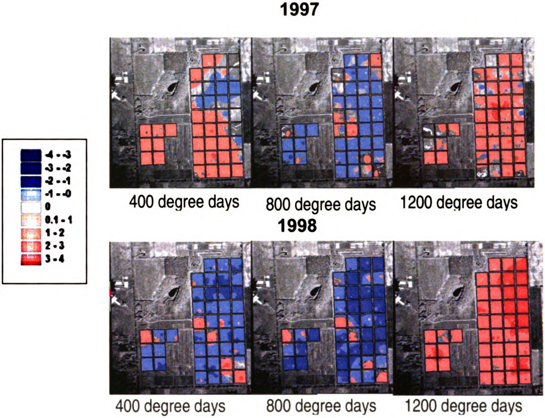


Figure 13. Results of the inverse distance weighted interpolations of the trap averages in 400 degree day intervals for 1997 and 1998. The maps show *C. septempunctata* dominance in blue, and *H. axyridis* dominance in red according t the legend above. Areas where neither species is dominant are transparent revealing the background photograph. The spatial resolution of the interpolations is 1 square meter. Images in this thesis are presented in color.

was uncommon. *Coccinella septempunctata* shows clear preference for the sucessional and agricultural treatments over the poplar habitats. The pattern of community dominance repeats and is consistent for the mid and late seasons regardless of the total abundance of the two species.

There is some spatial segregation based on the LTER treatment regime, the notable exception being the lack of *C. septempunctata* in the poplar treatments that *H. axyridis* uses.

Discussion:

The abundance and dispersion patterns of *C. septempunctata* did not change due to the arrival of *H.* axyridis in 1994 (Colunga and Gage 1998). This indicates that the long term fluctuations in the *C. septempunctata* population are due to some other factor. The long term population trend of *C. septempunctata* appears to exhibit a five to six year population cycle independent of the rest of the coccinellid community (LTER unpublished data). The pattern of mid season dominance followed by a late season decline in numbers as well as a contraction in dispersal repeated in the presence of *H. axyridis*.

The 400 degree day interval shows no clear pattern of dominance by either species. This could be the result of the LTER treatment. In wheat years *C. septempunctata* covered most of the habitat, while the early season soybean seemed to favor *H. axyridis*, but only one soybean year was available for analysis after *H. axyridis'* establishment. To determine if early season dominance is correlated with the LTER cultivar more soybean data needs to be analyzed.

Other interactions between the two species allow some additional interpretation. The point where the two dominance indexes crossed in 1995, 1997, and 1998 is remarkably consistent. Over the three years, it occurred within a 100 dd window, indicating that the population cycles of both species may be highly regulated. This regulation could be genetic, behavioral, related to generation times, or due to some other unknown environmental factor. The level of stochasticity in the dominance indexes in 1997 and 1998 indicate that the temporal segregation between the two species may be declining due to *H. axyridis* having become established. The rest of the system may be adjusting to its presence, lowering its dominance. This is also evidenced by the reduction in its total numbers, and the comparatively high proportion of neutral space.

The arrival of the soybean aphid (*Aphis glycines*) in 2000 further illustrates the importance of the temporal characteristics of these species. The soybean aphid arrived in 2000, and since its arrival, it has been a late season pest of soybean. The LTER has been colonized later than most areas of the state, and it is possible that the high populations of *C. septempunctata* aid in the delay of colonization. The spread of soybean aphid later in the season is hindered further by the then high prevalence of *H. axyridis*. The overall effect is fairly contiguous pest suppression mid season through harvest.

Without this temporal separation in niches the generalist behavior, lack of prey specificity, and common habitat would bring these two species into direct competition with each other, limiting one or both species' ability to thrive. The principle of competitive exclusion requires that two species vying for the same resource must compete, and one of those species must eventually push the other out of the niche. This push can be to less suitable prey to local extinction or into marginal habitat. This has been shown to happen with *H. axyridis*, forcing it to rely on cannibalism (Snyder et al 2000) or phytophagous resources (Slogget and Majerus 2000), but neither phenomenon has been in evidence in relation to competition with *C. septempunctata* in the LTER There is preliminary evidence that suggests that in times of limited prey availability in the row crop treatments, the two species move into separate alternative habitats: *H. axyridis* into the *Populus sp.* and arboreal treatments, and *C. septempunctata* into old field and early sucessional habitats. These observations, if shown to be significant by future analysis would further reduce the potential for competition between the species by spatial separation.

These two species as fairly new arrivals to North America have been able to establish populations and disperse widely; both have been successful invaders. The arrival of *H. axyridis* years after *C. septempunctata* seemed to set the stage for a competitive interaction and the eventual establishment of one species as the dominant member of the community; however, the segregation temporally between the two has allowed both to thrive. This phenomenon can be an effective pest management paradigm allowing consistent control of aphid pests throughout the latter two thirds of the Midwestern growing season. This control comes at a price; however, the rise in exotic species may have come at the expense of less competitive native species such as *Adalia bipunctata* L. which has not been observed in the LTER for several years (LTER unpublished data). The decline of native species is a plausible result of the arrival and establishment of exotics of the same guild and habitat preference. The costs to the environment of establishing exotics, even those considered beneficial, should be carefully weighed against their future benefits as biological control agents.

Chapter Four: The Microhabitat Preference and Response of the Dominant Members of the Coccinellid Complex to an Exotic Pest

Introduction:

The competitive exclusion principle states that two or more species can not coexist indefinitely on the same resource. Classic experiments on competition, such as those by G.F. Gause in the 1920's, have shown that one species can have a detrimental effect on another (Gause 1934), but this impact in a natural setting is much harder to quantify due to the spatial, temporal, and behavioral dynamics of the species niches. The niche of a species is defined by Ricklefs (1997) as "the ecological role a species plays in the community, and niche overlap is the sharing of niche space by two or more species; similarity of resource requirements, and tolerance of ecological conditions." To avoid the competitive exclusion principle's consequences, the niches of the species present in a community must not overlap completely. The separation in niches can be temporal, spatial, behavioral, or some other factor, but it must be sufficient to allow both species to coexist indefinitely. These separations in the niches can be hard to identify, much less quantify in a community, so the apparent absence of competition can be confounding.

The niches present in a community are also subject to outside influences such as invasive species. The introduction and establishment of an invasive exotic either via accidental or intentional introduction, represents a permanent alteration of the system. There are numerous examples of harmful introductions of plants, animals, and pathogens and their costly and damaging effects on native communities (Ruesink et al 1995). The entrance of an exotic into a niche previously filled by a native species, can drive the native out due to the inherent advantages of being non-native. Exotic species are generally free of their traditional predators and parasitoids, as well as their pathogens. Invaders generally are habitat and prey generalists, reproduce quickly, and have a means of rapid dispersal (Ricklefs 1997). The landscape level impacts of invasive species resemble the recolonization of islands in Wilson's classic experiments on island biogeography (Wilson and Macarthur 1967). As a new species moves in, it experiences a surge in numbers due to the advantages previously stated. As it establishes itself, if the niche it moves into is filled, the older resident is forced out either into marginal conditions or into local extinction. Later, after the invader has become firmly established, its advantage starts to wane. This could be due to the arrival of predators and pathogens or due to the adaptation of the ecosystem to its presence (Ricklefs 1997).

The continuing concern about the impacts of pesticide use and genetically modified crops is keeping the seemingly benign practice of classical biological control at the forefront of agricultural pest control. This practice seeks to control pest outbreaks by the introduction or augmentation of predators. These predators are sometimes native, but often the pest is an accidentally introduced exotic, so a predator from the same geographic area as the pest is imported. This brings two exotics into the same system and conflict with the endemic species in that system is often the result. Some of the earliest and most successful biological control agents imported into the Unites States were coccinellids (ladybeetles). They have been introduced numerous times throughout the country to control pests in crops ranging from citrus to forests to row crop agriculture (Gordon 1985).

Coccinellids are voracious predators of certain agricultural pests, especially aphids. In agricultural settings the coccinellid predator community provides protection on a variety of crops (Gordon 1985). This has led to their widespread use in biological control applications. Species have been moved from place to place to control outbreaks of endemic and exotic pests. The repeated introduction of exotic coccinellids (*Harmonia axyridis* Pallas and *Coccinella septempunctata* (L.)) in biological control has led to their establishment throughout the United States. *Coccinella septempunctata* was introduced after the 1950s and has become established in the northeastern United States (Schaefer et al. 1987). The introduction of *H. axyridis* into the United States was either intentional or accidentally via commerce (Day et al. 1994). Independent populations were first documented in 1988 (Chapin and Brou 1991), since it has expanded its North American range to become the most common ladybeetle in most of the United States. While these species represent a good weapon against soft bodied insect pests like aphids and mealy worms there is also evidence that they are having deleterious impacts on endemic populations of ladybeetles (Wheeler and Hoebeke 1995, Elliot et al. 1996, Colunga-Garcia et al. 1998). These introductions and the subsequent establishment in Southern Michigan have fundamentally altered the arthropod community ecology in the region. The effects on native coccinellid community structure are largely unknown due to a lack of knowledge about the community before the introduction of the exotics.

A diverse mix of urban, old field, riparian, wetland, and agricultural habitats characterizes the Southern Michigan landscape. This habitat diversity is reflected in the diversity of the arthropod communities. The high landscape diversity also provides abundant resources for generalist predators. *Harmonia axyridis* is adapted to arboreal habitats, but as a generalist it is able to exploit resources in old field and agricultural habitats as well. This flexibility allowed *H. axyridis* to become the dominant coccinellid in Michigan within five years of its first detection (Colunga-Garcia and Gage 1997). *Coccinella septempunctata* is prevalent primarily wheat, alfalfa, soybean, and old field habitats (Honek 1985, Ostrom et al. 1997) and was the dominant coccinellid before the arrival of *H. axyridis.* Even after the arrival of *H. axyridis, C. septempunctata* is still the second most common coccinellid in Southern Michigan.

The first populations of the soybean aphid (*Aphis glycines* Matsumura) in the north central region were documented in the late summer of 2000. A broad range was already established, as soybean aphids were documented in Illinois, Indiana, Iowa, Kentucky, Michigan, Minnesota, Missouri, Ohio, West Virginia, and Wisconsin. The heaviest infestations were in Michigan, southern Wisconsin, southeastern Minnesota, northern Illinois, and northern Indiana (DiFonzo and Hines, 2001). China and Eastern Asia are its traditional home range, and it is documented in the Philippines as well as Australia.

The establishment of a new pest on a vital cash crop is a cause for concern. Like all aphids, *Aphis glycines* is a vascular feeder, piercing the outer leaf surface to extract liquid form the vascular tissues of the soybean plant. Soybean is generally seen as a crop tolerant to insect damage. However, *Aphis glycines* populations are capable of extremely rapid reproduction and hundreds of individuals per leaf have been observed. These population levels especially when coupled with dry weather can cause significant yield loss (Ostile 2002). The soybean aphid is also capable of transmitting plant pathogens such as soybean mosaic virus, although the extent of transmission in the United States is unknown (Ostile 2002).

Understanding the impact of pest control introductions on endemic communities is essential to making good long-term management decisions, however, without a thorough understanding of the structure of the current community future impacts on biodiversity, ecosystem function, and competitive displacement of endemic species cannot be evaluated. For future decisions affecting coccinellid introductions a detailed examination of the coccinellid communities ecology including, niche overlap, competitive interactions, and preferred prey has to be done. Of the fourteen coccinellid species present in the LTER the dominant four were *Harmonia axyridis, Coccinella septempunctata, Coleomegilla maculata* (Degeer), and *Cycloneda munda* Say.

We hypothesized that the four dominant coccinellids would show segregation based on habitat type, and that the community would respond to the presence of soybean aphid by changing its dispersion patterns.

Materials and Methods

To begin drawing a detailed picture of coccinellid community structure and function, a monitoring system was designed to assess landscape level microhabitat preference among the four most prevalent coccinellids in Michigan, using the Kellogg Biological Station (KBS) Long Tern Ecological Research Site (LTER). The objective of this project is to describe the structure and function of the coccinellid community in an agricultural landscape. KBS in Southwestern Michigan is representative of the habitat types and cropping systems common to the region. In 1988 The National Science Foundation established a LTER there with the purpose of assessing the impacts of agriculture on biodiversity, community ecology, and ecosystem function. The site for this study is located in ancillary plots adjacent to the LTER main site. The habitat is highly fragmented, with row crops, perennial alfalfa populous, hardwood, and conifer plots. The landscape diversity is high, and this leads to a high degree of arthropod predator diversity. The LTER has been monitoring the coccinellid community for 13 years, assessing the impact of different land use regimes on the efficacy of endemic biological control.

During the 2001 and 2002 growing seasons, coccinellid adults were sampled using double-sided, yellow Pherocon AM™ un-baited cardboard sticky traps (22.5 x 14.0 cm). The traps were attached at plant canopy height, one meter, three meters, and five meters above the soil surface to either "t" posts as described by Maredia et al. (1992a), or affixed to fiberglass rods that were in turn attached to six foot steel fence posts. The sampling stations were arrayed at the edge of the field then 45 m in six were placed at intervals of 20m. The placement of the rows of monitoring stations was staggered to leave a trap free space in the center of each plot to avoid "trapping out" the fields. The second row of monitoring stations was placed 15m south of the first then a gap of 30m was left before the next row (See photo with trap locations at the top of Figures 14-19). This sampling regime provided a staggered grid where each row of sampling stations serves as a sub sample of the plot it is located in, providing for two equal sub samples nested within two replicates of the plots. Three hundred and fourteen traps in all were placed in rows across the plots. The plots are all approximately 1.15 hectares each for a total sampled area of 4.6 hectares. The plots were prepared as shown in Tables two and three. The crops were rotated for 2002 keeping with standard agricultural practice.

Date:	Action:	Plot:
4-28-2001	Disced with eight inch disc	Corn one and two soybean one and two
4-29-2001	Soil finished	Corn one and two soybean one and two
5-3-2001	Planted Pioneer™ 92B62 soybean at 150,000 seeds/ acre in 30" rows (roundup ready)	Soybean one and two
5-4-2001	Planted Pioneer™ 3730 corn at 26,000 seeds/acre 30"rows while applying 10 gallons/acre 28% nitrogen	Corn one and two
5-9-2001	Broadcast sprayed with Broadsroke+dual+atrizine™	Corn one and two
6-20-2001	Broadcast sprayed with Roundup Ultra™ and ammonium sulfate	Soybean one and two
6-21-2001	Sidedressed with 110lbs/acre of 28% nitrogen	Corn one
6-26-2001	Sidedressed with 110lbs/acre of 28% nitrogen	Corn two

Table 2 Preparation and planting regimens for the study plots in 2001.

The traps were replaced every second week. Coccinellid adults were identified, counted, recorded, and removed every week. Over 10,000 individual specimens are represented in this analysis.

Date:	Action Taken:	Treatment:
5-20 -2002	Soil finished	all four plots
5-21-2002	Planted to pioneer 37m34 corn at 28,000 seeds per acre	Corn one and two
5-24-2002	Broadcast sprayed plots 27-A and 27-C with 6 ounces per acre callisto, 1 quart per acre atrazine and 1 quart per acre dual	Corn one and two
	Planted pioneer 92b38 soybeans at 180,000 seeds per acre	Soybean one and two
6-27-2002	Sidedressed plots 27-A and 27-C with 125lbs of nitrogen or 42 gallons per acre of 28%	Corn one and two
	Broadcast sprayed with roundup ultra at 1 quart per acre	Soybean one and two

Table 3 Plot preparation and planting regimes in 2002

The habitat was blocked into three types, corn, soybean, and edge. Each block contained 20 sampling stations. The edge habitat consisted of 2 m transects along the corn soybean boundary. The edge areas were not prepped as the cropping systems were, merely left alone. This produced a weedy strip between the crops and around the edges of the entire plot. The plant community present in the edge areas consisted of a typical early sucessional community with species like pigweed, lambsquarter, dandelion, thistle and grasses. The diversity of the edge plots was as expected much higher than the crop treatments according to Simpson indexes ($D = 1/\sum Pi^2$) of the three treatments (Ricklefs 1997). Measured diversity was edge = 5.2, corn = 1.4, soybean = 1.1.

The location of the sampling stations was determined with a global positioning system then mapped in Arc GIS. The weekly trap catches were mapped by species and also plotted according to habitat. The three and five meter level traps are not included in this analysis to separate longer range movement from short term foraging flights. Coccinellids tend to fly higher when dispersing farther and low or at plant canopy height when actively searching for prey. The soybean aphid was sampled by counting the number of aphids on five soybean leaves within 2 m of each sampling station. The aphid count was then indexed in the following scale: 0=0, 1=1-10, 2=11-20, 3=21-30, 4=31-40, 4-41 and over.

The data was analyzed with SAS© to test whether the data met the assumptions of ANOVA analysis then with a one way analysis of variance to show the effect of the soybean aphid. Then a series of orthogonal contrasts to show the effect of increasing aphid populations and habitat preferences was done. The statistical model for the contrasts is $y_{ij} = \mu + \alpha_1 A_{1i} + \alpha_2 A_{2i} + \alpha_3 A_{3i} + \alpha_4 A_{4i} + \alpha_5 A_{5i} + e_{ij}$, where y_{ij} = predicted predator density, μ = the overall species mean, $\alpha_1 A_{1i} + \alpha_2 A_{2i} + \alpha_3 A_{3i} + \alpha_4 A_{4i} + \alpha_5 A_{5i}$ = the aphid scale values with their alpha values and, e_{ij} = the residual. All α values = .05. This model was used because it is ideal for examining repeated (in this case weekly) measurements for treatment effect (Kuehl 2000). The model also partitions the treatment sum of squares in ANOVA to minimize the effect due to the replicates. The results of the orthogonal contrasts, where significant, were then used to establish predictive linear models with the equation; $y=mx+b$, $y=$ predator population mean, m = slope or the best fit line, x = the aphid density and b = the x intercept. Least squares linear regression was the best fit, with alpha = .05.

The preference of the species for a habitat was statistically tested using the following linear orthogonal polynomial contrast model, $y_{ij} = \mu + \alpha_1 H_{1i} + \alpha_2 H_{2i} + \alpha_3 H_{3i} + e_{ij}$, where y_{ij} = predicted predator density, μ = the species mean, $\alpha_1 H_{1i} + \alpha_2 H_{2i} + \alpha_3 H_{3i}$ = the three habitat types and their alpha values and, e_{ij} = the residual. This model was used for the reasons stated above.

The aphid index was then interpolated using inverse distance weighting in ARC GIS 8.1™ and displayed on the maps as contour lines. The coccinellid dispersions were mapped with the same methodology and were displayed with color ramps to show intensity. The legend is classified by standard deviation from the mean, with the darker colors representing higher population densities. The resultant maps were then overlaid onto a high resolution aerial photograph of the study site to give a perspective on the surrounding habitat.

Results

Habitat Segregation

Each of the four dominant species was found in significant numbers in all microhabitats. However, all four species showed a marked preference for a particular

Year	**Species**	**Alpha**	**Pr>F**	R^2
2001	*Coccinella septempunctata*	.05	0001	.307
2001	*Coleomegilla maculata*	.05	.059	.104
2001	*Harmonia axyridis*	.05	.0042	.193
2001	*Cycloneda munda*	.05	.0105	.164
2002	*Coccinella septempunctata*	.05	<.0001	.112
2002	*Coleomegilla maculata*	.05	<.0001	.140
2002	*Harmonia axyridis*	.05	<.0001	.134
2002	*Cycloneda munda*	.05	.1336	.017

Table 4. 2001 ANOVA results and correlation coefficients for the response of the coccinellids to the habitat type index for 2001 and 2002. If the Pr>F is less than .05 the species showed a significant response to habitat. The correlation coefficient (R^2 **) indicates the strength of this response.**

habitat (Figures 14-17). The ANOVA (alpha = .05) analysis shows a significant treatment effect for all three microhabitats as well as all four coccinellids (Table 4). The more specific among the insects (*Coccinella septempunctata*) showed the highest R^2 value, while the more generalist ones had lower corollary values.

The orthogonal polynomial contrasts also showed significant differences in microhabitat for each species (Tables 5 and 6). *Coccinella septempunctata* showed significance when contrasting corn and soybean as well as soybean vs. edge, but not in corn vs. edge. *C. maculata* showed significance when contrasting corn vs. soybean but not corn vs. edge or soybean vs. edge. *H. axyridis* showed significant differences when contrasting corn vs. soybean and soybean vs. edge.

Contrast	*C. septempunctata*	*C. maculata*	*H. axyridis*	*C. munda*
Corn vs. Soybean	X	X	X	
Corn vs. Edge		X		X
Soybean vs. Edge	X		X	X

Table 5. 2001 Linear orthogonal contrasts between treatments for each species in 2001. Contrasts marked with an X are statistically significant using linear orthogonal contrasts. Significant contrasts show a difference in habitat preferred.

Contrast	*C. septempunctata*	*C. maculata*	*H. axyridis*	*C. munda*
Corn vs. Soybean	X	X	X	X
Corn vs. Edge		X		X
Soybean vs. Edge	X		X	X

Table 6. Linear orthogonal contrasts between treatments for each species in 2002. Contrasts marked with an X are statistically significant using quadratic linear contrasts. Significant contrasts show a difference in habitat preferred.

Each species average trap catch is graphed below by trap row (Figs. 14-17). As the graphs below indicate *C. septempunctata* and *H. axyridis* are significantly more likely to be found in soybean than corn. Corn is the overwhelming preference of *C. maculata*. While *C. munda* is the only species studied that was predominant in the edge habitats; this only occurred in 2001. In 2002 *C. munda* numbers were very low, and they showed no significant difference between treatments.. The averages by microhabitat correlate well with theoretical models of habitat as shown in figure 20. While none of the three species fits the true generalist pattern, *Harmonia axyridis* was displayed the most flexibility in microhabitat selection and is shown with the generalist model.

Aphid Responses:

Coccinella septempunctata preferred the soybean fields to the corn and was sampled in large numbers in the early season (Appendix 2, Figure 23). It actively fed on the soybean aphid, but its potential as a biocontrol agent is limited because in Michigan soybean aphid is a late season pest, and *C. septempunctata* numbers are at their highest in the middle of the growing season, tapering off quickly at approximately the same time as the soybean aphid reached its population peak. *C. septempunctata* populations were high in the early season and possibly had a direct impact by delaying soybean aphid colonization early in the season. The research area was successfully colonized later than most other areas in the state.

Year	**Species**	**Alpha**	**Pr>F**	R^2
2001	*Coccinella septempunctata*	.05	.0042	.478
2001	*Coleomegilla maculata*	.05	.1403	.269
2001	*Harmonia axyridis*	.05	.0001	.618
2001	*Cycloneda munda*	.05	.3816	.181
2002	*Coccinella septempunctata*	.05	.754	.030
2002	*Coleomegilla maculata*	.05	.6393	.030
2002	*Harmonia axyridis*	.05	.629	.032
2002	*Cycloneda munda*	.05	.966	.0023

Table 7. ANOVA results and correlation coefficients for the response of the coccinellids to the soybean aphid index for 2001 and 2002. If the Pr>F is less than .05 the species showed a significant response to the aphid. The correlation coefficient (R^2) indicates the strength of this response.

Cycloneda munda preferred the edges and weedy strips between the crops before the arrival of the soybean aphid. After the colonization of soybean aphid *C. munda* slowly moved into the soybean fields. The dispersion into soybean seems to be a direct response to the presence of soybean aphid, as its population in soybean rose linearly with the rise of soybean aphid numbers. *C. munda* moved into the fields after soybean aphid populations were high, helping to prevent an infestation (Appendix 2, Figure 22).

Harmonia axyridis is the most generalist of the coccinellids represented here. It is considered primarily an arboreal species but is adept at exploiting a number of habitats and prey. This is indicated in the maps by its continued sizeable presence in corn as well as soybean. *H. axyridis* was by far the most common coccinellid in the study and consequently was the main predator of the soybean aphid (Appendix 2, Figure 24).

Coleomegilla maculata was the least responsive to the presence of the soybean aphid (Appendix 2, Figure 21). This species prefers corn, where it feeds on corn pollen, mites and aphids in the tassels. It never moved in any appreciable numbers into soybean, indicating a possible lack of behavioral plasticity (i.e. not recognizing the soybean aphid as a food source).

The numerical response to the aphid was varied. The significant results of the linear orthogonal contrasts (Table 8) show a marked response in only two species in 2001 and none in 2002. In 2001 only *C. septempunctata* and *H. axyridis* showed response to the presence of the aphid.

Year	Species	Contrast	Pr>F	R^2	Linear Model
2001	*C. septempunctata*	0 vs.1	.005	.48	y= .79 x + .294
2001	*C. septempunctata*	0vs 2	.0097	.48	y= .79 x + .294
2001	*C. septempunctata*	0 vs. 3	.0004	.48	y= .79 x + .294
2001	*C. septempunctata*	0 vs. 4	.0097	.48	y= .79 x + .294
2001	*C. septempunctata*	0 vs. 5	.0170	.48	y= .79 x + .294
2001	*H. axyridis*	0 vs.1	.0003	.61	Y= 19x + 33.4
2001	*H. axyridis*	0vs 2	<.0001	.61	Y= 19x + 33.4
2001	*H. axyridis*	0 vs. 3	<.0001	.61	Y= 19x + 33.4
2001	*H. axyridis*	0 vs. 4	<.0001	.61	Y= 19x + 33.4
2001	*H. axyridis*	0 vs. 5	<.0001	.61	Y= 19x + 33.4

Table 8 Results of the linear orthogonal contrast for 2001 aphid scale test. Only the significant contrasts and models are shown.

None of the intermediate contrast levels (i.e. 2vs3 or 3v.s.4) for 2001 were significant but zero contrasted with any level was significant for the two exotic species. The aphid scale for 2002 was not significantly different than zero due to the low numbers of aphids so the contrasts were all insignificant, and no predictive equations could be developed.

Figure 14: The averages per row for the native Coccinellids in 2001. The study area is shown above the graphs with the corresponding row averages as bars directly below the actual sampling row. Significant differences in treatment are designated by letter. The Y axis is the average weekly trap catch for the six trap stations in the center of the rows. Images in this thesis are presented in color.

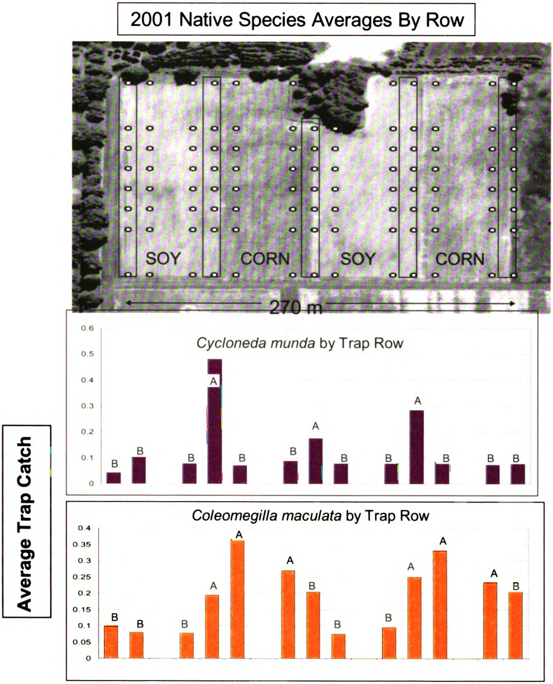

2001 Native Species Averages By Row
SOY
CORN
SOY
CORN
270 m
Average Trap Catch
Cycloneda munda by Trap Row
0.6
0.5
0.4
0.3
0.2
0.1
0
B B B A B B A B B A B B B
Coleomegilla maculata by Trap Row
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
B B B A A A B B B A A A B

Figure 14

Figure 15: The averages per row for the exotic Coccinellids in 2001. The study area is shown above the graphs with the corresponding row averages as bars directly below the actual sampling row. Significant differences in treatment are designated by letter. The Y axis is the average weekly trap catch for the six trap stations in the center of the rows. Different letters indicate significant differences in response to habitat. Images in this thesis are presented in color.

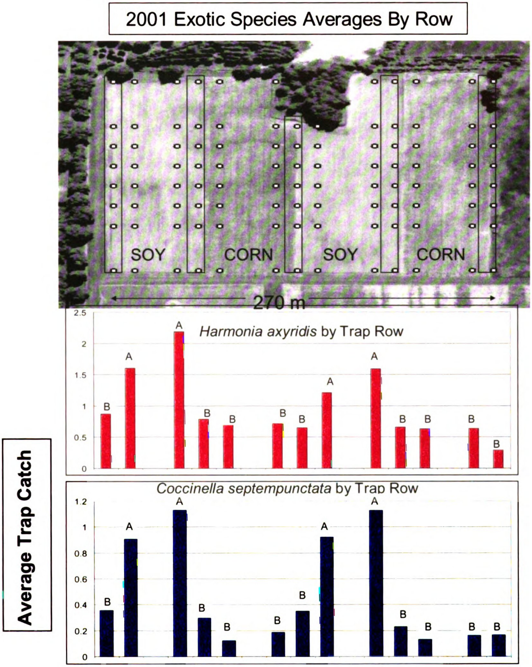

2001 Exotic Species Averages By Row
SOY
CORN
SOY
CORN
270 m
Average Trap Catch
Harmonia axyridis by Trap Row
2.5
2
1.5
1
0.5
0
B
A
A
B
B
B
B
A
A
B
B
B
B
Coccinella septempunctata by Trap Row
1.2
1
0.8
0.6
0.4
0.2
0
B
A
A
B
B
B
B
A
A
B
B
B
B

Figure 15

Figure 16: The averages per row for the native Coccinellids in 2002. The study area is shown above the graphs with the corresponding row averages as bars directly below the actual sampling row. Significant differences in treatment are designated by letter. The Y axis is the average weekly trap catch for the six trap stations in the center of the rows. Different letters indicate significant differences in response to habitat. Images in this thesis are presented in color.

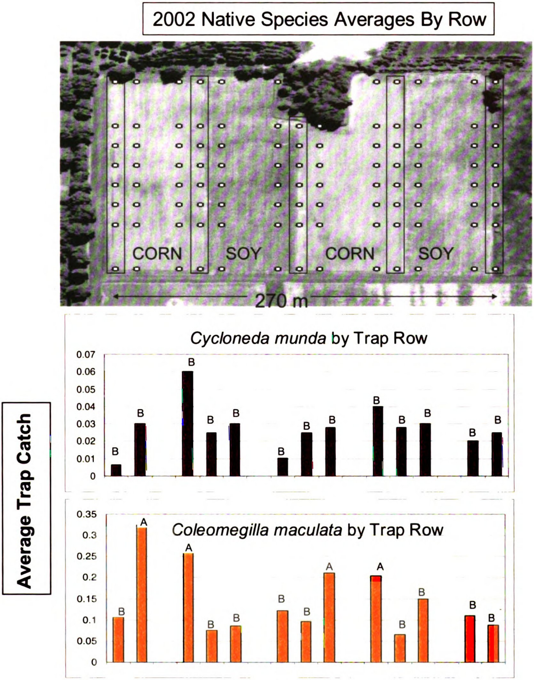

2002 Native Species Averages By Row
CORN
SOY
CORN
SOY
270 m
Average Trap Catch
Cycloneda munda by Trap Row
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0
B B B B B B B B B B B B B B
Coleomegilla maculata by Trap Row
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
B A A B B B B A A B B B B

Figure 16

Figure 17: The averages per row for the exotic Coccinellids in 2002. The study area is shown above the graphs with the corresponding row averages as bars directly below the actual sampling row. The Y axis is the average weekly trap catch for the six trap stations in the center of the rows. Different letters indicate significant differences in response to habitat. Images in this thesis are presented in color.

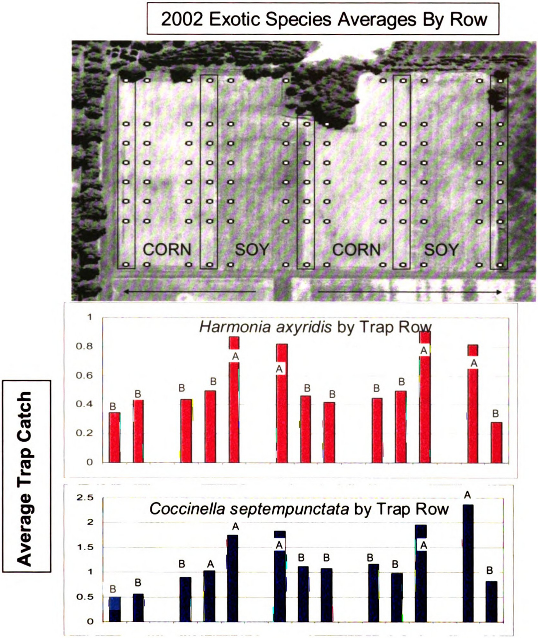
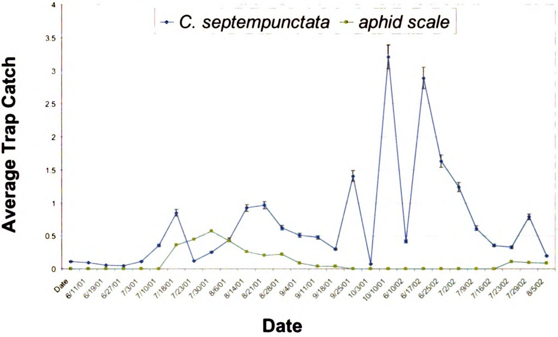

2002 Exotic Species Averages By Row
CORN
SOY
CORN
SOY
Average Trap Catch
Harmonia axyridis by Trap Row
0
0.2
0.4
0.6
0.8
1
B
B
B
B
A
A
B
B
B
B
A
A
B
Coccinella septempunctata by Trap Row
0
0.5
1
1.5
2
2.5
B
B
B
A
A
A
B
B
B
B
A
A
B

Figure 17

Figure 18. ***H. axyridis*** **and** ***C. septempunctata*** **and aphid scale vs. date for both years. The data points represent average trap catch at the center six traps stations in each row for the Coccinellids and the actual aphid scale sampled weekly. Error bars represent the standard error. Images in this thesis are presented in color.**

Figure 18
C. septempunctata and Aphid Scale vs. Date



H. axyridis and Aphid Scale vs. Date

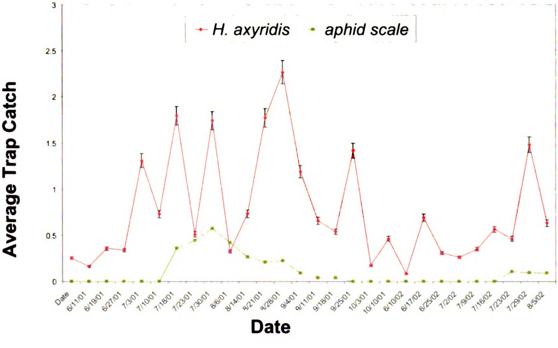
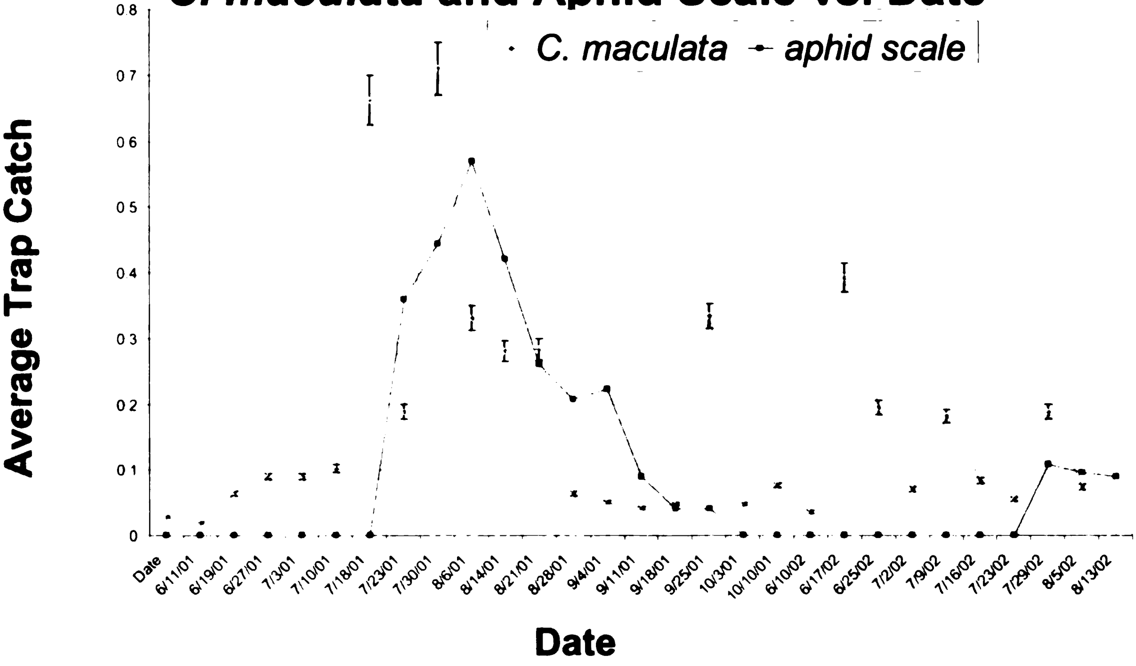


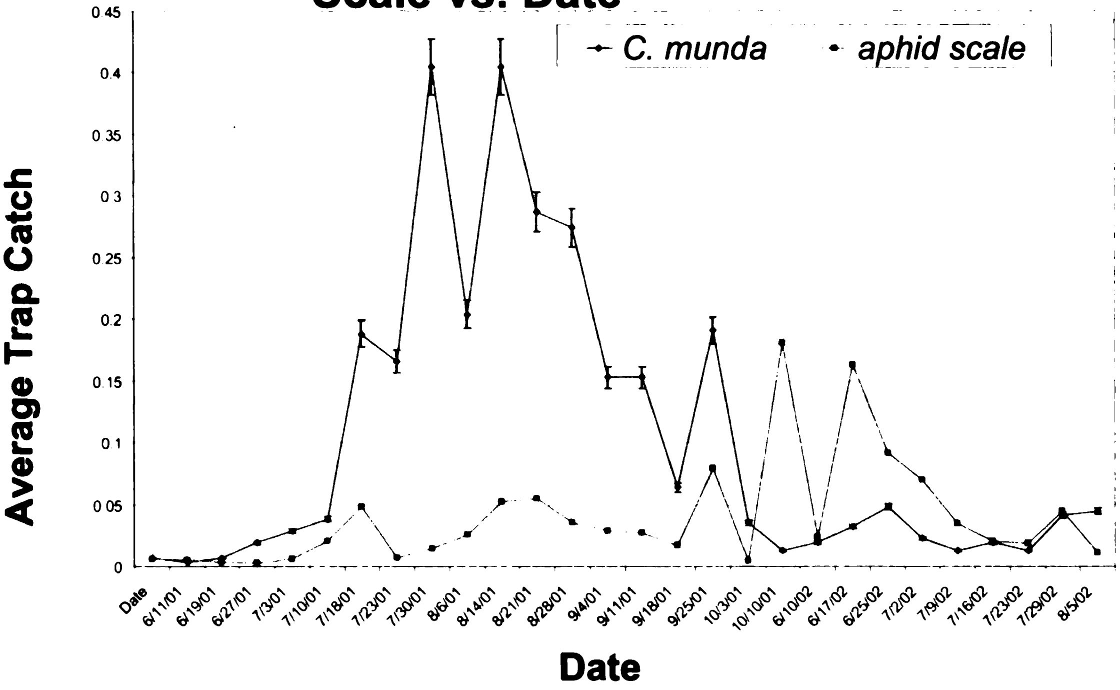
Figure 19. ***C. maculata*** **and** ***C. munda*** **and aphid scale vs. date for both years. The data points represent average trap catch at the center six traps stations in each row for the Coccinellids and the actual aphid scale sampled weekly. Error bars represent the standard error. Images in this thesis are presented in color.**

Figure 19

C. maculata and Aphid Scale vs. Date



C. munda and Aphid Scale vs. Date



Discussion

Habitat segregation

The results of the orthogonal contrasts provide a picture of habitat preference in this system. *Coccinella septempunctata* showed a significant difference in contrasts between corn and soybean as well as soybean and edge. *Coccinella septempunctata* was the most specific of the four species as represented by the highest correlation coefficient (R^2=.307) clearly preferring soybean. The potential greatest potential competition threat comes from *H. axyridis* but the two species' niches are separated temporally not entirely spatially (Chapter 3). *Coccinella septempunctata* is common early and in the middle of the growing season but its population drops markedly in the late season each year.

In stark contrast to *C. septempunctata*, *C. maculata* shows a definite preference for corn over both of the other treatments. It did utilize edge habitat but was comparatively uncommon in soybean. The soybean aphid (*Aphis glycines*) was abundant and readily available in soybean in 2001, so the relative isolation of *C. maculata* in corn indicates either a lack of behavioral plasticity on its part (failing to recognize the exotic aphid as a food source), a failure to thrive when eating the soybean aphid, or that it simply avoids competition with the larger more aggressive species in soybean. The former of these possibilities seems the most likely, but they both should be examined carefully to assess *C. maculata*'s potential as a biological control agent for *Aphis glycines*.

Cycloneda munda was the only species with a clear preference for the edge microhabitat rather than either of the row crop alternatives although this preference was only evident in 2001 because in 2002 its population was extremely small and no significant differences in habitat could be detected. In 2001 it did move into soybean after the soybean aphid became common, but even this dispersion was slow and originated form the edge microhabitat. *C. munda* prefers the more diverse edge microhabitat for reasons that are still unclear, perhaps it thrives in the increased vegetation diversity and its attendant increased prey diversity, or simply it avoids interspecific competition as none of the other species were as common, of preferred the edge habitat. The population of *C. munda* was the smallest of the species in the study; this follows the general assumption that it is primarily an arboreal species. The movement of *C. munda* into field crops seems to occur only when an abundant food source is present, so the lack of soybean aphid could explain its virtual absence in 2002. It has also possibly suffered from competition with *H. axyridis* as the long term population trend for *C. munda* at the KBS LTER since *H. axyridis* arrival has been negative (Colunga-Garcia and Gage 1998).

The most general microhabitat preference was that of *H. axyridis*. It was found in all treatments concurrently with all other species. Even as the most generalist predator in the study, it showed a marked preference for soybean over either of the two microhabitats. *H. axyridis* was by far the most common of the coccinellids in this study with a total trap catch of over 7000 individuals. Considered primarily an arboreal species in its Japanese home range, it has in North America exploited a number of habitat types and cropping systems. The appearance of *H. axyridis* in the United States before the soybean aphid created a novel scenario where an excellent biological control agent was widely established before the pest arrived.

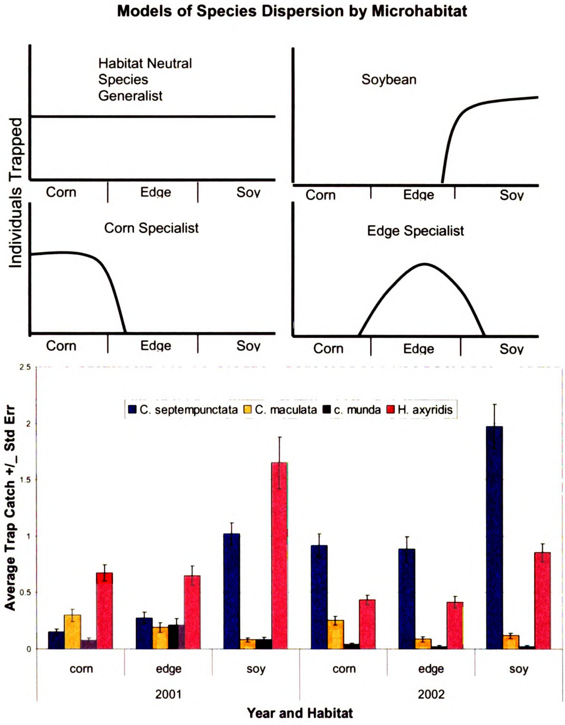


Figure20: Theoretical models of species habitat preferences and actual results. Images in this thesis are presented in color.

The theoretical dispersion models depicted in figure 20 are well represented by the four species studied with the exception of the microhabitat generalist. This does not necessarily mean that there are no generalists in the coccinellid guild. The presence of *Aphis glycines* as an abundant food source in soybean most likely drew the generalists into soybean to take advantage of an easily exploitable resource. *Harmonia axyridis* is the most generalist of the species studied but indicates a preference for soybean most likely due to resource availability. The soybean specialist profile fits *C. septempunctata* due to the temporal characteristics of the two species; the soybean aphid was a late season pest, while *C. septempunctata* was at its highest densities in the early to mid season before the arrival of the soybean aphid in the row crop.

The tendency for the coccinellids to isolate themselves from each other spatially minimizes the potential for direct competition between the adults of the community, allowing for seemingly high niche overlap. The overlap in spatial distribution occurred mainly in areas of abundant *Aphis glycines* colonies. With an ample food supply, the adults of the three species found in soybean did not appear to compete directly to the point of interspecific population regulation.

Aphid response

The soybean aphid was detected the week of July 23 in 2001 and during the week of July 28, 2002. These dates correspond to roughly 750 degree days (50° F. The aphid numbers in 2001 were much higher than in 2002, most probably due to the wetter, cooler summer in 2002. *Aphis glycines* is susceptible to fungal pathogens (Ostile, 2002), and the higher moisture in 2002 could have reduced aphid populations in 2002.

The most effective predator of the soybean aphid in the soybean was *H. axyridis* (Appendix 2, Figure 24) The temporal dynamics of both species dictate that they reach their population peaks at roughly the same time, both in the late season. The soybean aphid population in 2001 was rising until large numbers of *H. axyridis* arrived in the fields. The slow colonization of the soybean aphid indicates another possible control point in the system. The soybean aphid spends three generations on its overwintering host, buckthorn, before moving into the soybean fields. This initial population may have been regulated by the presence of *C. septempunctata* or one of the more arboreal community members such as *C. munda* or other members of the genus *Coccinella* attacking the soybean aphid on its winter host would reduce the number of winged adults that eventually moved into soybean and thereby be an important control point. More monitoring of the predators in buckthorn is needed to quantify the predator response on that host plant.

Chapter Five: Summary

Objectives

The four species studied showed a remarkable ability to segregate their niches to avoid competition as adults. The means of niche separation varied including temporal, habitat, and seemingly behavioral mechanisms. To summarize, objectives stated in chapter one are restated followed by a summary of the research findings:

Objective One: To gain a better understanding of the mechanism that allows the exotic species to coexist in the same habitat.

1. The exotic coccinellids were found in preliminary statistical analysis to not be competing. The spatial and temporal analysis of their habitat use shows that the mechanism of their niche separation is a temporal shift between the adults of the two species, with *C. septempunctata* dominating the early season and *H. axyridis* the late.

Objective Two: To gain a better understanding of the temporal, spatial, and habitat characteristics that separate the niches of the four dominant members of the community.

1. The four species were found to have varying mechanisms of niche separation. *C. maculata* isolates itself through use of corn as a primary habitat; it is the only coccinellid in the group to do so. Its ability to exploit a habitat the others can not is augmented by its ability to use pollen, including corn pollen, as an alternate food resource. It also showed no response to the soybean aphid.

2. *Cycloneda munda* also was present throughout the growing season and avoided competition by using an alternate habitat; thriving in the edges between the row crops and venturing into them only when food was abundant. When food was limited in the row crops, it remained in the edges or possibly stayed in the trees reflecting its arboreal nature.
3. *Harmonia axyridis* was found in all habitats but only in great numbers late in the growing season. This allows it to dominate the landscape in late summer. As a habitat generalist, it was able to exploit varying resources in seemingly opportunistically.
4. *Coccinella septempunctata* was most prevalent in the early season, mating and laying eggs before the other three species. This early season dominance coupled with its marked preference for soybean over edge or corn kept it in areas not utilized by the other species.

Objective Three: To gain a better understanding of the effects of an exotic prey species in the form of the newly arrived soybean aphid on the four dominant members of the community.

1. *Coleomegilla maculata* showed no significant response to the soybean aphid. It maintained its strong preference for corn in 2001 when the aphid was abundant as well as in 2002 when the aphid was scarce.
2. *Cycloneda munda* displayed an opportunistic ability to exploit the aphid as a resource. In 2001 when aphid populations were high, it moved into the soybean treatments In 2002 when the aphid populations dropped off, it remained in the edge treatments or possibly in the surrounding woods.

3. *Harmonia axyridis* was the most effective predator of the soybean aphid. It showed both a numerical and spatial response to the presence of the aphid at high of low densities. Its temporal characteristics match the aphid's well, with both populations peaking in the latter part of the growing season.
4. *Coccinella septempunctata* showed a strong preference for soybean, but its temporal characteristics made it an inefficient predator of the soybean aphid. The peak of *C. septempunctata's* population is too early in the season for it to be a large impact on the population of the soybean aphid. The high early and midseason populations could have played a significant role in delaying the colonization of the aphid in 2001, while in 2002 the very high numbers of *c. septempunctata* may have contributed to the marked decline in aphid colonies in 2002.
5. The soybean aphid did not cause a major shift in the spatial or temporal patterns of the dominant members of the coccinellid community. *C. munda* was the only species to show a marked spatial response to the soybean aphid.

Competition:

The debate about the role of competition in communities is referenced in chapter two, and a brief summary of the role of competition in this community is relevant here. The role of interspecific competition in this community currently seems minimal. This lack of competition in the community could be due to the results of past interactions which served to segregate the niches or a segregation by traits evolved independently of the other species. The recent arrival of two of the coccinellids studied would seem to favor the latter explanation due to the short amount of time the community has been given to adjust to the exotics. The addition of anovel food source in the form of the soybean aphid, a novel and rare occurrence, failed to elicit a response in any of the four species high enough to cause direct intraspecific competition. This research also sheds no light on the possible competitive interactions of the larval stages of these species. It is possible that the niche segregation displayed by the adults is a direct result of competition between the larvae.

Future directions:

There are several future research projects and data analyses that will further our knowledge of this community and its dynamics. The first is to analyze all 13 years of the LTER dataset to determine and quantify effects of different agricultural management practices on the coccinellid community. As previously stated the treatments range from certified organic to intensive conventional management. The analysis would use many of the tools (both spatial and statistical) already used herein. The effects of inputs on beneficial insects could play an important role in management decisions.

Second, I would like to test the effectiveness of *C. septempunctata* and *C. munda* control of the soybean aphid on its winter and spring host. Buckthorn is currently not monitored at the LTER for either the soybean aphid or coccinellids. The quantification of predation on the alternate host could provide an opportunity to interdict the pest before it moves into the crop. This research would require the identification of buckthorn surrounding the study site, then sampling with yellow sticky traps as in Maredia (1992), and developing an efficient means of sampling the aphid on this host.

Third, personal observations indicate that the application of Roundup® in genetically modified soybean in mid June had a temporary negative impact on the coccinellid community. The destruction of the weeds under the soybean killed up to one third of the vegetation in the field at that time. The coccinellid numbers declined precipitously for a short time. The potential side effects of this predator decrease include a pest outbreak. The genetically modified soybean would be monitored for three weeks pre and post herbicide application to quantify the population decline. For a control, a soybean field would be planted with the same variety, and a tractor and sprayer pass without the application of herbicide would be done at the same time the treatment fields were sprayed. The weed community and the potential coccinellid prey would be monitored for the entire period, as well as potential pests of the soybean.

The last proposed project is to quantify the temporal, spatial, and behavioral dynamics of the larvae of the dominant coccinellids in the field. The adult populations could be strongly influenced by interspecific egg predation, larval predation, and cannibalism of both specific and con-specific larvae (Snyder, 2000).

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Appendix 1

Record of Deposition of Voucher Specimens*

The specimens listed on the following sheet(s) have been deposited in the named museum(s) as samples of those species or other taxa, which were used in this research. Voucher recognition labels bearing the Voucher No. have been attached or included in fluid-preserved specimens.

Voucher No.: 2003-03

Title of thesis or dissertation (or other research projects):

Quantifying the Roles of Competition and Niche Separation in Native and Exotic Coccinellids, and the Changes in the Community in Response to an Exotic Prey Species

Museum(s) where deposited and abbreviations for table on following sheets:

Entomology Museum, Michigan State University (MSU)

Other Museums:

Investigator's Name(s) (typed)
Charles McKeown
Stuart Gage
Manuel Colunga Garcia

Date 5/4/2003

*Reference: Yoshimoto, C. M. 1978. Voucher Specimens for Entomology in North America. Bull. Entomol. Soc. Amer. 24: 141-42.

Deposit as follows:
Original: Include as Appendix 1 in ribbon copy of thesis or dissertation.

Copies: Include as Appendix 1 in copies of thesis or dissertation.
Museum(s) files.
Research project files.

This form is available from and the Voucher No. is assigned by the Curator, Michigan State University Entomology Museum.

Appendix 1.1

Voucher Specimen Data

Page 1 of 1 Pages

		Number of:							
Species or other taxon	Label data for specimens collected or used and deposited	Eggs	Larvae	Nymphs	Pupae	Adults ♀	Adults	Other	Museum where deposited
Harmonia axyridis	6-20-01 MI, Kalamazoo, KBS LTER 27 plots						3		
Harmonia axyridis	6-23-01 MI, Kalamazoo, KBS LTER 27 plots						1		
Harmonia axyridis	7-03-01 MI, Kalamazoo, KBS LTER 27 plots						5		
Harmonia axyridis	7-31-01 MI, Kalamazoo, KBS LTER 27 plots						1		
Coccinella septempunctata	7-10-01 MI, Kalamazoo, KBS LTER 27 plots						5		
Coccinella septempunctata	7-18-01 MI, Kalamazoo, KBS LTER 27 plots						1		
Coccinella septempunctata	7-31-01 MI, Kalamazoo, KBS LTER 27 plots						4		
Coleomegilla maculata	7-02-01MI, Kalamazoo, KBS LTER 27 plots						1		
Coleomegilla maculata	7-31-01 MI, Kalamazoo, KBS LTER 27 plots						9		
Cyclonedia munda	7-10-01 MI, Kalamazoo, KBS LTER 27 plots						1		
Cyclonedia munda	7-18-01 MI, Kalamazoo, KBS LTER 27 plots						1		
Cyclonedia munda	7-24-01 MI, Kalamazoo, KBS LTER 27 plots						1		
Cyclonedia munda	7-31-01 MI, Kalamazoo, KBS LTER 27 plots						7		
Aphis glycines	7-30-02 MI, Kalamazoo, KBS, LTER, 27 plots						8		

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

Charles McKeown

Stuart Gage

Manuel Colunga-Garcia

Date 4/8/2003

Voucher No. 2003-03

Received the above listed specimens for deposit in the Michigan State University Entomology Museum.

5 MAY 2003

Curator Date

Appendix 2 Soybean Aphid Response Maps

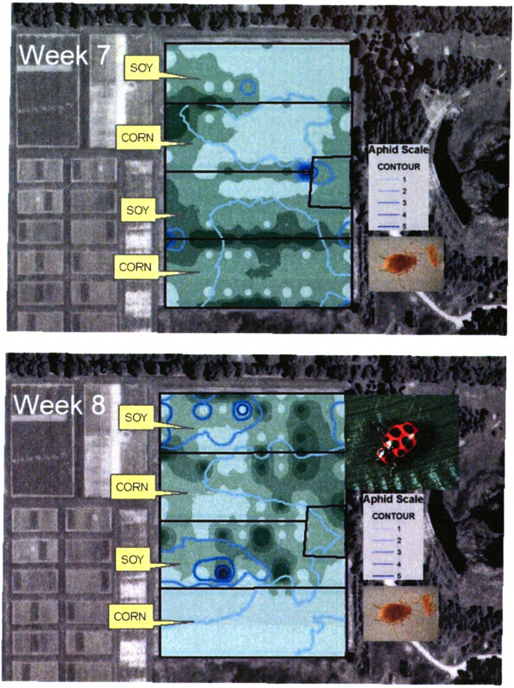
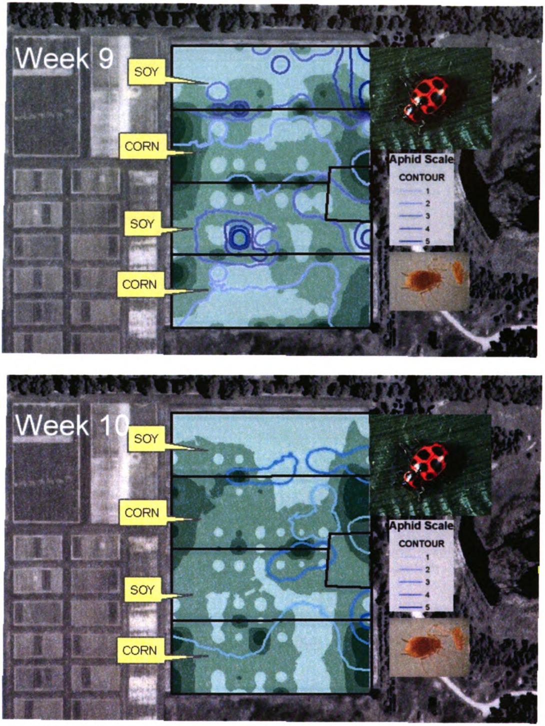


Figure 21 *C. maculata*



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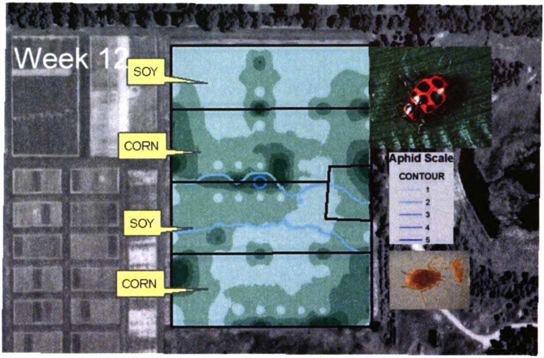

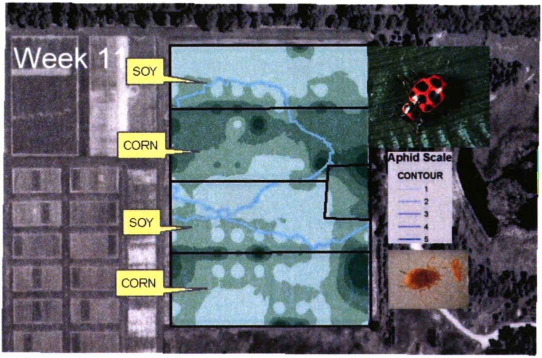

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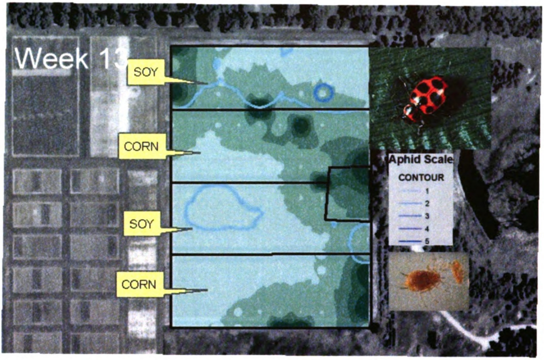

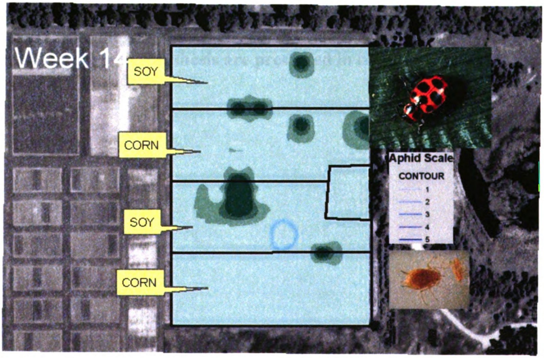

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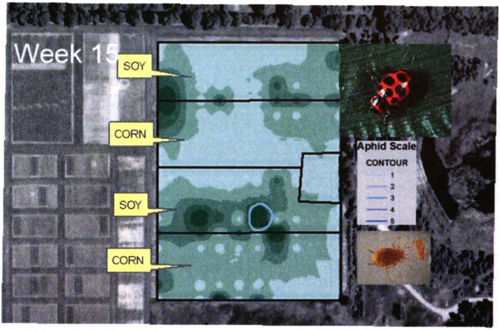


Figure 21 Cont. *C. maculata* dispersion maps with the aphid scale superimposed as contours for 2001. As the contour lines become closer the aphid intensity is higher. The predator is shown by standard deviation classification to emphasize the variation in the population spatially. Images in this thesis are presented in color.

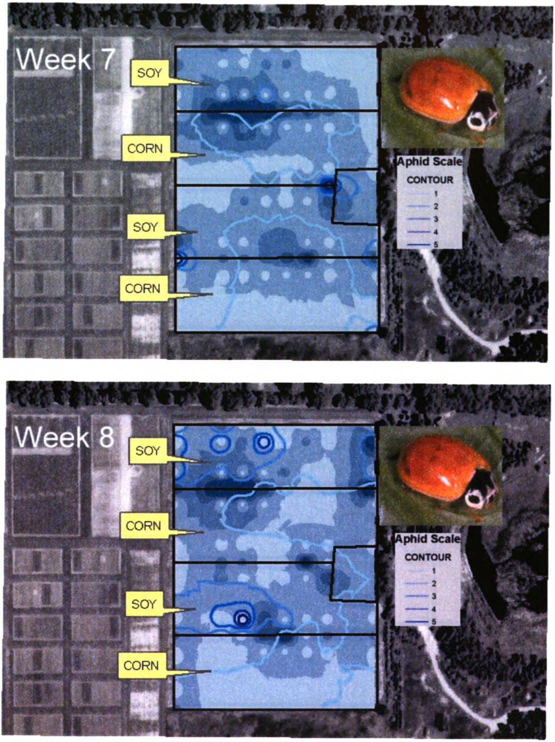


Figure 22 ***C. munda***

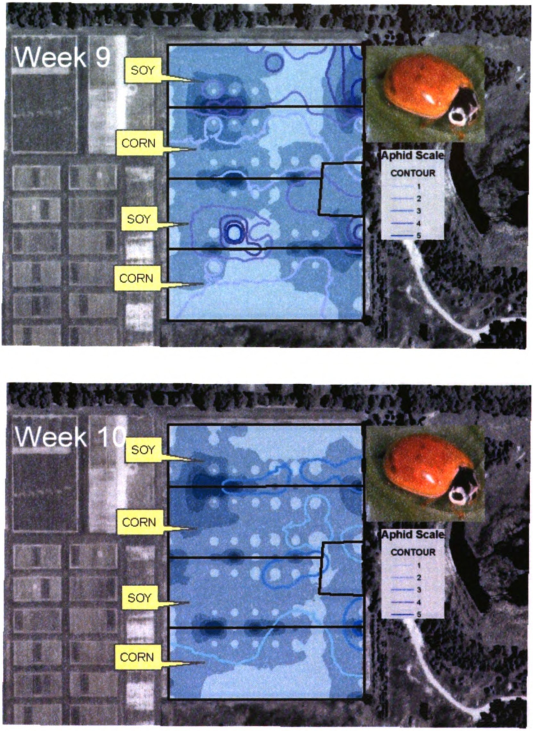
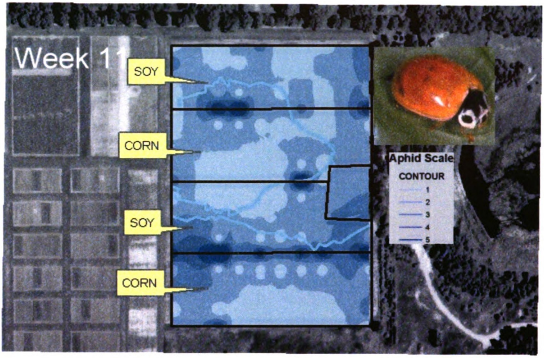
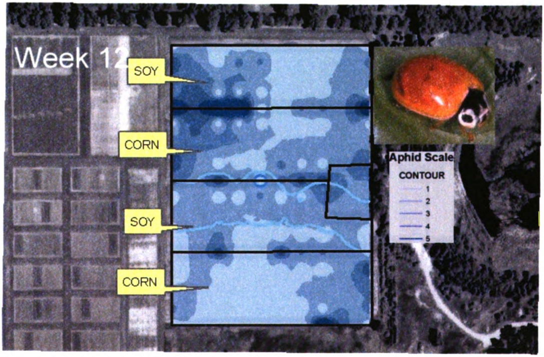


Figure 22 Cont. ***C. munda***





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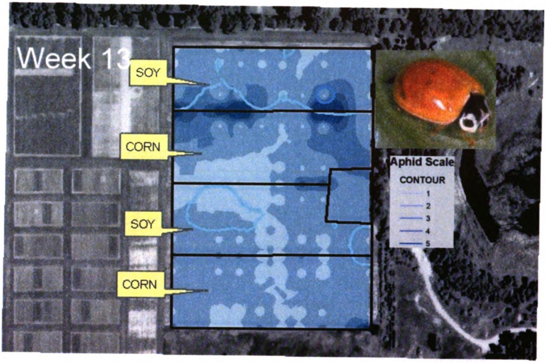

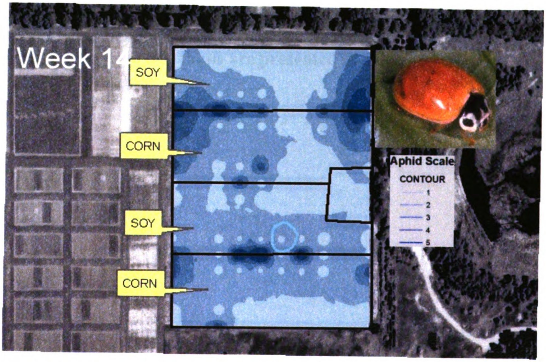

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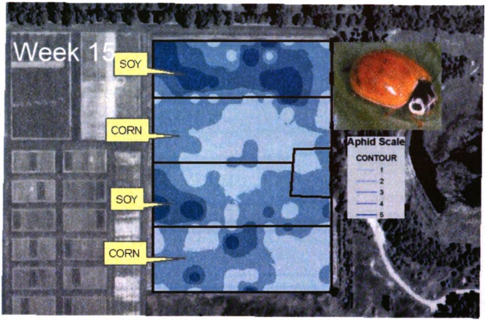


Figure 22 Cont. ***C. munda*** **dispersion maps with the aphid scale superimposed as contours for 2001. As the contour lines become closer the aphid intensity is higher. The predator is shown by standard deviation classification to emphasize the variation in the population spatially. Images in this thesis are presented in color.**

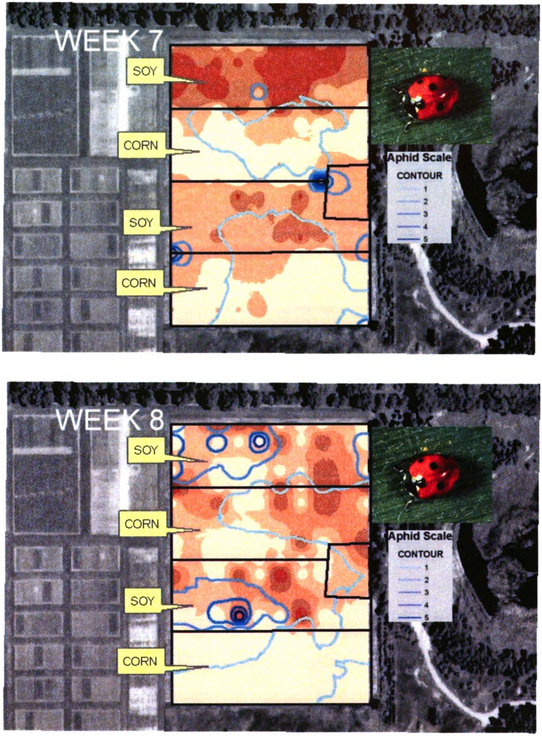
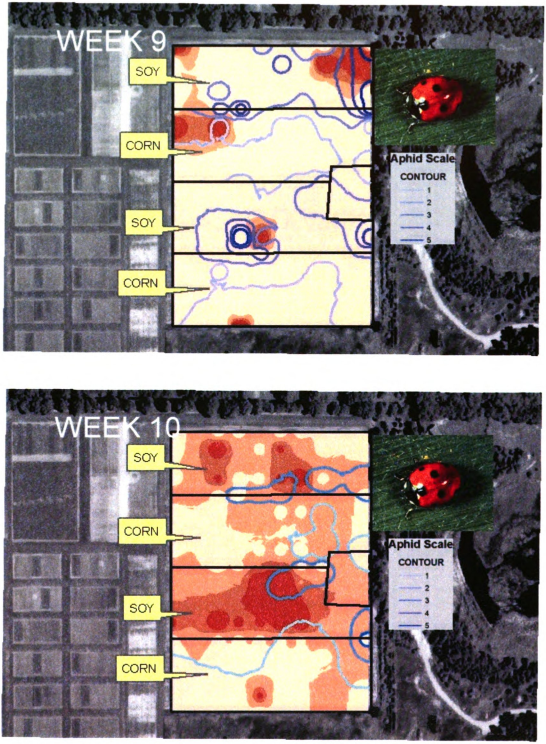


Figure 23 ***C. septempunctata***



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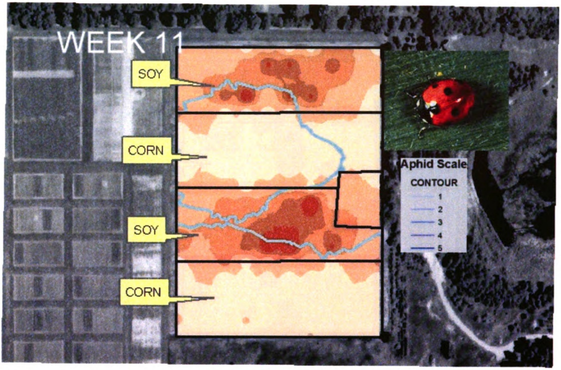


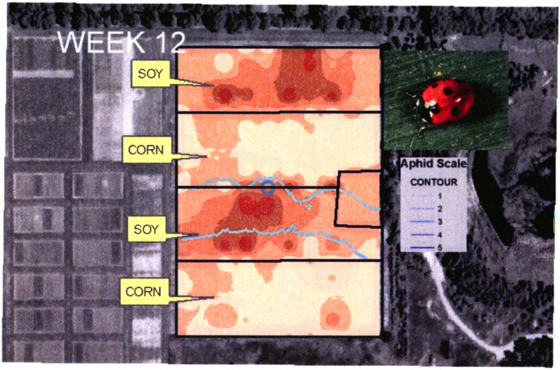
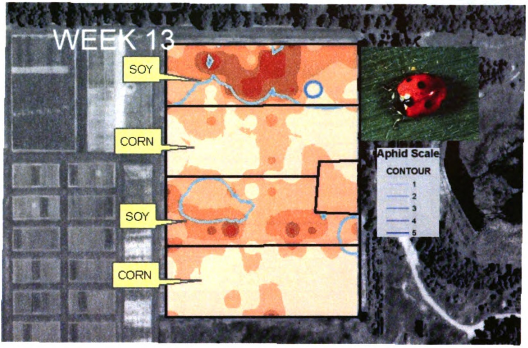


Figure 23 Cont. ***C. septempunctata***



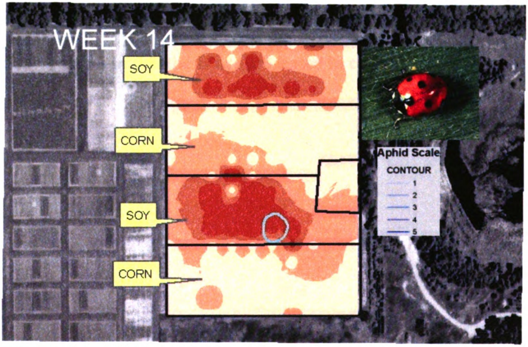


Figure 23 Cont. *C. septempunctata*

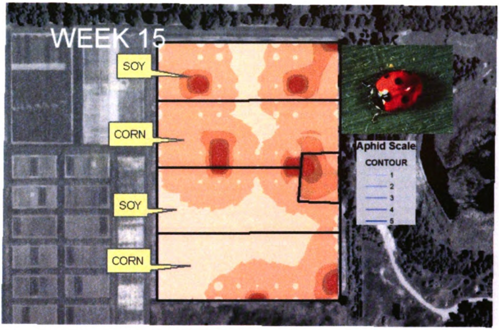


Figure 23 Cont. *C. septempunctata* **dispersion maps with the aphid scale superimposed as contours for 2001. As the contour lines become closer the aphid intensity is higher. The predator is shown by standard deviation classification to emphasize the variation in the population spatially. Images in this thesis are presented in color.**

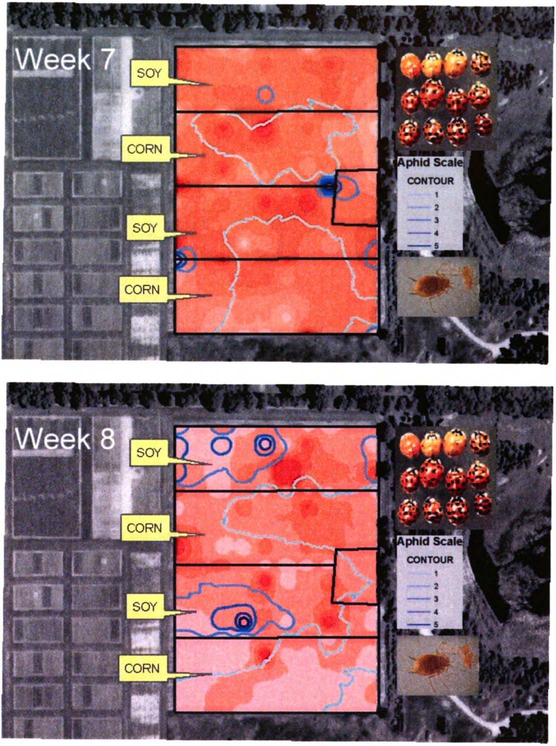
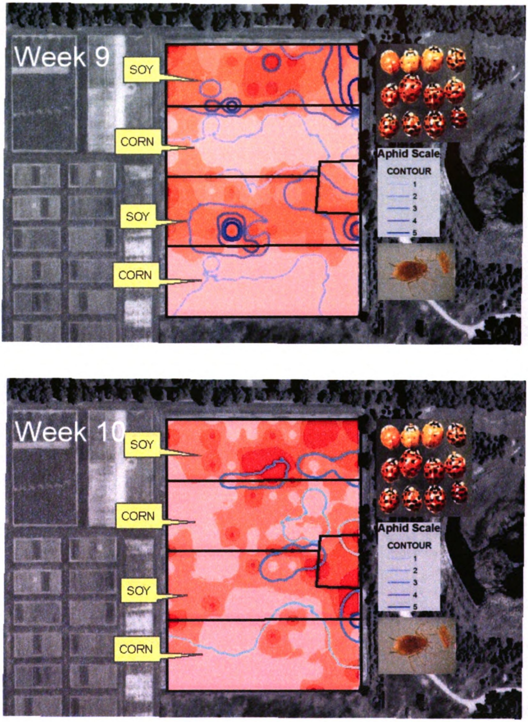


Figure 24 ***H. axyridis***



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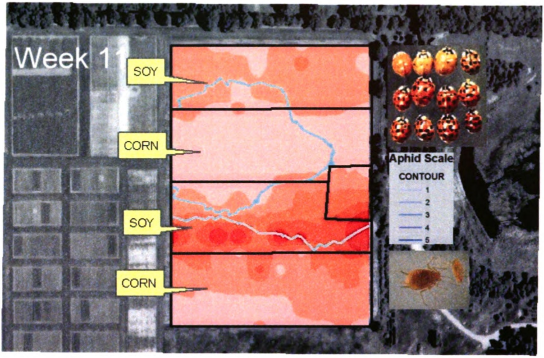


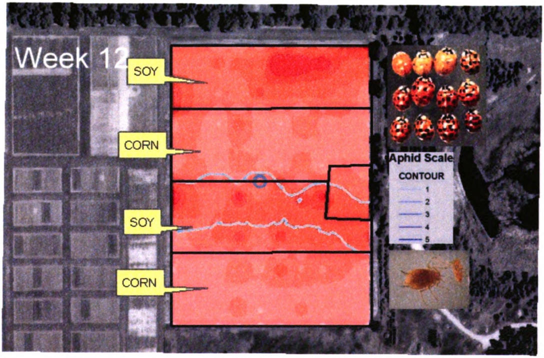
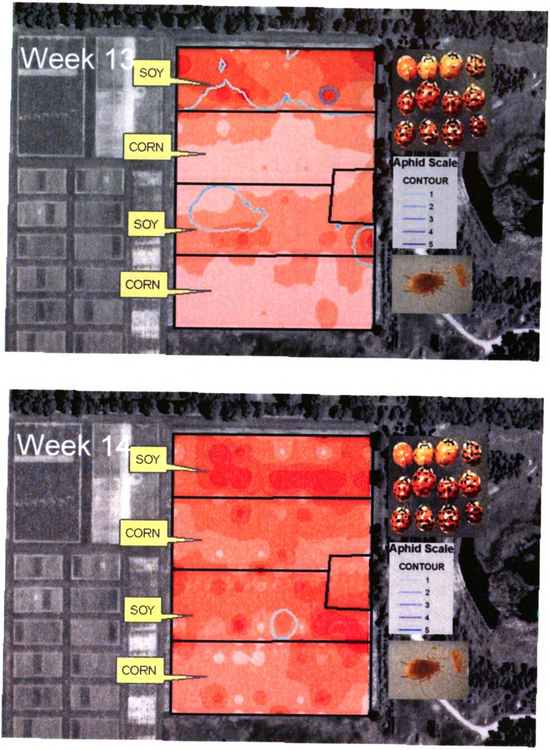


Figure 24 Cont. ***H. axyridis***



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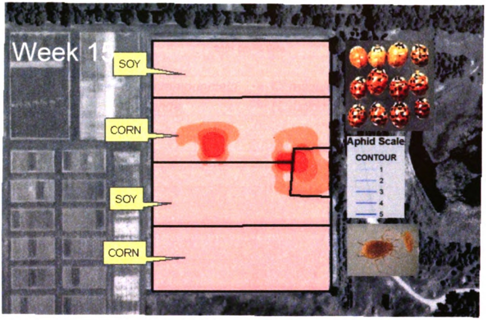
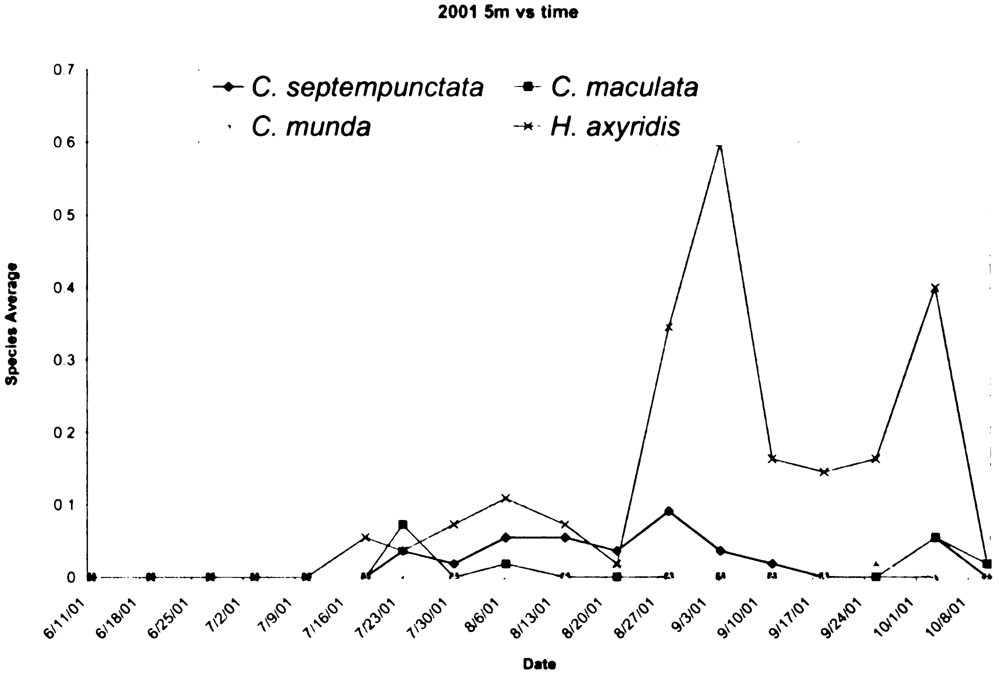
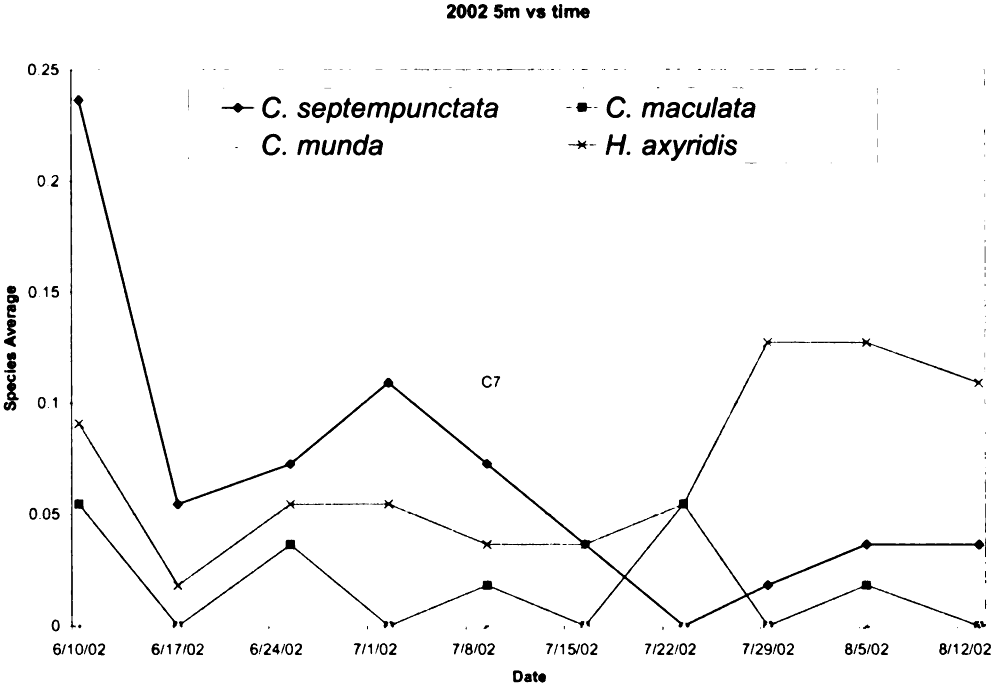


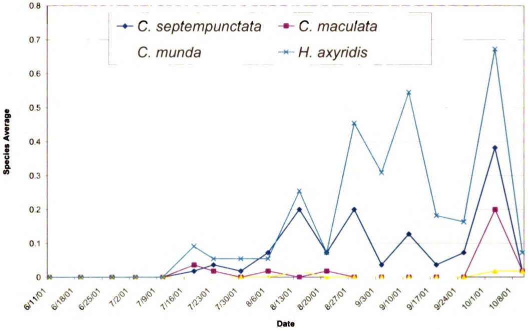
Figure 24 Cont. ***H. axyridis*** **dispersion maps with the aphid scale superimposed as contours for 2001. As the contour lines become closer the aphid intensity is higher. The predator is shown by standard deviation classification to emphasize the variation in the population spatially. Images in this thesis are presented in color.**

Appendix 3: Height Graphs

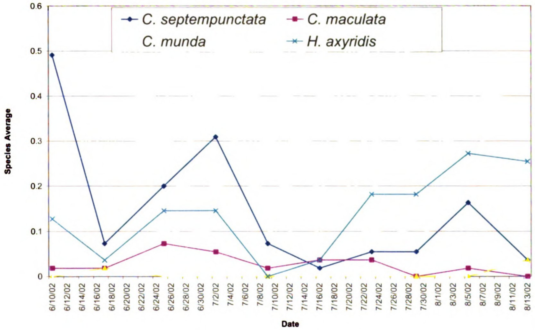
Images in this thesis are presented in color.



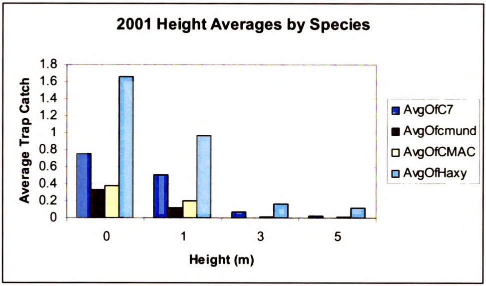


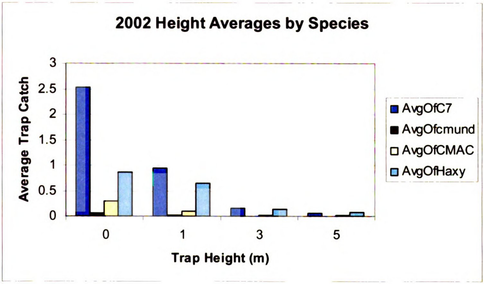


2001 3m vs time



2002 3m vs time


2001 Height Averages by Species
Average Trap Catch
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
0
1
3
5
Height (m)
AvgOfC7
AvgOfcmund
AvgOfCMAC
AvgOfHaxy


2002 Height Averages by Species
Average Trap Catch
3
2.5
2
1.5
1
0.5
0
0
1
3
5
Trap Height (m)
AvgOfC7
AvgOfcmund
AvgOfCMAC
AvgOfHaxy