

ABSTRACT

Title of Document:

THE ROLE OF RELATIVE ABUNDANCE
AND IDENTITY IN THE EFFECTIVENESS
OF GENERALIST PREDATORS AS
BIOCONTROL AGENTS OF *PIERIS RAPAE*
L. (LEPIDOPTERA: PIERIDAE)

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The importance of generalist arthropod predator assemblages in suppressing pests has recently received more attention. However, few studies have investigated the impacts of assemblage structure on pest mortality. This study assessed the influence of relative abundance and taxonomic identity among an assemblage of generalist predators in collards, (*Brassica oleracea* var. *acephala*), on the mortality of *Pieris rapae*. In field surveys and laboratory assays, I determined that *Coleomegilla maculata* was the numerically dominant while *Coccinella septempunctata* and *Podisus maculiventris* were numerically subdominant predators of *P. rapae* larvae.

Experimental mesocosms were used to determine whether numerically dominant predators alone, regardless of taxonomic identity, imposed greater *P. rapae* larval mortality than when in an assemblage. As numerically dominant species, only *C. septempunctata* imposed greater *P. rapae* larval mortality alone than when in an assemblage. This research highlights the importance of considering both relative abundance and identity in studies involving predator assemblages and biocontrol.

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EFFECTIVENESS OF GENERALIST PREDATORS AS BIOCONTROL AGENTS
OF *PIERIS RAPAE* L. (LEPIDOPTERA: PIERIDAE)

By

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Thesis submitted to the Faculty of the Graduate School of the
University of Maryland, College Park, in partial fulfillment
of the requirements for the degree of
Master of Science
2006

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ACKNOWLEDGEMENTS

I would like to gratefully acknowledge the support of my thesis advisor, Dr. Pedro Barbosa. Throughout my tenure here at the University of Maryland, Pedro has been an excellent mentor, and has been a constant source of encouragement and inspiration for me. His dedication to my intellectual and personal development during these past three years goes beyond description, and I cannot thank him enough for all his help. I would also like to thank the other members of my advisory committee: Drs. Robert F. Denno and Galen Dively. Their comments and suggestions have been instrumental in aiding me in the development of my experimental design, statistical analysis, and in the maintenance of arthropod colonies. I thank them for their wisdom and helpful advice.

I thank the past and present members of the Barbosa laboratory for their support, advice, and continuous encouragement. Drs. John Kemper and Astrid Caldas, as well as Eric Lind, Gwen Shlichta, Megan Paustian, and Raul Medina all contributed in one way or another to this research and for that I gratefully acknowledge them. I especially thank Scott Lewins, whom collaborated with me on certain aspects of this research. His help was critical to several components of my research, and I thank him for his support.

I thank Mike Newell, Mark Spicknall, Kevin Conover, and all the members of the Central Maryland Education and Research Center and Wye Education and Research Center for their help in setting up my collard plots at their farms. I also thank Jeffrey Aldrich, Don Weber, Zsofia Szendrei, and everyone at the Insect

Biocontrol Laboratory (USDA-ARS, Beltsville, MD) for helping me in the establishment of predator colonies.

I would like to thank the staff of the Department of Entomology here at the University of Maryland for their support and their warm spirit that always brought a smile to my face. In addition I would like to thank the faculty and students in the Department of Entomology for their encouragement, their help, and last but not least their friendship. I thank all those students who assisted in several aspects of my research.

I gratefully acknowledge the Cosmos Club Foundation and the Society for the Advancement of Chicanos and Native Americans in Science for their financial support.

I thank Silvana Marten-Rodriguez for her companionship, love, and support during these past three years. I also thank Akito Kawahara and Jeff Sosa for their constant help and encouragement during the various trials and tribulations of graduate school. Finally, I would like to thank my parents, Gustavo and Lilia Moreno, my sister, Erika Moreno, my brother-in-law, Richard Witmer, and of course my niece and nephew, Sofia and Ricky, for their love and support during all these years.

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CHAPTER 1:

Generalist Predator Assemblages and Species Abundance Distributions: A

Review

Historically, biological control efforts have assumed that the most effective control of pest species is achieved by single natural enemy species. This assumption has persisted in spite of a lack of rigorous experimental data. While there is evidence to suggest that generalist predators can reduce pest populations and decrease the probability of outbreaks (Chiverton 1986, Settle et al. 1996, Holland et al. 1996, Chang and Kareiva 1999, Symondson et al. 2002), studies evaluating the effectiveness of generalist predator assemblages relative to single species have been scarce until relatively recently. More research is now being conducted on the potential impact of naturally occurring generalist predator assemblages on prey suppression, in comparison to single predator species (Riechert and Bishop 1990, Cardinale et al. 2003, Snyder et al. 2006). Nevertheless, it remains largely unclear how effective assemblages of generalist predators may be at suppressing pests relative to single predator species.

In determining the effectiveness of predator assemblages, it may be necessary to understand how components of assemblage structure influence the effectiveness of predators and thus prey mortality. One particular component that has not been thoroughly investigated and may have an important influence on prey mortality is the relative abundance of predators in an assemblage. My research investigates the role of relative abundance among generalist predators in an assemblage on the mortality they

impose on prey. Specifically, I seek to understand whether abundance of a predator per se or its identity is important in determining its effectiveness as a biocontrol agent in an assemblage.

Classical vs. Conservation Biological Control

The three primary approaches in biological control are classical, augmentative, and conservation biological control. The role of natural enemy assemblages and communities in the biological control of pests is central to one of the three approaches, i.e., conservation biological control. In contrast, classical biological control, the most studied of the three approaches, involves the introduction of natural enemy species into agricultural systems in order to regulate pest populations. In the regulation of exotic pest species, the classical approach has typically been somewhat successful, both in terms of natural enemy establishment and pest regulation (Hawkins et al. 1999). Overall, however, only approximately 10-30% of natural enemy introductions have been successful (Hall et al. 1980). While a variety of factors may be responsible for the overall lack of success of these introductions, it is possible that some of the underlying assumptions of classical biological control are flawed (Symondson et al. 2002) and thus have contributed to some of the failures.

In classical biological control, certain traits of natural enemies have historically been assumed to be necessary for the effective control of pest species. One of the principle assumptions is that natural enemies should be highly prey specific (Debach and Rosen 1991, Hoy 1994). This philosophy has placed strong importance on the use of species with narrow diet breadths and high target-prey

specificity. A second assumption is that effective natural enemies should exert density dependent mortality on the pest (Debach 1964, DeBach and Rosen 1991, Van Driesche and Bellows Jr., 1996). That is, when the density of the target prey increases, there is a gradual increase in parasitism/predation. This creates a negative feedback, which works to drive target prey densities down and lower natural enemy pressure, maintaining a stable natural enemy-prey dynamic. A third assumption is that natural enemies should aggregate in areas of high prey density (Debach 1964, Van Driesche and Bellows Jr., 1996) Therefore, these assumptions have historically lead biological control practioners to focus on the introduction (and in augmentative biocontrol, the rearing) of aggregative, specialist natural enemies that exert density dependent mortality on pest populations (DeBach 1964, Hoy 1994). Given these traits it is not surprising that relatively little attention has been given to generalist predators or predator assemblages.

The ultimate goals of classical biological control are to reduce pest populations below threshold levels following introduction, and to ensure that the natural enemy will persist in the system via density dependency in order to maintain long-term pest suppression. However, the relative lack of successful establishment of introduced natural enemies (Hall et al. 1980, Murdoch et al. 1985), suggests that a different approach may be needed. There is increasing evidence that naturally-occurring generalist predators can exert significant mortality on pests, potentially preventing outbreaks (Chiverton 1986, Settle et al. 1996, Holland et al. 1996, Chang and Kareiva 1999, Symondson et al. 2002). Their effectiveness as bicontrol agents may be linked to traits that are not typically associated with specialist natural

enemies. Generalist predators, for example, are voracious, opportunistic feeders with minimal lag times between predation events (Ehler 1990, Symondson et al. 2002). Furthermore, they can persist temporally and spatially on non-pest prey during periods of low pest density (Settle et al. 1996, Symondson et al. 2002). Therefore, the accumulation of evidence on the effectiveness of predators and predator assemblages and the potential detrimental effects of classical biological control introductions have led to the greater interest in conservation biological control.

Rather than a focus on natural enemy introductions, conservation biological control tactics focus on the preservation of natural enemies communities already present in managed habitats, primarily through cultural and other agricultural practices (see Barbosa 1998, Barbosa et al. 2005). This alternative to classical biological control assumes that effective pest regulation may be better achieved by a local assemblage or community of natural enemies (Van Driesche and Bellows 1996, Pickett and Bugg 1998). This contention is represented in the species assemblage control hypothesis, which states that an assemblage of generalist predators can more effectively suppress pest populations than any single predator species (Reichert and Lockley 1984, Provencher and Reichert 1994, Reichert and Lawrence 1994, Reichert 1999).

The Influence of Multiple Predator Interactions on Prey Mortality

Theoretically, effective pest suppression via generalist predator assemblages is dependent on a multitude of interactions among predator species that dictate their collective impact as pest regulators (Polis et al. 1989, Soluk 1993, Kareiva 1994, Losey and Denno 1998). Implicit in the species assemblage control hypothesis is that

interactions among predator species lead to enhanced pest suppression. These interactions can be additive, in which the impact of the group of predators is equal to the sum of the individual predator impacts on the pest species (Snyder and Ives 2003). Alternatively, these interactions could be synergistic, in which the impact of the group is greater than the sum of the individual predator impacts (sensu Snyder et al. 2005). There are a number of possible mechanisms driving these implicit interactions. Additive and synergistic interactions may be the result of differential resource (i.e., prey) utilization among multiple predator species, whereby prey are more effectively exploited and consumed than they would be by any single species (Wilby and Thomas 2002, Wilby et al. 2005, Casula et al. 2006). This mechanism was first proposed by Howard and Fiske (1911) as the “sequence theory”. Synergism can also result when predatory activity by one species causes the prey to become more susceptible to another predator species (Soluk and Collins 1998, Losey and Denno 1998). This may be promoted by complementary hunting modes among predator species which induce prey escape from one habitat domain and facilitate prey capture in another (Schmitz 2005). The classic example of this form of synergistic interaction was provided in the Losey and Denno (1998) study, where the foraging activity of coccinellids on leaves caused pea aphids to fall to the ground, where they became more susceptible to ground foraging carabid predators.

Also implicit in the species assemblage control hypothesis is that antagonistic interactions are minimal and will ultimately not reduce the effectiveness of a predator assemblage. However, negative interactions such as interspecific competition, mutual interference, and intraguild predation may ultimately act to reduce pest suppression.

Competitive interactions among natural enemies, for example, can lead to mutual interference, displacement, and ultimately a reduction in prey mortality (Force 1970, Ables and Shepard 1976, Ehler and Hall 1982, Krause et al. 1990, Walter and Paterson 1995). The same risk or mortality-reducing effects on target pests may occur when interactions among species result in intraguild predation (Polis et al. 1989, Debach and Rosen 1991, Wissinger and McGrady 1993, Rosenheim et al. 1995, Finke and Denno 2004, 2005). However, natural assemblages can still be effective at reducing pest numbers despite the presumed negative effects of intraguild predation (Snyder and Ives 2003) and interference (Lang 2003, Snyder and Wise 1999). Furthermore, Riechert and Lockley (1984) argue that interactions like cannibalism and intraguild predation increase the probability of natural enemy subsistence in periods of low prey abundance.

The Importance of Assemblage Structure on Multiple Predator Interactions

Nevertheless, there remain many questions as to the effectiveness of predator assemblages, particularly with regard to their impact on pest species in comparison to single species in the assemblage. For example, many of the studies that have investigated the impacts of predator interactions on pest mortality have neglected to consider or incorporate several key traits of assemblage structure into their experimental design. One particular aspect of assemblage structure, the relative abundances of predators, has been largely overlooked in studying interactions among species. The outcomes of interactions among predators, and the impact of assemblages on pest mortality, may be influenced by the relative abundances of the

interacting species (Provencher and Riechert 1994, Letourneau and Dyer 1998, Moran and Scheidler 2002, Chang and Snyder 2004). One way to describe that relative abundance of species in a community is with species abundance distributions (SAD's). The SAD of a generalist predator community or assemblage typically describes a pattern of relative abundances that may, at least in part, determine the impact of assemblages of generalist predators. In the following section I provide a brief review of community or assemblage species abundance distributions, factors that may determine the observed patterns of relative abundance in a community, and how my proposed research seeks to determine the importance of relative abundance on the mortality imposed by generalist predators in assemblages

Species Abundance Distributions

Depictions of relative abundance such as species abundance distribution curves reflect a general pattern that is consistent regardless of taxa or habitat. This pattern reflects the presence of a few relatively abundant (or numerically dominant) species and many relatively scarce (or numerically subdominant) species (Sugihara 1980, Loreau 1992, Paarmann et al. 2001, Barbosa et al. 2003, Barbosa et al. 2005). This pattern of numerically dominant/subdominant species has been reported in a diverse array of organisms including mammals (Preston 1962), birds, planktonic crustaceans, and vascular plants, in both temperate and tropical regions (Brown 1984). While taxonomic identity has been the main unit of comparison in the development of community or assemblage SAD's, other SAD curves have been generated using biomass and productivity of organisms (Loreau 1992).

While several theories have been proposed to explain the mechanisms that lead to numerically dominant/subdominant dichotomy in communities and assemblages, most tend to fall under two categories: Causal and statistical (Loreau 1992). The Causal mechanism theory stresses the importance of ecological factors such as diet breadth and competition as the underlying forces explaining patterns of community or assemblage SAD's. This theory predicts that numerical dominance should be associated with more competitive species that have wide diet breadths, among other traits. In the case of generalist predator assemblages, causal factors such as competition, intraguild predation, mutual interference, limiting resources, foraging behavior, and intrinsic rate of species growth may be responsible for determining distribution of abundances (Loreau 1992). The statistical mechanism theory highlights the influence of independent, statistical, or historical factors in dictating the relative abundance of species in large communities (May 1981). Mathematical descriptions that assume causal mechanisms include the geometric series and Fisher's logarithmic series, whereas statistical mechanisms underlie the lognormal distribution (Frontier 1985). It has also been argued that the numerically dominant/subdominant pattern seen in communities may be driven by factors that are associated with both the causal and statistical theories (Loreau 1992). In this case, ecological factors may influence the relative abundance associated with numerically dominant species, while independent properties may determine the relative scarcity associated with numerically subdominant species.

My Research Questions and Study System

From a pest regulation perspective, it may be assumed that because there are several relatively scarce species in generalist predator assemblages, the key to effective control is to increase the abundance of all subdominant species. However, this approach may not only be unfeasible but also could result in an increased potential for antagonistic interactions and possible pest outbreaks (Letourneau and Dyer 1998, Moran and Scheidler 2002, Prasad and Snyder 2004, Mathews et al. 2004). The alternative assumption can also be made, in which only the numerically dominant species are assumed to be the most effective, in which case it would be better to focus conservation efforts on these species. Under this assumption, however, the potential additive or synergistic effects of the inclusion and conservation of numerically subdominant predator species may be neglected. In order to evaluate these alternate assumptions, it is critical to understand the impact of numerically dominant predators on pest mortality relative to the impact of an entire assemblage of generalist predators. Furthermore, it is also important to determine the influence of certain elements of predator identity, such as voraciousness, on the impact of numerically dominant predators relative to an entire assemblage. The question then becomes: do the numerically dominant predator species impose more pest mortality alone than an assemblage of generalist predators? A second and related question also must be asked, i.e., how important is the taxonomic identity of the numerically dominant predators in determining whether they impose greater pest mortality alone than an assemblage? These are the major questions that I propose to answer with my research.

Collards (*Brassica oleracea* var. *acephala*) serve as an ideal agroecosystem for addressing questions on generalist arthropod predators and pest mortality. A diverse assemblage of generalist predators is present in collard fields (Root 1973, Schellhorn and Sork 1997). Furthermore, *Pieris rapae* is one of the dominant lepidopteran pests of collards (*Brassica oleracea* var. *acephala*) and other crucifers in North America (Dempster 1967, Ashby 1974, Jones et al. 1987, Loader and Damman 1991, Schmaedick and Shelton 2000). I therefore investigated the impacts of relative abundance and identity on the mortality imposed by generalist predators found in collards on *P. rapae* larval mortality. I specifically tested two hypotheses: 1) Regardless of identity, the numerically dominant species will impose greater *P. rapae* larval mortality alone than when in an assemblage of generalist predators, and 2) the identity of the numerically dominant species is important in determining whether it will impose greater *P. rapae* larval mortality alone than when in an assemblage of generalist predators. The results of this research may be significant in developing sound conservation biological control strategies that alter the relative abundance of species in such a way as to enhance pest suppression.

Brief Overview of Research Objectives

The major objectives of this study will be addressed in the following chapters. In chapter 2, I discuss the research that I conducted to identify the potential predators of early instar *P. rapae* among the generalist arthropod predator community in collards in Maryland. Species abundance distributions were generated in order to

determine which species were numerically dominant and numerically subdominant. In chapter 3, I describe the feeding bioassays that were conducted in order to determine which of the potential predators found in the field consumed early instar *P. rapae*. The overall objectives of chapters 2 and 3 were therefore of importance in determining which predator taxa would be used in testing the hypothesis. In chapter 4, I provide a description of the experiments used to test the hypotheses stated above.

CHAPTER 2:

Assessing the Predatory Arthropod Fauna in Collards (*Brassica Oleraceae* Var. *Acephala*): A Microhabitat Breakdown of the Generalist Predator Community

INTRODUCTION

In many agroecosystems, generalist predators comprise a diverse and dominant component of the arthropod fauna (Barbosa 1998). Their use as biocontrol agents has recently gained more attention, and there is growing evidence that generalist predators can impose significant mortality on pests (Symondson et al. 2002). The potential of generalist predators has stimulated interest in conservation biological control, which seeks to sustain or enhance the performance and density of local natural enemy communities in managed habitats (Barbosa 1998, Pickett and Bugg 1998, Landis et al. 2000). However, in any given agroecosystem all of the species in the natural enemy assemblage, e.g., in the generalist predator assemblage, may not consume the target pest species. In addition, the target pest may not be the primary food source of predators, particularly those that are omnivorous. For instance, although carabid beetles are among the most abundant generalist predators in many crops, seeds may constitute the major component of their diet (Fawki and Toft 2005, Honek et al. 2006). Furthermore, some generalist predators may preferentially engage in intraguild predation rather than the consumption of pest herbivores (Polis et al. 1989, Denoth et al. 2002, Rosenheim et al. 1993, Finke and Denno 2002, 2003, 2005, Prasad and Snyder 2004). Conservation biological control should be aimed at the appropriate subset of the entire generalist predator community,

based on how natural enemies interact with each other and species that are potential prey. An important first step in developing sound conservation biological strategy should therefore be identifying the generalist predator taxa that are most likely to consume target pests.

In collards, (*Brassica oleracea* var. *acephala*), *Pieris rapae* L. (Lepidoptera: Pieridae), is a serious pest of collards in many areas of North America. Multiple studies have surveyed the assemblage of generalist arthropod predators found on collards plants (Root 1973, Schellhorn and Sork 1997). However, while the important generalist predators of *P. rapae* have been identified in other crucifer crops in several regions of the world (Dempster 1967, Ashby 1974, Jones et al. 1987, Schmaedick and Shelton 1999, Schmaedick and Shelton 2000), it is not clear which generalist predators are most likely to impose mortality on *P. rapae* larvae in collards, particularly in Maryland. Due to the relatively plant-adhering nature of *P. rapae* larvae (Harcourt 1961, Jones 1977), it is reasonable to assume that the predators that are most likely to consume *P. rapae* are those that primarily inhabit collard plants (i.e. the foliar microhabitat). However, there is little information on the importance of generalist predators in the epigeal and aerial microhabitats of collards as mortality agents of *P. rapae*. Nor is much known about the extent to which species in those assemblages overlap onto and forage on collard foliage. Generalist predators from these microhabitats or domains (sensu Schmitz 2005), may play an important role in exerting mortality on *P. rapae* populations, especially if they overlap onto collard plants. Thus, an assessment of the multiple microhabitats in collard agroecosystems

can be important in determining which generalist predators have the greatest potential to exert mortality on *P. rapae* populations.

Another potentially important factor to take into account when determining the potential effectiveness of predators is their relative abundance. A relatively specific and widespread pattern of species abundance has been documented in several communities, regardless of taxonomic identity of the community (Sugihara 1980, Loreau 1992, Paarmann et al. 2001, Barbosa et al. 2003, Barbosa et al. 2005). Typically, in most communities or assemblages, species abundance distribution is such that there is one or a few relatively abundant (or numerically dominant) species and the remaining species are relatively scarce (or numerically subdominant). In general, it is assumed that the numerically dominant predators exert greater mortality on *P. rapae* than numerically subdominant predators. However, this assumption has rarely been tested. The impact of relative abundance among generalist predators on pest mortality will be examined in greater detail in chapter 4. If indeed relative abundance of predators is a key factor in their effectiveness, it is important from a pest management standpoint to determine which predators in agroecosystems are numerically dominant and which are numerically subdominant.

In this chapter I report the results of my assessment of the community of generalist arthropod predators in three major microhabitats in collards, i.e., the foliar, epigeal (or ground-dwelling) and aerial microhabitats. Species abundance distributions were generated in order to determine which predators were numerically dominant and subdominant in each microhabitat. Furthermore, I determined which

generalist predators were most likely to impact larval *P. rapae* populations by focusing on the taxa that were found on, or overlapped into, the foliar microhabitat.

METHODS

Field Study Sites

Two collard (Vates variety) plots were established both at the Wye Research and Education Center (Queenstown, Maryland) and the Central Maryland Research and Education Center at Upper Marlboro (Upper Marlboro, Maryland). Collard plots at the Wye site were established on May 8, 2004. The plots were conventionally tilled, approximately 23m x 33m with 26 1m rows, 6.5 m apart from each other. One plot was surrounded by fallow fields 8m to the east and south, a corn field 4.5 m to the north, and the other collard plot to the west. The second plot was surrounded by a barley field 8 m to the west, a corn field 4.5 m to the north, and a fallow field 8 m to the south. At Upper Marlboro, two 23m x 33m no-till plots were also established on May 8. One plot contained 25 rows separated by 1 m, surrounded to the north, east, and west by grass, and a hay field 8 m to the south. The second plot was approximately 150 meters southwest of the first, had 26 rows, and was surrounded by a corn field 10 m to the northeast, a fallow field to east, and grasses 5 m to the north, west, and south.

Foliar Microhabitat Sampling

The assemblage of foliar generalist predators was sampled by visually inspecting plants and hand collecting predators found on collard plants. Ten plants were randomly selected within a 16m x 16m area in the center of each plot at each site. Each plant was searched for a 5 minute period once a week. Visual inspections typically took place between the hours of 1000 to 1200 (EST). All arthropods were collected and placed in vials with 90% ethyl alcohol and labeled by site, date, time, row, plot, and plant number. With the exception of spiders, most arthropods were identified to species or morphospecies (pending further identification). The sampling period at Wye started on June 15 and ended on August 2, 2004, while at Upper Marlboro it ran from June 16 to July 28, 2004.

Epigeal Microhabitat Sampling

The assemblage of epigeal or ground-dwelling, generalist predators was sampled using pitfall traps. A 16m x 16 m grid of 9 pitfall traps was placed in the center of each collard plot, at both sites. The 16m x 16 m grid was established by replacing a plant every 8 m with a pitfall trap within the center of the plot. Pitfall traps consisted of two 473 ml clear plastic cups (9.7 cm diameter opening; Solo Cup Co.[®], Urbana, Illinois), one inside the other. A plastic plate roof was placed above the trap to protect it from rain. Approximately 60 ml of antifreeze was added to each trap. Pitfalls were left open for a 24 hour period once a week and arthropods were collected per trap, per plot, and per site. Contents from each pitfall were placed in containers and labeled by site, date, time, row, plot, and trap number. Collections

were rinsed and stored in 90% ethyl alcohol at the lab. Arthropod predators were identified to lowest taxonomic level possible, typically to family. Efforts to further identify specimens to genus and species are currently underway. The sampling period lasted 8 weeks, starting at Wye on June 15 and ending on August 3, 2004, while at Upper Marlboro the period ran from June 17 to July 28, 2004.

Aerial Microhabitat Sampling

The aerial generalist predator assemblage was sampled by sweeping just above collard plants. Within a 16m x 16m area, in the center of each plot, ten sweep samples were taken. Ten plants within this central area were randomly selected as starting points. From the starting point plant, ten paces were taken along the row in a northward direction and for each pace two sweeps were taken. Sweeps were made using a 40 cm diameter heavy duty sweep net. Sweep samples typically took place between the hours of 1000 to 1200 (EST). The contents from the nets were transferred to plastic bags (Ziploc Co.®) and labeled by site, date, time, row, plot, and starting plant number. Collections were placed and stored in vials with 90% ethyl alcohol. Arthropod predators were identified to lowest taxonomic level, typically to species. The sampling period at Wye began on June 15 and ended on August 2, 2004, while at Upper Marlboro it ran from June 16 to July 28, 2004.

Species Abundance Distributions

In determining which generalist predators were numerically dominant and numerically subdominant in collard fields, I generated species abundance distribution

curves for the epigeal, foliar, and aerial microhabitats. Abundances of arthropod predator species/morphospecies were tabulated over the entire sampling period. Abundances of species/morphospecies represented both immature and adult individuals at both sites, for each microhabitat.

RESULTS AND DISCUSSION

Foliar Microhabitat

Arthropod predators found in the foliar microhabitat represented several families of the class Arachnida (including the families Araneidae, Lycosidae, Salticidae, Tetragnathidae, and Thomisidae) and Insecta (including the families Coccinellidae, Formicidae, Lampyridae, Miridae, Nabidae, Pentatomidae, and Syrphidae) (Table 2.1 lists the taxonomic authorities and rank order for all morphospecies/species collected in the foliar microhabitat). In the foliar microhabitat there were a total of 182 individuals of 20 species/morphospecies (Fig. 2.1). *Coleomegilla maculata* (Coccinellidae) (rank order 1) was the numerically dominant species, comprising 56% of the total number of individuals of all species/morphospecies. Of the numerically subdominant predators, only three species represented more than 5% of the total collection: *Nabis roseipennis* (Nabidae) (rank order 2; 12%), Tetragnathidae morphospecies 1 (rank order 3; 7%), and *Lygus lineolaris* (Miridae) (rank order 4; 6%). The remaining 16 numerically subdominant species comprised the remaining 19% of the total abundance of the assemblage.

Generalist predators found on the collard foliage potentially have the greatest probability of encountering *P. rapae* larvae, and thus may be assumed to be the most likely species to consume them. Indeed, there is evidence that the numerically dominant *Coleomegilla maculata* can have a significant impact on *P. rapae* in other crucifer crops (Schmaedick and Shelton 2000). In addition, congeneric species of the numerically subdominant *Nabis roseipennis*, *Coccinella septempunctata* (Coccinellidae) and members of the family Syrphidae have also all been shown to exert mortality on *P. rapae* (Ashby 1974, Schmaedick and Shelton 2000). While the numerically subdominant *Lygus lineolaris* may be considered a pest in several crops, it has been reported to also consume *P. rapae*, both in collards (Culliney et al. 1986) and cabbage (*Brassica oleracea* var. *capitata*) (Schmaedick and Shelton 2000). However, not all of the predators found in the foliar microhabitat are necessarily likely predators of *P. rapae* larvae. Web-building spiders such as Tetragnathidae and Araneidae, for instance, are not likely to capture relatively sedentary herbivores such as larval *P. rapae*.

Epigeal Microhabitat

The epigeal microhabitat had both the greatest number of species/morphospecies (85) and the greatest overall abundance (2720 individuals) relative to the two other microhabitats (Table 2.2, Fig. 2.2). The majority of the species/morphospecies collected pertain to families in the class Insecta, i.e., Staphylinidae, Carabidae, Formicidae, and from the family Lycosidae in the class Arachnida. The numerically dominant *Amisch sp.1* (Staphylinidae) (rank order 1)

comprised 21% of all individuals collected in the epigeal microhabitat. Only five other species/morphospecies comprised more than 5% of the total number of individuals collected; *Lasius alienus* (Formicidae) (rank order 2; 13%), *Pardosa* sp. 1 (Lycosidae) (rank order 3; 8%), *Pardosa* sp. 2 (rank order 4; 7%), *Pheidole bicarinata* (Formicidae) (rank order 5; 6%), and *Pardosa* sp. 3 (rank order 6; 5%). The remaining 79 species/morphospecies accounted for the remaining 39% of the total individuals collected. Four epigeal predator morphospecies were found to overlap into the foliar microhabitat; Lycosidae morphospecies 1, Lycosidae morphospecies 3, and a winged *Tetramorium* sp. 1 (Formicidae).

Several important inferences on the potential of epigeal generalist predators to consume *P. rapae* can be made from the findings presented here. First, despite the great diversity and abundance of epigeal predators, very few epigeal predators were found on collard plants. Epigeal predators that do not climb collard plants have very little contact with *P. rapae* larvae, and thus are not likely to play an important role in their mortality. Nevertheless, some epigeal predators such as staphylinid and carabid beetles may have climbed collard plants when sampling was not being conducted, such as at night (Vickerman and Sunderland 1975). In addition, I cannot eliminate the possibility that abiotic factors such as wind (Dempster 1967) or attack by foliar predators may knock *P. rapae* larvae off the plants, making them more susceptible to capture by predators that are restricted to the epigeal microhabitat. As for the epigeal predators that overlapped onto the collard foliage, there is evidence that the numerically subdominant *Pardosa* sp. 1 and other Lycosidae may be important predators of *P. rapae* in other crucifers (Ashby 1974, Schmaedick and Shelton 2000),

and thus should be considered as a potential predator of *P. rapae*. On the other hand, the numerically subdominant *Tetramorium* spp., represented by two alate adults, may have been transient species in search of mates or other resources and was an unlikely predator of *P. rapae*.

Aerial Microhabitat

The majority of the species/morphospecies found in the aerial microhabitat were from the order Heteroptera (Table 2.3, Fig. 2.3). There were 19 species/morphospecies and a total of 457 individuals found in the aerial microhabitat. *Lygus lineolaris* (rank order 1), the numerically dominant species, comprised nearly 70% of the total individuals. The numerically subdominant *Orius insidiosus* (Anthocoridae) (rank order 2, 10%) and *Coleomegilla maculata* (rank order 3, 8%) were the only two other species to comprise at least 5% of the total individuals collected. All other numerically subdominant species/morphospecies combined comprised 12% of the total individuals collected. Five species in the aerial microhabitat were found to overlap into the foliar microhabitat: *Lygus lineolaris*, *Coleomegilla maculata*, *Chauliognathus marginatus* (Cantharidae), *Geocoris punctipes* (Geocoridae), and *Nabis roseipennis*.

The five species found in both the aerial and foliar microhabitats are also potential predators of *P. rapae*. Aside from these five species, there is at least one more aerial species that, while not considered any further in this study, may exert substantial mortality on *P. rapae*. *Polistes* spp. (Vespidae) were observed foraging through the collard plots during sampling, but were able to evade the collecting nets

during sweep sampling. Furthermore, they also were observed, on multiple occasions, to attack and capture *P. rapae* larvae. *Polistes* spp. can exert significant suppression on lepidopteran pests in cabbage and other agricultural systems (Michener and Michener 1951, Rabb 1960, Gould and Jeanne 1984, Raveret and Richter 2000).

Conclusions

While there were certain limitations to this study, as noted earlier, I was successful in determining which generalist predators in my collard plots may be most likely to consume *P. rapae* larvae. These data also suggest that the predator assemblages of the foliar, epigeal, and aerial microhabitats in collard systems may be relatively distinct. These findings represent a first step in identifying the key predators of *P. rapae* in collards in Maryland.

Table 2.1. Taxonomic authorities and rank order of generalist arthropod predators captured in the foliar microhabitat in collards.

Taxa	Rank order
<i>Coleomegilla maculata</i>	1
<i>Nabis roseipennis</i>	2
Tetragnathidae morphospecies 1	3
<i>Lygus lineolaris</i>	4
Lycosidae morphospecies 3	5
Araneidae morphospecies 1	6
<i>Coccinella septempunctata</i>	7
Lycosidae morphospecies 1	8
Araneidae morphospecies 2	9
Salticidae morphospecies 1	10
<i>Podisus maculiventris</i>	11
Salticidae morphospecies 2	12
Thomisidae morphospecies 1	13
<i>Euschistus servus</i>	14
Lampyridae morphospecies 1	15
<i>Tetramorium</i> morphospecies 1	16
Syrphidae morphospecies 1	17
Salticidae morphospecies 3	18

Table 2.2. Taxonomic authorities and rank order of generalist arthropod predators captured in the epigeal microhabitat in collards.

Taxa	Rank order
<i>Amisch</i> morphospecies 1	1
<i>Lasius alienus</i>	2
<i>Pardosa</i> morphospecies 1	3
<i>Pardosa</i> morphospecies 2	4
<i>Pheidole bicarinata vinelandica</i>	5
<i>Pardosa</i> morphospecies 3	6
<i>Pterostichus lucublandus</i>	7
Formicidae morphospecies 1	8
<i>Pardosa</i> morphospecies 4	9
<i>Pardosa</i> morphospecies 5	10
<i>Pardosa</i> morphospecies 6	11
<i>Tetramorium caespitum</i>	12
<i>Bembidion semistrictum</i>	13
<i>Amisch</i> morphospecies 2.	14
<i>Aphaenogaster</i> morphospecies 1	15
Carabidae morphospecies 1	16
Staphylinidae morphospecies 1	17
<i>Stenolophus ochropezus</i>	18
Carabidae morphospecies 2	19
Staphylinidae morphospecies 2	20
Carabidae morphospecies 3	21
<i>Pardosa</i> morphospecies 7	22
Staphylinidae morphospecies 3	23
Staphylinidae morphospecies 4	24
<i>Coleomegilla maculata</i>	25
Staphylinidae morphospecies 5	26
Carabidae morphospecies 4	27
Carabidae morphospecies 5	28
Staphylinidae morphospecies 6	29
<i>Pardosa</i> morphospecies 8	30
Lycosidae morphospecies 1	31
Lycosidae morphospecies 2	32
Staphylinidae morphospecies 7	33
Staphylinidae morphospecies 8	34
<i>Pardosa</i> morphospecies 9	35
Carabidae morphospecies 6	36
Carabidae morphospecies 7	37
Carabidae morphospecies 8	38

Table 2.2 contd. Taxonomic authorities and rank order of generalist arthropod predators captured in the epigeal microhabitat in collards.

Taxa	Rank Order
Lycosidae morphospecies 3	39
Carabidae morphospecies 9	40
Staphylinidae morphospecies 9	41
Staphylinidae morphospecies 10	42
Staphylinidae morphospecies 11	43
<i>Monomorium minimum</i>	44
<i>Aphaenogaster</i> morphospecies 2	45
<i>Pardosa</i> morphospecies 10	46
Carabidae morphospecies 10	47
Lycosidae morphospecies 4	48
<i>Pardosa</i> morphospecies 10	49
Staphylinidae morphospecies 12	50
Staphylinidae morphospecies 13	51
Staphylinidae morphospecies 14	52
<i>Micracanthia humilis</i>	53
<i>Nabis roseipennis</i>	54
Carabidae morphospecies 11	55
Carabidae morphospecies 12	56
Carabidae morphospecies 13	57
Staphylinidae morphospecies 15	58
Staphylinidae morphospecies 16	59
Staphylinidae morphospecies 17	60
<i>Tetramorium</i> morphospecies 1	61
Formicidae morphospecies 2	62
<i>Pardosa</i> morphospecies 11	63
Thomisidae morphospecies 2	64
<i>Orius insidiosus</i>	65
<i>Barce fraternal</i>	66
<i>Melanolestes picipes</i>	67
Carabidae morphospecies 14	68
Carabidae morphospecies 15	69
Carabidae morphospecies 16	70
Carabidae morphospecies 17	71
Carabidae morphospecies 18	72
Staphylinidae morphospecies 18	73
Staphylinidae morphospecies 19	74
Staphylinidae morphospecies 20	75
Staphylinidae morphospecies 21	76
Staphylinidae morphospecies 22	77

Table 2.2 contd. Taxonomic authorities and rank order of generalist arthropod predators captured in the epigeal microhabitat in collards.

Taxa	Rank order
Staphylinidae morphospecies 24	79
Staphylinidae morphospecies 25	80
<i>Tetramorium</i> morphospecies 2	81
Mutillidae morphospecies 1	82
<i>Formica</i> (fusca) morphospecies 1	83
<i>Hypoponera</i> morphospecies 1	84
Formicidae morphospecies 3	85

Table 2.3. Taxonomic authorities and rank order of generalist arthropod predators captured in the aerial microhabitat in collards.

Taxa	Rank order
<i>Lygus lineolaris</i>	1
<i>Orius insidiosus</i>	2
<i>Coleomegilla maculata</i>	3
<i>Polymerus basalis</i>	4
Tetragnathidae morphospecies 2	5
<i>Monomorium minimum</i>	6
<i>Micracanthia humilis</i>	7
<i>Jalysus wickhami</i>	8
<i>Chauliognathus marginatus</i>	9
<i>Geocoris punctipes</i>	10
<i>Trigonotylus caelestialium</i>	11
<i>Lasius alienus</i>	12
<i>Harmonia axyridis</i>	13
Staphylinidae morphospecies 12	14
Salticidae morphospecies 4	15
<i>Nabis roseipennis</i>	16
<i>Sinea</i> morphospecies 1	17
Carabidae morphospecies 7	18
Staphylinidae morphospecies 19	19

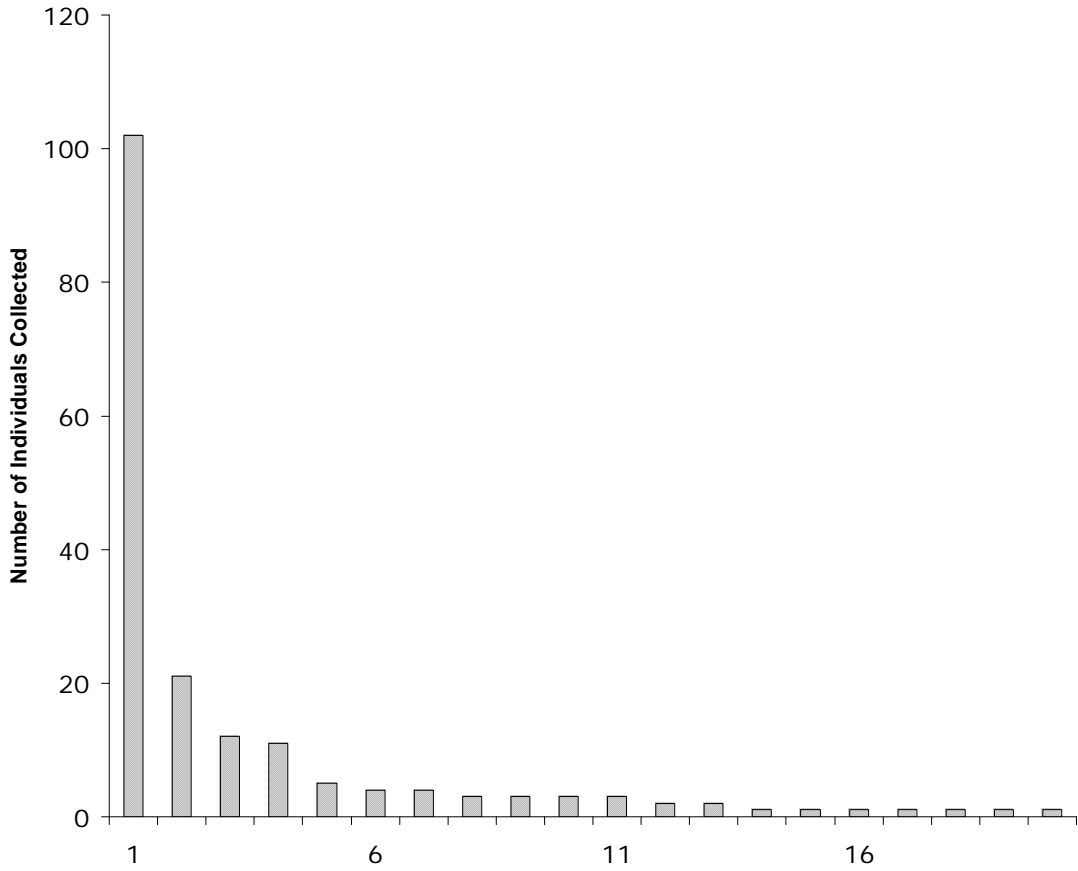


Figure 2.1. Total number of individuals of each species/morphospecies collected in the foliar microhabitat. Abundances shown here are combined from both sites. Numbers on the x-axis represent the rank order of the species/morphospecies from most to least abundant. The names of all species/morphospecies are listed by rank order in Table 2.1.

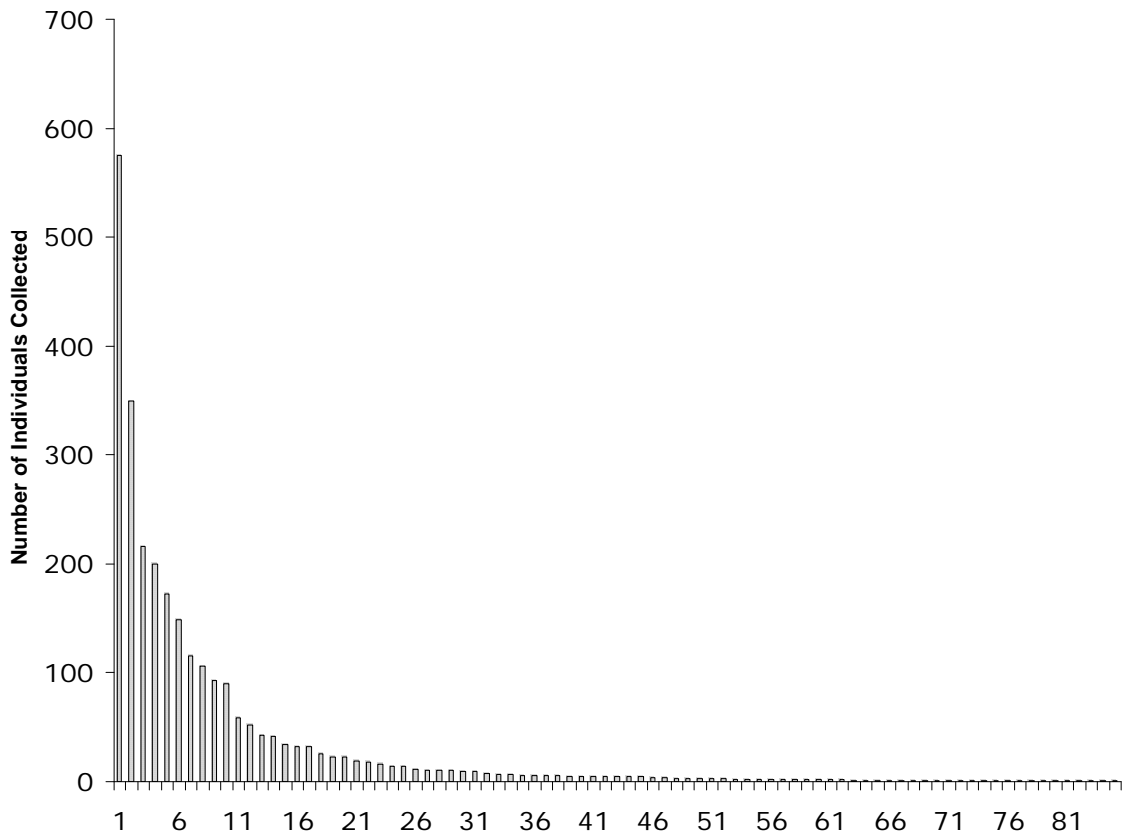


Figure 2.2. Total number of individuals of each species/morphospecies collected in the epigeal microhabitat. Abundances shown here are combined from both sites. Numbers on the x-axis represent the rank order of the species/morphospecies from most to least abundant. The names of all species/morphospecies are listed by rank order in Table 2.1.

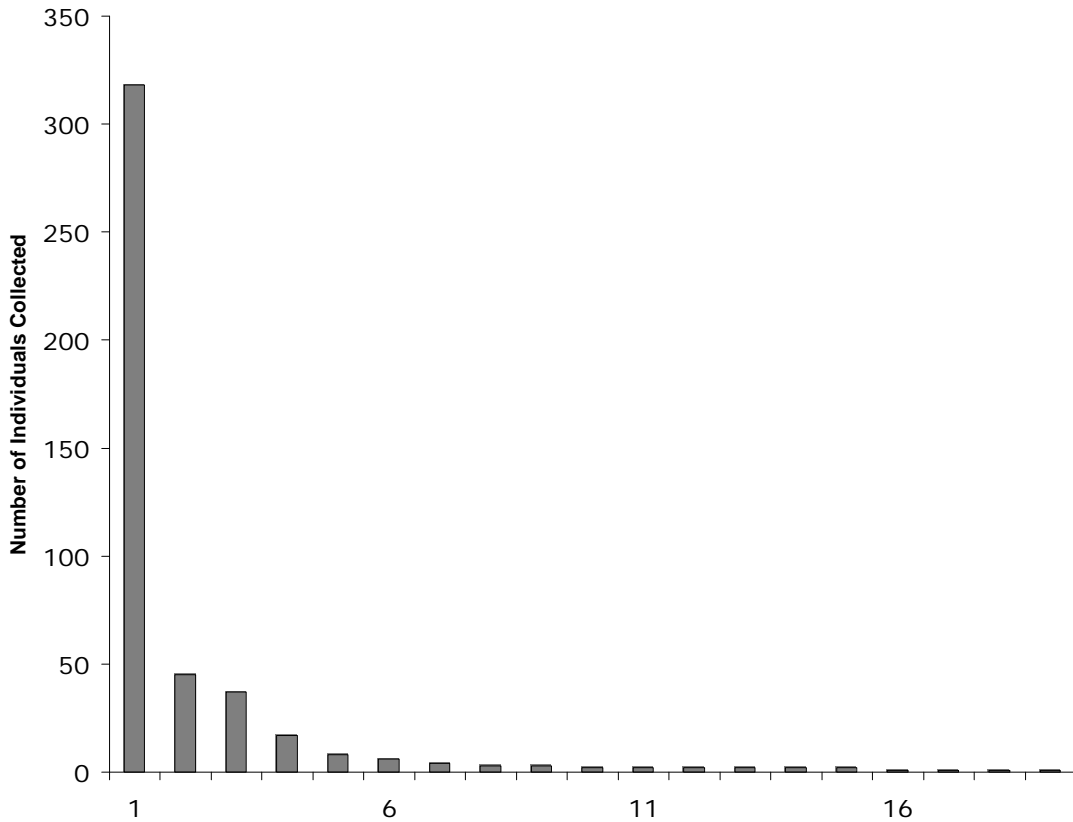


Figure 2.3. Total number of individuals of each species/morphospecies collected in the aerial microhabitat. Abundances shown here are combined from both sites.

Numbers on the x-axis represent the rank order of the species/morphospecies from most to least abundant. The names of all species/morphospecies are listed by rank order in Table 2.3.

CHAPTER 3:

Identifying the Major Generalist Predators of *Pieris Rapae* L. in collards

INTRODUCTION

Introduced from Europe in the late 19th century, *Pieris rapae* L. (Lepidoptera: Pieridae) is among the most damaging pests of collards, *Brassica oleracea* var. *acephala* (Cruciferae), in North America. While management of *P. rapae* in collards continues to rely heavily on the application of chemical insecticides, there is evidence that naturally occurring generalist arthropod predators in crucifers may act as effective biocontrol agents. Life table analysis of *P. rapae* in multiple crucifer crops indicates that generalist predators play an important role in imposing mortality on early larval stages (Moss 1933, Richards 1940, Harcourt 1961, Jones et al. 1987). Dempster (1964) and Ashby (1974) combined life table and serological analysis to further demonstrate that several members of the generalist predator assemblage in Brussel sprouts (*Brassica oleracea* var. *gemmifera*) and cabbage (*Brassica oleracea* var. *capitata*) can have an impact on early instar *P. rapae*. More recently, exclusion experiments and feeding bioassays have provided further evidence of the potential effectiveness of generalist predators as mortality agents of *P. rapae* in cabbage (Schmaedick and Shelton 1999, Schmaedick and Shelton 2000). In collards there is at least one study that has shown that the assemblage of generalist predators may impose substantial mortality on early instar *P. rapae* (Loader and Damman 1991), particularly on plants with low nitrogen levels. However, it is not clear which members of the generalist predator assemblage in collards are primarily responsible

for imposing mortality on *P. rapae*, particularly in Maryland. Therefore, while generalist arthropod predators may act as an important force in controlling *P. rapae* populations in collards, there is little information as to which predators in the assemblage are imposing significant mortality in this region of North America.

Starting with the species that were found to be numerically dominant and subdominant generalist predators in collards (Chapter 2), in this study I identified which of these potential predators actually consume *P. rapae* larvae. This was accomplished by conducting a series of laboratory feeding bioassays. Furthermore, I determined how voracious the predators that consume *P. rapae* are by measuring and comparing their per capita larval consumptions over a 24 hour period. Identity-specific traits such as voraciousness may play an important role in determining the level of mortality imposed by a generalist predator. The influence of relative abundance and identity among generalist predators on *P. rapae* larval mortality will be examined in greater detail in chapter 4.

METHODS

Initial Species Sorting

In chapter 2, I identified the numerically dominant and numerically subdominant predators that most likely consume early instar *P. rapae*. However, in testing which of these potential predators actually consume *P. rapae* larvae in feeding bioassays, I excluded species that possessed ecological or behavioral traits that would make their use in experiments inappropriate. Social insect species, such as ants and vespid wasps, were disregarded because their complex foraging behavior or social

life-style would have made determinations of feeding preferences unfeasible or would produce data of little validity. For example, in the absence of their nests the foraging behavior of individual ants and wasps would likely be abnormal, or at least significantly altered, and thus experiments would produce inaccurate or inappropriate data.

Generalist Arthropod Predators of *P. rapae* Larvae

To determine if the remaining potential predators were predacious on *P. rapae* larvae, I conducted a series of no-choice laboratory feeding bioassays during May through August 2005. I tested all of the potential predators that 1) were not eliminated by the criteria established in the initial species sorting (see above), and 2) were collected in the field in abundances of 5 or more individuals. A total of 9 species were tested: the numerically dominant foliar predator *Coleomegilla maculata* (n= 14) and the numerically subdominant foliar predators *Coccinella septempunctata* (n= 15), *Chauliognathus marginatus* (n= 5), *Geocoris punctipes* (n= 5), *Lygus lineolaris* (n= 7), *Pardosa* sp. (n= 5), *Nabis roseipennis* (n= 9), *P. maculiventris* (n= 6), and *Pterostichus* sp. (n= 5). The epigeal predator *Pterostichus* sp., despite its absence in the foliar microhabitat (see chapter 2), was included because carabids have been shown to consume *P. rapae* larvae in other crucifers (Dempster 1969), and because it was readily collected in the field in the year that these tests were conducted.

Predators used in the feeding trials were mainly collected in collard, alfalfa (*Medicago sativa*), and sweet corn (*Zea mays* var. *saccharata*) plots at the Beltsville,

Upper Marlboro, and Wye research farms during the summer of 2005. Foliar and aerial predators were collected by hand and sweep net, respectively, while a 16m X 16m grid of 9 pitfall traps (without a killing agent) were used to trap epigeal species. Only adult predators were used in the feeding trials. *P. rapae* larvae used in the feeding trials were obtained from colonies initiated with adults collected at the Wye and Upper Marlboro research farms.

Feeding trials were conducted in microcosms, comprised of a single 15 cm tall collard plant in a 774 sq. cm pot, covered by a 3.8 L. mesh bag (AZ Partsmaster Co.[®]). Ten 1st instar *P. rapae* were haphazardly placed on the leaves of the microcosm plant and an individual predator, starved for 24hr, was added. A control microcosm of 10 individual larvae and no predator was included to determine the number of missing larvae in the absence of a predator. Microcosms were placed into an environmental chamber at 16L: 8D, a temperature of 22° C (L) and 16° C (D) and 70% RH, and left alone for 24 hours. These conditions reflect the average environmental conditions in Maryland from May to August. After 24 hours, the number of missing/partially consumed larvae for each predator species and the number of missing *P. rapae* larvae in the control treatment was counted. All predator and control treatments were replicated at least 5 times with different individuals.

Differences in the mean number of missing larvae for each predator treatment and the number missing in the no predator control treatment were analyzed with an analysis of variance (ANOVA) using PROC MIXED (SAS Institute 1999). Because heterogeneous variance could not be corrected with data transformations, variance groupings were used in the model. Following the ANOVA, planned contrasts among

the predator species and the control were conducted, with p-values corrected with Bonferroni adjustments. Species with significantly greater levels of mean missing larvae compared to the control treatment were considered to be predators of *P. rapae* larvae.

Differences in Per Capita Consumption of *P. rapae* Larvae

Laboratory feeding bioassays were again conducted from May to September 2006 to determine 1) the per capita larval consumption for the predators of *P. rapae*, and 2) whether there were differences in per capita larval consumption among the predators of *P. rapae*. The species tested included the numerically dominant *Coleomegilla maculata* and the numerically subdominant *Coccinella septempunctata* and *Podisus maculiventris* (see results below). Although the numerically dominant *Nabis roseipennis* was also a predator of *P. rapae*, in the year in which these tests were conducted they were not collected in sufficient numbers to be included in the feeding trials.

Laboratory colonies of the three predators species tested were established. *Coleomegilla maculata* adults were obtained from a pre-existing laboratory colony at the Insect Biocontrol Laboratory (USDA-ARS, Beltsville, MD) and were provisioned with a combination of substitute bee pollen (Betterbee Inc.[®]) and first instar *P. rapae*. Some *C. maculata* adults were also collected in collard, sweet corn, and alfalfa fields in Beltsville, MD. *Coccinella septempunctata* adults were hand collected in alfalfa fields planted in Beltsville, MD and were fed with first instar *P. rapae* and aphids collected from alfalfa fields. Some early collection of *C. septempunctata* adults was

done in alfalfa fields in Piedmont Co., N.C. *Podisus maculiventris* adults were collected in the field using Podisus pheromone traps (developed by Jeffrey R. Aldrich, USDA ARS, Beltsville, MD) haphazardly placed on deciduous trees at the Patuxent Wildlife Refuge (Beltsville, MD) and the Central Maryland Research and Education Center at Beltsville, MD. *P. maculiventris* adults were fed *Leptinotarsa decimlineata* larvae from a pre-existing colony (Galen Dively, University of Maryland, College Park, MD) and first instar *P. rapae* larvae. All colonies were maintained in separate 0.3m X 0.3m X 0.3m plexiglass cages kept on a laboratory bench (at 21-25°C and 16:8 L:D), each containing cotton wicks soaked in water and shredded paper for shelter. First instar *P. rapae* used in the feeding trials were reared from field collected adults collected from the Wye and Upper Marlboro research farms.

The protocol of these laboratory feeding bioassays was the same as it had been in the previous laboratory feeding bioassays, as described above, with the only exception being that each species tested was replicated 15 times. The mean per capita larval consumption for each predator was determined by counting the number of missing/partially consumed larvae after 24 hours. A control of ten 1st instar *P. rapae*, in the absence of a predator, was included to determine background mortality of *P. rapae* larvae on plants (1.063 mean larvae missing). Data from the control treatment was used to calculate an adjusted mean per capita larval consumption for each predator.

The adjusted mean per capita larval consumption for *Coleomegilla maculata*, *Coccinella septempunctata*, and *Podisus maculiventris* was compared using a one way ANOVA with PROC MIXED (SAS Institute 1999). Least square means for the predator species were obtained and compared using the Tukey-Kramer post hoc test. As different predator and plant individuals were used for each replica, a repeated measures analysis was not necessary.

RESULTS

Generalist Arthropod Predators of *P. rapae* Larvae

There was significant variation in the mean number of missing *P. rapae* larvae among the predators and the control treatment ($F_{9,56}$, $p < 0.001$). *Coccinella septempunctata*, *Coleomegilla maculata*, *Nabis roseipennis*, and *Podisus maculiventris* had significantly more mean missing larvae than the control (Fig. 3.1; $p < 0.05$). There were no significant differences in the mean number of missing larvae among the other five predator species when compared to the number missing in the control treatment (Fig. 3.1; $p > 0.19$).

From the analysis of the laboratory feeding trials, we determined that four of the nine tested taxa were predators of *P. rapae* larvae: the numerically dominant *C. maculata* and the numerically subdominant *C. septempunctata*, *N. roseipennis*, and *P. maculiventris*. Because sample sizes were unequal among predators and in some cases were low, it may not be possible to definitively conclude from the feeding trials that *C. marginatus*, *G. punctipes*, *L. lineolaris*, *Pardosa* sp., and *Pterostichus* sp. were or were not predators of *P. rapae* larvae. However, when individuals of the 9 predator

species were placed in a petri dishes with *P. rapae* larvae following the feeding trials, only *C. maculata*, *C. septempunctata*, *N. roseipennis*, *P. maculiventris*, and *Pterostichus* sp. were observed eating larvae. While *Pterostichus* sp. may eat larvae when they come into contact with them, it appears from the feeding trials and the community assessment (see chapter 2) that they cannot climb or are not typically found on plants, and are thus not likely to impose significant mortality on *P. rapae* larvae.

Differences in Per Capita Consumption of *P. rapae* Larvae

On average, the numerically subdominant *Coccinella septempunctata* consumed nearly twice as much *P. rapae* larvae per capita as the other species (Fig. 3.2). However, overall there were no significant differences in the adjusted mean per capita larval consumption among the numerically dominant *Coleomegilla maculata* and the numerically subdominant *Coccinella septempunctata* and *Podisus maculiventris* (Fig 3.2, $F_{2,25}$, $p=0.10$).

DISCUSSION

Generalist arthropod predators may represent an important source of mortality in larval populations of *Pieris rapae* in collards (Loader and Damman, 1991). From the laboratory feeding trials, I identified four members of the generalist predator assemblage in collard fields in Maryland that consume early instar *P. rapae*: *Coleomegilla maculata*, *Coccinella septempunctata*, *Nabis roseipennis*, and *Podisus maculiventris*. With the exception of *P. maculiventris*, previous findings have found that *Nabis* spp., *Coccinella* spp., and *Coleomegilla maculata* are predators of early

instar *P. rapae* in different crucifer systems in other regions (Ashby 1974, Schmaedick and Shelton 2000). This study represents an initial step into identifying the potentially important predators of *P. rapae* occurring in collard plots in Maryland.

Due to the relatively few species tested in laboratory feeding trials with respect to the entire assemblage of foliar generalist predators, it is possible that the guild of *P. rapae* generalist arthropod predators in collards may not be restricted to the species identified here. Ants (Jones 1987, Jones et al. 1987), vespids (Jones and Ives 1979, Gould and Jeanne 1984), and syrphid larvae (Dempster 1969, Ashby 1974) have been reported as important predators of *P. rapae* in other crucifers, although in my study these predators were not tested due to complexities discussed above or because they were not collected in sufficient numbers to be included (e. g., syrphid larvae). A better method of assessing which predators consume *P. rapae* might involve combining laboratory feeding assays with other tests, such as serological methods, electrophoretic techniques, prey marking, or even direct observation in the field (Luck et al. 1988).

The voraciousness of predators in consuming *P. rapae* larvae was determined by measuring per capita larval consumption in laboratory feeding assays. The lack of significance in the differences in per capita consumption of early instar *P. rapae* by *C. maculata*, *C. septempunctata*, and *P. maculiventris* may indicate that these species are equally voracious in consuming *P. rapae*, all things being equal. However, further laboratory feeding assays encompassing longer periods of time are needed to determine if a lack of significant difference in per capita larval consumption is due to the time period used in my tests. The use of a longer experimental time period may be

particularly important for predators with long prey handling time or with time consuming foraging behavior, such as *P. maculiventris* (Wiedenmann 1991).

A knowledge of which generalist arthropod predators consume early instar *P. rapae* is an important step in developing sound biological control practices in collards. I was successful in determining four major predators of *P. rapae* larvae in collards grown in Maryland. From a conservation biological control perspective, management tactics could be focused on the preservation of *C. maculata*, *C. septempunctata*, *N. roseipennis*, and *P. maculiventris* populations in collards. However, as an assemblage, the collective impact of these predators on *P. rapae* larval mortality remains unclear. Also unclear is the impact that relative abundance and identity-specific traits, such as voraciousness, may have on the *P. rapae* larval mortality imposed by these generalist predators when in an assemblage. In the next chapter, I investigate these impacts using assemblages composed of the numerically dominant *C. maculata* and the numerically subdominant *C. septempunctata* and *P. maculiventris*.

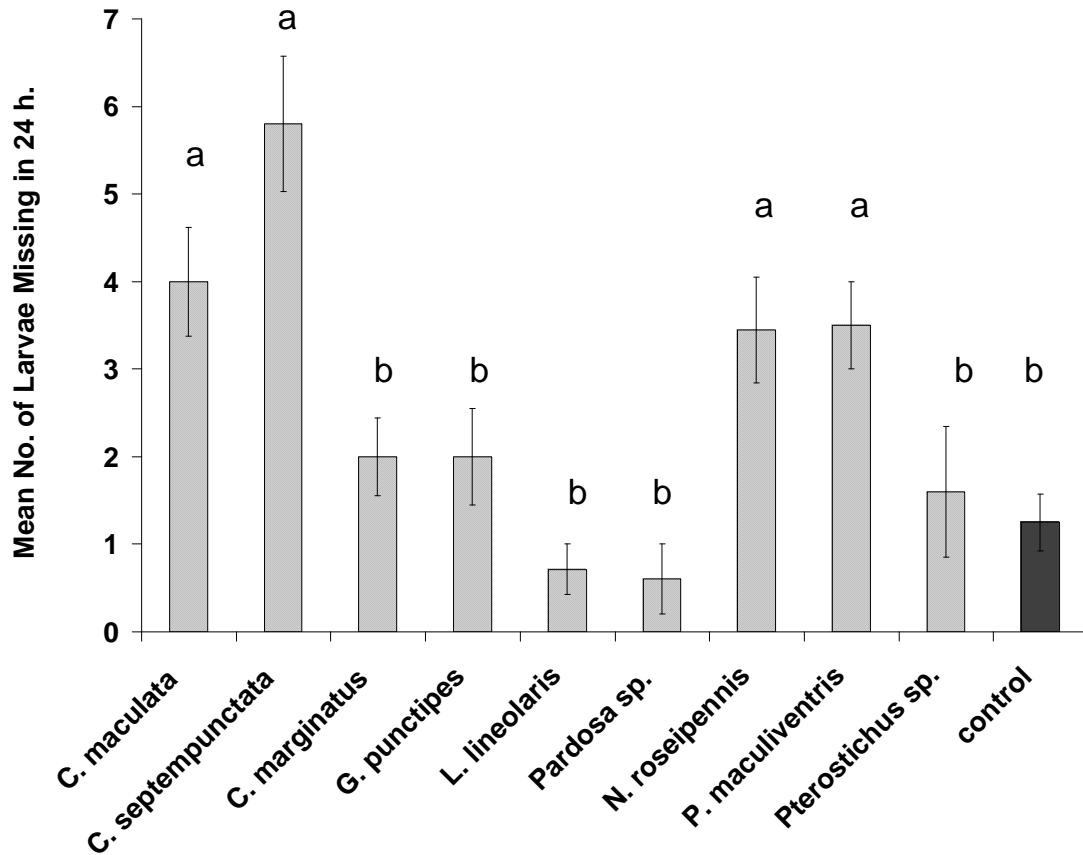


Figure 3.1. Mean number of larvae missing in 24 hours in the presence of each of nine generalist arthropod predator species/morphospecies and in a no predator control. P-values for contrasts between predators and the control were Bonferroni adjusted. Means with a different letter are significantly different at the $\alpha=0.05$ level. Data are presented as means \pm 1 SE.

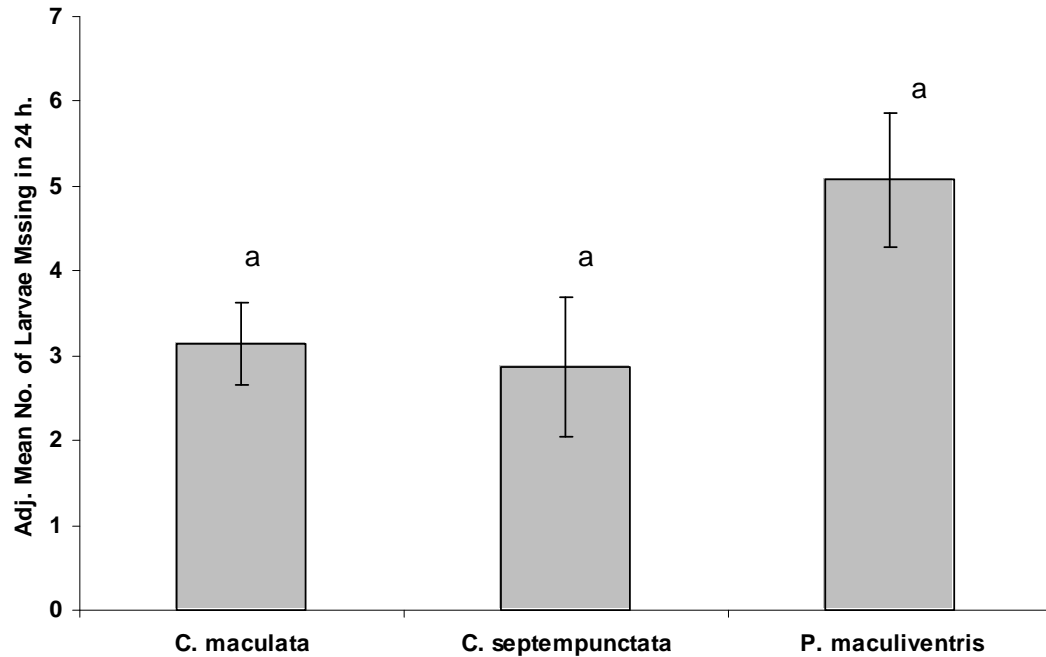


Figure 3.2. Adjusted mean per capita consumption of larvae (number of larvae missing in 24 hours) by *C. maculata*, *C. septempunctata*, and *P. maculiventris*. Adjusted means were calculated by subtracting mean number of missing larvae from the no predator control treatment from the mean per capita larval consumptions of each predator. P-values for contrasts between numerically dominant and numerically subdominant were Bonferroni adjusted ($\alpha=0.05$). Data are presented as means \pm 1 SE. Means with the same letter are not significantly different from each other.

CHAPTER 4:

The Influence of Relative Abundance and Identity on the Effectiveness of Generalist Predators as Biocontrol Agents of *Pieris Rapae* L.

INTRODUCTION

Among the principle assumptions of conservation biological control is one that proposes that a diverse and abundant community of natural enemies enhances the suppression of pest species. This principle underlies the Species Assemblage Control Hypothesis (Riechert and Lockley 1984, Provencher and Riechert 1994, Riechert and Lawrence 1997, Riechert 1999) that proposes that communities or assemblages of naturally occurring natural enemies can suppress pest populations more effectively than any one species in the assemblage or community. In the case of generalist predators this may be largely assumed to be the result of interactions among multiple species that enhance the mortality they impose on prey. These interactions may be additive, whereby the total impact of the assemblage is equal to the summed impacts of each species (Wootton 1994, Snyder and Ives 2003). Alternatively, it may result from synergistic interactions among predators where the impact of one predator may alter the behavior or habitat range of prey, making them more susceptible to attack by other predators (Soluk and Collins 1988, Losey and Denno 1999). However, negative interactions, such as intraguild predation and mutual interference, may also occur within generalist predator assemblages, potentially leading to lower levels of pest suppression (Rosenheim et al. 1993, Rosenheim et al. 1995). Ultimately, the interplay

of positive and negative interactions and the extent to which generalist predator assemblages are effective at regulating pests is still unclear.

Most of the studies that have investigated the impacts of predator assemblages have failed to consider the potential influences of assemblage structure on prey mortality. One particular aspect of assemblage structure that has not been investigated in this context is the distribution of relative abundance among predators. The relative abundance of predators in an assemblage may play a role in the type and strength of interactions that occur among species, which in turn may determine the impact of the assemblage on pest mortality (Provencher and Riechert 1994, Letourneau and Dyer 1998, Moran and Scheidler 2002, Chang and Snyder 2004). Typically, in predator assemblages, as well as in herbivore assemblages, there are only one or a few species that are relatively abundant (numerically dominant), while the majority of the members of the assemblage are relatively scarce (numerically subdominant) (Sugihara 1980, Loreau 1992, Paarmann et al. 2001, Barbosa et al. 2003, Barbosa et al. 2005). The widespread nature of this pattern suggests that the answer to certain questions might be important to the effective use of natural enemies in the biological control of pests. That is, given the pattern of relative abundance in generalist predator assemblages, how much pest mortality do the numerically dominant predators impose alone in relation to the entire assemblage? Does the addition of numerically subdominant species provide greater suppression of pests? While it has been assumed that numerically dominant predators are the key regulators of pests, it is not clear whether they alone impose greater mortality than an entire predator assemblage.

Shifts in predator abundance may also have drastic impacts on the levels of pest mortality imposed by a predator assemblage (Moran and Scheidler 2002, Prasad and Snyder 2004, Mathews et al. 2004). In conservation biological control one of the main goals is to enhance naturally occurring natural enemy populations through habitat manipulation and other tactics (Debach 1964, Van Driesche and Bellows Jr. 1996, Barbosa 1998). Clearly, such practices could lead to drastic changes in species abundance distribution within predator assemblages. What remains unclear is how changes in relative abundance can influence the effectiveness of species that typically occur as numerically dominant or numerically subdominant predators. For instance, if a numerically subdominant predator were to become numerically dominant e.g., due to habitat manipulations, can we expect that it will impose the same levels of pest mortality as the original numerically dominant predator? As numerically dominant species, are certain predators more voracious in consuming pests than others? Furthermore, will the numerically dominant predator, regardless of what species it is, always inflict greater pest mortality alone than the mortality imposed by the entire assemblage? That is, what is the importance of identity, in the context of predator voraciousness, on the impact of numerically dominant predators? None of these questions have been addressed experimentally.

I investigated the importance of relative abundance and identity among generalist species in predator assemblages in collards on the mortality imposed on *Pieris rapae* larvae, a major pest of crucifers. The assemblage evaluated consisted of *Coleomegilla maculata*, a numerically dominant predator, and *Coccinella septempunctata* and *Podisus maculiventris*, two numerically subdominant predators. I

specifically tested two hypotheses: 1. Regardless of identity, the numerically dominant species alone will impose greater *P. rapae* larval mortality than when in an assemblage of generalist predators, and 2. the identity of the numerically dominant species determines whether it alone will impose greater *P. rapae* larval mortality alone than when in an assemblage of generalist predators.

METHODS

Study System

Pieris rapae is one of the dominant lepidopteran pests of collards (*Brassica oleracea* var. *acephala*) in North America. A species-rich assemblage of generalist arthropod predators is present in collards in Maryland, and the pattern of relative abundance distribution is typical of most assemblages (see chapter 2). My field surveys indicated that *Coleomegilla maculata* was a numerically dominant predator and *Coccinella septempunctata* and *Podisus maculiventris* were numerically subdominant predators in collards during the months of May through August 2004 (see chapter 2). Based on laboratory feeding bioassays, I determined that *C. maculata*, *C. septempunctata*, and *P. maculiventris* are predators of early instar *P. rapae*, and that they each consume similar levels of *P. rapae* larvae over a 24 hour period, i.e., they have similar per capita consumption (see chapter 3).

Predator and *P. rapae* Collection and Colony Establishment

Colonies of *C. maculata*, *C. septempunctata*, *P. maculiventris*, and *P. rapae* were established in the lab. Adult *C. maculata* were obtained from a pre-existing colony established at the Insect Biocontrol Laboratory (USDA-ARS, Beltsville, MD) and were also collected in the field. *C. maculata* and *C. septempunctata* adults were primarily collected in crucifer, alfalfa (*Medicago sativa*), sweet corn (*Zea mays* var. *saccharata*), small grain, and vegetable fields at the Beltsville, Upper Marlboro, and Wye research farms during the summer of 2006 (see methods, chapter 2) Some early collection (April 2006) of *C. septempunctata* adults was done in alfalfa fields in Piedmont Co., N.C. At all locations, predators were collected both by hand and using sweep nets. *Podisus maculiventris* adults were collected in the field using *Podisus* pheromone traps (developed by Jeffrey R. Aldrich, USDA ARS, Beltsville, MD) haphazardly placed on deciduous trees at the Patuxent Wildlife Refuge (Beltsville, MD) and the Central Maryland Research and Education Center at Beltsville, MD. *P. rapae* adults were collected in crucifer fields at the same locations in Maryland from April to September 2006.

Predator colonies were housed in separate 0.3m X 0.3m X 0.3m plexiglas cages and provisioned with water and food (following the protocol described in the methods section of chapter 3). *P. rapae* adults were placed in 1m X 1m X 1m cages containing 2 six-week old collard plants, for feeding and oviposition. Adults were provided with sponges soaked in honey water. Every two days collard plants were checked for newly laid *P. rapae* eggs, and egg masses were transferred to 8” diameter

Petri dishes with fresh collard leaves. To slow down growth, *P. rapae* larvae were kept in refrigerators set at 16°C. Predators were kept in colonies until needed for the experiments described below.

Mesocosm Experiments

Experimental mesocosms were used to determine the influence of relative abundance and identity of numerically dominant predators on larval *P. rapae* mortality. Mesocosms consisted of 26.5 L pots (Olympia 2000, Nursery Supplies Inc.[®]) containing 3, four-week old collard plants. Nineteen liter mesh bags (AZ Partsmaster Co.[®]) supported by modified tomato trellices, were used to enclose the plants. Thirty 1st instar *P. rapae* were placed on the leaves of the three collard plants, ten of which were haphazardly placed on each plant, and allowed to settle for 24 hours prior to experimentation. Thirty larvae represented an amount that was larger than what could be consumed by each predator species in 48 hours, given the results of the 24-hour feeding bioassays (see chapter 3). Larvae were placed on mesocosm plants using paint brushes. Immediately before experimentation, each mesocosm was checked to ensure that there were a total 30 larvae on the plants.

Six predator treatments were established in the mesocosms (Table 4.1). Overall, the number of individuals was kept constant in all treatments. Three of the treatments consisted of assemblages of the three predator species. One assemblage (i.e., the *C. maculata* assemblage) mimicked the pattern of relative abundance found in the field (see chapter 2), in which *C. maculata* was numerically dominant. In the other two assemblages, i.e., the *C. septempunctata* and *P. maculiventris* assemblages,

the species that in the field were numerically subdominant, were made numerically dominant. The 4:1 ratio of numerically dominant to numerically subdominant individuals in the assemblage treatments was based on the relative abundance of numerically dominant and subdominant species determined in the field. Three additional treatments consisted of each predator as a single species at a total abundance equal to that of each assemblage treatment. The latter treatments represent each predator as a numerically dominant species in the absence of subdominant species.

For all treatments, individuals of the three predator species were haphazardly selected from their respective colonies and starved for 24 hours prior to being placed on the plants in each mesocosm. All mesocosms were randomly placed into an environmental chamber at 16L (22° C): 8 (16° C) and 70% RH (values based on the average environmental conditions in Maryland). The locations in chambers where mesocosms were placed were re-randomized for each replicate. After 48 hours, *P. rapae* mortality levels were measured for each treatment by counting the number of missing/ partially consumed larvae on all three plants. A control mesocosm of 30 *P. rapae* and no predators was also included to determine the background mortality of *P. rapae* larvae in the absence of predators (1.9 mean larvae missing). Values for missing larvae in the predator treatments were then adjusted for the background mortality to get a more accurate assessment of the prey consumption by single predator species and predator assemblages. Following the trials, the number of dead or missing *C. maculata*, *C. septempunctata*, and *P. maculiventris* individuals was noted for all treatments. The mean proportion of dead *C. maculata*, *C.*

septempunctata, and *P. maculiventris* individuals (i.e. number dead/number of total starting individuals) in the assemblage treatments (in which they were numerically dominant) and single treatments was then calculated. The experiments were repeated on a weekly basis from May to September 2006 and all treatments were replicated at least 12 times.

For statistical analyses, predator treatments were grouped by species (factor 1) and composition type, i.e., whether the predators were represented as single species or part of an assemblage (factor 2) (Table 4.2). The interaction between species and composition type was analyzed with a two-way ANOVA using PROC MIXED (SAS Institute, 1999). For the model, adjusted larval mortality was treated as a random effect, with composition type and species treated as fixed effects. Least square means were obtained and compared among treatments using Tukey's multiple comparison procedure.

In testing the hypotheses, I specifically focused on three sets of treatment comparisons: (1) comparisons of assemblages (in which each of the three species was numerically dominant) vs. treatments in which each numerically dominant species was alone (i.e., single), (2) comparisons of single treatments for each species and (3) comparisons of assemblage treatments (in which each of the three species was numerically dominant) (Table 4.3). The first set of comparisons (i.e. assemblage vs. single) was used to evaluate my hypotheses. If mean larval mortality in the single treatment was significantly greater than the assemblage treatment for *C. maculata*, *C. septempunctata*, and *P. maculiventris*, the results would support the hypothesis that the numerically dominant predator alone, regardless of identity, imposes greater

larval mortality than when in an assemblage of predators. If, however, mean larval mortality of the single treatment was significantly greater than the assemblage treatment for only one or two of the three species, this would support the hypothesis that the identity of the numerically dominant predator is important in determining whether it alone imposes greater larval mortality than when in an assemblage. While this first set of comparisons was used to directly test the hypotheses, the second (single vs single) and third (assemblage vs. assemblage) set of comparisons were used to determine the impact of individual species and the impact of assemblages composed of different numerically dominant species. Collectively, the results of all three comparisons can provide insights into the interactions occurring among the predator species.

Differences in the mean proportion of dead *C. maculata*, *C. septempunctata*, and *P. maculiventris* individuals in assemblages (in which they were numerically dominant) vs. single treatments was analyzed with Kruskal-Wallis tests using PROC NPARLWAY. These analyses were conducted to determine whether there were significant differences in the mortality of numerically dominant species when in an assemblage in contrast to when they were alone. Higher mortality levels of a numerically dominant species when in an assemblage than when represented as a single species could indicate that antagonistic interactions such as intraguild predation were occurring in an assemblage.

Intraguild Predation Trials

To determine whether any predators engage in intraguild predation, trials were conducted in test arenas that paired predators in all possible combinations. The test arenas were comprised of a single, 15 cm tall collard plant in a 774 sq. cm pot, covered by a 3.8 L mesh bag (AZ Partsmaster Co.[®]). A pairing consisted of a 24 hour starved individual of one species placed with another 24 hour starved individual of another species. After 48 hours each individual of both predator species were checked to see if it was alive. A control treatment was included where a predator individual was placed alone in the test arena. Predators for each pairing and control treatments were randomly selected from laboratory colonies. All pairing and control treatments were replicated 12 times during August 2006. I analyzed for differences in the mean percent survival of *C. maculata*, *C. septempunctata*, and *P. maculiventris* individuals when alone vs. when paired with other predators with Fisher's Exact Test using PROC FREQ.

RESULTS

Mesocosm Experiments

There was a significant interaction effect between species and composition type ($F_{2,69} = 8.08$, $p < 0.01$) indicating that the impact of predator species was dependent on whether it was represented as a numerically dominant species in an assemblage or as a single species. In comparisons of assemblage vs. single treatments for each species, *C. septempunctata* imposed significantly greater larval mortality in the single treatment than in the assemblage treatment ($p = 0.01$; Fig. 4.1). For both *C.*

maculata and *P. maculiventris* there were no significant differences between assemblage and single treatment means ($p > 0.23$).

Predator identity was clearly an important determinant of *P. rapae* larval mortality. In comparisons of single treatments, *C. septempunctata* and *P. maculiventris* both imposed significantly greater larval mortality than *C. maculata* ($p < 0.01$) but were not significantly different among each other ($p > .99$; Fig. 4.2). Assemblages varied significantly in the mortality imposed on *P. rapae* larvae depending on which species was numerically dominant. The assemblage where *P. maculiventris* was numerically dominant imposed significantly greater larval mortality than the assemblage where *C. septempunctata* was numerically dominant ($p = 0.03$), while neither of the former two imposed significantly different larval mortality than the assemblage where *C. maculata* was numerically dominant ($p > 0.15$, Fig. 4.3).

There was a significantly greater proportion of dead *C. septempunctata* individuals when it was the numerically dominant species in an assemblage than when it was represented as a single species. ($\chi^2 = 16.49$, $p < 0.01$; Fig. 4.5). There were no significant differences in the proportion of dead individuals when both *C. maculata* and *P. maculiventris* were the numerically dominant species in assemblages compared to their respective single treatments ($\chi^2 < 2.42$, $p > 0.12$; fig. 4.4, fig. 4.6). Intraguild predation of *C. septempunctata* by *P. maculiventris* was observed in the assemblage treatments on five occasions, four times in *C. septempunctata* assemblages, and once in the *P. maculiventris* assemblage. On one occasion intraguild predation of *C. maculata* by *P. maculiventris* was observed in the *C.*

maculata assemblage, however, no intraguild predation was observed between *C. maculata* and *C. septempunctata* in any of the assemblage treatments. A likely explanation for these results is provided by the experiments on intraguild predation.

Intraguild predation trials

From the intraguild predation trials I confirmed that *P. maculiventris* engages in intraguild predation on *C. septempunctata*, because the mean percent survival of *C. septempunctata* individuals was significantly greater when it was alone than when it was combined with *P. maculiventris* ($\chi^2= 10.99$, $p < 0.01$; Fig. 4.8). When combined with *C. maculata*, the mean percent survival of *C. septempunctata* individuals was not significantly different from that observed in the single treatment ($\chi^2= 0.37$, $p= 1.0$; Fig. 4.8). There were no significant differences in the mean percent survival of *C. maculata* individuals when combined with *P. maculiventris* ($\chi^2= 3.33$, $p= 0.22$) nor when combined with *C. septempunctata* compared to that observed in the single treatments ($\chi^2= 0$, $p= 1.0$; Fig. 4.7). There were also no significant differences in the mean percent survival of *P. maculiventris* individuals when combined with *C. maculata* ($\chi^2= 2.14$, $p= 0.48$) nor when combined with *C. septempunctata* compared to that observed in the single treatments ($\chi^2= 0$, $p= 1.0$; Fig. 4.9).

DISCUSSION

While it may be assumed that numerically dominant predators will exert greater pest mortality than an assemblage of arthropod predators, I found evidence that this assumption depends on the identity of the predator. Using an assemblage of three generalist predators found in collards, I found that only when *C. septempunctata*, a numerically subdominant predator in collards, was made a numerically dominant species, did the most abundant species alone impose greater *P. rapae* larval mortality than when in an assemblage (Fig. 4.1). On the other hand, when both *C. maculata* (the numerically dominant species in the field) and *P. maculiventris* (a numerically subdominant species in the field) were made numerically dominant, the levels of larval mortality imposed by these species alone were similar to the larval mortality imposed when they were in assemblages. These results support the hypothesis that identity, not abundance per se, is important in determining whether numerically dominant species impose greater *P. rapae* larval mortality alone than when in an assemblage of generalist predators. Furthermore, the results for *C. septempunctata* suggest that in some circumstances enhancing the abundance of a species that typically occurs as a subdominant predator, by the imposition of conservation biological control tactics, may result in greater mortality of pests

As important as species identity may be, the type of interactions that occur among numerically dominant and subdominant species may also be crucial in determining the impact of the most abundant species in predator assemblages. While not explicitly tested in this study, I was able to deduce the nature of interactions that

occurred among some of these predators by independently analyzing the impacts of single species and assemblages on larval mortality. As single species, *P. maculiventris* and *C. septempunctata*, while imposing similar levels of *P. rapae* larval mortality, were both more voracious predators than *C. maculata* (Fig. 4.2). However, in assemblages, there was a significant drop-off in larval mortality when *C. septempunctata* was numerically dominant compared to when *P. maculiventris* was numerically dominant (Fig. 4.3). Furthermore, when *C. maculata* was numerically dominant, the level of larval mortality imposed by the assemblage was not distinguishable from that of the other two assemblages. The differences in the impacts of single predators species vs. the impacts of species in assemblages suggests that interactions among numerically dominant and subdominant species could have influenced the impact they had on *P. rapae* mortality. If interactions among the species were strictly additive, then the larval mortality imposed by assemblages should be equal to the summed impacts of the individual numerically dominant and subdominant species. However, the larval mortality imposed by the assemblages did not appear to be additive for each numerically dominant species (Fig. 4.10). For this figure, the expected additive larval mortality of each assemblage was determined by calculating the per capita larval mortality imposed by each species from the single treatments, and then summing the per capita larval mortalities based on which species is numerically dominant and subdominant. The comparison suggests that while interactions in assemblages where *C. maculata* and *P. maculiventris* were numerically dominant were probably additive, they appear to have been antagonistic in

assemblages where *C. septempunctata* was the numerically dominant species, resulting in lower levels of larval mortality.

Intraguild predation was the most likely cause of the antagonistic interactions occurring in the assemblages where *C. septempunctata* was the numerically dominant species, since *P. maculiventris* was an asymmetric intraguild predator of *C. septempunctata* (Fig. 4.8). This was also the likely cause of the significantly greater proportion of dead *C. septempunctata* individuals as the numerically dominant species in assemblages versus when it was represented as a single species (Fig. 4.5). These results concur with the growing body of literature indicating that antagonistic interactions in predator assemblages such as intraguild predation can lead to a reduction in pest mortality (Polis et al. 1989, Rosenheim et al. 1993, Rosenheim et al. 1995, Snyder and Ives 2001, Finke and Denno 2004, 2005). However, my research expands on this theme by showing that intraguild predation by a numerically subdominant species, *P. maculiventris*, can potentially represent a significant source of mortality on *C. septempunctata* when it is numerically dominant. This in turn may have a substantial impact on the mortality that a numerically dominant species imposes on pests. On the other hand, the level of pest mortality imposed by an effective intraguild predator when it is numerically dominant, such as *P. maculiventris*, may not be substantially reduced in the presence of a numerically subdominant intraguild prey like *C. septempunctata*. Therefore, the relative abundances of predators may be an important component in determining the outcomes and impacts of intraguild predation on pest mortality.

Intraguild predation between adult *P. maculiventris* and adult *C. septempunctata* has been reported before (Mallampalli et al. 2002). Furthermore, Mallampalli et al. (2002) also found that adult *P. maculiventris* were not significant intraguild predators of adult *C. maculata*. What remains unclear, however, is why intraguild predation occurs among these predators, and the reasons why one coccinellid species appears to be preferred over the other. While not tested here, I suggest that, all things being equal, the interactions among the predators in this study may be influenced by their foraging behavior and size. In cases where prey are relatively sedentary, it has been shown that while mobile, widely foraging predators may exert strong mortality on prey, predators that employ a less mobile, sit and wait foraging strategy may act as top predators, imposing strong mortality on the mobile predators (Rosenheim et al. 2004a). Furthermore, intraguild predation by top predators may be stronger on larger mobile predators than smaller ones, due to the need of larger predators to consume more prey, which in turn, exposes them to more predation, relative to small predators (Rosenheim et al. 2004b). *P. maculiventris* is known to employ a low mobility foraging strategy, remaining relatively motionless for long periods of time while using vibrational, olfactory, and visual cues to detect prey (Wiedenmann 1991, Pfannenstiel et al. 1995). *C. maculata* and *C. septempunctata* are often described as mobile predators that extensively search plants for prey (Stubbs 1980, Nakamuta 1984, Harmon et al. 1998). Furthermore, the widely foraging *C. maculata* is a relatively smaller predator (typically 5-6 mm long) than the widely foraging *C. septempunctata* (typically 7-8 mm long). Thus, encounter rates may have been relatively greater between *P. maculiventris* and *C. septempunctata*

than between *P. maculiventris* and *C. maculata*. This could be due to the larger *C. septempunctata* having longer foraging bouts, causing greater leaf-borne vibrations, to its being more visible as it forages, or a combination of all three. This potentially may have caused *C. septempunctata* to be more easily detected by *P. maculiventris* than the smaller *C. maculata*. Therefore, other elements of predator identity, such as foraging behavior and size, may influence the level of pest mortality that is imposed by generalist predators in an assemblage. Further studies are needed to determine the prevalence of intraguild predation among these predators in the field, as well as to determine whether it is linked to their respective foraging behaviors.

My results imply that effective management of *P. rapae* populations may be better achieved through the conservation of a numerically dominant predator, albeit with two major caveats. The first caveat is that this result may be dependent on species identity, as the numerically dominant species in the field may not be the most voracious predator in relation to numerically subdominant species. The second caveat is that the impact of the numerically dominant predator on prey mortality may be diminished by the presence of numerically subdominant intraguild predators. If the numerically dominant predator in the field is not the most voracious species in the assemblage, numerically subdominant species may provide a substantial added source of prey mortality. If so, conservation tactics may be better targeted at increasing the abundance of effective numerically subdominant species. An in-depth knowledge of the arthropod predator community may be necessary in determining which conservation management strategy works best.

Table 4.1. List of treatments, the species included in each treatment, the number of individuals per species, and the number of replicates for each treatment. C.mac. refers to *C. maculata*, C.sep. to *C. septempunctata*, and P.mac. to *P. maculiventris*. Assemblage refers to treatments in which the predator is the numerically dominant species in the assemblage while single refers to numerically dominant species occurring alone.

Treatment	Species included	No. of individuals per species	No. of replicates
C.mac. assemblage	<i>C. maculata</i> <i>C.septempunctata</i> <i>P. maculiventris</i>	4 1 1	13
C.sep. assemblage	<i>C. septempunctata</i> <i>C. maculata</i> <i>P. maculiventris</i>	4 1 1	14
P.mac. assemblage	<i>P. maculiventris</i> <i>C. maculata</i> <i>C. septempunctata</i>	4 1 1	12
C.mac. single	<i>C. maculata</i>	6	12
C.sep. single	<i>C.septempunctata</i>	6	12
P.mac. single	<i>P. maculiventris</i>	6	12

Table 4.2. Breakdown of six predator treatments into species and composition categories. C.mac. refers to *C. maculata*, C.sep. to *C. septempunctata*, and P.mac. to *P. maculiventris*. Assemblage refers to treatments in which the predator is the numerically dominant species in the assemblage while single refers to numerically dominant species occurring alone.

Species	Composition type	Treatment
C.mac.	Assemblage	C.mac. assemblage
	Single	C.mac. single
C.sep.	Assemblage	C.sep. assemblage
	Single	C.sep. single
P.mac.	Assemblage	P.mac. assemblage
	Single	P.mac. single

Table 4.3. Summary of planned contrasts and the treatments that are compared.

C.mac. refers to *C. maculata*, C.sep. to *C. septempunctata*, and P.mac. to *P. maculiventris*. Assemblage refers to treatments in which the predator is the numerically dominant species in the assemblage while single refers to numerically dominant species occurring alone

Planned contrast	Treatments being compared	Relevance
1. Assemblage vs. Single	C.mac. assemblage vs. C.mac. single C.sep. assemblage vs. C.sep. single P.mac. assemblage vs. P.mac. single	Compares the impact of single numerically dominant species to the combined impact of numerically dominant and subdominant species
2. Single vs. Single	C.mac. single vs. C.sep. single C.sep. single vs. P.mac. single P.mac. single vs. C.mac. single	Determines the impact of single numerically dominant species
3. Assemblage vs. Assemblage	C.mac. assemblage vs. C.sep. assemblage C.sep. assemblage vs. P.mac. assemblage P.mac. assemblage vs. C.mac. assemblage	Determines the impact of numerically dominant species when subdominant species are added

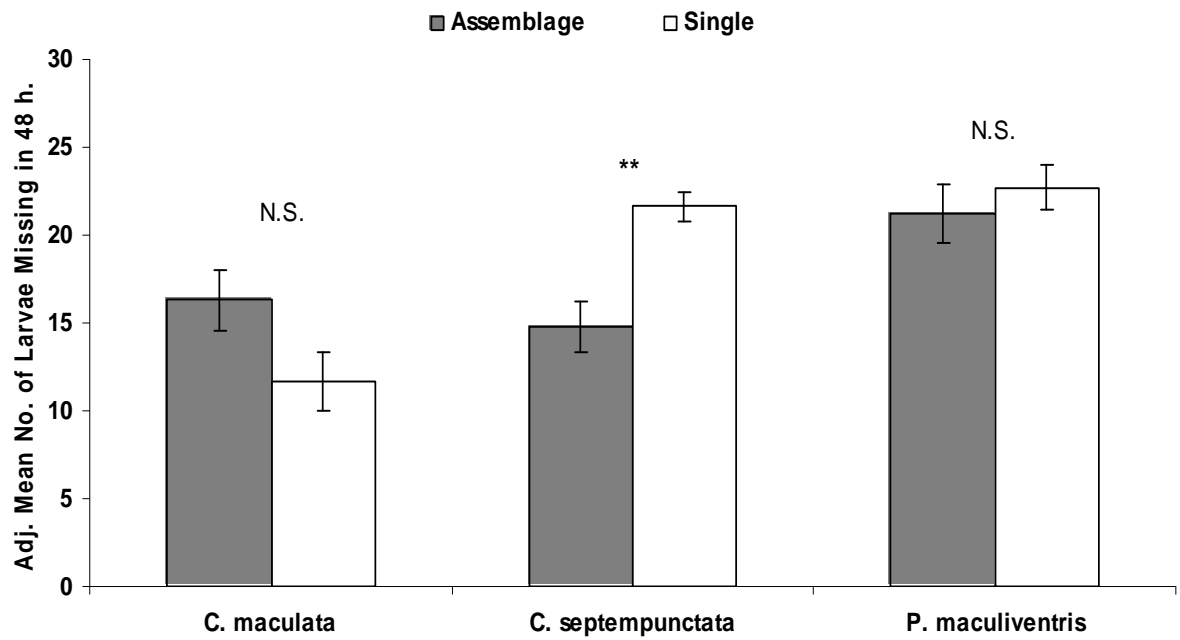


Figure 4.1. Adjusted mean larval mortality (number of larvae missing in 48 h.) of the numerically dominant *C. maculata*, *C. septempunctata*, and *P. maculiventris* when in assemblages vs. when represented as single species. P-values for contrasts between treatments were Bonferroni adjusted at the $\alpha=0.05$ level. Data are presented as means \pm 1 SE. N.S.= non significant, ** $p < 0.01$.

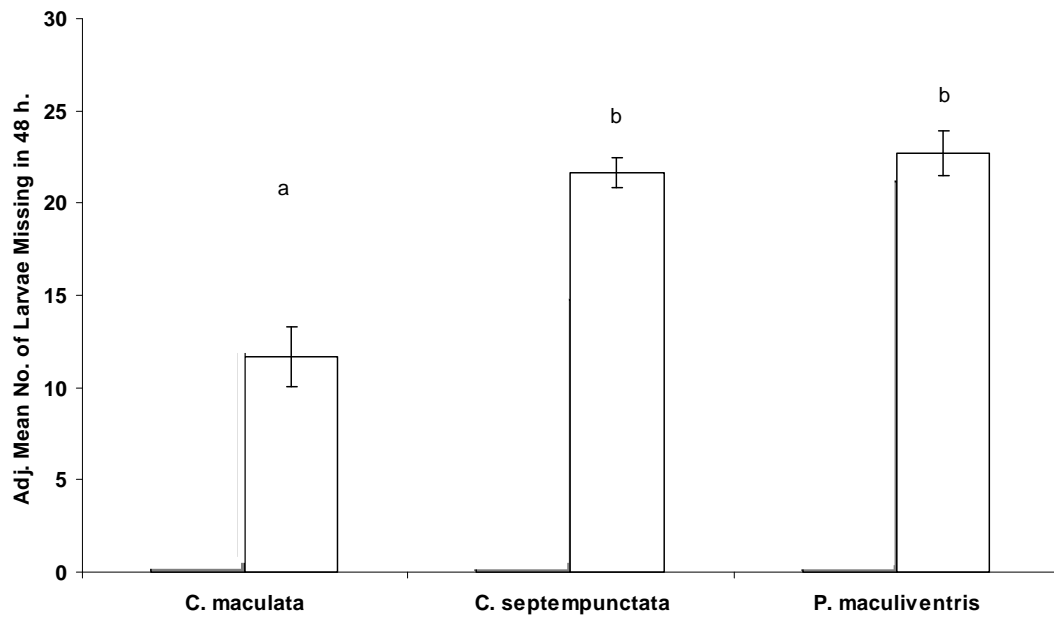


Figure 4.2. Adjusted mean larval mortality (number of larvae missing in 48 h.) of the numerically dominant *C. maculata*, *C. septempunctata*, and *P. maculiventris* when represented as single species. P-values for contrasts between treatments were Bonferroni adjusted at the $\alpha=0.05$ level. Data are presented as means \pm 1 SE. Means with the same letter are not significantly different from each other.

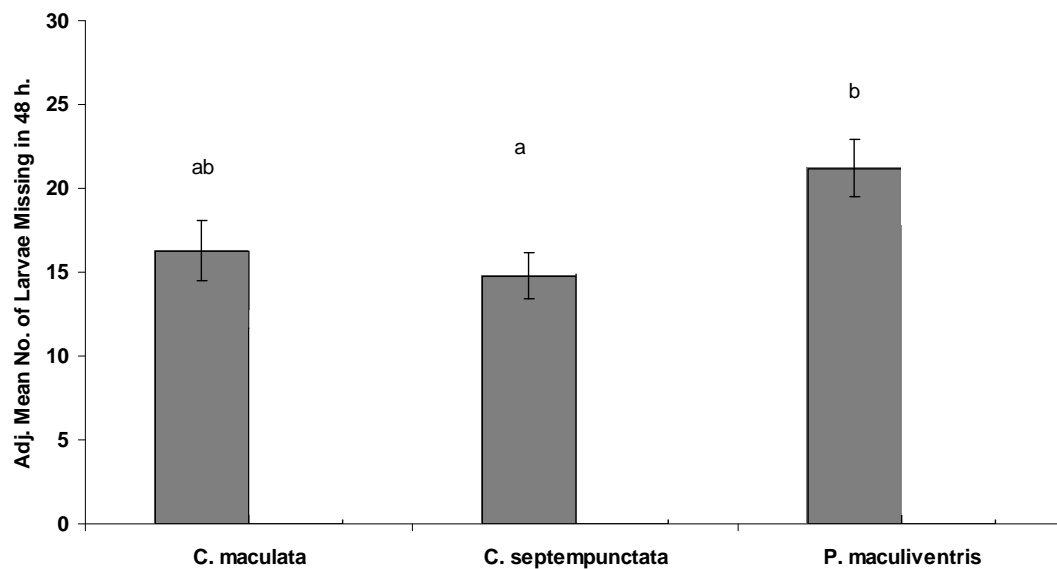


Figure 4.3. Adjusted mean larval mortality (Number of missing larvae in 48 h.) of the numerically dominant *C. maculata*, *C. septempunctata*, and *P. maculiventris* when in assemblages. P-values for contrasts between treatments were Bonferroni adjusted at the $\alpha=0.05$ level. Data are presented as means \pm 1 SE. Means with the same letter are not significantly different from each other.

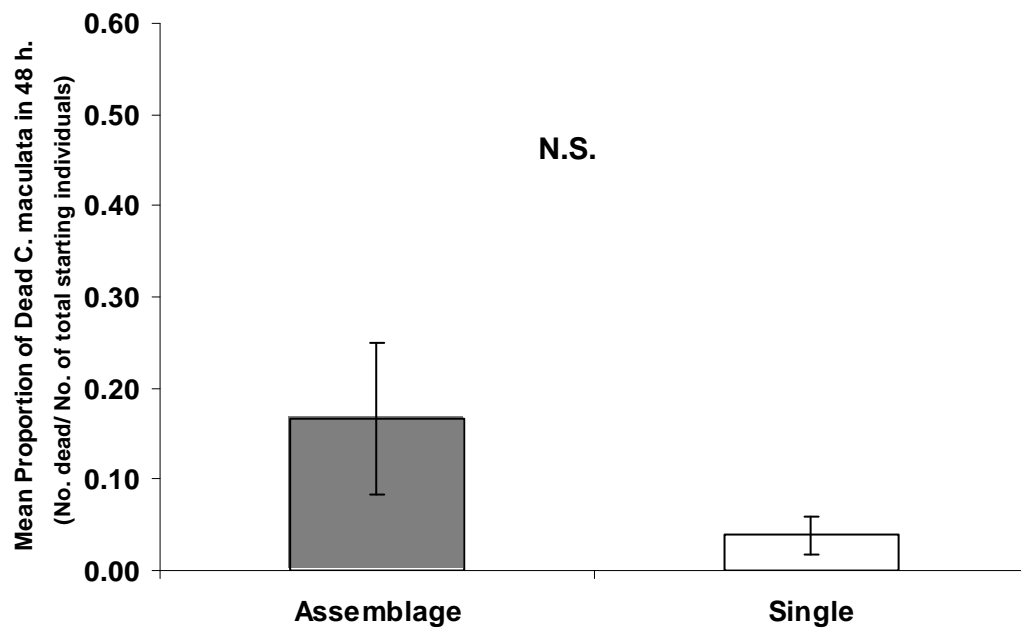


Figure 4.4. Mean proportion of dead *C. maculata* individuals (number of dead/number of total starting individuals) found in assemblage treatments (when the species is numerically dominant) vs. single treatments. N.S.= non significant, ** $p < 0.01$.

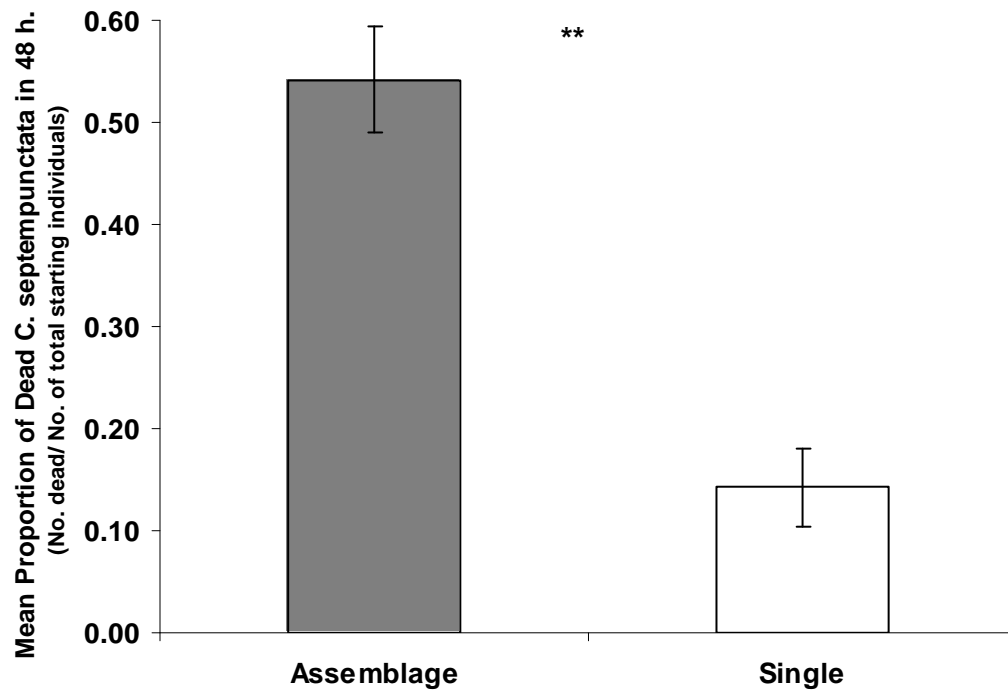


Figure 4.5. Mean proportion of dead *C. septempunctata* individuals (number of dead/number of total starting individuals) found in assemblage treatments (when the species is numerically dominant) vs. single treatments. N.S.= non significant, ** $p < 0.01$.

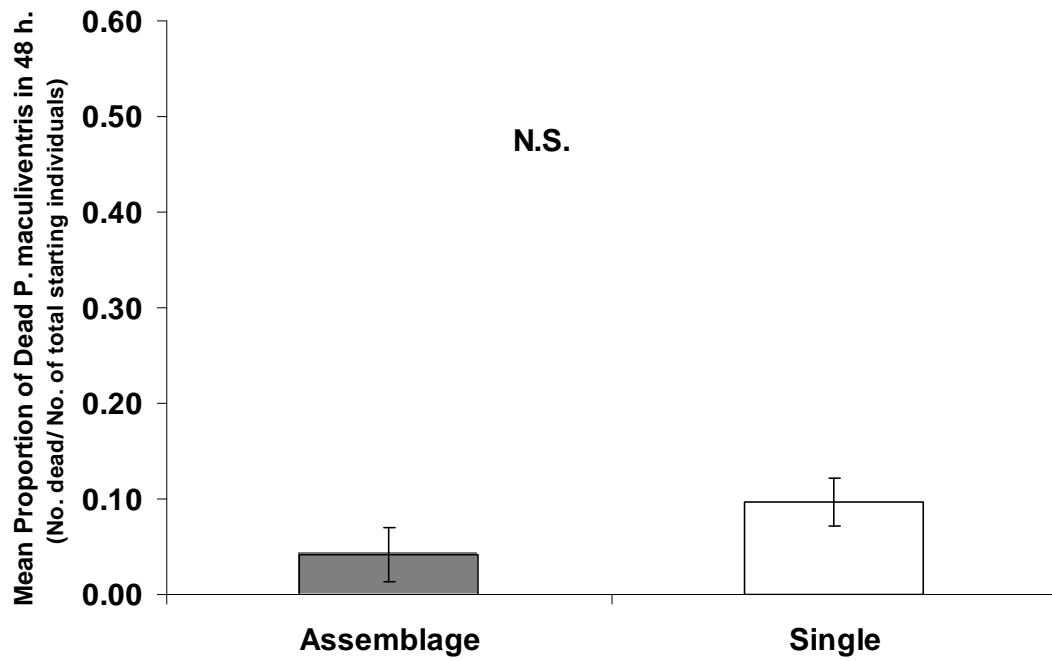


Figure 4.6. Mean proportion of dead *P. maculiventris* individuals (number of dead/number of total starting individuals) found in assemblage treatments (when the species is numerically dominant) vs. single treatments. N.S.= non significant, ** $p < 0.01$.

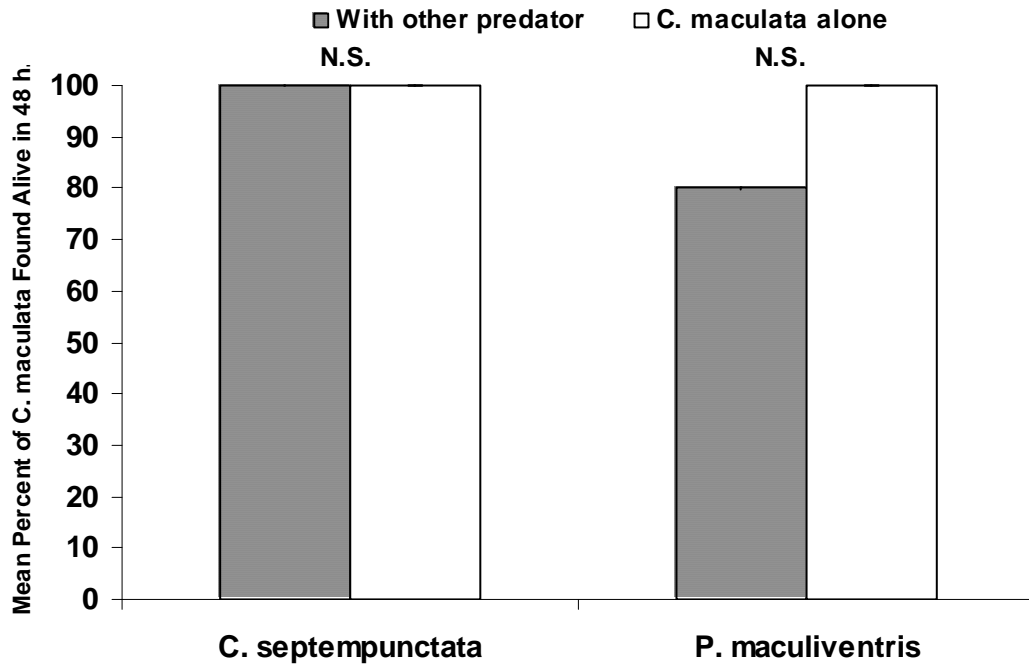


Figure 4.7. Mean percent survival of *C. maculata* individuals (Percent of predator individuals found alive in 48 h.) when paired with individuals of other predator species vs. when alone. N.S.= non significant, ** $p < 0.01$.

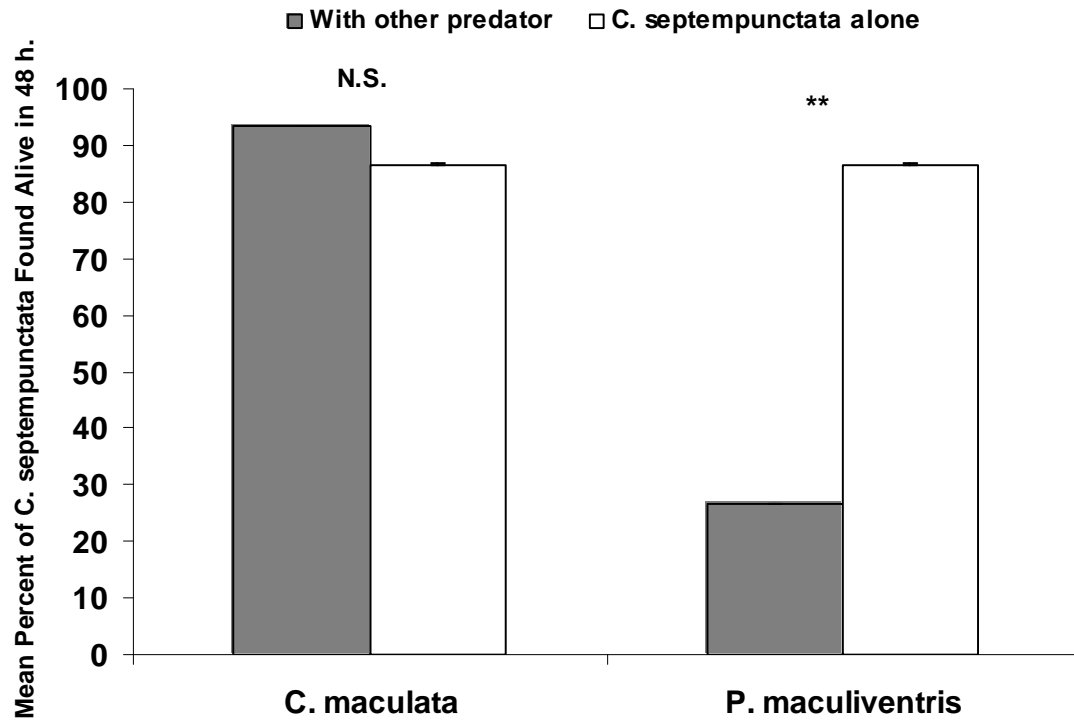


Figure 4.8. Mean percent survival of *C. septempunctata* individuals (Percent of predator individuals found alive in 48 h.) when paired with individuals of other predator species vs. when alone. N.S.= non significant, ** $p < 0.01$.

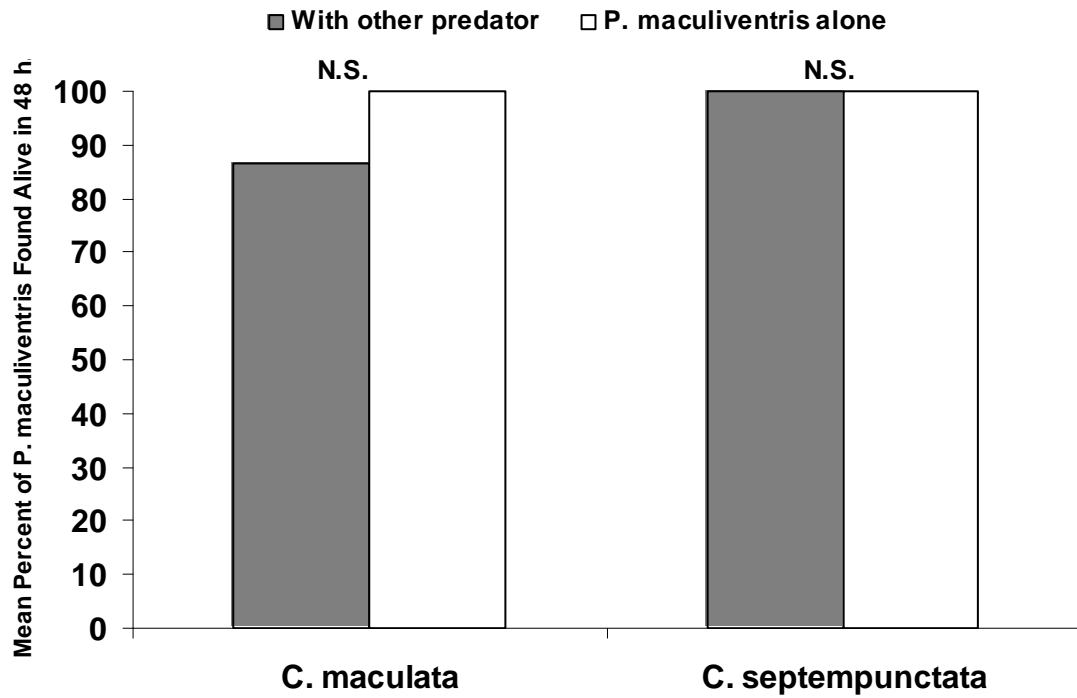


Figure 4.9. Mean percent survival of *P. maculiventris* individuals (Percent of predator individuals found alive in 48 h.) when paired with individuals of other predator species vs. when alone. N.S.= non significant, ** $p < 0.01$.

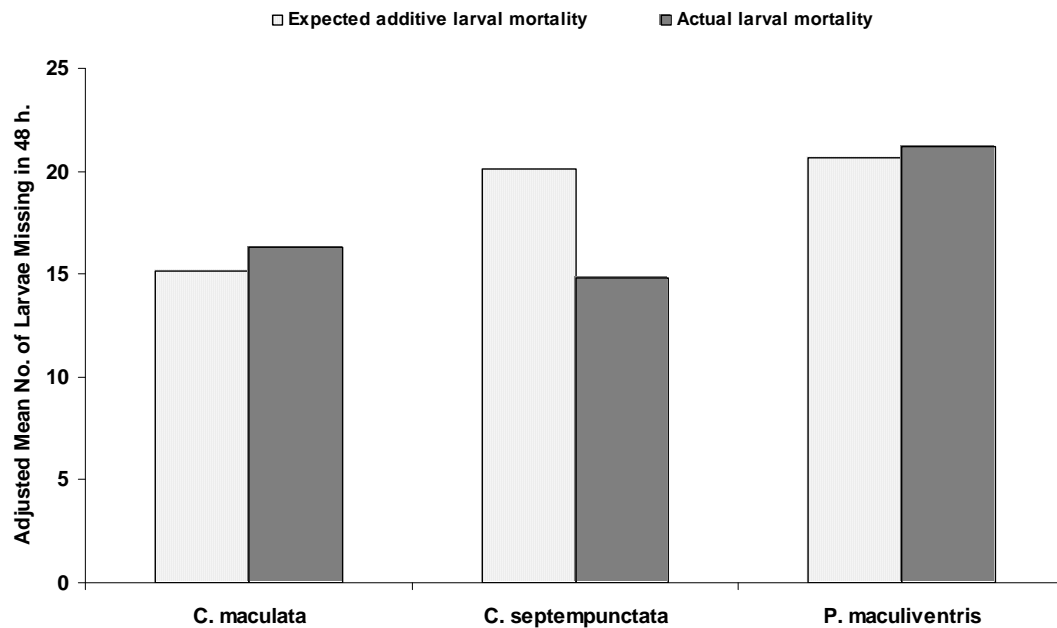


Figure 4.10. A comparison of the expected additive larval mortality vs. the actual mean larval mortality (Number of missing larvae in 48 h.) imposed by assemblages where *C. maculata*, *C. septempunctata*, and *P. maculiventris* were the numerically dominant species. Expected additive mortality for assemblages was determined by calculating the larval mortality imposed by each species from the single treatments, and then summing the per capita larval mortalities based on which species is numerically dominant and subdominant

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