5-2009

Comparisons of Native and Non-Native Lady Beetles: Habitat Distribution and Interactions with Prey and Competitors

Christy J. L. Finlayson

Recommended Citation

Finlayson, Christy J. L., "Comparisons of Native and Non-Native Lady Beetles: Habitat Distribution and Interactions with Prey and Competitors" (2009). *Electronic Theses and Dissertations*. 335.
http://digitalcommons.library.umaine.edu/etd/335

COMPARISONS OF NATIVE AND NON-NATIVE LADY BEETLES: HABITAT DISTRIBUTION AND INTERACTIONS WITH PREY AND COMPETITORS

By

Christy J.L. Finlayson

B.S. The University of Memphis, 1993

M.S. The University of Memphis, 1997

A THESIS

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Doctor of Philosophy

(in Biological Sciences)

The Graduate School

The University of Maine

May, 2009

Advisory Committee:

Andrei Alyokhin, Associate Professor of Applied Entomology, Advisor

Frank Drummond, Professor of Insect Ecology and Pest Management

Eleanor Groden, Professor of Entomology

Malcolm Hunter, Jr., Libra Professor of Conservation Biology and
Professor of Wildlife Ecology

Kevin Simon, Assistant Professor of Biological Sciences

LIBRARY RIGHTS STATEMENT

In presenting this thesis in partial fulfillment of the requirements for an advanced degree at the University of Maine, I agree that the Library shall make it freely available for inspection. I further agree that permission for "fair use" copying of this thesis for scholarly purposes may be granted by the Librarians. It is understood that any copying or publication of this thesis for financial gain shall not be allowed without my written permission.

Signature:

Date:

COMPARISONS OF NATIVE AND NON-NATIVE LADY BEETLES: HABITAT DISTRIBUTION AND INTERACTIONS WITH PREY AND COMPETITORS

By Christy J.L. Finlayson

Thesis Advisor: Dr. Andrei Alyokhin

An Abstract of the Thesis Presented
in Partial Fulfillment of the Requirements for the
Degree of Doctor of Philosophy
(in Biological Sciences)
May, 2009

Lady beetles (Coleoptera: Coccinellidae), as a group, are considered beneficial because they prey on plant pests. A number of studies suggest that non-native species introduced for biological control have replaced native species in agriculture. Agricultural and non-agricultural habitats were thus surveyed in Maine to determine if native species were still dominant in some areas. In 2004 and 2005, 3,487 and 2,903 beetles were collected, respectively, with non-native species dominant in all but one habitat (coniferous forest). Native species were found in very low numbers in all habitats surveyed.

Comparisons between species were then conducted to determine if differences exist that might provide an advantage to some species over others. Consumption of four aphid species by one native (*Coccinella trifasciata*) and three non-native (*Coccinella septempunctata*, *Harmonia axyridis*, *Propylea quatuordecimpunctata*) species were compared. *Harmonia axyridis* generally consumed the most aphids; *P. quatuordecimpunctata* consumed the fewest. *Coccinella trifasciata*, however, consumed the most of one aphid species, *Macrosiphum albifrons*. Direct competition for prey

was compared between native (*C. trifasciata*, *Coleomegilla maculata*, *Hippodamia convergens*) and non-native (*C. septempunctata*, *H. axyridis*, *Hippodamia variegata*, *P. quatuordecimpunctata*) species. *Harmonia axyridis* had the highest aphid consumption, shortest prey discovery time, and generally exhibited the most aggression towards other species. Consumption by *C. trifasciata* and *C. maculata* varied depending on with which species they were paired. Interactions between native and non-native species (same species as above) and the European fire ant (*Myrmica rubra*) tending aphid prey were compared. *Harmonia axyridis* consumed more aphids than all other species but *C. septempunctata*. *Hippodamia variegata* and *C. septempunctata* were effected the most by ant stings. These differences may explain, in part, the successful establishment of some non-native coccinellids in new habitats and suggest that asymmetric interactions between species may affect their ability to co-exist.

Studies evaluating relationships between newly sympatric coccinellids, tending ants, and plant-feeding insects were summarized. Research has been driven by concerns about the effects of invasive ants (primarily *Pheidole megacephala*, *Solenopsis invicta*, and *Linephithema humile*) on the effectiveness of pest control by coccinellids (primarily *Cryptolaemus montrouzieri* and *C. septempunctata*). Ants interfered with coccinellid predation in 56 of 77 studies.

ACKNOWLEDGMENTS

The author would like to thank the following for their assistance in the field and laboratory: Gary Sewell, Kristine Landry, Serena Gross, Erin Porter, Todd Finlayson, Melissa Lewis, Megan Patterson, Caroline Robinson, David Ginsberg, Allison Fleming, and Lauren Little. For providing access and guidance on their land, the author would like to thank Gary Sewell, Joseph Cannon, Pete Powers, John Jemison, Green Thumb Farm, Black Bear Food Guild, and Orono Land Trust. The author would also like to thank her Advisory Committee for the valuable input that they provided and her family and friends for their support. This research was supported by the Maine Agricultural and Forest Experiment Station, the National Science Foundation's GK-12 Teaching Fellows Program (Grant # DGE – 0231642 to S. Brawley *et al*.), the United States Fish and Wildlife Service, and the National Geographic Society Conservation Trust.

The first chapter of this dissertation has been published in the *Annals of the Entomological Society of America* (Finlayson CJ, Landry KM, Alyokhin AV. 2008. Abundance of native and non-native lady beetles (Coleoptera: Coccinellidae) in different habitats in Maine. *Annals of the Entomological Society of America* 101: 1078-1087). The research described in the second chapter is in press in the *Journal of Insect Science*. The third, fourth, and fifth chapters have been submitted to the *Journal of Insect Behavior, Environmental Entomology*, and *Biological Control,* respectively.

TABLE OF CONTENTS

Chapter

LIST OF TABLES

LIST OF FIGURES

Chapter 1

INTRODUCTION

Process of Biological Invasion

Introduced species are species that are not native to the location where they are released or found (Williamson 1996). Introduced species are often considered "invasive" when they cause detrimental effects in the location where they have been introduced. The control of introduced, or alien, species has been recognized as fundamental to the preservation of biodiversity (Williamson 1996, Perrings *et al*. 2000). The Convention on Biological Diversity was signed by over 150 countries at the 1992 Earth Summit in Rio de Janeiro, adopted as international law in 1993, and ratified by 176 countries in 1999. As part of an initiative to preserve biodiversity, one aim of this agreement was to "prevent the introduction of, control or eradicate those alien species which threaten ecosystems, habitats or species" (Glowka *et al*. 1994, Perrings *et al*. 2000).

By wind, water, and transport via animals, populations can be founded far from their native ranges. Although movements of populations into new habitats are natural occurrences, the frequency of non-native species introductions into habitats previously unoccupied by these species has increased with increases in the human population and with advances in human transportation and commerce (Williamson 1996, Mack *et al*. 1999, Perrings *et al*. 2000). Propagules ranging from gametes, seeds, and spores to groups of full-grown organisms are transported in ships' ballast water and cargo, via air travel and ground transportation in automobiles and trains, in containers and packing material. Between the years of 1980 and 1993, 38 of 47 harmful species known to have been introduced into the United States arrived via trade (Schmitz and Simberloff 1997). An estimated 50% of weeds and 39% of agricultural pests in the United States are non-native (USOTA 1993). Twenty-five percent of Florida's plant and animal species have been introduced by humans over the last 300 years (Schmitz and Simberloff 1997).

Biological invasions often occur as a result of the production and consumption of non-native species, the alteration or fragmentation of habitat, and the transport of people and goods (Mack *et al.* 1999). While some introductions occur inadvertently, others are deliberate. Species are intentionally introduced into new habitats for a variety of reasons. Humans carry seeds, plants, and animals with them when colonizing new lands. Plant and animal foods and the stock to produce these foods are exchanged from one region of the world to another as new and more successful varieties are developed. Game animals are specifically bred and introduced to native and non-native habitats in order to fortify recreational experiences such as hunting and fishing. For sentimental and aesthetic reasons, humans carry pets and plants with them when they move and grow ornamental gardens. Ground covers are introduced for erosion control (Schmitz and Simberloff 1997). Pollinators are often intentionally introduced to aid in fruit or vegetable production. Pests of agricultural crops are often controlled by the intentional introduction of their non-native natural enemies (Caltagirone and Doutt 1989, McEvoy and Cox 1991, Radcliffe and Flanders 1998).

Most introductions do not result in the establishment of self-sustaining populations (Williamson 1996). The exact mechanisms by which non-native species become invasive are largely unknown (Schmitz and Simberloff 1997). However, a number of variables are thought to influence the success of non-native species in establishing and maintaining populations, some credited to the inherent strength of the non-native species and some credited to the vulnerability of the habitat in question. The practical use of such characteristics is not yet possible. While there are some qualities that have shown to be common in successful invaders (relatedness to invaders, generalist habitat requirements and feeding strategies, propagation of many offspring), no general trend in characteristics has been determined enabling the prediction of invasive potential (Mack *et al* 1999). Assessments that might be conducted determining the invasion potential of a given habitat by a given invader are very site-specific. Systems with high natural diversity have been shown to be generally resistant to invasion (Drake *et al*. 1989). The same appears to be true for dry systems, arctic systems, and pelagic marine systems (Heywood 1995). Other systems with low diversity (Drake *et al*. 1989), such as agricultural systems (Perrings *et al*. 2002), and lakes, rivers, estuaries, and islands (Heywood 1995) are generally more susceptible to invasion. Other factors influencing the susceptibility of a system to invasion include proximity to human activity, level of disturbance, land-use, market and trade agreements and activity, and habitat fragmentation (Williamson 1996). Compared with its native habitat, an introduced species may need to overcome differences in climate, predators, prey, competition, and other biotic and abiotic factors, to establish a viable population (Perring *et al*. 2000). Additionally, when an introduced population is founded by very few individuals, the resulting population, even if quite large in number, may not contain the genotypic plasticity to deal with variables or changes in its new environment (Williamson 1996).

Some of these introduced species cause profound negative economic and ecological effects in the habitats in which they are introduced (Howarth 1991, Simberloff and Stiling 1996, Perrings *et al*. 2000, Louda *et al*. 2003). The proliferation of plant and animal invaders has completely altered some ecosystems, often resulting in changes in community structure, and changes and losses in biodiversity. Most terrestrial, freshwater, and marine ecosystems have been impacted by non-native species (Williamson 1996, Parker *et al*. 1999). In natural or unmanaged systems, non-native species cause direct damage by consuming natural resources, and possibly changing ecosystem structure and dynamics. Also, they may cause indirect damage by habitat destruction, disease transmission, and competition with indigenous species for natural resources, such as nutrition and nest sites. Direct and indirect effects are similar in agricultural or other managed systems, although the affected species may not be indigenous. Non-native species also cause damage by hybridizing with native species; introducing new alleles into a population can change gene frequency, change the gene pool, and effectively result in the extinction of both the native and non-native founders by the "melting" together of native and non-native populations (Williamson 1996).

The effects of non-native species are second only to habitat destruction in the world-wide endangerment of species (Glowka *et al* 1994, Perrings *et al*. 2000). In the United States, non-native species have been linked to 3 of 24 known extinctions and a decline in 42% of endangered and threatened species (Schmitz and Simberloff 1997).

The economic impacts of non-native species are difficult to estimate and must take into account direct and indirect resource loss and the costs associated with control of non-native species, such as pesticide use and manpower hours dedicated to all methods of management. In the United States, the annual economic impact of non-native species has been estimated from 1.2 (USOTA 1993) to 137 billion dollars (Pimentel *et al*. 1999). Costs associated with losses due to non-native plants constitute over one fourth of the United States' agricultural gross national product (Schmitz and Simberloff 1997). On many occasions, biological invasions have promoted the extensive use of and dependence on pesticides.

Although biological invasions will likely never be completely predictable (Perrings *et al*. 2000), broad-scale assessments might provide useful tools such as general models and bioindicators that can be more broadly applied. An understanding of pre-invasion system dynamics combined with knowledge regarding any small-scale, subtle changes that non-indigenous species produce when introduced into a new system before they become invasive is necessary. The prioritization of management efforts requires distinguishing small-scale from large-scale invasion effects, determining if traditional methods used to determine the impacts of non-indigenous species, such as measures of species richness, are adequate, or if more attention should be focused on the specifics of the ecosystem in question and its functioning (Parker *et al*. 1999).

Introduction and Establishment of Non-native Lady Beetle Species in North America

Lady beetles (Coleoptera: Coccinellidae) are small, oval-shaped insects often known for their bright red, orange, or yellow color and black dots. Approximately 4500 species of lady beetles exist worldwide, with approximately 475 species in 57 genera found in North America north of Mexico (Gordon 1985). Lady beetles are considered beneficial insects because, in temperate regions, they generally feed on the pests of plants. Their prey can include aphids; scale insects; thrips; mites; immature stages of Coleoptera, Lepidoptera, and Hymenoptera; fungal hyphae; fungal spores; and pollen (Hodek 1973, Gordon 1985). Some lady beetles do, however, feed on economically important plant species, particularly in tropical regions (Gordon 1985).

Lady beetles are often categorized based on their primary dietary preference(s). Some species are specialists; some species are generalists; while some species fall somewhere between. Some lady beetle species are exclusively predaceous; some are exclusively phytophagous; while others have a diverse diet depending on prey availability, habitat type, seasonality, and other variables (Hodek 1973). When a primary dietary preference is scarce, many lady beetles switch to a variety of secondary prey items (Gordon 1985, Koch 2003).

Lady beetles have been intentionally introduced into new habitats throughout the world for the control of pest species, such as aphids, in agricultural crops (Gordon 1985, Koch 2003). Lady beetles are highly mobile and do not always remain in the location of their original introduction, sometimes moving into adjacent habitats and establishing populations in areas where native lady beetles may or may not occur. Unintentional introductions have also occurred via transport as stowaways in plant exports and other cargo.

The first deliberate introduction of non-native lady beetles to North America took place in 1888 (Gordon 1985). After the cottony cushion scale insect had become a serious pest in California citrus groves, *Rodolia cardinalis* (Mulsant), an Australian lady beetle, was introduced among a number of other lady beetle species, and proved to be a huge success in the biological control of that pest. Between 1891 and 1892, 46 lady beetle species were introduced to North America from Australia, few of which became established (Gordon 1985). A period of inactivity in the introduction of lady beetle species took place as interest heightened in the use of parasitic Hymenoptera and in the development and implementation of pesticides as a widespread means of pest control. However, since the 1960's, there has been a renewed interest in using lady beetles for biological control, and a number of lady beetle introductions have proven useful in the control of pest species. Of the 179 known non-indigenous lady beetle species intentionally introduced in North America, approximately 16 species currently maintain viable populations. Eight lady beetle species have been established from unintentional introductions, with 5 of those a result of intentional introductions that established viable populations beyond the range of their intended habitats (Gordon 1985).

Non-native lady beetle species often establish populations in geographical ranges already inhabited by native or non-native lady beetle species. Introductions of non-native species have been corelated with decreases in numbers of native lady beetles (Elliot *et al.* 1996, Brown and Miller 1998, Colunga-Garcia and Gage 1998, Michaud 2002, Turnock *et al.* 2003) and in other non-native lady beetles (Brown 2003). In addition to outcompeting other lady beetles for food items (Michaud 2002), non-native species may also prey upon other aphidophagous insects (Dixon 2000).

The multicolored Asian lady beetle, *Harmonia axyridis* (Pallas), is probably the most well known example of an introduced biological control agent arguably "gone bad." This species has been intentionally released in North America on a number of occasions (Hodek and Honek 1996). *Harmonia axyridis* is native to Asia, with its distribution being delineated in the east by the Pacific Coast, in the west by the Altai Mountains, in the north by southern Siberia, and in the south by southern China (Korschefsky 1932, Dobzhansky 1933, Chapin 1965, Kuznetsov 1997). Individuals from Japan and/or Russia were released in California (1916, 1964, 1965), Washington (1978 to 1982), Nova Scotia (1981), and in Connecticut, Delaware, Georgia, Louisiana, Maine, Maryland, Mississippi, Ohio, Pennsylvania, and Washington D.C. (1978 to 1981) (Gordon 1985). There was no known record of temporary or permanent population establishment until 1988, when the first established population of *H. axyridis* was documented (Chapin and Brou 1991, Tedders and Schaefer 1994). Despite numerous intentional releases, it has been suggested that the current North American *H. axyridis* population originated from an unintentional introduction, likely at a seaport (Day *et al.* 1994), and radiated from one source population (Krafsur *et al.* 1997). Whatever its true origin was, *H. axyridis* quickly spread across North America and now occurs throughout much of the continental United States (Koch 2003).

Harmonia axyridis has proven to be successful in the control of pest species, such as aphids, on red pines, pecan, apple, citrus, soybean, sweet corn, cotton, tobacco, and winter wheat (Koch 2003). Cultures are relatively easy to rear in captivity (Matsuka and Niijima 1985); and until recently, *H. axyridis* could be easily obtained from commercial rearing facilities (Heimpel and Lundgren 2000). However, as concerns mount that *H. axyridis* may be becoming a significant pest species to non-target organisms, their availability has decreased (Koch 2003).

Introductions of *H. axyridis* have caused the displacement of indigenous lady beetles (Elliot *et al.* 1996, Brown and Miller 1998, Colunga-Garcia and Gage 1998, Michaud 2002, Turnock *et al*. 2003) and a decrease in other non-native lady beetles (Brown 2003). In addition to outcompeting other lady beetles for food items (Michaud 2002), *H. axyridis* may also prey upon other aphidophagous insects (Dixon 2000). *Harmonia axyridis* has also been shown to have a higher fecundity and fertility than other lady beetle species (Michaud 2002). *Harmonia axyridis* appears to be a true generalist, consuming a variety of insect species (Nakata 1995, Takizawa *et al*. 2000), plant matter such as pollen and fruit (Ratcliffe 2002, Ejbich 2003), and resorting to cannibalism in times of need (Osawa 1989, Snyder *et al*. 2000, Osawa 2002).

Harmonia axyridis has become a pest to humans. Similar to most species of lady beetles, *H. axyridis* overwinters in sheltered sites. Human dwellings serve well as their overwintering sites (Huelsman *et al*. 2002). The odor that lady beetles emit and the yellowish droplets that they excrete on windowsills irritate humans. Some humans have developed a form of rhinoconjunctivitis when exposed to *H. axyridis*. Documentation of the biting of humans by *H. axyridis* has also been recorded (Huelsman *et al*. 2002).

Harmonia axyridis is not the only alien species documented with negative effects where it has become established. A Palearctic species, the seven-spotted lady beetle, *Coccinella septempunctata* L., has been established in North America since 1973 (Angalet and Jacques 1975) and in the eastern United States since 1979 (Angalet 1979). Current populations were likely established by stowaways arriving to seaports or through intentional introductions for the control of pests in agriculture (Schaefer *et al*. 1987, Krasfur 1992); however, their exact origin is not certain (Obrycki and Kring 1998).

Coccinella septempunctata populations threaten native lady beetle species through intraguild predation and by competing for aphid prey (Ormord 1994). The decline of the native lady beetle, *Coccinella novemnotata* Herbst, in North America is correlated with the arrival of *C. septempunctata* (Wheeler and Hoebeke 1995). In South Dakota, populations of two native lady beetles (*Adalia bipunctata* (L.) and *Coccinella transversoguttata* Brown) declined with the arrival of *C. septempunctata* (Elliot *et al*. 1996). *Coccinella septempunctata* has also been documented to consume larvae of the endangered Karner blue butterfly (*Lycaeides melissa samuelis* Nabokov) (Schellhorn *et al*. 2005).

Also a Paleartic species, *Propylea quatuordecimpunctata* (L.) was released in North America to control greenbugs (Rogers *et al*. 1972); however, these releases are not believed to have led to its establishment in North America (Day *et al*. 1994). *Propylea quatuordecimpunctata* is thought to have become established in North America via ship traffic on the St. Lawrence Seaway (Chantal 1972). The first established population was found in Quebec in 1968 (Wheeler 1990), before intentional releases for the control of pests in agriculture were conducted. As a generalist predator of aphids, this species threatens native species through competition for prey (Gordon 1985).

Non-Native Lady Beetles in Maine: Current Status and Historical Record

Of the 51 lady beetle species currently documented to occur in Maine (Gordon 1985, Bourque *et al*. 2005), eight are non-native: *Coccinella hieroglyphica kirbyi* Crotch, *Stethorus punctum* (LeConte), *Stethorus punctillum* (Weise), *Epilachna varivestis* Mulsant, *Hippodamia variegata* (Goeze), *H. axyridis*, *C. septempunctata* and *P. quatuordecimpunctata* (Gordon 1985). *Propylea quatuordecimpunctata* was first documented in Maine in 1988 in Kennebec, Penobscot, and Aroostook Counties, where it is believed to have expanded its range from existing populations in Quebec (Wheeler 1990). Despite releases of over 80,000 *C. septempunctata* in Maine potato between 1964 and 1969 (Shands *et al*. 1972), it is unclear if current Maine populations are a result of these releases or by natural movement of accidental populations (Schaefer 1987).

Whether to determine the effectiveness of biological control or out of conservation concerns, it is important to understand the possible effects that alien introductions may be having on non-target, native species. Alyokhin and Sewell (2004) evaluated lady beetle populations on potato plots on the Aroostook Research Farm in northern Maine from 1971 to 2001. Until 1980, the dominant lady beetles species were *Hippodamia tredecimpunctata* (Say) and *Coccinella transversoguttata* Brown. Once *C. septempunctata* became established in 1980, its numbers increased until it became the dominant species. With the appearance of *H. axyridis* (1995) and *P. quatuordecimpunctata* (1996), the relative abundances of *H. tredecimpunctata* and *C. transversoguttata* continued to decrease. *Harmonia axyridis* and *P. quatuordecimpunctata* populations increased until 2001 (the last year of the study), perhaps signifying a shift in dominance as the two, newly established alien species increased in number. Dominance was then shared by the three alien species, with the two native species making up less than 15% of the lady beetle community. Although Alyokhin and Sewell (2004) provided some initial insight into interactions between native and non-native lady beetles, their study was rather limited in scope. Little is known about the effects that introduced lady beetles might be having on native lady beetle populations, prey populations, community structure, and ecosystem dynamics in the habitats where they are introduced.

Evans (2004) documented abundances of a non-native lady beetle species (*C. septempunctata*), several native lady beetle species, and their aphid prey in alfalfa in Utah in 1992-1994 and 1997-2001. Throughout the course of the study, aphid and native lady beetle abundance decreased as *C. septempunctata* abundance increased. Evans (2004) suggested that the reduction in prey density caused by the non-native lady beetle led to a concurrent reduction in native lady beetle abundance. Evans (2004) then artificially enhanced natural populations of aphids in an alfalfa field where a reduction in native species had previously coincided with an increase in non-native lady beetles. Native lady beetle abundance increased with increased aphid density. Based on this evidence, Evans (2004) suggested that native species have retreated from alfalfa fields to other habitats in response to the depletion of their food resources by *C. septempunctata*, but returned when prey species became more abundant. Therefore, in some cases, native species may still dominate in non-agricultural habitats while being replaced by non-native lady beetle species in agricultural ecosystems. This model of resource partitioning and optimal feeding is known as the "compression hypothesis" (MacArthur and Pianka 1966, MacArthur and Wilson 1967). To test this hypothesis, a survey of lady beetles was conducted in 2004 and 2005 in different habitats in Maine to determine if non-native lady beetle species have replaced native species in a variety of habitats.

Little is known about the factors that allow non-native lady beetle species to establish populations beside already existing native populations. To address these questions, an additional group of studies was conducted.

Chapter 2

ABUNDANCE OF NATIVE AND NON-NATIVE LADY BEETLES IN DIFFERENT HABITATS IN MAINE

Chapter Abstract

A number of studies suggest that non-native lady beetles may have replaced native lady beetles in some agricultural habitats. There is relatively little information, however, about lady beetle species composition outside of agricultural habitats. Evans (2004) suggested that native species have retreated to non-agricultural habitats in response to the arrival of non-native lady beetles (habitat compression hypothesis). To test this hypothesis, a survey of lady beetles was conducted in 2004 and 2005 in different habitats in Maine. From May to October, lady beetles were sampled in a variety of agricultural and non-agricultural habitats. A total of 3,487 and 2,903 lady beetles were collected in 2004 and 2005, respectively. Non-native lady beetles were found in a variety of habitats, including the ones that would have likely served as a refuge for native species if the habitat compression hypothesis applied to the surveyed areas. Native species were found in a higher proportion in agricultural habitats when compared to non-agricultural habitats and in very low numbers in all of the habitats surveyed. *Hippodamia tredecimpunctata tibialis* and *Coccinella transversoguttata*, the two native species that were once dominant here, made up only 1.09% and 0.07% of the total lady beetles collected, respectively. In this survey, evidence was detected showing that native lady beetles have retreated to non-agricultural habitats in response to the arrival of non-native lady beetles.

Introduction

Lady beetles are generally considered beneficial insects because they feed on the pests of crops including aphids, scale insects, thrips, mites, immature stages of Coleoptera, Lepidoptera, and Hymenoptera, fungi, and weed pollen (Hodek 1973, Gordon 1985). As a result, lady beetles have been intentionally introduced into new habitats throughout the world for the control of agricultural crop pests (Gordon 1985, Koch 2003, Koch and Galvan 2008). Unintentional introductions have also occurred via transport as stowaways in plant exports and other cargo (Chantal 1972, Schaefer *et al.* 1987, Day *et al.* 1994). With the increasing concern about the effects of invasive species on native ecosystems, non-native lady beetles (i.e., adventive, introduced, or exotic), which often establish populations in geographical ranges already inhabited by one or more native (i.e., indigenous) or non-native lady beetle species, have been receiving increased scrutiny. In addition to out-competing other lady beetles for food items (Michaud 2002), non-native species may also prey upon other lady beetle species (Dixon 2000, Yasuda *et al.* 2004). As a result, introductions of non-native lady beetles have been correlated with reductions in numbers of native lady beetles (Elliot *et al.* 1996, Brown and Miller 1998, Colunga-Garcia and Gage 1998, Michaud 2002, Brown 2003, Turnock *et al.* 2003, Alyokhin and Sewell 2004).

Of the 51 lady beetle species currently documented to occur in Maine (Gordon 1985, Bourque *et al.* 2005), the following eight are non-native: *Coccinella hieroglyphica kirbyi* Crotch, *Stethorus punctum* (LeConte), *Stethorus punctillum* (Weise), *Epilachna varivestis* Mulsant (Mexican bean beetle, an herbivorous pest species), *Hippodamia variegata* (Goeze), *Harmonia axyridis* (Pallas), *Coccinella septempunctata* L., and

Propylea quatuordecimpuncata L. (Gordon 1985). Relatively little is known about their impact on native lady beetles. Alyokhin and Sewell (2004) evaluated lady beetle populations in potato plots on the Aroostook Research Farm in northern Maine from 1971 to 2001. They reported that until 1980, the dominant lady beetles were the two native species *Hippodamia tredecimpunctata tibialis* (Say) and *Coccinella transversoguttata* Brown, but after *C. septempunctata* became established in 1980, it rapidly became the dominant species and densities of the two native species decreased significantly. With the appearance of *H. axyridis* (1995) and *P. quatuordecimpuncata* (1996), the relative abundances of *H. tredecimpunctata* and *C. transversoguttata* continued to decrease. *Harmonia axyridis* and *P. quatuordecimpunctata* populations increased until 2001 (the last year of the study), perhaps signifying a shift in dominance as the two, newly established non-native species increased in number. Dominance was then shared by the three non-native species, with the two native species making up less than 15% of the lady beetle community. Similarly, a 1998 survey in Cape Breton, Nova Scotia, found native lady beetle species, *Coccinella trifasciata perplexa* Mulsant and *Adalia bipunctata* (L.), greatly outnumbered by non-native species, *C. septempunctata*, *P. quatuordecimpunctata*, and *H. variegata* (Cormier *et al*. 2000).

Evans (2004) documented abundances of a non-native lady beetle species (*C. septempunctata*), several native lady beetle species, and their prey (pea aphids, *Acyrthosiphum pisum* [Harris]) in alfalfa in Utah in 1992-1994 and 1997-2001. Throughout the course of the study, pea aphid and native lady beetle abundance decreased as *C. septempunctata* abundance increased. Evans (2004) suggested that the reduction in prey density caused by the non-native lady beetle led to a concurrent reduction in native lady beetle abundance. Evans (2004) then artificially enhanced natural populations of pea aphids in an alfalfa field where a reduction in native species had previously coincided with an increase in non-native lady beetles. Native lady beetle abundance increased with increased pea aphid density. Based on this evidence, Evans (2004) suggested that native species have retreated from alfalfa fields to other habitats in response to the depletion of their food resources by *C. septempunctata*, but returned when prey species became more abundant. Therefore, in some cases, native species may still dominate in non-agricultural habitats while being replaced by non-native lady beetle species in agricultural ecosystems. This model of resource partitioning and optimal feeding is known as the "compression hypothesis" (MacArthur and Pianka 1966, MacArthur and Wilson 1967). To test this hypothesis, a survey of lady beetles was conducted in 2004 and 2005 in different habitats in Maine to determine if non-native lady beetle species have replaced native species in a variety of habitats.

When examining lady beetle populations in alfalfa micro-landscapes representing habitat loss, fragmentation, and isolation, Zaviezo *et al*. (2006) did not find differences in where native and non-native lady beetles were found. However, a mounting number of studies document greater abundances of non-native lady beetles compared to native lady beetles in a variety of geographic areas (Wheeler and Hoebeke 1995, Elliott *et al*. 1996, Brown and Miller 1998, Colunga-Garcia and Gage 1998, Michaud 2002, Turnock *et al*. 2003, Brown 2003, Alyokhin and Sewell 2004, Evans 2004), their focus almost exclusively on agricultural habitats. Little is known about lady beetle species composition in other habitats.

Materials and Methods

Study Area

Lady beetles were sampled in a variety of habitats (Table 2.1) at six locations across the state of Maine: commercial potato farm, Fryeburg, Maine (FR) (44.0560˚N, 70.9801˚W); Orono Land Trust Land, Orono, Maine (LT) (44.8974˚N, 68.6873˚W); the University of Maine's Rogers Farm, Orono, Maine (RF) (44.9311˚N, 68.6937˚W); commercial potato farm currently enrolled in the Conservation Reserve Program, Monticello, Maine (CR) (46.2743˚N, 67.8693˚W); on rural residential property, Presque Isle, Maine (PI) (46.5889˚N, 68.0704˚W), and the University of Maine's Aroostook Research Farm, Presque Isle, Maine (AF) (46.6528˚N, 68.0109˚W). Habitats at each location were situated within close proximity to each other. For logistical reasons, not all habitats were sampled during both years of the study.

Sampling Protocol

Determination of the best sampling method was based on information in the literature and validated by comparisons. In a comparison of the success of different methods in sampling coccinellids in alfalfa, Stephens and Losey (2004) found that when yellow sticky cards were deployed for over 10 days, they exceeded visual observation and sweep net sampling in the number of coccinellids collected per minute effort. In a two year, continuous study by Parajulee and Slosser (2003), yellow sticky cards were more efficient and effective in capturing coccinellids in cotton compared to a two-cycle vacuum sampler. Mensah (1997) found that of a variety of differently colored sticky cards, *Coccinella transversalis* (F.) and *A. bipunctata* in cotton were attracted the most

Table 2.1. Locations and habitats of sampling where 5 yellow sticky cards were deployed throughout each sampling season for 2-week periods.

Habitat	Locations						Dominant Vegetation
	FR	LT	RF	CR	PI	AF	
Apple			▦				*Malus* sp., *Elytrigia repens*, *Taraxacum* sp.
Coniferous forest		▦		▤			*Picea* sp., *Pinus* sp., *Abies* sp.
Deciduous forest		▦				▦	*Acer* sp., *Betula* sp.
Field		▦	▤	▤	▥	▦	*Phleum pratense*, *Trifolium* sp., *Cirsium* sp., *Vicia* sp., *Fragaria* sp.
Grain			▦			▦	*Hordeum* sp., *Avena* sp.
Mixed forest	▥	▦	▦	▤	▥	▦	*Acer* sp., *Abies* sp., *Thuja* sp., *Picea* sp., *Betula* sp., *Fagus* sp.
Mixed organic crops			▤				*Solanum lycopersicon*, *Allium* sp., *Brassica* sp., *Pisum* sp., *Phaseolus* sp.
Potato	▥		▦			▦	*Solanum tuberosum*
Riparian		▦	▦	▤		▦	*Alnus* sp., *Onoclea sensibilis*, *Cornus sericea*, *Impatiens capensis*, *Mentha* sp.
Shrub	▥	▦		▤		▦	*Solidago* sp., *Rubus* sp., *Prunus* sp., *Rosa* sp., *Cornus sericea*, *Alnus* sp.

Sampling season: In 2004 (horizontal lines), cards were collected and replaced during the weeks of: 17 May, 31 May, 14 June, 28 June, 12 July, 26 July, 9 Aug., 23 Aug., 6 Sept., 20 Sept, 4 Oct., and 18 Oct. In 2005 (vertical lines), cards were collected and replaced during the weeks of: 30 May, 13 June, 27 June, 11 July, 25 July, 8 Aug., 22 Aug, and 5 Sept. Boxes with horizontal and vertical lines represent habitats where 5 traps were deployed in both 2004 and 2005.

to those that were yellow, suggesting that yellow light in the range of 500 nm to 580 nm attracted these species the most because this is the range reflected the most by green foliage, where prey is typically found. Preliminary investigations determined that yellow sticky traps did not bias lady beetle samples compared to net sweeps, beating sheets, and visual observations, but were dramatically more productive and labor-efficient (Appendix A). Based on previous studies, preliminary data, and the ability to place cards at many locations over long periods of time, the study was limited to coccinellids collected by yellow sticky cards. Cards were situated both in close proximity to the ground and to vegetation, as the objective was to determine which coccinellid species were associated with different habitat types. Additionally, previous studies have shown that traps located closer to the ground are more effective in capturing coccinellids (Mensah 1997, Parajulee and Slosser 2003).

Samples were collected continuously from 17 May to 18 October 2004 and 30 May to 5 September 2005. Five, 15.24 cm x 30.48 cm yellow sticky strips TM (Olson Products, Medina, Ohio) with adhesive on both sides were deployed in each habitat in each location. Trap locations were determined randomly and spaced at least 50 meters apart within approximately 1-2 hectare (agricultural) and >2 hectare (non-agricultural) habitats. The cards were hung on stakes or directly from vegetation as close to foliage as possible without sticking to it; thus, the height of cards varied depending on vegetation structure. Cards were deployed in the same location unless changes in vegetation (i.e., growth, senescence) necessitated their vertical movement. Cards were replaced every two weeks at approximately the same time each day, with each location visited one day every two weeks (ex., Rogers Farm on Tuesday, 14 June; then Tuesday, 28 June, etc.). Cards were then brought to the laboratory and stored in the refrigerator. Captured lady beetles were removed from the traps and identified to species (Gordon 1985). Identifications were later confirmed by Donald Chandler (University of New Hampshire). Voucher specimens of each species were deposited in the Maine Forest Service Insect Collection in Augusta, Maine.

Statistical Analyses

The main focus of this study was based upon the assumption that non-native species establishment affects native populations. Therefore, analyses were limited to the lady beetle species with overlapping primary prey items (aphids) and three lady beetle species have been excluded from the analyses: *Psyllobora vigintimaculata* (Say) (a mildew-feeder), *E. varivestis* (a plant-feeder), and *Scymnus* sp. (feeding primarily on scale insects).

The data collected throughout the season were pooled for each trap position. For example, data were pooled from the 12 traps deployed throughout the 2004 season at the LT location in field habitat in position one. Similarly, data from the 12 traps deployed in field habitat at the LT location in position two were pooled; and so on, for locations three, four, and five. Thus, there were five trap positions in each habitat in each location where data were collected throughout each season.

Data normality was tested using the Wilk-Shapiro test (PROC UNIVARIATE, SAS Institute 2002). Count data that were not normally distributed were transformed using $\sqrt{X+0.001}$ transformations (Zar 1999). Means and standard errors reported in this paper were calculated from the untransformed data. To compare abundance of native and non-native lady beetles in different habitats, two-way ANOVA (PROC GLM, SAS Institute 2002) was used. Analyses were conducted separately for each location during each year of the study. Lady beetle origin (native or non-native) and habitat were used as the main effects. Different lady beetle species were pooled together. When an interaction between beetle origin and habitat was statistically significant, additional paired t-tests (PROC TTEST, SAS Institute 2002) were conducted comparing mean numbers of native beetles with non-native beetles within each habitat at that location. To determine if native and non-native species had similar habitat preferences, correlation analysis (PROC CORR, SAS Institute 2002) were used to compare their abundances in different habitats, where the same habitat types in different locations were considered separately.

Results

A total of 3,487 lady beetles were collected in 2004 and a total of 2,903 lady beetles were collected in 2005. Mean numbers of each species captured in each habitat in each location are provided in Appendix B. *Propylea quatuordecimpuncata*, *H. axyridis*, and *C. septempunctata* were the most numerous non-native species. Three other non-native species were also collected, but in very small numbers: *Coccinella hieroglyphica kirbyi*, *E. varivestis*, and *H. variegata*. Lady beetles collected that were native to the region were *P. vigintimaculata*, *Coleomegilla maculata lengi* Timberlake, *C. trifasciata*, *Hyperaspis* sp., *Hippodamia parenthesis* (Say), *H. tredecimpunctata*, *Mulsantina* sp., *Scymnus* sp., *Chilocorus* sp., *A. bipunctata*, *Anisosticta bitriangularis* (Say), *C. transversoguttata*, *Hippodamia convergens* Guérin-Méneville, *Calvia quatuordecimguttata* (L.), and *Anatis quindecimpunctata* (Olivier).

In both 2004 and 2005, *P. quatuordecimpuncata* was the most abundant species in field, potato, and mixed organic habitats; the mildew-feeding *P. vigintimaculata* in coniferous forest, deciduous forest, and mixed forest; and *H. axyridis* in apple. In grain, *P. quatuordecimpuncata* was the most abundant in Presque Isle, but *C. maculata* was the most abundant at the more southern, Orono location. Two habitats (riparian and shrub) differed in 2004 to 2005. In both of them, *P. vigintimaculata* was the most abundant in 2004, but *P. quatuordecimpuncata* was the most abundant in 2005.

When the data set was limited to aphidophagous species only, the totals became 2,338 in 2004 and 2,053 in 2005. In 2004, 66.19 ± 4.91% (mean ± standard error) of all aphidophagous lady beetles captured by yellow sticky traps were non-native species. Similarly in 2005, 67.24 ± 4.26% were non-native. Among non-native aphidophagous species, *P. quatuordecimpuncata* was by far the most numerous lady beetle collected (54.75% and 57.67% of the total number of aphidophagous lady beetles collected in 2004 and 2005, respectively), followed by *H. axyridis* (6.97% and 11.98%) and *C. septempunctata* (4.28% and 3.07%). The two most abundant native aphidophagous lady beetles were *C. maculata* (22.28% in 2004 and 14.95% in 2005) and *C. trifasciata* (3.21% in 2004 and 2.68% in 2005).

During both years of the study, there was considerable variation in the capture of aphidophagous lady beetles among sampled habitats at each location (Table 2.2). In 2004, mixed organic crops yielded the greatest number of lady beetles (native and non-native species combined), followed by grain and potato. Similarly, grain and potato yielded the highest numbers of beetles in 2005. In both 2004 and 2005, the fewest lady beetles were collected in coniferous forest, mixed forest, and deciduous forest.

Table 2.2. Mean (± standard error) number of aphidophagous lady beetles collected by yellow sticky cards (N = 5) throughout the sampling season in each habitat at each location in 2004 and 2005.

2004		Native		Non-Native		Total	
Location	Habitat	Mean	SE	Mean	SE	Mean	SE
CR	coniferous forest	1.20	0.8000	0.00	0.0000	1.20	0.8000
	field	2.20	1.1136	2.40	1.9391	4.60	2.9933
	mixed forest	0.60	0.2449	1.00	1.0000	1.60	1.1225
	riparian	1.80	1.1136	6.80	2.8879	8.60	3.0100
	shrub	2.20	1.2410	4.20	1.2806	6.40	1.6613
LT	coniferous forest	0.20	0.2000	0.00	0.0000	0.20	0.2000
	deciduous forest	0.40	0.2449	0.60	0.4000	1.00	0.4472
	field	11.00	0.4472	35.80	3.3377	46.80	3.0067
	mixed forest	0.40	0.4000	0.40	0.2449	0.80	0.3742
	riparian	0.40	0.4000	5.00	2.5495	5.40	2.9428
	shrub	4.80	1.1136	14.20	6.6963	19.00	6.8920
AF	deciduous forest	1.20	0.4899	9.00	4.0620	10.20	4.1881
	field	1.00	0.0000	11.00	1.0000	12.00	1.0000
	grain	3.80	0.8602	16.60	3.1241	20.40	3.6959
	mixed forest	0.40	0.4000	2.60	1.4000	3.00	1.4142
	potato	2.20	0.7348	20.00	4.6043	22.20	5.0339
	riparian	2.20	0.6633	8.60	2.5020	10.80	2.8178
	shrub	0.00	0.0000	9.20	1.8276	9.20	1.8276
RF	apple	3.80	1.4967	11.80	0.9695	15.60	1.9131
	field	11.80	2.5179	17.60	2.9428	29.40	2.2935
	grain	31.80	7.6118	40.20	13.1583	72.00	20.7340
	mixed forest	6.40	1.7205	9.00	3.9370	15.40	5.0060
	mixed organic crops	27.80	5.4900	48.60	13.5300	76.40	16.7946
	potato	22.60	4.4788	41.60	11.1203	64.20	15.3668
	riparian	0.40	0.2449	4.60	1.7205	5.00	1.7607

Table 2.2 (Continued). Mean (± standard error) number of aphidophagous lady beetles collected by yellow sticky cards (N = 5) throughout the sampling season in each habitat at each location in 2004 and 2005.

2005		Native		Non-Native		Total	
Location	Habitat	Mean	SE	Mean	SE	Mean	SE
FR	mixed forest	1.60	0.6000	4.40	1.8601	6.00	2.1679
	potato	2.80	0.9165	11.40	1.8055	14.20	1.9339
	shrub	1.60	0.4000	6.60	2.4617	8.20	2.2226
LT	coniferous forest	0.60	0.2449	0.40	0.2449	1.00	0.4472
	deciduous forest	0.00	0.0000	0.20	0.2000	0.20	0.2000
	field	4.20	0.8602	21.20	5.7393	25.40	5.5642
	mixed forest	1.00	0.6324	0.20	0.2000	1.20	0.5831
	riparian	1.20	0.2000	7.00	1.8974	8.20	1.8276
	shrub	4.80	3.1528	11.60	3.1241	16.40	2.2935
AF	deciduous forest	0.80	0.2000	16.40	5.1730	17.20	5.2288
	field	3.20	0.9165	10.20	2.0833	13.40	2.2494
	grain	4.20	0.7348	15.60	3.9699	19.80	4.5541
	mixed forest	0.40	0.2449	0.60	0.6000	1.00	0.5477
	potato	2.00	0.8367	18.60	2.8740	20.60	2.7857
	riparian	3.60	1.1662	2.60	1.2083	6.20	1.9339
	shrub	2.40	1.6613	33.40	15.7658	35.80	15.3375
PI	field	1.00	0.3162	1.80	0.6633	2.80	0.7348
	mixed forest	0.40	0.2449	1.40	0.6782	1.80	0.4899
RF	apple	3.40	0.7483	5.20	1.4967	8.60	2.1354
	grain	40.00	11.9541	48.80	7.9272	88.80	14.5959
	mixed forest	1.80	0.5831	13.00	2.7019	14.80	2.3108
	potato	27.20	7.0951	60.60	15.2302	87.80	21.3762
	riparian	2.00	0.8944	9.20	2.6533	11.20	2.5377

Statistically, the differences among the habitats were significant on the farm enrolled in the Conservation Reserve Program in Monticello in 2004 (ANOVA, DF = 4, 40, F = 2.89, p = 0.0342) and on the commercial potato farm in Fryeburg in 2005 (ANOVA, DF = 2, 24, F = 3.82, p = 0.0363). In all other cases, the difference was highly significant (ANOVA, p < 0.0001). The only exception was the rural residential property in Presque Isle sampled in 2005, where the difference between the two sampled habitats (field and mixed forest) was not significant (ANOVA, DF = 1, 16, F = 1.51, p = 0.2375).

Non-native lady beetles were generally more abundant during both years at each location (Figure 2.1, Table 2.3) with the exception of two locations where there was no

Figure 2.1 Abundance per trap (all collection dates pooled) of non-native and native lady beetles at different locations.

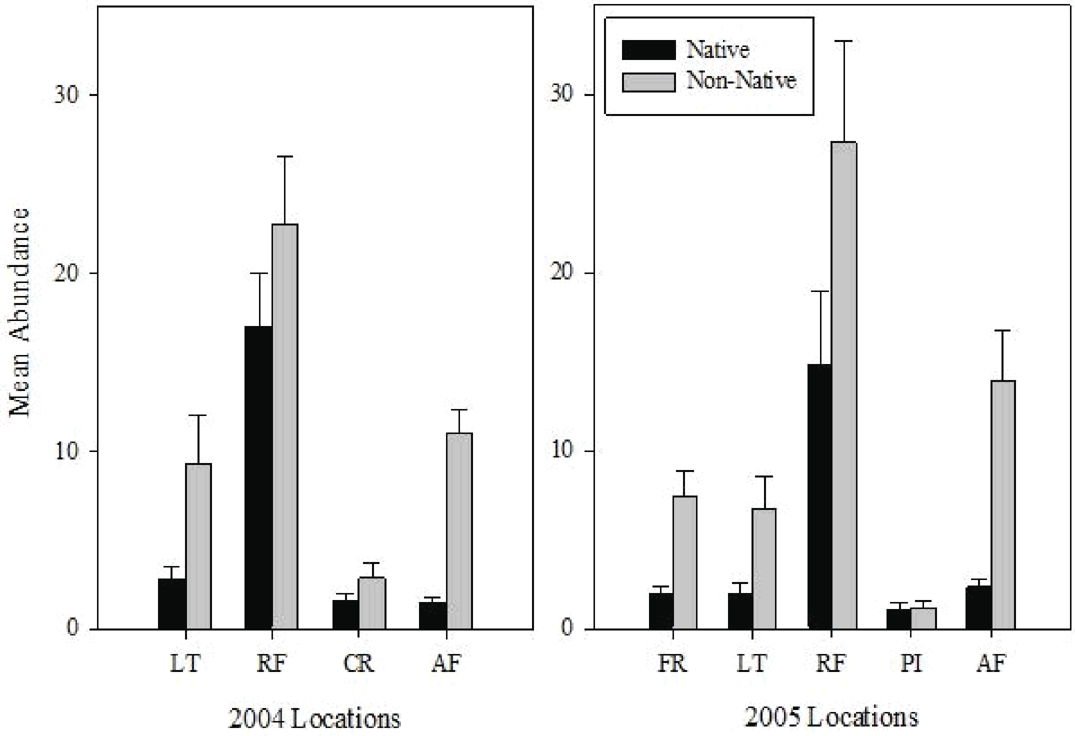


Table 2.3. Results of ANOVA comparing mean number of native and non-native aphidophagous lady beetles captured at the surveyed Maine locations.

Year	Location	DF	F	p
2004	LT	1, 48	15.45	0.0003
2004	RF	1, 56	5.04	0.0287
2004	CR	1, 40	0.31	0.5820
2004	AF	1, 56	106.48	<0.0001
2005	FR	1, 24	14.98	0.0007
2005	LT	1, 48	16.00	0.0002
2005	RF	1, 40	15.01	0.0004
2005	PI	1, 16	0.12	0.7388
2005	AF	1, 56	45.44	<0.0001

difference (the farm enrolled in the Conservation Reserve Program in Monticello in 2004 and on the rural residential property in Presque Isle in 2005). There were significant interactions between lady beetle origin and the habitat where they were captured at Orono Land Trust both in 2004 (ANOVA, DF = 5, 48, F = 3.95, p = 0.0044) and in 2005 (ANOVA, DF = 5, 48, F = 4.86, p = 0.0011) and at the Aroostook Research Farm in 2005 (ANOVA, DF = 6, 56, F = 5.33, p = 0.0002). Non-native lady beetles were more abundant in some of the habitats at these locations, and there was no significant difference between native and non-native species in the other habitats (Table 2.4). Never were the native species statistically more abundant than non-native species (Table 2.4). In the other locations sampled during the two years of the study, non-native species were more abundant than native species regardless of habitat, as evidenced by statistically

Table 2.4. Mean (± standard error) number of native and non-native aphidophagous lady beetles captured in different habitats at locations where the interaction between beetle origin and habitat was significant. t- and p-values are for the follow-up paired t-tests.

Location	Habitat	Origin	Mean	SE	t	p
LT (2004)	coniferous forest	native	0.20	0.2000	1.00	0.3739
		non-native	0.00	0.0000		
	deciduous forest	native	0.40	0.2449	0.22	0.8362
		non-native	0.60	0.4000		
	field	native	11.00	0.4472	8.01	0.0013
		non-native	35.80	3.3377		
	mixed forest	native	0.40	0.4000	0.26	0.8099
		non-native	0.40	0.2449		
	riparian	native	0.40	0.4000	6.70	0.0026
		non-native	5.00	2.5495		
	shrub	native	4.80	1.1136	0.99	0.3770
		non-native	14.20	6.6963		
LT (2005)	coniferous forest	native	0.60	0.2449	1.00	0.3739
		non-native	0.40	0.2449		
	deciduous forest	native	0.00	0.0000	1.00	0.3739
		non-native	0.20	0.2000		
	field	native	4.20	0.8602	3.67	0.0214
		non-native	21.20	5.7393		
	mixed forest	native	1.00	0.6324	0.86	0.4388
		non-native	0.20	0.2000		
	riparian	native	1.20	0.2000	3.95	0.0168
		non-native	7.00	1.8974		
	shrub	native	4.80	3.1528	1.37	0.2417
		non-native	11.60	3.1241		
AF (2005)	field	native	3.20	0.9165	3.24	0.0315
		non-native	10.20	2.0833		
	deciduous forest	native	0.80	0.2000	4.40	0.0117
		non-native	16.40	5.1730		
	grain	native	4.20	0.7348	3.30	0.0301
		non-native	15.60	3.9699		
	mixed forest	native	0.40	0.2449	0.10	0.9273
		non-native	0.60	0.6000		
	potato	native	2.00	0.8367	5.32	0.0060
		non-native	18.60	2.8740		
	riparian	native	3.60	1.1662	1.01	0.3688
		non-native	2.60	1.2083		
	shrub	native	2.40	1.6613	2.65	0.0571
		non-native	33.40	15.7658		

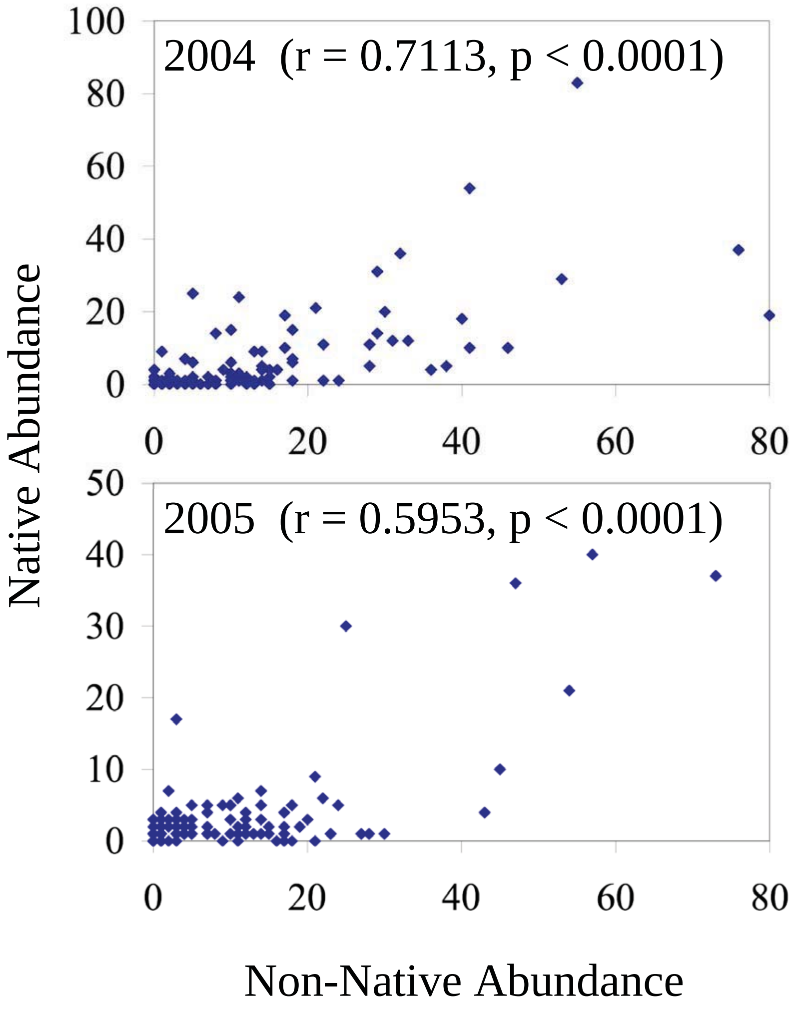
insignificant interaction terms (ANOVA, $p > 0.05$). There was a strong positive correlation between the abundance of non-native and native lady beetles (Figure 2.2) in 2004 ($r = 0.7113$, $p < 0.0001$) and 2005 ($r = 0.5953$, $p < 0.0001$); where non-native abundance was high, so was native abundance.

Discussion

Following their establishment in North America, non-native lady beetles now comprise a considerable proportion of the total lady beetle community in agricultural habitats (Wheeler and Hoebeke 1995, Elliott *et al*. 1996, Brown and Miller 1998, Colunga-Garcia and Gage 1998, Michaud 2002, Turnock *et al*. 2003, Brown 2003, Alyokhin and Sewell 2004). This survey indicates that a similar situation exists in other types of habitats as well, at least in the examined areas of Maine. Despite considerable variation in the number of lady beetles belonging to different species and collected in different habitats and locations, all surveyed communities of aphidophagous lady beetles had a large proportion of non-native species.

Based on the results of the correlation analyses, both native and non-native species appeared to prefer living in the same areas, suggesting that their abundances are strongly influenced by prey abundance (Kajita *et al*. 2000). This is likely to intensify competition for food and other resources, as well as intraguild predation. Competitive interactions between native and non-native species are asymmetric for some species, with the former at a competitive disadvantage compared to the latter (Michaud 2002, Yasuda *et al*. 2004). Therefore, competitive displacement of native lady beetles is a likely outcome of the establishment of non-native lady beetles in an area. Indeed, a number of studies

Figure 2.2. Abundance per trap (all collection dates pooled) of non-native and native lady beetles in 2004 and 2005.



that analyzed multi-year time series data on relative abundance of native and non-native lady beetles generally confirmed a decrease in the proportion of native beetles following the arrival of non-native species (Elliott *et al*. 1996, Brown and Miller 1998, Turnock *et al*. 2003, Evans 2000, 2004, Alyokhin and Sewell 2004).

Lady beetle densities were generally lower in non-agricultural habitats surveyed compared to agricultural habitats (Table 2.2). Furthermore, there was some indication that their abundance in non-agricultural habitats was in some cases influenced by proximity to agricultural habitats. For example, lady beetle mean abundance (Table 2.2) in mixed forest was 0.80 (2004) and 1.2 (2005) at Orono Land Trust, where there was no agriculture, but 15.40 (2004) and 14.80 (2005) at Rogers Farm.

There was no evidence that native lady beetles have retreated to and remain dominant in non-agricultural habitats in response to the arrival of non-native lady beetles in agricultural habitats. Native lady beetle captures were never greater than non-native lady beetle captures in any habitat, regardless of the location or proximity to agriculture. This is inconsistent with findings by Evans (2000, 2004), who observed that although native lady beetles declined dramatically in Utah alfalfa fields following the establishment of *C. septempunctata*, they still dominated in the native habitats. For example, on native riparian vegetation and adjacent sagebrush, *C. septempunctata* accounted for only 3% of adult lady beetles (Evans 2000). It is possible that differences in landscape and habitat structure made non-agricultural habitats in Maine more prone to invasion than non-agricultural habitats in Utah. Alternatively, it is possible that *P. quatuordecimpuncata* and *H. axyridis*, which were the dominant species in this survey, but absent in the study by Evans (2000, 2004), are more invasive than *C. septempunctata*.

Indeed, Brown and Miller (1998) and Alyokhin and Sewell (2004) reported replacement of *C. septempunctata* by the more recently arrived *H. axyridis*. Also, biological invasion is a dynamic and long-term process (Williamson 1996), so that non-native lady beetles in Utah might not have yet spread to more marginal habitats at the time of surveys (Evans 2000, Evans 2004).

The considerable presence of non-native lady beetles in non-agricultural habitats may be of substantial conservation concern. Non-native lady beetles may replace native species, thus decreasing diversity and altering system dynamics. The replacement of native species with non-native species may alter predator-prey interactions, as non-native species may or may not exhibit the same prey preferences. Additionally, non-native lady beetles may prey on species of ecological concern. For example, *C. septempunctata* has been documented to consume larvae of the endangered Karner blue butterfly (*Lycaeides melissa samuelis* Nabokov) (Schellhorn *et al*. 2005).

The exact ecological ramifications of the establishment of non-native lady beetles still remain to be determined. Many studies to-date, including this study, focus primarily on comparisons of numbers. This provides valuable, but somewhat limited, information. For example, the ecological role of an individual *H. axyridis* may not equal that of an individual *H. convergens*. Therefore, comparisons of numbers alone are not sufficient in fully assessing the effects of non-native species introductions on native communities. There was no evidence to support the "compression hypothesis" (MacArthur and Pianka 1966, MacArthur and Wilson 1967), which in this case, would have predicted that native lady beetles have retreated to and remain dominant in non-agricultural habitats in response to the arrival of non-native lady beetles in agricultural habitats. This survey indicates that non-native lady beetles now comprise a considerable proportion of the total lady beetle community in both agricultural and non-agricultural habitats in the examined areas of Maine. Because naturally occurring, native lady beetles are an important component of biological control programs (Obrycki and Kring 1998), it is essential to understand their interactions with potential biological control organisms, native or non-native to the area of release.

Chapter 3

DIFFERENTIAL CONSUMPTION OF FOUR APHID SPECIES BY FOUR LADY BEETLE SPECIES

Chapter Abstract

Consumption by one native (*Coccinella trifasciata*) and three non-native (*Coccinella septempunctata*, *Harmonia axyridis*, *Propylea quatuordecimpunctata*) lady beetle species were compared when paired with four different aphid species (*Macrosiphum albifrons*, *Macrosiphum euphorbiae*, *Macrosiphum pseudorosae*, and *Myzus persicae*) in the laboratory. In the field, the same lady beetle species were documented with and without aphids on host vegetation, *Lupinus polyphyllus*, *Solanum tuberosum*, and *Rosa multiflora*. In the laboratory, *H*. *axyridis* generally consumed the most aphid nymphs and adults, while *P. quatuordecimpunctata* consumed the fewest. The exception to this was *P. quatuordecimpunctata*, which consumed a greater number of *M*. *albifrons* nymphs, and *C*. *trifasciata*, which consumed a greater number of *M. albifrons* nymphs and adults, compared to the other two beetle species. Lady beetles generally consumed fewer *M*. *albifrons* compared with the other three aphid species. In the field, *P. quatuordecimpunctata* was the most abundant lady beetle found on lupine and potatoes.

Introduction

Lady beetles are known to be voracious predators of plant pests, such as aphids (Hodek 1973, Gordon 1985). It is often assumed that aphidophagous lady beetles are highly polyphagous, consuming most (if not all) aphid species that they encounter (Pedigo and Rice 2006). However, there is evidence that not every aphid species is equally suitable for every lady beetle species (Obrycki and Orr 1990, Phoofolo and Obrycki 1997, Kalushkov 1998, Michaud 2000, Kalushkov and Hodek 2004, Mignault *et al*. 2006). For example, Michaud (2000) conducted choice tests with seven lady beetle species and two aphid species, *Toxoptera citricida* (Kirkaldy) and *Aphis spiraecola* Patch. Although all lady beetles tested consumed both aphid species, four species (*Coccinella septempunctata* L., *Coleomegilla maculata fuscilabris* (Mulsant), *Coelophora inaequalis* F., and *Olla v-nigrum* Mulsant) were not able to complete their developmental cycle with either aphid species. Depending on the aphid species consumed and the addition of supplements (pollen) to the diet, the other three species (*Hippodamia convergens* Guerin, *Cycloneda sanguinea* (L.), and *Harmonia axyridis* Pallas), varied considerably in the number of eggs laid, egg viability, larval development time, and adult weight.

Lady beetles are commonly released to combat a diverse range of pests (Gordon 1985, Koch 2003), despite the fact that little is known about specific prey preferences of different species. A better understanding of prey range for aphidophagous lady beetles is important for two reasons. First, the replacement of native lady beetle species by non-native species with different prey preferences may favor some aphid species over others, thus leading to changes in the aphid community. Secondly, populations of lady beetles are intentionally increased in farms and home gardens to battle aphid infestations.

The success of such pest control measures depends upon the willingness of the lured or released lady beetles to consume the aphid pest in question. Despite sharing the same habitats, lady beetle species may differ in their consumption of aphid prey. In the laboratory, one native and three non-native lady beetle species were provided aphid prey of four different species and consumption recorded. To determine if potential differences documented in the laboratory were reflected in the field, lady beetle species were also documented with and without aphids in the field.

Materials and Methods

Study Species

The four lady beetle species chosen for this study are aphidophagous (Gordon 1985) and abundant in Maine. The native lady beetle species used was *Coccinella trifasciata perplexa* Mulsant, which is native from Labrador south to New Jersey and west to California and Alaska (Gordon 1985). The non-native lady beetle species used were *C. septempunctata*, *H. axyridis*, and *Propylea quatuordecimpunctata* (L.). These three species are Palearctic in origin and were both intentionally and inadvertently introduced in North America. *Coccinella septempunctata* has been established in North America since 1973 (Angalet and Jacques 1975), *H. axyridis* since 1988 (Chapin and Brou 1991, Tedders and Schaefer 1994), and *P. quatuordecimpuncata* since 1968 (Wheeler 1990).

Four aphid species were chosen to serve as the prey for the lady beetle species. The potato aphid, *Macrosiphum euphorbiae* (Thomas), feeds on over 200 plant species (Blackman and Eastop 1984). The green peach aphid, *Myzus persicae* (Sulzer), feeds on over 40 different plant families (Blackman and Eastop 1984). Hosts of the rose aphid, *Macrosiphum pseudorosae* (Patch), include the genus *Rosa* and a variety of herbaceous plants (Foottit and Maw 1997). The lupine aphid, *Macrosiphum albifrons* Essig, is a specialist, feeding only on plants in the genus *Lupinus* (Blackman and Eastop 1984). While *M. persicae* is believed to be Palearctic in origin (Blackman and Eastop 1984); the other three aphid species are Nearctic (Stroyan 1981, Blackman and Eastop 1984).

Laboratory Trials

Lady beetles were collected from the field 48-72 hours before test initiation and provided with water, but no food, for 48 hours before test initiation. Lady beetles were collected from a variety of locations in Orono, Maine (44.8835° N, 68.6721° W), that included mixed shrub (*Solidago* sp., *Rubus* sp., *Prunus* sp., *Rosa* sp., *Cornus sericea*, *Alnus* sp.), apple (*Malus* sp.), grain (*Hordeum* sp., *Avena* sp.), mixed organic crops (*Solanum lycopersicon*, *Allium* sp., *Brassica* sp., *Pisum* sp., *Phaseolus* sp.) and field (*Phleum pratense*, *Trifolium* sp., *Cirsium* sp., *Vicia* sp., *Fragaria* sp.).

Potato aphids and green peach aphids were obtained from colonies maintained in the laboratory. The colonies were originally founded by aphids collected from potato, *Solanum tuberosum* (Family: Solanaceae), in Presque Isle, Maine, and then maintained for at least 20 generations on excised potato foliage in the laboratory. Rose and lupine aphids were collected in the field from host vegetation (multi-flora rose, *Rosa multiflora* (Family: Rosaceae), and lupine, *Lupinus polyphyllus* (Family: Fabaceae), respectively), and then maintained in the laboratory on excised host vegetation for up to three days before use in trials.

In the beginning of each experiment, ten aphids belonging to the same species were placed using a paintbrush on an excised leaflet held within a 100 x 15 mm polystyrene Petri dish. Leaves used in trials were of the host plants from which aphids were collected in the field (see above). In each 24-hour trial, a single lady beetle previously housed in a separate Petri dish was added to the Petri dish containing the aphids by quickly exchanging lids between the two Petri dishes when the lady beetle was on the lid. After 24 hours, the number of aphids surviving was recorded. The experiment was conducted separately with adult wingless aphids and with 1st-2nd instar aphid nymphs. Sixty trials were conducted with each lady beetle species/aphid species pairing: 30 replicates with adult aphids and 30 replicates with the nymphs.

Lady beetles, aphid colonies, and test dishes were housed in Percival I-33VL Intellus environmental chambers at 16 (light):8 (dark) hour photoperiod and 20°C. Trials with potato and lupine aphids were conducted in 2005, from June 16 to August 12 and from June 2 to August 12, respectively. Trials with green peach and rose aphids were conducted in 2006, from 24 May to 16 August and from 10 August to 24 August, respectively.

Field Observations

In the field, lupine, potato, and multi-flora rose were observed for 30 minutes in various locations in Orono, ME (44.8974˚N, 68.6873˚W). The number of lady beetles on host vegetation or in contact with lupine, potato, or rose aphids was recorded. Observations were made between 10:00 am and 2:00 pm in areas approximately 0.1 hectare in size where the vegetation of interest was dominant (≥ 50%). Forty observation trials were conducted for each of the three species. Green peach aphids were not found in the field in numbers sufficient to conduct observations. Lupine aphid colonies were observed from 2 June to 12 July 2005, potato aphid colonies were observed from 17 June to 30 July 2005, and multi-flora rose aphid colonies were observed for rose aphid from 20 June to 24 August 2006.

Statistical Analyses

Normality of laboratory-generated data was tested using the Wilk-Shapiro test (PROC UNIVARIATE, SAS Institute Inc. 2002). The data were transformed using rank transformations (Conover and Iman 1989). Means and standard errors reported in this paper were calculated from the untransformed data. Differences between lady beetle species were analyzed separately for each aphid species using one-way ANOVA followed by Tukey's multiple comparison tests (PROC GLM, SAS Institute Inc. 2002). Analyses were conducted separately for aphid nymphs and adults.

Poisson regression (PROC GENMOD, SAS Institute Inc. 2002, SAS Institute Inc. 2005) was used to analyze lady beetle count data generated during field observations. Each plant species observed was analyzed separately, with the number of lady beetles as the response variable and lady beetle species and aphid presence/absence as the predictor variables. Overdispersion for lupine and rose aphid was corrected using a multiplicative overdispersion factor (Pearson chi-square divided by degrees of freedom) (Cox 1983, Allison 1999, SAS Institute Inc. 2005).

Results

Laboratory Trials

There were always significant differences in the numbers of aphids consumed by different lady beetle species (Table 3.1). *Harmonia axyridis* consumed the most nymphs and adults of the green peach aphid, the potato aphid, and the rose aphid compared with the other three beetle species, while *P. quatuordecimpunctata* consumed the fewest adults of these three aphid species and the fewest nymphs of the green peach aphid and the potato aphid. *Coccinella septempunctata* consumed the lowest numbers of rose aphid nymphs compared with the other three beetle species.

Lady beetles generally consumed fewer lupine aphids (Table 3.1) compared with the other three aphid species. *Coccinella trifasciata* and *P. quatuordecimpunctata* consumed a greater number of lupine aphid nymphs compared with the other two beetle species; *C. trifasciata* also consumed the greatest number of lupine aphid adults.

Field Observations

All four lady beetle species were found on potatoes, while only *H. axyridis* and *P. quatuordecimpunctata* were found on roses and only *C. trifasciata* and *P. quatuordecimpunctata* were found on lupines. There were significant differences in mean numbers of lady beetle species (Table 3.2) documented in two of the three vegetation types observed. The most abundant species in potatoes was *P. quatuordecimpunctata*, followed by *C. septempunctata* ($X^2 = 18.17$, $p < 0.0001$), *H. axyridis* ($X^2 = 22.02$, $p < 0.0001$), and *C. trifasciata* ($X^2 = 18.84$, $p < 0.0001$). On lupines, *P. quatuordecimpunctata* was more abundant than *C. trifasciata* ($X^2 = 5.52$, $p = 0.0188$).

Table 3.1. Mean (± standard error) aphid consumption by nymphs and adults of lady beetles (N = 30). Within each column, means with the same letter are not significantly different.

		Aphid Species							
		green peach		potato		rose		lupine	
Lady Beetle Species		nymphs	adults	nymphs	adults	nymphs	adults	nymphs	adults
C. trifasciata	Mean	8.70 b	8.90 b	7.13 b	7.57 b	7.33 b	7.97 b	0.90 a	0.33 a
	SE	0.2633	0.2769	0.3737	0.3380	0.2266	0.2372	0.1939	0.0998
C. septempunctata	Mean	8.47 b	8.73 b	6.97 b	7.60 b	6.37 c	6.77 b	0.00 b	0.00 b
	SE	0.1840	0.1914	0.4275	0.3575	0.2559	0.2333	0.0000	0.0000
H. axyridis	Mean	9.73 a	9.93 a	9.67 a	9.17 a	9.53 a	9.63 a	0.10 b	0.03 b
	SE	0.2030	0.0463	0.1107	0.2039	0.1244	0.1015	0.0557	0.0333
P. quatuordecimpunctata	Mean	8.47 b	6.73 c	8.00 b	5.33 c	8.13 b	6.03 b	0.63 a	0.10 b
	SE	0.2235	0.2488	0.3491	0.4271	0.2743	0.2420	0.1694	0.0557
	$F_{3,116}$	6.27	37.37	11.98	20.67	32.59	48.47	11.86	6.46
	p-value	<0.0006	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0004	<0.0006

Table 3.2. Mean (± standard error) number of lady beetles documented during field observations of host vegetation. For each plant/aphid species, mean beetles documented where aphids were present on vegetation are presented alongside mean beetles that were documented where aphids were absent. N = the number of observations, out of 40, where aphids were either present or absent.

		Plant/Aphid Species					
		potato		rose		lupine	
Lady Beetle Species		present	absent	present	absent	present	absent
	N	22	18	26	14	36	4
C. trifasciata	Mean	0.05	0.06	0	0	0.39	0
	SE	0.0455	0.0556			0.1505	
C. septempunctata	Mean	0.36	0.17	0	0	0	0
	SE	0.1050	0.0904				
H. axyridis	Mean	0.14	0.17	0.81	0.14	0	0
	SE	0.0749	0.0904	0.2355	0.0971		
P. quatuordecimpunctata	Mean	1.36	0.89	0.46	0.36	1.25	0.50
	SE	0.2421	0.1962	0.1491	0.1693	0.3766	0.2887

However, there was no difference in the abundance of the two species documented on rose (*P. quatuordecimpunctata* and *H. axyridis*). Although mean lady beetle numbers were higher in six out of the eight occasions where aphids were present compared to absent (Table 3.2), these differences were not significant.

Discussion

For all aphid species tested, consumption rates were different among the four lady beetle species. With the exception of the lupine aphid, *H. axyridis* was the most voracious predator, while *P. quatuordecimpuncata* removed the least prey. There may be a number of reasons for these differences. First, consumption rate may be affected by the size of the beetles or the size of the prey. *P. quatuordecimpuncata* is the smallest of the four beetle species, and may be satiated with fewer aphids compared with the other beetle species. The lupine aphid is larger than the other aphid species; fewer lupine aphids may satiate beetles compared with other aphid species. Consumption rate may also be affected by differences in handling (Pervez and Omkar 2005), nutritional suitability of prey (Houck 1991, Roger *et al*. 2001, Gagné *et al*. 2002), or chemical deterrence (Pasteels *et al*. 1983, Nishida and Fukami 1989).

Field observations generally supported laboratory trials. *Harmonia axyridis* consumed the most rose aphids in laboratory trials and was one of two species found in the field with rose aphids. *Coccinella trifasciata* consumed the most lupine aphids in laboratory trials and was one of two species found in the field with lupine aphids. The other beetle species found with rose and lupine aphids was *P. quatuordecimpunctata*. Of the beetle species compared in the laboratory, *P. quatuordecimpunctata* consumed the second largest number of rose and lupine aphids, although this difference was only statistically significant for lupine nymphs. It is also not surprising to find *P. quatuordecimpunctata* in all observations because this species is probably the most abundant lady beetle in Maine.

Three of the species tested in this study, *H. axyridis*, *C. septempunctata*, and *P. quatuordecimpunctata*, are not native to Maine (Gordon 1985). Because lady beetle species differ in their prey consumption, the replacement of native lady beetles by non-native lady beetles that has been reported in a number of studies (Elliot *et al*. 1996, Brown and Miller 1998, Colunga-Garcia and Gage 1998, Michaud 2002, Brown 2003, Turnock *et al*. 2003, Alyokhin and Sewell 2004) may favor some aphid species over others. As a result, the composition of aphid communities in the affected area will be altered, which may have important ecological and economic consequences.

Differences between lady beetle species may put some lady beetle species at a competitive advantage over others by contributing to successes or failures of non-native species in new habitats. For example, when compared with other coccinellid species, *H. axyridis* has been shown to have superior competitive abilities regarding its feeding rate (Michaud 2002), intraguild predation (Hironori and Katsuhiro 1997, Yasuda *et al*. 2001, Yasuda *et al*. 2004), and interactions with natural enemies (Dutcher *et al*. 1999, Saito and Bjørnson 2006). This species has been a highly successful invader, with populations established worldwide outside of its native range.

It is also interesting and important to consider the native ranges and relationships of species brought together from different geographic locations. In this study, *H. axyridis* and *C. septempunctata* consumed the lowest numbers of lupine aphid. *Coccinella* *trifasciata*, which is native to the area, consumed the most lupine adults. Lupine aphid is native to the area (Stroyan 1981). It is known to obtain toxic compounds from its host plant that have been shown to cause a "narcotizing effect" on *C. septempuctata* (Gruppe and Roemer 1988). Perhaps *C. trifasciata* has, over time, evolved the ability to feed in the presence of these compounds, while the relatively recent introduction of non-native lady beetles has not yet resulted in the same ability.

Chapter 4

COMPETITION FOR APHID PREY BETWEEN DIFFERENT LADY BEETLE SPECIES IN A LABORATORY ARENA

Chapter Abstract

Direct competition for aphid prey (Homoptera: Aphididae) was evaluated between and among several lady beetle species (Coleoptera: Coccinellidae). The behavior of three native (*Coccinella trifasciata*, *Coleomegilla maculata*, *Hippodamia convergens*) and four non-native (*Coccinella septempunctata*, *Harmonia axyridis*, *Hippodamia variegata*, *Propylea quatuordecimpunctata*) lady beetles was observed in laboratory arenas. The beetles were kept alone, paired with conspecifics, or paired with heterospecifics, and presented with potato aphids (*Macrosiphum euphorbiae*). *Harmonia axyridis* had the highest aphid consumption, shortest prey discovery time, and generally exhibited the most aggression towards other species. Prey consumption by *C. trifasciata* and *C. maculata* depended on with which species they were paired. There was generally a strong negative correlation between aphid consumption and prey discovery time, although for several species it was affected by interference from a heterospecific competitor. These results suggest that asymmetric interactions between lady beetle species may affect their ability to co-exist in the same habitat.

Introduction

Competition is often assumed when predatory species consuming the same prey species are found in the same area (Hairston *et al*. 1960). Persistent species that share prey and an evolutionary history together are often considered to have achieved a compromise over time, allowing them to co-exist by differentially exploiting the same prey species (MacArthur and Levin 1964, MacArthur and Levin 1967), for example, by foraging at different times (Pianka 1978). When species consuming the same prey are newly brought together, the ability of each to acquire the same necessary resources may allow their co-existence (Losey and Denno 1998, Hsu *et al*. 2001). Sharing prey items, however, does not mean that a sufficient share goes to each predator (Michaud 2002, Yasuda *et al*. 2004, Nunes and Hartz 2006, Blaustein and Chase 2007). Consumption by a more efficient predator may eventually result in the competitive exclusion of the less efficient predator (Hsu *et al*. 2001, Gakkhar *et al*. 2007).

Prey preferences (generalist or specialist) are often the primary consideration when evaluating the potential effects of introduced organisms on species of conservation concern and, in case of intentionally introduced natural enemies, on target pests (Symondson *et al*. 2002). However, it is also important to understand the allocation of prey going to each of the predators when considering their introduction alongside native or non-native competitors. If introduced species share prey with existing species, they may coexist. In this case, pest organisms would be controlled by a variety of predators, a favorable scenario that may result in a more comprehensive pest control program. Otherwise, if only one predator is responsible for controlling pest populations, they may reach damaging densities during periods of predator inactivity or low abundance. When considering species of conservation concern, the sharing of prey between non-native and native competitors may mean that non-native species introductions will not necessarily result in the extirpation of native species. On the other hand, non-native species that monopolize prey necessary to native species may require special consideration before their introduction, necessitate management after their introduction, or result in a decision not to introduce them.

Declines in native lady beetle abundances often coincide with the establishment of non-native lady beetle species (Elliot *et al.* 1996, Brown and Miller 1998, Colunga-Garcia and Gage 1998, Michaud 2002, Brown 2003, Turnock *et al.* 2003, Alyokhin and Sewell 2004), both as a result of intentional (Gordon 1985, Dreistadt and Flint 1996, Koch 2003) and unintentional introductions (Chantal 1972, Shaefer *et al.* 1987, Day *et al.* 1994). Because both native and non-native species are considered important for pest control (Hodek 1973, Gordon 1985), it is important to understand competitive interactions between co-existing species, and thus their effectiveness in controlling pests when found together. To evaluate direct competition and prey sharing between and among lady beetle species, beetles were presented with a limited food source in laboratory trials and their behavior documented.

Materials and Methods

Study Species

Aphidophagous lady beetle species abundant in Maine were chosen for the present study. Three species are native: the three-banded lady beetle *Coccinella trifasciata perplexa* Mulsant, the twelve-spotted lady beetle *Coleomegilla maculata lengi*

Timberlake, and the convergent lady beetle *Hippodamia convergens* Guérin-Méneville. The native range of *C. trifasciata* is north from New Jersey to Labrador and west to California and Alaska (Gordon 1985). *C. maculata* is native to eastern North America from Georgia to Ontario, and west to Texas and Minnesota (Gordon 1985). The range of *H. convergens* extends from British Columbia and Ontario south to South and Central America and the Antilles (Gordon 1985).

The non-native lady beetles used in the present study were the seven-spotted lady beetle *Coccinella septempunctata* L., the multicolored Asian lady beetle *Harmonia axyridis* (Pallas), the variegated lady beetle *Hippodamia variegata* (Goeze), and the fourteen-spotted lady beetle *Propylea quatuordecimpunctata* (L.). All four species are of Palearctic origin and were both inadvertently and intentionally introduced in North America. *Coccinella septempunctata* has been established in the eastern United States since 1979 (Angalet 1979). *Harmonia axyridis* was first documented as established in North America in 1988 (Chapin and Brou 1991, Tedders and Schaefer 1994), and now occurs throughout much of the continental United States (Koch 2003). *Hippodamia variegata* is widespread throughout northeastern North America (Gordon and Vandenberg 1991, Wheeler 1993, Wheeler and Stoops 1996, Hoebeke and Wheeler 1996, Ellis *et al*. 1999, Cormier *et al*. 2000). In Maine, *P. quatuordecimpunctata* was first documented in 1988 in Aroostook, Penobscot, and Kennebec Counties, where it is believed to have expanded its range from populations in Quebec dating to1968 (Wheeler 1990).

The potato aphid, *Macrosiphum euphorbiae* (Thomas), served as the prey. *M. euphorbiae* is common in Maine and native throughout North America (Blackman and Eastop 1984). It is known to feed on over 200 plant species including potato, apple, aster, and rose (Blackman and Eastop 1984) and is a common prey item for many lady beetle species (Shands *et al*. 1972, Gordon 1985, Hodek and Honěk 1996).

Insect Origins and Maintenance

Lady beetles were collected 48-72 hours before the initiation of each trial and provided with water, but no food, for 48 hours before trials began. Beetles were collected in Orono, Maine (44.8835° N, 68.6721° W), from a variety of habitats: mixed shrub (*Solidago* sp., *Rubus* sp., *Prunus* sp., *Rosa* sp., *Cornus sericea*, *Alnus* sp.), apple (*Malus* sp.), grain (*Hordeum* sp., *Avena* sp.), mixed organic crops (*Solanum lycopersicon*, *Allium* sp., *Brassica* sp., *Pisum* sp., *Phaseolus* sp.) and field (*Phleum pratense*, *Trifolium* sp., *Cirsium* sp., *Vicia* sp., *Fragaria* sp.) Potato aphids were obtained from a colony maintained in the laboratory. The colony was originally founded by aphids collected in Presque Isle, Maine (46.6528˚N, 68.0109˚W), from potato (*Solanum tuberosum*, Family: Solanaceae) fields and then maintained on excised potato foliage in the laboratory. Until used in trials, lady beetles and aphid colonies were housed separately in ventilated, 0.95 L Ball® glass jars (Jarden Home Brands, Inc., Daleville, Indiana) held within Percival I-33VL Intellus environmental chambers (Percival Scientific, Inc., Perry, Iowa) at 16 (light) : 8 (dark) hour photoperiod. The temperature was maintained at 20±1°C both during the photophase and scotophase. Trials were conducted from 16 May to 8 September 2006.

Competition Trials with Paired Lady Beetles

Each trial took place in an observation arena under a clear, ventilated plastic container (8.9-cm diameter and 9.5-cm height), turned upside-down and placed inside the bottom of a Petri dish. A cut potato leaf was placed in a small plastic vial with water. Using a paintbrush, 4 adult wingless aphids were placed on the upper surface of the leaf. The vial containing the vegetation and aphids was then placed in an upright position inside the observation arena. Adult lady beetle(s) were transferred to a different observation arena by allowing each lady beetle to crawl on to the tip of a paintbrush and then on to the interior of the arena. After a 10-minute period of adjustment, the cover holding the lady beetle(s) was switched with the cover under which the vial holding the leaf and aphids was housed, simultaneously exposing the lady beetle(s) to the aphids. Trials were conducted for 45 minutes. Time to prey discovery (of the first aphid), number of prey consumed by each beetle (documented to 0.25 aphid when the entire aphid was not consumed), and behavior (as a count of aggression delivered and received by each beetle in each trial) were recorded. The following behaviors were considered aggressive: chasing, grasping, biting, climbing upon, and attempting to or successfully stealing prey. Ten trials were conducted in random order with individuals of each species and with pairs of all combinations of each species, including conspecific pairings.

Prey Consumption and Discovery Time by Single Lady Beetles

To serve as a comparison with the paired trials described above, aphid consumption and time to prey discovery was also documented in trials with single lady beetles. These trials were conducted following the same protocol as described above, but with one individual introduced in each arena. Ten trials were conducted with each of the seven lady beetle species.

Measurements of Lady Beetle Weight and Size

Because differences in predator size have been used in some studies to explain differences in competition (Obrycki *et al*. 1998, Michaud 2002, Sato *et al*. 2003, Yasuda *et al*. 2004), the weight and volume of 20 lady beetles of each species were documented. The weight of each beetle was determined to the 0.0001 gram using an electronic Ohaus Adventurer Balance AR2140 (Ohaus Corp., Pine Brook, NJ). Width, length, and height were measured using a ruler mounted in the eyepiece of a Stereoscopic Zoom Microscope SMZ800 (Nikon Instruments Inc., Melville, NY) at 10x magnification. Volume was estimated by multiplying width (across the pronotum, dorsal side), length (from the frons of the head to the end of the elytra, dorsal side), and height (the greatest height below the elytra, laterally).

Statistical Analyses

The Wilk-Shapiro test (PROC UNIVARIATE, SAS Institute, Inc. 2002) was used to test data normality. Data were transformed using rank transformations (Conover and Iman 1981). Untransformed data were used to calculate the means and standard errors reported in this paper.

Behavioral data were analyzed using one-way ANOVAs followed by Tukey mean separation tests (PROC GLM, SAS Institute, Inc. 2002). Lady beetle species were used as an independent variable for each ANOVA. Aphid consumption, prey discovery time, aggression received, and aggression delivered were used as dependent variables. First, data were pooled from all trials conducted with a given species. This allowed the determination of which species consumed the overall largest number of aphids, was the quickest to discover its prey, etc. Analyses were conducted separately for beetles held alone, beetles paired with conspecifics, and beetles paired with heterospecifics (all species other than the species of interest pooled together) (Table 4.1). Secondly, the same dependent variables were evaluated separately for trials in which a given species was paired with each of the other species used in the study. This allowed pair-wise comparisons between all the tested species (Table 4.2).

Correlation analysis (PROC CORR, SAS Institute Inc. 2002) was used to test pair-wise comparisons for relationships between all possible combinations of the following: aphid consumption, prey discovery time, aggression delivered, and aggression received. In a given pair-wise comparison, the analyses were conducted for different variables within each species (e.g., correlation between aphid consumption and prey discovery time for *H. axyridis*) and for all combinations of variables between the two paired species (e.g., correlation between aphid consumption by *H. axyridis* and *C. septempunctata*) or the two individuals of the same species in conspecific trials. Most correlations between aphid consumption and prey discovery time were statistically significant. Therefore, for the ease of interpretation their results are reported separately (Table 4.3) from statistically significant comparisons between all other combinations of variables (Table 4.4). When considering aggression in a given set of pair-wise comparisons, aggression delivered by one species is equal to the aggression received by the other species. Thus, the same coefficient is produced when correlating Species One's aphid consumption with Species One's aggression delivered as when correlating Species One's aphid consumption with Species Two's aggression received.

Weights and volumes of different lady beetle species were compared using one-way ANOVA (PROC GLM, SAS Institute, Inc. 2002). Means were separated by Tukey tests.

Results

When all trials for each species were pooled (Table 4.1), there were differences between species in aphid consumption, prey discovery time, and aggression delivered. When beetles of the same species were paired together, *H. axyridis* consumed a significantly greater number of aphids than *P. quatuordecimpunctata*, but there were no statistically significant differences among other species. When paired with other species, *H. axyridis* consumed a significantly greater number of aphids than *H. variegata*, *P. quatuordecimpunctata*, *H, convergens*, and *C. maculata*. In single-beetle trials, *H. axyridis* consumed a significantly greater number of aphids than *H. variegata*, *P. quatuordecimpunctata*, *H. convergens*, and *C. trifasciata*.

There were no differences in prey discovery time between the different species in trials where the beetles were kept alone (Table 4.1). However, there were significant differences when the beetles were paired with conspecifics or with other species. When considering trials with conspecific pairings, *H. axyridis* had a significantly shorter prey discovery time compared to all other species but *C. septempunctata*. Similarly, *H. axyridis* had the shortest prey discovery time in pairings with other species. However, this was only significant in comparison with *H. convergens*. With the exception of *H.*

Table 4.1. Mean (± standard error) aphid consumption, prey discovery time, aggression delivered, and aggression received by seven lady beetle species during laboratory trials. Means in each column with the same letter are not significantly different.

		Aphid Consumption									Aggression Delivered					
		Alone			Same Species			Other Species			Same Species			Other Species		
		Mean		SE	Mean		SE	Mean		SE	Mean		SE	Mean		SE
native	*C. trifasciata*	1.30	B	0.3350	1.55	AB	0.2112	1.78	AB	0.1682	0.25	A	0.0993	0.22	B	0.0536
	C. maculata	1.60	AB	0.3712	1.55	AB	0.1983	1.42	BCD	0.1555	0.05	A	0.0500	0.23	B	0.0551
	H. convergens	1.20	B	0.2906	1.35	AB	0.1957	1.30	BCD	0.1403	0.10	A	0.0688	0.20	B	0.0521
non-native	*C. septempunctata*	1.70	AB	0.4230	1.50	AB	0.2763	1.48	ABC	0.1722	0.05	A	0.0500	0.13	B	0.0443
	H. axyridis	2.70	A	0.3000	1.95	A	0.2348	2.10	A	0.1730	0.10	A	0.0688	0.57	A	0.0645
	H. variegata	0.70	B	0.2603	0.75	AB	0.1230	0.84	D	0.1244	0.00	A	0.0000	0.13	B	0.0443
	P. quatuordecimpunctata	1.10	B	0.2333	1.03	B	0.1281	0.94	CD	0.1090	0.10	A	0.0688	0.33	B	0.0614
	N	10			20			60			20			60		
	p-value	.0146			0.0122			<0.0001			0.1544			<0.0001		
	F	2.90			2.85			5.99			2.07			6.27		
	DF	6, 63			6, 133			6, 413			6, 133			6, 413		

		Prey Discovery Time									Aggression Received					
		Alone			Same Species			Other Species			Same Species			Other Species		
		Mean		SE	Mean		SE	Mean		SE	Mean		SE	Mean		SE
native	*C. trifasciata*	18.00	A	4.8808	15.95	AB	3.1123	16.47	B	2.0206	0.25	A	0.0993	0.22	A	0.0536
	C. maculata	23.20	A	5.2235	20.30	A	2.7483	17.80	B	2.0052	0.05	A	0.0500	0.27	A	0.0576
	H. convergens	17.40	A	5.1082	18.40	A	3.0740	19.18	B	2.1783	0.10	A	0.0688	0.28	A	0.0587
non-native	*C. septempunctata*	15.50	A	5.1945	18.70	A	3.7516	20.80	AB	2.3348	0.05	A	0.0500	0.12	A	0.0418
	H. axyridis	11.20	A	2.6575	6.35	B	1.4713	13.23	B	1.9918	0.10	A	0.0688	0.35	A	0.0621
	H. variegata	27.40	A	6.0446	24.90	A	3.3276	28.13	A	2.1283	0.00	A	0.0000	0.27	A	0.0576
	P. quatuordecimpunctata	18.20	A	4.5651	17.85	A	3.3929	20.48	AB	2.1771	0.10	A	0.0688	0.27	A	0.0576
	N	10			20			60			20			60		
	p-value	.4273			0.0002			<0.0001			0.1544			0.1752		
	F	1.01			4.76			5.56			2.07			1.13		
	DF	6, 63			6, 133			4, 413			6, 133			6, 413		

axyridis, that exhibited a higher incidence of aggression to other species compared to the other species tested, there were no significant differences when considering aggression.

When paired with different species (Table 4.2), some lady beetle species differed in their aphid consumption, aggression delivered, and aggression received. *Coccinella trifasciata* consumed more aphids when paired with *C. maculata* and *H. convergens*; and *C. maculata* consumed more with *H. variegata* and *C. septempunctata*. *Harmonia axyridis* delivered the most aggression towards *C. trifasciata*, while *H. variegata* delivered the most aggression towards *H. axyridis*. Several species delivered a significantly different amount of aggression to some species compared to others: *H. axyridis* delivered the most aggression to *C. trifasciata*, *C. maculata*, *H. convergens*, and *P. quatuordecimpunctata*; while *H. axyridis* and *P. quatuordecimpunctata* delivered the most aggression to *H. variegata*.

In most pair-wise comparisons, there was a negative correlation between aphid consumption and prey discovery time (Table 4.3). However, there were also eight pair-wise comparisons where this relationship was either relatively weak ($r < 0.6500$) or not detected (Table 4.3): *C. maculata* with *C. septempunctata* and *H. axyridis*; *C. trifasciata* with *C. maculata*; *H. axyridis* with *C. trifasciata* and *P. quatuordecimpunctata*; *H. convergens* with *H. axyridis*; and *P. quatuordecimpunctata* with *C. maculata* and *H. axyridis*.

In addition, correlation analyses revealed a number of strong relationships between other measured parameters (Table 4.4). In six pair-wise comparisons, aphid consumption by one species was negatively correlated with aphid consumption by the other species confined in the same arena. In five comparisons aphid consumption by

Table 4.2. Mean (± standard error) aphid consumption, prey discovery time, aggression delivered, and aggression received by lady beetles paired in laboratory trials (N = 10). Means in each column with the same letter are not significantly different.

C. trifasciata (native)	Aphid Consumption			Prey Discovery Time			Aggression Delivered			Aggression Received		
with	Mean		SE	Mean		SE	Mean		SE	Mean		SE
C. trifasciata - alone	1.30	AB	0.3350	18.00	A	4.8808	NA		NA	NA		NA
C. trifasciata	1.70	AB	0.3350	15.40	A	4.0939	0.30	A	0.1528	0.20	B	0.1333
C. trifasciata	1.40	AB	0.2667	16.50	A	4.9063	0.20	A	0.1333	0.30	AB	0.1528
C. maculata	2.60	A	0.3712	6.50	A	2.4642	0.30	A	0.1528	0.20	B	0.1333
C. septempunctata	1.00	B	0.4216	25.70	A	5.8310	0.00	A	0.0000	0.20	B	0.1333
H. axyridis	1.30	AB	0.3667	17.10	A	5.2461	0.40	A	0.1633	0.80	A	0.1333
H. convergens	2.60	A	0.3055	9.10	A	2.5406	0.20	A	0.1333	0.00	B	0.0000
H. variegata	1.20	AB	0.3590	24.00	A	5.7774	0.10	A	0.1000	0.00	B	0.0000
P. quatuordecimpunctata	2.00	AB	0.3944	16.40	A	4.5023	0.30	A	0.1528	0.40	AB	0.1633
p-value	0.0073			0.0955			0.4856			0.0012		
F	2.87			1.77			1.33			3.89		
DF	8, 81			8, 81			7, 72			7, 72		

C. maculata (native)	Aphid Consumption			Prey Discovery Time			Aggression Delivered			Aggression Received		
with	Mean		SE	Mean		SE	Mean		SE	Mean		SE
C. maculata - alone	1.60	AB	0.3712	23.20	A	5.2235	NA		NA	NA		NA
C. maculata	1.60	AB	0.3055	18.30	A	3.8846	0.10	A	0.1000	0.00	B	0.0000
C. maculata	1.50	AB	0.2687	22.30	A	3.9890	0.00	A	0.0000	0.10	AB	0.1000
C. septempunctata	1.80	A	0.3590	12.60	A	4.2484	0.20	A	0.1333	0.10	AB	0.1000
C. trifasciata	0.40	B	0.2211	30.40	A	5.2898	0.20	A	0.1333	0.30	AB	0.1528
H. axyridis	1.00	AB	0.2687	19.90	A	4.7080	0.40	A	0.1633	0.60	A	0.1633
H. convergens	1.55	AB	0.2630	16.00	A	3.7977	0.20	A	0.1333	0.30	AB	0.1528
H. variegata	1.95	A	0.5080	13.30	A	5.5077	0.30	A	0.1528	0.10	AB	0.1000
P. quatuordecimpunctata	1.80	AB	0.4163	14.60	A	4.5073	0.10	A	0.1000	0.20	AB	0.1333
p-value	0.0262			0.0891			0.4877			0.0298		
F	2.33			1.80			1.22			1.79		
DF	8, 81			8, 81			7, 72			7, 72		

Table 4.2 (Continued). Mean (± standard error) aphid consumption, prey discovery time, aggression delivered, and aggression received by lady beetles paired in laboratory trials (N = 10). Means in each column with the same letter are not significantly different.

H. convergens (native)	Aphid Consumption			Prey Discovery Time			Aggression Delivered			Aggression Received		
with	Mean		SE	Mean		SE	Mean		SE	Mean		SE
H. convergens - alone	1.20	A	0.2906	17.40	A	5.1082	NA		NA	NA		NA
H. convergens	1.20	A	0.2906	19.80	A	4.6183	0.10	A	0.1000	0.10	B	0.1000
H. convergens	1.50	A	0.2687	17.00	A	4.2583	0.10	A	0.1000	0.10	B	0.1000
C. maculata	1.45	A	0.2833	16.40	A	3.6733	0.30	A	0.1528	0.20	AB	0.1333
C. septempunctata	1.30	A	0.3958	23.60	A	6.1738	0.20	A	0.1333	0.30	AB	0.1528
C. trifasciata	1.10	A	0.2769	22.60	A	5.4654	0.00	A	0.0000	0.20	AB	0.1333
H. axyridis	1.53	A	0.4331	8.50	A	4.2564	0.30	A	0.1528	0.70	A	0.1528
H. variegata	1.30	A	0.3350	20.00	A	5.6273	0.20	A	0.1333	0.00	B	0.0000
P. quatuordecimpunctata	1.10	A	0.3786	24.00	A	5.9759	0.20	A	0.1333	0.30	AB	0.1528
p-value	0.9568			0.3696			0.8922			0.0132		
F	0.32			1.10			0.53			2.39		
DF	8, 81			8, 81			7, 72			7, 72		

C. septempunctata (non-native)	Aphid Consumption			Prey Discovery Time			Aggression Delivered			Aggression Received		
with	Mean		SE	Mean		SE	Mean		SE	Mean		SE
C. septempunctata - alone	1.70	A	0.4230	15.50	A	5.1945	NA		NA	NA		NA
C. septempunctata	1.60	A	0.4269	18.10	A	5.1261	0.10	A	0.1000	0.00	A	0.0000
C. septempunctata	1.40	A	0.3712	19.30	A	5.7505	0.00	A	0.0000	0.10	A	0.1000
C. maculata	1.10	A	0.2769	21.30	A	6.5287	0.10	A	0.1000	0.20	A	0.1333
C. trifasciata	2.10	A	0.3786	9.20	A	2.6825	0.20	A	0.1333	0.00	A	0.0000
H. axyridis	1.10	A	0.5044	28.60	A	5.9744	0.10	A	0.1000	0.10	A	0.1000
H. convergens	1.40	A	0.4522	20.80	A	6.6145	0.30	A	0.1528	0.20	A	0.1333
H. variegata	1.60	A	0.5416	24.80	A	6.0824	0.00	A	0.0000	0.00	A	0.0000
P. quatuordecimpunctata	1.60	A	0.3399	20.10	A	4.9586	0.10	A	0.1000	0.20	A	0.1333
p-value	0.6632			0.5245			0.4338			0.5321		
F	0.73			0.90			1.02			0.82		
DF	8, 81			8, 81			7, 72			7, 72		

Table 4.2 (Continued). Mean (± standard error) aphid consumption, prey discovery time, aggression delivered, and aggression received by lady beetles paired in laboratory trials (N = 10). Means in each column with the same letter are not significantly different.

H. axyridis (non-native)	Aphid Consumption			Prey Discovery Time			Aggression Delivered			Aggression Received		
with	Mean		SE	Mean		SE	Mean		SE	Mean		SE
H. axyridis - alone	2.70	A	0.3000	11.20	A	2.6575	NA		NA	NA		NA
H. axyridis	1.80	A	0.3266	7.00	A	2.4449	0.10	B	0.1000	0.10	A	0.1000
H. axyridis	2.10	A	0.3480	5.70	A	1.7515	0.10	B	0.1000	0.10	A	0.1000
C. maculata	2.40	A	0.3786	12.40	A	4.7847	0.60	AB	0.1633	0.40	A	0.1633
C. septempunctata	1.80	A	0.4163	15.20	A	4.6303	0.10	B	0.1000	0.10	A	0.1000
C. trifasciata	2.10	A	0.4069	7.80	A	4.1708	0.80	A	0.1333	0.40	A	0.1633
H. convergens	2.00	A	0.4944	14.80	A	5.4667	0.70	AB	0.1528	0.30	A	0.1528
H. variegata	1.60	A	0.4761	22.50	A	6.3705	0.50	AB	0.1667	0.50	A	0.1667
P. quatuordecimpunctata	2.70	A	0.3667	6.70	A	2.3478	0.70	AB	0.1528	0.40	A	0.1633
p-value	0.2848			0.2262			0.0003			0.2787		
F	1.24			1.36			4.70			1.81		
DF	8, 81			8, 81			7, 72			7, 72		

H. variegata (non-native)	Aphid Consumption			Prey Discovery Time			Aggression Delivered			Aggression Received		
with	Mean		SE	Mean		SE	Mean		SE	Mean		SE
H. variegata - alone	0.70	A	0.2603	27.40	A	6.0446	NA		NA	NA		NA
H. variegata	0.80	A	0.2000	24.90	A	4.9608	0.00	B	0.0000	0.00	B	0.0000
H. variegata	0.70	A	0.1528	24.90	A	4.7057	0.00	B	0.0000	0.00	B	0.0000
C. maculata	0.95	A	0.3532	25.80	A	5.5394	0.10	B	0.1000	0.30	AB	0.1528
C. septempunctata	1.00	A	0.3651	26.30	A	5.0400	0.00	B	0.0000	0.00	B	0.0000
C. trifasciata	0.70	A	0.2603	31.80	A	5.5494	0.00	B	0.0000	0.10	B	0.1000
H. axyridis	0.90	A	0.3480	27.00	A	6.1046	0.50	A	0.1667	0.50	A	0.1667
H. convergens	0.70	A	0.2134	29.10	A	4.4508	0.00	B	0.0000	0.20	AB	0.1333
P. quatuordecimpunctata	0.80	A	0.3266	28.80	A	5.6071	0.20	AB	0.1333	0.50	A	0.1667
p-value	0.9989			0.9950			<0.0001			0.0028		
F	0.01			0.16			4.72			3.22		
DF	8, 81			8, 81			7, 72			7, 72		

Table 4.2 (Continued). Mean (± standard error) aphid consumption, prey discovery time, aggression delivered, and aggression received by lady beetles paired in laboratory trials (N = 10). Means in each column with the same letter are not significantly different.

P.quatuordecimpunctata (non-native)	Aphid Consumption			Prey Discovery Time			Aggression Delivered			Aggression Received		
with	Mean		SE	Mean		SE	Mean		SE	Mean		SE
P.quatuordecimpunctata - alone	1.10	A	0.2333	18.20	A	4.5651	NA		NA	NA		NA
P. quatuordecimpunctata	1.15	A	0.1833	17.50	A	5.0360	0.10	A	0.1000	0.10	B	0.1000
P. quatuordecimpunctata	0.90	A	0.1795	18.20	A	4.8185	0.10	A	0.1000	0.10	B	0.1000
C. maculata	0.90	A	0.3786	23.30	A	6.4894	0.20	A	0.1333	0.10	B	0.1000
C. septempunctata	1.10	A	0.2333	21.80	A	4.7768	0.20	A	0.1333	0.10	B	0.1000
C. trifasciata	0.60	A	0.1633	26.50	A	5.3754	0.40	A	0.1633	0.30	AB	0.1528
H. axyridis	0.60	A	0.2211	14.70	A	5.5459	0.40	A	0.1633	0.70	A	0.1528
H. convergens	1.15	A	0.2363	19.50	A	4.7170	0.30	A	0.1528	0.20	AB	0.1333
H. variegata	1.30	A	0.3000	17.10	A	5.4231	0.50	A	0.1667	0.20	AB	0.1333
p-value	0.4013			0.7767			0.2883			0.0170		
F	1.06			0.60			1.59			2.88		
DF	8, 81			8, 81			7, 72			7, 72		

Table 4.3. Correlations between aphid consumption and prey discovery time for single and paired lady beetles in trials (N = 10). Each row represents the relationship between aphid consumption and prey discovery time for the species in the left column when it was alone or paired with the species in the first row of the table.

	Species		alone	Ct	Cm	Hc	Cs	Ha	Hv	Pq
native	Ct	r	-0.8698	-0.7745	-0.3644	-0.8675	-0.8541	-0.7642	-0.9107	-0.7571
		p-value	0.0011	<0.0001	0.3005	0.0011	0.0017	0.0101	0.0002	0.0112
	Cm	r	-0.9524	-0.7942	-0.8559	-0.9011	-0.6469	-0.6235	-0.8016	-0.7745
		p-value	<0.0001	0.0061	<0.0001	0.0004	0.0432	0.0541	0.0053	0.0085
	Hc	r	-0.7994	-0.8708	-0.8199	-0.9091	-0.9039	-0.5518	-0.9431	-0.9184
		p-value	0.0055	0.0010	0.0037	<0.0001	0.0003	0.0982	<0.0001	0.0002
non-native	Cs	r	-0.8420	-0.8009	-0.8193	-0.8701	-0.8735	-0.9240	-0.9066	-0.8609
		p-value	0.0022	0.0054	0.0037	0.0011	<0.0001	0.0001	0.0003	0.0014
	Ha	r	-0.9389	-0.6010	-0.7980	-0.8140	-0.6836	-0.7743	-0.9708	-0.2439
		p-value	<0.0001	0.0661	0.0057	0.0042	0.0293	<0.0001	<0.0001	0.4970
	Hv	r	-0.9447	-0.7891	-0.8894	-0.9322	-0.7487	-0.8316	-0.8647	-0.8033
		p-value	<0.0001	0.0067	0.0006	<0.0001	0.0127	0.0029	<0.0001	0.0051
	Pq	r	-0.8818	-0.8734	-0.6182	-0.7900	-0.8852	-0.6361	-0.8284	-0.7502
		p-value	0.0011	0.0010	0.0568	0.0065	0.0007	0.0480	0.0031	0.0001

Ct = *Coccinella trifasciata*

Cm = *Coleomegilla maculata*

Hc = *Hippodamia convergens*

Cs = *Coccinella septempunctata*

Ha = *Harmonia axyridis*

Hv = *Hippodamia variegata*

Pq = *Propylea quatuordecimpunctata*

Table 4.4. Additional significant correlations between aphid consumption, prey discovery time, aggression delivered, and aggression received by lady beetles in trials (N = 10). Numbers (1 or 2) after species names differentiate paired beetles in pairings with the same species.

Correlation Between:	And:			
Aphid Consumption	Aphid Consumption		r	p-value
C. septempunctata	*C. trifasciata*	---	-0.9049	0.0002
C. trifasciata	*H. convergens*	---	-0.7356	0.0127
C. maculata	*H. axyridis*	---	-0.7098	0.0112
C. septempunctata	*H. convergens*	---	-0.8195	0.0053
H. axyridis	*H. convergens*	---	-0.9133	0.0003
H. axyridis	*P. quatuordecimpunctata*	---	-0.8497	0.0020
Aphid Consumption	Prey Discovery Time		r	p-value
C. trifasciata	*C. septempunctata*	---	0.8350	0.0017
C. septempunctata	*H. convergens*	---	0.7069	0.0002
C. septempunctata	*C. trifasciata*	---	0.7665	0.0112
H. convergens	*C. septempunctata*	---	0.8344	0.0022
P. quatuordecimpunctata	*H. variegata*	---	0.7107	0.0088
Prey Discovery Time	Prey Discovery Time		r	p-value
C. septempunctata	*C. trifasciata*	---	-0.7653	0.0085
C. septempunctata	*H. convergens*	---	-0.8138	0.0030
H. convergens	*P. quatuordecimpunctata*	---	-0.7001	0.0143
Aphid Consumption	Aggression Delivered by	or Aggression Received by	r	p-value
C. maculata	*C. maculata*	*C. trifasciata*	0.7994	0.0063
H. convergens	*H. convergens*	*H. axyridis*	0.7327	0.0029
C. septempunctata	*P. quatuordecimpunctata*	*C. septempunctata*	-0.7812	0.0080
Prey Discovery Time	Aggression Delivered by	or Aggression Received by	r	p-value
C. maculata	*C. maculata*	*C. septempunctata*	0.9225	<0.0001
C. maculata	*C. septempunctata*	*C. maculata*	0.8511	0.0017
H. convergens	*C. maculata*	*H. convergens*	0.8370	0.0002
C. septempunctata	*P. quatuordecimpunctata*	*C. septempunctata*	0.8392	0.0028
Aggression Received	Aggression Delivered by	or Aggression Received by	r	p-value
C. trifasciata 1	*C. trifasciata* 1	*C. trifasciata* 2	0.7003	0.0004

one species was positively correlated with prey discovery time by the other species. Also, aggressive behaviors were positively correlated with the prey discovery time in four of the comparisons. In three comparisons, prey discovery time of one species was negatively correlated with prey discovery time of the other species. There was a positive correlation between aphid consumption and aggression delivered/received (two comparisons), between prey discovery time and aggression delivered/received (four comparisons), and between aggression received and aggression received/delivered (one comparison). In one comparison, between *C. septempunctata* and *P. quatuordecimpunctata*, there was a negative correlation between aphid consumption and aggression delivered/received.

Coccinella septempunctata was the largest of the species tested (Table 4.5). Weights of other species were 74.76% (*H. axyridis*), 46.03% (*C. trifasciata*), 40.25% (*C.*

Table 4.5. Mean weight and volume (± standard error) of lady beetle species (N = 20) used in laboratory trials. Means in each column with the same letter are not significantly different.

		Measurements					
		Weight			Volume		
		Mean		SE	Mean		SE
native	*C. trifasciata*	0.0104	C	0.0007	20.41	D	1.2005
	C. maculata	0.0091	C	0.0008	15.10	DE	0.8356
	H. convergens	0.0087	C	0.0009	32.43	C	1.8409
non-native	*C. septempunctata*	0.0225	A	0.0017	78.87	A	2.6835
	H. axyridis	0.0168	B	0.0015	66.30	B	2.4081
	H. variegata	0.0040	D	0.0004	8.64	E	0.5435
	P. quatuordecimpunctata	0.0063	DC	0.0005	12.87	E	0.8090
	p-value	<0.0001			<0.0001		
	F	38.63			280.85		
	DF	6, 133			6, 133		

maculata), 38.65% (*H. convergens*), 28.02% (*P. quatuordecimpunctata*), and 17.83% (*H. variegata*) that of *C. septempunctata*. Volumes of other species were 84.06% (*H. axyridis*), 41.12% (*H. convergens*), 25.87% (*C. trifasciata*), 19.15% (*C. maculata*), 16.32% (*P. quatuordecimpunctata*), and 10.95% (*H. variegata*) that of *C. septempunctata*.

Discussion

Harmonia axyridis, a non-native species, had the highest aphid consumption when considering trials with single individuals, conspecifics, and other species; the shortest prey discovery time in trials with conspecifics and with other species (Table 4.1); and generally exhibited the most aggression towards other species (Table 4.2). A superior competitive ability of invasive species to utilize resources over native species has been documented in numerous studies (Melgoza *et al*. 1990, Petren and Case 1996, Kupfergberg 1997, Holway 1999, Byers 2000). These observations are also consistent with a number of studies that have documented the superior competitive abilities of *H. axyridis* among coccinellid species (Hironori and Katsuhiro 1997, Yasuda and Shinya 1997, Yasuda and Ohnuma 1999, Kajita *et al*. 2000, Yasuda *et al*. 2001, Michaud 2002, Snyder *et al*. 2004, Yasuda *et al*. 2004).

Coccinella septempunctata, *C. trifasciata*, and *C. maculata* generally followed *H. axyridis* in aphid consumption. *Coccinella septempunctata* and *H. axyridis* were also the heaviest and largest species among the seven species tested (Table 4.5). Despite *C. septempunctata*'s large size and being among the species consuming the most aphids, *C. septempunctata* generally did not deliver or receive more aggression than other species. Larger lady beetle species have been shown to be competitively favored over smaller ones (Obrycki *et al*. 1998, Michaud 2002, Sato *et al*. 2003, Yasuda *et al*. 2004), possibly because they are able to consume more because they are larger or because their size is intimidating to competitors. *Coccinella septempunctata* has also been documented to deter aggression by ants chemically (Tursch *et al*. 1971, Bhatkar 1982); chemical communication may, perhaps, be used by *C. septempunctata* to prevent aggression with other coccinellids.

It is worth noting that *H. axyridis*, *C. septempunctata*, *H. convergens*, *H. variegata*, and *P. quatuordecimpunctata* showed no difference in aphid consumption and prey discovery time whether they were kept alone or paired with any other species tested in the study, including conspecifics (Table 4.2). Perhaps if a given species is an efficient predator that can find and consume aphids quickly, its ability to acquire prey may not be significantly hindered by the presence of other lady beetles. Prey consumption by *C. trifasciata* and *C. maculata*, on the other hand, differed depending on with which species they were paired.

In addition to differences that were documented in aphid consumption, prey discovery time, and aggression, correlations between these variables provide insight into competitive interactions among and between different lady beetle species. There was generally a strong negative correlation between aphid consumption and prey discovery time, indicating that the shorter the amount of time it took to discover the first aphid, the more aphids were consumed. This seems intuitive; however, satiation or distraction by the other beetle may prevent continued prey consumption. This relationship was consistent with beetles in trials alone, in trials where beetles were paired with individuals of their own species, and in most (34 of 42) of the trials where beetles were paired with other species. In eight pairings with other species, the correlation was not documented or was very weak (Table 4.3), perhaps because the presence of the other beetle disrupted prey discovery and/or aphid consumption. Interestingly, six of these eight pair-wise comparisons showed significant correlations when comparing combinations of variables other than aphid consumption and prey discovery time (Table 4.4). For example, there was no correlation between aphid consumption and prey discovery time when considering *C. trifasciata* paired with *C. maculata* (Table 4.3, r = -0.3644, p = 0.3005). However, there was a positive correlation between aphid consumption by *C. maculata* and aggression delivered by that species towards *C. trifasciata* (Table 4.4). It is possible that these other documented correlations explain the lack of a relationship when considering aphid consumption and prey discovery time. In this case, aggression between these two species may disrupt prey discovery behavior.

It also is interesting to note discrepancies in the strength of the correlation between aphid consumption and prey discovery time when comparing lady beetles in trials when they were kept alone, paired with conspecifics, and paired with other species. For example, *H. variegata* showed a very strong correlation (Table 4.3) when alone (r = -0.9447, $p < 0.0001$), a strong correlation when paired with conspecifics (r = -0.8647, $p < 0.0001$), but a relatively weak correlation when paired with *C. septempunctata* (r = -0.7487, $p < 0.0001$). Such a difference may indicate interference from the heterospecific competitor. The influence, however, of other species did not always resulted in a decrease in the strength of this relationship. For example, the relationship for *C. septempunctata* alone (r = -0.8420, p = 0.0022) or with conspecifics (r = -0.8735, $p < 0.0001$) was not as strong as that when it was paired with *H. axyridis* (r = -0.9240, p =

0.0001). Similarly, the presence of conspecifics may stimulate prey searching; for *H. convergens*, the relationship between aphid consumption and prey discovery time was stronger when paired with conspecifics (r = -0.9091, p < 0.0001) compared to when it was alone (r = -0.7994, p = 0.0055).

Additionally, in six pair-wise comparisons (Table 4.4), more aphid consumption by one species was correlated with less aphid consumption by the other species. Similarly, in three comparisons, a short prey discovery time by one species was correlated with a long prey discovery time by the other species. These results imply that as prey are discovered and removed by a more efficient predator, foraging time can increase, and expectedly, aphid consumption can decrease for its competitor. In five pairings, a longer prey discovery time by one species was positively correlated with greater aphid consumption in the other species (and vice versa). This is also intuitive, as when an individual's competitor takes a long time to find prey, that leaves more prey and a greater likelihood of finding prey for that individual. On the other hand, if an individual's competitor finds prey quickly, there is less remaining for that individual.

Increased aggression delivered by *C. maculata* and *H. convergens* (Table 4.4) was correlated with increased aphid consumption by those species in trials with *C. trifasciata* and *H. axyridis*, respectively. Similarly, increased aggression delivered by *P. quatuordecimpunctata* was correlated with decreased consumption by *C. septempunctata*. In these cases, aggression may help deter other species from consuming prey. Expending time and energy on aggression may also distract the aggressor from foraging, thus decreasing prey consumption; however, this relationship was not documented in this study when considering consumption. On the other hand, species receiving aggression did show decreases in aphid consumption with increases in the aggression that they received. Interestingly, in one pair-wise comparison (*C. maculata* and *C. septempunctata*), increased aggression by *C. maculata* was correlated with its own increased prey discovery time, suggesting that it was distracted from foraging. On the other hand, in three other comparisons increases in aggression delivered were correlated with longer prey discovery times for the aggressor's competitor. In a conspecific pairing of *C. trifasciata*, aggression received by one conspecific was correlated with the aggression it delivered, meaning that aggressive interactions were not one-sided, but equally met by the other conspecific.

In conclusion, interactions between different lady beetle species result in differential prey sharing that favors some lady beetle species over others. Many of the correlations discussed above are intuitive. However, it is important to note that they are not consistently strong among and within all species. This information paired with differences in prey consumption, prey discovery time, and aggression, demonstrate that there are differences between species that are important when considering the co-existence of these species in the same location. There was not, however, a discreet separation between native and non-native species. Evidence also suggests that every aphid species is not equally suitable as prey for every lady beetle species (Obrycki and Orr 1990, Phoofolo and Obrycki 1997, Kalushkov 1998, Michaud 2000, Kalushkov and Hodek 2004, Mignault *et al*. 2006). Thus, while these results show that there are differences in different lady beetle species, these differences may not be consistent when considering different prey species.

The native lady beetle species used in this study, *C. maculata*, *C. trifasciata*, and *H. convergens*, are currently numerous in Maine. Native species, *Coccinella transversoguttata* Brown and *Hippodamia tredecimpunctata tibialis* (Say), that have experienced declines in abundance since non-native lady beetle introductions (Alyokhin and Sewell 2004), were excluded because they were not easily found in numbers sufficient for testing. It would be interesting and valuable to pair native species once numerous in Maine with both the non-native species now common and the native species that persist. The persistence of native species where several non-native species are now common may signify that these native species possess competitive abilities better suiting their persistence with the non-native lady beetles used in this study and now common in Maine, *H. axyridis*, *C. septempunctata*, *P. quatuordecimpunctata*, and *H. variegata*. Finally, this study was conducted in a relatively simple setting of a laboratory arena; increased environmental complexity may modify competitive abilities of certain species.

Chapter 5

BEHAVIORAL INTERACTIONS OF NATIVE AND NON-NATIVE LADY BEETLES WITH APHID-TENDING ANTS IN LABORATORY ARENAS

Chapter Abstract

Interactions between lady beetles and the European fire ant (*Myrmica rubra*) tending potato aphids (*Macrosiphum euphorbiae*) were compared in the laboratory. Lady beetle species native to North America (*Coccinella trifasciata*, *Coleomegilla maculata lengi*, *Hippodamia convergens*) and non-native species of Palearctic origin (*Coccinella septempunctata*, *Harmonia axyridis*, *Hippodamia variegata*, *Propylea quatuordecimpunctata*) were evaluated. *Harmonia axyridis* consumed a significantly greater number of aphids compared with all other species but *C. septempunctata*. Ant stings affected *H. variegata* and *C. septempunctata* to a greater extent than other species. Ants displayed a significantly greater amount of aggression towards *H. convergens* and *H. variegata* compared with *P. quatuordecimpunctata*. *Propylea quatuordecimpunctata*, *C. trifasciata*, and *H. axyridis* reacted significantly less to ants compared with *H. variegata*, *H. convergens*, *C. maculata*, and *C. septempunctata*. Differences in interactions with natural enemies may explain, in part, the successful establishment of some non-native coccinellids in new habitats.

Introduction

Some ant species tend plant-feeding insects, such as aphids, mealybugs, and scale insects, to exploit their sugary excrement known as "honeydew" as a food source (Auclair 1963, Way 1963, Buckley 1987, Völkl *et al.* 1999). Tending ants may move aphids to shelter them from unfavorable environmental conditions and clean them of debris such as their own sticky excrement, accumulations of which can promote fungal growth (Holdobler and Wilson 1990, Gonzalez Hernandez *et al.* 1999a). Ants may also provide protection to aphids from predators and parasites (Bartlett 1961, Way 1963, Buckley 1987, Vinson and Scarborough 1989, Charles 1993, Reimer *et al.* 1993, Jahn and Beardsley 1994, Gonzalez Hernandez *et al.* 1999a).

Generally considered beneficial because they feed on plant pests (Hodek 1973, Gordon 1985), lady beetles have been intentionally introduced to new locations worldwide for biological control in agricultural crops (Gordon 1985, Dreistadt and Flint 1996, Koch 2003). They have also been unintentionally introduced through plant exports and other cargo (Chantal 1972, Schaefer *et al.* 1987, Day *et al.* 1994). Reductions in native lady beetle numbers have been correlated with introductions of non-native lady beetles (Elliot *et al.* 1996, Brown and Miller 1998, Colunga-Garcia and Gage 1998, Michaud 2002, Brown 2003, Turnock *et al.* 2003, Alyokhin and Sewell 2004). It is believed that some non-native lady beetle species may outcompete native species for food (Michaud 2002). Because many lady beetle species feed primarily on plant-feeding insects, such as aphids, at least during part of their life cycle (Gordon 1985, Hodek and Honěk 1996), their competitive abilities may be in part determined by their interactions with tending ant species (Bartlett 1961, Vinson and Scarborough 1989, Hanks and Sadof

1990, Jahn and Beardsley 1994, Sloggett *et al*. 1998, Sloggett and Majerus 2000).

Many assessments of the relationships between lady beetle species have been made by measuring relative abundances (Elliot *et al*. 1996, Brown and Miller 1998, Colunga-Garcia and Gage 1998, Michaud 2002, Brown 2003, Turnock *et al*. 2003, Alyokhin and Sewell 2004), intraguild predation (Takahashi 1989, Elliot *et al*. 1996, Hough-Goldstein *et al*. 1996, Hironori and Katsuhiro 1997, Cottrell and Yeargan 1998, Yasuda and Ohnuma 1999, Dixon 2000, Kajita *et al*. 2000, Sakuratani *et al*. 2000, Lynch *et al*. 2001, Yasuda *et al*. 2001, Michaud 2002, Brown 2003, De Clerq *et al*. 2003, Yasuda *et al*. 2004), and direct competition (Dixon 2000, Michaud 2002, Yasuda *et al*. 2004) between lady beetle species. There has been little examination of indirect interactions that may influence lady beetle populations. Although a number of studies have documented differences in numbers of lady beetles and/or their prey in environments with and without ants (Chapin 1966, Bradley 1973, Bhatkar 1982, Jiggins *et al*. 1993, Sloggett *et al*. 1998, Dutcher *et al*. 1999, Corbara *et al*. 1999, Sloggett *et al*. 1999, Sloggett and Majerus 2000, Kaplan and Eubanks 2002), few studies have assessed differences between lady beetle species in their interactions with ants that might favor the survival of one species over another. Laboratory investigations were conducted with three native and four non-native lady beetle species presented with aphid prey that were protected by ants. Prey consumption and interactions with ants were evaluated to determine if different interactions with natural enemies may differentially affect the survival of different lady beetle species.

Materials and Methods

Study Species

Seven aphidophagous lady beetles species that are abundant in Maine were chosen for the present study. Three of those are native to the state: the three-banded lady beetle *Coccinella trifasciata perplexa* Mulsant, the twelve-spotted lady beetle *Coleomegilla maculata lengi* Timberlake, and the convergent lady beetle *Hippodamia convergens* Guérin-Méneville. *Coccinella trifasciata* is native from Labrador south to New Jersey and west to California and Alaska (Gordon 1985). The native range of *C. maculata* is restricted to eastern North America from Ontario to Georgia, and west to Texas and Minnesota (Gordon 1985). *Hippodamia convergens* is a widespread species, with its native range from British Columbia and Ontario south to South and Central America and the Antilles (Gordon 1985).

Four non-native lady beetles used in the study were the seven-spotted lady beetle *Coccinella septempunctata* L., the multicolored Asian lady beetle *Harmonia axyridis* (Pallas), the variegated lady beetle *Hippodamia variegata* (Goeze), and fourteen-spotted lady beetle *Propylea quatuordecimpunctata* (L.). All four species are Palearctic in origin and were both intentionally and inadvertently introduced in North America. *Coccinella septempunctata* has been established in North America since 1973 (Angalet and Jacques 1975) and in the eastern United States since 1979 (Angalet *et al*. 1979). The first established population of *H. axyridis* in North America was documented 1988 (Chapin and Brou 1991, Tedders and Schaefer 1994) and now this species occurs throughout much of the continental United States (Koch 2003). *Hippodamia variegata* is currently widespread throughout northeastern North America (Gordon and Vandenberg 1991, Wheeler 1993, Wheeler and Stoops 1996, Hoebeke and Wheeler 1996, Ellis *et al*. 1999, Cormier *et al*. 2000). The first established population of *P. quatuordecimpunctata* was found in Quebec in 1968 (Wheeler 1990). In Maine, it was first documented in 1988 in Kennebec, Penobscot, and Aroostook Counties, where it is believed to have expanded its range from existing populations in Quebec (Wheeler 1990).

The European red ant, *Myrmica rubra* (L.) is a Palearctic species native to Europe and northern Asia (Elmes 1975, Collingwood 1979, Elmes *et al*. 1999, Czechowski *et al*. 2000). It was first documented in the United States in 1908 in Forest Hills, Massachusetts (Wheeler 1908) and has since been observed in the United States in Maine, New Hampshire, Massachusetts, Rhode Island, New York, New Jersey, Pennsylvania, and Washington D.C., and in Canada, in Nova Scotia, New Brunswick, Québec, and Ontario (Groden *et al*. 2005). *Myrmica rubra* is known to commonly tend aphid colonies in its native range (Seifert 1996) and in Maine (Garnas 2005). In Maine, it is highly aggressive and known to have a profound impact on insect communities, including decreases in native ants and increases in plant-feeding insects (Garnas 2005). Therefore, *M. rubra* was used as a model species to test the comparative ability of different lady beetle species to secure aphid prey in the presence of tending ants.

The potato aphid, *Macrosiphum euphorbiae* (Thomas), served as the ant-tended prey. *Macrosiphum euphorbiae* is native to North America and common in Maine (Blackman and Eastop 1984). It is known to feed on over 200 varieties of plants including potato (*Solanum* sp.) (Blackman and Eastop 1984). It is also known to be tended by *M. rubra* (Finlayson personal observation) and is a common prey item for many lady beetle species (Shands *et al*. 1972, Gordon 1985, Hodek and Honěk 1996).

Insect Origins and Maintenance

Adult lady beetles were collected 48-72 hours before test initiation in Orono, Maine, from a variety of habitats: mixed shrub (*Solidago* sp., *Rubus* sp., *Prunus* sp., *Rosa* sp., *Cornus sericea*, *Alnus* sp.), apple (*Malus* sp.), grain (*Hordeum* sp., *Avena* sp.), mixed organic crops (*Solanum lycopersicon*, *Allium* sp., *Brassica* sp., *Pisum* sp., *Phaseolus* sp.) and field (*Phleum pratense*, *Trifolium* sp., *Cirsium* sp., *Vicia* sp., *Fragaria* sp.). Captured beetles were housed in Percival I-33VL Intellus environmental chambers (Percival Scientific, Inc., Perry, Iowa) at 20°C and 16 (light) : 8 (dark) hour photoperiod and provided with water, but no food, for 48 hours before test initiation.

Ten ant nests, each containing a queen and from 300 to 500 workers, were collected from an area of known infestation in suburban Bar Harbor, Maine (latitude: 44.385904, longitude: -68.209514), on 14 June 2006. Ants were housed in the laboratory in plastic containers (125-cm long, 67-cm wide, 15-in cm tall). To prevent ants from escaping, container walls were coated with Fluon® (ACG Chemicals Americas, Inc., Bayonne, New Jersey). For shelter, each nest was provided with a potato plant (15-cm diameter pot) and an inverted peat pot (10-cm diameter), under which a moist sponge supplied a constant supply of water. Twice a week, each nest was provided with six Drosophila larvae, 0.5 grams of granulated sugar, and 2.0 grams of chopped, boiled eggs. Potato aphids were obtained from a colony maintained in the laboratory. The colony was originally founded by aphids collected from potato (*Solanum tuberosum*, Family: Solanaceae) fields in Presque Isle, Maine, and then maintained for at least 20 generations on excised potato foliage in the laboratory. The colony was housed in Percival I-33VL Intellus environmental chambers at 20°C and 16 (light): 8 (dark) hour photoperiod.

Lady Beetle Consumption of Potato Aphids

Feeding trials were conducted to assure that the different beetle species used in these experiments would indeed feed on the species of aphid provided. In each trial, a single lady beetle was placed in a 100 x 15 mm polystyrene Petri dish with an excised leaf infested with ten late-instar aphid nymphs. Housed in a separate Petri dish, the lady beetle was added to the Petri dish containing the aphids by quickly exchanging lids between the two Petri dishes when the lady beetle was on the lid. After 24 hours, the number of surviving aphids was recorded. Five trials were conducted with each lady beetle species.

Ant-Aphid-Lady Beetle Interactions in Laboratory Arenas

Twenty trials for each lady beetle species were conducted from 15 June to 6 July 2006. Before trials, ten adult aphids were transferred to the main stem of potato plants using a soft-bristled paintbrush (these plants were different than plants used for nesting that were already in enclosures). Aphid numbers were counted every other day until reproduction was documented by the presence of nymphs. After one week, aphid numbers reached at least 20 individuals per plant, and plants were introduced to ant enclosures in an area opposite the plant used for nesting. Once ants were observed tending aphids (in contact with aphids, sometimes moving aphids, but not consuming aphids), a single lady beetle was introduced. Each of the ten ant nests was used in random order twice with an individual of each lady beetle species. Each trial contained only one beetle and individual beetles were not reused. The lady beetle was transferred from the Petri dish in which it was held by allowing it to crawl upon the end of a paintbrush. It was placed on the potato plant five to ten centimeters above the aphid colony. Behavior of ants and lady beetles, including aphid consumption, was then observed and documented for 20 minutes.

Based on preliminary observations, interactions between lady beetles and ants were divided into separate aggressive and reactive behavioral elements. The number of times (*f*, frequency) each element occurred during each trial was recorded and used to calculate modified aggression and reactions scores where elements were weighted based on energetic investment (Carlin and Holldobler 1986, Holway *et al*. 1998, Suarez *et al*. 1999, Garnas *et al*. 2007). The aggression score was used to compare differences in ant aggression towards different lady beetle species and calculated according to the following formula:

$$\text{Aggression Score} = -1*f\text{a} + 1*f\text{b} + 2*f\text{c} + 3*f\text{d} + 4*f\text{e} + 5*f\text{f}$$

Where, *f* refers to the frequency at which a particular behavioral element was observed in a trial and subscript letters refer to the following behavioral elements:

a	avoiding
b	prolonged antennation
c	opening mandibles
d	chasing
e	grasping/biting
f	stinging

Similarly, the reaction score was used to compare lady beetle response to ant aggression and calculated according to the following formula:

$$\text{Reaction Score} = -1*fA + 1*fB + 2*fC + 3*fD + 4*fE + 5*fF + 6*fG$$

Where, *f* refers to the number of times a particular behavioral element was observed in trials, and subscript letters refer to the following behavioral elements:

A	continuing behavior previous to contact
B	changing movement (behavior altered from previous activity)
C	pulling in legs/antennae
D	preening
E	turning on back/flailing legs/fluttering wings
F	backing away/running away
G	flying away

Lady Beetle Tolerance of Ant Stings

Different species of beetles appeared to exhibit different reactions to stings by *M. rubra* during the trials described above. Therefore, they were also subjected to intentional sting trials with agitated ants to compare the effects of ant stings. As described above with behavioral trials, a lady beetle was transferred from the Petri dish in which it was held by allowing it to crawl upon the end of a paintbrush. It was then transferred to a location near the ant nest and in the immediate proximity (within 1.5 cm) of patrolling ants by allowing it to crawl from the paintbrush into the observation arena. Twenty individuals of each species were tested, with one beetle per trial, and each of the ten ant nests used in random order twice with different individuals of each lady beetle species. The number of stings was recorded and lady beetles were removed after having been stung, on average, 14 times (range: 10-20). Because the ability to control stings was limited (the ants clung and continued stinging when lady beetles were removed), a higher level of precision in obtaining stings was not possible. Twenty additional individuals of each species were held throughout the course of this study under identical conditions with the exception that they were not introduced to ants and thus were not stung. These beetles served as controls. All beetles were held for 72 hours of observation following exposure to ant stings, or not stung, in the case of control beetles, and their behavior was documented. Beetles were provided with moisture and held in individual Petri dishes in Percival I-33VL Intellus environmental chambers at 20°C and 16 (light): 8 (dark) hour photoperiod.

Each beetle was assigned a response score based on its activity during the 72-hour observation period. The value of the response score increased as the effects observed increased in intensity from no effect, to a behavioral effect, a physical effect, and death, where, 0 = active or active when prodded; 1 = inactive or slow when prodded; 2 = impaired ambulatory locomotion, wings stretched out, or flips on back; or 3 = dead. When several effects of varying intensity were documented for a given beetle, the score assigned reflected only the observation with the highest value during the 72-hour period.

Statistical Analyses

Data normality was tested using the Wilk-Shapiro test (PROC UNIVARIATE, SAS Institute, Inc. 2002). Frequency data that were not normally distributed were transformed using $\sqrt{X+0.001}$ transformations (Zar 1999). Data from the aphid feeding trials, consumption during behavioral trials, and ant sting trials were transformed using rank transformations (Conover and Iman 1981). Means and standard errors reported in this paper were calculated from the untransformed data.

Mean numbers of potato aphids consumed by different lady beetle species were compared by one-way ANOVA (PROC GLM, SAS Institute, Inc. 2002). A split-plot ANOVA (PROC MIXED, SAS Institute Inc. 2002) was used, with beetle species as the plots and behaviors as the subplots, to compare behaviors among different lady beetle species, conducting a separate test for all ant behaviors and for all beetle behaviors. When interactions between beetle species and behavior were statistically significant additional one-way ANOVAs followed by Tukey mean separation tests (PROC GLM, SAS Institute, Inc. 2002) were conduced comparing the frequencies with which different lady beetle species displayed each behavior.

Aggression and reaction scores were compared among the tested lady beetle species using one-way ANOVAs followed by Tukey mean separation tests (PROC GLM, SAS Institute, Inc. 2002). To determine if there was a relationship between aggression and reaction scores or between aphid consumption during trials and aggression/reaction scores, correlation analysis (PROC CORR, SAS Institute Inc. 2002) were used.

The number of stings received by different lady beetle species was compared using one-way ANOVA (PROC GLM, SAS Institute Inc. 2002). To determine if different lady beetles responded differently to being stung by ants, a split plot ANOVA (PROC MIXED, SAS Institute Inc. 2002) was used with lady beetle species as the plots and exposure status to ant stings (stung experimental beetles and not stung control beetles) as the subplots. When interactions between beetle species and sting status were statistically significant, additional one-way ANOVAs were conducted followed by Tukey mean separation tests (PROC GLM, SAS Institute, Inc. 2002) comparing differences among the species separately for stung beetles, and control beetles. To determine if being stung made a difference for each species, the mean scores for the stung beetles were also compared with the mean scores for the control beetles (PROC TTEST, SAS Institute Inc. 2002).

Results

Verification of Lady Beetle Consumption of Potato Aphids

Lady beetles consumed, on average, 8.46 ± 0.34 (mean ± standard error) potato aphids during the 24-hour trial period (Table 5.1). There was no difference among the different species (ANOVA, DF = 6, 28, F = 1.17, p = 0.3478).

Table 5.1. Mean number (± standard error) of aphids (*Macrosiphum euphorbiae*) consumed (out of 10) after 24-hours with one each of seven lady beetle species (N = 5).

	Lady Beetle Species	Consumption
native	*C. trifasciata*	7.00 ± 0.6999
	C. maculata	9.20 ± 0.5107
	H. convergens	8.60 ± 0.4775
non-native	*C. septempunctata*	7.60 ± 0.8199
	H. axyridis	9.60 ± 0.4229
	H. variegata	9.20 ± 0.4091
	P. quatuordecimpunctata	8.00 ± 0.6849

Ant-Aphid-Lady Beetle Interactions in a Laboratory Arena

Different lady beetle species were found to interact differently with ants. When considering ant behaviors, the main effect of species (ANOVA, DF = 6, 114, F = 43.14,

$p < 0.0001$) and ant behavior (ANOVA, DF = 6, 798, F = 134.20, $p < 0.0001$) were both significant, as were interactions between species and ant behavior (ANOVA, DF = 36, 798, F = 14.34, $p < 0.0001$). Thus, one-way ANOVAs were conducted comparing the different lady beetle species for each ant behavior (Table 5.2). There were differences between beetle species in four ant behaviors: prolonged antennation, biting, grasping, and stinging. *Coccinella trifasciata* received a significantly higher frequency of prolonged antennation from ants compared with *H. axyridis*; however, there were no differences among the other beetle species. *Hippodamia convergens*, *H. variegata*, and *C. maculata* received significantly higher frequencies of ant biting, grasping, and stinging, compared with *C. trifasciata* and *P. quatuordecimpunctata*.

One-way ANOVAs were conducted comparing the different lady beetle species for each lady beetle behavior (Table 5.3) because the interaction between lady beetle species and lady beetle behavior was highly significant (ANOVA, DF = 48, 1064, F = 11.74, $p < 0.0001$). There were differences between beetle species in five behaviors: continuing behavior previous to contact, pulling in legs/antennae, turning on back, flailing legs, and running away. When confronted with ants, *C. septempunctata* continued its behavior previous to contact to a significantly greater extent compared with *H. convergens*, *H. variegata*, and *C. maculata*. *Hippodamia variegata* pulled in its legs and antenna significantly more frequently than *H. axyridis* and *P. quatuordecimpuncata*. Similarly, *H. variegata*, *C. maculata*, and *H. convergens* turned on their backs significantly more frequently than did *H. axyridis*, *C. trifasciata*, and *P. quatuordecimpuntata,* and flailed their legs significantly more frequently compared with *C. trifasciata* and *P. quatuordecimpuntata*. *Hippodamia convergens*, *C. septempunctata*,

Table 5.2. Mean frequency (± standard error) of ant behaviors in response to discovery of a lady beetle scored in determination of aggression score (N = 20). Letters associated with each mean are results of Tukey mean separation tests comparing beetle species for each behavior. For each behavior, means with the same letter are not significantly different.

		Ant Behaviors															
		avoiding				prolonged antennating				opening mandibles				chasing			
	Lady Beetle Species																
native	*C. trifasciata*	0.25	a	±	0.16	5.60	a	±	1.36	0.45	a	±	0.25	0.00	a	±	0.00
	C. maculata	0.15	a	±	0.11	2.20	ab	±	1.38	1.45	a	±	0.53	0.35	a	±	0.25
	H. convergens	0.10	a	±	0.07	2.65	ab	±	0.94	0.55	a	±	0.36	0.15	a	±	0.15
non-native	*C. septempunctata*	0.10	a	±	0.07	4.50	ab	±	1.09	2.10	a	±	1.03	0.05	a	±	0.05
	H. axyridis	0.10	a	±	0.07	1.20	b	±	0.49	0.10	a	±	0.07	0.00	a	±	0.00
	H. variegata	0.15	a	±	0.11	4.90	ab	±	1.75	0.75	a	±	0.34	0.00	a	±	0.00
	P. quatuordecimpunctata	0.05	a	±	0.05	2.55	ab	±	0.90	0.10	a	±	0.07	0.00	a	±	0.00
		$F_{6,133}$			p	$F_{6,133}$			p	$F_{6,133}$			p	$F_{6,133}$			p
		0.28			0.9462	3.04			0.0082	2.71			0.0611	1.67			0.1326

	Lady Beetle Species	biting				grasping				stinging			
native	*C. trifasciata*	3.05	c	±	1.12	0.05	c	±	0.05	0.35	c	±	0.25
	C. maculata	11.85	ab	±	2.44	2.85	ab	±	0.77	7.45	ab	±	2.03
	H. convergens	16.35	a	±	3.78	4.50	a	±	1.22	13.85	a	±	3.28
non-native	*C. septempunctata*	4.25	c	±	1.50	0.55	bc	±	0.25	0.60	c	±	0.29
	H. axyridis	5.80	bc	±	2.42	0.85	bc	±	0.75	3.55	bc	±	2.20
	H. variegata	14.95	a	±	2.70	6.10	a	±	1.93	11.05	a	±	2.26
	P. quatuordecimpunctata	0.65	c	±	0.28	0.05	c	±	0.05	0.65	c	±	0.28
		$F_{6,133}$			p	$F_{6,133}$			p	$F_{6,133}$			p
		10.14			< .0001	11.02			< .0001	13.05			< .0001

Table 5.3. Mean frequency (± standard error) of lady beetle behaviors in response to ant attack scored in determination of reaction score (N = 20). Letters associated with each mean are results of Tukey mean separation tests comparing beetle species for each behavior. For each behavior, means with the same letter are not significantly different.

		Lady Beetle Behaviors																			
	Lady Beetle Species	continuing behavior previous to contact				changing movement				pulling in legs/antennae				preening				turning on back			
native	*C. trifasciata*	1.15	ab	±	0.45	1.90	a	±	0.50	1.10	ab	±	0.37	0.20	a	±	0.20	0.00	d	±	0.00
	C. maculata	0.25	b	±	0.18	0.65	a	±	0.21	0.60	ab	±	0.17	0.05	a	±	0.05	1.15	ab	±	0.27
	H. convergens	0.45	b	±	0.22	3.00	a	±	0.61	0.85	ab	±	0.21	0.00	a	±	0.00	0.85	bc	±	0.27
non-native	*C. septempunctata*	2.35	a	±	0.62	2.90	a	±	0.71	1.15	ab	±	0.79	0.10	a	±	0.10	0.35	cd	±	0.15
	H. axyridis	1.20	ab	±	0.47	1.05	a	±	0.34	0.45	b	±	0.20	0.00	a	±	0.00	0.05	d	±	0.05
	H. variegata	0.35	b	±	0.17	3.15	a	±	0.61	1.60	a	±	0.37	0.00	a	±	0.00	2.45	a	±	0.66
	P.quatuordecimpunctata	1.40	ab	±	0.82	1.05	a	±	0.36	0.40	b	±	0.27	0.05	a	±	0.05	0.00	d	±	0.00
		$F_{6,133}$			p	$F_{6,133}$			p	$F_{6,133}$			p	$F_{6,133}$			p	$F_{6,133}$			p
		3.48			0.0032	1.00			0.4281	2.63			0.0194	0.56			0.7627	15.12			< .0001
	Lady Beetle Species	flailing legs				fluttering wings				backing away				running away				flying away			
native	*C. trifasciata*	0.00	c	±	0.00	0.00	a	±	0.00	0.00	a	±	0.00	0.60	de	±	0.31	0.00	a	±	0.00
	C. maculata	1.85	a	±	0.46	0.15	a	±	0.08	0.00	a	±	0.00	2.65	abc	±	0.50	0.20	a	±	0.12
	H. convergens	1.25	ab	±	0.38	0.05	a	±	0.05	0.00	a	±	0.00	3.75	a	±	0.58	0.00	a	±	0.00
non-native	*C. septempunctata*	0.55	bc	±	0.26	0.05	a	±	0.05	0.00	a	±	0.00	3.30	ab	±	0.80	0.20	a	±	0.12
	H. axyridis	0.25	bc	±	0.25	0.05	a	±	0.05	0.00	a	±	0.00	1.05	cde	±	0.32	0.05	a	±	0.05
	H. variegata	2.45	a	±	0.82	0.00	a	±	0.00	0.00	a	±	0.00	1.75	bcd	±	0.58	0.00	a	±	0.00
	P.quatuordecimpunctata	0.00	c	±	0.00	0.00	a	±	0.00	0.00	a	±	0.00	0.25	e	±	0.18	0.05	a	±	0.05
		$F_{6,133}$			p	$F_{6,133}$			p	$F_{6,133}$			p	$F_{6,133}$			p	$F_{6,133}$			p
		9.98			< .0001	1.41			0.2163	NA			NA	11.08			< .0001	1.8			0.1037

and *C. maculata* ran away significantly more frequently compared with *C. trifasciata* and *P. quatuordecimpunctata*. The following lady beetle behaviors did not differ between beetle species: changing movement, preening, fluttering wings, and flying away. Although lady beetles did back away from ants during preliminary observations, that behavior was not observed during trials, thus it was not included in the split-plot ANOVA comparing lady beetle species and lady beetle behaviors described above.

Aggression scores were significantly different among the tested lady beetle species (ANOVA, DF = 6, 133, F = 9.68, $p < 0.0001$) (Table 5.4). *Hippodamia convergens* and *H. variegata* were exposed to significantly more ant aggression than all other species except *C. maculata*. *Propylea quatuordecimpuntata*, on the other hand, provoked the least amount of aggression. Similarly, there was significant variation in reaction scores among the tested lady beetle species (Table 5.4). Reaction scores for *H. variegata*, *H. convergens*, *C. maculata*, and *C. septempunctata* were significantly higher (ANOVA, DF = 6, 133, F = 10.18, $p < 0.0001$) than those for the other three species. There was also a strong positive correlation between aggression and reaction scores ($r = 0.6196$, $p < 0.0001$).

Table 5.4. Aggression and reaction scores (mean ± standard error) from behavioral trials with different lady beetle species and *Myrmica rubra* (N = 20). Letters associated with each mean are results of Tukey mean separation tests comparing beetle species for each score. For each score, means with the same letter are not significantly different.

	Lady Beetle Species	Aggression Score				Reaction Score			
native	*C. trifasciata*	17.35	bc	±	4.89	8.45	b	±	2.01
	C. maculata	90.20	ab	±	19.94	29.05	a	±	3.65
	H. convergens	140.40	a	±	29.97	34.60	a	±	3.54
non-native	*C. septempunctata*	26.70	bc	±	6.62	27.90	a	±	5.36
	H. axyridis	39.85	bc	±	20.54	9.60	b	±	2.92
	H. variegata	130.75	a	±	20.20	34.85	a	±	7.22
	P. quatuordecimpunctata	8.10	c	±	2.55	3.80	b	±	1.46

Aphid consumption during behavioral trials differed between the different lady beetle species (Table 5.5) (ANOVA, DF = 6, 133, F = 6.15, $p < 0.0001$). *Harmonia axyridis* consumed a significantly greater number of aphids compared with all other species but *C. septempunctata*. When considering all species, there was a significant negative correlation between aphid consumption and aggression score ($r = -0.3251$, $p < 0.0001$) and between aphid consumption and reaction score ($r = -0.1882$, $p = 0.0260$).

Table 5.5. Consumption (mean ± standard error) of aphids by different beetle species during behavioral trials with *Myrmica rubra* (N = 20). Letters associated with each mean are results of Tukey mean separation tests comparing aphid consumption for each beetle species. Means with the same letter are not significantly different.

	Lady Beetle Species	Consumption			
native	*C. trifasciata*	0.45	bc	±	0.2112
	C. maculata	0.02	c	±	0.1094
	H. convergens	0.35	bc	±	0.1500
non-native	*C. septempunctata*	1.50	ab	±	0.5104
	H. axyridis	2.00	a	±	0.6407
	H. variegata	0.35	c	±	0.2209
	P. quatuordecimpunctata	0.40	bc	±	0.1522

Lady Beetle Tolerance of Ant Stings

Although there were no significant differences (DF = 6, 133, F = 2.18, $p = 0.9912$) in the number of stings received by each beetle species (mean = 14.40 stings, standard error = 0.2422), the main effect of species (ANOVA, DF = 6, 114, F = 10.94, $p < 0.0001$) and sting status (ANOVA, DF = 1, 133, F = 119.10, $p < 0.0001$) were both significant, as were interactions between species and sting status (ANOVA, DF = 6, 133, F = 14.98, $p < 0.0001$). For the lady beetles exposed to ant stings, response scores were significantly different among the species (DF = 6, 133, F = 6.45, $p < 0.0001$) (Table 5.6), with *H.*

Table 5.6. Mean scores (± standard error) for observations of different beetle species after having been stung by ants (N = 20). Letters associated with experimental means are results of Tukey mean separation tests comparing beetle species for experimental results. Means with the same letter are not significantly different. T and p-values refer to comparisons between experimental treatments and controls for each species.

	Lady Beetle Species	Experimental				Control			t	p
native	*C. trifasciata*	1.00	ab	±	0.1622	0.15	±	0.0819	-6.40	<0.0001
	C. maculata	0.45	bc	±	0.1846	0.40	±	0.1124	0.66	0.5181
	H. convergens	0.40	bc	±	0.1338	0.10	±	0.0688	-2.75	0.0128
non-native	*C. septempunctata*	1.10	a	±	0.1433	0.25	±	0.0993	-8.06	<0.0001
	H. axyridis	0.25	c	±	0.0993	0.35	±	0.1094	1.45	0.1625
	H. variegata	1.40	a	±	0.2224	0.30	±	0.1277	-5.79	<0.0001
	P. quatuordecimpunctata	1.00	abc	±	0.2176	0.30	±	0.1051	-3.75	0.0014

variegata and *C. septempuncata* having significantly higher scores than *H. axyridis*, *H. convergens*, and *C. maculata*. Control lady beetles not exposed to ants displayed similar response scores (mean score = 0.2643, standard error = 0.039) (DF = 6, 133, F = 1.14, p = 0.3444). When comparing beetles exposed to ant stings to the unexposed beetles of the same species, the former showed significantly higher response scores in five beetle species: *C. septempunctata*, *C. trifasciata*, *H. convergens*, *H. variegata*, and *P. quatuordecimpunctata*. There were no differences when comparing beetles stung to those not stung in the remaining two species, *C. maculata* and *H. axyridis*.

From the greatest to the least effects, these five species were *H. variegata*, *C. septempunctata*, *C. trifasciata*, *P. quatuordecimpunctata*, and *H. convergens*. The dominant condition (observed in 10 out of 20 trials) in experimental trials for *H. variegata* was “impaired ambulatory locomotion,” i.e., legs appearing to be non-functional and dragging behind the beetles. This condition was also observed seven times with *P. quatuordecimpunctata*, three times each with *C. maculata* and *C. trifasciata*, two times with *C. septempunctata*, in one trial with *H. convergens*, but in no trials with *H. axyridis*. This condition was not observed in control trials with any of the seven species.

Discussion

The three most aggressive ant behaviors documented (biting, grasping, and stinging) (Table 5.2) occurred most frequently with three lady beetle species: *H. convergens*, *H. variegata*, and *C. maculata*. *C. trifasciata*, *P. quatuordecimpunctata*, and *C. septempunctata* were generally documented to receive these behaviors the least. *Harmonia axyridis* was generally intermediate between these two groups. As expected, these patterns are reflected in aggression scores (Table 5.4).

Lady beetle behaviors in response to ant aggression (Table 5.3) followed a similar pattern to the groupings observed with ant behaviors. When there were differences between lady beetle species for a given behavior, *H. convergens*, *H. variegata*, *C. maculata*, and/or *C. septempunctata* generally had a higher frequency of reactive behaviors compared with *C. trifasciata* and/or *P. quatuordecimpunctata*. *Harmonia axyridis* was generally intermediate between these two groups. Again, these general groupings based on differences in lady beetle species considering individual behaviors were reflected in overall reaction scores (Table 5.4). Reaction scores for *H. variegata*, *H. convergens*, *C. maculata*, and *C. septempunctata* were significantly greater than those for *H. axyridis*, *C. trifasciata*, and *P. quatuordecimpunctata*.

It seems intuitive that high frequencies of aggression from ants would result in higher frequencies of reactive behaviors from lady beetles. It is interesting to note that despite the fact that *H. convergens* and *H. variegata* had the highest aggression scores, *C. septempunctata* had the highest reaction score relative to its aggression score. When interpreting these results, how the reaction by lady beetles might affect aggression by the ants must be considered. The most frequent reaction by *C. septempunctata* to ant aggression was to run away. Two possible explanations of why ant aggression does not escalate in this species are that running away is an effective method of avoidance, or that ants stop perceiving the retreating lady beetle as a threat. However, *H. convergens* ran away as much as *C. septempunctata*, yet ants were much more aggressive towards it. *Coccinella septempunctata* has been shown to deter attacks by ants chemically. *Coccinella septempunctata* was shown to use reflex bleeding to deter attacks by *Formica polyctena* when it used the ants' odor trails to locate aphid prey (Bhatkar 1982). Also, Tursch *et al*. (1971) found that *M. rubra* would not drink from water to which a defensive alkaloid produced by *C. septempunctata* had been added. It is possible that in this study behavioral activity documented for *C. septempunctata* in reaction scores coincided with chemical production that deterred further aggression by ants. Reflex bleeding was noted in three trials with *C. septempunctata*.

In the presence of ants, *H. axyridis* consumed more aphids than all other species except *C. septempunctata* (Table 5.5). There were no differences among lady beetle species in feeding trials conducted in Petri dishes in the absence of ants. *Harmonia axyridis* received a moderate level of aggression from ants, but had a relatively low reaction score compared to the other lady beetle species. This might reflect a better relative ability of *H. axyridis* to forage successfully on ant-protected aphids. Similarly, Dutcher *et al*. (1999) found that *H. axyridis* withstood fire ant (*Solenopsis invicta* Buren) aggression more successfully than *H. convergens*. While *H. convergens* was forced from plants housing its aphid prey and *S. invicta*, *H. axyridis* was able to remain. Alternatively, *H. axyridis* might have been a better forager in the relatively complex environment of the laboratory arenas, while that advantage disappeared in a simpler environment of Petri dishes. *Harmonia axyridis* is also a more voracious predator compared to *Cycloneda sanguinea* (L.) (Michaud 2002). Furthermore, in this study, *H axyridis* appeared to be highly tolerant of ant venom (Table 5.6). The ability of some species to tolerate *M. rubra* venom may have developed over time, as the ranges of the four non-native species tested overlap that of *M. rubra*.

The negative correlations between aphid consumption and aggression/reaction scores are also not surprising. One function of aphid-tending ants is to protect aphids from predators (Bartlett 1961, Way 1963, Buckley 1987, Vinson and Scarborough 1989, Jahn and Beardsley 1994). Aggression from ants should thwart predators from taking aphids. Time spent reacting to ant aggression would reduce time available for foraging and feeding.

Mean scores for ant sting trials for five of the seven lady beetle species tested were greater than each of these species' associated control trials. In two species, *H. axyridis* and C. *maculata*, venom was not documented to have any effects. Exocrine glands in ants are known to contain a variety of compounds that are used externally (Cavill and Robertson 1965). Although many of the constituents of *M. rubra*'s venom, Dufour, and mandibular gland excretions have been identified (Cammaerts-Tricot *et al.* 1976, Morgan *et al.* 1977, Evershed *et al.* 1981, Cammaerts *et al.* 1981a, Cammaerts *et al.* 1981b, Evershed *et al.* 1982, Attygale *et al.* 1983b, Cammaerts 1984, Cammaerts 1992), little is known about the effects of *M. rubra* envenomization on insects. Determinations of the effects of these compounds have been limited primarily to uses for communication with conspecifics such as in trail and foraging area delineation (Cammaerts-Tricot *et al.* 1976, Cammaerts *et al.* 1981a, Cammaerts *et al.* 1981b, Attygale *et al*. 1983a, Cammaerts 1984, Cammaerts 1992) and worker recruitment to foraging sites (Cammaerts-Tricot *et al*. 1976, Cammaerts 1978, Cammaerts *et al*. 1981a, Cammaerts *et al*. 1981b, Attygale *et al*. 1983a).

Aggression scores were higher in species that appear to have more exposed parts on which ants could grasp. When *H. convergens*, *H. variegata*, and *C. maculata* were observed to pull in their legs, their concealment was incomplete and ants could still bite them. On the other hand, when *H. axyridis*, *C. septempunctata*, *C. trifasciata*, and *P. quatuordecimpunctata* pulled in their legs, their appendages appeared to be completely retracted and ant aggression subsided. So, while interactions between ants and lady beetles may be behavioral and/or chemical, there may also be a physical component, ants acting as opportunists, grabbing what is available, causing aggression to escalate, or walking away when all parts are concealed.

Differences documented between lady beetle species may put some of them at a competitive advantage over others. In a number of earlier studies, *H. axyridis* has been found to be a superior competitor when compared to other lady beetle species due to intraguild predation (Hironori and Katsuhiro 1997, Yasuda *et al*. 2001, Yasuda *et al*. 2004), prey utilization (Michaud 2002), and tolerance of pathogenic microorganisms (Saito and Bjørnson 2006). It appears that it also performs better in the presence of an aggressive aphid-tending ant, *M. rubra*. While this study did not provide evidence that successful non-native species invariably have a competitive advantage over native species when dealing with an aggressive enemy, the differences between species provide further evidence that different lady beetle species have very different competitive abilities that may contribute to their successes or failures in new habitats.

Chapter 6

ECOLOGICAL INTERACTIONS BETWEEN COCCINELLIDS AND ANTS IN NEWLY SYMPATRIC SPECIES ASSEMBLAGES

Chapter Abstract

Research evaluating relationships between newly sympatric coccinellids, ants, and plant-feeding insects is summarized. Studies are limited to plant-feeding insects that serve as prey to coccinellids and sources of nutrition from their honeydew to ants. Three invasive ants, *Pheidole megacephala* (F.), *Solenopsis invicta* Buren, and *Linepithema humile* (Mayr), have driven the majority of these studies, as have coccinellid biological control organisms, *Cryptolaemus montrouzieri* Mulsant, *Coccinella septempunctata* L., and *Harmonia axyridis* (Pallas). Recent studies evaluate species-specific interactions, while older studies often consider coccinellids as a group. Many studies document increases in herbivore numbers due to ant attendance. Of 77 pairings between different ant and coccinellid species, ants interfered with coccinellid predation in 73%, exhibited no interference in 17%, and showed mixed effects in 10% of pairings. Several studies found an upper limit to care by ants, where as herbivore numbers increased relative to ant numbers, effective protection by ants decreased. On Midway Atoll, where the ant, *P. megacephala*, tends the treehopper, *Vanduzeea segmentata* Green, which is preyed upon by the coccinellid, *Coelophorus inaequalis* (F.), coccinellid numbers increased with increasing treehopper numbers, but decreased with increasing ant numbers. Coccinellid numbers with ants and treehoppers were greater when the ratio of ants to treehoppers

was less than two, compared to when it was greater than or equal to two. Suggestions for future work include evaluations of species-specific interactions and relative population densities, comparisons of species in native and non-native ranges, and assessments of the impacts of ant suppression in agricultural and non-agricultural systems.

Introduction

The relationship between coccinellids and phloem-feeding insects such as aphids, scales, and mealybugs and other insect pests, has been extensively documented (Biddinger *et al.* 2009, Evans 2009, Hodek and Honěk 2009; Obrycki *et al.* 2009). Many coccinellid species are predators of, and important control agents of, these pests in agriculture (Hodek 1973, Gordon 1985). The relationship between ants and phloem-feeding insects has also been extensively documented (Carroll and Janzen 1973, Buckley 1987, Lundgren 2009). Many ant species feed on the excrement (honeydew) of phloem-feeding insects. These ants receive sugars (and possibly some vitamins and amino acids) from the honeydew they consume (Auclair 1963, Way 1963, Carroll and Janzen 1973, Hölldobler and Wilson 1990, Völkl *et al.* 1999). Ants protect these insects by removing honeydew accumulations that can promote fungal growth (Hölldobler and Wilson 1990, Gonzalez Hernandez *et al.* 1999a). Through direct aggression or by providing refuge, ants also interfere with the activity of their predators, parasites, and parasitoids (Bartlett 1961, Way 1963, Buckley 1987, Vinson and Scarborough 1989, Charles 1993, Reimer *et al.* 1993, Jahn and Beardsley 1994, Gonzalez Hernandez *et al.* 1999a). In some cases, this "tending" by ants has been shown to support the persistence of, or contribute to increases in, tended insect populations (Addicott 1979, Bristow 1984, Mahdi and

Whittaker 1993, Sloggett and Majerus 2000). It is important to note, however, that some ant species are predators of, and thus valuable in the control of, the same kinds of insects described above as protected by ants, and other important agricultural pests such as caterpillars and herbivorous beetle larvae. The first documented case of management using biological control agents was that of the ant, *Oecophylla smaragdina* F. in China, where in the 4th century A.D., colonies were intentionally introduced to control leaf-feeding insects in citrus (van den Bosch and Messenger 1973).

When coccinellids and ants are present in the same system, coccinellid predation on ant-protected insects may be affected by tending ants. On the other hand, the ability of ants to obtain resources from tended insects may be hindered by coccinellids. Coccinellid predation on ant-tended insects diminishes resources available to ants, and may alter the behavior of the sternorrhynchans in ways that reduce their suitability for the ants. Ants must also expend energy to prevent predation by coccinellids, either through direct aggressive interactions with coccinellids or by having to shelter aphids, activities that distract ants from resource acquisition. Additionally, tended insects may not need to dedicate energy towards predator detection, defense, and avoidance, compared to their untended counterparts.

A number of studies have described relationships between coccinellids and ants that share the same insect resource. Takizawa and Yasuda (2006) reported that fewer *Coccinella septempunctata* L. remained on plants with *Aphis craccivora* Koch tended by the ant Lasius japonicus Santschi, compared to untended aphid colonies. Oliver *et al*. (2008) showed that *Adalia bipunctata* (L.) move away from and avoid laying their eggs near *Lasius niger* (L.). In the same study, however, the coccinellid, *Propylea japonica*

(Thunberg), remained for the same amount of time on plants tended and untended by ants. Associations between a myrmecophilous coccinellid, *Coccinella magnifica* Redtenbacher, and wood ants (*Formica rufa* L., group) tending *Cinara* sp. aphids were compared with non-myrmecophilous coccinellids (*C. septempunctata* in Sloggett *et al*., 1998; *Myrrha octodecimguttata* (Linnaeus), *Harmonia quadripunctata* (Pontoppidan), *Anatis ocelata* (Linnaeus), *Myzia* (=*Neomysia*) *oblongoguttata* (Linnaeus), and *C. septempunctata*, in Sloggett and Majerus, 2000). In these studies, different coccinellid species varied in their associations with ant-tended aphids, the different species handling aggression from the ants differently. These differences presumably resulted in differential effects on the ant-tended insects involved.

Extrapolation of information from these relationships to agricultural systems allows some speculation about the effects of similar species on pest populations and associated crop damage. While each of the species assemblages described above involve historically sympatric species, similar assemblages considered in agriculture often include at least one species that is not native to the location in question. Coccinellids have been introduced to new locations for the biological control of plant-feeding pests (Gordon 1985, Dreistadt and Flint 1996, Koch 2003, Biddinger *et al*. 2009) and all three guilds (coccinellids, ants, and plant pests) have been introduced unintentionally via plant exports and other cargo (Chantal 1972, Schaefer *et al*. 1987, Day *et al*. 1994). Introduced coccinellid species persist in some intended locations and disperse to other locations, where they may provide beneficial pest control or displace native coccinellids (Elliot *et al*. 1996, Brown and Miller 1998, Colunga-Garcia and Gage 1998, Michaud 2002, Brown 2003, Turnock *et al*. 2003, Alyokhin and Sewell 2004, Finlayson *et al*. 2008). Because a species can differ greatly in its introduced and native ranges (Tsutsui *et al*. 2000), a summary of studies evaluating interactions between newly sympatric coccinellids and tending ants is important to evaluate the effects of these new species assemblages. Many lady beetle species feed primarily on plant-feeding insects at least during part of their life cycle (Evans 2009, Hodek and Honěk 2009, Obrycki *et al*. 2009); thus, their survival and effect on target pest populations may, in part, be determined by their interactions with tending ants (Bartlett 1961, Vinson and Scarborough 1989, Hanks and Sadof 1990, Jahn and Beardsley 1994, Sloggett *et al*. 1998, Sloggett and Majerus 2000).

Here, I summarize studies investigating assemblages of newly sympatric coccinellids, ants, and the insects that they tend (and which coccinellids prey upon). I also present an evaluation of newly sympatric populations of *Coelophora inaequalis* (F.) (Coleoptera, Coccinellidae), *Vanduzeea segmentata* Green (Hemiptera, Membracidae), and *Pheidole megacephala* (F.) (Hymenoptera, Formicidae) on Eastern Island, Midway Atoll. Finally, based on research to date and current needs, I discuss directions for future research.

Materials and Methods

Literature Survey

Studies evaluated (n = 321) document the presence of coccinellids, ants, and plant-feeding insects in the same system. Studies included in the survey (n = 105) are limited to those evaluating newly sympatric assemblages where at least two of the three species have separate historical ranges, but now overlap. Plant-feeding insects are limited to phloem-feeders in the suborders Auchenorrhyncha and Sternorrhyncha, which serve as prey for coccinellids and are tended by ants. Surveys that document the utilization of the same herbivore without any information about the effects that ants have on coccinellid predation are included, but those that only document the presence of coccinellids and ants in the same location without evidence that they utilized the same phloem-feeding species have been omitted. Herbivores may obtain defensive chemicals from the plants on which they feed, and this may affect consumption by coccinellids (Auclair 1963, Buckley 1987, Bristow 1991, Hodek and Honěk 2009), but for simplicity, the influence of host plant was not considered. With so much attention on phloem-feeding pests in agriculture, where crop plants are often non-native, host plant origin could also be considered as part of a newly sympatric system. However, again, for the sake of simplicity, host plant origin was not considered.

Studies were categorized based on the relationships between coccinellids and ants. Research studies were categorized as "interference" when ant aggression disrupted coccinellid predation or when the presence of tending ants corresponded with lower coccinellid abundance or prey consumption compared to the same system where ants were absent. Studies in which ants showed no aggression towards coccinellids or where coccinellid abundance or predation was not different with and without ants are termed "no interference." Several studies with inconclusive results and evidence only of resource sharing are also included. Studies were also evaluated for trends, for example, in focus, species, and geographic distribution. When a study identified and associated results to one or more "dominant" species among a larger group of coccinellid, herbivore, and/or ant species, only the dominant species were included. For example, Michaud (1999) found that among 13 coccinellid species, *Cycloneda sanguinea* limbifer Casey, *C. inaequalis*, and *Harmonia axyridis* (Pallas) were the most abundant and the primary coccinellid predators of *Toxoptera citricida* (Kirkaldy); thus, only these three coccinellid species were included in the survey.

Midway Atoll Survey

The coccinellid-prey-ant community was evaluated on an invasive plant, *Verbesina encelioides* (Cavanilles) Bentham & Hooker ex Gray (Asteraceae), on Eastern Island (longitude: 28.2617, latitude: -177.383), Midway Atoll, a low coral atoll in the Northwestern Hawaiian Islands chain. Two surveys were conducted, one between 10 and 24 September 2007 and the other from 25 February to 17 March 2008. In each survey year, the entire 135-ha island was surveyed by walking transects spaced approximately 10 m apart. Survey points along the transects occurred at approximately 10-m intervals. At each survey point, the first *V. encelioides* stem encountered was evaluated. If a stem could not be located within a 2-m radius of the survey point, that point was bypassed. On each stem, coccinellids, ants, and plant-feeding insects tended by ants were counted and identified to species, with particular emphasis on a group of species previously noted as dominant on the island: the coccinellid (*C. inaequalis*), the ant (*P. megacephala*), and the treehopper (*V. segmentata*). In previous observations, *C. inaequalis* had been documented feeding on, and P. megacephala had been documented tending, *V. segmentata*. All other arthropod taxa were counted and identified when possible; this information, however, will be presented in a different manuscript.

Data were tested for normality using the Wilk-Shapiro test and transformed using log (n + 1) transformations (Sokal and Rohlf 1995). To quantify the relationship between coccinellids, treehoppers, and ants, the number of coccinellids on numbers of ants and treehoppers were regressed independently for each year. Correlation analyses were conducted to compare relationships among all combinations of *P. megacephala*, *V. segmentata*, and *C. inaequalis*. Mean numbers of *C. inaequalis* found with *P. megacephala* and *V. segmentata* were also evaluated. For each stem observed, a ratio was calculated by dividing the number of *P. megacephala* documented on that stem by the number of *V. segmentata* found on the same stem. Two-sample, independent t-tests were then conducted to compare mean numbers of *C. inaequalis* when the ratio was < 2 compared to when it was ≥ 2. All statistical analyses were conducted separately for 2007 and 2008 using SAS statistical software, version 9 (SAS Institute Inc. 2002). Means and standard errors reported in this paper were calculated from the untransformed data, as were the ratios of *P. megacephala* to *V. segmentata*.

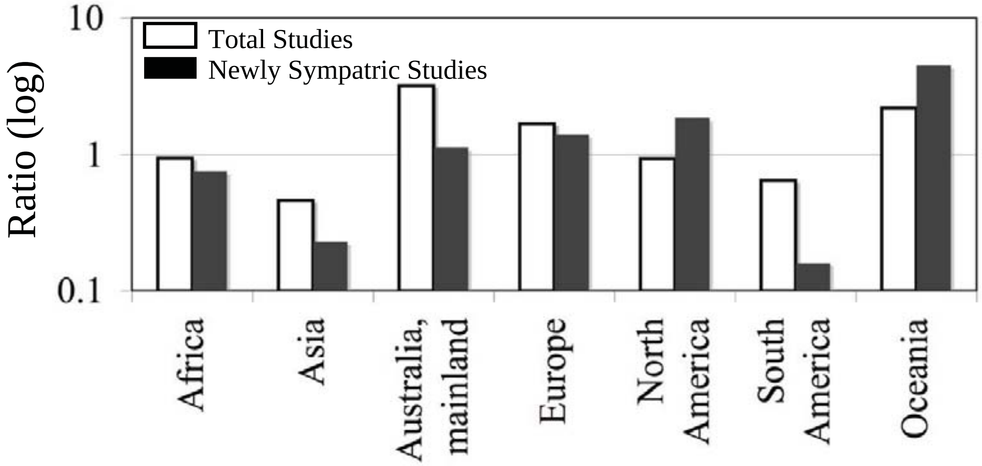
Results and Discussion

Literature Survey

105 of the 321 studies reviewed present information about newly sympatric species assemblages. An evaluation of the body of research reveals several trends discussed below:

- When considering the 321 studies (Figure 6.1), only Africa and North America are proportionally represented, i.e. the percent of studies in Africa (20%) and North America (16%) are comparable to the percent land area represented by each of those continents, 21.3% and 17.2%, respectively. Asia and South America are underrepresented based on geographic area, while mainland Australia is overrepresented in total

Figure 6.1. Ratio (log) of percent studies and percent land area for each continent. Ratios (log) greater than 1 indicate an overrepresentation of studies conducted in the continent relative to land area.



studies. Studies focusing on newly sympatric species assemblages are proportionally the most numerous on islands, in North America, and in Europe. Islands are often considered vulnerable to non-native species invasions, especially considering ants, as these ecosystems often have few or no native ant species. Studies largely represent locations where invasive ants are of concern because they tend pest populations, either affecting agricultural products or plants of conservation concern. For example, 41% of the 34 studies of newly sympatric species in North America involve the fairly recent introduction of the red imported fire ant, *Solenopsis invicta* Buren. This is not surprising, however, because if ants are concerned a hinderance, for example, to biocontrol, they will more likely be studied.

- The majority of studies evaluating newly sympatric assemblages took place in subtropical (20 – 35 degrees north and south latitude) locations (60 studies), with 23 in temperate (35 - 66.6 north and south latitude) and 22 in tropical (between 20 degrees north and 20 degrees south latitude) locations. Historically sympatric assemblages were studied more in temperate locations (17), with eight studies conducted in tropical and eight in subtropical locations. This may not stem from a greater proportion of non-native species in subtropical regions; these statistics are likely influenced by the location of research institutions with interest in these systems. These areas also have a moderate climate and are productive agriculturally, and many studies of newly sympatric species address concerns regarding agricultural loss due to pests tended by ants.

- The majority of studies (89% of 105 studies) involved pest populations on an agricultural commodity. The remainder of studies (11%) regarded species of conservation concern or ornamental interest.

- Coinciding with growing concerns about invasive species is the recognition that native species have value in biological control, where non-native species have often been introduced. Recent studies reflect this concern by evaluating different coccinellid species separately, comparing native and non-native species, where older studies often lump coccinellids into one group. Of the 105 studies evaluated, 30% examined coccinellids at the family level, while the remainder examined individual coccinellids (43% of studies) or conducted separate examinations for each of several species (27%).

- Several taxa have received a disproportionate amount of attention. Coccinellids introduced as biological control agents, *Cryptolaemus montrouzieri* Mulsant, and *Coccinella septempunctata*, have been evaluated in a number of systems with a variety of pests. So have the invasive ants *Pheidole megacephala*, *Solenopsis invicta*, and *Linepithema humile* (Mayr). The majority (70%) of studies evaluate recently introduced ant species that are considered aggressive and potentially disruptive to existing natural enemy/pest interactions, often with concern regarding effects on economically important crops or on unique fauna and flora.

Table 6.1 summarizes the results of studies that evaluated ant interference of predation by coccinellid species. Of the 77 coccinellid-ant pairings evaluated, the majority (73%) showed inference of coccinellid predation by ants. In only 17% did the ant not interfere with coccinellid predation. In the remaining 10% of pairings (eight pairings), evidence was mixed, with some studies documenting interference and others a lack of interference.

Based on the studies reviewed, coccinellids do not successfully control prey populations when they are tended by *P. megacephala* (Table 6.2). Six studies document the utilization of the same herbivore without any information about the effects that ants have on coccinellid predation (Catling 1971, Weaving 1980, Kfir *et al*. 1985, Carver *et al*. 1987, De Barro 1990, Handler *et al*. 2007). In its native range of Africa (Wheeler 1922), *P. megacephala* tends non-native prey (Catling 1971, Weaving 1980, Kfir *et al*. 1985) and interferes with coccinellid predation of non-native prey (Anneke 1959, Cudjoe *et al*. 1993) in agroecosystems. Outside of its native range, *P. megacephala* has interfered with coccinellid consumption of pests of pineapple (Illingworth 1931, Jahn 1992, Gonzalez-Hernandez *et al*. 1999a, Gonzalez-Hernandez *et al*. 1999b) and coffee (Reimer *et al*. 1993) in Hawaii, and of custard apples (Murray 1982) in Queensland, Australia. Successful control of pests tended by *P. megacephala* has been accomplished by controlling ant populations with insecticides (Reimer *et al*. 1990). When ant populations are reduced, coccinellids and other natural enemies can successfully control pests (Jahn 1992). On Palmyra Atoll in the Pacific Ocean, *P. megacephala* tends a non-

Table 6.1. Ant interference in coccinellid predation on pests.

Lady Beetle Species	Ant Interference?	Ant Species (Subfamily)	Citation
Adalia bipunctata (Linnaeus, 1758)	YES	*Formica propinqua* Creighton, 1940 (Formicinae)	Wimp and Whitham, 2001
	YES	*Formica rufibarbis* Fabricius, 1793 (Formicinae)	Kreiter and Iperti, 1986
	YES	*Lasius niger* (Linnaeus, 1758) (Formicinae)	Kreiter and Iperti, 1986
	NO	*Lasius niger* (Linnaeus, 1758) (Formicinae)	Stary, 1995
	YES	*Linepithema humile* (Mayr, 1868) (Dolichoderinae)	Hajek and Dahlsten, 1988
Adonia variegata Goeze, 1777	YES	*Monomorium carbonarium* (Smith, 1858) (Myrmicinae)	Elbanna, 2007
Anatis ocellata Linnaeus, 1758	NO	*Lasius niger* (Linnaeus, 1758) (Formicinae)	Stary, 1995
Azya luteipes Mulsant, 1850	YES	*Pheidole megacephala* (Fabricius, 1793) (Myrmicinae)	Reimer et al., 1993
Azya orbigera Mulsant, 1850	NO	*Azteca instabilis* (Smith, 1862) (Dolichoderinae)	Liere and Perfecto, 2008
Chilocorus angolensis Crotch	YES	*Pheidole megacephala* (Fabricius, 1793) (Myrmicinae)	Anneke, 1959
Chilocorus bipustulatus (Linnaeus, 1758)	YES	*Linepithema humile* (Mayr, 1868) (Dolichoderinae)	Bartlett, 1961
Chilocorus distigma Klug, 1835	NO	*Anoplolepis custodiens* (Smith, 1858) (Formicinae)	Steyn, 1954
	NO	*Technomyrmex detorquens* (Walker, 1859) (Dolichoderinae)	Vesey-Fitzgerald, 1939
Chilocorus hauseri Weise, 1895	YES	*Linepithema humile* (Mayr, 1868) (Dolichoderinae)	Bartlett, 1961
Chilocorus kuwanae Silvestri, 1909	YES	*Lasius niger* (Linnaeus, 1758) (Formicinae)	Itioka and Inoue, 1996
Chilocorus nigritus Fabricius, 1798	NO	*Technomyrmex* Mayr, 1872 (Dolichoderinae)	Vesey-Fitzgerald, 1941
	YES	*Technomyrmex* Mayr, 1872 (Dolichoderinae)	Vesey-Fitzgerald, 1953
	YES	*Camponotus grandidieri* Forel, 1886 (Formicinae)	Hill and Blackmore, 1980
	YES	*Camponotus maculatus* (Fabricius, 1782) (Formicinae)	Hill and Blackmore, 1980
	YES	*Monomorium floricola* (Jerdon, 1851) (Myrmicinae)	Hill and Blackmore, 1980
	YES	*Paratrechina longicornis* (Latreille, 1802) (Formicinae)	Hill and Blackmore, 1980

Table 6.1 (Continued). Ant interference in coccinellid predation on pests.

Lady Beetle Species	Ant Interference?	Ant Species (Subfamily)	Citation
Chilocorus Leach, 1815	YES	*Linepithema humile* (Mayr, 1868) (Dolichoderinae)	DeBach et al., 1951
Coccinella californica Mannerheim, 1843	YES	*Linepithema humile* (Mayr, 1868) (Dolichoderinae)	Hajek and Dahlsten, 1988
Coccinella novemnotata Herbst, 1793	YES	*Formica obscuripes* Forel, 1886 (Formicinae)	Philpott, 1997
Coccinella septempunctata Linnaeus, 1758	YES	*Formica integra* Nylander, 1856 (Formicinae)	Bugg and Ellis, 1990
	YES	*Formica nitidiventris* Emery, 1893 (Formicinae)	Bugg and Ellis, 1990
	YES	*Formica obscuripes* Forel, 1886 (Formicinae)	Philpott, 1997
	NO	*Formica propinqua* Creighton, 1940 (Formicinae)	Wimp and Whitham, 2001
	YES	*Formica subsericea* Say, 1836 (Formicinae)	Bugg and Ellis, 1990
	YES	*Lasius neoniger* Emery, 1893 (Formicinae)	Harmon and Andow, 2007
	YES	*Lasius niger* (Linnaeus, 1758) (Formicinae)	Katayama and Suzuki, 2002; Katayama and Suzuki, 2003
	NO	*Lasius niger* (Linnaeus, 1758) (Formicinae)	Stary, 1995
	YES	*Solenopsis invicta* Buren, 1972 (Myrmicinae)	Eubanks, 2001
	YES	*Tetramorium caespitum* (Linnaeus, 1758) (Myrmicinae)	Katayama and Suzuki, 2003
Coccinella transversoguttata Faldermann, 1835	YES	*Formica obscuripes* Forel, 1886 (Formicinae)	Philpott, 1997
Coelophora inaequalis (Fabricius, 1775)	YES	*Solenopsis invicta* Buren, 1972 (Myrmicinae)	Michaud and Browing, 1999
Coleomegilla maculata (De Geer, 1775)	YES	*Solenopsis invicta* Buren, 1972 (Myrmicinae)	Eubanks, 2001
	NO	*Solenopsis invicta* Buren, 1972 (Myrmicinae)	Sterling et al., 1979
Cryptolaemus montrouzieri Mulsant, 1853	YES	*Camponotus compressus* (Fabricius, 1787) (Formicinae)	Srikanth et al., 2001
	NO	*Anoplolepis custodiens* (Smith, 1858) (Formicinae)	Steyn, 1954
	YES	*Linepithema humile* (Mayr, 1868) (Dolichoderinae)	Smith and Armitage, 1931; Bennett and Hughes, 1959; Bartlett, 1961; Panis and Brun, 1974; Raciti et al., 1997

Table 6.1 (Continued). Ant interference in coccinellid predation on pests.

Lady Beetle Species	Ant Interference?	Ant Species (Subfamily)	Citation
Cryptolaemus montrouzieri Mulsant, 1853	NO	*Linepithema humile* (Mayr, 1868) (Dolichoderinae)	Panis, 1981; Daane et al., 2007
	YES	*Pheidole megacephala* (Fabricius, 1793) (Myrmicinae)	Murray, 1982
	YES	*Pheidole punctulata* Mayr, 1866 (Myrmicinae)	Kirkpatrick, 1927
	NO	*Tetramorium bicarinatum* (Nylander, 1846) (Myrmicinae)	Smith et al., 2004
Curinus coeruleus (Mulsant, 1850)	YES	*Pheidole megacephala* (Fabricius, 1793) (Myrmicinae)	Jahn, 1992
Cycloneda polita Casey, 1899	YES	*Formica obscuripes* Forel, 1886 (Formicinae)	Philpott, 1997
Cycloneda sanguinea limbifer Casey, 1899	YES	*Solenopsis invicta* Buren, 1972 (Myrmicinae)	Michaud and Browing, 1999
Cycloneda sanguinea (Linnaeus, 1763)	NO	*Solenopsis invicta* Buren, 1972 (Myrmicinae)	Sterling et al., 1979
Exochomus spp. Redtenbacher, 1843	YES	*Technomyrmex* Mayr, 1872 (Dolichoderinae)	Vesey-Fitzgerald, 1953
Exochomus troberti Mulsant, 1850	YES	*Camponotus acvapimensis* Mayr, 1862 (Formicinae)	Cudjoe et al., 1993
	YES	*Camponotus flavomarginatus* Mayr, 1862 (Formicinae)	Cudjoe et al., 1993
	YES	*Lepisiota capensis* (Mayr, 1862) (Formicinae)	Cudjoe et al., 1993
	YES	*Monomorium* Mayr, 1855 (Myrmicinae)	Cudjoe et al., 1993
	YES	*Paratrechina* Motschoulsky, 1863 (Formicinae)	Cudjoe et al., 1993
	YES	*Pheidole megacephala* (Fabricius, 1793) (Myrmicinae)	Cudjoe et al., 1993
Exochomus flavipes (Thunberg, 1781)	YES	*Pheidole megacephala* (Fabricius, 1793) (Myrmicinae)	Anneke, 1959
	NO	*Technomyrmex detorquens* (Walker, 1859) (Dolichoderinae)	Vesey-Fitzgerald, 1939
Exochomus ventralis (Gerst.)	NO	*Technomyrmex detorquens* (Walker, 1859) (Dolichoderinae)	Vesey-Fitzgerald, 1939
Harmonia axyridis (Pallas, 1773)	YES	*Formica obscuripes* Forel, 1886 (Formicinae)	Philpott, 1997
	YES	*Lasius neoniger* Emery, 1893 (Formicinae)	Harmon and Andow, 2007
	YES	*Lasius niger* (Linnaeus, 1758) (Formicinae)	Kaneko, 2002; Kaneko, 2004
	YES	*Solenopsis invicta* Buren, 1972 (Myrmicinae)	Dutcher et al., 1999; Eubanks, 2001

Table 6.1 (Continued). Ant interference in coccinellid predation on pests.

Lady Beetle Species	Ant Interference?	Ant Species (Subfamily)	Citation
Hippodamia convergens Guérin-Méneville, 1842	YES	*Formica obscuripes* Forel, 1886 (Formicinae)	Philpott, 1997
	YES	*Linepithema humile* (Mayr, 1868) (Dolichoderinae)	Bartlett, 1961; Hajek and Dahlsten, 1988
	YES	*Solenopsis invicta* Buren, 1972 (Myrmicinae)	Vinson and Scarborough, 1989; Dutcher et al., 1999; Eubanks, 2001
	NO	*Solenopsis invicta* Buren, 1972 (Myrmicinae)	Sterling et al., 1979; Tedders et al., 1990
Nephus bilucernarius (Mulsant, 1850)	YES	*Pheidole megacephala* (Fabricius, 1793) (Myrmicinae)	Gonzalez-Hernandez et al., 1999a; Gonzalez-Hernandez et al., 1999b
Olla v-nigrum (Mulsant, 1866)	YES	*Linepithema humile* (Mayr, 1868) (Dolichoderinae)	Hajek and Dahlsten, 1988
Rhyzobius Stephens, 1829	YES	*Iridomyrmex rufoniger* (Lowne, 1865) (Dolichoderinae)	Snowball and Milne, 1973; Milne, 1974
Rhyzobius lophanthae (Blaisdell, 1892)	YES	*Linepithema humile* (Mayr, 1868) (Dolichoderinae)	Bartlett, 1961
	NO	*Linepithema humile* (Mayr, 1868) (Dolichoderinae)	DeBach et al., 1951
Rodolia cardinalis (Mulsant, 1850)	YES	*Linepithema humile* (Mayr, 1868) (Dolichoderinae)	Bartlett, 1961; Quezada and DeBach, 1973
	NO	*Linepithema humile* (Mayr, 1868) (Dolichoderinae)	Bennett and Hughes, 1959
	YES	*Technomyrmex* Mayr, 1872 (Dolichoderinae)	Vesey-Fitzgerald, 1953
	YES	*Myrmecocystus mimicus* Wheeler, 1908 (Formicinae)	Quezada and DeBach, 1973
	YES	*Solenopsis xyloni* McCook, 1879 (Myrmicinae)	Quezada and DeBach, 1973
Rodolia chermesina Mulsant, 1850	YES	*Technomyrmex* Mayr, 1872 (Dolichoderinae)	Dupont, 1931; Vesey-Fitzgerald, 1953
Scymnus louisianae J. Chapin, 1973	YES	*Solenopsis invicta* Buren, 1972 (Myrmicinae)	Vinson and Scarborough, 1989
Scymnus loewii Mulsant, 1850	NO	*Solenopsis invicta* Buren, 1972 (Myrmicinae)	Sterling et al., 1979
Scymnus posticalis Sicard, 1913	NO	*Lasius niger* (Linnaeus, 1758) (Formicinae)	Kaneko, 2002; Kaneko, 2004
Scymnus sordidus Horn, 1895	NO	*Linepithema humile* (Mayr, 1868) (Dolichoderinae)	Bartlett, 1961
Scymnus Kugelann, 1794	YES	*Solenopsis invicta* Buren, 1972 (Myrmicinae)	Eubanks, 2001
	YES	*Linepithema humile* (Mayr, 1868) (Dolichoderinae)	Bartlett, 1961
Sticholotis ruficeps Weise, 1902	YES	*Pheidole megacephala* (Fabricius, 1793) (Myrmicinae)	Gonzalez-Hernandez et al., 1999b

Table 6.2. Studies evaluating the relationship between coccinellids, ant-tended insect herbivores, and the ant, *Pheidole megacephala*.

Lady Beetle Species Order Coleoptera Family Coccinellidae	Prey Species Order Hemiptera (Suborder, Family)	Host Plant Species (Family)	Location	Citation
Ants interfered with consumption of pests by coccinellids:				
Unidentified	*Dysmicoccus neobrevipes* Beardsley, 1959 (Sternorrhyncha, Pseudococcidae)	*Ananas comosus* (L.) Merr. (Bromeliaceae)	Hawaii, USA	Illingworth, 1931
Chilocorus angolensis Crotch *Exochomus flavipes* (Thunberg, 1781)	*Coccus hesperidum* Linnaeus, 1758 (Sternorrhyncha, Coccidae)	*Citrus sinensis* (L.) (Rutaceae)	South Africa	Anneke, 1959
Cryptolaemus montrouzieri Mulsant, 1853	*Planococcus citri* (Risso, 1913) (Sternorrhyncha, Pseudococcidae)	*Annona reticulate* L. (Annonaceae)	Queensland, Australia	Murray, 1982
Cryptolaemus montrouzieri Mulsant, 1853 *Azya orbigera* Mulsant, 1850	*Coccus viridis* (Green, 1889) (Sternorrhyncha, Coccidae)	*Pluchea indica* (L.) (Compositae)	Hawaii, USA	Bach, 1991
Curinus coeruleus (Mulsant, 1850)	*Dysmicoccus neobrevipes* Beardsley, 1959 (Sternorrhyncha, Pseudococcidae)	*Ananas comosus* (L.) Merr. (Bromeliaceae)	Hawaii, USA	Jahn, 1992
Exochomus troberti Mulsant, 1850	Phenacoccus manihoti Matile-Ferrero, 1977 (Sternorrhyncha, Coccidae)	*Manihot esculenta* Crantz (Euphorbiaceae)	Ghana	Cudjoe et al., 1993
Azya luteipes Mulsant, 1850	*Coccus viridis* (Green, 1889) (Sternorrhyncha, Coccidae)	*Coffea arabica* L. (Rubiaceae)	Hawaii, USA	Reimer et al., 1993
Nephus bilucernarius (Mulsant, 1850)	*Dysmicoccus brevipes* (Cockerell, 1893) (Sternorrhyncha, Pseudococcidae)	*Ananas comosus* (L.) Merr. (Bromeliaceae)	Hawaii, USA	Gonzalez-Hernandez et al., 1999a
Nephus bilucernarius (Mulsant, 1850) *Sticholotis ruficeps* Weise, 1902	*Dysmicoccus brevipes* (Cockerell, 1893) (Sternorrhyncha, Pseudococcidae) *Dysmicoccus neobrevipes* Beardsley, 1959 (Sternorrhyncha, Pseudococcidae)	*Ananas comosus* (L.) Merr. (Bromeliaceae)	Hawaii, USA	Gonzalez-Hernandez et al., 1999b
Ants and coccinellids utilized the same pest:				
Chilocorus cacti (Linnaeus, 1767)	*Aspidiotus aurantii* Maskell, 1879 (Sternorrhyncha, Diaspididae)	*Citrus* L. spp. (Rutaceae)	Swaziland	Catling, 1971
Hyperaspis Chevrolat in Dejean, 1837	*Hilda patruelis* (Stål, 1855) (Archaeorrhyncha, Tettigometridae)	groundnut crops	Zimbabwe	Weaving, 1980
Cheilomenes propinqua Mulsant *Cheilomenes lunata* (Fabricius 1775) *Exochomus flavipes* (Thunberg, 1781) *Hippodamia variegata* (Goeze, 1777) *Lioadalia flavomaculata* De Geer	*Cinara cronartii* Tissot and Pepper 1967 (Sternorrhyncha, Aphididae)	*Pinus* spp. (Pinaceae)	South Africa	Kfir et al., 1985
Cryptolaemus montrouzieri Mulsant, 1853	*Saccharicoccus sacchari* (Cockerell, 1895) (Sternorrhyncha, Pseudococcidae)	*Saccharum officinarum* L. (Poaceae)	Queensland, Australia	Carver et al., 1987
Orcus ovalis Blackburn, 1892	*Saccharicoccus sacchari* (Cockerell, 1895) (Sternorrhyncha, Pseudococcidae)	*Saccharum officinarum* L. (Poaceae)	Queensland, Australia	De Barro, 1990
Coelophora inaequalis (Fabricius, 1775) *Diomus notescens* (Blackburn, 1889) *Rhyzobius lophanthae* (Blaisdell, 1892)	*Pulvinaria urbicola* Cockerell, 1893 (Sternorrhyncha, Coccidae)	*Pisonia grandis* R. Br. (Nyctaginaceae)	Palmyra Atoll, Pacific Ocean	Handler et al., 2007

native scale insect that is destroying stands of *Pisonia grandis* R. Br., an important native tree; coccinellids present on the atoll have not been able to control the pest (Handler *et al*. 2007). On Coconut Island, Hawaii, *P. megacephala* removed all coccinellid larvae from plants where they tended the green scale, *Coccus viridis* (Green) (Bach 1991). However, because the plant, *Pluchea indica* (L.), is not native to Hawaii (Stone 1970), encouragement of prey populations by ants may be considered favorable, where damage to the plant is desirable.

All of the studies assessing relationships between coccinellids and *S. invicta* (Table 6.3) have been focused in agriculture in the southeastern United States, where the ant was introduced in the 1930s (Buren *et al*. 1974, Lofgren 1986). These studies report mixed findings. In the laboratory, coccinellid adults and larvae reduced prey in the absence of ants. But when ants were present, predation by coccinellids was reduced because ants killed the coccinellids (Vinson and Scarborough 1989). In pecan orchards, lady beetles were more abundant where ants were excluded, but only on certain sample dates (Dutcher *et al*. 1999). In cotton, ants reduced the numbers of *C. septempunctata* and *H. convergens* adults and larvae (Eubanks *et al*. 2002, Kaplan and Eubanks 2002, Kaplan and Eubanks 2005). Eubanks (2001) found that ant abundance was negatively correlated with numbers of coccinellids, aphids, leafhoppers, and treehoppers. Several other studies, however, failed to document interference by *S. invicta*. Sterling *et al*. (1979) documented early season control of *Aphis gossypii* Glover in cotton by *Scymnus loewii* Mulsant larvae regardless of whether ants were present undisturbed or reduced significantly by an insecticide (mirex). Clark and DeBarr (1996), found no differences in the numbers of prey or coccinellid with and without *S. invicta*. Although pests were

Table 6.3. Studies evaluating the relationship between coccinellids, ant-tended insect herbivores, and the ant, *Solenopsis invicta*.

Lady Beetle Species Order Coleoptera Family Coccinellidae	Prey Species Order Hemiptera (Suborder, Family)	Host Plant Species (Family)	Location	Citation
Ants interfered with consumption of pests by coccinellids:				
Hippodamia convergens Guérin-Méneville, 1842 *Scymnus louisianae* J. Chapin, 1973	*Aphis gossypii* Glover, 1877 (Sternorrhyncha, Aphididae)	*Gossypium hirsutum* L. (Malvaceae)	Texas, USA	Vinson and Scarborough, 1989
Coelophora inaequalis (Fabricius, 1775) *Cycloneda sanguinea limbifer* Casey, 1899	*Toxoptera citricida* (Kirkaldy, 1907) (Sternorrhyncha , Aphididae)	*Citrus* L. spp. (Rutaceae)	Puerto Rico	Michaud and Browing, 1999
Coccinella septempunctata Linnaeus, 1758 *Cycloneda sanguinea* (Linnaeus, 1763) *Harmonia axyridis* (Pallas, 1773) *Hippodamia convergens* Guérin-Méneville, 1842 *Olla v-nigrum* (Mulsant, 1866)	*Monellia caryella* Fitch 1855 (Aphis) (Sternorrhyncha, Aphididae)	*Carya illinoinensis* (Wangenh.) K. Koch (Juglandaceae)	Georgia and Alabama, USA	Dutcher et al., 1999
Harmonia axyridis (Pallas, 1773) *Hippodamia convergens* Guérin-Méneville, 1842	*Aphis craccivora* Koch, 1854 (Sternorrhyncha, Aphididae)	*Carya illinoinensis* (Wangenh.) K. Koch (Juglandaceae) *Vigna unguiculata* (L.) Walpers (Fabaceae)	Georgia and Alabama, USA	Dutcher et al., 1999
Coccinella septempunctata Linnaeus, 1758 *Coleomegilla maculata* (De Geer, 1775) *Harmonia axyridis* (Pallas, 1773) *Hippodamia convergens* Guérin-Méneville, 1842 *Scymnus* Kugelann, 1794 *Stethorus* Weise, 1885	Aphids (Sternorrhyncha, Superfamily Aphidoidea) Leafhoppers, treehoppers, froghoppers (Auchenorrhyncha; Cicadellidae, Membracidae, Cercopidae)	*Gossypium hirsutum* L. (Malvaceae) *Glycine max* (L.) Merr. (Fabaceae)	Alabama, USA	Eubanks, 2001
Coccinella septempunctata Linnaeus, 1758 *Hippodamia convergens* Guérin-Méneville, 1842	None	*Gossypium hirsutum* L. (Malvaceae)	Alabama, USA	Eubanks et al., 2002
Coccinella septempunctata Linnaeus, 1758 *Hippodamia convergens* Guérin-Méneville, 1842	*Aphis gossypii* Glover, 1877 (Sternorrhyncha, Aphididae)	*Gossypium hirsutum* L. (Malvaceae)	Alabama, USA	Kaplan and Eubanks, 2002
Coccinella septempunctata Linnaeus, 1758 *Hippodamia convergens* Guérin-Méneville, 1842	*Aphis gossypii* Glover, 1877 (Sternorrhyncha, Aphididae)	*Gossypium hirsutum* L. (Malvaceae)	Alabama, USA	Kaplan and Eubanks, 2005

Table 6.3 (Continued). Studies evaluating the relationship between coccinellids, ant-tended insect herbivores, and *Solenopsis invicta*.

Lady Beetle Species Order Coleoptera Family Coccinellidae	Prey Species Order Hemiptera (Suborder, Family)	Host Plant Species (Family)	Location	Citation
Ants did not interfere with consumption of pests by coccinellids:				
Coleomegilla maculata lengi Timberlake, 1943 *Cycloneda sanguinea* (Linnaeus, 1763) *Diomus terminatus* (Say, 1835) *Hippodamia convergens* Guérin-Méneville, 1842 *Olla v-nigrum* (Mulsant, 1866) *Scymnus* Kugelann, 1794 spp. *Scymnus loewii* Mulsant, 1850	*Aphis gossypii* Glover, 1877 (Sternorrhyncha, Aphididae)	*Gossypium hirsutum* L. (Malvaceae)	Texas, USA	Sterling et al., 1979
Hippodamia convergens Guérin-Méneville, 1842	*Monelliopsis pecanis* Bissell, 1983 (Sternorrhyncha, Aphididae) *Monellia caryella* Fitch 1855 (Aphis) (Sternorrhyncha, Aphididae) *Dysmicoccus morrisoni* (Hollinger, 1917) (Sternorrhyncha, Pseudococcidae)	*Carya* spp. (Juglandaceae)	Georgia, USA	Tedders et al., 1990
Chilocorus stigma (Say, 1835) *Coccinella septempunctata* Linnaeus, 1758 *Cycloneda munda* (Say, 1835) *Hippodamia convergens* Guérin-Méneville, 1842	*Toumeyella pini* King, 1901 (Sternorrhyncha, Coccidae) *Oracella acuta* Lobdell, 1930 (Sternorrhyncha, Pseudococcidae) Pseudophilippia quaintancii Cockerell, 1897 (Sternorrhyncha, Coccidae)	*Pinus taeda* L. (Pinaceae)	Georgia, USA	Clark and DeBarr, 1996
Coccinella Linnaeus, 1758 spp. *Coleomegilla* Timberlake, 1920 spp. *Hippodamia* Chevrolat in Dejean, 1837 spp. *Scymnus* Kugelann, 1794 spp.	*Aphis gossypii* Glover, 1877 (Sternorrhyncha, Aphididae)	*Gossypium hirsutum* L. (Malvaceae)	Texas, USA	Diaz Galarraga, 2003
Evidence inconclusive:				
Coleomegilla maculata (De Geer, 1775)	*Aphis gossypii* Glover, 1877 (Sternorrhyncha, Aphididae)	*Gossypium hirsutum* L. (Malvaceae)	Texas, USA	Reilly and Sterling, 1983
Ants and coccinellids utilized the same pest:				
Coccinella septempunctata Linnaeus, 1758 *Cycloneda* Crotch, 1871 *Hippodamia convergens* Guérin-Méneville, 1842 *Olla v-nigrum* (Mulsant, 1866) *Scymninae* Mulsant, 1846	*Aphis craccivora* Koch, 1854 (Sternorrhyncha, Aphididae)	*Vigna unguiculata* (L.) Walpers (Fabaceae)	Georgia, USA	Bugg and Dutcher, 1989
Coelophora inaequalis (Fabricius, 1775) *Cycloneda sanguinea limbifer* Casey, 1899 *Harmonia axyridis* (Pallas, 1773)	*Toxoptera citricida* (Kirkaldy, 1907) (Sternorrhyncha , Aphididae)	*Citrus* L. spp. (Rutaceae)	Puerto Rico and Florida, USA	Michaud, 1999

more abundant in association with ants, either coccinellid abundance was unaffected by the presence of ants (Diaz Galarraga 2003) or results were inconclusive due to low coccinellid densities (Reilly and Sterling 1983, Coppler *et al*. 2007).

Of the 27 evaluations of *L. humile* (Table 6.4), 14 documented interference with coccinellid predation and 9 documented a lack of interference. *Linepithema humile* attacked *C. montrouzieri* and *Hippodamia* sp., killing them or causing them to flee (Smith and Armitage 1931). In a different study, *C. montrouzieri* was more numerous with higher prey numbers, even in the presence of ants. Daane *et al*. (2007) concluded that adaptations in the coccinellids that mimicked prey facilitated predation, even in the presence of tending ants. Reproduction by *R. cardinalis* on prey tended and not tended by ants was the same, but it took longer for coccinellids to eliminate prey colonies that were tended by ants (Quezada and DeBach 1973). Several studies documented differences in coccinellid species preying on insects tended by *L. humile*. DeBach *et al*. (1951) reported that *Chilocorus* sp. Leach, numbers were five times greater on trees without ants compared to trees with ants. However, in the same system, *R. lophanthae* populations were twice as large on trees with ants. Bartlett (1961) reported that *L. humile* attacked all nine coccinellid species studied except *Scymnus sordidus* Horn.

Coccinellids commonly utilized as biological control agents were evaluated in 68% or 71 studies. For example, *C. montrouzieri* (Table 6.5) is often studied when its prey, often *Planococcus citri* (Risso), is tended by the Argentine ant, *L. humile*. Sometimes, *L. humile* interferes with pest management by *C. montrouzieri* (Bennett and Hughes 1959, Panis and Brun 1971, Raciti *et al*. 1997), but not always (Panis 1981, Danne *et al*. 2007). Many studies focus on the pests of a particular crop plant, such as

Table 6.4. Studies evaluating the relationship between coccinellids, ant-tended insect herbivores, and the ant, *Linepithema humile*.

Lady Beetle Species Order Coleoptera Family Coccinellidae	Prey Species Order Hemiptera (Suborder, Family)	Host Plant Species (Family)	Location	Citation
Ants interfered with consumption of pests by coccinellids:				
Cryptolaemus montrouzieri Mulsant, 1853	*Planococcus citri* (Risso, 1913) (Sternorrhyncha, Pseudococcidae) or *Pseudococcus citriculus* Green, 1922 (Sternorrhyncha, Pseudococcidae)	*Citrus* L. spp. (Rutaceae)	France	Poutiers, 1922
Cryptolaemus montrouzieri Mulsant, 1853	*Pseudococcus calceolariae* Maskell, 1879 (Sternorrhyncha, Pseudococcidae)	*Citrus* L. spp. (Rutaceae)	California, USA	Smith and Armitage, 1931
Cryptolaemus montrouzieri Mulsant, 1853 *Hippodamia* Chevrolat in Dejean, 1837	*Planococcus citri* (Risso, 1913) (Sternorrhyncha, Pseudococcidae)	*Citrus* L. spp. (Rutaceae)	California, USA	Smith and Armitage, 1931
Cryptolaemus montrouzieri Mulsant, 1853	*Planococcus citri* (Risso, 1913) (Sternorrhyncha, Pseudococcidae) or *Pseudococcus citriculus* Green, 1922 (Sternorrhyncha, Pseudococcidae)	*Citrus* L. spp. (Rutaceae)	South Africa Italy	Smit, 1934; Smit and Bishop, 1934 Costantino, 1935
Hyperaspis lateralis Mulsant, 1850 *Scymnus guttulatus* LeConte, 1852 *Scymnus nebulosus* LeConte, 1852 *Scymnus sordidus* Horn, 1895	*Planococcus citri* (Risso, 1913) (Sternorrhyncha, Pseudococcidae)	*Citrus* L. spp. (Rutaceae)	California, USA	Woglum, 1942
Chilocorus Leach, 1815	*Aspidiotus aurantii* Maskell, 1879 (Sternorrhyncha, Diaspididae)	*Citrus* × *limon* (L.) Burm.f. (Rutaceae)	California, USA	DeBach et al., 1951
Cryptolaemus montrouzieri Mulsant, 1853	*Pseudococcus longispinus* (Targioni-tozzetti, 1868) (Sternorrhyncha, Pseudococcidae)	*Cycas revoluta* Thunb. (Cycadaceae) *Nerium oleander* L. (Apocynaceae)	Bermuda	Bennett and Hughes, 1959
Chilocorus bipustulatus (Linnaeus, 1758) *Chilocorus hauseri* Weise, 1895 *Cryptolaemus montrouzieri* Mulsant, 1853 *Hippodamia convergens* Guérin-Méneville, 1842 *Rhyzobius lophanthae* (Blaisdell, 1892) *Rodolia cardinalis* (Mulsant, 1850)	None	None	California, USA	Bartlett, 1961
Rodolia cardinalis (Mulsant, 1850)	*Icerya purchasi* Maskell, 1878 (Sternorrhyncha, Margarodidae)	*Pittosporum tobira* (Pittosporaceae)	California, USA	Quezada and DeBach, 1973
Cryptolaemus montrouzieri Mulsant, 1853	*Planococcus citri* (Risso, 1913) (Sternorrhyncha, Pseudococcidae)	various ornamental plants	France	Panis and Brun, 1974
Adalia bipunctata (Linnaeus, 1758)	*Callipterinella callipterus* Hartig 1841 (Sternorrhyncha, Aphididae) *Euceraphis betulae* Koch 1855 (Sternorrhyncha, Aphididae) *Betulaphis brevipilosa* Börner 1940 (Sternorrhyncha, Aphididae)	*Betula pendula* Roth (Betulaceae)	California, USA	Hajek and Dahlsten, 1988
Cryptolaemus montrouzieri Mulsant, 1853	*Planococcus citri* (Risso, 1913) (Sternorrhyncha, Pseudococcidae)	*Citrus* L. spp. (Rutaceae)	Sicily	Raciti et al., 1997
Unidentified	*Aphis coreopsidis* Thomas 1878 (Sternorrhyncha, Aphididae)	*Baccharis halimifolia* Linnaeus (Asteraceae)	Florida, USA	Altfeld and Stiling, 2006

Table 6.4 (Continued). Studies evaluating the relationship between coccinellids, ant-tended insects, and *Linepithema humile*.

Lady Beetle Species Order Coleoptera Family Coccinellidae	Prey Species Order Hemiptera (Suborder, Family)	Host Plant Species (Family)	Location	Citation
Ants did not interfere with consumption of pests by coccinellids:				
Cryptolaemus montrouzieri Mulsant, 1853	*Planococcus citri* (Risso, 1913) (Sternorrhyncha, Pseudococcidae) or *Pseudococcus citriculus* Green, 1922 (Sternorrhyncha, Pseudococcidae)	*Citrus* L. spp. (Rutaceae)	South Africa	Bishop, 1931
Rhyzobius lophanthae (Blaisdell, 1892)	*Aspidiotus aurantii* Maskell, 1879 (Sternorrhyncha, Diaspididae)	*Citrus* × *limon* (L.) Burm.f. (Rutaceae)	California, USA	DeBach et al., 1951
Rodolia cardinalis (Mulsant, 1850)	*Icerya purchasi* Maskell, 1878 (Sternorrhyncha, Margarodidae)	*Citrus* L. spp. (Rutaceae)	Bermuda	Bennett and Hughes, 1959
Scymnus sordidus Horn, 1895	None	None	California, USA	Bartlett, 1961
Rodolia cardinalis (Mulsant, 1850)	*Icerya purchasi* Maskell, 1878 (Sternorrhyncha, Margarodidae)	*Pittosporum tobira* (Pittosporaceae)	California, USA	Quezada and DeBach, 1973
Cryptolaemus montrouzieri Mulsant, 1853	*Planococcus citri* (Risso, 1913) (Sternorrhyncha, Pseudococcidae)	*Citrus* L. spp. (Rutaceae)	France	Panis, 1981
Brumus quadripustulatus (Linnaeus, 1758) *Chilocorus bipustulatus* (Linnaeus, 1758)	*Saissetia coffeae* (Walker, 1852) (Sternorrhyncha, Pseudococcidae)	*Ficus carica* L. (Moraceae)	Italy	Monaco and D'Abbicco, 1987
Cryptolaemus montrouzieri Mulsant, 1853	*Pseudococcus viburni* Signoret, 1875 (Sternorrhyncha, Pseudococcidae) *Pseudococcus maritimus* Ehrhorn, 1900 (Sternorrhyncha, Pseudococcidae)	*Vitis* spp. (Vitaceae)	California, USA	Daane et al., 2007
Unidentified	*Aphis coreopsidis* Thomas 1878 (Sternorrhyncha, Aphididae)	*Baccharis halimifolia* Linnaeus (Asteraceae)	Florida, USA	Altfeld and Stiling, 2006, 2008
Evidence inconclusive:				
Cryptolaemus montrouzieri Mulsant, 1853 *Scymnus* Kugelann, 1794	*Pseudococcus longispinus* (Targioni-tozzetti, 1868) (Sternorrhyncha, Pseudococcidae)	*Persea americana* Mill. (Lauraceae)	Israel	Swirski et al., 1980
Ants and coccinellids utilized the same pest:				
Cryptolaemus montrouzieri Mulsant, 1853	*Saccharicoccus sacchari* (Cockerell, 1895) (Sternorrhyncha, Pseudococcidae)	*Saccharum officinarum* L. (Poaceae)	Queensland, Australia	Carver et al., 1987
Hippodamia convergens Guérin-Méneville, 1842	*Aphis nerii* Fonscolombe, 1841 (Sternorrhyncha, Aphididae)	*Nerium oleander* L. (Apocynaceae)	California, USA	Bristow, 1991
Eriopis connexa Germar, 1824 *Hippodamia variegata* (Goeze, 1777)	*Pseudococcus viburni* Signoret, 1875 (Sternorrhyncha, Pseudococcidae)	*Vitis vinifera* (Vitaceae) *Pyrus* L. and *Prunus* L. sp. (Rosaceae)	Chile	Curkovic et al., 1995

Table 6.5. Studies evaluating the relationship between ants, ant-tended insect herbivores (prey), and the coccinellid, *Cryptolaemus montrouzieri*.

Prey Species Order Hemiptera (Suborder, Family)	Host Plant Species (Family)	Ant Species Order Hymenoptera Family Formicidae (Subfamily)	Location	Citation
Ants interfered with consumption of pests by coccinellids:				
Planoococcus kenyae Le Pelley, 1935	*Coffea* L. (Rubiaceae)	*Pheidole punctulata* Mayr, 1866	Kenya	Kirkpatrick, 1927
Planococcus citri (Risso, 1913) (Sternorrhyncha, Pseudococcidae) or *Pseudococcus citriculus* Green, 1922 (Sternorrhyncha, Pseudococcidae)	*Citrus* L. spp. (Rutaceae)	*Linepithema humile* (Mayr, 1868) (Dolichoderinae)	France	Poutiers, 1922
Pseudococcus calceolariae Maskell, 1879 (Sternorrhyncha, Pseudococcidae)	*Citrus* L. spp. (Rutaceae)	*Linepithema humile* (Mayr, 1868) (Dolichoderinae)	California, USA	Smith and Armitage, 1931
Planococcus citri (Risso, 1913) (Sternorrhyncha, Pseudococcidae) or *Pseudococcus citriculus* Green, 1922 (Sternorrhyncha, Pseudococcidae)	*Citrus* L. spp. (Rutaceae)	*Linepithema humile* (Mayr, 1868) (Dolichoderinae)	France South Africa Italy	Poutiers, 1922 Smit, 1934; Smit and Bishop, 1934 Costantino, 1935
Pseudococcus longispinus (Targioni-tozzetti, 1868) (Sternorrhyncha, Pseudococcidae)	*Cycas revolute* Thunb. (Cycadaceae) *Nerium oleander* L. (Apocynaceae)	*Linepithema humile* (Mayr, 1868) (Dolichoderinae)	Bermuda	Bennett and Hughes, 1959
Planococcus citri (Risso, 1913) (Sternorrhyncha, Pseudococcidae)	ornamental plants	*Linepithema humile* (Mayr, 1868) (Dolichoderinae)	France	Panis and Brun, 1974
Planococcus citri (Risso, 1913) (Sternorrhyncha, Pseudococcidae)	*Annona reticulate* L. (Annonaceae)	*Pheidole megacephala* (Fabricius, 1793) (Myrmicinae)	Queensland, Australia	Murray, 1982
Planococcus citri (Risso, 1913) (Sternorrhyncha, Pseudococcidae)	*Citrus* L. spp. (Rutaceae)	*Linepithema humile* (Mayr, 1868) (Dolichoderinae)	Sicily	Raciti et al., 1997
Planococcus citri (Risso, 1913) (Sternorrhyncha, Pseudococcidae) *Planococcus lilacinus* Cockerell, 1905 (Sternorrhyncha, Pseudococcidae) *Planococcus minor* Maskell, 1897 (Sternorrhyncha, Pseudococcidae)	*Coffea* L. (Rubiaceae)	Formicidae	India	Reddy and Seetharama, 1997
Saccharicoccus sacchari (Cockerell, 1895) (Sternorrhyncha, Pseudococcidae)	*Saccharum* L. (Poaceae)	*Camponotus compressus* (Fabricius, 1787) (Formicinae)	India	Srikanth et al., 2001

Table 6.5 (Continued). Studies evaluating the relationship between ants, ant-tended insects, and the coccinellid, *Cryptolaemus montrouzieri*.

Prey Species Order Hemiptera (Suborder, Family)	Host Plant Species (Family)	Ant Species Order Hymenoptera Family Formicidae (Subfamily)	Location	Citation
Ants did not interfere with consumption of pests by coccinellids:				
Planococcus citri (Risso, 1913) (Sternorrhyncha, Pseudococcidae) or *Pseudococcus citriculus* Green, 1922 (Sternorrhyncha, Pseudococcidae)	*Citrus* L. spp. (Rutaceae)	*Linepithema humile* (Mayr, 1868) (Dolichoderinae)	South Africa	Bishop, 1931
Planococcus citri (Risso, 1913) (Sternorrhyncha, Pseudococcidae)	*Citrus* L. spp. (Rutaceae)	*Anoplolepis custodiens* (Smith, 1858) (Formicinae)	South Africa	Steyn, 1954
Planococcus citri (Risso, 1913) (Sternorrhyncha, Pseudococcidae)	*Citrus* L. spp. (Rutaceae)	*Linepithema humile* (Mayr, 1868) (Dolichoderinae)	France	Panis, 1981
Pulvinaria urbicola Cockerell, 1893 (Sternorrhyncha, Coccidae)	*Pisonia grandis* R. Br. (Nyctaginaceae)	*Tetramorium bicarinatum* (Nylander, 1846) (Myrmicinae)	Coringa Herald Group, Australia	Smith et al., 2004
Pseudococcus viburni Signoret, 1875 (Sternorrhyncha, Pseudococcidae) *Pseudococcus maritimus* Ehrhorn, 1900 (Sternorrhyncha, Pseudococcidae)	*Vitis* spp. (Vitaceae)	*Linepithema humile* (Mayr, 1868) (Dolichoderinae)	California, USA	Daane et al., 2007
Evidence inconclusive:				
Pulvinariella mesembryanthemi Vallot, 1829 (Sternorrhyncha, Coccidae)	*Carpobrotus edulis* (Aizoaceae)	*Crematogaster* Lund, 1831 (Myrmicinae) *Iridomyrmex* Mayr, 1862 (Dolichoderinae)	Western Australia	Collins and Scott, 1982
Planococcus citri (Risso, 1913) (Sternorrhyncha, Pseudococcidae)	*Citrus* L. spp. (Rutaceae)	Unidentified	Spain	Villalba et al., 2006
Ants and coccinellids utilized the same pest:				
Saccharicoccus sacchari (Cockerell, 1895) (Sternorrhyncha, Pseudococcidae)	*Saccharum officinarum* L. (Poaceae)	*Paratrechina* Motschoulsky, 1863 (Formicinae) spp. *Camponotus* Mayr, 1861 (Formicinae) *Tetramorium bicarinatum* (Nylander, 1846) (Myrmicinae) *Pheidole megacephala* (Fabricius, 1793) (Myrmicinae) *Iridomyrmex* Mayr, 1862 (sp. not humilis) (Dolichoderinae)	Queensland, Australia	Carver et al., 1987
Pulvinaria psidii Maskell, 1895 (Sternorrhyncha, Coccidae)	*Psidium* L. (Myrtaceae)	*Camponotus compressus* (Fabricius, 1787) (Formicinae)	Karnataka, India	Verghese and Ramachander, 1998

citrus, which is the focus of 25 of the 105 studies (Table 6.6).

Studies on islands (Table 6.7) document different assemblages compared with the continental studies, in which three invasive ant species dominate the literature (with the exception of *P. megacephala* in Hawaii and Palmyra Atoll (Table 6.2), *S. invicta* in Puerto Rico (Table 6.3), and *L. humile* in Bermuda and Sicily (Table 6.4)). The effects of the non-native *L. niger* on pests of citrus, peaches, and beans have been documented for Japan, where only *Scymnus posticalis* Sicard can consume ant-tended pests (Kaneko 2002, Kaneko 2004). The ants interfere with predation by the native *C. septempunctata* (Katayama and Suzuki 2003), *H. axyridis* (Kaneko 2002, Kaneko 2004) and other coccinellids (Shiga 1975, Itioka and Inoue 1996). In the Seychelles, *Technomyrmex* sp. interfered with scale predation by *R. cardinalis* and *Rodolia chermesina* Mulsant when these predators acted alone, but together they controlled the ant-tended pest (Vesey-Fitzgerald 1953). *Pisonia grandis* Robert Brown (Nyctaginaceae) is a forest tree native to the Coringa Herald Group in the Coral Sea, where it provides valuable habitat to seabirds; the exotic scale *Pulvinaria urbicola* Cockerell threatened the population of *P. grandis* on the Coringa Herald Group in the Coral Sea until *C. montrouzieri* was introduced (Smith *et al*. 2004).

Ant attendance increased prey populations in 22% of studies (Illingworth 1931, DeBach *et al*. 1951, Anneke 1959, Hamid *et al*. 1977, Collins and Scott 1982, Murray 1982, Samways 1983, Kreiter and Iperti 1986, Rü *et al*. 1990, Cudjoe *et al*. 1993, Reimer *et al*. 1993, Itioka and Inoue 1996, Stechmann *et al*. 1996, Verghese and Ramachander 1998, Chai 1999, Kaneko 2002, Kaplan and Eubanks 2002, Diaz Galarraga 2003, Kaneko 2004, Smith *et al*. 2004, Altfeld and Stiling 2006, Coppler *et al*. 2007, Daane *et al*. 2007).

Table 6.6. Studies evaluating the relationship between coccinellids, ant-tended insect herbivores (prey), and ants, in *Citrus* sp.

Prey Species Order Hemiptera (Suborder, Family)	Lady Beetle Species Order Coleoptera Family Coccinellidae	Ant Species Order Hymenoptera Family Formicidae (Subfamily)	Ant Interference?	Location	Citation
Aphis gossypii Glover, 1877 (Sternorrhyncha, Aphididae)	*Harmonia axyridis* (Pallas, 1773)	*Lasius niger* (Linnaeus, 1758) (Formicinae)	Yes	Japan	Kaneko, 2002; Kaneko, 2004
	Scymnus posticalis Sicard, 1913	*Lasius niger* (Linnaeus, 1758) (Formicinae)	No	Japan	Kaneko, 2002; Kaneko, 2004
Aspidiotus aurantii Maskell, 1879 (Sternorrhyncha, Diaspididae)	*Chilocorus* Leach, 1815	*Linepithema humile* (Mayr, 1868) (Dolichoderinae)	Yes	California, USA	DeBach et al., 1951
	Coccinella transversalis Fabricius, 1781 *Cryptolaemus montrouzieri* Mulsant, 1853 *Diomus notescens* (Blackburn, 1889) *Orcus australasiae* (Boisduval, 1835) *Rhyzobius lophanthae* (Blaisdell, 1892) *Stethorus nigripes* Kapur, 1948 *Stethorus* Weise, 1885 *Stethorus vagans* (Blackburn)	*Iridomyrmex rufoniger* (Lowne, 1865) (Dolichoderinae)	Yes	New South Wales, Australia	James et al., 1999
	Rhyzobius lophanthae (Blaisdell, 1892)	*Linepithema humile* (Mayr, 1868) (Dolichoderinae)	No	California, USA	DeBach et al., 1951
	Chilocorus distigma Klug, 1835	*Anoplolepis custodiens* (Smith, 1858) (Formicinae)	No	South Africa	Steyn, 1954
Coccus hesperidum Linnaeus, 1758 (Sternorrhyncha, Coccidae)	*Chilocorus angolensis* Crotch *Exochomus flavipes* (Thunberg, 1781)	*Pheidole megacephala* (Fabricius, 1793) (Myrmicinae)	Yes	South Africa	Anneke, 1959
	Rhyzobius Stephens, 1829	*Iridomyrmex rufoniger* (Lowne, 1865) (Dolichoderinae)	Yes	New South Wales, Australia	Snowball and Milne, 1973; Milne, 1974
	Coccinella transversalis Fabricius, 1781 *Cryptolaemus montrouzieri* Mulsant, 1853 *Diomus notescens* (Blackburn, 1889) *Orcus australasiae* (Boisduval, 1835) *Rhyzobius lophanthae* (Blaisdell, 1892) *Stethorus nigripes* Kapur, 1948 *Stethorus* Weise, 1885 *Stethorus vagans* (Blackburn)	*Iridomyrmex rufoniger* (Lowne, 1865) (Dolichoderinae)	Yes	New South Wales, Australia	James et al., 1999
Icerya purchasi Maskell, 1878 (Sternorrhyncha, Margarodidae)	*Cryptolaemus montrouzieri* Mulsant, 1853 *Rodolia iceryae* Janson, 1887	*Anoplolepis custodiens* (Smith, 1858) (Formicinae)	Yes	South Africa	Steyn, 1954
	Rodolia cardinalis (Mulsant, 1850)	*Myrmecocystus mimicus* Wheeler, 1908 (Formicinae) Solenopsis xyloni McCook (Myrmicinae)	Yes	California, USA	Quezada and DeBach, 1973
	Rodolia cardinalis (Mulsant, 1850)	*Linepithema humile* (Mayr, 1868) (Dolichoderinae)	No	Bermuda	Bennett and Hughes, 1959

Table 6.6 (Continued). Studies evaluating the relationship between coccinellids, ant-tended insects, and ants, in *Citrus* sp.

Prey Species Order Hemiptera (Suborder, Family)	Lady Beetle Species Order Coleoptera Family Coccinellidae	Ant Species Order Hymenoptera Family Formicidae (Subfamily)	Ant Interference?	Location	Citation
Icerya seychellarum seychellarum Westwood, 1855 (Sternorrhyncha, Margarodidae)	*Rodolia cardinalis* (Mulsant, 1850)	*Technomyrmex* Mayr, 1872 (Dolichoderinae)	No	Seychelles	Vesey-Fitzgerald, 1953
Planococcus citri (Risso, 1913) (Sternorrhyncha, Pseudococcidae)	*Cryptolaemus montrouzieri* Mulsant, 1853 *Hippodamia* Chevrolat in Dejean, 1837	*Linepithema humile* (Mayr, 1868) (Dolichoderinae)	Yes	California, USA	Smith and Armitage, 1931
	Hyperaspis lateralis Mulsant, 1850 *Scymnus sordidus* Horn, 1895 *Scymnus guttulatus* LeConte, 1852 *Scymnus nebulosus* LeConte, 1852	*Linepithema humile* (Mayr, 1868) (Dolichoderinae)	Yes	California, USA	Woglum, 1942
	Cryptolaemus montrouzieri Mulsant, 1853	*Linepithema humile* (Mayr, 1868) (Dolichoderinae)	Yes	Sicily	Raciti et al., 1997
	Cryptolaemus montrouzieri Mulsant, 1853	*Anoplolepis custodiens* (Smith, 1858) (Formicinae)	No	South Africa	Steyn, 1954
	Cryptolaemus montrouzieri Mulsant, 1853	*Linepithema humile* (Mayr, 1868) (Dolichoderinae)	No	France	Panis, 1981
Planococcus citri (Risso, 1913) (Sternorrhyncha, Pseudococcidae) or *Pseudococcus citriculus* Green, 1922 (Sternorrhyncha, Pseudococcidae)	*Cryptolaemus montrouzieri* Mulsant, 1853	*Linepithema humile* (Mayr, 1868) (Dolichoderinae)	Yes	France	Poutiers, 1922
				South Africa	Smit, 1934; Smit and Bishop, 1934
				Italy	Costantino, 1935
			No	South Africa	Bishop, 1931
Pseudococcus calceolariae Maskell, 1879 (Sternorrhyncha, Pseudococcidae)	*Cryptolaemus montrouzieri* Mulsant, 1853	*Linepithema humile* (Mayr, 1868) (Dolichoderinae)	Yes	California, USA	Smith and Armitage, 1931
Pseudococcus citriculus Green, 1922 (Sternorrhyncha, Pseudococcidae)	*Chilocorus kuwanae* Silvestri, 1909	*Lasius niger* (Linnaeus, 1758) (Formicinae)	Yes	Japan	Itioka and Inoue, 1996
Saissetia oleae (Olivier, 1791) (Sternorrhyncha, Coccidae)	*Rhyzobius* Stephens, 1829	*Iridomyrmex rufoniger* (Lowne, 1865) (Dolichoderinae)	Yes	New South Wales, Australia	Snowball and Milne, 1973; Milne, 1974
Toxoptera citricida (Kirkaldy, 1907) (Sternorrhyncha , Aphididae)	*Coelophora inaequalis* (Fabricius, 1775) *Cycloneda sanguinea limbifer* Casey, 1899	*Solenopsis invicta* Buren, 1972 (Myrmicinae)	Yes	Puerto Rico	Michaud and Browing, 1999

Table 6.7. Studies evaluating the relationship between coccinellids, ant-tended insect herbivores (prey), and ants on islands, with the exception of Hawaii and Palmyra Atoll, which are included in Table 5.1; Puerto Rico, which is included in Table 5.2; and Bermuda and Sicily, which are included in Table 5.3.

Lady Beetle Species Order Coleoptera Family Coccinellidae	Prey Species Order Hemiptera (Suborder, Family)	Host Plant Species (Family)	Ant Species Order Hymenoptera Family Formicidae (Subfamily)	Ant Interference?	Citation
Coringa Herald Group, Coral Sea, Australia					
Cryptolaemus montrouzieri Mulsant, 1853	*Pulvinaria urbicola* Cockerell, 1893 (Sternorrhyncha, Coccidae)	*Pisonia grandis* R. Br. (Nyctaginaceae)	*Tetramorium bicarinatum* (Nylander, 1846) (Myrmicinae)	No	Smith et al., 2004
Tongatapu Island, Kingdom of Tonga, Southwest Pacific					
Unidentified	*Pentalonia nigronervosa* Coquerel, 1859 (Sternorrhyncha, Aphididae)	*Musa x paradisiacal* (Musaceae)	*Pheidole oceanica* Mayr, 1866 (Myrmicinae) *Technomyrmex albipes* (Smith, 1861) (Dolichoderinae) *Tapinoma melanocephalum* (Fabricius, 1793) (Dolichoderinae)	Yes	Stechmann et al. 1996
Phillipines					
Menochilus sexmaculatus (Fabricius, 1781) *Scymnus* Kugelann, 1794	*Cerataphis palmae* (Ghesquiere, 1934) (Sternorrhyncha, Aphididae) *Aspidiotus destructor* Signoret, 1869 (Sternorrhyncha, Diaspididae) *Astegopteryx* Karsch 1890 (Sternorrhyncha, Hormaphididae)	*Cocos nucifera* (Arecaceae) *Cyrtostachys lakka* (Arecaceae)	*Oecophylla smaragdina* (Fabricius, 1775) (Formicinae)	NA - Shared	Sumalde and Calilung, 1982
Japan					
Scymnus ferrugatus Moll, 1785 *Scymnus ishidai* Araki, 1963	*Myzus persicae* (Sulzer, 1776) (Sternorrhyncha, Aphididae) *Hyalopterus amygdali* Blanchard 1840 (Sternorrhyncha, Aphididae)	*Prunus persica* (L.) Batsch (Rosaceae)	*Formica japonica* Motschoulsky, 1866 (Formicinae) *Lasius niger* (Linnaeus, 1758) (Formicinae) *Pristomyrmex pungens* Mayr, 1866 (Myrmicinae)	Yes	Shiga, 1975
Chilocorus kuwanae Silvestri, 1909	*Pseudococcus citriculus* Green, 1922 (Sternorrhyncha, Pseudococcidae)	*Citrus unshiu* Marc. (Rutaceae)	*Lasius niger* (Linnaeus, 1758) (Formicinae)	Yes	Itioka and Inoue, 1996
Harmonia axyridis (Pallas, 1773)	*Aphis gossypii* Glover, 1877 (Sternorrhyncha, Aphididae)	*Citrus reticulate* Blanco (Rutaceae)	*Lasius niger* (Linnaeus, 1758) (Formicinae)	Yes	Kaneko, 2002; Kaneko, 2004
Scymnus posticalis Sicard, 1913	*Aphis gossypii* Glover, 1877 (Sternorrhyncha, Aphididae)	*Citrus reticulate* Blanco (Rutaceae)	*Lasius niger* (Linnaeus, 1758) (Formicinae)	No	Kaneko, 2002; Kaneko, 2004
Coccinella septempunctata Linnaeus, 1758	*Aphis craccivora* Koch, 1854 (Sternorrhyncha, Aphididae)	*Vicia faba* (Fabaceae)	*Lasius niger* (Linnaeus, 1758) (Formicinae) *Tetramorium caespitum* (Linnaeus, 1758) (Myrmicinae)	Yes	Katayama and Suzuki, 2003

Table 6.7 (Continued). Studies evaluating the relationship between coccinellids, ant-tended insects, and ants on islands.

Lady Beetle Species Order Coleoptera Family Coccinellidae	Prey Species Order Hemiptera (Suborder, Family)	Host Plant Species (Family)	Ant Species Order Hymenoptera Family Formicidae (Subfamily)	Ant Interference?	Citation
Seychelles					
Rodolia chermesina Mulsant, 1850	*Icerya seychellarum seychellarum* Westwood, 1855 (Sternorrhyncha, Margarodidae)	*Cocos nucifera* (Arecaceae)	*Technomyrmex detorquens* (Walker, 1859) (Dolichoderinae)	Yes	Dupont, 1931
Chilocorus distigma Klug, 1835 *Exochomus ventralis* (Gerst.) *Exochomus flavipes* (Thunberg, 1781)	*Icerya seychellarum seychellarum* Westwood, 1855 (Sternorrhyncha, Margarodidae)	variety	*Technomyrmex detorquens* (Walker, 1859) (Dolichoderinae)	No	Vesey-Fitzgerald, 1939
Chilocorus nigritus Fabricius, 1798	*Eucalymnatus tessellatus* Signoret, 1873 (Sternorrhyncha, Coccidae)	*Cocos nucifera* (Arecaceae)	*Technomyrmex* Mayr, 1872 (Dolichoderinae)	No	Vesey-Fitzgerald, 1941
Exochomus spp.Redtenbacher, 1843	*Milviscutulus mangiferae* Green, 1889 (Sternorrhyncha, Coccidae)	*Cinnamomum verum* J.Presl (Lauraceae) *Mangifera* L. sp. (Anacardiaceae)	*Technomyrmex* Mayr, 1872 (Dolichoderinae)	Yes	Vesey-Fitzgerald, 1953
Rodolia chermesina Mulsant, 1850	*Icerya seychellarum seychellarum* Westwood, 1855 (Sternorrhyncha, Margarodidae)	Fruit and timber trees	*Technomyrmex* Mayr, 1872 (Dolichoderinae)	Yes	Vesey-Fitzgerald, 1953
Chilocorus nigritus Fabricius, 1798 *Chilocorus distigma* Klug, 1835 *Rodolia chermesina* Mulsant, 1850 *Rodolia cardinalis* (Mulsant, 1850) *Exochomus flavipes* (Thunberg, 1781)	*Chrysomphalus dictyospermi* (Morgan, 1889) (Sternorrhyncha, Diaspididae) *Parthenolecanium persicae persicae* Fabricius, 1776 (Sternorrhyncha, Coccidae) *Protopulvinaria pyriformis* Cockerell, 1894 (Sternorrhyncha, Coccidae)	*Cocos nucifera* (Arecaceae) *Psidium* L. (Myrtaceae) *Cinnamomum verum* J.Presl (Lauraceae)	*Technomyrmex* Mayr, 1872 (Dolichoderinae)	Yes	Vesey-Fitzgerald, 1953
Chilocorus nigritus Fabricius, 1798	*Pinnaspis buxi* (Bouche, 1851) (Sternorrhyncha, Diaspididae)	*Cocos nucifera* (Arecaceae)	*Technomyrmex* Mayr, 1872 (Dolichoderinae)	No	Vesey-Fitzgerald, 1953
Rodolia cardinalis (Mulsant, 1850) *Rodolia chermesina* Mulsant, 1850	*Icerya seychellarum seychellarum* Westwood, 1855 (Sternorrhyncha, Margarodidae)	*Casuarina* L. sp. (Casuarinaceae) *Citrus* L. sp. (Rutaceae) *Persea americana* Mill. (Lauraceae) *Artocarpus heterophyllus* Lam. (Moraceae)	*Technomyrmex* Mayr, 1872 (Dolichoderinae)	No	Vesey-Fitzgerald, 1953

Coccinellids were more abundant, more successful preying on herbivores, or met with less aggression from ants when the ratio of ants to prey decreased (DeBach *et al.* 1951, Itioka and Inoue 1996, Altfleld and Stiling 2006, 2008, Daane *et al.* 2007, Harmon and Andow 2007). Harmon and Andow (2007) showed that *L. niger* was better at deterring coccinellids from *Aphis fabae* Scopoli when the ratio of ants to aphids was high. With a greater relative number of ants, more ants moved to the perimeter of the colony where they detected intruders and protected the aphids more effectively. As the ratio decreased, a greater percentage of ants accompanied the colony compared to the perimeter, allowing predators to approach met with less aggression, and have greater foraging success. An exception to this was documented by Philpott (1997), where aggression of ants towards coccinellids was greater amidst more prey.

In 12% of studies, comparisons were made among several non-native coccinellids or among native and non-native coccinellids (Bennett and Hughes 1959, Bartlett 1961, Bugg and Ellis 1990, Reimer *et al.* 1993, Philpott 1997, Dutcher *et al.* 1999, Gonzalez-Hernandez *et al.* 1999b, Michaud 1999, Michaud and Browning 1999, Eubanks 2001, Wimp and Whitham 2001, Harmon and Andow 2007, Burgio *et al.* 2008). In Italy, Burgio *et al.* (2008) found that eggs of *A. bipunctata* (native) were consumed, presumably by ants, more than eggs of *H. axyridis* (non-native). Dutcher *et al.* (1999) found that *H. axyridis* (non-native) was less affected by fire ant (*S. invicta*) aggression than *H. convergens* (native). Ants bit and stung both species equally, ignoring some *H. convergens* individuals, but never *H. axyridis*. *Harmonia axyridis* remained on plants to a greater extent than *H. convergens* by biting ants, reflex bleeding, and exhibiting thanatosis. Philpott (1997) found that among native and non-native coccinellids, *C.*

septempunctata (non-native) fed the most and *H. axyridis* (non-native) the least with the ant, *Formica obscuripes* Forel, compared with the native species, *Coccinella novemnotata* Herbst, *Coccinella transversoguttata* Falderman, *Cycloneda polita* Casey, and *H. convergens*. However, while *C. septempunctata* received the second highest amount of aggression from ants, *H. axyridis* received the least. In Utah, *C. septempunctata* (non-native) was common on trees with and without ants and prey; however, *A. bipunctata* (native) was only found on trees devoid of ants and prey (Wimp and Whitman 2001). In cotton, Eubanks (2001) found that numbers of native (*C. maculata* and *H. convergens*) and non-native (*C. septempunctata* and *H. axyridis*) coccinellids were negatively correlated with ants.

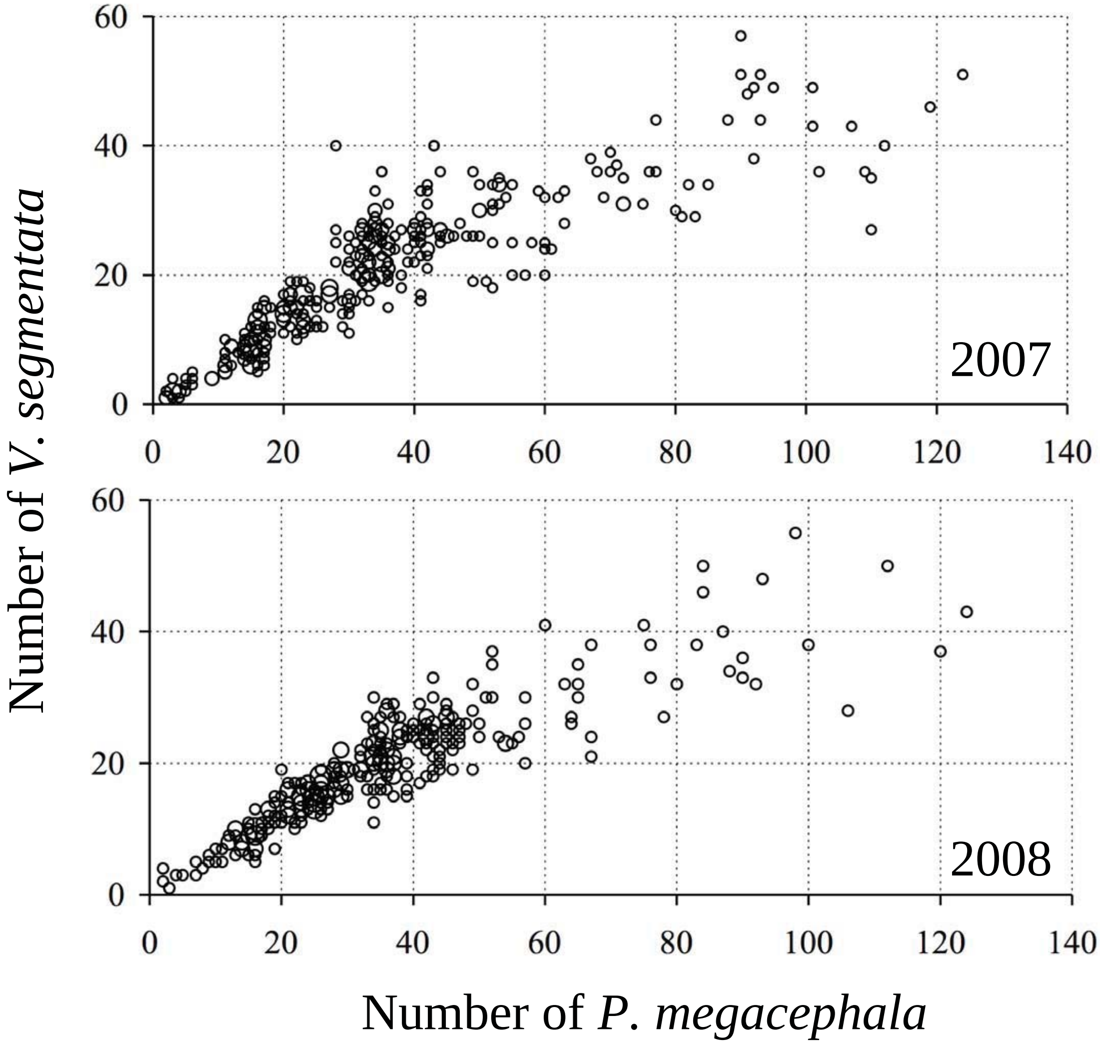
Midway Atoll Survey

Out of 1,062 stems examined in 2007 (Table 6.8), the ant *P. megacephala* was observed on 348 stems (mean ± SEM (throughout) = 35.00 ± 1.31 individuals per stem), the treehopper *V. segmentata* on 353 stems (19.97 ± 0.62 per stem), and the coccinellid *C. inaequalis* on 56 stems (1.14 ± 0.05 per stem). Of the 1,116 stems examined in 2008, *P. megacephala* was documented on 316 stems (35.00 ± 1.14 per stem), *V. segmentata* on 320 stems (18.96 ± 0.52 per stem), and *C. inaequalis* on 72 stems (1.11 ± 0.04 per stem). *Pheidole megacephala* and *V. segmentata* were found together on 334 stems (2007) and 308 stems (2008). There was a strong positive correlation (Figure 6.2) between numbers of *P. megacephala* and *V. segmentata* in 2007 ($r^2 = 0.9872$, $P < 0.0001$) and in 2008 ($r^2 = 0.8649$, $P < 0.0001$). There were no positive or negative correlations found of C. inaequalis numbers per stem with *P. megacephala* or with *V. segmentata* in 2007 or 2008.

Table 6.8. Total number of stems examined; number of stems on which *P. megacephala*, *V. segmentata*, and *C. inaequalis* were documented; number of stems on which combinations of these three species were documented together; mean (± standard error) number of individuals per stem; and correlations between pairs of species.

# stems	*P. megacephala*		*V. segmentata*		*C. inaequalis*		Correlation	
	Mean	SE	Mean	SE	Mean	SE	r	p-value
2007 - Total Number of Stems Examined = 1062								
348	35.00	1.3102						
353			19.97	0.6233				
56					1.14	0.0472		
334	36.34	1.3142	20.99	0.6129			0.8662	<0.0001
46	42.37	3.8166			1.13	0.0502	0.1885	0.5862
45			29.53	1.9953	1.13	0.0512	0.2707	0.3171
45	43.29	3.7875	29.53	1.9953	1.13	0.0512		
2008 - Total Number of Stems Examined = 1116								
316	35.00	1.1414						
320			18.96	0.5222				
72					1.11	0.0373		
308	35.77	1.1360	19.65	0.5034			0.8823	<0.0001
66	38.21	2.5315			1.11	0.0382	0.2689	0.4208
66			23.32	1.3022	1.11	0.0382	0.3505	0.3902
66	38.21	2.5315	23.32	1.3022	1.11	0.0382		

Figure 6.2. Number of *V. segmentata* found on *V. encelioides* stems with *P. megacephala* on Eastern Island, Midway Atoll, in 2007 and 2008.



Multiple regressions showed that there was a positive relationship between coccinellid numbers and treehopper abundance in 2007 (slope = 0.38, $r^2 = 0.13$, df = 333, $P < 0.0001$) and in 2008 (slope = 0.55, $r^2 = 0.11$, df = 307, $P < 0.0001$). So, with ant numbers held constant, the number of coccinellids increased by 0.38 (2007) and 0.55 (2008) with each additional treehopper. There was, however, a negative relationship between coccinellid numbers and ant abundance in 2007 (slope = -0.27, $r^2 = 0.13$, df = 333, $P < 0.0001$) and in 2008 (slope = -0.40, $r^2 = 0.11$, df = 308, $P < 0.0001$). In this case, with each additional ant, coccinellid numbers decreased by 0.27 (2007) and 0.40 (2008).

The mean ± SEM ratio of *P. megacephala* to *V. segmentata* was 1.73 ± 0.027 in 2007 (n = 334) and 1.80 ± 0.024 in 2008 (n = 308). There was a statistically significant difference in mean number of *C. inaequalis* when this ratio was < 2 compared to when it was ≥ 2 (Table 6.9). The number of *C. inaequalis* found with *P. megacephala* and *V. segmentata* was greater by a factor of 4.75 and 5.00 when the ant:treehopper ratio was < 2, in 2007 and 2008, respectively, compared to when it was ≥ 2. Coccinellids were found more often in colonies where the ants became outnumbered by the insects they tended.

Table 6.9. Mean (± standard error) number of *C. inaequalis* documented on *V. encelioides* stems with *P. megacephala* and *V. segmentata* in 2007 and 2008. *C. inaequalis* means are presented for two groups, those documented when the ratio between *P. megacephala* and *V. segmentata* was less than two and when it was greater than or equal to two.

	2007		2008	
	Ratio of *P. megacephala* to *V. segmentata*			
C. inaequalis	<2	≥2	<2	≥2
Mean	0.19	0.04	0.30	0.06
SE	0.0285	0.0206	0.0345	0.0264
N	251	83	228	80
p	< 0.0001		< 0.0001	
t-value	4.41		5.60	
DF	1, 332		1, 306	

What may be interpreted as a limit to protection by ants on Midway Atoll is supported by numerous published studies (Banks 1962, Banks and Macauley 1967, Addicott 1979, Cushman and Whitman 1991, Breton and Addicott 1992, Sakata 1994, 1995). Often, the benefits experienced by ant-tended insects are inversely density-dependent. Several studies with membracids also documented inverse density dependence (Morales 2000a, 2000b). However, Morales (2000a) found that density dependence between membracids and ants was not associated with predators. Positive density-dependence has, however, also been documented for ants and some membracids, *Publilia modesta* Uhler (Cushman and Whitman 1989), *Publilia concava* Say (McEvoy 1979), and *Enchenopa binotata* Say (Wood 1982).

These data support studies by Sloggett and Majerus (2000) and Altfeld and Stiling (2006, 2008) where coccinellid abundance was greater with ant-tended prey, presumably because untended prey was scarce. Only 19 (5.38%) and 12 (3.75%) stems were found with *V. segmentata* without *P. megacephala* on Midway Atoll in 2007 and 2008, respectively. These previous studies also suggest that non-myrmecophilous coccinellids will only feed on ant-tended prey when untended prey become scarce because, when given the choice, coccinellids would rather avoid ant aggression. On Midway Atoll, coccinellids were found more often with prey that became numerous with ants. Prey were seldom found untended. However, when prey numbers exceed half the number of tending ants, prey is functionally untended since they cannot be effectively protected from predators. If ant population numbers are limited by (thus rely on) nutrients supplied by the insects they tend, ant numbers may correspond with and thus grow in concert with tended populations. However, if ant populations are limited by another resource (such as appropriate nesting substrate), increases in tended insect numbers may provide resources beyond what ants require, becoming too much for ants to maintain. In this case, ants may be forced to tolerate the presence of coccinellids, at least until prey numbers fall below the untendable threshold.

Conclusions

The majority (73%) of studies documented ant interference in coccinellid predation on ant-tended herbivores. An examination of the species assemblage on Midway Atoll documented that coccinellids were five times more abundant on plants with ratios of ants to membracids of < 2, suggesting that there is a threshold for the ability of ants to protect tended herbivores against predation. Successful predation by coccinellids on ant-tended prey may also be due to physical or behavioral adaptations that allow them to feed in the presence of ants. These abilities may be specific to the coccinellid species, associated with the prey species, and/or their acceptance variable depending on the ant species. Additional studies evaluating the same species in its native and introduced locations will help discern the broad applicability and flexibility of existing adaptations and the speed at which new adaptations develop. Additional comparisons between different species in the same systems will provide information to evaluate the general versus specific nature of adaptations.

There is evidence supporting both density dependence and inverse density dependence between ants and the herbivores that they tend. The direction of density dependence is likely dynamic even within a species assemblage, changing with the shifting relative densities of each constituent. Thus, longer-term studies that evaluate population densities (instead of only presence or absence) as well as associated behaviors under a variety of conditions may help identify the circumstances under which these density relationships change. Understanding these dynamics will better enable stakeholders to better manage natural and agricultural habitats to improve their ecological and economic value.

Chapter 7

SUMMARY AND CONCLUSIONS

Summary

In Table 7.1, the results of chapters two, three, four, and five of this dissertation are summarized and presented side-by-side for comparison. From left to right, seven species are ordered from what would generally be considered the most to the least favorable result. For example, the most abundant species is listed on the left and the least abundant species is listed on the right. Similarly, the heaviest (weight) and largest (volume) species are listed on the left. The species that consumed the most aphids is listed on the left and the least on the right. When considering aggressive interactions with ants, receiving the least aggression and reacting the least are considered the more favorable conditions.

Conclusions

When considering the evidence from the four chapters collectively, several trends are evident. *Harmonia axyridis* consumed the most aphids, regardless of the company (alone, with conspecifics, with other lady beetle species, or with ants) or the aphid species, with the exception of the lupine aphid. When paired with other lady beetle species, *Harmonia axyridis* also had the shortest prey discovery time and generally exhibited the most aggression towards other species. Overall, *P. quatuordecimpunctata* consumed the fewest aphids, but was the most numerous in the survey, suggesting that a

Table 7.1. Summary of research comparing different lady beetle species. The number in parenthesis refers to the chapter in which the results were generated (1, 2, 3, or 4). Cm = *C. maculata* (native), Ct = *C. trifasciata* (native), Cs = *C. septempunctata* (non-native), Ha = *H. axyridis* (non-native), Hc = *H. convergens* (native), Hv = *H. variegata* (non-native), Pq = *P. quatuordecimpunctata* (non-native).

Abundance (1)	**Pq > Cm >> Ha > Cs > Ct >> Hc > Hv**
Prey Consumption – Aphids Only (2)	
GPA(n)	**Ha > Ct = Cs = Pq**
GPA(A)	**Ha > Ct = Cs > Pq**
PA(n)	**Ha > Ct = Cs = Pq**
PA(A)	**Ha > Ct = Cs > Pq**
RA(n)	**Ha > Ct = Pq > Cs**
RA(A)	**Ha > Ct = Cs = Pq**
LA(n)	**Ct = Pq > Ha = Cs**
LA(A)	**Ct > Cs = Ha = Pq**
Prey Consumption – Competing with Lady Beetles (3)	
Alone	**Ha ≥ Cs = Cm ≥ Ct = Hc = Hv = Pq**
Conspecifics	**Ha ≥ Ct = Cm = Cs = Hc = Pq ≥ Hv**
All Others	**Ha ≥ Ct ≥ Cs ≥ Cm = Hc ≥ Pq ≥ Hv**
Ct	**Cs ≤ Hv = Ha = Ct = Ct = Pq ≤ Hc = Cm**
Cm	**Ct ≤ Ha = Cm = Cm = Hc = Pq ≤ Cs = Hv**
Prey Consumption – Trials with Ants (4)	
	Ha ≥ Cs ≥ Ct = Hc = Pq ≥ Hv = Cm
Prey Discovery Time – Competing with Lady Beetles (3)	
Alone	**Ha = Cs = Hc = Pq = Ct = Cm = Hv**
Conspecifics	**Ha ≤ Ct ≤ Pq = Hc = Cs = Cm = Hv**
All Others	**Ha = Ct = Cm = Hc ≤ Pq = Cs ≤ Hv**
Weight (3)	**Cs > Ha > Ct = Cm = Hc = ≥ Pq ≥ Hv**
Volume (3)	**Cs > Ha > Hc > Ct = Cm > Pq = Hv**

Aggression Delivered – Competing with Lady Beetles (3)	
Conspecifics	**Ct = Hc = Ha = Pq = Cm = Cs = Hv**
All Others	**Ha > Pq = Cm = Ct = Hc = Cs = Hv**
Ha	**Ha = Ha = Cs ≤ Hv = Pq = Cm = Hc ≤ Ct**
Hv	**Cs = Hc = Ct = Hv = Hv = Cm ≤ Pq ≤ Ha**
Aggression Received – Competing with Lady Beetles (3)	
Conspecifics	**Hv = Cs = Cm = Pq = Ha = Hc = Ct**
All Others	**Cs = Ct = Cm = Pq = Hv = Hc = Ha**
Ct	**Ha ≥ Pq = Ct ≥ Cm = Cs = Hc = Hv**
Cm	**Ha ≥ Ct = Hc = Pq = Cm = Cs = Hv ≥ Cm**
Hc	**Ha ≥ Cs = Pq = Ct = Cm ≥ Hc = Hc = Hv**
Hv	**Ha = Pq ≥ Cm = Hc ≥ Ct = Hv = Hv = Cs**
Pq	**Ha ≥ Ct = Hc = Hv ≥ Pq = Pq = Cs = Cm**
Ant Behaviors – Trials with Ants (4)	
Aggression	**Pq ≤ Ct = Cs = Ha ≤ Cm ≤ Hv = Hc**
Antennation	**Ha ≤ Pq = Cm = Hc = Cs = Hv ≤ Ct**
Biting	**Pq = Ct = Cs ≤ Ha ≤ Cm ≤ Hv = Hc**
Grasping	**Pq = Ct ≤ Cs = Ha = Cm ≤ Hc = Hv**
Stinging	**Ct = Pq = Cs ≤ Ha ≤ Cm ≤ Hv = Hc**
Sting Score	**Ha ≤ Hc = Cm ≤ Pq ≤ Ct ≤ Cs = Hv**
Lady Beetle Behaviors – Trials with Ants (4)	
Reaction	**Pq = Ct = Ha ≤ Cs = Cm = Hc = Hv**
Continued	**Cs ≥ Ha = Pq = Ct ≥ Hc = Hv = Cm**
In Legs	**Pq = Ha ≤ Cm = Hc = Ct = Cs ≤ Hv**
On Back	**Pq = Ct = Ha ≤ Cs ≤ Hc ≤ Cm ≤ Hv**
Flailed Legs	**Pq = Ct ≤ Ha = Cs ≤ Hc ≤ Cm ≤ Hv**
Ran Away	**Pq ≤ Ct ≤ Ha ≤ Hv ≤ Cm ≤ Cs ≤ Hc**

lower consumption rate might support greater populations and actually be the favorable characteristic (compared with high prey consumption). *Propylea quatuordecimpunctata* was also among the smallest of the lady beetle species evaluated, suggesting that its nutritional needs may be less than the larger species. The other small species, *H. variegata*, also had low prey consumption, but was the least abundant. Ant stings affected *H. variegata* and *C. septempunctata* to a greater extent than other species. Ants displayed a significantly greater amount of aggression towards *H. convergens* and *H. variegata* compared with *P. quatuordecimpunctata*. *Propylea quatuordecimpunctata*, *C. trifasciata*, and *H. axyridis* reacted significantly less to ants compared with *H. variegata*, *H. convergens*, *C. maculata*, and *C. septempunctata*.

The first two species discussed, *H. axyridis* and *P. quatuordecimpunctata*, are examples of non-native species that appear to have become well established. *Hippodamia variegata*, another non-native species, did not fare as well in our evaluations. While *H. axyridis* and *P. quatuordecimpunctata* did well compared with native species, there was not a clear divide between native and non-native species.

Studies evaluating relationships between newly sympatric coccinellids, tending ants, and plant-feeding insects were summarized in the sixth chapter. Research has been driven by concerns about the effects of invasive ants (primarily *Pheidole megacephala*, *Solenopsis invicta*, and *Linephithema humile*) on the effectiveness of pest control by coccinellids (primarily *Cryptolaemus montrouzieri* and *C. septempunctata*). Several studies found an upper limit to care by ants, where as herbivore numbers increased relative to ant numbers, effective protection by ants decreased. Many studies document increases in herbivore numbers due to ant attendance. Ants interfered with coccinellid predation in 56 of 77 studies. Results, however, varied depending on the species participating in the ant:coccinellid pairings, with the ant, *P. megacephala*, the most effective at preventing predation of herbivores by coccinellids.

This research documents the importance of evaluating individual species for their invasive potential. Suggestions for future work include additional evaluations of species-specific interactions and relative population densities, comparisons of species in native and non-native ranges, and assessments of the impacts of ant suppression in agricultural and non-agricultural systems.

Bibliography

Addicott JF. 1979. A multispecies aphid-ant association: density dependence and species-specific effects. *Canadian Journal of Zoology* 57: 558-569.

Allison PD. 1999. Logistic Regression Using the SAS System: Theory and Application. SAS Institute Inc., Cary, North Carolina.

Altfeld L, Stiling P. 2006. Argentine ants strongly affect some but not all common insects on *Baccharis halmifolia*. *Environmental Entomology* 35: 31-36.

Altfeld L, Stiling P. 2008. Effects of aphid-tending Argentine ants, nitrogen enrichment and early-season herbivory on insects hosted by a coastal shrub. *Biological Invasions* 10.1007/s10530-008-9223-4.

Alyokhin A, Sewell G. 2004. Changes in lady beetle community following the establishment of three alien species. *Biological Invasions* 6: 463-471.

Angalet GW, Jacques JR. 1975. The establishment of *Coccinella septempunctata* L. in the continental United States. United States Department of Agriculture Co-operative Economic Insect Report 25: 883-884.

Angalet GW, Tropp JM, Eggart AN. 1979. *Coccinella septempunctata* in the United States: recolonizations and notes on its ecology. *Environmental Entomology* 8: 896-901.

Anneke, DP. 1959. The effect of parathion and ants on *Coccus hesperidium* L. (Coccidae: Hemiptera) and its natural enemies. *Journal of the Entomological Society of Southern Africa* 22: 245-274.

Attygalle AB, Cammaerts MC, Morgan ED. 1983a. Dufour gland secretions of *Myrmica rugulosa* and *Myrmica schencki* workers. *Journal of Insect Physiology* 29: 27-32.

Attygalle AB, Evershed RP, Morgan ED, Cammaerts MC. 1983b. Dufour gland secretions of workers of the ants *Myrmica sulcinodis* and *Myrmica lobicornis*, and comparison with six other species in *Myrmica*. *Insect Biochemistry* 13: 507-512.

Auclair JL. 1963. Aphid feeding and nutrition. *Annual Review of Entomology* 8: 439-490.

Bach CE. 1991. Direct and indirect interactions between ants (*Pheidole megacephala*), scales (*Coccus viridis*) and plants. *Oecologia* 87: 233-239.

Banks CJ. 1962. Effects of the ant, *Lasius niger* (L.) on insects preying on small populations of Aphis fabae Scop. on bean plants. *Annals of Applied Biology* 50: 669-679.

Banks CJ, Macauley EDM. 1967. Effects of *Aphis fabae* Scop. and of its attendant ants and insect predators on yields of field beans (Vicea faba L.). *Annals of Applied Biology* 60: 445-453.

Bartlett BR. 1961. The influence of ants upon parasites, predators, and scale insects. *Annals of the Entomological Society of America* 54: 543-551.

Bennett FD, Hughes IW. 1959. Biological control of insect pests in Bermuda. *Bulletin of Entomological Research* 50: 423-436.

Bhatkar AP. 1982. Orientation and defense of ladybeetles (Coleoptera, Coccinellidae) following ant trails in search of aphids. *Folia Entomologica Mexicana* 53: 75-85.

Biddinger DJ, Weber DC, Hull LA. 2009. Coccinellidae as predators of mites: Stethorini in biological control. *Biological Control*, in press.

Bishop HJ. 1931. Biological control of the citrus mealybug. *Farming in South Africa* 64: 7.

Blackman RL, Eastop VF. 1984. Aphids on the World's Crops: An Identification and Information Guide. John Wiley & Sons, New York.

Blaustein L, Chase JM. 2007. Interactions between mosquito larvae and species that share the same trophic level. *Annual Review of Entomology* 52: 489-507.

Bourque D, Chandler DS, Dearborn R, Donahue C, Michaud D. 2005. An annotated list of Maine beetle families. Special Insert. *Maine Entomological Society* 9(2).

Bradley GA. 1973. Effect of *Formica obscuripes* (Hymenoptera: Formicidae) on the predator-prey relationship between *Hyperaspis congressis* (Coleoptera: Coccinellidae) and *Toumeyella numismaticum* (Homoptera: Coccidae). *Canadian Entomologist* 105: 1113-1118.

Breton LM, Addicott JF. 1992. Density-dependent mutualism in an aphid-ant interaction. *Ecology* 73: 2175-2180.

Bristow CM. 1984. Differential benefits from ant attendance to two species of Homptera on New York Ironweed. *Journal of Animal Ecology* 53: 715-726.

Bristow CM. 1991. Are ant-aphid associations a tritrophic interaction? Oleander aphids and Argentine ants. *Oecologia* 87: 514-521.

Brown MW. 2003. Intraguild responses of aphid predators on apple to the invasion of an exotic species, *Harmonia axyridis*. *BioControl* 48: 141-153.

Brown MW, Miller SS. 1998. Coccinellidae (Coleoptera) in apple orchards of eastern West Virginia and the impact of invasion by *Harmonia axyridis*. *Entomological News* 109: 136-142.

Buckley R 1987. Interactions involving plants, Homoptera and ants. *Annual Review of Ecology and Systematics* 18: 111-135.

Bugg RL, Dutcher JD. 1989. Warm-season cover crops for pecan orchards: horticultural and entomological implications. *Biological Agriculture and Horticulture* 6: 123-148.

Bugg RL, Ellis RT. 1990. Insects associated with cover crops in Massachusetts. *Biological Agriculture & Horticulture* 7: 47-68.

Buren WF, Allen GE, Whitcomb WH, Lennartz FE, Williams RN. 1974. Zoogeography of the imported fire ant. *Journal of the New York Entomological Society* 82: 113-124.

Burgio G, Lanzoni A, Accinelli G, Maini S. 2008. Estimation of mortality by entomophages on exotic *Harmonia axyridis* versus native *Adalia bipunctata* in semi-field conditions in northern Italy. *BioControl* 53: 277-287.

Byers JE. 2000. Competition between two estuarine snails: implications for invasions of exotic species. *Ecology* 81: 1225-1239.

Caltagirone LE, Doutt RL. 1989. The history of the vedalia beetle importation to California and its impact on the development of biological control. *Annual Review of Entomology* 34: 1-16.

Cammaerts MC. 1978. Recruitment to food in *Myrmica rubra* L. *Biology of Behavior* 4: 159-172.

Cammaerts MC. 1984. Probable functions for a previously unrecognized pheromone in ants of the genus *Myrmica*. *Behavioural Processes* 9: 135-145.

Cammaerts MC. 1992. Anatomical origin and isolation of an ethological factor found on the last sternite of the workers of *Myrmica rubra* L. (Formicidae, Myrmicinae). *Journal of Insect Physiology* 38: 101-110.

Cammaerts MC, Evershed RP, Morgan ED. 1981a. Comparative study of pheromones emitted by different species of *Myrmica*. Pages 185-192 in Biosystematics of Social Insects. Academic Press, London.

Cammaerts MC, Evershed RP, Morgan ED. 1981b. Comparative study of the Dufour gland secretions of workers of four species of *Myrmica* ants. *Journal of Insect Physiology* 27: 59-65.

Cammaerts-Tricot MC, Morgan ED, Tyler RC, Braekman JC. 1976. Dufour's gland secretion of *Myrmica rubra*: chemical, electrophysiological, and ethological studies. *Journal of Insect Physiology* 22: 927-932.

Carlin NF, Holldobler B. 1986. The kin recognition system of carpenter ants (*Camponotus* spp.); I. Hierarchical cues in small colonies. *Behavioral Ecology and Sociobiology* 19: 123-134.

Carroll CR, Janzen DH. 1973. Ecology of foraging by ants. *Annual Review of Ecology and Systematics* 4: 231-257.

Carver M, Inkerman PA, Ashbolt NJ. 1987. *Anagyrus saccharicola* Timberlake (Hymenoptera: Encyrtidae) and other biota associated with *Saccharicoccus sacchari* (Cockerell) (Homoptera: Pseudococcidae) in Australia. *Journal of the Australian Entomological Society* 26: 367–368.

Catling HD. 1971. Studies on the citrus red scale, *Aonidiella aurantii* (Mask.), and its biological control in Swaziland. *Journal of the Entomological Society of Southern Africa* 34: 393-411.

Cavill GWK, Robertson PL. 1965. Ant venoms, attractants, and repellents. *Science* 149: 1337-1345.

Chai X. 1999. Predatory enemies of *Matsucoccus matsumurae* and their population dynamics. *Journal of Zhejiang Forestry College* 16: 336-340.

Chantal C. 1972. Additions a la faune coleopterique du Quebec. *Nature Canada* 99: 243-244.

Chapin EA. 1965. Coleoptera, Coccinellidae. Pages 189-254 in Insects of Micronesia. Bernice P. Bishop Museum, Honolulu, Hawaii.

Chapin EA. 1966. A new species of Myrmecophilous Coccinellidae, with notes on other Hyperspini (Coleoptera). *Psyche* 73: 278-283.

Chapin JB, Brou VA. 1991. *Harmonia axyridis* (Pallas) the third species of the genus to be found in the United States (Coleoptera: Coccinellidae). *Proceedings of the Entomological Society of Washington* 93: 630-635.

Charles JG. 1993. A survey of mealybugs and their natural enemies in horticultural crops in North Island, New Zealand, with implications for biological control. *Biocontrol Science and Technology* 3: 405-418.

Clark SR, DeBarr GL. 1996. Impacts of red imported fire ants (Hymenoptera: Formicidae) on striped pine scale (Homoptera: Coccidae) populations. *Journal of Entomological Science* 31: 229-239.

Collingwood CA. 1979. The Formicidae (Hymenoptera) of Fennoscandia and Denmark. *Fauna Entomologica Scandinavica* 8: 1-174.

Collins L, Scott JK. 1982. Interaction of ants, predators and the scale insect, *Pulvinariella mesembryanthemi*, on *Carpobrotus edulis*, an exotic plant naturalized in Western Australia. *Australian Entomological Magazine* 8: 73-78.

Colunga-Garcia M, Gage SH. 1998. Arrival, establishment, and habitat use of the multicolored Asian lady beetle (Coleoptera: Coccinellidae) in a Michigan landscape. *Environmental Entomology* 27: 1574-1580.

Conover WJ, Iman RL. 1981. Rank transformations as a bridge between parametric and non-parametric statistics. *American Statistician* 35: 124-129.

Coppler LB, Murphy JF, Eubanks MD. 2007. Red imported fire ants (Hymenoptera: Formicidae) increase the abundance of aphids in tomato. *Florida Entomologist* 90: 419-425.

Corbara B, Dejean A, Cerdan P. 1999. A myrmecophilous ladybird associated with the arboricolous ant *Dolichoderus bidens* (Dolichoderinae). *Actes Colloques Insect Sociaux* 12: 171-179.

Cormier CM, Forbes TA, Jones TA, Morrison RD, McCorquodale DB. 2000. Alien invasion: the status of non-native lady beetles (Coleoptera: Coccinellidae) in industrial Cape Breton, Nova Scotia. *Northeastern Naturalist* 7: 241-247.

Costantino G. 1935. Un nemico del Cotonello degli Agrumi: il *Cryptolaemus montrouzieri* Muls. *Bollettino della R. Stazione Sperimentale di Agrumicoltura e Frutticoltura in Acireale* 6: 7.

Cottrell TE, Yeargan KV. 1998. Intraguild predation between an introduced lady beetle, *Harmonia axyridis* (Coleoptera: Coccinellidae), and a native lady beetle, *Coleomegilla maculata* (Coleoptera: Coccinellidae). *Journal of the Kansas Entomological Society* 71: 159-163.

Cox DR. 1983. Some remarks on overdispersion. *Biometrika* 70: 269-274.

Cudjoe AR, Neuenschwander P, Copland MJW. 1993. Interference by ants in biological control of the cassava mealybug *Phenacoccus manihoti* (Hemiptera: Pseudococcidae) in Ghana. *Bulletin of Entomological Research* 83: 15-22.

Curkovic ST, Barria PG, González RR. 1995. Observaciones preliminares sobre insectos y acaros presentes en vides, perales, ciruelos y kakis detectados con trampas de agregacion. *Acta Entomologica Chilena* 19: 143-154.

Cushman JH, Whitman TG. 1989. Conditional mutualism in a membracid-ant association: temporal, age-specific, and density-dependent effects. *Ecology* 70: 1040-1047.

Cushman JH, Whitman TG. 1991. Competition mediating the outcome of a mutualism: protective services of ants as a limiting resource for membracids. *The American Naturalist* 138: 851-865.

Czechowski W, Radchenko A, Czechowska W. 2000. The Ants (Hymenoptera, Formicidae) of Poland. Warszawa, Poland.

Daane KM, Sime KR, Fallon J, Cooper ML. 2007. Impacts of Argentine ants on mealybugs and their natural enemies in California's coastal vineyards. *Ecological Entomology* 32: 583-596.

Day WH, Prokrym DR, Ellis DR, Chianese RJ. 1994. The known distribution of the predator *Propylea quatuordecimpunctata* (Coleoptera: Coccinellidae) in the United States, and thoughts on the origin of this species and five other exotic lady beetles in Eastern North America. *Entomological News* 105: 244-256.

De Barro PJ. 1990. Natural enemies and other species associated with *Saccharicoccus sacchari* (Cockerell) (Hemiptera: Pseudococcidae) in the Bundaberg area, southeast Queensland. *Journal of the Australian Entomological Society* 29: 87–88.

De Clercq P, Peeters I, Vergauwe G, Thas O. 2003. Interactions between *Podisus maculiventris* and *Harmonia axyridis*, two predators used in augmentative biological control in greenhouse crops. *BioControl* 48: 39-55.

DeBach P, Fleschner CA, Dietrick EJ. 1951. A biological check method for evaluating the effectiveness of entomophagous insects. *Journal of Economic Entomology* 44: 763-766.

Diaz Galarraga RR. 2003. Impact of the red imported fire ant upon cotton arthropods. Thesis, Texas A&M University.

Dixon AFG. 2000. Insect Predator-Prey Dynamics: Ladybird Beetles and Biological Control. Cambridge University Press, Cambridge, United Kingdom.

Dobzhansky T. 1933. Geographical variation in lady beetles. *American Naturalist* 67: 97-126.

Drake JA, Mooney HA, di Castri F, Groves RH, Kruger FJ, Rejmanek M, Williamson M (eds). 1989. Biological Invasions: A Global Perspective. John Wiley and Sons, Chichester.

Dreistadt SH, Flint ML. 1996. Melon aphid (Homoptera: Aphididae) control by inundative convergent lady beetle (Coleoptera: Coccinellidae) release on chrysanthemum. *Environmental Entomology* 25: 688-697.

Dupont PR. 1931. Entomological and mycological notes. Report of the Department of Agriculture, Seychelles. 1931: 11-13.

Dutcher JD, Estes PM, Dutcher MJ. 1999. Interaction in Entomology: Aphids, aphidophaga and ants in pecan orchards. *Journal of Entomological Science* 34: 40-56.

Ejbich K. 2003. Producers in Ontario and northern U.S. bugged by bad odors in wine. Wine Spectator 15 May: 16.

Elbanna SM. 2007. Insect interactions of three trophic levels on milkweed plant *Asclepias sinaica* (Boiss.) Musch. *International Journal of Agriculture & Biology* 9: 291-293.

Elliot N, Kieckhefer R, Kauffman W. 1996. Effects of an invading coccinellid on native coccinellids in an agricultural landscape. *Oecologica* 105: 537-544.

Ellis DR, Prokrym DR, Adams RG. 1999. Exotic lady beetle survey in northeastern United States: *Hippodamia variegata* and *Propylea quatuordecimpultctata* (Coleoptera: Coccinellidae). *Entomological News* 110: 73-84.

Elmes GW. 1975. Population studies on the genus *Myrmica* (Hymenoptera, Formicidae), with special reference to southern England. PhD thesis, University of London, London, United Kingdom.

Elmes GW, Wardlaw JC, Nielsen MG, Kipyatkov VE, Lopatina EB, Radchenko AG, Barr B. 1999. Site latitude influences on the respiration rate, fat content and the ability of worker ants to rear larvae: a comparison of *Myrmica rubra* (Hymenoptera: Formicidae) populations over their European range. *European Journal of Entomology* 96: 117-123.

Eubanks MD. 2001. Estimates of the direct and indirect effects of red imported fire ants on biological control in field crops. *Biological Control* 21: 35-43.

Eubanks MD, Blackwell SA, Parrish CJ, Delamar ZD, Hull-Sanders H. 2002. Intraguild predation of beneficial arthropods by red imported fire ants in cotton. *Environmental Entomology* 31: 1168-1174.

Evans EW. 2000. Morphology of invasion: body size patterns associated with establishment of *Coccinella septempunctata* (Coleoptera: Coccinellidae) in western North America. *European Journal of Entomology* 97: 469–474.

Evans EW. 2004. Habitat displacement of North American ladybirds by an introduced species. *Ecology* 85: 637-647.

Evans, E.W., 2009. Feeding by coccinellids on non-Hemipteran insects. *Biological Control*, in press.

Evershed RP, Morgan ED, Cammaerts MC. 1981. Identification of the trail pheromone of the ant *Myrmica rubra* L., and related species. *Naturwissenschaften* 68: 374-376.

Evershed RP, Morgan ED, Cammaerts MC. 1982. 3-ethyl-2,5-dimethylpyrazine, the trail pheromone from the venom gland of eight species of *Myrmica* ants. *Insect Biochemistry* 12: 383-391.

Finlayson CJ, Landry KM, Alyokhin AV. 2008. Abundance of native and non-native lady beetles (Coleoptera: Coccinellidae) in different habitats in Maine. *Annals of the Entomological Society of America* 101: 1078-1087.

Foottit RG, Maw E. 1997. Biological survey of Canada (terrestrial arthropods). Page 394 in Danks HV, Downes JA (eds), Insects of the Yukon. Canadian Museum of Nature, Ottawa.

Gagné I, Coderre D, Mauffette Y. 2002. Egg cannibalism by *Coleomegilla maculata lengi* neonates: preference even in the presence of essential prey. *Ecological Entomology* 27: 285–291.

Gakkhar S, Singh B, Naji RK. 2007. Dynamical behavior of two predators competing over a single prey. *Biosystems* 90: 808-817.

Garnas JR. 2005. European fire ants on Mount Desert Island, Maine: Population structure, mechanisms of competition and community impacts of *Myrmica rubra* L. (Hymenoptera: Formicidae). Thesis, University of Maine, Orono, Maine.

Garnas JR, Drummond FA, Groden E. 2007. Intercolony aggression within and among local populations of the invasive ant, *Myrmica rubra* (Hymenoptera: Formicidae), in coastal Maine. *Environmental Entomology* 36: 105-113.

Glowka L, Burhenne-Guilmin F, Synge H, McNeely JA, G'ndling L. 1994. A Guide to the Convention on Biological Diversity. International Union for the Conservation of Nature (IUCN), Gland, Switzerland.

Gonzalez Hernandez H, Johnson MW, Reimer NJ. 1999a. Impact of *Pheidole megacephala* (F.) (Hymenoptera: Formicidae) on the biological control of *Dysmicoccus brevipes* (Cockerell) (Homoptera: Pseudococcidae). *Biological Control* 15: 145-152.

Gonzalez-Hernandez H, Reimer NJ, Johnson MW. 1999b. Survey of the natural enemies of *Dysmicoccus* mealybugs on pineapple in Hawaii. *BioControl* 44: 47-58.

Gordon RD. 1985. The Coccinellidae (Coleoptera) of America north of Mexico. *Journal of New York Entomological Society* 93: 1-912.

Gordon RD, Vandenberg N. 1991. Field guide to recently introduced species of Coccinellidae (Coleoptera) in North America, with a revised key to North American genera of Coccinellini. *Proceedings of the Entomological Society of Washington* 93: 845-864.

Groden E, Drummond FA, Garnas J, Franceour A. 2005. Distribution of an invasive ant, *Myrmica rubra* (Hymenoptera: Formicidae), in Maine. *Journal of Economic Entomology* 98: 1774-1784.

Gruppe A, Roemer P. 1988. The lupin aphid (*Macrosiphum albifrons* Essig, 1911) (Hom., Aphididae) in West Germany: its occurrence, host plants and natural enemies. *Journal of Applied Entomology* 106: 135-143.

Hairston NG, Smith FE, Slobodkin LB. 1960. Community structure, population control, and competition. *The American Naturalist* 94: 421-425.

Hajek AE, Dahlsten DL. 1988. Distribution and dynamics of aphid (Homoptera: Drepanosiphidae) populations on Betula pendula in Northern California. *Hilgardia* 56: 1-33.

Hamid S, Shah MA, Anwar AM. 1977. Some ecological and behavioural studies on *Aphis craccivora* Koch (Hem.: Aphididae). Technical Bulletin, Commonwealth Institute of Biological Control 18: 99-111.

Handler AT, Gruner DS, Haines WP, Lange MW, Kanesshiro KY. 2007. Arthropod surveys on Palmyra Atoll, Line Islands, and insights into the decline of the native tree *Pisonia grandis* (Nyctaginaceae). *Pacific Science* 61: 485-502.

Hanks LM, Sadof CS. 1990. The effect of ants on nymphal survivorship of *Coccus viridis* (Homoptera: Coccidae). *Biotropica* 22: 210-213.

Harmon JP, Andow DA. 2007. Behavioral mechanisms underlying ants' density-dependent deterrence of aphid-eating predators. *Oikos* 116: 1030-1036.

Heimpel GE, Lundgren JG. 2000. Sex ratios of commercially reared biological control agents. *Biological Control* 19: 77-93.

Heywood V (ed). 1995. Global Biodiversity Assessment. Cambridge University Press, Cambridge, United Kingdom.

Hill MG, Blackmore PJM. 1980. Interactions between ants and the coccid *Icerya seychellarum* on Aldabra Atoll. *Oecologia* 45: 360-365.

Hironori Y, Katsuhiro S. 1997. Cannibalism and interspecific predation in two predatory ladybirds in relation to prey abundance in the field. *Entomophaga* 42: 53-163.

Hodek I. 1973. Biology of Coccinellidae. Dr. W. Junk N. V., Publishers, The Hague, Holland.

Hodek I, Honěk A. 1996. Ecology of Coccinellidae. Kluwer Academic, Boston.

Hodek I, Honěk A. 2009. Scale insects, mealybugs, whiteflies and psyllids (Hemiptera, Sternorrhyncha) as prey of ladybirds. *Biological Control*, in press.

Hoebeke ER, Wheeler AG. 1996. Adventive lady beetles (Coleoptera: Coccinellidae) in the Canadian Maritime Provinces, with new eastern U.S. records of *Harmonia quadripunctata*. *Entomological News* 107: 281-290.

Hölldobler B, Wilson EO. 1990. The Ants. Belknap Press of the Harvard University, Cambridge, Massachusetts.

Holway DA. 1999. Competitive mechanisms underlying the displacement of native ants by the invasive Argentine ant. *Ecology* 80: 238-251.

Holway DA, Suarez AV, Case TJ. 1998. Loss if intraspecific aggression in the success of a widespread invasive social insect. *Science* 282: 949-952.

Houck MA. 1991. Time and resource partitioning in *Stethorus punctum* (Coleoptera: Coccinellidae). *Enviromental Entomology* 20: 494–497.

Hough-Goldstein J, Cox J, Armstrong A. 1996. *Podisus maculiventris* (Hemiptera: Pentatomidae) predation on ladybird beetles (Coleoptera: Coccinellidae). *Florida Entomologist* 79: 64-68.

Howarth FG. 1991. Environmental impacts of classical biological control. *Annual Review of Entomology* 36: 485-509.

Hsu SB, Hwang TW, Kuang Y. 2001. Rich dynamics of a ratio-dependent one-prey two-predators model. *Journal of Mathematical Biology* 43: 377-396.

Huelsman MF, Kovach J, Jasinski J, Young C, Eisley B. 2002. Multicolored Asian lady beetle (*Harmonia axyridis*) as a nuisance pest in households in Ohio. Pages 243-250 in Jones SC, Zhai J, Robinson WH (eds), Proceedings of the 4th International Conference on Urban Pests. Pocahontas Press, Blacksburg, Virginia.

Illingworth JF. 1931. Preliminary report on evidence that mealybugs are an important factor in pineapple wilt. *Journal of Economic Entomology* 24: 877-889.

Itioka T, Inoue T. 1996. The role of attendant ants in the regulation and persistence of a population of the citrus mealybug *Pseudococcus citriculus* in a Satsuma Orange orchard. *Applied Entomology and Zoology* 31: 195-202.

Jahn G. 1992. The ecological significance of the big-headed ant in mealybug wilt disease of pineapple. Ph.D. Dissertation University of Hawaii at Manoa, Hawaii.

Jahn GC, Beardsley JW. 1994. Big-headed ants, *Pheidole megacephala*: interference with the biological control of mealybugs. Pages 199-205 in Williams DF (ed), Exotic Ants: Biology, Impact, and Control of Introduced Species. Westview Press, Boulder.

James DG, Stevens MM, O'Malley, KJ, Faulder RJ. 1999. Ant foraging reduces the abundance of beneficial and incidental arthropods in citrus canopies. *Biological Control* 14: 121-126.

Jiggins C, Majerus M, Gough U. 1993. Ant defence of colonies of *Aphis fabae* Scopoli (Hemiptera: Aphidadae), against predation by ladybirds. *British Journal of Entomology and Natural History* 6: 129-137 .

Kajita Y, Takano F, Yasuda H, Agarwala BK. 2000. Effects of indigenous ladybird species (Coleoptera : Coccinellidae) on the survival of an species in relation to prey abundance. *Applied Entomolofy and Zoology* 35: 473-479.

Kalushkov P. 1998. Ten aphid species (Sternorrhyncha: Aphididae) as prey for *Adalia bipunctata* (Coleoptera: Coccinellidae). *European Journal of Entomology* 95: 343-349.

Kalushkov P, Hodek I. 2004. The effects of thirteen species of aphids on some life history parameters of the ladybird *Coccinella septempunctata*. *BioControl* 49: 21-32.

Kaneko S. 2002. Aphid-attending ants increase the number of emerging adults of the aphid's primary parasitoid and hyperparasitoids by repelling intraguild predators. *Entomological Science* 5: 131-146.

Kaneko S. 2004. Positive impacts of aphid-attending ants on the number of emerging adults of aphid primary parasitoids and hyperparasitoids through exclusion of intraguild predators. *Japanese Journal of Entomology* 7: 173-183.

Kaplan I, Eubanks MD. 2002. Disruption of cotton aphid (Homoptera: Aphididae) – natural enemy dynamics by red imported fire ants (Hymenoptera: Formicidae). *Environmental Entomology* 31: 1175-1183.

Kaplan I, Eubanks MD. 2005. Aphids alter the community-wide impact of fire ants. *Ecology* 86: 1640-1649.

Katayama N, Suzuki N. 2002. Cost and benefit of ant attendance for *Aphis craccivora* (Hemiptera: Aphididae) with reference to aphid colony size. *Canadian Entomologist* 134: 241-249.

Katayama N, Suzuki N. 2003. Bodyguard effects for aphids of *Aphis craccivora* Koch (Homoptera: Aphididae) as related to the activity of two ant species, *Tetramorium caespitum* Linnaeus (Hymenoptera: Formicidae) and *Lasius niger* L. (Hymenoptera: Formicidae). *Applied Entomology and Zoology* 38: 427-433.

Kfir R, Kirsten F, Van Rensburg NJ. 1985. *Pauseia* sp. (Hymenoptera: Aphidiidae): a parasite introduced into South Africa for biological control of the black pine aphid, *Cinara cronartii* (Homoptera: Aphididae). *Environmental Entomology* 14: 597-601.

Kirkpatrick TW. 1927. The common coffee mealybug (*Pseudococcus lilacinus*, Ckll.) in Kenya Colony. Bulletin of the Department of Agriculture 18: 1-110.

Koch RL. 2003. The multicolored Asian lady beetle, *Harmonia axyridis*: a review of its biology, uses in biological control, and non-target impacts. *Journal of Insect Science* 3: 32.

Koch RL, Galvan TL. 2008. Bad side of a good beetle: the North American experience with *Harmonia axyridis*. Pages 23-35 in Roy HE, Wajnberg E (eds), From Biological Control to Invasion: The Ladybird *Harmonia axyridis* as a Model Species. Springer Netherlands.

Korschefsky R. 1932. Coccinellidae. Pages 439-447 in Schenkling S (ed), Coleopterorum catalogus, Berlin.

Krafsur ES, Kring TJ, Miller JC, Nariboli P, Obrycki JJ, Ruerson JR, Schaefer PW. 1997. Gene flow in the exotic colonizing lady beetle *Harmonia axyridis* in North America. *Biological Control* 8:207-214.

Krasfur ES, Obrycki JJ, Flanders RV. 1992. Gene flow in populations of the seven-spotted lady beetle, *Coccinella septempunctata*. *Journal of Heredity* 83:440-444.

Kreiter S, Iperti G. 1986. Effectiveness of *Adalia bipunctata* against aphids in a peach orchard with special reference to ant/aphid relationships. In Hodek I (ed) Ecology of Aphidophaga. Academia, Prague & Dr W. Junk, Dordrecht.

Kupferberg SJ. 1997. Bullfrog (*Rana catesbeina*) invasion of a California river: the role of larval competition. *Ecology* 78: 1736-1751.

Kuznetsov VN. 1997. Lady Beetles of Russian Far East. Memoir Seis Editor, CSE, Gainesville, Florida.

Liere H, Perfecto I. 2008. Cheating on a mutualism: indirect benefits of ant attendance to a coccidophagous coccinellid. *Environmental Entomology* 37: 143-149.

Lofgren, C.S., 1986. Pages 36-47 in Lofgren CS, Vander Meer RK (eds), Fire Ants and Leaf-cutting Ants: Biology and Management. Westview, Boulder, Colorado.

Losey JE, Denno RF. 1998. Positive predator-predator interactions: enhanced predation rates and synergistic suppression of aphid populations. *Ecology* 79: 2143-2152.

Louda SM, Pemberton RW, Johnson MT, Follett PA. 2003. Nontarget effects – the Achilles heel of biological control? *Annual Review of Entomology* 48: 365-396.

Lundgren JG. 2009. Relationships of natural enemies and non-prey foods. Springer International, Dordrecht, The Netherlands.

Lynch LD, Hokkanen HMT, Babendreier D, Bigler F, Burgio G, Gao ZH, Kuske S, Loomans A, Menzler-Hokkanen I, Thomas MB, Tommasini G, Waage JK, Lenteren JCv, Zeng QQ. 2001. Insect biological control and non-target effects: a European perspective. Pages 99-125 in Wajnberg E, Scott JK, Quinby PC (eds), Evaluating Indirect Ecological Effects of Biological Control. CABI Publishing, Wallingford, United Kingdom.

MacArthur R, Levins R. 1964. Competition, habitat selection, and character displacement in a patchy environment. *Proceedings of the National Academy of Sciences of the United States of America* 51: 1207-1210.

MacArthur R, Levins R. 1967. The limiting similarity, convergence, and divergence of coexisting species. *The American Naturalist* 101: 377-385.

MacArthur RH, Wilson EO. 1967. The Theory of Island Biogeography. Princeton University Press, Princeton, New Jersey.

MacArthur RH, Pianka ER. 1966. On optimal use of a patchy environment. *The American Naturalist* 100: 603-609.

Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA. 1999. Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecological Applications* 10: 689-710.

Mahdi T, Whittaker JB. 1993. Do birch trees (*Betula pendula*) grow better if foraged by wood ants? *Journal of Animal Ecology* 62: 101-116.

Matsuka M, Niijima K. 1985. *Harmonia axyridis*. Pages 265-268 in Singh P, Moore RF (eds), Handbook of Insect Rearing. Elsevier, Amsterdam.

McEvoy PB. 1979. Advantages and disadvantages to group living in treehoppers (Homoptera: Membracidae). *Miscellaneous Publications of the Entomological Society of America* 11: 1-13.

McEvoy P, Cox C. 1987. Successful biological control of ragwort, *Senecio jacobaea*, by introduced insects in Oregon. *Ecological Applications* 1: 430-442.

Melgoza G, Nowak RS, Tausch RJ. 1990. Soil water exploitation after fire: competition between *Bromus tectorum* (cheatgrass) and two native species. *Oecologia* 83: 7-13.

Mensah RK. 1997. Yellow traps can be used to monitor populations of *Coccinella transversalis* (F.) and *Adalia bipunctata* (L.) (Coleoptera: Coccinellidae) in cotton crops. *Australian Journal of Entomology* 36: 377-381.

Michaud JP. 1999. Sources of mortality in colonies of brown citrus aphid, *Toxoptera citricida*. *BioControl* 44: 347-367.

Michaud JP. 2000. Development and reproduction of ladybeetles (Coleoptera: Coccinellidae) on the citrus aphids *Aphis spiraecola* Patch and *Toxoptera citricida* (Kirkaldy) (Homoptera: Aphididae). *Biological Control* 18: 287–297.

Michaud JP. 2002. Invasion of the Florida citrus ecosystem by *Harmonia axyridis* (Coleoptera: Coccinellidae) and asymmetric competition with a native species, Cycloneda sanguinea. *Environmental Entomology* 31: 827-835.

Michaud JP, Browning HW. 1999. Seasonal abundance of the brown citrus aphid, *Toxoptera citricida*, (Homoptera: Aphididae) and its natural enemies in Puerto Rico. *Florida Entomologist* 82: 424-447.

Mignault M-P, Roy M, Brodeur J. 2006. Soybean aphid predators in Quebec and the suitability of *Aphis glycines* as prey for three Coccinellidae. *BioControl* 51: 89-106.

Milne WM. 1974. The relationship between ants and scale insects on citrus. CSIRO Division of Entomology Annual Report 1973–74. CSIRO, Sydney.

Monaco R, D'Abbicco M. 1987. Osservazioni biologiche sulla *Saissetia coffeae* Walk. (Rhynchota-Hom.-Coccidae) su fico (Ficus carica L.). *Entomologica* 22: 75-85.

Morales MA. 2000a. Mechanisms and density dependence of benefit in an ant-membracid mutualism. *Ecology* 81: 482-489.

Morales MA. 2000b. Survivorship of an ant-tended membracid as a function of ant recruitment. *Oikos* 90: 469-476.

Morgan ED, Tyler RC, Cammaerts MC. 1977. Identification of the components of Dufour gland secretion of the ant *Myrmica rubra* and responses to them. *Journal of Insect Physiology* 23: 511-515.

Murray DAH. 1982. Effects of sticky banding of custard apple tree trunks on ants and citrus mealybug, *Planococcus citri* (Rosso) (Pseudococcidae (Hem)) in southeast Queensland. *Queensland Journal of Agricultural and Animal Sciences* 39: 141-146.

Nakata T. 1995. Population fluctuations of aphids and their natural enemies on potato in Hokkaido. *Japanese Journal of Applied Entomology and Zoology* 30: 129-138.

Nishida R, Fukami H. 1989. Host plant iridoid-based chemical defense of an aphid, *Acyrthosiphon nipponicus*, against ladybird beetles. *Journal of Chemical Ecology* 15: 1837-1845.

Nunes DM, Hartz SM. 2006. Feeding dynamics and ecomorphology of *Oligosarcus jenynsii* (Gunther, 1864) and *Oligosarcus robustus* (Menezes, 1969) in the Lagoa Fortaleza, southern Brazil. *Brazilian Journal of Biology* 66: 121-132.

Obrycki JJ. 2009. Aphidophagy by Coccinellidae. *Biological Control*, in press.

Obrycki JJ, Giles KL, Ormord AM. 1998. Experimental assessment of interactions between larval *Coleomegilla maculata* and *Coccinellia septempunctata* (Coleoptera: Coccinellidae) in field cages. *Environmental Entomology* 27: 1280-1288.

Obrycki JJ, Kring TJ. 1998. Predaceous Coccinellidae in biological control. *Annual Review of Entomology* 43: 295-321.

Obrycki JJ, Orr CJ. 1990. Suitability of three prey species for Nearctic populations of *Coccinella septempunctata*, *Hippodamia variegata*, and *Propylea quatuordecimpunctata* (Coleoptera: Coccinellidae). *Journal of Economic Entomology* 83: 1292-1297.

Oliver TH, Jones I, Cook J, Leather SR. 2008. Avoidance responses of an aphidophagous ladybird, *Adalia bipunctata*, to aphid-tending ants. *Ecological Entomology* 33: 523-528.

Ormord AM. 1994. Interactions between larval *Coccinella septempunctata* L. and *Coleomegilla maculata* (DeGeer) (Coleoptera: Coccinellidae). MS Thesis, Iowa State University.

Osawa N. 1989. Sibling and non-sibling cannibalism by larvae of a lady beetle *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) in the field. *Researches on Population Ecology* 31: 153-160.

Osawa N. 1992. Effect of pupation site on pupal cannibalism and parasitism in the ladybird beetle *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae). *Japanese Journal of Entomology* 60: 131-135.

Panis A. 1981. Action des fourmis sur la biocénose parasitaire de la cochenille noire des agrumes en France (Homoptera, Coccoidea, Coccidae). *Fruits* 36: 47-48.

Panis A, Brun J. 1971. Essais de lutte biologique contre trois especes de Pseudococcidae (Homoptera, Coccoidea) en serres de plantes vertes. *Revue de Zoologie Agricole et de Pathologie Vegetale* 70: 42-47.

Parajulee MN, Slosser JE. 2003. Potential of yellow sticky traps for lady beetle survey in cotton. *Journal of Economic Entomology* 96: 239-245.

Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham K, Kareiva PM, Williamson MH, Von Holle B, Moyle PB, Byers JE, Goldwasser L. 1999. Impact: Toward a framework for understanding the ecological effects of invaders. *Biological Invasions* 1: 3-19.

Pasteels JM, Grégoire JC, Rowell-Rahier M. 1983. The chemical ecology of defense in arthropods. *Annual Review of Entomology* 28: 263-289.

Pedigo LP, Rice ME. 2006. Entomology and Pest Management. Pearson Prentice Hall., Upper Saddle River, New Jersey.

Perrings C, Williamson M, Barbier EB, Delfino D, Dalmazzone S, Shogren J, Simmons P, Watkinson A. 2002. Biological invasion risks and the public good: An economic perspective. *Conservation Ecology* 6(1): 1. URL: http://www.consecol.org/vol6/iss1/art1

Perrings C, Williamson M, Dalmazzone S (eds). 2000. The Economics of Biological Invasions. Edward Elgar Publishing, Inc., Northampton, Massachusetts.

Pervez A, Omkar. 2005. Functional responses of coccinellid predators: an illustration of a logistic approach. *Journal of Insect Science* 5: 5.

Petren K, Case TJ. 1996. An experimental demonstration of exploitation competition in an ongoing invasion. *Ecology* 77: 118-132.

Philpott S. 1997. Exotic ladybird beetles in Washington prairies and their interactions with native ants. Pages 141-147 in Dunn P and Ewing K (eds) The Ecology and Conservation of the South Puget Prairie Landscape. The Nature Conservancy, Seattle, Washington.

Phoofolo MW, Obrycki JJ. 1997. Comparative prey suitability of *Ostrinia nubilalis* eggs and *Acyrthosiphon pisum* for *Coleomegilla maculata*. *Biological Control* 9: 167-172.

Pianka ER. 1978. Evolutionary Ecology. Second Edition. Harper and Row, New York.

Pimental D, Lach L, Zuniga R, Morrison D. 1999. Environmental and economic costs of non-indigenous species in the United States. *BioScience* 50: 53-65.

Poutiers R. 1922. L'acclimatation de *Cryptolaeumus montrouzieri*, Muls. dans le midi de la France. *Annales des Epiphyties* 8: 3-18.

Quezada JR, DeBach P. 1973. Bioecological and population studies of the cottony-cushion scale, *Icerya purchasi* Mask., and its natural enemies, *Rodolia cardinalis* Mul. and *Cryptochaetum iceryae* Will., in southern California. *Hilgardia* 41: 631-688.

Raciti E, Tumminelli R, Conti D, Marano G, Barraco D, Dinatale A, Fisicaro R. 1997. Il cotonello degli agrumi. *Informatore Agrario* 53: 67-70.

Radcliffe EB, Flanders KL. 1998. Biological control of alfalfa weevil in North America. *Integrated Pest Management Reviews* 3: 225-242.

Ratcliffe S. 2002. National pest alert: Multicolored Asian lady beetle. USDA CSREES Regional Integrated Pest Management Program and the Pest Management Centers. URL: http://www.pmcenters.org/northcentrallMALB

Reddy KB, Seetharama HG. 1997. Integrated management of mealybugs in coffee. *Indian Coffee* 61: 26-28.

Reilly JJ, Sterling WL. 1983. Interspecific association between the red imported fire ant (Hymenoptera: Formicidae), aphids, and some predaceous insects in a cotton agroecosystem. *Environmental Entomology* 12: 541-545.

Reimer NJ, Beardsley JW, Jahn G. 1990. Pest ants in the Hawaiian Islands. Pages 40-50 in Vander Meer RK, Jaffe K, Cedeno A (eds), Applied Myrmecology: A World Perspective. Westview Press, Boulder, Colorado.

Reimer NJ, Cope M-L, Yasuda G. 1993. Interference of *Pheidole megacephala* (Hymenoptera: Formicidae) with biological control of *Coccus viridis* (Homoptera: Coccidae) in coffee. *Environmental Entomology* 22: 483-488.

Roger C, Coderre D, Vigneault C, Boivin G. 2001. Prey discrimination by a generalist coccinellid predator: effect of prey age or parasitism? *Ecological Entomology* 26: 163-172.

Rogers CE, Jackson HB, Eikenbary RD. 1972. Voracity and survival of *Propylea 14-punctata* preying upon greenbugs. *Journal of Economic Entomology* 65: 1313-1316.

Rü B, le Reyd G, Mapangou-Divassa S. 1990. Influence de l'exclusion des fourmis sur les populations de la cochenille du manioc *Phenacoccus manihoti* et de ses ennemis naturels au Congo. *Agronomie Tropicale* 45: 275-282.

Saito T, Bjørnson S. 2006. Horizontal transmission of a microsporidium from the convergent lady beetle, *Hippodamia convergens* Guérin-Méneville (Coleoptera: Coccinellidae), to three coccnellid species of Nova Scotia. *Biological Control* 39: 427-433.

Sakata H. 1994. How an ant decides to prey on or attend aphids. *Researches on Population Ecology* 36: 45-51.

Sakata H. 1995. Density-dependent predation of the ant *Lasius niger* (Hymenoptera: Formicidae) on two attended aphids *Lachnus tropicalis* and *Myzocallis kuricola* (Homoptera: Aphididae). *Researches on Population Ecology* 37: 159-164.

Sakuratani Y, Marsumoto Y, Oka M, Kubo T, Fuji A, Uotani M, Teraguchi T. 2000. Life history of *Adalia bipunctata* (Coleoptera: Coccinellidae) in Japan. *European Journal of Entomology* 97: 555-558.

Samways MJ. 1983. Interrelationship between an entomogenous fungus and two ant-homopteran (Hymenoptera: Formicidae-Hemiptera: Pseudococcidae & Aphididae) mutualisms on guava trees. *Bulletin of Entomological Research* 73: 321-331.

SAS Institute Inc. 2002. SAS Institute Inc., Cary, North Carolina.

SAS Institute Inc. 2005. Fitting Poisson Regression Models Using the GENMOD Procedure Course Notes. SAS Institute Inc., Cary, North Carolina.

Sato S, Dixon AFG, Yasuda H. 2003. Effect of emigration on cannibalism and intraguild predation in aphidophagous ladybirds. *Ecological Entomology* 28: 628-633.

Schaefer PW, Dysart RJ, Specht HB. 1987. North American distribution of *Coccinella septempunctata* (Coleoptera: Coccinellidae) and its mass appearance in coastal Delaware. *Environmental Entomology* 16: 368-373.

Schellhorn NA, Lane CP, Olson DM. 2005. The co-occurrence of an introduced biological control agent (Coleoptera: *Coccinella septempunctata*) and an endangered butterfly (Lepidoptera: *Lycaeides melissa samuelis*). *Journal of Insect Conservation* 9: 41-47.

Schmitz DC, Simberloff D. 1997. Biological invasions: A growing threat. *Issues in Science and Technology* – Online. University of Texas Press, Austin, Texas.

Seifert B. 1996. Ameisen Beobachten, Bestimmen. Naturbuch-Verlag, Augsburg.

Shands WA, Simpson GW, Wave HE, Gordon CC. 1972. Importance of arthropod predators in controlling aphids on potatoes in northeastern Maine. University of Maine Technical Bulletin 54. University of Maine, Orono, Maine.

Shiga M. 1975. Population dynamics of the green peach aphid, *Myzus persicae* (Sulzer), and the mealy plum aphid, *Hyalopterus arundinis* (Fabricius), in peach orchards. Pages 9-14 in Yasumatsu K, Mori H (eds), Approaches to Biological Control. University of Tokyo Press, Tokyo.

Simberloff D, Stiling P. 1996. How risky is biological control. *Ecology* 77: 1965-1974.

Sloggett JJ, Wood RA, Majerus MEN. 1998. Adaptations of *Coccinella magnifica* Redtenbacher, a myrmecophilous Coccinellid, to aggression by wood ants (*Formica rufa* Group). I. Adult behavioral adaptation, its ecological context and evolution. *Journal of Insect Behavavior* 11: 889-904.

Sloggett JJ, Majerus MEN. 2000. Aphid-mediated coexistence of ladybirds (Coleoptera: Coccinellidae) and the wood ant *Formica rufa*: seasonal effects, interspecific variability and the evolution of a coccinellid myrmecophile. *Oikos* 89: 345-359.

Sloggett JJ, Manica A, Day MJ, Majerus MEN. 1999. Predation of ladybirds (Coleoptera: Coccinellidae) by wood ants, *Formica rufa* L. (Hymenoptera: Formicidae). *Entomologist's Gazette* 50: 217-221.

Smit B. 1934. A study of the most important insect pests that confront the citrus grower in the Eastern Province. *South African Journal of Science* 31: 439-441.

Smit B, Bishop HJ. 1934. A study of the citrus mealybug and its association with ants in the Eastern Province. *Scientific Bulletin of the Department of Agriculture of South Africa* 125: 1-41.

Smith HS, Armitage HM. 1931. The biological control of mealybugs attacking citrus. *California Agricultural Experiment Station Bulletin* 509: 1-74.

Smith WE, Papacek D, Smith J. 2004. Biological control of *Pulvinaria urbicola* Cockerell Homoptera: Coccidae in a *Pisonia grandis* forest on North East Herald Cay in the Coral Sea. *General Applied Entomology* 33: 61-68.

Snowball GJ, Milne WM. 1973. Protection by ants as a deterrent to biological control of scales. CSIRO Division of Entomology Annual Report 1972–73. CSIRO, Sydney.

Snyder WE, Clevenger GM, Eigenbrode SD. 2004. Intraguild predation and successful invasion by introduced ladybirds beetles. *Oecologia* 140: 559-565.

Snyder WE, Joseph SB, Preziosi RF, Moore AJ. 2000. Nutritional benefits of cannibalism for the lady beetle *Harmonia axyridis* (Coleoptera: Coccinellidae) when prey quality is poor. *Environmental Entomology* 29: 1173-1179.

Sokal, R.R., Rohlf, F.J., 1995. Biometry. 3rd Edition. Freeman, New York.

Srikanth J, Easwaramoorthy S, Kurup NK. 2001. *Camponotus compressus* F. interferes with *Cryptolaemus montrouzieri* Mulsant activity in sugarcane. *Insect Environment* 7: 51-52.

Stary P. 1995. Natural enemy spectrum of *Aphis spiraephaga* (Hom.: Aphididae), an exotic immigrant aphid in Central Europe. *Entomophaga* 40: 29-34.

Stechmann D-H, Volkl W, Stary P. 1996. Ant-attendance as a critical factor in the biological control of the banana aphid *Pentalonia nigronervosa* Coq. (Hom: Aphididae) in Oceania. *Journal of Applied Entomology* 120: 119-123.

Stephens EJ, Losey JE. 2004. Comparison of sticky cards, visual and sweep sampling of coccinellid populations in alfalfa. *Environmental Entomology* 33: 535-539.

Sterling WL, Jones D, Dean DA. 1979. Failure of the red imported fire ant to reduce entomophagous insect and spider abundance in a cotton agroecosystem. *Environmental Entomology* 8: 976-981.

Steyn JJ. 1954. The pugnacious ant (*Anoplolepis custodiens* Smith) and its relation to the control of citrus scales at Letaba. Report of the Council for Scientific and Industrial Research, Pretoria.

Stone BC. 1970. The flora of Guam. *Micronesica* 6: 1-659.

Stroyan HLG. 1981. A North American lupin aphid found in Britain. *Plant Pathology* 30: 253.

Suarez AV, Tsutsui ND, Holway DA, Case TJ. 1999. Behavioral and genetic differentiation between native and introduced populations of the Argentine ant. *Biological Invasions* 1: 43-53.

Sumalde AC, Calilung VJ. 1982. Life history of *Cerataphis palmae* Ghesquire (Pemphigidae, Homoptera) on coconut. *Philippine Entomologist* 5: 273-290.

Swirski E, Izhar Y, Wysoki M, Gurevitz E, Greenberg S. 1980. Integrated control of the long-tailed mealybug, *Pseudococcus longispinus* [Hom: Pseudococcidae], in avocado plantations in Israel. *Entomophaga* 25: 415-426.

Symondson WOC, Sunderland KD, Greenstone MH. 2002. Can generalist predators be effective biocontrol agents? *Annual Review of Entomology* 47: 561-594.

Takahashi K. 1989. Intra- and interspecific predations of lady beetles in spring alfalfa fields. *Japanese Journal of Entomology* 57: 199-203.

Takizawa T, Yasuda H. 2006. The effects of attacks by the mutualistic ant, *Lasius japonicas* Santschi (Hymenoptera: Formicidae) on the foraging behavior of the two aphidophagous ladybirds, *Coccinella septempunctata brucki* Mulsant (Coleoptera: Coccinellidae) and *Propylea japonica* (Thunberg) (Coleoptera: Coccinellidae). *Applied Entomology and Zoology* 41: 161-169.

Takizawa T, Yasuda H, Agarwala BK. 2000. Effects of parasitized aphids (Homoptera: Aphididae) as food on larval performance of three predatory ladybirds (Coleoptera: Coccinellidae). *Applied Entomology and Zoology* 35: 2000.

Tedders WL, Reilly CC, Wood BW, Morrison RK, Lofgren CS. 1990. Behavior of *Solenopsis invicta* (Hymenoptera: Formicidae) in pecan orchards. *Environmental Entomology* 19: 44-53.

Tedders WL, Schaefer PW. 1994. Release and establishment of *Harmonia axyridis* (Coleoptera: Coccinellidae) in the Southeastern United States. *Entomological News* 105: 228-243.

Tsutsui ND, Suarez AV, Holway DA, Case TJ. 2000. Reduced genetic variation and the success of an invasive species. *Proceedings of the National Academy of Sciences* 97: 5948-5953.

Turnock WJ, Wise IL, Matheson FO. 2003. Abundance of some native coccinellids (Coleoptera: Coccinellidae) before and after the appearance of *Coccinella septempunctata*. *Canadian Entomologist* 135: 391-404.

Tursch B, Daloze D, Dupont M, Pasteels JM, Tricot MC. 1971. A defensive alkaloid in a carnivorous beetle. *Experientia* 27: 1380-1381.

United States Office of Technology Assessment (USOTA). 1993. Harmful non-indigenous species in the United States. United States Congress, United States Government Printing Office, Washington, D.C.

van den Bosch, R., Messenger, P.S., 1973. Biological Control. Intext Educational Publishers, New York.

Verghese A, Ramachander PR. 1998. Inter-specific association among prey, *Chloropulvinaria psidii* (Maskell) predator, *Cryptolaemus montrouzieri* Mulsant and ant, *Camponotus compressus* Fabricius in a guava ecosystem. *Pest Management in Horticultural Ecosystems* 4: 21-24.

Vesey-Fitzgerald D. 1939. Entomology. Report of the Department of Agriculture, Seychelles. 1939: 14-16.

Vesey-Fitzgerald D. 1941. Progress of the control of coconut-feeding Coccidae in Seychelles. *Bulletin of Entomological Research* 32: 161-164.

Vesey-Fitzgerald D. 1953. Review of the biological control on coconut palms in the Seycelles. *Bulletin of Entomological Research* 44: 405-413.

Villalba M, Vila N, Marzal C, Garcia Marí F. 2006. Influencia en el control biológico del cotonet *Planococcus citri* (Hemiptera: Pseudococcidae) de la liberación inoculativa de enemigos naturales y la eliminación de hormigas, en parcelas de cítricos. Boletín de Sanidad Vegetal, Plagas 32: 203-213.

Vinson SB, Scarborough TA. 1989. Impact of the imported fire ant on laboratory populations of cotton aphid (*Aphis gossypii*) predators. *Florida Entomologist* 72: 107-111.

Völkl W, Woodring J, Fisher MK, Lorenz MW, Hoffmann KH. 1999. Ant-aphid mutualism: the impact of honeydew production and honeydew sugar composition on ant preferences. *Oecologia* 118: 483-491.

Way MJ. 1963. Mutualism between ants and honeydew-producing Homoptera. *Annual Review of Entomology* 8: 307-344.

Weaving AJS. 1980. Observations on *Hilda patruelis* Stal. (Homoptera: Tettigometridae) and its infestation of the groundnut crop in Rhodesia. *Journal of the Entomological Society of Southern Africa* 43: 151-167.

Wheeler AG. 1990. *Propylea quatuordecimpunctata*: additional records of an adventive lady beetle (Coleoptera: Coccinellidae). *Entomological News* 101: 164-166.

Wheeler AG. 1993. Establishment of *Hippodamia variegata* and new records of *Propylea quaruordecimpunctata* in the eastern United States. *Entomological News* 104: 102-110.

Wheeler AG, Hoebeke ER. 1995. *Coccinella novemnotata* in northeastern North America: historical occurrence and current status (Coleoptera: Coccinellidae). *Proceedings of the Entomological Society of Washington* 97: 701-716.

Wheeler AG, Stoops CA. 1996. Status and spread of Palearctic lady beetles *Hippodamia variegata* and *Propylea quatuordecimpunctata* (Coleoptera: Coccinellidae) in Pennsylvania, 1993-1995. *Entomological News* 107: 291-298.

Wheeler WM. 1908. A European ant (*Myrmica laevinodis*) introduced into Massachusetts. *Journal of Economic Entomology* 1: 336-339.

Wheeler WM. 1922. The ants collected by the American Museum Congo Expedition. *Bulletin of the American Museum of Natural History* 45: 39-269.

Williamson M. 1996. Biological Invasions. Chapman & Hall, London, England.

Wimp GM, Whitham TG. 2001. Biodiversity consequences of predation and host plant hybridization on an aphid-ant mutualism. *Ecology* 82: 440-452.

Woglum RS. 1942. The Argentine ant. *California Citrogrower* 27: 155.

Wood TK. 1982. Ant-attended nymphal aggregations in the *Enchenopa binotata* complex (Homoptera: Membracidae). *Annals of the Entomological Society of America* 75: 649-653.

Yasuda H, Evans EW, Kajita Y, Urakawa K, Takizawa T. 2004. Asymmetric larval interactions between introduced and indigenous ladybirds in North America. *Oecologia* 141: 1432-1939.

Yasuda H, Kikuchi T, Kindlmann P, Sato S. 2001. Relationships between attack and escape rates, cannibalism, and intraguild predation in larvae of two predatory ladybirds. *Journal of Insect Behavior* 14: 373-384.

Yasuda H, Ohnuma N. 1999. Effect of cannibalism and predation on the larval performance of two ladybird beetles. *Entomologia Experimentalis et Applicata* 93: 63-67.

Yasuda H, Shinya K. 1997. Cannibalism and interspecific predation in two predatory ladybirds in relation to prey abundance in the field. *Entomophaga* 42: 153-163.

Zar JH. 1999. Biostatistical analysis, 4th Edition. Prentice Hall, Upper Saddle River, New Jersey.

Zaviezo T, Grez AA, Estades CF, Perez A. 2006. Effects of habitat loss, habitat fragmentation, and isolation on the density, species richness, and distribution of ladybeetles in manipulated alfalfa landscapes. *Ecological Entomology* 31: 646-656.

Appendix A. Comparison of four methods used to sample coccinellids.

Four methods commonly used to sample invertebrate populations were compared in the field from June 14 to September 20, 2004, and from July 11 to August 8, 2005:

<u>Yellow Sticky Traps</u>: Five, 6 x 12" yellow sticky strips TM (Olson Products, Medina, Ohio) with adhesive on both sides were deployed in each habitat in each location. Traps were hung on stakes or directly from the vegetation as close to foliage as possible without sticking to it. Traps were deployed for two weeks in the same location unless changes in vegetation necessitated their vertical movement.

<u>Visual Observation</u>: Visual observations were conducted at the same sites and on the same dates when sticky traps were deployed. Plants throughout the site were carefully inspected for 15 minutes by one field technician, and the number of observed coccinellids was recorded. The observations were made immediately after yellow sticky traps were removed and replaced.

<u>Beating Sheet</u>: Vegetation from throughout the habitat was shaken and beaten with a 24-inch, 1-inch diameter wooden stick for 10 minutes over a 28-in square canvas sheet supported by a 37-in wooden frame (BioQuip Products, Inc., Rancho Dominguez, California). Coccinellids that fell onto the canvas sheet were collected. The sampling was conducted immediately after visual observations were completed.

<u>Sweep net</u>: One hundred sweeps of the vegetation were made using a 15-in diameter sailcloth net with a 2-ft wooden handle (BioQuip Products, Inc., Rancho Dominguez, California). Samples were collected by sweep net following the collection of samples by beating sheet. Care was taken to intentionally avoid vegetation that was just sampled by beating sheet.

Appendix A (Continued). Comparison of four methods used to sample coccinellids.

The number of individuals collected by each method is listed below by species, first by totals for all habitats combined, then separately for each habitat:

2004

	all methods	sticky traps only	beating sheet only	sweep net only	observation only
Psyllobora vigintimaculata	1170	1151	7	9	3
Propylea quatuordecimpunctata	1149	1115	10	14	8
Coleomegilla maculata	274	271	0	0	3
Coccinella septempunctata	156	99	1	2	44
Harmonia axyridis	115	112	0	0	3
Coccinella trifasciata	74	67	0	7	0
Hippodamia parenthesis	56	55	1	0	0
Hippodamia tredecimpunctata	21	19	0	1	1
Hippodamia variegata	7	7	0	0	0
Mulsantina sp.	7	7	0	0	0
Chilocorus sp.	6	6	0	0	0
Anisosticta bitriangularis	3	3	0	0	0
Hyperaspis sp.	3	3	0	0	0
Coccinella hieroglypyhica	2	2	0	0	0
Epilachna varivestis	2	2	0	0	0
Adalia bipunctata	1	1	0	0	0
Anatis quindecimpunctata	1	0	0	0	1
Calvia quatuordecimguttata	1	1	0	0	0
Coccinella transversoguttata	1	1	0	0	0
Totals	3049	2922	19	33	63

2005

	all methods	sticky traps only	beating sheet only	sweep net only	observation only
Propylea quatuordecimpunctata	519	509	3	4	3
Coleomegilla maculata	228	226	0	0	2
Psyllobora vigintimaculata	198	189	3	4	2
Harmonia axyridis	44	41	0	1	2
Coccinella trifasciata	25	21	1	3	0
Coccinella septempunctata	21	16	0	0	5
Hippodamia parenthesis	10	9	1	0	0
Hippodamia tredecimpunctata	5	4	0	0	1
Chilocorus sp.	3	3	0	0	0
Hyperaspis sp.	2	2	0	0	0
Totals	1055	1020	8	12	15

Appendix A (Continued). Comparison of four methods used to sample coccinellids.

2004						**2005**					
	all methods	sticky traps only	beating sheet only	sweep net only	observation only		all methods	sticky traps only	beating sheet only	sweep net only	observation only
Field											
Propylea quatuordecimpunctata	243	224	9	10	0	*Propylea quatuordecimpunctata*	104	101	1	1	1
Coleomegilla maculata	74	71	0	0	3	*Coleomegilla maculata*	36	34	0	0	2
Coccinella trifasciata	53	46	0	7	0	*Coccinella trifasciata*	16	12	1	3	0
Coccinella septempunctata	48	29	1	2	6	*Coccinella septempunctata*	5	4	0	0	1
Hippodamia parenthesis	19	18	1	0	0	*Hippodamia parenthesis*	5	4	1	0	0
Hippodamia tredecimpunctata	9	8	0	1	0	*Hippodamia tredecimpunctata*	2	2	0	0	0
Psyllobora vigintimaculata	4	4	0	0	0	*Hyperaspis* sp.	2	2	0	0	0
Hyperaspis sp.	3	3	0	0	0	*Chilocorus* sp.	1	1	0	0	0
Chilocorus sp.	1	1	0	0	0						
Calvia quatuordecimguttata	1	1	0	0	0						
Coccinella hieroglypyhica	1	1	0	0	0						
Coccinella transversoguttata	1	1	0	0	0						
Hippodamia variegata	1	1	0	0	0						
Grain											
Propylea quatuordecimpunctata	235	233	0	0	2	*Propylea quatuordecimpunctata*	122	119	0	2	1
Coleomegilla maculata	93	93	0	0	0	*Coleomegilla maculata*	89	89	0	0	0
Coccinella septempunctata	71	33	0	0	38	*Coccinella septempunctata*	9	7	0	0	2
Harmonia axyridis	21	20	0	0	1	*Harmonia axyridis*	9	7	0	1	1
Hippodamia parenthesis	18	18	0	0	0	*Hippodamia parenthesis*	2	2	0	0	0
Psyllobora vigintimaculata	16	16	0	0	0	*Psyllobora vigintimaculata*	2	2	0	0	0
Hippodamia tredecimpunctata	9	8	0	0	1	*Hippodamia tredecimpunctata*	3	2	0	0	1
Coccinella trifasciata	8	8	0	0	0	*Coccinella trifasciata*	3	3	0	0	0
Hippodamia variegata	3	3	0	0	0						
Riparian											
Psyllobora vigintimaculata	303	295	3	2	3	*Psyllobora vigintimaculata*	56	54	0	1	1
Propylea quatuordecimpunctata	126	121	0	1	4	*Propylea quatuordecimpunctata*	47	45	2	0	0
Harmonia axyridis	5	4	0	0	1	*Harmonia axyridis*	2	2	0	0	0
Anisosticta bitriangularis	3	3	0	0	0						
Hippodamia tredecimpunctata	2	2	0	0	0						
Adalia bipunctata	1	1	0	0	0						
Coccinella septempunctata	1	1	0	0	0						
Mulsantina sp.	1	1	0	0	0						
Potato											
Propylea quatuordecimpunctata	246	242	0	0	2	*Propylea quatuordecimpunctata*	113	113	0	0	0
Coleomegilla maculata	90	90	0	0	0	*Coleomegilla maculata*	98	98	0	0	0
Coccinella septempunctata	35	35	0	0	0	*Coccinella septempunctata*	7	5	0	0	2
Harmonia axyridis	28	27	0	0	1	*Harmonia axyridis*	6	5	0	0	1
Hippodamia parenthesis	18	18	0	0	0	*Hippodamia parenthesis*	3	3	0	0	0
Psyllobora vigintimaculata	18	18	0	0	0	*Psyllobora vigintimaculata*	5	4	0	1	0
Coccinella trifasciata	6	6	0	0	0	*Coccinella trifasciata*	2	2	0	0	0
Hippodamia variegata	3	3	0	0	0						
Hippodamia tredecimpunctata	1	1	0	0	0						

Appendix A (Continued). Comparison of four methods used to sample coccinellids.

	2004						**2005**				
	all methods	sticky traps only	beating sheet only	sweep net only	observation only		all methods	sticky traps only	beating sheet only	sweep net only	observation only
Mixed Forest											
Psyllobora vigintimaculata	372	369	1	2	0	*Psyllobora vigintimaculata*	48	47	1	0	0
Propylea quatuordecimpunctata	41	41	0	0	0	*Propylea quatuordecimpunctata*	33	33	0	0	0
Coleomegilla maculata	16	16	0	0	0	*Coleomegilla maculata*	5	5	0	0	0
Epilachna varivestis	2	2	0	0	0						
Harmonia axyridis	2	2	0	0	0						
Coccinella septempunctata	1	1	0	0	0						
Deciduous Forest											
Psyllobora vigintimaculata	125	125	0	0	0	*Psyllobora vigintimaculata*	32	30	1	1	0
Propylea quatuordecimpunctata	74	74	0	0	0	*Propylea quatuordecimpunctata*	30	30	0	0	0
Coccinella trifasciata	3	3	0	0	0	*Coccinella trifasciata*	3	3	0	0	0
Anatis quindecimpunctata	1	0	0	0	1						
Chilocorus sp.	1	1	0	0	0						
Harmonia axyridis	1	1	0	0	0						
Coniferous Forest											
Psyllobora vigintimaculata	23	23	0	0	0	*Psyllobora vigintimaculata*	5	5	0	0	0
Mulsantina sp.	6	6	0	0	0						
Chilocorus sp.	1	1	0	0	0						
Apple											
Harmonia axyridis	57	57	0	0	0	*Harmonia axyridis*	27	27	0	0	0
Psyllobora vigintimaculata	18	18	0	0	0	*Psyllobora vigintimaculata*	7	7	0	0	0
Propylea quatuordecimpunctata	4	4	0	0	0						
Coleomegilla maculata	1	1	0	0	0						
Shrub											
Psyllobora vigintimaculata	291	283	3	5	0	*Psyllobora vigintimaculata*	43	40	1	1	1
Propylea quatuordecimpunctata	180	176	1	3	0	*Propylea quatuordecimpunctata*	70	68	0	1	1
Coccinella trifasciata	4	4	0	0	0	*Coccinella trifasciata*	1	1	0	0	0
Chilocorus sp.	3	3	0	0	0	*Chilocorus* sp.	2	2	0	0	0
Coccinella hieroglypyhica	1	1	0	0	0						
Harmonia axyridis	1	1	0	0	0						
Hippodamia parenthesis	1	1	0	0	0						

Yellow sticky traps collected the greatest numbers of individuals and the greatest numbers of species, compared with the other sampling techniques. Overall, yellow sticky traps collected 10 species in 2004 and two species in 2005 that were not collected by the other collection methods. With only one exception, all species collected by beating sheet, sweep net, and visual observation were also collected by yellow sticky traps, but in much greater numbers. Yellow sticky traps collected 22.82 (n = 37, SE = 5.14) times more beetles than all other methods combined. The exception, one individual of *Anatis quindecimpunctata*, was collected by visual observation from the stake holding the yellow sticky trap, approximately one inch below the yellow surface of the trap. Yellow sticky traps were only outperformed regarding the number of individuals of a given species collected in one instance. In 2004, 38 *C. septempunctata* individuals were documented during one observation period in grain, from what appeared to be the emergence of an overwintering group of adults.

Appendix B. Mean (± standard error) numbers of lady beetle species captured on yellow sticky cards (N = 5) throughout the sampling season in each habitat by location.

2004	Coniferous Forest		Field		Mixed Forest		Riparian		Shrub	
CR	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Non-native Species										
Coccinella hieroglyphica									0.20	0.2000
Coccinella septempunctata							0.20	0.2000		
Harmonia axyridis							0.40	0.4000		
Propylea quatuordecimpunctata			2.40	1.9391	3.60	1.3266	6.20	2.8879	3.20	0.7348
Native Species										
Chilocorus sp.					0.40	0.2449			0.20	0.2000
Coccinella trifasciata			0.20	0.2000	0.20	0.2000				
Coleomegilla maculata			0.80	0.8000						
Hippodamia parenthesis			0.20	0.2000					0.20	0.2000
Hyperaspis sp.			0.40	0.2449						
Mulsantina sp.	1.20	0.8000					0.20	0.2000		
Psyllobora vigintimaculata	1.60	0.6000	0.20	0.2000	3.20	1.2410	13.20	7.7614	10.00	5.8822
Scymnus sp.			0.80	0.5831			0.20	0.2000		

Location abbreviations: FR, commercial potato farm, Fryeburg, Maine; LT, Orono Land Trust Land, Orono, Maine; RF, University of Maine’s Rogers Farm, Orono, Maine; CR, commercial potato farm currently enrolled in the Conservation Reserve Program, Monticello, Maine; PI, rural residential property, Presque Isle, Maine; AF, University of Maine’s Aroostook Research Farm, Presque Isle, Maine.

Appendix B (Continued). Mean (± standard error) numbers of lady beetle species captured on yellow sticky cards (N = 5) throughout the sampling season in each habitat by location.

2004	Coniferous Forest		Deciduous Forest		Field		Mixed Forest		Riparian		Shrub	
LT	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Non-native Species												
Coccinella septempunctata					1.80	0.3742						
Harmonia axyridis					4.20	1.2410			0.20	0.2000		
Propylea quatuordecimpunctata			0.60	0.4000	29.80	3.6387	0.40	0.2449	4.80	2.6344	19.20	5.8600
Native Species												
Chilocorus sp.	0.20	0.2000			0.20	0.2000						
Coccinella transversoguttata					0.20	0.2000						
Coccinella trifasciata					6.40	1.2083					0.80	0.4899
Coleomegilla maculata					0.40	0.4000						
Hippodamia parenthesis					0.80	0.3742						
Psyllobora vigintimaculata	3.00	1.8974	6.20	3.8262	0.60	0.4000	2.40	0.8124	28.00	10.7098	4.40	1.5033
Scymnus sp.					0.40	0.2450	0.40	0.2450	0.20	0.2000		

Appendix B (Continued). Mean (± standard error) numbers of lady beetle species captured on yellow sticky cards (N = 5) throughout the sampling season in each habitat by location.

2004	Deciduous Forest		Field		Grain		Mixed Forest		Potato		Riparian		Shrub	
AF	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Non-native Species														
Coccinella hieroglyphica			0.20	0.2000										
Coccinella septempunctata			1.40	0.5099	1.60	0.5099			2.00	0.8367				
Harmonia axyridis	0.20	0.2000	0.20	0.2000					1.40	0.9274			0.20	0.2000
Propylea quatuordecimpunctata	8.60	4.2497	7.40	1.8601	14.80	2.9732	2.60	1.4000	16.60	5.1245	10.00	3.0332	9.00	1.6733
Native Species														
Adalia bipunctata											0.20	0.2000		
Anatis quindecimpunctata	0.20	0.2000												
Anisoticta bitriangularis											0.60	0.4000		
Calvia quatourdecimguttata			0.20	0.2000										
Chilocorus sp.	0.20	0.2000												
Coccinella trifasciata	0.60	0.6000	2.40	1.6912	0.60	0.4000			0.20	0.2000				
Coleomegilla maculata					1.40	0.5099	0.40	0.4000	0.80	0.5831	0.40	0.4000		
Hippodamia parenthesis			0.40	0.2449	1.60	0.5099			0.20	0.2000	0.40	0.4000		
Psyllobora vigintimaculata	24.80	9.5205					49.20	24.5039	0.40	0.2449	9.80	7.3716	39.00	20.3666

Appendix B (Continued). Mean (± standard error) numbers of lady beetle species captured on yellow sticky cards (N = 5) throughout the sampling season in each habitat by location.

2004	Apple		Field		Grain		Mixed Organic		Mixed Forest		Potato		Riparian	
RF	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Non-native Species														
Coccinella septempunctata			4.40	0.5099	2.40	0.4000	1.00	0.3162	0.20	0.2000	5.00	1.1402		
Epilachna varivestis							0.80	0.8000	0.40	0.4000				
Harmonia axyridis	11.00	0.8944	0.60	0.4000	2.20	0.4899	7.20	2.2226	0.60	0.4000	4.00	1.4832	0.20	0.2000
Propylea quatuordecimpunctata	0.80	0.3742	6.20	2.8531	27.20	7.0810	40.20	13.2151	8.20	3.4843	32.00	9.7417	4.40	1.5684
Native Species														
Chilocorus sp.							0.20	0.2000						
Coccinella trifasciata			0.20	0.2000	1.20	0.2000	1.00	0.5477			1.20	0.5831		
Coccinella transversoguttata					0.20	0.2000								
Coleomegilla maculata	3.80	1.4967	13.00	3.1623	35.60	11.6645	25.60	5.0458	4.40	1.6310	17.20	2.6344	0.40	0.2449
Hippodamia parenthesis			2.60	0.5099	0.80	0.4899	0.60	0.4000			3.60	1.2884		
Hippodamia variegata			0.20	0.2000			0.20	0.2000			0.60	0.2449		
Psyllobora vigintimaculata	0.80	0.4899			6.60	1.1662	0.60	0.4000	17.40	5.9211	3.20	2.9563	7.40	4.1061
Scymnus sp.	0.80	0.3742												

Appendix B (Continued). Mean (± standard error) numbers of lady beetle species captured on yellow sticky cards ($N = 5$) throughout the sampling season in each habitat by location.

2005	Mixed Forest		Potato		Shrub	
FR	Mean	SE	Mean	SE	Mean	SE
Non-native Species						
Coccinella septempunctata			4.20	1.5620		
Harmonia axyridis	1.80	1.1136	7.00	1.3038	5.40	1.8055
Propylea quatuordecimpunctata	2.60	1.0770	0.20	0.2000	1.20	0.8000
Native Species						
Chilocorus sp.	0.40	0.2449				
Coccinella trifasciata					0.20	0.2000
Coleomegilla maculata	0.20	0.2000	1.40	0.5099	0.20	0.2000
Hippodamia parenthesis			1.00	0.5477		
Psyllobora vigintimaculata	52.00	27.4062			2.80	1.1136
Scymnus sp.	0.20	0.2000			0.40	0.2450

Appendix B (Continued). Mean (± standard error) numbers of lady beetle species captured on yellow sticky cards (N = 5) throughout the sampling season in each habitat by location.

2005	Coniferous Forest		Deciduous Forest		Field		Mixed Forest		Riparian		Shrub	
LT	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Non-native Species												
Coccinella septempunctata					0.20	0.2000						
Harmonia axyridis	0.40	0.2449			0.60	0.2449			0.40	0.2449	1.00	0.6325
Propylea quatuordecimpunctata			0.20	0.2000	20.40	5.6798	0.20	0.2000	6.60	1.9391	10.60	3.2031
Native Species												
Chilocorus sp.	0.40	0.2449					0.20	0.2000			0.20	0.2000
Coccinella trifasciata					2.00	0.5477					0.20	0.2000
Coleomegilla maculata					0.40	0.2449						
Hyperaspis sp.					0.20	0.2000			0.40	0.2449	1.00	0.6325
Mulsantina sp.											3.20	3.2000
Psyllobora vigintimaculata	1.60	0.6782	4.20	1.1136	0.60	0.4000	3.20	1.8276	4.40	0.8718	3.60	1.3638
Scymnus sp.					1.00	0.5477			0.40	0.2450	0.60	0.4000

Appendix B (Continued). Mean (± standard error) numbers of lady beetle species captured on yellow sticky cards (N = 5) throughout the sampling season in each habitat by location.

2005	Deciduous Forest		Field		Grain		Mixed Forest		Potato		Riparian		Shrub	
AF	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Non-native Species														
Coccinella hieroglyphica			0.60	0.4000									0.20	0.2000
Coccinella septempunctata			0.60	0.4000	0.20	0.2000			3.20	0.7348			0.20	0.2000
Harmonia axyridis	1.60	0.8124	0.60	0.4000					4.00	0.8367			0.60	0.4000
Propylea quatuordecimpunctata	14.80	5.1127	8.40	1.6912	15.40	3.8678	0.60	0.6000	11.40	2.7129	2.60	1.2083	32.40	15.9455
Native Species														
Adalia bipunctata	0.20	0.2000	0.60	0.2449	0.20	0.2000							0.80	0.8000
Coccinella transversoguttata									0.20	0.2000				
Coccinella trifasciata	0.20	0.2000	1.00	0.3162	0.40	0.2449			1.00	0.6325	0.20	0.2000	0.80	0.5831
Coleomegilla maculata	0.20	0.2000												
Hippodamia convergens			0.20	0.2000										
Hippodamia parenthesis			0.20	0.2000					0.20	0.2000				
Hippodamia tredecimpunctata			0.40	0.2449	3.00	0.8367			0.40	0.2449	0.40	0.2449		
Hyperaspis sp.			0.40	0.2449										
Mulsantina sp.											0.80	0.3742		
Psyllobora vigintimaculata	12.80	3.7202	1.00	1.0000	2.20	1.1136	41.60	30.0576	0.20	0.2000	4.60	2.7677	23.80	10.9563
Scymnus sp.			0.20	0.2000							0.60	0.4000	0.40	0.4000

Appendix B (Continued). Mean (± standard error) numbers of lady beetle species captured on yellow sticky cards (N = 5) throughout the sampling season in each habitat by location.

2005	Field		Mixed Forest	
PI	Mean	SE	Mean	SE
Non-native Species				
Coccinella septempunctata	0.20	0.2000	0.20	0.2000
Harmonia axyridis	0.20	0.2000		
Propylea quatuordecimpunctata	1.40	0.5099	0.20	0.2000
Native Species				
Coccinella trifasciata	0.20	0.2000		
Psyllobora vigintimaculata	1.40	1.4000	8.40	3.0100

Appendix B (Continued). Mean (± standard error) numbers of lady beetle species captured on yellow sticky cards (N = 5) throughout the sampling season in each habitat by location.

2005	Apple		Grain		Mixed Forest		Potato		Riparian	
RF	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Non-native Species										
Coccinella septempunctata	0.20	0.2000	1.20	0.5831			2.20	0.9695		
Harmonia axyridis	3.20	1.0198	7.60	1.8601	0.60	0.2449	13.00	5.5136	1.20	0.8000
Propylea quatuordecimpunctata	1.80	0.3742	40.00	8.6197	12.40	2.7677	45.40	10.7219	8.00	2.2361
Native Species										
Adalia bipunctata					0.20	0.2000				
Chilocorus sp.	0.20	0.2000	0.20	0.2000	0.20	0.2000			0.20	0.2000
Coccinella trifasciata	0.60	0.4000	1.00	0.5477			3.20	1.4629		
Coleomegilla maculata	0.60	0.4000	36.20	12.8039	0.20	0.2000	21.80	6.3356	0.20	0.2000
Hippodamia convergens			1.60	1.6000						
Hippodamia parenthesis			0.60	0.4000			1.20	0.3742		
Hippodamia tredecimpunctata			0.20	0.2000			0.60	0.4000		
Hyperaspis sp.	0.40	0.2449			0.40	0.2449	0.20	0.2000	0.20	0.2000
Psyllobora vigintimaculata	1.80	0.5831	0.60	0.2449	23.60	9.1630	0.20	0.2000	4.00	2.2583
Scymnus sp.	0.80	0.4472							0.60	0.2450

BIOGRAPHY OF THE AUTHOR

Christy J. L. Finlayson was born in Duluth, Minnesota, raised in Bartlett, Tennessee, and graduated from Bartlett High School in 1989. She attended The University of Memphis and graduated in 1993 with a Bachelor of Science degree in Biology and Chemistry. She returned to The University of Memphis to earn a Master of Science degree in Biology, with an emphasis in ecotoxicology, in 1997. Christy is a candidate for the Doctor of Philosophy degree in Biological Sciences from The University of Maine in May, 2009.