EFFECTS OF *MEDICAGO SATIVA* L. AND *VICIA FABA*

L. ON NUTRITIONAL SUITABILITY OF

ACYRTHOSIPHON PISUM (HARRIS) FOR

COLEOMEGILLA MACULATA (DEGEER)

AND *HIPPODAMIA CONVERGENS*

GUERIN-MENEVILLE

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EFFECTS OF *MEDICAGO SATIVA* L. AND *VICA FABA*

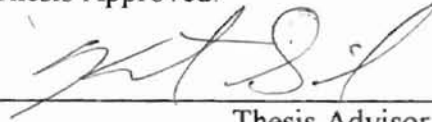L. ON NUTRITIONAL SUITABILITY OF

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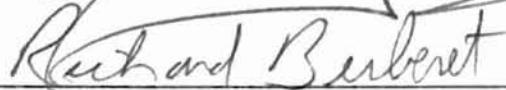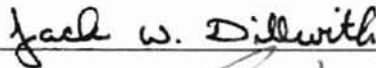
COLEOMEGILLA MACULATA (DEGEER)

AND *HIPPODAMIA CONVERGENS*

GUERIN-MENEVILLE

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PREFACE

The first chapter of this thesis is a literature review focusing on the suitability of prey, tritrophic interactions and the predatory insects *Coleomegilla maculata* and *Hippodamia convergens*. Also included is the biology of the herbivore *Acyrthosiphon pisum* as well as a detailed description of the lipid composition of this aphid when reared on *Medicago sativa* and *Vicia faba*. Subsequent chapters are formal manuscripts of the research I conducted during my M.S. program and are written in compliance with the publication policies and guidelines for manuscript preparation with the Entomological Society of America.

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Tritrophic interactions are the interactions among plants, prey, and natural enemies. Because plants can effect third trophic level processes (Faeth 1992), understanding the interactions among plants, prey, and predators is necessary when predicting predator-prey relationships. Not only may prey influence a predator directly but can also influence a predator indirectly via host plant. Predators may be affected by plant quality, variation characterizing populations and by reduced or altered

CHAPTER I

GENERAL INTRODUCTION

Tritrophic interactions are the interactions among plants, prey, and natural enemies. Because plants can affect third trophic level processes (Faeth 1992), understanding the interactions among plants, prey, and predators is necessary when predicting predator-prey relationships. Not only may prey influence a predator directly, but they can also influence a predator indirectly, via host plant. Predators may be influenced by plants indirectly via changing aphid populations and by reduced or enhanced prey suitability (Price 1997). Plant attributes and chemical constituents may alter the nutritional suitability or toxicity of aphids, thereby affecting natural enemy population dynamics by changing developmental times, mortality, or fecundity (Power 1992). Despite a wide range of evidence that plants affect the third trophic level, few studies have described the mechanisms of these interactions (Hodek and Honek 1996, Price 1997). The effect of prey suitability on the survival, development and fecundity of Coccinellidae has been evaluated for several species (Hodek and Honek 1996, Obrycki and Kring. 1998). However, little information exists concerning the relationship between *Acyrthosiphon pisum* Harris (Homoptera: Aphididae) and its host plants, and the subsequent effects on the population dynamics of Coccinellidae.

Compared with pea aphids (*Acyrthosiphon pisum* Harris) reared on *Vicia faba* L. (c.v. 'Windsor'), pea aphids reared on *Medicago sativa* L. (c.v. 'OK08') store 6-fold greater levels of myristic acid (Giles et al. 2000). This increase in myristic acid is primarily responsible for the 2.7- fold increase in total fatty acids and 1.17-fold increase in caloric content (K.L. Giles, unpublished data). Bashir (1973) demonstrated that increased quantities of myristic acid in artificial diets decrease the developmental times while increasing fecundity and adult size of *Olla abdomalis* (Say). *Coccinella*

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septempunctata (L.) exhibits increased survivorship and decreased developmental times when fed *A. pisum* with increased levels of myristic acid (Giles et al., unpublished data). Although the biochemical relationships between these host plants and pea aphids has been studied (Dillwith et al. 1993), little information exists relating findings to the population dynamics of lady beetles. Differences in fatty acid and subsequent caloric content may affect survival, development, size and fecundity of *Coleomegilla maculata* (DeGeer) (Coleoptera: Coccinellidae) and *Hippodamia convergens* (Guerin-Meneville) (Coleoptera: Coccinellidae).

Because host plant quality affects fatty acid storage in aphids (Dillwith et al. 1993), prey quality should be assessed on a nutritional level in order to isolate the mechanisms responsible for differences among predator-prey combinations. I tested the hypothesis that substantial variation in quantities and compositions of lipids stored by *A. pisum* resulting from different host plants will influence growth rate, survival, and fecundity of Coccinellidae. The overall goal of this study was to investigate the role of changing quantities and compositions of pea aphid lipids among host plants as determinants of survival, development, and fecundity of Coccinellidae.

Objectives

The specific objectives of my thesis were:

1. Determine the effect of *A. pisum* lipid levels and caloric content, as influenced by alfalfa and faba beans, on the preimaginal survival and development of *C. maculata* and *H. convergens*.

2. Determine the effect of *A. pisum* lipid levels and caloric content, as influenced by alfalfa and faba beans, on reproduction of adult *C. maculata* and *H. convergens*.

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I evaluated the survival, development, and reproduction of *C. maculata* and *H. convergens* that were supplied with pea aphids from either alfalfa or faba bean. I investigated whether differences in survival, development, and fecundity were the result of quantitative or qualitative differences in the nutritional value of pea aphids from the two host plants. Qualitative differences may be attributed to altered nutritional content of prey, for example the absence of an essential nutritional component, or presence of a plant derived toxin sequestered by prey. Quantitative differences are associated with differing levels, but a similar nutritional composition of prey. If there are qualitative differences in the nutritional value of prey, then coccinellid survival, development and fecundity would be different at both very high and low daily prey levels. If there are quantitative differences in the nutritional value of prey (as affected by differences in total nutrition) then Coccinellidae survival, development, and reproduction would be different at very low daily prey levels, but similar (would converge) at high daily prey levels (Giles et al. 2000).

Explanation of Thesis Format

This general introduction is followed by a literature review (Chapter II), then chapters III and IV, devoted to individual papers to be published, a general summary (Chapter V), and appendices. A list of references are provided for citations in the literature review and papers to be published. In paper I, the survival and development of *C. maculata* and *H. convergens* supplied with increasing daily prey levels of *A. pisum* reared *on M. sativa* and *V. faba* are examined. In paper II the reproduction *of C. maculata* and H. convergens supplied with increasing daily prey levels of *A. pisum* reared on *M. sativa* and *V. faba* is

studied. These papers follow the general guidelines of the Entomological Society of America for submission to scientific journals.

Biology and Life History of *Acyrthosiphon pisum*

Acyrthosiphon pisum (Harris) (Hemiptera: Aphididae), the pea aphid, is a common herbivore of legume crops including alfalfa, *Medicago sativa* L. and faba bean, *Vicia faba* (Müller and Hargrove 1997, Metcalf and Metcalf 1993). Pea aphids feed on and are vectors of several mosaic viruses of alfalfa, clover and ... pea aphids may reproduce ...

CHAPTER II

LITERATURE REVIEW

Biology and Life History of *Acyrthosiphon pisum*

Acyrthosiphon pisum (Harris) (Homoptera: Aphididae), the pea aphid, is a common herbivore of many legumes including alfalfa, *Medicago sativa* L. and faba beans, *Vicia faba* L. (Minks and Harrewijn 1987, Metcalf and Metcalf 1993). Pea aphids overwinter in either the egg stage or as ovoviviparous females in alfalfa, clovers, and other perennial plants, and in the southern U.S. pea aphids may reproduce all winter long on these plants.

Pea aphids exhibit both anholocyclic and holocyclic life cycles. Anholocyclic life cycles occur when pea aphids reproduce asexually or parthenogenetically, forming only clonal populations. Holocyclic life cycles occur when pea aphids reproduce sexually. In Northern latitudes, pea aphid holocyclic (sexual) life cycles often occur, whereas in the Southern latitudes, anholocyclic lifecycles occur. However, for pea aphids, both anholocyclic and holocyclic life cycles may occur, depending on daylength. In the spring, *A. pisum* numbers increase on winter host plants, before winged aphids (alates) begin to migrate to alternate legumous host plants. Winged migrants start new colonies on plants by giving birth to nymphs, which molt four times. In approximately 12 days, adult pea aphids begin reproducing. Female pea aphids produce 6 or 7 young each day until from 50 to 100 have been born; in one year between 7 and 20 generations of females can occur. Most adults are wingless, but when crowding occurs on a plant, winged aphids begin appearing and migrate to new host plants (Metcalf and Metcalf 1993).

In the fall, ovoviviparous females give birth to young, some winged males and some which become sexually-mature, egg-laying, wingless females. Eggs are laid

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primarily on stems and leaves of alfalfa and clover and are approximately 0.8 mm in length. Eggs are light green when newly laid but turn shiny black before hatching. These fertilized eggs overwinter and in the following spring give rise to ovoviviparous stem-mothers which repeat the cycle (Metcalf and Metcalf 1993).

Pea aphids have the ability to adapt to certain legumes and optimize development, survival and reproductive capacity. Their "performance" varies with respect to host plant and clone of pea aphid (Bergman et al. 1990). For example, pea aphids reared on faba beans (c.v. 'Windsor') are larger and are more fecund than those reared on alfalfa (cv. 'OK08') (Bergman et al. 1990).

Biotypes are known in many aphid species. Biotypes occur frequently among aphids, mainly due to their high reproductive rate (Minks and Harrewijn 1987). Harrington (1941) was the first to record the existence of pea aphid biotypes based on body size, feeding injury, and reproductive rates. He determined that there were at least five biotypes in the United States alone (Harrington 1945). Host preference, ability to transmit plant viruses, and resistance to pesticides often determine different biotypes of aphids.

Lipids of Aphididae

The pea aphid is a phloem feeder and removes fluid from stems, buds, and leaves (Minks and Harrewijn 1987, Metcalf and Metcalf 1993). Because phloem exudates have relatively low lipid levels, the diet of the aphids contains almost no lipid (Dillwith et al. 1993). Due to this dietary deficiency, aphids, including pea aphids have to synthesize nearly all required lipids (Buchner 1965, Houk and Griffiths 1980, Dasch et al. 1984, Dillwith et al. 1993).

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Most aphids, including pea aphids, synthesize the lipids necessary for growth, development, and reproduction. Most aphid species synthesize fatty acids *de novo*, and myristic acid is usually the most abundant of these fatty acids (Dillwith et al. 1993). There are two main steps involved in aphid fatty acid synthesis: (1) acetyl Co-A is converted by the multi-enzyme system acetyl Co-A carboxylase to malonyl Co-A; and (2) condensation of acetyl Co-A and malonyl Co-A units (catalyzed by fatty acid synthase and requires NADPH as a reducing agent) to produce long chain fatty acids. The fatty acid chains are elongated by two carbons for each complete condensation cycle. The enzyme thioesterase then releases either palmitic acid (16:0) or stearic acid (18:0). However, it is highly possible that thioesterase II cleaves fatty acids when they reach myristic acid (14:0). Thioesterase II has not been characterized in aphids, but is most likely present in most aphid species because of the abundance of myristic acid in aphids. Triglycerides, are reservoirs of fatty acids that store energy and serve as an energy reserve for many physiological processes (Dillwith et al. 1993). In the pea aphid, the stored lipids (triglycerides) are predominantly comprised of myristic acid (Dillwith et al. 1993, Neese 1995).

Most insects do not have the ability to synthesize sterols, therefore they need to acquire sterols in their diet (Clayton 1964, Minks and Harrewijn 1987), usually in the form of cholesterol. Several aphid species, however, have been reared through numerous generations on diets without cholesterol (Dadd and Krieger 1968, Ehrhardt 1968, Akey and Beck 1971, Srivastava and Auclair 1971, Minks and Harrewijn 1987). This indicates that a dietary supply of sterol is not required. Cholesterol in aphids is believed to be synthesized by bacterial symbionts, and it is assumed that this is available to the aphid in

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vivo (Ehrhardt 1968, Houk et al. 1976, Griffiths and Beck 1977, Minks and Harrewijn 1987). Campbell and Nes (1983) state that the primary role of the symbionts in aphid nutrition is not sterol synthesis but to aid in satisfying other nutritional requirements when aphids are under dietary stress (Minks and Harrewijn 1987). Unlike other aphid species, *A. pisum*, however, does not depend on endosymbionts for the biosynthesis of linoleic and myristic acids (de Renobales et al. 1986, de Renobales et al. 1990).

Response of Aphididae to Host Plants

Biochemical processes of aphids are significantly influenced by host plant species (Bergman et al. 1990, Dillwith et al. 1993). Suitability of diet can be estimated by aphid growth and reproductive rates (Bommarco and Ekbom 1996). Better nutrition of a host plant often yields larger aphids with greater reproductive potential (Minks and Harrewijn 1987). Aphids respond to lower quality host plants by storing energy in the form of lipids rather than expending the energy through reproduction (Bergman et al. 1990). When host plants are not highly suitable, aphids respond by reducing the turnover of storage fatty acids (Dillwith et al. 1993, Neese 1995). This response may allow aphids to survive when more suitable host plants become scarce or host nutrients are difficult to acquire, which often occurs during crowding (Minks and Harrewijn 1987, Dillwith et al. 1993).

The effect of host plant on aphid fatty acid composition has been documented for several aphid species. Dillwith et al. (1991) revealed that the spotted alfalfa aphid, *Therioaphis maculata* (Buckton), had higher triglyceride levels, when feeding on less suitable alfalfa cultivars or hosts with increased host plant resistance, than when on an optimal host. When feeding on more suitable hosts, the aphids do not store as much

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energy in the form of triglycerides, but instead devote the energy to growth and reproduction (Dillwith et al. 1991).

Acyrthosiphon pisum can survive and reproduce on several leguminous plants, however its biological and biochemical processes, including lipid utilization, and storage, are significantly influenced by host plant quality (Brown et al. 1969, Pimentel and Wheeler 1973, Karner and Manglitz 1985, Bergman et al. 1990, Hodek 1993, Dillwith et al. 1993, Neese 1995, Bommarco and Ekbom 1996). Pea aphids reared on alfalfa (c.v. 'OK08') have a mean fatty acid content of 30.7 μg/mg, whereas those reared on faba bean (c.v. 'Windsor') have a mean fatty acid content of 22.5 μg/mg (Neese 1995). These differences in the total fatty acid content of aphids from different host plants are primarily effected by differences in myristic acid levels (Neese 1995). For pea aphids reared on alfalfa, the lipid content is comprised of approximately 56% myristic acid, whereas those reared on faba beans have a lipid content with an average of 29% myristic acid (Bergman et al. 1990, Neese 1995). The difference in the myristic acid component is due primarily to metabolic responses of the aphids with respect to the suitability of the host (Bergman et al. 1990). Pea aphids reared on alfalfa store more lipids as triglycerides than pea aphids reared on faba bean (Neese 1995). These results indicate that on a more suitable host, pea aphids direct their energy into reproduction and on a less suitable host, the energy is stored in lipid reserves (Dillwith et al. 1993).

Temperature may also alter the physiological condition of the host plant and thus alter the physiology and biochemistry of the aphid (Minks and Harrewijn 1987). For instance, pea aphids reared on faba beans at 10°C have approximately four times the fatty

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acid content of those reared at 22°C (J. Dillwith, unpublished data, K.L. Giles, unpublished data).

Plants differ in the nature and quantity of toxic substances in their phloem, which may negatively effect aphids. Often, aphids are able to manipulate these substances to their benefit. For instance, both *Aphis cytisorum* Hartig and *Aphis nerii* (Boyer de Fonscolombe) sequester host plant defensive chemicals, including alkaloids and cardenolides, as a defense against predation (Minks and Harrewijn 1987).

Coccinellidae

Biology and Life History of Coccinellidae. Adults of Coccinellidae are most often oval, ranging in length from 0.8 to 18 mm, and are commonly three times as long as wide. The ventral surface is flat whereas the dorsal surface is convex (Minks and Harrewijn 1987). Coccinellids have five visible abdominal sternites, clubbed antennae, and their tarsi are divided into four segments on all six legs; the third segment is concealed by the bi-lobed second segment (Hodek and Honek 1996). The compound eyes are partially obscured due to a dorsal, forward-projecting part of the thorax that covers part of the head. Several species can release a bitter yellow defense fluid from glands near the tibial-trochantal joint (Minks and Harrewijn 1987).

Coccinellids have chewing mouthparts composed of heavily sclerotized mandibles, maxillae and labia with well-developed palpi and sensory structures (Minks and Harrewijn 1987). Both adults and larvae have functional eyes, although prey are detected only after contact. Most researchers agree that coccinellids rely solely on tactile stimulation with their maxillary palpi to recognize prey and initiate attack behaviors. The position of the forelegs in larvae may also serve as a sensory mechanism, channeling prey

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towards the palpi; adult forelegs do not appear to assist in prey capture (Storch 1976, Minks and Harrewijn 1987).

The first copulation does not take place until a few of days after emergence. For most species, just one copulation is sufficient to last the reproductive life of females, but adults commonly mate several times (Hodek and Honek 1996, Semyanov 1970). To maximize fitness, lady beetles must compromise between maximizing the number of eggs produced and increasing the survivorship of offspring (Hodek and Honek 1996). Fitness of larvae is correlated with egg size; the smaller the egg, the less likely survivorship becomes (Hodek and Honek 1996). In sub-optimal conditions, females may either preserve egg size and lessen the number of eggs laid, or decrease the size of the eggs and keep their number the same (Hodek and Honek 1996). However, Coccinellidae tend to preserve egg size and quality and therefore decrease the number of eggs oviposited when conditions deteriorate (Hodek and Honek 1996).

Coccinellidae commonly deposit their eggs on a substrate in batches, near a source of prey for the larvae (Hodek and Honek 1996, Obrycki et al. 1997). The time devoted to oviposition varies among species. Kawauchi (1991) showed that *Coccinella septempunctata*, *Propylea japonica* (Thunberg), and *Scymnus hoffmani* (Weise) had mean ovipositioned periods of 66, 77, and 49 days and produced a mean of 1660, 1481, and 110 eggs, respectively. Upon eclosion, larvae remain on the egg mass and consume unhatched eggs and dead larvae; occasionally they exhibit cannibalism of larvae. Typically, there are four instars, although some species may complete five instars (Hodek and Honek 1996).

For Coccinellidae there is only a slight amount of variation in the amount of time spent in each instar. Developmental time is shorter in species with larger eggs than those with smaller eggs (Stewart et. al. 1991). On average, healthy larvae spend approximately 23.7% of larval developmental time in the first instar, 16.9 % in the second, 19.3% in the third, and 39.7% in the fourth (Hodek and Honek 1996). The greatest food consumption and growth rate of the larvae occur during the last instar (Hodek and Honek 1996).

The later larval stages are more efficient in capture of prey than in small larvae. Adults are also generally less efficient predators than fourth instars (Hodek and Honek 1996). The voracity of larvae is dependent upon both the growth rate of the larvae and how effectively they can assimilate food (Hodek and Honek 1996). The weight of larvae fed an unlimited amount of food increases linearly with time (Mills 1981, Hodek and Honek 1996). Both growth rate and efficiency of food assimilation vary among species and with environmental factors such as temperature (Hodek and Honek 1996). According to one study, the average proportion of food intake (expressed as a percentage of the total food consumed during larval growth) for first instars is 5.9%, 11.1% for the second instars, 21.2% for third instars, and 61.8% for fourth instars (Okrouhla et al. 1983).

Larvae must reach a critical size before pupation can occur (Hodek and Honek 1996). The final instar uses its anal organ to attach to a substrate for pupation. Pale teneral adults emerge from the pupa and depending on temperature, attain full adult coloration after a couple of days.

Adult size may be determined by differences in larval size before pupation, or the growth rate during the latent period, or a combination of both (Hodek and Honek 1996).

Adult size differs slightly among individuals of the same species due to genetic differences, such as sex, even when larvae are in optimal environments (Hodek and Honek 1996). When larvae suffer adverse conditions, the variation in adult size increases considerably. Factors that ultimately affect adult size are food, temperature, and population density during the larval stages of development (Hodek and Honek 1996).

Lady beetles develop through one or several generations per year depending on temperature and prey availability (Hodek and Honek 1996). Most overwinter as adults in reproductive diapause and some *Coccinella* species and *Hippodamia* species overwinter in large aggregations (Minks and Harrewijn 1987). Most adults survive approximately one year in the field (Minks and Harrewijn 1987).

Suitability of Prey. Two categories of hosts for lady beetles may be described: those that are essential for completion of larval development and oviposition, and alternative foods that provide only a source of energy to prolong survival and prevent starvation (Hodek 1962, Hodek 1967, Mills 1981, Hodek 1993). Among essential hosts, some may be more optimal than others, providing for increased survival, developmental rates and fecundity (Hodek and Honek 1996). Alternative hosts may range from those being highly toxic to those being somewhat suitable in terms of survival in times of low prey densities or when essential hosts are unavailable (Hodek and Honek 1996). For instance, Blackman (1965, 1967) revealed that *Adalia bipunctata* (Linnaeus) can develop on *Aphis sambuci*, but has a substantially lower survival rate and weight of adults then when feeding on any of four essential prey. *Acyrthosiphon pisum* is considered to be more nutritious than *Aphis fabae* for *A. bipunctata* (Hariri 1966, Hodek and Honek 1996). This may be due to how easily *A. pisum* is assimilated or the lower nutritive value of *A.*

fabae. It may also be a combination of the two factors; nutritive value is low because an essential nutrient is unable to be easily assimilated by the predator (Blackman 1967; Hodek and Honek 1996).

There are a variety of acceptable prey for many Coccinellidae. The wide range of prey eaten by lady beetles led to the assumption that they are mainly generalists and food specificity exists only among major taxonomic groupings (Hodek and Honek 1996). Although many lady beetles are considered generalist predators in terms of accepted prey, they are primarily aphidophagous with regard to essential prey. Coccinellidae biology is negatively effected by consuming nutritionally less suitable prey. Adult *A. bipunctata* reared on *A. fabae* as larvae had low fecundity and low weight. When analyzed, these lady beetles had fairly low fat and glycogen contents. *Rhopalosiphum* (Lipaphis) *erysimi* may be a more suitable prey item than others for *C. septempunctata* due to its higher protein content (Atwal and Sethi 1963; Hodek and Honek 1996).

Environmental factors, such as temperature, may affect the amount of developmental time spent in each instar. Under controlled temperatures, lady beetle pre-imaginal developmental time may be used to estimate prey suitability. Obrycki and Orr (1990) investigated the effect of 2 aphid species (*Acyrthosiphon pisum and Rhopalosiphum maidis*) on the development of seven species of lady beetles, and found that the relative length of stadia varied significantly with prey species. Prey classified as unsuitable increased total developmental time. The exact cause of the variation is unknown, but is hypothesized to be caused by differences in the ability to assimilate food.

Eleven strains of five lady beetle species (*Adonia variegata* (Goetze), *C. septempunctata, Hippodamia tredecimpunctata* (Linnaeus), *Propylea*

quatuordecimpunctata (Linnaeus), and *Semiadalia undecimnotata* (Schneider) and two essential aphid species (*Diuraphis noxia* and *Schizaphis graminum*) were tested for suitability (Michaels and Flanders 1992). Among strains of the same species there were differences in larval development rates, larval survival rates, food consumption rates, and fecundity, indicating different levels of suitability of prey within populations of Coccinellidae.

Effects of Prey Level. Allocation of energy to growth or reproduction of Coccinellidae may depend on the quantity of food consumed (Hodek and Honek 1996). Beetle age and weight also affects energy allocation. With unlimited prey, larvae allocate all energy to body growth and necessary metabolic activities, and adults allocate energy into reproduction and metabolic activities. With limited amounts of food, lady beetles first partition energy into the basic costs of metabolism (i.e. maintaining life). Any remaining energy may be allocated to growth or reproduction (Hodek and Honek 1996).

In a laboratory study, one large *A. pisum* per day (average weight of 3.02 mg) has been shown to be sufficient for some individuals of both *C. septempunctata* and *C. maculata* to complete larval development (Ormond 1994, Obrycki et al.1997). When prey availability is increased to two aphids per day, survival is increased from 33.0% to 83.0% for *C. septempunctata* and from 63.0% to 78.9% for *C. maculata* (Ormond 1994, Obrycki et al. 1997).

Coccinellidae are able to complete development on only a fraction of the amount of prey for optimal development, however, developmental time typically increases and the pupae and adults are usually much smaller in size and mass (Hodek and Honek 1996). For example, *Harmonia axyridis* (Pallas) and *Propylea japonica* (Thunberg) grow more

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rapidly, achieve a higher weights, and exhibit increased survival rates with increasing availability of prey (Hukusima and Ohwaki 1972, Kawauchi 1979). Developmental times decreased and body size increased considerably in *Anatis mali* provided with increased quantities of food (Smith 1965). Developmental times decreased and body size increased for *C. maculata lengi* adults provided with increasing larval food quantities (dried *A. pisum*), but remained relatively constant after approximately 10 mg of dry prey (Smith 1965*). Anatis mali* shows more elasticity than *C. maculata lengi* in its capacity to adjust developmental rate and adult size to changes in food availability (Smith 1965). *Anatis mali* larvae fed an unlimited amount of food nearly doubled in adult weight (Smith 1965).

The amount of time spent in each instar varies with respect to food availability (Obrycki and Orr 1990). For instance, *A. bipunctata* larvae fed an unlimited amount of food (at 14 °C) had stadial lengths of 8.7, 5.6, 5.8, and 10.3 days, for the first through fourth instars, respectfully. With lower quantities of food, stadia were 17.7, 23.9, 14.7, and 35.6 days, respectively (Wratten 1973). A study conducted with *Hippodamia quinquesignata* (Kirby) yielded similar results (Kaddou 1960); individuals fed 1.2 aphids per day had a mean larval developmental time of 27.0 days, while those fed 15.5-29.5 aphids per day had a mean developmental time of only 8.1-8.5 days. Growth rates (accumulation of dry weight) of *A. bipunctata* larvae increase linearly with increasing amounts of food while developmental time decreases non-linearly. The quantity of food necessary to cover basal metabolic costs increases with each successive instar (Mills 1981). Although the amount of food consumed by *Hippodamia convergens* can influence

growth rate, the size of each instar is decreased only by extreme food scarcity (Hodek and Honek 1996).

Oviposition is also slowed by starvation (Hodek and Honek 1996). A 3.5 fold increase in daily consumption of the prey *Aphis gossypii* decreased the length of preoviposition time for *P. japonica* from 9.6 days to 4.3 days (Kawauchi 1981). For *H. convergens* reared on 1.2 mg food/ mg adult weight, the preoviposition period decreased by 6 days in comparison to those reared on 0.2 mg food / mg adult weight (Gutierriez et al. 1981).

Ferran et al. (1984) found a linear relationship between the weight of food consumed by *Semiadalia undecimnotata* (Schneider) and the number of eggs deposited in a 15-day period. The number of eggs laid by *C. septempunctata* is also directly proportionate to food consumption (Rhamhalinghan 1987). Although the consumption of prey influences the number of eggs deposited, it rarely influences egg size. Food availability only slightly influences the average size of each egg for *P. japonica*, however, egg distribution was substantially different (Kawauchi 1981).

The amount of food eaten by a lady beetle also affects sexual receptivity. Obata and Hidaka (1987) revealed that females reared on honey refused 46% to 80% of male copulation efforts and laid an average of 12-16 eggs per day while females reared on aphids rejected only 5% to 36% of male attempts and laid an average of 32-37 eggs per day.

Hippodamia convergens and *Coleomegilla maculata*

Hippodamia convergens adults are orange in color and usually have 12 black spots on the elytra (Chedester 1979, Hodek and Honek 1996). Eggs are yellow-orange in

color and are laid individually or in clusters. *Hippodamia convergens* larvae are black with pointed abdomens and orange stripes across the back. The ventral portion of the abdomen in adult male *H. convergens* is constricted at the fifth abdominal sternite at the medial portion of the segment, whereas the width of the fifth sternite is uniform in adult females (Chedester, 1979).

The ovipositional period begins from 7 and 15 days after mating (Chedester 1979). Both adult and larval *H. convergens* feed primarily on aphids (Chedester, 1979). Larvae consume up to 25 aphids per day while adults can consume about 56 / day (Clausen 1916, Chedester, 1979). *Hippodamia convergens* develops through four instars and was reported to develop from egg to adult in approximately 17 days when supplied with unlimited spotted alfalfa aphids, *T. maculata* (Simpson and Burkhardt 1960, Chedester, 1979). Chedester (1979) revealed that at $18°$ to $22°$ C, on a limiting diet of 25 greenbugs per day, *H. convergens* could complete development from egg to adult on average, in 32.7 days. The average larval development was completed in 21.4 days. The average egg incubation period and pupation period was 3.8 days and 7.5 days, respectively. On a diet of 25 greenbugs per day, with temperatures ranging between $22°$ and $30°$ C, *H. convergens* completed development from egg to adult in 27.7 days; and larval development required only 15.9 days. The egg incubation period was 3.5 days and pupation period 8.3 days (Chedester, 1979).

For H. convergens, required degree-days above a threshold of 12°C to complete pre-imaginal development was reported as 230 by Obrycki and Tauber (1982). The optimum temperature for survival and developmental rates is 24°C (Obrycki and Tauber 1982).

Coleomegilla maculata is a dark pink lady beetle with black spots on its elytra. Spindle-shaped oval yellow eggs are often laid in clusters and may be laid unattached or attached to a substrate. Larvae have elongated bodies and are black with yellow or orange markings. Eggs usually hatch within three or four days. Typically, *C. maculata* complete four larval instars with an occasional fifth instar completed (Hodek and Honek 1996). *Coleomegilla maculata* pupation period is between 3 and 12 days, depending on temperature. Adults may live from several months to over a year (Hodek and Honek 1996).

Coleomegilla maculata requires an accumulated 236 degree-days above 11.3 °C to complete pre-imaginal development from egg to adult emergence (Obrycki and Tauber 1978). The optimum temperature range for survival and development of *C. maculata* is between 24°C and 26.7 °C (Obrycki and Tauber 1978).

Coleomegilla maculata is a euryphagous lady beetle (one that is able to subsist on a wide variety of foods), whereas *Hippodamia convergens* is stenophagous (feeding on a limited variety of foods, primarily aphids) (Hodek 1973, Hagen 1987, Hodek and Honek 1996). In laboratory settings, *Coleomegilla maculata* is able to complete development on food items such as aphids, artificial diets, eggs, pollen, and powdered aphids (Hodek 1973, Giles 1992, Hodek and Honek 1996). However, *H. convergens* is primarily aphidophagous, surviving only on aphids, dry powdered aphids, and a few artificial diets (Hodek 1973, Hagen 1987, Hodek and Honek 1996). Both species can successfully reproduce and complete development on a diet of *A. pisum* (Hodek 1973, Obrycki and Tauber 1982, Hagen 1987, Giles et al. 1994, Hodek and Honek 1996). Obrycki et al. (1997) measured *C. maculata* mortality rates in spring of 1992 in an Iowa alfalfa field

containing *A. pisum*. First, second and third instars had mortality rates of 70.1%, 65.4%; and 32.1%, respectively. First through third instar mortality was 93.0%. In a similar study with *A. pisum*, the mortality of larval *H. convergens* ranged from 19% to 98%, most of the mortality occurring in the first and second instars (Kirby and Ehler 1977).

When supplied with an unlimited diet of *A. pisum*, *C. maculata* completed larval development in 13.7 days at 21.9°C (Smith 1965). Preimaginal developmental times for *C. maculata* supplied with 3.0 mg of *A. pisum* reared on *V. faba* cv. 'Windsor' was 26.7 days, whereas those supplied with unlimited *A. pisum* reared on *V. faba* decreased to 20.6 days (Obrycki et al. 1998). Larval developmental time for *H. convergens* supplied with an unlimited amount of *A. pisum* at 30°C was 14 days, the most time also being spent in the fourth instar (Rodriguez-saona and Miller 1999). Obrycki and Tauber (1982) found that with an unlimited supply of *A. pisum*, the average larval developmental time for *H. convergens* at 23°C was 12.0 days.

Coleomegilla maculata females supplied with an unlimited diet of *A. pisum* laid approximately 11.5 eggs per day and a mean total of 124.4 eggs (Phoofolo and Obrycki 1997). Field collected *H. convergens* supplied with an unlimited diet of *A. pisum* laid an average of 14.7 eggs per day and a mean total of 360.6 eggs (Rodriguez-saona and Miller 1994).

Tritrophic Interactions

Host plant effects (via consumption of prey) on the success of natural enemies has been shown in many ecological systems (Starks et al. 1972, Rice and Wilde 1989, Kareiva and Sahakian 1990, Campbell et al. 1992, Souissi and LeRu 1997, Bottrell et al. 1998, Giles et al. 2000). Host plant attributes can affect prey suitability by altering the

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access to prey, thus enhancing prey capture. Host plant chemical constituents can also affect prey suitability through acquired toxicity or poor nutritional value. Thus, a host plant (via consumption of prey) can alter the survival, development, weight, size, and fecundity of Coccinellidae (Kareiva and Sahakian 1990, Power 1992, Hodek and Honek 1996, Bottrell et al. 1998).

Understanding the dynamics of tritrophic interactions is necessary for predicting the degree of biological control among prey species. Plants respond chemically, morphologically, and physically to insect herbivory (Price 1997). These plant responses can affect herbivores by reducing growth and fecundity or even by killing them (Price 1997). Many researchers have suggested that host plants evolved these responses specifically for defense against herbivory (Price 1997). Additionally, these induced plant responses may also provide search cues for natural enemies and many researchers argue that plants evolved these defensive responses to attract insect natural enemies as a defense against herbivorous species (Faeth 1988, Faeth 1992).

The fitness and efficiency of predators feeding on herbivorous insects may be influenced by any plant feature that can affect growth, survivorship, and resistance to pathogens or fecundity (Bashir 1973, Price 1997). A host plant may increase effectiveness of biological control by releasing kairmones that attract predators of herbivores or by altered access to prey, thus enhancing prey capture (Faeth 1988). Plants may also influence predators indirectly by reducing or enhancing prey suitability (Price 1997).

Toxic Effects. There are two main possibilities why a particular aphid prey species may be toxic to certain Coccinellidae: (1) the aphids contain toxic substances, or

(2) they acquire them through host plant feeding. Many natural plant defense chemicals, which can be toxic or distasteful to predators, are sequestered by aphids (Birch et al. 1999). Plants differ in the nature and quantity of toxic substances accumulated in phloem and often, aphids utilize these substances for their benefit (Hodek and Honek 1996). Consequently, the population dynamics of a natural enemy species may be dramatically affected by feeding on prey populations among several host plants. For instance, both *C. septempunctata* and *P. japonica* die when fed naturally occurring *A. craccivora* in the spring, but survive in the summer. *Aphis craccivora* exploits a different host plant in the spring than in the summer; the host plant in the spring possibly contains a toxin the aphid is able to sequester (Takeda et al. 1964, Hodek and Honek 1996).

Antibiotic effects on predators often occur when aphids sequester toxins from host plants. Third instar *Megoura viciae* Buckton reared on *V. faba* are toxic to larval *Exochomus quadripustulatus* (Linnaeus) resulting in mortality within two days after feeding begins (Dixon 1958, Radwan and Lovei 1983, Hodek and Honek 1996). *Adalia bipunctata* (Linneaus) and *Adalia decempunctata* (Linneaus) avoid preying on *M. viciae* altogether. *Megoura viciae* was analyzed, but contained no compounds identified as toxins (Dixon 1958, Hodek and Honek 1996). *Aphis cytisorum* (Hartig) and *Aphis nerii* (Boyer de Fonscolombe) sequester host plant defensive chemicals, including alkaloids and cardenolides, which deter insect predators (Minks and Harrewijn 1987).

Antibiosis to entomophagous insects via aphids ingesting toxic substances from host plants is most commonly implicated as the causative factor for detrimental tritrophic effects. However, there is little quantitative evidence (van Emden and Wratten 1990, Hodek 1993, Hodek and Honek 1996, Price 1997, Bottrell et al. 1998). Okamoto (1966)

demonstrated that survivorship of *H. axyridis* varied greatly when prey were reared on different host plants. Larval *H. axyridis* were unable to survive on *Aphis craccivora* (=*medicaginis*) Koch reared on *V. faba*, but survived when *A. craccivora* were reared on *Robinia pseudoacacia.* Compounds that may be responsible for mortality in the former case are the amines canavanine and ethanolamine (Obatake and Suzuki 1985).

Nutritional Effects. Nutritive deficiency in prey as affected by host plants may decrease suitability for Coccinellidae (Hodek and Honek 1996). Differences in the nutritional content of prey may be attributed to plant quality, or it may be a result of altered biochemical processes in aphids in response to host plants (Bergman et al. 1990, Febvay et al. 1992, Dillwith et al. 1993, Neese 1995, Giles et al., in review). The effects of prey suitability have been studied extensively, however, very few studies have attempted to evaluate the nutritional effects on Coccinellidae (Smith 1965, Obrycki and Orr1990, Hodek 1993, Hodek and Honek 1996, Phoofolo and Obrycki 1997).

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CHAPTER III

PREIMAGINAL SURVIVAL AND DEVELOPMENT OF *COLEOMEGILLA*

MACULATA (DEGEER) AND *HIPPODAMIA CONVERGENS* GUERIN-MENEVILLE

(COLEOPTERA: COCCINELLIDAE) REARED ON *ACYRTHOSIPHON PISUM*

HARRIS: EFFECTS OF HOST PLANTS.

Abstract *Coleomegilla maculata* (DeGeer) and *Hippodamia convergens* Guerin-Meneville larvae were supplied daily with approximately 1.2, 2.2, 4.3, 8.2, or 16.4 mg of *Acyrthosiphon pisum* Harris reared on either *Medicago sativa* L. ('OK08') or *Vicia faba* L. ('Windsor') maintained at 22°C and a photoperiod of 16:8 (L:D). Myristic acid and total fatty acid content ($\mu g/mg$ aphid fresh weight) were confirmed to be 6.3 and 2.7 times greater, respectively, in *A. pisum* reared on *M. sativa* as compared to *V. faba*, resulting in a 1.17 fold increase in caloric content. Chi-square analysis indicated significant differences in survival between host plants at low daily prey levels (1.2 mg and 2.2 mg) for both *C. maculata* and *H. convergens*, but no differences were observed at higher prey levels. When *A. pisum* reared on *M. sativa* were supplied to *C. maculata* and *H. convergens* larvae at low prey levels, preimaginal developmental times were significantly reduced compared with those supplied with *A. pisum* reared on *V. faba* at the same prey levels. At higher daily *A. pisum* levels, *C. maculata* and *H. convergens* developmental times were not significantly different between host plants. At lower daily prey levels, *C. maculata* and *H. convergens* elliptical body area was larger when supplied with *A. pisum* reared on *M. sativa*, but similar in body area at higher daily prey levels. Convergence of survival ratios, developmental times, and body areas for *C. maculata* and *H. convergens* at high (less limiting) prey levels supports the hypothesis that differences in prey nutritional value between *A. pisum* reared on *M. sativa* and *V. faba* are quantitative and appear to be primarily influenced by differences in *A. pisum* myristic acid content.

Introduction

Because plants can affect third trophic level processes, understanding the interactions among plants, herbivores, and predators is necessary when predicting predator-prey relationships (Faeth 1992). Plants may influence predators through effects on herbivore population density, by altering the access to herbivores and increasing prey capture; or by changing suitability of herbivorous prey (Price 1997). Chemical constituents of plants may result in toxic or nutritionally unsuitable herbivorous prey, and may affect predator populations by increasing mortality, increasing developmental times, or reducing fecundity (Power 1992). Despite evidence that plants affect third trophic level processes, very few studies have investigated the mechanisms of these tritrophic interactions (Hodek and Honek 1996, Obrycki and Kring 1998).

Pea aphid, *Acyrthosiphon pisum* Harris, growth and reproductive performance varies with respect to host plant (Bergman et al. 1990). *Acyrthosiphon pisum* reared on faba beans (*Vicia faba* L. c.v. 'Windsor') are larger and reproduce faster than those reared on alfalfa (*Medicago sativa* L. cv. 'OK08') (Bergman et al 1990). Biochemical processes for *A. pisum*, including fatty acid storage, are influenced greatly with varied plant species and cultivars (Bergman et al. 1990, Febvay et al. 1992, Dillwith et al. 1993). Pea aphids reared on *M. sativa* store significantly more energy in the form of triglycerides, as compared to those reared on *V. faba*. Two to six fold increases in myristic acid content (μg/mg of aphid) are primarily responsible for the increase in total fatty acid for *A. pisum* reared on *M. sativa* (Bergman et al. 1990, Neese 1995, Giles et al. 2000). These differences in myristic acid content are primarily due to metabolic responses of the aphids in response to variations in suitability of host plants.

Differences in the nutritional quality of host plants can affect herbivore versus predator interactions and monitoring the nutritional changes of herbivorous prey is essential for evaluating prey suitability for predators (Giles et al. 2000). Myristic acid storage influences the caloric content and thus nutritional value of *A. pisum* and may have an effect on the population dynamics of predators (Giles et al. 2000). For example, Bashir (1973) demonstrated that higher levels of myristic acid in artificial diets promote faster developing larvae, increased size of adults, and higher fecundity for *Olla abdomalis* Say (Coleoptera: Coccinellidae). The effect of *A. pisum* on survival and development of Coccinellidae has been evaluated for several species (Hodek and Honek 1996, Obrycki et al. 1998). However, little is known about the effects of host plants on nutrient content of *A. pisum*, and subsequent population dynamics of Coccinellidae.

The goal was to describe interactions of *A. pisum* with each of two species of Coccinellidae as influenced by host plant (*M. sativa* or *V. faba*). Specifically, I evaluated the role that varied myristic acid sequestration in *A. pisum*, as influenced by host plants, has on the survival and development of *Coleomegilla maculata* (DeGeer) and *Hippodamia convergens* (uerin-Meneville).

Both *H. convergens* and *C. maculata* can survive, develop, and reproduce *on A. pisum*. *Hippodamia convergens* and *C. maculata* were chosen for this study because of their differences in prey specificity; *H. convergens* is primarily aphidophagous *and C. maculata* is polyphagous (Hodek and Honek 1996). This comparison in prey specificity may help to determine whether the observed differences in prey nutritional value derived from different host plants has a greater effect on more host specific predators as opposed to more generalist predators.

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Increasing prey levels (mg *A. pisum*/day) from aphid colonies on different host plants were evaluated in an effort to limit prey and evaluate if differences in prey nutritional value were quantitative or qualitative. Quantitative differences in prey nutritional value are simply differences in the total available useable calories as influenced by changes in nutritional components such as myristic acid. Qualitative differences in prey nutritional value occur when less suitable prey lack essential nutrients or contain compounds that may be toxic to predators. For my study, quantitative differences in nutritional value of *A. pisum* reared on the two host species would be evident if survival and development of *C. maculata* and *H. convergens* differed depending upon aphid host plants (*M. sativa* and *V. faba*) at low (limiting) prey levels, but were similar at high (less limiting) prey levels.

Materials and Methods

Aphid and coccinellidae colonies. Pea aphids were reared on *V. faba* L. cv. 'Windsor' and used as the infestation source for a colony maintained on *M. sativa* cv. 'OK08'. Aphid colonies were maintained on their respective host plants in separate growth chambers at 22°C and a photoperiod of 16:8 (L: D). Periodic analysis of fatty acid content was performed using gas chromatography (Bergman et al. 1991) on samples from each colony (n = 15-22 samples of ten-aphids) to measure variability within colonies during the experiment. Bomb calorimetry was used to measure caloric content of *A. pisum* from both colonies (n = three 5-g samples per colony). Protein content for *A. pisum* from each colony was quantified using proximate analysis (Official A. O. A. C. methods) (n = three pooled 5-g samples from each colony).

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Adult *C. maculata* and *H. convergens* were collected from alfalfa fields. Twenty

mating pairs of *C. maculata* and 16 pairs of *H. convergens* were maintained in half-pint

cardboard ice cream containers with a fine mesh cover in a chamber at 24°C and a

photoperiod of 16:8 (L: D). Each pair was provided daily with an unlimited supply of *A.*

pisum reared on faba beans, a moist cotton ball, and a supplementary diet of wheat-yeast-

honey mixture.

Lady Beetle Feeding Studies. Eggs from each female were collected daily,

placed in 5-ml glass vials stopped with cotton, and incubated in a table-top environmental

chamber at 24°C and a photoperiod of 16:8 (L:D). Upon eclosion, larvae reaching the

second instar were placed individually in vials stopped with cotton and fed one of the

following daily diet treatments (mean ± SE): 2 aphids (1.2 ± 0.03 mg), 4 aphids (2.2 ±

0.06 mg), 7 aphids (4.3 ± 0.12 mg), 14 aphids (8.2 ± 0.18 mg), or 28 aphids (16.4 ± 0.28

mg) per day reared on *M. sativa*, or 1 aphid (1.2 ± 0.06 mg) 2 aphids (2.1 ± 0.05 mg), 5

aphids (4.3 ± 0.09 mg), 10 aphids (8.2 ± 0.06 mg), or 20 aphids (16.4 ± 0.24 mg) reared

on *V. faba*. For similar dietary treatments, the weights of *A. pisum* provided per day from

M. sativa did not differ significantly ($P = 0.473$) from the weights of the aphids reared on

V. faba. Consistency of weights of aphids from each colony was maintained by weighing

samples of aphids throughout the experiment. To eliminate potential difficulties in prey

finding at the first instar, only larvae that survived to the second instar were used for this

study. A total of 54 individuals (second instars) were assigned to each treatment.

Because the fatty acid composition of pea aphids does not significantly vary

significantly among apterous life stages from either host plant (Neese 1995), apterous

adults and late (4th) stage nymphs were used as prey. I carefully used a consistent size of

aphid for feeding. Approximately 16 mg (16.4) was chosen as the highest daily prey level because it represented an adequate diet for maximal developmental rates but is well below the daily consumption capabilities of these predators (Obrycki and Orr 1990, Hodek and Honek 1996, Obrycki et al. 1998). All aphids for each treatment were consumed within 24 hours by the lady beetles at the fourth instar. This upper prey level (16.4 mg) eliminates the effects of satiation and allows the effect of prey levels to be analyzed quantitatively. I randomly assigned larvae from all parental lines to all treatments.

The larvae were checked daily to record mortality, molting, pupation, and adult emergence. Mean survival and developmental times for each life stage were calculated for each treatment. Upon adult emergence, sex was determined, and body length and width were measured. Body length and width were used to calculate elliptical body area [Π $\times 1/2$ (body length) $\times 1/2$ (body width) (Obrycki et al. 1998)].

Statistical Analysis. All analyses were performed using SAS version 6.12 for windows (SAS Institute 1996). A 0.05 significance level was chosen for all statistical analyses. Total fatty acid and myristic acid contents were compared among aphids from both colonies by analysis of variance (PROC MIXED). PROC MIXED was used because it does not assume equal variance among treatments.

Ratios for larval survival, pupal survival, preimaginal survival and sex were compared among treatments and between host plants using χ^2 analysis (PROC FREQ) or Fisher's exact test (two-tailed) when 50% of the cells had expected counts less than 5.

Developmental times (days) and adult body area (mm^2) among treatments were analyzed by analysis of variance (PROC MIXED). PROC MIXED was used because it supplies an ANOVA with both random and fixed effects. Because parental line may be a

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source of experimental error, parent line was included in analyses as a random factor. The data were pooled for analysis because preliminary analysis showed no significant interactions for sex of adults or parental line on developmental times and adult body area. Linear relationships among developmental times, adult body area and mg of aphids per day were analyzed by regression analysis (PROC GLM) for each host plant.

Voucher Specimens. Voucher specimens (*C. maculata* and *H. convergens* adults) are deposited in the Department of Entomology and Plant Pathology museum at Oklahoma State University, Stillwater.

Results

Aphid colonies. There were significant differences between aphids from alfalfa versus faba bean both in total fatty acid ($F = 53.17$; df = 2, 24; $P < 0.001$) and myristic acid ($F = 38.27$; df = 2, 24; $P = 0.001$) content (Table 1). *Acyrthosiphon pisum* reared on *M. sativa* had an average (± SE) total fatty acid content of 17.96 ± 1.7 µg per mg and an average myristic acid content of 12.62 ± 1.4 µg per mg fresh weight. The average total fatty acid and myristic acid content for *A. pisum* reared on *V. faba* was 6.59 ± 0.4 and 2.01 ± 0.3 µg per mg, respectively. The calorie content of *A. pisum* also varied significantly acid ($F = 259.01$; df = 2, 6; $P < 0.001$). For *A. pisum* reared on *M. sativa*, the average (± SE) calories per mg of aphid fresh weight was 1.195 ± 0.009. For aphids reared on *V. faba*, the average (± SE) calories per mg of aphid fresh weight was 1.021 ± 0.029. Proximate analysis of pooled samples revealed that *A. pisum* reared on *M. sativa* contained 10.9 percent protein and those reared on *V. faba* contained 10.6 percent protein.

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Coleomegilla maculata **survival and sex ratio.** *Coleomegilla maculata* survival increased with increasing daily prey levels from both host plants. Chi-square analysis with Fisher's exact test indicated a significant difference in the ratio of surviving *C. maculata* larvae with varied prey levels, but no significant differences between host plants at any one prey level (Tables 2 and 3). Chi-square analysis with Fisher's exact test indicated a significant difference among prey levels in pupal and preimaginal survival for *C. maculata*. There were also significant differences in pupal ($\chi^2 = 8.472$; df = 1; $P = 0.004$) and preimaginal survival ($\chi^2 = 8.704$; df = 1; $P = 0.003$) between host plants for the 1.2-mg prey levels (Tables 2 and 3). Larval, pupal and preimaginal survival ratios increased greatly before plateauing across the 8.2 and 16.4-mg prey levels (Table 3). Chi-square analysis with Fisher's exact test indicated a significant difference among all prey levels in the ratio of *C. maculata* females, however there were no significant differences between host plants (Tables 2 and 3).

Hippodamia convergens **survival and sex ratio.** As daily prey levels from both host plants increased, so did *H. convergens* survival. Chi-square analysis with Fisher's exact test indicated significant differences among prey levels in the ratio of surviving *H. convergens* larvae reared on faba beans, however no significant effects of prey level were detected for *H. convergens* larvae reared on alfalfa (Table 2). There were significant differences among prey levels in the ratio of *H. convergens* surviving the pupal stage and total preimaginal survival for both host plants (Table 2). Chi-square analysis with Fisher's exact test indicated significant differences in *H. convergens* larval, pupal and preimaginal survival between host plants at the lower prey levels (Table 4). There were significant differences between host plants in larval, pupal and preimaginal survival for the 1.2 mg

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prey levels ($\chi^2 = 37.133$; df = 1; $P < 0.001$; $\chi^2 = 8.975$; df = 1; $P = 0.003$; $\chi^2 = 33.753$; df

= 1; $P < 0.001$, respectively) and significant differences in larval and preimaginal survival

for the 2.1 or 2.2 mg prey levels ($\chi^2 = 7.053$; df = 1; $P = 0.008$; $\chi^2 = 7.782$; df = 1; $P =$

0.005, respectively; Table 4). Larval, pupal and preimaginal survival ratios increased

greatly before plateauing between the 8.2 and 16.4-mg prey levels (Table 4). Chi-square

analysis with Fisher's exact test indicated a significant difference among prey levels in the

ratio of *C. maculata* females, however there were no significant due to source of aphids

(Tables 2 and 4).

Coleomegilla maculata development. For *C. maculata*, larval and total

preimaginal developmental times were significantly different among daily prey levels and

between host plants, and the interaction between host plants and daily prey level was

significant (Table 5; Figs. 1 and 2). There was a significant curvilinear relationship of

decreasing developmental times and increasing prey levels from both alfalfa (larval: $r^2 =$

0.561; df = 2, 192; $P < 0.0001$; preimaginal: $r^2 = 0.506$; df = 2, 200; $P < 0.0001$) and faba

beans (larval: $r^2 = 0.713$; df = 2, 182; $P < 0.0001$; preimaginal: $r^2 = 0.600$; df = 2, 202; $P <$

0.0001; Figs. 1 and 2).

At the 1.2-mg ($P < 0.0001$), 2.1 or 2.2-mg ($P < 0.0001$) and 16.4-mg ($P =$

0.0343) daily prey levels, larval developmental times were significantly reduced for *C.*

maculata supplied with *A. pisum* reared on *M. sativa* versus *V. faba* (Fig. 1). Total

preimaginal developmental times were shorter for *C. maculata* supplied the 1.2-mg ($P < 0.$

0001), 2.1 or 2.2-mg ($P < 0.0001$) and 4.3-mg ($P = 0.0099$) daily prey levels with aphids

from alfalfa (Fig. 2). The minimum number of days (± SE) required for larval and

preimaginal development for *C. maculata* supplied with *A. pisum* reared on alfalfa were

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13.2 ± 0.4 and 20.7 ± 0.4, respectively (16.4-mg daily prey level; Figs. 1 and 2). The

maximum number of days were 23.2 ± 0.5 and 29.5 ± 0.5, respectively (1.2-mg daily prey

level; Figs. 1 and 2). The minimum number of days (± SE) required for larval and

preimaginal development for *C. maculata* supplied with *A. pisum* reared on faba beans

were 14.2 ± 0.4 and 21.6 ± 0.4, respectively (16.4-mg daily prey level; Figs. 1 and 2). The

maximum number of days were 27.4 ± 0.6 and 33.4 ± 0.8, respectively (1.2-mg daily prey

level; Figs. 1 and 2).

For *C. maculata* supplied with *A. pisum* from either of the colonies, pupal

developmental times (days ± SE), which ranged from 4.3 ± 0.2 to 5.1 ± 0.3, were not

significantly different among daily prey levels or between host plants, and no significant

interactions were detected (Table 5).

***Hippodamia convergens* development.** For *H. convergens* supplied *with A.

pisum* reared on either alfalfa or faba beans, larval and total preimaginal developmental

times were different among daily prey levels and between host plants and interactions

among host plants and daily prey levels were significant (Table 5; Figs. 3 and 4). There

was a significant curvilinear relationship of decreasing developmental times with increasing

prey levels from both alfalfa (larval: $r^2 = 0.669$; df = 2, 218; $P < 0.0001$; preimaginal: $r^2 =$

0.622; df = 2, 211; $P < 0.0001$) and faba (larval: $r^2 = 0.685$; df = 2, 187; $P < 0.0001$;

preimaginal: $r^2 = 0.703$; df = 2, 174; $P < 0.0001$; Figs. 3 and 4).

At all prey levels, larval ($P < 0.0001$) and preimaginal ($P < 0.0001$) developmental

times were significantly shorter for *H. convergens* supplied with *A. pisum* reared on alfalfa

versus faba beans (Figs. 3 and 4). The minimum number of days (± SE) required for larval

and preimaginal development for *H. convergens* supplied with *A. pisum* reared on alfalfa

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were 11.2 ± 0.5 and 19.9 ± 0.5, respectively (16.4-mg daily prey level; Figs. 3 and 4). The maximum number of days were 23.2 ± 0.5 and 31.3 ± 0.5, respectively (1.2-mg daily prey level; Figs. 3 and 4). The minimum number of days ($\pm$ SE) required for larval and preimaginal development when supplied with *A. pisum* reared on faba beans were 12.3 ± 0.4 and 21.1 ± 0.5, respectively (16.4-mg daily prey level; Figs. 3 and 4). The maximum number of days were 31.9 ± 0.7 and 40.2 ± 1.0, respectively (1.2- mg daily prey level; Figs. 3 and 4).

For *H. convergens* supplied with *A. pisum* from either alfalfa or faba beans, pupal developmental times (days $\pm$ SE) which ranged from 5.2 ± 0.2 to 6.1 ± 0.3 were not significantly different among daily prey levels or between host plants, and no significant interactions were detected (Table 5).

***Coleomegilla maculata* body size.** For *C. maculata* supplied with *A. pisum* reared on *M. sativa* or *V. faba*, adult elliptical body area (mm^2) significantly differed between host plants and among daily prey levels and a significant interaction between daily prey level and host plants was detected (Table 5, Fig. 5). There was a significant curvilinear relationship of increasing body area and increasing prey levels from alfalfa ($r^2 = 0.299$; df = 2, 182; $P < 0.0001$) and faba beans ($r^2 = 0.530$; df = 2, 195; $P < 0.0001$; Fig. 5).

At the 2.1or 2.2-mg and 4.3-mg daily prey levels, body area was significantly larger for *C. maculata* supplied with *A. pisum* reared on alfalfa ($P < 0.0090$; Fig. 5). For those supplied pea aphids reared on alfalfa, body area ranged from 14.4 ± 0.4 (16.4-mg daily prey level) to 9.5 ± 0.5 (1.2 mg daily prey level; Fig. 5). For those supplied with pea

aphids reared on faba beans, body area ranged from 15.2 ± 0.3 (16.4-mg daily prey level) to 8.2 ± 0.6 (1.2-mg daily prey level; Fig. 5).

Hippodamia convergens **body size.** For *H. convergens* supplied with *A. pisum* reared on *M. sativa* or *V. faba*, adult elliptical body area (mm^2) significantly differed between host plants and among daily prey levels, however, a significant interaction between daily prey level and host plants was not detected (Table 5, Fig. 6). There was a significant curvilinear relationship of increasing body area and increasing prey levels from alfalfa ($r^2 = 0.667$; df = 2, 200; $P < 0.0001$) and faba beans ($r^2 = 0.685$; df = 2, 155; $P < 0.0001$; Fig. 6).

At the 1.2-mg, 2.1or 2.2-mg and 4.3-mg daily prey levels, body area was larger for *H. convergens* supplied with *A. pisum* reared on alfalfa ($P < 0.0497$; Fig. 6). For those supplied pea aphids reared on alfalfa, body area (mm ± SE) ranged from 18.5 ± 0.4 (16.4-mg daily prey level) to 9.7 ± 0.4 (1.2-mg daily prey level; Fig. 6). For those supplied with aphids reared on faba beans, body area ranged from 18.4 ± 0.4 (16.4-mg daily prey level) to 7.5 ± 1.0 (1.2-mg daily prey level; Fig. 6). (Af\dditional data are included in appendix pg. 127).

Discussion

Effect of Prey Levels and Host Plant on *C. maculata* and *H. convergens*. Studies showing decreased developmental times and higher survivorship have demonstrated that aphids, including *A. pisum*, are very suitable larval prey for *C. maculata* and *H. convergens* (Smith 1965, Karner and Manglitz 1984, Phoofolo and Obrycki 1997, Obrycki et al. 1997, Eigenbrode et al. 1998). However, low prey levels and consumption of less suitable aphid prey during larval stages can result in lower survival, longer developmental

times, and decreased weight and size in Coccinellidae (Smith 1965, Mills 1981, Hodek and Honek 1996, Phoofolo and Obrycki 1997, Obrycki et al. 1998).

In this study, decreasing prey levels resulted in significantly reduced survival of both *C. maculata* and *H. convergens*. My results of *C. maculata* and *H. convergens* preimaginal survivorship compare closely with those of Obrycki et al. (1998). *Coleomegilla maculata* fed the 1.2-mg daily prey level had significantly higher pupal and total preimaginal survival when provided aphids from alfalfa versus faba bean. There was no significant difference at higher prey levels. Similarly *H. convergens* fed the 1.2-mg daily prey level of aphids reared on alfalfa had significantly higher larval, pupal, and preimaginal survival. Increased survival was also observed for *H. convergens* larval and total preimaginal periods at the 2.2-mg daily prey level from alfalfa. Host plant did not significantly affect the survival of *H. convergens* at the higher prey levels (Table 4). Convergence of survival ratios (statistically similar) as prey levels from each host plant increase for both *C. maculata* and *H. convergens*, suggests that differences in survival can be attributed to quantitative differences in the nutritional value of prey.

Significant decreases in larval and preimaginal developmental times at the lower prey levels for *C. maculata* and *H. convergens* fed pea aphids reared on *M. sativa* suggest a host plant effect on the third trophic level at limiting daily prey levels. We observed a quadratic effect of decreasing prey levels on developmental times for both *C. maculata* and *H. convergens*. Similarly, for *A. bipunctata*, developmental rates decreased non-linearly as food levels increased (Mills 1981). For *C. maculata* reared on *A. pisum* from either *M. sativa* or *V. faba*, the lower limit for preimaginal developmental time occurs when supplied between 8.2 and 16.4-mg fresh weight of prey per day, whereas for *H.*

convergens it is at least 16.4-mg of *A. pisum* per day (Figs. 2 and 4). My results compare

closely with previously reported studies examining minimum developmental times for *C.*

maculata and *H. convergens* (Smith 1965, Obrycki and Tauber 1978, Obrycki and Tauber

1982, Obrycki et al. 1998).

The minimum preimaginal developmental times for *C. maculata* and *H. convergens*

reflects approximately a one-day difference between host plants (16.4-mg; Figs. 2 and 4).

At the 1.2-mg prey level, *C. maculata* and *H. convergens* preimaginal developmental

times between host plants were 4 days and 9 days apart, respectively. The different

responses between the two species may be due to differences in food specificity; *C.*

maculata is highly polyphagous and may be able to more easily assimilate nutritional

differences of prey than the primarily aphidophagous *H. convergens* (Hodek and Honek

1996). Preimaginal development at the higher prey levels were statistically similar for *C.*

maculata, suggesting that quantitative nutritional differences between *A. pisum* colonies

and not antibiosis are causing differences in developmental times for those fed the lower

treatment levels. Additionally, significant interactions further support this conclusion. For

H. convergens larval and preimaginal development, host plant did have a significant effect

for all prey levels (Figs. 3 and 4). However, similar to *C. maculata*, the differences in

developmental times still converged (significant interactions) between host plants at the

higher treatment levels, suggesting that the differences in developmental time for *H.*

convergens can be attributed to quantitative differences in nutritional value of prey.

Adult body area was significantly larger for both *H. convergens* and *C. maculata*

larvae fed low prey levels of *A. pisum* (during the larval stage) reared on *M. sativa*, as

opposed to *V. faba*. Body area is statistically similar between host plants at the higher

daily prey levels, again suggesting that the differences in body area for both *C. maculata*

and *H. convergens* can be attributed to quantitative differences in nutritional quality of

prey. Growth rates (accumulation of body mass) of *A. bipunctata* larvae increased linearly

with increasing amounts of food (Mills 1981). Both the size and the dry weight of *C.*

maculata lengi adults increased with increasing larval food quantities, but remained

relatively constant after approximately 10 mg of dry prey (Smith 1965). Linear

relationships between prey consumption and growth have been well documented for insect

predators, including Coccinellidae (Mills 1981, Baumgaerter et al. 1981). In this study,

adult elliptical body area increased quadratically with increasing levels of prey. However

adult body size is often determined by factors besides prey consumption and assimilation

(Figs. 5 and 6) (Hodek and Honek 1996). For instance, Rodriguez-Saona and Miller

(1990) found that *H. convergens* reared at different temperatures varied in body size.

Hippodamia convergens reared at 18°C and 22°C were significantly larger than those

reared at 26°C and 30°C (Rodriguez-Saona and Miller 1990).

The different amounts of fatty acids between aphids reared on *M. sativa* and *V.*

faba provide significant nutritional differences to both *H. convergens* and *C. maculata.*

Over a 6-fold increase in myristic acid for pea aphids reared on *M. sativa* is primarily

responsible for the 2.7-fold increase in fatty acids, resulting in a 1.17-fold increase in

calories (Table 1). The differences in fatty acid levels, which effect the quantitative

differences in the nutritional value of *A. pisum* between host plants, appear to affect the

survival, development and size of *C. maculata* and *H. convergens*. Convergence of

survivorship, developmental times and adult body area at high (less limiting) daily *A.*

pisum levels supports this conclusion. In a laboratory study, Bashir (1973) demonstrated

that increased quantities of myristic acid in artificial diets decreased the developmental times and increased adult size of *O. abdomalis*.

To further support my results, I manipulated the fatty acid content of pea aphids reared on *V. faba*, using temperature. Pea aphids reared on faba beans at 10°C store significantly more energy in fatty acid fractions, mainly as myristic acid, than those reared at 24°C (K.L. Giles unpublished data). Using this information, I was able to manipulate development of Coccinellidae within host plant. Using only the 4.0-mg prey level and the methods as previously described, I observed decreased developmental times after supplying *C. maculata* and *H. convergens* with pea aphids reared on *V. faba* at 10°C (R. Stockland, unpublished data). Thus, I manipulated developmental time among and within host plants and saw a predictable affect. This data further supports the hypothesis that that quantitative differences in the nutritional value (as affected by fatty acid content) of *A. pisum* reared on *M. sativa* versus *V. faba* affect Coccinellidae biology.

Implications for Tritrophic Interactions. The effect of host plant, for herbivorous pests, on the success of biological control of these pests has been observed in many ecological systems (Starks et al. 1972, Rice and Wilde 1989, Kareiva and Sahakian 1990, Campbell et al. 1992, Souissi and LeRu 1997, Bottrell et al. 1998). Host plant attributes or their chemical constituents affect natural enemy processes at the third trophic level and can affect prey suitability for predators through acquired toxicity or poor nutritional value, which result in lower survival, slower development, low weight, small size, or decreased fecundity (Kareiva and Sahakian 1990, Power 1992, Hodek and Honek 1996, Bottrell et al. 1998). Despite numerous studies on tritrophic interactions, direct evidence demonstrating that plant toxins affect natural enemies via prey consumption is

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uncommon (van Emden and Wratten 1990, Hodek and Honek 1996, Price 1997, Bottrell et al. 1998, Giles et al. 2000).

My study supports the hypothesis that quantitative differences in the nutritional value of prey as affected by fatty acid content between *A. pisum* reared on *M. sativa* versus *V. faba* appear related for differences in *C. maculata* and *H. convergens* survival, developmental times and adult body area. Further evaluation of the effects of essential minerals or amino acids may provide additional insight towards quantifying prey suitability.

Because qualities of host plants can affect fatty acid storage in aphid prey (Dillwith et al. 1993), prey nutritional value should be quantified on a nutritional basis in order to identify the mechanisms responsible for differences in predator biology. Evaluating the relationships among host plants, prey nutritional value, and predator biology may be important for developing pest management programs that can include the effects of natural enemies on different host plants.

Acknowledgments

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Table 3.1. Relationship between weight of *A. pisum* for each daily diet treatment, and estimated myristic acid, fatty acid and caloric content.

Treatments				
	pea aphids	myristic acid	fatty acid	
Host plant	mg day^{-1} ± SE	µg^a	µg^a	cal^b
Alfalfa	1.2 ± 0.03	15.1	21.5	1.434
Faba bean	1.2 ± 0.06	2.4	7.9	1.225
Alfalfa	2.2 ± 0.06	28.7	39.6	2.629
Faba bean	2.1 ± 0.05	4.3	13.8	2.143
Alfalfa	4.3 ± 0.12	54.3	77.2	5.138
Faba bean	4.3 ± 0.09	8.6	28.3	4.388
Alfalfa	8.2 ± 0.18	103.5	147.3	9.799
Faba bean	8.2 ± 0.06	16.5	54.0	8.369
Alfalfa	16.4 ± 0.28	207.0	294.6	19.597
Faba bean	16.4 ± 0.24	33.0	108.1	16.737

^{a}Estimated from results of lipid analysis (µg mg^{-1} aphid).

^{b}Calories estimated from result of bomb calorimetry.

Table 3.2. Ratios of *C. maculata* and *H. convergens* surviving the larval, pupal, and total preimaginal stages and ratio of females resulting from increasing daily prey levels of *A. pisum* reared on *M. sativa* or *V. faba*.

| Response variable | Effects of Prey Level | | | | | |
| | Alfalfa | | | Faba Beans | | |
	$\chi 2$	df	P	$\chi 2$	df	P
C. maculata						
Larval Survival	70.407	4	0.001	93.033	4	0.001
Pupal Survival	9.857	4	0.043	84.459	4	0.001
Total Survival	48.986	4	0.001	141.946	4	0.001
Female	17.059	4	0.002	34.670	4	0.001
H. convergens						
Larval Survival	6.328	4	0.176	103.333	4	0.001
Pupal Survival	16.476	4	0.002	62.732	4	0.001
Total Survival	19.015	4	0.001	12.443	4	0.001
Female	51.863	4	0.001	32.305	4	0.001

Table 3.3. Survival and female ratios of *C. maculata* fed increasing daily levels of *A. pisum* reared on either *M. sativa* or *V. faba.*

| | Daily prey level of *A. pisum* (mg/day) from each host plant | | | | | | | | | |
| | 1.2 | | 2.2 | | 4.3 | | 8.2 | | 16.4 | |
Variable	*M.s.*[a]	*V.f.*[b]	*M.s.*	*V.f.*	*M.s.*	*V.f.*	*M.s.*	*V.f.*	*M.s.*	*V.f.*
Larval	0.556	0.444	0.944	0.870	0.981	0.963	1.000	1.000	0.926	0.981
Pupal	0.767	0.375[c]	0.784	0.915	0.924	0.981	0.888	0.944	0.940	1.000
Total	0.426	0.167	0.741	0.796	0.907	0.944	0.889	0.944	0.870	0.981
Female	0.364	0.222	0.375	0.200	0.614	0.449	0.576	0.721	0.767	0.717
n[d]	54	54	54	54	54	54	54	54	54	54

[a] Pea aphids reared on *M. sativa.*

[b] Pea aphids reared on *V. faba.*

[c] Paired underlined values represent significant differences ($P < 0.05$) for 2 x 2 χ^2 tests between host plants

Table 3.3 Survival and female ratios of *C. maculata* fed increasing daily levels of *A. pisum* reared on

either *M. sativa* or *V. faba* (continued).

at each mg level.

[d] Total number of *C. maculata* larvae per treatment at beginning of experiment.

Table 3.4. Survival and female ratios of *H. convergens* fed increasing daily levels of *A. pisum* reared on either *M. sativa* or *V. faba*.

Daily prey level of *A. pisum* (mg/day) from each host plant

| Variable | 1.2 | | 2.2 | | 4.3 | | 8.2 | | 16.4 | |
	$M.s.^a$	$V.f.^b$	M.s.	V.f.	M.s.	V.f.	M.s.	V.f.	M.s.	V.f.
Larval	0.889	0.315^c	0.981	0.833	0.944	0.926	0.981	0.944	0.944	0.981
Pupal	0.708	0.294	0.774	0.600	0.804	0.920	0.962	0.922	0.922	0.981
Total	0.630	0.093	0.759	0.500	0.759	0.852	0.944	0.870	0.870	0.963
Female	0.303	0	0.158	0.111	0.281	0.333	0.636	0.550	0.868	0.705
n^d	54	54	54	54	54	54	54	54	54	54

[a] Pea aphids reared on *M. sativa*.

[b] Pea aphids reared on *V. faba*.

[c] Paired underlined values represent significant differences ($P < 0.05$) for 2 x 2 χ^2 tests between host plants

Table 3.4. Survival and female ratios of *H. convergens* fed increasing daily levels of *A. pisum* reared on

either *M. sativa* or *V. faba* (continued).

at each mg level.

[d] Total number of *H. convergens* larvae per treatment at beginning of experiment.

Table 3.5. **ANOVA results (Proc Mixed Procedure, SAS) for *C. maculata* and *H. convergens* developmental times (days) and adult size (body area) reared on increasing daily prey levels of *A. pisum* (prey level) from alfalfa and faba beans.**

Response Variable	Tests of fixed effects			
	Source of variation	df	F	P
C. maculata				
DEVELOPMENTAL TIMES				
Larval	Host plant	354	50.72	0.0001
	Prey level	354	265.66	0.0001
	Host plant × Prey level	354	6.39	0.0001
Pupal	Host plant	384	0.26	0.6083
	Prey level	384	0.74	0.5625
	Host plant × Prey level	384	0.71	0.5821
Total Preimaginal	Host plant	384	45.55	0.0001
	Prey level	384	147.63	0.0001
	Host plant × Prey level	384	5.13	0.0005
ADULT BODY AREA (mm²)[a]	Host plant	349	4.56	0.0334
	Prey level	349	75.89	0.0001
	Host plant × Prey level	349	6.72	0.0001
H. convergens				
DEVELOPMENTAL TIMES				
Larval	Host plant	386	228.99	0.0001
	Prey level	386	430.19	0.0001
	Host plant × Prey level	386	27.51	0.0001
Pupal	Host plant	366	0.71	0.4013
	Prey level	366	1.55	0.1882
	Host plant × Prey level	366	1.81	0.1259

Table 3.5. ANOVA results (Proc Mixed Procedure, SAS) for *C. maculata* and *H. convergens* developmental times (days) and adult size (body area) reared on increasing daily prey levels of *A. pisum* (prey level) from alfalfa and faba beans (continued).

| Response Variable | Tests of fixed effects | | | |
	Source of variation	df	F	P
Total Preimaginal	Host plant	367	14.69	0.0001
	Prey level	367	188.32	0.0001
	Host plant × Prey level	367	1.48	0.0001
ADULT BODY AREA $(mm^2)^a$	Host plant	333	14.69	0.0002
	Prey level	333	188.32	0.0001
	Host plant × Prey level	333	1 48	0.2090

Host plants were *M. sativa* and *V. faba*. Daily prey levels from *M. sativa* were (mean ± SE) 1.2 ± 0.03, 2.2 ± 0.06, 4.3 ± 0.12, 8.2 ± 0.18, or 16.4 ± 0.28 mg/day of pea aphids. The daily prey levels from *V. faba* were (mean ± SE) 1.2 ± 0.06, 2.1 ± 0.05, 4.3 ± 0.09, 8.2 ± 0.06, or 16.4 ± 0.24 mg.

[a]Calculated using equation from an ellipse [$\pi \times \frac{1}{2}$ (body length) $\times \frac{1}{2}$ (body width)]. Additional replications represent individual developments to the adult stage but with missing data on developmental times.

Fig. 1. Larval developmental times (± SE) for *C. maculata* with increasing daily

levels of *A. pisum* reared on alfalfa or faba bean.

* indicates means for each treatment are significantly different $P < 0.05$.
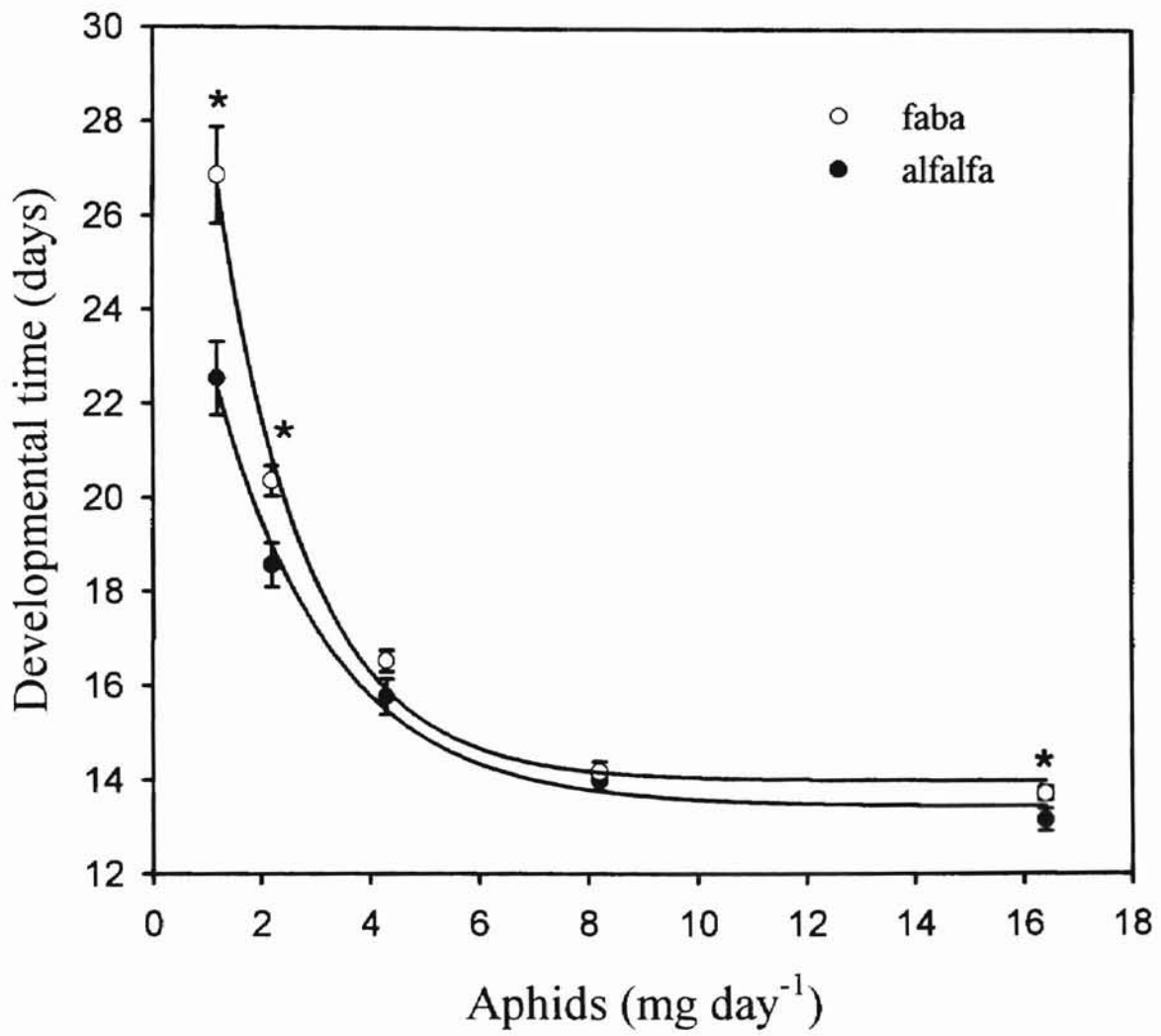
Fig. 2. Preimaginal developmental times (± SE) for *C. maculata* with increasing

daily levels of *A. pisum* reared on alfalfa or faba bean.

* indicates means for each treatment are significantly different $P > 0.05$.
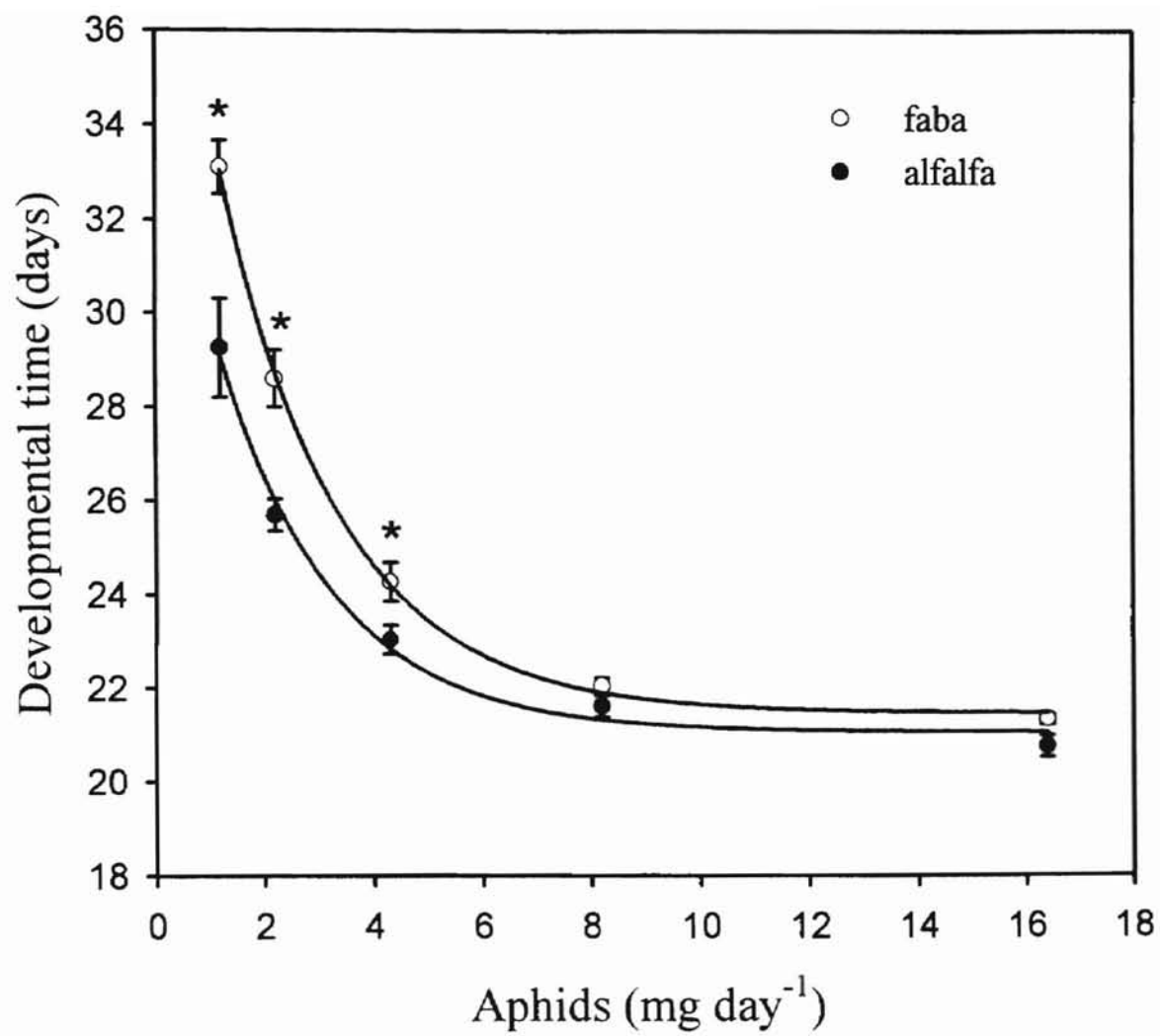
Fig. 3. Larval developmental times (± SE) for *H. convergens* with increasing daily

levels of *A. pisum* reared on alfalfa or faba bean.

*indicates means for each treatment are significantly different $P < 0.05$.
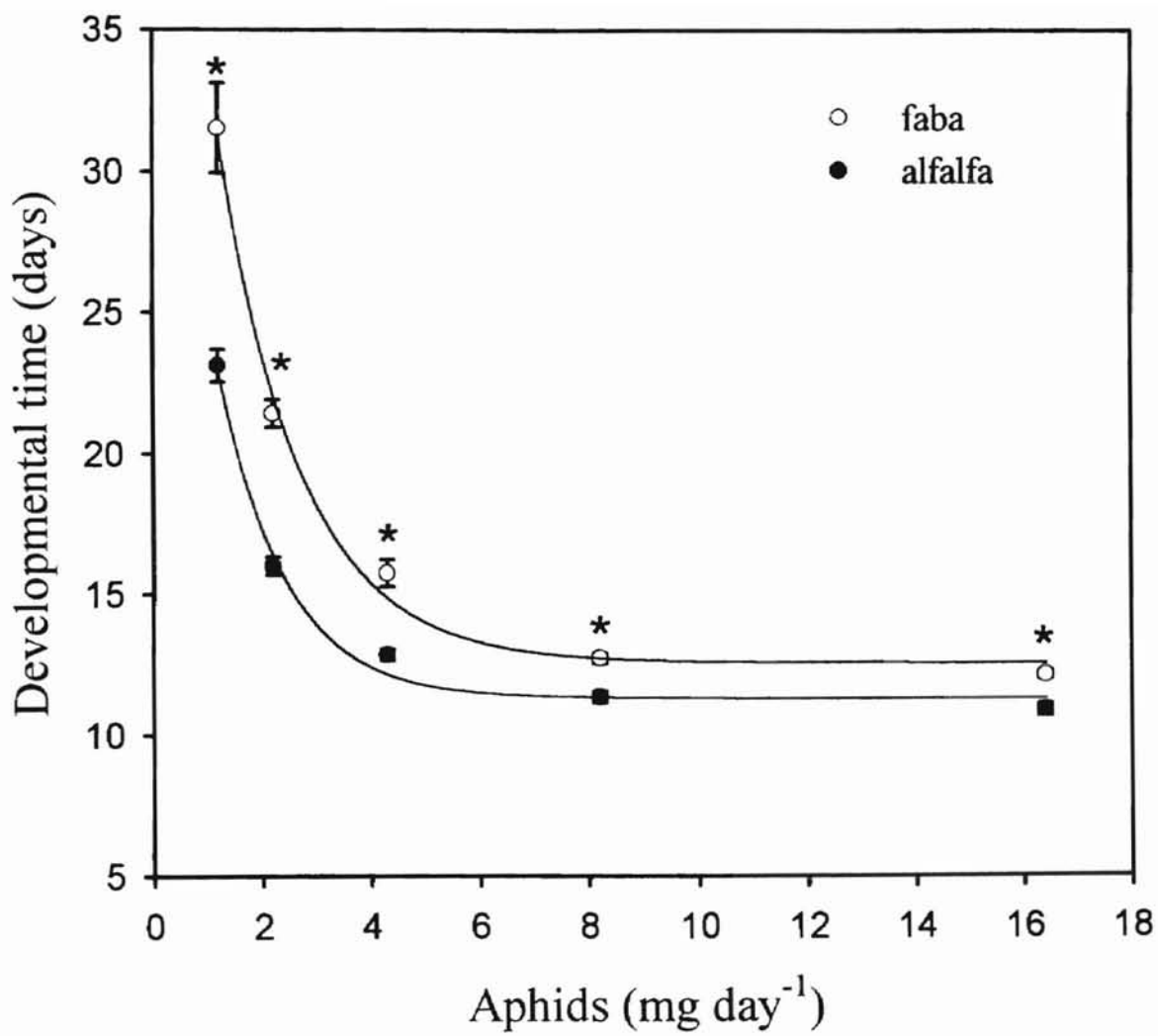
Fig. 4. Preimaginal developmental times (± SE) for *H. convergens* with increasing

daily levels of *A. pisum* reared on alfalfa or faba bean.

* indicates means for each treatment are significantly different $P < 0.05$.
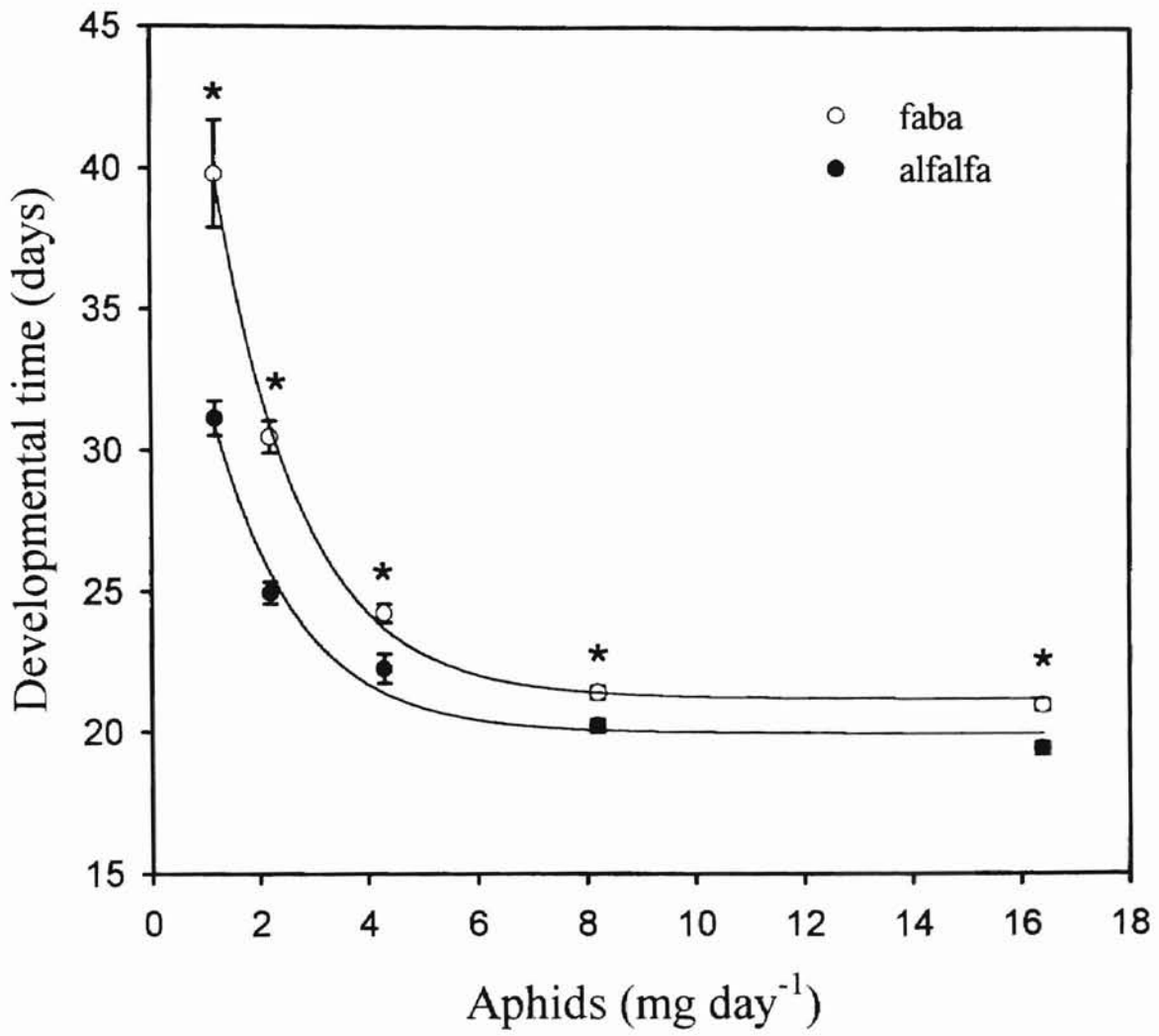
Fig. 5. Adult body area (± SE) for *C. maculata* with increasing daily levels of *A. pisum* reared on alfalfa or faba bean.

*indicates means for each treatment are significantly different $P < 0.05$.
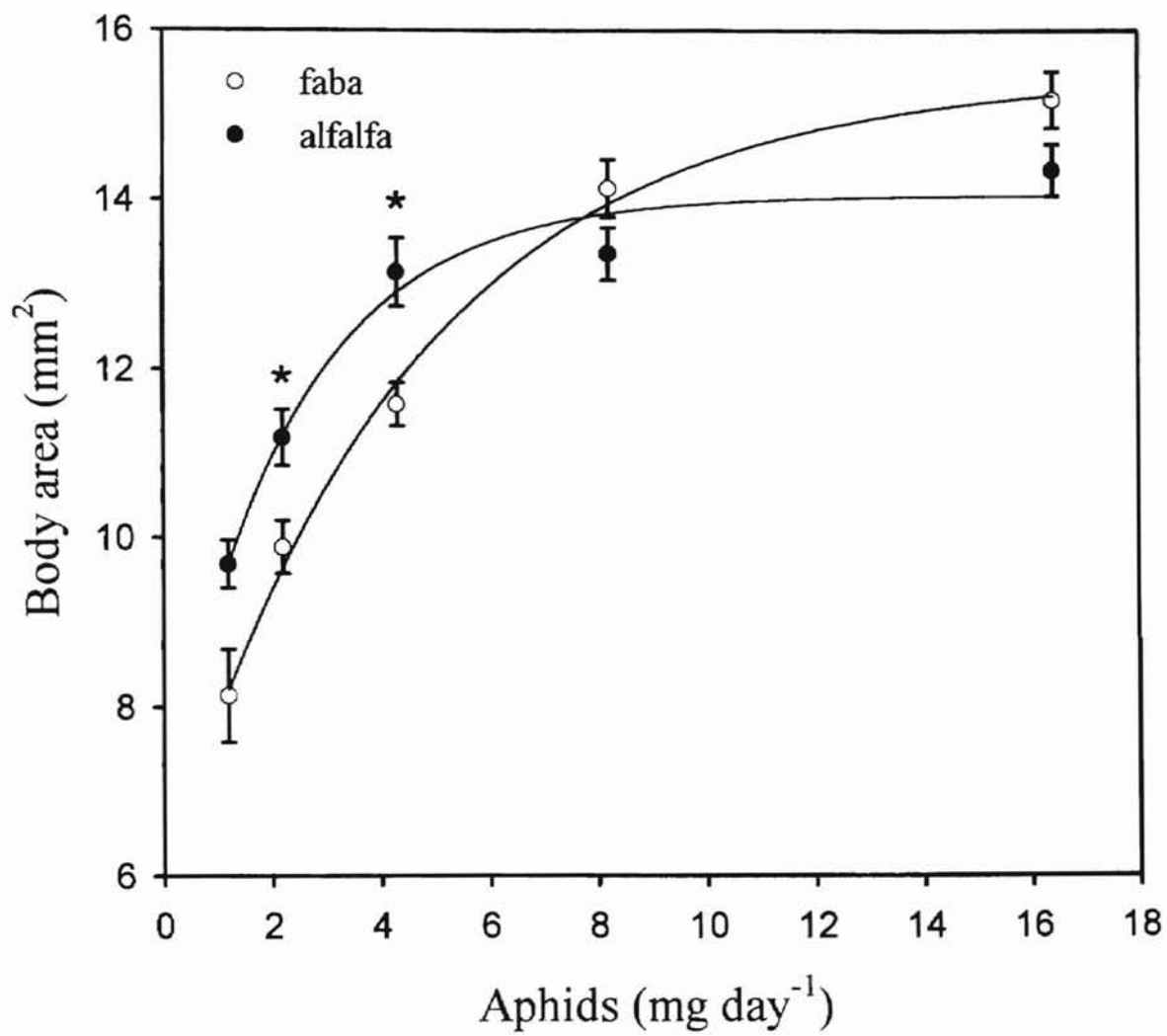
Fig. 6. Adult body area (± SE) for *H. convergens* with increasing daily levels of *A. pisum* reared on alfalfa or faba bean.

*indicates means for each treatment are significantly different $P < 0.05$.

Body area (mm^2) versus Aphids (mg day^{-1})
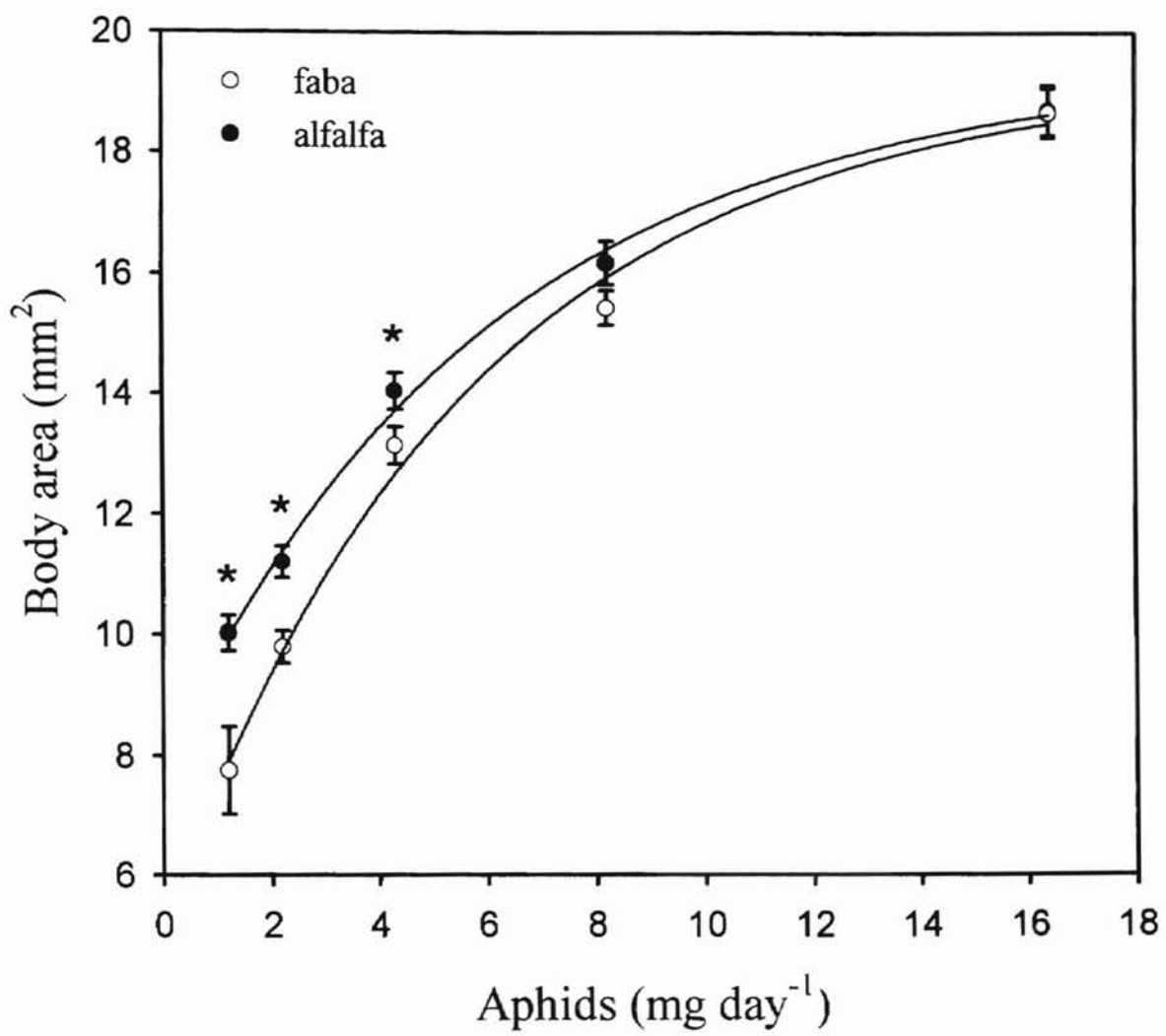
○ faba
● alfalfa

CHAPTER IV

REPRODUCTION OF *COLEOMEGILLA MACULATA* (DEGEER) AND

HIPPODAMIA CONVERGENS GUERIN-MENEVILLE (COLEOPTERA:

COCCINELLIDAE) REARED ON LIMITING LEVELS OF *ACYRTHOSIPHON*

PISUM HARRIS: EFFECTS OF ALFALFA (*MEDICAGO SATIVA*) AND FABA

BEANS (*VICIA FABA*).

Abstract. *Coleomegilla maculata* (DeGeer) and *Hippodamia convergens* Guerin-Meneville larvae were supplied daily with approximately 2.2, 4.3, or 16.4 mg of *Acyrthosiphon pisum* Harris reared on either *Medicago sativa* L. ('OK08') or *Vicia faba* L. ('Windsor') maintained at 22°C and a photoperiod of 16:8 (L:D). After emergence, females were placed individually with a male and supplied with unlimited daily diets of *A. pisum* reared on *M. sativa* and *V. faba*. In a second study, *C. maculata* and *H. convergens* larvae were fed an unlimited daily diet consisting of a mixture of pea aphids reared on *M. sativa* and *V. faba*, but upon emergence, mating pairs of each species were fed 4.4 mg, 8.6 mg, or 32.8 mg of pea aphids reared on either alfalfa or faba beans. Preoviposition period, the total number of eggs, the total number of fertile eggs, and percent fertility were measured for 30 days following the first oviposition period. Myristic acid and total fatty acid content (μg/mg aphid fresh weight) were confirmed to be 6.3 and 2.7 times greater, respectively, in *A. pisum* reared on *M. sativa* than in those reared on *V. faba*, resulting in a 1.17 fold increase in calories. Consumption of *A. pisum* with increased fatty acid levels during the larval or adult stage did not influence the preoviposition period, the total number of eggs laid, the number of fertile eggs or percent fertility. However, this study suggests that the minimum amount of *A. pisum* necessary for *C. maculata* and *H. convergens* to begin ovipositing occurs between 4.3 mg and 16.4 mg per day.

Introduction

Chemical constituents of plants may result in toxic or nutritionally unsuitable prey that may affect the mortality, development and reproduction of predator populations (Power 1992). Therefore, quantifying the results of tritrophic interactions is necessary when examining predator-prey population dynamics (Faeth 1992). Predator populations are influenced by host plants of their herbivorous prey through (1) altering prey population levels and thus prey availability for predators, (2) altering prey composition or physiological processes, thereby reducing or enhancing prey suitability for predators, or (3) altering access to prey, thus reducing prey capture (Price 1997). The effects of host plants on the survival and development of aphidophagous Coccinellidae have been demonstrated in several systems (Rice and Wilde 1989, Hodek and Honek 1996, Kareiva and Sahakian 1990, Campbell et al. 1992, Bottrell et al. 1998, Obrycki et al. 1998). Although tritrophic interactions among host plants, aphids and Coccinellidae have been studied extensively, relatively few studies have attempted to identify the mechanisms of these interactions, including their effects on reproduction (Hodek and Honek 1996).

Host plant species have been shown to affect the growth and reproductive performance of *Acyrthosiphon pisum* Harris (pea aphids) by altering biochemical processes (Bergman et al. 1990). *Acyrthosiphon pisum* reared on *Vicia faba* (c.v. 'Windsor') are larger and more fecund than those reared on *Medicago sativa* (c.v. 'OK08') (Bergman et al 1990). Additionally, *A. pisum* reared on *M. sativa* store significantly more energy, mainly myristic acid (14:0), as compared to those reared on *V. faba* (Bergman et al. 1990, Febvay et al. 1992, Dillwith et al. 1993, Giles et al. 2000). Up

to six fold increases in myristic acid content (µg/mg of aphid) are primarily responsible for the increase in total fatty acid in *A. pisum* reared on *M. sativa* (Bergman et al. 1990, Neese 1995, Giles et al. 2000). Varied levels of myristic acid content reflect differences in the metabolic responses of *A. pisum* to host plants (Bergman et al. 1990). Pea aphids reared on more suitable host plants, such as faba beans, direct their energy into reproduction, whereas pea aphids reared on less suitable host plants, such as alfalfa, store energy in lipid reserves (Dillwith et al. 1993).

The nutritional value of prey can affect predator-prey dynamics so monitoring biochemical and nutritional properties of prey relative to predator survival and reproduction is necessary for evaluating prey suitability (House 1969, Hodek and Honek 1996, Thompson 1999). Production and storage of fatty acids, including myristic acid, influence the nutritional properties of *A. pisum* for Coccinellidae and may have an effect on the next trophic level (Giles et al 2000). Bashir (1973) found that increasing levels of myristic acid in artificial diets for *Olla abdomalis* Say (Coleoptera: Coccinellidae) decreased developmental time, increased adult size, and resulted in adults which were more fecund.

The effects of prey suitability on the reproduction of Coccinellidae have been evaluated for several species (Hodek and Honek 1996, Obrycki et al. 1998). However, little is known about the tritrophic relationships among host plants, pea aphids, and reproduction in lady beetles. The main objective of this study was to compare reproductive rates of *Coleomegilla maculata* (DeGeer) and *Hippodamia convergens* Guerin-Meneville when fed *A. pisum* from *M. sativa* versus those from *V. faba*. I evaluated the effect of both larval and adult diet on reproduction. In each study, I

evaluated daily pea aphid (mg *A. pisum*/day) diets from separate host plants, known to allow differential survival and larval development, on the reproduction of Coccinellidae. In the first study, larval diet was limited and adult diet was unlimited. In the second study, larval diet was unlimited and adult diet was limited. Both studies were conducted in order to evaluate the effects of consuming aphids from different host plants, on reproduction of each Coccinellidae species. In each study, increasing, yet still limiting, prey levels (mg *A. pisum*/day) from *A. pisum* colonies on each host plant were evaluated in an effort to limit prey and determine if differences in the nutritional value of aphids were quantitative. Quantitative differences in prey nutritional value are simply differences in the total available calories as influenced by changes in nutritional components such as myristic acid. Qualitative differences in the nutritional value of prey can occur when less suitable prey lack essential nutrients for the predator or contain toxic compounds. Quantitative differences in *A. pisum* nutritional value between host plants would be evident if reproductive parameters of *C. maculata* and *H. convergens* were different between pea aphids reared on separate host plants (*M. sativa* and *V. faba*) at low (very limiting) prey levels, but similar at higher (less limiting) prey levels.

Hippodamia convergens and *C. maculata* were chosen for this study because of their different prey specificities; *H. convergens* being primarily aphidophagous and *C. maculata* being highly polyphagous (Hodek 1973, Hagen 1987, Giles 1992, Hodek and Honek 1996). This difference in prey specificity may further allow us to determine whether observed differences in prey nutritional value has a greater effect on the reproduction of a primarily aphidophagous predator as opposed to a more generalist predator.

Materials and Methods

Aphid and Coccinellidae colonies. Pea aphids were reared on *V. faba* (cv. 'Windsor') and used as the infestation source for a colony maintained on *M. sativa* (cv. 'OK08'). Aphid colonies were maintained on their respective host plants in separate growth chambers at 22°C and a photoperiod of 16:8 (L:D). Periodic fatty acid analysis was performed using gas chromatography (Bergman et al. 1991) on each aphid colony (n = 15-22 ten-aphid samples) to measure variability within colonies. Bomb calorimetry was used to measure caloric content of *A. pisum* from both colonies (n = three 5-g samples per colony). Percentage protein for *A. pisum* from each colony was quantified using proximate analysis (Official A. O. A. C. methods) (n = three pooled 5-g samples from each colony).

Adult *C. maculata* and *H. convergens* were collected from north-central Oklahoma alfalfa fields and separated into mating pairs. Mating pairs were maintained in half-pint cardboard ice cream containers with a fine mesh cover in an environmental chamber at 24°C and a photoperiod of 16:8 (L:D). Each pair was provided daily with an unlimited supply of *A. pisum* reared on faba beans, a moist cotton ball, and a supplementary diet of wheat-yeast honey mixture. Totals of 11 and 7 females were used to produce larvae for experiments for *H. convergens* and *C. maculata*, respectively.

Effect of larval diet on reproduction. Eggs from mating pairs were removed daily and placed into 5-ml vials stopped with a cotton plug. Upon eclosion, larvae were placed individually into vials stopped with cotton plugs and fed one of six daily diet treatments (mean ± SE): 4 aphids (2.2 ± 0.3 mg), 7 aphids (4.3 ± 0.6 mg), or 28 aphids (16.4 ± 1.3 mg) of pea aphids reared on alfalfa; or 2 aphids (2.2 ± 0.3 mg), 5 aphids (4.3

± 0.4 mg), or 20 aphids (16.4 ± 1.2 mg) of pea aphids reared on faba beans. Aphid weights were measured using a Satorius M3P digital microbalance.

Because the fatty acid composition of pea aphids does not vary among apterous life stages from either host plant, apterous adults and late stage nymphs of consistent size were used as prey (Neese 1995). The highest daily prey level of 16.4 mg was chosen because it represented an adequate diet for maximal larval development for each Coccinellidae species but is well below the daily consumption capabilities of these predators at later instars (Obrycki and Orr 1990, Hodek and Honek 1996, Obrycki et al. 1998, R. Stockland unpublished data). For all treatments, all aphids were consumed by Coccinellidae larvae within 24 hours at the fourth instar.

Upon adult emergence, 6 –10 females of each species reared on the same larval diet were placed individually into ice cream containers with one male from a different parental line, and a moist cotton ball. If a male died, another male was placed with the remaining female. Mating pairs were supplied with an unlimited mixture of pea aphids from alfalfa and faba beans and maintained at 24°C and a photoperiod of 16:8 (L:D). For each mating pair, pre-oviposition time, the number of eggs per day, and the total number of fertile eggs were recorded for 30 days following onset of oviposition. Eggs were collected daily from each cage and placed in a 5-ml glass vial stopped with a cotton plug. I used larval emergence as the measure of fertility. If a female did not oviposit in 45 days following emergence, reproduction was recorded as zero.

Effect of adult diet on reproduction. Eggs were collected from mating pairs as previously described. Upon eclosion, larvae were placed individually into vials stopped with a cotton plug and fed daily an unlimited amount of a mixture of pea aphids reared on

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alfalfa and faba beans. Upon adult emergence, females of each species were individually placed into ice cream containers with one male from a different parental line and a moist cotton ball. Six to seven pairs were assigned one of the following daily diet treatments (mean ± SE): 8 aphids (4.4 ± 0.12 mg), 14 aphids (8.6 ± 0.36 mg), or 56 aphids (32.8 ± 0.56 mg) of pea aphids reared on alfalfa; or 4 aphids (4.4 ± 0.10 mg), 10 aphids (8.6 ± 0.12 mg), or 40 aphids (32.8 ± 0.48 mg) of pea aphids reared on faba beans. Aphid weights were measured as previously described. The methods used and the reproductive parameters measured are as previously described.

For comparison, an additional set of mating pairs was established in order to determine the maximum reproductive capacity of *C. maculata* and *H. convergens*. Eggs were collected from mating pairs as previously described. Upon eclosion, three *C. maculata* larvae and nine *H. convergens* larvae were given (daily) an unlimited amount of a mixture of *A. pisum* reared on *M. sativa* and *V. faba*. Upon adult emergence, females were placed individually into ice cream containers with one male from a different parental line and a moist cotton ball. The mating pairs were supplied daily with an unlimited mixture of *A. pisum* reared on *M. sativa* and *V. faba*. The methods used and the reproductive parameters measured are as previously described.

Statistical Analysis. All analyses were performed using SAS version 6.12 for windows (SAS Institute, 1996). Pre-oviposition time, total number of eggs laid, total number of fertile eggs, and percent fertility were analyzed using PROC MIXED. Coccinellidae which did not oviposit within 45 days of emergence were excluded from the analysis of preoviposition period. PROC MIXED was used because it supplies an ANOVA with both random and fixed effects. Because parental line may be a source of

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experimental error, parent line was included in analyses as a random factor. For *C. maculata* and *H. convergens* larvae and adults supplied with an unlimited amount of a mixture of *A. pisum* reared on alfalfa and faba beans, preoviposition time, total number of eggs, total number of fertile eggs, and percent fertility were analyzed by PROC MEANS. A 0.05 significance level was chosen for all statistical analyses.

Results

Aphid lipid analysis. There were significant differences among aphid colonies for both total fatty acid content ($F = 53.17$; df = 2, 24; $P < 0.001$) and myristic acid ($F = 38.27$; df = 2, 24; $P < 0.001$). *Acyrthosiphon pisum* reared on *M. sativa* had an average total fatty acid content of 17.96 ± 1.7 ($\pm$ SE) and an average myristic acid content of 12.62 ± 2.2 µg per mg aphid fresh weight, respectively. The average total fatty acid and myristic acid content for *A. pisum* reared on *V. faba* was 6.59 ± 0.4 ($\pm$ SE) and 2.01 ± 0.3 µg per mg aphid fresh weight, respectively. The calorie content of *A. pisum* also varied significantly acid ($F = 259.01$; df = 2, 6; $P < 0.001$). For *A. pisum* reared on *M. sativa*, the average ($\pm$ SE) calories per mg of aphid fresh weight was 1.195 ± 0.009. For aphids reared on *V. faba*, the average ($\pm$ SE) calories per mg of aphid fresh weight was 1.021 ± 0.029. Proximate analysis of pooled samples revealed that *A. pisum* reared on *M. sativa* contained 10.9 percent protein and those reared on *V. faba* contained 10.6 percent protein.

Effect of larval diet on *C. maculata* reproduction. For *C. maculata*, reproductive parameters of adults supplied with limiting larval *A. pisum* diets from either *M. sativa* or *V. faba* were highly variable with no distinguishable trends. We found no significant effects of daily prey levels or host plants on preoviposition time, total eggs,

total fertility, or percent fertility (Tables 1 and 2). Additionally, the interactions of host plants and daily prey levels were not significant for all reproductive parameters measured (Tables 1 and 2).

Effect of larval diet on *H. convergens* reproduction. Similar to *C. maculata*, the reproductive parameters of *H. convergens* adults supplied with limiting larval *A. pisum* diets from either *M. sativa* or *V. faba* were highly variable with no distinguishable trends. Preoviposition time was not statistically different among daily prey levels and between host plants and the interaction of host plants and daily prey levels was not significant (Tables 1 and 2). The total number of eggs, fertile eggs, and percent fertility were not statistically different among daily prey levels and between host plants, but, an interaction between host plant and prey level was detected (Tables 1 and 2).

Effect of adult diet on *C. maculata* reproduction. For *C. maculata*, reproductive parameters of adults supplied with adult *A. pisum* diets from either *M. sativa* or *V. faba* were highly variable with no distinguishable trends between host plants. An analysis of preoviposition time was not possible due to the high number of females that did not oviposit (Tables 3 and 4). The total number of eggs laid was not statistically different between host plants and among daily prey levels, and there was not a significant interaction between host plant and daily prey level (Tables 3 and 4). The total number of fertile eggs was not statistically different between host plants and approached significance among daily prey levels, but a significant interaction between host plant and prey level was observed (Tables 3 and 4). Adults supplied with 32.8 mg of pea aphids reared on alfalfa had a significantly greater number of fertile eggs than all other treatments (Tables 3 and 4). Percent fertility was not statistically different between host

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plants, however it was significantly different among daily prey levels; a significant interaction between host plant and daily prey level was not detected (Tables 3 and 4). Adults supplied with 32.8 mg of aphids reared on alfalfa had a significantly greater percentage of fertile eggs than those reared on any of the other daily diet treatments (Tables 3 and 4).

Effect of adult diet on *H. convergens* reproduction. For *H. convergens*, reproductive parameters of adults supplied with adult *A. pisum* diets from either *M. sativa* or *V. faba* were highly variable with no distinguishable trends between host plants. Preoviposition time was not statistically different between host plants, and among daily prey levels; analysis of interaction between host plant and daily prey level was not possible due to the high number of females that did not oviposit (Tables 3 and 4). The total number of eggs laid was not statistically different between host plants, but was significantly different among daily prey levels; there was no significant interaction between host plant and daily prey level (Tables 3 and 4). The total number of fertile eggs was not statistically different among daily prey levels or between host plants, nor was there a significant interaction between host plant and daily prey level (Tables 3 and 4). Percent fertility was not statistically different between host plants, however it was significantly different among daily prey levels; a significant interaction between host plant and daily prey level was not detected (Tables 3 and 4). Adults supplied with 32.8 mg of pea aphids reared on alfalfa did not differ significantly from those supplied with 32.8 mg of pea aphids reared on faba beans. However, those fed 32.8 mg of pea aphids reared on alfalfa had a significantly greater percentage of fertile eggs than those fed 2.1 or 4.3 mg of pea aphids regardless of host plant (Tables 3 and 4).

The average preoviposition period (mean ± SE) for *C. maculata* supplied with an unlimited amount of a mixture of *A. pisum* reared on *M. sativa* or *V. faba* as both larvae and adults was 30.5 ± 7.5 days. The total number of eggs laid (mean ± SE) for *C. maculata* supplied with the unlimited treatment was 58.3 ± 31.3, the total number of fertile eggs (mean ± SE) was 41.3 ± 22.4 and the percent fertility (mean ± SE) was 47.0% ± 23.5 (Table 5). The average preoviposition period (mean ± SE) for *H. convergens* supplied with the unlimited larval and adult mixed diet was 6.9 ± 1.3 days. The total number of eggs laid (mean ± SE) for *H. convergens* supplied with the unlimited treatment was 295.9 ± 122.3, the total number of fertile eggs (mean ± SE) was 226.3 ± 113.0 and the percent fertility (mean ± SE) was 47.4% ±15.1 (Table 5).

Discussion

Many Coccinellidae, including *C. maculata* and *H. convergens*, are sensitive to changes in prey nutritional value (Smith 1965, Soberon 1985, Hodek 1993, Bull et al. 1993, Phoofolo and Obrycki 1997, Obrycki and Orr 1990). Decreased prey levels or consumption of toxic or less suitable prey by larvae of Coccinellidae can result in lower survival, longer developmental times, decreased weight and size, and reduced fecundity of emerging adults (Smith 1965, Hodek and Honek 1996, Phoofolo and Obrycki 1997, Stockland et al., unpublished data). Hariri (1966a, b) found *A. fabae* to be a fairly unsuitable prey item for *Adalia bipunctata* (Linnaeus). Larvae reared on *A. fabae* had lower weights, less fat and glycogen content, and their fecundity was reduced by 50% (Hodek and Honek 1996). *Harmonia axyridis* (Pallas) adults supplied with *Myzus persicae* (Sulzer) had an oviposition period that was 2.2 days shorter than those maintained on *Amphorophora oleracea* (Hukusima and Kamei 1970). When supplied

with *A. pisum, C. maculata* laid an average of six eggs per mg of prey, whereas *C. maculata* supplied with *R. maidis* produced only four eggs per mg of prey (Smith 1965).

Prey levels can also have an effect on egg production and preoviposition period. For instance, Ferran et al. (1984) found a linear relationship between the weight of food consumed as an adult and the number of eggs produced by *Semiadalia undecimnotata* in a 15-day period; a 3.5 fold increase in daily consumption of *Aphis gossypii* decreased the preoviposition period from 9.6 to 4.3 days. The preoviposition period of *H. convergens* also decreased from 12 days to 6 days with an increase of 1-mg *A. gossypii* per mg adult weight per day (Gutierrez et al. 1981, Hodek and Honek 1996).

The different amounts of fatty acids sequestered in pea aphids reared on *M. sativa* versus *V. faba* provide significant differences in nutrients available to Coccinellidae. *Coleomegilla maculata* and *H. convergens* larvae supplied daily with low prey levels of *A. pisum* reared on *M. sativa* ('OK08') had significantly higher survival, shorter developmental times, and were larger as adults compared with those supplied with aphids reared on *V. faba* ('Windsor') (Chapter III). However, developmental times and body areas began to converge (were statistically similar) at higher daily prey levels. Convergence of survival ratios and developmental times for *C. maculata* and *H. convergens* at high prey levels supported the hypothesis that differences in prey nutritional value between *A. pisum* reared on *M. sativa* and *V. faba* are quantitative and appear to be primarily influenced by differences in myristic acid content (Chapter III).

The differences in fatty acid levels and caloric content between aphid colonies were hypothesized to have an impact on the reproductive parameters of *C. maculata* and *H. convergens*. *Coleomegilla maculata* and *H. convergens*, like many other insect natural

enemies, have the ability to survive and develop at low prey levels, however the effects of larval diet levels on adult reproduction has not been extensively studied (Hodek and Honek 1996, Obrycki et al. 1998, Stockland et al., unpublished data). Under the experimental conditions of this study, we did not detect any significant effects of increased fatty acid levels (*A. pisum* reared on *M. sativa*) in the larval diet on the reproductive parameters of either *H. convergens* or *C. maculata*. There were no significant effects of host plant or prey level on any of the reproductive parameters analyzed for *C. maculata* fed the limiting prey levels as larvae (Tables 1 and 2). However, these results also suggest that at higher prey levels, the reproductive parameters measured were somewhat higher for Coccinellidae supplied with pea aphids reared on alfalfa. Even with negligible fecundity effects between host plants, preimaginal stages developed faster when supplied with pea aphids reared on alfalfa (Chapter 3). The decreased developmental time for Coccinellidae feeding on aphids from alfalfa would shorten the generation time considerably, resulting in an increase in population growth.

For *H. convergens*, host plant and daily prey level (when larval prey was different) did not have a significant effect on any of the reproductive parameters analyzed, however there was a significant interaction between host plant and prey level for total number of eggs laid, total number of fertile eggs and percent fertility. There were some significant differences in reproductive parameters between host plants for the 4.3 mg and 2.1 or 2.2 mg prey levels, however these differences do not support the hypothesis that consumption of pea aphids with increased fatty acid levels and a higher caloric content in the larval stage influences the reproduction of *H. convergens*.

Likewise, there were no significant effects of increased fatty acid levels in *A. pisum* between host plant in the adult diet on the reproductive parameters of *H. convergens* and *C. maculata*. There were no significant differences between host plants and among prey levels for the total number of eggs laid and the total number of fertile eggs (Table 3 and 4). There was not a significant effect of host plant on percent fertility, however the effect of prey level was significant (Tables 3 and 4). *Coleomegilla maculata* adults fed 32.8 mg of pea aphids reared on faba beans had a significantly higher percent fertility than all other daily diet treatments (Tables 3 and 4). For *H. convergens*, there was not a significant effect of host plant on any of the reproductive parameters examined (Tables 3 and 4). However, there was a significant effect of daily prey level on percent fertility (Tables 3 and 4). Adults fed 32.8-mg of pea aphids reared on faba beans had a significantly higher percent fertility than those fed the 4.4 and 8.6-mg treatment levels (Tables 3 and 4). Similar to *C. maculata*, these differences do not support the hypothesis that consumption of pea aphids with increased fatty acid levels and a higher caloric content in the adult stage influences the reproductive parameters of *H. convergens*.

For both *C. maculata* and *H. convergens* supplied with the limited daily prey levels as adults, only a few adults laid eggs; egg laying was sporadic, and production of fertile eggs was rare. Primarily, only the adults fed the 32.8-mg daily prey level reproduced, and it is difficult to evaluate the full effects of adult diet on reproduction without further studies at higher prey levels.

The results of my study on the effects of adult diet on reproduction on *both C. maculata* and *H. convergens* suggest that there is a minimum amount of prey necessary for these predators to begin ovipositing and a minimum amount to food required for egg

quality to be sufficient for a larva to eclose. For instance, Ibrahim (1955) found that with a minimum of 30 aphids daily, *Coccinella undecimpunctata aegyptiaca* Reiche would begin to oviposit, and there was a positive correlation between the consumption of aphids and egg production. Similar results were found for *C. septempunctata* (Ghanim et al. 1984, Hodek and Honek 1996). For insect predators, only a part of the energy in assimilated matter is used for food conversion and respiration. The remaining energy may be converted to body tissues, reserves for diapause, or egg production. On low prey level diets, there may be no energy left over to gain body tissue, make reserves, or produce eggs (Hodek and Honek 1996). The prey levels in this study were likely too low to fully evaluate the effect of adult diet on the reproduction of *C. maculata* and *H. convergens*. With unlimited food, larvae or adults allocate all energy to body growth, reproduction and necessary metabolic activities. For example, *C. maculata* supplied with an unlimited amount of *A. pisum* laid approximately 11.5 eggs per day and had a fecundity of 124.4 eggs (Phoofolo and Obrycki 1997). Field collected *H. convergens* supplied with an unlimited amount of *A. pisum* laid an average of 14 7 eggs per day and laid an average of 360.6 eggs in their lifetime (Rodriguez-saona and Miller 1994).

The differences observed in fatty acid content between *A. pisum* reared on either *M. sativa* or *V. faba*, do not appear to affect the reproductive parameters of *C. maculata* and *H. convergens*. *Coleomegilla maculata* and *H. convergens* fed the unlimited diet laid more eggs and had a higher number of fertile eggs than those fed the limited daily prey levels as either larvae or adults, suggesting that prey level does influence adult reproduction. However, at the higher daily prey levels, the reproductive parameters measured were somewhat higher for Coccinellidae supplied with pea aphids reared on

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alfalfa. Even with negligible fecundity effects between host plants, preimaginal stages developed faster when supplied with pea aphids reared on alfalfa (Chapter III). The decreased developmental time for Coccinellidae feeding on aphids from alfalfa would shorten the generation time considerably, resulting in an increase in population growth. Further studies with higher daily prey levels from both host plants are necessary to fully evaluate the effect of *A. pisum* from separate host plants on reproduction.

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Table 4.1. Reproductive measures (means ± SE) of *C. maculata* and *H. convergens* for 30 days supplied as larvae with *A. Pisum* reared on increasing levels of *M. sativa* or *V. faba*.

| | Daily prey level of *A. pisum* (mg day^{-1}) at the larval stage from each host plant | | | | | |
| | 2.2 | | 4.3 | | 16.4 | |
Variable	*M. sativa*[a]	*V. faba*[b]	*M. sativa*	*V. faba*	*M. sativa*	*V. faba*
C. maculata						
Preovipostion period	5.0 ± 5.7	12.0 ± 6.6	6.0 ± 8.1	12.0 ± 6.6	15.0 ± 8.1	16.5 ± 5.7
Total number of eggs laid	24.9 ±14.5	13.3 ±12.8	8.7 ±14.4	35.7 ±14.8	8.5 ±15.3	20.9 ±12.2
Total number of fertile eggs	14.8 ± 5.4	4.0 ± 4.8	3.9 ± 5.4	10.1 ± 5.6	7.4 ± 5.6	5.0 ± 4.6
Percent fertility	59.7 ±18.9	9.6 ±16.7	7.1 ±18.9	20.8 ±18.9	25.8 ±20.4	10.7 ±15.8
H. convergens						
Preovipostion period	10.8 ± 2.2	8.2 ± 2.6	8.6 ± 2.7	8.6 ± 2.2	3.9 ± 2.5	4.7 ± 2.6

Table 4.1. Reproductive measures (means ± SE) of *C. maculata* and *H. convergens* for 30 days supplied as larvae with *A. Pisum* reared on increasing levels of *M. sativa* or *V. faba* (continued).

	Daily prey level of *A. pisum* (mg day^{-1}) at the larval stage from each host plant					
	2.2		4.3		16.4	
Variable	*M. sativa*[a]	*V. faba*[b]	*M. sativa*	*V. faba*	*M. sativa*	*V. faba*
Total number of eggs laid	158.6 ±62.1	36.1 ±53.8	63.9 ±62.1	330.7 ±62.1	223.1 ±62.1	195.6 ±65.8
Total number of fertile eggs	77.4 ±46.1	15.2 ±39.9	48.9 ±46.1	229.0 ±46.1	176.0 ±46.1	120.9 ±48.9
Percent fertility	50.2 ±11.3	16.1 ± 9.8	16.0 ±11.3	62.2 ±11.3	45.5 ±11.3	38.0 ±11.9

[a] Pea aphids reared on *M. sativa*.

[b] Pea aphids reared on *V. faba*.

Means followed by different letters indicate significant differences at $P > 0.005$.

Table 4.2. ANOVA results (Proc Mixed Procedure, SAS) for *C. maculata* and *H. convergens* reproductive parameters supplied with increasing daily prey levels of *A. pisum* as larvae from alfalfa and faba beans.

Response Variable	Source of variation	df	F	P
		Tests of fixed effects		
C. maculata				
Preoviposition time	Host plant	6	0.74	0.4234
	Prey level	6	0.69	0.5362
	Host plant × Prey level	6	0.09	0.9128
Total eggs	Host plant	34	0.70	0.4071
	Prey level	34	0.15	0.8585
	Host plant × Prey level	34	1.04	0.3633
Total fertility	Host plant	34	0.35	0.5557
	Prey level	34	0.26	0.7726
	Host plant × Prey level	34	1.62	0.2136
Percent fertility	Host plant	34	1.31	0.2599
	Prey level	34	0.72	0.4936
	Host plant × Prey level	34	1.52	0.2336
H. convergens				
Preoviposition time	Host plant	24	0.12	0.7275
	Prey level	24	2.78	0.0823
	Host plant × Prey level	24	0.28	0.7558
Total	Host plant	40	0.60	0.4421

Table 4.2. ANOVA results (Proc Mixed Procedure, SAS) for *C. maculata* and *H. convergens* reproductive parameters supplied with increasing daily prey levels of *A. pisum* as larvae from alfalfa and faba beans (continued).

| Response Variable | | Tests of fixed effects | | |
	Source of variation	df	*F*	*P*
eggs	Prey level	40	2.11	0.1347
	Host plant × Prey level	40	5.56	0.0074
Total fertility	Host plant	40	0.32	0.5777
	Prey level	40	3.22	0.0504
	Host plant × Prey level	40	4.55	0.0166
Percent fertility	Host plant	40	0.03	0.8702
	Prey level	40	0.32	0.7267
	Host plant × Prey level	40	6.93	0.0026

Daily larval prey levels from *M. sativa* were (mean ± SE) 2.2 ± 0.03, 4.3 ± 0.12, or 16.4 ± 0.28 mg / day of pea aphids. The daily prey levels from *V. faba* were (mean ± SE) 2.1 ± 0.05, 4.3 ± 0.09, or 16.4 ± 0.24 mg.

Table 4.3. Reproductive measures (means ± SE) of *C. maculata* and *H. convergens* for 30 days supplied as adults with increasing levels of A. pisum reared on *M. sativa* or *V. faba.*

| Variable | Daily prey level of *A. pisum* (mg day^{-1}) at adult stage from each host plant | | | | | |
| | 4.4 | | 8.6 | | 32.8 | |
	M. sativa[a]	*V. faba*[b]	*M. sativa*	*V. faba*	*M. sativa*	*V. faba*
C. maculata						
Preoviposition period	-	-	-	-	-	-
Total number of eggs laid	0.0	0.0	0.0	8.0 ± 5.2	21.3 ± 5.6	3.9 ± 5.2
Total number of fertile eggs	0.0	0.0	0.0a	3.9 ± 3.2a	14.3 ± 3.4b	1.6 ± 3.2a
Percent fertility	0.0	0.0	0.0a	6.9 ± 7.1a	33.4 ± 7.7b	10.9 ± 7.1a
H. convergens						
Preoviposition period	-	-	5.0 ±11.6	-	18.5 ± 5.8	14.0 ± 6.7

Table 4.3. **Reproductive measures (means ± SE) of *C. maculata* and *H. convergens* for 30 days supplied as adults with increasing levels of A. pisum reared on *M. sativa* or *V. faba* (continued).**

	Daily prey level of *A. pisum* (mg day^{-1}) at adult stage from each host plant					
	4.4		8.6		32.8	
Variable	M. sativa[a]	V. faba[b]	M. sativa	V. faba	M. sativa	V. faba
Total number of eggs laid	0.0	0.0	1.0 ±11.6a	0.0a	27.4 ±10.8a	26.1 ±10.8a
Total number of fertile eggs	0.0	0.0	0.0a	0.0a	23.0 ± 9.9a	15.7 ± 9.9a
Percent fertility	0.0	0.0	0.0a	0.0a	38.7 ± 9.4b	18.4 ± 9.4ab

[a] Pea aphids reared on *M. sativa*.

[b] Pea aphids reared on *V. faba*.

Means followed by different letters indicate significant differences at *P* < 0.05.

Table 4.4. ANOVA results (Proc Mixed Procedure, SAS) for *C. maculata* and *H. convergens* reproductive parameters supplied with increasing daily prey levels of *A. pisum* as adults from alfalfa and faba beans.

Response Variable	Source of variation	df	*F*	*P*
			Tests of fixed effects	
C. maculata				
Preoviposition time	Host plant	0	2.07	-
	Prey level	0	0.01	-
	Host plant × Prey level	-	-	-
Total eggs	Host plant	28	0.49	0.4882
	Prey level	28	2.73	0.0829
	Host plant × Prey level	28	2.86	0.0738
Total fertility	Host plant	28	1.20	0.2830
	Prey level	28	3.13	0.0595
	Host plant × Prey level	28	3.50	0.0439
Percent fertility	Host plant	28	0.72	0.4023
	Prey level	28	5.09	0.0131
	Host plant × Prey level	28	2.15	0.1355
H. convergens				
Preoviposition time	Host plant	1	0.26	0.7016
	Prey level	1	1.08	0.4882
	Host plant × Prey level	-	-	-
Total eggs	Host plant	32	0.01	0.9350
	Prey level	32	3.84	0.0321

Table 4.4. ANOVA results (Proc Mixed Procedure, SAS) for *C. maculata* and *H. convergens* reproductive parameters supplied with increasing daily prey levels of *A. pisum* as adults from alfalfa and faba beans (continued).

| Response Variable | Tests of fixed effects | | | |
	Source of variation	df	*F*	*P*
	Host plant × Prey level	32	0.00	0.9982
Total fertility	Host plant	32	0.08	0.7780
	Prey level	32	2.40	0.1067
	Host plant × Prey level	32	0.09	0.9187
Percent fertility	Host plant	32	0.69	0.4120
	Prey level	32	5.79	0.0071
	Host plant × Prey level	32	0.73	0.4910

Daily prey levels from *M. sativa* were (mean ± SE) 4.4 ± 0.12, 8.6 ± 0.24, or 32.8 ± 0.56 mg / day of pea aphids. The daily prey levels from *V. faba* were (mean ± SE) 4.2 ± 0.10, 8.6 ± 0.18, or 32.8 ± 0.48 mg.

Table 4.5. Reproductive measures (means ± SE) of *C. maculata* and *H. convergens* supplied with an unlimited supply of a mixture of *A. pisum* reared on *M. sativa* or *V. faba* as larvae and adults.

	Preoviposition Period	Total Number of eggs laid	Total Number of fertile eggs	Percent fertility
C. maculata	30.5 ± 7.5	58.3 ± 31.3	41.3 ± 22.4	47.0 ± 23.5
H. convergens	6.9 ± 1.3	295.9 ± 122.3	226.3 ± 113.0	47.4 ± 15.1

CHAPTER V

SUMMARY

Differences in the nutritional content of aphid prey for Coccinellidae may be attributed to plant quality or may be the result of altered biochemical processes in aphids in response to host plant (Bergman et al. 1990, Febvay 1992, Dillwith et al. 1993, Neese 1995). Despite convincing evidence that plants affect third trophic level organisms, very few studies have described the mechanisms of these interactions (Hodek and Honek 1996, Price 1997). The goal of this thesis was to determine the effect of lipid levels of *Acyrthosiphon pisum* Harris, as influenced by two host plants, *Medicago sativa* L. cv. 'OK08' (alfalfa) and *Vica faba* L. cv. 'Windsor' (faba beans), on the survival, development and reproduction of *Coleomegilla maculata* (DeGeer) and *Hippodamia convergens* Guerin-Meneville.

Myristic acid and total fatty acid content (μg/mg aphid fresh weight) were confirmed to be 6.3 and 2.7 times greater, respectively, in *A. pisum* reared on *M. sativa* in comparison to *A. pisum* reared on *V. faba*, resulting in a 1.17 fold increase in caloric content. I tested whether the different amounts of fatty acids of pea aphids reared on *M. sativa* versus *V. faba* provide significant nutritional differences for Coccinellidae. *Coleomegilla maculata* and *H. convergens* larvae supplied with low daily prey levels of *A. pisum* reared on *M. sativa* had significantly higher survival rates, shorter developmental times, and were larger as adults in comparison to those supplied with aphids reared on *V. faba*. Survivorship, developmental times, and body areas converged between host plants at higher daily prey levels. Convergence of survival rates, developmental times, and adult body size for *C. maculata* and *H. convergens* (most evident for the polyphagous *C. maculata*) at high prey levels supported the hypothesis

that substantial variation in quantities and compositions of lipids stored by *A. pisum* resulting from different host plants will influence growth rate, survival, and fecundity of Coccinellidae. Additionally, differences in prey nutritional value between *A. pisum* reared on *M. sativa* and *V. faba* are quantitative and appear to be primarily influenced by differences in myristic acid content.

The results of the studies performed on the effects of larval and adult diet on *C. maculata* and *H. convergens* reproduction suggest that increased fatty acid content as influenced by host plant does not influence the preoviposition period, the total number of eggs laid, or the number of fertile eggs or percent fertility. These studies suggest that the minimum amount of daily prey (as adults) necessary for *C. maculata* and *H. convergens* to begin ovipositing occurs between 4.3 mg and 16.4 mg. Further studies at higher daily prey levels are necessary to fully evaluate the effect of adult diet (as influenced by increasing prey suitability) on reproduction.

The nutritional value of host plants can affect fatty acid storage in aphid prey (Dillwith 1993). Therefore, prey nutritional value should be described on a nutritional basis in order to quantify the mechanisms responsible for differences in predator biology. Nutritional models for tritrophic interactions should be formulated when evaluating prey suitability in ecological systems. Evaluating the relationships among host plants, prey nutritional biochemistry, and predator biology may be important for developing insect pest management programs that can include the efficiency of control provided by natural enemies on different host plants. The influence of host plant on aphid fatty acid storage appears to affect the survival and development of Coccinellidae, and may influence the level of biological control among host plants. However, the results pertaining to the

effects of host plant on fatty acid storage and their influence on the reproduction of

Coccinellidae were inconclusive. My results suggest that at higher prey levels, the

reproductive parameters measured were somewhat higher for Coccinellidae supplied with

pea aphids reared on alfalfa. Even with negligible fecundity effects of Coccinellidae

supplied with pea aphids reared between host plants, preimaginal stages developed faster

when supplied with pea aphids reared on alfalfa (Chapter 3). The decreased

developmental time for Coccinellidae feeding on pea aphids from alfalfa does, however,

shorten the generation time considerably, resulting in an increase in population growth.

APPENDIX

Table A1. Survival ratios of *C. maculata* and *H. convergens* among daily *A. pisum* diet treatments.

Host Plant	*A. pisum* mg day^{-1} ± SD	n	*C. maculata* Instar		
			2nd	3rd	4th
M. sativa	1.2 ±0.2	54	0.981	0.882	0.667
V. faba	1.2 ±0.3	54	0.944	0.882	0.533
M. sativa	2.2 ±0.3	54	1.00	1.00	0.962
V. faba	2.1 ±0.3	54	1.00	0.963	0.904
M. sativa	4.3 ±0.6	54	1.00	0.981	1.00
V. faba	4.3 ±0.4	54	1.00	1.00	0.963
M. sativa	8.2 ±0.9	54	1.00	1.00	1.00
V. faba	8.2 ±0.3	54	1.00	1.00	1.00
M. sativa	16.4 ±1.3	54	1.00	1.00	0.926
V. faba	16.4 ±1.2	54	0.981	1.00	1.00
			H. convergens Instar		
			2nd	3rd	4th
M. sativa	1.2 ±0.2	54	1.00	1.00	0.889
V. faba	1.2 ±0.3	54	0.963	0.846	0.386
M. sativa	2.2 ±0.3	54	1.00	1.00	0.981
V. faba	2.1 ±0.3	54	0.963	0.962	0.900
M. sativa	4.3 ±0.6	54	0.963	0.981	1.00
V. faba	4.3 ±0.4	54	0.981	1.00	0.943
M. sativa	8.2 ±0.9	54	1.00	0.981	1.00
V. faba	8.2 ±0.3	54	1.00	1.00	0.944
M. sativa	16.4 ±1.3	54	0.981	1.00	0.962
V. faba	16.4 ±1.2	54	1.00	1.00	0.981

Table A2. *Coleomegilla maculata* development (days) at 24° C, 16:8 (L:D) on increasing numbers of *A. pisum* reared on *M. sativa* or *V. faba*, and statistical comparisons between treatments.

Host Plant	*A. pisum* mg day^{-1}	Stage					
		egg	1st	2nd	3rd	4th	pupal
M. sativa	1.2 ± 0.2	3.3 ± 0.1 a	4.3 ± 0.2 ab	3.1 ± 0.1 bc	4.0 ± 0.2 b	11.7 ± 0.5 b	5.0 ± 0.4 a
V. faba	1.2 ± 0.3	3.2 ± 0.1 a	4.6 ± 0.2 a	3.7 ± 0.1 a	5.2 ± 0.2 a	14.7 ± 0.5 a	4.5 ± 0.6 a
M. sativa	2.2 ± 0.3	3.2 ± 0.1 a	4.1 ± 0.2 bc	3.0 ± 0.1 cd	3.0 ± 0.2 c	9.0 ± 0.4 d	4.6 ± 0.3 a
V. faba	2.1 ± 0.3	3.2 ± 0.1 a	4.2 ± 0.2 bc	3.4 ± 0.1 ab	3.6 ± 0.2 b	10.0 ± 0.4 c	5.1 ± 0.3 a
M. sativa	4.3 ± 0.6	3.2 ± 0.1 a	3.7 ± 0.2 d	2.7 ± 0.1 def	2.9 ± 0.2 cd	6.8 ± 0.4 e	4.3 ± 0.2 a
V. faba	4.3 ± 0.4	3.3 ± 0.1 a	4.2 ± 0.2 abc	2.7 ± 0.1 de	3.0 ± 0.2 c	6.9 ± 0.4 e	4.8 ± 0.2 a
M. sativa	8.2 ± 0.9	3.2 ± 0.1 a	3.7 ± 0.2 d	2.4 ± 0.1 ef	2.7 ± 0.2 cde	5.4 ± 0.4 g	4.5 ± 0.3 a
V. faba	8.2 ± 0.3	3.2 ± 0.1 a	4.0 ± 0.2 bcd	2.4 ± 0.1 ef	2.8 ± 0.2 cde	6.4 ± 0.4 fg	4.9 ± 0.2 a
M. sativa	16.4 ± 1.3	3.3 ± 0.1 a	3.6 ± 0.2 d	2.3 ± 0.1 f	2.4 ± 0.2 e	4.9 ± 0.4 g	4.4 ± 0.3 a
V. faba	16.4 ± 1.2	3.2 ± 0.1 a	3.9 ± 0.2 cd	2.7 ± 0.1 def	2.5 ± 0.2 de	5.0 ± 0.4 g	4.5 ± 0.2 a

Letters indicate significant differences among treatments. Chi squared analysis with Fisher's exact test.

Table A3. *H. convergens* development (days) at 24° C, 16:8 (L:D) on increasing numbers of *A. pisum* reared on *M. sativa* or *V. faba*, and statistical comparisons between treatments.

Host Plant	*A. pisum* mg day^{-1}	egg		1st		2nd		3rd		4th		pupal	
M. sativa	1.2 ± 0.2	3.4 ± 0.2	a	3.3 ± 0.1	ab	2.7 ± 0.1	b	3.2 ± 0.1	c	14.5 ± 0.4	b	5.6 ± 0.2	a
V. faba	1.2 ± 0.3	3.4 ± 0.2	a	3.3 ± 0.1	ab	3.0 ± 0.1	a	5.3 ± 0.2	a	20.9 ± 0.6	a	5.8 ± 0.6	a
M. sativa	2.2 ± 0.3	3.4 ± 0.2	a	2.9 ± 0.1	cd	2.1 ± 0.1	cd	2.9 ± 0.2	cd	8.5 ± 0.4	d	5.4 ± 0.2	a
V. faba	2.1 ± 0.3	3.5 ± 0.2	a	3.4 ± 0.1	a	2.4 ± 0.1	bc	3.7 ± 0.2	b	12.1 ± 0.4	c	6.1 ± 0.3	a
M. sativa	4.3 ± 0.6	3.5 ± 0.2	a	2.8 ± 0.1	cd	1.9 ± 0.1	de	2.4 ± 0.2	e	6.0 ± 0.4	f	6.1 ± 0.2	a
V. faba	4.3 ± 0.4	3.4 ± 0.2	a	3.1 ± 0.1	bc	2.4 ± 0.1	bc	2.9 ± 0.2	c	7.5 ± 0.4	e	5.5 ± 0.2	a
M. sativa	8.2 ± 0.9	3.6 ± 0.2	a	2.6 ± 0.1	d	1.9 ± 0.1	e	2.2 ± 0.2	e	4.9 ± 0.4	g	5.4 ± 0.2	a
V. faba	8.2 ± 0.3	3.3 ± 0.2	a	3.0 ± 0.1	bc	2.2 ± 0.1	cde	2.4 ± 0.2	e	5.3 ± 0.4	fg	5.4 ± 0.2	a
M. sativa	16.4 ± 1.3	3.6 ± 0.2	a	2.6 ± 0.1	d	2.0 ± 0.1	cde	2.1 ± 0.2	e	4.6 ± 0.4	g	5.2 ± 0.2	a
V. faba	16.4 ± 1.2	3.4 ± 0.2	a	2.9 ± 0.1	cd	2.2 ± 0.1	cd	2.5 ± 0.1	e	4.8 ± 0.4	g	5.6 ± 0.2	a

Letters indicate significant differences among treatments. Chi squared analysis with Fisher's exact test.

Table A4. Coccinellidae body area for each daily diet treatment, and statistical comparisons among daily prey levels (weights) for body area.

Treatments		_C. maculata_		_H. convergens_	
Host plant	_A. pisum_ mg day^{-1}	Body area		Body area	
M. sativa	1.2 ± 0.2	9.53 ± 0.5 (20)	ab	9.72 ± 0.4 (32)	b
V. faba	1.2 ± 0.3	8.19 ± 0.6 (11)	a	7.45 ± 1.0 (4)	a
M. sativa	2.2 ± 0.3	11.21 ± 0.4 (39)	c	10.91 ± 0.4 (40)	c
V. faba	2.1 ± 0.3	9.98 ± 0.4 (39)	b	9.61 ± 0.5 (23)	b
M. sativa	4.3 ± 0.6	13.13 ± 0.4 (40)	d	13.79 ± 0.4 (40)	e
V. faba	4.3 ± 0.4	11.62 ± 0.3 (49)	c	12.90 ± 0.4 (44)	d
M. sativa	8.2 ± 0.9	13.39 ± 0.3 (47)	de	16.02 ± 0.4 (47)	f
V. faba	8.2 ± 0.3	14.17 ± 0.3 (49)	ef	15.26 ± 0.4 (40)	f
M. sativa	16.4 ± 1.3	14.38 ± 0.4 (42)	fg	18.48 ± 0.4 (45)	g
V. faba	16.4 ± 1.2	15.19 ± 0.3 (48)	g	18.43 ± 0.4 (47)	g

Elliptical body area was measured using the equation [$\Pi \times 1/2$ (body length) $\times 1/2$ (body width) (Obrycki et al. 1998)]. Letters indicate significant differences among treatments. PROC MIXED with LSMeans comparison.

VITA

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Master of Science

Thesis: EFFECTS OF *MEDICAGO SATIVA* L. AND *VICIA FABA* L. ON NUTRITIONAL SUITABILITY OF *ACYRTHOSIPHON PISUM* (HARRIS) FOR *COLEOMEGILLA MACULATA* (DEGEER) AND *HIPPODAMIA CONVERGENS* GUERIN-MENEVILLE

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