SUITABLILTY OF GREENBUGS (*SCHIZAPHIS GRAMINUM*) PARASITIZED BY *LYSIPHLEBUS TESTACEIPES* AS A FOOD SOURCE FOR PREDATORY COCCINELLIDAE: *COCCINELLA SEPTEMPUNCTATA* AND *HIPPODAMIA CONVERGENS*

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PREFACE

Chapter I of this thesis is a literature review on the suitability of greenbugs (*Schizaphis graminum*) parasitized by *Lysiphlebus testaceipes* (Cresson), as a food source for predatory Coccinellidae: *Coccinella septempunctata* (L.) and *Hippodamia convergens* (Guerin-Meneville). The biology of each insect species is included as well as the description of intraguild predation of *L. testaceipes* mummies by Coccinellidae predators. The following chapters are a formal manuscript of the research I conducted during my Master of Science program and are written in compliance with the publication policies and guidelines for manuscript preparation with the Entomological Society of America.

Completing and pursuing this degree would not have been possible without the provision of health and direction from God, and the support and motivation from my family and fiancée. I would like to thank my advisors, Dr. Tom Royer and Dr. Kristopher Giles, for their assistance and advice throughout this research project. I also would like to extend my thanks to Dr. Jack Dillwith for his valuable advice and Dr. Mark Payton for his assistance especially from the statistical point of view. In addition, I would like to also thank Dennis Kastl and Doug Jones for their technical support. Above all, I want to extend my special thanks to my sponsor W.K. Kellogg Foundation (AED) for their financial and academic support in every way whenever I have a need.

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CHAPTER I

INTRODUCTION

In Oklahoma, more than 6 million acres of winter wheat are planted each year and about 3-4 million acres are harvested for grain at an average yield of 34 bushels per acre (Krenzer et al. 1999). Overall, 50-60% of planted wheat is grazed (Hossain et al. 2004 and Thomson 1990), so planting dates vary depending on location and intended purpose of the crop. Livestock can graze without significantly reducing grain yield potential from mid-November until the first hollow stem appears (Krenzer et al. 1999). Wheat grain is generally harvested in late May or early June (Royer and Krenzer 2000).

Winter wheat is infested by a number of arthropods, including the greenbug, *Schizaphis graminum* Rondani; the Russian wheat aphid, *Diuraphis noxia* Mordviko; bird cherry-oat aphid, *Rhopalosiphum padi* L; the English grain aphid, *Sitobion avenae* Fabricius; the corn leaf aphid, *Rhopalosiphum maidis* Fitch, as well as other pests. Aphids especially greenbugs are the most consistent pests; outbreaks occur somewhere in Oklahoma almost every year with widespread outbreaks reported every 5-10 years (Starks and Burton 1977).

Greenbugs are attacked by several predators and parasites, including coccinellid lady beetles and parasitic wasps (Royer et al. 1998). The commonly encountered Coccinellidae species in Oklahoma wheat fields are *Hippodamia convergens* Guerin-Meinville, *Hippodamia sinuate* Muslant, *Coccinella septempunctata* L. and *Coleomegilla maculata* De Geer (Teetes et al. 1973, and Obrycki and Kring 1998).

Lysiphlebus testaceipes is very active and often responsible for the collapse of aphid population outbreaks in sorghum and small grains, although the population reduction often takes place after economic damage has been realized (Stark and Burton 1977). Recently Jones et al. (2003) found that *L. testaciepes* can provide predictable control of greenbugs in winter wheat during the fall and spring. *Coccinella septempunctata* L. and *H. convergens* are also commonly found in wheat fields along with *L. testaceipes*. Adults and larvae of *H. convergens* are reported to contribute greatly to greenbug control in wheat and sorghum (Teetes et al. 1973).

Lysiphlebus testaceipes, *C. septempunctata* and *H. convergens* all occur in wheat fields during the growing season and all prey on greenbug and other cereal aphids. In spring, cereal aphid populations decline rapidly, almost exclusively due to parasitizism by *L. testaceipes*. However, numerous coccinellid larvae and adults area also present at that time (Giles unpublished). It is not understood if these larvae can utilize the parasitized greenbugs as a suitable food source, or what impact their feeding may have on the parasitoid population structure. Since these three natural enemies co-exist in winter wheat throughout the growing season, it is important to understand their ecological relationship to better incorporate them into a comprehensive integrated pest management plan (Royer et al. 1998).

The overall goal of this study was to characterize some aspects of intraguild relationships between *C. septempunctata*, a euryphagous predator, *H. convergens*, an aphidophagous predator, and the solitary aphidiid parasitoid, *Lysiphlebus testaceipes*. I tested the hypothesis that parasitized greenbug mummies were an acceptable, suitable food source for *C. septempunctata* and *H. convergens*.

Objectives. The objectives of this research were:

1. Determine which larval instars of *C. septempunctata* and *H. convergens* are able to feed on *S. graminum* mummies parasitized by *L. testaceipes*.

2. Determine if *C. septempunctata* and *H. convergens* larvae demonstrate a preference between unparasitized *S. graminum* and mummies parasitized by *L. testaceipes*
3. Determine the effect of *S. graminum mummies* parasitized by *L. testaceipes* as a food source on the survival, growth and development and of *C. septempunctata* and *H. convergens* larvae.

Explanation of the Thesis Format

Chapter I of this thesis is the general introduction and is followed by a literature review (Chapter II) and two chapters (III and IV) the Materials and Methods and Results of the individual studies. Chapter V is a Discussion and is followed by a summary and the appendices. The first study reports on an evaluation of the capability of *C. septempunctata* and *H. convergens* larval stadia to feed on greenbugs mummies parasitized by *L. testaceipes*. The second study examines the preference of *C. septempunctata* and *H. convergens* for unparasitized or parasitized *S. graminum* in a choice situation. The final study examines the growth, development and survival of *C. septempunctata* and *H. convergens* larvae when provided daily with various combinations of *S. graminum* aphids and *S. graminum* mummies parasitized by *L. testaceipes*. The individual studies follow the style guidelines of the Entomological Society of America for submission to scientific journals.

CHAPTER II

LITERATURE REVIEW

Wheat production in Oklahoma: Winter wheat (*Triticum aestivum* L.) is grown in the southern Great Plains of the United States (Krenzer et al. 1999). The southern Great Plains has unique soil types, climate and environmental conditions that are suitable for the production of winter wheat for grain only, forage only and as a dual purpose forage and grain crop (Krenzer et al. 1999). There appears to be a small risk of Hessian fly infestations which allows the producers to plant wheat in the late summer. This early planting lengthens the fall vegetative growth period and increases fall forage production relative to October plantings (Krenzer et al. 1999). Extended snow cover is rare so livestock can graze during winter (Hossain et al. 2004). In Oklahoma, more than 6 million acres of arable land is planted into winter wheat every year, and about 50-55% of that acreage is grazed (Thomson 1990). In 1998, about 4.3 million acres of wheat was harvested for grain at an average yield of 34 bushels per acre (Krenzer et al. 1999).

Wheat production practices in Oklahoma differ with the intended use of the crop. Wheat grown for forage is typically planted two to six weeks before the recommended planting date for grain-only production (Krenzer et al. 1999), and seeded at a higher rate. Recommended planting dates vary with production area, but wheat for forage and grain production is generally planted from the 15th of September to the 10th of October, while wheat for grain only is planted from 10th October to 30th October.

Appropriate soil tillage for wheat production involves a wide range of options in the U.S. In the areas like the southeast where rainfall is plentiful, moldboard plowing is often recommended. Deep plowing and full or near-full tillage allow producers to create a seedbed conducive to; maximum seed-soil contact for rapid moisture imbibition and germination, optimum seed placement, maximum fertilizer distribution, maximum mechanical weed control and in-furrow insecticide or fungicide treatments if needed (Smith 1995). The rate of seeding also differs with location, wheat type (spring or winter) initial soil moisture and expected rainfall, soil fertility, date and method of planting and intended use. Winter wheat tends to tiller more and is therefore seeded at rates 25-50% lower than spring wheat grown in the same location (Smith 1995).

If soil moisture and temperature are suitable, wheat immediately germinates and emerges from the soil as a seedling. Stem formation (tillering) begins with the appearance of the first tillers and continues until the stem starts to elongate (jointing). Jointing is initiated in January to March as the weather warms up, and the stem of the tiller becomes hollow and extends upward. The earliest formation of this stem hollowing is known as "first hollow stem" (Krenzer et al. 1999). Livestock grazing does not significantly reduce grain production until the first hollow stem occurs (Krenzer et al. 1999). Once first hollow stem is reached, plants start to grow and tillers extend dramatically in length. Heading begins as the flower spike emerges from the flag leaf sheath and this continues until flowering is complete. The head matures and is harvested in late May or early June (Royer and Krenzer 2000).

Arthropod Pests of Wheat: Several arthropods are injurious to wheat, including the Hessian fly (*Mayetolia destructor* Say), the greenbug (*Schizaphis graminum* Rondani), the Russian wheat aphid (*Diuraphis noxia* Mordviko), the bird cherry-oat aphid (*Rhopalosiphum padi* L.) the English grain aphid (*Sitobion avenae* Fabricius), and the corn leaf aphid (*Rhopalosiphum maidis* Fitch) and the rice root aphid (*Rhopalosiphum rufiabdominalis*). Other pests include armyworms *Pseudaletia unipuncta* (Hayworth) and *Spodoptera frugiperda* (J.E. Smith); cutworms (*Euxoa auxilaris* Grote and *Agrotis* *orthogonis* Morrison); false wireworms in the family Tenebrionidae; mites including the brown wheat mite [*Petrobia latens* (Müller)], wheat curl mite [*Aceria tosichella* (Keifer)], and winter grain mite [*Pentalius major* (Puges)]; and white grubs (*Cyclocephala spp.* and *Phyllophaga spp.*) (Royer et al.1998). The most consistent and common of these pests in winter wheat are aphids; outbreaks are persistent in Oklahoma with widespread outbreaks reported every 5-10 years (Starks and Burton 1977).

Schizaphis graminum

Description: *Schizaphis graminum* is approximately 1.6 mm long, light green in color, with a darker green dorsal abdominal stripe (Almand et al. 1973). The eyes, the distal leg segments, tips of the cornicles and antennae are black. Female greenbugs reproduce mainly by parthenogenesis when ambient temperatures exceed their developmental threshold of 5°C (Walgenbach et al. 1988). Greenbugs develop through four nymphal stages in about seven days under favorable conditions (Metcalf and Metcalf 1993). Under optimum conditions, adult females begin reproduction immediately and produce about 80 offspring during a 25-day period. Alate (winged) and apterous (wingless) forms may be present in the same colony (Young and Teetes 1977, Almand et al. 1969). Alate females begin reproducing 24 to 48 hours after the last molt (Wadley 1931). Paedogenesis (reproduction by nymphs) occurs in approximately 2% of alate immature greenbugs (Wood and Starks 1975). Reproductive rates of 3.5 nymphs per day by parthenogenic females and ca. one egg per day by oviparous females were described by Wadley (1931). Webster and Starks (1987) recorded a birth rate of six nymphs per day by biotype E greenbugs on TAM 105 wheat at 26-28°C. Up to 33 generations can occur per year, although the mean number is 21 per year (Webster and Phillips 1918). In the autumn, alate males and apterous non-parthenogenetic females (sexuales) may be produced in response to increased scotophase. After mating, female sexuales deposit eggs that overwinter. Apterous parthenogenetic females, known as 'fundatrices', hatch from the eggs in spring (Dixon 1985). In the southern Great Plains, however, *S. graminum* is believed to overwinter almost exclusively as parthenogenetic females (Webster and Phillips 1918, Wadley 1931).

Pest Status: *Schizaphis graminum* was first described in Italy in 1847 (Rondani 1847). It is believed to be European in origin although this is now disputed (Shufran et al. 2000, Porter et al. 1997). It was first recorded in the United States in 1882 in Virginia (Hunter and Glenn 1909), and has been a serious pest of small grain crops in North America ever since then (Porter et al. 1997). In the United States, greenbugs feed on a wide range of graminaceous species, many of which serve as secondary hosts when winter wheat and other grain crops are not present (Michaels 1986). Over the past century greenbugs have expanded their range of preferred hosts to include barley, sorghum, and Kentucky bluegrass and have apparently been found to have several different biotypes capable of flourishing on many host plants previously thought to be resistant to their feeding (Beregovoy et al. 1988, Porter et al. 1997). Presently, greenbugs are a serious but sporadic pest of wheat and sorghum in Oklahoma (Royer personal communication).

The greenbug can affect both sorghum and wheat from seedling through heading. The greenbug, because of its general distribution and great prolificacy, causes a loss of from 1 to possibly 3% of the wheat crop of the entire world. Wheat or small-grain fields infested by the greenbug usually show distinct small deadened areas that usually appear in the field during the late winter or early spring (Metcalf and Metcalf 1993

Nature of Damage: Greenbugs feed by inserting stylets formed by mandibles and maxillae into the host plant tissue to feed on phloem sap, which results in chlorosis. In sorghum, injury is detectable by the appearance reddish spots on the leaves that are believed to be in response to toxins (Burton 1986), which cause chlorophyll reductions (Peters et al. 1988). The reddened areas enlarge as the greenbug numbers increase. As feeding continues, the leaf finally dies, turning brown from the outer edges toward the centre (Almand et al. 1969). In wheat, the two leaf stage is the most susceptible to greenbug feeding injury (Pike and Schaffner 1985), resulting in both root and shoot biomass reductions that persist throughout the entire growing season and result in yield reductions (Kindler et al. 2002).

Natural Enemies: Greenbugs are attacked by several predators and parasites, including lady beetles, parasitic wasps, spiders, damsel bugs, lacewing larvae and syrphid fly larvae (Royer et al. 1998). The most important natural enemies in the southern Great Plains are the parasitic Hymenoptera and Coccinellidae (Kring and Gilstrap 1983, and Kring et al. 1985). Abundance of natural enemies in cereal aphid population outbreaks has shown a characteristic lag time of about 1-2 weeks, suggesting that native aphid predators do not always hold cereal aphid populations in check. However, Giles et al. (2003) suggests that aphid outbreaks occur sporadically because native natural enemies usually regulate aphid increases.

Lysiphlebus testaceipes

Distribution and Importance: Hymenopteran parasitoids of the greenbug in Oklahoma include the primary parasitoids *Aphelinus nigritus* (Howard), *Aphelinus varipes* (Forester), *Diaeretiella rapae* (McIntosh) and *Lysiphlebus testaceipes* (Cresson), of which *L. testaceipes* is the most important (Jackson et al. 1970, Walker et al. 1973 and Archer et al. 1974). Several hyperparasitoids, including *Aphidencyrtus aphidivorus* (Mayr), *Pachyneuron siphonophorae* (Ashmead), *Charips sp.* and *Asaphes lucens* (Provancher) have also been identified.

Lysiphlebus testaceipes is a common solitary parasitoid of aphids that is found throughout temperate regions of North and South America (Krombein et al, 1979). Webster (1909) suggested that *L. testaceipes* was responsible for holding the pest in check in America. This parasite is very active and is often responsible for the collapse of aphid populations on sorghum and small grains, although the pest reduction often occurs after economic damage has been realized (Stark and Burton 1977). The relatively high developmental threshold and low degree-day requirement of this species suggests that it may be best adapted to warm climates and may be most effective during late-spring and summer in the southern Great Plains region (Elliott et al. 1999). Recent research suggests that *L. testaceipes* wasps are active throughout winter in winter wheat except for extended periods of cold (Jones 2001).

Biology and life History: *Lysiphlebus testaceipes* is a slender, dark greenish to black parasite (< 3mm) with long antennae that attacks aphids in several aphid genera (Flint and Dreistat 1995, and Hoffman and Frodsham 1993). Female *L. testaceipes* deposits an egg in an aphid host which hatches in about two days (Webster and Phillips

1912). The larvae emerges and develops first by consuming the hemolymph and later all the internal organs of the host. Larval movement expands the host exoskeleton, giving it a swollen appearance (Hardee et al. 1990). The larva cuts a hole in the bottom of the aphid, attaches the aphid to a leaf with silk and glue, and the dead greenbug changes color to become a brown "mummy" (Weeden et al. 1997). Once attached, the parasitoid larva pupates. The aphid mummies, which remain on leaves after the aphids die, can be easily detected. The wasp larva completes feeding in about 6-8 days, after developing through four instars, then molts to the pupal stage. After 4-5 days, the wasp chews a circular opening dorsally in the aphid mummy to emerge and begin another generation (Hardee et al. 1990). The newly emerged wasp mates and begins to search for new aphids to attack. *Lysiphlebus testaceipes* disperses either by flying (adult wasps) or by the larvae being carried inside winged aphids when they undergo long migration flights. When parasitized, greenbug adults stop reproducing in about three days (Spencer 1926), but adult parasitized greenbugs less than three days old, do not reproduce at all (Eikenbary and Rogers 1974).

Lysiphlebus testaceipes has a developmental threshold of 6.6°C and takes 9.3 days to develop from egg to adult at 26°C, in contrast to requiring over 49 days at 10°C (Elliott et al. 1994). Archer et al. (1973) evaluated the effects of temperature on *Lysiphlebus testaceipes* mummies, and found a few insects emerged after 90 days of storage at 4.4 and 1.7°C. This suggests that *L. testaceipes* may be able to overwinter in mummies. However, Royer et al. (2001) indicated that little is known about overwintering habits or other basic ecological characteristics exhibited by this parasite, despite its importance as a natural enemy of cereal aphids.

Coccinellidae

Distribution and importance: Predaceous coccinellids have been associated with biological control more often than any other predatory organisms. They are important natural enemies of various pest species, especially aphids, whiteflies, mealybugs, scale insects and mites. The beneficial status of these beetles has a rich history that is recognized by the general public and biological control practitioners (Blackman 1965).

Hodek (1970) proposed that Coccinellidae are the most important aphidophagous insects that regulate aphid populations. Adult coccinellids are highly mobile and capable of traveling many hundreds of kilometers to and from overwintering sites (Hodek 1973). Of the 64 genera and 453 species of aphidophagous Coccinellidae indigenous to America (Gordon 1985), *Hippodamia convergens* Guerin-Meinville, *Hippodamia sinuate* Muslant, *Coccinella septempunctata* L. and *Coleomegilla maculata* Timberlake are commonly encountered in Oklahoma winter wheat fields (Teetes et al. 1973, Michels et al. 1997, Obrycki and Kring 1998).

Biology of Coccinellidae: Lady beetles are nearly hemispherical in shape, and the most common species are red, brown or tan, usually with black spots; a few are black, sometimes spotted with red. Lady beetle larvae are carrot-shaped with flattened, gradually tapering bodies, distinct body regions, long legs and warty or spiny backs.

Lady beetles overwinter as adults. Some species, such as *H. convergens* congregate in enormous hibernation clusters while other species overwinter singly or in small clusters (Mahr and Ridgway 1993). In spring they disperse and seek out aphids or other prey that can serve as adult and larval food and lay eggs adjacent to the prey on the leaf surface. Some species scatter individual eggs, while other species lay compact clusters of 10-20 eggs. The eggs of aphid-feeding species are usually yellow to orange in color, and 1-15mm long (Mahr and Ridgway 1993). After hatching, the larvae remain on the egg shell for up to one day and often eat nonviable sibling eggs before dispersing in search of food. Larvae grow through 4 instars and a pupal stage before emerging as adults (Hodek and Honek 1996).

Hippodamia convergens

Distribution and Importance: *Hippodamia convergens* is a well known and common native lady beetle in North American (Sloderbeck et al, 1996) that is often sold by insectaries for aphid control (Hoffman and Frodsham 1993). It is an important predator of aphid and mite pests on cultivated crops. Adults are highly mobile, capable of migrating hundreds of miles under some circumstances (Hagen 1962), a characteristic which often considerably reduces its effectiveness as a natural pest control agent. Experiments by Kring et al. (1985) demonstrated that *H. convergens* and other Coccinellidae were not very effective for greenbug control in early season grain sorghum, but were important later in the growing season when temperatures increased. The feeding behaviour of *H. convergence* in Oklahoma during the winter wheat growing season has not been well documented.

Biology and Life History: *Hippodamia convergens* beetles are slightly elongated in shape and can range from 4-7 mm in length. Their orange wing covers typically have six small black spots on each wing cover (Rice and Mahr 1995, Sloderbeck et al 1996). However, the number of spots can vary, ranging from no spots to a full complement of 13 spots (Hoffman and Frodsham 1993). The section of the body behind the head is black with white margins, and two converging white lines (Rice and Mahr 1995, Sloderbeck et al. 1996), which are common to all individuals (Hoffman and Frodsham 1993).

Adults and larvae feed primarily on aphids (Rice and Mahr 1995, Sloderbeck et al. 1996). They are voracious predators: adults eat about 30-60 greenbugs per day while the larvae can consume 20-100 per day, depending on instar (Hunter and Glenn 1909). They have been reported to feed on pea, melon, cabbage, potato, green peach and corn leaf aphids. If aphids are scarce, adults and larvae may feed on small insect larvae, insect eggs, mites, mealybugs, scales and occasionally, nectar and honey dew secreted by aphids (Hoffman and Frodsham 1993, Carr 1955).

Development from egg to adult may take only two to three weeks, and adults life for weeks or months depending on the location, availability of prey and time of the year (Hoffman and Frodsham 1993). *Hippodamia convergens* requires temperatures above 15°C to complete development beyond the second instar (Obrycki and Tauber 1982), and complete development requires approximately 350 degree-days when fed greenbugs in the laboratory (Michels and Behle 1991). They require fewer greenbugs to reach maturity as ambient temperature increased (517 greenbugs at 20°C vs. 230 greenbugs at 30°C). In the United States resident populations are active throughout spring and summer if aphids are present. One or two generations are completed each year, depending on the length that favorable climatic conditions occur. The adults enter winter hibernation usually in a protected site (Sloderbeck et al. 1996). In early spring, after temperatures warm, adults migrate with prevailing winds from overwintering sites (Flint and Dreistadt 1998).

Coccinella septempunctata

Distribution and importance: This aphidophagous coccinellid is native to much of Asia, Europe and North Africa (Hodek 1973). It was introduced, and now is permanently established in every state of the continental United States (USDA-APHIS 1991). In many areas of North America, it has become one of the dominant coccinellid species in agricultural habitats (Gordon 1985, Obrycki et al. 1982). *Coccinella septempunctata* was first introduced into southern California in 1956 from shipments originating from India. Additional shipments from Europe to the Beneficial Insects Research Laboratory, Newark, Delaware, were released during the years 1958 to 1973 (Angalet and Jacques 1975). Large numbers of beetles were found overwintering in aggregations centered in New Jersey and following this discovery, sub-colonization efforts were initiated in Oklahoma (Cartright et al. 1979).

Biology and Life History: The adults of *C. septempunctata* are more oval than elongated, with a distinctly domed shape. They measure 7-8mm (~1/3 inches) with a distinctive white or pale spot on either side of the head and, typically, a 1- 4 - 2 pattern of black spots on orange or red forewings. *C. septempunctata* commonly occurs in alfalfa fields where it feeds on larvae of the alfalfa weevil as well as on pea aphids (Honek 1980). Adult lady beetles are frequently observed in the field feeding on these larvae in spring and early summer although such use of prey may occur from opportunistic attacks upon encounter as predators search alfalfa primarily for aphid prey (Hodek 1962 and Dixon 2000).

They grow through one or two generations per year in the northeastern region of the United States, the adults being most common from mid- to late summer. Adult beetles usually overwinter near the fields where they feed and reproduce. In spring, emerging lady beetles feed on the aphids before laying eggs. Larvae mature in 10 to 50 days, depending on the availability of aphids. Hodek and Cerkasov (1960) reported that over its wide distributional range, *C. septempunctata* exhibits at least four types of voltinism. It expresses a univoltine summer generation followed by hibernation in the cool northern latitudes. In the lower latitudes under hot dry conditions, it is also univoltine, with a late spring generation followed by a long aestivo-hibernation. But in the drier, hotter Mediterranean they express a bivoltine condition which is intrrupted during the summer with aestivation.

Intraguild predation (IGP)

Definition: Agro ecosystems have a three major trophic level communities consisting of primary producers (crop), primary consumers (pests) and secondary consumers (natural enemies of pests). The interaction between species usually leads to predation, competition, mutualism, comensalism or amensalism (Root 1967). Predation, competition and mutualism (Pianka 1994) are three important interactions that structure biotic populations and communities. Polis et al. (1989) and Polis and Holt (1992) documented the fourth species interaction that may influence the structure on communities; a combination of competition and predation that they called intraguild predation (IGP). Polis et al. (1989) defined the concept of intraguild predation by using the term "guild" to refer to the organisms that share a common food source either through predation or parasitism. He later defined it as "the killing and eating of the species that use similar, often limiting, resources and thus are potential competitors."

Types of Intraguild Predation: Rosenheim et al. (1995) used 'predation' to refer to the trophic interaction between biological control agents and reported that this concept may be unidirectional, where one species will be called an intraguild predator and the other the intraguild prey, or bidirectional, when both species prey on each other. He described two types: symmetric and asymmetric. Symmetric or bidirectional IGP commonly occurs when predaceous antagonists are equally able to kill each other and is independent of age, structure or social behaviour (Polis et al. 1989). Asymmetric or unidirectional IGP occurs when one of the antagonists is superior to the other (Hindayana et al. 2001).

Intraguild Predation and Biological Control: Rosenheim et al. (1995), in a review, identified intraspecific interactions within the same trophic level as a major factor that shapes the assembly of guilds and leads to instability in the natural communities, citing works by Holt 1977 and Polis and Holt 1992. Intraguild predation is common when generalist predators belong to a guild (Lucas et al. 1998), especially in aphid antagonist guilds which are composed of generalist and specialist predators as well as parasitoids (Müller et al. 1999).

Few studies have attempted to address the effects of intraguild predation on biological control (Rosenheim et al. 1995), possibly due to the technical challenges associated with such studies in the field. However, the potential for using multiple biological control agents has received a lot of attention (Dennis 1991). Furguson and Stiling (1996) reported the effects of multiple natural enemies on a prey population as being synergistic, additive or non-additive. Hochberg and Lawton (1990) add that they could have an antagonistic effect, resulting in an increase in the prey population if sufficient interference exists among the natural enemies. Despite adaptations that lady beetles possess which increase their foraging efficiency on well distributed and short-lived aphid colonies (Majerus 1994), they have shown little to no success when used as the sole biological control agent.

Polis and Holt (1992) argued that intraguild predation is a perfect example of the interference that could occur between natural enemies. Such antagonistic interference could result in a reduction in the mortality of the host, especially if the competing organisms engage in a trophic interaction (predation and parasitism), which prevails within most biological control agents (Goetel et al. 1990, Rosenheim et al. 1995, Roy and Pell 2000).

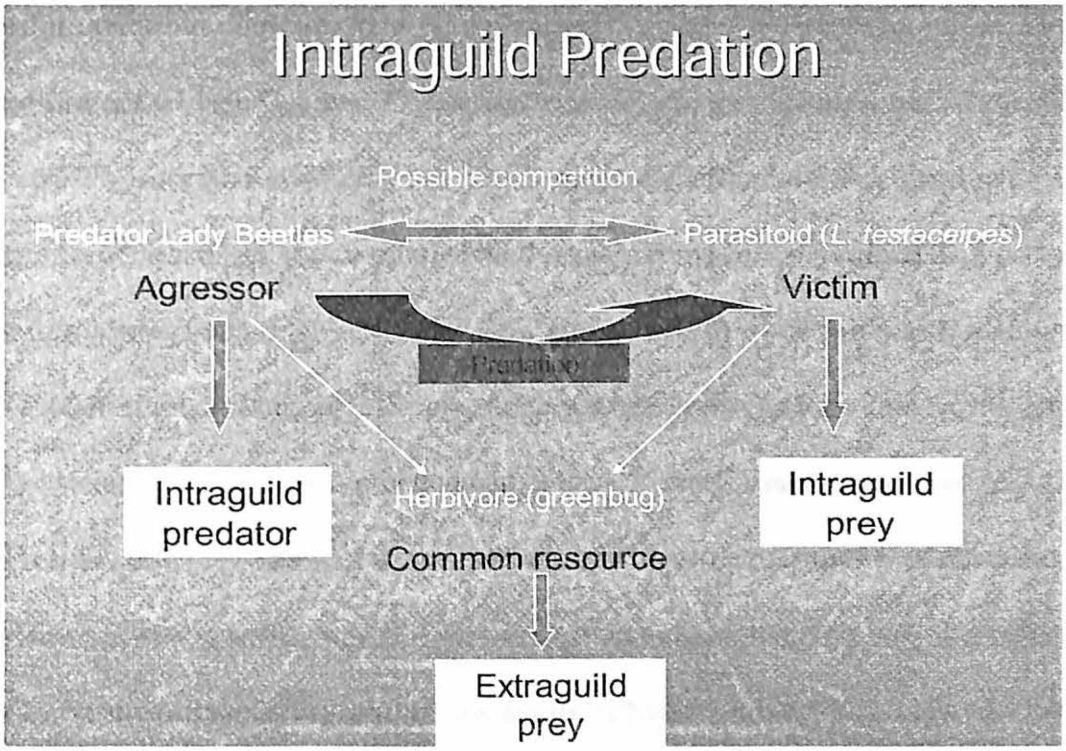
It appears that manipulative field experiments involving more than a single biological control agent are rare (Rosenheim et al. 1995). Their extensive experience with augmentative biological control has rarely produced evidence of outbreaks that occurred as a result of releases, which suggests that disruption is rarely caused by intraguild predation. They stated that the only field-documented disruption in biological control associated with intraguild predation arose from predators including mites, insects and fish.

Intraguild Predation in Coccinellidae: Lady beetles are very voracious and abundant predators in many agro ecosystems (Yasuda and Shinya 1997). Intraguild predation relationships that include coccinellid beetles can be characterized as intraspecific (cannibalism) or interspecific. The incidence of cannibalism and intraguild predation (Takahashi 1987, Agarwala and Dixon 1992, Yasuda and Shinya 1997) is affected by the relative abundance of prey compared to predator. Cannibalism and intraguild predation increase when larvae disperse from plants and remain low when the species emigrate early. The result of cannibalism and intraguild predation depends on the relative sizes and the stage of development of the prey and the predator. The younger larvae and eggs are more vulnerable to cannibalism by older larvae than the older larvae to the younger larvae (Agarwala and Dixon 1992). In the same way, a smaller species is more vulnerable as prey to the larger species in intraguild predation (Lucas et al. 1998, Phoofolo and Obrycki 1998, Hindayana et al. 2001).

Elliott and Keickhefer (1990) and Elliott et al. (1996) observed the occurrence of intraguild interactions among aphidophagous lady beetles, which may have accounted for changes in the beetles' guild structure, and resulted in restructuring of insect communities and species composition in lady beetle guilds in the U.S. A typical example of such restructuring was observed with the intraguild predation by *Harmonia axyridis* of aphidophagous lady beetles in North America (Day et al. 1994). *Harmonia axyridis* and *C. septempunctata* appear to coexist in Japan (Yasuda and Shinya 1997). Although both are capable of preying on each other and the larvae of both species are similar in size, their developmental times are different. The larvae of *C. septempunctata* develop more rapidly than *H. axyridis* larvae, so at similar ages, they are larger than those of *H. axyridis*. Therefore the larvae of the former species can attack and feed on the latter.

This implies that smaller, inactive species are likely to become prey for the larger active individuals irrespective of species. This could result in either interspecific (predation between species) or intraspecific intraguild predation (predation within species). Rosenheim et al. (1995) recognized two types of unidirectional IGP between predators and parasitoids. In the first instance, predators feed directly on immature parasitoids that develop externally on the host, or on the free living adults. Secondly, the predators feed on the parasitized host and indirectly consume the immature parasitoid. Meyhofer and Klug (2002) studied the mortality risks of *Lysiphlebus fabarum* from intraguild predation by *C. septempunctata* and observed that the larval developmental stages and the pupa of this parasitoid are the intraguild prey to various predator species, but they could not quantify specific predation risks. Figure 1 illustrates an example of such an intraguild interaction, and the hypothesized interaction that may be occurring in the winter wheat system that occurs in Oklahoma.

Figure 1. Schematic description of intraguild predation by coccinellid lady beetles.



Intraguild Predation

Possible competition

Predator Lady Beetles ⟷ Parasitoid (*L. testaceipes*)

Agressor

Victim

Predation

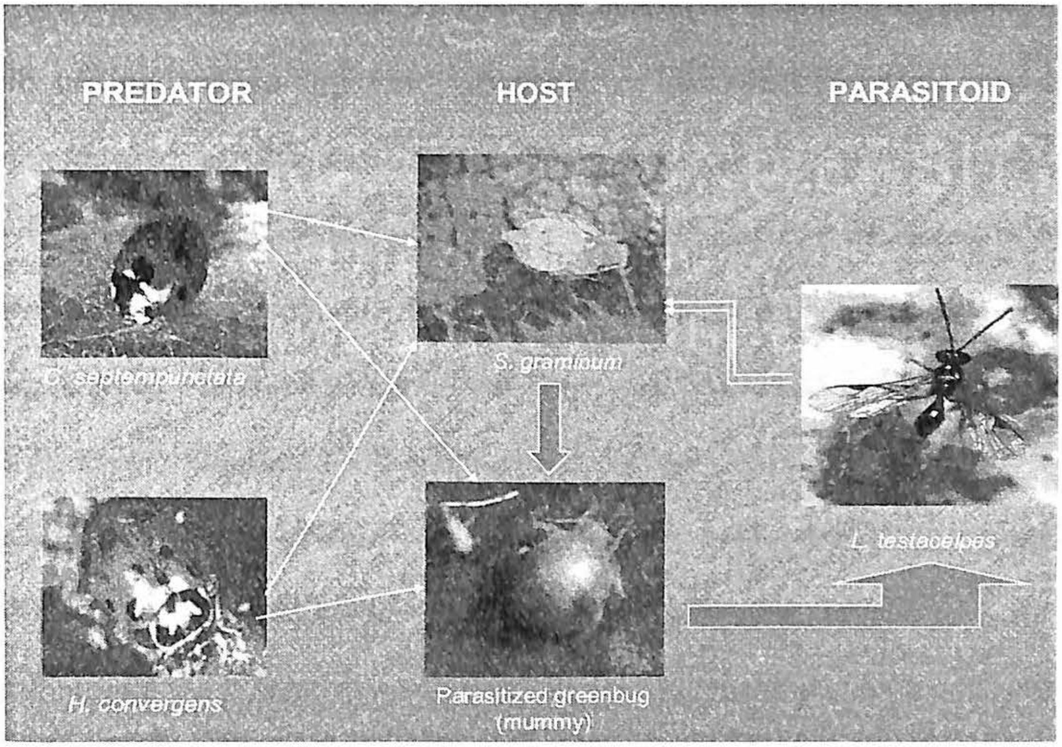
Intraguild predator

Herbivore (greenbug)

Common resource

Intraguild prey

Extraguild prey



PREDATOR

HOST

PARASITOID

C. septempunctata

S. graminum

L. testaceipes

H. convergens

Parasitized greenbug
(mummy)

Nutritional Ecology of Coccinellidae

Prey Suitability in Coccinellidae: Predaceous coccinellids are known to feed on a wide range of food. Besides feeding on Homoptera and phytophagous mites, they often eat young instars of Lepidoptera, Coleoptera and Hymenoptera, small nematocerous Diptera and Thysanoptera. Thompson (1951) suggested that the foods listed as acceptable to coccinellids are unreliable, and some new criteria of suitability, other than acceptability should be adopted. Hodek (1973) argued that observed acceptability (when the non-essential or primary prey is accepted) has been mistaken for real suitability (which is suitable for normal development) of prey even by most experienced workers.

Hodek (1973) found that the wide variety of food consumed by predaceous coccinellids has led to many scientists to assume that food specificity among coccinellids exists only between major taxonomic groupings. There is evidence to support Hodek's claims. Observations reported as early as 1907 indicated that some aphids are not suitable to certain Coccinellids (Hodek 1973). Blackman (1965) reviewed studies on the dietary specificity of Coccinellidae and found that the larvae of *C. septempunctata* were able to develop on *Aphis fabae* and *Megoura viciae*; although a diet of *M. viciae* caused a slight increase in development time and resulted in smaller adults. Other studies showed that the *C. septempunctata* readily attacked alfalfa weevil larvae as well as aphids, but failed to reproduce when maintained on a diet the weevil larvae only (Richards and Evans 1998, Evans et al. 1999). Obryicki and Phoofolo (1997) reported that some species of Coccinellidae can reproduce on relatively wide ranging diets of aphid and non-aphid prey, while others reproduce little when aphids are absent in their diet.

Effects of Nutritional Quality and Quantity: Coccinellid lady beetles depend on both temperature and food quality for their development and fecundity. Development rate increases with temperatures only up to a certain temperature (the upper development threshold) then remains flat or slows until the lethal temperature threshold is reached (Jarosik et al. 2000). Hodek (1962) distinguished between essential prey (which provides the essential nutrients) and alternative prey (which serves solely as an energy source, but does not allow development). Dixon (2000) distinguished between nursery prey, patches of which may cause predator oviposition, and the broader category of food prey consumed by the predators to sustain themselves. These distinctions are well illustrated by lady beetles that prey especially on aphids (Hodek 1973; Gordon 1985; Hodek and Honek 1996 and Dixon 2000). Although some species in this group have quite broad diets and reproduce readily after eating non-aphid prey (Putnam 1957; Schanderl et al. 1988, Phoofolo and Obrycki 1997), numerous observations demonstrate that certain accepted prey do not enable development or can be toxic. These different relations have most often been described for aphids and aphidophagous coccinellids like *H. convergens* and *C. septempunctata* (Hodek and Honek 1996).

When suitable food is in short supply, adult Coccinellids can (1) survive starvation for quite a long time, (2) take only a limited amount of food or, (3) switch to a substitutive (alternative) food, of insect and or plant origin. Therefore, feeding on several types of food "mixed feed" is generally observed as an emergency feature, compelled by shortages of "right" food (Hodek and Honek 1996).

Hodek (1962) described the best criterion to determine the suitability of food as that which provides the experimental evidence in which the predator is able to develop on a particular prey. Food, (quantity and quality), significantly influences the rate of larval growth (increase in weight) and development (duration of instars). Several studies revealed that decreasing food amounts increase developmental time and slow larval growth. Food consumption during different instars is a product of instar duration and feeding voracity. The latter depends on its growth rate and physiological efficiency of food assimilation. The nutritive value of aphids can vary with temperature and host plant (Giles et al. 2001), due to differences in fatty acid content. As these factors vary among species and diet, it becomes difficult to make comparisons Hodek and Honek (1996). The consensus is that further work on food suitability in the context of coccinellid ecology is needed. Since both crops are grown in Oklahoma and both serve as host for greenbug and its associated array of natural enemies, it is critical that the interactions among *S. graminum*, *L. testaceipes*, *C. septempunctata* and *H. convergens* are elucidated.

CHAPTER III

MATERIALS AND METHODS

Greenbug Rearing Procedures: Greenbugs; 'Biotype E' were maintained in a greenhouse colony on sorghum grown in fritted clay and sphagnum moss medium. Sorghum was selected as the host plant because it is able to withstand greenbug infestations longer than wheat without dying. Both crops are grown in Oklahoma (Oklahoma Agric. Statistics Service 2004) and 'Biotype E' greenbugs are common, and use both crops as a food source (Royer et al. 1998, Royer 2004). *L. testaceipes* and both species of ladybeetles also occur in both crops (T. Royer, personal communication). Rearing methods consisted of three steps. First, sorghum plants were planted in pots in the greenhouse and covered with nylon-screened plastic cages. When the plant stems reached ~8 mm in diameter, they were placed into larger cages, and infested with greenbugs which were allowed to settle and multiply. New plants were replaced as infested plants began to senesce.

***Lysiphlebus testaceipes* Rearing Procedures:** A colony of *L. testaceipes* was maintained in the laboratory under room temperature and 12:12 photoperiod and reared on 'Biotype E' greenbugs in wooden cages covered with fine mesh. Sorghum plants were placed in the cages and greenbugs were released onto the plants and allowed to settle and establish for 2-4 days. Aphid mummies were collected from the field and held in isolation until adult wasps emerged. Newly emerged wasps were collected, held in a cold chamber and identified. Adult *L. testaceipes* wasps were removed from the cages with an aspirator and released into sorghum-reared colonies of unparasitized greenbugs kept on plants in three fine mesh cages. Wasp colonies were provided with unparasitized greenbug-infested plants periodically to maintain wasp colonies.

Ladybeetle Rearing Procedures: *Coccinella septempunctata* and *H. convergens* were collected from the field, separated into mating pairs and maintained in half pint cardboard ice cream containers with a fine mesh cover in a growth chamber set at 22 °C and a photoperiod of 16:8 (L:D). Beetles were fed an unlimited supply of pea aphids (*Acyrthosiphon pisum*) and an artificial supplementary diet made from honey and wheast. When egg laying commenced, the male beetles were removed to avoid egg consumption and female disruption. Eggs from at least three mating pairs were allowed to hatch under the same conditions, and upon eclosion, the larvae were separated into 5-ml individual glass vials stopped with nylon screened caps. In all cases, larvae were reared exclusively on 4 mg of greenbugs per day until they were subjected to experimental treatments.

Production of Mummies: Greenbugs were pulled out of the laboratory colony and placed on un-infested sorghum plants contained in nylon-screened cages. They were allowed to settle, establish and multiply for ca. 3-5 days. Adult *L. testaceipes* wasps were collected from the laboratory wasp colony using an aspirator and released into the cage containing greenbug-infested sorghum plants. Seven to ten days after the *L. testaceipes* wasps were released into the cages of greenbugs, newly formed mummies were located and hand-picked daily from the sorghum plants using a fine pair of forceps. The mummies were placed in 5-ml plastic vials, labeled with date of collection, and stored in the growth chamber at 6°C, which is below their lower development threshold (Elliot et al 1994b), and a photoperiod 16:8 (L:D).

Feeding Capability Study: This study was conducted to determine the capability of each instar of *C. septempunctata* and *H. convergens* for consuming greenbug mummies parasitized by *L. testaceipes.* Twenty *C. septempunctata* larvae and twenty *H. convergens* larvae (five larvae per instar) were placed individually in vials stopped with nylon-screened caps. Larvae were fed one of the following diet treatments of newly-formed greenbug mummies: first instar larvae were fed four mummies; second instar larvae were fed eight mummies; third instar larvae were fed sixteen mummies; fourth instar larvae and adult beetles were fed 4mg mummies that were weighed on a Satorius M 3P micro-balance. Larvae were observed daily to record visual evidence (determined by finding opened, empty mummy shells) that the mummies had been fed upon.

Prey Preference Study: This study was conducted to determine if larvae of *C. septempunctata* and *H. convergens* demonstrate a preference for unparasitized greenbugs or greenbug mummies parasitized by *L. testaceipes.* Twenty fourth instar *C. septempunctata* larvae and twenty fourth instar *H. convergens* larvae that had been starved for 24 hours were provided with 10 unparasitized greenbugs or 10 greenbug mummies that had been parasitized by *L. testaceipes* in a no-choice test and observed for 30 minutes. The time they required to completely consume an individual prey item was recorded. In a separate experiment, fourth instar *C. septempunctata* larvae and twenty fourth instar *H. convergens* larvae were starved for 24 hours then presented with 10 unparasitized, and 10 parasitized greenbug mummies in a choice test to determine their preference. The prey items were placed at the center of the Petri-dish, and then a larva was released in the center of the dish and allowed to search, and feed. The number of encounters, and attacks on each diet item were recorded under a choice situation for 30 minutes. The insect's general behaviour was also observed and recorded to contribute to the understanding of their preference abilities. At the end of thirty minutes, the number of parasitized and unparasitized greenbugs that were consumed was recorded and a comparison of consumed prey types was used as an indication of preference for one prey relative to the other (Murdoch 1969).

Data were analyzed for each species. Pairwise t-tests were used to compare the number of prey encountered to the number attacked and to the number consumed for each prey item using PROC MIXED in SAS (Littell, et. al 1996). A paired t test (PROC TTEST in SAS) was used to compare attack rate between greenbugs and mummies, and consumption rate between greenbugs and mummies. An alpha value of 0.05 was chosen as the significance level for all comparisons.

Prey Suitability Study: This study was conducted to the effects of greenbug mummies parasitized by *L. testaceipes* on the development of *C. septempunctata* and *H. convergens* larvae. The diet treatments were selected using two criteria. First, the diet amount was limited to 4 mg of diet/day because Giles et al. (2003) showed that limited diets are required to quantitatively evaluate effects on development, and that in nature, larvae are often feeding in "starvation mode" where they are not obtaining unlimited food. Second, all larvae being fed a diet that contained any mummies were also provided with water once the diet treatment was applied. Preliminary experiments conducted to develop the protocols indicated that larvae fed greenbugs were able to complete their development to adulthood, but that larvae fed mummies without any water died within two days. Therefore, water was provided to all larvae that received a diet containing mummies through a cotton wick to assure that they received adequate water to eliminate any mortality that could be attributed to dehydration.

Prior to the application of diet treatments, all larvae received a daily supply of 4mg of greenbugs. Upon reaching the third instar, sets of five individuals were randomly selected to receive one of the five diets: 4mg of greenbugs per day (GB); 4mg of a 50/50 ratio of greenbugs and greenbug mummies per day beginning at 3rd instar (MIX3); 4mg of greenbug mummies per day beginning at 3rd instar (MUM3); 4mg of a 50/50 ratio of greenbug and greenbug mummies per day beginning at 4th instar (MIX4); or 4mg of greenbug mummies per day, beginning at 4th instar (MUM4).

The insects were checked twice daily for visual evidence of molting until they died or emerged as adults. The elliptical body area of emerged adults was calculated by measuring the body length and width using the Obrycki et al. (1998) formulae: [½(body length)הּ] × [½(body width)הּ].

Differences in development time and elliptical body size in the prey suitability study were analyzed as a randomized complete block design using PROC MIXED (Littell et al. 1996) in SAS. For purposes of analysis, blocks were considered to be a specific rearing period (6 levels) and treatments were diets (5 levels). When the ANOVA was significant for treatment comparisons, pairwise t tests were performed using a DIFF option in an LSMEANS statement. This analysis was performed for each species of lady beetle separately. A chi square test with PROC FREQ in SAS was used to compare sex ratios and survival (larval and pupal) among treatments in the prey suitability study. An alpha value of 0.05 was chosen as the significance level for all comparisons.

CHAPTER IV

RESULTS

Feeding Capability Study: *Coccinella septempunctata* and *H. convergens* larvae fed on parasitized greenbugs. The first instar larvae of both species were not able to consume mummies. Second instar larvae attempted to feed and partially consumed mummies. Third and fourth instar larvae completely consumed the mummies provided to them (Table 1).

Prey Preference Study: In the first experiment, the prey handling time for *H. convergens* ($t = -11.90$; df = 19; $P = <.0001$) and *C. septempunctata* ($t = -4.22$; df = 14; $P = 0.0009$), larvae was significantly different between the two prey items. For both species, larvae took longer to consume mummies compared to greenbugs (Table 2).

C. septempunctata, demonstrated no significant difference in the number of greenbugs or mummies attacked or consumed compared to the number encountered ($t = 0$; df = 19; $P = 1.00$). One hundred % of both prey items that were encountered were attacked and consumed (Table 3). There was also no difference between the number of greenbugs attacked or consumed compared to the number encountered ($t = 1.91$; df = 19; $P = 0.0717$) for *H. convergens*. However, they consumed significantly fewer mummies than they encountered ($t = 2.64$; df = 19; $P = 0.0163$). Larvae tended to encounter and ignore; encounter and reject; or encounter, attack then stop feeding on mummies prior to consuming them.

Prey Suitability Study: Results are summarized in Table 4. The average length for larval and preimaginal development of GB *C. septempunctata* larvae was 11.8 ± 0.3 days and 21.4 ± 0.4 days . The average length for larval and preimaginal development of

Table 1. Consumption of parasitized greenbugs by larvae and adults of *Coccinella septempunctata* and *Hippodamia convergens.*

	Observation	**# of mummies provided**	**# of mummies consumed**	
			C-7	*HC.*
1st instar	1	2	0	0
	2	2	0	0
	3	2	0	0
	4	2	0	0
	5	2	0	0
	Total	**10**	**0**	**0**
2nd instar	1	4	4*	2*
	2	4	3*	4*
	3	4	4*	4*
	4	4	4*	4*
	5	4	4*	3*
	Total	**20**	**19**	**17**
3rd	1	16	16	16
	2	16	16	16
	3	16	16	16
	4	16	16	16
	5	16	16	16
	Total	**80**	**80**	**80**
4th	1	30	30	16
	2	30	30	16
	3	30	30	16
	4	30	30	16
	5	30	30	16
	Total	**150**	**150**	**150**
Adults	1	30	30	30
	2	30	30	30
	3	30	30	30
	4	30	30	30
	5	30	30	30
	Total	**150**	**150**	**150**

* Feeding was attempted but mummies were only partially consumed

C-7 = *Coccinella septempunctata*, HC = *Hippodamia convergens*

Table 2. Mean handling time (± SEM) of unparasitized and parasitized greenbugs by *C. septempunctata* and *H. convergens* fourth instar larvae in a choice test.

	Mean duration (seconds)	
	C. septempunctata	*H. convergens*
Unparasitized greenbugs	79.14 ± 9.6a*	49.10 ± 6.0*
Parasitized mummies	119.54 ± 9.6	120.80 ± 6.0

Values within columns, if the first is followed by an asterix* are significantly different (*P* > 0.05, Fisher's protected Least Significant Difference Procedure).

Table 3. Encounters, attacks and number consumed (mean ± SEM) of unparasitized greenbugs (GB) and mummies parasitized by *Lysiphlebus testaceipes* (MUM) by 4th instar larvae of *Coccinella septempunctata* and *Hippodamia convergens*.

Species	Prey	N	# Encountered	# Attacked	# Consumed
C-7	GB	10	5.3 ± 0.40a	5.3 ± 0.40a	5.3 ± 0.40a
	MUM	10	5.6 ± 0.38a	5.6 ± 038a	5.6 ± 0.38a
HC	GB	10	4.1 ± 0.53a	3.6 ± 0.60a	3.5 ± 0.40a
	MUM	10	4.4 ± 0.36a	3.6 ± 0.54ab	3.2 ± 0.58b

C-7 = *Coccinella septempunctata,* HC = *Hippodamia convergens*
Values within a row, followed by the same letter are not significantly different (*P* > 0.05, Fisher's protected Least Significant Difference Procedure).

Table 4. Effects of diet on development times and adult elliptical area at 22°C for *C. septempunctata* and *H. convergens* in prey suitability studies.

		Developmental Time (Days ±SEM)					
	Treatment*	3rd instar	4th instar	Larval	Pupal	Preimaginal	Adult Eliptical area (mm^2 ± SEM)
C. septempunctata							
N = 27	GB	3.0 ± 0.1bc	4.8 ± 0.16c	11.7 ± 0.2b	5.6 ± 0.2b	21.4 ± 0.3b	0.73 ± 0.01a
N = 25	MIX3	3.3 ± 0.1b	6.9 ± 0.3a	14.3 ± 0.4a	7.9 ± 0.3a	26.3 ± 0.5a	0.52 ± 0.01b
N = 30	MUM3	6.9 ± 0.2a	-	-	-	-	-
N= 30	MIX4	2.9 ± 0.1bc	5.8 ± 0.2b	12.6 ± 0.2b	5.9 ± 0.2b	22.3 ± 0.2b	0.71 ± 0.01a
N = 30	MUM4	2.8 ± 0.2c	-	-	-	-	-
H. convergens							
N = 30	GB	3.0 ± 0.0b	3.5 ± 0.1c	10.5 ± 0.1c	3.9 ± 0.05b	18.5 ± 0.1c	0.38 ± 0.005a
N = 28	MIX3	3.1 ± 0.1b	5.7 ± 0.2a	12.8 ± 0.2a	4.9 ± 0.1a	21.6 ± 0.2a	0.32 ± 0.004c
N = 30	MUM4	3.8 ± 0.1a	-	-	-	-	-
N = 28	MIX4	3.0 ± 0.0b	4.0 ± 0.1b	11.0 ± 0.1b	4.7 ± 0.2a	19.7 ± 0.2b	0.36 ± 0.002b
N = 29	MUM4	3.0 ± 0.1b	-	-	-	-	-

* All larvae received 4 mg of food/day and all larvae received unparasitized greenbugs until diet treatments were applied.

GB - unparasitized greenbugs only beginning at 1st instar;
MIX3 - 50/50 mixture of unparasitized and parasitized greenbugs beginning at 3rd instar
MUM3 - parasitized greenbugs beginning at 3rd instar
MIX4 - a 50/50 mixture of unparasitized and parasitized greenbugs beginning at 4th instar
MUM4 - parasitized greenbug mummies beginning at 4th instar.

Means in a column within the same species followed by the same letter are not significantly different ($P > 0.05$) according to Fisher's Protected Least Significant Difference Procedure.

GB *H. convergens* larvae was 10.5 ± 0.2 and 18.5 ± 0.2 days (Fig. 4 and 5). There were significant effects of diet in the larval and preimaginal development for *C. septempunctata* ($F = 32.2$; df = 2; P <0001; $F = 55.43$; df = 2; P <0001) and *H. convergens* larvae: ($F = 94.84$; df = 2; P <0001; $F = 98.27$; df = 2; P <0001). MIX3 *C. septempunctata* larval and preimaginal development was significantly different ($Pt <$ 0.001) from both MIX4 and GB larvae. There was no difference between *C. septempunctata* MIX4 and GB larvae. However, MIX4 larval and preimaginal development for *H. convergens* was significantly different (Pt <0.001) from GB larvae.

Larval development of MIX3 *C. septempunctata* larvae was increased by about 2.6 days, pupal development by 2.3 days and preimaginal development by about 5.0 days. (Fig 2-5). Average length for larval development of MIX3 *H. convergens* larvae was increased by 2.3 days, pupal development by 1 day and preimaginal development by 3.2 days (Fig. 2-5). MIX4 preimaginal development of *H. convergens* was increased by about 3 days.

Survivorship: MUM3 *C. septempunctata* and *H. convergens* larvae molted into fourth instars, but did not survive to pupation (Fig. 6 and 7). MUM4 larvae of both species did not pupate, but survived to the prepupal stage and then died. The χ^2 analysis indicated a difference in larval survivorship (Table 5) but did not indicate any significant effect on survivorship of sexes between any larvae in either species (Table 6).

Body size: There was a significant difference in the adult elliptical body area (P $| t | = 0.001$) for GB, MIX3 and MIX4 larvae of both species. MIX3 adults were significantly smaller (Table 2 and Fig. 8). However, there was no difference in adult body size for MIX4 adults compared to GB adults ($P\ | t | = 0.0978$) in *C. septempunctata*.

Table 5. Effects of diets on survivorship of *C. septempunctata* (C-7) and *H. convergens* (HC).

		Proportion Surviving			
	Treatment	3rd Instar	4th Instar	Larval	Preimaginal
C-7					
	GB	0.97	0.97	0.90	0.90
	MIX3	1.00	1.00	0.83	0.93
	MUM3	1.00	1.00	0.00*	0.00*
	MIX4	1.00	1.00	1.00	1.00
	MUM4	1.00	1.00	0.00*	0.00*
HC					
	GB	1.00	1.00	1.00	1.00
	MIX3	1.00	1.00	0.93	0.93
	MUM3	1.00	1.00	0.00*	0.00*
	MIX4	1.00	1.00	0.93	0.93
	MUM4	1.00	1.00	0.00*	0.00*

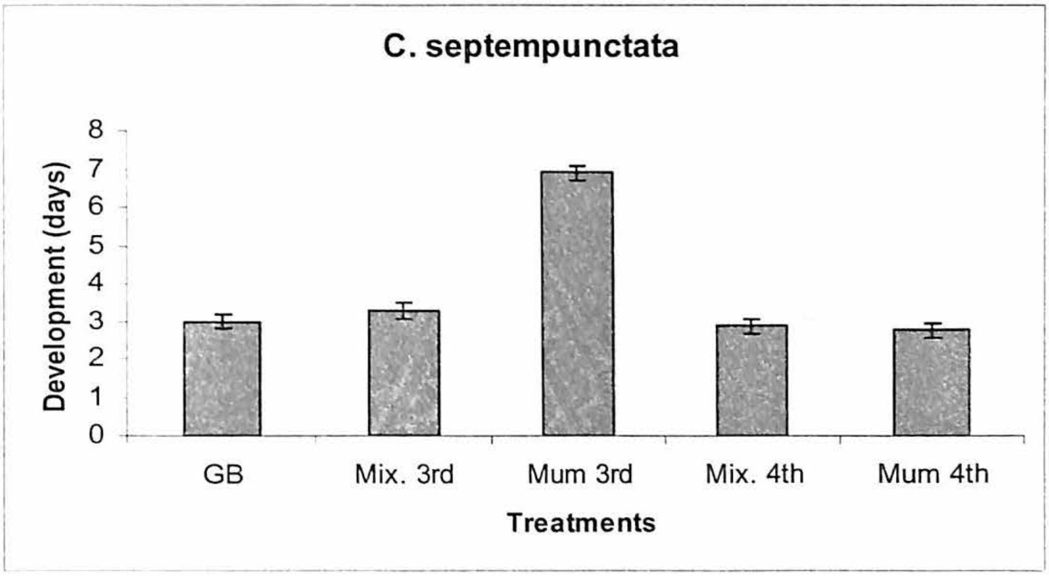
GB – Unparasitized greenbugs only at 1st instar
MIX3 – Mixture of unparasitized and parasitized greenbugs at 3rd instar
MUM3 – Parasitized greenbugs at 3rd instar
MIX4 - Mixture of unparasitized and parasitized greenbugs at 4th instar
MUM4 - Parasitized greenbugs at 4th instar
Survival values followed by an asterix * are significantly different (P chi square < 0.05) from 100% survival, according to chi square test (Proc FREQ), SAS Institute.

Table 6. Effects of diet on female/male ratio of surviving *C. septempunctata* and *H. convergens* in prey suitability studies

				Sex	
	Treatment	N	# Females	# Males	F/M ratio
C. septempunctata					
	GB	27	12	15	0.80
	MIX3	25	10	15	0.67
	MUM3	0	0	0	-
	MIX4	30	12	18	0.66
	MUM4	0	0	0	-
					***P* = 0.926**
H. convergens					
	GB	30	14	16	0.88
	MIX3	28	11	17	0.65
	MUM3	0	0	0	-
	MIX4	28	15	13	1.25
	MUM4	0	0	0	-
					***P* = 0.563**

* All larvae received 4 mg of food/day; all larvae received unparasitized greenbugs until diet treatments were applied
GB - unparasitized greenbugs only beginning at 1st instar;
MIX3 - 50/50 mixture of unparasitized and parasitized greenbugs beginning at 3rd instar
MUM3 - parasitized greenbugs beginning at 3rd instar
MIX4 - a 50/50 mixture of unparasitized and parasitized greenbugs beginning at 4th instar
MUM4 - parasitized greenbug mummies beginning at 4th instar.
P values are the probability of chi square (Proc FREQ, SAS Institute) that the female/male ratio for each treatment is not different from 1.0

Figure 2. Effects of diet on average development times (±SEM) for 3^{rd} instar larvae of *C. septempunctata* and *H. convergens* in prey suitability studies.



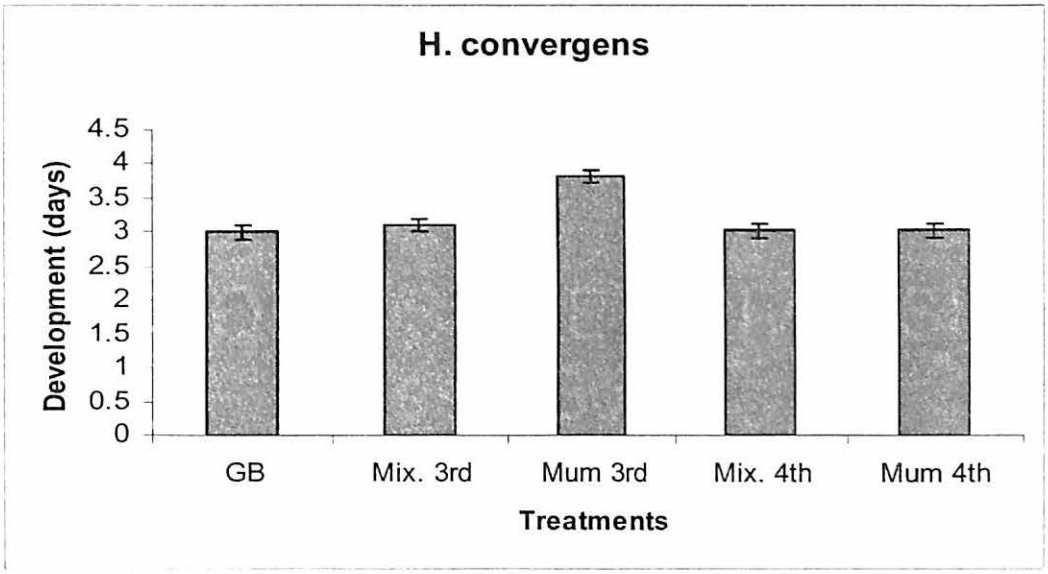
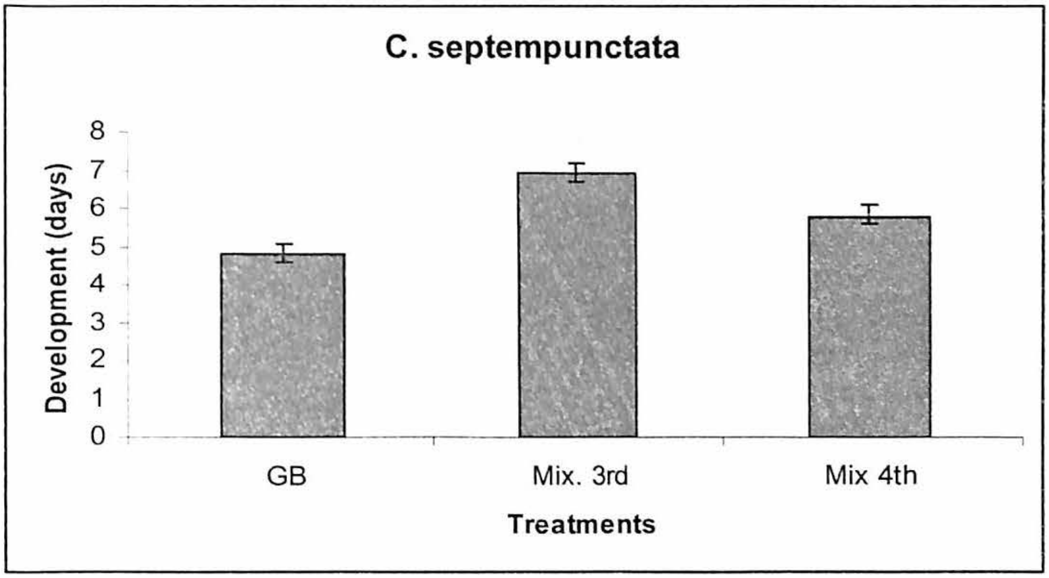


Figure 3. Effect of diet on average development times (±SEM) for 4th instar larvae of *C. septempunctata* and *H. convergens* in prey suitability studies.



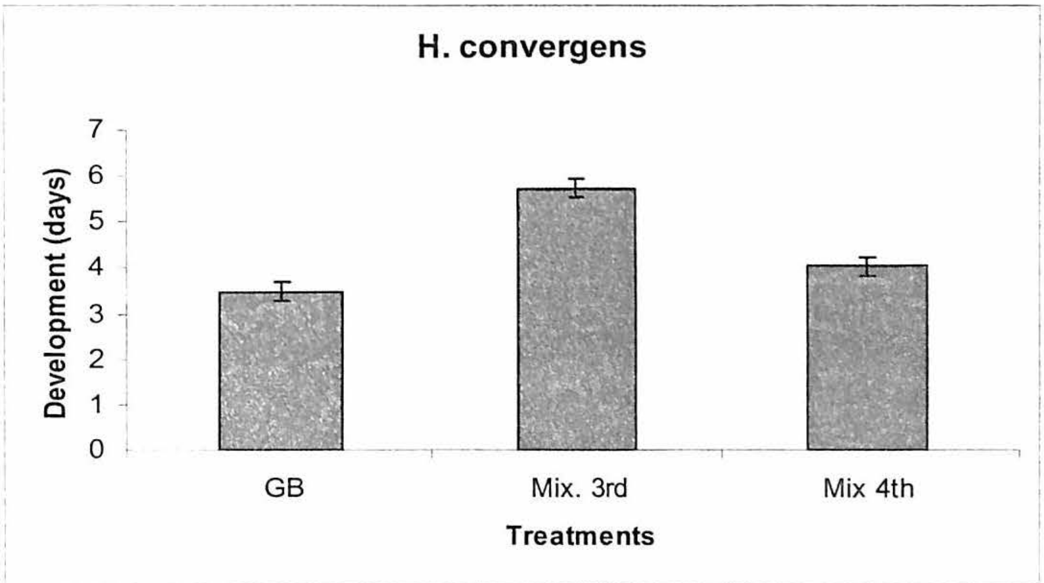
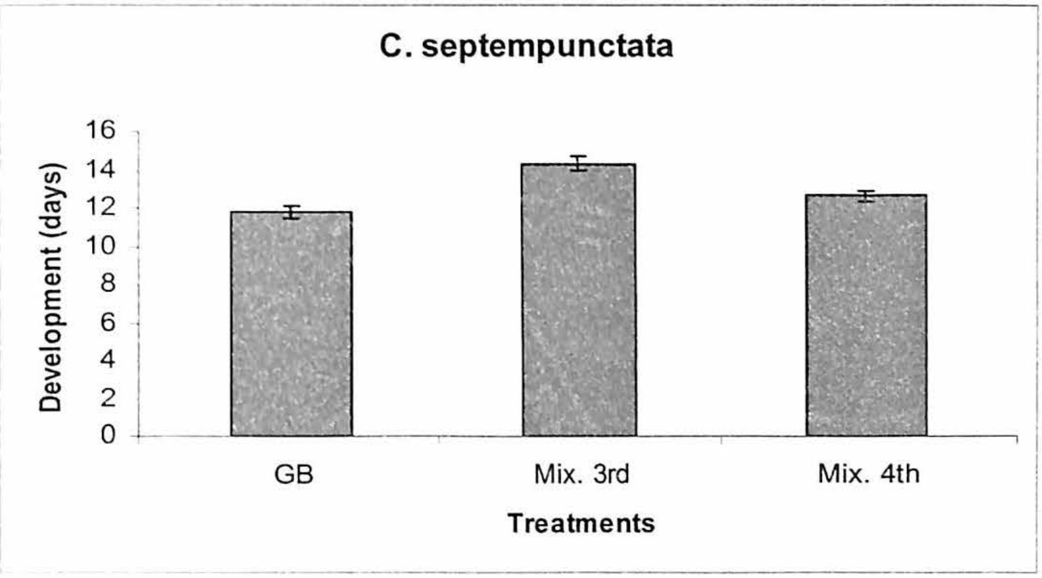


Figure 4. Effect of diet on average larval development times (±SEM) of *C. septempunctata* and *H. convergens* in prey suitability studies.



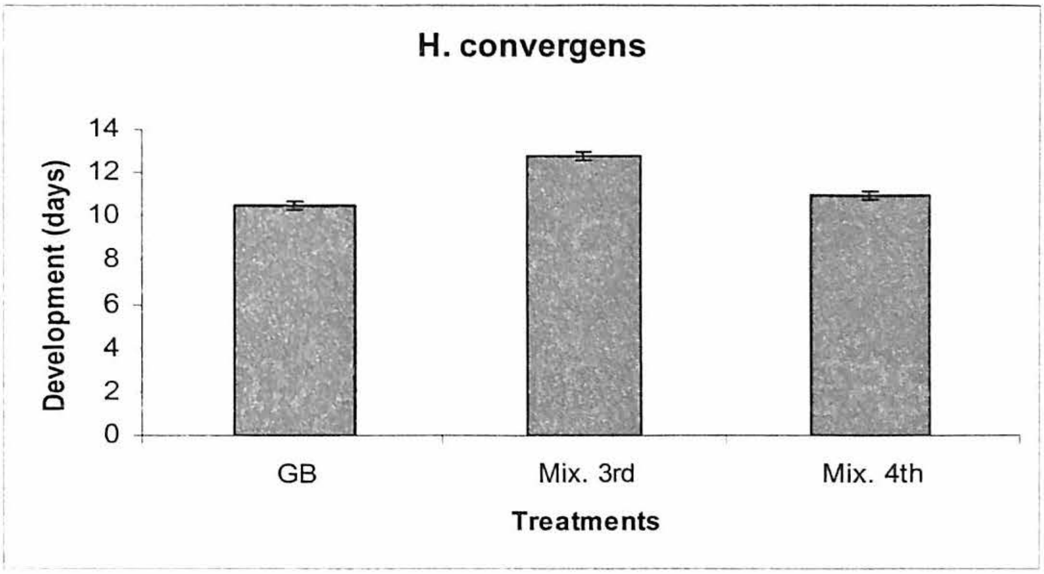


Figure 5. Effect of diets on average preimaginal development times (±SEM) of *C. septempunctata* and *H. convergens* in prey suitability studies.

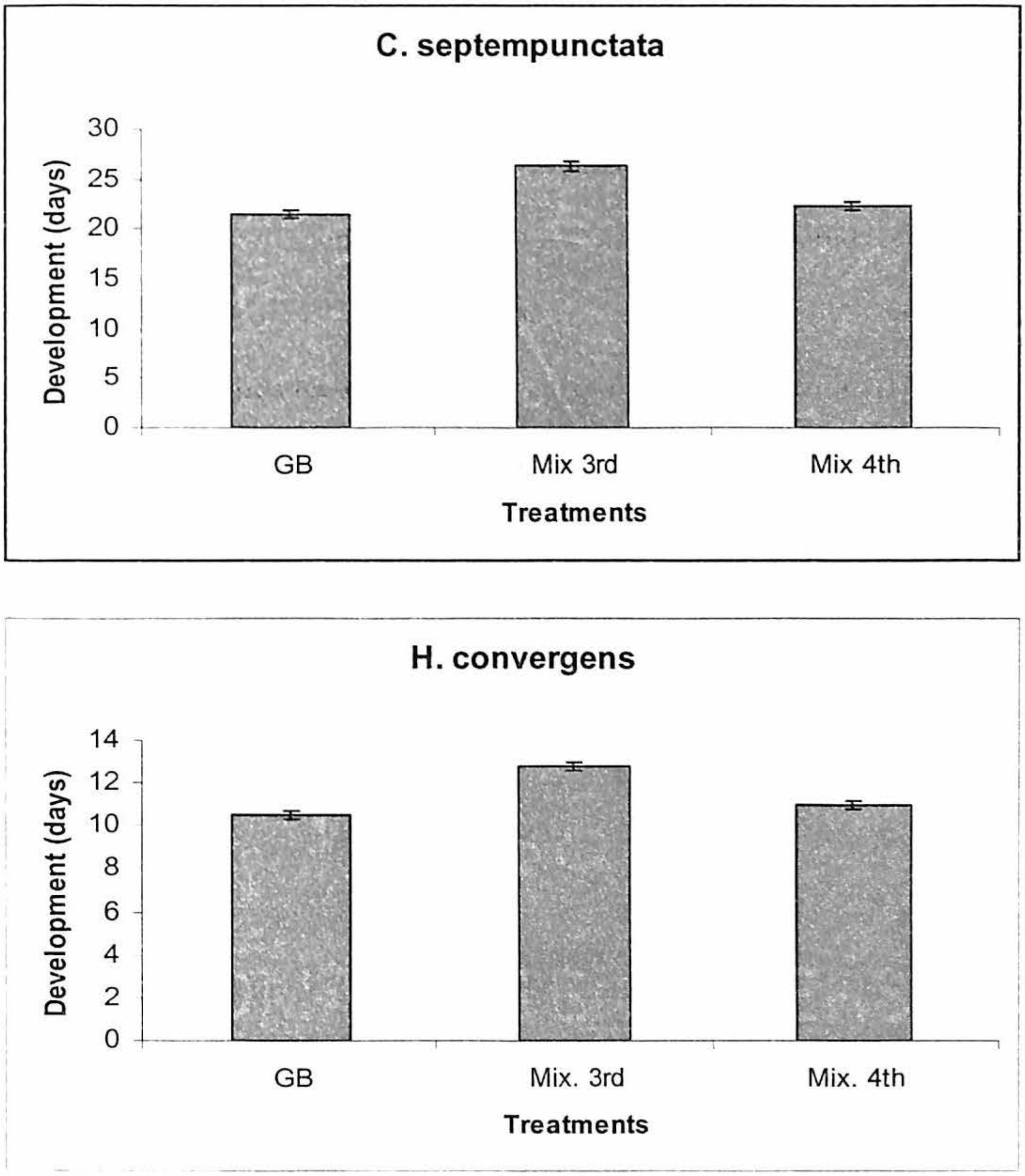
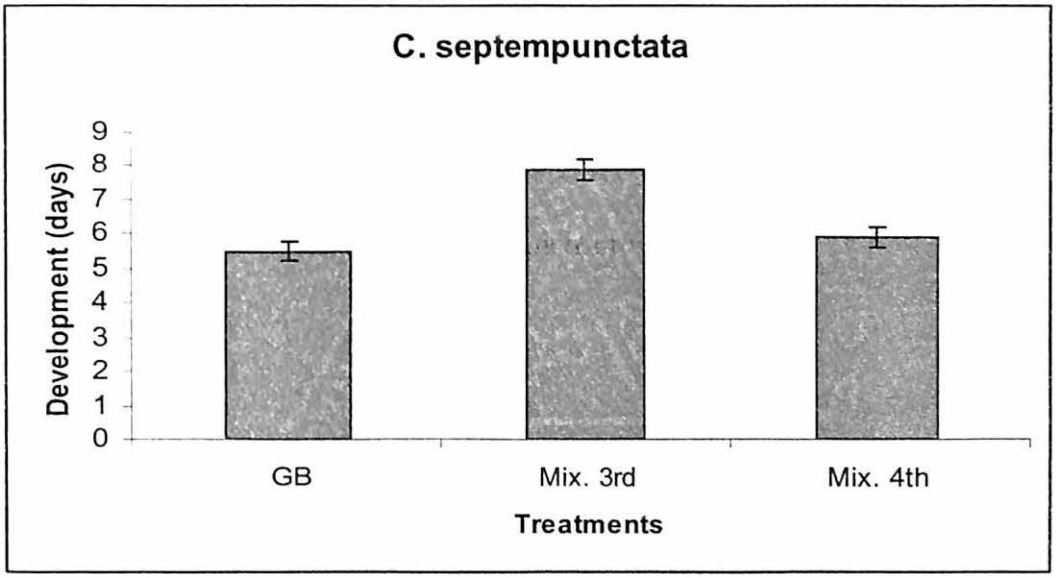


Figure 6. Effects of diet on average pupal development times (±SEM) of *C. septempunctata* and *H. convergens* in prey suitability studies.



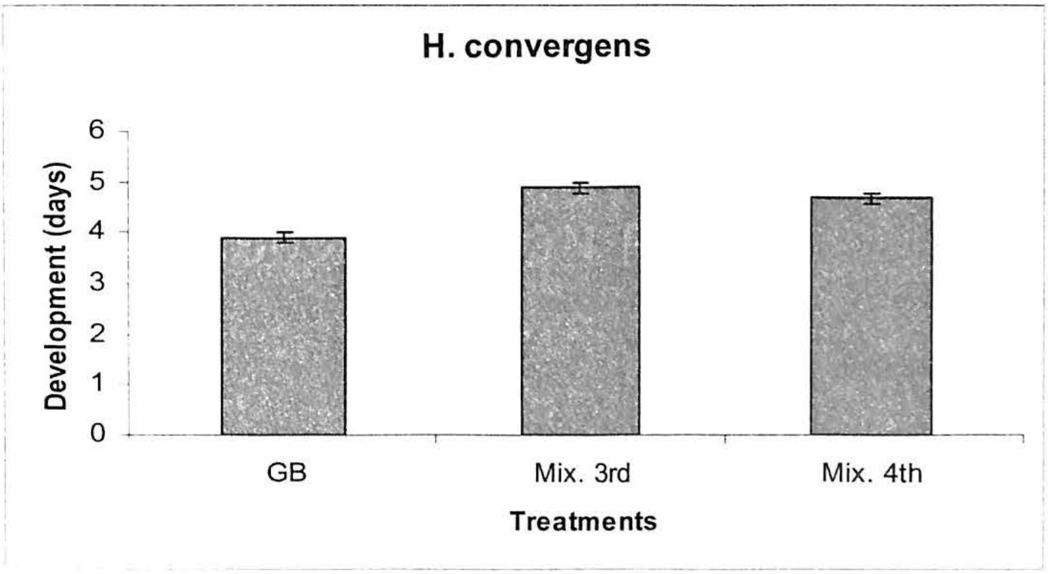


Figure 7. Effects of diet on survivorship of *C. septempunctata* larvae in prey suitability studies.

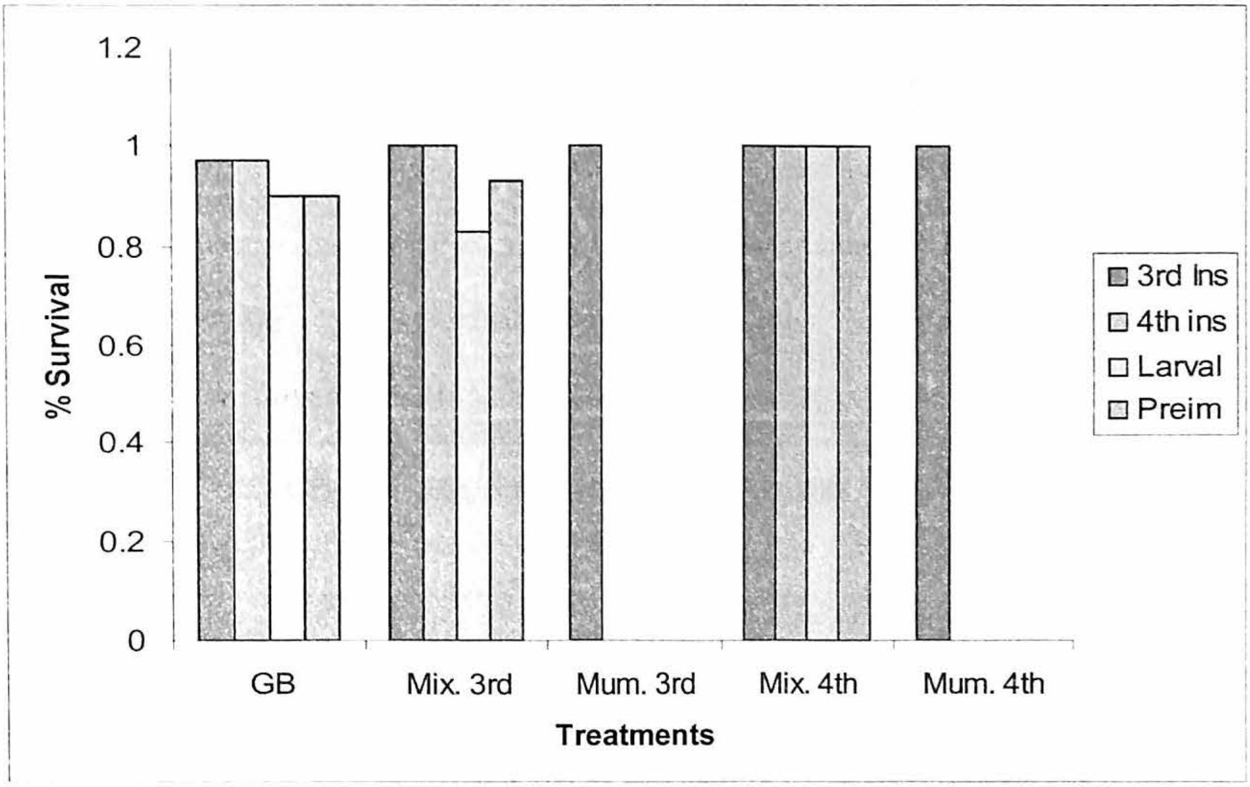


Figure 8. Effects of diet on survivorship of *H. convergens* larvae in prey suitability studies.

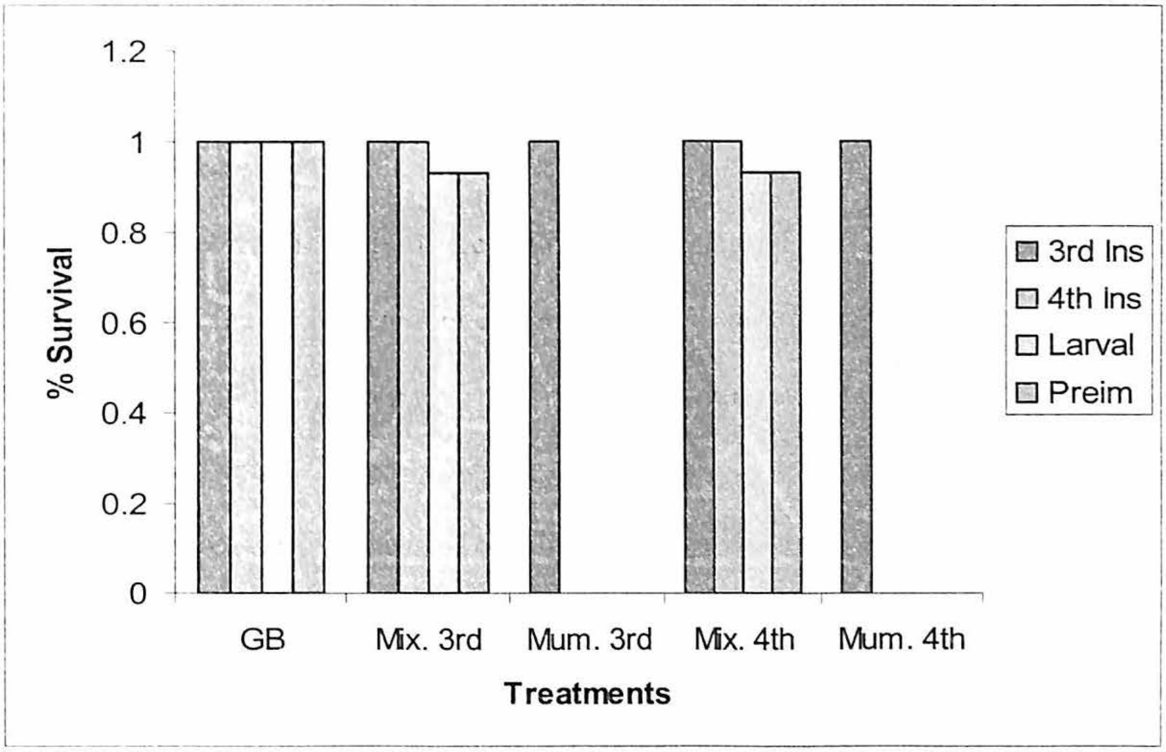
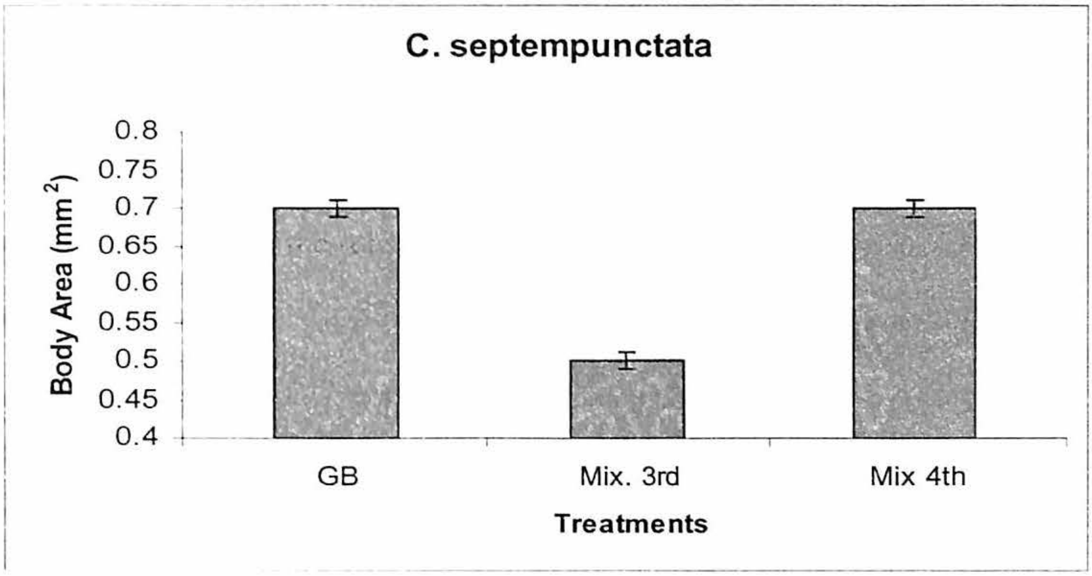
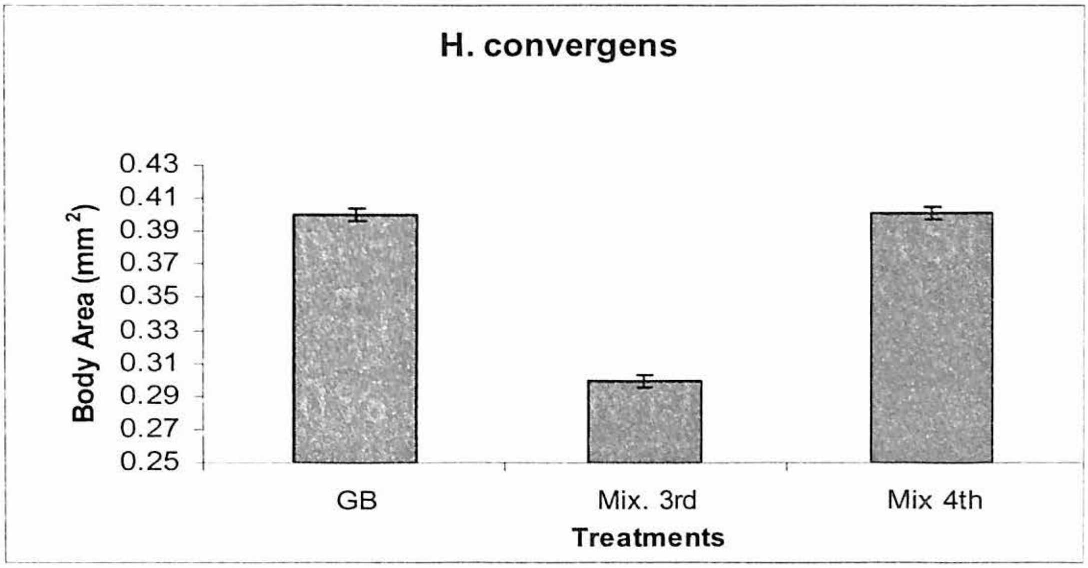


Figure 9. Effect of diets on eliptical area (mm^2) for *C. septempunctata* and *H. convergens* in prey suitability studies.





CHAPTER V

DISCUSSION

Lady beetle feeding capability: Meyhofer and Klug (2002) reported that asymmetric IGP occurs when one co-occurring antagonistic species is inferior to the other. In predator-parasitoid interactions, the predator (superior antagonist) it is an intraguild predator and the parasitoid (inferior antagonist) becomes an intraguild prey. Several coccinellid and aphidiid species have common aphid prey (Hagen 1986 and Majerus 1994). Because of their aphidophagous behaviour, coccinellids feed on the aphid prey and any parasitic Hymenoptera that have already attacked the aphid. Although most coccinellids feed on a wide range of prey types in nature (Hodek and Honek 1996), not all larval instars were able to successfully consume all kinds of prey they come into contact with.

The results of this study demonstrated that the first instar larvae of both *C. septempunctata* and *H. convergens* were not able to consume greenbug mummies parasitized by *L. testaceipes*. The second instar larvae attempted to eat, but only partially consumed mummies, which could be due to the protective mummy shelter they were unable to penetrate. However, the third and fourth instar larvae and adults of both species were able to completely consume the parasitized mummies. Thus, third and fourth instar larvae are intraguild predators of greenbug mummies containing *L. testaceipes* pupa. Second instar larvae were only able to partially consume mummies, thus they weaker intraguild predators of greenbug mummies parasitized by *L. testaceipes*, and thus contribute to parasitoid mortality.

The study further supports the results reported by Brodeur and Rosenheim (2000) on the risks aphid parasitoids face. They found that among other mortality risks, predation by aphidophagous predators was a major source of mortality. They were able to determine that developing offspring of aphid parasitoids are threatened by predation when a predator attacks the host aphids. Several studies of other species indicate that parasitized aphids face the same risk of predation as unparasitized aphids regardless of the stage of development and the foraging behaviour of the predator. Colfer and Rosenheim (1995) showed that *L. testaceipes* pupae are preyed upon by coccinellid beetles in cotton, but did not show that such predation affected the regulation of the host cotton aphid.

Lady beetle prey preference: In nature, most coccinellids feed on a wide range of prey types (Hodek and Honek 1996), but their prey is not always equivalent in nutritional value (Smith 1965, Mills 1981, Obrycki and Orr 1990). Crawley and Krebs (1992), using optimal foraging models, predicted that predators searching for prey should select the most profitable prey type and reject the unprofitable prey. Steven and Krebs (1986) added that such decisions would minimize loss of opportunity time and maximize energy return. Therefore, if parasitism alters prey suitability and profitability, the detection and recognition of a sign left by the parasitoid female, or morphological or physiological changes provoked by a developing immature parasitoid would provide strong advantages to a predator.

The results of this study showed that *C. septempunctata* and *H. convergens* larvae did not exhibit any measurable preference between parasitized and unparasitized greenbugs. Even their first encounter did not seem to influence the choice they made in the next encounter. Hoelmer et al. (1994), Brower and Press (1988) and Ruberson and Kring (1991) point out that most studies of egg predators have shown that they avoid parasitized prey containing larvae or pupae. Furthermore, Fritz (1982) suggested that the differential preference observed is a function of the physiological changes provoked by the developing parasitoid.

There was no significant difference in the amount of time required for a larva to consume a single mummified greenbug even though it was assumed that the larvae were randomly presented with different developmental stages of the immature parasitoid.

Since these larvae did not display any measurable preference, it suggests that parasitized mummies could be an alternative prey for these two predators. Putman (1959) found that nine out of ten coccinellid species he tested consumed less attractive prey (mites), but did not switch from extensive to intensive search behavior. My observations did not suggest that *C. septempunctata* larvae switch searching behaviors based upon the prey they encountered, but *H. convergens* larvae demonstrated a weak switching behavior. In conclusion, results of this study suggest that these two species do not discriminate between unparasitized and greenbug mummies parasitized by *L. testaceipes*.

Prey suitability: Hauge et al. (1998) assumed that a mixture of prey species may provide a higher nutritional diversity regardless if they are unselective in their prey choices. Thus, such a diet would be beneficial in terms of improved performance; that is, low mortality, faster development and larger adult body size and weight.

Alternatively, many coccinellid larvae have been shown to be sensitive to changes in the nutritional value of prey and decreased prey levels, or to the effect of toxic or less suitable prey. All can result in lower survival, longer developmental times, decreased weight and size and reduced fecundity of emerging adults as reported by (Smith 1965, Hodek 1973 and Phoofolo and Obrycki 1997). Blackman (1967) showed that prey of low quality slowed larval development and produced smaller adult animals, and concluded that coccinellids frequently accept alternative food which serves only as a source of energy but does not allow development.

The results of this study show that one varied diet had an adverse impact on larval development of both *C. septempunctata* and *H. convergens.* The third and fourth instar larvae that were fed mummies did not survive to pupae. Larvae fed a mixture of mummies and greenbugs were able to pupate, but developmental time was delayed and their adult body size was smaller those that were fed greenbugs. I did not evaluate the effects of diet on adult fertility or fecundity.

Although this experiment does not fully represent the interactions of these species in nature, it suggests that greenbugs may possess specific, essential nutrients which are required for growth, development and survival to maturity that are lacking in greenbug mummies parasitized by *L. testaceipes.* Giles et al (2001) showed that growth and development of both *C. septempunctata* and *H. convergens* were affected when fed *Acyrthosiphon pisum* (Harris) that had been reared on different host plants and had differing levels of myristic acid. An alternative hypothesis would be that parasitized greenbugs may contain some toxins that affect coccinellid larval development. The results obtained from this experiment show that parasitized greenbugs are not a suitable food source for *H. convergens* and *C. septempunctata.* However, the question still remains as to the root causes of these effects.

SUMMARY

The greenbug is an important pest of winter wheat in Oklahoma. Several predaceous coccinellids and an aphidophagous parasitic wasp are important natural enemies of the greenbug and co-occur with greenbugs throughout the winter wheat growing season. In order to understand the interactions between plants herbivores and predators, it is important to identify or predict the predator-prey relationships (Rice and Wilde 1989). Predation and parasitism play important roles in biological control but there is no consensus on the role that competition plays (DeBach 1964). Although many predatory insects appear to be opportunistic generalists in their diets, the suitability of different prey for predators' growth, development and reproduction can vary widely (Eubanks and Denno 2000).

The goal of this thesis was to determine the suitability of greenbugs parasitized by *Lysiphlebus testaceipes* as a food source for predatory Coccinellidae: *Coccinella septempunctata* and *Hippodamia convergens.* The first study confirmed that the first instar larvae of *C. septempunctata* and *H. convergens* are not able to consume mummies, while the second instar larvae partially consume them. However, third and fourth instar larvae and the adults of both species were able to completely consume greenbugs parasitized by *L. testaceipes.*

The second study examined if *H. convergens* and *C. septempunctata* demonstrated preference towards greenbugs that are parasitized by *L. testaceipes* or unparasitized greenbugs in a choice experiment. The results of this study suggested no preference was demonstrated by either species, and would likely feed on parasitized greenbug mummies if encountered.

The third study tested whether third and fourth instar larvae of *C. septempunctata* and *H. convergens* would be able to develop, grow and survive to adulthood when supplied with a diet of mummies only or a mixture of mummies and greenbugs. The results suggested that a diet of mummies alone will not sustain larvae to maturity; however, both instars were able to survive to maturity when fed a mixed diet of mummies and greenbugs. A mixed diet of greenbugs and greenbug mummies delayed larval development and reduced adult body size compared to larvae that were fed an equivalent amount of greenbugs. Future research is needed to examine these relationships in the field, and to evaluate the impact that intraguild predation has on *L. testaceipes*.

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APPENDIX

Table A1. ANOVA results (PROC MIXED, SAS Institute) for diet effects on development times and adult elliptical area of *C. septempunctata* and *H. convergens*.

Response Variable	Sources of Variation	Tests of Fixed Effects df	*F*	*P*
C. septempunctata				
Third Instar	Treatment	4, 132	116.57	<.0001
Fouth Instar	Treatment	2, 74	27.17	<.0001
Larval	Treatment	2, 74	32.21	<.0001
Pupal	Treatment	2, 74	28.46	<.0001
Preimaginal	Treatment	2, 74	55.43	<.0001
Adult Eliptical Area	Treatment	2, 79	237.75	<.0001
H. convergens				
Third Instar	Treatment	4, 141	46.86	<.0001
Fouth Instar	Treatment	2, 78	97.98	<.0001
Larval	Treatment	2, 78	94.48	<.0001
Pupal	Treatment	2, 83	15.93	<.0001
Preimaginal	Treatment	2, 78	98.27	<.0001
Adult Eliptical Area	Treatment	2, 78	50.84	<.0001

Table A2. Effects of diet on survivorship of *C. septempunctata* and *H. convergens* in prey suitability studies.

Response Variable	Source of Variation	df	χ^2	P
Survival				
C. septempunctata				
3rd Instar	Treatment	4	4.0	0.402
4th Instar	Treatment	2	4.0	0.402
Larval	Treatment	2	13.9	0.007*
Preimaginal	Treatment	2	131.4	< 0.001*
H. convergens				
3rd Instar	Treatment	4	0	1.00
4th Instar	Treatment	2	0	1.00
Larval	Treatment	2	6.2	0.19
Preimaginal	Treatment	2	134.7	< 0.001*

P-values followed by an asterix * are significantly different ($P = 0.05$) according to chi square test (Proc FREQ), SAS Institute.

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