

SUITABILITY OF *BREVICORYNE BRASSICAE*,
LIPAPHIS ERYSIMI AND *MYZUS PERSICAE*
(HEMIPTERA: APHIDIDAE) FROM WINTER CANOLA
FOR DEVELOPMENT AND SURVIVAL OF
HIPPODAMIA CONVERGENS (COLEOPTERA:
COCCINELLIDAE) AND *CHRYSOPERLA CARNEA*
(NEUROPTERA: CHRYSOPIDAE)

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Title of Study: SUITABILITY OF *BREVICORYNE BRASSICAE*, *LIPAPHIS ERYSIMI* AND *MYZUS PERSICAE* (HEMIPTERA: APHIDIDAE) FROM WINTER CANOLA FOR DEVELOPMENT AND SURVIVAL OF *HIPPODAMIA CONVERGENS* (COLEOPTERA: COCCINELLIDAE) AND *CHRYSOPERLA CARNEA* (NEUROPTERA: CHRYSOPIDAE)

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Abstract: Winter canola (*Brassica napus* L.) is a high energy oilseed crop recently introduced to the Southern Great Plains growing region. As a cruciferous plant, it introduces to typically low-prey landscapes a habitat with very high populations of potentially toxic cabbage aphids (*Brevicoryne brassicae* L.) and turnip aphids (*Lipaphis erysimi* Kalténbach). These aphids are capable of sequestering plant volatiles from host plants to arm themselves with a potent chemical defense system, dependent upon the distribution and concentration of these compounds within the plant. Also a frequent pest of winter canola, the green peach aphid (*Myzus persicae* Sulzer) is a generalist herbivore unable to sequester such toxic compounds. This study attempts to conclusively evaluate the suitability of all three aphid species commonly attacking winter canola for two abundant natural enemies that occur in Southern Great Plains, the convergent lady beetle (*Hippodamia convergens* Guérin-Ménéville) and the common green lacewing (*Chrysoperla carnea* Stephens) and determine whether these predators exhibit preferences among these aphid species. Prey species and daily prey quantity provided to predator larvae significantly affected developmental times and adult weights. Diets of turnip and cabbage aphids always resulted in slower developmental times and smaller adult weights than diets of green peach aphids and pea aphids. While developmental times of each predator decreased as daily prey quantity increased, adult weight of predators was significantly less when fed diets of *Brassica* specialist aphids. Survival of predators on all four diets was relatively high regardless of daily prey quantity. These results indicate that although cabbage and turnip aphids were suitable prey for *H. convergens* and *C. carnea*, qualitative differences likely exist between *Brassica* specialist aphids and the green peach aphid. Furthermore, green peach aphids feeding on winter canola should be considered high-quality prey items, as each predator's performance on these aphids was very similar to that of pea aphids. While no preferences for aphid prey were detected, larvae of each predator species frequently consumed more green peach aphids than either cabbage or turnip aphids. These results suggest winter canola has the potential to serve as a source habitat for *H. convergens* and *C. carnea*.

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CHAPTER I

INTRODUCTION

The Oklahoma landscape has long been composed of grasslands, whether native or agricultural, supporting many beneficial arthropods that provide economically valuable services to producers. The substantial reduction in insecticide applications in winter crops since the development of Glance n' Go (see Giles et al. 2003) has recently been altered with the widespread adoption of a novel biofuel crop requiring intensive management of frequent aphid outbreaks (Franke et al. 2009). Initial sampling efforts have documented large numbers of aphid natural enemies, but such insects have not been observed maintaining pest populations below economic thresholds (Chown and Giles 2006, Giles et al. 2011). The primary predators of aphids in winter canola are the convergent lady beetle (*Hippodamia convergens* Guérin-Méneville) and the common green lacewing (*Chrysoperla carnea* Stephens). These natural enemies are capable of substantially reducing aphid populations in nearby winter wheat (Kring et al. 1985, Rice and Wilde 1988, Elliott et al. 1996), but their ability to develop on diets of aphids from winter canola has not been studied. The accumulation of glucosinolates by two of the three aphid species that commonly occur in winter canola has been shown to cause significant mortality in many natural enemies, and such aphids may escape predation through this chemical defense system (Francis et al. 2001, Bridges et al. 2002, Kazana et al. 2007, Pratt et al. 2008, Kos et al. 2011).

Winter canola in the Southern Great Plains is a valuable crop for producers, but its ecological role in the landscape is uncertain. Its attractiveness to predators, parasitoids and pollinators - due to the large aphid populations and abundant floral resources in late spring - undoubtedly encourages heavy parental investment in the habitat, but may serve as an ecological sink if predators struggle to complete development within this system. In addition, late spring applications of broad-spectrum foliar insecticides may further reduce beneficial insect populations and lead to resistant pest populations. Incorporation of biological control in pest management decisions may decrease overall costs (economic and environmental) of controlling pests in winter canola, but basic information on pest-natural enemy interactions is required for the development of a more holistic pest management program. This research aims to quantify the suitability of aphids reared on winter canola for the development and survival of two of the most common predators in winter canola (*H. convergens* and *C. carnea*) and to describe predator preference for aphids that feed on winter canola.

Objectives

- I. Evaluate the suitability of the winter canola aphids *Brevicoryne brassicae*, *Lipaphis erysimi* and *Myzus persicae* for development, survival and adult body weight of *Hippodamia convergens* and *Chrysoperla carnea*.
- II. Determine if *H. convergens* and/or *C. carnea* exhibit a feeding preference for *M. persicae* over *B. brassicae* and/or *L. erysimi*.

CHAPTER II

REVIEW OF LITERATURE

Oklahoma Winter Canola Production

Canola (*Brassica napus* L.) is a recently developed variation of oilseed rape, a crop in production as far back as 1200 CE (Anonymous 1981). Oil from rapeseed crops has been used as fuel for lanterns and early combustion engines, but had limited utility in other markets due to high erucic acid content (50%). Low erucic acid (less than 2%) varieties of rapeseed (“canola”) were developed in Canada in 1974 following the reduced need for traditional rapeseed oil as a lubricant in steam-driven machinery (Daun 1986). Spring and summer canola varieties have been produced in large acreages in northern latitudes since the 1970’s, and with the development of winter-hardy varieties, production has spread into the lower latitudes of the United States including the Southern Great Plains (USDA/NASS 2013).

Winter canola has gained popularity with producers in Oklahoma as a rotation crop with winter wheat (*Triticum aestivum* L.) (Boyles et al. 2012), providing an excellent economic return of up to \$400 per acre (Peeper and Boyles 2008). In addition, Roundup-Ready varieties can be used to reduce encroachment of weedy grasses and forbs that would otherwise reduce profitability of winter wheat. Winter canola can also provide a temporal buffer against insect pests and winter wheat pathogens common in continuous wheat production (Blackshaw et al. 2001). With such

potential value, it comes as little surprise that winter canola production has increased from a few hundred to over 250,000 acres since 2001 (USDA/NASS 2013).

Because of the low erucic acid content, the oil-rich seeds of winter canola can be crushed to extract an edible oil that has gained popularity with consumers due to its health benefits. Much of the infrastructure needed to crush the seeds already exists in the Great Plains, and the remaining seed meal solids can be used as high-energy feed for livestock (Bell 1993). Canola oil can also be converted to biodiesel with minimal processing (Ardebili et al. 2011), and may be produced from used cooking oil that would otherwise be discarded (Tickell 2000, Ghobadian et al. 2009).

Insect Pest Management in Winter Canola

Several insect species are capable of damaging winter canola leaves, buds and seed pods, including both crucifer specialists and generalist insects. Flea beetles (Coleoptera: Chrysomelidae) were initially found to consume young seedlings entirely, but such damage has been minimized with the development of a pyrethroid seed treatment (Dosdall and Stevenson 2005, Lenssen et al. 2007). Some of the most damaging insects in the Great Plains region include the diamondback moth (*Plutella xylostella* L.) and multiple aphid species (Sternorrhyncha: Aphididae). Diamondback moths are active from early October through spring, and have been most damaging to young seedlings despite neonicotinoid seed treatments (Boyles et al. 2012). Aphids are viewed to be the most serious pest in winter canola, capable of reaching 17,000 individuals per plant and reducing yields to nearly zero (K.L.G. unpublished data).

As a cruciferous plant (Brassicales: Brassicaceae), winter canola produces secondary metabolites known as glucosinolates as part of an intricate chemical defense against herbivores (Mithen 2001). These compounds are produced in nearly all parts of the plant and kept spatially separated from myrosinase, an enzymatic β -thioglucosidase that catalyzes the hydrolysis of glucosinolates into their volatile counterparts (Hopkins et al. 2009). These compounds, primarily

isothiocyanates and nitriles, serve to deter herbivory and in many cases attract natural enemies of the herbivore (Dicke 1999, Turlings et al. 2002, Mumm et al. 2008). All glucosinolates are composed of three primary structures: a β -thioglucoside, an N-hydroxysulfate and a variable side chain (Hopkins et al. 2009). This variable functional group contributes, in large part, to the hydrolysis products formed by the degradation of glucosinolates. The glucosinolates gluconapin, progoitin, glucobrassin and 4-hydroxyglucobrassicin are the predominant species found in winter canola tissues, though nine other species are known to occur (Shahidi and Gabon 1989, Fahey et al. 2001).

In the Southern Great Plains, winter canola is planted most often in September and grown through May (Boyles et al. 2012). As young plants emerge from the soil, they are susceptible to damage from a number of insect pests (Boyles et al. 2012). These seedlings are often protected from insect damage by an insecticidal seed treatment that limits herbivore damage through early spring (Boyles et al. 2012). Seed treatments not only allow producers to delay applications of foliar insecticides, but also permit colonization of fields by beneficial natural enemies, particularly aphid parasitoids which are able to remain active at temperatures as low as 4°C (Royer et al. 2001, Jones et al. 2007). Many aphid predators arrive en masse as warm southern winds push insects northward in mid-spring. These predator populations may help combat increasing aphid numbers and serve as a source of beneficial insects for temporally separated crops planted in spring (Parajulee and Slosser 1999, French et al. 2001). However, it is often at this time that broad-spectrum insecticides are applied to maintain aphid populations below economic thresholds, which results in reductions of non-target species (Giles et al. 2009, Boyles et al. 2012).

Canola producers in the Southern Plains rely on a simple insecticide-based management plan to prevent economic losses to insect pests (Royer and Giles 2008). Because of a lack of basic ecological information, producers are not able to implement a comprehensive pest management program for winter canola that incorporates the use of insecticides, the impact of plant defenses

(glucosinolates), biological control by natural enemies, and conservation of important pollinating species such as the honey bee (*Apis mellifera* L.). The basic life history studies described in this thesis address whether common insect predators are able to utilize aphids on winter canola as a food source, and are a first step towards integrating their impact into pest management decisions.

Aphids in Winter Canola

The production of winter canola in the Southern Great Plains has faced tremendous setbacks due in part to the large numbers of aphid pests that commonly attack winter canola and reduce seed yield. The most frequent and damaging aphids in the spring are cabbage aphids (*Brevicoryne brassicae* L.) and green peach aphids (*Myzus persicae* Sulzer), although turnip aphids (*Lipaphis erysimi* Kalténbach) may also occur throughout the growing season and during seed pod formation in late spring (W.P.J. personal observation). These aphids are known to occur in very high numbers and can kill young plants in the fall (in the case of turnip aphids) and cause substantial injury to flowers and seed pods in late spring (primarily green peach and cabbage aphids) (Royer and Giles 2008, Boyles et al. 2012). Similar outbreaks had not been observed on spring and summer canola varieties grown in northern regions and aphids were not expected to become major pests on winter varieties (Berglund et al. 2007).

Turnip and cabbage aphids are specialist herbivores of *Brassica* crops capable of feeding on a wide range of cruciferous vegetables (Bridges et al. 2002). Cabbage aphids have a thick layer of lipids attached to their cuticle, which gives them a characteristic white, fuzzy appearance. This waxy coating has been implicated in the “unpalatability” of these aphids to coccinellids (Tsaganou et al. 2004, George 1957). When switched to a diet of cabbage aphids from one of high quality, adult *Harmonia axyridis* (Pallas) reduced prey consumption by 90% (Honěk 1996). Turnip aphids have also been identified as a sub-optimal prey for multiple species of lady beetles and lacewings, but are not described as wholly unsuitable (Chen and Liu 2001, Liu and Chen 2001, Acheampong and Stark 2004, Farooq and Tasawar 2008).

Green peach aphids have a wide range of accepted host plants, and do not feed exclusively on cruciferous plants (van Emden et al. 1969). This species has been described as a suitable prey item for many lady beetle species, and development duration on green peach aphid diets is similar to those observed for diets consisting of *Acyrtosiphon pisum* or *Aphis fabae* (Francis et al. 2000, Blackman 1965). Chen and Liu (2001) found no significant effects of a green peach aphid diet on development duration of *C. carnea* relative to a diet of *Aphis gossypii*.

Natural Enemies in Winter Canola

The most common natural enemies attacking winter canola aphids in the Southern Great Plains are the convergent lady beetle (*Hippodamia convergens* Guérin-Méneville), seven-spotted lady beetle (*Coccinella septempunctata* L.), the common green lacewing (*Chrysoperla carnea* Stephens) and the parasitoid wasps *Lysiphlebus testacipes* (Cresson) and *Diaeretiella rapae* (M'Intosh) (Kring et al. 1985, Jones 2001, Giles et al. 2003, Jones 2005). These natural enemies are also common in nearby winter wheat fields, and are known to disperse among crops. Despite co-occurrence of natural enemies in Oklahoma canola-wheat systems, these predators and parasitoids have not been observed regulating aphid pests below economic thresholds in canola (Parajulee and Slosser 1999, Slosser et al. 2000, French et al. 2001).

Coccinellidae. Lady beetles are common in most habitats across North America and capable of lengthy flights (Hagen 1962). Though highly variable in size, shape and color, most are easily recognized by their red-orange color and presence of black spots on the elytra. Of the nearly 4,000 species of lady beetles worldwide, only 453 aphidophagous species are known to occur in North America (Gordon 1985). The most common lady beetle species found in the Southern Great Plains region include *H. convergens*, *Coleomegilla maculata* (De Geer), *Hippodamia sinuate* (Mulsant), *Harmonia axyridis* (Pallas), *C. septempunctata*, and *Olla v-nigrum* (Mulsant) (Teetes et al. 1973, Michels et al. 1997). However, the native *H. convergens* and the exotic *C. septempunctata* are regarded as the most abundant in this region (Teetes et al.

1973, Elliott et al. 2006). Because aphids in crop systems are a primary source of prey for lady beetles, this group of predators is considered particularly beneficial in crops regularly experiencing aphid outbreaks (Kring et al. 1985, Rice and Wilde 1988, Elliott et al. 1996, Jones 2001).

Hippodamia convergens is known to substantially reduce aphids in winter wheat (Jones 2001, Michels et al. 2001) and is found in many other winter and summer crops including alfalfa, cotton, soybean and corn (Elliott et al. 1996, Michels et al. 2001). This species is implicated as an intraguild predator of the aphid parasitoid *Lysephlebis testacipes* (Cresson) (Lebusa 2004, Mullins 2008, Royer et al. 2008, Mullins et al. 2011) in winter wheat, but can also serve as intraguild prey (Sloggett et al. 2009). *Hippodamia convergens* is considered a voracious predator and capable of consuming up to 100 aphids per day as a late instar, resulting in >400 aphids consumed over all larval stadia (Hodek 1996, El-Heneidy et al. 2008).

Lady beetle eggs are laid in clusters of 5-50 eggs, often distributed along the undersides of leaves and twigs (Honěk 1996). Larvae often consume siblings after hatching, before departing the egg mass in search of food. Cannibalism and interspecific predation occur frequently among lady beetles and may facilitate survival when normal prey items are scarce (Agarwala and Dixon 1992, Hodek 1996, Obrycki et al. 1998, Snyder et al. 2000). Larvae undergo three molts over an approximately 14-day larval period before spending up to several days as an immobile fourth instar, often termed a “prepupa” (Hodek 1996). The final larval molt is shed to form the pupa, which is typically attached to substrate at the caudal end and not encased within a cocoon. Although unprotected, pupae are able to make sharp movements of the anterior end upwards when stimulated (Honěk 1996). The duration of larval and pupal stages varies considerably due to differences in prey, water availability and ambient temperature (Honěk 1996, Michels and Behle 1991, Phoofolo et al. 2007, Royer et al. 2008).

Following successful pupation, *H. convergens* adults have a pre-ovipositional period ranging from 6 to 12 days, depending on food availability and quality (Gutierrez et al. 1981).

While *H. convergens* lays approximately 20 eggs per day, coccinellid reproduction is indeterminate and adults of this species may lay hundreds of eggs in a lifetime, often producing multiple generations within a year (Honěk 1996). Adults may mate and produce a successive generation in their existing habitat, or overwinter/diapause in dense vegetation or other protected sites, often feeding on plant-based foods (e.g. pollen) when aphid prey are scarce (Schuster et al. 1976, Hemptinne and Desprets 1986). Diapause is not limited to winter months as food availability is known to be the primary regulating force of *H. convergens* diapause. Pollen and nectar are also consumed to increase nutrient reserves in preparation for long periods of dormancy, lengthy flights and periods of low prey availability (Hagen 1962). In fact, plant-based foods have been documented as essential for successful reproduction of lady beetles (Ugine and Losey 2013)

The likelihood of a lady beetle surviving to adulthood is highly dependent upon both the quality and quantity of their prey (Hodek and Honěk 1996, Agarwala 2008). Under food stress caused by either low-quality prey or scarce food resources, these predators tend to exhibit a slowed development rate, increased mortality through the pupal stage, and decreased ovipositional capacity as adults (Omkar and Srivastava 2003, Royer et al. 2008, Takizawa et al. 2000). The developmental delay is an adaptive strategy to prolong the larval stages until nutrient quotas or a critical weight needed for successful molting are met (Davidowitz et al. 2003, Phoofolo et al. 2008). However, this strategy is not completely successful as larvae that are provided a severely limited diet during the final instar often do not successfully compensate for the effects of starvation (Baumgaertner et al. 1981).

Chrysopidae. Much of the natural enemy research within Oklahoma winter crops has focused on lady beetles and aphid parasitoids. However, sampling efforts from 2011 through 2013 in both winter wheat and winter canola indicate green lacewings (Chrysopidae) outnumber lady beetles by as much as 4:1 (Donelson and Giles 2012, Giles et al. 2012, Casi N. Jessie unpublished data). Lacewing larvae are predaceous and typically feed on small, soft-bodied prey such as

aphids, scales and insect larvae. In fact, green lacewings are commercially available and released in orchards, greenhouses and row crops throughout the world to control pests (Afzal and Khan 1978, Tulisalo 1984, Nordlund et al. 1991, Henry et al. 2001). Green lacewings are particularly well adapted to agricultural systems due to their short generation times and low prey requirements for survival and reproduction (Hagen et al. 1970, Tauber 1974).

Chrysoperla species are common in many environments throughout North America, with widely overlapping distributions extending from central Mexico to Canada. *Chrysoperla rufilabris* is restricted to the eastern half of the continent, whereas *C. carnea* can be found throughout the United States, preferring more xeric environments than does *C. rufilabris* (Tauber and Tauber 1983). Adult green lacewings are bright green with small, slender bodies and large membranous wings.

Green lacewing eggs are laid singly on stalks to reduce the likelihood of predation and cannibalism (Ruzicka 1997), though cannibalism does often occur and may prevent local extinction when prey populations are low (Duelli 1981, Bar and Gerling 1985). Larvae undergo two molts over approximately 11 days (Nasreen et al. 2011, Principi and Canard 1984). Following a short pre-pupal period during the third instar, larvae locate a pupation site and spin a cocoon made from silk-like thread produced by the malpighian tubules and secreted through the anus (Gepp 1984). Once the cocoon is spun, a larva spends approximately two days as a pre-pupa (Kuznetsova 1969) before shedding its final exuvium and forming the puparium (Canard and Principi 1984). Although the lacewing is now encased in its cocoon, the pupa is exarate with a limited range of motion in the abdomen (Canard and Principi 1984).

Following approximately 13 days of pupation, the decticious pupa may use its mouthparts in combination with pressure exerted on the cephalic end of the cocoon to create an opening from which it emerges (Canard and Principi 1984). At this critical point, the pupa (considered a pharate adult) searches for solid substrate to which it attaches and emerges from the puparium as an adult (Canard and Principi 1984). Failure of the pupa to locate such a substrate may often result in

death. The pre-ovipositional period of green lacewings is generally much shorter than coccinellids, usually lasting three to four days under optimal temperature and photoperiod (Canard and Principi 1984). Most green lacewings, including *C. carnea*, are facultatively multivoltine and may lay eggs for the duration of their adult lifespan, up to 82 days (Kuznetsova 1969).

Green lacewing larvae are highly mobile, voracious predators capable of consuming over 400 aphids during the larval stages (Balasubramani and Swamiappan 1994, Canard and Principi 1984), but *C. carnea* larvae can still complete development on as few as two aphids per day (Atlihan et al. 2004). Pre-imago lacewings feed via extra-oral digestion, injecting salivary enzymes into prey through long jaws formed from fused mandibles and maxillae (Canard and Duelli 1984, Canard 2001). Larvae are adept at manipulating prey with their jaws to ensure complete digestion, often making sharp, lateral movements after penetrating prey to ensure laceration of internal tissues (Canard and Duelli 1984). Following liquefaction, fluids are siphoned through the lacewing's alimentary canal for further digestion (Canard 2001).

As with many other insects, the quantity and quality of prey for larvae interact to have a significant influence on the duration of larval and pupal stages, ultimately affecting adult body size and reproductive potential (Hydorn and Whitcomb 1979, Canard and Principi 1984, Balasubramani and Swamiappan 1994 and 1998, Liu and Chen 2001, Giles et al. 2000, Atlihan et al. 2004, Jessie 2012). Often, preimaginal duration and adult body size are correlated, such that rapidly developing larvae tend to become large adults (Dixon 2000, Michaud 2005, Omkar and James 2004). Unlike the larvae, adult *C. carnea* are pollinivorous/glyciphagous, and feed primarily on pollen, nectar and aphid honeydew (Principi 1984). Some strains of *C. carnea* have been reported to feed on live aphids, but still require floral resources for oviposition (Tauber and Tauber 1983).

Tritrophic Interactions

Aphid prey species may be characterized as suitable or unsuitable depending on whether the organisms can successfully complete development to adulthood and lay viable eggs on the diet (Michaud 2005). This suitability is due in part to the biology of aphid prey, but also the host plant on which it feeds. Giles et al. (2000, 2001) demonstrated the host plant's relationship to aphid nutritional value and subsequent effects on predator development. Pea aphids reared on *Vicia faba* L. had much lower myristic and fatty acid content than did conspecifics reared on *Medicago sativa* L. *Chrysoperla rufilabris* and *H. convergens* larvae supplied with *V. faba*-reared aphids had significantly longer development times than larvae provided *M. sativa*-reared aphids. Altered nutrition or toxic effects on the third trophic level are common, and have been heavily studied within the host plant order Brassicales (Francis et al. 2001, Bridges et al. 2002, Kazana et al. 2007, Pratt et al. 2008, Kos et al. 2011).

Because cabbage and turnip aphids are specialist herbivores of cruciferous plants, they have developed specialized mechanisms of coping with toxic host plant volatiles. These insects feed on their hosts extracellularly, avoiding the rupture of cell walls and subsequent release of the myrosinase enzyme. Glucosinolate compounds are taken up with the plant fluids and sequestered within aphid tissues (Pratt et al. 2008). Cabbage and turnip aphids are also capable of producing a myrosinase that is evolutionarily distinct from the myrosinase produced by their host plants (Jones et al. 2001). As predators attack aphids and tissues are damaged by feeding, hydrolysis of stored glucosinolates occurs very rapidly and produces volatile nitriles and isothiocyanites; the aphid is thus referred to as a "walking mustard oil bomb" (Kazana et al. 2007). In addition to overcoming its host's defenses, this process allows aphids to become chemically defended from predation - further reducing the likelihood of successful biological control. Cabbage aphids have been shown to sequester over 150 $\mu\text{mol/g}$ of aliphatic glucosinolates by the time they become adults; up to 20 times higher than in plants (Rossiter et al. 2003, Kos et al. 2011). Contrary to cabbage and turnip aphids, the green peach aphid is a generalist herbivore capable of feeding on a

wide range of host plants and has adapted to feeding on crucifers by excreting the intact plant defense compounds in their honeydew. This excretion results in a total glucosinolate concentration less than 5 $\mu\text{mol/g}$ in green peach aphids (Merritt 1996).

Francis et al. (2001) examined green peach and cabbage aphids reared on three plants with variable glucosinolate concentrations and their relative influence on mortality rates of two-spot lady beetle (*Adalia bipunctata* L.) larvae. The green peach aphid was shown to have caused mortality rates similar to aphids reared on plants containing no glucosinolates, whereas cabbage aphid diets containing as little as 5.8 $\mu\text{mol/g}$ glucosinolates caused 40% mortality. Furthermore, cabbage aphids containing higher glucosinolate levels (148 -185 $\mu\text{mol/g}$) caused 100% mortality during the larval stage. These results are similar to those of Kazana et al. (2007) and Pratt et al. (2008) who demonstrated significant negative effects on lady beetles supplied with aphids containing even moderate (10 $\mu\text{mol/g}$) amounts of glucosinolates. Both turnip and cabbage aphids have been shown to accumulate glucosinolates from winter canola, and such compounds are likely to impact the development and survival of predators that consume these aphids (Hopkins et al. 2009, Cibilis-Stewart 2013)

Prey Preferences of Natural Enemies

Hoden and Honěk (1996) categorize aphid prey as accepted or rejected by lady beetle predators. Often, accepted prey items are of poor quality or contain toxins which may impair development or cause mortality. When accepted prey is neither essential nor alternative, it is often referred to as unsuitable. Many lady beetles have a wide range of accepted foods, which may result in reduced preimaginal and adult performance when accepted foods are of low quality (Hodek 1966, Blackman 1967, Nedved and Salvucci 2008). It should be expected, therefore, that such predators would have been selected to preferentially reduce or avoid consumption of prey items not suitable for their development. However, Nedved and Salvucci (2008) describe the apparent preference of *C. septempunctata* for the aphid species *Aphis sambucci* (L) despite its

negative consequences on lady beetle survival. *Adalia bipunctata* larvae also did not discriminate between high and low-quality prey items (Ferrer et al. 2008). Fréchette et al. (2006) suggested lady beetles often exhibit preference for habitat rather than specific food items, but also found *A. bipunctata* adults were reluctant to lay eggs in the presence of toxic vetch aphid (*Megoura viciae* Buckton). Also, adults may exhibit preferences for oviposition sites in relation to the presence and/or quality of food resources (Hodek 1996). Such preferences are likely to have greater impact on larval diet than do larval preferences, as the limited mobility of pre-imago lady beetles restricts preferences to small spatial units often composed of limited numbers of prey species (Evans and Dixon 1986, Seagraves 2009). Assessments of prey preference in predaceous chrysopids typically reveal indiscriminate consumption of prey items by larvae (Cheng et al. 2010, Hydorn and Whitcomb 1979), although Chen and Liu (2001) and Liu and Chen (2001) found both *C. carnea* and *C. rufilabris* consumed more green peach aphids than turnip aphids.

CHAPTER III

MATERIALS AND METHODS

Host Plant Production

All host plants were planted weekly in 15-cm pots with a 50:50 mix of potting soil and fritted clay absorbent material. Winter canola (*Brassica napus*) cultivar ‘Wichita’ pots were watered every other day and provided with a liquid 20-20-20 (N:P:K) fertilizer weekly. Faba bean (*Vicia faba* cultivar ‘Windsor’) were planted with a slow-release 15-9-12 pellet fertilizer and watered every four days. Uninfested winter canola and faba bean plants were transferred to insect colonies when they reached 25 and 7 days in age, respectively.

Aphid Colonies

Colonies of cabbage aphids (*Brevicoryne brassicae*), turnip aphids (*Lipaphis erysimi*) and green peach aphids (*Myzus persicae*) were established from individuals collected from winter canola fields in the spring of 2012. Field-collected aphids were isolated on winter canola leaves and screened for the presence of aphid parasitoids. Aphids were then transferred to colony cages containing at least 15 winter canola plants. Each colony was reared independently in double-walled fine mesh cages at 24°C and a photoperiod of 16:8 (L:D). Dead leaves were removed daily and pots/plants were replaced weekly with fresh 25-day-old winter canola. Stock colonies of pea aphids (*Acyrtosiphon pisum* Harris) reared on faba bean were maintained in large, single-walled

mesh boxes kept at 24°C and a photoperiod of 16:8 (L:D). Pea aphids were collected daily to prevent plant death and fresh plants were added to the colonies weekly. All winter canola aphids used in experiments were removed individually with a fine camel-hair brush and transferred to experimental containers.

Lady beetle Colonies

Adult *H. convergens* were collected from winter canola fields in central Oklahoma during the spring of 2012 and transferred to 0.25 liter cardboard containers topped with nylon mesh lids. All adult lady beetles were kept in table-top environmental growth chambers maintained at 24°C and a photoperiod of 16:8 (L:D). They were provided with an unlimited supply of fresh *A. pisum* and a moistened cotton ball. Eggs of field-collected lady beetles were removed and placed into 30ml plastic cups with lids. Hatching larvae were isolated and reared to adults (F1) on *ad libitum* pea aphids. Colonies of F1 individuals were kept in large cardboard containers with ventilated lids. Mating F1 pairs (n=10), reared from at least five field-collected pairs, were isolated and provided with pea aphids and moistened cotton balls. To encourage oviposition, mating pairs were also provided a honey-wheat-yeast mixture (Planet Natural Garden Supply, Bozeman, MT) and fresh faba leaves. Egg clutches laid by mating pairs were collected daily and placed separately into 30ml plastic cups before being used in experiments.

Lacewing Colonies

Adults and eggs of green lacewings were collected from central Oklahoma winter wheat and canola fields during the spring of 2012. Adults were kept in double-walled fine mesh cages and provided daily with a honey-wheat-yeast mixture and water to encourage oviposition. Eggs were collected from cages weekly by using a ball of fine nylon mesh to gently brush eggs off cage surfaces, which were then collected individually and isolated in 30ml cups. Upon eclosion, larvae were identified as *C. carnea* (Tauber 1974) and reared to adults on an *ad libitum* diet of

pea aphids. F1 adults and subsequent generations were placed in cages and provided a dilute honey-wheat-yeast mixture, *A. pisum* and water. Subsequent batches of eggs were removed individually with forceps and transferred to 30ml plastic cups for use in experiments.

Experiment I: Evaluation of Aphid Suitability

Upon eclosion, lady beetle and lacewing larvae were supplied daily with 2, 4, or 8mg of late-instar apterous pea aphids, cabbage aphids, turnip aphids or green peach aphids collected from laboratory colonies. Twenty larvae of each predator species were assigned to each aphid species-weight treatment. Larvae were systematically checked every 24 h for evidence of mortality, molting, pupation or emergence as adults. Each day, old prey items were removed and replaced with freshly collected aphids. No water was provided, as the aphid diet provided enough moisture for development (Michaud 2005). The duration of each successive life stage was recorded to determine the effects of each diet treatment on development and survival of the predator species. After emergence, adult predators were sexed and weighed on a digital microbalance to record live weights. Representative lacewing and lady beetle specimens from each diet treatment were deposited in the K. C. Emerson Entomology Museum, Department of Entomology and Plant Pathology, Oklahoma State University, Stillwater, Oklahoma.

Data analyses were performed with SAS version 9.3 for Windows (SAS Institute, July 2011). Durations of development (days) and adult live weights (mg) were compared among diet treatments using ANOVA (PROC MIXED) and significant interactions were compared using LSMEANS. Tests of effect slices were performed to determine the relative contribution of each source of variation to the developmental metrics measured. Cumulative survivorship (the total number of individuals surviving to each successive life stage) was evaluated via construction of 2x4 contingency tables (PROC FREQ) and analyzed for significance using Fisher's Exact Test. Egg batch (for lacewings) and parental line (for lady beetles) were included as a random variable

to account for variation among larval genotypes. Aphid weights were analyzed using ANOVA (PROC MIXED). A 0.05 significance level was used for all statistical analyses.

Experiment II: Tests of Predator Preference

Ten cabbage aphids, turnip aphid, or green peach aphids were placed in the center of a 9cm petri dish arena to produce three diet treatments for a no choice preference test. Separately, 10 cabbage aphids + 10 green peach aphids, and 10 turnip aphids + 10 green peach aphids were placed in the center of a 9cm petri dish arena to produce two diet treatments for a choice preference test. For each test and treatment, a single 3rd instar *C. carnea* or 4th instar *H. convergens* reared on pea aphids and starved for 24 hours was then released into an arena and allowed to feed for thirty minutes. All treatments for each test were replicated with twenty separate individual predators of each species. The numbers of prey items encountered, attacked and consumed were recorded following presentation of the prey items. By exposing larvae to both prey items simultaneously during the choice test, preference can be determined by comparing differences in encounter and consumption ratios among individuals. The number of encounters and consumptions were compared separately for each test among the aphid treatments for each predator species using ANOVA (PROC MIXED) and the ratios of consumptions to encounters were compared using paired t-tests (PROC TTEST). A 0.05 significance level was used for all analyses.

CHAPTER IV

RESULTS

Experiment I: Duration of Development

Hippodamia convergens. Significant interactions between prey species and prey levels were detected for total larval development time ($F = 10.51$; $df = 6, 216$; $p < 0.0001$). Overall, *H. convergens* larvae developed fastest on diets of green peach aphids and pea aphids, while those provided with either turnip aphids or cabbage aphids developed slowest within each prey level (Table 2). For first-instar lady beetles assigned to the 2-mg and 4-mg prey levels, larvae supplied with green peach aphids developed the fastest (2.6 ± 0.15 and 2.8 ± 0.14 days, respectively), and larvae supplied with cabbage aphids developed the slowest (3.3 ± 0.13 and 3.0 ± 0.21 days, respectively). At the 8-mg level, first-instar larvae provided pea aphids developed fastest (2.1 ± 0.16 days) while those given cabbage aphids were slowest to develop (3.2 ± 0.19 days). Second and third-instars also developed fastest on green peach and pea aphid diets, whereas those provided cabbage or turnip aphids took longer to develop. By the fourth instar, larvae were spending an average of 14.8 ± 0.41 days developing within the 2-mg turnip aphid treatment and only 6.8 ± 0.24 days within the 2-mg pea aphid treatment. At the 8-mg level, fourth-instars provided with turnip aphids took 7.2 ± 0.47 days to pupate versus 5.4 ± 0.26 days for larvae provided pea aphids (Table 2). Total larval development times ranged from 15.3 ± 0.38 to $26.2 \pm$

1.18 days within the 2-mg treatments, 14.0 ± 0.41 to 23.4 ± 1.01 days within the 4-mg treatments, and 13.0 ± 0.38 to 17.1 ± 0.70 days within the 8-mg treatments (Table 3).

Pupal durations were significantly different among prey species at the 4-mg and 8-mg prey levels and the interaction between prey species and prey level was found to be significant for pupal durations as well ($F = 9.98$; $df = 6, 178$; $p < 0.0001$; Table 1). Among all diet treatments, mean duration of *H. convergens* pupal stages ranged from 5.5 ± 0.12 days for larvae supplied with 8-mg of pea aphids to 8.8 ± 0.53 days for larvae supplied with 4mg of turnip aphids. Lady beetles within the 2-mg prey level spent much less time in pupation. Interestingly, pupal durations for larvae provided cabbage aphids and turnip aphids were highest within the 4-mg daily prey level (7.9 ± 0.38 and 8.8 ± 0.53 , respectively).

Larval + pupal duration was also significantly affected by the interaction of prey species and prey level ($F = 3.6$; $df = 6, 177$; $p < 0.0022$). Even when prey levels were high, significant differences were detected among prey species (see Table 3). Larval + pupal duration ranged from 18.3 ± 0.31 days when provided with 8 mg of pea aphids to 33.5 ± 0.52 days when provided with 2 mg of turnip aphids.

Chrysoperla carnea. Prey species and prey level interacted to have significant effects on larval duration of *C. carnea* ($F = 9.85$; $df = 6, 223$; $p < 0.0001$). Duration of the first instar for *C. carnea* ranged from 2.9 ± 0.15 days for 8 mg of green peach aphids to 4.6 ± 0.17 days for 2 mg of turnip aphids. Second-instars developed fastest on pea aphids and green peach aphids at the 8-mg prey level (3.0 and 3.0 ± 0.11 , respectively). Within the 2-mg prey level, second instar duration ranged from 3.4 ± 0.13 days when provided with pea aphids to 7.7 ± 0.65 days when provided with turnip aphids. Lacewing larvae spent an average of 18.1 ± 1.11 days in the third instar when provided with 2 mg of turnip aphids, but spent only 5.6 ± 0.21 days as third-instars when provided with 8 mg of cabbage aphids.

Overall, *C. carnea* larvae developed fastest on diets of green peach aphids and pea aphids and developed slowest on diets of turnip aphids and cabbage aphids within each prey level (Table

5). Total larval development times ranged from 19.9 ± 0.77 to 30.4 ± 1.30 days within the 2-mg treatments, 15.9 ± 0.26 to 23.5 ± 0.46 days within the 4-mg treatments, and 11.1 ± 0.38 to 13.8 ± 0.59 days within the 8-mg treatments (Table 6).

Pupal duration was significantly affected by the interaction of prey species and prey level ($F = 2.58$; $df = 6, 206$; $p = 0.0197$; Table 4). Mean duration of *C. carnea* pupal stages ranged from 10.5 ± 0.16 days for 8 mg of green peach aphids to 13.8 ± 0.32 days for 2 mg of pea aphids (Table 6).

Larval + pupal duration was also significantly affected by the interaction of prey level and prey species ($F = 14.41$; $df = 6, 206$; $p < 0.0001$; Table 4). Total development times for *C. carnea* ranged from 44.8 ± 0.87 days in the 2-mg turnip aphid treatment to 21.9 ± 0.20 days for the 8-mg green peach aphid treatment (Table 6).

Experiment I: Predator Survival

Hippodamia convergens. There were no significant differences in cumulative survivorship found within any prey level and no significant differences were detected among prey levels for each diet species (Table 7, $p > 0.0719$). Larval survivorship was lowest for those provided 4 mg of pea aphids (0.850). Cumulative pupal survivorship ranged from 0.600 for 8 mg of turnip aphids to 0.950 for 4 mg of green peach aphids. One adult in the 2-mg green peach aphid treatment emerged unsuccessfully from the puparium. Total cumulative survivorship was lowest (0.600) for the 8-mg turnip aphid treatment (Table 7).

Chrysoperla carnea. No differences in larval, pupal or adult survival were detected among *C. carnea* within any of the three prey levels, and comparisons of survival among prey levels revealed no significant differences (Table 8, $p > 0.1530$). Mortality in the adult stage was more frequent in lacewings than lady beetles, with cumulative survivorship as low as 0.842 among larvae supplied with 8 mg of turnip aphids. Cumulative survival through the adult stage

was highest for lacewings provided 4 mg and 8 mg of pea aphids (0.950). The lowest cumulative (0.700) survivorship was observed within the 2-mg green peach aphid treatment.

Experiment I: Adult Body Weight

Hippodamia convergens. Adult weight was significantly affected by the interaction of prey level and prey species ($F= 13.42$; $df = 6, 182$; $p < 0.0001$). Adult weights were not significantly different between the 2-mg and 4-mg prey levels for both cabbage aphid ($t = -1.29$; $df = 182$; $p = 0.1993$) and turnip aphid diets ($t = 0.78$; $df = 182$; $p = 0.4367$), whereas adults within the pea aphid treatments were significantly different at all prey levels (Table 2). Within the 2-mg prey level, adult weights of larvae provided with cabbage or turnip aphids were not significantly different ($t = -0.04$; $df = 182$; $p = 0.9690$), but were significantly different at the 8-mg daily prey level ($t = 3.51$; $df = 182$; $p = 0.0006$). Among larvae provided green peach or pea aphids, adult weights were not significantly different at the 2-mg ($t = -0.80$; $df = 182$; $p = 0.4226$) or 4-mg ($t = 1.90$; $df = 182$; $p = 0.0592$) daily prey levels, but were found to be significantly different at the 8-mg daily prey levels ($t = -5.17$; $df = 182$; $p < 0.0001$).

Chrysoperla carnea. Daily prey level and prey species interacted to have significant effects on adult body weight (Table 6; $F= 8.10$; $df = 6, 190$; $p < 0.0001$). Within each prey level, larvae provided with a pea aphid diet became the largest adults, whereas those provided with either cabbage aphid or turnip aphid diets were significantly smaller. Despite similar larval+pupal duration between green peach aphid and pea aphid diets, adult weights were significantly higher within the pea aphid treatments at the 2-mg ($t = -2.51$; $df = 190$; $p = 0.0130$), 4-mg ($t = -3.91$; $df = 190$; $p = 0.0001$) and 8-mg ($t = -3.78$; $df = 190$; $p = 0.0002$) daily prey levels (Table 6).

Experiment II: Predator Preference

Hippodamia convergens. Fourth instar larvae did not attack every prey item encountered (Table 9), but every attacked item was completely consumed. In no-choice trials, consumptions

ratios (# of consumptions / # of encounters) were highest among lady beetle larvae provided green peach aphids (0.95 ± 0.02) and lowest among those provided cabbage aphids (0.93 ± 0.03), but were not significantly different ($F = 0.14$; $df = 59$; $p = 0.8666$; Table 9). Lady beetles encountered ($F = 22.40$; $df = 59$; $p < 0.0001$) and consumed ($F = 26.25$; $df = 59$; $p < 0.0001$) more green peach aphids than either of the other species in no-choice tests. In choice trials, the consumption ratio for turnip aphids and green peach aphids were not significantly different ($t = 1.07$; $df = 19$; $p = 0.2967$). The difference in consumptions ratios for larvae provided cabbage aphids and green peach aphids was also not significant ($t = 0.41$; $df = 19$; $p = 0.6855$; Table 9).

Chrysoperla carnea. Third instar larvae completely consumed any prey item attacked, but not all encountered aphids were attacked (Table 10). Among diet treatments in no-choice trials, the consumption ratios were not significantly different ($F = 0.39$; $df = 59$; $p = 0.6802$). The encounter and consumption rates were also similar for *C. carnea* larvae in each scenario (Table 10). In choice trials, no significant differences were detected between consumption ratios for both the turnip aphid and green peach aphid treatments ($t = -0.64$; $df = 19$; $p = 0.5303$) and the cabbage aphid and green peach aphid treatments ($t = 1.03$; $df = 19$; $p = 0.3157$).

TABLES

Table 1. Results from analysis (PROC MIXED) of increasing daily prey level of four aphid species on preimaginal duration and adult body weight of *Hippodamia convergens*.

Response variable^a	Source of variation^b	df	F	p
Larval	Prey species	3, 218	92.74	<0.000
	Prey level	2, 218	69.45	<0.000
	Prey species x Prey level	6, 216	10.51	<0.000
Pupal	Prey species	3, 180	17.47	<0.000
	Prey level	2, 181	9.3	0.0001
	Prey species x Prey level	6, 178	9.98	<0.000
Larval + Pupal	Prey species	3, 180	38.27	<0.000
	Prey level	2, 181	28.5	<0.000
	Prey species x Prey level	6, 177	3.6	0.0022
Adult live weight	Prey species	3, 182	64.39	<0.000
	Prey level	2, 182	44.94	<0.000
	Prey species x Prey level	6, 182	13.42	<0.000

^aDevelopmental times were recorded in days. Adult live weights were recorded in milligrams.
^bPrey species were *Brevicoryne brassicae*, *Lipaphis erysimi*, *Myzus persicae* or *Acyrtosiphon pisum*. Prey levels were 2, 4, or 8 mg per day.

Table 2. Means (\pm SE) of larval developmental times of *Hippodamia convergens* in response to daily prey levels and prey species at 23.8 ± 0.04 °C and 61.2 ± 0.39 %RH.

Prey level	Prey species	Instar Development Time (days)			
		First	Second	Third	Fourth
2mg	<i>L. erysimi</i>	2.9 \pm 0.07a	2.6 \pm 0.11a	7.0 \pm 0.25a	14.8 \pm 0.41a
	<i>B. brassicae</i>	3.3 \pm 0.13a	2.9 \pm 0.26a	5.3 \pm 0.33b	10.8 \pm 0.32b
	<i>M. persicae</i>	2.6 \pm 0.15b	2.6 \pm 0.13a	3.3 \pm 0.19c	10.0 \pm 0.47b
	<i>A. pisum</i>	3.1 \pm 0.14a	2.4 \pm 0.11b	3.1 \pm 0.18c	6.8 \pm 0.24c
4mg	<i>L. erysimi</i>	2.8 \pm 0.16a	2.5 \pm 0.11b	4.4 \pm 0.23b	12.3 \pm 0.47a
	<i>B. brassicae</i>	3.0 \pm 0.21a	3.7 \pm 0.20a	5.1 \pm 0.35a	11.6 \pm 0.72b
	<i>M. persicae</i>	2.8 \pm 0.14a	2.4 \pm 0.11b	2.9 \pm 0.16c	5.9 \pm 0.38c
	<i>A. pisum</i>	3.0 \pm 0.18a	2.5 \pm 0.11b	3.3 \pm 0.17c	5.9 \pm 0.14c
8mg	<i>L. erysimi</i>	2.8 \pm 0.14ab	2.5 \pm 0.14b	3.8 \pm 0.16ab	7.2 \pm 0.47a
	<i>B. brassicae</i>	3.2 \pm 0.19a	2.9 \pm 0.08a	4.2 \pm 0.34a	6.8 \pm 0.44a
	<i>M. persicae</i>	2.4 \pm 0.11bc	2.5 \pm 0.11b	2.8 \pm 0.16c	6.5 \pm 0.29a
	<i>A. pisum</i>	2.1 \pm 0.16c	2.4 \pm 0.11b	3.2 \pm 0.17bc	5.4 \pm 0.26b

Statistical analyses are reported within each daily prey level. Values in each column followed by the same letter are not significantly different ($p > 0.05$).

Table 3. Means (\pm SE) of developmental times and adult live weights for *Hippodamia convergens* in response to daily prey levels and prey species at 23.8 ± 0.04 °C and 61.2 ± 0.39 %RH.

Prey level	Prey species	Development Time (days)			Adult weight (mg)
		Larval	Pupal	Larval + Pupal	
2mg	<i>L. erysimi</i>	26.2 \pm 1.18a	6.1 \pm 0.22a	33.5 \pm 0.52a	6.473 \pm 0.18b
	<i>B. brassicae</i>	22.2 \pm 0.61b	6.7 \pm 0.28a	29.2 \pm 0.65b	6.449 \pm 0.20b
	<i>M. persicae</i>	18.4 \pm 0.77c	6.2 \pm 0.17a	23.9 \pm 0.73c	8.555 \pm 0.51a
	<i>A. pisum</i>	15.3 \pm 0.38d	6.8 \pm 0.18a	22.2 \pm 0.49d	9.034 \pm 0.20a
4mg	<i>L. erysimi</i>	21.9 \pm 0.67a	8.8 \pm 0.53a	29.9 \pm 0.71a	5.993 \pm 0.60c
	<i>B. brassicae</i>	23.4 \pm 1.01a	7.9 \pm 0.38b	31.5 \pm 0.88a	7.281 \pm 0.27b
	<i>M. persicae</i>	14.0 \pm 0.41b	5.9 \pm 0.14c	19.9 \pm 0.49b	12.940 \pm 0.64a
	<i>A. pisum</i>	14.5 \pm 0.27b	6.5 \pm 0.13c	20.9 \pm 0.30b	11.819 \pm 0.31a
8mg	<i>L. erysimi</i>	16.2 \pm 0.65a	7.3 \pm 0.33ab	22.6 \pm 0.93ab	8.328 \pm 0.61c
	<i>B. brassicae</i>	17.1 \pm 0.70a	7.6 \pm 0.32a	24.2 \pm 0.95a	10.663 \pm 0.54b
	<i>M. persicae</i>	14.2 \pm 0.39b	6.7 \pm 0.21b	20.8 \pm 0.56b	10.041 \pm 0.36b
	<i>A. pisum</i>	13.0 \pm 0.38b	5.5 \pm 0.12c	18.3 \pm 0.31c	13.041 \pm 0.27a

20 initial replicates for each prey level by species combination. Statistical analyses are reported within each daily prey level. Values in each column followed by the same letter are not significantly different ($p > 0.05$).

Table 4. Results from analysis (PROC MIXED) of increasing daily prey level of four aphid species on developmental durations and adult body weights of *Chrysoperla carnea*.

Response variable^a	Source of variation^b	df	F	p
Larval	Prey species	3, 224	64.53	<0.0001
	Prey level	2, 58.1	352.88	<0.0001
	Prey species x Prey level	6, 223	9.85	<0.0001
Pupal	Prey species	3, 206	3.29	0.0216
	Prey level	2, 206	102.63	<0.0001
	Prey species x Prey level	6, 206	2.58	0.0197
Larval + Pupal	Prey species	3, 206	86.18	<0.0001
	Prey level	2, 206	593.73	<0.0001
	Prey species x Prey level	6, 206	14.41	<0.0001
Adult live weight	Prey species	3, 190	39.15	<0.0001
	Prey level	2, 190	171.78	<0.0001
	Prey species x Prey level	6, 190	8.1	<0.0001

^aDevelopmental times were recorded in days. Adult live weights were recorded in milligrams.
^bPrey species were *B. brassicae*, *L. erysimi*, *M. persicae* and *A. pisum*. Prey levels were 2, 4, or 8 mg per day.

Table 5. Means (\pm SE) of larval developmental times of *Chrysoperla carnea* in response to prey species and daily prey levels at 23.8 ± 0.04 °C and 61.2 ± 0.39

Prey level	Prey species	Instar Development Time (days)		
		First	Second	Third
2mg	<i>L. erysimi</i>	4.6 \pm 0.17a	7.7 \pm 0.65a	18.1 \pm 1.11a
	<i>B. brassicae</i>	4.3 \pm 0.12a	5.4 \pm 0.30b	14.8 \pm 0.47b
	<i>M. persicae</i>	4.0 \pm 0.13a	4.0 \pm 0.27c	15.6 \pm 0.88b
	<i>A. pisum</i>	4.0 \pm 0.11a	3.4 \pm 0.13c	12.6 \pm 0.66c
4mg	<i>L. erysimi</i>	4.0 \pm 0.15a	4.9 \pm 0.18a	14.7 \pm 0.39a
	<i>B. brassicae</i>	4.4 \pm 0.11a	4.4 \pm 0.15a	10.9 \pm 0.16b
	<i>M. persicae</i>	3.8 \pm 0.14a	3.6 \pm 0.20b	8.5 \pm 0.17c
	<i>A. pisum</i>	4.3 \pm 0.21a	3.2 \pm 0.15b	9.3 \pm 0.21c
8mg	<i>L. erysimi</i>	3.5 \pm 0.11b	3.7 \pm 0.26b	6.6 \pm 0.41a
	<i>B. brassicae</i>	4.4 \pm 0.21a	4.3 \pm 0.23a	5.6 \pm 0.21a
	<i>M. persicae</i>	2.9 \pm 0.15c	3.0 \pm 0.11b	5.6 \pm 0.21a
	<i>A. pisum</i>	3.1 \pm 0.05c	3.0 \pm 0.00b	5.8 \pm 0.19a

Statistical analyses are reported within each daily prey level. Values in each column followed by the same letter are not significantly different ($p > 0.05$).

Table 6. Means (\pm SE) of developmental times and adult body weights of *Chrysoperla carnea* in response to prey species and daily prey levels at 23.8 ± 0.04 °C and 61.2 ± 0.39 %RH.

Prey level	Prey species	Development Time (days)			Adult weight (mg)
		Larval	Pupal	Larval + Pupal	
2mg	<i>L. erysimi</i>	30.4 \pm 1.30a	13.3 \pm 0.23ab	44.8 \pm 0.87a	3.616 \pm 0.12bc
	<i>B. brassicae</i>	24.4 \pm 0.57b	13.4 \pm 0.35ab	37.6 \pm 0.81b	3.729 \pm 0.11c
	<i>M. persicae</i>	23.5 \pm 1.01b	12.8 \pm 0.29a	35.6 \pm 1.23c	3.594 \pm 0.11b
	<i>A. pisum</i>	19.9 \pm 0.77c	13.8 \pm 0.32b	33.2 \pm 0.86d	4.130 \pm 0.21a
4mg	<i>L. erysimi</i>	23.5 \pm 0.46a	11.8 \pm 0.43a	35.0 \pm 0.50a	3.727 \pm 0.18c
	<i>B. brassicae</i>	19.7 \pm 0.30b	10.8 \pm 0.18b	30.4 \pm 0.37b	4.292 \pm 0.07b
	<i>M. persicae</i>	15.9 \pm 0.26c	11.2 \pm 0.18ab	27.1 \pm 0.26c	4.188 \pm 0.08b
	<i>A. pisum</i>	16.8 \pm 0.27c	11.4 \pm 0.17a	28.2 \pm 0.32c	4.949 \pm 0.09a
8mg	<i>L. erysimi</i>	13.8 \pm 0.59a	11.2 \pm 0.12a	24.4 \pm 0.37a	4.987 \pm 0.17c
	<i>B. brassicae</i>	13.9 \pm 0.42a	11.4 \pm 0.13a	25.0 \pm 0.26a	4.792 \pm 0.16c
	<i>M. persicae</i>	11.1 \pm 0.38b	10.5 \pm 0.16b	21.9 \pm 0.20b	5.978 \pm 0.10b
	<i>A. pisum</i>	11.9 \pm 0.20b	11.0 \pm 0.20a	22.8 \pm 0.24b	6.726 \pm 0.21a

20 initial replicates for each prey level by species combination. Statistical analyses are reported within each daily prey level. Values in each column followed by the same letter are not significantly different ($p > 0.05$).

Table 7. Effects of daily prey levels and prey species on cumulative^a survivorship of *Hippodamia convergens* larval, pupal and adult stages

Prey level	Stage	Prey Species				Fisher's Exact	
		<i>L. erysimi</i>	<i>B. brassicae</i>	<i>M. persicae</i>	<i>A. pisum</i>	df	<i>P</i>
2mg	Larval	0.950	1.000	0.950	1.000	3	1.0000
	Pupal	0.750	0.850	0.900	0.750	3	0.5857
	Adult	0.750	0.850	0.850	0.750	3	0.7949
4mg	Larval	1.000	0.950	1.000	0.850	3	0.1852
	Pupal	0.850	0.800	0.950	0.700	3	0.2353
	Adult	0.850	0.800	0.950	0.700	3	0.2353
8mg	Larval	0.950	1.000	1.000	1.000	3	1.0000
	Pupal	0.600	0.900	0.900	0.800	3	0.0719
	Adult	0.600	0.900	0.900	0.800	3	0.0719

No significant differences in survival were detected within the three prey levels at the $p = 0.05$ significance

^aCumulative survivorship includes proportions of individuals surviving previous life stages.

Table 8. Effects of daily prey levels and prey species on cumulative^a survivorship of *Chrysoperla carnea* larval, pupal and adult stages

Prey level	Stage	Prey Species				Fisher's Exact	
		<i>L. erysimi</i>	<i>B. brassicae</i>	<i>M. persicae</i>	<i>A. pisum</i>	df	P
2mg	Larval	0.900	1.000	1.000	1.000	3	0.2405
	Pupal	0.799	0.950	0.800	0.850	3	0.5222
	Adult	0.750	0.850	0.700	0.850	3	0.6509
4mg	Larval	0.950	1.000	1.000	1.000	3	1.0000
	Pupal	0.850	1.000	0.950	1.000	3	0.1852
	Adult	0.800	0.900	0.900	0.950	3	0.6096
8mg	Larval	0.950	0.900	0.950	1.000	3	0.8988
	Pupal	0.950	0.800	0.950	1.000	3	0.1530
	Adult	0.800	0.800	0.850	0.950	3	0.5222

No significant differences in survival were detected within the three prey levels at the p = 0.05 significance
^aCumulative survivorship includes proportions of individuals surviving previous life stages.

Table 9. Number of encounters and consumptions and the ratios of consumptions / encounters for fourth instar <i>Hippodamia convergens</i> .					
Scenario	Prey species	N	# Encountered	# Consumed	Ratio
No-choice	<i>Cabbage</i>	20	3.0 ± 0.15a	2.8 ± 0.10a	0.93 ± 0.03a
	<i>Turnip</i>	20	3.1 ± 0.14a	2.9 ± 0.13a	0.94 ± 0.03a
	<i>Green peach</i>	20	4.2 ± 0.13b	4.0 ± 0.15b	0.95 ± 0.02a
Choice	<i>B. brassicae</i>	20	2.1 ± 0.12a	1.8 ± 0.09a	0.89 ± 0.05a
	<i>M. persicae</i>		2.2 ± 0.12a	2.0 ± 0.13a	0.92 ± 0.04a
	<i>L. erysimi</i>	20	2.3 ± 0.10a	1.9 ± 0.10a	0.86 ± 0.05a
	<i>M. persicae</i>		2.4 ± 0.13a	2.2 ± 0.14a	0.93 ± 0.04a

Values within each grouped column followed by the same letter are not statistically different ($p > 0.05$).

Table 10. Number of encounters and consumptions and the ratios of consumptions / encounters for third instar *Chrysoperla carnea* .

Scenario	Prey species	N	# Encountered	# Consumed	Ratio
No-choice	<i>B. brassicae</i>	20	3.2 ± 0.14a	3.2 ± 0.13a	0.99 ± 0.01a
	<i>L. erysimi</i>	20	3.2 ± 0.17a	3.1 ± 0.17a	0.97 ± 0.02a
	<i>M. persicae</i>	20	3.6 ± 0.18a	3.4 ± 0.15a	0.97 ± 0.02a
Choice	<i>B. brassicae</i>	20	2.2 ± 0.13a	2.0 ± 0.10a	0.95 ± 0.03a
	<i>M. persicae</i>		2.2 ± .013a	2.0 ± 0.14a	0.92 ± 0.04a
	<i>L. erysimi</i>	20	1.9 ± 0.13a	1.7 ± 0.11a	0.92 ± 0.04a
	<i>M. persicae</i>		2.2 ± 0.09b	2.1 ± 0.07b	0.97 ± 0.02a

Values within each grouped column followed by the same letter are not statistically different (p > 0.05).

CHAPTER V

DISCUSSION

Winter canola is a high-energy oilseed crop with abundant floral and aphid resources especially during the warm spring months. The rotation of long-term winter wheat habitats within the Southern Great Plains with this new high-energy crucifer crop alters plant and herbivore resources and may influence natural enemy life history and dynamics in these landscapes. In these wheat-canola landscapes, aphidophagous predators are able to utilize highly suitable greenbugs (*Schizaphis graminum*) and other cereal aphids, but because of abundant annual infestations of canola aphids, predators are now faced with increasing proportions of chemically defended prey. Indeed, turnip and cabbage aphids, which are commonly found on canola, have the potential to disrupt predator development via accumulation of glucosinolates from their host plants (Francis et al. 2000). Glucosinolate concentration in *Brassica* species is highly variable, however, and their expression may also vary among individual plant tissues and in response to herbivore feeding (Hopkins et al. 2009). For example, the mortality of *Adalia bipunctata* lady beetles provided with cabbage aphid diets has ranged from approximately 40% on *B. napus* to 100% mortality on *Sinapis alba*, *B. nigra* and artificial diets containing 1% sinigrin (Francis et al. 2001, Kazana et al. 2007, Pratt et al. 2008). Other lady beetles, such as *Coccinella septempunctata*, are known to successfully consume and develop on diets of cabbage aphids from *B. nigra* host plants (Blackman 1967, Pratt et al. 2008). In fact, turnip aphids from mustard (*B.*

campestris L.) have been described as a higher-quality prey than green peach aphids for *C. septempunctata* (Omkar and Srivastava 2003).

Aphid performance on different *Brassica* genotypes is related to the distribution and concentration of these metabolites within the plant. Kos et al. (2012) reported cabbage aphid performance on white cabbage cultivars (*B. oleracea* convar. *capitata* var. *alba*) was best on plants with the highest aliphatic glucosinolates. Recall that aliphatic glucosinolates are selectively accumulated in specialist herbivores, and increased concentration of aliphatic glucosinolates within plants will ultimately have negative effects on predator development (Francis et al. 2001, Kos et al. 2012). For example, Kos et al. (2011) investigated life history traits of *C. carnea* provided with cabbage aphids reared on multiple cabbage cultivars. Despite significant effects of plant cultivar on development time and adult weight, survival was on average 92% for this predator.

The effects of host plant and aphid species on predator development and survival raises important questions about the suitability of *Brassica*-specialist aphids in canola, a plant selectively bred to contain both low levels of erucic acid and glucosinolates (Shahidi and Gabon 1989). Levels of aliphatic glucosinolates in winter canola are similar to levels in broccoli (*B. oleracea* var. *italica*) when attacked by cabbage aphids, over 60 μmol per gram (Chaplin-Kramer et al. 2011, Cibilis-Stewart 2013). However, little is known about the ability of turnip aphids to sequester glucosinolates from winter canola. If cabbage and turnip aphids are sequestering high levels of glucosinolates from winter canola, predator abundance within the winter wheat-canola growing region may decline. Many natural enemies utilizing winter canola in the Southern Great Plains are also faced with a habitat requiring intensive management of insect populations not typically required in winter wheat habitats. Producers often make multiple insecticide applications throughout spring to combat aphid outbreaks, which also pose a high mortality risk to insects utilizing the aphid prey. Applications in late spring also present a significant risk to pollinators attracted to floral resources common at this time (Appendix A2).

Predator Life History in Winter Canola

While many lady beetle species are susceptible to the effects of low prey availability and quality (Giles et al. 2002), *Chrysoperla* species are notoriously resilient to stress from low prey availability (Hassan et al. 1985, Hagley 1989, Nordlund et al. 1991) as well as low prey quality (Giles et al. 2000, Kos et al. 2011, Jessie 2012). Longer development times are expected when prey levels are low and/or are nutritionally inadequate (Atlihan et al. 2004, Giles et al. 2002, Jessie 2012). Among diet treatments, development times were significantly different for both *H. convergens* and *C. carnea* at the 2-mg daily prey level. Fewer significant differences were detected at higher prey levels, but diets of *Brassica* specialists always resulted in significantly slower development than other diets. Differences in development times were substantial, with both *C. carnea* and *H. convergens* requiring over a week longer to reach the adult stage on turnip aphid diets when compared to pea aphid diets at the 2-mg daily prey level.

Few studies have compared development rates of *Chrysoperla* spp. on fixed quantities of daily prey, and differences in development duration are frequently attributed to lower consumption rates of turnip aphids relative to green peach aphids (Liu and Chen 2001). The fastest development times for both predator species occurred among larvae supplied with either green peach aphids or pea aphids, regardless of prey level. Lacewing larvae took 35.6 ± 1.23 and 33.2 ± 0.86 days to develop on limited daily levels of green peach and pea aphids, respectively. Liu and Chen (2001) found *C. carnea* took 25.5 ± 0.4 days to develop on low daily prey levels of green peach aphids, and Jessie (2012) found *C. rufilabris* larvae took 30.3 ± 0.7 days to complete development on 2 mg of daily pea aphid prey. Lady beetles spent only 23.9 ± 0.73 and 22.2 ± 0.49 days in preimaginal stages when provided with 2 mg of daily green peach and pea aphid prey, respectively. Giles et al. (2001) found *H. convergens* took approximately 30 days to complete development when provided with 2 mg of pea aphids per day.

Because differences in development duration were much greater at low prey levels, cabbage and turnip aphids from winter canola host plants are suspected to be quantitatively

(available calories) different from green peach aphid and pea aphid prey (Giles et al. 2002). However, significant differences were detected between *Brassica* specialists and other prey at the 8-mg level for both lacewings and lady beetles, suggesting qualitative (nutritional and/or toxic) differences may exist among these diets. Giles et al. (2000) found similar results when feeding *C. rufilabris* pea aphids reared on two different host plants, alfalfa (*Medicago sativa*) versus faba bean (*Vicia faba*). Despite varying daily prey quantity, lacewing larvae were more affected by the qualitative differences of the prey. In this study, if cabbage aphids and turnip aphids sequester high levels of glucosinolate compounds from winter canola, development times are unlikely to converge even if more aphids are consumed (>8 mg) each day. Unlike quantitative differences, the effects of toxins and/or nutritional deficiencies are often difficult to compensate for with increased prey consumption alone, and may only be offset by ingestion of high-quality prey in mixed diets (Mehrparvar et al. 2013).

While cumulative larval survival for both lady beetles and lacewings was high, pupal and pharate (among lacewings) stages experienced the lowest survival. Many lady beetles died within the pupal stage, especially when prey levels were low. These results are consistent with the findings of Phoofolo et al. (2009) who observed a weight threshold for successful pupation among lady beetle fourth instars, and failure to accumulate enough mass resulted in failure to successfully pupate. This strategy may exist for other predators of clustered or ephemeral prey such as lacewings (Canard and Principi 1984), but was not observed for *C. carnea* in this experiment.

Both lacewings and lady beetles were able to complete development on all aphid prey species and at each prey level without significant difference in survival, indicating all aphid prey are suitable for the survival of *H. convergens* and *C. carnea*. Michaud (2005) described prey suitability as the ability of the larva to complete development on a monospecific diet, with survival being most important. With the exception of the turnip aphid diet, pupal success of lady beetles was higher as prey levels increased. When convergent lady beetles were provided with 8

mg of daily turnip aphid prey, only 60% of larvae survived to the adult stage. While this was not significantly different from other treatments ($p = 0.0719$), 40% mortality is undoubtedly an important cost to consider. Although this may indicate a toxic qualitative difference in turnip aphid diets relative to the other aphid species, survival of green lacewings provided with turnip aphids was unexpectedly high and contrasts with previous studies reporting cumulative survival of 0.149 for *C. carnea* larvae provided with turnip aphids from cabbage host plants (Liu and Chen 2001). A possible explanation for our observations of *C. carnea* survival on turnip aphids may likely be due to effects from the first trophic level (winter canola versus cabbage host plants). Unpublished data on glucosinolate concentration of winter canola plants and aphids used in this thesis indicate high levels of indole glucosinolates in both winter canola leaf tissue and *Brassica*-specialist aphids (Appendix A1). High mortality rates are typically observed when predators feed on *Brassica*-specialist aphids containing high concentrations of aliphatic glucosinolates, as this group of glucosinolates typically form volatile isothiocyanate compounds when degraded (Rossiter et al. 2003). Indole glucosinolates, on the other hand, produce unstable isothiocyanates that quickly form nonvolatile indoylcarbinols less likely to cause mortality (Hopkins et al. 2011).

Convergence of development rates at 8 mg of daily prey would be expected if differences in diet suitability were due solely to caloric content (Giles et al. 2000, 2002); yet such results were not observed in this thesis. As previously stated, despite significant statistical interactions between prey species and daily prey levels (indicating convergence of development times), development duration for each predator remained different among prey species at the highest prey level, indicating qualitative differences among prey. Typically, shorter development times strongly correlate with adult body size and fecundity (Michaud 2005). However, adult live weights of both predator species were increasingly greater for pea aphid and green peach aphid diets as prey levels increased; and may indicate predators were not able to compensate for the effects of lower prey quality as daily prey quantity increased.

Interestingly, adult weights for lady beetles were not significantly different between the green peach aphid and cabbage aphid diets at 8 mg of daily prey. This was not observed among lacewing adults, as significant differences were detected among *Brassica*-specialist aphid, green peach aphid and pea aphid diets. This suggests the apparent convergence of development times as daily prey levels rise masks qualitative differences in specialist aphid diets for each predator species. Taken independently, the similarities among development times at high prey levels (8 mg) would suggest that predators are able to compensate for quantitative differences in aphid prey suitability. Few studies have been conducted on the relative effects of indole glucosinolate accumulation by herbivores on predaceous insects, but the high levels of such compounds in the aphid prey used in this thesis are a potential source of qualitative differences in diet suitability. Identifying glucosinolate concentration and distribution in field-grown winter canola plants with large aphid populations can further clarify mechanisms of qualitative differences in winter canola aphid prey.

Biological Control in Winter Wheat-Canola Systems

Lady beetles and lacewings are important regulators of insect pest populations in winter wheat systems (Kring et al. 1985, Rice and Wilde 1988, Jones 2001, Michels et al. 2001, Elliott et al. 2006), and overall pest suppression in the winter crop landscape is likely to be affected by increasing proportions of less suitable / potentially toxic prey from winter canola fields. As winter canola becomes a persistent feature in the Southern Great Plains, natural enemies are likely to create new associations with the novel plant and become increasingly familiar with the resources available (see Pimentel 1991). Increasing natural enemy diversity within winter canola may also help maximize use of aphid resources and regulate pest populations below economic injury levels (Jones 2001, Snyder and Ives 2003, Gardiner and Landis 2007). Indeed, diversity of specialist predators is expected to maximize the regulation of prey populations as competitive and intraguild interactions among species drive the partitioning of resources and niche overlap is

reduced (Finke and Snyder 2008). However, lacewings and lady beetles co-occur in space and time and share aphid prey resources, making them more likely to encounter each other given the lack of clear preferences for aphid prey in winter canola. Observations during no-choice and choice experiments revealed no measurable differences in prey preferences for *H. convergens* and *C. carnea*, which indicates niche overlap is likely to occur in the wild. This overlap may contribute to natural enemy mortality as multiple predators are more likely to encounter fellow guild members as they compete for shared prey (Straub et al. 2008).

Because *C. carnea* and *H. convergens* co-occur in high numbers, the potential for competition and intraguild predation may reduce the overall contribution these predators make to biological control (Rosenheim et al. 1993, Straub et al. 2008). Rosenheim et al. (1993) found decreased aphid suppression when multiple predator species attacked *A. gossypii* compared to one predator (*C. carnea*) acting alone. This is due to the overall negative effect of predator-predator interactions on suppression of shared prey (Rosenheim et al. 1993). Given the abundance of aphid prey in winter canola throughout the growing season, however, predators should be less likely to become intraguild predators (Lucas et al. 1998, Kajita et al. 2000). Further examination of how these predators may interact with other natural enemies and pest management strategies would shed light on proximate causes of frequent aphid outbreaks.

Large populations of aphids are frequent in winter canola throughout the spring and provide abundant prey resources for natural enemies (Royer and Giles 2008, Boyles et al. 2012). High survival rates of these two predators indicate aphid suitability is not the primary reason for the failure of natural enemies to regulate winter canola aphids below economic thresholds. Because of frequent, large aphid populations in winter canola, predators may experience higher development rates and exhibit a reproductive numerical response to increasing prey density (Murdoch 1972). Relative to biological control in winter wheat, winter canola should serve as an attractive resource for *H. convergens*, a species known to disperse from areas of low prey density in search of food (Giles et al. 1994). However, as aphid populations become increasingly

attractive to predator species, the need to protect winter canola seed pods from aphid damage often results in applications of broad-spectrum foliar insecticides which substantially reduce natural enemy abundance in winter canola fields (Franke et al. 2009, Casi N. Jessie unpublished data). As a result, heavily managed winter canola fields may function as an ecological sink regardless of prey suitability or intraguild predation.

The ability of common green lacewings and convergent lady beetles to successfully develop on winter canola aphids is an indication of biological control services they may provide and their potential benefit to the cropping system. Both species are known to occur in high numbers in winter wheat fields, and the results of these studies indicate winter canola has the potential to be a source habitat for these predators. However, reproductive potential of adults may be significantly reduced if larvae feed on *Brassica* specialists (turnip and cabbage aphids) more frequently. Atlihan et al. (2004) observed decreased fecundity of *C. carnea* as preimaginal duration increased with low daily prey quantity. Longer development times and lower adult weights are frequently observed with lower prey quality and are likely to negatively impact female fecundity (Dixon 2000). Female ovipositional capacity in winter canola may be lower than in winter wheat if predator larvae are primarily consuming *Brassica*-specialist prey. Overall, one would expect winter canola to remain a viable habitat choice for lady beetles and lacewings as females are searching for oviposition sites. Further examination of winter canola's relative attractiveness to females as ovipositional habitat will clarify the role it plays in predator life-history traits, particularly as winter canola production spreads across the growing region.

Large aphid populations in winter canola would likely attract female lady beetles searching for ovipositional sites, but lacewings are known to oviposit in habitats regardless of the presence of aphid prey. It is known, however, that *C. carnea* is the most common predator (Casi N. Jessie unpublished data) and frequently lay eggs in winter canola (W.P.J. unpublished data). Relative to predator performance in neighboring winter wheat crops, winter canola aphids are likely to serve as superior prey, as larvae provided diets of *Brassica* specialist aphids had longer

development times but higher survival than has been found in larvae provided parasitized aphids from winter wheat (Lebusa 2004, Mullins 2008, Royer et al. 2008, Jessie 2012). However, when parasitism rates are low in winter wheat fields, predators may experience significantly higher survival, as unparasitized greenbugs are considered high-quality prey (Honěk 1966). The abundant floral resources in winter canola are likely to positively influence predator development and fecundity.

Aphidophagous predators such as lacewings and lady beetles are known to rely on plant-based foods (Principi and Canard 1984, Hodek 1996). Such foods serve as alternative energy resources for flight and diapause, allowing for sustained development and survival when typical aphid prey is scarce (Lundgren 2009). When combined with aphid prey, foods such as pollen and nectar can increase reproductive performance in lady beetles, resulting in faster larval development and adult size in winter canola (Evans 2000, Omkar 2006). The typical low prey availability in winter wheat may limit the ability of natural enemy populations to persist, but the addition of abundant floral resources in winter canola may extend their ability to survive such conditions. Further examination of the role floral resources play in predator development will help to determine if combined aphid/pollen diets can offset the developmental and reproductive costs of feeding solely on Brassica-specialist aphids.

Conclusions and Future Directions

Aphids from winter canola are suitable for the survival of *H. convergens* and *C. carnea*, but significantly affect both the duration of larval and pupal development as well as adult weight. Both lady beetle and lacewing development took up to 11 days longer when provided turnip aphids relative to the control when daily prey was most limited, and adult weight was reduced by as much as 36% when fed turnip aphids at the 8 mg daily prey level relative to the pea aphid control.

No preferences for any aphid species were detected, but both predators often consumed

more green peach aphids. The lack of clear preferences among winter canola aphids is an indication both predator species should readily feed on all three aphid species, and prey preferences should not negatively influence biological control of aphid pests in winter canola. While increased levels of daily turnip aphid and cabbage aphid prey resulted in faster development times, adult live weights of predators were only marginally improved at the highest prey levels, indicating a qualitative difference in these specialist aphids relative to green peach aphid and pea aphid prey. Despite demonstrated reduced suitability of *Brassica*-specialist aphids from winter canola for *H. convergens* and *C. carnea*, the results from this study are further indication that the addition of a high-energy biofuels crop (winter canola) to traditional winter wheat landscapes may benefit aphidophagous predators primarily because of consistent and abundant alternative prey resources. The sheer number of aphids that occur in late spring in winter canola can provide nearly unlimited resources for developing predators, and green peach aphids may be regarded as a high-quality prey species. Furthermore, floral resources of winter canola habitats are expected to benefit natural enemy populations by providing additional, non-aphid foods to species commonly utilizing pollen and nectar. In addition, delays in development rates may be reduced if predators are consuming multiple aphid species, rather than developing on monospecific diets of *Brassica*-specialist aphids.

In our experiments, turnip aphid diets resulted in the slowest development times among both lady beetles and lacewings. Some green lacewings took more than 50 days to develop from a newly hatched larva to an adult, raising important questions about whether such delays to predator development could negatively impact biological control. Such a delay would be likely during fall and early spring months, as aphid resources are typically small (clustered populations of less than 50 individuals are common during this time). As aphid populations increase in early spring, a broad-spectrum insecticide is more likely to be applied (Appendix A2). While this may substantially reduce aphid populations, it is also likely to cause significant mortality to immature predators nearing adult stages. The overall contribution that natural enemies are expected to make

to aphid control in winter canola may therefore be limited by their ability to develop rapidly enough to escape frequent broad-spectrum insecticide applications. A delay in insecticide applications made in early spring may have the potential to facilitate a numerical response of predators as they complete development and lay additional eggs in winter canola. This method of conserving natural enemies known to occur in high numbers in winter canola may further be enhanced with the incorporation of natural enemy presence into sampling protocols and economic thresholds for each aphid species.

Large aphid populations in winter canola have caused severe economic damage (Giles et al. 2009) and regulation of these aphid populations by natural enemies has not yet been observed. These annual infestations of aphids in winter canola have resulted in regular use of synthetic pyrethroids (Franke et al. 2009), and mortality associated with spring applications of insecticides may be the greatest threat to predators within the Southern Great Plains. Detailed studies on natural enemy life histories and their relationship to pest management strategies within winter canola are needed to determine whether this crop may serve as an ecological source or sink habitat. Indeed, any delay made to insecticidal applications in early spring has the potential to facilitate predator development and enhance biological control of aphid pests.

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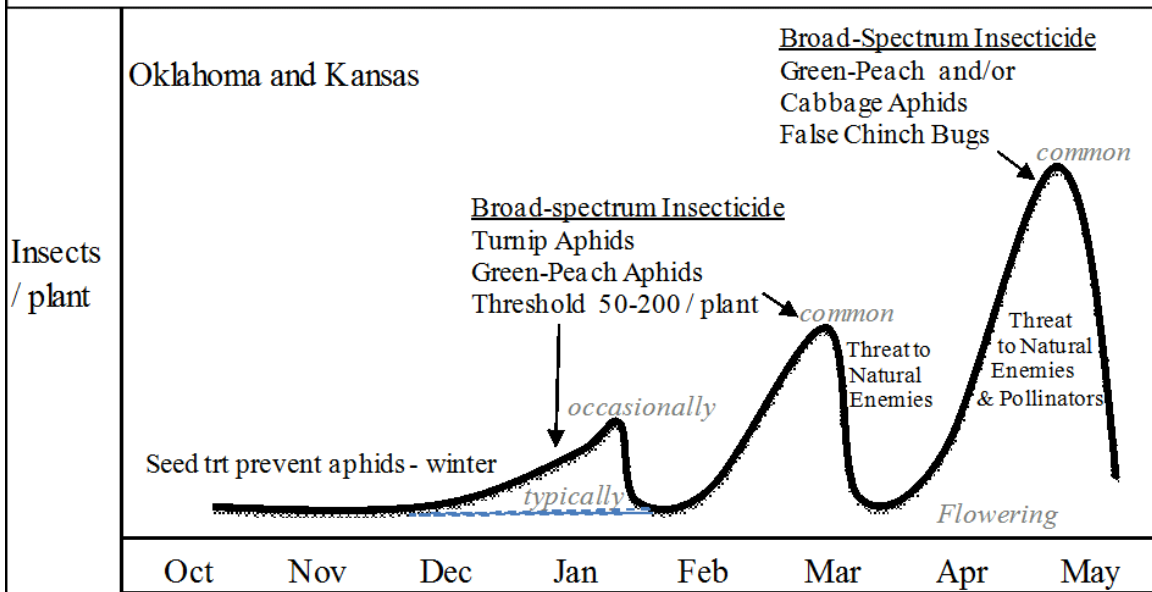
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APPENDICES

A1. Mean (\pm SE) concentration of glucosinolates identified in aphids feeding on winter canola host plants and vegetative tissues of winter canola host plants.				
Glucosinolate compound	Concentration (nmol/15 aphids)			nmol/150mg
	<i>L. erysimi</i>	<i>B. brassicae</i>	<i>M. persicae</i>	Leaf tissue
Indolyl-3-methyl	2.676 ± 0.437	1.459 ± 0.166	0.047 ± 0.047	2.934 ± 1.724
4-hydroxy-indolyl-3-methyl	0.361 ± 0.113	1.121 ± 0.032	0.000 ± 0.000	0.401 ± 0.258
4-methoxy-indolyl-3-methyl	0.757 ± 0.047	1.085 ± 0.064	0.017 ± 0.017	0.620 ± 0.338
N-methoxy-indolyl-3-methyl	0.406 ± 0.049	0.363 ± 0.034	0.015 ± 0.010	0.577 ± 0.342
Total	4.200 ± 0.467	4.029 ± 0.242	0.079 ± 0.062	4.533 ± 2.619
No aliphatic glucosinolate compounds were detected in aphid or winter canola host plant samples. Six replicates of 15 aphids or approximately 150mg of leaf tissue were included in each treatment.				

A2. Current pest dynamics with broad-spectrum insecticides in winter canola



VITA

William Paul Jessie

Candidate for the Degree of

Master of Science

Thesis: SUITABILITY OF *BREVICORYNE BRASSICAE*, *LIPAPHIS ERYSIMI* AND *MYZUS PERSICAE* (HEMIPTERA: APHIDIDAE) FROM WINTER CANOLA FOR DEVELOPMENT AND SURVIVAL OF *HIPPODAMIA CONVERGENS* (COLEOPTERA: COCCINELLIDAE) AND *CHRYSOPERLA CARNEA* (NEUROPTERA: CHRYSOPIDAE)

Major Field: Entomology and Plant Pathology

Biographical:

Education:

Completed the requirements for the Bachelor of Science in Natural Resource Ecology and Management at Oklahoma State University, Stillwater, Oklahoma in December, 2008.

Completed the requirements for the Bachelor of Science in Zoology at Oklahoma State University, Stillwater, Oklahoma in May, 2009.

Experience: Graduate Research Assistant in Integrated Pest Management Laboratory (June 2011 - December 2013), Graduate Teaching Assistant in Introduction to Entomology (Fall 2012, 2013), Department of Entomology and Plant Pathology, Oklahoma State University, Stillwater, Oklahoma.

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