DIVERSITY, RELATIVE ABUNDANCE,

MOVEMENT, AND FITNESS OF INSECT

PREDATORS IN WINTER CANOLA AGRICULTURAL

LANDSCAPES IN THE UNITED STATES SOUTHERN

PLAINS

By

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"Look at the world – so close, and I'm halfway to it!
Look at it all – so big – do I even dare?
Look at me – there at last! I just have to do it. Should I? No. Here I go!
Just smell the grass. The dirt. Just like I dreamed they'd be.
Just feel that summer breeze – the way it's calling me.
For like the first time ever, I'm completely free!
I could go running, and racing, and dancing, and chasing, and leaping, and bounding.
Hair flying, heart pounding.
And splashing, and reeling, and finally feeling that's when my life begins!"
- Tangled

iii

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Abstract: In general, landscape diversification in agricultural production systems is possibly correlated with increased biological pest suppression services. In the Southern Great Plains, continuous winter wheat systems are being successfully rotated with winter-adapted canola to maximize pest suppression and net profits. Despite the rapid adoption of winter canola into Oklahoma wheat agrolandscapes, it remains unknown how this new cropping system affects arthropod communities. Our studies focused on documenting arthropod diversity and abundance in canola-wheat and canola-pasture interfaces, quantifying predator movements within and among the interfaces, and documenting the impact of winter canola pollen on lady beetle larval survival, development, and fitness. During 2011, 2012, and 2013, arthropods were sampled at 22 locations of canola-wheat and 10 locations of canola-pasture interfaces with yellow sticky traps during canola flowering season (April-May). Surprisingly, pasture fields, mostly devoid of green vegetation, had the highest mean Shannon diversity index but the lowest mean field abundances. Wheat fields had the highest predator and parasitoid wasp abundances and the lowest herbivore abundances. Unique protein marks were applied at field interfaces (egg whites in canola, cow's milk in wheat, and soy milk in pasture) to mark insects and indirect enzyme-linked immunosorbent assays (ELISA) were used to document adult lady beetle and green lacewing movements. Green lacewings were the predominant predator trapped followed by lady beetles. Both predators showed similar movement trends based on protein marks; both had frequent movements within and out of canola (emigration) with less movement from wheat or pasture into canola (immigration). In addition, in a laboratory study we supplied *Hippodamia convergens* larvae with *Myzus persicae* and winter canola pollen which revealed that supplementing limited daily prey quantities with canola floral resources increased survival, decreased developmental time, and increased adult body weight. Winter canola does not appear to support the diverse and abundant arthropod communities documented within winter wheat and pasture habitats common in the Southern Great Plains; however, predatory insects are frequently visiting winter canola and may be utilizing available floral resources as a supplement before returning to wheat fields.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER I

GENERAL INTRODUCTION

Wheat (*Triticum aestivum* L., Poaceae) has a long history of production in the Great Plains ecoregion of the United States, and for over 100yr, winter-adapted cultivars have been grown successfully in the Southern Plains. The success of this crop is partially attributed to an extensive amount of research that resulted in improved arthropod pest management practices. Recently, the wheat agrolandscape has been diversified with the introduction of a rotational crop, winter canola (*Brassica napus* L., Brassicaceae), grown primarily to optimize weed management. Canola production in Oklahoma has increased from a few small research plots in 2001 (Boyles and Peeper 2008) to over 30,000 hectares harvested in 2016 (USDA NASS 2016), and recommended rotations have been shown to boost subsequent wheat yields by as much as 22% (Bushong et al. 2012).

The two crops have drastically different plant physiologies that influence arthropod herbivore and natural enemy assemblages and subsequent pest management decisions. Aphid (Aphididae) pest assemblages do not overlap between wheat and canola fields (Elliott et al. 2014) because of unique adaptations to their host plant. Cereal aphids on wheat are highly suitable prey for many natural enemies, including green lacewings and lady beetles. Predators exhibit fast development, high survival, and large adult body weights when reared on cereal aphids, including the greenbug, *Schizaphis graminum* Rondani, and bird cherry-oat aphid, *Rhopalosiphum padi* L. (Phoofolo et al. 2007, Khan et al. 2013). However, canola aphids, particularly the *Brassica*-specialist cabbage aphids, *Brevicoryne brassicae* L., and turnip aphids, *Lipahis erysimi* Kaltenbach, are known to sequester toxic plant compounds (i.e., glucosinolates) while feeding on many

Brassica species (Jessie et al. 2015). Studies have shown glucosinolates and their toxic metabolites are harmful to natural enemies causing delayed development, decreased survival, and potentially reduced fitness (Chen and Liu 2001, Kazana et al. 2007, Jessie et al. 2015).

Not only are natural enemies exposed to toxic prey in canola ecosystems, they are also vulnerable to pest management decisions. The diverse natural enemy community assemblage in winter wheat is known to provide consistent and reliable pest suppression (Rice and Wilde 1988, Jones 2001, Brewer and Elliott 2004, Giles et al. 2008, Elliott et al. 2014, Safarzoda et al. 2014). Winter wheat is rarely treated with insecticides because sampling efforts and area-wide pest management programs have incorporated natural enemy impact into pest management decision recommendations (Giles et al. 2003, Giles et al. 2008). Alternately, because winter canola is a relatively new crop in the Southern Plains, pest management research is still focused on insecticide efficacy and subsequent net-returns. The lack of well-developed management plans for this growing region has left pest suppression decisions to the discretion of canola producers, who routinely apply insecticidal treatments rather than invest in scouting efforts that would optimize economic returns (Franke et al. 2009, K. L. Giles, unpublished data). Fortunately, many studies have documented relatively high numbers of beneficial arthropods in canola, including natural enemies of aphid pests (French et al. 2001, Chown and Giles 2006, Elliott et al. 2014); however, there are no published studies describing the dynamics of these natural enemies in the Southern Plains.

The most common and potentially important natural enemies of crop pests are highly mobile and more likely to survive and reproduce in diverse cropping systems that have a range of spatial and temporal resources (French et al. 2001, Brewer and Elliott 2004, Bianchi et al. 2006, Gurr et al. 2017). Indeed, winter canola herbivores and the large amount of non-prey resources (i.e., pollen and nectar) available during late spring months provide natural enemies with additional resources that may conserve their populations in the agricultural landscape (agrolandscape). However, the abundance, diversity, and movement of natural enemies within the unique wheat-canola systems of the Southern Plains have not been described.

Describing the role of natural enemies in wheat-canola systems of the Southern Great Plains requires: 1) documentation of arthropod abundance, diversity, and movement within and between available habitats; 2) detailed life history studies on natural enemies that utilize canola resources; 3) population dynamics studies at field and agrolandscape levels; and 4) natural enemy exclusion experiments that quantify pest suppression. My goal was to address components 1 and 2, in particular trends in abundance, diversity, and movement at habitat interfaces and life history outcomes for key predators that utilize canola resources.

Objectives

I. Quantify arthropod diversity and functional trait communities (i.e., herbivores, predators, and parasitoids) in winter vegetation habitats (wheat, canola, and uncultivated pasture) throughout north-central Oklahoma where canola has been incorporated into agrolandscapes.

II. Quantify the relative abundance of dominant predatory arthropods and document their movement between available vegetation habitats (wheat, canola, and uncultivated pasture).

III. Determine suitability of winter canola pollen as a supplemental food source for *Hippodamia convergens*.

Explanation of Dissertation Format

The first study describes an extensive field-based study designed to identify and monitor arthropod communities at winter canola-wheat and canola-pasture interfaces. Predator movement trends were determined by utilizing a mark-capture technique and unique protein markers. A second laboratory study examined the effects of winter canola pollen as a dietary supplement for *H. convergens* survival, development, and growth. This general introduction (Chapter I) is followed by a thorough review of the literature (Chapter II), then Chapters III and IV describe the two studies, respectively, in manuscript form for future submission to Environmental Entomology. Chapter V provides a general conclusion to the overall dissertation.

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CHAPTER II

REVIEW OF THE LITERATURE

Winter Wheat

<u>Production</u>

Winter wheat (*Triticum aestivum* L.) is an annual, cool-season grass (Poaceae) that has been cultivated in the United States since the early 19th century. It is grown primarily in the Great Plains ecoregion of the United States and production extends from Texas to South Dakota and from Colorado to Michigan, but it is also grown in the Pacific-Northwest region. Kansas is the largest winter wheat producing state with over 3.44 million hectares planted in the fall of 2016; Oklahoma and Texas rank second and third, respectively, with over 2 million hectares each (USDA NASS 2017). Cultivation and production methods vary across the Southern Plains and can change yearly. Wright et al. (2010) surveyed over 9,000 Oklahoma wheat producers finding 28% used a reduced tillage approach, 29% used conservation tillage, and 43% used intensive tillage prior to planting during early fall months (September-October). Available wheat cultivars are adapted for production in the Southern Plains and as temperatures decrease during winter months, wheat seedlings undergo dormancy until early spring when tillering and erect growth with node formation begins (Wise et al. 2011). As temperatures increase in late spring, wheat begins to head and mature. In Oklahoma, wheat is typically harvested during June which can be delayed by rains for several weeks (Edwards et al. 2015). In addition, winter wheat is frequently grown as a dual-purpose crop providing forage for cattle during winter months and grain yield after harvest. Since 2000, Oklahoma wheat

producers have increased dual-purpose production (both grain and forage) from 49 to 63% and slightly increased forage-only production from 20 to 24%, while grain-only systems decreased from 31 to 13% (Hossain et al. 2004, Wright et al. 2015).

<u>Important Arthropod Pests</u>

Because wheat provides green vegetation during winter months in the Southern Plains when other vegetation is dormant, many arthropods (including pests) utilize this crop. The most common and damaging arthropods in wheat are: aphids (Aphididae); army cutworms (*Euzoa auxiliaris* Grote), armyworms, fall armyworms (*Spodoptera frugiperda* JE Smith), and pale western cutworms (Noctuidae); wire worms (Elateridae); grasshoppers (Orthoptera); Hessian fly (*Mayetiola destructor* Say, Cecidomyiidae); and several mite species (Acari) (PMSP for winter wheat in the Southern Great Plains 2012, Royer and Giles 2015a). Historically, the most economically important pest is the greenbug (*Schizaphis graminum* Rondani). This aphid pest has a worldwide distribution on small grains and weedy grasses, with more than 70 host plants (see Royer et al. 2015). First reports of greenbug in the United States occurred in 1882 and within 30yr it had caused significant damage to Oklahoma winter wheat fields (Jackson et al. 1970). Greenbugs can be found annually in wheat fields but widespread outbreaks occur every 5-7yr (Burton et al. 1985).

Wingless (apterous) greenbugs can be identified by their light green color, dark dorsal stripe, two dark-tipped cornicles on the posterior of their abdomen, and dark colored 'feet' and antennae (Royer et al. 2015). Winged greenbugs (alates) differ in appearance with yellowish heads and lack the dark dorsal stripe; their long wings are membranous and transparent. Apterous greenbugs are parthenogenic females that give birth to live young. Males only exist as alates but females can develop wings as well. Winged females can reproduce either asexually with live birth or sexually with eggs. Day length and temperature influence greenbug reproduction in that those occurring in the southern US (south of the 35th parallel) have parthenogenic female populations

with overwintering nymphs and adults (anholocyclic); whereas, greenbugs in northern regions produce male and female forms with overwintering eggs (holocyclic) (Daniels 1956).

Temperature also has an effect on development and survival and therefore can limit greenbug populations geographically. Greenbugs cannot withstand temperatures below -26°C; this prohibits greenbug colonization in much of the US during cold winter months but north-central Oklahoma and central-south Texas remain above this supercooling temperature and therefore can support greenbugs in winter wheat throughout the growing season (Jones et al. 2008). Greenbug populations can grow exponentially with a female greenbug birthing 60-80 nymphs during her 25d life span (Walgenbach et al. 1988). Nymphs develop into adults within 5d of being born and can begin reproducing within a day of becoming an adult (Walgenbach et al. 1988). Despite this exponential growth, greenbug populations rarely reach outbreak proportions due to abiotic and biotic conditions (i.e., weather, crowding, and host plant condition) as well as natural enemy presence.

Greenbugs feed on plant sap (phloem) with piercing-sucking mouthparts and cause visible plant injury. A range of greenbug biotypes are differentiated from each other based on feeding style and subsequent phenotypic plant damage (Saxena and Chada 1971). Regardless of biotype, the extent of damage to wheat plants includes decreases in fertile tillers per plant (Burton et al. 1985), seed heads (Kindler et al. 2002), and seeds per head (Burton et al. 1985, Kindler et al. 2002); all of which result in significant yield loss (Fenton and Fisher 1940, Burton et al. 1985, Kindler et al. 2002, 2003). Kindler et al. (2003) estimated winter wheat yield loss based on greenbug density per tiller in both drought (34.3kg/ha) and non-drought conditions (14.5kg/ha).

The seedling stage is the most susceptible to greenbug injury (Burton et al. 1985) with fall economic thresholds (ET) at ≤10 aphids per plant whereas spring thresholds approach 20 aphids per plant (Royer et al. 2015). Young seedlings can be killed by low numbers whereas wheat plants that have reached the boot stage, which is early seed head formation (Wise et al. 2011), suffer little yield loss even with high levels of greenbug (Burton et al. 1985). Therefore, ET are low in the fall

8

to avoid widespread plant death and reduced yields, but spring ET are higher because established plants can sustain some feeding injury (Burton et al. 1985, Giles et al. 2000, 2003). Reliable aphid sampling plans have been developed for both spring and winter wheat producers (Elliott and Kieckhefer 1986, Elliott et al. 1990, Feng and Noweierski 1992, Boeve and Weiss 1997, Giles et al. 2000). For the Southern Great Plains, Giles et al. (2000, 2003) developed a binomial sequential sampling plan for greenbug in winter wheat that integrates parasitoid wasp activity, wheat prices, and control costs. This plan (Glance 'n Go) provides producers with a user-friendly pest management approach that incorporates the effects of naturally occurring parasitism (http://myfields.info/dashboard).

Another common cereal aphid, the bird cherry-oat aphid (BCOA, *Rhopalosiphum padi* L.), can occasionally reach outbreak proportions in the Southern Plains (PMSP for winter wheat in the Southern Great Plains 2012). Unlike the greenbug, BCOA are olive green with a red region on their abdomen (Royer and Giles 2015a) and require alternating host plants (Dixon 1971). This aphid is an important vector of barley yellow dwarf virus (BYDV), and both aphid and disease incidence can reach damaging levels when wheat is infested during early fall months (Ismail et al. 2003, Hunger et al. 2012, K. L. Giles, unpublished data).

Integrated Pest Management

For winter wheat production fields in the Southern Great Plains, integrated pest management (IPM) incorporates several strategies for effective arthropod pest control including justifiable use of insecticides, habitat manipulations, host-plant resistance, and biological control (Giles et al. 2008, PMSP for winter wheat in the Southern Great Plains 2012). Larger area-wide approaches that reduce pest numbers and increase net-profitability have also been utilized in wheat production systems in the Southern Plains (Giles et al. 2008).

Chemical Control Historically, wheat producers have managed insect pests upon detection or, more simply, applied routine sprays. Wratten et al. (1990) conducted a survey of winter wheat producers in England concerning pest management practices and found an alarming percentage

"irrationally spraying". Because this approach is unsustainable in the Southern Plains where yields are relatively low, winter wheat producers regularly rely on pest scouting to inform judicious management decisions and rarely utilize costly sampling help outside of the farming practice (Royer et al. 2015). Wheat producers utilize insecticidal seed treatments and/or foliar insecticides as management tools for aphid suppression. Seed treatments can be used justifiably as a preventative measure in areas where aphids regularly infest, however, there are only three available products recommended for aphid control and they are all systemic (i.e., distributed throughout the plant) neonicotinoids that target acetylcholine receptors within pests. Seed treatments can prevent aphid and BYDV infestation/infections and can preserve yield (Royer et al. 2005), but profitability depends on preventing infestations and plant damage that may occur.

Foliar insecticides approved for use in winter wheat include organophosphates (e.g., chlorpyrifos, malathion, dimethoate), pyrethroids (e.g., lambda-cyhalothrin, gamma-cyhalothrin, zeta-cypermethrin), sulfoximine (e.g., sulfoxaflor), and butenolides (e.g., flupyradifurone) (Oklahoma State University 2016). Because of costs, foliar sprays are rarely used alone for pest prevention, except as a low cost tank mix effort during spring (with top-dress fertilizer applications). If field scouting identifies aphid populations exceeding ET in the absence of parasitoid wasps, then foliar insecticides are justified and profitable to use.

Cultural Control Several cultural controls have been shown to be effective for managing pest populations in winter wheat, particularly aphids. Grazing cattle on wheat has been shown to reduce aphid populations (both greenbugs and BCOA) and BYDV incidence, although it is not a consistent and reliable pest management strategy (Arnold 1981, Ismail et al. 2003). Delayed fall planting during cooler temperatures allows producers to avoid aphid colonization and subsequent disease incidence (Royer et al. 2005, Hunger et al. 2012). Strip-cropping canola (*Brassica napus* L., Brassicaceae) and wheat, versus wheat monocultures, was shown to reduce aphid populations in wheat while simultaneously conserving natural enemies (Nassab et al. 2013). In a meta-analysis, Lopes et al. (2016) examined 50 scientific papers on wheat-based intercropping systems and found

pest populations are always less in intercropping systems compared to wheat monocultures. In the Southern Great Plains, compared with vast wheat monoculture landscapes, large-scale diverse cropping landscapes were also associated with lower aphid populations in local wheat fields (Giles et al. 2008).

Host Plant Resistance According to Jarošová et al. (2016), BYDV can only be prevented by killing the aphid vectors directly (via insecticides) or plant resistance. There are a few problems with this approach: 1) there are several aphid species that transmit the virus which may require separate management approaches, and 2) resistant cultivars are usually species/strain specific and mechanisms of resistance are not always fully known. Resistant cultivars have been developed for various greenbug biotypes during the last 40yr using two genes, *Gb2* and *Gb3* (Jarošová et al. 2016). The resistance selected for in these cultivars primarily function to reduce aphid reproductive abilities as well as prolong nymph development (Lazer et al. 1995, Webster and Porter 2000, Giles et al. 2008, PMSP for winter wheat in the Southern Great Plains 2012). This antibiosis effect reduces greenbug population growth and may prevent yield loss through preserved fertile tillers and seeds per plant (Burton et al. 1985). Kindler et al. (2002) determined resistant wheat cultivars tolerate 50% more greenbug damage than susceptible cultivars; however, regardless of cultivar, where populations are high greenbugs can damage wheat especially during the seedling stage when plants are most vulnerable.

Biological Control Winter wheat in the Southern Plains provides a green refuge for natural enemies during months when other vegetation is dormant. There are a large number of natural enemy species that readily feed on or parasitize aphids and other wheat pests. Elliott et al. (2006) used a D-vac sampling method to document the natural enemy assemblages in Oklahoma wheat fields. Lady beetles (Coccinellidae), green lacewings (Chrysopidae), damsel bugs (Nabidae), spiders (Araneae), ground beetles (Carabidae), and rove beetles (Staphalynidae) were the most abundant natural enemies (Elliott et al. 2006). The diversity and abundance of predators collected suggests strong top-down regulatory forces occurring within wheat fields. Lady beetles are well-

studied natural enemies in winter wheat and regularly co-occur with low greenbug populations; several studies have documented suppression of aphids in the Central and Southern Plains by these common predators (Fenton and Fisher 1940, Arnold 1981, Kring et al. 1985, Rice and Wilde 1988, Michels et al. 2001, Brewer and Elliott 2004). However, lady beetles alone are not always considered reliable biological control agents (Royer et al. 2015) due in part to the high mortality risk of immature and egg stages (Kirby and Ehler 1977) and fluctuating yearly populations (Elliott and Kieckhefer 1990). Sole reliance on biological control by predators for aphid management in wheat may not yield consistent results across regions or growing seasons. Exclusion cage studies revealed variable abilities among the common predatory species to impose regulatory effects on aphids in Colorado, Texas, and Oklahoma even when augmentative releases occurred (Michels et al. 2001, Jones 2001, Randolf et al. 2002, Lee et al. 2005). However, relatively stable populations of the parasitoid wasp *Lysiphlebus testaceipes* Cresson (Braconidae) provide significant aphid control in the Southern Great Plains (Fenton and Fisher 1940, Arnold 1981, Harvey et al. 1982, Rice and Wilde 1988, Fernandes et al. 1998, Jones 2001, Giles et al. 2003, Elliott et al. 2014). Indeed, producers consider the presence of the native greenbug parasitoid *L. testaceipes* in Oklahoma winter wheat as a reliable predictor of overall aphid suppression (Giles et al. 2003), and as a result are less likely to use insecticides in their fields despite the presence of aphids (Edwards et al. 2015).

Studies have shown that aphid resistant cultivars of wheat and sorghum, *Sorghum bicolor* L. (a summer crop in the Southern Plains), have little to no negative effects on natural enemies, including the two most common lady beetles in the Southern Great Plains: *Coccinella septempunctata* L. and *Hippodamia convergens* Guérin-Menéville (Giles et al. 2005, Ayyanath et al. 2008). Wheat host-plant resistance targeting aphids is also compatible with parasitoid activity. The predominant greenbug parasitoid *L. testaceipes* is capable of controlling greenbug populations without negative tri-trophic side effects (Fuentes-Grandados et al. 2001, Dogramaci et al. 2005). However, Dogramaci et al. (2005) showed that *L. testaceipes* was unable to prevent greenbug

damage in resistant sorghum hybrids when greenbug infestations were initially very high. At low and intermediate greenbug infestations, *L. testaceipes* was able to suppress greenbug populations and prevent significant plant damage.

According to scientists who study aphid biological control in wheat, consistent regulation of aphids is most likely to occur from a combination of predators and parasitoids in more diverse winter wheat cropping systems (Rice and Wilde 1988, Jones 2001, Brewer and Elliott 2004, Giles et al. 2008, Nassab et al. 2013, Lopes et al. 2016). Areas surrounding field crops can significantly influence natural enemy presence and abundance, especially when additional food resources and refuges are available (Bowie et al. 1999, Grez and Prado 2000, Brewer and Elliott 2004, Bianchi et al. 2006, Gardiner et al. 2009, Scherber et al. 2010, Schellhorn et al. 2015, Gurr et al. 2017). Enhancing the agricultural landscape (agrolandscape) with varying crop types (i.e., intercropping and mixed cropping) often results in an overall higher natural enemy abundance and lower pest abundance (Verkerk et al. 1998, Brewer and Elliott 2004, Giles et al. 2008, Gurr et al. 2017). In many cropping systems, pest management decisions based on regions or areas, rather than individual fields, can greatly improve pest density predictions (Hutchison et al. 2010) while benefiting natural enemies (Chandler et al. 2008, Schellhorn et al. 2015). Giles et al. (2008) and Vitale et al. (2014) summarized data from an area-wide wheat IPM program that was focused on non-chemical pest control tactics and diverse cropping systems. Overall, higher natural enemy numbers, lower pest numbers, and higher on-farm net profits occurred in more diverse wheat cropping systems.

Winter Canola

History

Canola, *B. napus*, was developed from traditional rapeseed in Canada and currently it is the second largest oilseed crop produced worldwide. Selection for canola was geared toward creating rapeseed germplasm with low levels of erucic acid in seed oil coupled with low concentrations of glucosinolates in the remaining meal post-oil extraction (Boyles et al. 2012).

Historically, rapeseed was cultivated in Asia for cooking oil while production in Europe targeted lamp oil and lubrication uses (Raymer 2002, Boyles et al. 2012). Producers in Canada used rapeseed oil as a lubricant but transitioned its use during the mid-twentieth century toward cooking oil. This transition resulted in the development of a germplasm with lower levels of erucic acid and glucosinolate concentrations (Boyles et al. 2012); in fact, canola is abbreviated from CANadian Oil Low Acid. United States production was initiated once the Food and Drug Administration (FDA) recognized canola as safe in terms of food production (USDA ERS 2016) and the pronouncement by the American Heart Association (1986) that Americans needed to reduce saturated fats in their diet.

Worldwide canola production has increased from 6 million hectares in 1961 to over 36 million hectares in 2014 (Food and Agriculture Organization of the United Nations 2017). The United States produced almost 2.8 million hectares of both spring and winter varieties in 2016 with North Dakota leading the way (≥590,000ha) and Oklahoma as a distant second (≥32,000ha; USDA NASS 2017). The recent increase in winter canola production throughout the Great Plains illustrates the profitability of canola adoption into current agricultural production systems. Bushong et al. (2012) documented greater wheat yields and overall higher net returns when winter canola and wheat are rotated.

Growth and Production

Recently, winter canola cultivars were developed specifically for production in the Southern Great Plains. Plant breeders have developed winter canola that survives cold, dry winters through vernalization (Kacperska 1984) and preserves a waxy leaf coating that prevents moisture loss (Desneux and Ramirez-Romero 2009). Cultivars adapted to the Southern Great Plains have been researched since 1991, primarily in Kansas, and in a 3yr period the number of regional cultivars available have increased from 7 (Boyles et al. 2012) to 22 (Lofton et al. 2015). When selecting a cultivar producers must consider winter survival, low pH tolerance, yield, heat tolerance, blackleg resistance, sulfonylurea herbicide residue tolerance, open-pollination versus hybrid, and

herbicide resistance. Although winter survival is dependent on environmental conditions as well as management practices, genetics primarily influence the potential of a specific cultivar to survive winter temperatures in this region. Most canola cultivars are open-pollinated but a small number of hybrids are available. Hybrids typically produce larger seeds, which can aid in planting but are more costly to produce (Boyles et al. 2012). Herbicide resistance drives cultivar selection because most producers have incorporated canola into their wheat systems specifically for grassy weed management. Three common types of herbicide-resistant cultivars available are imidazolinone resistance, glyphosate resistance, and glufosinate resistance; most cultivars available in Oklahoma are Roundup Ready® (glyphosate) resistant (Godsey and Boyles 2012).

Planting depends on abiotic conditions, but it is recommended 6wk prior to first expected frost (≤25°C); in north-central Oklahoma, where winter canola is produced, planting is recommended during the first 2wk of September (Boyles et al. 2012). This allows canola seedlings, which are vulnerable to insect damage, grazing, and abiotic conditions, to accumulate enough biomass to survive harsh winter months. Despite being able to use small-grain planting equipment for canola, seeds are smaller (≤2mm diameter) than that of cereals and, therefore, soil preparation is important for planting and establishment. There are three types of tillage applications in Oklahoma canola production: conventional, reduced, and in some areas, producers utilize no-till systems.

Following emergence, surviving plants overwinter in the rosette stage and require a series of freeze acclimation and de-acclimation events for successful seed production in the spring (Zanewich and Rood 1995, Trischuk et al. 2014). Although rare, canola producers are able to graze livestock on canola during the winter, but unfortunately, this can reduce yields and seed must not be treated with insecticide (Boyles et al. 2012). Typically, it is better to graze young cattle as their lower weight results in less plant damage from trampling (Boyles et al. 2012). However, it is important for producers to be aware of nitrogen levels, especially in the petioles where it is more concentrated, prior to grazing because nitrate toxicity is harmful to cattle (Zhang et al. 2005).

As temperatures (≥40°C) and day length increase during early spring months, canola begins to bolt and produce reproductive structures. Canola inflorescences are clustered racemes containing 5-7 yellow flowers each, and flowers produce a seedpod containing 10-30 seeds (Musil 1950). Flowering normally occurs for 3-4wk during late March through April but can be delayed under cold weather conditions. Occasionally, canola continues to flower through early May. While non-hybrid canola is mostly self-pollinated (70-80%), pollen can be transferred by insects, animals (including humans), and wind (Boyles et al. 2012). Oklahoma canola producers frequently encourage placement of commercial beehives along field margins in an attempt to increase pollination rates and seed production (W. P. Jessie, personal communication). In fact, Bommarco et al. (2012) documented positive effects of insect pollination on canola yield and seed quality.

Maturation and ripening of seedpods takes place during late spring to early summer and lasts several weeks. Canola harvest can be accomplished by pushing (best for tall, thick stands), swathing (for large areas), desiccation (for uneven stand maturity), or direct combining (Boyles et al. 2012). Regardless of method, canola harvest requires more time than winter wheat, and the greatest concern during harvest is prevention of premature pod shattering. Pushing is recommended for tall, thick canola stands and is accomplished by using a "pusher" to horizontally lodge plants without inhibiting further seed pod ripening. Swathing occurs when plants are physically cut and left in the field for later harvest. This method protects pods from shattering due to wind as well as hail, but requires the field to have uniform maturity because once the plants are cut there is no further seed ripening. Desiccation (via herbicide) is used when neither pushing nor swathing are viable and is most useful when fields are unevenly mature or in situations where plant lodging has already occurred. Boyles et al. (2012) suggest direct combining as a more efficient method for canola harvest because it requires a single pass through a field, and it typically results in a higher seed recovery and better quality (i.e., very little chaff).

Pests and Management

Weeds Canola fields are typically infested with grassy weeds, including Italian ryegrass (*Lolium multiflorum* Lamarck) and volunteer wheat, and broadleaf weeds, for example the hard to eradicate wild radish (*Raphanus raphanistrum* L.). Herbicide-resistant cultivars were developed to optimize for grassy and broadleaf weed management in canola fields. Grey et al. (2006) tested the effects of three herbicide-resistant winter canola cultivars and the corresponding use of herbicides (e.g., imazamox, glyphosate, and glufosinate) on weed control and re-emergence. Treatments with imazamox and glyphosate provided the most reliable and consistent control of many common grassy and broadleaf weeds without negative effects on canola yield; however, glufosinate treatments resulted in varying levels of weed control and therefore cultivars with glufosinate resistance were not recommended (Grey et al. 2006). In Oklahoma, Bushong et al. (2012) documented the positive effects on wheat yields in canola-wheat rotations when herbicide-resistant canola cultivars were utilized; rotations without herbicide applications had lower yields than rotations with herbicide applications. Glyphosate resistant cultivars were the best economic choice for use in canola-wheat rotations because of low cost and successful one-time application of herbicide (Bushong et al. 2012).

Pathogens Blackleg fungus, *Leptosphaeria maculans* Desmazières, is the most serious disease found in canola systems throughout the world. This fungus can infect canola seeds (thereby infecting subsequent seedlings), closely related weed species (allowing for quick dispersal into neighboring canola), and remaining stubble (Boyles et al. 2012). Spores can be spread long distances through the air and by rain but infected seeds are the main route of pathogen spread. Producers can protect canola crops by planting disease-free, certified seed treated with fungicide (e.g., Acceleron IDL810, Helix Lite, Helix XTra, Dynasty, Prosper, and Prosper FX). However, seed treatments do not protect canola seedlings from fungus already present in the environment (Boyles et al. 2012). If producers identify blackleg on stubble or in non-canola agricultural fields, tillage or deep-plowing can reduce inoculation; however, care must be taken not to overturn the infected stubble because fungal spores can persist in soil for ≤5yr (Boyles et al. 2012). Proper tillage

and planting equipment usage and sanitation can also prevent blackleg spread in fields. The best defense against field-wide blackleg fungal infection is the incorporation of fungal-resistant cultivars and crop rotation (Dominiak-Olsen et al. 2015). Other diseases of concern for winter canola in the Southern Great Plains include sclerotinia stem rot (caused by *Sclerotinia sclerotiorum* fungus), Alternaria black spot (caused by *Alternaria* spp.), downy mildew fungus (*Peronospora parasitica*), and powdery mildew fungus (*Erysiphe cruciferarum*). However, these pathogens are dependent upon uncommon warm moist conditions and therefore occur sporadically in this region.

   Arthropod Pests Insect surveys in winter canola, especially in the Southern Great Plains, are limited, but French et al. (2001) monitored arthropods using plant counts and D-vac (Dietrick 1961) samples in Oklahoma in all but the harshest winter months (March-December). Aphids (details described below) were, and continue to be, the most frequent and damaging arthropod pest in winter canola, especially in the Southern Plains. Other pests that infrequently infest winter canola include army cutworms, diamondback moths (*Plutella xylostella* L., Plutellidae), flea beetles (*Phyllotreta* spp., Chrysomelidae), grasshoppers, root maggots (Anthomyiidae), false chinch bugs (*Nysius raphanus* Schilling, Lygaeidae), and fall armyworms. In the Pacific Northwest, canola seedpod weevil, *Ceutorhynchus assimilis* Paykull, (Curculionidae) can severely reduce seed weight (Buntin 1999); but this direct pest has not been found in the Southern Plains region. Although rare, plant injury can also come from non-arthropod animals. For instance, bird (horned lark, *Eremophila alpestris* L.; Alaudidae) populations can completely decimate pre-emerged and newly emerged canola seedlings (Schillinger and Werner 2016).

   Currently, in the Southern Great Plains, the three most common aphid species include two *Brassica*-specialists, the turnip aphid (*Lipaphis erysimi* Kaltenbach) and cabbage aphid (*Brevicoryne brassicae* L.), and the generalist green peach aphid, *Myzus persicae* Sulzer (Elliott et al. 2014). Turnip and green peach aphids can occur in winter canola throughout the growing season, however, cabbage aphids are found only during flowering and congregate on the racemes near field edges (Buntin and Raymer 1994, Parker et al. 2003). Cibils-Stewart et al. (2015) suggest that

cabbage aphids are adapted to feeding on canola reproductive structures. These researchers documented positive effects (i.e., higher growth rates, higher fecundities, and shorter generation times) of feeding on the reproductive portions of canola versus vegetative portions. Regardless of species, aphid feeding can significantly delay canola growth, survival, and subsequent canola yield, but Buntin and Raymer (1994) consider turnip and green peach aphids the most important of the three species. Because of the consistent frequency with which winter canola becomes infested with aphids during early winter months, insecticidal seed treatments are currently the foundation of early-season pest management (Royer and Giles 2015b). Winter canola seeds treated with clothianidin are effective against early-season aphids and are compatible with beneficial insects, such as pollinators. Despite detection of insecticide residues in nectar and pollen, Cutler and Scott-Dupree (2007) found that there were no differences in honey bee (*Apis mellifera* L., Apidae) weight between seed-treated canola fields and non-treated fields.

Foliar insecticide sprays for pest management are justified when economic thresholds are reached, however, sampling plans require intensive research and few exist for frequent canola pests (Buntin and Raymer 1994). Oklahoma producers regularly spray insecticides in the spring to prevent aphid buildup and damage, however, these applications are not based on insect counts (K. L. Giles, unpublished data). Unfortunately, and not surprisingly, canola pesticide run-off poses a serious threat to aquatic invertebrates (Bunzel et al. 2015) and therefore each insecticide application needs to be justified to minimalize economic and environmental costs. Recently, a sampling plan was developed for cabbage aphids in Australia that incorporates edge effects (as these aphids typically infest field edges) into sequential plant counts until a decision on aphid management is reached (Severtson et al. 2016). This approach allows for the justifiable use of foliar sprays, and sprays can be targeted towards a portion of the field rather than the entire field (Severtson et al. 2016). Currently, there are no sampling plans for canola aphids in the Southern Great Plains, but it is recommended that during the winter rosette stage plants be treated with an insecticide when aphid numbers ≥100-200 per plant. During spring months, when plants are budding and beginning to

bloom, treatment should be applied when the number of aphid-infested racemes ≥15% (Royer and Giles 2015b).

<u>Natural Enemies</u>

Few field-level studies have been conducted on natural enemies within winter canola systems, but many laboratory and field-cage studies have demonstrated significant potential for natural enemies to provide some degree of pest suppression. French et al. (2001) conducted a survey of predatory natural enemies in Oklahoma winter canola research plots prior to statewide canola production, which revealed the presence of lady beetles, green lacewings, damsel bugs, and brown lacewings (Hemerobiidae). A common parasitoid wasp collected from cabbage aphids in *Brassica* cropping systems is *Diaeretiella rapae* McIntosh (Desneux et al. 2006); and Elliott et al. (2014) were the first to document this parasitoid emerging from all three common Oklahoma canola aphids during canola flowering. *Diaeretiella rapae* has been observed emerging from aphids on canola seedlings during fall months (Desneux et al. 2006), which may aid in preventing aphid populations from reaching economic levels. This parasitoid is capable of suppressing cabbage aphid populations on greenhouse winter canola (Neuville et al. 2016) and can tolerate pyrethroid insecticides without altering host handling behaviors (Desneux et al. 2004). Chown and Giles (2006) sampled a single 0.81ha plot of winter canola multiple times during spring and documented that, despite high natural enemy abundance (≥2,000 lady beetles and ≥3,000 parasitized aphids), aphid populations were not reduced. They concluded that without reliable natural biological control, winter canola aphid management must rely on integration of additional tactics to protect yields, such as seed treatments, resistant cultivars, and foliar insecticidal sprays.

Despite large numbers of insect predators regularly found in winter canola, they may be limited by host plant factors (Chown and Giles 2006, Jessie et al. 2015). Host plants play a significant role in aphid toxicity; for example, when reared on *Sinapis alba* L. (mustard), cabbage aphids are considered toxic prey for the two-spot lady beetle (*Adalia bipunctata* L.*)*, but when reared on *B. napus* cabbage aphids are considered suitable alternative prey (Francis et al. 2000).

Interestingly, lady beetles can feed on canola-reared cabbage aphids but there are minor sub-lethal effects on development and reproduction (Francis et al. 2000). *Brassica*-specialist aphids are able to sequester compounds, i.e., glucosinolates, when feeding on winter-adapted canola (Jessie et al. 2015), and this attribute renders aphids as toxic prey for predatory natural enemies (Francis et al. 2000, Chen and Liu 2001, Kazana et al. 2007, Jessie et al. 2015). Jessie et al. (2015) documented reduced survival of *H. convergens* larvae supplied with canola-reared turnip aphids or cabbage aphids but green lacewings were less affected. The authors demonstrated that *Brassica*-specialist aphids sequester high levels of toxic glucosinolates and are not fully suitable prey for lady beetles and green lacewings (Jessie et al. 2015). However, because of its wide host plant range, the green peach aphid is not capable of sequestering toxic plant compounds when feeding on winter canola and was shown to be essential prey for lady beetles (Francis et al. 2000, Jessie et al. 2015).

Canola Landscapes and Arthropods

With the recent rapid adoption of winter canola in Oklahoma winter wheat landscapes it is imperative to understand how this newly diversified system influences established natural enemy communities as well as pest populations. Researchers in other countries have studied how incorporating canola, and other closely related *Brassica* spp., can affect agricultural landscape heterogeneity and arthropod communities (Grez and Prado 2000, Bukovinsky et al. 2003, Kienegger et al. 2003, Seress et al. 2003, Macfadyen and Muller 2013). Intercropping *Brassica* spp. with either flower strips or other *Brassica* crops has been documented to reduce cabbage aphids compared to monocultures (Bukovinsky et al. 2003, Kienegger et al. 2003, Seress et al. 2003); however, natural enemy dynamics appear to depend on which crops are utilized. Kienegger et al. (2003) documented the positive effects of flowering strips in broccoli (*B. oleracea* L.) fields on carabid (Carabidae) and syrphid fly (Syrphidae) abundances compared to monocropped broccoli; but green lacewings, lady beetles, and parasitoid wasps were not affected by the flower-broccoli intercropping. Alternatively, Bukovinsky et al. (2003) documented increases in natural enemy abundances (parasitoid wasps, green lacewings, and syrphid flies) and decreases in cabbage aphid

populations when Brussel sprouts (*B. oleracea*) were under sowed with black mustard (*B. nigra* L.).

Macfadyen and Muller (2013) monitored insect movement within and among Australian canola systems and surrounding habitats (including cereal crops and uncultivated fields) and found that predatory arthropods tended to move more frequently between canola and cereal crops while parasitoid wasps moved from native perennial vegetation into canola more frequently. The authors also showed that timing of predatory Neuropteran (e.g., brown and green lacewings) and Coleopteran (e.g., lady beetles and carabid beetles) movement peaked when canola fields were in bloom. Parajulee et al. (1997) monitored pest and predator abundance in experimental cotton (*Gossypium hirsutum* L.) plots relayed with canola and wheat in western Texas, and despite the use of small plot sizes (4 crop-rows by 100m), predatory arthropods were documented sheltering in the relay crops during the time when cotton was not in production. Furthermore, predator abundance was higher in canola intercropped with cotton than in wheat (Parajulee et al. 1997); however, this was not observed in a later study with smaller plot sizes (4 crop-rows by 23m) (Parajulee and Slosser 1999). Additional field studies are needed in order to better assess how arthropod communities are altered by incorporation of winter canola into established winter agrolandscapes. This is especially important in the Southern Great Plains given the rise in winter canola production over the last decade.

Chrysopidae

<u>Distribution and Taxonomy</u>

Green lacewings, specifically *Chrysoperla* spp., are a cryptic cosmopolitan group of very closely related predatory species. Commonly found in agroecosystems, including row crops (Wheeler et al. 1968, Afazal and Khan 1978, Tassan et al. 1979, Woolfolk and Inglis 2004, Elliott et al. 2006, Freier et al. 2007) and orchards (Elkarmi et al. 1987, Hagley 1989, Atlihan et al. 2004), chrysopids are frequently studied for their utility in IPM programs and are mass-reared and released as biological control agents (Cranshaw et al. 1996, van Lenteren et al. 1997, Tauber et al. 2000,

Henry and Wells 2007). Recently, there has been substantial disagreement among experts regarding species identification within this genus. Historically, researchers relied on morphological characteristics and geographic distributions for species identification (Tauber 1974, Agnew et al. 1981, Garland 1985, Tauber et al. 2000, Tauber 2003). Conversely, research into unique adult courtship 'songs' reveals arguably more reliable species-specific features for identification (Henry 1985, Henry and Wells 2007). Green lacewings use tremulations (abdominal vibrations), or songs, for courtship and both sexes will perform duets prior to copulation. Wells and Henry (1992) documented song types for green lacewings collected across North America presumed to be *Chrysoperla plorabunda* Fitch and discovered three different song morphs in which the majority of tested females would only respond to their specific song type. The authors concluded that *C. plorabunda* was comprised of at least three separate species. Subsequently, researchers have begun to utilize song variations for *Chrysoperla* species identification around the world (Henry et al. 1999, Henry et al. 2003, Taki et al. 2005, Henry et al. 2006, Henry and Wells 2007, Henry et al. 2009). According to Brooks (1994, as referenced by Henry et al. 2001), there are 36 recognized *Chrysoperla* species; however, Henry et al. (2001) cautions this number is conservative in its identifications and *Chrysoperla* systematics remains inconclusive.

Development

Female green lacewings randomly lay eggs on the undersides of leaves and other substrates (Frechette and Coderre 2000, Frechette et al. 2006). Eggs, small and green, are attached to a substrate via a silk stalk (Afzal and Khan 1978, Canard et al. 1984) which is most likely a means of protection from intra-specific predation (Růžička 1997). Cannibalism occurs at high rates in green lacewings especially during the egg stage when the last laid eggs are more susceptible to predation (Fréchette and Coderre 2000, Fréchette et al. 2006). The eggs begin to turn gray prior to hatching after which newly eclosed larvae remain immobile on the egg stalk for a few hours to a few days without feeding (Canard et al. 1984). Once larvae climb down from the stalk they begin to search for prey. Green lacewing larvae are highly mobile and have voracious appetites for soft-

23

bodied arthropods (Afzal and Khan 1978). There are three larval instars (Canard et al. 1984) and appetites increase with each subsequent larval molt (Balasubramani and Swamiappan 1994, Chen and Liu 2001). Typically, the duration of the first and second instar is approximately 2-4d each and the third instar lasts approximately 6d (Burke and Martin 1956, Afzal and Khan 1978, Hydorn and Whitcomb 1979, Giles et al. 2000, Chen and Liu 2001, Khan et al. 2013).

Chrysoperla spp. undergo a pre-pupation period, which starts when larvae begin construction of their silken spherical cocoon produced with silk glands located in their hindgut (Canard et al. 1984). Preimaginal development typically lasts between 18-24d, depending on prey quality and quantity as well as relative humidity (Burke and Martin 1956, Afzal and Khan 1978, Hydorn and Whitcomb 1979, Tauber and Tauber 1983, Giles et al. 2000, Chen and Liu 2001, Khan et al. 2013). Pre-pupation culminates after approximately 4d with the appearance of the darkened larval skin at one end of the cocoon and the lacewing pupa remains in the cocoon for an additional 7-11d (Afzal and Khan 1978, Khan et al. 2013). Finally, cued by scotophase (the dark phase of a light/dark cycle), the pharate adult emerges by cutting a hinged circle in the side of the cocoon and climbs up a substrate to undergo the 'final molt' (Duelli 1980, Canard et al. 1984). Adult green lacewings will remain on a substrate until the following night before they first take flight (Duelli 1980).

Adult Flight and Reproduction

Adults are nocturnal fliers (Duelli 1980, Keulder and van den Berg 2013), and have specialized eyes adapted for nocturnal vision (Kral and Stelzl 1998). Duelli (1980) documented *C. carnea* Stephens (=*Chrysopa carnea*) nocturnal flights and showed newly emerged adults have obligatory migration flights (i.e., adaptive dispersal flight) that occur nightly for several consecutive nights and individuals can fly up to 40km in a single night. Adult *C. carnea* typically fly downwind between 2-8m off the ground; however, gravid females tend to fly at lower elevations (2.6m) than unmated females and females without mature eggs (Duelli 1980). During the adaptive dispersal flight, adults do not respond to food or mate stimuli, even in flight simulations; however,

approximately 3d after adult emergence, green lacewings begin to react to environmental stimuli which coincides with reproductive maturity (van Emden and Hagen 1976, Duelli 1980). Sexually mature adults participate in species-specific courtship songs wherein one adult oscillates their abdomen and sends vibrations through a substrate to the receiving lacewing; both adults will continue to 'sing' to each other before copulation (Henry 1985, Henry and Wells 2007). Females produce the most number of eggs following the first copulation and appear to lay eggs continuously until sperm depletion, which then triggers sexual receptivity for additional copulations (Henry and Busher 1987). *Chrysoperla plorabunda* and *C. downesi* Smith females copulate an average of two times throughout their lifespan; however, males usually mate with multiple (≥20) females (Henry and Busher 1987). Female *C. plorabunda* and *C. downesi* produce an average of 774.5 eggs during their lifespan (Henry and Busher 1987); comparatively, *C. carnea* produces between 300-806 eggs depending on preimaginal diet (Atlihan et al. 2004, Khan et al. 2013). *Chrysoperla* adult longevity is highly variable, especially considering some species are capable of diapausing for several months. Atlihan et al. (2004) documented average longevity for *C. carnea* to be 41.5d. Similarly, Khan et al. (2013) determined female *C. carnea* have an average lifespan of 51.2d and the average lifespan for males was 32.4d.

<u>Larval and Adult Diets</u>

The feeding habits of green lacewings differ significantly between larvae and adults. Larvae have a unique feeding strategy termed extra-oral digestion (EOD) in which initial prey digestion happens outside the predator's digestive track (Cohen 1995, 1998). Once a prey item is captured, the lacewing larva's hollow, sickle-shaped mandibles pump digestive enzymes into the prey where breakdown of non-chitinous materials occurs; this predigested food is sucked back through the mandibles for further digestion within the lacewing gut (Cohen 1995, 1998). Although primarily opportunistic predators of soft-bodied arthropods, larvae will supplement their diet with non-prey resources (Limburg and Rosenheim 2001, Patt et al. 2003, Hogervorst et al. 2008). Limburg and Rosenheim (2001) observed 136 *C. plorabunda* larvae on cotton plants and almond

trees and documented 21% of larvae utilized extra-floral nectar. However, there was an inverse relationship between aphid density and extra-floral nectar feeding which suggests the larvae were supplementing their diets with extra-floral nectar when aphids, or other prey, were scarce (Limburg and Rosenheim 2001). This is unsurprising because green lacewing larvae are limited to a small foraging area as their limited mobility prevent movement from one depleted aphid patch to a larger patch. *Chrysoperla carnea* larvae have been documented feeding on aphid honeydew in the presence of aphids and, when starved, will preferentially feed on honeydew prior to feeding on aphids (Hogervorst et al. 2008). Furthermore, Patt et al. (2003) documented the positive effects (i.e., faster development and larger adult size) pollen has on *C. carnea* larvae when mixed with a low-quality prey diet. These authors used stable isotope analysis to determine pollen provides green lacewing larvae with an additional source of essential nitrogen as well as other trace nutrients (Patt et al. 2003).

Larval developmental time and survival are influenced by diet quality and quantity as well as abiotic conditions, particularly relative humidity. Tauber and Tauber (1983) documented the effects of relative humidity on green lacewing survival, development, and growth; they demonstrated significant interspecific variation. For example, *C. rufilabris* Burmeister is better adapted to more mesic habitats (≥55%RH) than *C. carnea,* which explains the prevalence of *C. rufilabris* in the more humid southeastern US.

Suboptimal (i.e., low quality and/or quantity) larval diets can negatively affect green lacewing larval development and survival (Hydorn and Whitcomb 1979, Greenburg et al. 1994, Chen and Liu 2001) as well as alter adult performance (Hydorn and Whitcomb 1979, Giles et al. 2000, Atlihan et al. 2004, Gonzalez et al. 2015). Hydorn and Whitcomb (1979) provided *C. rufilabris* (=*Chrysopa rufilabris*) with four different prey types in order to document the differential responses to each prey. The authors concluded that larvae reared on a mixed aphid species diet developed more quickly and had a higher survival than larvae reared on the other prey types, including adult *Drosophila melanogaster* Meigan (Drosophilidae). However, not all aphids are

optimal for green lacewing development. Chen and Liu (2001) found that all *C. rufilabris* larvae provided with turnip aphids (*L. erysimi*) died prior to adult emergence, whereas larvae provided with *Aphis gossypii* Glover or *M. persicae* had 100% survival. Furthermore, tri-trophic interactions (specifically lower-nutrient host plants and volatile secondary metabolites) can prolong larval development and reduce survival (Legaspi et al. 1994, 1996, Giles et al. 2000, Jessie et al. 2015). Giles et al. (2000) analyzed the fatty acid content of pea aphids (*Acyrthosiphon pisum* Harris) reared on a high quality host plant (alfalfa, *Medicago sativa* L., Fabaceae) versus a low quality host (faba bean, *Vicia faba* L.) and found that aphids reared on alfalfa had a higher fatty acid content which allowed for greater green lacewing survivorship, reduced developmental time, and larger adults. Some aphids can sequester host plant volatiles and become toxic for predators (Kazana et al. 2007, Jessie et al. 2015). Jessie et al. (2015) documented the sub-lethal negative effects (i.e., longer development and smaller adult size) of *Brassica*-specialist aphid diets (*L. erysimi* and *B. brassicae*), which contained high levels of plant glucosinolates, on *C. carnea* and lady beetle (*H. convergens*) larvae.

In addition to suboptimal quality diets, low quantity diets can negatively affect larval survival, development, and subsequent adult fitness (Zheng et al. 1993, Giles et al. 2000, Atlihan et al. 2004). *Chrysoperla carnea* larvae supplied with ≤10 aphids (*Hyalopterus pruni* Geoffroy) per day had a lower survivorship, prolonged preimaginal development, lengthened pre-ovipositional period, and reduced fecundity compared to larvae provided ≥20 aphids per day (Atlihan et al. 2004). However, Jessie (2012) documented *C. rufilabris* larvae surviving at a high rate to adulthood on a daily diet with as few as two large pea aphids (*A. pisum*) or 10 greenbugs (*S. graminum*).

Chrysoperla adults feed solely on aphid honeydew and floral resources such as pollen and nectar (Burke and Martin 1956, Venzon et al. 2006, Villenave et al. 2006). Symbiotic yeasts located within the diverticulum (an outgrowth of the crop) aid in digestion of these food sources (Hagen et al. 1970, Afzal and Khan 1978, Woolfolk and Inglis 2004, Woolfolk et al. 2004). Newly emerged adults do not contain symbiotic yeasts (Woolfolk and Inglis 2004), but acquire them via trophallaxis

with older adults (Hagen et al. 1970). Females tend to lay eggs randomly around accessible floral resources, as pollen and nectar are essential for egg development (Hagen et al. 1970, van Rijn 2012). Additionally, the breakdown of aphid honeydew by the symbiotic yeasts provides essential amino acids necessary for ovigenesis (Hagen et al. 1970). Flowering plants provide variable access to floral nectar, pollen, and extra-floral nectaries, which can influence how green lacewings utilize flower resources. van Rijn (2012) found that while green lacewings may not be able to feed on some flowering species due to inaccessible floral nectaries, pollen is still accessible and consumed. In a groundbreaking study, Gonzalez et al. (2015) analyzed the nectar and pollen of 11 native Mediterranean plants associated with olive orchards and found that those species with higher concentrations of trehalose in both types of plant resources (pollen and nectar) increased adult *C. carnea* longevity and fecundity.

Biological Control

Chrysopids possess several characteristics that enable them to be effective natural enemies, such as high consumption rates of a variety of prey types. Aphids are a common pest for which green lacewings are utilized as biological control agents (Hassan et al. 1985, Hagley 1989, Messina et al. 1995, Balasubramani and Swamiappan 1998, Chen and Liu 2001, Khan et al. 2013). The unique feeding strategy (EOD) allows for efficient food consumption (i.e., reduced handling times) as well as possibly protecting larvae from the negative effects of consuming suboptimal prey (Cohen 1995, 1998). Green lacewings have been utilized as biological control agents for over 60yr, with the first records of mass-rearing (Finney 1948) and release (Doutt and Hagen 1949) in pear orchards for mealybug suppression. Culturing green lacewings was studied extensively during the mid-20th century and focused on how best to rear lacewings on artificial diets (Ru et al. 1976, Elkarmi et al. 1987, Balasubramani and Swamiappan 1998, Cohen and Smith 1998). By the turn of the century, van Lenteren et al. (1997) documented 64 commercial insectaries that provided biological control agents worldwide; of which 26 were located in Europe and 10 in North America. However, only two European companies produced and sold green lacewings and with only the egg

stages of *C. carnea* and *C. rufilabris* available for purchase. By 2007, 40 North American companies advertised selling green lacewings but of these only four companies actually had rearing facilities (Henry and Wells 2007).

Releasing natural enemies for pest control (or augmentation) is the most common method for utilizing green lacewings in both field crop and greenhouse IPM programs (compared to conservation biological control). Augmentation occurs when large numbers of green lacewings (i.e., eggs, larvae, or adults) are released in a field for pest suppression, and this approach can provide immediate or more long-term pest control depending on which life stage is released. Releasing adult green lacewings is problematic because they are highly dispersive (Trouvé et al. 1996), but releases of eggs or larvae place predators and pests together in time and space and can lead to successful suppression (Nordlund et al. 2001). For example, following the release of *C. carnea* eggs in a dwarf apple orchard, apple aphid (*Aphis pomi* DeGeer) populations were reduced when predator to prey ratios were ≥1:20 (Hagley 1989). Additionally, *C. rufilabris* (Nordlund et al. 1991) and *C. carnea* (Sablon et al. 2013) have been documented as effective predators of Colorado potato beetle larvae, *Leptinoarsa decemlineata* Say (Chrysomelidae), in both laboratory and field studies.

Conservation biological control incorporates natural enemies already present within an agroecosystem and maintains/enhances their populations and impacts through attractants, alternative resources (prey/hosts), and refuges (e.g., field margins) (Gurr et al. 2017). Artificial food sprays (attractants) were developed for *Chrysoperla* spp. over 50yr ago (Hagen et al. 1976) with mixed success. Wade et al. (2008) conducted a meta-analysis on artificial food sprays and success rates for conservation biological control and found, of the 104 publications on Neuroptera and artificial food sprays, a success rate of 77% in which either Neuropteran populations increased, pest populations decreased, or both. The authors suggest that, while more research is needed to definitively classify artificial food sprays as an effective method for conserving natural enemies, sprays can be a useful tool in IPM programs (Wade et al. 2008). Refuge habitat not only provides

natural enemies with sanctuary from inhospitable conditions (i.e., mechanical manipulations such as tillage and harvest), but can provide alternative prey/hosts when these resources are not available in the primary crop habitat. Natural enemy recruitment in refuges can also serve as a medium for broadening prey/host ranges. Colares et al. (2015) showed how natural enemies, including *Chrysoperla* spp., can be recruited as biological control agents on novel prey (sugarcane aphid, *Melanaphis saccari* Zehntner) when offered established prey (greenbugs). Conserving natural enemies, and in particular green lacewings, within established agroecosytems can significantly benefit and enhance biological pest suppression services.

Green lacewings also compliment IPM programs because they have a high tolerance to many insecticides, including DDT (Doutt and Hagen 1949), pyrethroids (Lawrence 1974, Mizell and Schiffhauer 1990), organophosphates (Hagley 1989), and Bt toxin (Romeis et al. 2004, Li et al. 2008). Mizell and Schiffauer (1990) tested 20 different pesticides (including three fungicides and two acaricides) on *C. rufilabris* eggs, larvae, and adults and found that each life stage has a different tolerance depending on the class of pesticides with carbamates being the most toxic to all life stages. Unfortunately, green lacewings are susceptible to a common insecticide used in canola management (Boyles et al. 2012); Amarasekare and Shearer (2013) documented the lethal effects lambda-cyhalothrin has on both larvae and adult green lacewings. This recent study coupled with current sampling methods for green lacewings (that likely underrepresent populations due to low detectability of larvae and adults) illustrates the need for understanding impacts of winter canola in historical monoculture wheat agroecosystems. Incorporating biological control services of green lacewings into IPM programs, specifically for evolving winter canola-wheat landscapes with higher pesticide inputs, will require a thorough understanding of their population dynamics within managed heterogeneous agricultural landscapes.

Coccinellidae

Distribution and Taxonomy

Lady beetles are common predatory beetles found throughout the world in a diversity of habitats ranging from agricultural systems, wooded areas, and urban gardens (Hodek and Honěk 1996). Approximately 6,000 lady beetle species have been described worldwide (Nedvěd and Kovář 2012) with nearly 470 species in the United States (Gordon 1985). There are two common lady beetle species in the agroecosystems of the Southern Great Plains. The convergent lady beetle, *H. convergens*, is native to North America and is found in most agricultural habitats, including winter wheat fields. The seven-spotted lady beetle, *C. septempunctata* is a Palearctic species introduced into the United States as a biological control agent. Because it is a habitat and prey generalist, this exotic beetle was able to establish quickly, and extend its distribution from initial introduction sites to all states in the US (Cartwright et al. 1979, Obrycki et al. 1987, Schaefer et al. 1987, Elliott et al. 1996).

Development

The lady beetle life cycle begins with the egg stage and many species are believed to oviposit in areas that minimize both intra- and inter-specific competition (Hemptinne and Dixon 1991, Růžička 2001). Typically, larvae hatch after 5-7d and are highly mobile. Once sclerotized, larvae begin to look for food choosing soft-bodied organisms to prey upon and continue to increase the quantity of daily prey consumed as they develop (Campbell and Cone 1999, Cardoso and Lázzari 2003). The larval stage consists of four instars with three distinct molts (Nedvěd and Honěk 2012); and depending on lady beetle species, larvae are able to complete development after 14-35d. On average, the first instar comprises 24% of the developmental time, second instar 17%, third instar 19%, and fourth instar 40% (Hodek and Honěk 1996). Pupation begins once a critical weight is reached in the final instar (Phoofolo et al. 2009) and the larva affixes itself to a substrate (Nedvěd and Honěk 2012). Pupation can last up to 14d and after emergence adults remain on the empty pupal case while elytra and other chitinous structures harden (Nedvěd and Honěk 2012).

A large number of studies have demonstrated larval development is influenced by availability of prey and non-prey resources, or lack thereof, as well as temperature (Michels and

Behle 1991, Babu 1999, Rodriguez-Saona and Miller 1999, Srivastava and Omkar 2003, El-Heneidy et al. 2008, Nedvěd and Honěk 2012). Phoofolo et al. (2007) documented the effects of *ad libitum* (unlimited) versus limited diets on *H. convergens* preimaginal development and showed that larvae developed significantly faster when provided with daily *ad libitum* aphids, but had slower development when provided with limited optimal prey levels and suboptimal prey (Phoofolo et al. 2007). All lady beetle larvae develop faster as temperatures increase to an optimal species-specific threshold (Michels and Behle 1991, Srivastava and Omkar 2003, Omkar and James 2004, Nedvěd and Honěk 2012).

<u>Larval and Adult Diets</u>

While lady beetle diets vary extensively across the family Coccinellidae (including but not limited to herbivory, phytophagy, and predation), most are predators of a variety of soft-bodied insects, including sternorrhynchan Hemiptera such as aphids, mealybugs (Pseudococcidae), and scales (Coccidae) (Hodek and Evans 2012). Not all accepted prey are optimal for larval growth, and Michaud (2005) classified lady beetle prey as either suitable, adequate, or marginal. Aphids, in particular, have been identified as suitable prey, and in some cases critical, for lady beetle development (Ferrer et al. 2008). Greenbugs (*S. graminum*) and BCOA (*R. padi*) that infest wheat are essential prey for *H. convergens* development and reproduction (Phoofolo et al. 2007).

Adult coccinellids feed on similar prey as their larvae, however it is debated whether quantity is more important than quality for reproducing females (Evans 2003, Phoofolo et al. 2007). Reproduction is complex and varies among species, but in general, females require a substantial amount of nutrients in order to produce eggs and actively search for ovipositional sites, and therefore prey quality can influence lady beetle fecundity (Hariri 1966). For gravid females, it is more energetically costly to move around in habitats with small aphid populations but there is also a cost associated with laying eggs in aphid-sparse habitats (Evans 2003). Aphidophagous lady beetles have coevolved with aphids resulting in closely synchronized life cycles with aphid colony development (Hemptinne and Dixon 1991), lower starvation thresholds (Hemptinne and Dixon

1991, Phoofolo et al. 2008), and efficient searching capacity for locating small aphid patches in crop monocultures (Giles et al. 1994, Grez and Predo 2000, Michels et al. 2001). When gravid females colonize habitats with low essential prey density they rely on non-insect food for nutrition delegated towards metabolic maintenance rather than for reproduction (Evans 2003), however there is a balance between allocating nutrients for oöcyte production and energy for ovipositional site searching (Ferrer et al. 2010). Non-insect foods, such as honeydew, nectar, and extra-floral resources, are converted and stored as fat in lady beetles and not utilized for reproduction (Hagen 1962, Hemptinne and Dixon 1991). Flower pollen, however, has been shown to offset suboptimal diets for the two-spot lady beetle (*A. bipunctata*) by improving weight and fertility (DeClercq et al. 2005).

<u>Reproduction</u>

For most species, lady beetle males become sexually mature during the pupal stage when testes develop; therefore, males are ready to mate shortly after adult emergence (Hodek and Ceryngier 2000). On the other hand, females require a pre-ovipositional period for an average of 11d following adult emergence (Hodek and Ceryngier 2000, Omkar and Srivastava 2002). Temperature as well as prey quality and quantity can greatly influence the length of pre-oviposition (Hariri 1966, Munyaneza and Obrycki 1997, Hemptinne et al. 2001, Raak-van den Berg et al. 2011).

In a pivotal study, the two-spot lady beetle (*A. bipunctata*) was used to determine mate recognition cues and it was documented that males, while less active than females, modify their mate searching to an area restricted search pattern once contact with a female has occurred (Hemptinne et al. 1996). This led the authors to suggest that mate recognition occurs via female elytra properties and that a contact pheromone is likely present (Hemptinne et al. 1996). Males have a series of behaviors that precede copulation, including approach, watch, examine, mount, and attempt copulation (Omkar and Srivastava 2002, Omkar and James 2005). Once the male mounts the female, he shakes his body so that insemination, via the spermatophore, is ensured (Hodek and

Ceryngier 2000). About 60min after copulation, the spermatophore empties within the female's bursa copulatrix and is then ejected from the female's body (Hodek and Ceryngier 2000, Omkar and Srivastava 2002). Some female lady beetles will consume the emptied spermatophore (Hodek and Ceryngier 2000). A female may shake off a male attempting to copulate if she is gravid, has recently mated, or is not sexually mature (Omkar and Srivastava 2002). Mate acceptance can be influenced by age (i.e., older females being more accepting of copulation than younger females), melanism, and size (Hodek and Ceryngier 2000, Pervez et al. 2004). Lady beetles often engage in multiple matings which have been shown to enhance female fecundity as well as fertility (Omkar and James 2005).

Lady beetle ovipositional rates are described as triangular fecundity functions because rates are accelerated following sexual maturity and then, once the maximum number of eggs in ovarioles is achieved, the rate slowly declines until the death of the female (Dixon and Agarwala 2002). Oviposition usually occurs on the underside of leaves near young aphid colonies (Nedvěd and Honěk 2012) and eggs can be laid singly or in clusters. Duration of lifetime oviposition as well as overall fecundity varies by species and is dependent on temperature and both larval and adult food quality and quantity (Nedvěd and Honěk 2012).

Biological Control

The biological control services that lady beetles are capable of providing have been extensively studied (Michaud 2012). Most researchers agree that lady beetles are capable of reducing pest populations, particularly aphids (Arnold 1981, Kring et al. 1985, Rice and Wilde 1988, Michels et al. 2001). While there are successful examples, including the famous vedalia lady beetle (*Rodolia cardinalis* Mulsant) introduced from Australia in 1887 for control of cottony cushion scale (*Icerya purchasi* Maskell), studies have also shown the ineffectiveness of relying solely on lady beetles to provide long-term control of aphids (Jones 2001, Randolf et al. 2002, Freier et al. 2007, Michaud 2012). There are several possible explanations as to why lady beetles are not consistently reliable biological control agents, including yearly fluctuating populations

(Elliott et al. 1996), high mortality in the egg stage (Kirby and Ehler 1977), sub-optimal foraging for larvae (Kindlmann and Dixon 1993), and the negative effects of intraguild predation (Takizawa et al. 2000, Royer et al. 2008, Mullins et al. 2013). Intraguild predation, a risk many natural enemies take when foraging, occurs when organisms within the same trophic level consume one another (Polis et al. 1989, Polis and Holt 1992, Brodeur and Rosenheim 2000). In Oklahoma, Mullins et al. (2011) documented the frequent occurrence of parasitized aphids in field-collected lady beetle digestive tracks. Unfortunately, consuming parasitized aphids can decrease lady beetle reproductive potential by retarding larval development, survival, and weight gain (Takizawa et al. 2000, Mullins et al. 2013, Royer et al. 2008).

Conservation biological control approaches have the greatest potential for utilizing the prey suppression impacts of lady beetles in IPM programs, especially considering the shortcomings reported in classical and augmentation biological control (see Michaud 2012). Enhancing current lady beetle populations in agroecosystems is considered paramount for pest suppression and many studies have shown moderate to high success with artificial food sprays (Hagen and Hale 1974, Wade et al. 2008), alternative food resources (see Obrycki et al. 2009), and refuge habitat enhancement (Cottrell and Yeargan 1999). However, it remains unclear as to how lady beetles contribute to overall pest suppression in complex agroecosystems compared to single crop monocultures, and Obrycki et al. (2009) cite the need for more detailed field research on lady beetle diets and movements within agroecosystems to better understand and capitalize on their biological control impact.

Agrolandscapes

Definitions

The 'landscape' concept was first described in the 1940s (Watt 1947) but has taken on new meaning with increasing concern for preserving biodiversity and conservation biology. Forman and Godron (1986) classify a landscape as a land area with differing, but consistent, structure, function, and disturbance patterns that allow for a heterogeneous mixture of habitats, or patches, within an

overall specific land area type, or matrix. Landscapes are defined by spatial and temporal scales; for example, a meadow can be considered a landscape in which the areas of uncultivated vegetation are the matrix (or dominant land cover), the edges (or margins) of the meadow and bare ground are patches within the overall matrix, and the meadow structure/successional stage is influenced by time.

Agricultural landscapes, or agrolandscapes, are recognized as a definable system where integrated pest management programs can be developed and evaluated. Until recently, researchers referred to agrolandscapes in terms of crop diversity within a field, such as monocultures (a single crop) versus polycultures (more than two crops) (Andow 1991), or the system was referred to more generally as 'habitat heterogeneity' (Scherber et al. 2010). However, it is now widely accepted that an agrolandscape incorporates the field in which a particular crop is planted as well as the surrounding habitat, including both small (e.g., field margins, ditches, and roads) and large patches (e.g., forests, uncultivated areas, and other crops), and the microhabitats within a field (e.g., bare ground or cover crops between crop rows). Additional factors include past cultivation practices which influence agrolandscapes by changing soil properties, which have a cascading temporal effect on above- and belowground ecosystem functions (Crotty et al. 2016). Indeed, agrolandscapes are shaped by a large number of management practices that vary depending on cropping system. Tillage, harvest, chemical applications (i.e., fertilizers, herbicides, and insecticides), and cultural practices (e.g., strip cropping, intercropping, and crop rotation) can influence the structure (i.e., spatial dynamics) and function of any agrolandscape.

Landscape Heterogeneity and Pest Suppression

Past landscape ecology research studies focused primarily on describing relationships between landscape components and biodiversity (Forman and Godron 1986). Heterogeneous landscapes are correlated with positive effects on arthropod abundance and diversity, but also with pest suppression and conservation of indigenous natural enemies (Bowie et al. 1999, Grez and Prado 2000, Elliott et al. 2002, Brewer and Elliott 2004, Bianchi et al. 2006, Gardiner et al. 2009,

Scherber et al. 2010, Schellhorn et al. 2015, Zhao et al. 2015, Gurr et al. 2017). There are limited number of studies, however, that have demonstrated the effects of landscape diversity on pest suppression and subsequent crop protection (Gurr et al. 2017). Scherber et al. (2010) determined herbivore populations are more likely to be influenced by vegetational diversity (bottom-up effects) than are higher trophic levels but, overall, vegetation heterogeneity shapes multitrophic interactions. Hendrickx et al. (2007) determined that agrolandscape intensification (i.e., management practices) had more influence on beneficial species diversity than did habitat diversity. Bianchi et al. (2006) concluded that heterogeneous landscapes have an overall positive effect on natural enemy abundances, and in 45% of the studies they reviewed landscape heterogeneity resulted in greater pest suppression. However, landscape heterogeneity can have variable impacts on natural enemy assemblages (Bianchi et al. 2006, Hendrickx et al. 2007, Bertrand et al. 2016). For example, Bertrand et al. (2016) found that spider and carabid beetle communities and the potential for biological control were not influenced by surrounding landscape spatial structure in winter wheat fields. Rather, inclusion of temporal scales allowed for detection of pest suppression, and the authors stressed the need for landscape studies that include a range of temporal scales in order to account for non-spatial variability in predator assemblages in landscape studies (Bertrand et al. 2016).

While homogeneous agrolandscapes (monocultures) tend to support higher densities of herbivores and natural enemies, likely due to rapid prey/host location and utilization (Andow 1991), heterogeneous agrolandscapes (polycultures) are characterized as having higher levels of arthropod movement (Altieri and Whitcomb 1979, Andow 1991, Giles et al. 1994, Grez and Prado 2000, Schellhorn et al. 2015, Madeira et al. 2016). Andow (1991) summarized movement studies and determined that heterogeneous agrolandscapes had higher immigration and emigration rates than did homogeneous landscapes despite having lower insect abundances than monocultures. Arthropod movement appears to be critical for conservation of natural enemies and biological control in cropping systems. Early and frequent colonization of natural enemies into crop fields

within diverse agrolandscapes is more likely to lead to effective pest suppression (Altieri and Whitcomb 1979, Gurr et al. 2017). Understanding how natural enemies move within agrolandscapes would allow researchers and pest management practitioners to design heterogeneous agrolandscapes that optimize natural enemy colonization and subsequent pest suppression.

Gurr et al. (2017) summarized recent research on the effects of habitat management on natural enemy conservation and found that non-crop habitats are critical sources for natural enemy recolonization into annual crops within agrolandscapes. Typically, habitat management in conservation biological control efforts involves provisioning of pollen, nectar, and alternative prey/hosts, and refuge habitats (Landis et al. 2000). In addition, food sprays and semiochemicals can aid in attracting natural enemies to a particular crop and/or retain biological control agents that were released in a crop; but success thus far has been highly variable, particularly with generalist predators (Symondson et al. 2002). However, there are adverse effects of habitat management such as increasing intra- and interspecific competition and potentially increasing pest diversity and abundance (Gurr et al. 2017). Tscharntke et al. (2016) summarized why the availability, or lack thereof, of non-crop habitats can promote or suppress biological control services within agrolandscapes and determined that outcomes are the result of species-specific pest and natural enemy requirements. Generally, however, habitat diversity through management enhances natural enemies within agrolandscapes (Landis et al. 2000, Brewer and Elliott 2004, Gurr et al. 2017).

Natural Enemy Movement in Agrolandscapes

There are many factors that contribute to arthropod movement within agrolandscapes, especially in classical, augmentation, and conservation biological control programs (Lavandero et al. 2004). Frequent movement of arthropods between habitat patches are often responses to vegetational cues, weather conditions, prey/host resources, and intra- or interspecific interactions (i.e., predator avoidance, or competition) (Schellhorn et al. 2014). For example, vegetational cues such as herbivore-induced plant volatiles have been shown to attract parasitoids to their hosts (Vet

and Dicke 1992); and lady beetles are well known for moving to habitats when aphid prey are most abundant (Giles et al. 1994, Grez and Prado 2000, Elliott et al. 2002). Movement can be either directed or passive (i.e., random); many insects, despite their small size, are capable of long-distance, self-directed movements (Schellhorn et al. 2014). However, passive movement via wind, phoresy, and anthropogenic transport is especially common with insects (Schellhorn et al. 2014). Insects with directed movement are able to respond to resources or environmental conditions and adjust their movements accordingly; however, random movers have unbiased directionality and are not able to differentiate between source or sink habitats (Armsworth and Roughgarden 2005). Obligatory dispersal movement, a type of random movement, is observed following successful adult emergence for several natural enemy species, including green lacewings (Schellhorn et al. 2014). Adult green lacewings have adaptive dispersal flights that occur for several consecutive nights following adult emergence to allow for reproductive maturation (Duelli 1980). These insects do not respond to environmental cues or stimuli until after sexual maturation (Duelli 1980). Lady beetles, however, exhibit directed movement, and consistently track aphid populations within various habitat types (Giles et al. 1994, Grez and Prado 2000, Elliott et al. 2002).

Immigration and emigration are mediated by habitat factors and, ultimately, these movements may influence ecosystem services, including pest suppression. Dunning et al. (1992) characterized four ecosystem processes that affect arthropod movements in heterogeneous landscapes. Landscape complementation occurs when a single species requires critical resources (e.g., food, shelter, or oviposition sites) from differing habitat patches and thus depends on frequent movements between the different patches in order to survive and reproduce successfully. Bird cherry-oat aphid (*R. padi*) has a complex life cycle that requires multiple host plant species for successful development and reproduction (Dixon 1971). Landscape supplementation occurs when a single species requires critical resources from one habitat patch but can supplement other resources from either the same or different habitat patches. Source and sink habitats also may influence arthropod movement. For example, when one habitat patch, capable of attracting and

sustaining an arthropod population, has a high level of emigration events (species moving out of the patch) then the habitat is considered a source for that species in the landscape (Chisholm et al. 2014). Conversely, if a population is attracted into a habitat patch but death rates exceed birth rates then the habitat patch is considered a sink for that species. The final ecological process characterized by Dunning et al. (1992) is the neighborhood effect; that is, neighboring (or close) habitat patches influence immigration and emigration behavior in a species for a particular habitat patch. Duelli et al. (1990) documented the importance of neighboring habitat for predator colonization in a particular patch. Spiders were collected in higher abundances in wheat fields in close proximity to undisturbed patches, such as meadows; whereas carabid and rove beetles had higher colonization events among crop patches. Spillover occurs when populations from one habitat patch exceed carrying capacity and the dispersal of individuals into neighboring patches occurs. Madeira et al. (2016) documented the spillover of predatory arthropods from wheat fields into neighboring calcareous grasslands.

Quantifying Arthropod Movement

Movement of arthropods within agrolandscapes is often quantified by examining spatial distribution patterns and abundances of arthropod taxa as well as functional trait groups. This approach is a reliable method for conservation biological control programs which aim to manipulate natural enemies, and other beneficial arthropods (i.e., pollinators), for targeted ecosystem services, such as pest suppression and pollination (Lavandero et al. 2004). Lima and Zollner (1996) stressed the importance of combining behavioral ecology with landscape ecology for a more comprehensive understanding of animal dispersal behaviors and habitat selection. They argued that behavioral studies on animal movements operate on a small scale that focuses on individual movements (i.e., analyzing random walks); ecological landscape studies, on the other hand, have focused on large-scale assessments of animal movement but these studies often ignore individual behaviors (Lima and Zollner 1996). By incorporating behavioral ecology with landscape ecology, animal movement studies can provide researchers with a more realistic understanding of habitat selection.

Mark-recapture techniques have proven essential for documenting large-scale arthropod movement among habitats. Insects can be marked either internally or externally depending on ease of methodology and analysis (Hagler and Jackson 2001, Lavandero et al. 2004). Internal marks (e.g., pollen/sugar, stable carbon isotope, and molecular) are usually obtained by insects naturally in their environment. Villenave et al. (2006) collected adult green lacewings from several cropping systems and analyzed ingested pollen to determine the extent of floral feeding. The authors discovered that pollen is collected from many asynchronous flowering species distributed across several different habitat patches thus revealing spatial and temporal movement patterns for adult green lacewings (Villenave et al. 2006). External marks (e.g., dyes/dusts, branding, and radar) can either be applied directly to an insect, such as with branding, or can be obtained from the environment (e.g., dye). Ives (1981) captured lady beetles in oat and alfalfa fields and marked their elytra with field-specific enamel paint in order to document movement. It was determined lady beetles were constantly moving among different habitats and their movements were triggered by high temperatures and aphid abundances (Ives 1981).

A recent development in arthropod movement studies involves the inexpensive method of protein marking (Hagler et al. 1992, Jones et al. 2006). Insects can acquire unique protein marks by contact with a sprayed surface or by being directly sprayed. Using indirect enzyme-linked immunosorbent assay (ELISA) methods to detect chicken egg albumin in egg whites, bovine casein in milk, and soy protein in soy milk allows researchers to spray large areas of habitat, capture naturally occurring arthropods that have been marked, and document movement in the landscape. The ability to apply protein marks over a large area changes how researchers can quantify animal movements because, in the past, mark-recapture studies have underestimated insect movement because of low recapture rates (see Turchin et al. 1991). This inexpensive and highly sensitive mark and detection method allows for monitoring of insect community movement within agrolandscapes (Hagler and Miller 2002, Jones et al. 2006) and tracking natural enemy movements (Hagler and Jackson 1998, Hagler et al. 2002, Hagler and Naranjo 2004), but there are some drawbacks with

this marking-capture-detection method. First, a laboratory must be properly equipped to conduct indirect ELISA. Secondly, each mark has a different detection ability post-application; for instance, the egg protein can be contracted from a surface for several weeks following a protein spray but the soy has a lower detection ability (Jones et al. 2006). Finally, mark sensitivity can be dampened by abiotic, cultural practices (i.e., overhead irrigation), and physical contact (Hagler et al. 2014). Overall, the use of inexpensive protein marks provides researchers with a novel way of marking naturally occurring arthropods across large-scale areas in order to document animal movement.

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58

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CHAPTER III

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Diversity, relative abundance, and movement of arthropods in winter canola agricultural landscapes

Introduction

Winter wheat (*Triticum aestivum* L., Poaceae) has been successfully grown as a low-profit margin crop for over 100yr in the Southern Great Plains primarily because of scientific advancements that maximize production while minimizing pest impacts. Oklahoma is second to Kansas in winter wheat production with over 2 million hectares harvested in 2016 (USDA NASS 2017); however, annual weed management issues, damaging pest populations, and decreases in wheat prices present significant production challenges for growers throughout the region. Fortunately, comprehensive integrated pest management programs have been developed that 1) optimize insect pest suppression in wheat fields through conservation of insect natural enemies and judicious insecticide use, and 2) allow for long-term management of troublesome weeds through crop rotation and selective herbicide use (Giles et al. 2003, Giles et al. 2008, Royer et al. 2015, Royer and Giles 2017). Winter canola (*Brassica napus* L., Brassicaceae) was introduced into Oklahoma wheat production systems in 2001 (Boyles and Peeper 2008) as the only viable rotational crop for this region and canola production has increased to over 30,000 hectares in 2016 (USDA NASS 2017). Producers primarily utilize herbicide-resistant canola cultivars and are able to suppress the most important weed pests, reduce disease pressure common in continuous

73

wheat production systems, and increase subsequent wheat yields in the rotation by 10-22% (DeVuyst et al. 2009, Bushong et al. 2012).

With steady increases in yearly Oklahoma winter canola production, it remains unknown how this relatively new crop, while adding complexity to the winter agricultural landscape (agrolandscape), is affecting arthropod communities, particularly pests and their natural enemies. Pest suppression services by naturally occurring biological control agents have not been quantified in canola-wheat landscapes, but are likely influenced by agrolandscape diversity (Altieri and Whitcomb 1979, Bowie et al. 1999, Brewer and Elliott 2004, Gardiner et al. 2009). Natural enemy-pest interactions within agrolandscapes are complex because mobile natural enemies feed on or parasitize a range of herbivores, and pests are often crop specific and vary in their nutritional suitability. For example, winter wheat, a graminaceous plant, is host to several cereal aphid (Aphididae) species including *Schizaphis graminum* Rondani and *Rhopalosiphum padi* L., which have been shown to be highly suitable prey for commonly found lady beetle (Coccinellidae) species (Phoofolo et al. 2007). On the other hand, canola aphids, which are not found in cereal crops (Elliott et al. 2014) because of adaptations to cruciferous plants, are able to sequester toxic plant compounds called glucosinolates and are less suitable prey for common insect predators (Jessie et al. 2015). Specifically, the two common *Brassica*-specialist aphids (*Brevicoryne brassicae* L. and *Lipaphis erysimi* Kaltenbach) are known to have deleterious effects on green lacewing (Chrysopidae) and lady beetle development and survival (Francis et al. 2000, Chen and Liu 2001, Kazana et al. 2007, Jessie et al. 2015). However, another frequent and damaging pest in winter canola, green peach aphid (*Myzus persicae* Sulzer), does not sequester glucosinolates and is highly suitable prey for many natural enemies (Jessie et al. 2015). This dichotomy between winter canola and winter wheat in terms of prey availability and prey quality may significantly influence natural enemy populations and ultimately pest suppression services.

Because of their mobility and willingness to feed on a range of herbivores, generalist natural enemies are more likely to survive and reproduce in diverse cropping systems that have a

range of spatial and temporal resources (Giles et al. 1994, Bowie et al. 1999, Grez and Prado 2000, French et al. 2001, Brewer and Elliott 2004, Bianchi et al. 2006, Schellhorn et al. 2015). Theoretically, winter canola rotations into primarily wheat agrolandscapes should be beneficial for natural enemy communities because of availability of additional herbivore species as well as floral and extra-floral food resources (i.e., pollen, nectar). Winter canola can also act as a shelter, or refuge, habitat during periodic disturbances in wheat, including pest management decisions (i.e., insecticidal sprays). Macfadyen and Muller (2013) documented the frequency of arthropod movement among Australian canola systems and surrounding habitats (including cereal crops and uncultivated habitats), and found that generalist predators regularly moved among canola and cereal crops whereas parasitoid wasps were more likely to move from native, perennial vegetation into canola. Abundance, diversity, and movement of natural enemies and pest species in the unique canola-wheat landscapes of the Southern Plains are unknown. Indeed, because winter wheat and canola represent the only habitat with green vegetation for pests and natural enemies during winter and early spring months in the Southern Great Plains, dynamics are therefore likely to be restricted to these crops and uncultivated grassland that may serve as overwintering sites.

A few critical first steps towards identifying how canola influences arthropods in traditional winter wheat landscapes in the Southern Plains include quantifying arthropod abundance, diversity, and movement within and between available habitats. Typically, habitat functionality is described in terms of whether a habitat is a population source or sink for specific taxa. Source habitats support a higher number of birth rates than death rates and have higher emigration rates compared to immigration, whereas sink habitats have high death and low emigration rates (Schellhorn et al. 2014). Habitat functionality can vary for different taxa and so a source habitat for one natural enemy could potentially be a sink for another (Chisholm et al. 2014). If canola is functioning as a source habitat for natural enemies in winter agrolandscapes, we may expect abundance, diversity, and emigration to be higher than in other habitats. Because abundance and diversity of key natural enemies is linked to greater pest suppression in agrolandscapes,

conservation of source habitats should be prioritized in comprehensive pest management programs (Evans 2016, Tscharntke et al. 2016).

The first objective for this study is to quantify arthropod diversity and functional trait communities (i.e., herbivores, predators, and parasitoids) in winter vegetation habitats (wheat, canola, and uncultivated grassland, referred to as pasture) throughout north-central Oklahoma where canola has been incorporated into agrolandscapes. Documenting arthropod communities within canola-wheat landscapes provides necessary baseline data for development of hypotheses that predict outcomes of arthropod interactions among trophic levels within and between vegetation habitats (Rosenheim et al 1995, Evans 2016). We hypothesize that herbivore communities will differ among canola, wheat, and pasture habitats because of plant physiologies and herbivore-specific nutritional requirements. We expect minor differences in natural enemy communities because the majority of indigenous natural enemies in this region are generalists (French et al. 2001, Elliott et al. 2006) and therefore do not have specialized lower-trophic level preferences.

The second objective for this study is to quantify the relative abundance of dominant predatory arthropods and document their movement between available habitats (canola, wheat, and pasture). Knowledge of movement patterns provides evidence of how these arthropods behave in agrolandscapes and which habitats might be functioning as natural enemy sources or sinks (Schellhorn et al. 2014). Despite abundant herbivore and floral resources, we hypothesize that winter canola is a sink habitat for natural enemies, particularly predators, because of the lower nutritional quality of prey items available in canola compared to prey in wheat (Francis et al. 2000, Kazana et al. 2007, Phoofolo et al. 2007, Jessie et al. 2015) and because of regular use of broad-spectrum insecticides. If canola functions as a sink habitat for indigenous predators then immigration rates into canola will be higher than emigration out of canola and abundance within canola will be lower compared to neighboring wheat and pasture habitats. Quantifying immigration and emigration trends in canola-wheat landscapes will provide initial valuable information on how natural enemies function in this agrolandscape in the Southern Plains.

Materials and Methods

Locations and Experimental Design

Using yellow sticky traps (Pherocon AM, Trécé Incorporated, Adair, Oklahoma), arthropod movement, diversity, and relative abundance was summarized in north-central Oklahoma and south-central Kansas during late-spring months (April-May) in 2011, 2012, and 2013 as winter canola was flowering. Arthropod trapping began when approximately 50% of canola plants were in bloom. Data was collected from up to 22 locations (Fig. 3.1) where a winter canola field (C^W) interfaced with a winter wheat field (W^C). In addition, data was collected from up to 10 locations where a winter canola field (C^P) interfaced with an uncultivated area, or 'pasture', (P^C). Canola-wheat locations were as close as 0.2km and as far away as 1.6km to canola-pasture locations. The structure of the uncultivated areas varied depending on location but these sites were selected because 1) grazing cattle were not present during the sampling period, and 2) sites had not been in agricultural production for at least 3yr. Furthermore, USDA NASS CropScape (2016) categorizes the uncultivated areas used in this study as 'grass/pasture' and preliminary sampling efforts determined these areas are dominated by warm-seasons grasses. All locations were large enough to contain a sampling area of at least 100m wide at the interface between the two field types and 230m deep into each field, or habitat. Interfaces were typically ditches or roads and not separated by more than 20m. Sampling occurred in the same general geographic areas each year, but no field was used for two consecutive years because canola is rotated out of production to avoid pathogen buildup (Boyles et al. 2012).

The 22 canola-wheat and 10 canola-pasture locations were not uniformly oriented across years because we chose to include all possible field orientations. With the exception of low rainfall for Cherokee, OK in 2012, mean weather conditions (including wind speed) were similar across all locations and years (Table 3.1). Weather data was collected from Oklahoma mesonet sites closest to each location for each year (Oklahoma Mesonet 2017). Mesonet sites are located across Oklahoma in every county and record weather conditions every five minutes. Because field

locations changed each year of the study, the most appropriate mesonet site was used based on proximity to each field location.

Parallel to the interface between the fields (Fig. 3.2) three wooden posts (1.5m) were placed 40m apart along a linear transect 10m from crop or pasture edge. These border posts were within a 20x100m area that received a unique protein application to mark habitat/predators and document movement. Additionally, five parallel 3-post transects were placed in each field at 40m intervals up to 230m from the field edge. Each post had two yellow sticky traps (trap sides): one facing (F) towards the interface between fields and one directed away (A). Traps were labeled with corresponding deployment date, location, field type, location within the field, and trap side; and stapled onto designated posts. Depending on weather conditions, traps were replaced at 2-4 day intervals and a maximum of six times. Traps were collected from wooden posts by placing a sheet of wax paper over the sticky traps to prevent loss, movement, and cross contamination of protein-marked arthropod specimens (Hagler et al. 2014). All traps were stored at -17.79°C until processed in the laboratory.

Protein Mark-Capture to Document Predator Movement

Within the 20x100m border area (plot), unique protein markers (Jones et al. 2006, Sivakoff et al. 2011) were sprayed just prior to initial yearly trap deployment with a 4-nozzle handheld boom attached to a 5gal backpack sprayer at a rate of 10gal per plot. Winter canola plots were sprayed with a 5% dilution of chicken egg whites (Papetti's Froze'n Ready Frozen Liquid Angel Whites); winter wheat plots were sprayed with cows' milk (Borden whole milk); and pasture plots were sprayed with soy milk (Kikkoman Pearl Organic Soymilk; Ben E. Keith, Oklahoma City, OK). Prior to spraying (Day 0), all backpacks were designated for a single protein mark for use throughout the entire study (2011-2013). To prevent protein contamination (Hagler et al. 2014) within fields and among locations, technicians were designated to spray a single protein for each year of the study and wore disposable coveralls and rubber boots during sprays, but did not assist in experimental protocols outside of the sprayed plot.

78

After each plot was sprayed with a designated protein marker, yellow sticky traps were immediately stapled to each wooden post within the field and were then collected and replaced as previously described. In 2011, all plots were re-sprayed with the designated protein within 10d to ensure the protein mark would still be transferable and detectable. Subsequently, it was determined that the egg protein did not need to be re-sprayed due to its long lasting detectability in the field (J. R. Hagler, unpublished data); however, the milk and soy proteins were re-sprayed in plots during 2012 and 2013 on approximately Day 10.

All traps were processed in the laboratory where adult lady beetles (Coccinellidae) identified to species, and green lacewings (Chrysopidae) were counted, removed individually with disposable toothpicks, and placed in 5ml centrifuge tubes color-coded by insect family. The centrifuge tubes were then stored at -17.79°C prior to shipment to the USDA-ARS in Maricopa, Arizona for protein detection analysis using indirect ELISA procedures developed by Jones et al. (2006) and Sivakoff et al. (2011). For a video detailing the ELISA protocol see Hagler and Machtley (2016). To prevent Type I errors, we used a conservative threshold for detecting positive protein marks on green lacewings and lady beetles (Sivakoff et al. 2011).

Mean green lacewing, lady beetle, *Hippodamia convergens* Guérin-Méneville, and *Coccinella septempunctata* L. abundances were compared among field types (C^W, W^C, C^P, and P^C) using generalized linear mixed models with SAS software, Version 9.4 of the SAS system for Microsoft Windows. Copyright © 2013 SAS Institute Inc. SAS and all other SAS Institute Inc. product or service names are registered trademarks or trademarks of SAS Institute Inc., Cary, NC, USA. A generalized linear mixed model was used to compare the proportion of positive protein marks between field types. Proportion marked with egg, milk, or soy protein were transformed ($arcsin(\sqrt{Y})$) and analyzed with a generalized linear mixed model to compare field*trap side (F or A) to determine emigration and/or immigration movement. For all analyses, year and location were random effects to account for variability in sampling effort across years. Degrees of freedom were

adjusted with the Kenward-Rodger method. When significant differences were detected, using a significance level of α=0.05, least squares means were compared.

<u>Arthropod Diversity and Relative Abundance</u>

A subset of the data was used for comprehensive arthropod identification and quantification. Traps in the subset of data were from 15 canola-wheat locations and 7 canola-pasture locations collected on the three middle sample days (2nd, 3rd, and 4th) and from transects at three distances (30, 110, and 190m) from field interface. All arthropods were identified to family and some arthropods were identified to subfamily or species, with the exception of spiders being identified to order. In addition to the previously recorded Chrysopidae and Coccinellidae, other taxa summarized included: brown lacewings (Hemerobiidae); braconid wasps (Braconidae); ichneumon wasps (Ichneumonidae); ground beetles (Carabidae); syrphid flies (Syrphidae); lygus bugs (Lygaeidae) including false chinch bugs (*Nysius ericae* Schilling) and big-eyed bugs (*Geocoris punctipes* Say); damsel bugs (Nabidae); minute pirate bugs (Anthocoridae); leafhoppers (Cicadellidae); psyllids (Psyllidae); rove beetles (Staphylinidae); soldier beetles (Cantharidae); blister beetles (Meloidae); leaf beetles (Chrysomelidae) including flea beetles (Alticinae) and cucumber beetles (*Diabrotica* spp.); scarab beetles (Scarabaeidae); weevils (Curculionidae); click beetles (Elateridae); spiders (Araneae); and aphids (Aphididae). Hyperparasitoid wasps, *Alloxysta* spp. (Figitidae), were also quantified. Additionally, small aphid parasitoid species, *Lysiphlebus testaceipes* Cresson and *Diaeretiella rapae* M'intosh, were identified for five canola-wheat locations and one canola-pasture location in 2013 on Day 2, 3, and 4.

Shannon diversity indices ($|n/N*\ln(n/N)|$) were used to calculate taxa diversity in each field, where n is the total of a single species in each field type and N is the total number of all taxa trapped. Indices and mean arthropod abundances were compared among field types (C^W, W^C, C^P, and P^C) using generalized linear mixed models with year and location as random effects and degrees of freedom adjusted with the Kenward-Rodger method. Least squares means comparisons were conducted when significant differences (α=0.05) were detected.

Results

Arthropod Diversity and Relative Abundance

Diversity Shannon diversity indices for arthropods caught on sticky traps were compared among the four field types (C^W, W^C, C^P, and P^C) and significant differences were detected ($F_{3,120.4}=3.05$, p=0.031). Despite an overall lower relative abundance of arthropods caught in pasture (P^C), these fields had the greatest taxa diversity (Table 3.2) compared to wheat ($t_{124.4}=2.08$, p=0.040) and canola fields (C^W: $t_{124.4}=-2.97$, p=0.004; C^P: $t_{115.3}=-2.09$, p=0.039). Wheat fields (W^C) had the second greatest taxa diversity but was not significantly different compared to interfacing canola fields (C^W; $t_{115.3}=-1.18$, p=0.239) and from canola that interfaced pasture fields (C^P; $t_{124.4}=-0.22$, p=0.826). Diversity did not differ for the two types of canola fields ($t_{124.4}=0.67$, p=0.505), however, C^P fields had a slightly greater taxa diversity than C^W fields.

Herbivores Eleven herbivore taxa were identified on sticky traps representing nine insect families (Table 3.3). Herbivores were higher in mean abundance in canola fields, regardless of interfacing field type (pasture or wheat). The most abundant herbivores found on sticky traps were leafhoppers, false chinch bugs, aphids, psyllids, and flea beetles, respectively (Table 3.4). Leafhoppers were the highest in abundance in C^W fields with similar abundances in C^P fields (p=0.100), however, abundances in C^W fields were greater than in W^C and P^C fields (p≤0.001). False chinch bugs were most abundant in C^P fields, and while abundances were not significantly higher than in P^C fields (p=0.152), there was significant difference in abundances in C^P fields compared to W^C and C^W fields (p≤0.046). False chinch bug abundance in the other field types did not significantly differ (p≥0.506). Surprisingly, despite little-to-no green vegetation, P^C fields had significantly higher trap catches of aphids (p≤0.005) and psyllids (p≤0.006) compared to other field types. Aphids were least abundant in C^W fields; however, there was no significant difference compared to W^C and C^P fields (p≥0.598). Psyllid numbers were similar in W^C, C^W, and C^P fields (p≥0.956). Flea beetle abundances were similar among all field types (p≥0.185); however, flea beetle abundance was highest in P^C fields and lowest in C^W fields.

Predators Eighteen predator taxa were identified on sticky traps representing 14 arthropod families (Table 3.3). Predators were higher in abundance in W^C fields and lower in abundance in both types of canola fields. The most abundant predators trapped were green lacewings, syrphid flies, rove beetles, lady beetles, and minute pirate bugs, respectively (Tables 3.3 and 3.4). Green lacewings and lady beetles are discussed in the following section. Syrphid flies were captured most in W^C fields, followed by P^C fields but there was no significant abundance differences between these field types (p=0.455). Syrphid fly abundance in both types of canola fields was similar to abundances in PC fields (p≥0.112). Rove beetles were most abundant in P^C fields (p≤0.001); and both types of canola fields and W^C fields had similar abundances (p≥0.506). Minute pirate bug abundance was similar in all field types (p≥0.083).

Parasitoids and Hyperparasitoids Parasitoids from two insect families (Braconidae and Ichneumonidae) and a hyperparasitoid from one family (Figitidae) were most abundant in W^C fields (p≤0.0001; Table 3.3, Table 3.4). Ichneumonid wasps were most abundant in C^W fields and least abundant in W^C fields (p=0.039), however, there were no differences among C^W, C^P, and P^C fields (p≥0.131) and no differences among C^P, P^C, and W^C fields (p≥0.540). Braconid aphid parasitoids were most abundant in W^C fields (p≤0.001), however, abundances were not different among C^W, P^C, and C^P fields (p≥0.431). Species identification of braconid wasps were determined in 2013, and *L. testaceipes* was the most common species (99%) identified. *Alloxysta* hyperparasitoids were significantly more abundant in W^C fields (p≤0.006); abundances were similar among the other field types (p≥0.267).

Protein Marking and Abundance of Coccinellidae and Chrysopidae

Coccinellidae A total of 8,341 lady beetles (Table 3.5) were trapped during the 3yr study and *H. convergens* was the predominant species (52%), followed by *C. septempunctata* (46%), *Olla v-nigrum* Mulsant (2%), *Harmonia axyridis* Pallas (0.26%), and *Coleomegilla maculata* DeGeer (0.12%). Total lady beetle (all species combined) abundance was similar across field types ($F_{3,286.2}$=2.58, p=0.054); however, W^C fields had the highest mean trap captures of lady beetles

compared with C^W which had the lowest (p=0.010). Separating data for primary lady beetle species revealed interesting trends. *Hippodamia convergens* (Fig. 3.3B) abundance varied among field types ($F_{3,285.3}$=5.91, p=0.001), and were most abundant in W^C fields compared to C^W, and P^C fields (p≤0.004). Abundance in W^C and C^P fields were similar (p=0.056), and abundance in C^P, C^W, and P^C fields were similar (p≥0.075). Surprisingly, *C. septempunctata* (Fig. 3.3C) abundances were not significantly different among field types ($F_{3,285.7}$=2.49, p=0.060), however, P^C fields had higher *C. septempunctata* abundance compared to C^W fields (p=0.048), and abundance was greater in W^C fields compared to C^W fields (p=0.0378). *Coccinella septempunctata* abundances were in similar in P^C and W^C fields (p=0.631), and C^P and C^W fields (p=0.965).

Total lady beetle abundance for each trap side (Fig. 3.4) was significantly different among field types ($F_{7,578.3}$=2.18, p=0.035). In canola-wheat interfaces (Fig. 3.4A), W^C fields had the greatest lady beetle abundance (all species combined), however, abundances were similar for both facing (F) and away (A) trap sides (p=0.218). Abundances differed between W^C-A traps and both traps sides in C^W fields (p≤0.003), but W^C-F traps were similar to C^W-F and C^W-A traps (p≥0.063). Lady beetle abundance in C^W fields was not significantly different between the trap sides (p=0.959). In canola-pasture fields (Fig. 3.4B) there were no significant differences between trap side for either field type (p≥0.341).

Hippodamia convergens abundance differed significantly by field type and trap side ($F_{7,577.3}$=4.36, p≤0.0001). Abundances of *H. convergens* in canola-wheat interfaces (Fig. 3.5A) were significantly higher on W^C, regardless of trap side, compared to C^W-A traps (p≤0.029) and C^W-F traps (p≤0.043). Abundance did not differ between trap sides in C^W fields (p=0.878) or W^C fields (p=0.262). In canola-pasture fields (Fig. 3.5B), there were no significant differences in *H. convergens* abundance between trap side for either field (p≥0.070).

Coccinella septempunctata trap side abundances were significantly different among field types ($F_{7,579.2}$=2.14, p=0.038; Fig. 3.6). In canola-wheat landscapes (Fig. 3.6A), *C. septempunctata* abundances were the highest on W^C-A traps compared to both traps sides in C^W fields (p≤0.011),

but abundance was similar to W^C-F traps (p=0.258). Abundance on W^C-F traps was similar to both trap sides in C^W fields (p≥0.152). In canola-pasture interfaces, *C. septempunctata* abundances were similar in both CP and PC fields, regardless of trap side (p≥0.069).

Protein marks were compared for all lady beetle species combined because only three of five species had positive protein marks (Fig. 3.7). There were 8,124 lady beetles analyzed for ELISA proteins, of which 185 beetles had positive egg protein marks (2.28%), 128 had positive milk marks (1.58%), and 40 had positive soy marks (0.49%). Most positive protein marks detected were reflective of specific proteins sprayed at designated interfaces; however, a smaller number of positive milk marks collected at canola-pasture interfaces and positive soy marks at canola-wheat interfaces reflect expected movement within agrolandscapes where different locations were within 1.63km (Fig. 3.8, 3.11). The proportion of lady beetles marked with egg protein were not significantly different among field types or trap side ($F_{7,592}$=1.15, p=0.327; Fig. 3.8); those trapped in canola-wheat interfaces (Fig. 3.8A) had more egg marks than those from canola-pasture interfaces (Fig. 3.8B). The proportion of lady beetles with milk marks were similar among field types and trap sides ($F_{7,592}$=1.67, p=0.115). In canola-wheat interfaces, more lady beetles with milk marks were trapped in W^C, regardless of trap side (p=0.698), compared to those on C^W-F traps (p≤0.035), however milk marks were similar to those on C^W-A traps (p≥0.228). In canola-pasture fields, lady beetles with milk marks (reflecting movement from nearby canola-wheat interfaces) were similar among C^P and P^C fields, regardless of trap side (p≥0.472). While the proportion of lady beetles trapped with soy marks were significantly different among field types and trap sides ($F_{7,592}$=2.21, p=0.032), there were no differences in canola-pasture fields (p≥0.162), aside from between P^C-F and P^C-A traps (p=0.038). Interestingly, and again reflective of lady beetle movement from nearby canola-pasture interfaces, soy marks were detected on lady beetles trapped in canola-wheat interfaces, however there were no significant differences between crops and trap sides (p≥0.209).

Chrysopidae A total of 35,325 green lacewings were trapped during the study; abundances (Fig. 3.9) were significantly different among the four field types ($F_{3,296}=25.63$, p≤0.0001). Green lacewing abundance was greatest in W^C fields (p≤0.0001) and was lowest in P^C (p≤0.020); however, abundance was similar between the two types of canola fields (p=0.821). Trap side abundance (Fig. 3.10) was significantly different for green lacewings collected in the four field types ($F_{7,592}=13.51$, p≤0.0001). In canola-wheat interfaces (Fig. 3.10A), green lacewing abundance was greatest in W^C regardless of trap side (p≤0.0001); however abundance was similar for both trap sides in C^W fields (p=0.368). In canola-pasture fields (Fig. 3.10B), abundances were similar on both trap sides in C^P fields (p=0.207); however, abundance on C^P-F were greater than on P^C-F and P^C-A traps (p≤0.028). Green lacewing abundance was similar on C^P-A, P^C-F, and P^C-A traps (p≥0.160).

Of the 34,636 green lacewings analyzed for ELISA proteins, 762 had egg protein marks (2.20%), 412 had milk protein marks (1.19%), and 95 had soy protein marks (0.27%). As with lady beetles, smaller numbers of milk and soy protein marks collected at canola-pasture and canola-wheat interfaces, respectively, reflect overall green lacewing movement within agrolandscapes. The proportion of green lacewings with egg marks was significantly different across field types and trap sides ($F_{7,592}=4.04$, p=0.0002). In canola-wheat interfaces (Fig. 3.11A), there were no differences in the proportion with egg marks (p≥0.213); however, in canola-pasture fields (Fig. 3.11B) there were significantly higher egg marks on both trap sides in C^P fields compared to egg marks on P^C-A (p≤0.004) and P^C-F traps (p≤0.001). Proportion of green lacewings with egg marks trapped in P^C did not differ between trap side (p=0.578). Proportion of green lacewings marked with milk protein were significantly different across field types and trap sides ($F_{7,592}=6.11$, p≤0.0001); W^C traps had the greatest proportion of marked green lacewings compared to C^W traps (p≤0.022). Proportion of green lacewings marked with milk protein were similar between C^W-F and -A traps (p=0.863). In canola-pasture fields, some green lacewings did test positive for milk protein (reflective of overall agrolandscape movement); however, there proportion with milk marks

were similar on both trap sides in C^P and P^C fields (p≥0.122). Proportion of green lacewings marked with soy protein was significantly different across field types and trap sides ($F_{7,592}$=4.69, p≤0.0001); P^C-A traps had the greatest proportion of soy marks in canola-pasture fields (p≤0.001), but proportions were not significantly different among P^C-F, C^P-F, and C^P-A traps (p≥0.503). There were green lacewings marked with soy protein collected in canola-wheat interfaces, and the greatest proportion were collected on W^C-F traps, but there were no significant differences of proportion marked with soy protein on both trap sides in C^W and W^C fields (p≥0.190).

Discussion

Southern Great Plains winter landscapes have recently been diversified with the introduction of winter canola as a rotational crop in traditional continuous wheat production systems. It is important to understand how arthropods are responding to this new crop in Oklahoma agrolandscapes. My study was aimed at characterizing arthropod communities utilizing these winter habitats, specifically canola, wheat, and uncultivated pastureland, during mid-to-late spring months.

Utilization of yellow sticky traps did not appear to influence arthropod trap activities, and this was expected because sampling efforts were concentrated to small areas of each field. Furthermore, many arthropods have limited eyesight which may have impeded trap detection/attractiveness. For example, Nakamuta (1984) determined *C. septempunctata* visually cue in on prey at 7mm distance during light phases, and required 2mm distance during dark phases to detect prey. Therefore, flying lady beetles would only be able to detect the yellow traps within close proximity. In addition, if there was a sampling bias with the traps then we would not have been able to document the significant differences in arthropod abundances among field types. Attractive traps would have resulted in similar trap abundances regardless of field type. Furthermore, highly mobile adult arthropods were sampled more frequently than apterous arthropods, such as spiders. However, we consider our robust sampling effort successfully captured the diverse arthropod communities present within Oklahoma early-spring agrolandscapes. We

suspect additional sampling efforts (i.e., pit-fall traps, sweep net samples, and/or D-vac samples) would have documented the same diversity in each field type, however, taxa abundances would have differed.

My first objective was to describe arthropod diversity and relative functional trait group abundances. Sticky trap capture data was used to describe arthropod activity, and more specifically individuals that fly or walk into traps. Mid-to-late spring in the Southern Plains represents an important time where arthropods are initiating movement among habitats and exploiting resources required for reproduction. Trap data therefore reflects the activity of most of the above ground species that utilize early-spring vegetation habitats; this study focused primarily on winter crops and pastures. As expected, pasture habitats were the most taxa rich; however, this richness did not equate to abundance. Gurr et al. (2017) stated that non-crop habitats often support large numbers of arthropods; however, pasture habitats had the lowest mean trap abundance for the entire study. Alhmedi et al. (2007) documented higher arthropod abundances in nettle strips (*Urtica dioica* L.) along field margins of wheat and canola compared to within cropping systems; however, their study took place in a single location for one season which could have under-estimated geographic and temporal variations in arthropod communities. Although the structure of pasture habitats in the current study was inconsistent across locations and years, it was mostly devoid of green vegetation during sampling (C. N. Jessie, unpublished data). This habitat may be serving as an over-wintering refuge or shelter habitat for many different taxa as suggested by Gurr et al. (2017). Further studies should focus on this seemingly important habitat in winter agrolandscapes as a means of harboring pests and natural enemies during winter months.

Functional trait groups revealed an interesting dynamic in that both types of canola fields (canola interfaced with wheat and canola interfaced with pasture) had relatively high herbivore abundances whereas wheat fields had the lowest; however, predators and parasitoids were more abundant in wheat fields. The sampling methodology was highly biased toward alate (winged) insects and therefore we might expect distributions of apterous (wingless) herbivores and natural

enemies to differ slightly. Nonetheless, the high abundance of herbivores in canola and the lack of significant predators and parasitoids suggest that natural enemies may not be synchronized with herbivores and therefore are less likely to exert top-down control commonly observed in long-term wheat habitats (Giles et al. 2003, Brewer and Elliott 2004).

Herbivores

The most abundant herbivores collected in our study were leafhoppers, and they were most abundant in canola fields. While leafhoppers are vectors for many plant pathogens, they are not considered significant pests in the Southern Great Plains (Boyles et al. 2012). However, mean field abundance for leafhoppers was higher than the next abundant herbivore which implies leafhoppers may be an under-represented concern for Oklahoma canola producers. More research is needed to determine how leafhopper abundance and damage potential are possibly influencing canola production systems. On the other hand, false chinch bugs are a known pest in Oklahoma winter canola and can occasionally reach economic thresholds; however, outbreaks usually occur during mild and dry springs (such as 2011) when newly budding plants are infested (Boyles et al. 2012).

Aphids, and to a lesser extent flea beetles and psyllids, were significantly more abundant in pasture fields compared to canola and wheat fields; this is surprising because sampling efforts in pasture fields during all three years of the study revealed very little green vegetation and no flowering plants (C. N. Jessie, unpublished data). These herbivores were primarily alates and could be ephemeral visitors in pasture fields; it is likely that aphids, dispersed primarily by wind, were transient founder alates dispersing to pasture habitats (Dixon 1971). Although we did not identify aphids to species, we suspect the majority were either cereal or cruciferous species known to infest wheat and canola fields in this region given their consistent prevalence in these systems (Giles et al. 2000, French et al. 2001, Chown and Giles 2006, Elliott et al. 2014).

Natural Enemies

As expected, braconid wasps were significantly more abundant in wheat fields compared to other field types because of the dominant parasitoid species, *L. testaceipes*, which is a key cereal

aphid parasitoid in the Southern Great Plains (Archer et al. 1974, Arnold 1981, Kring and Gilstrap 1983, Giles et al. 2003, Brewer and Elliott 2004, Jones et al. 2005, Elliott et al. 2014). Elliott et al. (2014) documented aphid-parasitoid interactions in wheat and canola fields throughout Oklahoma using D-vac sampling methods and plant counts, respectively, to collect aphids and quantify apparent parasitism rates. The authors found that *L. testaceipes* emerged from cereal aphids only and *D. rapae* was the predominant parasitoid species to emerge from canola aphids (Elliott et al. 2014). In the present study, *L. testaceipes* was the most abundant arthropod collected in all field types, which suggests that, despite being a cereal aphid specialist, this species actively moves throughout the agrolandscape in high numbers (Fig. 3.12).

Fourteen different predator taxa were collected during our study, which far exceeds other predator sampling studies in wheat and/or canola fields (Parajulee et al. 1997, Parajulee and Slosser 1999, French et al. 2001, Chown and Giles 2006, Elliott et al 2006, Safarzoda et al. 2014). While lady beetles are well-studied natural enemies in winter wheat (Fenton and Fisher 1940, Kring et al. 1985, Rice and Wilde 1988, Michels et al. 2001), green lacewings were the most common predator trapped in canola and wheat fields and may therefore play a greater role in biological control than previously thought. In the smaller subset of data where all arthropods were counted, syrphid flies and rove beetles were most abundant in pasture fields and, surprisingly, least abundant in canola fields. Bowie et al. (1999) documented adult syrphid fly movements into canola by examining digested pollen content and determined syrphid flies that had fed on canola pollen were more likely to move into wheat but remain within 4m of the field edge rather than move farther into the wheat field. My study could have under-estimated adult syrphid fly abundances given our closest transect of sticky traps were 30m from the crop interface, but given the significant floral resources in canola, low captures were unexpected.

Lady beetle populations fluctuate yearly and, typically, large populations occur every 5-7yr (Elliott and Kieckhefer 1990); annual fluctuations were evident in the present study with a greater number of lady beetles collected in 2011 (n=6,096) compared to 2012 and 2013 (n=1,449

and n=796, respectively). *Hippodamia convergens* was, unsurprisingly, the predominant coccinellid species captured. Like most aphidophagous lady beetles, this native species has coevolved with aphids (Hemptinne and Dixon 1990, 1991, Michels et al. 2001, Phoofolo et al. 2008) and many cereal aphids are considered essential prey for successful *H. convergens* survival and reproduction (Phoofolo et al. 2007). *Coccinella septempunctata* was the second most abundant lady beetle species trapped in our study, and unlike *H. convergens*, was more abundant in pasture fields. Hesler and Peterson (2008) monitored lady beetles in the Northern Great Plains and documented *C. septempunctata* feeding on aphids in non-crop habitats, which is interesting considering this generalist species was released in the US as a biological control agent in agricultural productions systems (Cartwright et al. 1979). Indeed, *C. septempunctata* has been observed aggregating to high aphid populations in agricultural fields (Giles et al. 1994, Elliott et al. 2002), but may have moved to/within pastures for refuge or mating (Lima and Zollner 1996).

Protein Mark-Capture of Lady Beetles and Green Lacewings

Based on positive protein marks, lady beetles moved into winter canola but did not appear to remain in the crop. In fact, there were no significant differences in positive egg marks in any of the field types, suggesting lady beetles in Oklahoma agrolandscapes frequently move among available habitat patches. Describing lady beetle movements, Evans (2003) determined that appetitive flights are common when prey, particularly aphids, are abundant and hectic trivial flights occur when prey are scarce. However, lady beetles are known to consume non-prey resources such as pollen and nectar during prey scarcity (Hagen 1962, Hemptinne and Dixon 1990, Evans 2003, De Clercq et al. 2005) and this could explain why lady beetles frequented canola fields without remaining in the habitat. Furthermore, Ives (1981) documented frequent lady beetle movements in agrolandscapes dominated with grasses and legumes. Clearly, lady beetles are frequently moving among different habitats during mid-to-late spring in the Southern Plains and further studies are needed to describe behaviors that drive these movements (Lima and Zollner 1996).

My study revealed that green lacewings were most abundant in wheat fields, and, similar to lady beetles, readily moved into canola acquiring egg protein marks before moving farther into canola or into adjacent wheat fields. Green lacewings were seldom collected in pasture fields and furthermore protein marks in canola-pasture landscapes showed very little movement out of canola. We expected high numbers of green lacewings in winter canola because of the abundant floral resources and herbivore prey present; however, like other common natural enemies these species may be well adapted to the highly suitable prey resources found in wheat fields. Further research is needed to determine green lacewing dynamics in canola and wheat, especially since studies have under-estimated the pest suppression services provided by these organisms (Jones 2001).

Potential Influence of Canola on Arthropods in Southern Plains Agrolandscapes

Dunning et al. (1992) describe four landscape processes that serve to explain arthropod movement and predict habitat functionality. The first process is landscape complementation in which a single species must move among different habitats for spatially separate resources. The species will be in greater abundance when the required habitat patches are closer together. This may explain our observations of *L. testaceipes* activity; while cereal aphids are highly preferred hosts (Elliott et al. 2014) we documented *L. testaceipes* presence in canola fields up to 190m from the nearest wheat interface (Fig. 3.12). Macfadyen and Muller (2013) documented a similar phenomenon in Australia with multiple braconid wasp species moving from native perennial vegetation into canola fields but the wasps were not observed emerging from parasitized canola herbivores. The authors suggest that braconid wasps visit canola for its floral resources and use native vegetation habitats for shelter and host habitat.

The second type of landscape process characterized by Dunning et al. (1992) is landscape supplementation, which occurs when a single species requires critical resources from one habitat patch but can supplement other resources from either the same or different habitat patches. Populations are more abundant when the relevant habitat patches are closer together than spatially farther apart, similar to landscape complementation (Dunning et al. 1992). This process could

describe green lacewing abundance and movement within our study; in canola-wheat landscapes, abundances and movement were relatively high in both crops but there were significantly more green lacewings in wheat fields. However, when we compared canola-wheat abundances with canola-pasture there was a drastic difference; populations were higher in canola-wheat landscapes compared to canola-pasture likely due to the abundant floral resources in canola and suitable prey in wheat.

The third process Dunning et al. (1992) describe is the dynamic between source and sink habitats. While this process is extremely hard to document without quantifying birth and death rates, we expected winter canola to be a potential sink habitat because of lower nutritional prey (Francis et al. 2000, Chen and Liu 2001, Kazana et al. 2007, Jessie et al. 2015) and frequent insecticide use. However, we can categorize winter canola as a potential source or sink habitat based on predator abundance and movement. If canola were a source habitat for green lacewings or lady beetles, we would expect it to harbor higher abundances compared to other habitats and have higher emigration rates compared to surrounding habitats. However, we documented that wheat (and pasture for *C. septempunctata*) had the highest predator abundance, furthermore, protein marks revealed lady beetles and green lacewings were frequently visiting canola fields and emigrating at equal rates into surrounding habitats. We hypothesize that these predators were visiting canola fields for the abundant floral resources and then leaving the habitat for wheat. Lady beetles are known for ovipositing near young aphid colonies (Hemptinne and Dixon 1990), and therefore these predators are likely returning to wheat to oviposit near preferred and essential prey. Adult predators visiting canola are at a much higher risk of mortality and sub-lethal consequences incurred by both reduced prey quality (and toxicity) and frequent insecticidal sprays, resulting in an overall sink effect. Lower captures in canola compared to wheat provide some evidence, but future research should focus on describing population dynamics in winter canola and wheat to clarify source-sink relationships for common predatory insects.

The final ecological process influencing population abundances and movement within landscapes are neighborhood effects, occurring when neighboring (or nearby) habitat patches influence movement of a species in a particular habitat patch (Dunning et al. 1992). Spillover occurs when populations from one habitat patch exceed carrying capacity and the dispersal of individuals into neighboring patches occurs. Madeira et al. (2016) documented spillover effects of generalist predators from wheat fields into neighboring calcareous fields; for example, spider abundances were highest at 10m within a wheat field but decreased gradually into neighboring calcareous fields. In the present study, lady beetle abundances showed a possible gradual spillover effect from wheat into canola fields, because abundances were significantly higher in wheat on the away (A) traps indicating lady beetles are moving from wheat toward canola. However, in canola-pasture fields there were no significant differences in abundances on either trap side in either field type. Green lacewings have a similar spillover effect because abundances are higher in canola-wheat interfaces compared to abundances in canola-pasture, and abundances are significantly higher in wheat fields compared to the other habitats; therefore, green lacewings are likely spilling over from wheat fields into canola

Documenting natural enemy communities within canola-wheat landscapes provides necessary baseline data for development of hypotheses that predict outcomes of arthropod interactions among trophic levels within and between vegetation habitats (Rosenheim et al 1995, Evans 2016). Overall, there is a strong indication of top-down herbivore suppression occurring in Oklahoma winter agrolandscapes, particularly in wheat fields. Given time and opportunities for adaptation to this relatively new winter vegetation habitat, pest suppression commonly observed in wheat fields may spillover into canola fields (Nassab et al. 2013, Royer et al. 2015, Lopes et al. 2016). Future research should focus on quantifying predator and parasitoid biological control potential within the entire agrolandscape and defining how canola's abundant non-prey resources (pollen and nectar) influence natural enemy-pest dynamics.

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Tables and Figures
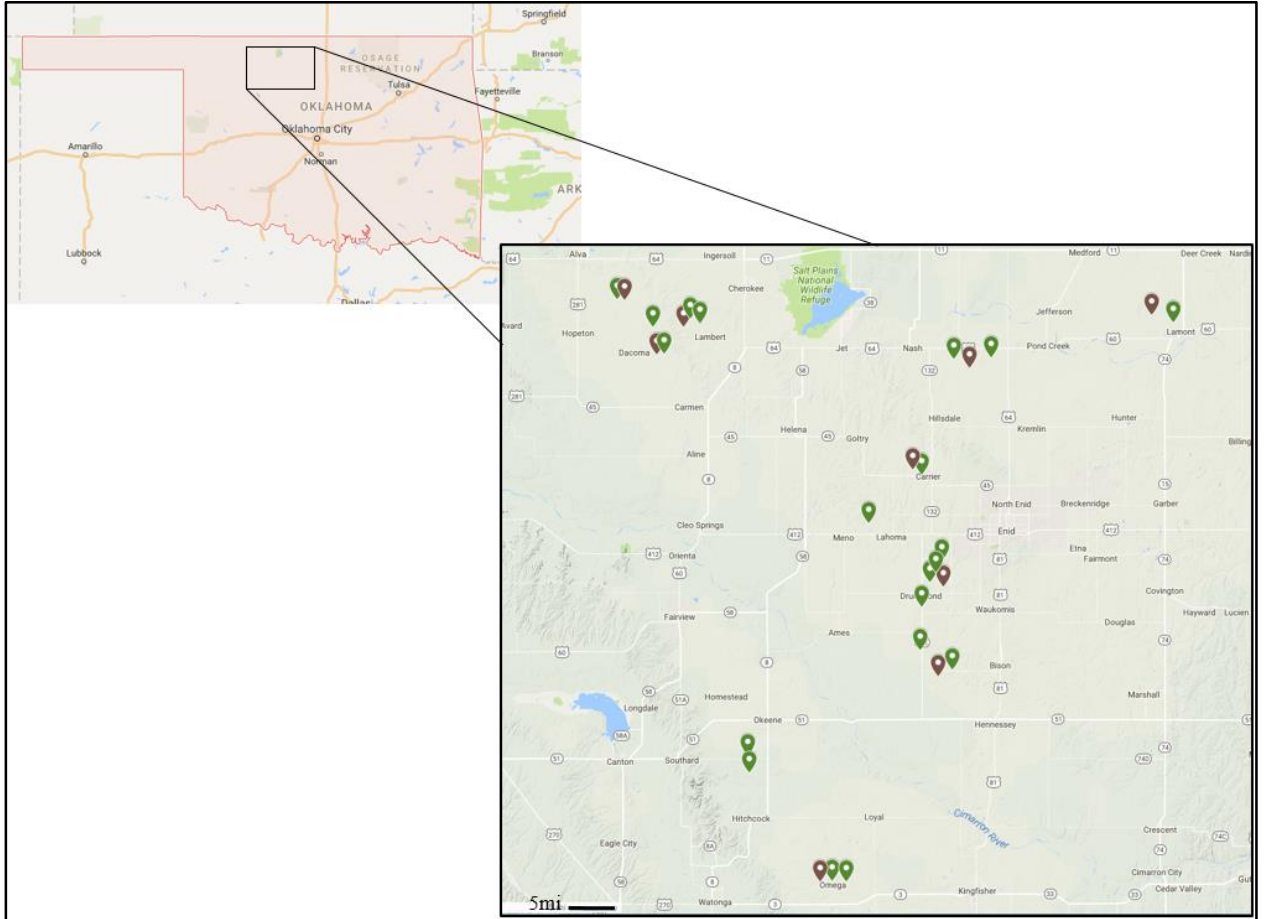
Figure 3.1. Field locations of canola-wheat (green, n=22) and canola-pasture (gray, n=10) in north-central Oklahoma in 2011, 2012, and 2013.

Table 3.1. Average temperature and wind condtions (±SEM) and total rainfall (in) recorded by Oklahoma mesonet stations closest to each location for 2011, 2012, and 2013.

Abiotic Conditions	2011			2012				2013		
	Cherokee	Fairview	Kingfisher	Cherokee	Fairview	Lahoma	Medford	Alva	Fairview	Lahoma
Avg. Temp. (°F)	59.858 ± 1.386	61.052 ± 1.410	62.751 ± 1.582	59.816 ± 1.171	60.142 ± 1.146	59.240 ± 1.102	59.509 ± 1.126	54.896 ± 1.961	55.771 ± 1.871	54.437 ± 1.804
Max. Temp. (°F)	73.475 ± 1.931	74.764 ± 2.029	76.138 ± 2.011	70.858 ± 1.404	71.153 ± 1.532	69.921 ± 1.341	70.165 ± 1.265	67.194 ± 2.432	67.818 ± 2.328	66.671 ± 2.314
Min. Temp. (°F)	43.557 ± 1.374	45.401 ± 1.212	46.572 ± 1.471	47.890 ± 1.853	48.915 ± 1.538	48.499 ± 1.491	47.946 ± 1.670	42.975 ± 2.028	44.757 ± 1.889	42.774 ± 1.837
Avg. Wind (mph)	10.837 ± 0.997	10.980 ± 0.830	11.396 ± 0.815	9.122 ± 0.931	9.181 ± 0.750	10.295 ± 0.847	9.724 ± 0.914	13.039 ± 0.885	11.271 ± 0.746	12.591 ± 0.803
Max. Wind (mph)	20.607 ± 1.430	20.572 ± 1.106	22.093 ± 1.274	18.089 ± 1.665	18.969 ± 1.622	20.045 ± 1.591	18.651 ± 1.530	23.705 ± 1.459	20.297 ± 1.198	22.204 ± 1.143
Min. Wind (mph)	2.345 ± 0.430	2.558 ± 0.475	1.870 ± 0.378	1.890 ± 0.389	1.699 ± 0.382	2.633 ± 0.484	2.518 ± 0.392	3.778 ± 0.536	2.872 ± 0.476	3.533 ± 0.604
Max Wind Gust (mph)	57.440 ± 1.766	57.580 ± 1.624	53.190 ± 1.648	53.550 ± 2.426	49.320 ± 2.313	46.840 ± 2.233	50.490 ± 2.374	51.070 ± 1.925	47.070 ± 1.608	42.810 ± 1.488
Rain (in)	0.780	1.160	1.330	0.070	3.000	1.920	1.870	2.430	2.430	1.640
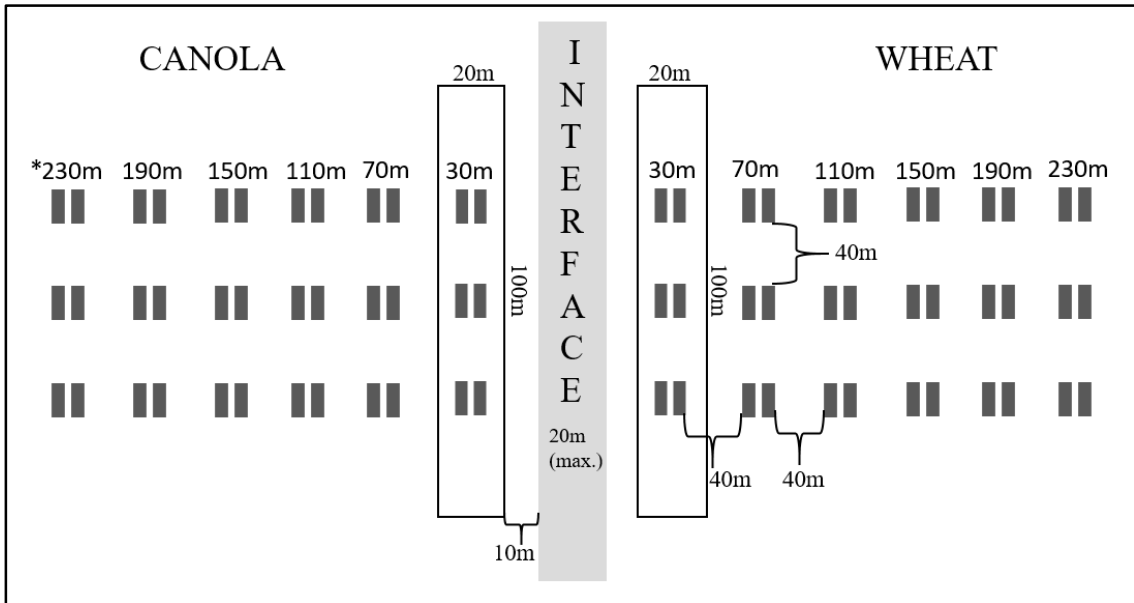
Figure 3.2. Experimental design for canola-wheat locations (n=22). The interface (grey rectangle) is the area between the two crops and the outlined rectangle is where protein applications were applied. * signifies trap distance from the interface. Each ‖ represents two yellow sticky traps, one facing the interface (trap side F) and one directed away (trap side A). Canola-pasture locations (n=10) had identical design.

Table 3.2. Mean Shannon diversity index and abundance per field (± SEM) for four field types based on number of taxa (family, subfamily, or species) trapped on yellow sticky traps in north-central Oklahoma during winter canola flowering season in 2011, 2012, and 2013.

Field	Diversity Index	Abundance/field
C^{W*}	1.433 ± 0.072b**	1343.200 ± 181.550
W^C	1.534 ± 0.076b	1405.090 ± 128.397
C^P	1.539 ± 0.088b	1108.620 ± 195.644
P^C	1.799 ± 0.071a	946.000 ± 137.608

* C^W refers to traps in canola that interfaced wheat. W^C are traps in wheat interfaced with canola. C^P are traps in canola interfaced with pasture. P^C are traps in pasture interfaced with canola.

** Different letters next to diversity indices indicate significant differences among the field types. $F_{3,120.4}$=3.05, p=0.312, α=0.05.

Table 3.3. Mean abundance per field (±SEM) for arthropods collected on yellow sticky traps in north-central Oklahoma during winter canola flowering in 2011, 2012, and 2013. Arthropods are separated into functional trait groups and the most abundant taxa are bolded.

Herbivore		C^W*		W^C		C^P		P^C		Grand Total	
Aphididae		**91.298 ±**	**14.099**	**129.622 ±**	**15.725**	**115.619 ±**	**23.952**	**221.238 ±**	**39.283**	**128.902 ±**	**10.805**
Chrysomelidae	**Alticinae**	**5.089 ±**	**1.091**	**6.667 ±**	**1.549**	**7.762 ±**	**2.435**	**10.381 ±**	**2.842**	**6.894 ±**	**0.881**
	Diabrotica spp.	0.422 ±	0.175	0.933 ±	0.209	0.238 ±	0.168	0.286 ±	0.140	0.545 ±	0.102
Cicadellidae		**511.022 ±**	**130.121**	**130.222 ±**	**22.908**	**306.524 ±**	**101.591**	**88.429 ±**	**27.851**	**281.439 ±**	**50.110**
Curculionidae		0.356 ±	0.096	0.200 ±	0.088	0.619 ±	0.244	0.762 ±	0.181	0.409 ±	0.067
Lygaeidae	**N. raphanus**	**144.444 ±**	**38.347**	**129.889 ±**	**35.079**	**286.905 ±**	**105.251**	**183.667 ±**	**64.593**	**168.386 ±**	**26.502**
	Other	2.311 ±	0.758	1.533 ±	0.488	2.048 ±	0.705	1.524 ±	0.563	1.879 ±	0.337
Pentatomidae		0.089 ±	0.053	0.022 ±	0.022	0.095 ±	0.095	0.095 ±	0.066	0.068 ±	0.027
Psyllidae		**7.222 ±**	**1.106**	**9.400 ±**	**1.476**	**6.952 ±**	**2.032**	**24.143 ±**	**10.089**	**10.614 ±**	**1.798**
Scarabaeidae		1.689 ±	0.548	1.378 ±	0.278	1.714 ±	0.666	3.429 ±	0.699	1.864 ±	0.264
Tingidae		0.178 ±	0.092	0.067 ±	0.038	0.143 ±	0.104	0.048 ±	0.048	0.114 ±	0.038
	Total Herbivore	**764.11 ±**	**135.534**	**409.933 ±**	**50.202**	**728.619 ±**	**155.650**	**534.000 ±**	**99.828**		
Predator											
Anthocoridae		**6.556 ±**	**1.903**	**4.111 ±**	**0.777**	**8.048 ±**	**2.745**	**3.238 ±**	**0.990**	**5.432 ±**	**0.844**
Araneae		2.222 ±	0.368	7.222 ±	0.763	2.143 ±	0.459	7.238 ±	1.177	4.712 ±	0.411
Cantharidae		0.178 ±	0.097	0.422 ±	0.093	0.238 ±	0.153	2.143 ±	0.934	0.583 ±	0.165
Carabidae		2.067 ±	0.335	2.244 ±	0.434	2.143 ±	0.410	6.952 ±	1.502	2.917 ±	0.342
Chrysopidae		**44.756 ±**	**7.569**	**103.156 ±**	**13.110**	**48.571 ±**	**11.682**	**12.905 ±**	**5.156**	**60.205 ±**	**6.205**
Coccinellidae		**6.867 ±**	**1.405**	**15.222 ±**	**4.390**	**9.143 ±**	**2.526**	**22.286 ±**	**14.746**	**12.530 ±**	**2.846**
	C. septemunctata	1.511 ±	0.627	7.178 ±	3.102	2.476 ±	1.220	17.810 ±	13.361	6.189 ±	2.400
	C. maculata	0.044 ±	0.031	0.044 ±	0.031	0.048 ±	0.048	0		0.038 ±	0.017
	H. axyridis	0.133 ±	0.075	0		0.095 ±	0.066	0		0.061 ±	0.028
	H. convergens	5.022 ±	0.887	7.911 ±	1.629	6.524 ±	1.573	4.333 ±	1.622	6.134 ±	0.730
	O. v-nigrum	0.156 ±	0.063	0.089 ±	0.053	0		0.143 ±	0.104	0.106 ±	0.033
Elateridae		0.311 ±	0.134	2.311 ±	0.826	0.952 ±	0.263	12.381 ±	4.527	3.015 ±	0.844
Hemerobiidae		0.800 ±	0.235	1.733 ±	0.290	0.905 ±	0.447	0.952 ±	0.460	1.159 ±	0.165
Lygaeidae	*G. punctipes*	0.889 ±	0.313	0.378 ±	0.132	0.762 ±	0.292	0.905 ±	0.275	0.697 ±	0.133
Meloidae		1.489 ±	0.409	2.067 ±	0.649	0.857 ±	0.242	1.524 ±	0.461	0.088 ±	0.019
Nabidae		0.022 ±	0.022	0		0		0.048 ±	0.048	0.015 ±	0.011
Redjuviidae		0.133 ±	0.113	0.022 ±	0.022	0		0.143 ±	0.078	0.076 ±	0.041
Staphylinidae		**16.133 ±**	**3.654**	**15.822 ±**	**1.900**	**9.714 ±**	**1.616**	**25.476 ±**	**3.850**	**16.492 ±**	**1.588**
Syrphidae		**10.556 ±**	**3.469**	**44.644 ±**	**12.825**	**7.571 ±**	**3.781**	**32.286 ±**	**11.234**	**25.159 ±**	**5.060**
	Total Predator	**92.956 ±**	**9.700**	**199.667 ±**	**18.682**	**91.048 ±**	**13.408**	**129.286 ±**	**21.403**		
Parasitoid											
Braconidae	**Aphid parasitoids**	**244.600 ±**	**43.118**	**581.800 ±**	**88.790**	**133.048 ±**	**25.714**	**186.476 ±**	**47.771**	**332.561 ±**	**37.989**
	D. rapae **	0.600 ±	0.183	1.667 ±	0.685	1.111 ±	0.772	1.560 ±	1.082	1.179 ±	0.312
	L. testaceipes ***	194.500 ±	42.262	509.667 ±	99.066	126.222 ±	54.290	253.556 ±	107.830	314.654 ±	46.647
Ichneumonidae		**167.489 ±**	**92.611**	**13.222 ±**	**1.749**	**64.857 ±**	**30.413**	**8.333 ±**	**1.450**	**73.250 ±**	**32.290**
	Total Parasitoid	**430.911 ±**	**99.520**	**651.556 ±**	**88.963**	**210.571 ±**	**36.866**	**227.286 ±**	**61.597**		
Hyperparasitoid											
Figitidea	**Alloxysta spp.**	**55.200 ±**	**13.471**	**144.244 ±**	**41.159**	**78.381 ±**	**25.956**	**56.238 ±**	**14.910**	**89.409 ±**	**15.776**

*C^w refers to traps in canola that interfaced wheat. W^C are traps in wheat interfaced with canola. C^P are traps in canola interfaced with pasture. P^C are traps in pasture interfaced with canola.

**D. rapae* was only identified for 2012 and 2013 trapping seasons.

***L. testaceipes* was only identified for 2012 and 2013 trapping seasons.

Table 3.4. Mean field captures (±SEM) for the most abundant taxa* collected on yellow sticky traps in north-central Oklahoma during winter canola flowering season in 2011, 2012, and 2013.

Functional Group	Family		C^W**	W^C	C^P	P^C	F	df	P
Herbivore	Aphididae		91.298 ± 14.099b***	129.622 ± 15.725b	115.619 ± 23.952b	221.238 ± 39.283a	6.47	3;120.9	0.0004
	Chrysomelidae	Alticinae	5.089 ± 1.091a	6.667 ± 1.549a	7.762 ± 2.435a	10.381 ± 2.842a	0.80	3;117.8	0.4970
	Cicadellidae		511.022 ± 130.121a	130.222 ± 22.908b	306.524 ± 101.591ab	88.429 ± 27.851b	6.28	3;118.9	0.0005
	Lygaeidae	*Nysius raphanus*	144.444 ± 38.347b	129.889 ± 35.079b	286.905 ± 105.251a	183.667 ± 64.593ab	1.79	3;116.7	0.1551
	Psyllidae		7.222 ± 1.106b	9.400 ± 1.476b	6.952 ± 2.032b	24.143 ± 10.089a	4.00	3;123.0	0.0093
Predator	Anthocoridae		6.556 ± 1.903a	4.111 ± 0.777a	8.048 ± 2.745a	3.238 ± 0.990a	1.64	3;120.9	0.1840
	Staphylinidae		16.133 ± 3.654b	15.822 ± 1.900b	9.714 ± 1.616b	25.476 ± 3.850a	5.84	3;112.6	0.0010
	Syrphidae		10.556 ± 3.469b	44.644 ± 12.825a	7.571 ± 3.781b	32.286 ± 11.234ab	4.18	3;117.9	0.0075
Parasitoid	Braconidae	Aphid parasitoids	244.600 ± 43.118b	581.800 ± 88.790a	133.048 ± 25.714b	186.476 ± 47.771b	8.52	3;120.1	≤0.0001
	Ichneumonidae		167.489 ± 92.611a	13.222 ± 1.749b	64.857 ± 30.413ab	8.333 ± 1.450ab	1.67	3;112.0	0.1775
Hyperparasitoid	Figitidea	*Alloxysta* spp.	55.200 ± 13.471b	144.244 ± 41.159a	78.381 ± 25.956b	56.238 ± 14.910b	5.42	3;118.0	0.0016

* Chrysopidae and Coccinellidae are discussed in a separate analysis.

** C^W refers to traps in canola interfaced with wheat. W^C are traps in wheat interfaced with canola. C^P are traps in canola interfaced with pasture. P^C are traps in pasture interfaced with canola.

*** Different letters within each row indicate signficant differences for each taxa at α=0.05.

Table 3.5. Total lady beetle species abundance (percentage within field) collected on yellow sticky traps in north-central Oklahoma from 2011-2013 during winter canola flowering season (April-May).

Year	Field[**]	Lady Beetle Species[*]					Grand Total
		H. convergens	*C. septempunctata*	*H. axyridis*	*C. maculata*	*O. v-nigrum*	
2011	**C^W**	915 69%	389 29%	8 1%	2 0%	10 1%	1,324
	W^C	1,309 43%	1,728 57%	2 0%	4 0%	4 0%	3,047
	C^P	473 76%	145 23%	4 1%	1 0%	0 0%	623
	P^C	209 19%	890 81%	1 0%	0 0%	2 0%	1,102
2012	**C^W**	175 65%	88 33%	3 1%	0 0%	4 1%	270
	W^C	612 71%	229 27%	0 0%	2 0%	14 2%	859
	C^P	74 56%	55 42%	0 0%	0 0%	2 2%	131
	P^C	61 32%	123 65%	0 0%	1 1%	4 2%	189
2013	**C^W**	239 74%	38 12%	3 1%	0 0%	43 13%	323
	W^C	207 56%	88 24%	0 0%	0 0%	77 21%	372
	C^P	48 71%	10 15%	0 0%	0 0%	10 15%	68
	P^C	14 42%	16 48%	1 3%	0 0%	2 6%	33
Grand Total		**4,336 52%**	**3,799 46%**	**22 0%**	**10 0%**	**172 2%**	**8,341**

*A total of 6 lady beetle adults were unable to be identified.

** C^W refers to traps in canola that interfaced wheat. W^C are traps in wheat interfaced with canola. C^P are traps in canola interfaced with pasture. P^C are traps in pasture interfaced with canola.
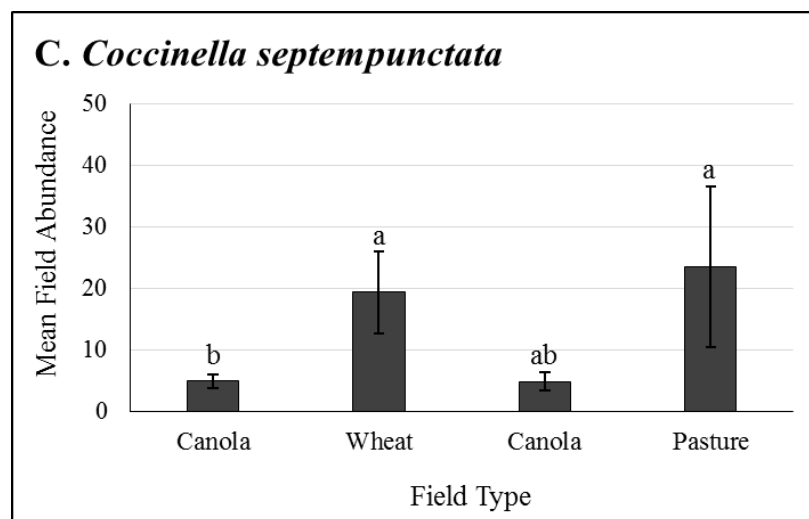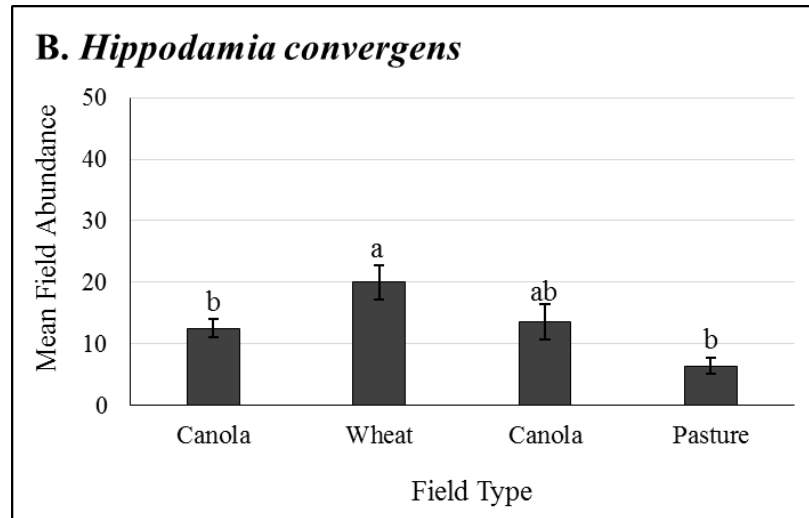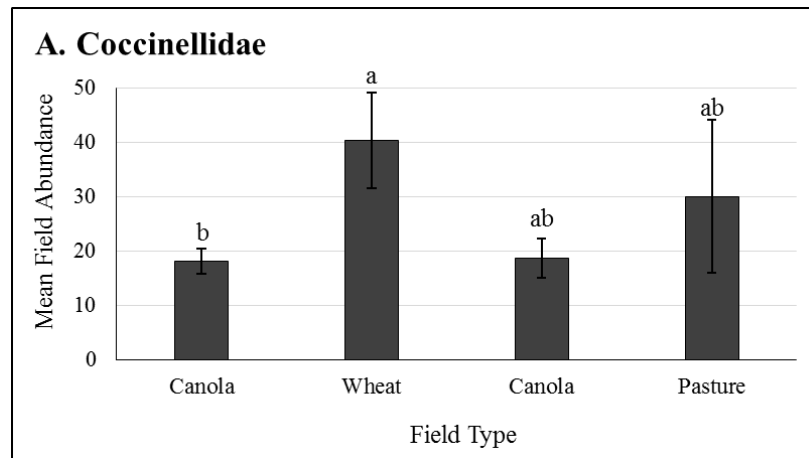
Figure 3.3. Mean field abundance (±SEM) in four field types for all lady beetle species combined (A), *Hippodamia convergens* (B), and *Coccinella septempunctata* (C) for all three years (2011-2013) during canola flowering season. Different letters indicate significant differences (α=0.05).
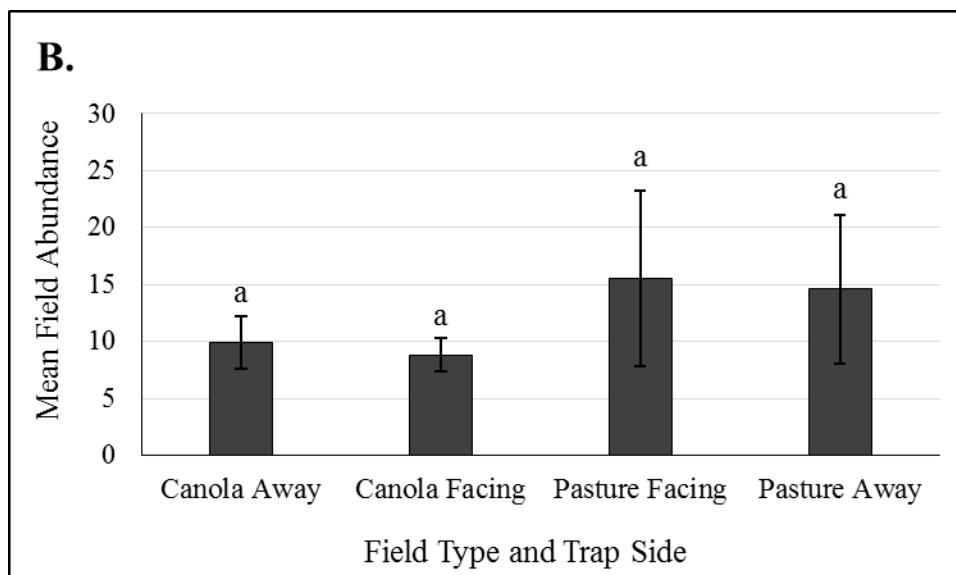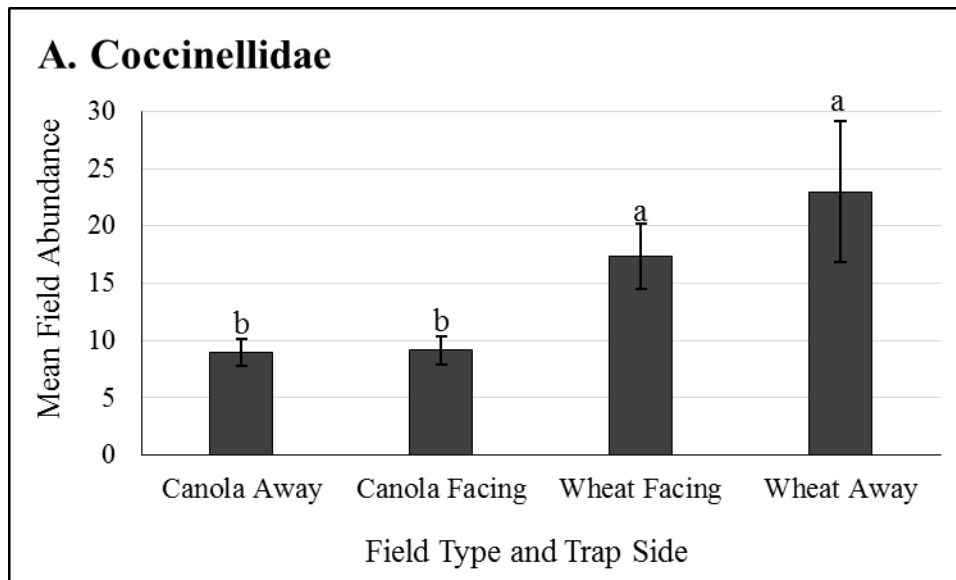
Figure 3.4. Field type and trap side mean abundances (±SEM) for all lady beetles in canola-wheat (A) and canola-pasture (B) landscapes for all three years (2011-2013) during canola flowering season. Different letters indicate significant differences (α=0.05).
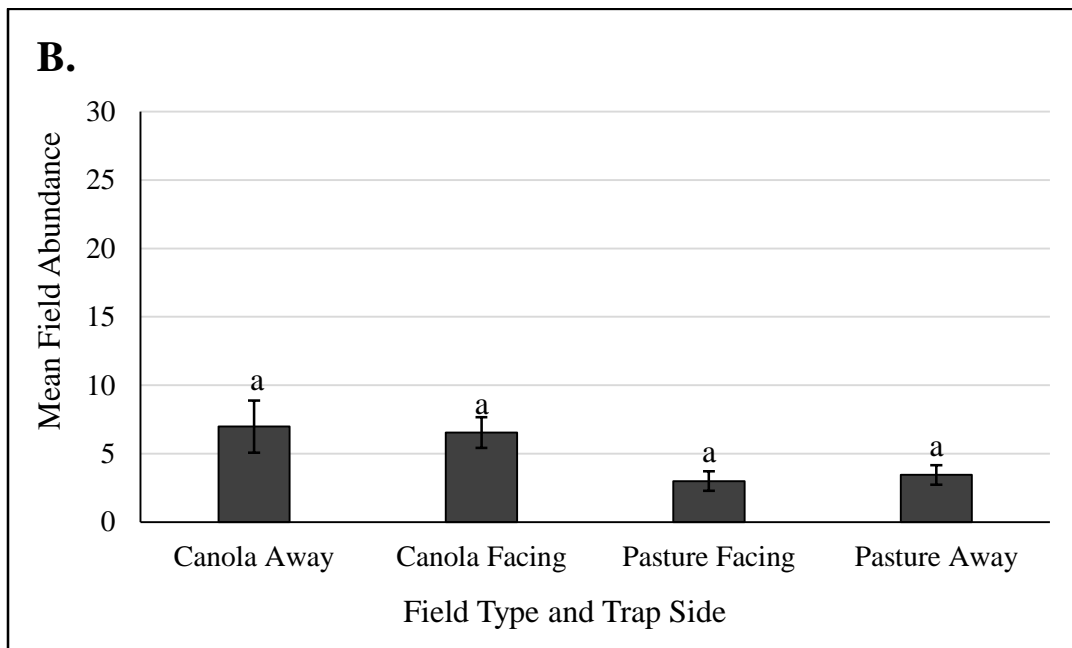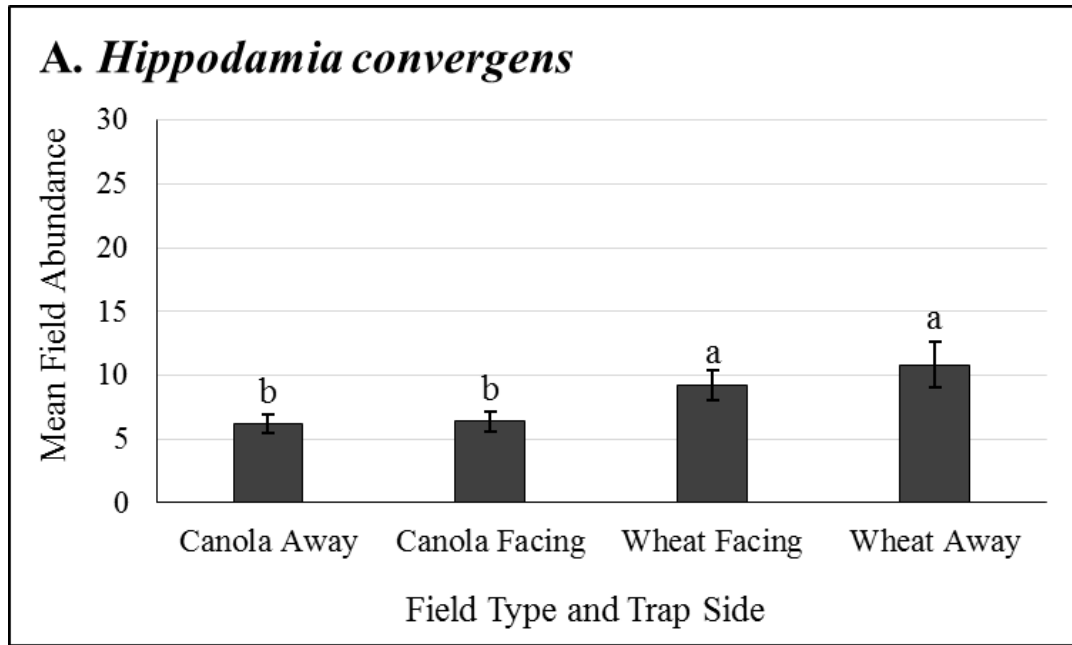
Figure 3.5. Field type and trap side mean abundances (±SEM) for *Hippodamia convergens* in canola-wheat (A) and canola-pasture (B) landscapes for all three years (2011-2013) during canola flowering season. Different letters indicate significant differences (α=0.05).
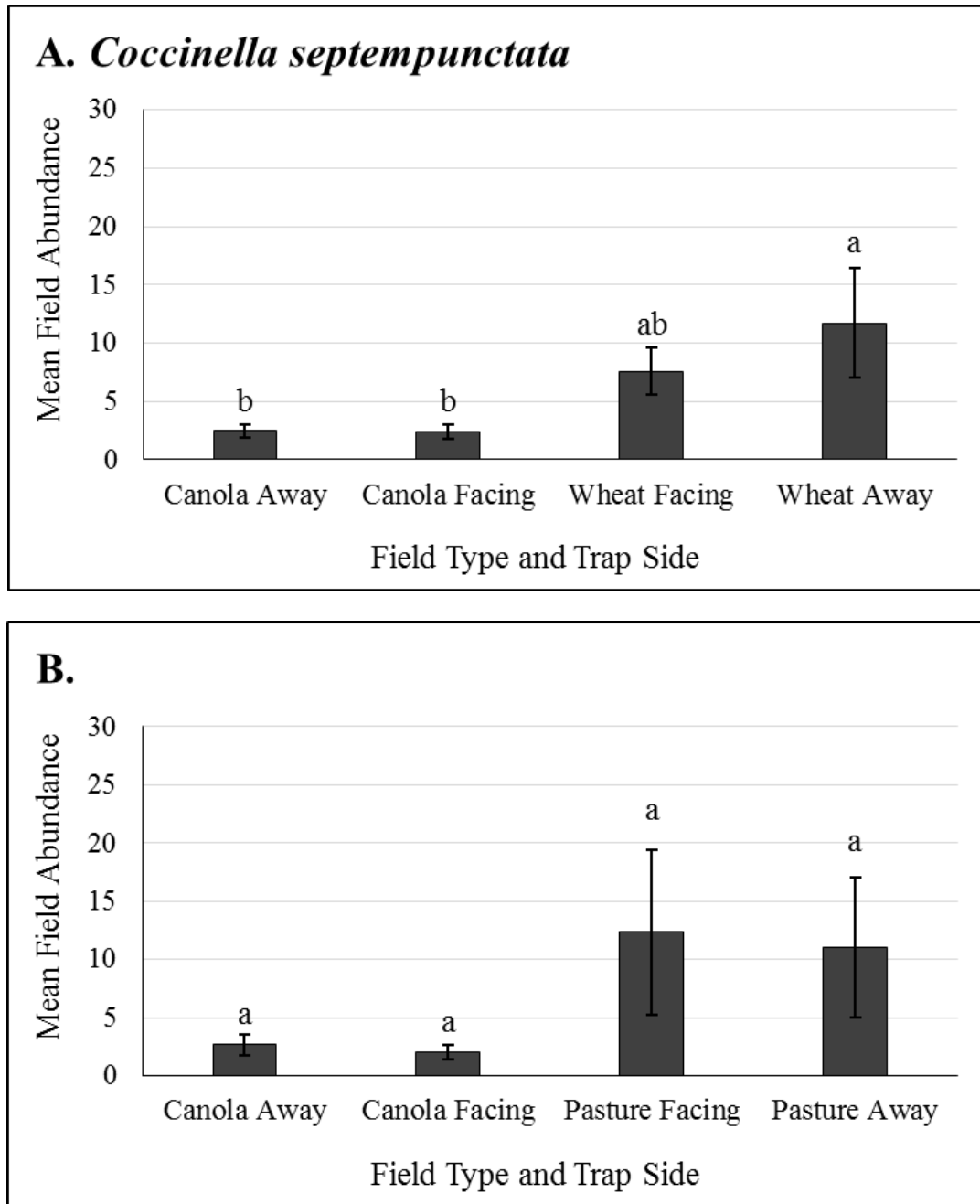
Figure 3.6. Field type and trap side mean abundances (±SEM) for *Coccinella septempunctata* in canola-wheat (A) and canola-pasture (B) landscapes for all three years (2011-2013) during canola flowering season. Different letters indicate significant differences (α=0.05).
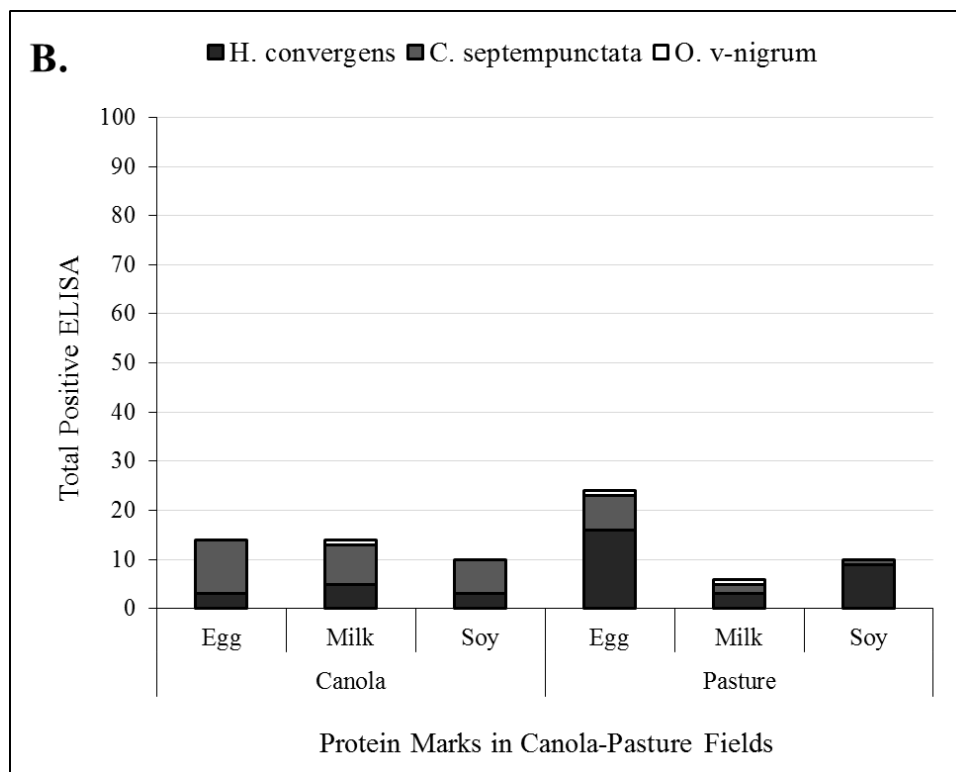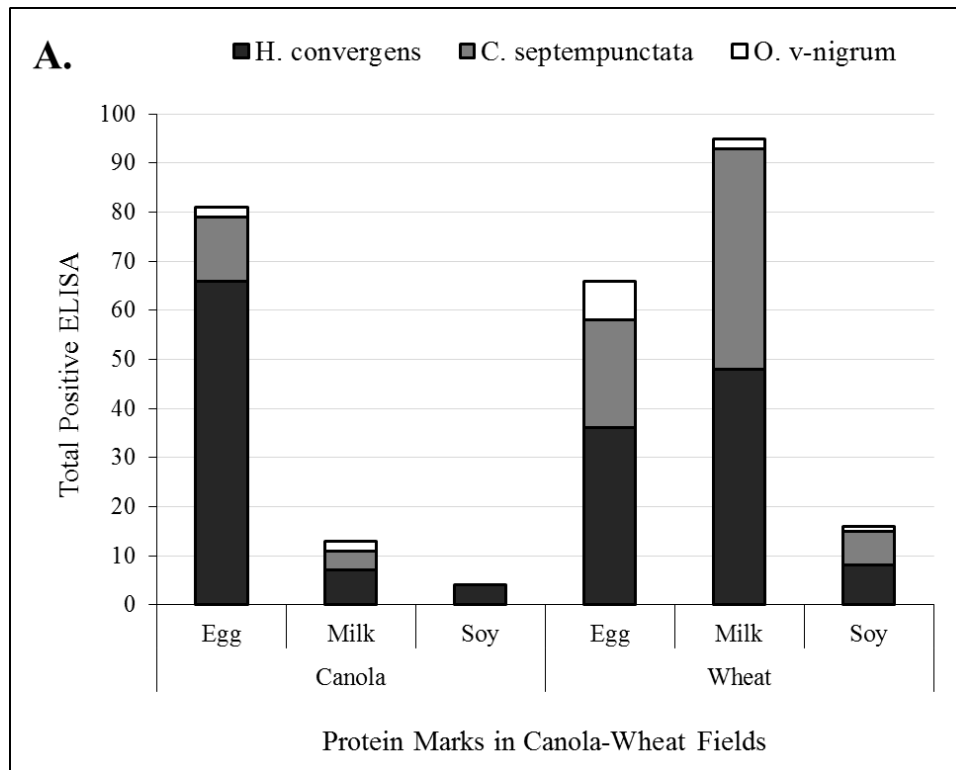
Figure 3.7. Coccinellid species proportions for total positive ELISA marks (egg from canola, milk from wheat, and soy from pasture fields) for all three years of the study.
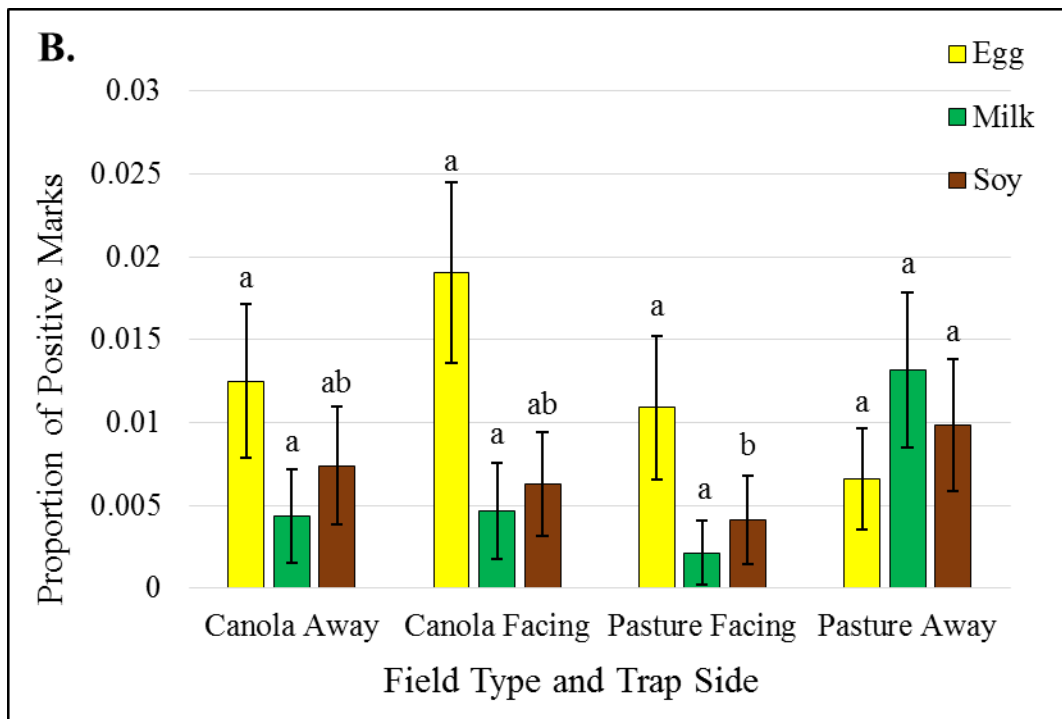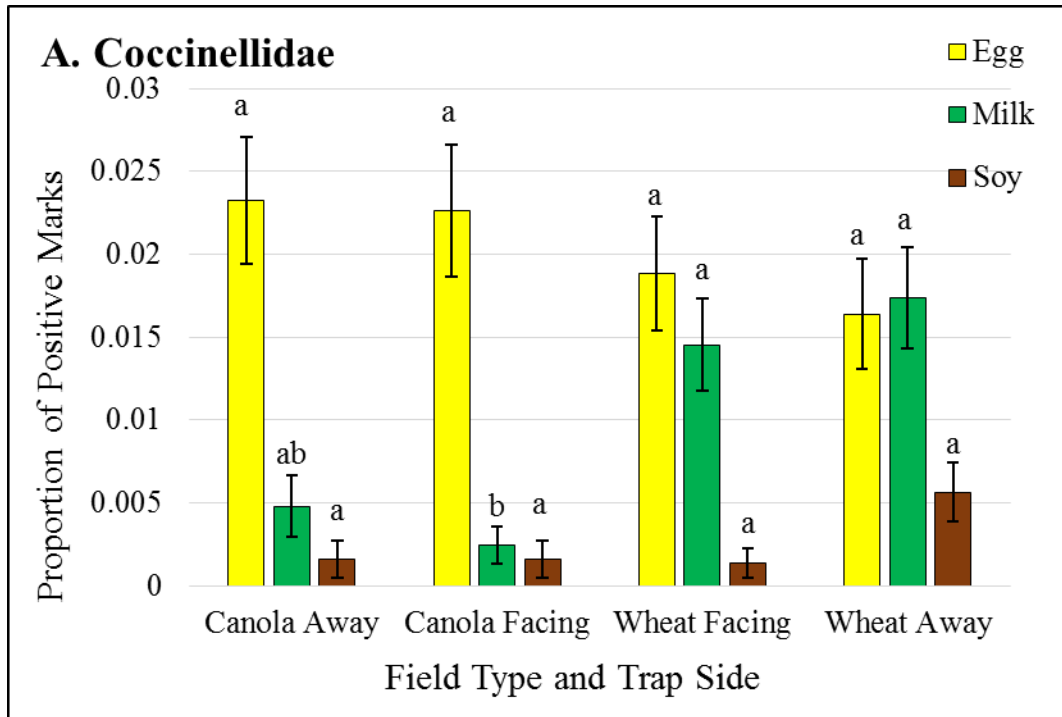
Figure 3.8. Proportion of positive ELISA marks (egg from canola, milk from wheat, and soy from pasture fields) for lady beetles by field type and trap side for all years. Different letters indicate significant differences ($\alpha=0.05$) of protein marks ($\arcsin(\sqrt{Y+1})$ transformed) among field type and trap side for each protein.

114
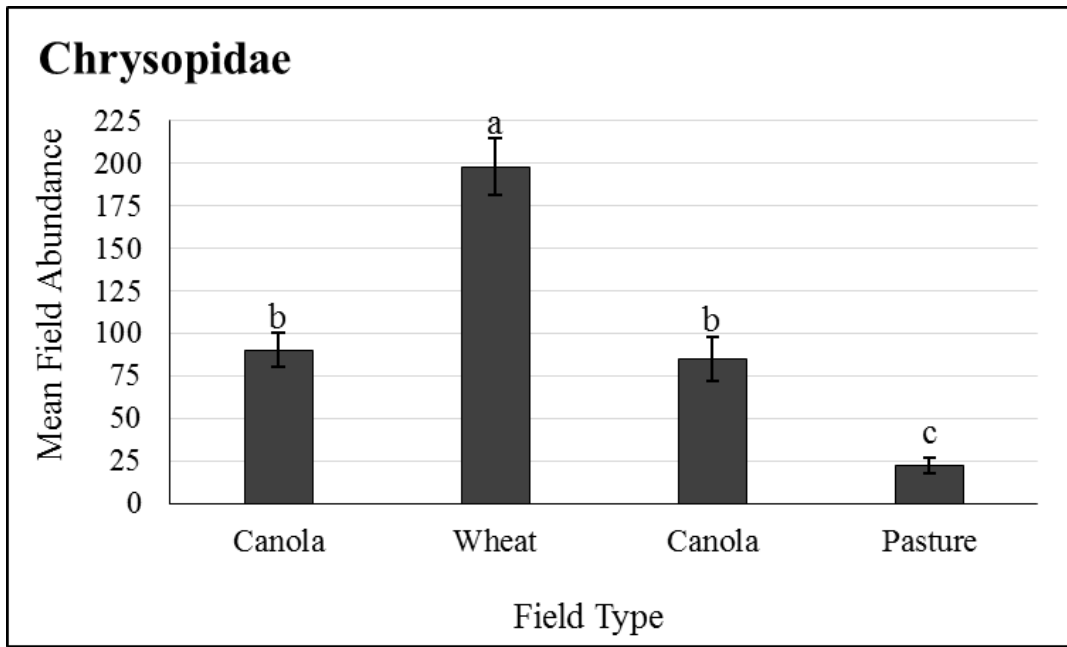
Figure 3.9. Mean field abundance (±SEM) of green lacewings in four field types for all three years (2011-2013) during canola flowering season. Different letters indicate significant differences (α=0.05).
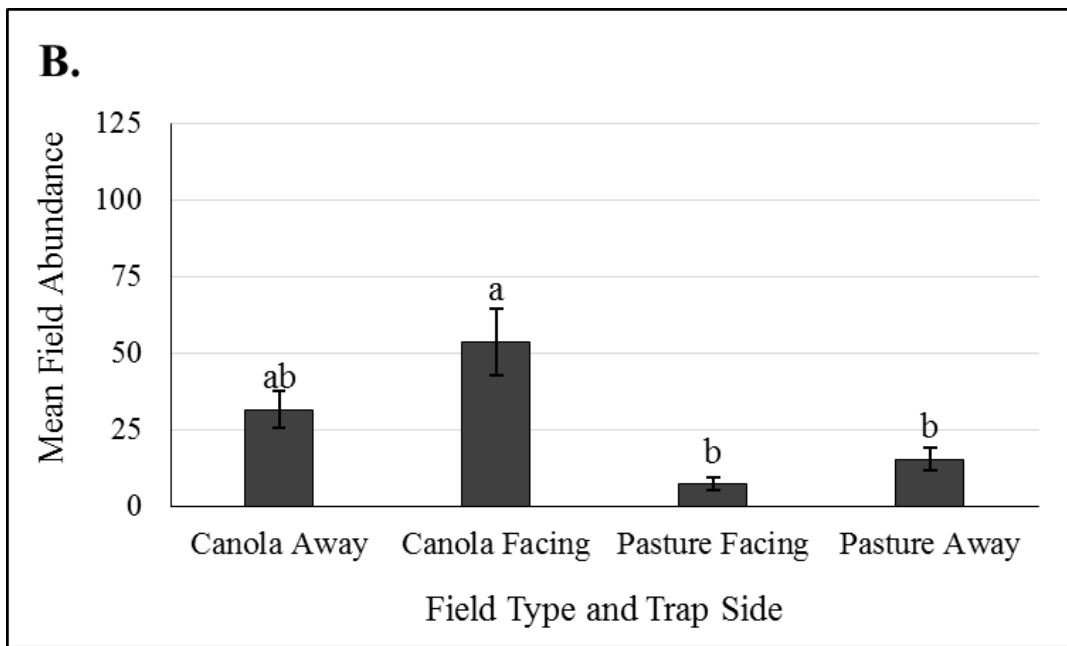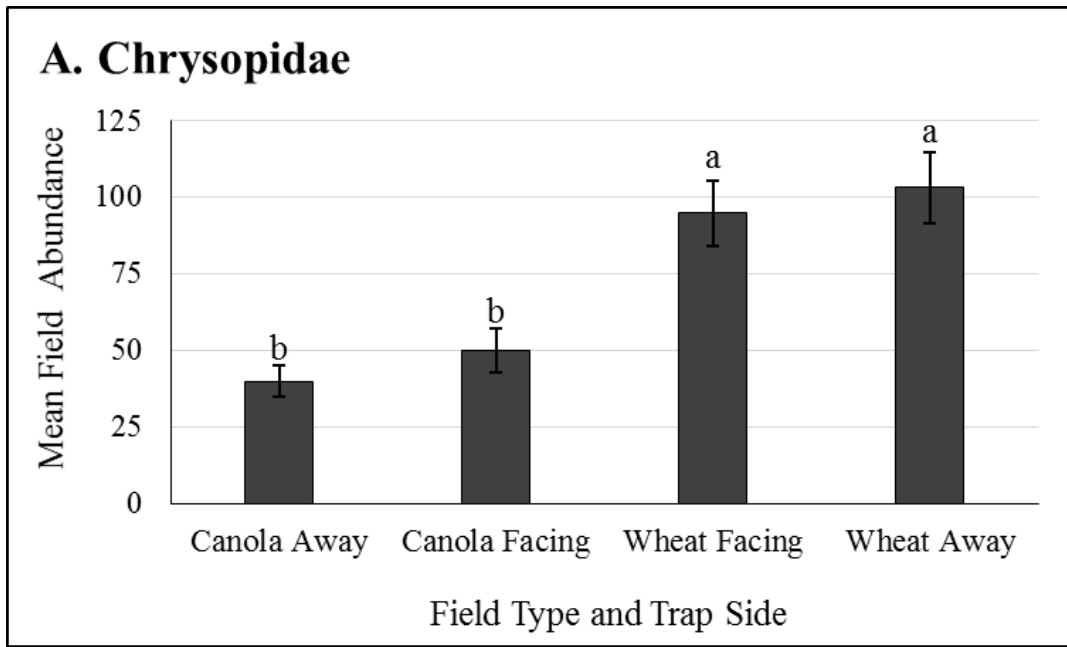
Figure 3.10. Field type and trap side mean abundances (±SEM) for green lacewings in canola-wheat (A) and canola-pasture (B) landscapes for all three years (2011-2013) during canola flowering season. Different letters indicate significant differences (α=0.05).
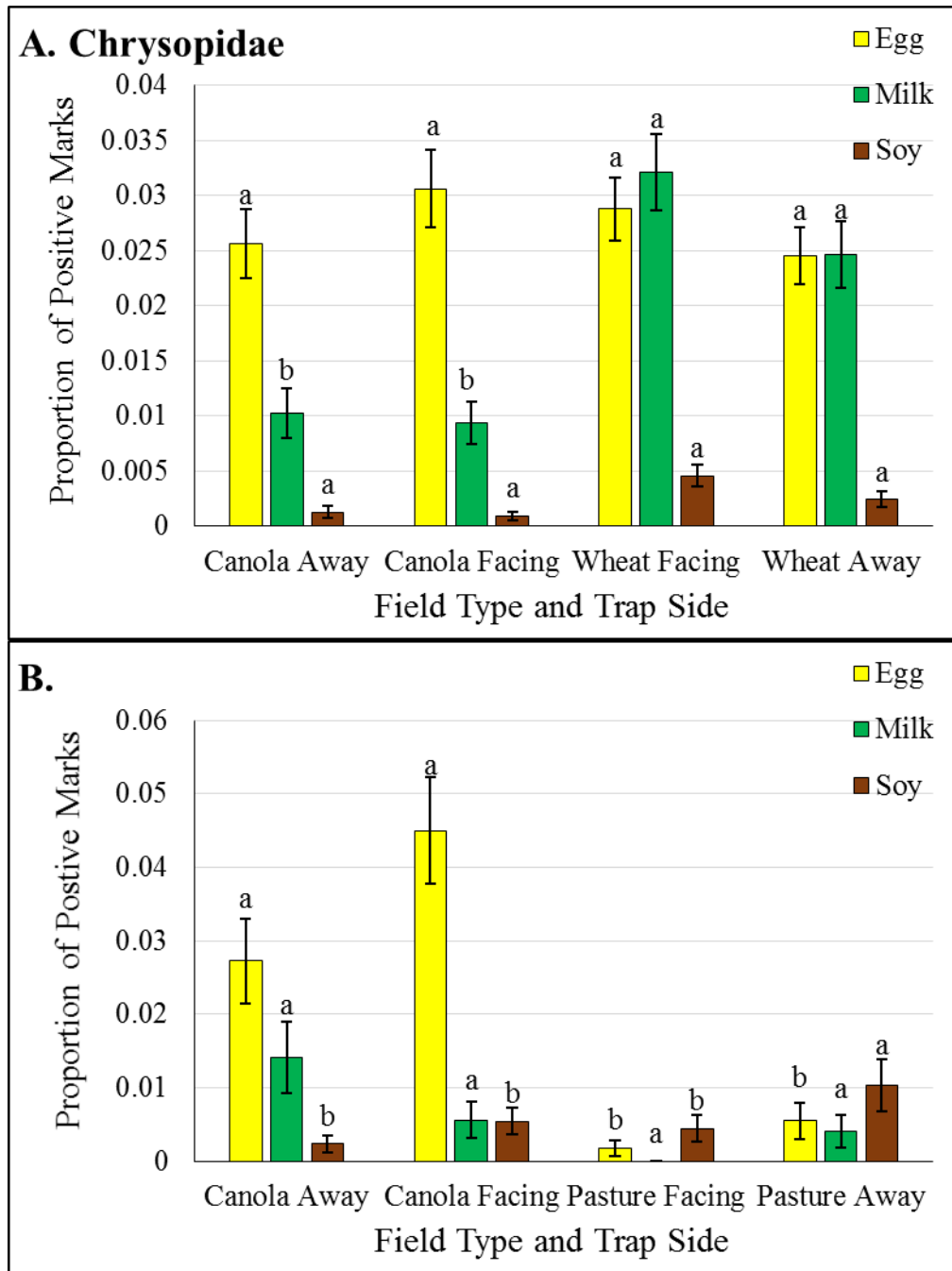
Figure 3.11. Proportion of positive ELISA marks (egg from canola, milk from wheat, and soy from pasture fields) for green lacewings by field type and trap side for all years. Different letters indicate significant differences (α=0.05) of protein marks ($\arcsin(\sqrt{Y+1})$ transformed) among field type and trap side for each protein.

Figure 3.12. *Lysiphlebus testaceipes* spatial distribution (mean abundance) in canola-wheat interfaces (A) and canola-pasture interfaces (B) on yellow sticky traps from five locations in 2013.

CHAPTER IV

MANUSCRIPT TWO

Effects of winter canola pollen as a dietary supplement on *Hippodamia convergens* survival, development, and growth

Introduction

The Oklahoma winter agrolandscape consists primarily of wheat (*Triticum aestivum* L., Poaceae), with over 1.4 million hectares harvested in 2016 (USDA NASS 2017). However, wheat production systems have recently been diversified with the introduction of winter canola (*Brassica napus* L., Brassicaceae) as a rotational crop (Bushong et al. 2012). Oklahoma canola production has increased from a few research plots in 2001 to over 30,000 hectares harvested in 2016 (USDA NASS 2017). Cultivars with herbicide resistance are prevalent in this region and allow growers an opportunity to maximize weed pest suppression, reduce disease pressure, and increase wheat yields – all of which improve the net profitability of winter wheat in the Southern Plains (DeVuyst et al. 2009, Bushong et al. 2012). However, the impact of canola on naturally occurring arthropods within the winter agrolandscape is unknown.

Natural enemy abundance and diversity in the Central and Southern Plains winter cropping systems have been extensively studied in wheat fields (Fenton and Fisher 1940, Arnold 1981, Kring et al. 1985, Rice and Wilde 1988, Jones 2001, Michels et al. 2001, Brewer and Elliott 2004, Elliott et al. 2006, Elliott et al. 2014). Past research has shown lady beetles (Coccinellidae)

are the predominant predator group sampled in winter wheat, and the native convergent lady

beetle, *Hippodamia convergens* Guérin-Méneville, is frequently the most abundant (Elliott et al.

2006); but Chapter III of this dissertation has documented the overwhelming abundance of green

lacewings that far exceeds lady beetles in all sampled field types. Previous studies of natural

enemies were limited in winter canola and have only been conducted in small research plots.

French et al. (2001) sampled for pests and natural enemies in 8x8m plots of winter canola along

with 12 other field crops in Oklahoma, including wheat, and found relatively high numbers of *H.*

convergens and *Coleomegilla maculata* DeGeer. Unfortunately, their study was conducted prior

to large-scale winter canola introductions into wheat production systems; they did not determine

if canola could support indigenous natural enemy communities.

Female coccinellids require a considerable amount of nutrients for egg production and

oviposition (Hariri 1966). However, when aphid (Aphididae) prey are scarce, females rely on non-

prey resources to survive (Evans 2003); therefore, female lady beetles must balance energy costs

associated with remaining in low aphid population habitats and utilizing non-prey resources with

searching for alternative ovipositional sites in other habitats (Ferrer et al. 2010). Indeed, non-prey

resources (honeydew, nectar, and sap) are converted and stored as fat and are not used for

reproduction (Hagen 1962, Hemptinne and Dixon 1990). Flower pollen as a supplemental food

source, however, has been shown to improve immature growth, weight gain, and fertility in *Adalia*

bipunctata L. females when suboptimal prey are available (De Clercq et al. 2005).

Aphidophagous coccinellids oviposit near aphid colonies (Hemptinne and Dixon 1991) and

adults are known to track small aphid populations within crop fields (Giles et al. 1994, Grez and

Prado 2000, Elliott et al. 2002). Adult lady beetles, however, are capable of directed flight and can

move among different habitats, whereas larvae have limited mobility and remain within their natal

habitat and feed on available resources until adult emergence. Therefore, female oviposition sites

dictate where larvae survive and develop. Locally adapted winter canola can attract natural enemies

from surrounding habitats because it has alternative prey/host and floral resources (e.g., pollen and

nectar) (Landis et al. 2000, Gurr et al. 2017), but the suitability of these resources for survivorship, growth, and reproduction have not been fully quantified (Jessie et al. 2015). The purpose of this laboratory study was to determine potential outcomes of lady beetle larvae in winter canola. Specifically, the objective was to examine the suitability of winter canola pollen as a supplemental food source during prey scarcity for *H. convergens* larval survival, development, and growth. Based on previous studies examining flower pollen as a food source for insect predators, we hypothesized that larvae will be able to offset the negative consequences of feeding on low quantities of prey by consuming canola pollen.

Materials and Methods

Aphid Colonies

Pea aphids (*Acyrthosiphon pisum* Harris) were reared on faba bean (*Vicia faba* L., cultivar 'Windsor'), planted in 15.2x12.7cm plastic pots with a 1:1 mixture of potting soil and clay absorbent. Twelve seeds were sown in each pot and fertilized weekly with water-soluble 20:20:20 nitrogen:phosphorus:potassium (NPK) fertilizer. Plants were allowed to grow for 10-12d and watered as needed. When plants were approximately 22cm in length they were added to one of three separate pea aphid colonies containing six plants. Colonies were enclosed within a wooden framed cage (24x18x24cm) with a plastic top and fine mesh screen (530µm) on each side with a Velcro mesh opening. Plants were maintained in the laboratory at 24.2±0.5°C under florescent gro-lux wide spectrum 40-watt bulbs (15:9 light:dark [L:D]). Each week, old and damaged plants were replaced with uninfested 10d plants. Pea aphids were harvested as needed by dislodging aphids from plants onto a piece of paper.

Green peach aphids (*Myzus persicae* Sulzer) were reared on winter canola (cultivar 'Wichita'). Canola was planted and maintained at 18±2.5°C and 16:8 L:D in a greenhouse. Four canola seeds were planted in 15.2x12.7cm plastic pots with a 1:1 potting soil and clay absorbent mixture, and all plants were fertilized (20:20:20 NPK) weekly. To ensure appropriate vegetative growth, two types of bulbs were used in the greenhouse: 400-watt high-pressure sodium and 400-

watt metal halide. Because of the cooler temperatures in the greenhouse, plants required approximately three weeks of growth before being placed in one of three green peach aphid colonies. Old, damaged plants were replaced as needed with three-week old uninfested canola plants. Each colony (identical to pea aphid cages) contained at least three pots of canola. Aphids were harvested from leaves with a small paintbrush as needed.

Ladybeetle Colony

Adult *H. convergens* were collected early spring 2016 from winter canola and wheat fields throughout north-central Oklahoma and maintained in 118ml plastic containers for egg collection at 24.2±0.5°C, 39±0.5% RH, and 15:9 L:D. All lady beetles were supplied with *ad libitum* pea aphids and provided fresh cut faba bean leaves daily. Eggs were collected daily as needed and larvae were reared to adults; eggs collected from F1 mating pairs were then used in the pollen diet suitability study. Eggs were collected daily as needed and labeled with mating pair identification. Prior to hatching, eggs (F2) were isolated in 60ml plastic containers and randomly assigned to one of nine diet treatments (see below).

Canola Floral Resource Feeding Study

Canola anthers (pollen source) and flowers (pollen and nectar source) were collected daily from untreated field and lab-reared plants. Plants from canola fields were uprooted and transplanted into large 5gal buckets and maintained in the laboratory at 24.2±0.5°C, 39±0.5% RH, and 15:9 L:D. Very low numbers of insects were found on field-collected plants; however, all arthropods were removed from plants to prevent herbivore-induced plant volatiles (Vet and Dicke 1992) and/or insect damage. Flowers were collected from canola plants and anthers (with pollen) were removed, placed into microcentrifuge tubes, and stored in plastic bags in a deep freeze (-17.78°C) until pollen was needed for the experiment.

Eight food resource combinations and a control were evaluated (Table 4.1). The control diet treatment consisted of 4mg of green peach aphids (GPA) daily; this limited amount has been shown to support *H. convergens* larval development and survival (Jessie et al. 2015). Additionally,

Giles et al. (2001) documented that low diet levels approaching 4mg per day allow for isolation of diet suitability effects while avoiding confounding effects of predator satiation. The other diet treatments had one of two aphid-to-pollen rations (12:4mg or 4:12mg), a present/absent water source, and a present/absent canola flower for each aphid-to-pollen ratio (Table 4.1). All diet treatments containing canola flowers had six replications (36 total larvae evaluated), and the remaining treatments, including control, had 15 replications (105 total larvae evaluated). A moistened cotton ball was used to provide a water source. Treatments with a canola flower contained flowers from laboratory plants (see above). Regardless of flower presence, based on laboratory measurements total pollen quantities were consistently 4.3±0.25mg or 12.2±0.25mg, respective of diet treatment. As F2 *H. convergens* eggs hatched, larvae were randomly assigned to one of nine diet treatments, and were monitored daily for molting, pupation, adult emergence, or death. Old aphid prey were removed daily and replaced with fresh aphids; however, pollen, flowers, and water were refreshed every other day because they were never fully consumed and therefore remained available for ≥48hr. Emerging adults were placed in a freezer for 24-36hr before weight (mg) and sex were recorded.

Statistical Analysis

A general linear mixed model (GLIMMIX) was used to analyze nine response variables and was generated using SAS software, Version 9.4 of the SAS system for Microsoft Windows. Copyright © 2013 SAS Institute Inc. SAS and all other SAS Institute Inc. product or service names are registered trademarks or trademarks of SAS Institute Inc., Cary, NC, USA. Development time in days for first through total preimaginal stages were compared among treatment combinations using a multinomial distribution. Mean adult body weights were compared across treatment combinations using a Gaussian distribution. Gender was analyzed using a binary distribution, and proportions of females to males for each treatment combination were compared. All tests used a significance level of α=0.05. The control diet treatment (4mg aphids) was considered a limited quantity check and was not included in statistical analyses.

Results

<u>Survival</u>

Cumulative survival (Fig. 4.1), although not included in the analysis, revealed the control treatment (4mg GPA) had fewer *H. convergens* surviving to adulthood (53%). Of larvae supplied with 12:4mg (aphid:pollen) treatments, those supplied with flowers and those supplied with water and flowers ('water+flower') had 100% survival; whereas larvae supplied with water or neither flower or water ('none') had 96% survival. Within the 4:12mg diet treatments, larvae supplied with flowers or 'none' had 100% survival, compared to larvae supplied with water only (86%) or water+flower (83%).

<u>Development</u>

Developmental time (Table 4.2) was not significantly different for first, second, or third instars ($F_{7,61}=1.47$, p=0.194; $F_{7,60}=0.71$, p=0.665; $F_{7,60}=1.03$, p=0.60, respectively). First stadium duration ranged from 2.7-3.2d, and larvae supplied with 12:4mg and flowers took the longest to molt whereas larvae supplied with 4:12mg and flowers molted faster. Larvae supplied with the control treatment spent an average of 2.7d as a first instar. Second stadium duration ranged from 1.5-1.9d; larvae supplied with 4:12mg and water had the longest duration and larvae supplied with 12:4mg and flowers had the shortest duration. Larvae supplied with the control treatment took an average of 2.0±0.17d to molt from second to third instar. Third stadium duration ranged from 2.0-2.4d, and larvae supplied with 4:12mg and water+flowers took the longest to molt, whereas larvae supplied with 4:12mg and flowers had the quickest development. Larvae supplied with the control treatment spent an average of 2.7±0.21d in the third instar. Fourth stadium duration (Fig. 4.2) was significantly different among diet treatments ($F_{7,53}=5.28$, p≤0.0001). Larvae supplied with only 4:12mg took longer to pupate, and larvae supplied with 12:4mg and flowers pupated fastest. In fact, all larvae supplied with 12:4mg diet treatments were quicker to pupate than larvae supplied with any of the 4:12mg treatments or control treatment. Larvae supplied with the control treatment spent an average of 6±0.54d in the fourth stadium. Total larval duration (Fig. 4.3) was significantly

different among treatments ($F_{7,53}$=4.88, p=0.0003), and larvae supplied with 12:4mg and flowers had the shortest larval duration whereas larvae supplied with 4:12mg and 'none' took the longest to pupate. Larvae supplied with the control treatment had longer larval duration compared to larvae supplied with 12:4mg and 4:12mg treatments.

Duration of pupal stage was not significantly different across diet treatments ($F_{7,56}$=0.56, p=0.783); pupal duration ranged from 5.2-5.8d, and larvae supplied with 4:12mg and water+flowers and 4:12mg and flowers had the shortest and longest pupal periods, respectively. Larvae supplied with the control treatment had slightly longer pupation period than larvae supplied with 4:12mg and flowers. Overall, total preimaginal development (Fig. 4.4) was significantly different among diet treatments ($F_{7,52}$=4.52, p=0.0001). Larvae supplied with 12:4mg and flowers had the fastest immature development whereas those supplied with 4:12mg and 'none' had the longest development. Larvae supplied with the control treatment had longer developmental duration compared to all other analyzed diet treatments.

<u>Adult Weight and Sex Ratios</u>

Adult body weight (Fig. 4.5) was significantly different across diet treatments ($F_{7,48.81}$=16.13, p≤0.0001); all larvae supplied with 12:4mg diet treatments had significantly higher weights compared to larvae supplied with 4:12mg diet treatments (p≤0.01) or control treatment. Larvae supplied with 4:12mg treatments had adult weights ranging from 11.33 to 12.30mg, and larvae supplied with 12:4mg treatments ranged from 7.23 to 15.97mg adult weight. Larvae supplied with control treatment had lower adult body weight (10.95mg) compared to the other analyzed diet treatments.

The proportion of emerging adult females to males was not significantly different among diet treatments ($F_{7,62}$=0.40, p=0.901). Higher proportions of females emerged from 12:4mg and 'none' treatments (72%), 12:4mg and water+flower treatments (68%), and 4:12mg and water+flower treatments (66%). Larvae supplied with 4:12mg and water treatment had the lowest

proportion of emerging females (46%), but larvae supplied with control treatment had the lowest proportion of emerged females (23%).

Discussion

The purpose of this study was to determine if lady beetles, particularly the native *H. convergens*, could utilize canola pollen as a dietary supplement during prey scarcity. Medeiros et al. (2010) confirmed *H. convergens* adults frequently feed on a variety of different flowering plants; however, *Brassica* species were not identified. Given its rapid introduction into historical wheat production systems, it is critical to understand how winter canola affects natural enemy populations - especially lady beetles - which are well documented within cereal agrolandscapes.

Overall, *H. convergens* larval survival and adult weight were not negatively affected by canola pollen, and in fact, both were slightly enhanced for larvae supplied with canola pollen. This was especially apparent when compared to lady beetles supplied with 4mg of aphids without a pollen source. While larvae supplied with high daily aphid quantities had greater larval survival and subsequent heavier adults, larvae supplied with suboptimal aphid quantities and canola pollen had higher survival rates and body weights compared to larvae not provided with pollen. Similarly, De Clercq et al. (2005) documented enhanced larval survival and adult weight of *Adalia bipunctata* L. when simultaneously supplied with bee pollen and nutritionally suboptimal prey. Clearly, canola pollen has a positive effect on *H. convergens* larval survival and adult weight especially when aphid quantities are suboptimal. Furthermore, adult lady beetle body weight correlates with subsequent fitness, and canola pollen feeding could potentially increase lady beetle reproductive capabilities in canola production systems (Nedvěd and Honěk 2012); but this needs further study.

Hippodamia convergens development was only affected by canola pollen coupled with daily prey quantities during the fourth instar, and this likely influenced the differences observed for total larval development and preimaginal development. It is clear that the higher daily prey quantities increased fourth stadium duration, however, within the limited prey treatments (4:12mg), larvae provided with flowers were faster to pupate than those supplied with water or 4:12mg and

126

'none' treatment. Lady beetles will readily consume plant sap and extra-floral nectaries when prey is scarce (Hodek and Evans 2012); however, extra-floral plant feeding was not evaluated during this study.

Given the frequency of adult lady beetle movement observed among winter canola and wheat habitats, it is critical to understand if lady beetles can successfully utilize canola floral resources. Adults are highly mobile and females will selectively search for and oviposit in young aphid colonies. Therefore, subsequent generations are forced to forage within natal habitats because of their relatively limited mobility, and must overcome nutritionally or quantitatively inadequate prey by feeding on non-prey resources. The current study verified that supplemental feeding on winter canola pollen benefits lady beetle larval survival, development, and growth. Therefore, winter canola-wheat rotations in the Southern Great Plains have the potential to enhance indigenous lady beetle populations, and the abundant floral resources provided during canola bloom can supplement lady beetle diets when aphids and other prey are scarce.

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Table 4.1. Diet treatments for *H. convergens* larvae supplied with green peach aphids and canola pollen at two ratios, and with or without supplemental water and canola flowers.

Aphids	Pollen	Water	Flower
12mg	4mg	-	-
12mg	4mg	Yes	-
12mg	4mg	-	Yes
12mg	4mg	Yes	Yes
4mg	12mg	-	-
4mg	12mg	Yes	-
4mg	12mg	-	Yes
4mg	12mg	Yes	Yes
4mg	-	-	-
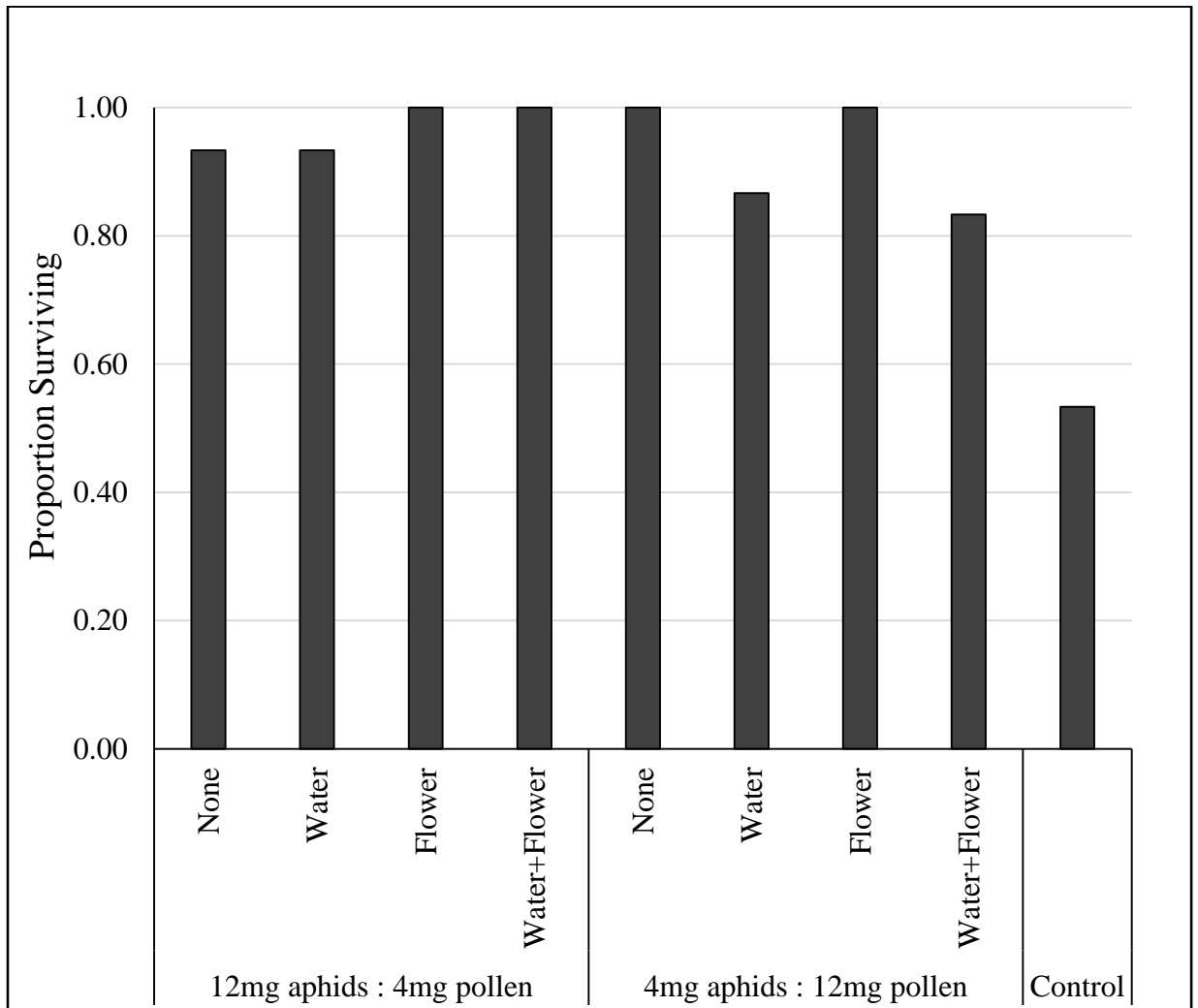
Figure 4.1. Cumulative survival for *H. convergens* supplied with green peach aphids and canola pollen at two ratios, and with or without supplemental water and canola flowers. The control diet consisted of 4mg of aphids. "None" refers to no water or flower were provided to larvae.

Table 4.2. Average developmental duration (d) for each life stage of *H. convergens* supplied with one of nine diet treatments.

				First		Second		Third		Fourth[ł]		Total Larval[ł]		Pupal		Preimaginal[ł]	
Aphid*	Pollen**	Water	Flower	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM
12	4	-	-	2.933 ± 0.067a[Ł]		1.867 ± 0.091a		2.200 ± 0.107a		4.000 ± 0.234		10.929 ± 0.305		5.643 ± 0.169a		16.571 ± 0.402	
12	4	Yes	-	3.000 ± 0.098a		1.867 ± 0.091a		2.133 ± 0.091a		3.615 ± 0.213		10.539 ± 0.215		5.462 ± 0.183a		16.000 ± 0.182	
12	4	-	Yes	3.167 ± 0.167a		1.500 ± 0.224a		2.333 ± 0.211a		3.167 ± 0.167		10.167 ± 0.167		5.500 ± 0.224a		15.667 ± 0.211	
12	4	Yes	Yes	2.667 ± 0.211a		1.667 ± 0.211a		2.167 ± 0.167a		3.833 ± 0.167		10.333 ± 0.211		5.500 ± 0.224a		15.833 ± 0.167	
4	12	-	-	2.933 ± 0.067a		1.800 ± 0.145a		2.333 ± 0.126a		5.267 ± 0.248		12.333 ± 0.333		5.600 ± 0.131a		17.933 ± 0.371	
4	12	Yes	-	3.143 ± 0.097a		1.929 ± 0.165a		2.250 ± 0.131a		4.833 ± 0.207		12.071 ± 0.370		5.385 ± 0.140a		17.539 ± 0.447	
4	12	-	Yes	2.667 ± 0.211a		1.833 ± 0.167a		2.000 ± 0.000a		4.167 ± 0.167		10.667 ± 0.333		5.667 ± 0.211a		16.333 ± 0.211	
4	12	Yes	Yes	2.833 ± 0.167a		1.600 ± 0.245a		2.400 ± 0.245a		4.200 ± 0.200		11.000 ± 0.316		5.200 ± 0.200a		16.200 ± 0.200	
4	-	-	-	2.733 ± 0.153		2.000 ± 0.169		2.692 ± 0.208		6.000 ± 0.535		13.125 ± 0.743		5.750 ± 0.164		18.875 ± 0.789	

* Green peach aphids (*M. persicae*) in milligrams (mg).

** Total canola pollen available in treatment in milligrams (mg).

ł Average fourth, total larval, and preimaginal durations were significantly different (α<0.05).

Ł Columns with the same letter indicate no significant differences across diet treatments.
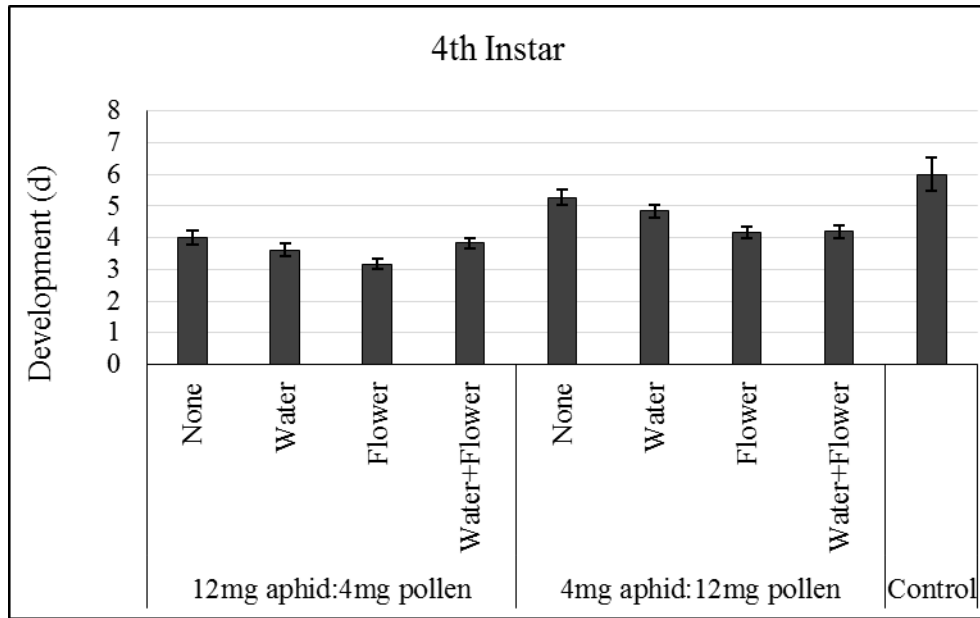
Figure 4.2. Mean development (d) of fourth instar *H. convergens* supplied with green peach aphids and canola pollen at two ratios, and with or without supplemental water and canola flowers. The control diet consisted of 4mg of aphids. "None" refers to no water or flower were provided to larvae.
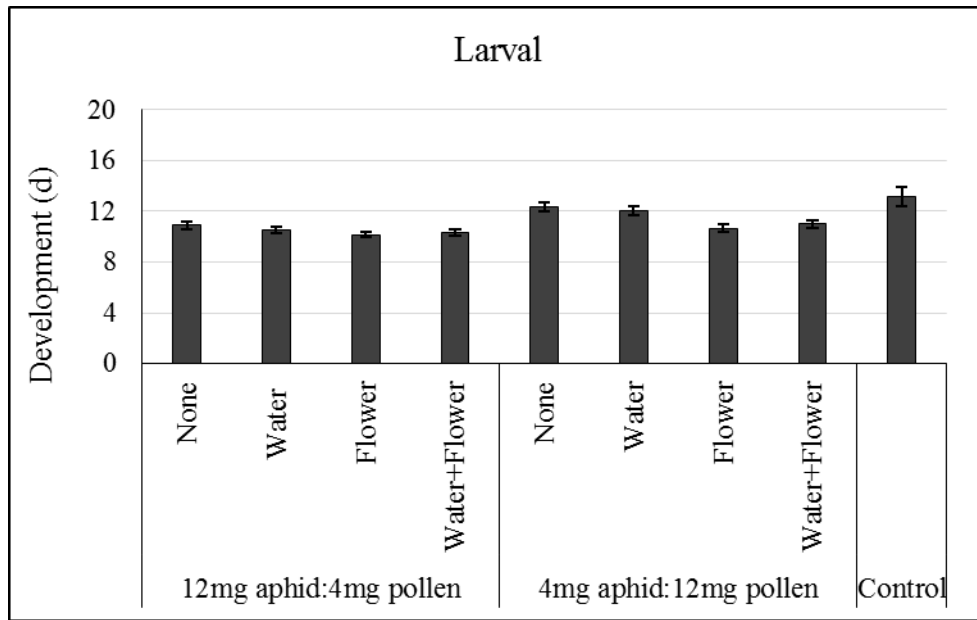
Figure 4.3. Mean larval duration (d) for *H. convergens* supplied with green peach aphids and canola pollen at two ratios, and with or without supplemental water and canola flowers. The control diet consisted of 4mg of aphids. "None" refers to no water or flower were provided to larvae.
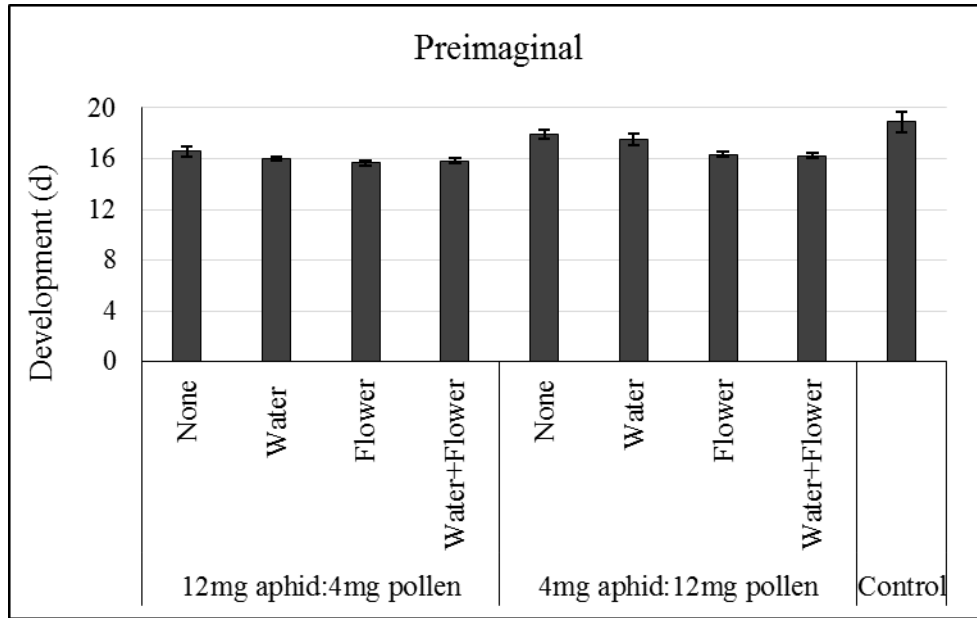
Figure 4.4. Mean preimaginal duration (d) for *H. convergens* supplied with green peach aphids and canola pollen at two ratios, and with or without supplemental water and canola flowers. The control diet consisted of 4mg of aphids. "None" refers to no water or flower were provided to larvae.
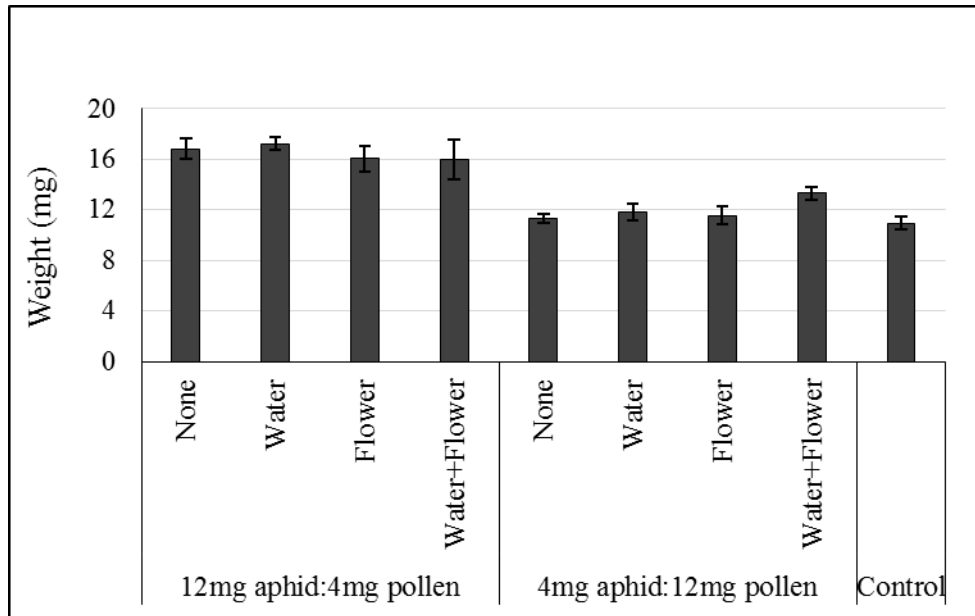
Figure 4.5. Mean adult weight (mg) for *H. convergens* supplied with green peach aphids and canola pollen at two ratios, and with or without supplemental water and canola flowers. The control diet consisted of 4mg of aphids. "None" refers to no water or flower were provided to larvae.

CHAPTER V

GENERAL CONCLUSIONS

Winter wheat (*Triticum aestivum*) has been grown in the Southern Great Plains ecoregion for more than 100yr, and Oklahoma is the second largest US producer with approximately 1.4 million hectares harvested in 2016 (USDA NASS 2017). As with many continuous monoculture production systems, winter wheat producers have regularly dealt with weedy pest encroachment and arthropod pest outbreaks. Because of the low-profit margin for winter wheat, research has focused on viable rotational crop options to reduce risk and improve productivity. Winter-adapted canola cultivars (*Brassica napus*) are successful in wheat rotations because they allow for adequate weed management. Rotations can increase subsequent wheat rotation yields by as much as 22% and overall net returns (Bushong et al. 2012). Currently, Oklahoma canola production is approximately 30,000 hectares, and this is expected to increase (USDA NASS 2017).

A dichotomy exists between wheat and canola in regards to plant physiology, and this difference has a profound effect on arthropod communities and trophic-level interactions. Wheat, a graminaceous crop, is host to many cereal aphids which are known to be essential (i.e., highly suitable) prey for many natural enemies, including lady beetles and green lacewings. Ultimately, consumption of cereal aphids promotes high survival, fast development, and optimal growth (Phoofolo et al. 2007, Khan et al. 2013). Alternatively, canola is a crucifer with its own unique aphid assemblage (Elliott et al. 2014). Many *Brassica* specialist aphids are capable of sequestering toxic host plant compounds, and these compounds, termed glucosinolates, have negative effects on predator survival, development, and growth (Chena and Liu 2001, Kazana et

139

al. 2007, Jessie et al. 2015). While wheat and canola have unique aphid assemblages, limited arthropod sampling has revealed small differences in higher trophic level communities (French et al. 2001).

The overall purpose of the studies outlined in this dissertation was to evaluate how arthropod communities are affected in winter canola, wheat, and pasture systems. In the first study, arthropod diversity and abundances were monitored at canola-wheat and canola-pasture interfaces. Furthermore, predator movements were documented within and among canola-wheat and canola-pasture interfaces. In the second experiment, *Hippodamia convergens* larvae were provided canola pollen and larval survival, development, and growth was quantified to determine suitability of pollen as a dietary supplement.

Surprisingly, pasture habitats had the highest taxa diversity but the lowest overall abundance compared to canola and wheat fields. The most abundant herbivores in all sampled habitats were leafhoppers followed by false chinch bugs and aphids. Aphid parasitoid wasps (Braconidae) were the dominant parasitoid in canola, wheat, and pasture fields. The most common predators were green lacewings followed by syrphid flies, rove beetles, and lady beetles. Unique protein marks revealed that both lady beetles and green lacewings frequently move within and among crop habitats as well as uncultivated pastureland; however, a higher rate of movement appears to be occurring from winter canola (emigration) compared to wheat and pasture fields, although overall abundances are higher in wheat. The data tentatively suggests that winter canola is not functioning as a source or sink habitat for green lacewings and lady beetles, but rather, canola functions as a complemental landscape feature (see Dunning et al. 1992).

The canola pollen feeding study indicated that supplementing low prey quantities with canola floral resources has positive effects on lady beetle survival, development, and growth. The studies documented within this dissertation reveal that while winter canola does not appear to support the diverse and abundant arthropod communities common in other Oklahoma winter vegetation habitats, predatory insects are frequently visiting winter canola fields and may be

utilizing abundant floral resources to improve overall fitness. Furthermore, this dissertation serves as a necessary baseline for documenting natural enemy communities within canola-wheat landscapes, and provides a foundation for further hypothesis development focused on predicting outcomes of arthropod interactions among trophic levels within and between vegetation habitats (Rosenheim et al 1995, Evans 2016).

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Phoofolo, M. W., K. L. Giles, and N. C. Elliott. 2007. Quantitative evaluation of suitability of the greenbug, *Schizaphis graminum*, and the bird cherry-oat aphid, *Rhopalosiphum padi*, as prey for *Hippodamia convergens* (Coleoptera: Coccinellidae). Biological Control 41: 25-32.

Rosenheim, J. A., H. K. Kaya, L. E. Ehler, J. J. Marois, and B. A. Jaffee. 1995. Intraguild predation among biological-control agents: theory and evidence. Biological Control 5:303-335.

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APPENDICES

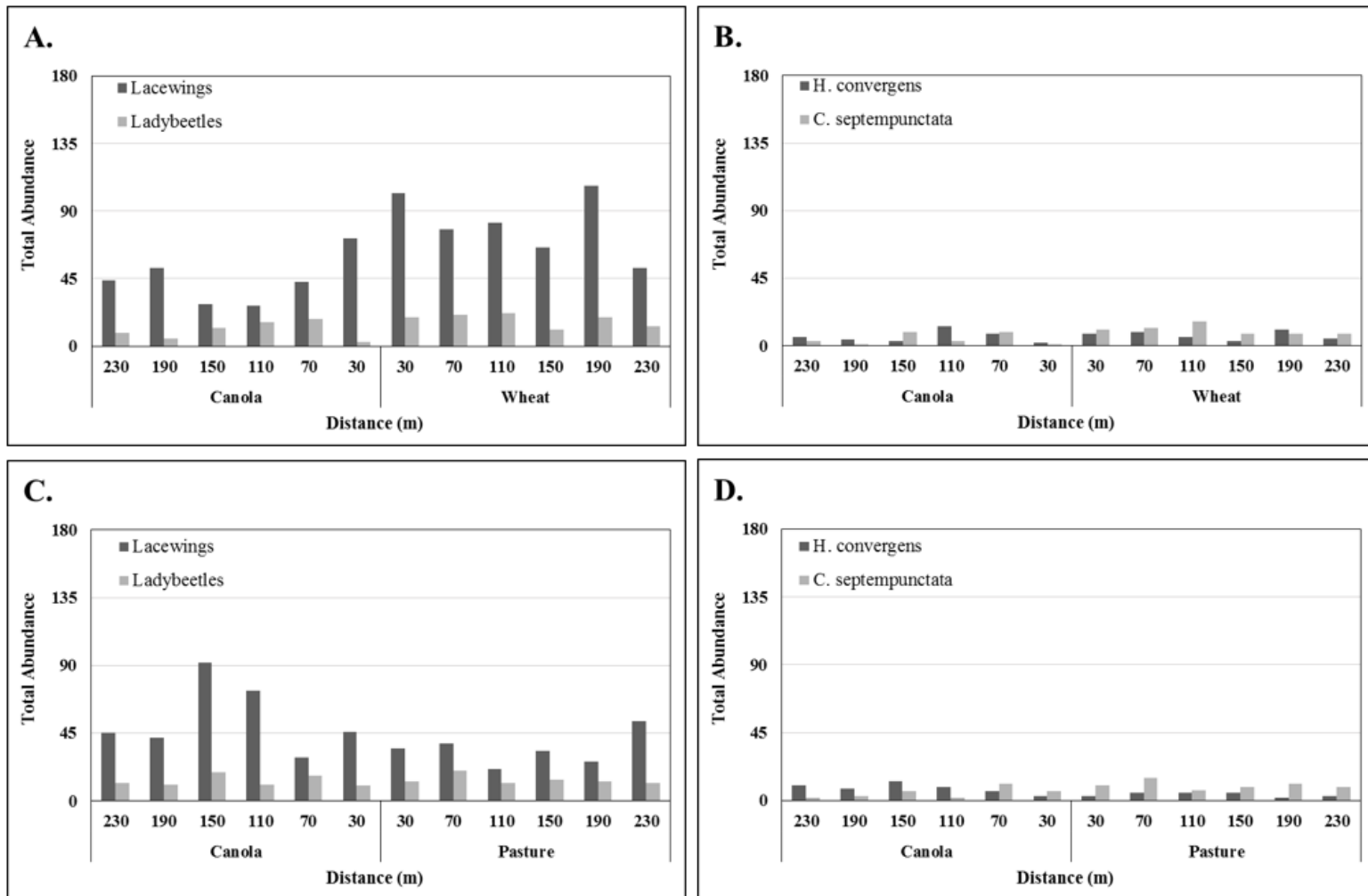Appendices start on the following page.

Appendix A. 2011 Carmen East Diverse abundances over 5 sample periods for green lacewings and lady beetles (A, C) in canola-wheat fields and canola-pasture fields, respectively, and abundances for two lady beetle species (B, D) in the two landscape types.
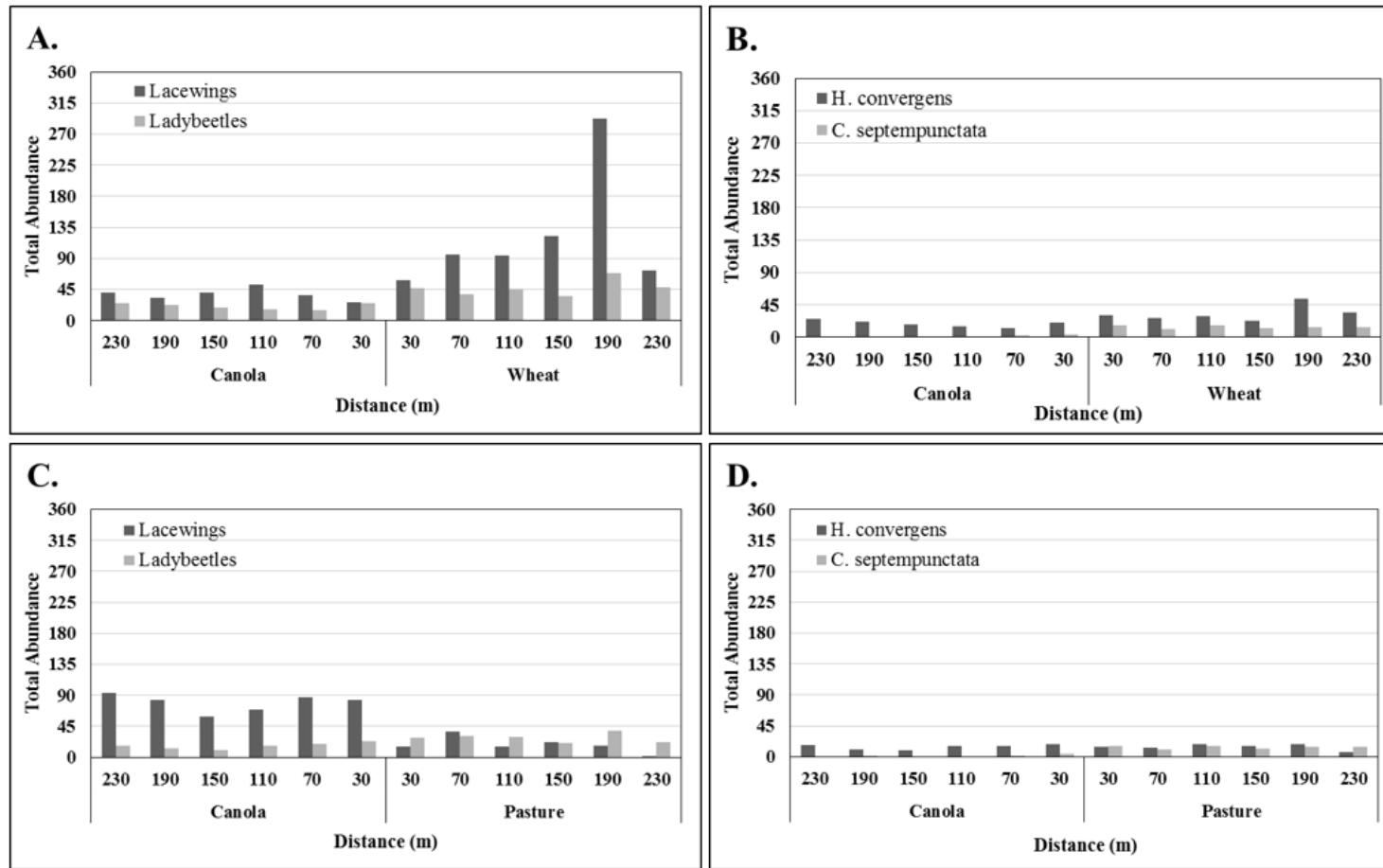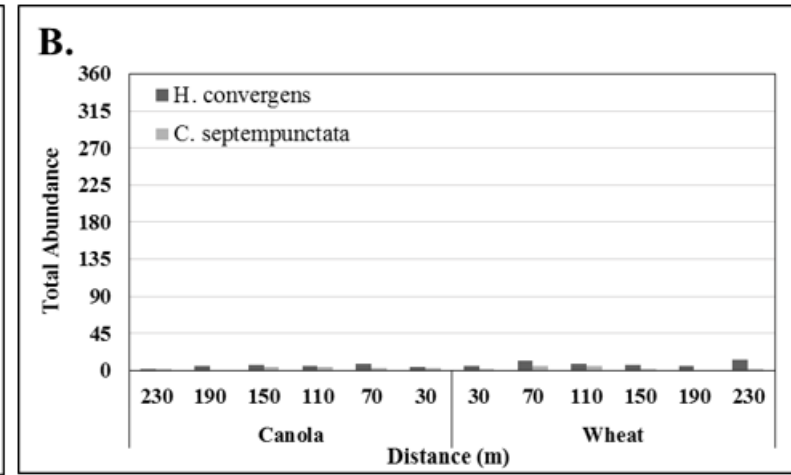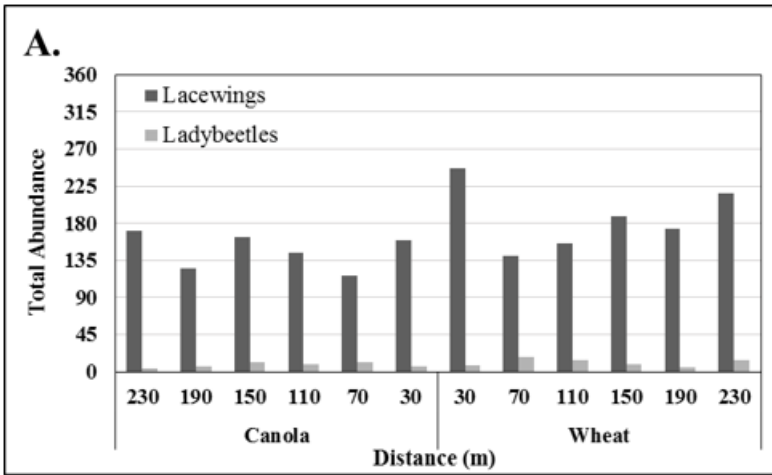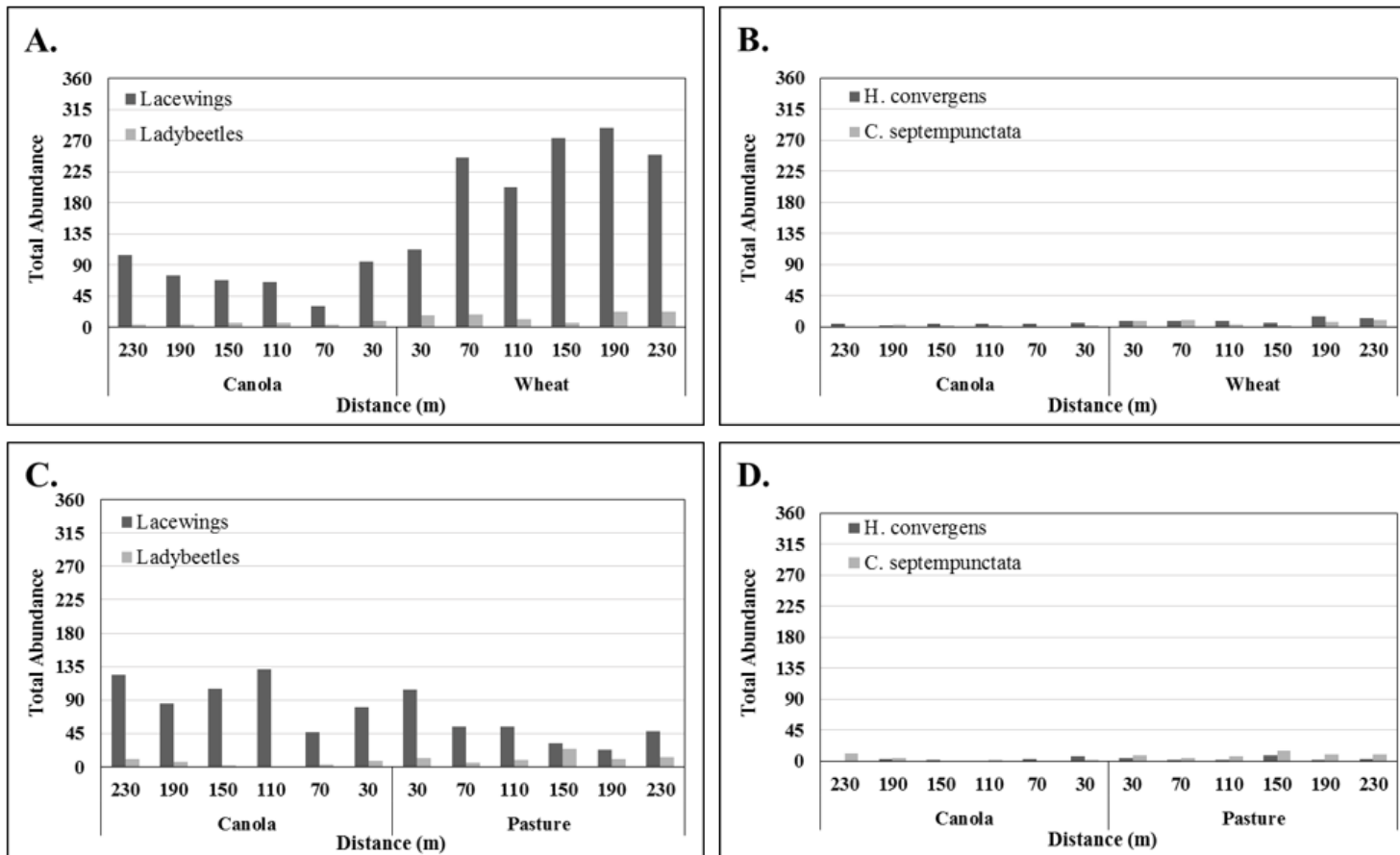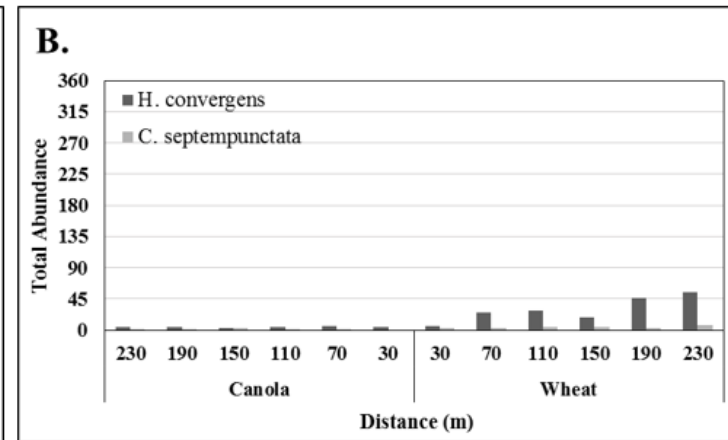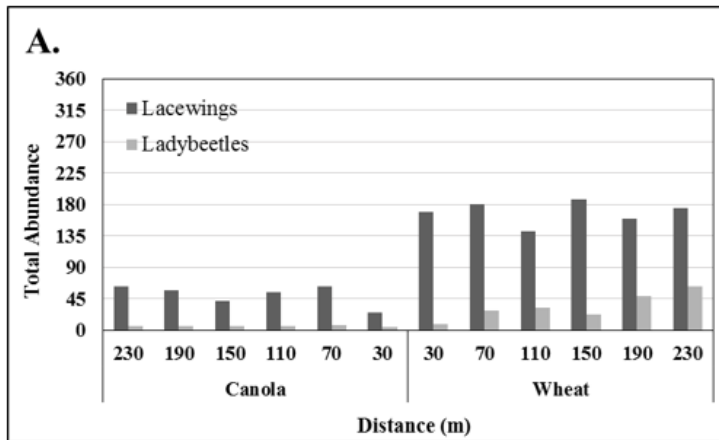
Appendix B. 2011 Carmen North Diverse abundances over 5 sample days for green lacewings and lady beetles (A, C) in canola-wheat fields and canola-pasture fields, respectively, and abundances for two lady beetle species (B, D) in the two landscape types.
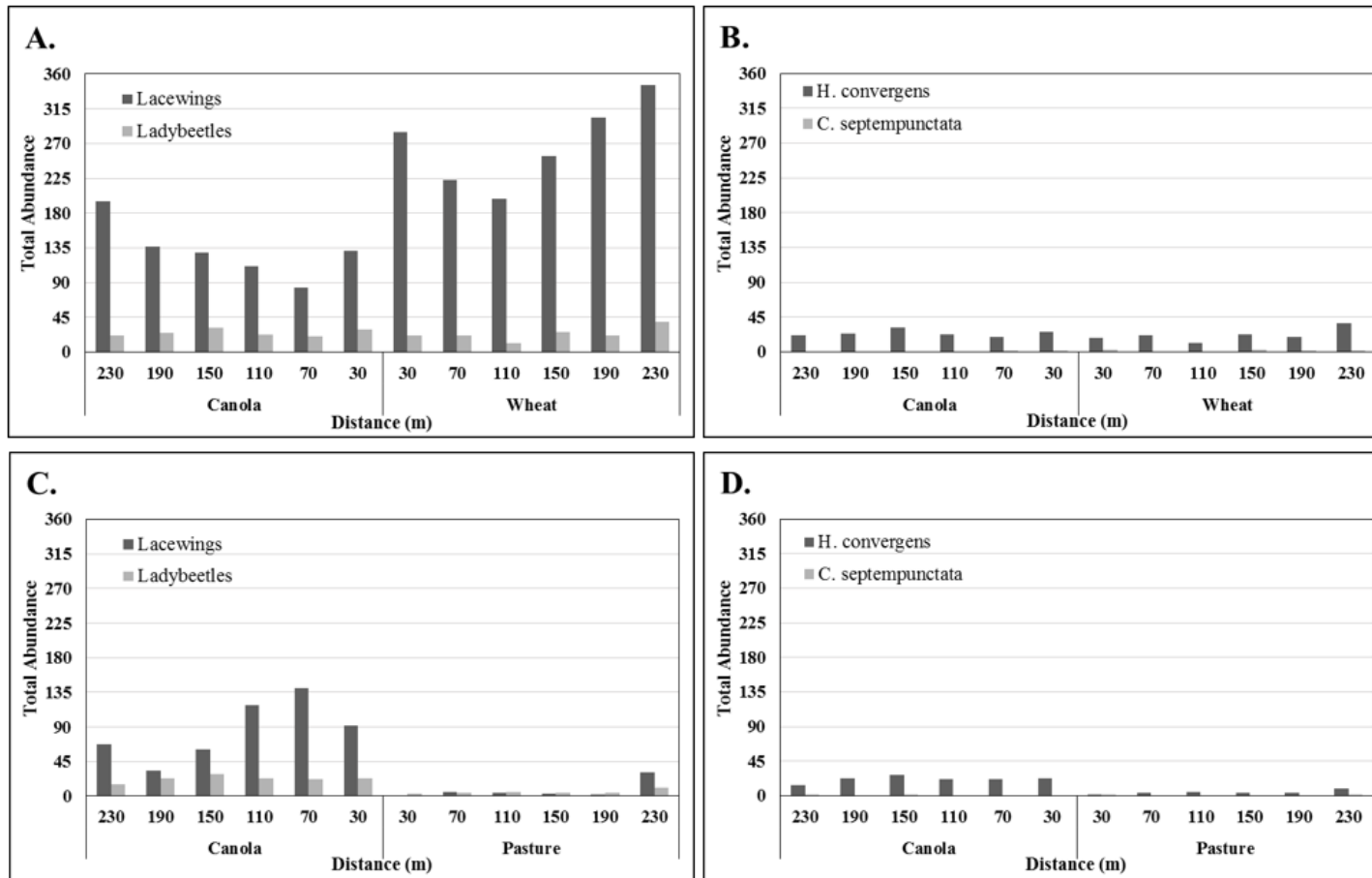
Appendix C. 2011 Carmen Simple abundances over 5 sample periods for green lacewings and lady beetles (A) and two predominant lady beetle species (B).
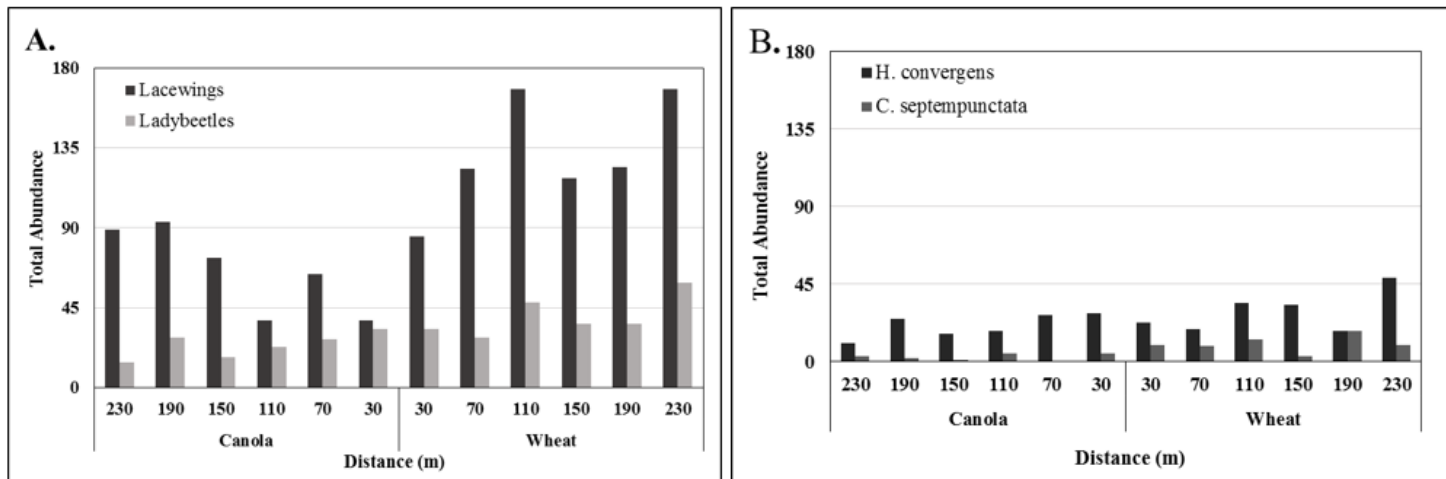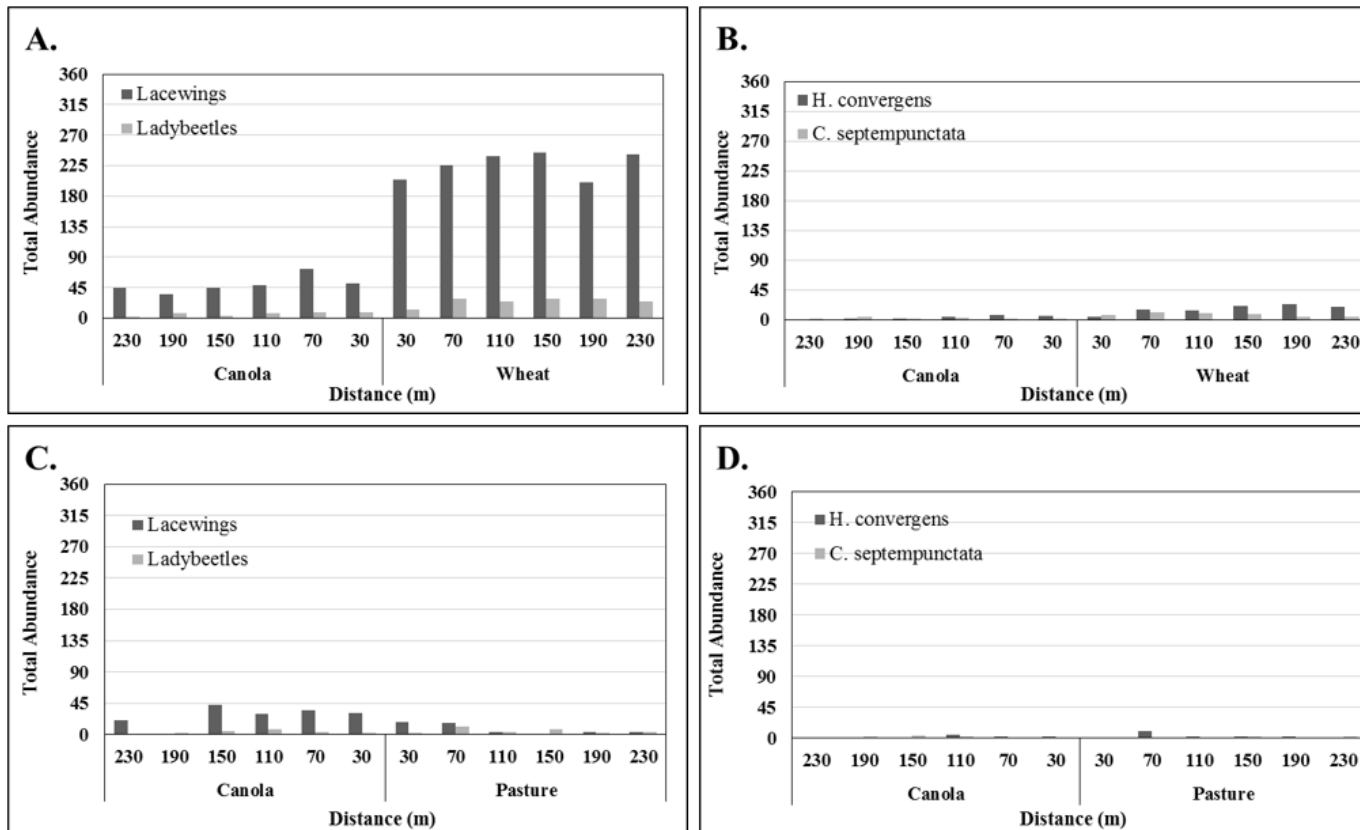
Appendix D. 2011 Nash Diverse abundances over 5 sample periods for green lacewings and lady beetles (A, C) in canola-wheat fields and canola-pasture fields, respectively, and abundances for two lady beetle species (B, D) in the two landscape types.
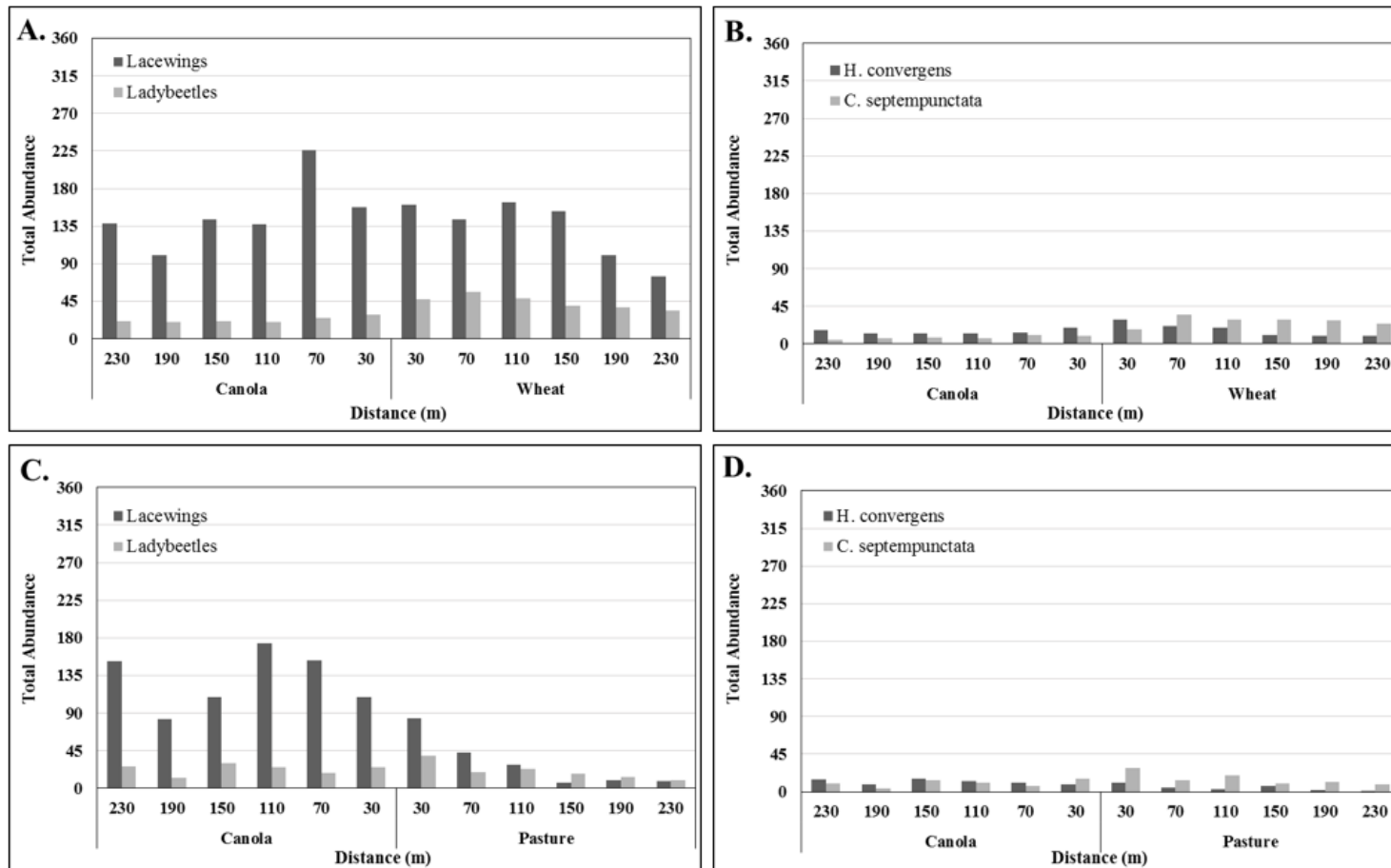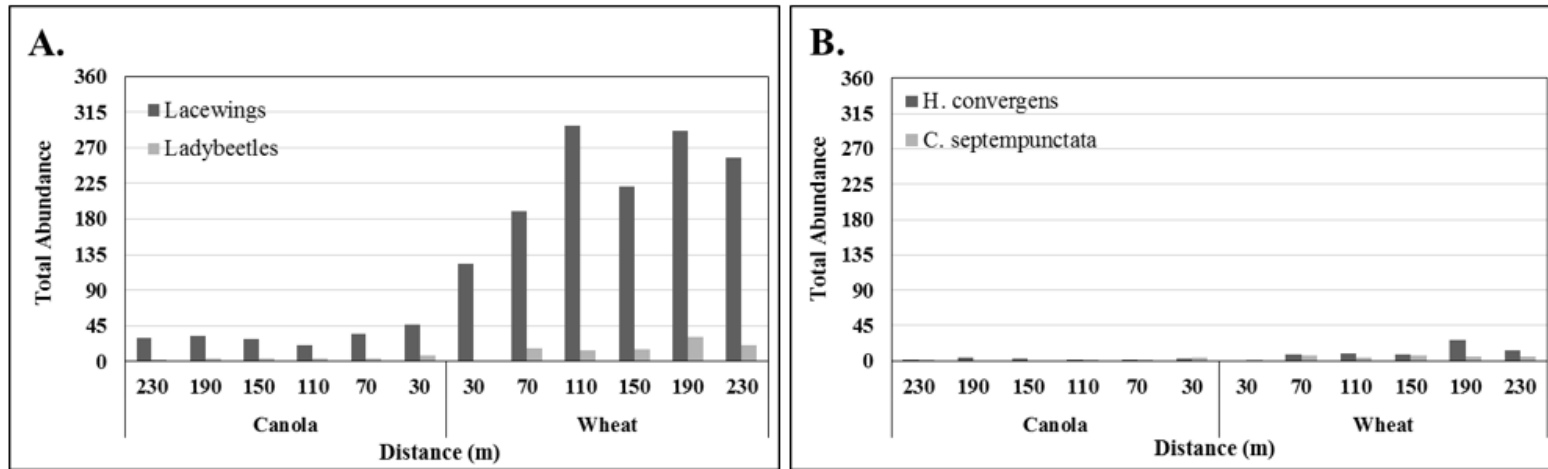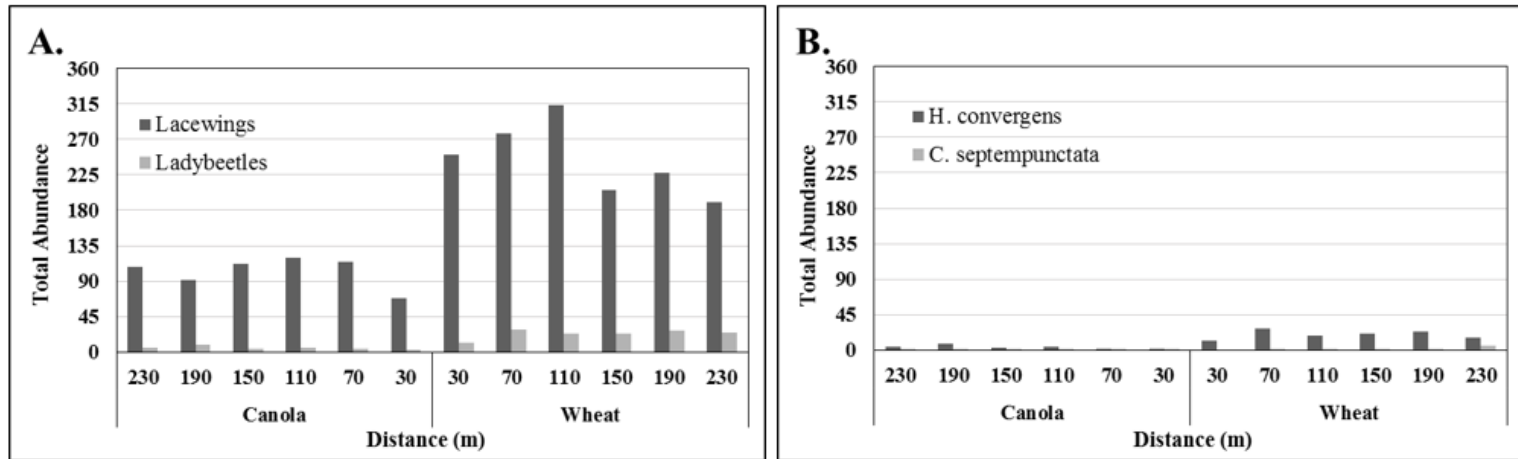
Appendix E. 2011 Nash North Simple abundances over 3 sample periods for green lacewings and lady beetles (A) and two predominant lady beetle species (B).
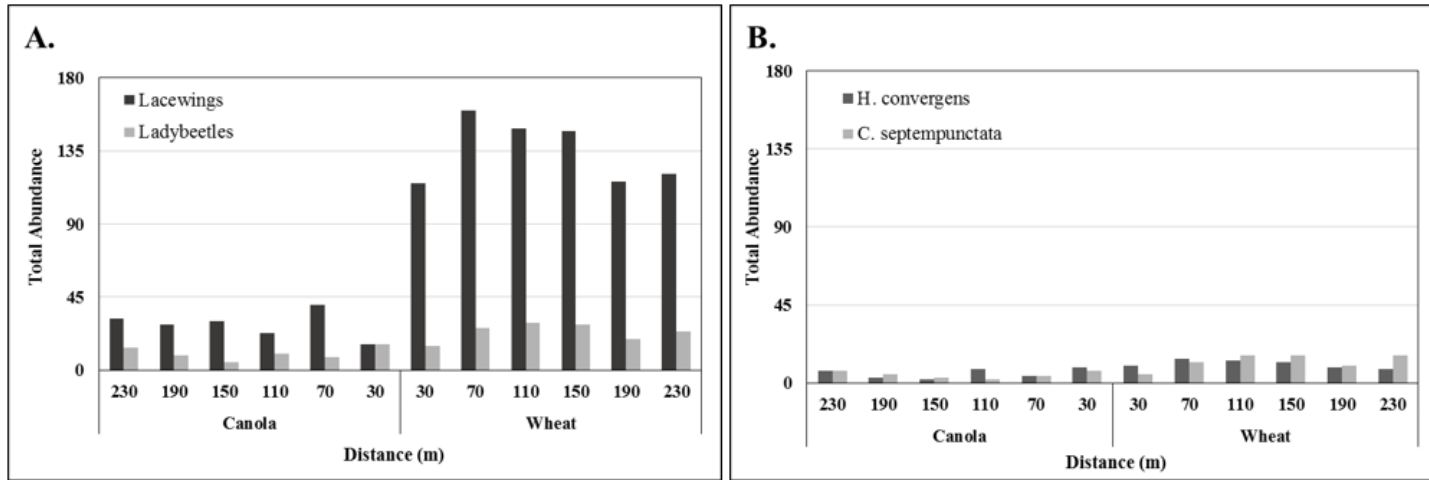
Appendix F. 2011 Okeene Simple abundances over 5 sample periods for green lacewings and lady beetles (A) and two predominant lady beetle species (B).
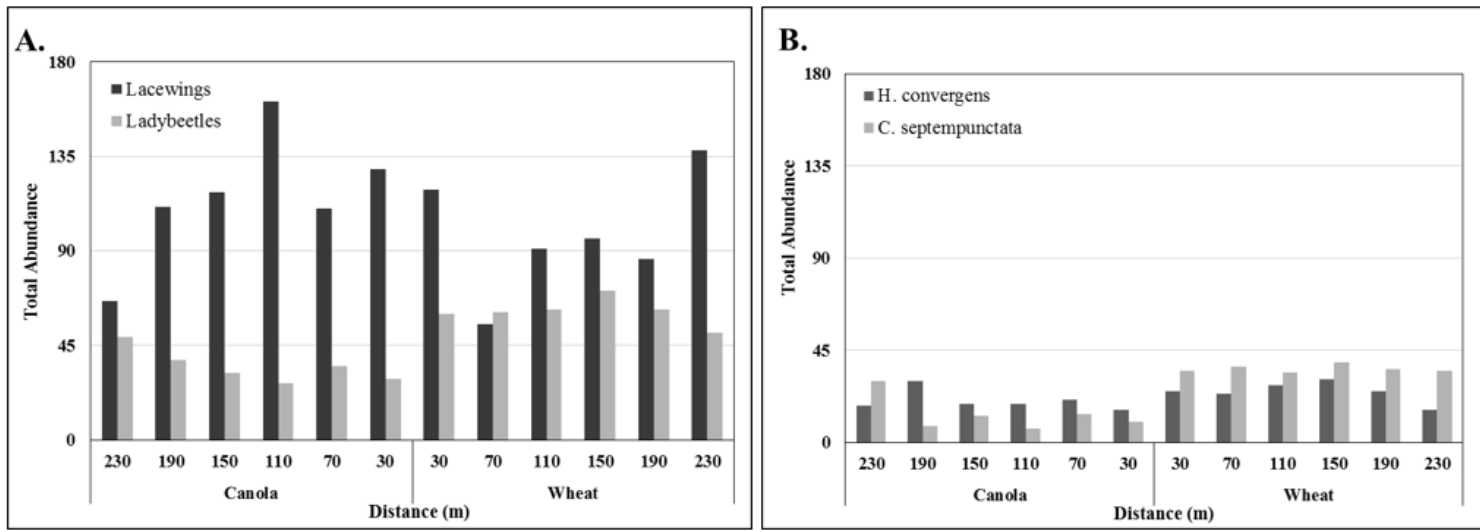
Appendix G. 2011 Omega Simple abundances over 5 sample periods for green lacewings and lady beetles (A) and two predominant lady beetle species (B).
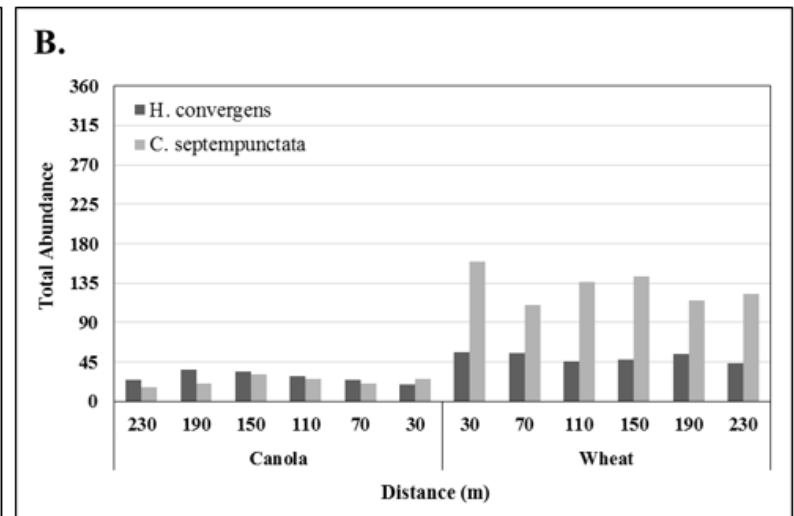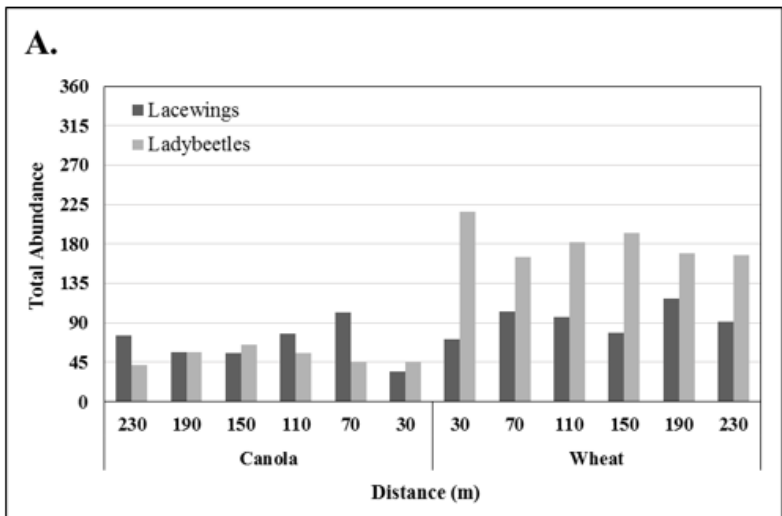
Appendix H. 2011 Omega North Diverse abundances over 5 sample periods for green lacewings and lady beetles (A, C) in canola-wheat fields and canola-pasture fields, respectively, and abundances for two lady beetle species (B, D) in the two landscape types.
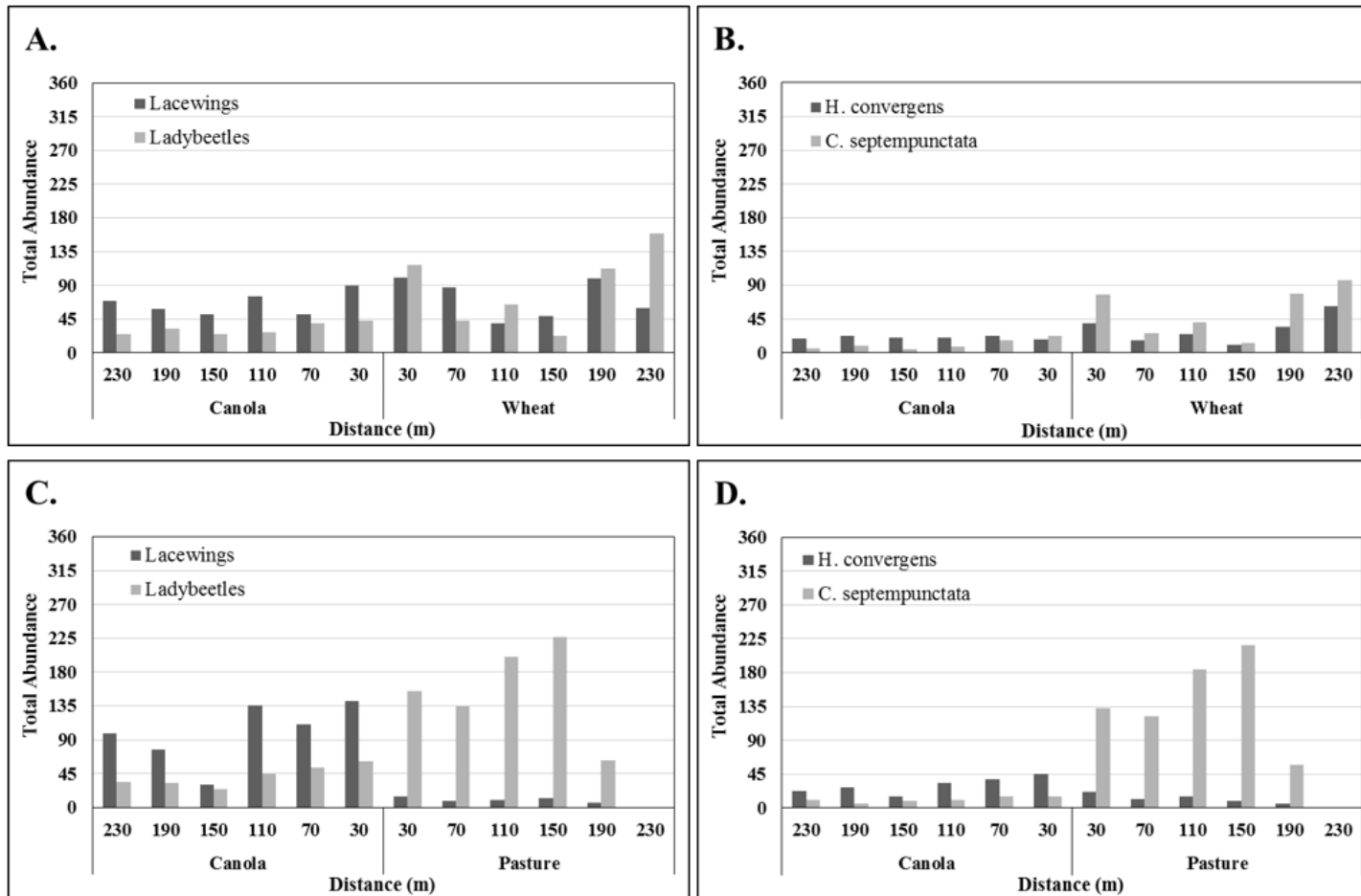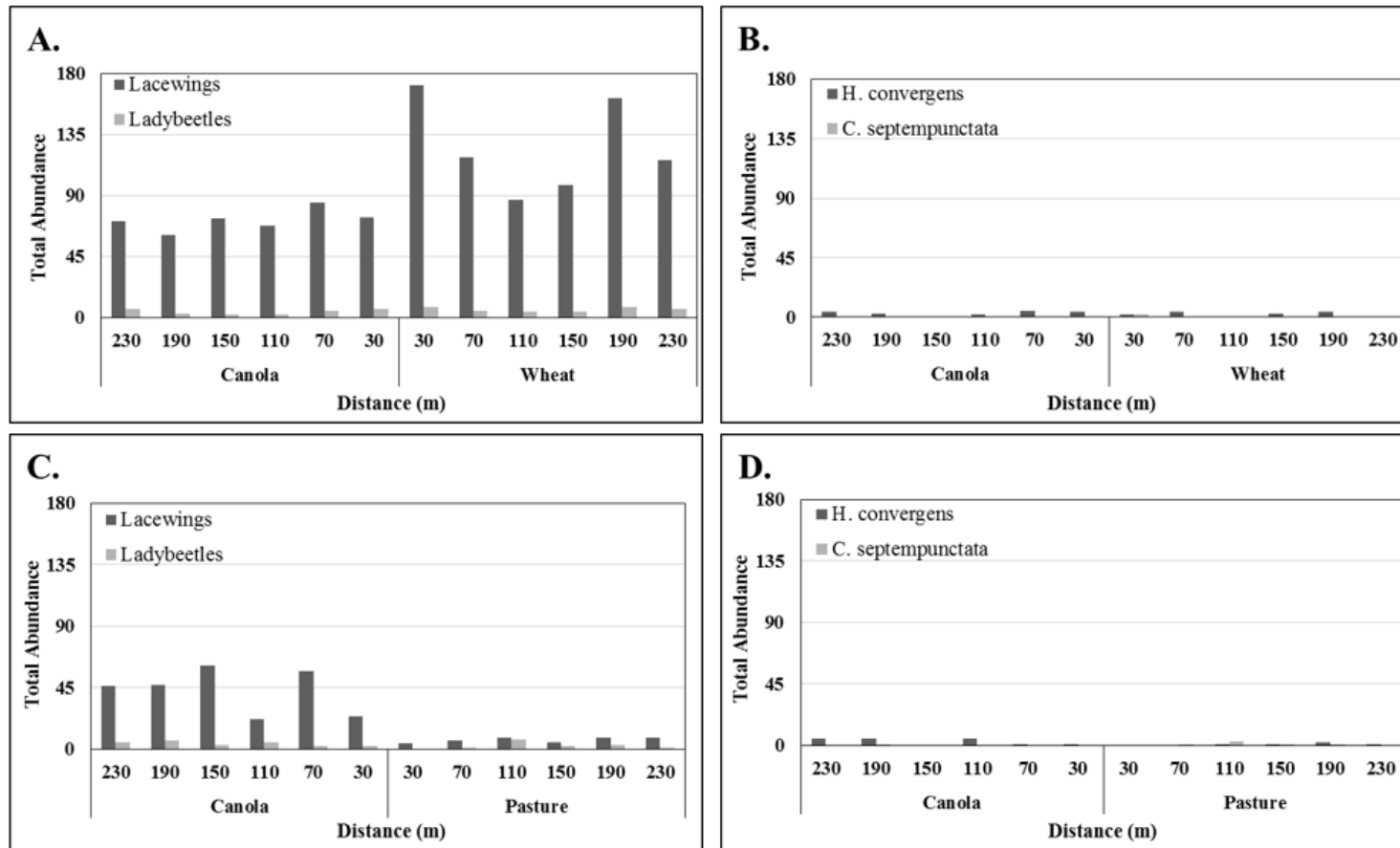
Appendix I. 2012 Carmen Diverse abundances over 1 sample period for green lacewings and lady beetles (A, C) in canola-wheat fields and canola-pasture fields, respectively, and abundances for two lady beetle species (B, D) in the two landscape types.
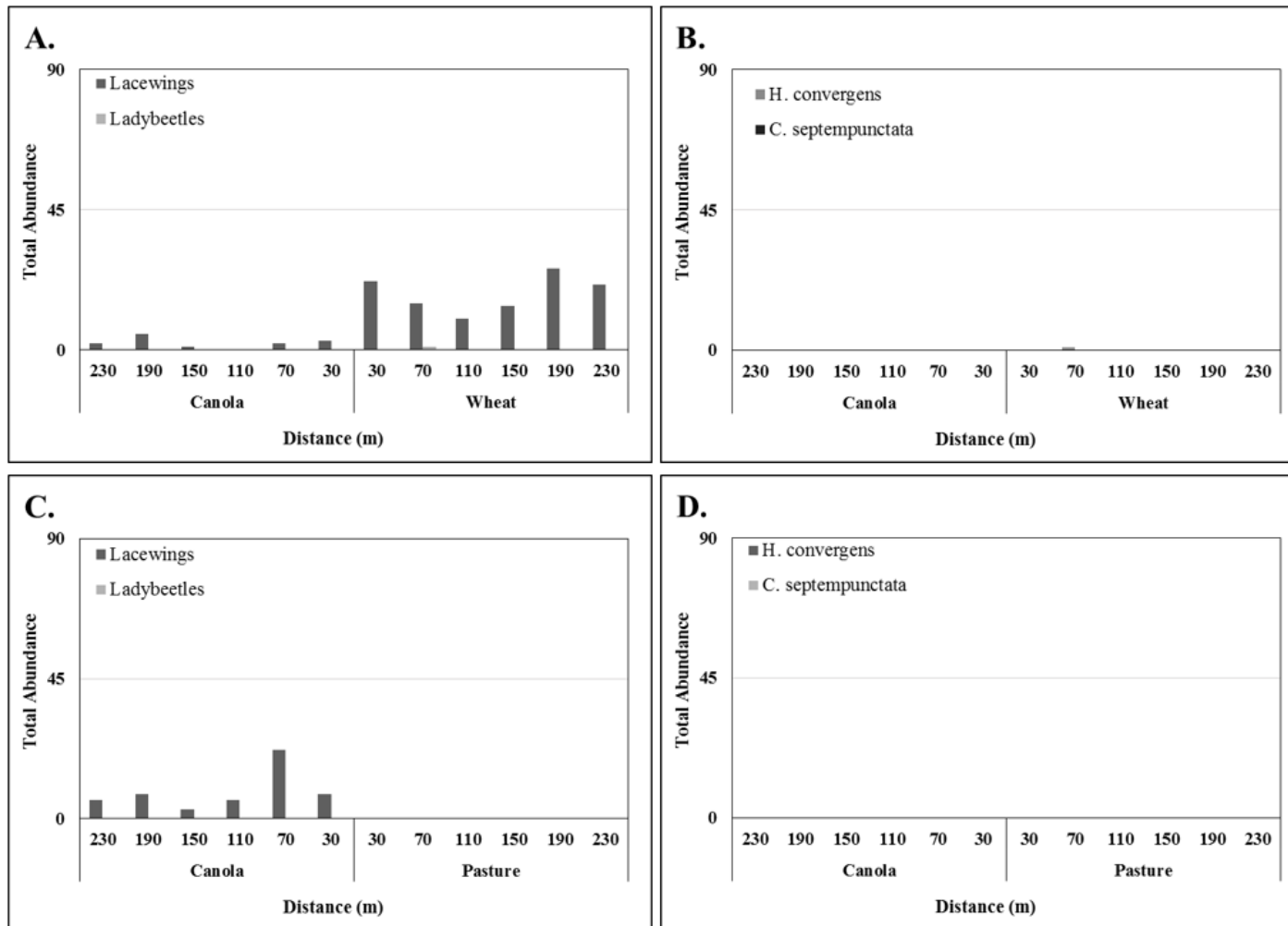
Appendix J. 2012 Drummond North Diverse abundances over 5 sample period for green lacewings and lady beetles (A, C) in canola-wheat fields and canola-pasture fields, respectively, and abundances for two lady beetle species (B, D) in the two landscape types.

Appendix K. 2012 Drummond North Simple abundances over 5 sample periods for green lacewings and lady beetles (A) and two predominant lady beetle species (B).

**Appendix L.** 2012 Drummond South Diverse abundances over 5 sample period for green lacewings and lady beetles (A, C) in canola-wheat fields and canola-pasture fields, respectively, and abundances for two lady beetle species (B, D) in the two landscape types.

Appendix M. 2012 Drummond South Simple abundances over 5 sample periods for green lacewings and lady beetles (A) and two predominant lady beetle species (B).

Appendix N. 2012 Lamont Diverse abundances over 5 sample period for green lacewings and lady beetles (A, C) in canola-wheat fields and canola-pasture fields, respectively, and abundances for two lady beetle species (B, D) in the two landscape types.
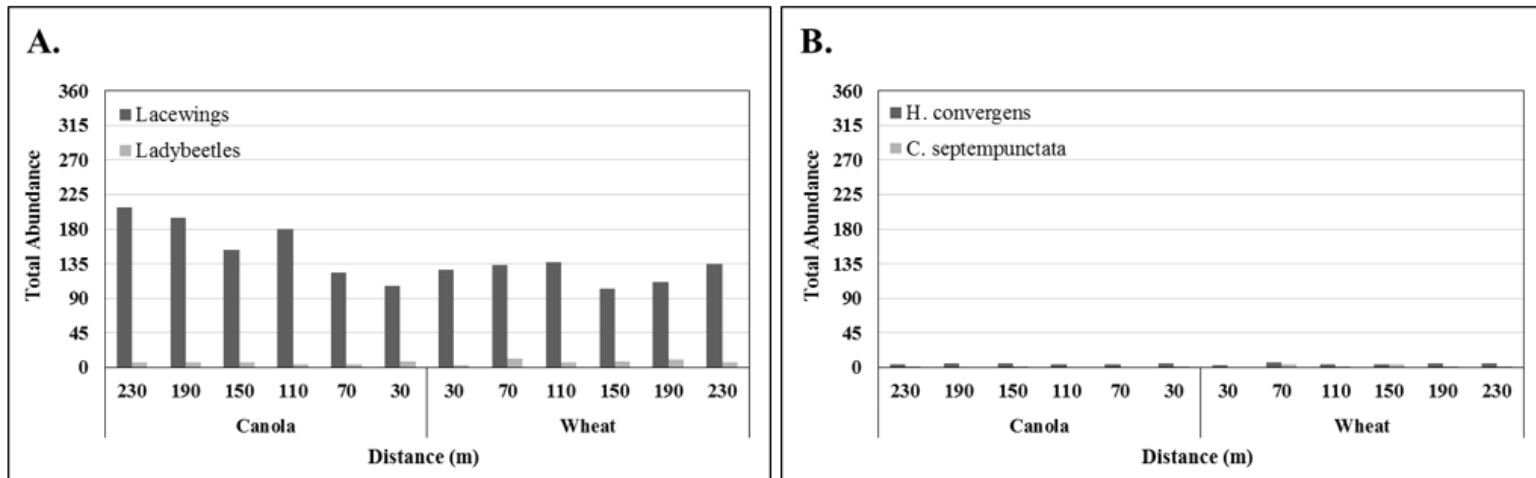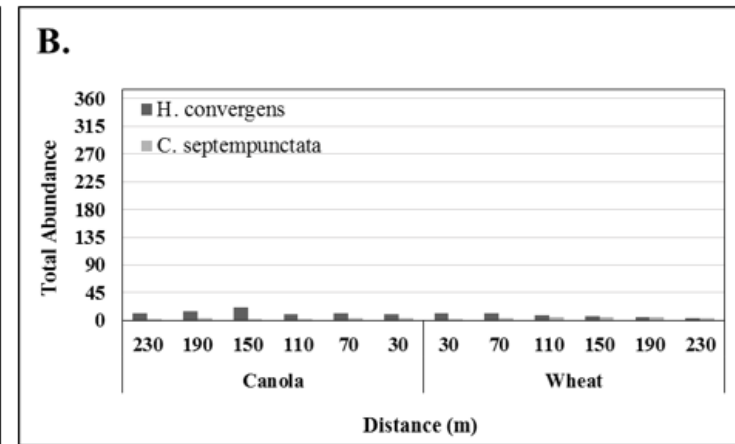
Appendix O. 2012 Okeene North Simple abundances over 5 sample periods for green lacewings and lady beetles (A) and two predominant lady beetle species (B).

Appendix P. 2012 Okeene South Simple abundances over 5 sample periods for green lacewings and lady beetles (A) and two predominant lady beetle species (B).

Appendix Q. 2013 Alva Diverse abundances over 2 sample period for green lacewings and lady beetles (A, C) in canola-wheat fields and canola-pasture fields, respectively, and abundances for two lady beetle species (B, D) in the two landscape types.

Appendix R. 2013 Carrier Diverse abundances over 6 sample period for green lacewings and lady beetles (A, C) in canola-wheat fields and canola-pasture fields, respectively, and abundances for two lady beetle species (B, D) in the two landscape types.
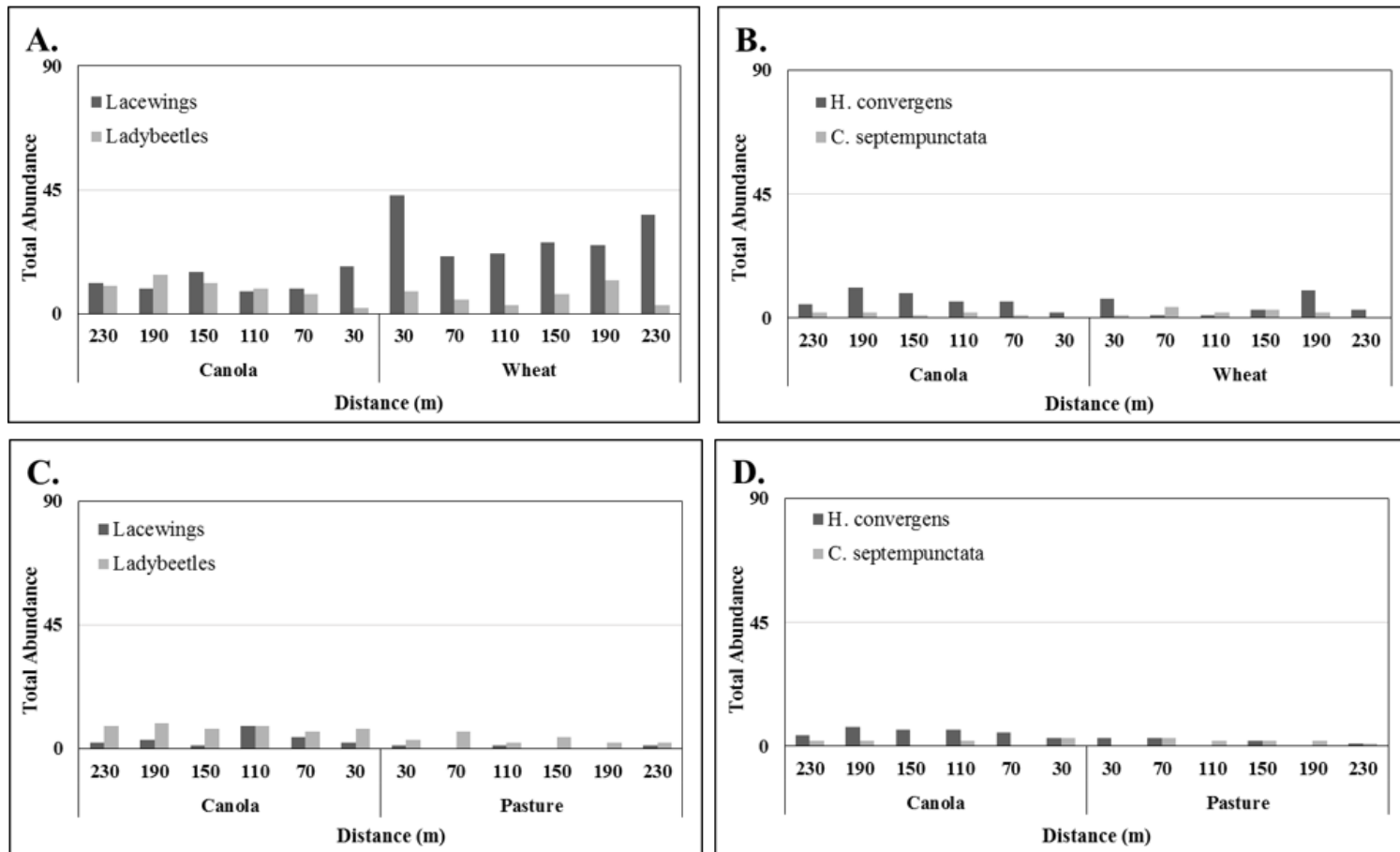
Appendix S. 2013 Drummond Fox Simple abundances over 6 sample periods for green lacewings and lady beetles (A) and two predominant lady beetle species (B).
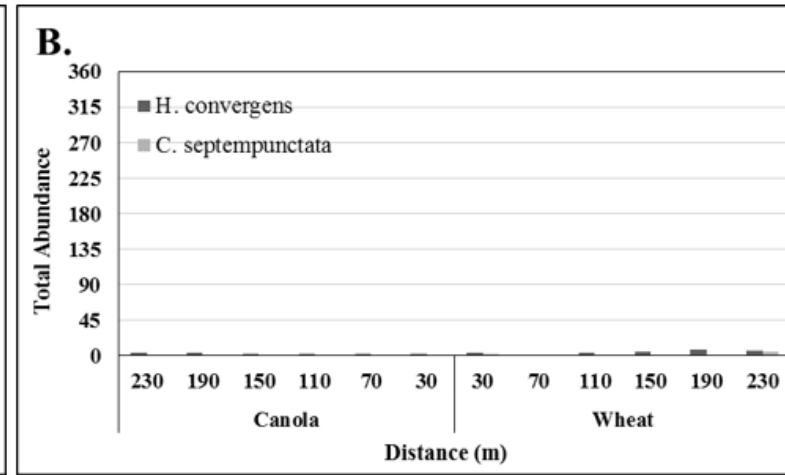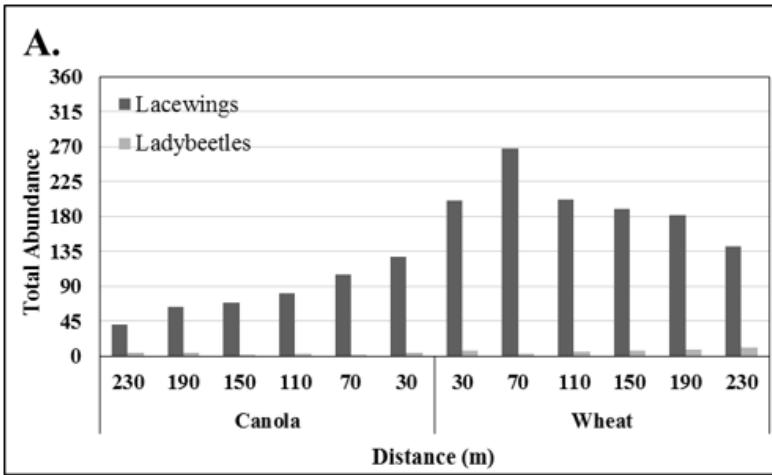
Appendix T. 2013 Drummond Simple abundances over 6 sample periods for green lacewings and lady beetles (A) and two predominant lady beetle species (B).

Appendix U. 2013 Okeene North abundances over 6 sample periods for green lacewings and lady beetles (A) and two predominant lady beetle species (B).
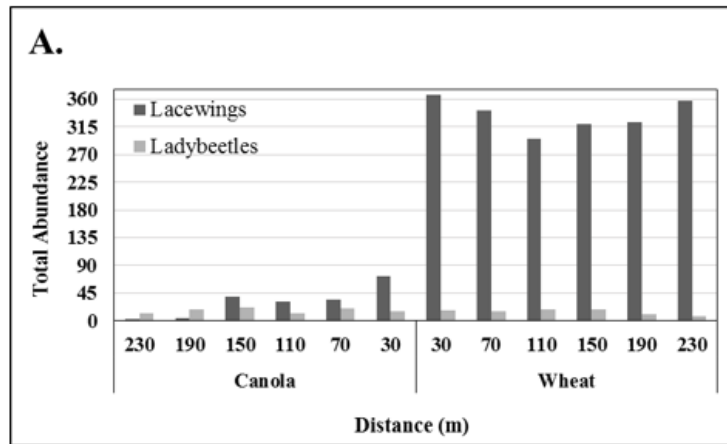
Appendix V. 2013 Okeene South abundances over 6 sample periods for green lacewings and lady beetles (A) and two predominant lady beetle species (B).
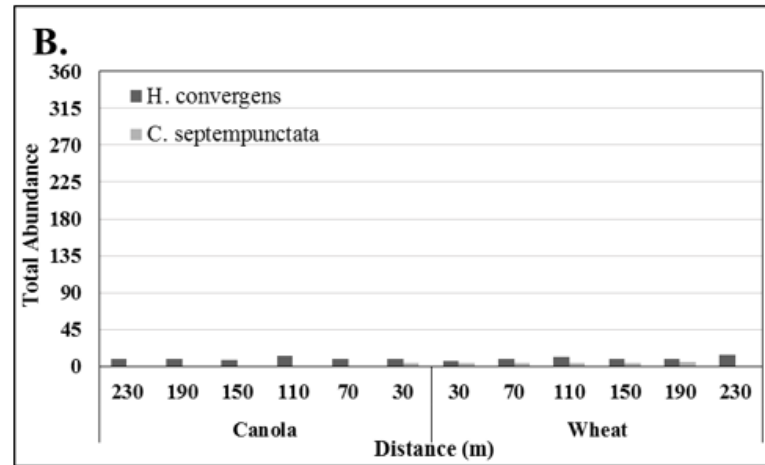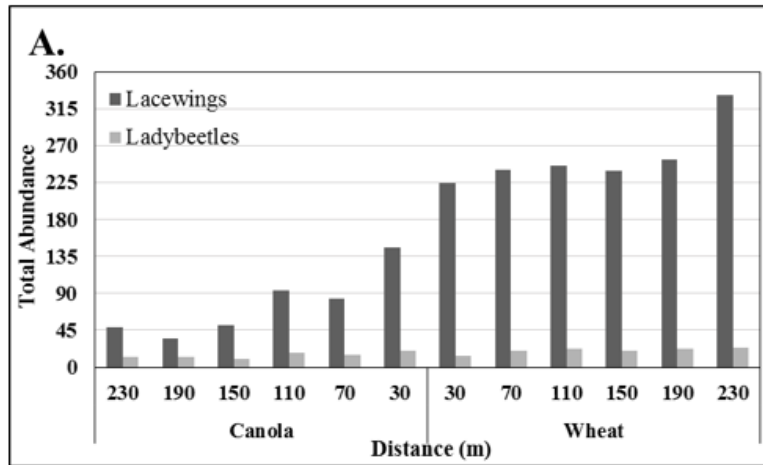
Appendix W. Total positive ELISA results for Chrysopidae, Coccinellidae, *Hippodamia convergens*, and *Coccinella septempunctata* for each field type in 2011, 2012, and 2013. Egg whites were sprayed in both canola fields (CW and CP), cows' milk in wheat, and soy milk in pasture.
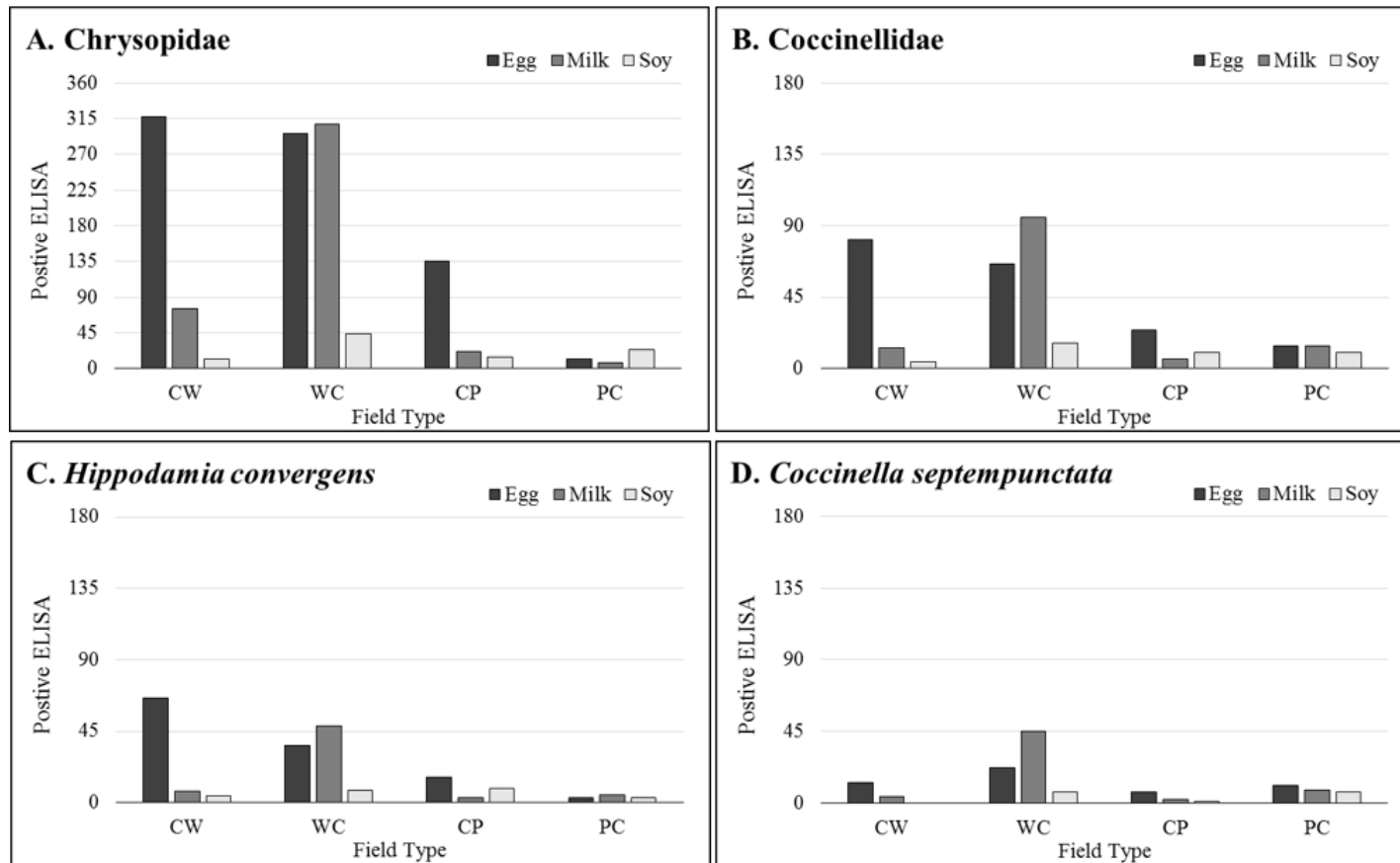
VITA

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