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BEHAVIOURAL RESPONSES OF AN INTRAGUILD PREDATOR: THE EFFECTS OF INTRAGUILD PREDATION ON POPULATION DYNAMICS

by

Angela G. Brommit

A Thesis
Submitted to the Faculty of Graduate Studies through Biological Sciences in Partial Fulfillment of the Requirements for the Degree of Master of Science at the University of Windsor

Windsor, Ontario, Canada

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ABSTRACT

Omnivores feed at more than one trophic level and affect population dynamics within communities. Behavioural observations demonstrated that the omnivore, *Dicyphus hesperus*, preferred more vulnerable herbivores as prey over intraguild prey. Regardless of prey type, *D. hesperus* exhibited a Type II functional response indicating that the omnivore was limited by the time taken to find prey at low densities and limited by the time taken to eat prey at high densities. Satiation limited the rate of consumption of prey, however, satiation of *D. hesperus* occurred at different rates for different types of prey.

Population level experiments showed that the presence of *D. hesperus* had a neutral effect on spider mite population regulation and enhanced whitefly population suppression. Although the presence of the omnivore had a negative effect on intraguild prey populations, herbivore suppression was not disrupted. The omnivore's preference for herbivorous insects resulted in a low incidence of intraguild predation.
CO-AUTHORSHIP STATEMENT

I certify that this thesis, and the research to which it refers, are the product of my own work, and that any ideas or quotations from the work of other people, published or otherwise, are fully acknowledged in accordance with the standard referencing practices of this discipline. I acknowledge the input of my supervisors Dr. S.L. VanLaerhoven and Dr. D.R. Gillespie in the preparation of each of the manuscripts presented within. I certify that the manuscripts were written by me and that the input of the co-authors occurred during the development of the methodology and the editorial process.
ACKNOWLEDGEMENTS

I would like to thank my co-supervisors Drs. Sherah VanLaerhoven and Dave Gillespie for this opportunity, as well as their guidance and feedback throughout this project. Thank you to my committee members Drs. Maria Cioppa and Hugh MacIsaac. I would like to thank my lab mates Jennifer Rosati, Jonathon Bennett and Henry Murillo for their input and advice. I would like to thank Dan Edelstein for his statistical help. I would like to thank the NSERC Biocontrol Network and the University of Windsor for funding support. Lastly, I thank my family and friends for their support over the years.
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Chapter 1

General introduction

In natural environments, natural enemies – predators, parasitoids, and pathogens – are major biotic factors that limit the population levels of phytophagous insects, thereby maintaining phytophagous insects at lower levels than would be expected given the abundance of their food sources (Holt and Lawton 1993). Species within a community are usually linked by direct and indirect interactions including various forms of predation and competition (Holt 1977). Understanding the multiple predator effects that govern herbivore population dynamics will further our understanding of species interactions and ultimately, community structure.

The goal of this thesis was to investigate the mechanisms governing omnivorous interactions within natural enemy communities, specifically intraguild predation and the outcomes on population dynamics. The population dynamics between predator and prey species are governed by numerous mechanisms including (but not limited to) predator functional and numerical responses to prey density, availability of food resources (both target and nontarget prey species), prey preference, and the degree of polyphagy (Symondson et al. 2002). Some of these mechanisms will be discussed in more detail in subsequent sections.

Types of Omnivory

Omnivores are often extreme generalists feeding on resources that belong to different trophic levels; therefore, they are able to persist in variable environments (Coll and Guershon 2002). Omnivorous species were once thought to be rare in food webs because it was believed that omnivory destabilized local food webs (Pimm and Lawton
1978). Empirical observations have, however, shown that omnivory is very common in both natural and managed communities of terrestrial arthropods (Polis et al. 1989; Polis 1991; Coll and Guershon 2002). Zoophytophagous omnivory (Figure 1-1), as defined by diet, can be facultative or obligatory depending on the relative importance of prey and plant materials needed to develop (Coll and Guershon 2002). Facultative omnivores are opportunistic and supplement their diet to increase fitness. For example, western flower thrips *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae) are primarily herbivorous, but they will consume the eggs of *Phytoseiulus persimilis* Athias-Henriot (Acarina: Phytoseiidae) (Jenssen et al. 2003). Obligate omnivores derive some benefit from plants that cannot be derived from prey and they must, therefore, consume both resources to complete their diet. For example, Gillespie and McGregor (2000) found that plant feeding by *Dicyphus hesperus* Knight (Heteroptera: Miridae) was required in order to acquire water necessary for prey feeding and development.

Omnivores can be defined in various ways depending on their resource use and interactions with other members of the food web. True omnivores, or zoophytophagous omnivores, are consumers that feed on both animal and vegetable materials (Coll and Guershon 2002), whereas trophic omnivory is defined as feeding on more than one trophic level (Pimm and Lawton 1978) (Figure 1-1). True omnivory, therefore, fits within the more broad definition of trophic omnivory. Trophic omnivory also includes intraguild predation and cannibalism, in which predators consume potential competitors (Coll and Guershon 2002) (Figure 1-1). Over the next few sections I will review intraguild predation and its effects on population dynamics.
Intraguild predation

Intraguild predation is a widespread and important interaction in many natural communities (Polis et al. 1989). Members of a guild are organisms within a community that use similar resources and thus are potential competitors. Intraguild predation occurs between members of the same guild when these members engage in predator-prey interactions with one another (Polis et al. 1989) (Figure 1-1). Most predators eat what they can subdue as diets are usually established by size ranges and predators eat from all trophic levels (Polis et al. 1989; Polis 1991; Cohen et al. 1993). Therefore, most generalist intraguild predators are larger than their intraguild prey.

Intraguild predation offers a number of benefits for the intraguild predator. First, predation on guild members, as with any food item, yields nutritional gains. As trophic level increases, there is an increase in nitrogen within the organism, thus feeding on prey from higher trophic levels supplies more nitrogen resources to the predator with fewer prey items (Deniro and Epstein 1981). Second, feeding on other guild members results in a direct reduction of competition. Finally, an intraguild predator, in the case of mutual predation, can consume the more vulnerable life stages of its own future intraguild predators, thereby eliminating them (Polis et al. 1989). It is clear that the impact of intraguild predation on population dynamics is more complex than predation or competition alone.

There are two types of intraguild predation: coincidental intraguild predation and omnivorous intraguild predation (Polis et al. 1989). Coincidental intraguild predation generally occurs when an intraguild predator attacks an herbivore that has already been attacked by an intermediate predator (i.e. a parasitoid), thereby killing the intermediate
predator via its offspring. Omnivorous intraguild predation occurs when the intraguild predator consumes the intermediate predator directly (Polis et al. 1989; Rosenheim and Harmon 2006). It has been suggested that omnivorous intraguild predation would have a greater potential to disrupt biological control than coincidental intraguild predation in cases where the predator does not distinguish between parasitized and unparasitized hosts (Rosenheim and Harmon 2006).

Rosenheim and Harmon (2006) did a meta-analysis of the literature using 25 published articles to determine: (1) whether intraguild predation led to elevated herbivore populations and (2) whether coincidental intraguild predation was less disruptive to biological control than omnivorous intraguild predation. Rosenheim and Harmon (2006) noted that, across all studies, intraguild predators had variable effects on herbivore populations ranging from dramatic decreases in herbivore populations to outbreaks in herbivore populations and this duality in the literature led to an overall effect size that was not different from zero. They concluded that experimental literature on intraguild predation in insect communities does not support any single, dominant outcome for herbivore populations. Given that the effect of intraguild predators is not unilateral, other mechanisms, such as the type of intraguild predator present, may be responsible for the variation in population outcomes.

Rosenheim and Harmon (2006) propose that for both coincidental and omnivorous intraguild predation, preference for the intermediate predator (intraguild prey) (Figure 1-1) relative to the herbivore will be a key determinant in the overall effect on population dynamics. They found that the coincidental intraguild predator, which chooses between parasitized and unparasitized prey, most often did not distinguish
between parasitized and unparasitized prey early during the parasitoid’s development and developed an increasing preference for unparasitized hosts as the parasitoid matured. Therefore, their results suggested that the addition of a coincidental intraguild predator to herbivore/intermediate predator systems would result in a lower overall herbivore population. Predicting preference for an omnivorous intraguild predator is more difficult. Rosenheim and Harmon (2006) found that the effects of an omnivorous intraguild predator were more varied than the effects of a coincidental intraguild predator. Omnivorous intraguild predators were just as likely to elevate herbivore density as they were to decrease herbivore density. The role of intraguild predation in population dynamics is clearly complex, but it is an important interaction as scientists continue to exploit natural enemies for the biological control of herbivorous insects in natural and managed systems.

Most naturally occurring herbivorous insect populations are attacked by both monophagous and polyphagous natural enemies (Hassell and May 1986), yet biological control practices were rooted in classical biocontrol by specialist natural enemies (Symondson et al. 2002). The role of specialists versus generalist predators as effective biocontrol agents has long been debated (Koss and Synder 2005). Specialists employ a search and destroy strategy and have higher prey mortality per natural enemy. Generalists subsist on nontarget food resources allowing them to persist in the environment. Therefore, they are always present and may reduce the magnitude of pest outbreaks and/or maintain pests at a lower population after specialists have reduced pest numbers. Omnivorous generalists, due to their persistence at low prey densities, may decouple the dynamics of omnivore and prey populations (Coll and Guershon 2002).
other words, fluctuations in specific prey populations would have no effect on omnivore populations. This is in contrast to the highly coupled population dynamics between specialist predators and their prey. There is growing evidence that generalist predators can effectively suppress pest populations (Symondson et al. 2002; Chang and Kareiva 1999). In addition, generalist predators can simultaneously attack different unrelated prey species and impact several pest populations.

The different strategies used by specialists and generalists, when combined together, may have an additive effect that further reduces herbivore populations. For this reason, the debate pertaining to generalist and specialist predators has shifted from concerns of superiority to potential interference between natural enemies when generalists and specialists are used together in multi-species systems of biocontrol. Intraguild predation may result in the elimination of the intermediate predator (specialist) or coexistence of the intraguild predator and intermediate predator. For coexistence to occur, the intermediate predator must be superior to the intraguild predator at exploiting shared resources (Polis et al. 1989). Rosenheim and Harmon (2006) note, however, that there is no reason why the intraguild predator could not be the best competitor (and therefore the best biological control agent) and simultaneously improve herbivore suppression while exploiting the intermediate predator as a food source. This situation, of course, would be unstable and eventually lead to the exclusion of the intermediate predator and/or the shared prey.

Another concern is that the predation pressure experienced by a particular herbivore species may be alleviated when their omnivorous natural enemies also feed on other prey species or other host plants (Coll and Guershon 2002). Therefore, the impact
of a generalist species upon a single species of prey will also depend on the composition of the other species in the generalist’s diet (Holt 1977). Before adding an omnivore to an herbivore/intermediate predator system, it is important to determine the alternative food sources that would be available to a generalist predator and examine any prey preferences the generalist may have.

**Prey preference of an omnivore**

Despite the potential number of prey species available to generalist predators, they often have preferences for certain prey species which could have important consequences for prey populations (Richards 1982). A predator’s preference for different prey species may be an active choice and/or a passive selection (Pastorok 1981). An active choice preference is dependent on the selectivity of the predator for different prey species. A passive selection preference is based on prey vulnerability (i.e. prey escape responses such as mobility), thus it is the prey that determines the outcome of the encounter, not a choice made by the predator (Pastorok 1981).

In addition, preference may be influenced not only by the abundance and susceptibility of the prey species in question, but also by the abundance and susceptibility of alternative prey species (Holt and Lawton 1994). For example, if a generalist predator has no preference for species A or species B, then the indirect effects of species A on species B and species B on species A will depend on their abundance such that an increase in species A would relax predation on species B and vise versa (Holt and Lawton 1994). If a generalist predator has a preference for either species, then the outcome of the interactions between the prey species and the shared natural enemy becomes more complicated.
Prey preference by an intraguild predator predicts three outcomes on herbivore population dynamics. First, if the intraguild predator prefers the intraguild prey (intermediate predator) over the shared prey, then the herbivore could be released from predation. Second, if the intraguild predator prefers the herbivore over the intraguild prey, then control of the herbivore population will be enhanced. Third, if the intraguild predator exhibits no preference between the herbivore prey or intraguild prey, then control of the herbivore population may not be impacted depending on the ratio of herbivore to intraguild prey as the intraguild predator would have the highest predation on the most numerous prey.

So far, previous studies have supported the above predictions. Snyder and Ives (2001) found that pea aphid (*Acyrthosiphon pisum* (Harris) (Homoptera: Aphididae)) populations were released from regulation by *Aphidius ervi* Haliday (Hymenoptera: Braconidae) when the generalist predator *Pterostichus melanarius* (Illiger) (Coleoptera: Carabidae) preferred aphids parasitized by *A. ervi* to unparasitized aphids. Heinz and Nelson (1996) found that population suppression of *Bemisia argentifolii* (Powell and Bellows) (Homoptera: Aleyrodidae) was increased when the generalist predator *Delphastus pusillus* Leconte (Coleoptera: Coccinellidae) showed a partial preference for the pest insect compared to the parasitoid. McGregor and Gillespie (2005) found no preference in *Dicyphus hesperus* Knight (Heteroptera: Miridae) for parasitized and unparasitized whitefly (*Trialeurodes vaporariorum* Westwood (Homoptera: Aleyrodidae)) and consequently found no influence of intraguild predation on whitefly populations when the generalist predator *D. hesperus* was present with the parasitoid *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae).
In addition to predator prey preference, the mobility of prey may affect its vulnerability to predation. If an intermediate predator is more mobile than an herbivore, the herbivore could be more vulnerable to predation by the intraguild predator than the intermediate predator. For example, mobility could increase predator success rate by increasing the encounter rate or it could decrease success rate by enabling the prey to escape (Eubanks and Denno 2000).

The nutritional quality of food items may also influence feeding choices of omnivores (Agrawal et al. 1999). Interestingly, this includes plant quality, as this can affect the diet of omnivores as well. The western flower thrips, *F. occidentalis*, showed increased predation on spider mite (*Tetranychus turkestani* Ugarov and Nikolski (Acari: Tetranychidae)) eggs and decreased herbivory when plant quality was reduced (Agrawal et al. 1999). Janssen et al. (2003) found that an increase in plant quality resulted in a decrease in predation of *Phytoseiulus persimilis* eggs by western flower thrips. Eubanks and Denno (1997) found that when high quality bean pods were made available, omnivorous big-eyed bugs (*Geocoris* spp. (Hemiptera: Lygaeidae)) shifted their behaviour away from predation, thus resulting in an increase in aphid numbers. In contrast, Weiser and Stamp (1998) found that it may be maladaptive for zoophytophagous species to feed only on plants when prey are abundant, as supplementing a prey diet with plant material may have negative effects (i.e. lower developmental rates, lower survival rates) on the performance of omnivores. It is clear that in order to predict the efficiency of a generalist predator as a biocontrol agent, it is important to understand its prey preference and how preferences can affect the population dynamics of prey and other natural enemies.
The effectiveness of a predator population on the suppression of a pest population will also depend, to some extent, on the searching efficiency of the predator population. The searching efficiency of a predator population is influenced by many factors including (but not limited to) prey density (functional response), prey distribution, predator density (numerical response) and any alternative prey or competing predator species (Hassell 1978). The numerical response of a predator is a predator’s ability to increase its numbers with increasing prey density. Functional response is defined as changes in the prey consumption rate by predators with respect to changes in prey density over a given time interval (Solomon 1949; Holling 1959a; Holling 1959b). The functional response curve is defined by two parameters, the attack coefficient and the handling time. The attack coefficient (or instantaneous search rate) is the probability that a given predator will encounter a given prey during its searching lifetime (Hassell 1978). The attack coefficient is influenced by many aspects such as predator versus prey mobility, success rate of the predator, distribution of the prey, size and complexity of the arena, and motivation of the predator. The handling time refers to the amount of time spent chasing, killing, eating and digesting a single prey item (Hassell 1978). Holling (1959a) recognized three types of functional response curves: Type I where the response rises linearly to a plateau; Type II where the number of prey eaten per predator increases decelerating to a plateau (the maximum number of prey that can be eaten by each predator per unit time); and Type III where the response is represented be a sigmoidal increase in hosts attacked.

Holling’s (1959b) disc equation assumes that predators are primarily time-limited (handling time and search time), but this is not always the case. Predators may also be
digestion limited (Sabelis 1992, van Rijn et al. 2005). As an example, if a predator requires 10 minutes to consume a prey item, they could potentially consume 6 prey items in one hour, assuming there was unlimited prey and no satiation. However, the same predator may, in reality, only consume 4 prey in one hour as a result of the time it takes to empty the gut. It is clear that satiation can influence foraging behaviour, and therefore, it is important that satiation patterns for predators be determined for alternate prey in order to understand the predation process.

Species within a community are usually linked by direct and indirect interactions through interspecific competition. Interspecific competition is defined as the negative effects that one species has upon another by consuming or controlling access to a resource that is limited in availability or through susceptibility to shared predators and can be mediated through interference competition, exploitative competition, apparent competition and cannibalism (Holt 1977). Interference competition occurs when one species reduces the access of a competitor to a limited resource through behavioural interactions. Exploitation competition occurs when two consumer species indirectly compete for a limited shared resource (Polis et al. 1989).

Apparent competition arises when multiple prey species increase a predator population, thereby indirectly limiting each others densities (Holt 1977). For example, a food-limited predator, when feeding on a single prey type, is maintained at a certain equilibrium density and in turn, maintains the prey at a certain density. However, the appearance of a second prey species may increase the density of the predator thereby increasing predation levels on both prey species, causing both prey species to equilibrate at lower densities or causing the exclusion of one prey species from the community (Holt
Thus, predator density is partly determined by the diversity and abundance of prey species (Holt 1977).

The concept of apparent competition may be important in biological control. According to predator-mediated apparent competition theory, the addition of an intraguild predator should not disrupt suppression of herbivore populations. If the intraguild predator consumes the occasional intermediate predator, the effect may be an increase in the density of the intraguild predator, which would result in greater predation pressure on the herbivore population, ultimately resulting in a lower equilibrium density of the pest species. Herne and Putman (1966) posited that *Panonychus ulmi* (Koch) (Acari: Tetranychidae) was maintained at a low density in peach orchards by the phytoseiid *Typhlodromus caudiglans* Schuster (Acari: Phytoseiidae) even though *T. caudiglans* frequently subsidized its diet with alternative prey. *Typhlodromus caudiglans* was able to increase its density by consuming additional food sources, thereby increasing the predation pressure on the pest species and is an example of successful pest suppression through predator-mediated apparent competition.

**Summary**

As biological control practices increasingly advance toward the use of assemblages of natural enemies in pest reduction, it becomes ever more important to understand the impact of intraguild interactions on population dynamics. The theoretical predictions regarding the effects of intraguild predation on the stability of food webs are mixed. The addition of an intraguild predator to a food web may decrease the stability of the system resulting in the exclusion of either the intermediate predator or the intraguild predator, or it could stabilize the system (Polis and Holt 1992; Holt and Polis 1997;
Mylius et al. 2001). Therefore, it is important that we back up theoretical predictions with empirical evidence.

Some important mechanisms to explore when examining the potential impact of an omnivorous predator on population dynamics are predator preferences for intraguild prey versus shared prey, searching efficiency of a predator population and the effects of interspecific competition. Over the next three chapters, I will address several of these issues with the goal of gaining a deeper understanding of multi-trophic level interactions between omnivores, specialist predators and their prey. I begin with a chapter on the use of observational studies to examine the mechanisms of prey preference by omnivores. I assess the preference of the intraguild predator (omnivore) for the intraguild prey versus shared prey via encounter rate, predation rate, success ratio, and handling time and I compare the time invested in prey feeding and searching for prey with the time invested in plant feeding. In the third chapter, I measure an omnivore’s ability to impact population dynamics in a multi-species system using functional response curves and satiation patterns. The fourth chapter is an empirical study on population dynamics. I measure the population dynamics of the intermediate predator and the shared prey with and without the presence of an omnivore (intraguild predator) and alternative food source. Finally, I conclude with a chapter that ties the concepts and findings of the previous chapters together.
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Predator \rightarrow \textbf{Intraguild predator}

Herbivore \rightarrow \textbf{Omnivore}

Plant

Herbivore

Plant

a) True omnivory

b) Trophic omnivory

Figure 1-1: Hypothetical food webs depicting true omnivory and trophic omnivory.

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Chapter 2

Determining prey preference in an omnivore: Predation behaviour of an intraguild predator in the presence of intraguild prey and shared prey

Introduction

Omnivory is very common in terrestrial arthropods in both natural and managed communities (Polis et al. 1989; Polis 1991; Coll and Guershon 2002). Omnivores are often extreme generalists feeding on resources that belong to different trophic levels, therefore, they are able to persist in variable environments (Coll and Guershon 2002). Omnivory can be defined in various ways depending on their resource use and interactions with other members of the food web. True omnivores, or zoophytophagous omnivores, are consumers that feed on both animal and plant food sources (Coll and Guershon 2002) whereas trophic omnivory is defined as feeding on more than one trophic level (Pimm and Lawton 1978). True omnivory, therefore, fits within the definition of trophic omnivory. Trophic omnivory also includes intraguild predation, in which predators consume potential competitors (Coll and Guershon 2002).

Intraguild predation is a widespread and important interaction in many natural communities (Polis et al. 1989). Members of a guild are organisms within a community that use similar resources and thus are potential competitors. Intraguild predation occurs between members of the same guild when these members engage in predator-prey interactions with one another (Polis et al. 1989). Intraguild predation offers a number of benefits for the intraguild predator such as nutritional gains and a reduction in the number of competitors (Polis et al. 1989).
The nutritional quality of food items may influence feeding choices of omnivores (Agrawal et al. 1999). Nitrogen is a critical nutrient required for the growth and development of organisms (Fagan et al. 2002). The nitrogen content in herbivorous insects is generally lower than that of predatory insects and may be a limiting growth factor for predatory insects in terrestrial ecosystems (Fagan et al. 2002). As trophic levels increase, there is an increase in nitrogen (Deniro and Epstein 1981). It has been suggested that predator performance is enhanced by eating more nitrogen rich prey via intraguild predation (Denno and Fagan 2003). Furthermore, nitrogen content varies among herbivore species, suggesting that some herbivores are more beneficial to eat than others (Fagan et al. 2002). McGregor et al. (1999) found that whitefly (Trialeurodes vaporariorum Westwood (Homoptera: Aleyrodidae)) were a better-quality food item for the growth and development of Dicyphus hesperus Knight (Heteroptera: Miridae) compared to spider mites (Tetranychus urticae Koch (Acari: Tetranychidae)). Diet choice by an intraguild predator, therefore, may play an important role in determining the population dynamics of potential prey.

Despite the potential number of prey species available, generalist predators often have discernable preferences for certain insect species which could have important consequences for prey populations (Richards 1982). A predator's preference for different prey species may be an active choice by the predator and/or a passive selection due to the vulnerabilities of the prey (Pastorok 1981). Mobility is a prey trait that may affect a prey's vulnerability to predation. If an intraguild prey is more mobile than an herbivorous prey, the herbivore could be more vulnerable to predation by the intraguild or higher order predator than the intraguild prey if the herbivore is unable to escape the...
higher order predator (Eubanks and Denno 2000). Alternately, a mobile intraguild prey may be encountered by the higher order predator more frequently, thereby increasing the frequency that prey type is killed by the predator compared to a less mobile or stationary herbivorous prey type.

Prey preference by an intraguild predator predicts three outcomes on herbivore population dynamics. First, if the intraguild predator prefers the intraguild prey over the shared prey, then the herbivore could be released from predation. Second, if the intraguild predator prefers the herbivore over the intraguild prey, then regulation of the herbivore population will be enhanced. Third, if the intraguild predator exhibits no preference between the herbivore prey or intraguild prey, then regulation of the herbivore population may not be impacted depending on the ratio of herbivore to intraguild prey as the intraguild predator would have the highest predation on the most numerous prey.

It is clear that prey preference of an intraguild predator can have important consequences on intraguild and herbivore prey population dynamics. This can have important consequences for regulation of herbivorous species in natural and managed ecosystems. Biological control is the use of natural enemies - predators, parasitoids, and pathogens - to maintain low levels of phytophagous insect populations. Biological control practices are moving toward the use of assemblages of natural enemies in pest reduction, however, the ability of specialist and generalist natural enemies to coexist in managed ecosystems is still unclear (Abram 2006). One thing that is clear is the importance of determining the alternative food sources that would be available to a generalist predator and to examine any prey preferences the generalist may have before adding a generalist predator to an herbivore/intermediate predator system.
Dicyphus hesperus is a zoophytophagous mirid that feeds not only a variety of prey, but also on a variety of host plants including mullein (Verbascum thapsus L. (Scrophulariaceae)) and tomato (Lycopersicon esculentum Mill. (Solanaceae)) (McGregor et al. 1999; Gillespie and McGregor 2000; Sanchez et al. 2004). This generalist omnivore is currently used as a biological control agent to suppress pest populations of greenhouse whitefly (T. vaporariorum) and two-spotted spider mites (T. urticae) in tomato greenhouses in British Columbia, Ontario and Quebec, Canada (McGregor et al. 1999; Sanchez et al. 2003). Also present in this system are the specialist natural enemies of those pest species, namely the parasitoid Encarsia formosa Gahan (Hymenoptera: Aphelinidae) and the predatory mite Phytoseiulus persimilis Athias-Henriot (Acarina: Phytoseiidae). As a higher order predator, D. hesperus engages in intraguild predation by preying upon the specialist natural enemies of the herbivore species. In this chapter, feeding preferences of an intraguild predator (omnivore) for intraguild prey versus shared prey are assessed. In addition, behavioural activities such as the amount of time spent prey feeding, searching for prey, plant feeding and resting and grooming are compared for different sets of prey species.

Materials and Methods

Insect origins and rearing

Predator

Dicyphus hesperus were originally collected from white stem hedge nettle, Stachys albens A. Gray (Lamiaceae) in the foothills of the Sierra Nevada Mountains at an elevation of ca. 300 m near Woody, CA USA (Lat 35°42.9'N, long 116°49.1'W).
Colonies were maintained on tobacco plants, *Nicotiana tabacum* L. (Solanaceae) at 24 °C with a 16 h light and 8 h dark diel cycle. Adult *D. hesperus* oviposited on caged plants for 7 days, prior to removal of adults from the plants. Eggs were allowed to hatch and nymphs were fed previously frozen eggs of *Ephesitia kuehniella* Zeller (Lepidoptera: Pyralidae) *ad libitum*, until development to adult. This procedure allowed for synchronized cohorts of adults.

**Prey**

Two-spotted spider mites were reared on tomato leaves. *Encarsia formosa* and *P. persimilis* were ordered from Koppert Biological Systems, Scarborough, Ontario, Canada and greenhouse whitefly were obtained from Applied Bionomics, Sidney, British Columbia, Canada. Only the pupal stages of greenhouse whitefly and *E. formosa* were used during these experiments.

**Experimental Setup**

Adult *Dicyphus hesperus* females (1 week old) were starved for 72 h prior to the start of each experiment. Arenas consisted of a piece of tomato leaf (Early Cascade Hybrid) placed upside down in a 5 cm diameter Petri dish. Predatory females were provided two treatments of prey consisting of either spider mites and *P. persimilis* (20 of each), whitefly and *E. formosa* (20 of each), or whitefly and spider mites (20 of each) randomly placed on the tomato leaf. The following behaviours were recorded for 2 h from the start of each experiment using EthoLog (Ottoni, 2000): time spent searching (walking), number of times *D. hesperus* encountered prey and which prey type was encountered (spider mite, *P. persimilis*, whitefly, *E. formosa*), time spent eating prey (spider mite, *P. persimilis*, whitefly, *E. formosa*) and time spent plant feeding. Each *D. hesperus* female
was only used once. Each treatment was replicated 20 times. Prey were not replaced during the experiment.

Statistical analysis

Encounter rate was calculated for each species by dividing the total number of encounters for each species by the total time spent searching (i.e. walking). Predation rate for each species was measured as the number of prey killed per hour. The success ratio for each species was calculated as the number of encounters followed by feeding, divided by the total number of encounters with that prey. Handling time for each species was measured as the mean time spent eating one prey item. These data were analyzed using a MANOVA (SPSS v. 13.0). To compare differences in time allocated to the different behaviours paired t-tests with a Bonferroni correction was used with an alpha of \( P = 0.017 \) (SPSS v. 13.0).

Results

*Dicynopus hesperus* had a higher predation rate (\( F_{1,36} = 6.391, P = 0.016 \)) and marginally higher success ratio (\( F_{1,36} = 3.123, P = 0.086 \)) for whitefly pupae than for *E. formosa* pupae when presented at the same time (Table 2-1). No differences in encounter rate (\( F_{1,36} = 0.545, P = 0.465 \)) and handling time (\( F_{1,36} = 1.633, P = 0.210 \)) were measured for *D. hesperus* attacking whitefly and *E. formosa* (Table 2-1).

Mean encounter rate was greater for *D. hesperus* attacking spider mites than *P. persimilis* (Table 2-2: \( F_{1,35} = 15.635, P < 0.001 \)). In addition, *D. hesperus* had a higher predation rate (\( F_{1,35} = 229.123, P < 0.001 \)) and success ratio (\( F_{1,35} = 92.361, P < 0.001 \)) for spider mites than for *P. persimilis* when offered together (Table 2-2). There was no
difference in mean handling time for *D. hesperus* attacking spider mites and *P. persimilis* (Table 2-2: $F_{1,35} = 2.295, P = 0.139$).

*Dicyphus hesperus* had a higher encounter rate ($F_{1,33} = 9.372, P = 0.004$), predation rate ($F_{1,33} = 67.448, P < 0.001$), success ratio ($F_{1,33} = 12.050, P = 0.001$) and handling time ($F_{1,33} = 101.392, P < 0.001$) for whitefly pupae than for spider mites when present at the same time (Table 2-3).

In the presence of whitefly and *E. formosa*, *D. hesperus* spent more time prey feeding than searching for prey (Table 2-4: $t_{1,19} = -8.27, P < 0.001$) and plant feeding (Table 2-4: $t_{1,19} = -11.24, P < 0.001$). In the presence of whitefly and *E. formosa*, *D. hesperus* spent more time searching for prey than plant feeding (Table 2-4: $t_{1,19} = 3.16, P = 0.005$).

In the presence of spider mites and *P. persimilis*, *D. hesperus* spent more time prey feeding than searching for prey (Table 2-5: $t_{1,19} = -4.53, P < 0.001$) and plant feeding (Table 2-5: $t_{1,19} = -19.14, P < 0.001$). In the presence of spider mites and *P. persimilis*, *D. hesperus* spent more time searching for prey than plant feeding (Table 2-5: $t_{1,19} = 25.33, P < 0.001$).

In the presence of spider mites and whitefly, *D. hesperus* spent more time prey feeding than searching for prey (Table 2-6: $t_{1,19} = -43.13, P < 0.001$) and plant feeding (Table 2-6: $t_{1,19} = -34.95, P < 0.001$). In the presence of spider mites and whitefly, *D. hesperus* spent marginally more time searching for prey versus plant feeding (Table 2-6: $t_{1,19} = 2.57, P = 0.019$).
Discussion

The intraguild predator fed on both the intraguild prey and the shared prey when presented simultaneously. The presence of spider mites and whitefly did not prevent predation on *P. persimilis* and *E. formosa*. Therefore, *D. hesperus* and *P. persimilis* interact by both competing for prey and through intraguild predation by *D. hesperus* on *P. persimilis*. Similarly, *D. hesperus* and *E. formosa* interact by both competing for prey and through intraguild predation. In both cases the intraguild predator had a higher predation rate and success ratio for the shared prey than for the intraguild prey despite equal numbers of both prey types. Thus, intraguild predation on the specialist natural enemy (intraguild prey) is likely to be minimized in natural settings as the herbivore is present in much higher numbers than the intraguild prey. Higher encounter rate for the herbivore prey, combined with a preference for the herbivore prey, suggests that competition for the herbivore prey is likely to be the more important interaction regulating population dynamics between these species.

*Dicynphus hesperus* had a preference for spider mites over the intraguild predator *P. persimilis*. This preference appears to be caused by trait differences in the prey types (passive selection) as opposed to being an active choice of the predator. *Dicynphus hesperus* had a higher encounter rate for the herbivorous mite than for the predaceous mite. This was partly due to the fact that the predaceous mites would often wander on and off the leaf surface, whereas the herbivorous mites tended to stay on the leaf surface. Therefore, as *D. hesperus* searched the leaf, it encountered more of the herbivorous mites. This indicates that the more mobile *P. persimilis* had an advantage over spider mites by decreasing the number of times it encountered the intraguild predator. In
addition, the predatory mites that were encountered but not killed escaped by running away from *D. hesperus*, resulting in a lower success ratio for this prey type.

Venzon et al. (2001) studied the foraging behaviour of an intraguild predator, *Orius laevigatus* (Fieber) (Heteroptera: Anthocoridae), with an intraguild prey, *P. persimilis*, and a shared prey, spider mites, on cucumber leaf discs in Petri dishes. They found no difference between predation rates of spider mites and *P. persimilis* by the intraguild predator. However, the density of *P. persimilis* was four times lower than that of spider mites and they multiplied the predation rate of *P. persimilis* by four to compensate for the lower densities. Therefore, they assumed that predation by the intraguild predator would increase by a magnitude of 4 if the density was increased by an equal magnitude. This may have been a false assumption and could explain the difference between their results and the results of this study. Venzon et al. (2001) also found an equal encounter rate between spider mites and *P. persimilis*, but they followed the same procedure as described above. In contrast to the results of this study, Venzon et al. (2001) found the same success ratio for the intraguild predator consuming spider mites and *P. persimilis*, but the handling times for the two prey types differed. This may be attributed to differences between *O. laevigatus* and *D. hesperus* (the intraguild predator species) in their ability to subdue the different prey species.

Differences in prey mobility do not explain the differential predation by *D. hesperus* on the herbivore prey, whitefly, in the presence of *E. formosa* parasitized whitefly, as both prey types were immobile. Although encounter rate for whitefly and *E. formosa* were similar, the omnivore killed more whitefly than parasitized whitefly. There are two possible explanations. The first possibility is that parasitized whitefly were
harder to feed upon by the omnivore. Parasitized pupae have a hardened cuticle, which may have made cuticle penetration more difficult for the omnivore (Hoelmer et al. 1994). In addition, as a parasitoid matures inside the whitefly pupae, the fluid contents of the whitefly are used up and air pockets form inside the pupal case. These air spaces may interfere with fluid uptake by *D. hesperus* (Hoelmer et al. 1994).

Castañé et al. (2004) found that two other mirid predators, *Dicyphus tamaninii* Wagner and *Macrolophus caliginosus* Wagner, had a strong preference for unparasitized whitefly pupae versus those parasitized by *E. formosa*. In contrast, McGregor and Gillespie (2005) measured intraguild predation by *D. hesperus* on greenhouse whitefly pupae versus pupae that had been parasitized by *E. formosa* and concluded that although *D. hesperus* readily consumed parasitized pupae, they did not display a preference between the two prey types. Labbe et al. (2006) using the same host-parasitoid-predator system measured predation by *D. hesperus* in non-choice experiments and observed that *D. hesperus* did not preferentially attack parasitized versus unparasitized whiteflies.

The second possibility is that the omnivore was able to distinguish between parasitized and unparasitized whitefly, and chose unparasitized whitefly. The nutritional quality of food items may influence feeding choices of omnivores (Agrawal et al. 1999). Nitrogen is a critical nutrient required for the growth and development of organisms. The nitrogen content in herbivorous insects is generally lower than that of predatory insects and may be a limiting growth factor for predatory insects in terrestrial ecosystems (Fagan et al. 2002). As trophic levels increase, there is an increase in nitrogen, which may promote intraguild predation, as predator fitness is predicted to increase by eating more nitrogen rich prey (Denno and Fagan 2003). Thus, *D. hesperus* might be expected to
choose the specialist natural enemies as prey. However, Matsumura et al. (2004) evaluated the relationship between predator performance and prey nitrogen content using the intraguild predator *Pardosa littoralis* Banks (Araneae: Lycosidae), when fed a diet of intraguild prey *Grammonota trivittata* Banks (Araneae: Linyphiidae), or *Prokelisia dolus* Wilson (Hemiptera: Delphacidae) as the herbivorous prey. They found predator performance decreased as a result of intraguild predation and concluded that predator performance was likely based on foraging efficiency rather than nitrogen content.

Similarly, Kagata and Katayama (2006) demonstrated that *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) (an intraguild predator) expressed a decrease in growth when fed *Coccinella septempunctata* L. (Coleoptera: Coccinellidae) (intraguild prey) compared to aphids (*Acyrthosiphon pisum* Harris and *Aphis craccivora* Koch (Homoptera: Aphididae)) (herbivorous prey). They offered two explanations for the reduction in predator performance when predators engaged in intraguild predation. First, there was a cost associated with intraguild predation. In this case, the intraguild predator did not have a large advantage over the intraguild prey and risked becoming the intraguild prey. Also, prey consumption decreased because the intraguild predator was less efficient at capturing and subduing the intraguild prey compared to the herbivorous prey. Second, nitrogen-use efficiency decreased when fed the intraguild prey compared to the herbivorous prey. Kagata and Katayama (2006) suggested that if *C. septempunctata* larvae have more nitrogen than *H. axyridis* requires then *H. axyridis* would release nitrogen in excess of their requirements in order to maintain nitrogen homeostasis. Furthermore, nitrogen content varies among herbivore species, suggesting that some herbivores are more beneficial to eat than others (Fagan et al. 2002).
McGregor et al. (1999) found that whitefly were a better-quality food item for the growth and development of *D. hesperus* compared to spider mites. Fittingly, this study found that *D. hesperus* had a higher encounter rate, predation rate and success ratio for whitefly than for spider mites when offered together. This suggests that *D. hesperus* has a strong preference for whitefly over spider mites and that *D. hesperus* is foraging optimally.

Although whitefly are a superior food for the growth and development of *D. hesperus* compared to spider mites, there may be another explanation for the observed preference between these two herbivores. Whitefly pupae are immobile, whereas spider mites are mobile. In this study the immobile whitefly pupae remained randomly placed on the tomato leaflet throughout the trial, whereas spider mites were able to move about. Even though they did not move off the leaf, they did redistribute themselves in such a manner that resulted in *D. hesperus* encountering them less often compared to the whitefly pupae. This indicates that the increased mobility of spider mites provides them with an advantage over whitefly pupae, by decreasing the number of times they are encountered by the intraguild predator. It is hard to say whether spider mite mobility or the nutritional gains of whitefly were responsible for the higher success ratio of *D. hesperus* for whitefly. Although spider mites are mobile, they are not that fast and they are considerably smaller than *D. hesperus*. In actuality, *D. hesperus*, upon encountering spider mites, would often be the one to walk away, perhaps in search of higher quality whitefly.

*Dicypthus hesperus* is an obligate omnivore, as plant feeding is required in order to acquire water necessary for prey feeding (via extra-oral digestion) and nutrients that enhance growth and development (Gillespie and McGregor 2000). During extra-oral
digestion digestive enzymes are injected into prey and the liquefied contents are withdrawn through the stylets. As plants can be an alternative food source for *D. hesperus*, it was important to examine the amount of time *D. hesperus* spent prey feeding and searching for prey versus plant feeding. *Dicyphus hesperus* spent more time prey feeding and searching for prey than plant feeding under all three prey combinations.

Eubanks and Denno (1999) advocate that zoophytophages that endure periods of prey scarcity by feeding on plants usually have lower survival rates than individuals feeding consistently on prey. This is consistent with Sanchez et al. (2004) who compared the success of developing *D. hesperus* nymphs raised on prey versus mullein and found that on mullein without prey 30% of nymphs completed development, whereas about 90% completed development on most host plants with prey. Although *D. hesperus* can survive on mullein and, in fact, plant feeding is required for prey feeding and development (Gillespie and McGregor 2000), prey items are a higher quality food item. In other words, it is beneficial for *D. hesperus* to incorporate both animal and plant material into its diet rather than subsist on plant material alone when prey are also available. In addition, Roitberg et al. (2005) examined the physical impact of plant feeding on the mouthparts of an omnivore and the possible loss of feeding efficiency on prey as a result. They demonstrated that a stylet-feeding insect, *D. hesperus*, suffers mandibular stylet wear with age as a result of plant feeding and suggested that stylet wear will reduce prey feeding efficiency. Mandibular stylet wear as well as the nutritional gains of prey feeding when prey are present assist in explaining why more time was invested by *D. hesperus* in prey feeding and searching for prey than in plant feeding.
Water is lost continually through extra-oral digestion and plant feeding is one way to regain water (Pollard 1988; Gillespie and McGregor 2000). Gillespie and McGregor (2000) posit that plant feeding in *D. hesperus* to gain water may occur in proportion to predation levels irrespective of prey quantity or quality. This explains why *D. hesperus* did not spend all its time prey feeding or searching for prey.

In summary, the presence of the shared prey did not prevent predation on the intraguild prey. However, the intraguild predator, through active choice and passive selection, preferred the herbivore prey over the intraguild prey. In addition, the intraguild predator expressed a preference for one herbivorous species over the other. This study suggests that differential escape success, nutritional quality and other prey defenses of the intraguild prey and the shared prey are important traits to consider when determining preference and the effect of intraguild predation on a prey population. Given the greater number of herbivore prey than intraguild prey in real life food webs, and the preference for herbivore prey, the population dynamics of the intraguild predator and intraguild prey are more likely regulated by competitive interactions than intraguild predation. With respect to regulation of managed agro-ecosystems, the addition of the omnivore *D. hesperus* should result in enhanced herbivore population suppression, with minimal intraguild interactions.
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history traits in the zoophytophagous predator *Dicyphus hesperus*. Entomologia Experimentalis et Applicata 112: 7-19

Table 2-1: Mean (±SE) encounter rate, predation rate, success ratio and handling time for starved *Dicyphus hesperus* females when provided whitefly and *Encarsia formosa* pupae.

<table>
<thead>
<tr>
<th></th>
<th>Whitefly</th>
<th><em>E. formosa</em></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Encounter rate</td>
<td>26.14 ± 6.34/h</td>
<td>20.42 ± 3.30/h</td>
<td><em>F</em>₁,₃₆ = 0.545 <em>P</em> = 0.465</td>
</tr>
<tr>
<td>Predation rate</td>
<td>2.50 ± 0.34/h</td>
<td>1.27 ± 0.24/h</td>
<td><em>F</em>₁,₃₆ = 6.391 <em>P</em> = 0.016</td>
</tr>
<tr>
<td>Success ratio</td>
<td>0.71 ± 0.06</td>
<td>0.49 ± 0.07</td>
<td><em>F</em>₁,₃₆ = 3.123 <em>P</em> = 0.086</td>
</tr>
<tr>
<td>Handling time</td>
<td>12.28 ± 1.27 min</td>
<td>9.41 ± 1.89 min</td>
<td><em>F</em>₁,₃₆ = 1.633 <em>P</em> = 0.210</td>
</tr>
</tbody>
</table>
Table 2-2: Mean (±SE) encounter rate, predation rate, success ratio and handling time for starved *Dicyphus hesperus* females when provided two-spotted spider mites and *Phytoseiulus persimilis*.

<table>
<thead>
<tr>
<th></th>
<th>Spider mites</th>
<th>P. persimilis</th>
</tr>
</thead>
</table>
| Encounter rate | 12.88 ± 0.73/h | 7.56 ± 0.92/h | $F_{1,35} = 15.635$ $P < 0.001$  
| Predation rate  | 4.37 ± 0.13/h     | 1.15 ± 0.17/h     | $F_{1,35} = 229.123$ $P < 0.001$  
| Success ratio   | 0.91 ± 0.02       | 0.41 ± 0.05       | $F_{1,35} = 92.361$ $P < 0.001$  
| Handling time   | 5.32 ± 0.31 min   | 4.70 ± 0.24 min   | $F_{1,35} = 2.295$ $P = 0.139$  

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Table 2-3: Mean (±SE) encounter rate, predation rate, success ratio and handling time for starved *Dicyphus hesperus* females when provided two-spotted spider mites and whitefly pupae.

<table>
<thead>
<tr>
<th></th>
<th>Spider mites</th>
<th>Whitefly</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Encounter rate</td>
<td>20.23 ± 3.5/h</td>
<td>62.73 ± 10.15/h</td>
<td>$F_{1, 33} = 9.372 \ P = 0.004$</td>
</tr>
<tr>
<td>Predation rate</td>
<td>1.12 ± 0.22/h</td>
<td>4.02 ± 0.21/h</td>
<td>$F_{1, 33} = 67.448 \ P &lt; 0.001$</td>
</tr>
<tr>
<td>Success ratio</td>
<td>0.68 ± 0.07</td>
<td>0.95 ± 0.03</td>
<td>$F_{1, 33} = 12.050 \ P = 0.001$</td>
</tr>
<tr>
<td>Handling time</td>
<td>3.17 ± 0.23 min</td>
<td>12.07 ± 0.74 min</td>
<td>$F_{1, 33} = 101.392 \ P &lt; 0.001$</td>
</tr>
</tbody>
</table>
Table 2-4: Mean (±SE) time spent prey feeding, searching and plant feeding for starved *Dicyphus hesperus* females when provided whitefly and *Encarsia formosa* pupae.

<table>
<thead>
<tr>
<th>Behavior</th>
<th>Mean (±SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Prey feeding</td>
<td>1.18 ± 0.08/h a</td>
</tr>
<tr>
<td>Searching</td>
<td>0.44 ± 0.05/h b</td>
</tr>
<tr>
<td>Plant feeding</td>
<td>0.23 ± 0.03/h c</td>
</tr>
</tbody>
</table>

Means in each column followed by the same letter are not significantly different (P > 0.017).
Table 2-5: Mean (±SE) time spent prey feeding, searching and plant feeding for starved *Dicyphus hesperus* females when provided two-spotted spider mites and *Phytoseiulus persimilis*.

<table>
<thead>
<tr>
<th>Behavior</th>
<th>Mean (±SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Prey feeding</td>
<td>0.95 ± 0.05/h a</td>
</tr>
<tr>
<td>Searching</td>
<td>0.77 ± 0.03/h b</td>
</tr>
<tr>
<td>Plant feeding</td>
<td>0.18 ± 0.02/h c</td>
</tr>
</tbody>
</table>

Means in each column followed by the same letter are not significantly different (P > 0.017).
Table 2-6: Mean (±SE) time spent prey feeding, searching and plant feeding for starved *Dicyphus hesperus* females when provided two-spotted spider mites and whitefly pupae.

<table>
<thead>
<tr>
<th>Behavior</th>
<th>Mean (±SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Prey feeding</td>
<td>1.66 ± 0.04/ha</td>
</tr>
<tr>
<td>Searching</td>
<td>0.17 ± 0.02/h</td>
</tr>
<tr>
<td>Plant feeding</td>
<td>0.11 ± 0.02/h</td>
</tr>
</tbody>
</table>

Means in each column followed by the same letter are not significantly different (P > 0.017). The amount of time spent searching for prey versus plant feeding was marginally different (P = 0.019).
Chapter 3

Functional response of an omnivore: Intraguild prey versus shared prey

Introduction

Most naturally occurring herbivorous insect populations are attacked by both monophagous and polyphagous natural enemies (Hassell and May 1986) and these predator-prey relationships can be exploited to regulate herbivorous insect populations both in natural environments and in managed systems. Omnivory, which is defined as feeding on more than one trophic level (Pimm and Lawton 1978) is a common form of predation (Polis et al. 1989; Polis 1991; Coll and Guershon 2002). Intraguild predation is a type of omnivory defined as predation that occurs between organisms that exploit a common resource (Polis et al. 1989). Omnivores are often extreme generalists that feed on a variety of resources and with such flexible diets are able to persist in variable environments (Coll and Guershon 2002).

The nutritional quality of food items influences feeding choices of omnivores (Agrawal et al. 1999). Nitrogen is a critical nutrient required for the growth and development of organisms (Fagan et al. 2002). The nitrogen content in herbivorous insects is generally lower than that of predatory insects and may be a limiting growth factor for predatory insects in terrestrial ecosystems (Fagan et al. 2002). As trophic levels increase, there is an increase in nitrogen and this may promote intraguild predation (Denno and Fagan 2003). Furthermore, nitrogen content varies among herbivore species, suggesting that some herbivores are more beneficial to eat than others (Fagan et al. 2002). McGregor et al. (1999) found that greenhouse whitefly (Trialeurodes vaporariorum...
Westwood (Homoptera: Aleyrodidae)) were a better-quality food item for the growth and development of *Dicypus hesperus* Knight (Heteroptera: Miridae) compared to two-spotted spider mites (*Tetranychus urticae* Koch (Acari: Tetranychidae)). Diet choice by an intraguild predator, therefore, may play an important role in determining the population dynamics of potential prey.

Predation pressure experienced by a focal herbivore may be alleviated when omnivorous natural enemies feed on other prey species or other host plants (Coll and Guershon 2002). The impact of a generalist predator on the population dynamics of any one species of prey will also depend on the demographics of other species in the generalist’s diet (Holt 1977). Before adding an omnivore to an herbivore/intermediate predator system, it will be important to determine the alternative food sources that would be available to a generalist predator and examine the impact of the generalist predator on population dynamics of each of the potential prey species within the food web.

The ability of a predator population to regulate an herbivore population depends to some extent on the searching efficiency of the predator population. The searching efficiency of a predator population is influenced by many factors including (but not limited to) prey density (functional response), prey distribution, predator density (numerical response) and any alternative prey or competing predator species (Hassell 1978). Numerical response of a predator is its ability to increase its numbers with increasing prey density and occurs between generations. Functional response of a predator is defined as changes in prey consumption rate with changes in prey density and occurs within a generation (Solomon 1949; Holling 1959a; Holling 1959b). Within this
chapter, the functional response of an omnivorous predator to prey density in a homogeneous environment is evaluated.

The functional response curve is defined by two parameters, the attack coefficient and the handling time. The attack coefficient (or instantaneous search rate) is the probability that a given predator will encounter a given prey during its searching lifetime (Hassell 1978). The attack coefficient is influenced by many aspects such as predator versus prey mobility, success rate of the predator, distribution of the prey, size and complexity of the arena, and motivation of the predator. The handling time refers to the amount of time spent chasing, killing, eating and digesting a single prey item (Hassell 1978).

Holling (1959a) recognized three types of functional response curves: Type I where the response rises linearly to a plateau; Type II where the number of prey eaten per predator increases decelerating to a plateau (the maximum number of prey that can be eaten by each predator per unit time); and type III where the number of prey consumed is slow initially, usually attributed to learning by the predator to recognize and find the prey, followed by a rapid increase in prey consumption per predator, which then decelerates to a plateau.

Holling’s (1959b) disc equation, which describes the functional response curve, assumes that predators are primarily time-limited (handling time and search time), but this is not always the case. Predators may also be digestion limited (Sabelis 1992, van Rijn et al. 2005). In other words, if a predator requires 10 minutes to consume a prey item they could potentially consume 6 prey items in one hour assuming there was unlimited prey and no satiation. However, the same predator may, in reality, only
consume 4 prey in one hour as a result of gut fullness. It is clear that satiation influences foraging behaviour and therefore it is important that satiation patterns for predators be determined for alternate prey in order to understand the predation process.

*Dicyphus hesperus* is a zoophytophagous mirid that feeds not only on a variety of prey, but also on a variety of host plants including mullein (*Verbascum thapsus* L. (Scrophulariaceae)) and tomato (*Lycopersicon esculentum* Mill. (Solanaceae)) (McGregor et al. 1999; Gillespie and McGregor 2000; Sanchez et al. 2004). *Dicyphus hesperus*, a generalist predator, is currently used as a biological control agent to suppress pest populations of greenhouse whitefly (*T. vaporariorum*) and two-spotted spider mites (*T. urticae*) in tomato greenhouses in British Columbia, Ontario and Quebec, Canada (McGregor et al. 1999; Sanchez et al. 2003). Also present in this system are the specialist natural enemies of those pest species, namely the parasitoid *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) and the predatory mite *Phytoseiulus persimilis* Athias-Henriot (Acarina: Phytoseiidae). *Dicyphus hesperus* also engages in intraguild predation by preying on the specialist natural enemies of the pest species.

The goal of this study was to compare the functional response of *D. hesperus* when feeding on greenhouse whitefly, two-spotted spider mites, *E. formosa*, and *P. persimilis*, in order to estimate the potential effect of intraguild predation when *D. hesperus* is used in combination with *E. formosa* and *P. persimilis* to control whitefly and spider mites on tomato plants in greenhouses. The following questions were addressed: (1) Are the functional response parameters different for a predator when they feed on different prey? (2) What is the potential effect of intraguild predation by *D. hesperus*?
Materials and Methods

Insect origins and rearing

Predator

_Dicyphus hesperus_ were originally collected from white stem hedge nettle, _Stachys albens_ A. Gray (Lamiaceae) in the foothills of the Sierra Nevada Mountains at an elevation of ca. 300 m near Woody, CA USA (Lat 35°42.9’N, long 116°49.1’W).

Colonies were maintained on tobacco plants, _Nicotiana tabacum_ L. (Solanaceae) at 24 °C with a 16 h light and 8 h dark diel cycle. Adult _D. hesperus_ oviposited on caged plants for 7 days, prior to removal of adults from the plants. Eggs were allowed to hatch and nymphs were fed previously frozen eggs of _Ephesitia kuehniella_ Zeller (Lepidoptera: Pyralidae) _ad libitum_, until development to adult. This procedure allowed for synchronized cohorts of adults.

Prey

Two-spotted spider mites were reared on tomato leaves. _Encarsia formosa_, and _P. persimilis_ were supplied by Koppert Biological Systems, Scarborough, Ontario, Canada and greenhouse whitefly were supplied by Applied Bionomics, Sidney, British Columbia, Canada. Only the pupal stages of greenhouse whitefly and _E. formosa_ were used during these experiments.

Experimental Setup

Functional response

Prior to each experiment, 1 week old adult _D. hesperus_ females were fed the test prey for 24 h and then starved for 24 h. Arenas consisted of a piece of tomato leaf (Early Cascade Hybrid) placed upside down in a 5 cm diameter Petri dish. Different prey
densities were offered to *D. hesperus* females. The densities tested were 1, 3, 6, 9, 15, 18, 30, 40, and 50 for all prey types (whitefly, *E. formosa*, spider mites, and *P. persimilis*). One individual *D. hesperus* female and one density of prey species was tested per arena, and the number of dead prey was recorded 6 h after omnivore release. Each predatory female was only used once. Every prey density was replicated 10 times for each of the 4 prey types. Prey were not replaced during the experiment.

Data were fit to a modified Holling’s (1959b) disc equation, the “random-predator” equation (Rogers, 1972), which is considered more appropriate as it incorporates the depletion of prey over time (Hazzard and Ferro, 1991):

$$\frac{Na}{TP} = \frac{aN}{1 + aT_hN},$$

where \(Na\) is the number of prey attacked, \(T\) is the total time of prey exposure, \(P\) is the number of predators, \(N\) is the initial prey density, \(a\) is the attack rate and \(T_h\) is the handling time.

*Satiation*

Before each experiment, 1 week old adult *D. hesperus* females were fed the test prey for 24 h and then starved for 24 h. Arenas consisted of a piece of tomato leaf placed upside down in a 5 cm diameter Petri dish. One predatory female was placed in an arena with 20 individuals of the same prey and allowed to feed for 6 hours. There were 4 prey types, consisting of whitefly, *E. formosa*, spider mites, and *P. persimilis*. Every hour, the number of dead prey was recorded, the prey were removed and replaced with another 20 individuals.
**Statistical analysis**

**Functional response**

Data on prey killed were analyzed using a one-way analysis of variance (ANOVA) of the mean number of prey killed at each density (Wells and McPherson 1999). Functional response parameters were calculated and the curve was plotted for untransformed data, using nonlinear regression (STATISTICA v. 6.0). Significance of the regression models was evaluated by ANOVA and the variance explained by the model was expressed by the coefficient of determination (as per Moura et al. 2006).

In order to test for a difference between the parameters (attack coefficient and handling time) of the four prey types a model incorporating indicator variables (Juliano and Williams 1985; Neter and Wasserman 1974) was used:

\[
N_a = \frac{[a_b + d_a(s)]N}{TP} = \frac{[a_b + d_a(s)]N}{1 + [a_b + d_a(s)]*[T_{h_b} + d_{h_b}(s)]N},
\]

where \( s \) is the indicator variable for prey populations. Parameters for two prey types were analyzed at a time. One prey type was represented by \( a_b \) for attack coefficient and \( T_{h_b} \) for handling time and \( s = 0 \), \( s = 1 \) for the other prey type. The parameters \( d_a \) and \( d_{h_b} \) are therefore estimates of the differences in the attack coefficient and handling times, respectively, between the two prey types being analyzed. There were 6 comparisons in total. The differences between parameters for the four prey types were tested using t-tests of the hypotheses that \( d_a = 0 \) and \( d_{h_b} = 0 \) (Juliano and Williams 1985; Neter and Wasserman 1974).

**Satiation**

Data were analyzed using repeated measures analysis of variance with observations of consumption rate repeated in time (SPSS v. 14.0).
Results

**Type of Functional Response.** The proportion of all 4 prey types consumed by *D. hesperus* during 6 h declined with increasing prey density, representing a type II functional response (Figures 3-1 to 3-4). The modified Holling’s (1959) disk equation fit the observed data and the estimated models accounted for a significant portion of the initial variance of the data for all prey species (Table 3-1). The mean number of prey consumed by *D. hesperus* across all prey densities was affected by prey type ($F_{3,356} = 2.523, P = 0.058$). *Dicyphus hesperus* ate marginally more whitefly pupae ($P = 0.093$) and spider mites ($P = 0.075$) than *E. formosa* pupae across all prey densities (Table 3-2). *Dicyphus hesperus* was able to find all 4 prey species when offered at low densities (Figures 3-1 to 3-4).

**Parameters of Functional Response.** The attack coefficients (or instantaneous search rate) (a) (hours$^{-1}$) for *D. hesperus* with whitefly, *E. formosa*, spider mites and *P. persimilis* as prey were similar (Table 3-3). However, the attack coefficient for *D. hesperus* with whitefly was marginally higher than with *P. persimilis* as prey ($P = 0.077$). Handling time, or time taken for *D. hesperus* to find, capture and consume prey (in minutes) was shortest with spider mites and *P. persimilis*, followed by whitefly pupae and longest when consuming *E. formosa* pupae (Table 3-3).

**Satiation.** The number of prey consumed by *D. hesperus* in one hour changed over time ($F_{5,180} = 16.60, P < 0.001$). There was an effect of prey type on the mean number of prey consumed by *D. hesperus* ($F_{1,36} = 14.03, P < 0.001$). Overall, *D. hesperus* consumed more *E. formosa* pupae, spider mites and *P. persimilis* than whitefly pupae and

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more spider mites than *E. formosa* pupae. The hourly consumption of prey by *D. hesperus* changed depending on prey type (*F*15,180 = 4.44, *P* < 0.001). Whitefly were consumed at the highest rate during the first hour, then consumption steadily declined until the 4th hour, at which point, consumption increased for 2 hours and then declined again (Figure 3-5). In contrast, consumption of *E. formosa* by *Dicyphus hesperus* remained relatively constant over time (Figure 3-5). Consumption of spider mites by *Dicyphus hesperus* slowly declined over time, whereas consumption of *P. persimilis* increased over the first two hours and then slowly declined over time (Figure 3-6).

**Discussion**

Holling's (1959b) disc equation or functional response models illustrate the principle of time budget in behavioural ecology. This model assumes that a predator spends its time on only two types of activities, searching for prey (the attack coefficient) and prey handling which includes the time spent chasing, killing, eating and digesting. It assumes that predation is limited by the effective searching rate at low prey densities and by the time needed to handle prey at high prey densities. This means that the number of attacked prey will increase with an increase in total time, prey density, and/or attack rate, but will decrease as handling time increases. This is because handling time takes away from searching time. Within this model, consumption rate of a predator is limited because even if prey are so abundant that no time is needed for searching for prey, a predator still needs to spend time on prey handling. The attack coefficient determines how rapidly the curve approaches the upper asymptote or maximum number of prey that can be eaten.
The attack coefficient is influenced by many aspects, such as predator versus prey mobility, success rate of the predator, distribution of the prey, size and complexity of the arena, and motivation of the predator (Hassell 1978). *Dicyphus hesperus* had similar attack coefficients when feeding on each of the four prey species, suggesting that *D. hesperus* had similar abilities to find each of the four prey species, but did have a marginally easier time finding whitefly versus *P. persimilis*. This could be because *P. persimilis* is highly mobile and whitefly pupae are stationary (see Chapter 2). Montserrat et al. (2000) measured the functional response of *Dicyphus tamaninii* Wagner when feeding on whitefly and found a similar attack coefficient (a = 0.185 h⁻¹).

According to the model, handling time includes time spent pursuing, subduing, and consuming each prey item, plus resting, grooming and the effects of satiation (Mills 1982). However, predators also spend their time laying eggs, consuming alternative prey and/or plant feeding and these activities are not addressed in Holling’s (1959b) disc equation. It is for this reason that the handling times derived from the functional response experiments in this chapter are longer than the handling times measured in chapter 2. The handling times from chapter 2 are actual observed times and only span the time the proboscis of the insect was inserted into the prey item (actual feeding time), whereas functional response handling times are assumed to include everything mentioned above. As was found in the behavioural observation study (Chapter 2), there was no difference in handling time for *D. hesperus* when consuming the intraguild prey, *P. persimilis* compared to the herbivorous prey, spider mites. This was not entirely unexpected as spider mites and *P. persimilis* are similar in size.
In contrast to the results in the behavioural observation study (Chapter 2), *D. hesperus* had a longer handling time for the intraguild prey, *E. formosa* compared with the herbivorous prey, greenhouse whitefly. As a result of the high handling time for *E. formosa*, *D. hesperus* showed the lowest maximal intake of parasitized pupae. The longer handling time of *E. formosa* could be the result of parasitism-induced hardening of the whitefly cuticle in parasitized pupae, which may have made cuticle penetration more difficult (Hoelmer et al. 1994). In the behavioural observation trials it was observed that *D. hesperus*'s proboscis would often come out of the parasitized pupae as *D. hesperus* moved the pupae around to change the angle of insertion of the proboscis. *Dicyphus hesperus*, due to the hardened cuticle of the parasitized whitefly often experienced difficulty in reinserting the proboscis and would sometimes give up and move on to another prey item. The parasitized and unparasitized pupae were fairly close together on the leaf surface and *D. hesperus*, in abandoning the parasitized pupae would promptly encounter another prey item. This explanation could account for the lack of difference found in the handing times of parasitized versus unparasitized pupae in the observational study.

Between the two herbivorous prey types, handling time was longer for whitefly than spider mites, as was found in the behavioural observation study (Chapter 2). It is likely that larger individuals require longer handling times because there is more mass to consume (Juliano and Williams 1985) and spider mites are less than half the size of whitefly pupae. Although handling time for *D. hesperus* was longer when consuming whitefly pupae compared to spider mites, the maximal intake of whitefly was similar to spider mites, suggesting a preference for whitefly. Montserrat et al. (2000) determined
the functional response of *Dicyphus tamaninii* Wagner when feeding on whitefly and found a similar handling time ($T_h = 0.381 \text{ h}^{-1}$).

During the satiation trials, *D. hesperus* consumed more *E. formosa* pupae, spider mites and *P. persimilis*, than whitefly pupae. Although whitefly appears to be the preferred prey, *D. hesperus* becomes satiated on whitefly faster than the other prey species. The longer handling time of whitefly limits the number of prey *D. hesperus* can consume in 6 h compared to spider mites and *P. persimilis*. In contrast, consumption of *E. formosa* by *D. hesperus* remained relatively constant over time. It appears that, when feeding on *E. formosa*, *D. hesperus* does not really become satiated because of the amount of time involved in handling each prey item.

*Dicyphus hesperus* consumed more spider mites than *E. formosa* and this is probably due to the extreme differences in handling times. *Dicyphus hesperus* is able to consume higher numbers of spider mites gradually becoming satiated, probably a result of a lower handling time. This is contrasted with consumption of *P. persimilis* by *D. hesperus*, which increased during the first two hours and then slowly declined over time. The initial increase during the first two hours may be because *P. persimilis* are highly mobile and *D. hesperus* had to learn how to capture and feed on this prey.

*Dicyphus hesperus* exhibited a type II functional response for all prey types in a homogeneous environment, which is the most common response of predators to changes in prey density. A type II functional response suggests that *Dicyphus hesperus* is most effective at regulating prey populations and cause maximum mortality when prey densities are below its saturation plateau or upper asymptote.
A shortcoming of the functional response model is that it requires predators to interact for a fixed period of time, thereby assuming that the amount of time predators spend in a patch is not influenced by the number of prey in that patch (Montserrat et al. 2004). This is contrary to foraging theory, which predicts predators will leave patches with few prey quicker than patches where prey is abundant (Charnov 1976). Predators may leave patches with only a few prey, thereby allowing those prey to persist in the environment. Therefore, to truly understand a predator’s foraging behaviour, these studies must be repeated at larger spatial scales to allow the predator the opportunity to leave a patch when prey are scarce. Should a predator decide to leave patches with low prey densities, the functional response curves would change.

There are several variables that could affect a predator’s prey consumption rates and they include (but are not limited to) environmental factors such as temperature and time of day, the inclusion of males, the size and complexity of the arena, and predator age (Hazzard and Ferro 1991). It is also important to note that the availability of alternative prey may influence predator behaviour, thereby altering the predation experienced by the prey of interest via the predator’s functional response (Holling 1959b). In addition, preferences may change as the relative densities of the prey species available change (Symondson et al. 2002). For example, alternative prey may lower predation on a focal prey through predator preference or satiation. Although the addition of alternative prey may reduce per capita predation on a target prey, it must be kept in mind that functional response is an individual response. The overall impact of alternative prey is, therefore, the combination of changes to the predator’s numerical and functional response (Harmon and Andow 2004).
Recall, a predator’s numerical response is to increase its numbers with increasing prey densities. To determine the net effect of an increase in predator numbers (numerical response) and a decrease in individual predator foraging efficiency (functional response) in the presence of alternative prey, one must determine the relative contribution of each mechanism (Harmon and Andow 2004). Furthermore, the numerical response of a predator (population growth) must be large enough to offset the reduction in per capita predation in order to maintain target herbivore suppression in the presence of alternative prey (Harmon and Andow 2004). Therefore, it is important to re-examine the functional response of the predator in the presence of more than one prey species in order to gain a better understanding of the predation rates.

In summary, *Dicyphus hesperus* showed a significant decelerating increase in consumption of all four prey species as prey density increased (Type II functional response). *Dicyphus hesperus* had similar attack coefficients for all four prey species. *Dicyphus hesperus* differed in its ability to handle the different prey species and was most efficient at consuming spider mites and least efficient at consuming *E. formosa*. *Dicyphus hesperus* had the highest maximal intake with whitefly and spider mites. Although whitefly is the preferred prey for *D. hesperus*, *D. hesperus* becomes satiated on whitefly faster than the other prey species. From a practical point of view, *D. hesperus* would make a good biocontrol agent for whitefly and spider mites and should not disrupt herbivore population regulation through intraguild predation because *D. hesperus* appears to have a preference for whitefly and maximal intake rates were lowest for *P. persimilis* and *E. formosa*. This is the first step in determining the foraging efficiency of *D*.56

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hesperus and its effects on the population dynamics of herbivores and their natural enemies. Future studies need to incorporate more prey choices and larger arenas.
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Holling CS (1959b) Some characteristics of simple types of predation and parasitism. Canadian Entomologist 91: 385–398


Figure 3-1: Functional response of *Dicyphus hesperus* at different prey densities of greenhouse whitefly.
Figure 3-2: Functional response of *Dicyphus hesperus* at different prey densities of *Encarsia formosa*.
Figure 3-3: Functional response of *Dicyphus hesperus* at different prey densities of two-spotted spider mites.
Figure 3-4: Functional response of *Dicyphus hesperus* at different prey densities of *Phytoseiulus persimilis*.

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Figure 3-5: Mean (±SE) number of greenhouse whitefly and *Encarsia formosa* consumed per hour by *Dicyphus hesperus*.
Figure 3-6: Mean (±SE) number of two-spotted spider mites and *Phytoseiulus persimilis* consumed per hour by *Dicyphus hesperus*.
Table 3-1: Results of the ANOVAs testing the fit of the modified Holling's (1959) disk equation to the observed data for *Dicyphus hesperus* fed different densities of greenhouse whitefly, *Encarsia formosa*, two-spotted spider mites and *Phytoseiulus persimilis*.

<table>
<thead>
<tr>
<th>Prey Species</th>
<th>$F_{(2, 88)}$ statistic</th>
<th>p-value</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Greenhouse whitefly</td>
<td>752.13</td>
<td>P &lt; 0.01</td>
<td>0.81</td>
</tr>
<tr>
<td><em>Encarsia formosa</em></td>
<td>990.23</td>
<td>P &lt; 0.01</td>
<td>0.85</td>
</tr>
<tr>
<td>Two-spotted spider mites</td>
<td>2172.77</td>
<td>P &lt; 0.01</td>
<td>0.94</td>
</tr>
<tr>
<td><em>Phytoseiulus persimilis</em></td>
<td>1703.57</td>
<td>P &lt; 0.01</td>
<td>0.92</td>
</tr>
</tbody>
</table>
Table 3-2: Mean (±SE) number of *Encarsia formosa*, *Phytoseiulus persimilis*, two-spotted spider mites and whitefly killed by *Dicyphus hesperus* across all prey densities in 6 h.

<table>
<thead>
<tr>
<th>Prey type</th>
<th>N</th>
<th>Mean # of prey killed</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Encarsia formosa</em></td>
<td>90</td>
<td>6.72 ± 0.44a</td>
</tr>
<tr>
<td><em>P. persimilis</em></td>
<td>90</td>
<td>7.83 ± 0.55a</td>
</tr>
<tr>
<td>Spider mites</td>
<td>90</td>
<td>8.59 ± 0.60a</td>
</tr>
<tr>
<td>Whitefly</td>
<td>90</td>
<td>8.52 ± 0.27a</td>
</tr>
</tbody>
</table>

Means in each column followed by the same letter are not significantly different (P > 0.05).
Table 3-3: Attack coefficients (a) (hours\(^{-1}\)) and handling times (T\(_h\)) (minutes) for *Dicyphus hesperus* with greenhouse whitefly, *Encarsia formosa*, two-spotted spider mites and *Phytoseiulus persimilis* as prey on caged tomato leaves for 6 h.

<table>
<thead>
<tr>
<th>Prey species</th>
<th>Attack Coefficient + SE</th>
<th>Handling time + SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Whitefly</td>
<td>0.184 ± 0.02a</td>
<td>17.16 ± 1.32b</td>
</tr>
<tr>
<td><em>E. formosa</em></td>
<td>0.156 ± 0.01ab</td>
<td>22.86 ± 1.50c</td>
</tr>
<tr>
<td>Spider mites</td>
<td>0.153 ± 0.01ab</td>
<td>13.86 ± 0.78a</td>
</tr>
<tr>
<td><em>P. persimilis</em></td>
<td>0.145 ± 0.01b</td>
<td>15.78 ± 0.96ab</td>
</tr>
</tbody>
</table>

Means in each column followed by the same letter are not significantly different (P > 0.05). The attack coefficients for *D. hesperus* with whitefly and *P. persimilis* as prey are marginally different (P = 0.077).
Chapter 4

Population dynamics of the intermediate predator and prey in the presence/absence of an intraguild predator and alternative food source

Introduction

Understanding the mechanisms governing dynamic interactions within natural enemy communities with respect to intraguild predation and its effects on the population dynamics of all the species involved is an important step to understanding food webs. Intraguild predation, a subset of omnivory, is defined as predation that occurs between organisms that exploit a common resource, and is a frequent interaction in many natural communities (Polis et al. 1989). Rosenheim (1998) posited that the outcome of asymmetric intraguild predation interactions for herbivore populations would depend on the preference of the intraguild predator for the intraguild prey (intermediate predator) versus the herbivore. When the intraguild predator prefers the intraguild prey, regulation of herbivore populations is destabilized (Synder and Ives 2001). When the intraguild predator prefers the herbivore over the intraguild prey, regulation of the herbivore population is increased, resulting in lower herbivore populations than when the intraguild prey is present alone (Heinz and Nelson 1996; Colfer and Rosenheim 2001). Finally, when the intraguild predator exhibits no particular preference between the intraguild prey and the herbivore, there is a neutral effect on the regulation of the herbivore population (Castañé et al. 2004; McGregor and Gillespie 2005). This is because the herbivore is present in higher numbers than the intraguild prey, thus the intraguild predator consumes more herbivores than intraguild prey.
Regulation of herbivore populations may be alleviated when their omnivorous natural enemies also feed on other prey species or other host plants (Coll and Guershon 2002). Alternative prey can either increase predation on a focal herbivore or decrease predation on a focal herbivore. Harmon et al. (2000) found that *Coleomegilla maculata* (DeGeer) (Coleoptera: Coccinellidae) had higher densities on alfalfa, *Medicago sativa* (L.), interspersed with pollen-producing dandelion, *Taraxacum officinale* (Weber), than on alfalfa alone, which resulted in an increase in predation on pea aphids, *Acyrthosiphon pismum* (Harris) (Homoptera: Aphididae) on alfalfa. On the other hand, Koss and Snyder (2005) found that the addition of an alternative prey (green peach aphid, *Myzus persicae* Sulzer) resulted in decreased predation by several predatory hemipterans (*Geocoris* spp. and *Nabis* spp.) on Colorado potato beetles, *Leptinotarsa decemlineata* Say, on potatoes, *Solanum tuberosum* L. Therefore, the presence of the preferred prey (aphids) disrupted suppression of the target herbivore (Colorado potato beetle).

In addition to intraguild predation, an important interaction within food webs for the regulation of predator guilds is interspecific competition. Interspecific competition is defined as the negative effect that one species has upon another by consuming or controlling access to a resource that is limited in availability or through susceptibility to shared predators and can be mediated through interference competition, exploitative competition, and apparent competition (Holt 1977). Interference competition occurs when one species reduces the access of a competitor to a limited resource through behavioural interactions. Exploitation competition occurs when two consumer species compete directly for a limited-shared resource (Polis et al. 1989). Apparent competition arises when competitors indirectly limit each others densities by increasing the
population of a shared predator (Holt 1977). Thus, predator density is partly determined by the diversity and abundance of prey species (Holt 1977).

The concept of apparent competition between prey species may be important in regulation of herbivore populations. According to predator-mediated apparent competition theory, the addition of an intraguild predator should not disrupt suppression of herbivore populations. If the intraguild predator consumes the occasional intermediate predator, the effect may be an increase in the density of the intraguild predator, which would result in greater predation pressure on the herbivore population, ultimately resulting in a lower equilibrium density of the pest species. Herne and Putman (1966) posited that *Panonychus ulmi* (Koch) was maintained at a low density in peach orchards by the phytoseiid *Typhlodromus caudiglans* Schuster even though *T. caudiglans* frequently subsidized its diet with alternative prey. *Typhlodromus caudiglans* was able to increase its density by consuming additional food sources, thereby increasing the predation pressure on the pest species and is an example of herbivore population regulation through predator-mediated apparent competition.

*Dicyphus hesperus* Knight (Heteroptera: Miridae) is a zoophytophagous omnivore that feeds not only a variety of prey, but also on a variety of host plants including mullein (*Verbascum thapsus* L. (Scrophulariaceae)) and tomato (*Lycopersicon esculentum* Mill. (Solanaceae)) (McGregor et al. 1999; Gillespie and McGregor 2000; Sanchez et al. 2004). The plant feeding ability of *D. hesperus* may facilitate survivorship during a period of low or absent prey (Bugg et al. 1987; Eubanks and Denno 1999). Mullein is the best host plant for *D. hesperus* because it provides the highest quality nutrients, females can produce eggs and nymphs can develop to maturity in the absence of prey. In
comparison, tomato plants provide medium quality nutrients and do not support adult egg production or nymphal development in the absence of prey (Sanchez et al. 2004).

*Dicyphus hesperus* is currently used as a biological control agent to suppress herbivore populations of greenhouse whitefly (*Trialeurodes vaporariorum* Westwood (Homoptera: Aleyrodidae)) and two-spotted spider mites (*Tetranychus urticae* Koch (Acari: Tetranychidae)) in tomato greenhouses in Canada (McGregor et al. 1999; Sanchez et al. 2003). Mullein is used as a banker plant in these greenhouses to help establish and manage populations of *D. hesperus* (Sanchez et al. 2003). Sanchez et al. (2003) studied population dynamics of *D. hesperus* in greenhouses in the presence and absence of mullein and found that *D. hesperus* was always more abundant in greenhouses with mullein than in greenhouses with tomato plants alone. Therefore, the use of mullein as a supplementary resource may increase predator numbers thereby increasing predation pressure on herbivores. Also present in this greenhouse food web are the specialist natural enemies of those herbivore species, namely the parasitoid *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) and the predatory mite *Phytoseiulus persimilis* Athias-Henriot (Acarina: Phytoseiidae). *Dicyphus hesperus* engages in intraguild predation by preying on the specialist natural enemies of the herbivore species and this could impact herbivore population dynamics.

The goal of this study was to examine the population dynamics of intraguild prey (specialist natural enemies) and herbivore populations in the presence and absence of an intraguild predator (*D. hesperus*) and alternative food source (mullein). Based on the results of the behavioural observation and functional response studies, I hypothesized that the presence of *D. hesperus* would result in lower population levels of whitefly and
spider mite compared to food webs without *D. hesperus*. The presence of *D. hesperus* was expected to have no effect on population levels of *P. persimilis* and *E. formosa*, based on the preference exhibited by *D. hesperus* in chapter 2 and 3 for the herbivore species. The presence of mullein, an alternative food source to prey for the intraguild predator, was expected to reduce feeding on the herbivores by *D. hesperus*. However, as *D. hesperus* was not expected to affect intraguild prey populations, the presence of mullein was expected to have no effect on population levels of the intraguild prey.

**Methods**

**Insect origins and rearing**

*Predator*

*Dicypethus hesperus* were originally collected from white stem hedge nettle, *Stachys albens* A. Gray (Lamiaceae) in the foothills of the Sierra Nevada Mountains at an elevation of ca. 300 m near Woody, CA USA (Lat 35°42.9′N, long 116°49.1′W). Colonies were maintained on tobacco plants, *Nicotiana tabacum* L. (Solanaceae) at 24 °C with a 16 h light and 8 h dark diel cycle. Adult *D. hesperus* oviposited on caged plants for 7 days, prior to removal of adults from the plants. Eggs were allowed to hatch and nymphs were fed previously frozen eggs of *Ephesitia kuehniella* Zeller (Lepidoptera: Pyralidae) *ad libitum*, until development to adult. This procedure allowed for synchronized cohorts of adults.

*Prey*

Two-spotted spider mites were reared on tomato leaves. *Encarsia formosa*, and *P. persimilis* were ordered from Koppert Biological Systems, Scarborough, Ontario,
Canada and greenhouse whitefly were obtained from Applied Bionomics, Sidney, British Columbia, Canada.

**Experimental setup**

The experiment consisted of 4 treatments with 1 treatment per (1m³) mesh cage within the greenhouse. Each cage consisted of 4 tomato plants (Early Cascade Hybrid) which were approximately 30 cm at the start of the experiment, spider mites, whitefly, *P. persimilis* and *E. formosa*. The experimental design was a full-factorial design with the presence/absence of mullein and the presence/absence of *D. hesperus* (Table 4-1). On day 1, 80 adult spider-mites and 80 adult whitefly were released into all 4 treatments and were evenly dispersed on the plants. On day 12, 8 adult *E. formosa* and 16 adult *P. persimilis* were released into all 4 treatments. On day 18, an additional 8 *E. formosa* were released into all 4 treatments. On day 20, 15 *D. hesperus* were released into treatments C and D (Table 4-1). Each treatment was replicated 8 times, with a new replicate started every few days. One tomato plant from each cage of the 4 treatments was removed every 20 days until the experiment ended at 80 days. It was assumed that all insect populations were distributed equally over the four tomato plants and therefore each plant represented the population fluctuations within each cage. Upon removal of the tomato plant, all life stages of all insect species were counted. Temperature in the greenhouse was recorded every hour for the duration of the experiment using ACR Smart Button Data Loggers.

**Statistical Analysis**

To determine differences in mean population levels across time between treatments, all life stages for each prey species within each cage were summed. Log-transformed (log₁₀) numbers of whitefly, spider mites, *E. formosa* and *P. persimilis* were
analyzed using repeated measures analysis (for days 40, 60 and 80) with presence/absence of *D. hesperus* and mullein as factors (SPSS 14.0, SPSS Inc.). Data for percent parasitism was not log-transformed.

**Results**

Considerable variance in temperature occurred, but conditions were comparable for all cages between different runs of the experiment (Table 4-2). Spider mite numbers changed over time ($F_{2,27} = 19.61, P < 0.001$). However, there was no interaction between time and the presence of *D. hesperus* or mullein (time*D. hesperus*: $F_{2,27} = 0.305, P = 0.740$; time*mullein*: $F_{2,27} = 0.051, P = 0.951$; T*D*M: $F_{2,27} = 2.355, P = 0.114$) (Figure 4-1). By day 20, spider mite populations had begun to increase and this continued until day 40 across all treatments. By day 60 spider mite populations were declining for all treatments and this continued through until the end of the experiment (day 80) (Figure 4-1). The presence of either *D. hesperus* or mullein did not affect the mean number of spider mites (*D. hesperus*: $F_{1,28} = 0.087, P = 0.770$; mullein: $F_{1,28} = 0.069, P = 0.795$; D*M: $F_{1,28} = 0.364, P = 0.551$) (Figure 4-1).

*Phytoseiulus persimilis* numbers changed over time ($F_{2,27} = 15.644, P < 0.001$). However, there was no interaction between time and the presence of *D. hesperus* or mullein (time*D: $F_{2,27} = 0.345, P = 0.711$; time*mullein*: $F_{2,27} = 0.007, P = 0.993$; T*D*M: $F_{2,27} = 0.031, P = 0.970$) (Figure 4-2). The mean number of *P. persimilis* was marginally lower in the presence of *D. hesperus* ($F_{1,28} = 3.152, P = 0.087$). The presence of mullein did not affect the mean number of *P. persimilis* (mullein: $F_{1,28} = 1.436, P = 0.241$) (Figure 4-2). There was no interaction between presence of *D. hesperus* and
mullein on the mean number of *P. persimilis* (D*M: F$_{1,28}$ = 0.301, P = 0.587). By day 20, *P. persimilis* numbers were still very low for all treatments. However, by day 40, *P. persimilis* numbers were increasing and continued to increase until day 60 for all treatments. By day 80, *P. persimilis* numbers had begun to decline slightly. Releasing *D. hesperus* resulted in a slower increase in *P. persimilis* numbers and a slightly lower overall population density than not releasing *D. hesperus* (Figure 4-2).

Whitefly numbers changed over time (F = 23.103, P < 0.001). However, there was no interaction between time and the presence of *D. hesperus* or mullein (time*D: F$_{2,27}$ = 1.385, P = 0.268; time*mullein: F$_{2,27}$ = 0.460, P = 0.636; T*D*M: F$_{2,27}$ = 2.557, P = 0.096) (Figure 4-3). The presence of *D. hesperus* reduced the mean number of whitefly (F$_{1,28}$ = 5.314, P = 0.029). There was no effect of the presence of mullein and no interaction effect on the mean number of whitefly (mullein: F$_{1,28}$ = 1.055, P = 0.313; D*M: F$_{1,28}$ = 1.583, P = 0.219) (Figure 4-3). At day 40, the whitefly populations did not differ between treatments, however by day 60 whitefly populations had declined in the *D. hesperus* alone treatment. By day 80, whitefly populations for the 4 treatments were similar again. Therefore, releasing *D. hesperus* resulted in an earlier decline in whitefly density than not releasing *D. hesperus* (Figure 4-3).

*Encarsia formosa* numbers changed over time (F$_{2,27}$ = 15.405, P < 0.001). However, there was no interaction between time and the presence of *D. hesperus* or mullein (time*D: F$_{2,27}$ = 0.002, P = 0.998; time*mullein: F$_{2,27}$ = 0.632, P = 0.539; T*D*M: F$_{2,27}$ = 2.135, P = 0.138) (Figure 4-4). The mean number of *E. formosa* was marginally lower in the presence of *D. hesperus* (F$_{1,27}$ = 3.014, P = 0.094). There was no effect of mullein and no interaction effect on the mean number of *E. formosa* (mullein:
By day 20, *E. formosa* numbers were still low for all treatments. By day 40, *E. formosa* numbers had begun to increase for all treatments. Releasing *D. hesperus* resulted in a larger decline in *E. formosa* density as well as a lower population density at the end of the experiment than not releasing *D. hesperus* (Figure 4-4).

There was no affect of time and no interaction between time and the presence of *D. hesperus* or mullein on the percent parasitism rate of whitefly by *E. formosa* (time: \(F_{2, 27} = 2.923, P = 0.100\); time*D: \(F_{2, 27} = 0.842, P = 0.459\); time*mullein: \(F_{2, 27} = 0.420, P = 0.668\); T*D*M: \(F_{2, 27} = 0.046, P = 0.955\)). There was no effect of the presence of either *D. hesperus* or mullein on the percent parasitism rate of greenhouse whitefly by *E. formosa* (*D. hesperus*: \(F_{1, 11} = 1.405, P = 0.261\); mullein: \(F_{1, 11} = 0.359, P = 0.561\); D*M: \(F_{1, 11} = 1.817, P = 0.205\)) (Figure 4-5). In general, there was an increase in percent parasitism from day 20 through to day 80 (Figure 4-5).

**Discussion**

The impact of generalist predators on herbivore populations in combination with a specialist natural enemy may be additive, such that prey suppression may be greater than the sum of their individual impact; neutral, such that prey suppression is less than the sum of their individual impacts but equal to that of the specialist alone or negative, such that prey suppression is below that of the specialist alone. Rosenheim (1998) posited that the outcome of asymmetric intraguild predation interactions for herbivore populations would depend on the preference of the intraguild predator for the parasitoid/predator versus the prey. Based on the observation studies in chapter 2, in which the intraguild predator was
found to prefer the shared herbivores over the intraguild prey, we expected to find
enhanced, and possibly additive, herbivore population suppression when the omnivore
was present with the specialist natural enemies (intraguild prey).

*Phytoseiulus persimilis* reached maximum population levels by day 60 and
population levels had begun to decline by day 80, most likely due to declining prey
populations. The mean number of *P. persimilis* was marginally lower in the presence of
*D. hesperus*. Although intraguild predator had a negative impact on the population of the
intraguild prey, there was a neutral effect on herbivore population suppression. Given the
higher predation rate and success ratio *D. hesperus* has for the herbivore prey over the
intraguild prey (Chapter 2), herbivore populations likely experienced higher predation
rates by *D. hesperus* than the intraguild prey, especially with the higher mean population
densities compared to that of the intraguild prey but it did not result in enhanced
population suppression of spider mites. The fact that spider mite population suppression
was not enhanced by the presence of *D. hesperus* as predicted may be because *D.
hesperus* prefers whitefly over spider mites (Chapter 2 and 3).

This is further demonstrated as the presence of the intraguild predator, *D.
hesperus*, enhanced the population regulation of the herbivore prey, whitefly, with only a
marginal impact of intraguild predation on the intraguild prey, *E. formosa*. Furthermore,
the presence of *D. hesperus* did not affect percent parasitism rates of greenhouse whitefly
by *E. formosa*. Similarly, Bennett (2006) examined the population dynamics of whitefly
and *E. formosa* in the presence and absence of *D. hesperus* on a larger experimental scale
with commercial-sized tomato plant arenas and concluded that *D. hesperus*, in
combination with *E. formosa*, reduced whitefly populations more than *E. formosa* alone.

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His study also demonstrated that intraguild predation by *D. hesperus* reduced the population of the intraguild prey, *E. formosa*. However, in contrast to the present study, Bennett (2006) found that the presence of *D. hesperus* had a positive effect on percent parasitism of whitefly by *E. formosa*. There was a lower number of parasitized individuals in the absence of *D. hesperus*. Bennett (2006) had higher release rates of the parasitoid and suggested that intraspecific competition among parasitoids caused the decline in the population reproductive rate. The presence of *D. hesperus* alleviated intraspecific pressure through intraguild predation, resulting in a higher per capita oviposition success rate of *E. formosa*.

In contrast to Bennett’s (2006) study, which consisted of a simpler food web of one herbivore prey type, one intraguild prey type and the intraguild predator, the current study incorporated the possibility for more complex interactions with two herbivore prey types, two intraguild prey types and the intraguild predator. Therefore, in the current study, the observed decline in *E. formosa* numbers in the presence of *D. hesperus* may have been the result of the significant decline in whitefly numbers due to the increased predation pressure on the herbivore by the addition of the generalist omnivore. The population dynamics of the spider mites and predatory mites in the absence of intraguild predation are typically unstable, with the predatory mites eradicating the spider mite population (Janssen and Sabelis 1992; van Baalen and Sabelis 1995; Pels and Sabelis 1999). The same is true of the population dynamics of whitefly and *E. formosa*. As a result, the populations of both specialist natural enemies (*P. persimilis* and *E. formosa*) go extinct. Therefore, the highly coupled population dynamics of the parasitoid-host
(predator-prey) relationship may account for the decline in parasitoid numbers in the presence of the generalist more than intraguild interactions.

For all treatments, both natural enemy populations remained below the population levels of the herbivores throughout the experiment. The intensity of interspecific interactions between predators such as intraguild predation, interference competition, and cannibalism have been known to change with prey density and effect a prey’s predation risk accordingly (Vance-Chalcraft and Soluk 2005). For example, intraguild predation by Coccinella septempunctata L. (Coleoptera: Coccinellidae), on Coleomegilla maculata (DeGeer) (Coleoptera: Coccinellidae), was observed at low pea aphid Acrthosiphon pisum (Harris) (Homoptera: Aphididae) densities (prey) but not at high prey densities (Obrycki et al. 1998). The simplest explanation for decreasing intensity of interspecific interactions with increasing herbivore density is that the intraguild predators are able to find herbivorous prey more easily. Therefore, an increase in herbivore density may result in a decrease in intraguild predator aggression and ultimately result in an increase in predation risk for herbivorous prey (Vance-Chalcraft and Soluk 2005). Likewise, intraguild predation events may increase as herbivore populations decrease in response to predation.

Several studies have examined the effects of intraguild predation and its consequences for continued herbivore population suppression. Heinz and Nelson (1996) found that the population suppression of Bemisia argentifolii was increased when the generalist predator Delphastus pusillus showed a partial preference for the herbivore compared to the parasitoid. On the other hand, Synder and Ives (2001) found that pea aphid populations were released from regulation when the intraguild predator
Pterostichus melanarius had a preference for immobile aphid mummies parasitized by *Aphidius ervi*. McGregor and Gillespie (2005) conducted greenhouse experiments to examine the influence of intraguild predation by *D. hesperus* through the predation of whitefly pupae parasitized by *E. formosa* and its effects on whitefly populations. They found that although there was a negative impact of intraguild predation on *E. formosa* populations, there was a neutral effect on the population regulation of whitefly. Castañé et al. (2004) monitored populations of greenhouse whitefly and *E. formosa*, as well as populations of two mirid bugs, *Dicyphus tamaninii* Wagner and *Macrolophus caliginosus* Wagner, in greenhouses. They found that whitefly control was not impeded by intraguild predation on *E. formosa* as the two mirid bugs exhibited no preference for parasitized pupae. Venzon et al. (2001) studied the effects of the presence/absence of an intraguild predator, *Orius laevigatus* (Fieber), on the population dynamics of an intraguild prey, *P. persimilis*, and a shared prey, spider mites on cucumber plants in cages in a greenhouse. They found no effect of the presence of the intraguild predator on the numbers of spider mites and predatory mites. Overall, the effects of intraguild predation on herbivore regulation are varied and depend a great deal on the component species that comprise the community.

Increasing habitat complexity generally increases the abundance of arthropod natural enemies (Root 1973, Langellotto and Denno 2004). It has been suggested that interspersing mullein plants in tomato crops may enhance early season establishment of *D. hesperus* and help preserve predator populations in the greenhouse in the absence of prey, thus acting as a reservoir which would allow *D. hesperus* to respond quicker to increasing herbivore populations (Sanchez et al. 2003). Similarly, Eubanks and Denno
(2000) found lower prey populations when bean pods were present in field plots as a result of higher predator populations in the presence of the bean pods.

In this case, increasing habitat complexity by interspersing mullein in tomato greenhouses also introduces a high quality alternative food source into the increasingly complex food web. The presence of an alternative food source (mullein) may reduce intraguild predation and cannibalism thereby contributing to increased numbers of natural enemies (Langellotto and Denno 2004). However, there is one concern in using mullein to enhance establishment of *D. hesperus* and maintain the predator population in the scarcity of prey and that is that when prey populations begin to increase again *D. hesperus* may remain on the mullein plants as *D. hesperus* can complete its life cycle on mullein (Sanchez et al. 2004). There is, however, considerable evidence to suggest that *D. hesperus* will not remain on mullein once prey populations begin to increase. Eubanks and Denno (1999) suggested that the survival of zoophytophages that endure periods of prey scarcity by feeding on plants usually have lower survival rates than individuals feeding consistently on prey. This is consistent with Sanchez et al. (2004) who compared the success of developing *D. hesperus* nymphs raised on prey versus mullein and found that on mullein without prey 30% of nymphs completed development, whereas about 90% completed development on most host plants with prey.

Although *D. hesperus* can survive on mullein and, in fact, plant feeding is required for prey feeding and development (Gillespie and McGregor 2000), prey items are a higher quality food item. In other words, it is beneficial for *D. hesperus* to incorporate both animal and plant material into its diet rather than subsist on plant material alone when prey are also available. This suggests that, *Dicyphus hesperus* is
primarily carnivorous and should abandon mullein as prey populations increase on tomato plants (Sanchez et al. 2004). Furthermore, through mark recapture experiments, Sanchez et al. (2003) observed that higher proportions of *D. hesperus* were found on tomato plants during weeks with the highest whitefly density and the presence of mullein did not hinder the movement of *D. hesperus* between mullein and tomato plants. In addition, VanLaerhoven et al. (unpublished) examined the effects of habitat complexity on *D. hesperus* and found that although *D. hesperus* could remain on high quality mullein plants and complete its life cycle (Sanchez et al. 2004), the presence of mullein actually increased between plant movement by *D. hesperus*. Kereliuk (2007) examined the relationship between plant quality and prey consumption in *D. hesperus* and found that prey consumption was higher on mullein than on tomato.

In the current study, the presence of mullein did not result in measurable differences in population dynamics of herbivore prey or intraguild prey over time. The presence of mullein also did not result in measurable differences in the percent parasitism rate of greenhouse whitefly by *E. formosa*. Similarly, Sanchez et al. (2003) found that whitefly population dynamics were not impacted by the presence of mullein. Overall, it appears that the concurrent use of mullein with *D. hesperus* will not disrupt herbivore regulation and may contribute to enhanced biological control of herbivore species.

*Dicynthus hesperus* is not only a trophic omnivore, feeding at more than one trophic level (Pimm and Lawton 1978), but also a true omnivore, feeding on both plant and animal materials (Coll and Guershon 2002). Zoophytophagous omnivory, as defined by diet, can be facultative or obligatory depending on the relative importance of prey and plant materials needed to develop (Coll and Guershon 2002). Facultative omnivores are
opportunist and supplement their diet to increase fitness. In this context, plants are considered to be a suboptimal food and facultative omnivores are assumed to switch between plant and prey materials based on the availability of prey (Agrawal et al. 1999; Gillespie and McGregor 2000). Obligate omnivores, on the other hand, derive some benefit from plants that cannot be derived from prey and they must therefore consume both resources to complete their diet.

_Dicyphus hesperus_ is an obligate omnivore as plant feeding is required in order to acquire water necessary for prey feeding (via extra-oral digestion) and nutrients that enhance growth and development (Gillespie and McGregor 2000). During extra-oral digestion digestive enzymes are injected into prey and the liquefied contents are withdrawn through the stylets. Water is lost continually through extra-oral digestion and plant feeding is one way to regain water (Pollard 1988; Gillespie and McGregor 2000). Gillespie and McGregor (2000) posit that plant feeding in _D. hesperus_ to gain water may occur in proportion to predation levels irrespective of prey quantity or quality. However, the evidence presented above suggests that the predicted increase in plant feeding associated with an increase in predation will only serve to increase predator populations because of an increase in predator fitness.

In addition, plants damaged by herbivores can release volatiles that attack natural enemies. McGregor and Gillespie (2004) found that _D. hesperus_ was strongly attracted to olfactory cues given off by whitefly-infested tomato leaves. Therefore, it is possible that as herbivore numbers increase on tomato plants _D. hesperus_ will be drawn to those plants by olfactory cues, and abandon mullein plants until prey become scarce again. VanLaerhoven et al. (2006) examined patch retention times for _D. hesperus_ on tomato
and mullein independently and found that patch retention times were shortest when no prey were available. VanLaerhoven (unpublished data) examined retention times and movement decisions of *D. hesperus* in combined tomato/mullein landscapes and even in the absence of prey, the omnivore moved readily between tomato and mullein. Ostfeld and Keesing (2000) stated that dispersal among food resources is typical of many generalist populations in response to fluctuating resources. These studies support the conclusion that *D. hesperus* will migrate from mullein plants to tomato plants as herbivore numbers increase on tomato plants.

Although intraguild predation by *D. hesperus* had a negative effect on the intraguild prey population dynamics, the presence of the intraguild predator had a neutral effect on spider mite population regulation and a positive effect on whitefly population regulation. The presence of mullein did not interfere with enhanced whitefly population suppression in the presence of *D. hesperus*, as it is beneficial for *D. hesperus* to both plant and prey feed when prey are available. Furthermore, several studies using the same generalist predator found similar results. The increasing numbers of biological control agents that are used are changing simple tritrophic interactions into more complex food web interactions and it is becoming ever more important that we understand these interactions. The degree of intraguild predation and its impact on herbivore suppression will depend on the species composition of the food web as well as the predator preferences and herbivore vulnerabilities of those species (Denno and Finke 2006). Understanding multiple predator effects will further our understanding of species interactions and ultimately community structure.
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Table 4-1: The experimental design was a full-factorial design with the presence/absence of mullein and the presence/absence of *D. hesperus*.

<table>
<thead>
<tr>
<th></th>
<th>Mullein plant</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>-</td>
</tr>
<tr>
<td><em>D. hesperus</em></td>
<td>Treatment A</td>
</tr>
<tr>
<td>-</td>
<td></td>
</tr>
<tr>
<td>+</td>
<td>Treatment C</td>
</tr>
</tbody>
</table>

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Table 4-2. Temperature for the 8 runs of 4 treatments for the duration of the experiment.

<table>
<thead>
<tr>
<th>Run</th>
<th>Temperature °C</th>
<th>Min - Max</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean (±SE)</td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>25.27 ± 0.13</td>
<td>12 - 42</td>
</tr>
<tr>
<td>2</td>
<td>25.25 ± 0.13</td>
<td>12 - 42</td>
</tr>
<tr>
<td>3</td>
<td>24.39 ± 0.12</td>
<td>13 - 43</td>
</tr>
<tr>
<td>4</td>
<td>24.29 ± 0.11</td>
<td>13 - 41</td>
</tr>
<tr>
<td>5</td>
<td>24.47 ± 0.11</td>
<td>13 - 41</td>
</tr>
<tr>
<td>6</td>
<td>24.56 ± 0.10</td>
<td>13 - 41</td>
</tr>
<tr>
<td>7</td>
<td>24.56 ± 0.10</td>
<td>10.5 - 43.5</td>
</tr>
<tr>
<td>8</td>
<td>24.57 ± 0.10</td>
<td>10.5 - 43.5</td>
</tr>
</tbody>
</table>
Figure 4-1: Mean (±SE) number of two-spotted spider mites in the presence/absence of *Dicynhus hesperus* and mullein.
Figure 4-2: Mean (±SE) number of Phytoseiulus persimilis in the presence/absence of Dicyphus hesperus and mullein.

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Figure 4-3: Mean (±SE) number of greenhouse whitefly in the presence/absence of *Dicacyphus hesperus* and mullein.
Figure 4-4: Mean (±SE) number of *Encarsia formosa* in the presence/absence of *Dicynhus hesperus* and mullein.

*Dicynhus hesperus* added
Figure 4-5: Percent parasitism of greenhouse whitefly pupae by *Encarsia formosa* in the presence/absence of *Dicyphus hesperus* and mullein.

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In natural environments, natural enemies – predators, parasitoids, and pathogens – are major biotic factors that limit the population levels of phytophagous insects, thereby maintaining phytophagous insects at lower levels than would be expected given the abundance of their food sources (Holt and Lawton 1993). Understanding multiple predator effects will further our understanding of species interactions and ultimately, community structure. Species within a community are linked by direct and indirect interactions such as predation and various forms of competition (Holt 1977). The effectiveness of a predator population on the suppression of an herbivore population depends to some extent on the searching efficiency of the predator population.

In chapter 2, observational studies were used to assess preferences of an intraguild predator for intraguild prey versus shared prey when offered simultaneously. Intraguild predation is a type of omnivory in which predators consume potential competitors (Polis et al. 1989). Omnivores are often extreme generalists feeding on resources that belong to different trophic levels and are, therefore, able to persist in variable environments (Coll and Guershon 2002). *Dicyphus hesperus* Knight (Heteroptera: Miridae) is a zoophytophagous omnivore that feeds not only a variety of prey, but also on a variety of host plants including mullein (*Verbascum thapsus* L.) and tomato (*Lycopersicon esculentum* Mill.) (McGregor et al. 1999; Gillespie and McGregor 2000; Sanchez et al. 2004). Prey preference of an intraguild predator can have important consequences for intraguild prey and herbivorous prey populations.
Behavioural observations showed that the intraguild predator fed on both the intraguild prey and the shared prey, however, the intraguild predator had a higher predation rate and success ratio for the shared prey compared to the intraguild prey. This suggested that *D. hesperus* had a preference for the herbivores.

*Dicypus hesperus* had a higher encounter rate for the herbivorous spider mites (*Tetranychus urticae* Koch (Acari: Tetranychidae)) than for the predacious mites *Phytoseiulus persimilis* Athias-Henriot (Acarina: Phytoseiidae), likely because *P. persimilis* are more mobile than spider mites. The increased mobility of *P. persimilis* resulted in a lower encounter rate with *D. hesperus* and most of the predatory mites that were encountered, but not killed, escaped by running away.

Encounter rates for the herbivore greenhouse whitefly (*Trialeurodes vaporariorum* Westwood (Homoptera: Aleyrodidae)) and parasitoid *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) were similar which is not surprising as both species were immobile. In both cases, the interguild predator spent the same amount of time feeding or handling per intraguild prey and per shared prey. There could be several explanations for the observed preference of the intraguild predator for whitefly. The preferential predation on unparasitized whitefly pupae could be a result of parasitism-induced hardening of the whitefly cuticle in parasitized pupae, which may have made cuticle penetration more difficult (Hoelmer et al. 1994). In addition, as a parasitoid matures inside the whitefly pupae, the fluid contents of the whitefly are used up and air pockets form inside the pupal case. These air spaces may interfere with fluid uptake by *D. hesperus* (Hoelmer et al. 1994).
In both cases, the herbivores were more vulnerable than the intraguild prey to predation by the intraguild predator which resulted in the observed preference for the herbivores. It has been suggested that the nutritional quality of food items may influence feeding choices of omnivores as well (Agrawal et al. 1999). As trophic levels increase, there is an increase in nitrogen, and it has been suggested that this may promote intraguild predation, as predator fitness is predicted to increase by eating more nitrogen rich prey (Denno and Fagan 2003). Furthermore, nitrogen content varies among herbivore species, suggesting that some herbivores are more beneficial to eat than others (Fagan et al. 2002). McGregor et al. (1999) found that whitefly were a better-quality food item for the growth and development of *D. hesperus* compared to spider mites. Fittingly, this study found that *D. hesperus* had a higher encounter rate, predation rate and success ratio for whitefly than for spider mites when offered together. This suggests that *D. hesperus* has a strong preference for whitefly over spider mites and that *D. hesperus* is foraging optimally.

*Dicyphus hesperus* is an obligate omnivore as plant feeding is required in order to acquire water necessary for prey feeding (via extra-oral digestion) and nutrients that enhance growth and development (Gillespie and McGregor 2000). During extra-oral digestion digestive enzymes are injected into prey and the liquefied contents are withdrawn through the stylets. As plants can be an alternative food source for *D. hesperus*, I examined the amount of time *D. hesperus* spent prey feeding and searching for prey versus plant feeding. *Dicyphus hesperus* spent more time prey feeding and searching for prey than plant feeding under all three prey combinations. Sanchez et al. (2004) examined developmental success of *D. hesperus* nymphs raised on prey versus
mullein and found that on mullein without prey 30% of nymphs completed development, whereas about 90% completed development on most host plants with prey. Therefore, it is beneficial for *D. hesperus* to incorporate both animal and plant material into its’ diet rather than subsist on plant material alone when prey are also available. Water is lost continually through extra-oral digestion and plant feeding is one way to regain water (Pollard 1988; Gillespie and McGregor 2000). Gillespie and McGregor (2000) posit that plant feeding in *D. hesperus* to gain water may occur in proportion to predation levels irrespective of prey quantity or quality. Therefore, *D. hesperus* did not spend all its time prey feeding or searching for prey.

The functional response of a predator is often used as a means to understand the searching efficiency of a predator population. Functional response is defined as changes in the prey consumption rate by predators with changes in prey density and occurs within a generation (Solomon 1949; Holling 1959a; Holling 1959b). In chapter 3, I used a modified version of Holling’s (1959b) disc equation, the “random-predator” equation (Rogers, 1972) to determine the functional response parameters of an omnivore when fed different prey species and examined the potential impact of intraguild predation on the prey populations. *Dicyphus hesperus* showed a significant decelerating increase in consumption of all four prey species as prey density increased (Type II functional response).

The functional response curve is defined by two parameters, the attack coefficient and the handling time. The attack coefficient (or instantaneous search rate) is the probability that a given predator will encounter a given prey during its searching lifetime and is influenced by many aspects such as predator versus prey mobility, success rate of
the predator, distribution of the prey, size and complexity of the arena, and motivation of the predator (Hassell 1978). The handling time refers to the amount of time spent chasing, killing, eating and digesting a single prey item (Hassell 1978). *Dicyphus hesperus* had similar attack coefficients when feeding on each of the four prey species separately, indicating that *D. hesperus* had similar abilities to find each of the four prey species. *Dicyphus hesperus* differed in its ability to handle the different prey species, requiring the lest amount of time to consume spider mites followed by *P. persimilis* and whitefly and requiring the most amount of time to consume *E. formosa*. *Dicyphus hesperus* had the highest maximal intake with whitefly and spider mites in part due to the different handling times of each species.

Holling’s (1959b) disc equation assumes that predation is limited by the effective searching rate at low prey densities and by the time needed to handle prey at high prey densities. This means that the number of attacked prey will increase with an increase in total time, prey density, and/or attack rate, but will decrease as handling time increases. This is because handling time takes away from searching time. According to the model, handling time includes time spent pursuing, subduing, and consuming each prey item, plus the effects of satiation (Mills 1982). When the handling times from the behavioural observation study (chapter 2) are compared to the handling times generated from Holling’s disc equation (chapter 3), it is clear that Holling’s disc equation over-estimated handling times. A smaller handling time means more time can be allocated to searching and consuming other prey items. This may be important in determining the foraging efficiency of a predator, especially for use in biocontrol programs. Therefore, functional
response experiments should be conducted together with behavioural observation experiments.

Holling’s (1959b) disc equation assumes that predators are primarily time-limited (handling time and search time), but this is often not the case. Predators may also be digestion limited (Sabelis 1992, van Rijn et al. 2005), therefore, satiation may influence foraging behaviour. Satiation patterns for D. hesperus were determined for alternate prey in order to better understand omnivore foraging efficiency. Although whitefly is the preferred prey for D. hesperus, D. hesperus became satiated on whitefly faster than the other prey species, thereby consuming a smaller quantity of whitefly compared to E. formosa, spider mites and P. persimilis. In addition, Dicyphus hesperus consumed more spider mites than E. formosa, indicating that the number of prey consumed by D. hesperus is highly correlated with the amount of time required to consume each prey type as well as satiation levels.

The results of chapter 2 and 3 indicated that D. hesperus, an intraguild predator, preferred herbivore species over intraguild prey. Therefore, I predicted that the addition of D. hesperus to an existing predator-prey/parasitoid-host community would enhance suppression of the herbivore populations. I also addressed whether the addition of an alternative food source (mullein) would affect population levels of intraguild prey or shared prey. Studies have shown that alternative prey can increase predation on a focal herbivore, decrease predation on a focal herbivore, or have a neutral effect (Harmon et al. 2000; Koss and Snyder 2005).

Although intraguild predation by D. hesperus had a negative effect on natural enemy populations, the presence of D. hesperus had a neutral effect on suppression of
spider mite populations and enhanced suppression of whitefly populations. The population dynamics of the spider mites and predatory mites in the absence of intraguild predation are typically unstable, with the predatory mites eradicating the spider mite population (Janssen and Sabelis 1992; van Baalen and Sabelis 1995; Pels and Sabelis 1999). The same is true of the population dynamics of whitefly and *E. formosa*. As a result, the populations of both specialist natural enemies (*P. persimilis* and *E. formosa*) go extinct. The highly coupled population dynamics of the parasitoid-host (predator-prey) relationship may account for the decline in natural enemies in the presence of the generalist more than intraguild interactions.

In this study, intraguild predation did not interfere with herbivore population suppression. For all treatments, natural enemy populations remained below the population levels of the herbivores throughout the experiment. The intensity of interspecific interactions between predators such as intraguild predation, interference competition, and cannibalism have been known to change with prey density and affect a prey’s predation risk accordingly (Vance-Chalcraft and Soluk 2005). Therefore, intraguild predation would be expected to increase as herbivore populations decrease in response to predation. At the point where the incidence of intraguild predation is high, herbivore population levels would be very low and intraguild predation would provide the means for the omnivore to persist in the system.

Another means for omnivores to persist in the system is through the use of high quality plant food sources. Interspersing mullein plants in tomato crops enhances early season establishment of *D. hesperus* when prey are absent and help preserve predator populations in the greenhouse during periods of prey scarcity, thus acting as a reservoir
which would allow \textit{D. hesperus} to respond quicker to increasing herbivore populations (Sanchez et al. 2003). Depending on the foraging strategy of the omnivore, the presence of high quality plant food sources may alter consumption of insect prey. In this case, increasing habitat complexity by interspersing mullein in tomato greenhouses also introduces a high quality alternative food source into the increasingly complex food web. The presence of an alternative food source (mullein) may reduce intraguild predation and cannibalism, thereby contributing to increased numbers of natural enemies (Langellotto and Denno 2004).

This study demonstrated that the presence of mullein did not interfere with enhanced whitefly population suppression in the presence of \textit{D. hesperus}. Sanchez et al. (2003) demonstrated that the presence of mullein did not hinder the movement of \textit{D. hesperus} between mullein and tomato plants. Sanchez et al. (2004) found that \textit{Dicyphus hesperus} was primarily carnivorous and that a greater proportion of nymphs completed development on host plants with prey than on mullein without prey. McGregor and Gillespie (2004) found that \textit{D. hesperus} was strongly attracted to olfactory cues given off by whitefly-infested tomato leaves. VanLaerhoven et al. (2006) examined patch retention times for \textit{D. hesperus} on tomato and mullein and found that patch retention times were shortest when no prey were available. These studies suggest that \textit{D. hesperus} will migrate from mullein plants to tomato plants as herbivore numbers increase on tomato plants and support the use of mullein as an alternative plant to assist in establishment and maintenance of \textit{D. hesperus} populations in greenhouses.

Understanding the mechanisms governing dynamic interactions within natural enemy communities with respect to intraguild predation and outcomes on population
dynamics is an important step to understanding food webs. The increased use of biological control agents are changing simple tritrophic interactions into more complex food web interactions and it is becoming ever more important that we understand these interactions. The degree of intraguild predation and therefore its impact on herbivore suppression will depend on the species composition of the food web as well as the predator preferences and herbivore vulnerabilities of those species (Denno and Finke 2006). This study showed that when determining preference of an intraguild predator and its impact on a prey population, differences in prey vulnerabilities should be considered.

From a practical point of view, D. hesperus would make a good biocontrol agent for whitefly and spider mites, as is not predicted to disrupt herbivore population suppression through intraguild predation because D. hesperus appeared to have a preference for whitefly and maximal intake rates were lowest for the specialist natural enemies P. persimilis and E. formosa. This is just the first step in determining the foraging efficiency of D. hesperus and its effects on the population dynamics of herbivores and their natural enemies. Future studies need to incorporate more prey choices and larger arenas.
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VITA AUCTORIS

Angela Brommit was born in 1975 in Kentville, Nova Scotia. She graduated from King’s County Academy High School in Kentville in 1993. From there, Angela attended Carleton University in Ottawa, Ontario where she obtained a Bachelor of Arts in Law and Psychology and a Bachelor of Science in Biology. She is currently a candidate for the Master’s degree in Biological Sciences at the University of Windsor and hopes to begin her Ph.D. in the fall of 2007.