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CAUSES AND CONSEQUENCES OF VARIATION IN OMNIVORY WITHIN FOOD WEBS: AN EMPIRICAL AND THEORETICAL EXPLORATION

by

Jonathan A. Bennett

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ABSTRACT

Omnivores feed at more than one trophic level and as such increase the complexity of food web interactions. Using manipulative experiments and stable isotopes, I found that the omnivorous insect, *Dicyphus hesperus*, fed more often on plant material when prey became scarce. Variability was found within populations, suggesting differences in feeding decisions among individuals. By examining the spatial distribution of resources and the foraging behaviors of *D. hesperus* and its intraguild prey, *Encarsia formosa*, I found that the distribution of prey resources was altered by the omnivore to favor itself. The omnivore also disrupted the distribution of the parasitoid, though it relieved intraspecific pressure within parasitoid populations. A theoretical examination of spatial dynamics showed that coexistence can be achieved between a competitively dominant intraguild predator and its intraguild prey through trade-offs in foraging scale and dispersal ability. Here, omnivory was more equivalent to competition than predation, and omnivore preference was relatively unimportant.

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 the 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 and the input of Dr. J.L. Shipp in the preparation of the manuscript "Foraging strategies, resource distributions, and intraguild predation: Intraguild interactions between an omnivore and a parasitoid". 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.

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STATEMENT OF ORIGINALITY

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 the discipline. I also certify that the work embodied within this thesis is the result of original research and has not been submitted for a higher degree to any other University or Institution.

TABLE OF CONTENTS

CHAPTER

LIST OF TABLES

CHAPTER

IV. CHAPTER IV

LIST OF FIGURES

CHAPTER

II. CHAPTER 2

III. CHAPTER 3

IV. CHAPTER 4

Chapter 1

General introduction

The understanding of food web dynamics is essential to tackling many of the ecological problems facing the world today (de Ruiter et al. 2005). This necessarily means understanding the interactions that occur within food webs. If we understood each of these interactions independently, we might understand the dynamics of the food web as a whole. However, much of our ecological understanding is imperfect, so we must compartmentalize food webs to make them more tractable. In this thesis, I will explore omnivory as an interaction in both mechanism and in its effect on community structure and function. Here I refer to omnivory as feeding at more than one trophic level (Pimm and Lawton 1978). Omnivory is a widespread trophic interaction which is inherently complex (Arim and Marquet 2004; Coll and Guershon 2002; Polis 1991). By feeding on more than one trophic level, omnivores have the potential to link large numbers of organisms that otherwise may never influence each other and thus are capable of having widespread effects throughout the entire food web.

Omnivory, as a blanket term, can encompass a variety of feeding ecologies. Mostly, omnivory is used to describe both intraguild predation (IGP) and 'true omnivory'. IGP is the consumption of a potential competitor (Polis et al. 1989), otherwise termed within-chain omnivory (Pimm 1982). There are numerous examples within the literature, most coming from insect, aquatic, or marine food webs. True omnivory is the consumption of both plant and animal tissue (Coll and Guershon 2002), though many true omnivores are generalists that also consume competitors.

Types of omnivory

IGP occurs for a variety of reasons (Polis et al. 1989). As most predators will feed on any organism within a certain size range, despite trophic position, it is common for large predators to consume smaller predators with which they share prey (e.g. Denno et al. 2004). The consumption of parasitized prey also fits this category. Insect predators commonly consume parasitoid larvae along with their host (Colfer and Rosenheim 2001; Kester and Jackson 1996; McGregor and Gillespie 2005; Snyder and Ives 2001). This may also include the incidental consumption of insects by large herbivores (Smith and Balda 1979).

Age-structured IGP is a common result of ontogenetic diet shifts. As a species matures, its diet may change either in type or in size. This change can involve the inclusion of former competitors in the diet (Polis et al. 1989). This is often seen in both food webs with fish (Polis et al. 1996) and in arthropod communities (Walzer et al. 2004). Age-structured IGP can also be symmetrical, with both species feeding on the immature stages of the other, as is seen in predatory mites (Venzon et al. 2001).

Some forms of IGP are unrelated to size. Facultative hyperparasitoids are common and consume both the shared host and primary parasitoids (Rosenheim et al. 1995), though the size difference between the parasitoids is likely negligible. Social generalists, such as ants, will often consume competitors many times their size (Holway et al. 2002). It is arguable that ants act as a much larger organism when foraging due to the number of individuals involved in the act of predation.

Omnivory involving plant and prey diets can be facultative or obligate (Coll and Guershon 2002). A facultative omnivore supplements its diet to increase its fitness. This can be seen in the inclusion of plant material in mantid diets (Beckman and Hurd 2003) and predation of mite eggs by predominantly herbivorous thrips (Janssen et al. 2003). Obligate omnivores have diets which are not nutritionally complete without including both resources. This is the case with the omnivorous mirid *Dicyphus hesperus* Knight (Heteroptera), which requires the water obtained by plant feeding to complete development (Gillespie and McGregor 2000), but different plants have been shown to differentially enhance fitness suggesting some sort of nutritive benefit (Sanchez et al. 2004).

Though there are different types of omnivore, all experience a benefit due to a certain amount of plasticity in their diet. In the next few sections, I will review the methods used to determine omnivory, the factors influencing variation in the degree of omnivory, and some of the effects that omnivory has on communities and food webs.

Manipulative experiments

The most common way to determine the interactions between species within a food web is to add and remove species. The determination of indirect effects is often problematic and difficult to separate from direct effects. Very little work has been done to directly test the factors affecting the degree of omnivory or the relative effects of competition and predation on an interaction. A number of theories have been suggested as to why omnivory occurs. The dietary plasticity that comes with being an omnivore allows for an increased degree of persistence in a variable environment (Coll and Guershon 2002). That being said, it is commonly thought that the degree of omnivory will be based on the relative abundances of different resources. The quality of those food sources is also important (Agrawal and Klein 2000; Diehl 2003; Janssen et al. 2003). The increased acquisition of nitrogen when feeding at a higher trophic level was at first believed to be an important factor determining the prevalence of omnivory (Fagan et al. 2002), though later work downplayed its importance (Matsumura et al. 2004). Nutrient balancing behaviors have been observed in both omnivores and generalist predators (Gadd and Raubenheimer 2000; Mayntz et al. 2005), so the idea that omnivory is related to nutrient specific needs is not entirely unfounded. To my knowledge, there has been no definitive work in the factors controlling omnivory.

Numerous studies have commented on the role of omnivory in food webs. Of the studies directly testing food web theory, the simplest are microcosm studies. Microcosms offer the ability to control many of the variables within an experiment while the variables of interest are manipulated. Though they do offer excellent control, microcosms also introduce artifacts pertaining to the relatively homogeneous environment and spatial constraints. Some of the simplest investigations into omnivory in food webs have been done using microbial food webs. Omnivores have been found to achieve higher densities than specialist predators (Morin and Lawler 1996). When varying the number of species exhibiting IGP, omnivory was found to increase persistence time within microbial microcosms, but was unable to offset the destabilizing effects of increasing food chain length (Holyoak and Sachdev 1998). Within similar microcosms, low productivity was found to exclude the intraguild predator, whereas increasing productivity allowed for coexistence (Morin 1999). However, high productivity was found to exclude the IG prey (Diehl and Feissel 2001). This supports the widely held belief that coexistence is only possible when the intraguild prey is the superior competitor, and that at low resource levels the IG predator should be excluded (Polis et al. 1989).

At a somewhat larger scale, mesocosms allow for greater heterogeneity. In a study examining the effect of predator diversity on a simplified food web, an omnivorous species was introduced along with several strict predators (Bruno and O'Connor 2005). In the absence of omnivory, predator diversity was found to maximize algal biomass. The inclusion of the omnivore disrupted the cascade through direct feeding on the algae. The scale of this study precluded any density-mediated indirect effects or population level effects as only five individuals were present within any given mesocosm. This effect on trophic cascading is confirmed by some field studies (Finke and Denno 2003; Finke and Denno 2004), but seems to contradict others. Plots containing mantids as the IG predator and spiders as the IG prey were established in old field habitat (Moran et al. 1996). Mantids induced behavioral shifts among the spiders, increasing emigration rates of the IG prey. Mantids exhibited weak interactions with all herbivorous species, but still managed to induce a cascade, resulting in an increase in plant biomass. The differences among these studies could be due to trait-mediated indirect interactions, which have recently been assigned importance when considering cascades (Schmitz et al. 2004). Preferences and consumption rates are also likely to differ between the species.

Other field studies have investigated the resiliency of food webs containing omnivory to perturbation (Fagan 1997). Field plots were established containing either a strict predator or an omnivore as the top consumer. This factor was then crossed with a disturbance in the form of an aphicide. Omnivory was found to stabilize the food web against disturbance, with only the community in the omnivorous treatment remaining similar to that found within the no aphicide control. This is likely due to the flexible foraging strategy of the omnivore allowing it to quickly adapt to changes in secondary productivity.

Most studies of omnivory were not designed to test the effects of omnivory on food webs. In general, these studies were designed to quantify the effects of omnivory on a particular species or omnivory was noted during observation, but was not the interaction of interest. Of these studies, a large number of them are located within the biological control literature. Biological control is essentially the process of manipulating a food web. Natural enemies are added in order to attain control of some pest species. Often, these natural enemies engage in omnivory, either through intraguild predation for generalist predators and facultative hyperparasitoids (Rosenheim et al. 1995) or through the consumption of plant material for omnivorous predators (Coll and Guershon 2002; Eubanks et al. 2003).

The results of these interactions can vary. In some cases, intraguild predation disrupts biological control (Brodeur and Rosenheim 2000; Rosenheim 2005). This is the case with biological control of psyllid pests on eucalyptus trees in California (Erbilgin et al. 2004). Here, introduction of generalist predators into cages with the psylllid and its parasitoid increased parasitoid mortality, resulting in declines in psyllid mortality. No effect was seen on psyllid abundance in the field due to generalist predators. This suggests that spatial constraints may play a role in determining the outcomes of these interactions. Intraguild predators can also enhance suppression of pests. Ladybird beetles can cause increased control of aphid populations, despite the presence of IGP on the parasitoid through predation on parasitized hosts (Colfer and Rosenheim 2001). This type of result is expected to occur as long as the predator has at least a partial preference for unparasitized hosts. IGP can also have non-disruptive effects on pest mortality (Rosenheim et al. 2004). In this study, the small body size of the mite reduced intraguild predation by a spider on a predatory mite. Non-disruptive dynamics are also seen with fire ants in cotton crops (Harvey and Eubanks 2005), though this is not always the case (Eubanks 2001; Eubanks et al. 2002). IGP yields a series of complex interactions within a guild of aphid predators (Lucas et al. 1998), with the importance of intraguild interactions varying between species, but affected by prey density for all species.

Omnivory including plant tissues can enhance the performance of generalists as is seen in a number of heteropteran insects (Eubanks and Denno 1999; Eubanks and Denno 2000; Sanchez et al. 2003). These studies suggest that plant food quality may be an important factor determining omnivore function. Another way plant quality may affect the interaction between an omnivore and its prey is through plant defenses (Agrawal 2000). Both low quality plants (Janssen et al. 2003; Magalhaes et al. 2005) and induced plant resistance (Agrawal et al. 1999) have been shown to increase mite egg consumption by omnivorous thrips. In both cases, the omnivore is supplementing an otherwise poor diet with prey. In the case of induced plant defenses, the benefit is two-fold for the plant, a reduction in herbivory as well as increased consumption of the herbivore. However, this interaction is not quite that straightforward, as thrips will also eat the eggs of predacious mites. Consumption of mite eggs was higher on low quality plants, but more predator eggs were killed on this plant type as spider mite eggs are partially protected by webbing (Magalhaes et al. 2005). There was no difference on high quality plants. This mode of consumption with partial preference may have large effects on the population dynamics of the two mite species.

Though these are not tests of food web theory per se, these biological control experiments can give us an idea of the types of factors that are important in determining the effects of omnivory in food webs. Of the experiments listed above, we can say that spatial constraints, body size ratios, preferences, prey ratios, and the quality of alternative foods may be important in omnivorous interactions. It is unclear to what degree these variables operate in isolation, but it seems likely that they are interconnected.

Diet analysis

Diet analysis is a relatively straightforward way to analyze the strength of trophic interactions. Stable isotope analysis is commonly used to investigate trophic structure and involves the tracking of ^{15}N and ^{13}C through the food web (Deniro and Epstein 1978; Deniro and Epstein 1981). As trophic level increases, there is a consequent increase in the ratio of ^{15}N to ^{14}N. This increase can be quantified and then used to determine trophic position (Post 2002). Trophic position is the estimated position that an organism occupies within the food web. If the animal feeds at both the third and fourth trophic level, then its trophic position would be somewhere between three and four. When using carbon isotopes, one can determine the source of the diet as there is little variation between trophic transfers compared to the variation between plant sources. For many species this is relatively straightforward, but omnivores generally have a wider diet breadth which can increase the variance in their isotopic signature. Recently, it has been proposed that variation in isotopic signatures can be used to determine the amount of omnivory (Bearhop et al. 2004). Variation has been found on both temporal and spatial scales for ant omnivory using similar methods showing that these ants function slightly above the level of a primary predator on average, dependant on a number of conditions (Mooney and Tillberg 2005). Dietary mixing models are commonly used to explain these differences. These models use average fractionation rates to determine the relative contribution of diet sources (Lubetkin and Simenstad 2004; Phillips 2001; Phillips and Koch 2002), though they are sensitive to isotopic variation within the diet source (Phillips and Gregg 2001).

Most attempts to determine trophic structure have not included temporal variance, but have looked at the isotopic signature at a single point in time. Using this method, researchers have been able to reclassify stream insects formerly thought to be predacious as omnivores (Lancaster et al. 2005). Other studies have examined the degree of omnivory in ants (Bluthgen et al. 2003; Tillberg and Breed 2004), fish (Cabana and Rasmussen 1994; Motta and Uieda 2005; Post 2002; Vander Zanden et al. 1997; Vander Zanden and Rasmussen 1999), freshwater invertebrates (Branstrator et al. 2000; Kling et al. 1992; Parkyn et al. 2001; Vander Zanden and Rasmussen 1999), marine invertebrates (Schmidt et al. 2003), and predators within detrital webs (Halaj et al. 2005; McNabb et al. 2001). This technique has since been used to look for generalities within food webs. Post used this technique to show that ecosystem size was the greatest predictor of food chain length as opposed to productivity (Post et al. 2000b) and to link the littoral and pelagic zones of lakes (Post et al. 2000a). In these papers, food chain length was determined by looking at the trophic position of the top predator in the system and comparing this metric among lakes. Others have used this approach to show that omnivory is increased in small lakes and suggest spatial compression as the cause (McCann et al. 2005).

Stable isotope analysis shows a great deal of promise as a technique for determining omnivory, though a large amount of variation exists that has yet to be accounted for. The variation in consumer fractionation rates is quite large (Vander Zanden and Rasmussen 2001; Vanderklift and Ponsard 2003), though a large proportion of this can be accounted for through comparison to a basal resource (Post 2002). Variation within populations and individuals does occur within basal groups like plants (Dawson et al. 2002; Evans 2001; Farquhar et al. 1989; Handley and Scrimgeour 1997). Quantification of the effects of this variation needs further attention.

Gut content analysis provides another method of diet determination. Traditionally, this involved the visual identification of the diet, but new DNA based approaches offer a much more efficient methodology (Harwood and Obrycki 2005; Harwood et al. 2004; Juen and Traugott 2005). However, this methodology is still being developed.

Theoretical analysis

The earliest theoretical treatments of omnivory in food webs were that of Pimm and Lawton (Pimm 1980; Pimm 1982; Pimm and Lawton 1978). Increasing omnivory was found to increase the proportion of unstable food chains. At the highest ranks of omnivory, almost all food chains were unstable except with weak interaction strengths. The importance of weak interactions agrees with a number of more recent studies (Deruiter et al. 1995; Emmerson and Yearsley 2004; McCann et al. 1998; Raffaelli and Hall 1996). For the models that showed stability, increasing omnivory led to shorter return times. This suggests that omnivores are flexible in nature, allowing them to adapt rapidly to changes (Fagan 1997), though this flexibility is not found within the models used by Pimm, as these are rather rigid in structure. From Pimm's models, he concluded that omnivory should be statistically rare due to the low number of stable systems. This supposition has been rebuffed by a number of authors (Arim and Marquet 2004; Fagan 1997; McCann and Hastings 1997; Polis 1991). Pimm did not represent food webs as flexible. Real food webs are flexible with many organisms that have adaptive traits (Abrams 1996; Abrams and Matsuda 2004; Fryxell and Lundberg 1994; Galef 1996; Krivan 2000; Krivan 2003; Krivan and Schmitz 2003; Schmitz et al. 1997). Omnivores feed on more than one food as a risk-spreading strategy (Fagan 1997), which allows for persistence under a multitude of environmental conditions (Coll and Guershon 2002; Holt and Lawton 1994; Polis 1991; Polis et al. 1989) and diffuses the effects of consumption across multiple trophic levels (Polis and Strong 1996).

This issue was re-evaluated by McCann and Hastings (1997) using a two-species type II functional response and a preference parameter, to simulate the degree of omnivory. In most cases where the food web was unstable prior to omnivory, the inclusion of omnivory was found to stabilize the system and increase minimum population densities, except when omnivory was strong. If the initial conditions led to stable dynamics, omnivory tended to destabilize the system. The stabilizing effects of omnivory are consistent with empirical results (Fagan 1997; Holyoak and Sachdev 1998).

Holt and Polis (1997) took three commonly used models pertaining to predation and competition and modified them to include omnivory. The authors draw two generalizations from these models which they apply to IGP in general. First, intraguild predators are able to persist at lower basal resource levels than strict predators because they can use the resource directly. Second, coexistence requires the intraguild prey be a superior competitor to withstand the predation pressure. Holt and Polis provide a mathematical basis for some common sense properties of food webs, but these properties are only applicable in situations where all other things are equal. Otherwise, any number of exogenous factors affecting natural systems would upset these properties. However, all three models used by Holt and Polis were concerned with the same interaction, but each model approached it from a slightly different perspective. These small shifts in the assumptions change the behavior of each of the models and should serve as a caution when interpreting the results of theoretical models.

There are four ways in which plant feeding omnivores differ from strict prey feeders (Coll and Izraylevich 1997). The first is that the relative size of the resource is unimportant and it is thus most likely prey density and plant quality that influence the interaction. Second, plants do not move. There is no change in the probability of finding the plant. Third, the plant and prey are often spatially correlated. Fourth, there should be differences in the nutritional quality of the prey and the plant which will influence diet mixing. To encompass these differences, Coll and Izraylevitch (1997) do not treat the plant explicitly, but use a cumulative carrying capacity for both species when feeding on the resource. They also include a nonlinear preference function incorporating consumer density and the toxicity of the plant, with predator growth rates dependent on diet choice. They found that at elevated plant toxicity levels, predators were better able to suppress prey through the reduction of the negative effects of competition and enhanced stability of the model. These results are consistent with a number of empirical studies discussed earlier (Agrawal and Klein 2000; Agrawal et al. 1999; Janssen et al. 2003; Magalhaes et al. 2005) which showed that poor quality plant foods increased predation rates. This model was revisited and adapted a few years later to explore a larger range of possibilities for resource availability and preference (Lalonde et al. 1999). They found that an intermediate mix of plant feeding and predation was most likely to yield stable populations.

Another set of studies considers dynamics in a simple chemostat environment (Kooi et al. 2002; Kuijper et al. 2003). The studies were undertaken as an admitted oversimplification of natural systems, but all conditions can be easily maintained at constant levels for experimental tests of the model. This allows direct comparison of theoretical and experimental results. The model includes nutrient dynamics, essentially expanding the system to four trophic levels. The study found that IGP with less consumption of the intraguild prey demonstrated a wide variety of dynamic behaviors that appear ecologically plausible. As many previous investigations have found, the IG prey must be a superior competitor for coexistence. In that case, if the interaction shifts more towards competition than predation, the IG predator will be excluded. However, with a small degree of omnivory, multiple stable states exist in which only the IG predator or the IG prey exist with both systems being resistant to invasion by the other competitor. High nutrient densities were found to complicate dynamics, but this behavior was eliminated by the inclusion of a weak IG interaction between the predator and the resource species. The authors suggest that if complex dynamics are so easily eliminated by weak interactions and IGP is so wide spread in nature, then the complex dynamics generated by many simple models may be artifacts.

The effect of space on food web dynamics has recently drawn a lot of interest. In particular, spatial compression of the food web is believed to be important in determining the stability of food webs. Webs that are more compressed will likely suffer increased competition. This effect was modeled using lake food webs where weak and intermediate couplings between systems lead to stability (McCann et al. 2005). The destabilizing effects of spatial coupling can be reduced by the inclusion of omnivory, with higher degrees of omnivory required to offset elevated degrees of spatial compression. These results confirm other results which found the trophic position of trout to be lower in smaller lakes (Post et al. 2000b). Both large spatial scales as well as omnivory function similarly to increase stability as they provide refuges for prey when prey populations are at low abundances. The spatial scale allows the predator to transfer to a new environment, while omnivory allows the predation pressure to shift to another species.

This adaptive foraging behavior was more closely examined in another recent paper. Krivan and Diehl (2005) explore the possibility that an omnivore will feed only on the less profitable prey if the more profitable prey is unavailable. The more profitable food type is always attacked upon encounter, whereas the less profitable food type is attacked if the more profitable food type is below a certain critical density. The study found that in general, adaptive foraging increased the region in parameter space leading to permanence. This only occurred in regions where the predator would otherwise be excluded and had no effect on the prey. This result is intuitive from a behavioral aspect as the predator is only trying to optimize its own fitness and not that of the model, thus it increases its chance of survival. Whether omnivory was adaptive or not, coexistence was most likely when prey consumed the shared resource more efficiently, which is consistent with a number of other theoretical models.

Synthesis

To date, theoretical explorations of omnivory have delivered few generalizations. The most commonly observed occurrence is that the intraguild prey should be a more efficient competitor for coexistence to occur. Also, omnivory can stabilize an otherwise unstable system, by offering a refuge to prey through diet switching. This type of variable interaction strength is somewhat analogous to the weak and intermediate interaction strengths which are generally agreed to promote stability. A final generalization is that stable omnivorous webs will destabilize at extremes of productivity. Though these generalizations seem to hold, they do not tell us much about how dynamics occur in the real world. In order for food web ecology to have value in applied areas, we must have specific knowledge of dynamics (de Ruiter et al. 2005). To expand our knowledge base, there are a number of factors that appear important in the experimental literature which have yet to be fully examined in theory.

Age structure is important in determining when intraguild predation will occur (Polis et al. 1989). The literature is littered with examples of how this occurs in nature (Polis et al. 1996; Venzon et al. 2001; Walzer et al. 2004), but there have been few theoretical treatments of this in regards to food webs. Invulnerable life stages have been included in theoretical investigations (Mylius et al. 2001) and age structure has been used to look at multitrophic interactions (Gutierrez et al. 1990), but this approach was largely descriptive. Another aspect which has seen not received theoretical consideration is reciprocal IGP. This is common in many age structured populations (Polis et al. 1989; Rosenheim et al. 1995), but has not been examined by any sort of theoretical means.

Omnivory involving plants takes two forms, species that supplement their diet with plant material and species that require plant material (Coll and Guershon 2002). There are bound to be a number of interesting differences in how this plays out in terms of dynamics. Plant material has been modeled as suboptimal food (Lalonde et al. 1999), but to my knowledge, it has never been addressed as a required food.

Spatial constraints can affect food web dynamics. This affects the degree of omnivorous behavior (Post et al. 2000b) and may affect the dynamics of intraguild interactions (Erbilgin et al. 2004). Some aspects of space have been addressed (McCann et al. 2005), but a number of aspects have yet to be explored. Spatial complexity is often considered when looking at foraging behaviors (Cobb and Watzin 2002; Gols et al. 2005), yet has not been applied to omnivory in food webs. It seems likely that heterogeneous environments may lead to dynamic model behavior.

There are a number of ways in which feeding preferences have been examined empirically (Janssen et al. 2003; Venzon et al. 2001) and theoretically (Coll and Izraylevich 1997; Krivan and Diehl 2005; Lalonde et al. 1999). Generally, what we find is that preference for the intraguild prey can stabilize dynamics. However, there are a number of ways that foraging behavior can be affected by preference that have yet to be examined. Preferences have not been examined for species feeding at three trophic levels as do most omnivorous Heteroptera (Eubanks et al. 2003). Neither have a number of issues that are considered important in optimal foraging theory been examined. This includes nutrient mixing which appears to be important in diet choice (Mayntz et al.

2005; Mayntz and Toft 2001; Mayntz et al. 2003; Simpson et al. 2004). Along a similar line, plant quality has been addressed empirically (Agrawal and Klein 2000; Agrawal et al. 1999; Diehl 2003; Eubanks and Denno 1999; Eubanks and Denno 2000; Janssen et al. 2003; Magalhaes et al. 2005; Sanchez et al. 2003; Sanchez et al. 2004) and in theoretical models (Coll and Izraylevich 1997; Lalonde et al. 1999), but never with multiple plant species of variable quality within a theoretical food web.

Another area which warrants further inquiry is the occurrence of trait-mediated interactions within food webs containing omnivory. Trait-mediated interactions are indirect interactions that involve changes in behavior. Recently, the role of trait-mediated interactions in food webs has received a lot of attention (Abrams et al. 1996; Bolker et al. 2003; Krivan and Schmitz 2004; Peacor and Werner 2000; Peacor and Werner 2001; Schmitz et al. 2004; Werner and Peacor 2003). This attention has not yet included the role of omnivory in affecting these interactions, but given the number of direct links in a food web with omnivory and the already dynamic behavior of these webs, trait-mediated indirect interactions are sure to abound and have profound effects throughout the web.

Over the next three chapters, I will address several of these issues. I will begin with a chapter on the use of both manipulative experimentation and stable isotope analysis to determine the factors affecting the occurrence of omnivory, commenting on both the benefits and limitations of such a technique. The second chapter is an empirical investigation of the interplay between the effect of the spatial arrangement of resources on relative foraging success and how foraging can in turn alter that spatial arrangement. I look at the arrangement of both the intraguild prey and the shared prey with and without the presence of an intraguild predator and compare these results with expectations derived from an analysis of foraging behaviors. In the third chapter, I take a theoretical perspective on the some of the factors that may affect the stability of omnivorous interactions. Specifically, I address the trade-off between foraging scale and dispersal time in a patchy environment and how this trade-off is affected by varying degrees of omnivory.

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Chapter 2

Measuring variation in omnivory within a greenhouse insect community using stable isotopes

Introduction

Omnivory, defined as feeding at more than one trophic level (Pimm 1982), is widespread in nature (Arim and Marquet 2004; Coll and Guershon 2002). Therefore, it is important to understand the mechanisms which influence variation in the occurrence and degree of omnivory. Variation in the degree of omnivory may arise from: age related differences among individuals (Branstrator et al. 2000; Polis et al. 1989); differences in food quality (Diehl 2003; Janssen et al. 2003; Magalhaes et al. 2005; Singer and Bernays 2003); risk associated with foraging (Singer and Bernays 2003); nutritional needs (Gadd and Raubenheimer 2000); or food availability (Mooney and Tillberg 2005). However, omnivory is not a simple interaction between two species and may involve numerous indirect interactions (Bruno and O'Connor 2005; Diehl 1995). This complexity suggests that monitoring only population dynamics is insufficient to infer the degree of omnivory in the absence of other more direct measurements of the interaction.

Diet composition is one way to infer the relative strength of trophic interactions for an omnivore. Stable isotope analysis is often used to determine diets and has been used to measure the degree of omnivory (Bluthgen et al. 2003; Mooney and Tillberg 2005). Nitrogen is generally used as an indicator of trophic position (Deniro and Epstein 1981) and carbon as an indicator of the plant source (Deniro and Epstein 1978). Most commonly, the interpretation of omnivory using stable isotopes involves the determination of trophic position using average fractionation rates within a dietary mixing model, though these models are sensitive to the degree of variation in the isotopic signature of diet sources (Phillips 2001; Phillips and Gregg 2001). The variation within isotopic signatures has also been proposed as an indicator of diet breadth and omnivory (Bearhop et al. 2004; Matthews and Mazumder 2004). Variation in $\delta^{13}C$ and $\delta^{15}N$ can be considered as indicators of dietary variation within the population. When coupled with abundance estimates, a time integrated measure of changes in diet composition should prove robust in interpreting the relationships between omnivory and community dynamics.

Dicyphus hesperus Knight (Heteroptera: Miridae), is an omnivorous insect which requires both plant and prey in its diet (McGregor et al. 1999). It is currently used as a biological control agent for greenhouse whitefly, *Trialeurodes vaporariorum* Westwood (Homoptera: Aleyrodidae), on greenhouse tomato, *Lycopersicon esculentum* Mill (Solanaceae), in Ontario, Quebec, and British Columbia, Canada. Also within this system the parasitoid, *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae), is routinely used for biological control for whitefly, and mullein, *Verbascum thapsus* L. (Scrophulariaceae) is included as a supplemental high quality plant food for *D. hesperus* (Sanchez et al. 2003). Intraguild predation occurs, with *D. hesperus* feeding on parasitized whitefly (McGregor and Gillespie 2005). To investigate the factors affecting dietary changes and thus the degree of omnivory, we established a series of cages where the omnivore would be subjected to varying populations of whitefly and their parasitoid. Dietary changes were tracked using stable isotope analysis and then compared with known changes in prey abundance.

Materials and methods:

Plant and insect sources

For greenhouse trials, tomato plants var. Rhapsody, were grown hydroponically in rockwool growing medium in a greenhouse at the Agriculture and Agri-Food Canada Greenhouse and Processing Crops Research Centre (GPCRC) in Harrow, Ontario, Canada. Plants were watered and fertilized through a fertigation system. The nutrient solution contained 230 ppm NO_3, 10 ppm NH_4, 60 ppm P, 460 ppm K, 200 ppm Ca, 80 ppm Mg, 3 ppm Fe and 0.5ppm Mn with an EC of 2800 μScm^{-1} and a pH of 5.5. Tomato plants for the feeding trials were cultivated in BM2 germinating mix soil (Berger Peat Moss Co.) at the University of Windsor greenhouse in Windsor, Ontario, Canada. Plants were grown under natural light supplemented with high pressure sodium lights (16:8 light : dark cycle), flooded daily, and fertilized with 4 mL of 20-20-20 fertilizer (Plant-Prod®) mixed in 1 L of water once per week. Mullein plants, *Verbascum thapsus* L. (Scrophulariaceae), were grown from seeds originally collected in Summerland, British Columbia, Canada. They were cultivated from seed at the University of Windsor greenhouse, and then transferred to the GPCRC for use in the greenhouse cage trials. The mullein plants at both locations were maintained using the same method as tomato.

Colonies of *D. hesperus* were established from individuals originally collected on white hedge nettle, *Stachys albens* Gray (Lamiaceae), at 500 m elevation in the Sierra Nevada Mountains in California, at 25° 42' N, 118° 50'W. Colonies were kept at 24°C and 16h light photoperiod. Insects were reared on tobacco, *Nicotiana tabacum* L.

(Solanaceae) and fed a diet of *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) eggs. *Encarsia formosa* were obtained from Koppert Biological Systems (EN-STRIP) as parasitized whitefly pupae. Adult parasitoids were allowed to emerge before use in the greenhouse trials, but were presented to *D. hesperus* as parasitized whitefly pupae on the card for the feeding trials. Whiteflies for the greenhouse cage trials were obtained from a colony maintained on tomato at the GPCRC. The whiteflies for the colony were collected from commercial greenhouses in southwestern Ontario. Whiteflies for the feeding trials were collected from a colony grown on tomato in the University of Windsor greenhouse. The whiteflies for this colony were started from the colony at the GPCRC.

Feeding trials

To determine the fractionation rate for *D. hesperus* fed on diets of whitefly and parasitized whitefly, individual *D. hesperus* were placed within 500 mL styrofoam cups, each containing a covered water reservoir and a tomato leaflet with the petiole inserted into the reservoir. Depending on the treatment, the leaflet was either clean or infested with whitefly pupae. Into each of the cups with a clean leaf, a single card containing approximately 80 parasitized pupae was inserted. Prey were replaced for both treatments every 2-3 days to ensure constant prey availability. At the end of 30 days, *D. hesperus* individuals were collected for isotopic analysis. Samples were taken of each of the diet components throughout the experiment. This experiment was repeated a second time, with samples of all dietary components as well as tobacco and mullein leaves collected for isotopic analysis. Tobacco and mullein were collected along with tomato to compare differences among plant materials within the diet. All samples were frozen at -10°C until they could be analyzed.

Greenhouse cage trials

Cage trials were conducted within a greenhouse at the GPCRC. Cages were constructed using 3.8 cm ABS plastic pipe and covered with polypropylene non-woven fabric (Agryl-P17), a commonly used insect barrier due to its small mesh size. All cages were 1.44 m^2 at the base and 2 m in height. Each cage enclosed six tomato plants and a single potted mullein plant suspended in the center of the cage near the top. Mullein was included to facilitate the establishment and survival of the omnivorous *D. hesperus* (Sanchez et al. 2003).

Into all cages, 30 whiteflies were introduced and allowed three weeks to establish within the cage before omnivore and parasitoid introduction. Thirty-six *D. hesperus* individuals were introduced into each cage with the introduction split evenly among adults at an even sex ratio, late instar juveniles, and early instar juveniles. In order to create a variable parasitism environment, five cages received 15 initial adult females (high release rate) and five cages received five adult females (low release rate). Both whitefly and *E. formosa* were re-released into the cages at their initial release rates at weeks 7, 9, 10, and 11. Mullein plants were also reintroduced as necessary. Beginning in the sixth week, six leaves were removed each week to record whitefly and parasitoid populations and up to five adult *D. hesperus* individuals were removed every two weeks for isotopic analysis. The number of *D. hesperus* captured was determined by the number of individuals caught within 10 minutes of searching the cage. The leaves removed for insect counts were selected using a directed sampling scheme due to the aggregated and structured nature of whitefly populations (van Lenteren and Noldus 1990). Three leaves were removed from two plants each week, according to a schedule ensuring two weeks between samples from a particular plant. Leaves were taken at the 4th, 8th, and 12th leaf position from the top of the plant to target both early and late whitefly instars. Whitefly nymphs, pupae, and parasitized pupae were counted on each leaf by visual scans aided by the use of a stereomicroscope. Other losses of prey and natural enemies may have occurred during weekly crop maintenance, as senescing basal leaves and secondary shoots were removed from the plant using commercial propagation practices. All removed leaves were placed on the floor of the cage for a period of one week to minimize any losses of natural enemies and prey. The experiment was conducted for 13 weeks from the introduction of whiteflies into the cages. This allowed for at least two generations of all insects. At the completion of the experiment, tomato leaf tissue was collected from a number of plants for isotopic analysis.

Isotope analyses

All samples were dried at 70°C for 72 h before analysis. Plant tissues were analyzed as individual leaves. Each individual leaf was homogenized using a mortar and pestle and then weighed to approximately 450 μg. Healthy and parasitized whitefly pupae were grouped according to source, whether it be a specific leaf or card. Samples were weighed to approximately 250 μg for analysis. Each sample contained a minimum of 10 whitefly or *E. formosa* pupae. *Dicyphus hesperus* were analyzed individually as whole insects. In cases where the weight of the insect exceeded 600 μg, the insect was homogenized and a sample of 300 μg was taken. All samples were placed into tin capsules and analyzed for $\delta^{13}C$ and $\delta^{15}N$ at the University of Windsor stable isotope laboratory using a Thermo Finnigan Flash 1112 elemental analyzer coupled to a Thermo Finnigan Delta Plus mass spectrometer, operating in continuous flow mode. The samples from the cage trials and the initial feeding trials were analyzed at a different time than the samples from the second feeding trial. The precision was better than 0.1‰ for δ^{13}C and 0.3‰ for δ^{15}N for the initial run and 0.2‰ for δ^{13}C and 0.3‰ for δ^{15}N for the second run. Fractionation rates were calculated as the difference between the average δ^{13}C and δ^{15}N values for *D. hesperus* individuals and the average isotopic composition of their diet, assuming an equal contribution of both plant and prey. Fractionation rates between *E. formosa*, whitefly, and tomato were also calculated using means. Average differences between plant types were also calculated by comparing mean δ^{13}C and δ^{15}N values of plants grown under the same conditions.

Statistical analysis

The isotopic signatures of *D. hesperus* from the feeding trials and diet components were rank transformed and first compared using multivariate analysis of variance (MANOVA) to identify possible variation between trials in both δ^{13}C and δ^{15}N. Due to a significant interaction effect between trial and sample type, trials were analyzed separately. To identify which sample types varied between trials, each sample type was analyzed independently using MANOVA. Differences between diet components and *D. hesperus* within feeding trials were analyzed following rank transformation using MANOVA for δ^{13}C and δ^{15}N. When necessary, *post hoc* analysis was conducted using Tukey's HSD test. *Dicyphus hesperus* individuals from the feeding trials were only compared for the first feeding trial due to the loss of samples of individuals fed on healthy whitefly in the second trial. The isotopic signature of different plant types grown under the same conditions were also compared using MANOVA for both δ^{13}C and δ^{15}N. Data for δ^{13}C were rank transformed prior to analysis.

Linear regression was used to examine how both insect counts and isotope data from the cage trials varied with time. Insect counts were summed to give a value for total prey and then transformed using the natural logarithm. Both the mean and coefficient of variation (variance to mean ratio) of the $\delta^{13}C$ and $\delta^{15}N$ measurements for each cage were regressed against time individually using linear regression. Values for $\delta^{13}C$ as well as both sets of coefficients of variation were rank transformed prior to analysis. All statistical analyses were conducted using SPSS 13.0 (SPSS 2004).

Results

Significant differences in isotopic signature between feeding trials were identified as an interaction between the sample type and the trial (Wilks' lambda = 0.52, $P = 0.07$). Univariate results indicated that this response was due to a difference in $\delta^{13}C$ ($F_{5,36} = 5.88$, $P < 0.001$). Both tomato and *E. formosa* harvested from the greenhouse at the University of Windsor varied between trials (Wilks' lambda = 0.002, $P = 0.043$, and Wilks' lambda = 0.06, $P = 0.004$ respectively). This variation was also due to differences in $\delta^{13}C$ for both tomato ($F_{1,2} = 22.06$, $P = 0.009$) and *E. formosa* ($F_{1,5} = 20.41$, $P = 0.001$). Significant differences were found among samples in the first feeding trial (Fig. 2-1, Wilks' lambda = 0.16, $P = 0.003$) and occurred for both $\delta^{13}C$ ($F_{5,14} = 8.70$, $P = 0.001$) and $\delta^{15}N$ ($F_{5,14} = 9.49$, $P < 0.001$). *Dicyphus hesperus* fed on *E. formosa* was distinct from both the tomato ($P = 0.017$) and *E. formosa* ($P = 0.031$) for $\delta^{13}C$, but for $\delta^{15}N$, only from *E. formosa* ($P = 0.016$). The $\delta^{13}C$ values for *D. hesperus* fed on whitefly

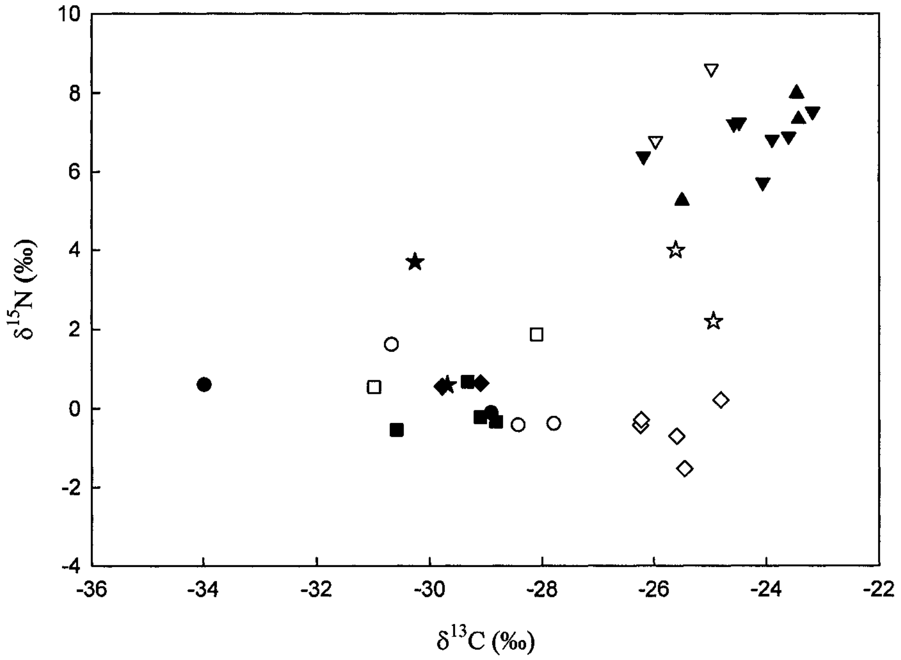

Figure 2-1: Isotopic signature of diet components and omnivores from the feeding trials. Filled symbols indicate the first trial and hollow the second. Symbols are as follows: tomato (★), whitefly (■), *E. formosa* from leaf (♦), *E. formosa* from card (●), *D. hesperus* fed whitefly (▲), and *D. hesperus* fed *E. formosa* (▼).

differed from both tomato ($P = 0.017$) and whitefly ($P = 0.014$), but for $\delta^{15}N$ only from whitefly ($P = 0.005$). No differences were found between the isotopic signatures of any of the prey items. In the second trial, there were differences between diet components (Wilks' lambda = 0.12, $P = 0.005$), but only for $\delta^{15}N$ ($F_{4,10} = 7.03$, $P = 0.006$). *Dicyphus hesperus* was significantly enriched in ^{15}N relative to *E. formosa* ($P = 0.048$), but not tomato. *Encarsia formosa* was depleted compared to tomato ($P = 0.039$), but was not significantly different from whitefly. No other differences were found between diet components.

All fractionation rates are reported as mean (±standard error). The average fractionation rate for *D. hesperus* fed *E. formosa* and tomato was 6.45 (±0.34) parts per thousand (‰) for $\delta^{13}C$ and 5.81 (±0.13)‰ for $\delta^{15}N$ in the first trial and 1.65 (±0.50)‰ for $\delta^{13}C$ and 6.01 (±0.92)‰ for $\delta^{15}N$ for the second trial. *D. hesperus* fed whitefly and tomato differed from their diet by 5.69 (±0.68)‰ for ^{13}C and 5.79 (±0.82)‰ for ^{15}N in the first trial. No viable results were obtained in the second trial due to sample contamination and loss. Both whitefly and *E. formosa* were depleted in ^{15}N from the tomato plants in both trial 1 (whitefly -2.25‰, *E. formosa* -1.78‰) and trial 2 (whitefly -2.56‰ and *E. formosa* -3.61‰). Both whiteflies (0.51‰) and *E. formosa* (0.71) were mildly enriched in ^{13}C in the first trial, but in the second trial *E. formosa* was mildly depleted (-0.74‰) and whiteflies were substantially depleted (-2.91‰). Samples of the same type were all highly variable. To highlight this, the range of values found within any given treatment were plotted alongside the average fractionation rates (Fig. 2-2). The proportion of cages from which we were able to get estimates for variability varied

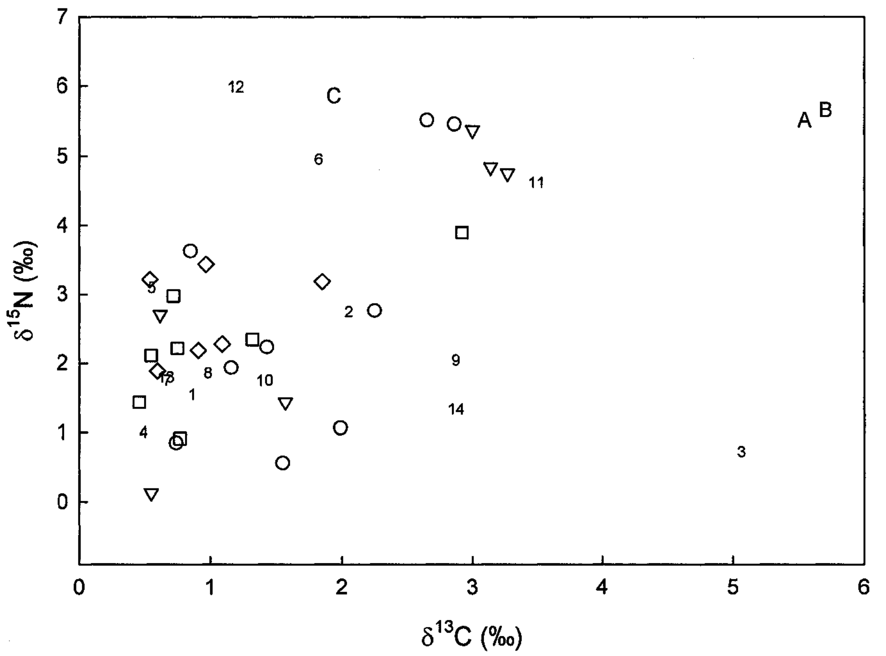

Figure 2-2: Range of isotopic values found within feeding trials, between dietary sources, and within cage trials. Also included are the average fractionation rates for *D. hesperus* fed on whitefly in trial 1 (A), *E. formosa* in trial 1 (B), and *E. formosa* in trial 2 (C). Isotopic ranges are as follows for trial 1: *D. hesperus* fed *E. formosa* (1), *D. hesperus* fed whitefly (2), *E. formosa* card (3), whitefly (4), tomato (5), and *E. formosa* leaf (7). For trial 2: *D. hesperus* fed *E. formosa* (8), *E. formosa* card (9), *E. formosa* leaf (10), tomato (13), and whitefly (14). Different plant types harvested at the same time as trial 2 are mullein (11), and tobacco (12). From the cage trials: tomato (6), *D. hesperus* cages week 6 (○), week 8 (▽), week 10 (□), and week 12 (◇).

between sampling periods, depending on the number of individuals caught. Often, no more than one individual could be found within the allotted sampling time and thus those cages were excluded from our analysis of variability.

No significant differences were found between tomato, tobacco, or mullein grown under the same conditions, though there were sizeable differences between the average $\delta^{13}C$ and $\delta^{15}N$ values. Mullein leaves were enriched in ^{13}C relative to both tobacco (1.06‰) and tomato (1.23‰) with very little difference between tomato and tobacco (0.17‰). Tomato leaves were enriched in ^{15}N relative to tobacco (2.77‰) and mullein (2.62‰). There was very little difference between tobacco and mullein (0.15‰). The range of values for some of these plants was quite large which likely contributed to the lack of significant differences (Fig. 2-2).

Total prey showed a weak but significant decline over time (Fig. 2-3, $R^2 = 0.061$, $p = 0.04$). This decline in available prey coincided with declines in both $\delta^{13}C$ (Fig. 2-4, $R^2 = 0.296$, $P < 0.001$) and $\delta^{15}N$ (Fig. 2-4, $R^2 = 0.338$, $P < 0.001$). Within cage variability in $\delta^{13}C$ declined over time ($R^2 = 0.253$, $P = 0.005$), but there was no change in the variability of $\delta^{15}N$. Within cage variation is depicted as the range of values found within cages (Fig. 2-2).

Discussion

The isotopic signature of *D. hesperus* was distinct from each of the diets that it was subjected to. This result is dependent on the assumption that the contribution of plant and prey to the isotopic signature of *D. hesperus* are equivalent, though the consumption of

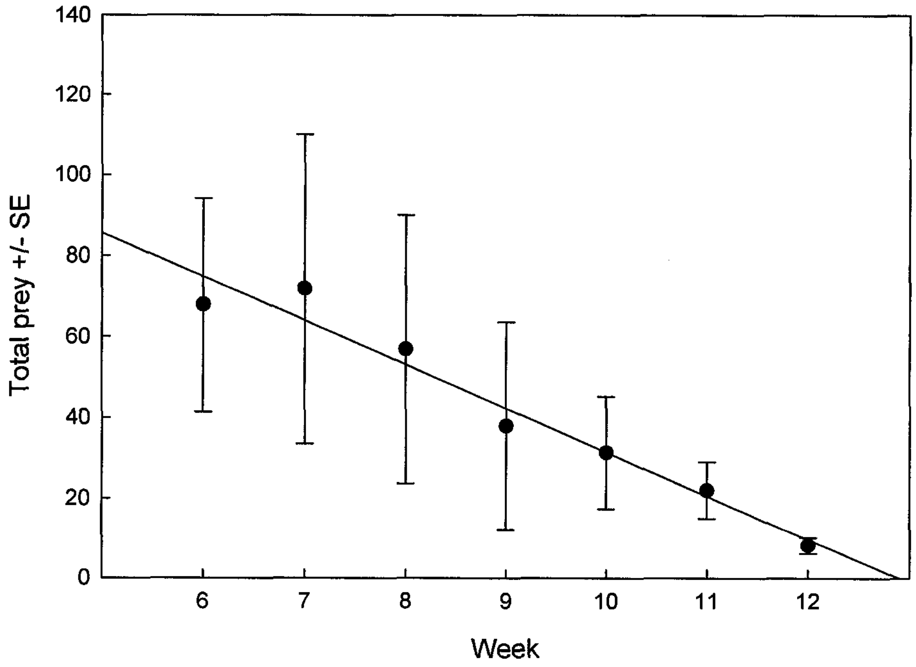

Figure 2-3: Changes in the cumulative abundance of immature whitefly and *E. formosa* over time. The line represents a weak linear regression line ($R^2 = 0.061$, $P < 0.05$).

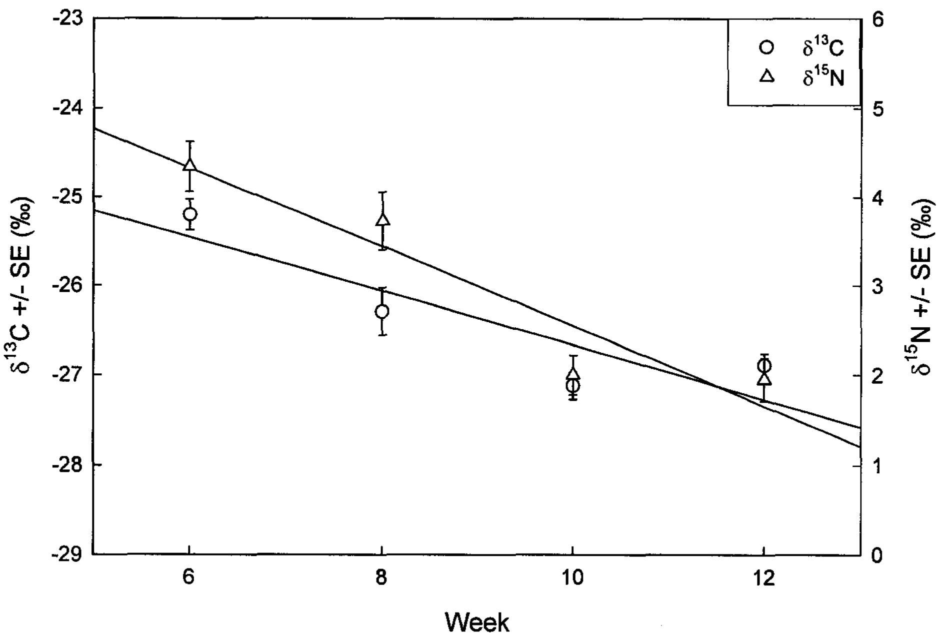

Figure 2-4: Changes in mean isotopic signature of *D. hesperus* over time. The lines represent linear regression lines for both $\delta^{13}C$ ($R^2 = 0.296$) and $\delta^{15}N$ ($R^2 = 0.338$).

plant material may decrease when prey are abundant. Also, some evidence shows that plant material may not be assimilated as readily as prey (Patt et al. 2003). However, the diets themselves were isotopically indistinguishable, thus there should be little error associated with the assumption. The goal of this study was to measure the relative proportions of whitefly versus *E. formosa* in the diet of *D. hesperus* under a variety of conditions. The inability to distinguish between whitefly and their parasitoid eliminated this possibility. Other studies have had similar failures when comparing the $\delta^{15}N$ of parasitoids and their hosts (Tooker and Hanks 2004). Some success has been reported using carbon and nitrogen isotopes (Langellotto et al. 2005), but this study used adult parasitoids and hosts for isotopic analysis. In the current study, immature whiteflies and parasitoids were used because this stage is the predominant stage where predation by *D. hesperus* occurs. It is not surprising that immature parasitoids are not distinct as fractionation occurs due to discrimination against the heavy isotope during metabolic processes (Deniro and Epstein 1978; Deniro and Epstein 1981), but there is no excretion of wastes by the parasitoid until just prior to emergence (Hoddle et al. 1998). If wastes are not excreted, then there is no enrichment of the heavier isotopes. Similarly, the lack of difference between *D. hesperus* fed on whitefly versus *E. formosa* may be due to the consumption of these wastes during predation.

The magnitude of variation among plant species was unexpected. The range of values obtained from tomato, tobacco and mullein plants were quite large. All three of these plant groupings showed ranges around 5‰ for $\delta^{15}N$. Intra-population and intra-individual differences in $\delta^{15}N$ are not uncommon in plants. Plant $\delta^{15}N$ can vary with age (Handley and Scrimgeour 1997) and with small differences in microhabitat (Dawson et al. 2002; Handley and Scrimgeour 1997). Within-plant variation in $\delta^{15}N$ is usually between 2-3‰, but can be as much as 7‰ (Dawson et al. 2002). Within tomatoes, $\delta^{15}N$ varies depending on leaf age (Zanne et al. 2006) and can vary with nitrogen source due to differences in the assimilation of ammonium and nitrate (Evans 2001; Evans et al. 1996). Differences have also been noted between phloem and xylem and between different plant organs (Evans 2001; Yoneyama et al. 1997).

Carbon signatures were also variable within plant groups and in the case of tomato grown at the University of Windsor, between trials. Variation was seen within *E. formosa* and whitefly, but these insects may reflect the variation in the signature of the plant source (Spence and Rosenheim 2005). Genetic differences among plants can lead to differences in ^{13}C discrimination rates (Farquhar et al. 1989; Monneveux et al. 2003; Sandquist and Ehleringer 2003) and may also show an interaction with the environment (Comstock et al. 2005). Plant size can influence carbon isotope discrimination (Martin et al. 1999). Variation in humidity and temperature also may affect carbon isotope discrimination (Comstock and Ehleringer 1992; Monneveux et al. 2003; Sinclair et al. 2004; Xu and Zhou 2005), as may soil moisture (Dawson et al. 2002; Farquhar et al. 1989; Martin et al. 1999; Smedley et al. 1991). Shaded leaves can vary by up to 5‰ in $\delta^{13}C$ within a single tree (Le Roux et al. 2001) with a variety of other evidence pointing towards the influence of light (Dawson et al. 2002; Farquhar et al. 1989). Plant organs can also vary in $\delta^{13}C$ (Yoneyama et al. 1997).

Given the variety of factors influencing isotopic discrimination, it is difficult to pinpoint any one factor that may have influenced the variability within and between feeding trials. Between trial differences may have been due to inconsistency in watering effort as there was a change in staff. Within trial variation can be attributed to either within plant differences or inherent variation between individuals, as conditions were otherwise consistent for all individuals. Leaf age and size likely affected the isotopic signature of these plants. Within pot resource heterogeneity may have influenced the isotopic composition of different plant sections, given the sectored nature of many plants, including tomato (Zanne et al. 2006).

Given the amount of within-plant variation in isotopic signature, it is surprising that there have been no trophic studies to my knowledge that have taken this into account. This source of variation needs to be accounted for, especially given the heterogeneous nature of plants as a resource (Orians et al. 2002; Orians and Jones 2001). Many of the factors which influence the resource heterogeneity within the plant are the same which influence isotopic heterogeneity. Shading of individual leaves can alter $\delta^{13}C$ (Le Roux et al. 2001) and can also alter nitrogen content and the amount of secondary plant compounds making them more appealing to herbivorous insects (Crone and Jones 1999; Nichols-Orians 1991). Some species avoid younger leaves because of secondary compounds (Bryant 1981; Lawrence et al. 2003) and others prefer them (Cizek 2005), yet these leaves are likely to vary in isotopic composition (Zanne et al. 2006). The best approach to including this variation would be to sample plant material at known feeding sites as in Spence and Rosenheim (2005), but to compare each forager to the leaf tissue that they feed on individually, without making a homogenate of a variety of leaf tissues. Such an approach should reduce the variation associated with fractionation estimates.

With fractionation rates between 5 and 6 ‰ for *D. hesperus*, the variation associated with the diet makes the use of $\delta^{15}N$ in a diet mixing model problematic (Phillips 2001).

Further, the uncertainty associated with the mean isotopic values for any of these food sources would amplify the error associated with the fractionation rates a great degree (Phillips and Gregg 2001). The use of variation in determining the degree of omnivory (Bearhop et al. 2004) is still applicable in a very qualitative sense. The negative correlation of both $\delta^{13}C$ and $\delta^{15}N$ with time suggest that diets were changing. The weak decline in total prey availability coincides with this change in mean isotopic signature. The relationship may have been stronger, but sampling of whitefly is problematic given their aggregated distribution (Hoddle et al. 1998), which resulted in a large error in population estimates. The variation in isotopic signature over time indicates decreasing omnivory and a move towards a more herbivorous feeding habit. The decrease in the variation of $\delta^{13}C$ over time can be interpreted as the move towards a single dietary carbon source. However, mullein and tomato were isotopically indistinct when taken from the University of Windsor greenhouse. It may also be that fluctuating environmental conditions affected the plants or the insects. The variability in signatures within each cage at any given sampling date should reflect variability in diet choice within the population. Age-related differences should be minimal as all individuals sampled were reproductive adults, though differences related to sex may still apply. The fact that the variability in $\delta^{15}N$ did not change over time suggests that the dietary differences were independent of the amount of prey available. Thus, we can infer that differences exist between *D. hesperus* individuals in their diet choices and this variance in feeding habits appears to be independent of variation in prey abundance. However, prey availability does influence the average trophic position of *D. hesperus* individuals. In order to reduce the uncertainty of estimates of trophic position, more work needs to be done to determine how within-plant variability and herbivore preferences affect fractionation rates.

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Chapter 3

Foraging strategies, resource distributions, and intraguild predation: Intraguild interactions between an omnivore and a parasitoid

Introduction

When two species compete, their relative success may depend on how the resources are arranged within the environment (Amarasekare 2003). Differential resource use and spatial dynamics have also been suggested as a means of coexistence for complexes of parasitoids (Bonsall et al. 2004; Comins and Hassell 1996; Lei and Hanski 1998), bees (Steffan-Dewenter and Kuhn 2003) and vertebrates (Brown et al. 1994; Marion et al. 2005). Coexistence is also possible for species of marine snails which graze differentially at varying algal abundance levels (Schmitt 1996) and for hummingbirds and bees which feed on nectar at different depths within the flower (Laverty and Plowright 1985). As a forager feeds, it modifies the way in which resources are distributed. How the distribution of these resources is modified will depend on the feeding behavior of the forager. If an animal feeds until it has exhausted the patch where it is feeding and then searches for a new patch, it will have a different effect on the arrangement of resources than an animal that spends less time within a patch, only partially depleting it before leaving. These effects can accumulate over time and lead to a modification of the resource distribution within the habitat, which may favor one species over the other or may permit coexistence. Similarly, species which differ in their competitive ability, yet compete for a single patchy resource, can coexist if resources are only available to the superior competitor at high patch densities (Chase et al. 2001; Richards et al. 2000; Wilson et al. 1999).

Exploitative competition does not usually occur in isolation. In any situation where organisms interact, the possibility exists for a multitude of direct and indirect interactions (Abrams et al. 1996; Krivan and Schmitz 2004; Sih et al. 1998; Werner and Peacor 2003). As the number of organisms involved increases, so does the number of possible interactions. Many attempts have been made to identify these interactions and to determine in which ways they are related. These questions have been addressed from the level of food webs down to individual behaviors (Eubanks and Denno 2000; Krivan and Schmitz 2004; Peacor and Werner 2000; Relyea and Yurewicz 2002). A number of such studies have focused on the interactions between multiple natural enemies which share prey (Schmitz and Sokol-Hessner 2002; Sih et al. 1998; Sokol-Hessner and Schmitz 2002; Vance-Chalcraft and Soluk 2005). One interaction which has received a large amount of attention is intraguild predation, the consumption of a competitor by a predator.

An intraguild predator will compete with and consume its intraguild prey (Polis et al. 1989), and may also modify the behavior of the intraguild prey (Raymond et al. 2000). Most studies of intraguild predation do not consider the influence of spatial dynamics on these interactions. The degree of intraguild predation varies between habitat types (Griffen and Byers 2006) and can vary with the degree of distributional overlap at a small scale (Nakashima and Akashi 2005). However, neither study considered modification of resource distribution at the patch scale and its effect on competition between the intraguild predator and prey.

Competition, both between and within species can also be affected by population densities (Gurevitch et al. 1992; Post et al. 1999; Wise 2006). The importance of intra- and interspecific competition can depend on the relative number of conspecific and heterospecific individuals. Intraguild predation can also depend on the relative density of prey types (Diehl and Feissel 2001; Lucas et al. 1998; MacRae and Croft 1997). Thus, it is of interest to identify how density affects intraguild interactions and how intraguild interactions affect density-dependent intraspecific interactions. We tested the effects of intraguild interactions through predator addition using the omnivorous predator *Dicyphus hesperus* Knight (Heteroptera: Miridae) and the parasitoid *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) at multiple parasitoid densities.

Dicyphus hesperus is currently used for control of the greenhouse whitefly, *Trialeurodes vaporariorum* Westwood (Homoptera: Aleurodidae), on greenhouse tomato, *Lycopersicon esculentum* Mill (Solanaceae) (McGregor et al. 1999). The diet of *D. hesperus* is supplemented with mullein, *Verbascum thapsus* L. (Scrophulariaceae) to help in the establishment of *D. hesperus* populations (Sanchez et al. 2003). The most common biological control method for whitefly involves multiple releases of the parasitoid *E. formosa* before the first occurrence of whitefly within a greenhouse (Onillon 1990). This method has proven successful but can be unstable in small greenhouses (van Lenteren et al. 1996). Both *D. hesperus* and *E. formosa* compete for whitefly and exhibit similar overall fecundity and prey consumption rates (Gillespie et al. 2004; Hoddle et al. 1998; McGregor et al. 1999). However, *D. hesperus* will prey on parasitized whitefly pupae (McGregor and Gillespie 2005), therefore intraguild predation could have important effects on the population dynamics of both the intraguild predator and prey

(Holt and Polis 1997). *Dicyphus hesperus* is omnivorous and requires plant material for predation, though it is able to sustain itself on a plant diet when no prey is available (Gillespie and McGregor 2000). Both *D. hesperus* and *E. formosa* respond to odors from whitefly infested plants (Birkett et al. 2003; McGregor and Gillespie 2004), suggesting similar capabilities for patch location at larger scales, though there is some previous evidence to the contrary for *E. formosa* (van Lenteren et al. 1996). Recent work suggests that *D. hesperus* is efficient at finding prey patches on a plant and tends to consume these patches in their entirety (S.L. VanLaerhoven *unpublished data*). In contrast, a high percentage of *E. formosa* individuals were predicted to be inefficient at finding patches at similar host densities and would not fully exploit these patches when found (van Roermund and van Lenteren 1997).

We hypothesized that *D. hesperus* would cause significant declines in whitefly populations, but that *E. formosa* populations would remain at low levels. Trade-offs in foraging strategies were also expected to minimize the competition between these two species. This is in part due to *D. hesperus* reallocating its foraging time, with an increased proportion spent feeding on mullein. Treatments containing *D. hesperus* were expected to have fewer patches of whitefly than treatments without the predator. Foraging by *E. formosa* was hypothesized to reduce patch size, but not the number of patches. Both the resulting spatial arrangement of whitefly and the adaptive foraging behavior of *D. hesperus* were expected to allow *E. formosa* to persist within patches missed by *D. hesperus* at low densities. Elevated parasitoid release rates were expected to subsidize *E. formosa* populations allowing for higher population densities.

Materials and methods:

Insect collection and rearing

Colonies of *D. hesperus* were established from individuals originally collected on white hedge nettle, *Stachys albens* Gray (Lamiaceae), at 500 m elevation in the Sierra Nevada Mountains in California, at 25° 42' N, 118° 50'W. Colonies were kept at 24°C and 16h light photoperiod. Insects were reared on tobacco, *Nicotiana tabacum* L. (Solanaceae) and fed a diet of *Ephestia kuehniella* Zeller (Lepidoptera: Pyraloidea) eggs. *Encarsia formosa* were obtained from Koppert Biological Systems (EN-STRIP) as parasitized whitefly pupae. Parasitoids were allowed to emerge before use. Whiteflies were obtained from a colony maintained on tomato at the Agriculture and Agri-Food Canada Greenhouse and Processing Crops Research Centre (GPCRC). The whiteflies for the colony were collected from commercial greenhouses in southwestern Ontario.

Experimental setup

All experiments were conducted within a greenhouse at the GPCRC in Harrow, Ontario. Cages were constructed using 3.8 cm ABS plastic pipe and covered with polypropylene non-woven fabric (Agryl-P17), which is used as an insect barrier due to its small mesh size. All cages were 1.2 m^2 at the base and 2m in height. Each cage enclosed six tomato plants, *Lycopersicon esculentum* var. Rhapsody, grown in rockwool growing medium and a single potted mullein plant was suspended in the center of the cage near the top. Mullein was included to facilitate the establishment and survival of the omnivorous *D. hesperus* (Sanchez et al. 2003).

The experiment was treated as a 2x2 factorial design with the presence or absence of *D. hesperus* and high or low *E. formosa* release rates for a total of four treatments with five replicates per treatment. Into all cages, 30 whitefly were introduced and allowed three weeks to establish within the cage before predator and parasitoid introduction. Initial predator introductions included 12 each of *D. hesperus* adults, late instar juveniles, and early instar juveniles. Parasitoids were introduced at 15 adult female *E. formosa* for the high release rate treatments and 5 adult females for treatments with low release rates. Both whitefly and *E. formosa* were re-released into the cages at their initial release rates at weeks 7, 9, 10, and 11. Six leaves per week and up to five *D. hesperus* individuals every two weeks were removed for other analyses not considered in this paper. Other losses of prey and natural enemies may have occurred during weekly crop maintenance, as senescing basal leaves and secondary shoots were removed from the plant using commercial propagation practices. All removed leaves were placed on the floor of the cage for a period of one week to minimize any losses of natural enemies and prey.

The experiment was conducted for 13 weeks from the introduction of whiteflies into the cages. This allowed for at least two generations of all insects. One week before completion of the experiment, the primary apical meristem was removed due to space constraints within the cages. This prevented further vertical growth of the plants. As a result, the first leaf from the top was 1-2 weeks old when the plants were removed for analysis. Three days before the completion of the experiment, yellow sticky cards were introduced to trap all mobile insects within the cages. At completion, sticky cards were removed and all remaining mobile insects were collected using a vacuum aspirator. Tomato plants were vertically sectioned, bagged and stored at 4^{o}C until all insects could be counted. Upon analysis, each leaf was numbered according to the plant it came from and its vertical position. Whitefly nymphs, pupae, and adults, parasitized pupae, *E. formosa* adults, and both unparasitized and parasitized exuviae were counted on each leaf by visual scans aided by the use of a stereomicroscope.

Data analysis

To determine differences in mean population levels between treatments, all life stages of all insects within each cage were summed. Abundances of whitefly nymphs, pupae, and parasitized pupae were compared using negative binomial regression with *D. hesperus* and *E. formosa* treatments tested factorially. *Dicyphus hesperus* abundance was compared between cages with high and low parasitoid release rates using a T-test. The highest values were removed from both treatments due to the presence of an outlier in the low parasitoid treatment. Parasitism rates were calculated for both pupae and exuviae as the number of individuals at each stage that were parasitized divided by the total number of healthy and parasitized individuals at that stage. Parasitism was determined by the characteristic color change from white to black as *E. formosa* pupates. This method does not consider possible parasitism before the change in coloration. A general linear model was used to test for treatment effects on parasitism with the same factorial design as was used for the count data. Both pupal and exuvial parasitism were included as dependent variables and exact P values were calculated within the MANOVA option of the GLM procedure within SAS v. 9.1.3 (SAS Institute 2005).

A number of methods were used to assess possible treatment effects on whitefly and *E. formosa* distributions. To compare how the insects were distributed vertically on the plant, the insects at each leaf position were summed for each cage. These per leaf sums were then converted to a proportion of the total for the cage. The use of proportions removes any treatment differences in the means. These data were then categorized due to an inflated number of zeros. The categories were arranged based on the percentage of the total from lowest to highest as 0%, $0>x\leq10\%$, $10>x\leq20\%$, $20>x\leq30\%$, and >30%. The categorical data were then analyzed using a cumulative logit model, which has been suggested as a means of dealing with zero-inflated data while using a single set of parameters (Min and Agresti 2005), unlike many other models which use multiple parameter sets to describe the data (Martin et al. 2005). The model was structured as predator treatment*position + parasitoid treatment*position + predator treatment*parasitoid treatment*position, with position treated as a continuous variable. In this way, any effect of treatment on position appears as an interaction effect. Whitefly nymphs, whitefly pupae, and parasitized pupae were analyzed separately.

It is possible for any forager to reduce patch size or the number of patches available. Each of these components can potentially affect the success rate of the foraging organism and may do so in different ways depending on foraging behavior. To assess the probability of either *D. hesperus* or *E. formosa* finding a patch, leaf counts of whitefly stages were converted to binary presence and absence data. The probability of finding a patch is the expected probability given a random search strategy. These data were then analyzed using logistic regression with random effects. Each life stage was analyzed separately with predator and parasitoid treatments as fixed factors and accounting for the random effects of specific cages. To analyze the size of the available patches, the data set was truncated by removing all zero values for each whitefly stage separately. The resultant data were then analyzed using negative binomial regression with random effects. All treatment and random effects were specified in the same way as in the patch probability model. All statistical analyses were conducted using SAS v. 9.1.3 (SAS Institute 2005)

Results

A number of differences were found among treatments for all life stages (Figure 3-1). The addition of *D. hesperus* lowered the abundance of total whitefly by 76.6%. Whitefly nymph abundance was reduced by 78.2% ($X^2_{1,20} = 19.40$, $P < 0.0001$) and whitefly pupae by 71.5% ($X^2_{1,20} = 6.94$, $P = 0.0084$) compared to cages where *D. hesperus* was absent. Predator addition reduced the number of pupae which had been parasitized by *E. formosa* by 84.7% ($X^2_{1,20} = 14.66$, $P = 0.0001$). Elevated parasitoid release rates decreased the abundance of whitefly by 47.8%, with nymphs reduced by 40.4% ($X^2_{1,20} = 4.09$, $P = 0.0432$) and pupae by 66.1% ($X^2_{1,20} = 4.44$, $P = 0.0352$). Increasing the release rate of *E. formosa* had no effect on the number of *E. formosa* pupae present. No differences were found in *D. hesperus* abundance between high (mean 4.75, s.d. 3.86) and low (mean 4.25, s.d. 2.36) *E. formosa* treatments. Interaction effects between predator and parasitoid treatments were found to be significant for parasitized pupae ($X^2_{1,20} = 5.04$, $P = 0.0247$), but not for either whitefly life stage.

Overall, predator addition was found to lower the parasitism rates by 59.6% (Figure 3-2, Wilks' lambda = 0.436, $P = 0.002$). Pupal parasitism was reduced 67.9% ($F_{1,16} = 7.23$, $P = 0.0162$) and exuvial parasitism 55.5% ($F_{1,16} = 14.28$, $P = 0.0016$). Release rates of *E. formosa* did not affect the percent parasitism, but there appeared to be an interaction

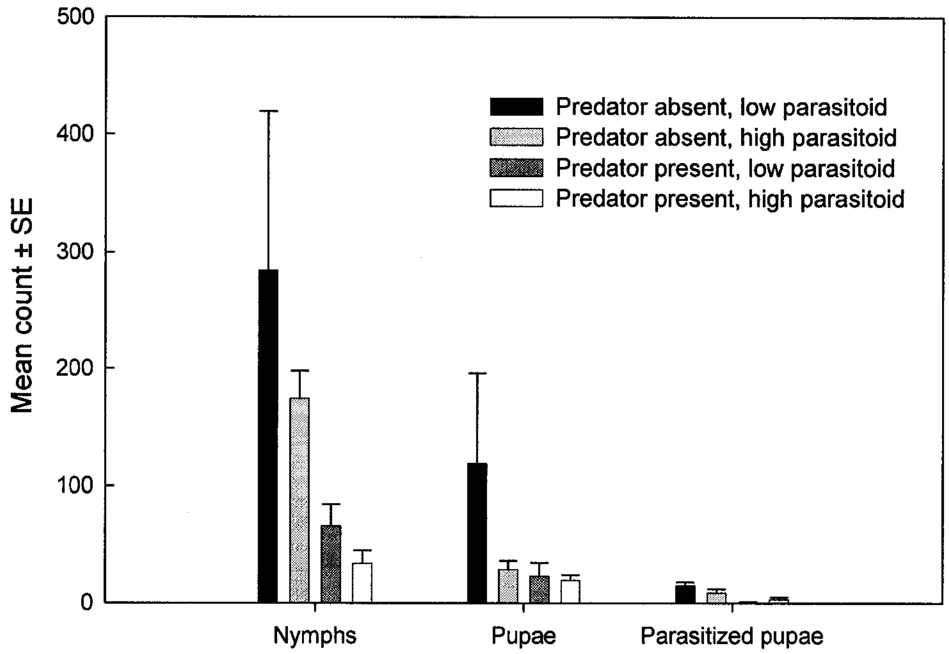

Figure 3-1: Mean population sizes of immature life stages of *E. formosa* and whiteflies after exposure to predator and parasitoid treatments. Predator addition reduced populations of all life stages, while parasitoid release rates only affected whitefly populations. Intraspecific interactions in parasitoid populations were modified by predator addition.

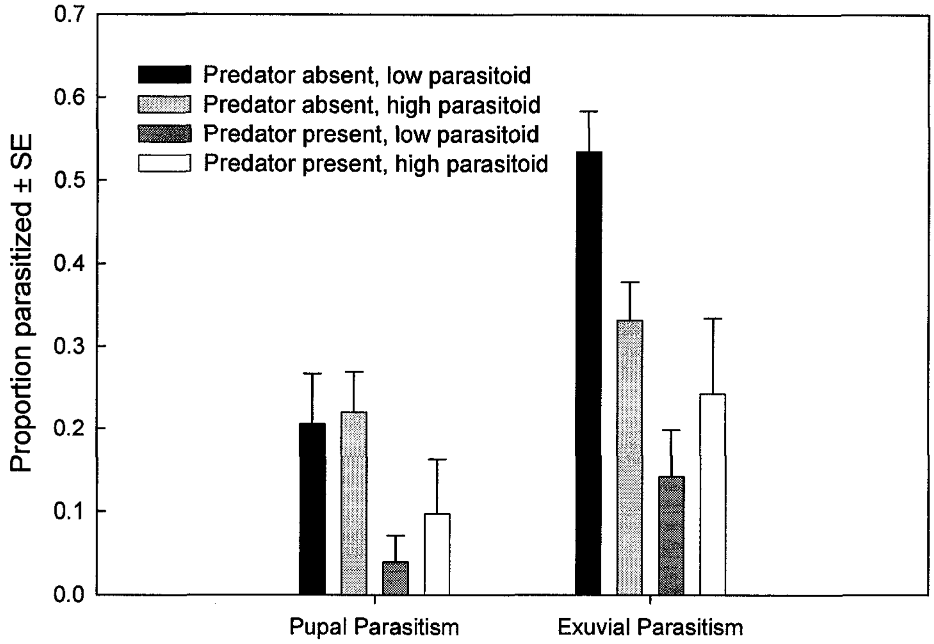

Figure 3-2: Mean pupal and exuvial parasitism rates for predator and parasitoid treatments. Parasitism rates were reduced by the addition of the predator, but were unaffected by variation in parasitoid release rates. Predator addition affected the effect of parasitoid release rates on the parasitism rate of exuviae, but not for pupae.

between the two treatments (Wilks' lambda = 0.734, $P = 0.0986$), though it was not statistically significant. Univariate analysis suggested that the interaction was present when considering parasitism rates measured by looking at exuviae ($F_{1,16} = 5.69$, $P = 0.0297$), but not when measuring parasitism in pupae. This may reflect the accuracy of pupal parasitism estimates or the time scale difference between the estimates.

The presence of *D. hesperus* changed the vertical distribution of both whitefly nymphs (Figure 3-3, $X^2_{1,423} = 7.43$, $P = 0.0064$), and parasitized pupae (Figure 3-4, $X^2_{1,315} = 4.83$, $P = 0.0280$), but had no effect on the distribution of healthy pupae. In the absence of *D. hesperus*, whitefly nymphs were distributed in a log-normal shaped curve from the apex of the plant. When the predator was added, this distribution was disrupted, shifting the peak down the plant and increasing the proportion found lower on the plant. The parasitized pupae were also distributed in a log-normal shaped curve when *D. hesperus* was absent, but this distribution appeared more chaotic with the predator, with more pupae found lower on the plant.

The proportion of available patches occupied by whitefly nymphs was lower ($F_{1,2176} = 12.20$, $P = 0.0005$), but not the proportion of patches occupied by pupae in the presence of *D. hesperus* (Figure 3-5). Mean patch sizes of both whitefly nymphs ($F_{1,608} = 22.46$, $P < 0.0001$) and pupae ($F_{1,329} = 6.48$, $P = 0.0114$) were lower in cages where the generalist was added (Figure 3-6). There were no effects of *E. formosa* treatment on patch occupancy or patch size.

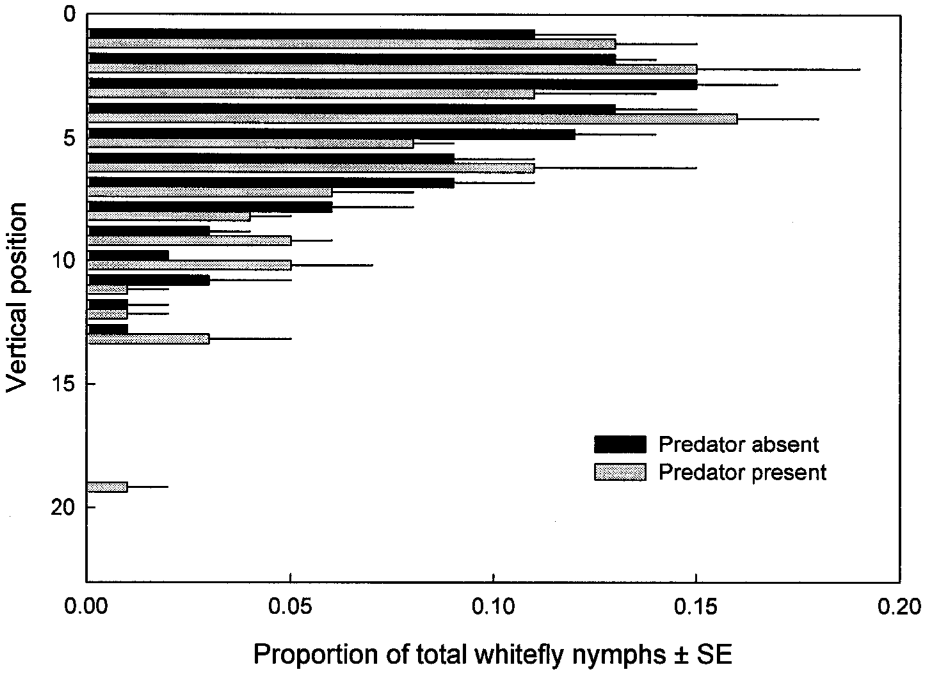

Figure 3-3: Mean vertical distribution of whitefly nymphs in the presence and absence of the generalist predator, *Dicyphus hesperus*. Whitefly nymphs appear to be distributed lower on the tomato plant when the predator is present.

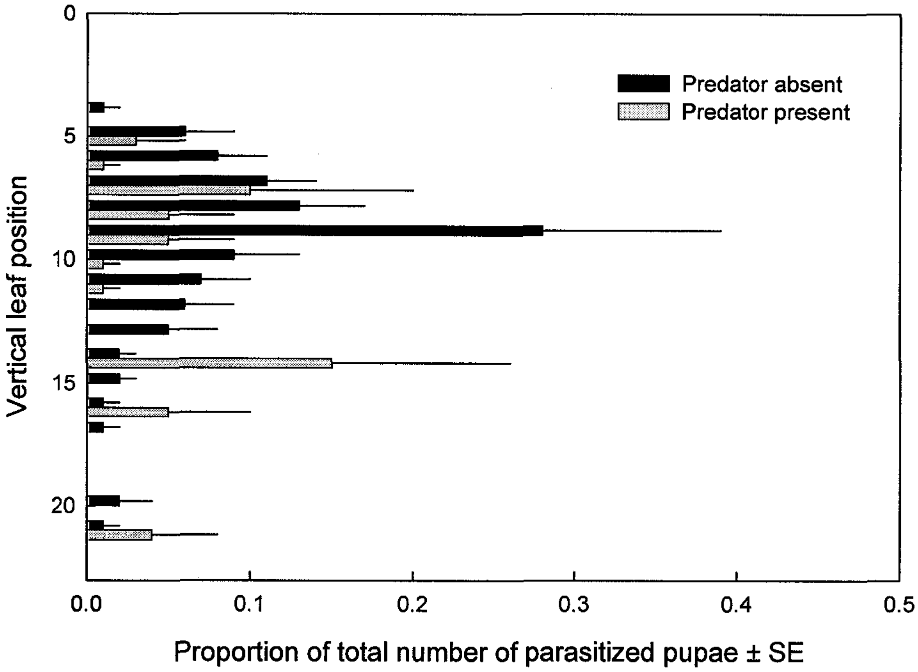

Figure 3-4: Mean vertical distribution of parasitized pupae in predator presence and absence treatments. A significant amount of chaos was found in the distribution of parasitized pupae when the predator was included.

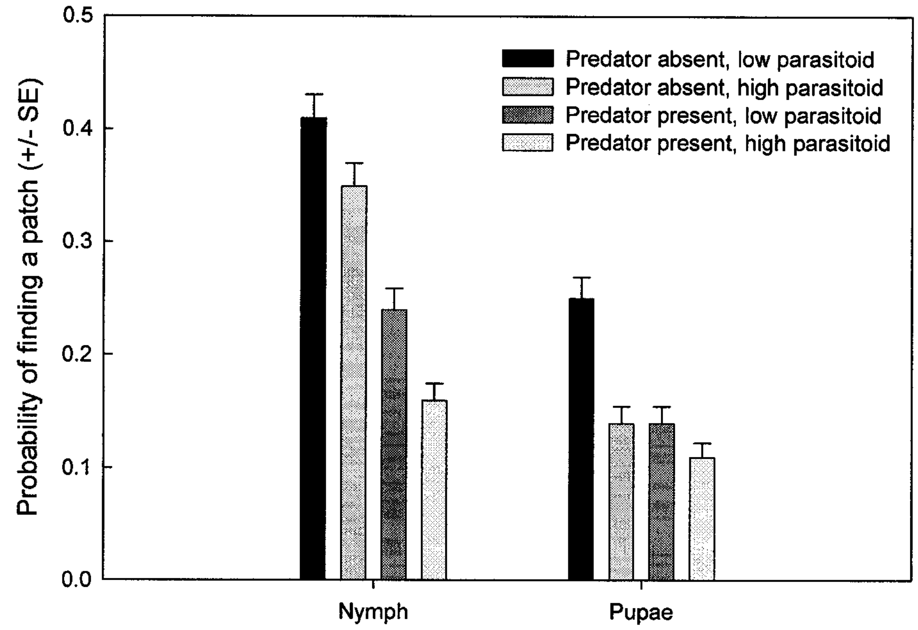

Figure 3-5: Mean probability of finding a patch of whitefly nymphs or pupae, assuming a random search, in all predator and parasitoid treatments. Whitefly nymphs were found on a smaller proportion of available patches in treatments including the predator. No other significant effects were found.

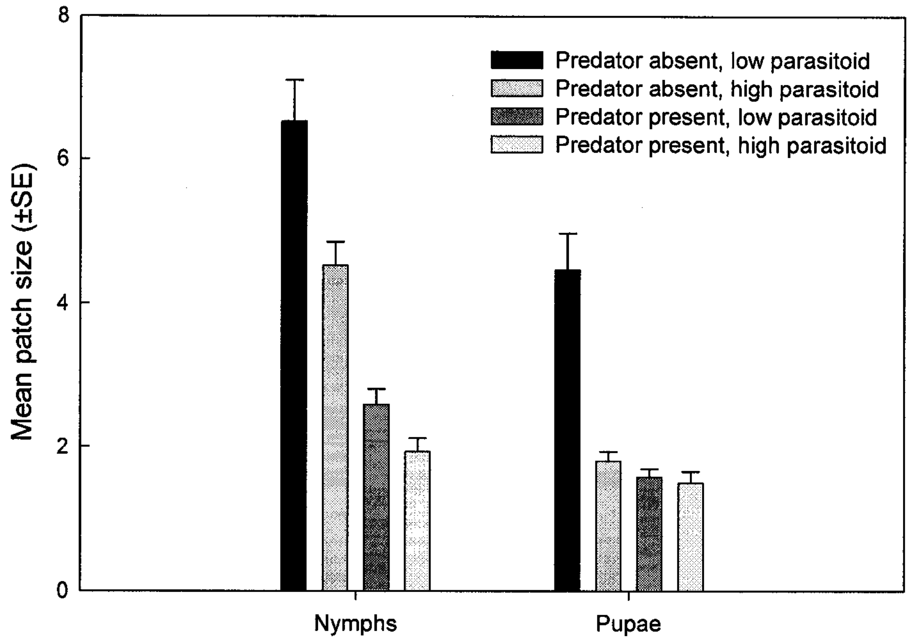

Figure 3-6: Mean patch size for immature whitefly for all predator and parasitoid treatments. Patch sizes were reduced in the presence of the predator, but were unaffected by variation in the parasitoid release rate.

Discussion

Both the generalist predator and the specialist parasitoid reduced whitefly populations. *Dicyphus hesperus* also reduced the population size of the parasitoid *E. formosa*, but *D. hesperus* abundances were unaffected by higher parasitoid release rates. However, *E. formosa* populations were affected by increased intraspecific competition at higher release rates. Increasing the number of adult parasitoids added to the cages decreased the abundance of whitefly nymphs and pupae, but not the number of parasitized pupae. The reduction in whitefly populations is unsurprising as *E. formosa* has been used as a successful biological control agent for many years (Onillon 1990), but the lack of an effect on parasitoid population abundances was contrary to expectations.

The intraspecific interactions for *E. formosa* in this study varied with predator treatment. A significant interaction effect between predator and parasitoid treatments was found for parasitized pupae, with a lower number of parasitized individuals being found in treatments with higher parasitoid release rates when no predator was present. This suggests that the parasitoids released into the cages had a far lower per capita rate of oviposition success in absence of the predator. This trend was not apparent when looking at pupal parasitism rates, but was consistent with exuvial parasitism. The disparity between pupal and exuvial parasitism may exist for a number of reasons. First, late instar nymphs do not exhibit the pronounced color change seen in parasitized pupae. Thus, they could have been misclassified as healthy pupae when in fact they may not have reached the pupal stage yet or may have been parasitized. The misclassification of late instar nymphs could have led to underestimation of the proportion of parasitized pupae. Second, the two measures are related to much different time scales. Exuviae exist on the leaves for some time after emergence of the adult insect. In this way, examining exuviae integrates the degree of parasitism over a much longer time than pupae, which are an estimate at a given point in time for only a single life stage.

The reduction in parasitoid efficiency in the absence of the predator can be attributed to intraspecific competition among parasitoids causing a decline in the population reproductive rate. *Encarsia formosa* kills whitefly both by parasitizing the host and by host feeding. Increasing the ratio of *E. formosa* adults to whiteflies released into the cages could therefore lead to an increase in the number of host feeding events and a reduction in the number of immature whiteflies (Burnett 1967). The reduction in immature whitefly would lead to increased competition for surviving hosts and a reduction in oviposition rates for individual wasps. Superparasitism also increases at elevated parasitoid densities, reducing the survivorship of offspring for *E. formosa* (van Lenteren et al. 1996) as well as other parasitoid species (Montoya et al. 2000; Sallam et al. 2002). These effects of *E. formosa* release rate vary depending on the size of the greenhouse, with lower release rates showing more stable control in small greenhouses (van Lenteren et al. 1996). Given the relatively small size of the enclosures, our results appear consistent with these findings.

These intraspecific effects on the abundance of parasitized pupae do not appear in the presence of the predator. Competition and predation interact in a wide variety of studies (Gurevitch et al. 2000). The reduction of parasitoid populations by the predator may have alleviated intraspecific pressure, resulting in a greater per capita oviposition success rate for *E. formosa.*

It was expected that *D. hesperus* would be minimally affected by competition with *E. formosa* due to its ability to feed on immature parasitoids (McGregor and Gillespie 2005). The parasitoid likely would have been extirpated if the populations had not been externally subsidized. Asymmetric intraguild predation nearly always leads to exclusion of the intraguild prey when the intraguild predator is the superior competitor (Holt and Polis 1997; Kuijper et al. 2003; Polis and Holt 1992; Polis et al. 1989). It appears that *D. hesperus* is a superior competitor, though the reasons for this conclusion require explanation.

Populations of *E. formosa* are reduced by 85% by *D. hesperus*, with overall percent parasitism reduced by 60%. In the absence of other evidence, many would conclude that the reduction in parasitism rate was a result of intraguild predation. Many studies have used changes in the percent parasitism as an indicator of the degree of intraguild predation (e.g. Snyder and Ives 2003). For this supposition to be true, there would have to be no other indirect interactions affecting the ability of the parasitoid to successfully parasitize the host. *Dicyphus hesperus* shows no preference for either healthy or parasitized pupae in choice experiments (McGregor and Gillespie 2005), but further work suggests that *D. hesperus* may prefer unparasitized hosts under some conditions (J.A. Bennett *unpublished data*). This suggests that factors other than intraguild predation may be affecting the interaction between the two species. The foraging behavior of aphid parasitoids was modified when subjected to the scent of known aphid predators (Taylor et al. 1998) leading to a negative association between the intraguild predator and intraguild prey (Raymond et al. 2000). This type of effect is likely to contribute greatly to the interaction between the predator and its intraguild prey (Peacor and Werner 2001) and cannot be ignored when making inferences about the degree of intraguild predation.

Encarsia formosa has been shown to respond to the volatiles of whitefly infested bean plants (Birkett et al. 2003). It is likely that *E. formosa* will show a similar response to tomato plants infested with whitefly. The possibility exists that this response is attenuated by the presence of *D. hesperus* as has been observed in another herbivore-parasitoid-predator system (Raymond et al. 2000). Similarly, plant feeding by *D. hesperus* may obscure the odor released by whitefly as seen in other multiple herbivore systems (Rodriguez-Saona et al. 2003). *Dicyphus hesperus* will also feed upon mobile prey (McGregor et al. 1999) and therefore may directly interfere with adult *E. formosa* through attempted feedings, though no evidence has yet been found for this.

Part of the reduction in total parasitism rate and the number of immature parasitoids can be explained using the spatial distribution of resources and the foraging behavior of both species. In the absence of any type of natural enemy, whiteflies tend to distribute themselves in a regular fashion (van Lenteren and Noldus 1990). Most adult whiteflies lay their eggs at the top of the plant, with some individuals laying eggs further down. If the distribution is plotted along the height of the plant, it resembles a log-normal curve, heavily weighted towards the apex of the plant. Later life stages follow the same distributional pattern, but are found further down the plant. When only *E. formosa* is included, a similar curve can be seen, with parasitized pupae distributed in a similar fashion. This suggests that they do not disrupt the whitefly from their normal habit and that they do not host feed extensively at any given position. However, if *D. hesperus* is included, the pattern becomes less structured. This chaos is likely due to large scale patch depletion by *D. hesperus.* The average distribution of parasitized pupae reflected this change in whitefly distribution. It also appears that an increasing proportion of the whitefly nymphs are found lower on the plant when the predator is present. Adult whitefly do not appear to be disturbed by the foraging habits of the specialist *E. formosa* (*personal observation*) which only feed on immature whitefly (Nell et al. 1976). The generalist *D. hesperus* will feed on mobile prey (McGregor et al. 1999), and has been observed feeding on adult whitefly (D.R. Gillespie *unpublished observation*). Failed feeding attempts on adult whitefly could force the whitefly to relocate and oviposit lower on the plant changing the vertical distribution of eggs and thus immature whitefly. Similarly, *D. hesperus* may also attempt to feed on adult *E. formosa,* interfering with the foraging of the parasitoid. This interference may force *E. formosa* to forage on lower leaves, resulting in the observed distributional difference in parasitized pupae. From this evidence, one can conjecture that *D. hesperus* modifies the distribution of available prey, but there is no evidence that *E. formosa* does. This modification of whitefly distribution can then be viewed within the context of possible effects on parasitoid and predator foraging success.

The changes in whitefly distribution can manifest in both the probability of finding a patch or the size of that patch. In this case, a patch is a single leaf. The probability of finding a leaf where whiteflies were present decreased in the presence of *D. hesperus* when considering pre-pupal stages, but not for pupae. However, the mean patch size was depressed for both whitefly stages. It was expected that *D. hesperus* would reduce the total number of patches more so than the size of the patches as it tends to completely exhaust patches when foraging (S.L. VanLaerhoven *unpublished data*). The lack of reduction of the number of patches of pupae could be due to the patch size used in this study. A tomato leaf contains a number of leaflets which each have the possibility of containing a patch of whiteflies. It may be that there were fewer leaflets with whiteflies present which might have been the relevant patch scale for these insects. However, there is no data to corroborate this hypothesis. This reduction in both the probability of finding a patch and the size of the patches when found can influence the foraging success of both species.

Encarsia formosa has previously been shown to be better suited to foraging in environments where resources are clumped (van Roermund and van Lenteren 1997). The foraging habits of *E. formosa* generally involve random walking on the plant and searching for available hosts by antennal drumming, but not the use of visual cues or any other known localization cue (van Lenteren et al. 1976). The inability of this insect to locate prey or hosts through means other than tactile cues would greatly reduce the foraging efficiency as resources become increasingly sparse. Such a limitation would decrease the amount of area covered in a set amount of time and thus the search rate of the forager. Slower search rates have been linked to lowered foraging success in heterogeneous environments (Marion et al. 2005).

Dicyphus hesperus is a visual predator and is several times larger than *E. formosa*. These size and behavior differences should reduce the effect of decreased patch size and increased distances between patches as the larger predator can search larger areas at an increased rate. *Dicyphus hesperus* also feed on plant material, allowing subsistence between predation events. This suggests that the generalist is able to modify the environment in a way that makes it more favorable for itself.

The coexistence of species sharing a single resource has been related to differences in foraging efficiency at various levels of resource abundance for a variety of animals (Brown et al. 1994; Chase et al. 2001; Laverty and Plowright 1985; Schmitt 1996). Similarly, the modification of resource availability by a number of plants has been considered an important method of altering competitive interactions (Chesson et al. 2004; Suding et al. 2004). Here we find that the alteration of resource patterning by the intraguild predator results in a foraging environment that should favor exclusion of the intraguild prey. This suggests that despite similarities in foraging rates for both species, that *D. hesperus* is a superior competitor. This combination of a superior competitor and intraguild predator greatly reduces any possibilities for species coexistence (Holt and Polis 1997; Kuijper et al. 2003; Polis and Holt 1992; Polis et al. 1989).

Encarsia formosa was expected to reduce patch sizes, but although they reduced overall whitefly abundances, showed no significant effects on either the number of patches or the size of those patches. The variability observed concerning intraspecific effects within *E. formosa* populations (van Lenteren et al. 1996) may have contributed to the lack of spatial effects for this species within the study. We are unable to say definitively that *E. formosa* did not affect the spatial distribution of whitefly, as there were no treatments which contained no natural enemies, but comparison to previous work suggests that any effect if present would be minimal (van Lenteren and Noldus 1990).

This study also has implications for biological control. *Dicyphus hesperus* in combination with *E. formosa* reduced all populations of whitefly by about 75% more than *E. formosa* alone on average. From a biological control perspective, this shows an added measure of control over existing programs using only *E. formosa*. No conclusions can be reached regarding the effect of *D. hesperus* by itself due to the absence of cages without *E. formosa, but D. hesperus* does appear to have a stronger effect than the parasitoid. Overall, high parasitoid release rates reduced whitefly populations by almost 50% more than lower release rates. This includes an approximately 40% reduction in the presence of *D. hesperus*, suggesting the efficacy of a combined solution would be greater than either species in isolation though the effects do not appear additive. However, *D. hesperus* has the added advantage that only a single introduction is required and that the population is able to subsist in the absence of prey by feeding on mullein (Sanchez et al. 2003). These factors suggest that *D. hesperus* will be effective regardless of the other natural enemies present.

Within the study of community dynamics, it is widely recognized that there are a multitude of possible direct and indirect effects that can result when species interact. To predict the outcomes of these interactions, one must know the mechanisms that contribute to the net effect as different components of the interaction will be affected by environmental and biotic variability in different ways. Numeric and behavioral interactions need to be considered in the context of spatial and temporal variation. The ability of any organism to influence its environment must also be considered in the same light. Patterns of resource abundance and distribution influence the foraging species and are influenced by those same species. The accuracy with which we can predict the outcome of competition is likely to be influenced by this interplay between an organism and its environment. The analysis of this interaction is not overly complicated or expensive and can shed considerable light on competition. As competition is an integral part of intraguild predation, these mechanics need also be included in considerations of this subject. Until all aspects are included, it will remain difficult to form predictive hypotheses for these systems.

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Chapter 4

Foraging scale and coexistence in omnivorous food webs

Introduction

Food webs are complex. It is the job of the ecologist to analyze these webs, disentangle them, and present them in a format that can be understood. The food web as a whole may be too complex, but insight can be gained through the study of smaller subsets within these webs. Any set of interactions is generally more complex than they first appear and may include any number of direct and indirect interactions (Abrams et al. 1996; Bolker et al. 2003; Krivan and Schmitz 2004; Schmitz and Suttle 2001). Omnivory is one type of interaction that by its very nature includes both direct and indirect effects.

Omnivory can be defined as feeding at more than one trophic level (Pimm and Lawton 1978) and is common throughout nature (Arim and Marquet 2004; Coll and Guershon 2002; Polis et al. 1989). Intraguild predation (IGP), a subset of omnivory, is the consumption of a potential competitor (Polis et al. 1989). Therefore, by definition, intraguild predation includes both indirect (competition) and direct (predation) effects. Given the prevalence of this interaction, there is a paucity of theoretical explorations compared with the volume of theory surrounding both predation and competition. Early investigations indicated that IGP destabilized food webs and thus should be statistically rare (Pimm 1982; Pimm and Lawton 1978). Since that time, intraguild predation has been shown to lead to a variety of community dynamics (Holt and Polis 1997; McCann and Hastings 1997). Evidence suggests that many factors may play a significant role in determining the stability of omnivorous systems.

A large body of work has placed emphasis on the role of interaction strengths. Weak interactions have the ability to stabilize food chains, but may destabilize them if the omnivory is too strong (Emmerson and Yearsley 2004; McCann and Hastings 1997; McCann et al. 1998; Neutel et al. 2002). Further studies have found that the intraguild predator must also be an inferior competitor on the shared resource to enable coexistence (Holt and Polis 1997; Kooi et al. 2002; Kuijper et al. 2003), though adaptive foraging may stabilize these systems through the occasional removal of the intraguild prey (IGPrey) from the diet of the intraguild predator (IGPredator) (Krivan and Diehl 2005).

Very little research has considered the spatial dynamics within omnivorous systems. Omnivory has been observed to stabilize food webs as they become spatially compressed (McCann et al. 2005), but to our knowledge, no studies have examined how space may stabilize the effects of omnivory. A large volume of theory concerns the effects of space on predatory and competitive interactions (Amarasekare 2003; Amarasekare et al. 2004; Holt 2002; Polis et al. 1996). The most general result that comes from these theories is that space enables options. There are a multitude of trade-offs that can arise when spatial dynamics are also included in the model. One of the most common is the dispersal-competitive ability trade-off (Amarasekare 2003), in which a lack of competitive ability is compensated for by increased dispersal ability.

Competitors vary in their mobility and thus may vary in the scale at which they use resources. In a patchy environment, an increase in scale would mean access to more resource patches, assuming a random distribution of patches. Traveling between patches necessarily incurs an associated cost. It is the trade-off between resource access, travel between patches, competitive ability within these patches, and degree of omnivory that we will explore with this model. We predicted that this series of trade-offs would enable coexistence in omnivorous systems across all sets of competitive abilities.

The Model

We start with a simple Lotka-Volterra model for a three species food chain with IGP as outlined by Holt and Polis (1997):

$$\frac{dP}{dt} = P(b'a'R + \beta\alpha N - m')$$
$$\frac{dN}{dt} = N(abR - m - \alpha P)$$
$$\frac{dR}{dt} = R[r(1 - R/K) - aN - a'P]$$

Within this model, *P, N,* and *R* refer to the IGPredator, the IGPrey, and the shared resource respectively. The variables *a*, *a*', and α refer to the consumption of resource by the IGPrey, the consumption of resource by the IGPredator, and the consumption of the IGPrey by the IGPredator, respectively. Conversion rates from prey consumption to new births are represented by *b* for the IGPrey and by *b*' and β for the IGPredator consuming the shared resource and IGPrey, respectively. The intrinsic rate of resource increase is represented by *r*, with mortality rates for the IGPrey and IGPredator represented by *m* and *m*' respectively. The parameter *K* represents the maximum resource density. This model was modified to incorporate predator choice as well as spatial concepts.

Space can be included by modeling a series of patches in a finite environment. This approach is similar to how metapopulation models approach patch dynamics (e.g. Wilson and Abrams 2005), but differs in that the absolute number of patches is considered instead of the proportion of patches occupied. The number of patches *S* within the environment is a function of the patch renewal rate s, the maximum number of patches K_S, and the rate at which patches are depleted by the consumers. The inclusion of patches requires that the equation for resources be reparameterized such that the maximum resource abundance becomes a function of the within patch carrying capacity K_R and S. This results in the following model:

$$\frac{dR}{dt} = R[r(1-\frac{R}{SK_R}) - aN - a'P]$$

$$\frac{dS}{dt} = S[s(1-S/K_S) - F(N,S) - F(P,S)]$$

The functional response of the consumers was modeled to include multi-species preference functions and spatial considerations. The multi-species preference function, denoted W, was added to allow consumption by the IGPredator to vary depending on preference and the relative abundance of food sources (McCann et al. 2005). The function is:

$$W = \frac{wR}{wR + (1-w)N}$$

The variable w represents a relative preference for either species at equal abundances. Preference for the IGPrey is simply $(1-W)$. This parameter can be set between 0 and 1, with 0 representing pure predation and 1 representing pure exploitative competition. Any value between these two extremes would indicate some degree of omnivory.

Space was considered as the scale at which each of the consumers treat the patchy environment. The consumers were assigned patch fidelity scores M such that these scores range from $1/S$, representing an individual that views the environment as completely mixed, to 1, for an individual that experiences the resources at an individual patch scale. The number of patches that an individual visits per unit time is 1/M.

Therefore, fidelity scores are a means of fixing the number of patches visited and thus the amount of resource accessed.

Each movement between patches must carry a cost in dispersal time. For the sake of simplicity, metabolic costs and costs associated with risks were ignored. This time spent moving between patches would limit the amount of time spent feeding so that an individual which feeds at five patches will spend five times the amount of time moving than an individual which feeds in only one patch. This dispersal time D represents the average dispersal time between patches, given complete patch occupancy. The amount of time spent dispersing T_D was represented as:

$$T_D = \frac{DK_S}{MS}$$

Dispersal time will increase as fewer patches remain occupied and will affect both IGPredator and IGPrey such that species having lower fidelity scores will disperse more often. This dispersal time has an upper bound equivalent to the fidelity score at full patch capacity where all of the organism's time is spent dispersing. These values then alter the functional response of each consumer as:

$$F(P,R) = W\frac{a'R}{M'S}(1 - T_D')$$

$$F(P,N) = (1 - W)\frac{\alpha N}{M'S}(1 - T_D')$$

$$F(N,R) = \frac{aR}{MS}(1 - T_D)$$

For consumer effect on patch dynamics, we will assume that both resources and consumers are distributed randomly among patches. If both are distributed randomly, then the average density of resources per patch and the average consumption per patch will give the average probability that a patch is depleted Therefore, the effect of the two consumers on the resource patches is:

$$F(P,S) = \frac{F(P,R)}{R}$$
$$F(N,S) = \frac{F(N,R)}{R}$$

Given these additions to the model, the resultant series of equations are:

$$\frac{dP}{dt} = P[b' F(P,R) + \beta F(N,R) - m']$$
$$\frac{dN}{dt} = N[b[F(N,R) - F(P,R) - m]$$
$$\frac{dR}{dt} = R[r(1 - \frac{R}{K_R S}) - F(P,R) - F(P,N)]$$
$$\frac{dS}{dt} = S[s(1 - \frac{S}{K_S}) - F(P,S) - F(N,S)]$$

This model was analyzed over a variety of parameter sets using computer simulations conducted within Stella v.8.0 (ISEE 2003). The model was integrated using Euler's method at time intervals of 1. All parameters for the IGPrey were held constant throughout the analysis. Initial parameters can be found in Table 4-1. These values were chosen as they led to stability for IGPrey in absence of the IGPredator at a patch renewal rate of $s = 0.2$. The model was re-examined in the same fashion at $s = 0.5$ as this patch renewal rate results in cyclic dynamics for the IGPrey in isolation. At all times, the attack and consumption rates, a' and α, were considered equivalent. To determine coexistence values, preference (w), and thus the degree of omnivory (McCann and Hastings 1997), was set at 0, 0.10, 0.25, 0.50, 0.75, 0.90, and 1 to investigate the range in interactions between the two species. This range of interactions was tested for an IGPredator that had fidelity scores (M') of 0.20, 0.50, and 0.80. This range of values

Table 4-1: Initial conditions yielding stable or cyclic IGPrey dynamics.

Parameter	**Stable initial conditions**	**Cyclic initial conditions**
R_0	5000	5000
N_0	100	100
P_0	100	100
S_0	500	500
K_R	100	100
K_S	1000	1000
a	0.3	0.3
b	0.1	0.1
b'	0.05	0.05
β	0.1	0.1
m	0.2	0.2
m'	0.2	0.2
r	0.5	0.5
M	0.5	0.5
D	0.25	0.25
s	0.1	0.5

covers situations where the number of patches visited by the IGPredator is larger, equal, and smaller than the IGPrey. To determine coexistence parameters, dispersal times between patches (*D*') were varied incrementally between 0.001 and the upper limit for dispersal time in increments of 0.001 at attack rates (*a*') ranging between 0.1 and 1.0 in increments of 0.1. All simulations were run for 5000 time intervals. Regions in parameter space where both species coexisted were recorded as well as whether populations were stable or fluctuating. In cases where coexistence lay between increments in *D*', it was recorded as such. Further investigations into the effects of preference, competitive ability, and fidelity on population dynamics were conducted at a broader range of parameter sets. All values for equilibrium densities were taken as the value at time = 1000. All cyclical abundances are reported as the maximum and minimum values obtained between time = 1000 and time = 2000.

Results

Community dynamics followed a regular pattern as dispersal times increased. An example of this pattern can be found in Figure 4-1. At very low dispersal times, neither species was consistently able to exist. However, within this band where both species were generally excluded, the IGPredator would occasionally show stable dynamics. As dispersal times continued to increase, this progressed towards conditions under which the IGPredator excluded the IGPrey, and then to coexistence. At higher dispersal times, the IGPredator was excluded by the IGPrey. This pattern held for all competitive and omnivorous systems.

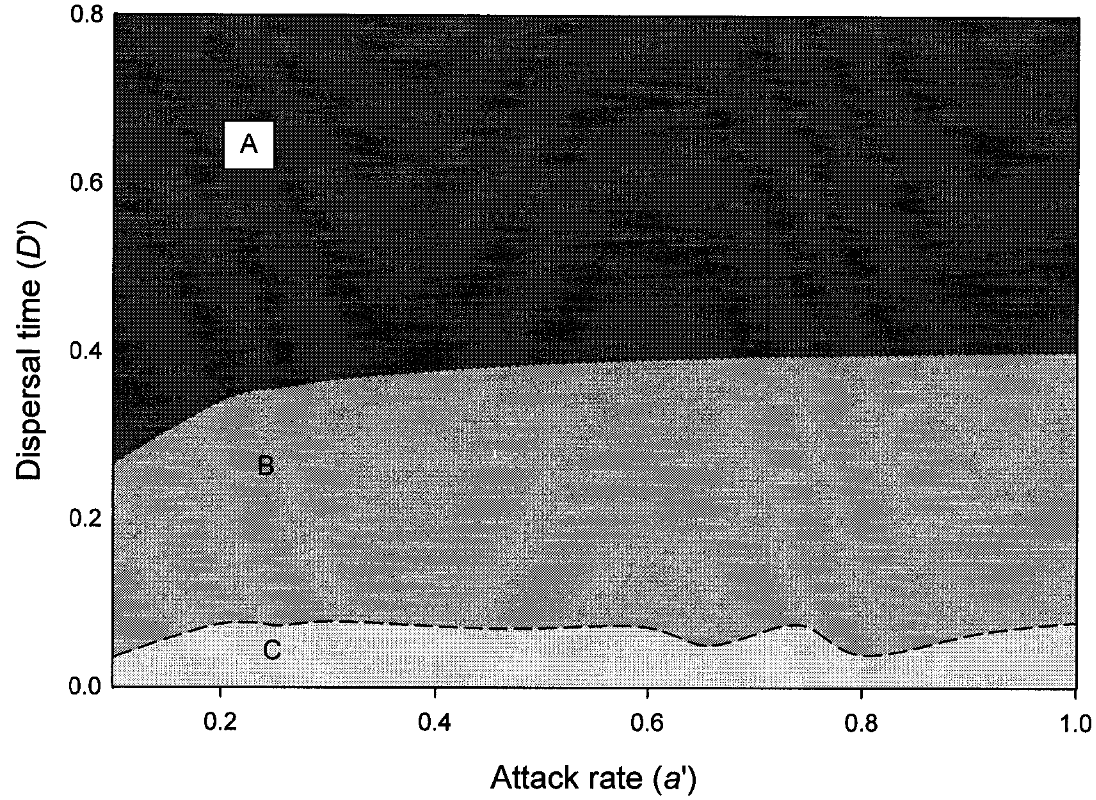

Figure 4-1: Stable states for the system when starting with stable dynamics and an IGPredator with a fidelity score of 0.8 across a range of attack rates and dispersal times. Region A represents parameter space where the IGPredator is excluded. Region B represents parameter values where the IGPrey is excluded. Region C represents parameter values where both species are excluded except for the sporadic occurrence of the IGPredator. Coexistence occurs along the boundary of regions A and B.

Stable coexistence was found for each parameter set when conditions were set to give stable dynamics for the IGPrey (Figure 4-2). Both pure exploitative competition and omnivory showed a single stable equilibrium. Coexistence bandwidths were generally broad for a strict predator, but became restricted to higher attack rates at higher fidelities. As preference scores moved from competition towards predation, the dispersal time allowing for coexistence was reduced by a small amount. This effect was exaggerated at higher fidelities as the theoretical limit for dispersal time increased.

A similar pattern of community dynamics were exhibited under cyclic initial conditions compared to stable initial conditions (Figure 4-3), with coexistence occurring in either limit cycles or chaos. Omnivorous systems remained most comparable to competition (Figure 4-4). Omnivorous and competitive systems had a broader range of dispersal times supporting coexistence, but still reduced compared to strict predation. However, coexistence bandwidth tended to decline with increasing preference for the IGPrey in omnivorous systems, but increased with increasing fidelity. Community dynamics again moved from both species being excluded to IGPrey exclusion to coexistence to IGPredator exclusion as dispersal times increased (Figure 4-3). However, there were a few exceptions to this pattern. Under all fidelities, there existed a range of attack rates for which we could not find exact coexistence conditions where there was an abrupt switch from IGPrey exclusion to IGPredator exclusion. The occurrence of these conditions increased with increasing fidelity. At high attack rates at patch fidelity = 0.2 (Figure 4-4a), there was no overlap between IGPredator and IGPrey exclusion. Also of note, an interesting anomaly occurred at low attack rates at $M' = 0.8$, where a large increase in coexistence bandwidth was found for a variety of preferences.

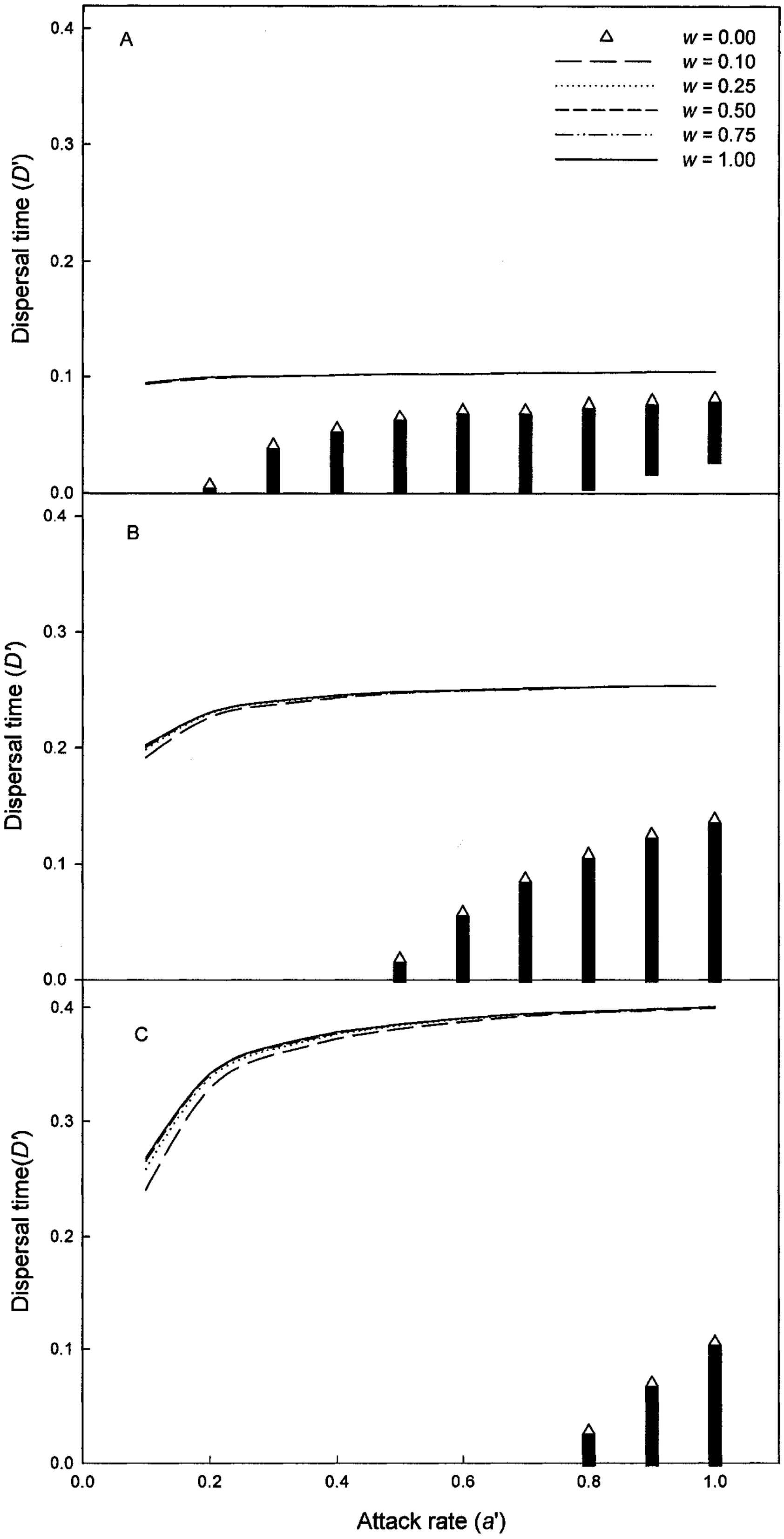A
B
C
△ w = 0.00
w = 0.10
w = 0.25
w = 0.50
w = 0.75
w = 1.00
Dispersal time (D')
Dispersal time(D')
0.0
0.1
0.2
0.3
0.4
0.0
0.2
0.4
0.6
0.8
1.0
Attack rate (a')

Figure 4-2: Dispersal times and attack rates leading to coexistence across a range of preferences when initial conditions yielded stable dynamics for the IGPrey. Lines connect the equilibrium points for omnivorous and competitive systems. Coexistence regions for strictly predatory systems are denoted by a series of points. Tight clustering of points may appear as bars. The graphs represent a range of fidelity scores: (A) $M' = 0.2$, (B) $M' = 0.5$, (C) $M' = 0.8$.

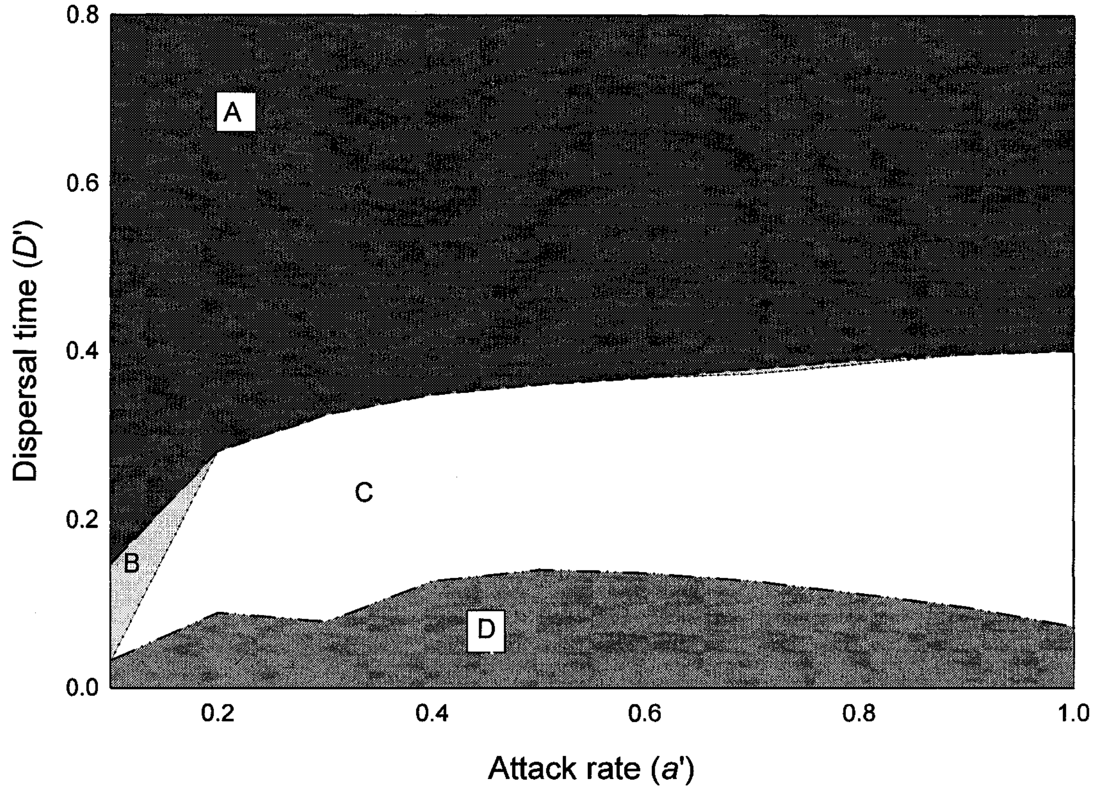

Figure 4-3: Stable states for the system when starting with cyclic dynamics and an IGPredator with a fidelity score of 0.8 across a range of attack rates and dispersal times. Region A represents values for which the IGPredator is excluded. Region B and the boundary between regions A and C represent areas of coexistence. Region C represents areas where the IGPrey is excluded. Region D represents areas where both species are excluded except for the sporadic occurrence of the IGPredator.

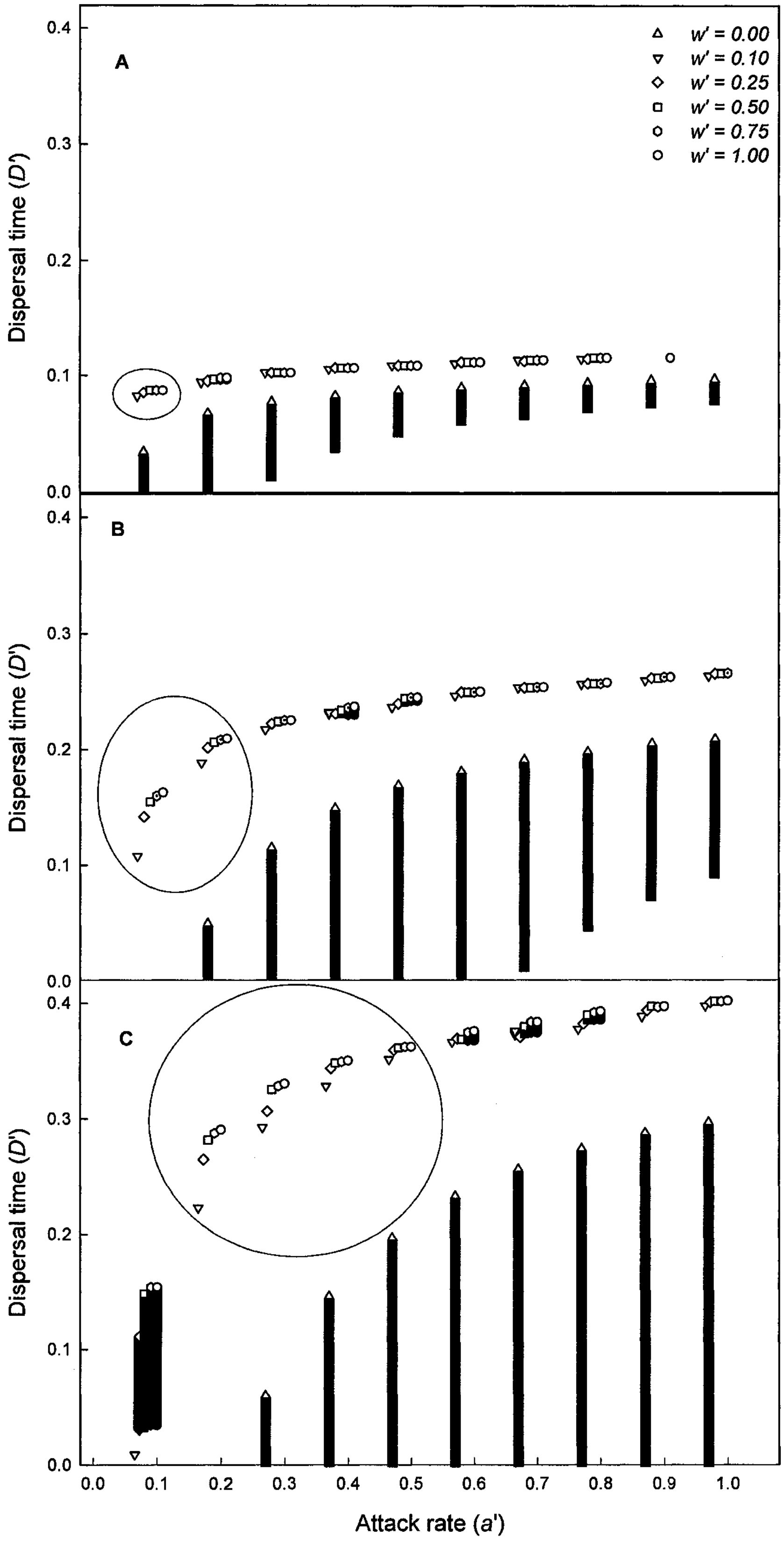
A
B
C
△ w' = 0.00
▽ w' = 0.10
◇ w' = 0.25
□ w' = 0.50
○ w' = 0.75
○ w' = 1.00
Dispersal time (D')
0.0
0.1
0.2
0.3
0.4
Attack rate (a')
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0

Figure 4-4: Dispersal times and attack rates leading to coexistence across a range of preferences when initial conditions yielded cyclic dynamics for the IGPrey. Each point represents a parameter set at which coexistence occurred. Tight clustering of points may appear as bars. The graphs represent a range of fidelity scores: (A) $M' = 0.2$, (B) $M' = 0.5$, (C) $M' = 0.8$. Regions within the ellipse represent parameter regions where IGPrey exclusion abruptly shifted to IGPredator exclusion and we were unable to ascertain coexistence conditions.

Under stable conditions, relative preference had little effect on the equilibrium abundances of the IGPrey or the IGPredator (Figure 4-5). This effect held for the IGPredator as both an inferior and superior within-patch competitor, though there were changes in relative abundances, with both species achieving higher maximum abundance as the superior competitor. The data shown are for a single fidelity score ($M' = 0.80$), though similar trends were found at other fidelities. Increasing fidelity led to declines in the equilibrium abundance of the IGPredator, though this was slightly offset by increasing the attack rate (Figure 4-6). An opposite result was found for the IGPrey. These results were found at null preference for the IGPredator ($w = 0.50$), but held for all omnivorous and competitive systems.

The dynamics if the system were much more complicated when initial conditions were set to produce population cycles. The largest range of dispersal values leading to coexistence occurred at different combinations of fidelity scores and attack rates, with the range of conditions declining with increasing preference for the IGPrey (Figure 4-4). When dispersal values, fidelity scores, and attack rates were held constant, incremental increases in preference led to a variety of dynamics for the IGPredator. When the IGPredator experiences resources at a larger scale than the IGPrey, coexistence was not possible over the entire range of values for a single combination of attack rate and dispersal time (Figure 4-7). Both the mean abundance and the range of values tend to decrease with increasing preference in a stable and predictable fashion until a boundary where higher preferences for the IGPrey can no longer support the IGPredator. When the fidelity of the IGPrey and the IGPredator are equal, a stable decline in the abundance of the IGPredator occurs as the preference value moves away from a purely competitive

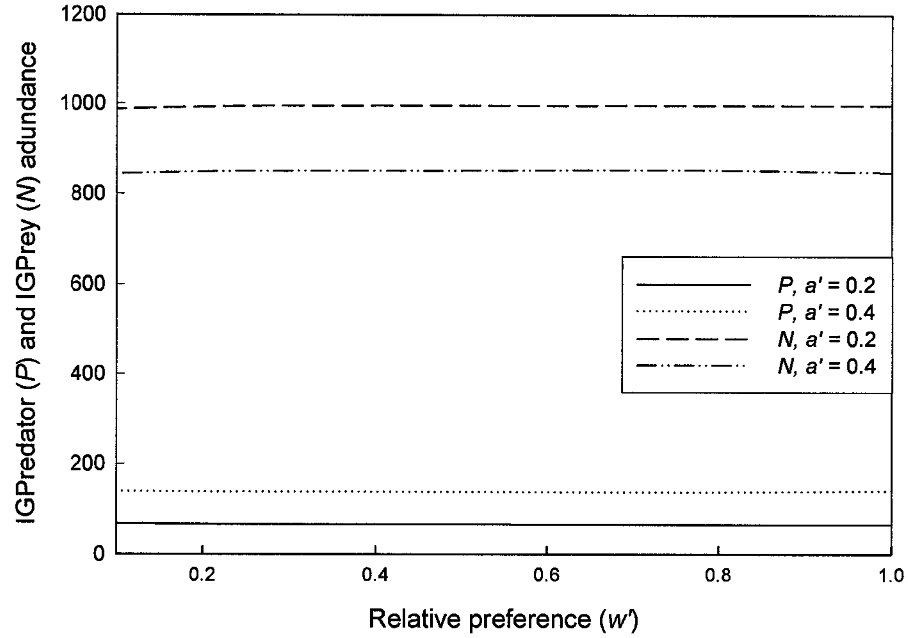

Figure 4-5: Equilibrium densities for both IGPredator and IGPrey across a range of preferences. Results are from M' = 0.8 and represent the IGPredator as both a superior and inferior competitor.

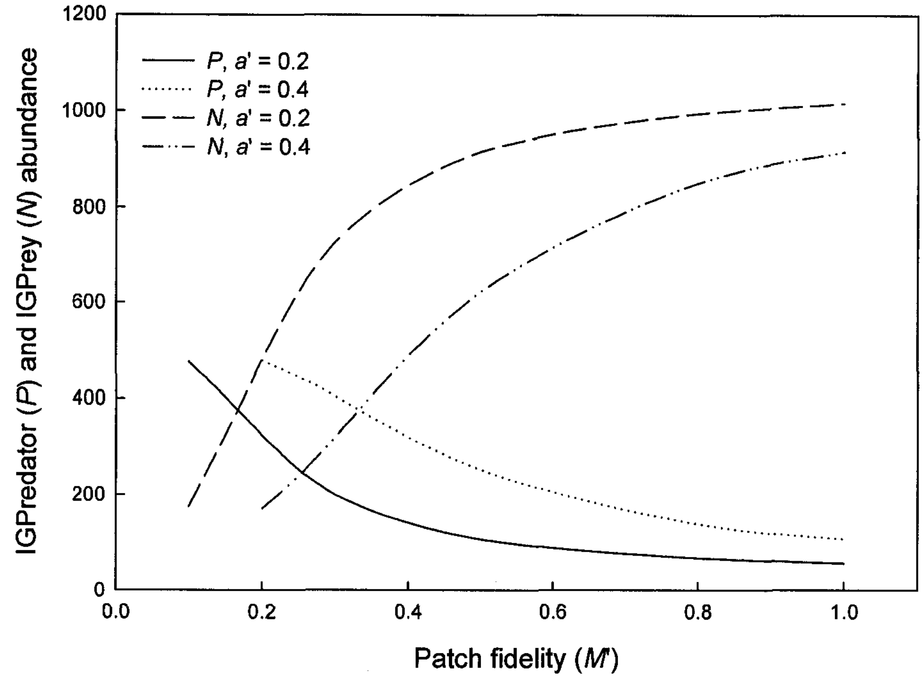

Figure 4-6: Equilibrium densities across a range of fidelity scores for both the IGPredator and IGPrey. All results are taken from the null preference point ($w = 0.5$) and represent the IGPredator as both a superior and inferior competitor.

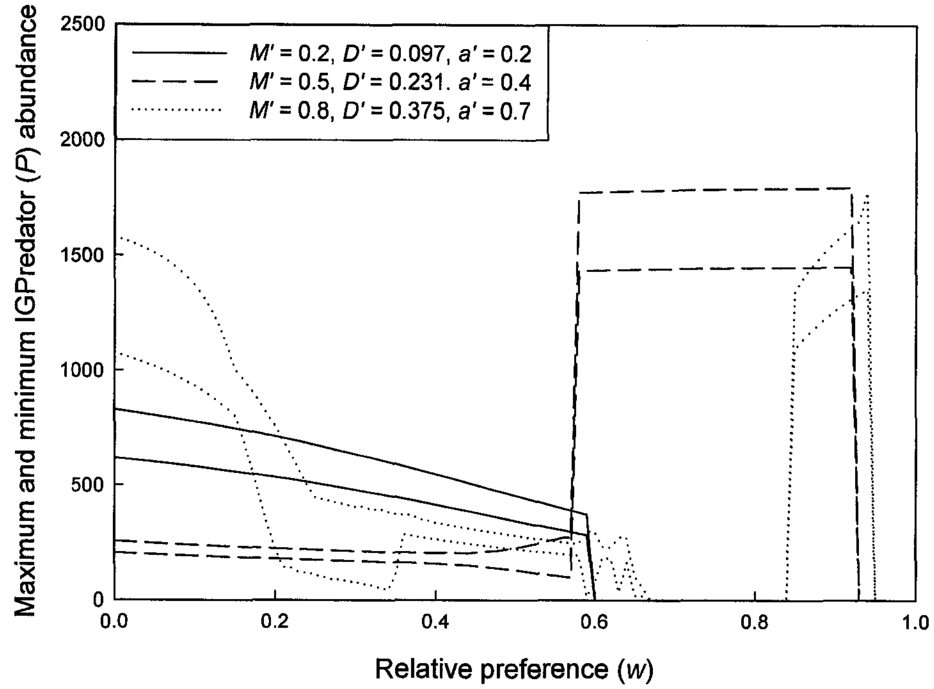

Figure 4-7: Maximum and minimum abundances of the IGPredator obtained across a range of relative preferences under conditions favorable for coexistence for each fidelity score.

relationship. A transition zone occurs just around the null preference point where the cycles begin to get more chaotic. An abrupt change occurs just after preference moves beyond a preference of 0.5 where the abundance of the IGPredator increases six-fold and the cycles restabilize. This stabilization of the cycles does not infer systemic stability, as the IGPrey drop to very low abundances which then leads to a collapse of the system. If the IGPredator experiences resource at a smaller scale than the IGPrey, the effect of preference becomes less predictable. Declines in the mean abundance occur with increasing preference. The range of values tends to wax and wane giving no firm inference on the effect of preference over this range of values. After we reach the same transition zone as just mentioned, the dynamics become extremely chaotic until the IGPredator is excluded. As preference increases and the IGPredator behaves more like a predator which occasionally consumes the resource, we see a resurgence of the predator with a sharp increase in abundance as preference for the IGPrey increases. This increase behaves similarly to the increase at a fidelity of 0.5 as does the decline of IGPrey, again resulting in a loss of system stability.

The largest effect of attack rate on coexistence was on the range of values for which coexistence is possible. If we look specifically at population dynamics over the entirety of each of those intervals, we find a number of patterns. Dynamics tend to be more predictable for parameter sets that give a wider range of coexistence possibilities. For a fidelity of 0.8, at attack rates of both 0.10 and 0.80, the range of values is wider (Figure 4), and the system dynamics are more predictable (Figure 4-8). Conversely, at an attack rate of 0.90, the coexistence bandwidth is narrower and the dynamics are less predictable. At an attack rate of 0.10, the IGPredator becomes more tightly bounded with increasing

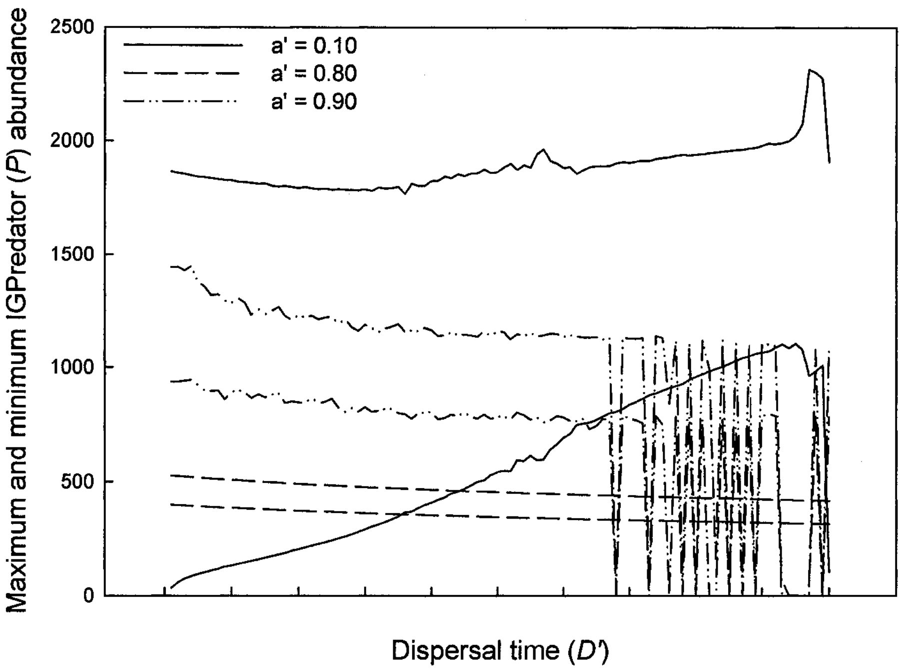

Figure 4-8: Maximum and minimum abundances of the IGPredator obtained across a range of dispersal times for a series of attack rates which enabled coexistence. Data are from *M'* = 0.8. As each attack rate yielded different coexistence bandwidths, units of dispersal time are not equivalent on scale.

dispersal cost, suggesting a more stable system. The cycling at the attack rate of 0.80 remained relatively stable as it does at all points with a broad range of coexistence conditions. At the higher attack rate (*a*' = 0.90), the reduced range results in extinction of the IGPrey at the lower end of the range and inconsistency of coexistence at the higher end. Similar patterns existed at other fidelities.

Discussion

Coexistence between an intraguild predator and its intraguild prey within food webs was enabled under a variety of conditions by including a spatial component in the model. Spatial scale has been shown to be important in determining food web stability and omnivory has been shown to stabilize spatially compressed food webs (McCann et al. 2005). We show that a spatial component can stabilize simple food webs where IGP has been shown to be destabilizing previously. Competitively dominant IGPredators have always been assumed to displace the IGPrey (Holt and Polis 1997; Kooi et al. 2002; Kuijper et al. 2003). In our model, dispersal costs and foraging costs have been shown to offset this increased local competitive ability. A large, less mobile IGPredator may be competitively dominant, but by moving among patches an easily consumed more mobile IGPrey may be able to coexist. Similarly, IGPrey may escape exclusion by reducing the amount of time spent dispersing and concentrating on feeding, though it may not consume resources at the same rate.

There are a number of assumptions implicit within this model that need to be addressed. The first is that the number of patches visited is a constant. This is unlikely to be true in actuality. Optimal foraging theory predicts that patch leaving behavior be based on both maximization of energy gain and risk avoidance (Stephens and Charnov 1982). Risk is ignored in this model. Patch leaving is not based upon the remaining resource at each patch as it is in energy maximization models. In our model, patch leaving can be considered the time averaged propensity of the organism for remaining in a patch given the trade-offs it will experience in time spent dispersing. The inclusion of more biologically realistic behavior may increase the realism of the model, but was excluded due to the increase in complexity in an already somewhat complex model.

The use of a type I functional response was chosen to reduce the complexity of the model. The limitation of a type II response can allow coexistence if the organism with the type II response is the superior competitor (Armstrong and McGehee 1980). Similarly, the inclusion of a type II response may limit the differences in potential resource use by competitors with different fidelity scores. Preliminary analysis using a type II functional response did not show qualitative differences in the model, though a more detailed examination would be necessary before drawing any conclusions.

It was also assumed that the attack rate was equivalent when preying upon both the IGPrey and the resource to reduce the complexity. This attack rate necessarily assumes that all resources encountered are consumed. In actuality, there can be differences in the rate at which each organism is consumed due to differences in defensive capability of the two prey, incurring a greater cost when feeding upon the IGPrey (Polis et al. 1989). The use of this assumption is unlikely to yield more than cosmetic differences in the model as it would only cause slight differences in the functional response for each item that would have been compensated for through a change in some other parameter.

The assumption that the IGPrey would convert resources to young at a higher efficiency than the IGPredator and that the IGPrey was a more nutritious food item for the IGPredator were based on allometric assumptions. It was assumed that the IGPrey would be larger than the resource and that the IGPredator would be larger than the IGPrey. This assumption may not hold across all systems. Thus energy transfer would be consistent with differences in size. Unequal conversion efficiencies can affect model outcomes under adaptive omnivory (Krivan and Diehl 2005). However, initial investigations showed no qualitative differences in the behavior between the two assumptions.

Systems with omnivory much more closely resembled exploitative competition systems than tritrophic systems with strict predation. The set of parameters enabling coexistence was always narrower in competitive and omnivorous systems than strictly predacious systems. In this sense, omnivory reduced the stability of the model as has been suggested by others (Pimm and Lawton 1978). Under most conditions, coexistence was possible and gave rise to at least one stable state when initial conditions promoted stability of the IGPrey. When the initial conditions caused limit cycles in the IGPrey, a variety of coexistence conditions were then possible. It is under these conditions that the model exhibited the variety of dynamics found in other studies (Holt and Polis 1997; McCann and Hastings 1997). Under certain parameter sets, the dynamics of the IGPredator are stable even when the environmental conditions lead the IGPrey to cycle. It is when these two conditions abut in parameter space that coexistence does not occur. Conversely, increased asynchrony of the cycling may lead to an increase in coexistence bandwidth (Wilson and Abrams 2005), which may account for the broad range of coexistence conditions found under a number of conditions.

These bands of coexistence occurred at different ranges of attack rates depending on the fidelity score of the IGPredator. Fidelity scores influence the relative amount of resource available to the consumer. Decreasing the fidelity score is similar to increasing the amount of resource available to the IGPredator. The increase in available resources leads to greater fluctuations for the IGPredator across all attack rates at lower fidelities. At higher fidelities, larger attack rates are required to induce cycling within the population of the IGPredator, leading to a larger range of attack rates for which coexistence does not occur. The range of dispersal values at each attack rate that can induce coexistence generally declines as attack rates increase. This may be related to the increasing amplitude of the oscillations of the IGPredator at elevated attack rates, resulting in an IGPrey population oscillating at low abundances. Any reduction in dispersal costs will increase the abundance of the IGPredator, increasing the probability of extinction for the IGPrey.

Under stable conditions, preference had no real effect on the dynamics of the system or the abundance of its components. This can be explained by the preference function. This function bases preference on the relative abundances of the prey choices. Throughout all sets of parameters, the IGPrey should remain at approximately 10% of the abundance of the resource, due to its conversion efficiency. Even at high relative preferences, the encounter rate is going to be highly skewed, reducing the contribution of the IGPrey to the diet. This reduction in IGP can constitute a weak interaction, which is widely accepted to contribute to the stability of omnivorous systems (Emmerson and

Yearsley 2004; McCann and Hastings 1997; McCann et al. 1998; Neutel et al. 2002). Adaptive foraging has been shown to lead to an increase in the stability of omnivorous systems, by having the omnivore drop the IGPrey from its diet when its abundance becomes too low (Krivan and Diehl 2005). In our model the preference is adaptive, causing changes in the feeding of the omnivore, but also leading to stability.

The role of preference is much more complicated under cyclic dynamics. This is likely due to the sensitivity of chaotic systems to initial parameters. We do see that declines in IGPredator abundance tend to coincide with increasing preference for the IGPrey. The parameter sets which allow coexistence also narrow with increased inclusion of IGPrey into the diet. These results are surprising as the amount of IGPrey included into the diet is minimal at any preference value due to the preference function and the large difference in relative abundances between the IGPrey and the resource. The anomalous effects of preference in this case likely changes the cycling just enough to alter the synchrony of the IGPredator and the IGPrey. The transition zone between beneficial and non-beneficial IGP does appear to be relatively consistent across parameter sets. This small degree of IGP may be enough to limit the IGPrey and allow dominance of the IGPredator. This switch only occurs when the attack rate is high and happens at a higher preference at higher fidelity scores. This suggests that some combination of preference, prey availability, and attack rate are responsible for determining the threshold which increases the competitive benefit of IGP to the IGPredator. The exact relationship is unknown.

The findings of this model indicate that intraguild predation can lead to stable dynamics over a variety of conditions. The IGPredator can be locally competitive dominant and still coexist with the IGPrey as long as some other trade-off is involved. More spatially exact models should provide more detailed insight into how space affects omnivory. In many ways, the results of omnivory are similar to the results for competition. The incorporation of competitive exclusion theory into the study of omnivory would rapidly enhance our understanding of this widespread interaction.

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Chapter 5

General discussion and conclusions

There are numerous means by which species can interact within communities and food webs (Abrams et al. 1996; Bolker et al. 2003; Krivan and Schmitz 2004; Schmitz and Suttle 2001). Some of these interactions are direct such as predation or interference competition. Most others are indirect as in exploitative competition and trait-mediated interactions. Omnivory involves many of these interactions (Bruno and O'Connor 2005; Diehl 1995) and they all must be considered in the context of both temporal and spatial variation (Holt 2002; Polis et al. 1996). For a thorough understanding of omnivory, we must understand the mechanisms behind the variation. Very little work has actually been able to quantify omnivory as the relative consumption of different diet components, and at the same time quantify environmental variation. Omnivory has been suggested to vary with age related differences among individuals (Branstrator et al. 2000; Polis et al. 1989) variation in food quality (Diehl 2003; Janssen et al. 2003; Singer and Bernays 2003), risk associated with foraging (Singer and Bernays 2003), nutritional needs (Gadd and Raubenheimer 2000), and food availability (Mooney and Tillberg 2005). However, most such studies are theoretical or are studied at a small scale.

Stable isotope analysis is commonly used to describe food webs and has often been used to identify omnivory within these food webs. One of these attempts was able to identify both temporal and spatial variability in omnivory (Mooney and Tillberg 2005), though most isotope studies are purely descriptive and do little to help explain how and why omnivory varies. My study is the first, I believe, to apply the use of stable isotopes in manipulative food web experiments. By establishing multiple communities of similar composition, we were able to track the diet of *Dicyphus hesperus* using stable isotopes, and compare these with changes in the abundance of prey. Using this method, we found that the average trophic position of *D. hesperus* declined over time. This decline coincided with declines in total prey availability, suggesting an increasing degree of herbivory. Also within *D. hesperus* populations, there was a large amount of variation in the trophic position of individuals. Variation in isotopic signature has been suggested as a means to identify niche width and omnivory (Bearhop et al. 2004; Matthews and Mazumder 2004). This variability did not decline with time, which suggests that some individuals are more likely to consume plants than prey, regardless of prey availability. It is unclear whether these differences are static or if they vary. This coupling of diet analysis and community dynamics should prove a powerful tool in food web ecology.

There are a number of limitations to the stable isotope technique that we found through our experiments. We were unable to differentiate between healthy and parasitized whitefly pupae. Previous work had found that parasitoids were distinct from their hosts in their carbon signature (Langellotto et al. 2005), but this study used adult parasitoids and hosts. The consumption of parasitoid waste products which remain within the host until emergence seems to be the most likely means for the lack of discrimination. If wastes are not excreted, then there is no enrichment of the diet with heavier isotopes.

We also found a great deal of variation in the isotopic signatures of plants. Variation in plant isotopic signatures is common within and between populations, and even within individuals (Dawson et al. 2002; Evans 2001; Farquhar et al. 1989; Handley and

Scrimgeour 1997). These differences can be due to a variety of factors, making it difficult to determine the exact reason for the large amount of variance. Even within-plant isotopic signatures can vary between plant organs and between leaves, so it is surprising that this is as yet not addressed within trophic studies. This isotopic variation coincides with variation in plant characteristics which may change the palatability of the plant to consumers. Given this correlation, it seems likely that herbivores may only feed on certain parts of the plant and that the use of the average isotopic signature for an entire plant may be increasing the error associated with fractionation rates. This variation needs to be accounted for in future studies.

This first part of the study found that omnivory varied both within a population and over time. The next question we addressed was how this interaction is affected by spatial considerations. The spatial arrangement of resources has very pronounced effects on the foraging ability of different animals (Amarasekare 2003). Consequently, if that arrangement varies, so will the foraging efficiency of the animal. As an animal feeds, it also modifies its environment by depleting resources. Thus, animals may modify their own foraging efficiency through the consumption of the resource. An animal should then be able to modify the foraging abilities of competitors in the same way. This idea has been demonstrated in a somewhat different fashion in a number of systems where resources are unavailable to certain competitors below a minimum resource density (Brown et al. 1994; Chase et al. 2001; Laverty and Plowright 1985; Schmitt 1996) as well as in plant communities where modification of resource availability affects competitive interactions (Chesson et al. 2004; Suding et al. 2004). However, to my knowledge, this coexistence mechanism has yet to be applied to a system where competitive abilities vary continuously with variation in resource availability. Intraguild predation adds another layer of complexity to these interactions through the consumption of the competitor (Polis et al. 1989) and through behavioral modification of that competitor (Raymond et al. 2000).

I used the same whitefly, parasitoid, and omnivore system to explore this theory. Both the omnivore and parasitoid reduced whitefly densities. Whitefly populations were further reduced when both species were present at the same time, though it is unlikely that the effects are additive. This suggests that the use of both biological control agents would prove beneficial to whitefly control programs. However, the interactions were more complicated than that. In absence of the omnivore, elevated intraspecific pressure was found at higher parasitoid release rates, reducing parasitoid populations. This finding concurs with a number of other studies which show density related negative intraspecific effects in parasitoid populations (van Lenteren et al. 1996). This pressure was alleviated when the omnivore was present. The omnivore also altered the distribution of whitefly. There were shifts in the vertical position of both whitefly and the parasitoid, suggesting either behavioral alteration of the prey or preferential feeding by the omnivore at certain heights along the plants within the cages. The number of patches and the size of these patches was also reduced through predation by the omnivore. The parasitoid, when used in isolation, had little effect on prey distribution. This arrangement of resources is unlikely to be beneficial to the parasitoid as it is a tactile forager (van Lenteren et al. 1976), which would greatly restrict its search rate. As the omnivore is much larger and a visual predator, it is concluded that the spatial arrangement of resources favors the omnivore. This suggests that the omnivore modified the arrangement of prey in such a way that it increased its competitive ability. The results of this study are valid only within a confined environment and may vary if the organisms are given the chance to disperse over larger distances.

The outcomes of many competitive interactions are determined through the spatial arrangement of resources (Amarasekare 2003). It is likely that in most cases, foraging in a patchy environment will alter resource distributions through patch depletion and elimination. I am as yet unaware of any study which examines the effects of consumption induced variation in the arrangement of patchy resources with resultant changes in competitive abilities. These types of interactions ought to be common with future work aimed at explicitly testing this theory.

I then took a theoretical approach to this theory and modeled a system with intraguild predation so that the intraguild predator and the intraguild prey could differ in their competitive abilities and the scale at which they forage. Foraging scale was modeled as the number of patches visited, with each patch visited incurring a certain cost in dispersal time. Patches were modeled as an implicit indicator of space. As patches became depleted, dispersal times increased, acting to reduce the efficiency of foraging at a larger scale. Omnivory was originally thought to destabilize food webs (Pimm 1982; Pimm and Lawton 1978), but has since been shown to lead to a broader range of dynamics (Holt and Polis 1997; McCann and Hastings 1997). Most models of omnivory look at trade-offs between competitive abilities and predation on the intraguild prey (Holt and Polis 1997; Kooi et al. 2002; Kuijper et al. 2003). Theoretical explorations of the spatial component of omnivorous systems are rare. Omnivory can stabilize spatially compressed food webs (McCann et al. 2005), but as far as I know, no studies have examined how spatial considerations stabilize the effects of omnivory. I found that a competitively dominant intraguild predator was able to coexist with the intraguild prey over a variety of conditions, dependent on the trade-offs in foraging scale and dispersal time.

I also found that omnivory much more closely followed the dynamics of a purely competitive system than that of a strictly predaceous food chain. Within most food chains or food webs, there is a reduction in biomass as trophic level increases. This reduction in biomass will manifest as lower availability of the intraguild prey relative to the shared resource. By the inclusion of a preference function that is dependent on the relative densities of the different food items, the amount of intraguild prey in the diet was greatly reduced. Even if the intraguild prey is highly preferred and it is converted much more efficiently into births compared to the shared prey, it still had little effect on the dynamics of the intraguild predator, due to the lower relative abundance of the intraguild prey. This adaptive preference maintains a weak direct interaction between the intraguild predator and the intraguild prey. Weak interactions are commonly found to promote stability (Emmerson and Yearsley 2004; McCann and Hastings 1997; McCann et al. 1998; Neutel et al. 2002). It is also similar to the findings where adaptive foraging increased stability, through the removal of the intraguild prey from the diet at low densities (Krivan and Diehl 2005).

This model suggests that omnivorous systems like this one are more akin to competition than predation, although early suggestions were contrary to this finding (Polis et al. 1989). The next step would be to look at the competitive exclusion literature and see how the principles within that large body of work can be applied to omnivory. It is my belief that this would rapidly advance our understanding of this interaction as mechanisms analogous to competitive exclusion would more appropriately describe omnivory within food webs.

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