

An Abstract Of The Thesis Of

Ian V. MacRae for the degree of Doctor of Philosophy in Entomology presented on October 27, 1994.

Title: Interspecific Predation and Cannibalism of Immatures by Adult Female *Metaseiulus occidentalis*, *Typhlodromus pyri* (Acari: Phytoseiidae) and *Zetzellia mali* (Acari:

Stigmaeidae)

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Brian A. Croft

Interspecific predation and cannibalism and associated rates of oviposition were assessed for adult female *Metaseiulus occidentalis* (Nesbitt) and *Typhlodromus pyri* Scheuten when provided non-limiting amounts of either eggs, larvae, protonymphs, or deutonymphs. Tests with all four stages of phytoseiids and larvae of *Tetranychus urticae* Koch were carried out at 25°C. At 15 and 12.5°C only larvae of phytoseiids and larvae of *T. urticae* were prey items. Predation by *T. pyri* was higher than *M. occidentalis* at 12.5 and 15°C, but more similar at 25°C. *M. occidentalis* did not feed appreciably on phytoseiid larvae at 15° and 12.5°C. Neither phytoseiid oviposited at 12.5°C when fed phytoseiid larvae, but *T. pyri* did at 15°C. We concluded that *T. pyri* was a more active predator at low temperatures and early-season predation on *M. occidentalis* immatures by *T. pyri* could contribute to displacement of *M. occidentalis* from apple orchards in western Oregon.

The effects of prey species and prey density on the rates of inter- and intraspecific predation and oviposition of the two phytoseiid mite predators *Metaseiulus occidentalis* (Nesbitt) and *Typhlodromus pyri* Schueten were investigated through a series of laboratory experiments. Adult female predators were given mixed populations of phytoseiid larvae and larvae of a more preferred prey, the spider mite, *Tetranychus urticae* Koch, at different rates and proportions. *T. pyri*, more of a generalist predator, consistently showed higher rates of predation and cannibalism on phytoseiid immatures at most prey populations and proportions. Manly Preference Indices indicated that *T. pyri* switched to feed on phytoseiid immatures at higher population levels and proportions of *T.*

urticae than did *M. occidentalis*. This ability to readily utilize phytoseiid immatures as prey indicated that maintaining both predators in a biological control program at low prey densities may require the use of active selective techniques that favour *M. occidentalis*.

The differential impact of *Zetzellia mali* on the phytoseiids *Metaseiulus occidentalis* and *Typhlodromus pyri* was studied in laboratory experiments and by analysis of population data from experimental orchard plots containing either of the phytoseiid species, similar numbers of prey mites, and high or low populations of *Z. mali*. Five hypotheses were evaluated to explain why *Z. mali* had more impact on *M. occidentalis* in the field than on *T. pyri*. Given equal opportunity, *Z. mali* adult females did not consume greater numbers of *M. occidentalis* eggs than *T. pyri* eggs nor did adult females of either phytoseiid species inflict greater mortality on *Z. mali* eggs or larvae through attack or consumption. There was no difference in the within tree association of *Z. mali* adult females with the eggs of either phytoseiid species nor were there differences in the way prey mites (all stages) were spatially partitioned between adult female *Z. mali* as compared with adults and deutonymphs of either of the two phytoseiids. The foraging area of adult female *Z. mali* and the oviposition locations of the two phytoseiids from both field and laboratory assessments were compared using spatial statistical procedures. *M. occidentalis* laid significantly more eggs in the primary foraging area of adult female *Z. mali* than did *T. pyri*. This spatial difference was the only factor tested which might explain the observed greater impact of *Z. mali* on *M. occidentalis*. Impact of these interspecific interactions and competition on the persistence of predatory mite guilds for the biological control of plant-feeding mites are discussed.

Interspecific Predation and Cannibalism of Immatures by Adult Female *Metaseiulus occidentalis*, *Typhlodromus pyri* (Acari: Phytoseiidae) and *Zetzellia mali* Schueten (Acari: Stigmaeidae)

by
Ian V. MacRae

A Thesis

submitted to

Oregon State University

in partial fulfilment of
the requirements for the
degree of
Doctor of Philosophy

Completed October 27, 1994
Commencement June 1995

Doctor of Philosophy thesis of Ian V. MacRae presented on October 27, 1994.

Approved:

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Major Professor, representing Entomology

Redacted for Privacy

Chairman of Department of Entomology

Redacted for Privacy

Dean of Graduate School

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Ian V. MacRae, author

I dedicate this thesis to my mother, Miriam Belle, and my father, George Duncan.

“Ich bin ein Croftite” - Phillippe Rossignol, 1994.

Acknowledgments

I wish to thank the members of my committee for their guidance and help. They have all listened to my ideas and given valuable feedback, often helping me see parts of my own project in a much different, and perhaps more complete, framework. They have offered input and have graciously taken time to help revise the chapters from this thesis which have already been submitted for publication. Their attention has enabled me to complete this thesis in an efficient manner and aided me in furthering my career. Most of all, I would like to thank them for encouraging me in my research and treating me as a colleague. I would like to thank my supervisor, Dr. Brian Croft for a productive and insightful experience. He taught me the importance of publishing in a timely way and that our responsibility as scientists is not over until we tell others what we have found. In addition, he gave me many of the skills I will need as a researcher. I would like to thank Kevin Currans for his assistance and support in so many things. From computers to irrigation pumps, if it was broken or I couldn't figure it out, Kevin was there to help and provide the right answers. I would also like to acknowledge the input and support of the 'Croftites' who shared my time in the lab: John Dunley, who became a close friend and helped Brian teach me much about phytoseiids; Chris Murphy, who put up with me in the same office for several years and guided me through computer learning pains; Ray Drapek, Ray-Bob-A-Loo-Bob, who helped me learn about GIS, Darin Allred, who was always ready to lend his hand to any task to help out, regardless of the difficulty. All became good friends, all shared their talents freely. I also received help from a number of other faculty and grad students over my tenure at OSU, and to all of you I say thank you.

I could never have even started down the path of graduate school if not for the support of my family. My mother and father, both of whom have always told me I could do anything to which I set my mind. They have always shown both their love for me and their faith in me. My sisters, Shannon and Heather, and my brother, Scott have always been there for me, and I hope I can always be there for them. I have saved the most important for last; my wife, Colleen. What can I say other than without you I could have done none of this. You are my strength and my passion; I love you dearly, Doll.

Table of Contents

Chapter 1 - Introduction	1
Chapter 2 - The Influence of Temperature on Interspecific Predation and Cannibalism by <i>Metaseiulus occidentalis</i> and <i>Typhlodromus pyri</i>	8
Introduction	8
Methods and Materials	9
Results	11
Temperature	11
Prey Stage	16
Prey Species	16
Discussion	18
Chapter 3 - Inter- and Intraspecific Predation by Adult Female <i>Metaseiulus occidentalis</i> and <i>Typhlodromus pyri</i> at Varying Densities and Proportions of <i>Tetranychus urticae</i> and Phytoseiid Larvae	20
Introduction	20
Methods and Materials	21
Experiment 1	22
Experiment 2	23
Experiment 3	23
Results and Discussion	23
Experiment 1	23
Experiment 2	30
Experiment 3	31
Conclusion	32
Chapter 4 - Differential Impact of <i>Zetzellia mali</i> on <i>Metaseiulus occidentalis</i> and <i>Typhlodromus pyri</i>	33
Introduction	33
Methods and Materials	35
<i>Z. mali</i> predation on phytoseiid eggs	36
Phytoseiid predation on <i>Z. mali</i> immatures	37
Comparison of prey population levels in phytoseiid plots	37
Within-tree spatial associations of <i>M. occidentalis</i> with <i>Z. mali</i> vs. <i>T. pyri</i> with <i>Z. mali</i>	38
Within-leaf spatial associations of phytoseiid egg distribution with <i>Z. mali</i> a)	
Adult <i>Z. mali</i> foraging	39
b) Phytoseiid oviposition location on individual leaves	39
Results and Discussion	40
Conclusions	51
Summary	53

Table Of Contents (continued)

Literature Cited	58
Appendices	63
Appendix 1: Vitae	64

List of Figures

- Figure 2.1. Mean cumulative prey eaten by adult female *T. pyri* (Tp) and *M. occidentalis* (Mo) at 25°C, 15°C, and 12.5°C, respectively over 10 days. 15**
- Figure 3.1: Mean Manly Prey Preference indices for adult female *M. occidentalis* (n=10) and *T. pyri* (n=10) feeding on mixed populations of phytoseiid and *T. urticae* larvae (index for phytoseiid larvae as prey). 27**
- Figure 3.2: Mean cumulative oviposition over 5 days of adult female *M. occidentalis* (n=10) and *T. pyri* (n=10) feeding on mixed populations of phytoseiid and *T. urticae* larvae. 29**
- Figure 4.1. Spatial location of mites in the field digitized on a generalized apple leaf using GIS software (Grass 4.0) 50**

List of Tables

- Table 2.1.** Mean consumption of prey and oviposition rate per day per individual of mated female *Metaseiulus occidentalis* and *Typhlodromus pyri* feeding on larvae at 25°, 15°, and 12.5° C over 10 days. 13
- Table 2.2.** Mean prey consumption and oviposition rate per day per individual mated female *Metaseiulus occidentalis* and *Typhlodromus pyri* feeding on all stages at 25° C over 10 days. 17
- Table 3.1:** Mean cumulative number of phytoseiid larvae eaten over 5 days by adult female *Metaseiulus occidentalis* (n=10) and *Typhlodromus pyri* (n=10) when offered mixed populations of phytoseiid and *Tetranychus urticae* larvae. Numbers in brackets are 95% C.I.'s and means in the 24
- Table 4.1:** Mean number of eggs eaten per day per female *Zetzellia mali* (n=10), over 7 days, and the mean oviposition per day associated with each species of prey. 42
- Table 4.2.** Mean daily number of *Metaseiulus occidentalis* and *Typhlodromus pyri* eggs eaten and corresponding oviposition (+/- 2 S.D.'s) by adult female *Zetzellia mali* (n = 16) over 7 days. Phytoseiid eggs are separated into two age classes; 0-24 hours old and 24-48 hours old. 42
- Table 4.3:** Mean number of *Zetzellia mali* eggs (+/- 2 S.D.'s) eaten and mean number of eggs laid by female *Metaseiulus occidentalis* and *Typhlodromus pyri* per female per day, over 6 days. 45
- Table 4.4:** Comparison of correlation coefficients of *Metaseiulus occidentalis* eggs with adult female *Zetzellia mali* and *Typhlodromus pyri* eggs with adult female *Zetzellia mali*, in high *Zetzellia mali* population plots throughout the growing season, 1991. 45
- Table 4.5:** Comparison of correlation coefficients of adult and deutonymph *Typhlodromus pyri* with total prey mites, adult and deutonymph *Metaseiulus occidentalis* with total prey mites, and adult and deutonymph *Zetzellia mali* with total prey mites, in high *Z. mali* population plots throughout the growing season, 1991. 47

Interspecific Predation and Cannibalism of Immatures by Adult Female *Metaseiulus occidentalis*, *Typhlodromus pyri* (Acari: Phytoseiidae) and *Zetzellia mali* Schueten (Acari: Stigmaeidae)

CHAPTER 1 - INTRODUCTION

Sharing the same habitat often leads to interactions between species such as predation, competition, mutualism, commensalism, neutralism, etc., which significantly influence community structure. If species share resources, these interactions are likely to take the form of competition. Among predators, mutual predation, either between individuals of the same species (cannibalism or intra-specific competition) or those of different species (interspecific competition) can result in an immediate removal of competitors thus increasing access to the common resource (Polis and Meyers 1989). This differs from competition when mortality of competitors is caused indirectly or when there is lowered reproduction from resource depletion. Both forms of competition can be avoided by resource partitioning among the species sharing the resource (Schoener 1974).

Biological control involves introducing natural enemies (predators and parasitoids) to suppress pest populations, ideally below levels which cause damage to the crop. Classical biological control of an introduced pest involves exploration of the pest's home range, finding natural enemies which limit it there and importing these agents to do likewise where the pest has been introduced (DeBach 1964). Augmentative release, the periodic introduction of one or more natural enemies, not necessarily from the pest's home range, can have two forms; inundative, where control is a function of the natural enemies released, and inoculative, where control is a function of its progeny (DeBach 1964). Establishment of long-term biological control mostly involves the latter. Although augmentative release does not have as successful a record as classical biological control, there is increasing evidence for its usefulness (Parella et al. 1992).

The establishment or release of several species of natural enemies into a shared habitat represents the formation of a guild. If the species have no history of co-evolution, they may be subject to intense interspecific competition, especially when the prey (the common resource) decrease as the target pest is controlled. This disruption of pest (prey) populations is the ultimate goal of biological control and in these cases even natural enemies which have co-evolved and have methods of partitioning scarce resources may have strong competition. However, this competition may not be destabilizing; interspecific predation of immatures may contribute to long-term regulation of mite communities by stabilizing generalist predator populations, enhancing their persistence at low prey densities (Yao and Chant 1989, MacRae and Croft 1993).

The introduction of multiple species into a guild of natural enemies provides an excellent opportunity to observe long term competition and the success of biological control. From a practical viewpoint, interspecific competition can diminish the overall control effect and lead to the displacement of species less able to compete. This has been demonstrated both in the field (Chant 1958, McMurtry et al. 1982) and in the lab (Yao and Chant 1989). If the presence of multiple natural enemies always resulted in the persistence of the species which exerted the best control of the pest, it would not be a problem. However, such competition may result in a natural enemy which is less able to control the pest population persisting and displacing the other species. A number of traits have been identified as being desirable in a successful natural enemy (such as good searching potential, host specificity, a life history synchronized with that of the pest) (Doutt and DeBach 1964, Huffaker et al. 1977). Some of these factors, however, may carry a cost to competitive fitness. Consequently, the more intrinsically inferior species may be extrinsically superior in a situation termed counter-balanced competition and the less effective natural enemy may persist (Zwolfer 1971, Pschorn-Walcher 1977).

It may be possible to avoid such competition in synthetic guilds by matching certain compatible ecological and life history traits. This was the goal of a long-term field experiment involving the introduction of the two phytoseiid mites, *Metaseiulus occidentalis* Nesbitt and *Typhlodromus pyri* Schueten, to control the pest mites, Two-Spotted Spider Mite, *Tetranychus urticae* Koch, European Red Mite *Panonychus ulmi* (Koch), and the apple rust mite, *Aculus schlechtendali* Nalepa, in apple (Croft and MacRae 1992a). Both of the phytoseiids are native species and are known to overlap in their distribution in Oregon (Croft et al. 1990). Both are also successfully used individually in biological control programs for spider mites (Helle and Sabelis 1985).

Members of the family Phytoseiidae are free-living, predatory, terrestrial mites often occurring on crops where they prey on phytophagous mites (Krantz 1978). They are efficient predators, generally moving much more rapidly than their prey, searching well, and have rates of reproduction and developmental periods that lead to overlapping generations wherein all four life stages (egg, protonymph, deutonymph and adult) are simultaneously present. Their ability to control Tetranychid (spider mite) populations has led to increasing interest in their use as biological control agents for these and other phytophagous mites (Chant 1985).

Many phytoseiids show definite prey preference among spider mites, often based on the web-building behaviour of phytophagous mites (Krantz 1978) or on a response to plant kairomones released by leaves being fed upon by phytophagous mites (Sabelis and Van de Baan 1979, Dicke 1988, Zhang and Sanderson 1992). Such preferences have been shown for *M. occidentalis* (which shows a preference for *T. urticae* as prey) and for *T. pyri* (which prefers *P. ulmi*) (Sabelis and Van de Baan 1979, Dicke and De Jong 1988, Dicke et al. 1988). Some species are relatively prey specific, accepting only tetranychids and other smaller mite species as prey, as does *M. occidentalis*, or are more generalist in

their feeding habits, able to exploit not only a wide variety of acarine prey but also pollen and plant juices, as does *T. pyri* (Overmeer 1985).

In Oregon, *M. occidentalis* is more prevalent in the warmer, drier intermountain valleys. Westgard et al. (1972) found it was the predominant phytoseiid species in pear orchards in the Rogue River valley and Croft et al. (1990) found it likewise to be the most numerous species in the Hood River Valley. Haddam et al. (1986) found that in the wetter Willamette Valley, *T. pyri* was more numerous in apple orchards than was *M. occidentalis*.

Croft et al. (1990) proposed management techniques for mixed populations of these two species. The complementary ecological and life history attributes of *M. occidentalis* and *T. pyri* may allow them to be used in conjunction against phytophagous mites in apple. It was hypothesized that *M. occidentalis*, with its preference for warmer, drier climates, would have population peaks in mid-summer and concentrate their predation on *T. urticae*. It was thought that *T. pyri* would peak earlier in the season, and then again in the fall, concentrating its predation on *P. ulmi*. Both phytoseiids will feed and reproduce readily on *A. schlechtendali* (Dicke et al. 1990) and so should be able to persist when spider mites are scarce. It was hypothesized that *T. pyri*, with its greater functional response, would function to maintain the pest mite populations at low levels and *M. occidentalis*, with its much narrower prey specificity and higher rate of reproduction, would function as a population responder, reacting to pest population outbreaks. Mixed populations of greater numbers of *T. pyri* with approximately 20% *M. occidentalis* to respond to pest mite outbreak situations should provide an adequate predator guild to control spider mite infestations (Croft pers com).

An experimental orchard was established, composed of 20 plots. Each plot contained 5, 7-yr-old 'Red Delicious' apple trees, pruned to 2-3 m height, grown in 25 gal plastic pots filled with soil. In the first year, into each plot was introduced a unique population

treatment: one of 5 prey types (A, no pest mites added; B, apple rust mites added; C, European Red Mite added; D, European Red Mite and two-spotted spider mite added; E, apple rust mite suppressed and two-spotted spider mite added), and one of 4 predator types (1, no predators; 2, *T. pyri* added; 3, *M. occidentalis* added; 4, both predators added, each at levels $\sim 1/2$ of 2 or 3). This resulted in 20 prey-predator treatments (Croft and MacRae 1992a). These treatments were maintained or changed through 4 years of the experiment via yearly introductions of predators and phytophagous mites and through chemical exclusion of certain species (see Croft and MacRae 1992a, 1992b, 1993, and 1994 for details on yearly prey-predator treatments). The plots were sampled bi-weekly through the growing season. Natural populations of the egg predator *Zetzellia mali* Ewing (Acarina: Stigmaeidae) were also present, and from the second year onwards were chemically suppressed in some plots.

During the first year, populations of both phytoseiids were numerous and they controlled all species of pest mites. The plots with mixed populations of phytoseiids, however, were ranked as having better levels of biological control than were the single predator plots (Croft and MacRae 1992a). In the second year, with very low pest mite numbers, interactions between the predators in the system became apparent. *M. occidentalis* populations were suppressed and even displaced from some plots where *T. pyri* and *Z. mali* were present (Croft and MacRae 1992b). Because populations of *M. occidentalis* persisted in plots where it was the only predator, it was assumed that this shift in species abundance was the result of interspecific competition. Population data from late in the season of 1990 indicated that it may have been direct competition in the form of *T. pyri* eating immature *M. occidentalis*. In addition, the presence of *Z. mali* had an adverse effect on populations of both phytoseiids, but more so on *M. occidentalis* (Croft and MacRae 1992b, 1993). Because the stigmaeid's obligate prey are eggs and young immatures, it was thought this impact must be due to predation on phytoseiid

immatures. Other researchers have suggested that predation on immature stages of other predators in mixed acarine systems may be important. Chant (1959) observed that in unsprayed English apple orchards, *Euseius findlandicus* (Oudemans) was the dominant species, displacing *Phytoseius macropilis* (Banks) and *T. pyri*, apparently through destruction of eggs and larvae of the latter two phytoseiids. Yao and Chant (1989) showed that *Amblyseius degenerans* (Berlese) displaced *Phytoseiulus persimilis* Athias-Henriot, through predation of immatures in laboratory colonies.

It was decided to experimentally evaluate and compare the effect of various environmental factors on the rates of inter- and intraspecific competition in *M. occidentalis*, *T. pyri* and *Z. mali*. The displacement of *M. occidentalis* occurred principally during the fall of the first year and the spring of the second (Croft and MacRae 1992a). The outcome of interspecific competition is influenced by the individual species' response to environmental variables (Park 1962). It was hypothesized that at lower temperatures, *T. pyri* is more active, has a higher rate of reproduction and more readily accepts phytoseiid immatures as prey than does *M. occidentalis*. Consequently, the rates of intra- and interspecific predation of the two phytoseiids were described and compared at a series of sequentially lowering temperatures (Chapter 1 - The Influence of Temperature on Interspecific Predation and Cannibalism by *Metaseiulus occidentalis* and *Typhlodromus pyri*). In addition, as populations of the preferred prey species, *T. urticae*, *P. ulmi* and *A. schlechtendali* were lowered in the fall of the first year and continued to be low in the spring of the second year, it was hypothesized that *T. pyri* accepted phytoseiid immatures as prey at higher densities of preferred prey (i.e. spider mites) than did *M. occidentalis*. The rates of intra- and interspecific predation were, therefore, also described and compared at a variety of prey populations and proportions (Chapter 2 - Inter- and Intraspecific Predation by Adult Female *Metaseiulus occidentalis* and *Typhlodromus pyri* at Varying Densities and Proportions of *Tetranychus urticae* and Phytoseiid Larvae).

Field data indicated the presence of *Z. mali* appeared to have a greater impact on *M. occidentalis* at low prey densities than it did on *T. pyri*. This phenomena was investigated in the third chapter (Differential Impact of *Zetzellia mali* on *Metaseiulus occidentalis* and *Typhlodromus pyri*).

CHAPTER 2 - The Influence of Temperature on Interspecific Predation and Cannibalism by *Metaseiulus occidentalis* and *Typhlodromus pyri**

Introduction

There is mixed opinion about the value of using multiple natural enemies to achieve biological control of arthropod pests. Positive effects may come from additive impacts of parasitoids and predators (Waage and Hassell 1982); negative ones can arise from competition among species with similar foraging strategies or prey preferences (Ehler and Hall 1982).

Predaceous phytoseiid mites appear to interact in ways that relate to these phenomena (Helle and Sabelis 1985). For example, interspecific predation by one phytoseiid may limit short-term biological control by another, especially if the second shows a greater numerical response to pest mites than the first. This is the case with the specialist predator, *Metaseiulus occidentalis* (Nesbitt), which is suppressed by the more general feeder, *Typhlodromus pyri*, Scheuten in Oregon apple orchards (Croft and MacRae 1992a). At the other extreme, predation by adult phytoseiids on their immatures may be a mechanism that contributes to long-term regulation of mite communities. This would enhance the persistence of generalist predator species at low spider mite populations, ensuring continued control of pest mite populations (Chant 1959, McMurtry et al. 1980, Yao and Chant 1989). A greater understanding of these complex interactions is needed to better manage multiple phytoseiid species in the same system, which may result in improved biological control.

In experiments with *M. occidentalis* and *T. pyri*, interspecific competition was demonstrated in plots that received inoculative releases of equal densities of these two

* Published as: MacRae, I.V. and B.A. Croft. 1993. Influence of temperature on interspecific predation and cannibalism by *Metaseiulus occidentalis* and *Typhlodromus pyri* (Acarina: Phytoseiidae). *Env. Ent.* 22(4): 770-775.

predators (Croft and MacRae 1991, 1992, Croft et al. 1992). *M. occidentalis* was more abundant during mid-summer of the first year after releases because of greater reproduction when temperatures were warm and prey were abundant, but *T. pyri* oviposited more rapidly in late-season and the next spring when it was cool and prey were scarce. In the second season, a shift in species abundance occurred, *T. pyri* became more common and *M. occidentalis* declined, but *M. occidentalis* was very abundant in single species release plots without *T. pyri*. We hypothesized that in addition to its greater reproduction at low temperatures, the feeding of *T. pyri* on *M. occidentalis* contributed to the shift in species abundance.

In this study, we assessed predation and oviposition by adult female *T. pyri* and *M. occidentalis* when fed phytoseiid immatures in the laboratory at 15° and 12.5°C. These are temperatures close to those that prevailed in the field when displacement of *M. occidentalis* occurred. We also studied these factors at 25°C, which is near-optimum for development and reproduction of both phytoseiids (Helle and Sabelis 1985). Rates of cannibalism and interspecific predation by adult female phytoseiids were compared to their predation on the spider mite, *Tetranychus urticae* Koch. *T. urticae* is prey for both *M. occidentalis* and *T. pyri* in the field, and many data exist on the temperature-mediated responses of phytoseiids to this spider mite (Helle and Sabelis 1985).

Methods and Materials

Experimental arenas of 1 cm² were constructed by subdividing 7 x 6 cm plastic tiles into 20 units using "Tanglefoot" (Grand Rapids, Mich) adhesive. Tile served as a substrate rather than leaf disks to prevent predators from feeding on plant fluids (Chant 1959). Each arena had a hole (0.25 cm diameter) filled with a cotton wick to supply free

water to predators. Tiles rested on water saturated sponges contained in a tray of water. Cotton fibers placed in the center of an arena provided a site for oviposition by predators after feeding on prey. Experiments were run at constant spring (12.5° and 15°C), and mid-summer (25°C) temperatures. RH 55-65 % was maintained in all tests.

A 5-day old mated female of either *M. occidentalis* or *T. pyri* reared on *T. urticae* was taken from a laboratory colony and placed onto each arena. Female predators were starved for 24 h before prey were presented. Preliminary tests determined non-limiting amounts of prey types. Because of the small arena size and amounts of food presented, it was assumed that searching was non-limiting to predation and oviposition. Prey presented at 25°C were either 10 eggs, larvae, protonymphs, or deutonymphs of the same or the other phytoseiid species, or 20 larvae of *T. urticae*. A female was given the same prey type throughout a trial in non-limiting amounts, replaced daily. Six prey-predator combinations were tested: *M. occidentalis* females-*M. occidentalis* immatures, *M. occidentalis* females-*T. pyri* immatures, *M. occidentalis* females-*T. urticae* larvae and three similar ones with *T. pyri* adult females as predators and the same prey. At 12.5°C and 15°C only phytoseiid larvae (10) and *T. urticae* larvae (20) were offered as prey. This was because the greatest feeding response was on larvae, and larvae allowed the greatest discrimination in feeding rates. Consumed prey and eggs oviposited were counted for each female predator every 24 hours; each test was run for 10 d or until death of the adult female predator. Consumed prey were identified by their shriveled appearance. Each test was replicated 10 times. The effect of temperature on the rates of predation and oviposition was analyzed by a Hierarchical Analysis of Variance (ANOVA) and significantly different means separated by Least Significant Difference (LSD) (Steele and Torrie 1980). The effects of stage and species were similarly analysed by a 2-way ANOVA and LSD. Mean cumulative consumption per day over a 10-day period and confidence intervals (95%) for the last day were calculated.

Results

Three factors were tested for their influence on interspecific predation, cannibalism and oviposition by predators:

Temperature: Rates of interspecific predation and cannibalism by *M. occidentalis* and *T. pyri* on larvae of either phytoseiid decreased significantly with temperature (Figs. 1.1a, 1.1c, 1.1e Table 1.1). At 25°C, predation rates on phytoseiid larvae were significantly higher for *T. pyri* than for *M. occidentalis* (Fig. 1.1a, Table 1.1). At 15°C, *T. pyri* fed on larvae of both phytoseiids at relatively high frequencies (*i.e.*, comparable to rates for *M. occidentalis* at 25°C), but predation by *M. occidentalis* was significantly less (Fig 1.1c, Table 1.1). At 12.5°C, *T. pyri* continued to feed on larvae of *M. occidentalis* and somewhat on *T. pyri*, but *M. occidentalis* fed on neither phytoseiid larvae after day 3 (Fig 1.1e). Rates of oviposition when feeding on phytoseiid larvae showed similar effects of temperature. At 25°C, oviposition by both phytoseiids was low (compared to feeding on *T. urticae*, see below), from 0.35-0.40 eggs per day (Table 1.1). *T. pyri* oviposited at 15°C (0.19-0.25 eggs per day); *M. occidentalis* did not. Neither predator oviposited at 12.5°C.

There also were significant differences at 25°, 15° and 12.5° C in predation rates by both females phytoseiids on *T. urticae* larvae (Figs. 1.1b and 1.1d, Table 1.1); however from 25° to 15°C, rates decreased less drastically than when feeding on phytoseiid larvae (Figs. 1.1b and 1.1d). While still actively foraging on *T. urticae*, predation of *M. occidentalis* on *T. urticae* larvae at 15°C was significantly lower than that of *T. pyri* (Fig 1.1c, Table 1.1). At 12.5°C, predation by *M. occidentalis* on *T. urticae* larvae essentially stopped (Fig 1.1f, Table 1.1), but *T. pyri* continued to feed at a low level.

Temperature affected oviposition of both predators when feeding on *T. urticae* larvae, but over a wider range than when feeding on phytoseiids. *M. occidentalis* feeding on *T.*

urticae oviposited 2.13 eggs per day, which was more than *T. pyri*'s 1.02 per day (Table 1.1). At 15°C, there was no difference in oviposition between the two predators, with *M. occidentalis* laying 0.70 eggs per day to *T. pyri*'s 0.83 eggs per day. Neither phytoseiid oviposited when feeding on *T. urticae* larvae at 12.5°C.

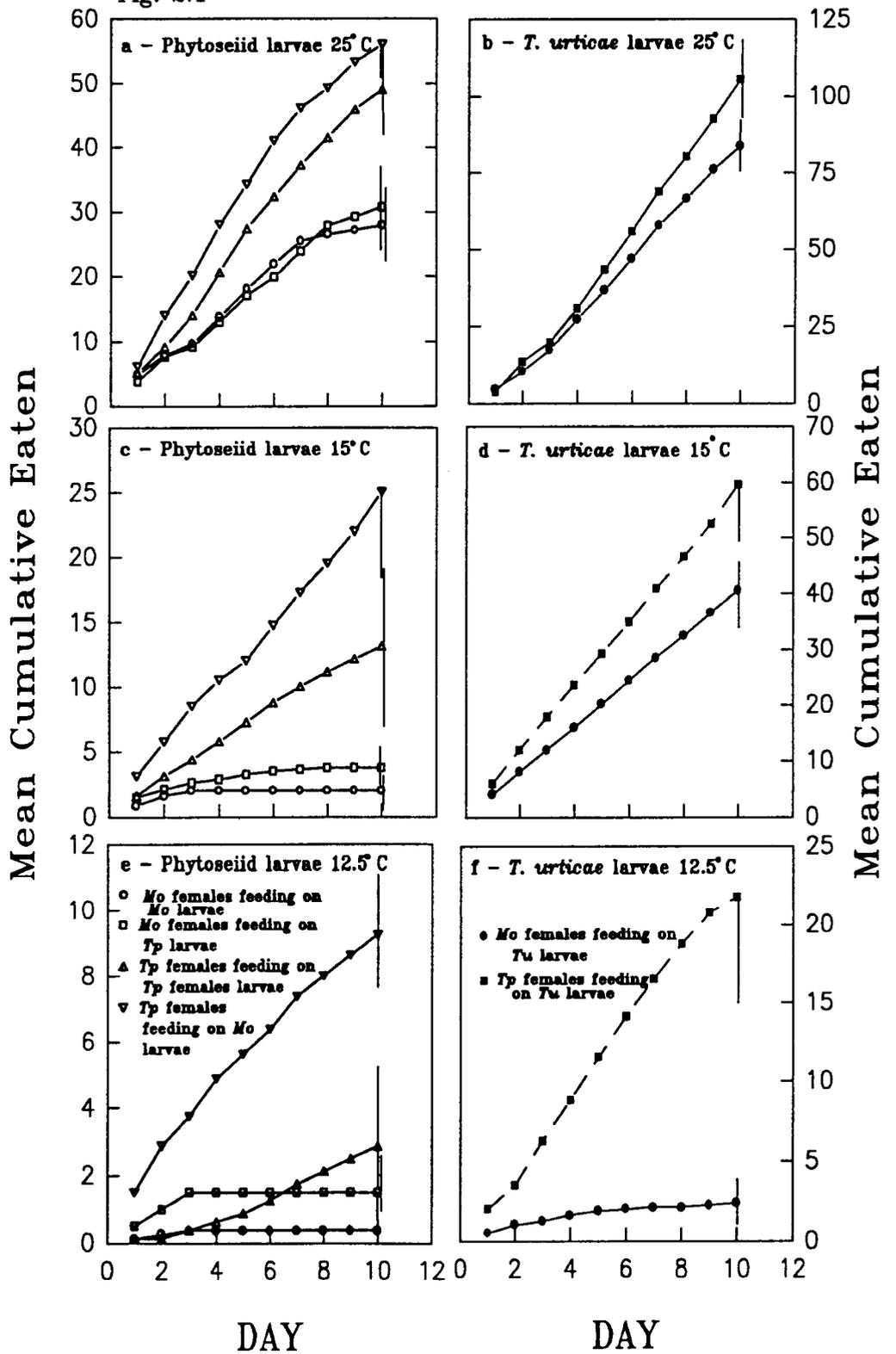
Table 2.1. Mean consumption of prey and oviposition rate per day per individual of mated female *M. occidentalis* and *T. pyri* feeding on larvae at 25°, 15°, and 12.5° C over 10 days.

Temp ° C	Predator Species	Prey Species	Mean Pred. Rate	Oviposition Rate	No. larvae eaten / 1 egg laid
25° C	<i>M. occidentalis</i>	<i>M. occidentalis</i>	2.79c	0.38b	7.34
	<i>M. occidentalis</i>	<i>T. pyri</i>	3.08cd	0.38b	8.80
	<i>M. occidentalis</i>	<i>T. urticae</i>	8.37e	2.13d	3.93
	<i>T. pyri</i>	<i>M. occidentalis</i>	5.60e	0.40b	14.00
	<i>T. pyri</i>	<i>T. pyri</i>	4.90d	0.38b	12.89
	<i>T. pyri</i>	<i>T. urticae</i>	10.55f	1.02c	10.34
15° C	<i>M. occidentalis</i>	<i>M. occidentalis</i>	0.20a	0.00a	N/A
	<i>M. occidentalis</i>	<i>T. pyri</i>	0.38b	0.00a	N/A
	<i>M. occidentalis</i>	<i>T. urticae</i>	4.05d	0.70b	5.79
	<i>T. pyri</i>	<i>M. occidentalis</i>	2.51bc	0.25b	10.04
	<i>T. pyri</i>	<i>T. pyri</i>	1.31b	0.19b	6.89
	<i>T. pyri</i>	<i>T. urticae</i>	5.96e	0.83bc	7.18
12.5° C	<i>M. occidentalis</i>	<i>M. occidentalis</i>	0.04a	0.00a	N/A
	<i>M. occidentalis</i>	<i>T. pyri</i>	0.15a	0.00a	N/A
	<i>M. occidentalis</i>	<i>T. urticae</i>	0.24a	0.00a	N/A
	<i>T. pyri</i>	<i>M. occidentalis</i>	0.93b	0.00a	N/A
	<i>T. pyri</i>	<i>T. pyri</i>	0.29ab	0.00a	N/A
	<i>T. pyri</i>	<i>T. urticae</i>	2.18bc	0.02a	N/A

Means in a column followed by the same letter are not significantly different ($P = 0.05$) by LSD (Steele and Torrie 1980)

Figure 2.1. Mean cumulative prey eaten by adult female *T. pyri* (*Tp*) and *M. occidentalis* (*Mo*) at 25°C, 15°C, and 12.5°C, respectively over 10 days (1a,c and e are for phytoseiid larvae as prey; 1b,d and f are for *T. urticae* larvae). Vertical bars are 95% confidence intervals.

Fig. 2.1



Prey Stage: This factor was evaluated for phytoseiid immatures only (Table 1.2) and had significant effects on predation by adults of both phytoseiids. The highest rates of cannibalism and interspecific predation by adult female phytoseiids was on larvae, followed by protonymphs, eggs, and deutonymphs, respectively. Both species showed the highest oviposition rate when feeding on larvae or eggs, followed by protonymphs and then deutonymphs (Table 1.2). Another factor (the ratio of immatures consumed to number of eggs laid per day) was different among prey stages; *e.g.*, 4.75 eggs eaten : 1 egg laid per female per day, versus 9.9 protonymphs eaten : 1 egg laid per female per day for *M. occidentalis* females feeding on its own immatures (Table 1.2). The lowest ratios of immatures eaten/eggs laid were for adult females consuming phytoseiid eggs.

Prey Species: Not surprisingly, there were more spider mite larvae than phytoseiid larvae eaten by both predators at all temperatures tested (Fig 1.1, Table 1.1). With phytoseiid immatures, *M. occidentalis* did not show any differences in consumption within prey stage, but *T. pyri* did at some temperatures (Table 1.2). At 25°C, *T. pyri* females ate more *M. occidentalis* eggs and protonymphs than those of their own. *T. pyri* females ate fewer *T. pyri* eggs than *M. occidentalis* females did of either species (Table 1.2). This was the only case where predation by *T. pyri* was less than that for *M. occidentalis* at any temperature. *T. pyri* ate significantly more larvae of *M. occidentalis* than its own at 12.5°C, however this difference did not carry over to oviposition rates between these two prey items (Table 1.2). *T. pyri* produced less eggs per phytoseiid larvae consumed than *M. occidentalis* (Table 1.1), but this trend did not hold true across all predator life stages (Table 1.2).

Table 2.2. Mean prey consumption and oviposition rate per day per individual mated female *M. occidentalis* and *T. pyri* feeding on all stages at 25° C over 10 days.

Predator Stage (Prey Stage)	Predator species	Prey species	Mean no. consumed	Oviposition rate	No. prey items eaten / 1 egg laid
Adults (Eggs)	<i>M. occidentalis</i>	<i>M. occidentalis</i>	1.33b	0.28c	4.75
	<i>M. occidentalis</i>	<i>T. pyri</i>	1.75bc	0.24bc	7.29
	<i>T. pyri</i>	<i>M. occidentalis</i>	2.18c	0.32c	6.82
	<i>T. pyri</i>	<i>T. pyri</i>	1.01b	0.21b	4.81
Adults (Larvae)	<i>M. occidentalis</i>	<i>M. occidentalis</i>	2.79c	0.38cd	7.34
	<i>M. occidentalis</i>	<i>T. pyri</i>	3.08c	0.35cd	8.80
	<i>T. pyri</i>	<i>M. occidentalis</i>	5.60d	0.40d	14.00
	<i>T. pyri</i>	<i>T. pyri</i>	4.90d	0.38cd	12.89
Adults (Proto- nymphs)	<i>M. occidentalis</i>	<i>M. occidentalis</i>	1.49bc	0.15b	9.90
	<i>M. occidentalis</i>	<i>T. pyri</i>	1.76bc	0.11ab	16.00
	<i>T. pyri</i>	<i>M. occidentalis</i>	4.31d	0.23bc	18.74
	<i>T. pyri</i>	<i>T. pyri</i>	2.54c	0.25c	10.16
Adults (Deuto- nymphs)	<i>M. occidentalis</i>	<i>M. occidentalis</i>	0.43a	0.10a	4.30
	<i>M. occidentalis</i>	<i>T. pyri</i>	0.86ab	0.90e	9.56
	<i>T. pyri</i>	<i>M. occidentalis</i>	1.68bc	0.13ab	12.92
	<i>T. pyri</i>	<i>T. pyri</i>	1.34bc	0.09a	14.89

Means in a column followed by the same letter are not significantly different ($P = 0.05$) by LSD (Steele and Torrie 1980).

Discussion

Typhlodromus pyri demonstrated greater rates of interspecific predation and cannibalism than *M. occidentalis* at the three temperatures tested with the exception of cannibalism of eggs at 25°C. The same trend held for predation on eggs of *T. urticae*. These responses to temperature were expected given the geographic distribution of *T. pyri* in cooler, wetter regions of Oregon and higher abundance of *M. occidentalis* in warmer, drier areas (Croft et al. 1990). The greater feeding by *T. pyri* on phytoseiid larvae in the laboratory at 15° and 12.5°C indicated that interspecific predation by *T. pyri* on *M. occidentalis* immatures could contribute to displacement of *M. occidentalis* in the field as suggested earlier (Croft and MacRae 1991, 1992a,b, Croft et al. 1992). Because *T. pyri* can actively forage on spider mites at 12.5°C, a decrease in prey populations in spring may intensify interspecific competition between these two predators. Also in early summer, *T. pyri* would be able to prey on both spider mites and phytoseiid immatures, whereas the latter option would be unavailable to *M. occidentalis*.

The greatest predation on phytoseiid immatures by both predators was on larvae. Croft and McMurtry (1972) found that *M. occidentalis* had the greatest feeding response to larvae when fed different immature stages of *T. urticae*. These trends in feeding behavior were not well correlated with the nutritional value of phytoseiid and tetranychid life stages, however. The ratio of phytoseiid immatures eaten/mean eggs oviposited per day indicated that eggs were the most nutritious life stage. Greater consumption of larvae likely reflects the fact that smaller, motile prey stimulate a greater feeding response by phytoseiid adults than do eggs (Croft and McMurtry 1972, Croft 1972).

Although both predators preyed more heavily and oviposited more when feeding on *T. urticae* than on phytoseiid immatures, the latter were of significant value nutritionally as reflected by oviposition rates, especially for *T. pyri*. Most likely, spider mites illicit feeding responses in phytoseiids that are related to their searching response to

kairomones as has been reported for *T. pyri* and *M. occidentalis* (e.g., Dicke 1988, Dicke et al. 1988, Zhang and Sanderson 1992). The tendency of *T. pyri* to feed more on *M. occidentalis* eggs than on its own may indicate that it has a mechanism to differentiate egg species. The somewhat higher nutritional value of phytoseiids to *T. pyri* than to *M. occidentalis* might be related to the acceptance by *T. pyri* of a wider range of food types (Dicke and DeJong 1988, Dicke et al. 1988). This may also explain the fact *T. pyri* is more likely to prey upon phytoseiid immatures. This wider acceptance of alternate prey types is probably associated with its tendency not to disperse to other habitats as rapidly as *M. occidentalis* (Dunley and Croft 1990) and allows it to be a regulator of spider mites at low population densities (Helle and Sabelis 1985, Croft et al. 1992). In contrast, the greater efficiency of *M. occidentalis* in converting larvae of *T. urticae* to eggs and its lesser tendency to feed on phytoseiid immatures, may reflect its more specialized food habits, its capability to rapidly respond to outbreaks of spider mite pests, and its ability to rapidly disperse to other habitats (Helle and Sabelis 1985, Croft et al. 1992, Dunley and Croft 1990).

CHAPTER 3 - Inter- and Intraspecific Predation by Adult Female *Metaseiulus occidentalis* and *Typhlodromus pyri* at Varying Densities and Proportions of *Tetranychus urticae* and Phytoseiid Larvae*

Introduction

Maintaining the structure of a guild of biological control agents becomes increasingly difficult as the population density of available prey decreases and interspecific competition among natural enemies increases. Predation on immatures of closely related species is a form of direct competition, where potential competitors are removed from the system (Yao and Chant 1989). Intraguild predation and predation of immatures is also a response to lowered food availability and may serve to stabilize the predator's population over time (Polis 1981, Polis and Myers 1989). Both behaviours may enhance the persistence of generalist predators at low prey densities (McMurtry et al. 1984, MacRae and Croft 1993). Interspecific predation and cannibalism may also be a shift in prey as a response to a decline in more typical prey while same or similar species numbers remain temporarily high (Murdoch and Marks 1973).

Such interactions appear to occur between the phytoseiids, *Metaseiulus occidentalis* (Nesbitt) and *Typhlodromus pyri* Schueten when they co-occur in a biological control program for pest mites on apple. When *T. pyri* and *M. occidentalis* were initially introduced into field plots alone and together in approximately equal densities (Croft and MacRae 1992a and b), both phytoseiids were abundant and exerted appreciable biological control of the pest mites, *Panonychus ulmi* Koch, *Tetranychus urticae* (Koch) and *Aculus schlechtendali* Nalepa (Croft and MacRae 1992a). In the second year, however, a shift in species abundance occurred: *T. pyri* populations increased while those of *M. occidentalis* declined (Croft and MacRae 1992b). This trend continued in the third year with *M.*

* Submitted as: MacRae, I.V. and B.A. Croft. Inter- and Intraspecific Predation by Adult Female *Metaseiulus occidentalis* and *Typhlodromus pyri* at Varying Densities and Proportions of *Tetranychus urticae* and Phytoseiid Larvae. *Oecologia*.

occidentalis disappearing completely in some plots (Croft and MacRae 1993). It was concluded that this shift resulted from interspecific competition because it did not occur where *M. occidentalis* was introduced without *T. pyri*. In subsequent laboratory experiments, it was found that at low temperatures, *T. pyri* had a greater propensity to feed on phytoseiid immatures than *M. occidentalis* (MacRae and Croft 1993). *T. pyri*'s ability to feed on *M. occidentalis* immatures during fall and spring, when temperatures were low plus its higher reproduction at lower temperatures, contributed to the displacement of *M. occidentalis*. We hypothesized that, because *T. pyri* was a more general feeder than *M. occidentalis*, it would have a greater tendency to prey on phytoseiid immatures at lowered prey population densities and would shift more rapidly to phytoseiid immatures from spider mites than would *M. occidentalis*.

In this study we assessed the effect of prey density on interspecific predation and cannibalism of phytoseiid larvae and oviposition by adult female *M. occidentalis* and *T. pyri*. Mixed populations of phytoseiid larvae and larvae of the spider mite, *Tetranychus urticae* Koch, were presented in various ratios to adult female *M. occidentalis* and *T. pyri* to determine if rates of interspecific predation or cannibalism were affected either by decreasing spider mite populations, or increasing proportions of phytoseiid larvae, or a combination of the two.

Methods and Materials

All trials were conducted in 5 cm² arenas constructed on tile substrates with sticky barriers. All individual larvae and adult female mites used were taken from laboratory colonies. Adult female *T. pyri* or *M. occidentalis* of approximately the same age were placed on arenas and not fed for 24 hours to produce similar levels of hunger. Prey larvae (a combination of phytoseiid larvae and the more preferred prey, *T. urticae* larvae according to the proportions outlined below) were transferred with a camel hair brush into the arenas daily at 24 hr intervals. All unconsumed prey were removed daily and replaced

with fresh individuals for 7 days (the first two days were considered a period of acclimation of the females to the arenas and the feeding regimen and these data were not used in analyses). Prey species, number of prey consumed, and oviposition by predators were recorded daily. Each experiment was replicated ten times using fresh adult female predators for each trial and each replication within each trial. Larvae not consumed were removed and destroyed each day. Mean cumulative consumption was calculated over the 5 day experimental period and compared within each prey level and proportion treatment. Results were analysed by a one-way ANOVA and significant differences differentiated with a Fisher's LSD test (SAS Institute 1987). Because comparisons between different prey numbers and proportions were not possible directly, Manly's prey preference indices were calculated for each combination (Manly 1974, Clements and Harmsen 1993). Indices were compared with a 2-way ANOVA and significant differences differentiated with Fisher's LSD. Manly preference indices were calculated only for adult female phytoseiids feeding on prey populations / proportions that included both phytoseiid and *T. urticae* larvae. This was because the sum of the preference indices for all prey species in the system equals unity for any predator; the preference index for any prey population / proportion where available prey was only one species (either phytoseiid or *T. urticae* larvae) was, therefore, not meaningful.

Three experiments involving different prey levels / proportions were conducted:

Experiment 1: Decreasing total prey with constant prey species proportions - To evaluate the effect of decreased available prey, trials were conducted in which sequentially lower prey populations in a constant proportion of prey species of phytoseiids to tetranychids (1:2 respectively) were offered. Any adult female phytoseiid received the same prey number and proportion for the duration of the experiment. The prey numbers and proportions were 8 : 16, 6 : 12, 4 : 8, and 2 : 4 (phytoseiid larvae : *T. urticae* larvae).

As prey density changes, a change in the prey preference index will indicate prey switching on the part of the predator (Chesson 1983).

Experiment 2: Constant total prey with varying prey species proportions - To evaluate the effect of increasing the proportion of phytoseiid larvae in the available prey population, a series of trials were conducted in which the total number of prey offered was kept constant at 20 individuals but the proportion of phytoseiid larvae to tetranychid larvae was varied. Any adult female phytoseiid received the same prey proportion for the duration of the experiment. The prey proportions were 4 : 16, 8 : 12, 12 : 8, 16 : 4, and 20 : 0 (phytoseiid larvae : *T. urticae* larvae respectively).

Experiment 3: Decreasing total prey varying prey species proportions - To evaluate the effect of both decreased prey population and varying prey species proportion, trials were conducted in which lowering prey numbers and an increasing proportion of phytoseiid larvae were offered. An adult female phytoseiid received the same prey number and proportion of phytoseiid larvae for the duration of the experiment. The prey populations and proportions used were 2 : 16, 4 : 12, 6 : 8, 8 : 4, 10 : 0 (phytoseiid larvae : *T. urticae* larvae respectively).

Results and Discussion

Experiment 1: In this first series of tests, the species of phytoseiid larvae offered as prey had no effect on the cumulative number of phytoseiid larvae eaten by either predator. Both *M. occidentalis* and *T. pyri* consumed as many larvae of their own species as those of the other phytoseiid (Table 2.1). This was in contrast with earlier studies with eggs which showed *T. pyri* has a greater feeding rate and preference for *M. occidentalis* eggs over their own (MacRae and Croft 1993). Overall in this study, however, *T. pyri* showed significantly greater predatory behaviour than did *M. occidentalis* at all but the first level of available prey (10 phytoseiid larvae : 20 *T. urticae* larvae). This was not surprising, because earlier tests evaluating the effect of temperature on interspecific predation and

cannibalism in these two species indicated that *T. pyri* would more readily utilize phytoseiid larvae as prey than would *M. occidentalis* (MacRae and Croft 1993).

Table 3.1: Mean cumulative number of phytoseiid larvae eaten over 5 days by adult female *M. occidentalis* (n=10) and *T. pyri* (n=10) when offered mixed populations of phytoseiid and *T. urticae* larvae. Numbers in brackets are 95% C.I.'s and means in the same row followed by different letters are significantly different at alpha = 0.05.

Experimental Conditions of Density / Proportions	No. of phytoseiid larvae : no. of <i>T. urticae</i> larvae	<i>M. occidentalis</i> females on <i>M. occidentalis</i> larvae	<i>M. occidentalis</i> on <i>T. pyri</i> larvae	<i>T. pyri</i> on <i>M. occidentalis</i> larvae	<i>T. pyri</i> on <i>T. pyri</i> larvae
Decreasing total prey, constant proportions	10 : 20	0.3 (+/-0.48) a	0.4 (+/-0.52) a	1.0 (+/-0.67) a	0.6 (+/-0.70) a
	8 : 16	0.2 (+/-0.18) a	0.3 (+/-0.46) ab	1.4 (+/-0.93) b	1.2 (+/-0.63) b
	6 : 12	0.4 (+/-0.49) a	0.5 (+/-0.28) a	6.7 (+/-0.90) b	7.4 (+/-2.88) b
	4 : 8	2.5 (+/-0.72) a	2.6 (+/-0.71) a	10.7 (+/-3.57) b	11.2 (+/-2.74) b
	2 : 4	6.3 (+/-3.57) a	5.9 (+/-0.77) a	9.6 (+/-0.97) b	9.6 (+/-0.92) b
Constant total prey (=20), changing proportions	4 : 16	1.2 (+/-0.40) a	1.2 (+/-1.14) a	6.0 (+/-2.06) b	4.2 (+/-2.15) b
	8 : 12	3.9 (+/-0.77) a	3.6 (+/-1.35) a	7.9 (+/-2.64) b	14.4 (+/-3.57) c
	12 : 8	5.7 (+/-1.79) a	4.8 (+/-2.35) a	22.6 (+/-7.71) b	24.6 (+/-4.67) b
	16 : 4	15.3 (+/-6.68) a	16.8 (+/-6.06) a	31.2 (+/-6.30) b	32.8 (+/-5.69) b
	20 : 0	18.0 (+/-1.63) a	16.9 (+/-3.43) a	34.3 (+/-3.34) c	27.2 (+/-3.51) b
Decreasing total prey, changing proportions	2 : 16	0.4 (+/-0.39) a	0.4 (+/-0.52) a	2.6 (+/-1.17) b	1.8 (+/-1.03) ab
	4 : 12	1.4 (+/-0.86) a	0.7 (+/-0.68) a	7.9 (+/-2.64) b	7.2 (+/-0.92) b
	6 : 8	2.3 (+/-1.08) a	1.8 (+/-1.40) a	11.3 (+/-3.43) b	13.2 (+/-1.40) b
	8 : 4	5.0 (+/-2.09) a	3.9 (+/-1.79) a	19.9 (+/-2.64) b	19.5 (+/-2.37) b
	10 : 0	18.1 (+/-1.72) a	17.1 (+/-3.68) a	33.5 (+/-3.86) c	26.8 (+/-4.01) b

When Manly's Preference Index was used to compare mean cumulative consumption across the various populations of prey, *T. pyri* began to show a more equal prey preference for phytoseiid and *T. urticae* larvae at higher numbers of available prey than did *M. occidentalis* (compare values at 4 phytoseiid larvae : 8 *T. urticae* larvae versus 2 phytoseiid larvae : 4 *T. urticae* larvae) (Figure 2.1a). The trend indicated by the prey preference indices is that *T. pyri* will accept phytoseiid larvae as prey when preferred prey levels are still relatively high. Even at the highest prey level (8 phytoseiid larvae : 16 *T. urticae* larvae), although the only significant difference is between *T. pyri* feeding on *M.*

occidentalis and *M. occidentalis* cannibalizing larvae, *T. pyri* showed greater preference for phytoseiid larvae than *M. occidentalis*. When only 12 total prey per day were available, *T. pyri* had a preference index of ~ 0.5 , indicating no preference between feeding on phytoseiid larvae or those of *T. urticae*. *M. occidentalis* continued to show a preference for *T. urticae* larvae until the available prey per day fell to 6. The fact that the preference index changed with prey density indicated that both predators were undergoing a switching behaviour and that *T. pyri* did so at higher total prey densities than did *M. occidentalis*.

Cumulative oviposition values were extremely variable both between and within species (Figure 2.2a). There was no significant difference in cumulative oviposition between the two phytoseiids at any prey combination treatment, but there did seem to be a trend for *M. occidentalis* to have consistently greater rates of oviposition except at the lowest level of prey. This corresponded with studies indicating *M. occidentalis* had a higher intrinsic rate of reproduction than does *T. pyri* when their preferred prey (tetranychid mites) were plentiful (Sabelis 1985). Field studies have indicated that *M. occidentalis* oviposits less than *T. pyri* at low prey densities (Croft et al. 1992, Croft and MacRae 1992b). It was apparent that the species of phytoseiid larvae offered as prey did not have a significant effect on the rate of oviposition by either predator. The only significant differences in oviposition within species was between prey populations at the highest and lowest levels. While differences in oviposition at these two extremes are to be expected due simply to the decrease in available prey, wide variance prevented differentiation of oviposition rates at intermediate prey levels. Our interpretation of these results was that while replications were sufficient to provide discrimination for feeding behaviours, oviposition is intrinsically a more variable behaviour at low prey levels than is prey attack.

Figure 3.1: Mean Manly Prey Preference indices for adult female *M. occidentalis* (n=10) and *T. pyri* (n=10) feeding on mixed populations of phytoseiid and *T. urticae* larvae (index for phytoseiid larvae as prey). Experiments are: a - decreasing total prey, constant prey species proportion; b - constant total prey, increasing proportion of phytoseiid larvae; c - decreasing total prey, increasing proportion of phytoseiid larvae. Vertical bars represent 95% CI's and different letters represent significantly different means at alpha = 0.05.

Fig. 3.1a

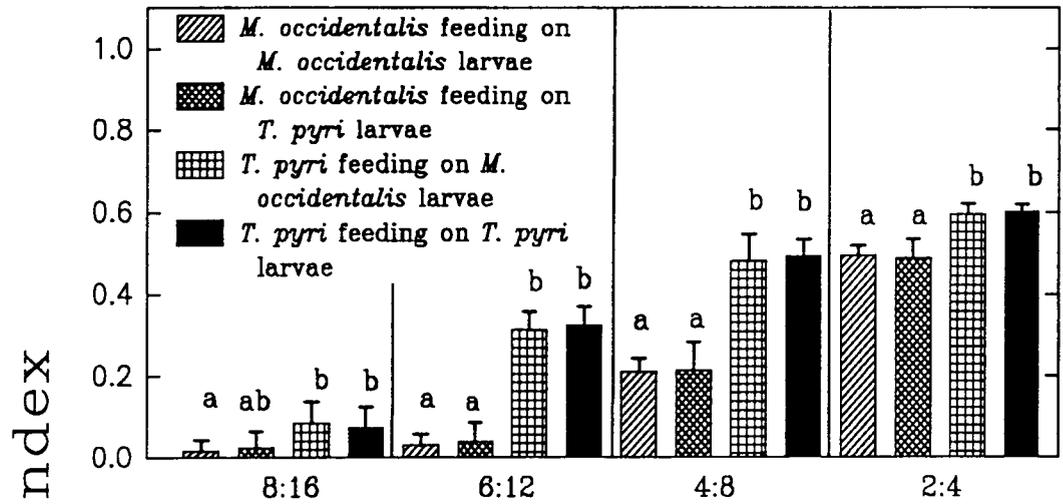
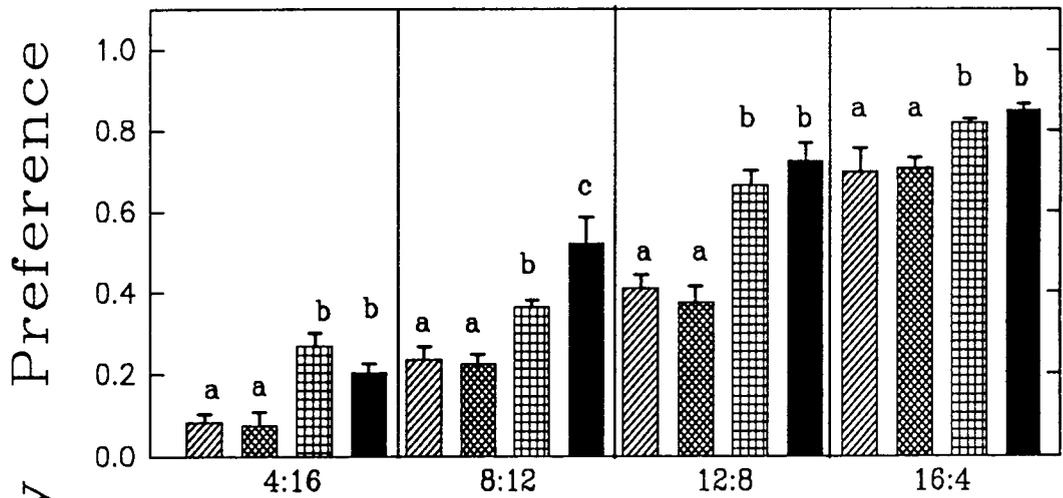
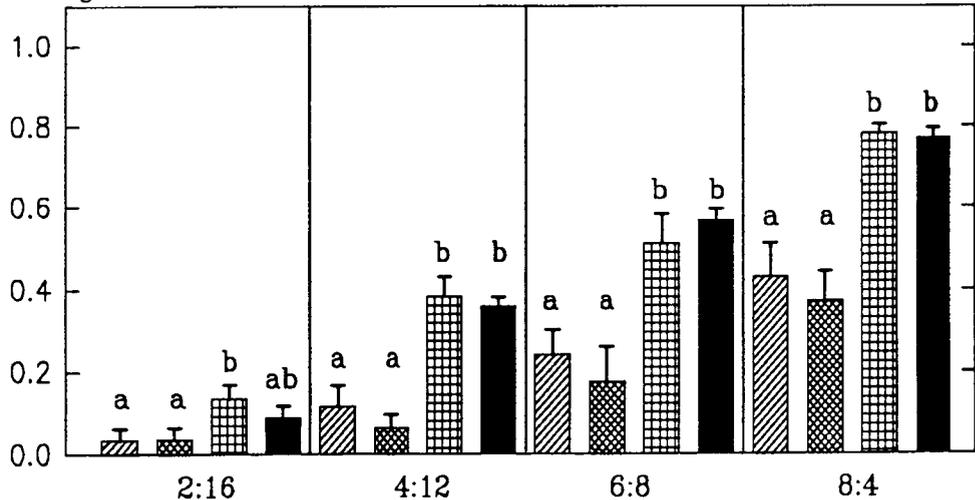


Fig. 3.1b



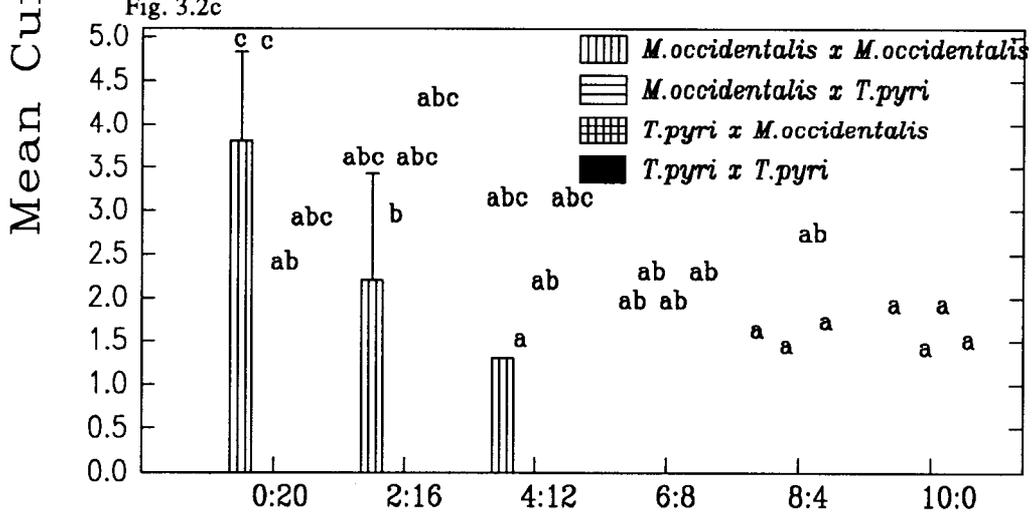
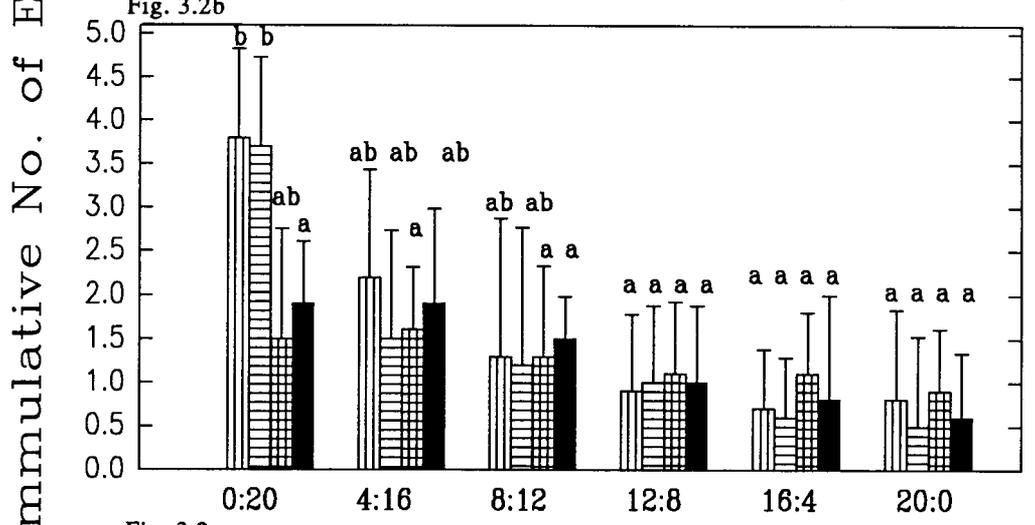
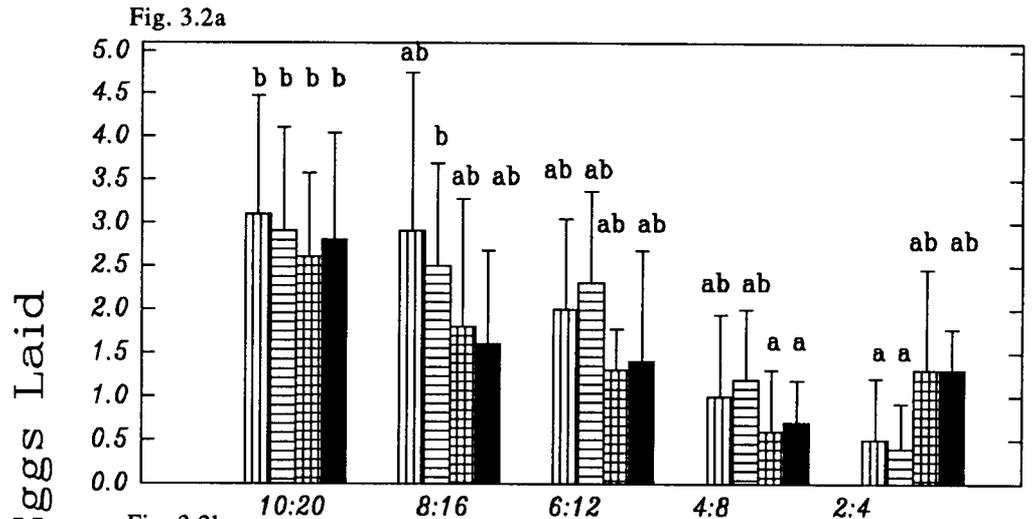
Manly

Fig. 3.1c



No. of Phytoseiid Larvae : *T. urticae* Larvae

Figure 3.2: Mean cumulative oviposition over 5 days of adult female *M. occidentalis* (n=10) and *T. pyri* (n=10) feeding on mixed populations of phytoseiid and *T. urticae* larvae (a - decreasing total prey, constant prey species proportion; b - constant total prey, increasing proportion of phytoseiid larvae; c - decreasing total prey, increasing proportion of phytoseiid larvae). Vertical bars represent 95% CI's and different letters represent significantly different means at $\alpha = 0.05$.



No. of Phytoseiid Larvae : *T. urticae* Larvae

Experiment 2: In this series of trials, the species of phytoseiid larvae offered as prey had an effect on the cumulative number of larvae eaten by a predator in only two of the five prey density / proportions that included phytoseiids. At 8 phytoseiid larvae : 12 *T. urticae* larvae, *T. pyri* consumed more of its own larvae than those of *M. occidentalis*. Also, when all larvae offered as prey were phytoseiids (20 phytoseiid larvae : 0 *T. urticae* larvae), *T. pyri* consumed significantly more *M. occidentalis* larvae (Table 2.1). These two cases seem to be anomalies considering that the species of phytoseiid larvae being offered as prey had no effect on cumulative feeding by the adult predators at any of the other prey density / proportions. However, as a whole, there seemed to be greater variability in *T. pyri*'s feeding patterns on phytoseiid larvae in this experiment than in the other two. *M. occidentalis* did not consume more of one species of phytoseiid larvae than another at any of the prey ratios tested, nor did it show the variability in feeding on the two species of phytoseiid larvae shown by *T. pyri*. At all prey proportions, *T. pyri* consumed significantly greater numbers of phytoseiid larvae than did *M. occidentalis*, following the same pattern seen with decreasing prey and constant prey species proportions (experiment 1). The Manly Prey Preference indices for this experiment again showed *T. pyri* having a significantly greater preference for phytoseiid larvae than did *M. occidentalis* when greater numbers of tetranychid larvae were present (Figure 2.1b).

At the highest density of prey (0 phytoseiid larvae : 20 *T. urticae* larvae), *M. occidentalis* tended to oviposit more than *T. pyri*. The species of phytoseiid larvae offered as prey had no effect on cumulative oviposition in either *T. pyri* or *M. occidentalis* in any of the 5 treatments in which they were included (Figure 2.2b). Cumulative oviposition was again highly variable but there was a significant difference in oviposition rates of *M. occidentalis* at only two of six prey density / proportions: when there were no phytoseiid larvae (0 phytoseiid larvae : 20 *T. urticae* larvae), and when there were no tetranychid larvae (20 phytoseiid larvae : 0 *T. urticae* larvae) (Figure 2.2b). There was also a trend

for a general decrease in the rate of oviposition as phytoseiid larvae made up an increasing proportion of the available prey, although variability in the data precludes differentiation of oviposition rates at intermediate proportions of phytoseiid to tetranychid larvae. This apparent trend, reinforced by the significant difference seen in oviposition by *M. occidentalis* at the highest and lowest proportions of tetranychid larvae, indicates that, unlike tetranychid larvae, phytoseiid larvae are not sufficient prey to allow oviposition. This observation supported previous findings (MacRae and Croft 1993).

Experiment 3: In this series of experiments, the species of phytoseiid larvae offered as prey had an effect on the cumulative number of larvae eaten by a predator in only one of five prey population / proportions that included phytoseiids. When there were no tetranychid larvae present (10 phytoseiid larvae : 0 *T. urticae* larvae), *T. pyri* consumed significantly more *M. occidentalis* larvae than those of *T. pyri* species (Table 2.1). The species of phytoseiid present in the prey population had no effect on the number of phytoseiid larvae consumed by *M. occidentalis*. Again, *T. pyri* consumed significantly more phytoseiid larvae at all prey populations and proportions than did *M. occidentalis*. The prey preference indices reflected the pattern seen in the previous two experiments, i.e. *T. pyri*'s preference for phytoseiid larvae was greater than that of *M. occidentalis* at all prey populations and proportions with the exception of the first density / proportion (2 phytoseiid larvae : 16 *T. urticae* larvae) (Figure 2.1c). Here, *T. pyri*'s preference index for cannibalism was not significantly greater than the preference indices of *M. occidentalis* for phytoseiid larvae of either species. At lower levels of prey, the difference in preference indices between the two predators was much more noticeable. While *M. occidentalis*'s preference indices for phytoseiid larvae were equal to approximately 0.4 at the lowest prey population level (8 phytoseiid larvae : 4 *T. urticae* larvae), *T. pyri* showed virtually no preference for either phytoseiid or tetranychid larvae when there were 6 phytoseiid larvae :

8 *T. urticae* larvae. *T. pyri* will obviously make the switch to feeding on phytoseiid larvae at much higher densities of spider mites than will *M. occidentalis*.

The species of phytoseiid present in the prey population had no effect on the mean cumulative oviposition of either phytoseiid at all six prey density / proportions (Figure 2.2c). For both phytoseiids, there was an observable trend of decreasing oviposition with decreasing prey availability.

Conclusion

Although neither predator appeared to be much affected by the species of phytoseiid larvae present in the prey population, *T. pyri* exploited phytoseiid larvae as prey at much higher population and proportion levels of *T. urticae* and than did *M. occidentalis*. The ability to readily accept phytoseiid larvae as prey is consistent with *T. pyri*'s ability to utilize a much wider variety of food sources than does *M. occidentalis* (Croft and MacRae 1992), and is consistent with earlier research investigating the effect of temperature on interspecific predation and cannibalism in these two phytoseiids (MacRae and Croft 1993).

The ability of a generalist predator to more readily switch prey types and rely on conspecifics or closely related species may help stabilize its population when more preferred prey is unavailable. *T. pyri* is a more generalist feeder than is *M. occidentalis* and has demonstrated a greater ability to switch prey types to phytoseiid larvae when tetranychid larvae become less numerous. This behaviour may contribute to *T. pyri*'s observed greater stability and persistence in long-term apple plots where these two predators are being experimentally evaluated as biological control agents of the spider mites *P. ulmi*, *T. urticae*, and the eriophyid, *A. schlechtendali* (Croft and MacRae 1992b, 1993, Croft et al. 1992).

CHAPTER 4 - Differential Impact of *Zetzellia mali* on *Metaseiulus occidentalis* and *Typhlodromus pyri**

Introduction

Interspecific competition has its greatest influence in structuring communities during what Weins (1977) called resource "crunch" years. Although the goal of biological control programs is a continuous period of lowered prey availability, there may be a crash of the pest population due to unusually high impact of other mortality factors (e.g. environmental conditions). Such a decrease in available food resources will seem like a "crunch" year to the introduced biological control agents. If multiple species are introduced in a guild of biological control agents, interspecific competition between them at this time may weaken the overall control effect and have a negative effect on the local persistence of certain guild members.

Direct competition in the form of mutual predation has been suspected as an important mechanism structuring predatory mite communities, particularly among the Phytoseiidae. Chant (1959) suggested that predation on eggs and larvae of other phytoseiid species by *Euseius finlandicus* Oudemans was responsible for its dominance in unsprayed apple orchards in England. In a study evaluating the effects of predatory mite releases in avocado, McMurtry et al. (1984) speculated that mutual predation was responsible for reduced populations of native phytoseiids after the introduction of exotic predatory mites while tetranychid mite populations were unaffected. Interspecific predation on immatures by adult female *Amblyseius* (*Neoseiulus*) *degenerans* has been shown experimentally to be responsible for decreased populations of *Phytoseiulus persimilis* Athias-Henriot in a mixed acarine system (Yao and Chant 1989). In field

* Submitted as: MacRae, I.V. and B.A. Croft. Differential impact of *Zetzellia mali* (Acari: Stigmaeidae) on *Metaseiulus occidentalis* and *Typhlodromus pyri* (Acari: Phytoseiidae). J. Appl. Ecol.

experiments, Croft and MacRae (1992) found that when prey populations declined to very low levels, competition between predatory mites influenced the species composition of the predatory mite guild. If an introduced guild of biological control agents is to become established, the species being introduced must somehow partition common resources during times of scarcity.

Zetzellia mali (Ewing) is an important predator of tetranychid mites on apple where it feeds principally on the eggs of *Panonychus ulmi* Koch (Santos 1976), and *Tetranychus urticae* Koch (Santos 1976) and on eggs of several predaceous phytoseiid mites, the latter of which are similar in morphology and size (Santos 1982, Clements and Harmsen 1990, 1993). Santos (1991) reported that *Z. mali* does not preferentially forage or use kairomones, but, rather, locates its prey through random encounter. At low spider mite densities, phytoseiid eggs may represent an alternate food source. While phytoseiids may cause some reciprocal mortality of stigmatids, it has been suggested that feeding by *Z. mali* on phytoseiid eggs at low tetranychid densities may impair the ability of phytoseiids to further control spider mites (Johnson and Croft 1981, Croft and McGroarty 1977, Clements and Harmsen 1990). Alternatively, predation by *Z. mali* on phytoseiids may improve biological control by reducing over-exploitation of pest mites by phytoseiids (Croft and MacRae, 1992). The ability of *Z. mali* to persist at low prey densities on a wide variety of alternate food sources (White and Laing 1977) and its superior competitive abilities in comparison to phytoseiids at low prey densities (Clements and Harmsen 1992, Clements et al. 1991) may enable it to significantly contribute to biological control for tetranychid mites (Croft and MacRae, 1993).

In field trials designed to evaluate the efficacy of single and mixed populations of the phytoseiids *Metaseiulus occidentalis* Nesbitt and *Typhlodromus pyri* (Schueten) to control spider mites on apple, it was found that lower levels of either phytoseiid mite were associated with high population densities of *Z. mali* (Croft and MacRae 1992, 1993).

Field trials were conducted in an experimental apple orchard which contained plots of different phytophagous mite species. Pest mites were exposed to predation by *M. occidentalis* or *T. pyri* (see Croft and MacRae 1992 for details of the experimental design). In plots with low tetranychid populations, *Z. mali* had a greater impact on *M. occidentalis* than on *T. pyri* populations in those plots with only one species of phytoseiid present. Population data from the field indicated the impact was mostly on *M. occidentalis* immatures (Croft and MacRae 1993). Eventually, *M. occidentalis* disappeared from plots with high *Z. mali* populations while *T. pyri* persisted until the end of the season, although *Z. mali* populations were similar in number in both plots. *M. occidentalis* persisted until the end of the season only in plots with low *Z. mali* populations. In another test, similar numbers of *M. occidentalis* were introduced into apple trees with different levels of *Z. mali* and low levels of spider mites. Establishment of *M. occidentalis* was excellent in trees with low *Z. mali* populations but poor where stigmaeid numbers were high (Croft and MacRae 1993).

As the effect of the presence of *Z. mali* was greater on *M. occidentalis* than on *T. pyri*, a combination of laboratory and field trials was conducted to better understand the relationships between these three species.

Methods and Materials

Based on the field observations that the impact appeared to be concentrated on immature populations, several hypotheses were evaluated to explain the differential impact of *Z. mali* on *M. occidentalis* and *T. pyri*: 1) *Z. mali* consumes more *M. occidentalis* eggs than *T. pyri* eggs, 2) *T. pyri* imposes greater mortality on *Z. mali* than does *M. occidentalis*, 3) there were more phytophagous mites available in field plots with *T. pyri* than in plots with *M. occidentalis*, leading to larger populations of *T. pyri* and to less feeding on *T. pyri* eggs by *Z. mali* than on *M. occidentalis* eggs, 4 a) *M. occidentalis* eggs

were more closely spatially associated with adult *Z. mali* within apple trees than were *T. pyri* eggs or, b) the within tree spatial association of the older stages of *T. pyri* and of adult *Z. mali* with phytophagous prey mites permitted greater partitioning of the existing resources than did that of the older stages of *M. occidentalis* and of adult *Z. mali* with phytophagous prey mites, and 5) the oviposition locations of *M. occidentalis* on individual apple leaves were more closely associated with the main foraging area of *Z. mali* than were the oviposition locations of *T. pyri*.

***Z. mali* predation on phytoseiid eggs:** To assess the suitability of phytoseiid eggs as prey, adult female *Z. mali* were placed on 18 cm diameter leaf disks. Female *Z. mali* were collected from trees in the experimental orchard that had high prey populations (in this case, *A. schlechtendali*). Although the prey populations were abundant, they were obviously not uniform and so the *Z. mali* females were starved for 12 hr to standardize hunger levels. They were then offered 10 eggs per day of either the spider mite, *P. ulmi*, or of the phytoseiids, *M. occidentalis* or *T. pyri*, replaced daily for 7 days. Because *Z. mali* does not appear to show prey preference (Santos 1991), an adult female stigmatid was offered the same species and age class of eggs throughout the experiment to simplify the experimental manipulation. *P. ulmi* eggs were collected from the field during June while phytoseiid eggs were randomly selected from laboratory reared colonies and assumed to be representative of all age classes of eggs. These tests were replicated 10 times each and mean daily consumption and mean daily oviposition were compared for each species of prey with a 1-way Analysis of Variance (Steele and Torrie 1980).

Because *Z. mali* seemed to prefer feeding on younger rather than older phytoseiid eggs (or may be more successful on younger eggs), a second experiment was conducted to assess the impact of egg age on consumption by *Z. mali*. Adult female *Z. mali* were placed on 18 cm leaf disks, starved for 12 hours to standardize hunger levels and then fed 10 eggs per day of either *M. occidentalis* or *T. pyri*, replaced daily for 7 days. Two age

classes of phytoseiid eggs were offered, 0-24 hr old and 24-48 hr old. Daily feeding and oviposition by *Z. mali* were recorded. Trials of predation on each species and age class of phytoseiid egg were replicated 16 times. Effects of age and species on the mean daily feeding rate of *Z. mali* on phytoseiid eggs were analyzed using a 2-way ANOVA, and significantly different feeding rates were separated by Least Significant Difference (LSD) (Steele and Torrie 1980). Mean daily oviposition was analysed in the same way.

Phytoseiid predation on *Z. mali* immatures: Adult female *M. occidentalis* and *T. pyri* were placed on 1 cm² arenas constructed on plastic tiles and bounded with Tanglefoot adhesive. Adult female phytoseiids were taken from colonies and were well-fed. They were, therefore, starved for 24 hr to standardize hunger levels and then fed 20 *Z. mali* eggs per day, replaced daily, for 6 days. *Z. mali* eggs were randomly selected from field samples and transferred to arenas using a fine camel-hair brush. Daily feeding and oviposition were recorded. Trials were replicated 16 times for each species of adult female phytoseiid. These experiments were also repeated using *Z. mali* larvae as prey. Completely consumed prey were characterized by a shriveled appearance while individuals killed by phytoseiid attack but not eaten appeared as partially consumed, desiccated eggs and physically damaged, unmoving larvae. These partially consumed individuals were included in mortality counts due to the low likelihood of their survival. Mean feeding rates of *M. occidentalis* and *T. pyri* females on *Z. mali* eggs were compared with a 1-way ANOVA, as were the accompanying mean daily oviposition rates and the mean rates of mortality to *Z. mali* caused by both phytoseiid species. Results of trials using *Z. mali* larvae as food for *M. occidentalis* and *T. pyri* adult females were analysed in the same way.

Comparison of prey population levels in phytoseiid plots: Initial observations of the differential impact of *Z. mali* on *M. occidentalis* and *T. pyri* were made in field studies (Croft and MacRae, 1992). From these studies detailed population and distribution data

were available for individual life stages of all species present. Plots in the experimental orchard were composed of 5 replicate trees sampled bi-weekly to monitor mite populations and monthly for statistical analysis. To monitor mite populations, bi-weekly samples of 10 leaves were taken, picked bottom to top, from each of the five trees in each plot. Every 4 weeks, 40 leaves, sampled in the same way, were taken from all 5 trees in each plot. Leaves were stored and examined under a dissecting microscope at 30X in the same order as they were sampled. The species, life stage group, and density of all mites present were recorded. Populations of the eriophyid *Aculus schlechtendali* Nalepa, consisting of all active life stages, were estimated as 8 density categories: 0/leaf, 0-10/leaf, 10-100/leaf, 100-200/leaf, 200-300/leaf, 300-400/leaf, 400-500/leaf, and >500/leaf.

Cumulative mite days for 1991 were calculated for the three prey mite species present (*P. ulmi*, *T. urticae*, and *A. schlechtendali*) in plots that held either *M. occidentalis* or *T. pyri* as the only species of phytoseiid present, and that also had high *Z. mali* populations. Mean cumulative mite days were calculated for species of prey mites in plots with *M. occidentalis* plus *Z. mali* and plots with *T. pyri* plus *Z. mali*. The mean cumulative mite days of each prey species in the *M. occidentalis* plots were then compared to those in the *T. pyri* plots with two-sample t-tests.

Within-tree spatial associations of *M. occidentalis* with *Z. mali* vs. *T. pyri* with *Z. mali*: Field population data also were used to calculate the correlation of the presence of *M. occidentalis* eggs with the presence of adult female *Z. mali*, and the presence of *T. pyri* eggs with the presence of adult female *Z. mali* within trees in plots that held only single species populations of phytoseiids and high populations of *Z. mali*. Also, to ascertain if there was some difference in the manner in which the resource of prey mites was partitioned between *Z. mali* and the two phytoseiids, correlation coefficients were calculated for adult *Z. mali* and total prey; combined adults and deutonymphs of *M. occidentalis* and total prey; and combined adults and deutonymphs of *T. pyri* and total

prey (combined adults and deutonymphs were used as they account for the greatest amount of predation by phytoseiids). Correlation coefficients were compared and significantly different coefficients separated according to Zar (1984).

Within-leaf spatial associations of phytoseiid egg distribution with *Z. mali* a)

Adult *Z. mali* foraging: Leaves were examined in the field through June and July with a 16X hand lens at different times throughout the day, at different times over several days during both light and dark periods. The presence and estimated positions on the leaf of adult female *Z. mali* were recorded at the time of observation onto a generalized leaf pattern. The generalized leaf pattern and observed locations of the adult female *Z. mali* (N=480 individuals) were digitized using the Geographical Information System (GIS) software GRASS (US Army CERL 1991). This computer software was used to calculate and indicate on the generalized leaf outline the area of the 76th percentile densest occurrence of female *Z. mali*.

Leaves with *Z. mali* were also brought into the laboratory through the same period and examined under a dissecting microscope. Individual adult females searching for prey were observed for 15 minutes and their location and movement noted. Locations of *Z. mali* on the leaf were divided into the central 1/3 of the leaf, including the mid-rib, the adjacent 1/3 of the leaf, incorporating the middle of the area between the mid-rib and leaf edge, and the outer 1/3 of the leaf and the time spent in each area rounded to the nearest minute. A total of 112 individuals were observed for 1680 minutes (28 hr) of foraging time. The mean amount of time spent by *Z. mali* females in each of the three areas was calculated as the proportion of overall observation time.

b) Phytoseiid oviposition location on individual leaves: The within-leaf distribution of 550 eggs of both *M. occidentalis* and *T. pyri* were recorded throughout the growing season by noting their location on leaves taken during regular sampling of single

predator release plots. Using GRASS, locations were digitized onto the same generalized leaf pattern as were the locations of searching adult female *Z. mali* observed in the field. The generalized leaf pattern was divided into 18,000 grid cells, each roughly the size of a single phytoseiid egg (the eggs of *T. pyri* and *M. occidentalis* are approximately the same size). By treating each grid cell as a quadrat of a mapped area (the generalized leaf pattern), the total number of eggs per quadrat could be counted and the variance to mean ratio of egg occurrence could be calculated over that mapped area. Variance to mean ratio values of distributions greater than one suggest clustered patterns of objects, and thus a *t*-statistic and significance level can be calculated comparing the ratio value to 1.00. The variance to mean ratios of the distribution of *M. occidentalis* eggs and those of *T. pyri* were compared to each other. GRASS was also used to calculate the number of eggs of both phytoseiid species outside the area of the 76th percentile densest occurrence of female *Z. mali* in the field observations (laboratory observations indicated that *Z. mali* females spent approximately 76% of their foraging time on or around the mid-rib). The number of phytoseiid eggs outside this area were compared by species with a chi-square analysis.

Results and Discussion

Although *Z. mali* fed on slightly more *P. ulmi* eggs than on phytoseiid eggs, the difference was not significant (Table 3.1). In addition, there was no significant difference in the mean daily oviposition by *Z. mali* females feeding on eggs of the three different mite species (Table 3.1). This does not agree with Clements and Harmsen's (1990) findings wherein *Z. mali* took significantly fewer phytoseiid eggs than those of *P. ulmi* or their recent study (1993) in which *Z. mali* showed a significant preference for *P. ulmi* eggs over those of *T. caudiglans*. Sample sizes of *P. ulmi* eggs were lower in the present study than in that of Clements and Harmsen's (1990) and this may have contributed to the difference

in results. The lack of any difference in feeding and oviposition indicates that phytoseiid eggs are as suitable as food items as are *P. ulmi* eggs.

The species of phytoseiid egg being consumed had no effect on the mean feeding rate of *Z. mali* females (Table 3.2). However, phytoseiid egg age did affect the feeding rate of *Z. mali*, with significantly greater numbers of 0-24 hr old eggs being eaten per day than 24-48 hr old eggs (Table 3.2). It may be that the chelicerae of *Z. mali* cannot effectively penetrate the additional cuticle of the larvae developing inside older phytoseiid eggs.

Table 4.1: Mean number of eggs eaten per day per female *Zetzellia mali* (n=10), over 7 days, and the mean oviposition per day associated with each species of prey.

Species of egg eaten	Mean no. eggs eaten per day per female (+/- 2S.D.)	Mean oviposition per day per female (+/- 2S.D.)
<i>Panonychus ulmi</i>	1.7 +/- 1.2 a	1.2 +/- 0.8 a
<i>Metaseiulus occidentalis</i>	1.2 +/- 1.1 a	1.5 +/- 1.0 a
<i>Typhlodromus pyri</i>	1.2 +/- 1.5 a	1.2 +/- 0.9 a

Means within the same column followed by the same letter are not significantly different at $\alpha = 0.05$.

Table 4.2. Mean daily number of *M. occidentalis* and *T. pyri* eggs eaten and corresponding oviposition (+/- 2 S.D.'s) by adult female *Z. mali* (n = 16) over 7 days. Phytoseiid eggs are separated into two age classes; 0-24 hours old and 24-48 hours old.

	<i>M. occidentalis</i>		<i>T. pyri</i>	
	0 -24 h old eggs	24-48 h old eggs	0 -24 h old eggs	24-48 h old eggs
Mean no. of eggs eaten per day per female <i>Z. mali</i>	1.80 +/- 0.28 b	0.75 +/- 0.31 a	1.73 +/- 0.31 b	0.82 +/- 0.29 a
Mean daily oviposition per female <i>Z. mali</i>	1.20 +/- 0.29 b	0.31 +/- 0.33 a	2.00 +/- 0.46 b	0.64 +/- 0.51 a

Means within rows followed by the same letter are not significantly different at $\alpha = 0.05$.

Z. mali eggs and larvae were not very suitable prey for either *M. occidentalis* or *T. pyri* (Table 3.3). This agrees with observations by Clements and Harmsen (1990, 1993). Both species of phytoseiid attacked *Z. mali* immatures but generally did not fully consume them. Attack by either phytoseiid, however, resulted in mortality to the stigmaeid in all observed cases. After 6 days, the cumulative mean number of *Z. mali* eggs or larvae eaten was less than 1 for either phytoseiid species. Indeed, trials could only be run for 6 days. After this time, phytoseiid females began to die from either being caught in the arena's tanglefoot barrier as they attempted to emigrate or from starvation. There was no oviposition by phytoseiids feeding on either stigmaeid eggs or larvae after the 24 hr starvation period. There was no significant difference in the levels of mortality to *Z. mali* eggs and larvae caused by either phytoseiid (Table 3.3).

A two-sample t-test indicated that there were significantly more cumulative mite days of *P. ulmi* in *M. occidentalis* plots with high *Z. mali* populations (4924.0) than in similar *T. pyri* plots (2972.7) ($P = 0.000$). The same was true for cumulative mite days for *A. schlehtendali* (1196.933 in *M. occidentalis* plots and 729.1 in *T. pyri* plots; $P = 0.000$; numbers of apple rust mites represent cumulative population categories, not raw numbers). There was no significant difference in the number of *T. urticae* in either of the phytoseiid plots (16.6 in *M. occidentalis* plots and 8.8 in *T. pyri* plots; $P = 0.1396$). These results run counter to the proposed hypothesis of greater prey mite numbers in *T. pyri* plots. *T. pyri* in plots with high *Z. mali* populations had less available prey overall than did *M. occidentalis* in similar plots. The lessened impact of *Z. mali* on *T. pyri*, therefore, is not likely due to more prey being available.

The eggs of both phytoseiid species were equally associated spatially with adult *Z. mali* within trees (Table 3.4). With the exception of the first sample date (April 27) and the last two (August 22 and September 09) there was no difference at any of the sample dates in the correlation coefficients of *M. occidentalis* or *T. pyri* eggs with *Z. mali* in their

respective single species phytoseiid plots that had high *Z. mali* populations (Table 3.4). The eggs of both phytoseiids appeared to be less positively associated with *Z. mali* as the growing season progressed. The difference in the correlation coefficients in the early and late season was not unexpected. April 27 was too early for *M. occidentalis* to be ovipositing actively and its eggs were recovered rarely, if at all, even from the plots that held low populations of *Z. mali* (Croft and MacRae 1993). Similarly, by the last two sample dates, any remaining *M. occidentalis* had dispersed due to low prey numbers.

Table 4.3: Mean number of *Zetzellia mali* eggs (+/- 2 S.D.'s) eaten and mean number of eggs laid by female *Metaseiulus occidentalis* and *Typhlodromus pyri* per female per day, over 6 days.

Species of predator	Mean number of <i>Z. mali</i> eggs eaten /female /day	Mean number of <i>Z. mali</i> eggs attacked /female /day	Mean number of eggs laid /female /day
<i>Metaseiulus occidentalis</i>	0.155 +/- 0.091 a	8.94 +/- 2.24 a	0 a
<i>Typhlodromus pyri</i>	0.133 +/- 0.092 a	9.78 +/- 3.45 a	0 a

Means in the same column followed by the same letter are not significantly different at $\alpha = 0.05$.

Table 4.4: Comparison of correlation coefficients of *Metaseiulus occidentalis* eggs with adult female *Zetzellia mali* and *Typhlodromus pyri* eggs with adult female *Z. mali*, in high *Z. mali* population plots throughout the growing season, 1991.

DATE	<i>Typhlodromus pyri</i> r	<i>Metaseiulus occidentalis</i> r	Z - Value	P - Value
04 / 27	0.138	N / A	N / A	N / A
05 / 09	0.105	N / A	N / A	N / A
05 / 23	0.164	0.035	0.9955	P > 0.50
06 / 06	0.194	0.139	0.4303	P > 0.50
06 / 27	0.213	0.289	0.8591	0.20 < P < 0.50
07 / 18	0.245	0.185	0.7299	0.20 < P < 0.50
08 / 01	0.229	0.153	1.1284	0.10 < P < 0.20
08 / 22	0.070	N / A	N / A	N / A
09 / 09	0.052	N / A	N / A	N / A

n=100 leaves for *T. pyri*, n=150 leaves for *M. occidentalis*.

N/A indicates periods when *M. occidentalis* eggs were not recovered in the samples.

There was no significant difference in the spatial correlation of combined adults and deutonymphs of either the two phytoseiids with total prey mites and the correlation of adult *Z. mali* with total prey mites, except for the last two sample dates (Table 3.5). Consequently, it may be assumed that, with the exception of the last two dates, there was no difference in the spatial partitioning of the prey mite resource between the feeding stages of *Z. mali* and *M. occidentalis* or between those of *Z. mali* and *T. pyri*. Also, a Tukey-type multiple comparison of the correlation coefficients for the last two sample dates showed that, while there was no significant difference between the correlation coefficients of the older stages of *M. occidentalis* and the total prey mites and the correlation coefficient of the older stages of *T. pyri* and the total prey mites, adult *Z. mali* were significantly more closely associated with prey mites than were either phytoseiid species (Table 3.5). The lowered availability of prey at this time (see Croft and MacRae 1993 for details) may have caused the phytoseiids to forage more widely between leaves in search of a much reduced prey supply. *Z. mali* can survive on much lower levels of prey than can either phytoseiid, is much less active, and travels less often from leaf to leaf (Santos 1982). Thus, localized populations of *Z. mali* may be clustered around the few remaining prey at this time.

The foraging area of *Z. mali* appears to be localized around the mid-rib, corroborating the observations of Santos (1976). Of 480 adult female *Z. mali* observed on leaves in the orchard, 398 (82.9%) were found on or around the mid-rib of the leaf (Fig. 3.1a). Of the 1680 m of laboratory observations, 1276 m (76.0% of the total observation time) were spent on or around the mid-rib. As *Z. mali* moves relatively slowly, individuals spent most of the observation periods in the leaf area in which they were first observed. Of the remaining 404 m of laboratory observations, 252 m (15% of the observation time) was spent on the middle 1/3 of the leaf and the remaining 151 m (9% of the observation time) was spent at the leaf's edge.

Table 4.5: Comparison of correlation coefficients of adult and deutonymph *Typhlodromus pyri* with total prey mites, adult and deutonymph *Metaseiulus occidentalis* with total prey mites, and adult and deutonymph *Zetzellia mali* with total prey mites, in high *Z. mali* population plots throughout the growing season, 1991.

DATE	<i>Typhlodromus pyri</i> r	<i>Metaseiulus occidentalis</i> r	<i>Zetzellia mali</i> r	Chi Square	P - Value
04 / 27	.0681 a	.0285 a	.0594 a	0.1135	0.50 < P < 0.75
05 / 09	.0742 a	.0264 a	.2292 a	3.3746	0.05 < P < 0.10
05 / 23	.1204 a	.0525 a	.2614 a	3.5114	0.05 < P < 0.10
06 / 06	.1631 a	.0776 a	.2866 a	3.5019	0.05 < P < 0.10
06 / 27	.1027 a	.1117 a	.2575 a	2.2064	0.10 < P < 0.25
07 / 18	.0298 a	.0467 a	.1552 a	1.2611	0.50 < P < 0.75
08 / 01	.1113 a	.0637 a	.1634 a	0.7515	0.50 < P < 0.75
08 / 22	.1068 a	.0011 a	.3582 b	16.702	P < 0.001
09 / 09	.0725 a	.0183 a	.6823 b	70.1325	P < 0.001

n = 100 for *T. pyri*, n = 150 for *M. occidentalis*, n = 250 for *Z. mali*.

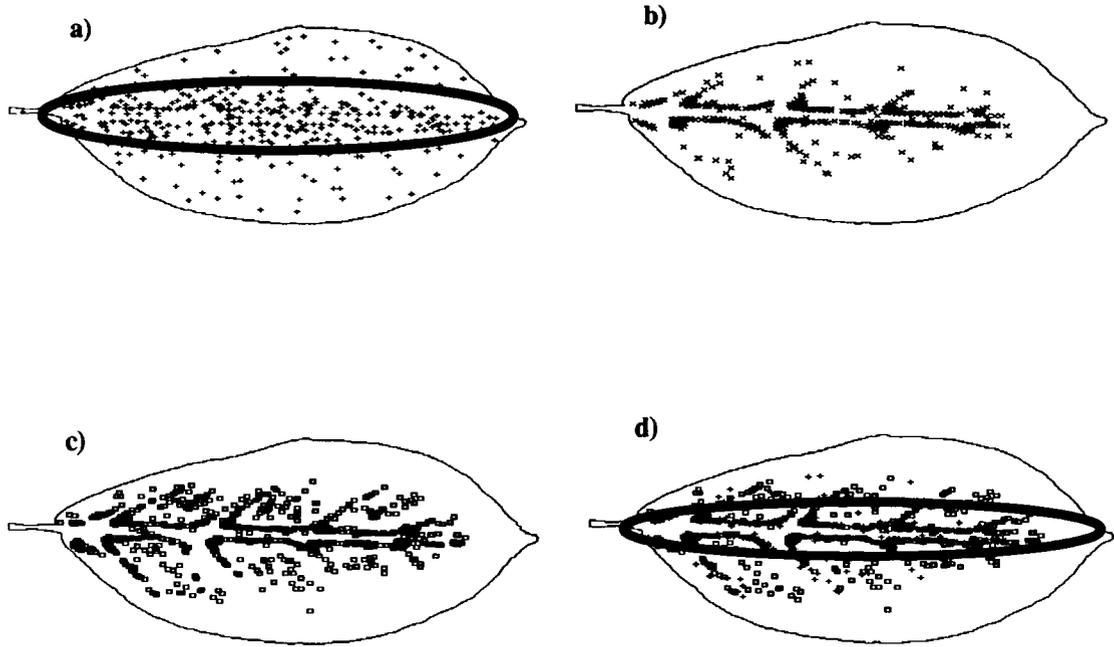
Coefficients within a row followed by the same letter are not significantly different, at $\alpha = 0.05$, according to a Tukey-type multiple comparison.

Eggs of both *M. occidentalis* and *T. pyri* were aggregated, although *M. occidentalis* eggs were more clumped. This pattern was visible when egg distributions for the entire season were examined (Fig 3.1b and 3.1c). The variance to mean ratio of *M. occidentalis* eggs was 2.940 and that of *T. pyri* was 1.935 ($P < 0.001$ for either of these values being equal to 1.00). In addition, significantly more *T. pyri* eggs (196 of 550) were found outside the primary *Z. mali* foraging area (the area of the 76th percentile densest occurrence of female *Z. mali*) than those of *M. occidentalis* (91 of 550) (Fig 3.1b,c,d). A chi-square analysis indicated this difference to be significant ($P < 0.001$).

These data indicate that *M. occidentalis* prefers to oviposit closer to the mid-rib than does *T. pyri*. This difference in distribution places more *M. occidentalis* eggs within the primary foraging area of *Z. mali*. The region outside this foraging area constitutes a refugium where eggs may be less available to predation by *Z. mali*. With significantly more of its eggs in this refugium, *T. pyri* would be less affected by *Z. mali* predation than would *M. occidentalis*. All other life stages of these two predators would be much more active in moving from leaf to leaf and also are much less likely to be attacked by *Z. mali*.

Figure 4.1. Spatial location of mites in the field digitized on a generalized apple leaf using GIS software (Grass 4.0): a) Adult female *Z. mali* (n=480), b) eggs of *T. pyri* (n=550), c) eggs of *M. occidentalis* (n=550), and d) eggs of *T. pyri* and *M. occidentalis*. (Oval represents area of the 76th percentile densest distribution of individuals, some points represent more than one individual).

Fig. 4.1



Conclusions

In these tests, we have shown that when *Z. mali* is given equal access to both *M. occidentalis* and *T. pyri* eggs, it neither consumes more eggs of either phytoseiid, nor does either phytoseiid inflict greater mortality on *Z. mali*. In addition, there does not appear to be a difference in the within-tree associations of the eggs of either phytoseiid and the stigmaeid, neither is there a greater partitioning of available food resources by *Z. mali* with *T. pyri* than with *M. occidentalis*. The only difference we could measure which may explain the differential impact of *Z. mali* on the two phytoseiid species is that of their respective egg distributions. It would appear that when phytophagous mites are rare, *T. pyri* is better able to avoid interactions with *Z. mali* that lead to direct competition (i.e. contact of *Z. mali* with phytoseiid eggs) than is *M. occidentalis*, by ovipositing its eggs in a more dispersed way on individual leaves. The existence of an actual refugium depends on equal rates of encounter by predators on prey (Jeffries and Lawton 1984). For the concept of a refugia to be valid here, there must be an assumption that *Z. mali*'s rate of walking does not change when it ventures away from the mid-rib. While the stigmaeid's walking rate was not specifically measured, there did not appear to be a noticeable difference between its speed during the 404 minutes of observation time when the stigmaeid was away from the mid-rib and the 1276 minutes of observation time when it was foraging in the middle area of the leaf.

It has been reported that within-tree and within-orchard distributions of phytoseiids and their population dynamics in relation to their prey are very important in the persistence of local populations over time (Janssen and Sabelis 1992, Nyrop 1988, Walde et al. 1992). Certainly these relationships are far more important than within-leaf distributions when considering the persistence of species in phytoseiid / tetranychid communities. The importance of within-leaf egg distributions in phytoseiid / stigmaeid systems, as was

demonstrated in this study, is probably important only because *Z. mali* is so much less mobile than are phytoseiids.

In a series of studies (Croft and MacRae, 1992, 1993) we have examined the interactions of plant-feeding mites with the three predatory mites, *Metaseiulus occidentalis*, *Typhlodromus pyri*, and *Zetzellia mali*. *Z. mali* has shown a consistent pattern of influence over both pest mites and phytoseiids. It has a greater ability to regulate pest mite populations than was expected (Croft and MacRae 1993) providing that high densities of this predator are present early in the season and pest mite populations are not excessively high. Consequently, the inclusion of *Z. mali* in an introduced guild of predators for control of pest mites is desirable, but this species may need to be managed if the long-term persistence of the complete guild of phytoseiids is to be maintained (Croft and MacRae 1993). There are several chemical pesticides that may be used selectively to reduce populations of *Z. mali* but which do not appreciably affect either phytoseiid or phytophagous mites, e.g. endosulfan (Croft and MacRae 1992, 1993, Croft 1994).

SUMMARY

This study was initially proposed as a complement to an extensive field study of the factors that affect biological control of phytophagous mites by *M. occidentalis* and *T. pyri* (Croft et al. 1992, Croft and MacRae 1992a, 1992b, 1993). My focus was to be the specific mechanisms involved in the interspecific competition between the phytoseiids. Later, after field studies were underway, it became apparent that direct competition was probably of greatest importance and it was decided to concentrate research efforts in that direction. It was also decided that study of *Z. mali* must be included to understand the interactions between the two phytoseiids (Croft and MacRae 1993). In making conclusions about biological control success and competition by these mites, I have tried to relate the results from this study with those arising out of the field studies (Croft et al., Croft and MacRae 1992a, 1992b, 1993, Croft 1994).

When both phytoseiids were fed phytoseiid immatures and *T. urticae* larvae at a series of decreasing temperatures, *Typhlodromus pyri* demonstrated it was a more active predator at low temperatures than was *M. occidentalis*. It accepted phytoseiid immatures as prey at temperatures low enough to stop predation by *M. occidentalis*. This might be expected because of the prevalence of *T. pyri* in cold, wet habitats in Oregon (Croft et al. 1990).

It was hypothesized that *T. pyri* would have higher rates of predation on phytoseiid immatures because of its wider acceptance of alternate prey than *M. occidentalis* (Helle and Sabelis 1985, Dicke et al. 1988). This was the case in this study (chapter 1). However, even this greater predation of phytoseiid immatures by *T. pyri* did not predict its impact on *M. occidentalis* in some of the field plots in the second year. Apparently, *T. pyri* is capable of excluding *M. occidentalis* as prey declines, even in the absence of *Z. mali* (Croft and MacRae 1991b). This effect may have been the result of both direct and

indirect competition as plant feeding mites (prey) were reduced to very low levels. The results of the feeding trials indicate, however, that the direct impacts between the two phytoseiids are substantial.

Based on the differences in feeding behaviours of the two predators seen in Chapter 1, I decided to assess the switching behaviour of both phytoseiids between a more preferred prey (spider mites) and phytoseiid immatures. When provided diets of mixed *T. urticae* and phytoseiid larvae at different population levels and proportions, *T. pyri* showed higher rates of predation and cannibalism on phytoseiid immatures at most prey populations and proportions. Manly Preference Indices indicated that *T. pyri* switched to phytoseiid immatures as prey at higher levels of an alternate, more preferred prey than did *M. occidentalis*. This means it did not have to be as starved as *M. occidentalis* before it utilized conspecific immatures or those of closely related species as food. Neither did *T. pyri* have to encounter phytoseiids at as great a rate as *M. occidentalis* did before it began accepting them as suitable prey. This rapid switching of prey is indicative of a generalist predator (Murdoch and Marks 1973).

Again, the ability of *T. pyri* to readily cannibalize and prey on closely related species reflects its wider range of alternate prey. This is also inferred by the relatively higher nutritional value of phytoseiid immatures to *T. pyri* (Chapter 2). The ability to utilize guild members as food probably contributed to *T. pyri*'s persistence while the more specialist predator, *M. occidentalis*, was displaced when spider mite densities lowered. The persistence of *T. pyri* over *M. occidentalis* in the second year of the experimental orchard demonstrates the benefit of intraguild predation as a form of competition (Polis and Meyer 1989). Not only is *T. pyri* able to attack *M. occidentalis* immatures during the early and late season and thereby depress the latter's densities, but it secures a greater proportion of the remaining food resources which it can channel into increased

reproduction at these temperature. In addition, *M. occidentalis* immatures themselves become food sources contributing to further displacement.

The impact of *T. pyri* on *M. occidentalis* populations may be heavier than indicated by these trials. Predation by immature *T. pyri* on immature *M. occidentalis* was not investigated in these studies and may account for a significant proportion of this mortality. Recent work indicates that although *M. occidentalis* larvae feed and those of *T. pyri* do not, the other immature stages (protonymphs and deutonymphs) of *T. pyri* are much more active as predators than are those of *M. occidentalis* (Croft and Croft 1993, Zhang and Croft in prep). Zhang and Croft (in prep) found that only larval *T. pyri* were less active than comparable stage *M. occidentalis*, indicating that at all other stages, *T. pyri* is a more active forager. Preliminary observations also seemed to indicate that *T. pyri* foraged for longer periods than did *M. occidentalis* (unpublished data). This corresponds with *M. occidentalis* populations responding to prey numbers more closely than that of *T. pyri*, putting more of it's resource gain into reproductive effort rather than increased foraging (Croft and MacRae 1992a, Zhang and Croft in prep). The combination of a wide acceptance of alternate prey and very active predatory behaviour at younger ages may mean that *T. pyri* immatures are imparting high mortality on comparable or younger stages of *M. occidentalis*.

From the field data, it was obvious that *Z. mali* had a greater impact on *M. occidentalis* than on *T. pyri*, displacing the former from systems with low spider mite populations, even in the absence of *T. pyri* (Croft and MacRae 1993). It was not, at first apparent why this should be so. *Z. mali* adult females did not consume greater numbers of *M. occidentalis* eggs than *T. pyri* eggs nor did adult females of either phytoseiid species inflict greater mortality on *Z. mali* eggs or larvae through attack or consumption. There was no difference in the within-tree association of *Z. mali* adult females with the eggs of either phytoseiid species nor were there differences in the way prey mites (all stages) were

spatially partitioned between adult female *Z. mali* as compared with adults and deutonymphs of either of the two phytoseiids. It was found that *M. occidentalis* laid significantly more eggs in the primary foraging area of adult female *Z. mali* than did *T. pyri*. The field data demonstrated that the impact of egg predation by *Z. mali* contributed to the displacement of *M. occidentalis* from certain plots in the experimental orchard (Croft and MacRae 1993).

Because *M. occidentalis* appears to be less successful in the competition for scarce resources under the environmental conditions of the experimental orchard, the impact of egg predation by *Z. mali* becomes more important when *T. pyri* is also included in the system. The impact of *Z. mali* on population levels of *M. occidentalis* was not due to any intrinsic factor of the three predators, but rather, was the result of a behavioural interaction. The negative impact of *Z. mali* on the persistence of *M. occidentalis* at low prey levels demonstrates how a less suitable natural enemy (for biological control purposes) can contribute to the displacement of a more valuable species.

All three predators make valuable contributions to the overall biological control provided by the complex. *M. occidentalis* has shown that it responds well to outbreaks of *T. urticae*, *P. ulmi*, and *A. schlechtendali* in the presence of *T. pyri* (Croft and MacRae 1992a); *T. pyri* is capable of regulating populations of these three pest mites at low densities, either in the presence or absence of *M. occidentalis* (Croft and MacRae 1992b); and *Z. mali* is also an efficient predator of these pest mites and can also successfully attack the eggs of *P. ulmi*, unlike either phytoseiid (Santos 1976, Croft and MacRae 1993). Its potential negative impact on the two phytoseiids should be considered before including this species in a mixed species biocontrol system. It may prove very useful in maintaining low spider mite populations over the long term. It may be advisable to exclude *Z. mali* when initially setting up the system, allowing the phytoseiids to become well established, or when introducing phytoseiids for short term control. The interactions of these three

species, however, dictate that active management practices must be used to ensure their persistence in a biocontrol guild under the environmental conditions of the experimental orchard. The use of selective pesticides that are more toxic to *T. pyri* and *Z. mali* than to *M. occidentalis* may contribute to the persistence of the latter in this guild. For example, Croft (1990) reviews the effects of a multitude of pesticides to these and other natural enemies. It may be that in warmer and more arid habitats, *M. occidentalis* may be favoured enough to persist without management inputs.

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APPENDIX

APPENDIX: VITAE

Ian V. MacRae B.Sc. (Biology) 1980 University of Prince Edward Island
Charlottetown, P.E.I., Canada

M.Sc. (Biology)1988 University of Victoria
Victoria, B.C., Canada

Supervisor: Dr. Richard Ring
Thesis: An Evaluation of *Cricotopus myriophylli* Oliver (Dipter:
Chironomidae) As A Potential Biocontrol for Eurasian Watermilfoil