ECOLOGICAL CONSEQUENCES OF GENETIC VARIATION IN FORAGING BEHAVIORS OF A PREDATORY MITE

by

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Abstract

Foraging traits such as prey consumption rate and the efficiency with which predators convert their prey into offspring are important determinants of local predator-prey dynamics. However, in environments with patchy prey distribution, predator dispersal and aggregation in response to prey-induced volatile cues becomes more critical. My dissertation addressed predator-prey population dynamics in response to variation in four foraging traits in the predatory mite*, Phytoseiulus persimilis* (Acari: Phytoseiidae): consumption rate, conversion efficiency, dispersal, and olfactory response related to prey.

The dispersal response and olfactory sensitivity in predatory mites is modified by prey-related cues. For example, the dispersal response increased with decreasing prey density in a patch and increasing prey-related volatiles from outside the prey patch. The olfactory response of predatory mites also increased with increasing numbers of prey per plant or with the length of time a plant was infested by prey. These results formed the basis for development of bioassays used to examine genetic variation in dispersal and olfactory response of predatory mites.

Through artificial selection I documented additive genetic variation in all four traits. After relaxation of selection, high-level phenotypes were stable compared to their low counterparts. There were significant genetic correlations between some of the foraging traits. However, there were no correlations between foraging traits and life-history traits. The existence of genetic variation and covariation among the foraging traits suggests that predatory mites must be able to adopt different foraging strategies in the evolution of prey-finding in a tritrophic system.

High consumption, high conversion efficiency and high dispersal response phenotypes interacted differently with prey in a spatially complex landscape. All foraging traits were comparable in terms of predator-prey densities and plant damage; but they were lower than the unselected control. Spatial association and correlation analysis showed that all foraging traits were positively associated with prey; but the strongest association was observed for the high conversion efficiency and dispersal lines. The variability in foraging behaviors of the predatory mite affects its ability to locate patchily distributed prey, thereby influencing foraging efficiency and population dynamics. This research provides new information about the critical link between predator foraging and population dynamics relevant to biological control.

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Table of Contents

List of Figures x
List of Tables xiii
Acknowledgements xiv
CHAPTER 1 - Introduction 1
Acarine Predator-Prey System 2
Influence of Predator Foraging Behaviors on Predator-Prey Interactions 4
Prey Consumption and Reproduction 4
Aggregation in Response to Prey-Induced Volatiles 4
Dispersal Response 5
Genetics of Foraging Behaviors in Natural Enemies 7
Objectives 8
References 9
Chapter 2-Resource-Dependent Giving-Up Time of the Predatory Mite, *Phytoseiulus persimilis* 21
Abstract 21
Introduction 21
Materials and Methods 24
Mites 24
Leaf Disks 24
Wind Tunnel 25
Statistical Analysis 26
Results and Discussion 27
Acknowledgements 31
References 31
Figures and Tables 36
CHAPTER 3- *Phytoseiulus persimilis* Response to Herbivore-Induced Plant Volatiles as a Function of Mite-days 39
Abstract 39

Introduction 40
Materials and Methods 42
Source Material 42
Spider Mite Counts and Damage Ratings 42
Bioassay of Response of *P. persimilis* to *T. urticae*–Induced Plant Volatiles 43
Statistical Analysis 44
Results and Discussion 45
Acknowledgements 48
References 49
Figures 53
CHAPTER-4- Genetic Variation of Foraging Behaviors and Associated Life Histories in a Predatory Mite 55
Abstract 55
Introduction 57
Materials and Methods 64
Study Species 64
Phenotypic Assays of *P. persimilis* 65
Artificial Selection Lines 67
Correlated Responses to Selection 70
Statistical Analysis 72
Results 74
Response to Selection, Stability and Heritability of Phenotypes 74
Correlated Responses to Selection 78
Discussion 83
References 95
Figures and Tables 108
CHAPTER 5- Ecological Consequences of Genetic Variation in Foraging Behaviors of a Predatory Mite: Spatio-Temporal Dynamics of a Predatory Mite and its Prey 117
Abstract 117
Introduction 118
Materials and Methods 125

Study Organisms 125
Foraging Traits 127
Greenhouse Experimental Design 128
Population Counts 129
Spatial Distribution and Association 129
Statistical Analysis 131
Results 132
Foraging Traits 132
Population Counts 133
Spatial Distribution of Predators 134
Spatial Distribution of Prey 136
Spatial Association between Predator and Prey 137
Correlation between Predator and Prey Densities 138
Discussion 139
References 146
Figures and Tables 157
CHAPTER 6- Conclusions 166
Implications for Biological Control 169
Appendix A - Chapter 2 172
SAS CODES 172
Appendix B - Chapter 3 173
SAS CODES 173
Appendix C - Chapter 4 175
SAS CODES 183
Appendix D - Chapter 5 186
SAS CODES 189

List of Figures

Figure 2-1 Effect of local prey density and volatiles on giving-up time of satiated *P. persimilis* from a prey patch. Circles denote tests run with 5 predators per petri dish and triangles those with only a single predator per petri dish. 36

Figure 2-2 Effect of local prey density and volatiles on giving-up time of starved *P. persimilis* from a prey patch. Circles denote test run with 5 predators per petri dish and triangle those run with only a single predator per petri dish. 37

Figure 3-1 Response of *P. persimilis* in relation to number of mite-days resulting from adult female *T. urticae* density and the duration of infestation 53

Figure 3-2 Response of *P. persimilis* in an arena bioassay in relation to (a) *T. urticae* density per leaf, (b) average leaf damage as per LDI scale and (c) percentage of predator responding over the duration of *T. urticae* infestation per plant 54

Figure 4-1 Diagram of the selection regime of two replicates A) bidirectional selection, B) alternating selection. For all traits the high and the low line were selected simultaneously. An unselected control line (not shown in diagram) was maintained under laboratory conditions. Arrows indicate selection lines for each trait. 108

Figure 4-2 Mean ± SE prey consumption rate per generation for *P. persimilis* to different selection regimes. 109

Figure 4-3 Mean ± SE conversion efficiency per generation for *P. persimilis* to different selection regimes. 110

Figure 4-4 Mean ± SE dispersal response per generation for A) high lines and B) low line in *P. persimilis* to different selection regimes. 111

Figure 4-5 Mean ± SE olfactory response per generation for A) high line and B) low line in *P. persimilis* to different selection regimes. 112

Figure 4-6 Correlated response in the dispersal ability of A) consumption lines, B) conversion efficiency lines and C) olfactory lines in the presence of 5 or 40 prey eggs. Phenotypic means ± SE are indicated for each line. 113

Figure 4-7 Correlated response in the olfactory response of A) consumption lines, B) conversion efficiency lines and C) dispersal lines to infested or clean plant volatiles. Phenotypic means ± SE are indicated for each line. 114
Figure 5-1 Mean predator numbers per array at four sampling periods. Vertical bars indicate ± SE for the experiment. 157
Figure 5-2 Mean prey numbers per array at predator release ratios of A) 1:10 and B) 1:30 sampled at four time periods. Vertical bars indicate ± SE for the experiment. 158
Figure 5-3 Mean plant damage ratings per array at four sampling periods. Vertical bars indicate ± SE for the experiment. 159
Figure 5-4 Example maps of spatial association patterns of predator and prey populations per array during the course of the experimental period. A) unselected control, B) consumption, C) conversion efficiency and D) dispersal response. Red color indicates spatial association index, X>0, positive association between predator and prey, green color indicates spatial association index, X<0, negative association or dissociation between predator and prey, white color indicates spatial association index, X=0, random pattern of predator and prey. 160
Figure A-1 Frequency distribution of consumption phenotypes in *P. persimilis* per generation. 175
Figure A-2 Frequency distribution of conversion efficiency phenotypes in *P. persimilis* per generation. 176
Figure A-3 Frequency distribution of dispersal response phenotypes in *P. persimilis* per generation. 177
Figure A-4 Frequency distribution of olfactory response phenotypes in *P. persimilis* per generation. 178
Figure A-5 Response of prey consumption rate to selection in *P. persimilis* relative to the cumulative selection differential for both high and low lines. The linear regression for high replicate 1: $r^2 = 0.78$, $F_{1,5} = 17.22$, $P = 0.01$; high replicate 2: $r^2 = 0.99$, $F_{1,5} = 14072.8$, $P < 0.0001$ and low line: $r^2 = 0.44$, $F_{1,2} = 3.89$, $P = 0.11$). 179
Figure A-6 Response of conversion efficiency to selection in *P. persimilis* relative to the cumulative selection differential for both high and low lines. The linear regression for high

replicate 1: $r^2 = 0.64$, $F_{1,4} = 7.28$, $P = 0.05$; high replicate 2: $r^2 = 0.78$, $F_{1,4} = 14.59$, $P = 0.02$ and low line: $r^2 = 0.37$, $F_{1,4} = 2.24$, $P = 0.21$). 180

Figure A-7 Response of dispersal to selection in in *P. persimilis* relative to the cumulative selection differential for both high and low lines. The linear regression for high replicate 1: $r^2 = 0.98$, $F_{1,4} = 235.90$, $P < 0.0001$ and high replicate 2: $r^2 = 0.99$, $F_{1,4} = 850.01$, $P < 0.0001$ and low line: $r^2 = 0.89$, $F_{1,4} = 30.39$, $P = 0.005$. 181

Figure A-8 Response of olfaction to selection in *P. persimilis* relative to the cumulative selection differential for both high and low lines. The linear regression for high line: $r^2 = 0.76$, $F_{1,4} = 12.86$, $P = 0.02$; low line 2: $r^2 = 0.02$, $F_{1,4} = 0.08$, $P = 0.78$. 182

List of Tables

Table 2-1 Mean ± SE number *T. urticae* eggs consumed by predators at the end of the observation period (6h). 38

Table 4-1 Realized heritability estimates of foraging traits in *P. persimilis*. 115

Table 4-2 Intrinsic rate of increase (r_m) ± SE generated from jackknifes $l_x m_x$ data for cohorts of *P. persimilis* selection lines..... 116

Table 5-1 Levels of response in specific predator foraging traits and the unselected control after selection plateaued. Means within columns followed by the same letter are not statistically different at P<0.0001. 162

Table 5-2 Levels of response in specific predator foraging traits immediately before and after greenhouse experiments. 163

Table 5-3 Influence of type of foraging trait, predator release ratio and time of interaction on the number of predators, prey and associated plant damage. P-values highlighted in bold highlight are significant. 164

Table 5-4 Influence of type of foraging trait, predator release ratio and time of interaction on spatial distribution indices: aggregation (I_a), gap (V_j) and patch (V_i). P-values highlighted in bold are significant..... 165

Table A-1 ANOVA table to determine the levels of response in specific predator foraging traits and the unselected control after selection plateaued. 186

Table A-2 ANOVA table to determine the effect of foraging behavior, predator release ratio and time on the number of predator, prey and associated prey damage. 187

Table A-3 ANOVA table to determine the effect of foraging trait, predator release ratio and time on spatial distribution parameters including aggregation (I_a), gap (V_j) and patch (V_i) indices. 188

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CHAPTER 1 - Introduction

The ability of arthropod predators to find and attack prey is a key attribute for suppressing prey populations. Theoretical treatments (Hassell and May 1985; Pels et al. 2002) and empirical evidence (Murdoch et al. 1996) suggest that even subtle differences in predator foraging can lead to significant differences in predator-prey population dynamics and prey suppression. Knowledge of the population impact of different predator foraging traits should allow us to understand the responses of predator-prey systems in different environments to deliberate manipulations, as might occur in biological control. Unfortunately, there is a large gap between behavioral studies at individual levels and population dynamics studies of interactions relevant to biological control (Ives 1995). One way to link behavior and population dynamics is to focus on the influence of specific predator foraging traits affecting both natural enemy fitness and prey suppression.

The rate at which predators consume prey and the efficiency with which predators convert their food (i.e., prey) into offspring, determine predator impact on the local predator-prey dynamics, as described by the functional and numerical response. In patchy environments, traits related to predator movement between patches become equally important to both local (i.e., within-patch) and regional (i.e., among patches) dynamics (Hassell 1978; Berryman and Gutierrez 1999). Local consumption rate and conversion efficiency still affect regional dynamics to the extent that they determine local prey availability; but predator dispersal and colonization of prey patches affect the number of predators remaining in a “source” patch, as well as the number of predators that colonize new prey patches. Thus, these predator traits will interact to affect the predator-prey ratio in each local patch, which in turn affects the stability of

the interaction (Hassell 1978; Berryman 1999) and effectiveness of biological control (Hussey and Bravenboer 1971).

Acarine Predator-Prey System

The twospotted spider mite, *Tetranychus urticae* Koch, is a generalist herbivore. It is highly polyphagous and feeds on over 180 host plants, including over 100 cultivated species (van de Vrie et al. 1972). The spider mite is widely distributed in the United States and all over the world. *Tetranychus urticae* mainly colonize the underside of leaves, but also the top of plants, where mites produce webbing in which all stages live and most activity (e.g., feeding, mating, oviposition) takes place. Adult females deposit eggs close to where they feed, and immatures do not move very far from where they hatch (Suski and Naegele 1968; Kondo and Takafuji 1985). Mites pass through five stages of development: egg, larva, protonymph, deutonymph, and adult. The population goes through a generation every 7 to 21 days, depending on the ambient temperatures in their environment. In this way, clusters, or patches, of spider mite-infested leaves develop. As mite feeding destroys leaf tissue within a patch, mites move to new, uninfested parts of a plant. Because of the explosive growth potential of mite populations (Sabelis 1981), mites can rapidly infest and kill entire plants. Because of their ability to disperse, they can rapidly infest large areas.

The predatory phytoseiid mite, *Phytoseiulus persimilis* Athias Henriot, is a specialist predator on tetranychids and the most frequently used biological control agent for spider mites, especially in greenhouses (van Lenteren and Woets 1988). The predatory mite was introduced into The Netherlands from Chile in 1958 (Dosse 1958) and subsequently shipped to other parts of the world, including the United States. *Phytoseiulus persimilis* are extremely small and are orange to bright reddish in color. Phytoseiid mites reproduce by pseudoarrhenotoky, which is

characterized by obligate fertilization of all eggs followed by a loss and/or heterochromatization of the paternal chromosomes in embryos that develop into males, resulting in haploid condition of the males (Hoy 1979; Schulten 1985; Perrot-Minnot et al. 2000). Under normal conditions, the sex ratio is female-biased, usually close to 0.83 (Helle and Sabelis 1985), and each female can produce upto 60 eggs in her lifetime (McMurty and Rodriguez 1987). *Phytoseiulus persimilis* has five developmental stages: egg, non-feeding larva, protonymph, deutonymph and adult (Sabelis 1981). When predatory mites invade a spider mite-infested plant, the predator population is likely to deplete the local spider mite population (Chant 1961; Takafuji et al. 1983). Although this means the local predator-prey interaction is limited and ephemeral, the interaction may persist on a regional scale due to repeated dispersal from and colonization of patches by both species (Diekmann et al. 1988; Nachman 1987, 1988, 1991; Sabelis et al. 1991; Walde 1991, 1994; Jansen and Sabelis 1992). As prey density drops to zero, *P. persimilis* will leave (Takafuji 1977; Bernstein 1984; Zhang and Sanderson 1993) and seek other patches. Successful colonization of new spider mite patches by the predator is important for the persistence of the predator population and for biological control (Sabelis et al. 1999; Walde and Nachman 1999; McCauley et al. 2000).

Because of their economic importance, the acarine predator-prey system is well studied. There exists a framework of information about the demography and behavior of both species of mites, mathematical models of both local and metapopulation dynamics, and experimental and theoretical studies offering extensive information on biological control (Helle and Sabelis 1985; Sabelis and Harmsen 1992; Sabelis et al. 1999; Walde and Nachman 1999; Pels et al. 2002). Thus, this system provides an appropriate model to study the effect of behavior on predator-prey population dynamics in patchy environments

Influence of Predator Foraging Behaviors on Predator-Prey Interactions

Prey Consumption and Reproduction

The success of *P. persimilis* as a control agent is largely attributed to its strong numerical response (Eveleigh and Chant 1982). One component of the numerical response is the rate of predator reproduction in prey patches (Sabelis 1985a). There is a direct linear relation between predator reproduction and prey consumption (Sabelis 1981). Predators are generally found feeding in densely packed prey colonies (Bancroft and Margolies 1999); so individual consumption rate is relatively constant and close to the maximum possible. When prey decreases in the immediate vicinity of a predator, the predator will simply move to an adjacent area where prey are still plentiful (Sabelis et al. 1998). Thus, for most of the time a predator is in a prey patch the rate of predation and reproduction is close to its maximum (Sabelis et al. 1999). It is only when prey becomes scarce in the patch as a whole that the per capita predation rate drops.

Aggregation in Response to Prey-Induced Volatiles

A second component of the predator numerical response is aggregation, which leads to a high local predator-prey ratio. *Phytoseiulus persimilis* aggregate on a plant in response to prey density (Jarosik 1990). *Phytoseiulus persimilis* uses local cues from the prey to find spider mite colonies on a plant (Hoy and Smilanick 1981; Zhang and Sanderson 1992). Predators search along the shoots, stems, leaf ribs and leaf edges, areas where prey colonies are often founded (Sabelis and Dicke, 1985). Signals associated with prey, such as exuviae, feces, webbing, and eggs (Sabelis and van de Baan 1983), are detectable in the immediate vicinity of the prey patch. A foraging predator uses them all to decide whether to stay in or leave a patch (Sabelis 1981); this decision may be further enhanced by plant volatiles produced when attacked by spider mites

(Maeda et al. 1998; Mayland et al. 2000). When *P. persimilis* locates prey-associated cues in a patch, it exhibits reduced walking speed and a more tortuous walking path (Sabelis 1981), both of which increase patch residence time of the individual forager and lead to aggregation of predator populations.

Prey-induced plant volatiles may have an important influence on the *P. persimilis-T. urticae* population interaction (Dicke and Sabelis 1988). In olfactometer tests, predatory mites were attracted to the odor of plants infested by *Tetranychus* mites in preference to the odor of uninfested plants (Sabelis and van de Baan 1983; Sabelis et al. 1984; Dicke 1994) or plants infested with non-prey herbivores (Dicke et al. 1990a, b; Turlings et al. 1990; Takabayashi et al. 1991). These prey-induced plant volatiles may be utilized by *P. persimilis* in both long-range and local foraging (Sabelis and Dicke 1985; Zemek and Nachman 1999). At long range, volatiles may attract a predator to or cause it to search more intensively around a prey-infested plant (Janssen 1999). Once a predator is on a plant, the same volatiles that attract predators may also be important in local arrestment (Sabelis et al. 1984).

Dispersal Response

In general, good searching ability is an important natural enemy trait contributing to successful biological control (van Lenteren and Woets 1988). Successful colonization of new patches is related to the number of dispersers produced in patches (Sabelis et al. 1999). Production of potential colonists, in turn, is affected by predator consumption rates and conversion efficiency on local patches. If predators stay in a patch until all prey are eliminated, local predator population growth rates should be high, local prey populations should show an immediate decrease, and the local interaction period will be short. Because of the latter, the patch will produce few dispersing predators. If, on the other hand, predators continually disperse

during the interaction, the local predator population growth rate will be lower, the local prey population will decrease at a lower rate (or even increase, depending on the predator-prey ratio), and the interaction period will be longer. This patch will produce more predators to find and colonize other patches (Pels et al. 2002). That is, the global outcome depends on the balance between the length of local predator-prey interactions and local production of predators (van Baalen and Sabelis 1995). Circumstances that enhance predator dispersal -- aggregation, consumption, and reproduction -- have been suggested to lead to greater impact on the pest population (Jarosik 1990, Berlinger et al. 1996). However, models of mite predator-prey interactions in patchy environments do not necessarily predict both local and regional persistence (Hassell 1978; Nachman 1987; Sabelis et al. 1998; Pels and Sabelis 1999; Pels et al. 2002).

The matter of when a natural enemy should leave a patch (Hamilton and May 1977; Bernstein et al. 1988, 1991; Sjerps and Haccou 1994) is important because the timing of predator dispersal can affect both local and regional dynamics (Johst and Brandl 1997). Short-lived arthropods, such as predatory mites, are not likely to acquire information about the global distributions of their resources (which, furthermore, change all the time), so these foragers probably rely on local environmental stimuli which generally provide adequate, but not necessarily optimal, information (Cowie and Krebs 1979). Some *P. persimilis* may disperse while prey numbers are still in decline (Bernstein 1983; Zemek and Nachman 1998), but many will stay until almost all prey are consumed (Takafuji et al. 1983; Sabelis and van der Meer 1986). Foraging decisions, such as when to disperse, may be modified by environmental cues (e.g., host or prey density, presence of competitors, odors) and habituation to such cues (Waage 1979).

Residence time in *P. persimilis* seems to depend on the interaction between consumption rate (as a measure of prey density) and prey-related plant volatiles (Margolies et al. 1997; Maeda et al. 1998; Mayland et al. 2000; Maeda and Takabayashi 2001a; Jia et al. 2002). The response of predators to steep odor gradients associated with prey colonies depends on the predator feeding status; well-fed predators that happen to walk out of an odor patch frequently turn back to it (Sabelis et al. 1984). However, if a predator is starved it is less likely to turn around, but more likely to be attracted to a distant odor source, hence resulting in leaving a patch. Thus, food depletion ultimately leads to dispersal. These behaviors cause predators to remain in profitable prey patches and abandon unprofitable ones (Takafuji 1977; Fernando and Hassell 1980; Ryoo 1986; Bernstein 1984; Zhang et al. 1992).

Timing and rate of dispersal may also be affected by plant volatiles coming from sources outside the local prey patch. When, for instance, predators perceive prey-induced volatiles produced by nearby plants, they may leave a local patch even if abundant food remains (Maeda et al. 1998; Mayland et al. 2000; Maeda and Takabayashi 2001a). Such volatiles may offer information on availability of prey in the general environment beyond the limits of the locally-available patch, and may aid discovery of distant prey. Variability in responsiveness of predators to prey-induced plant volatiles would then lead to different dispersal rates (Jia et al. 2002) and, potentially, to different local dynamics.

Genetics of Foraging Behaviors in Natural Enemies

Documentation of genetic variation in foraging traits is important to determine potential response to selection and for evaluating applications of natural enemies for biological control (Mackauer 1976; Lewis et al. 1990; Hoy 1990; Hopper et al. 1993; Bruins et al. 1994). In a few tritrophic systems there is evidence of a genetic component in foraging behaviors, including the

response of natural enemies to plant chemicals for host acceptance (Mollema 1991; Powell and Wright 1992) and attraction to host-infested plants (Prevost and Lewis 1990; Gu and Dorn 1999; Wang et al. 2003). Early work on the chemical basis of attraction of *P. persimilis to T. urticae*-induced plant volatiles (Sabelis and van de Baan 1983; Dicke et al. 1990b) pointed to significant phenotypic variation in the olfactory response. Quantitative genetic studies also revealed significant additive genetic variation for this trait (Margolies et al. 1997; Margolies 1999; Jia et al. 2002; Maeda 2005, 2006).

The existence of natural genetic variation in dispersal rate, and its impact on the local predator-prey interaction, were demonstrated by Pels and Sabelis (1999). They found consistent differences in dispersal response of two different populations of *P. persimilis*; one line dispersed only after all prey were eliminated, while in the other some females began dispersing while prey were still present. Jia et al. (2002) also found substantial phenotypic variation in prey consumption and oviposition of *P. persimilis*. Genetic variation has also been detected in dispersal tendency, olfactory response, prey consumption and fecundity in the predatory mite, *Neoseiulus womersleyi* (Shicha) (Maeda 2005; 2006).

Objectives

This research examined changes in predator-prey population dynamics in response to variation in four ecologically-relevant foraging traits of a predatory mite, *P. persimilis*: consumption, conversion efficiency, dispersal and olfactory response with the aim to ultimately link predator behavior to population dynamics and prey suppression.

The specific objectives of this study were to:

1) Quantify the genetic components of phenotypic variation in four ecologically-relevant foraging traits in the predatory mite, *P. persimilis* using standardized laboratory bioassays: 1) prey consumption, 2) efficiency with which predators convert their prey (food) into offspring, 3) dispersal response and 4) olfactory response.

2) Examine the impact of the foraging phenotypes developed through artificial selection on the predator-prey interaction in a spatially complex landscape.

The overall hypothesis is that the presence of genetic variation and covariation in foraging behaviors of predatory mites will critically impact predator performance and predator-prey dynamics in heterogeneous environments. The first and second chapters focused on development of laboratory bioassays to test predator dispersal response and olfactory response, respectively. In the third chapter, I examined the genetic components of phenotypic variation in ecologically-relevant foraging traits of the predatory mite, *P. persimilis*: consumption rate, conversion efficiency, dispersal response and olfactory response to *T. urticae*-induced plant volatiles using artificial selection regimes. In chapter four, I tested the impact of high predator foraging phenotypes developed through artificial selection experiments on predator-prey interactions and spatial distribution of predator and prey in a heterogeneous landscape.

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Chapter 2-Resource-Dependent Giving-Up Time of the Predatory Mite, *Phytoseiulus persimilis*

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Abstract

We examined the effect of prey (*Tetranychus urticae*) egg density on leaving rate of the predatory mite, *Phytoseiulus persimilis*, from leaf disks using predators with different feeding experiences and levels of external volatile cues related to their prey. Predators stayed longer on disks with prey eggs than on those without prey eggs. However, at each prey egg density predators stayed longer in the absence of prey-related volatiles from an external source. Starved predators stayed longer in a prey patch than those that had not experienced starvation. At each prey density, starved *P. persimilis* consumed a greater proportion of prey eggs than non-starved predators. The total prey consumption of starved predators appears to be related to their longer residence time on source disks compared to satiated predators and also the per capita consumption rate was greater for starved predators compared to satiated predators.

Introduction

The predatory mite, *Phytoseiulus persimilis* Athias-Henriot (Acari: Phytoseiidae), is a specialist feeder on the tetranychid mites, specifically the twospotted spider mite, *Tetranychus urticae* Koch (Acari: Tetranychidae), and therefore is the most frequently used biological control agent for spider mites, especially in greenhouses (van Lenteren and Woets 1988). Spider mite populations develop in patches, both within a plant and among plants within a habitat. An important determinant of effective short-term biological control, as well as regional persistence

of the predator, is predator efficiency within the entire area of pest infestation. This depends in part on colonization of new prey patches, which is affected by how long predators stay in a prey patch, how many predators (potential colonists) are produced in a patch, and how offspring are distributed among patches. Studies have shown that subtle differences in predator foraging behavior can lead to significant differences in predator-prey population dynamics (Pels et al. 2002). Thus the timing of dispersal from a prey patch is likely to be one of the critical behaviors influencing the predator-prey interaction.

Foraging decisions, such as when to disperse, are primarily based on innate behaviors which may be modified by environmental cues (e.g., host or prey density, presence of competitors, odors) and habituation to such cues (Waage 1979). Predators evaluate resources within the patch as well as the habitat to determine their residence time (Stephens and Krebs 1986). Because short-lived arthropods such as predatory mites are not likely to acquire information about the regional distribution of their resources, which furthermore change all the time, these foragers probably rely on local environmental stimuli which may provide adequate, but not necessarily optimal, information about prey availability. Some *P. persimilis* may disperse while prey numbers are still in decline (Bernstein 1983; Zemek and Nachman 1998), but many will stay until almost all prey are consumed (Takafuji et al. 1983; Sabelis and van der Meer 1986; Maeda et al.1998). Food depletion ultimately will affect leaving as predators become hungry. Starved *P. persimilis* females turn less and walk faster (Bernstein 1983) and are more likely to move upwind (Sabelis and van der Weel 1993) than satiated predators, even without upwind volatiles. All of these behaviors will likely result in starved predators rapidly leaving the plant in search of food elsewhere. However, when predators encounter food (e.g., infested plants), they remain on the plant.

Predator foraging decisions are modified by environmental cues as well as by the internal physiological state of the predator (i.e., starved or satiated). Among the cues used by predatory mites that may help them determine when to leave a patch are volatile chemicals that originate from the plant on which the prey feed (Sabelis and Dicke 1985; Sabelis and Afman 1994; Mayland *et al*., 2000). Herbivore-induced plant volatiles (HIPV) from distant sources shorten the residence time of *P. persimilis* in a prey patch (Maeda et al.1998; Mayland et al. 2000), while local prey-related cues, including locally-produced HIPV, lengthen the residence time of *P. persimilis* (Mayland et al. 2000). These factors have a similar interactive effect on the emigration rate of a related predatory mite, *Amblyseius womersleyi* (Maeda and Takabayashi 2001) and may represent a general phenomenon. However, our current knowledge is insufficient to assess how the cues interact as local prey availability decreases, as it will when predators freely consume prey. Our study tests the hypothesis that predator dispersal rate from a prey patch will be affected by both local rewards (prey eggs) and distant cues about potential rewards (HIPV). Therefore, our objectives were to determine the effects and relative importance of resource (prey egg density) levels in a patch and *T. urticae*-infested plant volatiles from outside the patch on leaving rate of satiated and starved *P. persimilis*.

The experimental set up consisted of two components: 1) a leaf disk assay to determine the effect of local resource-level (prey egg density) on *P. persimilis* dispersal, and 2) a wind tunnel, within which the experiment was conducted, to examine the effect of distant *T. urticae*-infested or uninfested plant volatiles on *P. persimilis* dispersal from the leaf disk.

Materials and Methods

Mites

The *T. urticae* population was maintained on lima beans (*Phaseolus lunatus* cv. 'Sieva') in a rearing room under 400 W high-pressure sodium vapor lamps on a 16:8 (L: D) photoperiod at temperatures ranging from 25 ±1^{o}C. Bean plants were reared in a greenhouse under similar conditions. *P. persimilis* were obtained from Koppert Biological Systems, Inc. (Watsonville, California), a commercial producer of beneficial arthropods. Voucher specimens are in the Kansas State University Museum of Entomological and Prairie Arthropod Research under Lot No. 135 and 154 for *T. urticae* and *P. persimilis*, respectively.

Leaf Disks

To investigate the effect of resource-level on dispersal rate of *P. persimilis*, we used a petri dish bioassay similar to that described in Maeda and Takabayashi (2001); a leaf disk (2.2 cm diam) and a square piece of leaf (2.2 x 2.2 cm) were placed 60 mm apart on water-saturated cotton wool in plastic petri dish (9 cm). When we were ready to test a predator the leaf disk was connected to leaf square by a bridge made of parafilm (30 x 3 mm). Our objective was to measure the time for predators to leave the leaf disk, or source. Spider mite eggs served as prey because they are immobile and also are a preferred prey life stage (Fernando and Hassell 1980). We established the prey egg densities on the leaf disks: 5, 10, 20 or 40 eggs plus an uninfested leaf disk as a control. To obtain the required prey egg densities, we introduced ten adult female spider mites and allowed them to oviposit for 24 h prior to testing. We then removed eggs to achieve the appropriate density. The leaf square on the other end of the bridge served as a sink to arrest predators that dispersed from the source. The sink was heavily infested with spider mites to ensure that predators that dispersed from the leaf disks would not move back to the leaf

disk (Maeda and Takabayashi 2001). After *T. urticae* eggs were established on source and sink, five satiated or starved *P. persimilis* adult females were introduced onto each leaf disk. After 1 h of acclimatization, the leaf disk was connected to the leaf square by a bridge and the petri dishes were placed in a wind tunnel.

Wind Tunnel

To examine the effect of *T. urticae*-infested or uninfested plant volatiles on leaving time of the predators in the petri dishes, tests were conducted in 2 plexiglass wind tunnels (each 1.5 m L x 0.5 m W x 0.25 m H) positioned in a fume hood to draw air through the length of the wind tunnels; air flow was 3 cm s^{-1} at the downwind end of the wind tunnels. Depending on the treatment, twenty *T. urticae*-infested or uninfested lima bean plants were placed at the upwind end of each wind tunnel as a potential source of volatiles (Dicke et al. 1990a). The five petri dishes with 0, 5, 10, 20 or 40 prey eggs and the predatory mites were placed in the downwind end of each wind tunnel, 1 m from the upwind plants. To prevent predators from perceiving volatile cues released from the infested leaf square which might influence their leaving time from the source disk, the petri dishes were oriented so the bridge was at 90º angle to the wind direction. We defined a predatory mite as resident if it remained on the source disk or on the bridge, or dispersed if it crossed the bridge and reached the leaf square.

To examine the effect of starvation on leaving time, *P. persimilis* adult females were held without food for 24h in a small glass vial (2.5 cm diam x 5.5 cm H) and maintained in an environmental chamber (24°C, 60-70% RH, L: D 16:8). The predatory mites were then introduced onto the leaf disk to measure dispersal rate similar to procedures described above.

Previous work reported no difference in giving-up time when one, five or ten predators were placed on a prey-infested plant (Mayland 1998). However, to determine whether predator

density affected leaving rate on the small leaf disks in our study, tests were conducted with either one or five female *P. persimilis* introduced onto the each leaf disk. A single predator was tested at low (5 eggs) or high prey density (40 eggs) per petri dish in order to determine the effects of interference on predator dispersal rate at these prey densities.

Statistical Analysis

The experimental unit was a single petri dish because petri dishes with the 5 different prey densities were exposed to the same condition of volatiles. There were a total of 20 replicates for each treatment combination (prey egg density, volatiles and feeding experience). The number of predatory mites that left the source leaf disk was observed continuously for the first half hour and then every half hour for a total of 6h. We also recorded the number of prey eggs that were consumed by the end of experiment. We analyzed the giving-up time (GUT) of satiated and starved *P. persimilis*, which in the context of our study we defined as the time when 80% of the predators (4 out of 5 predators introduced onto source/leaf disk) had left the source. We used this criterion because in some treatments a single predatory mite remained on the leaf disk at the end of the 6-h experimental period. The same criteria was used to conduct a life test analysis (PROC LIFETEST) to compare leaving rates among single predator and five predators per petri dish using log-rank test (SAS Institute 2002). Statistical analysis was performed by analysis of variance using the PROC MIXED in SAS (SAS Institute 2002). The number of *T. urticae* prey eggs consumed by satiated and starved predators at each prey egg density and volatile condition was analyzed the by analysis of variance using PROC GLM in SAS (SAS Institute 2002).

Results and Discussion

The foraging behavior of *P. persimilis* was influenced both by local and distant cues, including herbivore-induced plant volatiles (HIPV) from outside the prey patch. The most important factors for retaining predators in a prey patch were the presence and density of prey eggs irrespective of external volatile cues or feeding experience of the predator. For example, on disks lacking prey, predators left very quickly whether or not *T. urticae*-infested plants were present upwind. These findings are consistent with previous studies that have shown that predatory mites are detained by the presence of prey eggs and prey products (Maeda and Takabayshi 2001; Mayland et al. 2000; Sabelis and Dicke 1985). Retention of predators within a patch may result, at least in part; from area-restricted searching behavior because *P. persimilis* are known to exhibit a reduction in search speed and an increase in the number of turns following prey capture (Eveleigh and Chant 1982). When prey were available on the source disk, the giving-up time of *P. persimilis* was significantly affected by both prey density on the source disk ($F = 889.54$, $df = 4,344$, $P < 0.0001$) and the presence of upwind volatiles ($F = 35.23$, $df = 1,36$, $P < 0.0001$). Regardless of the upwind treatment, the giving-up time increased with increasing prey density (Fig. 2-1). This is consistent with previous reports of prey density-dependent dispersal rates of *P. persimilis* (Takafuji and Chant 1976; Takafuji 1977; Bernstein 1983; Maeda et al. 1998; Vanas et al. 2006). Predators left the source significantly faster in the presence of infested plants upwind than in the presence of uninfested plants at prey egg densities ≥ 10 (Fig. 2-1). On control leaf disks, the giving-up time was within 5.0 min regardless of the upwind treatment. There was a significant interaction between local prey density and external volatiles on predator leaving time at prey densities ≥ 20 ($F = 44.23$, $df = 4,344$, $P < 0.0001$). When prey was scarce predators left the source regardless of the upwind treatment; but as prey

became abundant the presence of volatiles upwind reduced predator giving-up time. We interpret this to mean that when prey are scarce, predators leave the source regardless of the likelihood of finding prey elsewhere. However, as prey become more abundant locally, predators are more likely to stay so the influence of external HIPV on predator dispersal is more likely to be noticed.

Other investigators have shown that HIPV from outside the prey patch influence the leaving rate of *P. persimilis* (Maeda et al. 1998; Mayland et al. 2000). Residence time of *P. persimilis* in a prey patch seems to depend on the interaction between consumption rate (as a measure of prey density) and response to plant volatiles (Margolies et al. 1997; Maeda et al. 1998; Mayland et al. 2000; Jia et al. 2002). When predatory mites perceive distant volatiles in the air stream their behavioral response is altered. This change in behavior could be interpreted as attraction to upwind plants or as non-directed stimulation of movement. Predators outside a prey patch appear to use HIPV to find prey-infested plants (Janssen 1999), but in addition predators within a prey patch may use HIPV to define the limits of the patch. When the environment is flooded with volatiles the predators will not immediately perceive being outside the patch and will be more likely to expand their movement beyond the source disk

The hunger status of *P. persimilis* also has a significant influence on foraging behavior (Bernstein 1983; Sabelis and van der Weel 1993; Maeda and Takabayashi 2005). The giving-up time of *P. persimilis* from a source leaf disk was significantly affected by starvation ($F = 91.51$, $df = 1, 36$, $P < 0.0001$). Additionally, giving-up time of starved predators followed the same trend of satiated predators; i.e., giving-up time is longer in the presence of uninfested than infested plants upwind at prey egg densities ≥ 20 ($P < 0.0001$, Fig.2-2). On control leaf disks (no prey eggs) the giving-up time was less than 5 min regardless of the upwind treatment.

The degree of hunger also affected response to external volatile cues. For example, in the presence of leaf volatiles from *T. urticae*-infested leaves, hungry predators showed intensified positive anemotactic (i.e., upwind) movement (Sabelis and Dicke, 1985) whereas the response of satiated predators is to move downwind. There was a significant interaction between prey density and feeding experience at prey densities ≥ 20 ($F = 285.52$, df = 4,344, $P < 0.0001$). Hunger status influenced residence time in *P. persimilis*, but differences in response between satiated and starved predators increased as local prey density increased. Specifically, when prey were abundant on the source disk, starved predators remained significantly longer than satiated predators. Other differences in dispersal behavior have been noted between well-fed and starved *P. persimilis*. Sabelis et al. (1984) showed that satiated predators that pass a steep odor gradient at the end of the patch turn back frequently, but starved predators walk less and turn faster. These behaviors cause predators to remain in profitable prey patches and to abandon unprofitable ones (Takafuji 1977; Bernstein 1984; Zhang et al. 1992). Predatory mites are likely to stay in prey patches until all prey are consumed (Takafuji et al. 1983; Sabelis and van der Meer 1986). Thus, food depletion ultimately leads to dispersal.

The number of prey eggs consumed by starved *P. persimilis* was greater than satiated predators at each prey density ($F=33.92$, df=1, $P<0.0001$) and volatile condition ($F=50.78$, df=1, $P < 0.0001$) (Table 2-1). There was no significant interaction between feeding experience and volatile condition on proportion of prey eggs consumed ($F=1.80$, df=1, $P=0.18$). The per capita consumption rate was also greater for starved predators than satiated predators at each prey egg density ($F=17.71$, df=1, $P<0.0001$) and volatile condition ($F=40.84$, df=1, $P<0.0001$). Hence the greater total prey consumption of starved predators appears to be related to their longer residence time on source disks compared to satiated predators. Regardless of the feeding status,

predators consumed fewer prey eggs when exposed to leaf volatiles from infested leaves than from uninfested leaves (Table 2-1). Hence, *P. persimilis* giving-up time seems to depend on the interaction between consumption rate (as a measure of prey density) and HIPV. Based on this conclusion we might expect that predator density would affect giving-up time. While this may be true for longer interactions, within the time frame of our tests the giving-up time of a single predator at low (5 eggs) and high prey density (40 eggs) per petri dish was similar to that of five predators at comparable densities (Fig. 2-1). There was no significant difference in the leaving rates of satiated predators (one or 5) at 5 prey eggs ($\chi^2 = 0.91$, df= 4, P=0.922) or 40 prey eggs ($\chi^2 = 0.68$, df= 4, P=0.87) at either volatile condition. Similarly, there was no significant difference in the leaving rates of starved predators (one or 5) at 5 prey eggs ($\chi^2 = 6.51$, df= 4, P=0.08) or 40 prey eggs ($\chi^2 = 4.18$, df= 4, P=0.24) at either volatile condition. This is consistent with reports that *P. persimilis* emigration rate is independent of predator density when prey are at very low or at high densities (Bernstein 1984; Zemek and Nachman 1998).

Many studies have considered the problem of when a natural enemy should leave a resource patch. Knowledge of factors that affect predator giving-up time has applications for pest management because the timing of natural enemy dispersal can affect the ratio of natural enemies to pest both within a patch and throughout a region, which in turn affects pest suppression. If predator response to HIPV has an impact on the ability of a predator population to reduce a prey population, it will affect the predator's success as a biological control agent (Hopper et al. 1993; Lewis et al. 1990). The impact of the volatiles on giving-up time, and hence population dynamics, is likely to be modified by interactions among predators, either locally (Bernstein 1984) or from a distance (Janssen et al. 1997). With more specific information on the role of HIPV in relation to other cues available to predator, we may be able to manipulate these

volatiles to increase efficiency of the biological control agent (Dicke et al. 1990b; Lewis and Martin 1990; Tumlinson 1988; Vet and Dicke1992).

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Figures and Tables

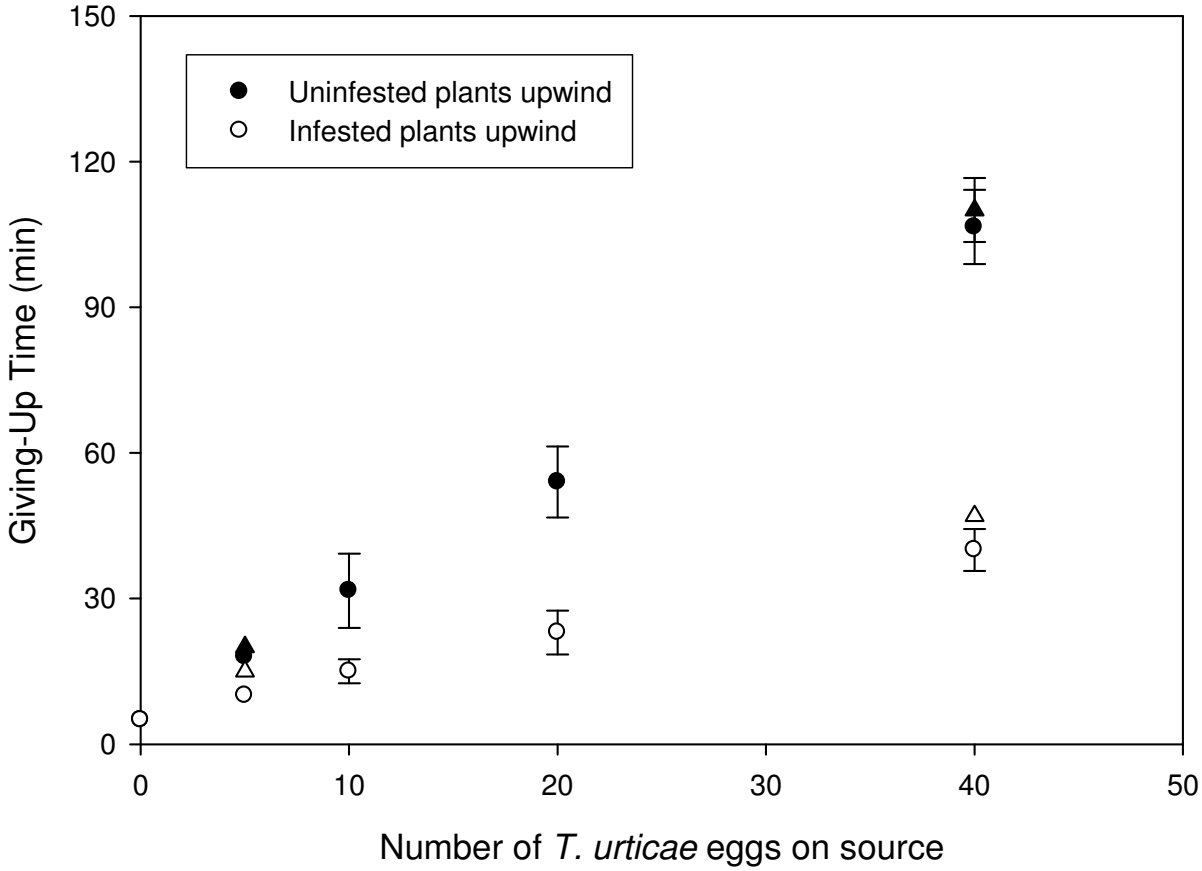

Figure 2-1 Effect of local prey density and volatiles on giving-up time of satiated *P. persimilis* from a prey patch. Circles denote tests run with 5 predators per petri dish and triangles those with only a single predator per petri dish.

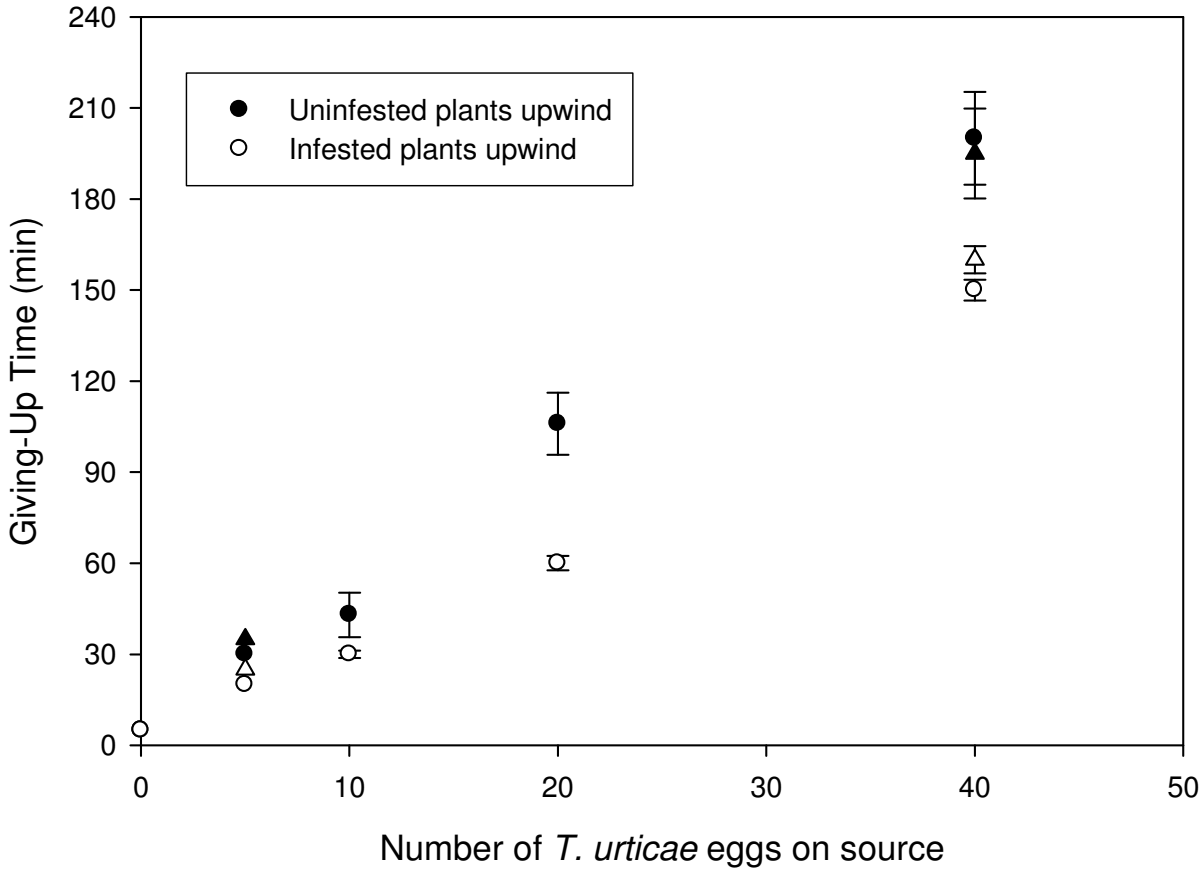

Figure 2-2 Effect of local prey density and volatiles on giving-up time of starved *P. persimilis* from a prey patch. Circles denote test run with 5 predators per petri dish and triangle those run with only a single predator per petri dish.

Prey density	Upwind plants	Prey eggs consumed by predator	
		Satiated	Starved
0	Uninfested	-	-
	Infested	-	-
5	Uninfested	4.00 ± 0.26	5.00 ± 0.46
	Infested	3.00 ± 0.12	2.70 ± 0.31
10	Uninfested	5.15 ± 1.09	6.95 ± 1.70
	Infested	3.31 ± 0.75	5.90 ± 2.40
20	Uninfested	6.75 ± 1.39	9.50 ± 1.49
	Infested	4.45 ± 0.75	6.75 ± 0.85
40	Uninfested	9.27 ± 1.10	20.80 ± 2.50
	Infested	7.05 ± 1.12	11.15 ± 1.27

Table 2-1 Mean ± SE number *T. urticae* eggs consumed by predators at the end of the observation period (6h).

CHAPTER 3- *Phytoseiulus persimilis* Response to Herbivore-Induced Plant Volatiles as a Function of Mite-days

Experimental and Applied Acarology 40: 231-239.

Abstract

The predatory mite, *Phytoseiulus persimilis (*Acari: Phytoseiidae), uses plant volatiles (i.e., airborne chemicals) triggered by feeding of their herbivorous prey, *Tetranychus urticae* (Acari: Tetranychidae), to help locate prey patches. The olfactory response of *P. persimilis* to prey-infested plants varies in direct relation to the population growth pattern of *T. urticae* on the plant; *P. persimilis* responds to plants until the spider mite population feeding on a plant collapses, after which infested plants do not attract predators. It has been suggested that this represents an early enemy-free period for *T. urticae* before the next generation of females is produced. We hypothesize that the mechanism behind the diminished response of predators is due to extensive leaf damage caused by *T. urticae* feeding, which reduces the production of volatiles irrespective of the collapse of *T. urticae* population on the plant. To test this hypothesis we investigated how the response of *P. persimilis* to prey-infested plants is affected by: 1) initial density of *T. urticae*, 2) duration of infestation, and 3) corresponding leaf damage due to *T. urticae* feeding. Specifically, we assessed the response of *P. persimilis* to plants infested with two *T. urticae* densities (20 or 40 per plant) after 2, 4, 6, 8, 10, 12 or 14 days. We also measured leaf damage on these plants. We found that predator response to *T. urticae*-infested plants can be quantified as a function of mite-days, which is a cumulative measure of the standing adult female

mite population sampled and summed over time. That is, response to volatiles increased with increasing numbers of *T. urticae* per plant or with the length of time plant was infested by *T. urticae*, at least as long at the leaves were green. Predatory mites were significantly attracted to plants that were infested for 2 days with only 20 spider mites. This suggests that the enemy-free period might only provide a limited window of opportunity for *T. urticae* because relatively low numbers of *T. urticae* per plant can attract predators. Leaf damage also increased as a function of mite-days until the entire leaf was blanched. *T. urticae* populations decreased at this time, but predator response to volatiles dropped before the entire leaf was blanched and before the *T. urticae* population decreased. This result supports our hypothesis that predator response to plant volatiles is linked to and limited by the degree of leaf damage, and that the quantitative response to *T. urticae* populations occurs only within a range when plant quality has not been severely compromised.

Introduction

Arthropod natural enemies use many sensory cues to aid the search for food, but the use of chemical cues is probably most common (Roland 1990; Vet and Dicke 1992). Plant volatiles are probably important in directing parasitoids and predators to search in appropriate habitats (Bell 1984; Lewis and Martin 1990; Turlings et al.1990; Takabayashi and Dicke 1996), but plant volatiles that are produced only in response to herbivore feeding offer natural enemies more reliable information on the actual presence of food (Vet and Dicke 1992). The phytoseiid mite, *Phytoseiulus persimilis* Athias–Henriot (Acari: Phytoseiidae), is a specialist predator of tetranychid mites and the most frequently used biological control agent for twospotted spider mites, *Tetranychus urticae* Koch (Acari: Tetranychidae), especially in greenhouses (van Lenteren and Woets 1988). Among the cues that predatory mites may use to find prey-infested

plants are volatile chemicals that originate from the plant on which the prey feed (Sabelis and van de Baan 1983; Dicke et al. 1990c; Maeda and Takabayashi 2001). Previous studies have demonstrated that *P. persimilis* are attracted to the odor of plants infested by its prey, *T. urticae*, in preference to the odor of uninfested plants (Sabelis and van de Baan 1983; Sabelis et al. 1984; Dicke 1994; Janssen 1999) or plants infested with non-prey herbivores (Dicke et al. 1990a, b; Turlings et al. 1990; Takabayashi et al. 1991).

Maeda and Takabayashi (2001) demonstrated that the intensity of response of *P. persimilis* to *T. urticae*-infested plant volatiles was highly correlated with the amount of volatiles produced by *T. urticae*-infested plants. The density of *T. urticae* females on kidney bean plants was proportional to the production of *T. urticae*-induced plant volatiles until the collapse of the adult spider mite population; however, the plants didn't attract predators until 40 spider mites had fed on the plants for at least 12 days. The authors also found that in the interval between the collapse of initial adult *T. urticae* numbers and appearance of the second generation females infested plants did not attract predatory mites. They hypothesized this was a temporary enemy-free period for *T. urticae*. We suggest a mechanism for this response that may lead to an enemy-free period. That is, the diminished response of predators results from extensive leaf damage caused by *T. urticae* feeding, which reduces the production of volatiles irrespective of the collapse of *T. urticae* population on the plant. To test our hypothesis we investigated three factors that might affect the production of *T. urticae* -infested plant volatiles: 1) densities of *T. urticae* per plant, 2) duration of *T. urticae* infestation, and 3) level of leaf damage corresponding to *T. urticae* infestation.

Materials and Methods

Source Material

Lima bean, *Phaseolus lunatus* cv. 'Sieva', served as the host plant for *T. urticae* in all experiments. Plants were grown in the greenhouse under 400 W high-pressure sodium vapor lamps that were set at a 16:8 (L: D) h photoperiod and 22–25°C. Irrigation and fertilizer regime was uniform for all plants. Lima bean plants were sown on two consecutive days. Plants with two fully expanded cotyledons were used for the study. New growth was clipped of periodically to maintain two leaves on the plant.

The population of *T. urticae* used in experiments derived from a colony maintained on lima beans in a rearing room under light and temperature conditions as described above. *P. persimilis* were obtained from Koppert Biological Systems, Inc. (Romulus, MI USA), a commercial producer of beneficial arthropods. One-week old adult female predators were used in the experiment.

Spider Mite Counts and Damage Ratings

The number of adult female *T. urticae* present on each infested leaf and leaf damage was recorded prior to use in the experiment. Mite-days were calculated as the cumulative number of adult female *T. urticae* per plant through time (14-day period). We visually assessed the degree of *T. urticae* -related leaf-feeding injury using a leaf damage index (LDI) similar to that of Nachman and Zemek (2002), which was modification of a procedure developed by Hussey and Parr (1963). The symptoms were ranked according to an ordinal scale as follows: 0, no damage; 1, incipient damage, one or two small feeding patches; 2, feeding patches tending to coalesce, but only 2/3 of leaf affected; 3, 2/3 of leaf with feeding marks as chlorotic patches; 4, dense feeding marks over entire leaf but appearance still green; and 5, as 4, but leaf blanched and

beginning to shrivel. LDI was calculated as an average of four plants per treatment-time combination.

Bioassay of Response of P. persimilis *to* T. urticae*–Induced Plant Volatiles*

The response of predators to *T. urticae*-induced plant volatiles was examined on a 40 cm diameter circular arena encircled with a sticky material (Insect Coating, The Tanglefoot Company, MI, USA) to prevent predators from leaving. The size of the arena was based on previous studies which showed that adult female *P. persimilis* exhibited increased turning rates and decreased walking speed within 20 cm of prey-infested plants (Mayland 1998). Three arenas were set up side-by-side (one for each treatment and one for the control) with a vertical cardboard divider (60 cm H x 55 cm W) to reduce air movement and possible drift of volatiles. To further reduce the effect of air movement on predator orientation and activity, the arenas were located in a small room (3 m x 1.2 m) that was closed of when running a test. A 40W fluorescent lamp located above the arenas provided illumination. Room temperature and humidity were maintained at 25 ±1°C and 60%, respectively. Tests were usually conducted from 1000 to 1200 h. For each repetition of the experiment, one 2.2 cm diam leaf disk was cut from infested parts of a plant infested with 20 or 40 *T. urticae*; these served as sources of *T. urticae*-infested plant volatiles. However, volatile production is not limited to the site of damage but is produced systemically (Dicke et al. 1990b; Turlings and Tumlinson 1992; Potting et al. 1995; Röse et al. 1996). A leaf disk cut from an uninfested plant served as the control. All spider mites eggs and webbing were removed from each of the leaf disks before disks were placed, one per arena, in the center on moist cotton wool. This was done 2 h prior to testing to allow suffcient time for the volatiles to diffuse in air (Jia et al. 2002). During this 2 h period predators were held without food in an empty glass vial (2.5 cm diam and 5.5 cm H) sealed with parafilm.

This procedure allowed the predator to empty their gut contents without affecting their foraging ability (Sabelis 1981). Following the protocol of Jia et al. (2002), 10– 12 adult female *P. persimilis* were released from the edge of the arena and the number of predatory mites that found the central leaf disk within 10 min was recorded. Predators were continuously observed after release in the arena and the time for each predator to reach the central leaf disk was recorded. Predators were immediately removed from the arena when they encountered the central disk to avoid recounting of the same individuals. Thus, the arena bioassay tested *P. persimilis* attraction to leaf disks from a distance, and the comparison between the control and treated disks allowed us to test whether the response differed from that expected under random (non-attracted) movement. The surface of the arena was always cleaned between trials to minimize contamination between runs. Tests at each of the three inoculation levels were run 2, 4, 6, 8, 10, 12, and 14 days post-inoculation. Experiments were conducted over a four-month period (March–June) with eight replicates per treatment-time combination, hence a total of 32 (8 x 4) replicates per treatment-time combination.

Statistical Analysis

We analyzed the response of the predators, which in the context of our study we defined as the proportion of predators that found the central leaf disk placed in the arena in the first 10 min (Mayland 1998). The experimental design was a randomized complete block with repeated measures and nested blocking factors. A mixed-model analysis was conducted using treatment, time (days after inoculation), and their interaction as fixed effects, and experiment as random effects. Time was also a repeated measures factor. Models were fit assuming numerous standard structures for the serial correlation, and the best-fitting model was selected using Akaike's Information Criterion (Littell et al. 1996; Guerin and Stroup 2000). F-tests for fixed

effects and t-tests for pairwise comparisons were performed based on the chosen correlation structure (Littell et al. 1996). All tests used a 0.05 type I error rate. All computations were done using PROC MIXED in SAS (SAS Institute 2001).

Results and Discussion

P. persimilis were attracted to leaf disks from *T. urticae*-infested plants, whereas leaf disks from control plants, which were mechanically-damaged, elicited no or a weak response (Fig. 3c). There was a significant difference in response of *P. persimilis* to leaf disks from 20 and 40 *T. urticae*-infested plants compared to the uninfested plant (t_{21} = -41.02, P < 0.0001 and t_{21} = 51.90, P < 0.0001) respectively (Fig. 3-2c). This supports the assumption that leaf volatiles produced by the herbivorous prey were involved in the response. Volatiles released by mechanical damage (i.e., cutting) are different from those released by spider mite feeding and the former do not attract *P. persimilis* while the latter do (reviewed by Turlings et al. 1995; Takabayashi and Dicke 1996; Dicke et al. 1998). The response of *P. persimilis* to *T. urticae*-infested plant volatiles increased with increasing *T. urticae* density per plant ($F_{2,\ 14.9}$ =349.86, P < 0.0001) (Fig. 3-2a, c). Additionally, the responsiveness of *P. persimilis* to *T. urticae*-infested plant volatiles also increased with the duration of infestation of *T. urticae* on the plant ($F_{6,\ 16}$ =280.36, P < 0.0001) (Fig. 3-2a, c). Thus, the response of *P. persimilis* to *T. urticae*-infested plants may be quantified using mite-days, which is a measure of the standing adult female *T. urticae* population on a plant sampled and summed over time (Fig. 3-1).

The response of *P. persimilis* to plant volatiles was similar for 20 *T. urticae* on a plant for 4d or 40 *T. urticae* for 2d which equals 80 mite-days ($t_{14.1}$ = -1.08, P =0.21). Similarly, response of *P. persimilis* to plant volatiles was similar for 20 *T. urticae* on a plant for 8d or 40 *T. urticae* for 4d which equals160 mite-days ($t_{24.3}$ =3.32, P =0.28) (Fig. 3-1). These data support the

concept that plant volatile production is related to cumulative *T. urticae* populations over time. However, the mite-day concept did not hold at higher levels. For example, there was a significant difference in the response of *P. persimilis* at 240 mite-days between the two combinations tested, i.e., 20 *T. urticae* on a plant for 12d vs. 40 *T. urticae* for 6d ($t_{42.4}$ =4.96, P <0.05) (Fig. 3-1). The attractiveness of *P. persimilis* to prey-infested plants shows a typical unimodal curve with linear increase in predator response corresponding to an increase in *T. urticae* density. However after the peak of *T. urticae* density, predator response starts to decrease (Maeda and Takabayashi 2001). The mite-days concept may not be a reliable indicator of plant volatile production beyond a certain density and/or duration of *T. urticae* infestation because of differences in induction potential for plant volatiles related to differences in *T. urticae* demography (i.e., changes in age class distribution over time). However, we did not evaluate these changes.

Leaf damage due to *T. urticae* feeding increased as a function of mite-days, i.e., average LDI per plant increased with increasing *T. urticae* density and duration of infestation until the entire leaf was blanched (Fig. 3-2a, b). The average response of *P. persimilis* to 20 or 40 *T. urticae*-infested plant corresponds to LDI values of 4.8 and 4.2, respectively (Fig. 3-2b, c). Adult populations of *T. urticae* began to decrease after the LDI reached 4.5; but predator response to plant volatiles dropped before this time (Fig. 3-2b, c). Mite-days can be applied to leaf damage until the leaf appears green with dense feeding symptoms of *T. urticae*; beyond this level of damage mite-days cannot be used for quantifying predator response to volatiles. This suggests that the reduction in predator's response under conditions of severe leaf damage may be related to a reduction in plant ability to produce volatiles.

Our results confirm previous reports that the response of *P. persimilis* to plant volatiles corresponds with *T. urticae* densities and the duration of spider mite infestation on the plant (Sabelis et al. 1984; Maeda and Takabayashi 2001; Gols et al. 2003). Progressive increase in *T. urticae* density, duration of infestation, and mite-days resulted in corresponding increases in the level of attraction of *P. persimilis* (Fig. 3-2a, c). We observed a significant response of predators when 20 or 40 *T. urticae* were introduced on the plant at 2 days ($t_{9.96}$ =9.44, $P < 0.0001$ and $t_{9.96}$ =14.60, $P < 0.0001$, respectively) (Fig. 3-2a, c). Gols et al. (2003) using whole plants as odour sources also found that relatively low density of spider mites (only 1or 4) on a plant for 2 days caused *P. persimilis* to be significantly attracted to *T. urticae*-induced plant volatiles in a Y-tube olfactometer. Although our experimental set-up was different from the Y-tube olfactometer used by Gols et al. (2003), both studies show similar results in that few spider mites per plant and infestation period of only 2 days is suffiicient to increase predator response. Plants with 20 *T. urticae* for 12d resulted in 70% of the predator's response, and plants with 40 *T. urticae* at 8d resulted in 74% predator response (Fig. 3-2a, c). One explanation for the shift in time of the peak response of the predators may be because there were higher numbers of adult female *T. urticae* on plants inoculated with 40 *T. urticae*; this may have resulted in larger quantities of volatiles being produced, or volatiles being produced sooner, compared to plants infested with 20 *T. urticae*. We found that relatively low numbers of spider mites per plant will attract predatory mites to the plants and this would reduce the enemy-free period available for spider mites. We also found that the response of predators to volatiles is linked to plant damage rather than directly to *T. urticae* populations, and that predator response decreases because leaf damage caused by *T. urticae* feeding reduces the plant's ability to produce volatiles. As the plant reaches a damage threshold, it may cease production of volatiles. Various factors are known to influence

the quality and quantity of volatiles produced, including plant species or cultivar, leaf growth stage, herbivore species, and abiotic conditions (light intensity, time of year, and water stress) (Sabelis and Dicke 1985; Dicke et al. 1990a; Takabayashi et al. 1994). Nevertheless, for a specified set of genetic and environmental conditions, mite-days may provide a quantitative assessment of *P. persimilis* response to *T. urticae*-infested plant volatiles within a given range of *T. urticae* density and duration of infestation. Successful colonization of new spider mite patches by the predator is important for the persistence of the predator population and for biological control (Sabelis et al. 1999; Walde and Nachman 1999). Because herbivore-induced plant volatiles increase the probability of the predator finding a rich prey patch, it can directly increase predator foraging and fecundity, thus contributing to predator population fitness. Investigations of the role of plant volatiles, in combination with other factors that underlie variation in predator behavioral response, will contribute to a better understanding of how *P. persimilis* forages for *T. urticae*. It may also lead to a greater ability to manipulate plant volatiles to increase the efficiency of this biological control agent.

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Figures

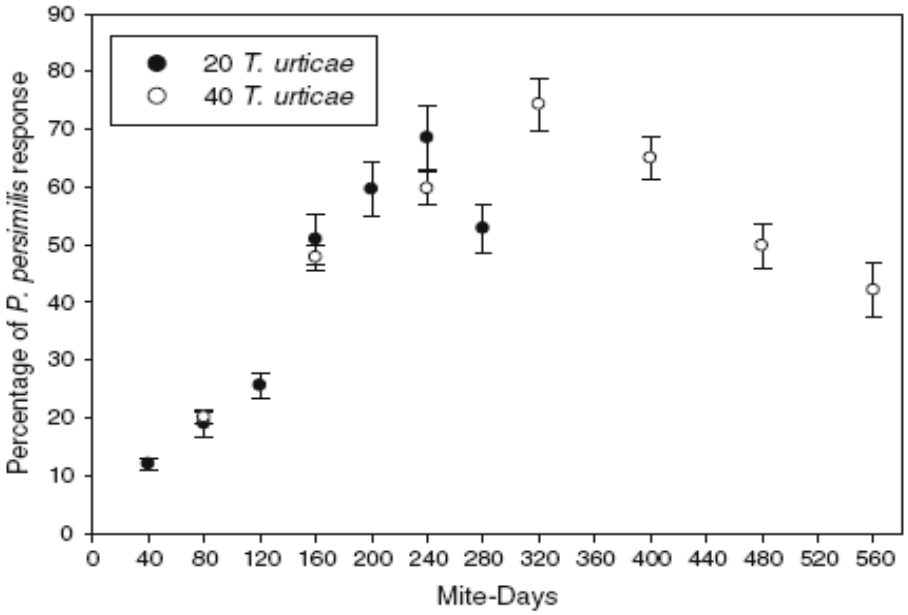

Figure 3-1 Response of *P. persimilis* in relation to number of mite-days resulting from adult female *T. urticae* density and the duration of infestation

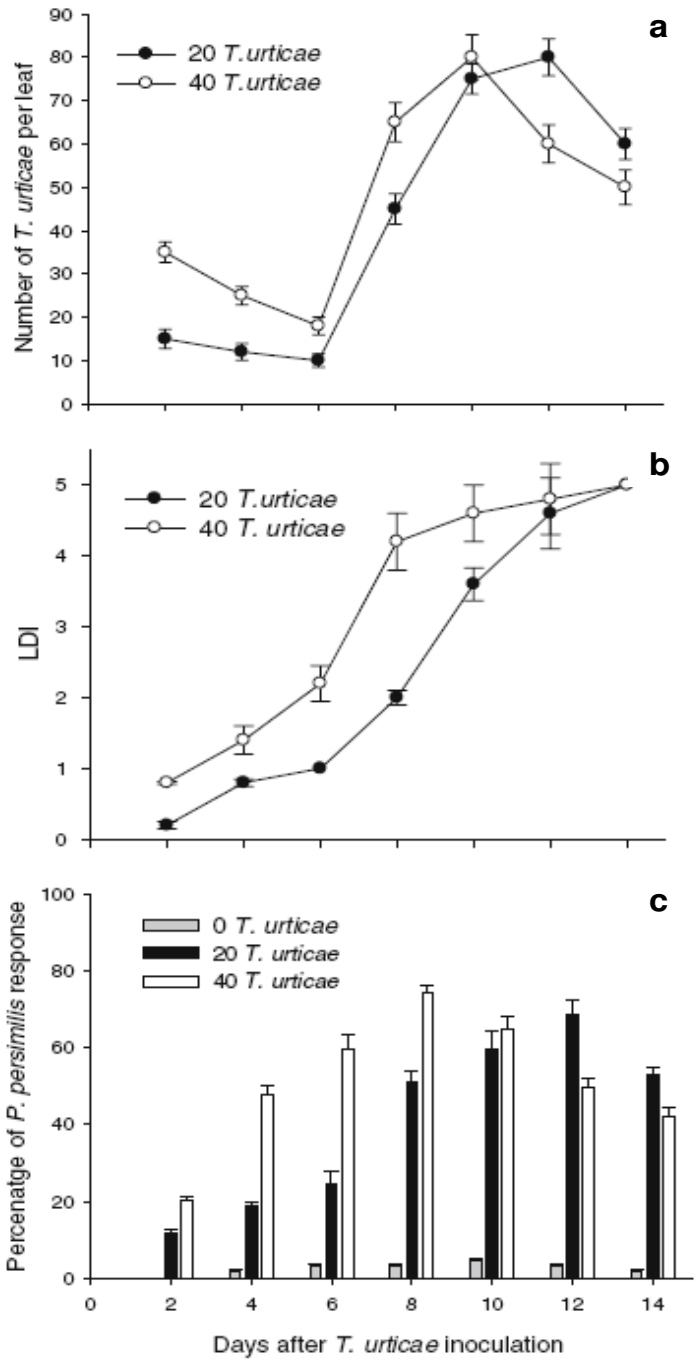

Figure 3-2 Response of *P. persimilis* in an arena bioassay in relation to (a) *T. urticae* density per leaf, (b) average leaf damage as per LDI scale and (c) percentage of predator responding over the duration of *T. urticae* infestation per plant

CHAPTER-4- Genetic Variation of Foraging Behaviors and Associated Life Histories in a Predatory Mite

Abstract

For any complex phenotype to evolve in response to ecological conditions, it is essential that the phenotypic variation be controlled in part by heritable genetic variation. This heritable genetic variation in a population will determine how rapidly a phenotype will change in response to selection. However, the existence of genetic correlations with other phenotypes may hinder the direction and/or rate of this response to selection. One such complex trait is foraging behavior, which is composed of many related phenotypic components and has obvious links to individual fitness in nature. Despite steady progress in the study of foraging behavior, key questions about the evolutionary or genetic mechanisms that contribute to the maintenance of genetic variation, and the effect of this variation on individual fitness, remain unanswered. We conducted a quantitative genetic analysis for four ecologically-relevant components of foraging behavior including prey consumption rate, conversion efficiency, dispersal and olfactory response in a predatory mite, *Phytoseiulus persimilis.* To quantify the portion of the phenotypic variation caused by genetic effects, we conducted a set of bidirectional artificial selection experiments on aforementioned foraging traits. Significant additive genetic variation was detected in both directions of selection for nearly all of the foraging traits with the single exception being the low-olfactory line. To confirm that the patterns observed in the first set of selection experiments were in fact the result of responses to selection and not stochastic changes in allele frequencies caused by genetic drift, we performed a temporally distinct second replicate of selection. In this second set of selection experiments we imposed selection only in the

direction of, and for the traits which maintained, the selection response after the selection was relaxed in the first set of experiments. Thus, in the second set of experiments we created an additional high consumption line, high conversion efficiency line, and a high dispersal response line. The response to selection in the second replicate was similar to that obtained in the first set of selection experiments. After successful selection of the lines, we assessed correlated responses in consumption, conversion efficiency, dispersal and olfactory response at the conclusion of selection for all lines subjected to selection regime I. We detected significant genetic correlations between some foraging traits that were used in the selection treatments. For example, consumption and dispersal both responded in a manner consistent with a correlated response to selection. We also measured correlation among foraging traits and life-history traits such as hatching time (time to emerge from egg), hatching percent, development time (time from nymph to adult ecdysis), survivorship from egg to adult and daily fecundities. There was no evidence of genetic correlations between the selected lines with hatching time, hatching percent and survivorship except for a marginally significant correlation between low consumption and development time. The high- and low-consumption and conversion efficiency lines had significantly different fecundities than control line, whereas the high- and low-dispersal and olfaction lines were comparable to the control. These results indicate that certain traits like consumption and dispersal likely share a common genetic basis, and depending on the mode of selection applied to this variation (and covariation) constraints on their independent evolution could occur. Finally, we assessed the fitness of foraging phenotypes to evaluate their potential competitiveness in the field. The fitness estimates in the low-consumption and low-conversion efficiency line were significantly diminished compared to their respective high lines and the unselected control. The dispersal and olfactory response lines did not differ in their fitness

compared to the unselected control. This study provides the first comprehensive examination of genetic variation and covariation in a suite of ecologically-relevant foraging traits that potentially impact the foraging success and fitness consequences of a predatory mite.

Introduction

How animals forage for food is a core issue in ecology. This process forms the basis of trophic interactions and plays a fundamental role in shaping population dynamics, food webs, and communities. Foraging is the expression of a complex phenotype that is composed of numerous behavioral and physiological components, including olfactory cues, movement dynamics, and consumption efficiency. At a genetic level there is tremendous variation in foraging traits among individuals of a species owing to the interaction of many genes (Sokolowski 2001). In addition, the foraging success of an individual is influenced by factors such as the distribution and suitability of resources and the risks associated with searching for food (Stephens and Krebs 1986). Furthermore, ecological factors not directly related to foraging, such as variation in life-history traits, may also affect foraging success (Roitberg et al. 1992). For example, variation in body size can affect locomotory skills (Roff 1991). Together, the genes, the life-history, and the landscape produce wide variation in foraging phenotypes. Theoretical treatments (e.g., Hassell and May 1985; Pels et al. 2002) and empirical evidence (e.g., Murdoch et al. 1996; Hanski et al. 2004) suggest that even subtle differences in predator foraging success caused by variation in any of these factors can lead to significant differences in predator-prey population dynamics. Therefore, we expect the evolution of foraging traits will depend on the relationship and interaction between the standing genetic variation and the

environmental variance in the trait, which ultimately gives rise to the phenotypic variation upon which natural selection can act.

Three conditions are necessary for local adaptation to occur in foraging behavior (Carriere and Roitberg 1996): 1) a proportion of the phenotypic variation must be heritable; 2) phenotypic variation in foraging must have consistent fitness consequences; and 3) gene flow between populations associated with different habitats must be negligible to allow evolutionary divergence in locally-adapted foraging behaviors. Although these conditions are true for simple phenotypes, the evolution of multivariate phenotypes is much more complex. Foraging behaviors are a composite set phenotype made up of many related phenotypic components that must evolve together for entire behavior to respond to selection. The manner in which suites of phenotypes respond to selection has and continues to be a central paradigm of evolutionary theory (Lande and Arnold 1983; Roff 1992; Stearns 1992). Selection favoring the increase in one trait may be constrained by a fitness trade-off between the trait under selection and a second trait that is genetically correlated with the trait under selection, for example offspring size and offspring number. However, only trade-offs that are the result of significant additive genetic covariation will be evolutionarily significant (Roff et al. 1999). Trade offs that are the result of genetic covariation will persist on evolutionary time scales because the genetic correlations are likely the result of either pleiotropy or tight linkage between the genes underlying each of these two phenotypes (Falconer and Mackay 1996). Therefore, to accurately predict the response of multiple phenotypic traits to selection, we must not only estimate the genetic variation of a trait but also the genetic covariation with other traits as the combination of these two factors will determine the rate and direction of future evolutionary change (Lande and Arnold 1983; Arnold 1986).

In this study we were particularly interested in the evolution of responses to herbivore-induced plant volatiles by arthropod predators. Although understanding the genetic basis of such traits is extremely important for predicting the long-term population dynamics in multitrophic systems, only a handful of studies have provided strong evidence of a genetic component in foraging behaviors. These include host acceptance (Mollema 1991; Powell and Wright 1992) and attraction to host-infested plants (Prevost and Lewis 1990; Gu and Dorn 1999, Wang et al. 2003) in response to plant chemicals. We have started to address the evolution of foraging under the presence of plant volatiles by conducting a set of artificial selection experiments focusing on several specific yet variable predator foraging traits, including response to herbivore-induced plant volatiles, that potentially affect both predator fitness and population dynamics. In general, artificial selection experiments provide a powerful tool to estimate genetic variation. Additionally, artificial selection can be used to estimate the strength and sign of genetic correlations that underlie multiple phenotypic components by quantifying the correlated response to selection on additional specific predator foraging traits.

We examined genetic variation in and covariation among predator foraging traits in a tritrophic system consisting of a bean plant (*Phaseolus lunatus* L.), the twospotted spider mite, *Tetranychus urticae* Koch, and the phytoseiid mite, *Phytoseiulus persimilis* Athias-Henriot. Early work on the chemical basis of attraction of *P. persimilis* to *T. urticae*-induced plant volatiles (Sabelis and van de Baan 1983; Dicke et al. 1990) demonstrated significant phenotypic variation in the olfactory response. While subsequent work reported significant phenotypic and genetic variation in response to spider mite-induced plant volatiles, dispersal in response to prey density and prey consumption rate was demonstrated in both *P. persimilis* (Margolies et al. 1997, Jia et al. 2002, Pels and Sabelis 1999) and the closely-related predatory mite *Neoseiulus*

womersleyi (Shicha) (Maeda 2005, 2006). However, the potential interaction of these traits with each other or with other ecological factors is unknown but presumably important in the population dynamics of this system and the evolution and maintenance of genetic variation in these traits in natural populations. Thus, this analysis of genetic variation and covariation in foraging traits is the first step needed to develop a comprehensive and predictive model of the evolutionary response to natural selection in a complex environment.

Phytoseiulus persimilis is a specialist predator on tetranychid mites (van Lenteren and Woets 1988) and is commonly used as a biological control agent for twospotted spider mites. In biological control, we are particularly concerned with the impact of foraging on the simple trophic interaction of a natural enemy and its target. One of the earliest and simplest formulations of this interaction is the Lotka-Volterra predator-prey model, which couples predator and prey population dynamics in homogeneous environments via predator consumption rate (which reduces prey population growth) and the rate of conversion of prey eaten into predators produced (which affects predator population growth). These two variables, consumption and conversion efficiency, reflect the basic link between predator foraging and population dynamics assuming, prey are always available. However, when predators must find prey in heterogeneous landscapes, predator dispersal and ability to find new resources affect both individual foraging success and regional predator-prey dynamics. In this case, the local consumption rate and conversion efficiency will affect regional dynamics, because by affecting local per capita prey availability they affect the dispersal rate of predators. In turn, when predators leave a prey patch they reduce the local predator population, while at the same time increasing colonization of other prey patches. Thus, traits that affect predator dispersal from patches are equally important to local and regional (i.e., among patch) dynamics (Hassell 1978;

Berryman and Gutierrez 1999). These traits will interact to affect the predator-to-prey ratio in each local patch, which in turn affects the stability of the species interaction (Hassell 1978; Berryman 1999).

The local interaction between *P. persimilis* and *T. urticae* is limited and ephemeral because when *P. persimilis* invade a spider mite-infested plant the predators quickly eliminate the local spider mite population (Chant 1961; Takafuji et al. 1983). This outcome is the result of a strong predator numerical response and its voraciousness. One component of the numerical response is predator aggregation (Nachman 2006). These predators locate and remain in prey patches in response to cues associated with prey density, including direct cues such as exuviae, feces, webbing, and eggs (Sabelis and van de Baan 1983), and important indirect cues such as prey-induced plant volatiles (Maeda et al. 1998; Mayland et al. 2000). At long range, volatiles attract predators to prey-infested plants or cause them to search more intensively around a prey-infested plant (Janssen 1999). Once a predator is on a plant, the same volatiles that attract predators are also important in local arrestment (Sabelis et al. 1984). This results in predator aggregation. The other component of the numerical response is the predator reproductive rate (Sabelis 1985), which is directly related to the rate of prey consumption (Sabelis 1981). Predators are generally found feeding in densely-packed prey colonies (Bancroft and Margolies 1999), so individual consumption rates are relatively constant and close to the maximum possible (Sabelis et al. 1999). When prey density decreases in the immediate vicinity of a predator, the predator will simply move to an adjacent area where the prey are still plentiful. It is only when prey density becomes scarce in the entire patch that the per capita predation rate drops.

Although the local interaction within a patch is generally unstable, the predator-prey interaction may persist on a regional scale as a result of repeated dispersal from and colonization

of new patches by both prey and predators (Diekmann et al. 1988; Nachman 1987, 1988, 1991; Sabelis et al. 1991; Walde 1991, 1994; Jansen and Sabelis 1992; Walde and Nachman 1999; McCauley et al. 2000). Predators usually disperse from occupied patches when prey density approaches zero (Takafuji 1977; Bernstein 1984; Zhang and Sanderson 1993; Zemek and Nachman 1998). However, some individuals disperse more readily, which extends the duration of the local interaction and ultimately results in the production of more dispersers (van Baalen and Sabelis 1995). That is, if predators stay in a patch until all prey are eliminated, local predator population growth rates should be high, local prey populations should show an immediate decrease, and the local interaction period will be short. Because the interaction is brief, the patch will produce few dispersing predators. If, on the other hand, predators continually disperse during the interaction, the local predator population growth rate will be lower, the local prey population will decrease at a lower rate (or even increase), and the interaction period will be longer. This patch will produce more predators to find and colonize other patches (Pels et al. 2002). Successful colonization of new prey patches is positively related to the number of dispersers produced in occupied patches (Sabelis et al. 1999); therefore dispersal rate is related to regional foraging success (Pels and Sabelis 1999). Furthermore, because the rate of local prey depletion is affected by predator consumption rates and conversion efficiency, these traits must also affect the length of the local interaction.

The major objective of this study was to quantify the genetic components of phenotypic variation in four ecologically-relevant foraging traits in the predatory mite, *P. persimilis* using standardized laboratory bioassays (Jia et al. 2002; Nachappa et al. 2006a, b). To this end multiple replicated selection regimes were used to create lines of *P. persimilis* with high and low levels (relative to an unselected control population) of the four described foraging traits:

consumption rate, conversion efficiency, dispersal response to prey density, and olfactory attraction to *T. urticae*-induced plant volatiles. A first replicate of selection was initiated with an unconventional approach via a combination of both mass selection and family selection to achieve sufficient sample sizes and a significant selection response.

We were particularly interested in the rate of and limits to the selection response. Selection limits may be imposed on a population either because of constraints by correlated traits or because all the alleles affecting the trait are either fixed or lost. It is also possible that artificial selection on dispersal is opposed by natural selection on dispersal or some correlated traits. We examined this possibility by relaxing artificial selection on the foraging traits to see if natural selection acting alone would reverse the changes obtained by direct selection on the trait.

To confirm the first replicate of selection, a second temporally distinct replicate of selection followed a more conventional approach, which imposed artificial selection every other generation with random mating in the other generations for the stable phenotypes obtained in the previous replicate. This approach was used to again ensure sufficient sample sizes and a significant selection response.

After stable replicated selection lines were produced, our second objective was to investigate the correlated responses in consumption, conversion efficiency, dispersal and olfactory response for all lines subjected to selection regime I. We also measured genetic correlations between life history traits, including time to emerge from egg, hatching percent, development time (time from nymph to adult ecdysis), and survivorship from egg to adult for lines in selection replicate I. Finally, we estimated fitness in terms of intrinsic rate of increase (r_m) for each foraging phenotypes in replicate I. To our knowledge this is the first experimental selection study that examines the genetic basis of a suite of ecologically-relevant foraging traits

that are likely to be critical for predator performance and predator-prey dynamics in heterogeneous landscape (Sabelis et al. 1999).

Materials and Methods

Study Species

The predatory mite *Phytoseiulus persimilis* (Acari: Mesostigmata: Phytoseiidae) is globally distributed and represents one of most important biological control agent for tetranychid mites in a number of agricultural systems (Helle and Sabelis 1985 a, b). This predator is of Chilean origin (Dosse 1958) and was subsequently shipped to other parts of the world, including the United States (Hussey and Scopes 1977). Phytoseiid mites reproduce by pseudoarrhenotoky, which is characterized by obligate fertilization of all eggs followed by a loss and/or heterochromatization of the paternal chromosomes in embryos that develop into males, resulting in a haploid condition of the males (Hoy 1979; Schulten 1985; Perrot-Minnot et al. 2000). Under normal conditions, the sex ratio is female-biased, usually close to 0.83 (Helle and Sabelis 1985b) and each female can produce 60 eggs in her lifetime (McMurty and Rodriguez 1987). *Phytoseiulus persimilis* has 5 developmental stages: egg, non-feeding larva, protonymph, deutonymph and adult (Sabelis 1981). Development time (egg to adult) at 25^{o} C is approximately 3 days, generation time (egg to egg) is 5 days, and average adult lifespan is 25 days (Takafuji and Chant 1976). Nymphs and adults feed on all stages of their tetranychid prey but preferentially consume prey eggs (Sabelis 1981); when prey are abundant, adults will consume 24 prey eggs per day (Sabelis 1981). Predators maximally produce 6 offspring per day, or one predator egg produced for every 0.13 prey eggs consumed (Nachappa unpublished).

Replicate selection lines were initiated from a source population of *P. persimilis* that were purchased from Koppert Biological Systems, Inc. (Romulus, Michigan), a commercial

supplier of beneficial arthropods. *Phytoseiulus persimilis* were reared on twospotted spider mites, *Tetranychus urticae* Koch (Acari: Prostigmata: Tetranychidae), in the laboratory for one generation under 24±1°C, 60-70% relative humidity, 16:8 h (L: D) photoperiod to allow the predators to acclimate to laboratory conditions. *Tetranychus urticae* (prey) were maintained on lima beans (*Phaseolus lunatus* cv. 'Sieva') under the same temperature and photoperiod regime. Selection lines were maintained in 1.89 l. mason jars with the metal lids removed and replaced with fine mesh screen to allow air exchange. *T. urticae*-infested bean plants were added to the jars every other day. Every week the bottom layers, consisting of dry leaves with few spider mites or predators, were discarded. Seven to 10 day old adult female predators were used for all experiments.

Phenotypic Assays of P. persimilis

Consumption and Conversion Efficiency Consumption and conversion efficiency were measured in a bioassay developed by Jia et al. (2002). *Phytoseiulus persimilis* were placed in a vial 2.5-cm diam x 5.5- cm ht along with a 2-cm diam bean leaf disk that had 40-50 one-day old *T. urticae* eggs. The vial was sealed with parafilm and maintained in an environmental chamber at 24±1°C, 60-70% relative humidity, and 16:8 h L: D photoperiod for 24 h, after which the number of prey eggs left on the disk was counted. In addition, predator eggs generated within the 24-h period were also counted. Consumption rate was defined as the number of prey eggs consumed by a predatory mite within 24 h and conversion efficiency was the ratio of the number of prey eggs consumed to the number of predator eggs laid in that time.

Dispersal Response Dispersal response of *P. persimilis* was measured in a Petri dish bioassay modified from Maeda and Takabayashi (2001) and Nachappa et al. (2006a). A 2.2-cm diam leaf disk with *T. urticae* eggs was placed on water-saturated cotton wool in 90-cm diam

plastic petri dish. Ten *T. urticae* (prey) adult females were introduced on the leaf disk and allowed to oviposit for 24 h; eggs were removed to achieve the appropriate density on the leaf disk or source. Five *P. persimilis* adult females were then introduced onto each leaf disk and allowed a 30 min acclimatization period, after which we connected a 30 x 5 mm parafilm bridge to the disk; predators that walked onto and out along the bridge were counted as dispersed. Predators were observed continuously and were removed as soon as they came to or passed the midpoint of the bridge. The time taken to disperse was then recorded. Typically, bidirectional selection is imposed under the same test conditions for high and low lines. However, we selected the high- and low-dispersal lines under different environmental test conditions (i.e., prey egg density). Previous research has shown that the dispersal speed of an individual *P. persimilis* is significantly affected by the density of prey (40 vs. 5 prey eggs) (Nachappa et al. 2006a). Thus, in this study the high dispersal line represents those individuals that dispersed from the leaf disk in the presence of 40 eggs, while the low dispersal line is comprised of individuals that remained on the leaf disk in the presence of only 5 eggs. Because the high and low dispersal lines were selected under different environmental test conditions it is difficult to directly compare the high and low selection lines. Unselected controls for both the high and low selection lines were maintained under each environmental test condition.

Olfactory Response Attraction of *P. persimilis* to *T. urticae*–induced plant volatiles was examined using a 40-cm diam circular arena as in Jia et al. (2002) and Nachappa et al. (2006b). Selection for high- and low-olfactory response lines was conducted using two different levels of volatiles; we used a low level of volatiles to select for the high-olfaction line and high levels of volatiles to select for the low-olfaction line. To achieve high or low volatile production we manipulated prey density on bean plants for different durations of time (for details see Nachappa

et al. 2006b). Leaf disks (2.2 cm diam) were cut from the manipulated plants which served as source of the two different volatiles levels in the selection experiments. Test conditions were similar to those followed in Nachappa et al. (2006b). Phenotyping was performed in two arenas that were set up side-by-side with a vertical cardboard divider (60 cm ht x 55 cm w) between to reduce air movement and possible drift of volatiles. In the center of one arena we placed a leaf disk from a *T. urticae*-infested plant; in the other we placed a leaf disk from an uninfested plant as a control. For each trial, 10 to 12 adult female predatory mites were starved for 2 h and then released at the edge of the arena. We recorded the number of predators that found the central leaf disk (source of volatiles) in the arena in the first 10 minutes. The high-olfaction line consisted of individuals that found the central leaf disk in the presence of low-level of volatiles in the vicinity (arena). The low-olfaction line consisted of individuals that did not find the leaf disk despite a high-level of volatiles in the arena. Similar to the dispersal selection lines, the high- and low olfactory response lines were selected under different environmental conditions, hence we maintained control lines for both the high and low dispersal lines. Comparisons between the test disks (infested plant) and control disks (clean plant) allowed us to test whether the response differed from that expected under random (non-attracted) movement. Thus, this selection procedure focused on olfactory sensitivity.

Artificial Selection Lines

To determine whether observed phenotypic changes that have occurred in response to selection are the result of selection rather than effects of random genetic drift it is essential that all selection experiments be replicated (Falconer and Mackay 1996; Morgan et al. 2003). Generally, this replication would occur contemporaneously for all replicate lines within each selection treatment. However, it was logistically impossible to maintain contemporaneous

replicate lines when performing selection on foraging behavioral phenotypes in *P. persimilis*. Thus, rather than eliminating replication from our selection experiment, we created replicates that were temporally separated. In the first replicate of selection, because of limitations in the number of offspring created and scored each generation, we used two generations of individual selection followed by family selection and random mating to increase population sizes (See Selection Lines I below). In the temporally distinct second replicate of the selection experiment (See Selection Lines II below), we used a more typical selection regime by alternating a generation of individual selection with a generation of random mating, thus allowing us to use a consistent selection regime and still obtain population sizes large enough to phenotype and use for artificial selection.

Selection Lines – I Bidirectional selection was initiated using a combination of mass individual selection (Falconer and Mackay 1996) and family selection (Lynch 1980) to develop the initial replicate of the selected lines (Fig. 4-1A). Consumption and conversion efficiency lines were initiated by phenotyping 300 to 350 individuals from a randomly mating population, whereas the dispersal and olfactory response lines were initiated from 170 to 200 individuals. From these initial populations, one line was selected for increased trait values, one line for decreased trait values. Further, for the dispersal and olfactory response lines a randomly mated population with respect to the trait under selection served as the unselected control because the high and low lines for these foraging traits were tested under different environmental conditions. The proportion selected as breeders in each generation was the 20% extremes (high and low) of the base population distribution. The same percentage of individuals was selected from each generation to form the subsequent generations. We tested even-aged individuals, such that adults were allowed to oviposit for only 3 to 4 days and then removed. Because of this procedure only

a small number of offspring were available for the following round of selection. The result was that population size was reduced to 10-20 individuals after two generations of individual mass selection for consumption and conversion efficiency and three generations of selection for dispersal and olfactory response. Thus, to increase our sample size we modified the selection protocol at generation 2 to family selection. For family selection a whole family is chosen to represent the breeders for the next generation as a unit according to its mean phenotypic value (Falconer and Mackay 1996). These families are then mixed within lines to produce the subsequent generations. Each family was founded by a single mated female and was maintained in a 0.5 l mason jars under laboratory conditions. Family selection was started with 10-20 families, of which 3-4 families were selected to continue each line. From each of these families, 8-10 adult female *P. persimilis* were selected as mothers and their offspring were pooled to form the next generation. At generation 3, each line was randomly mated within each line (i.e., selection was not imposed) because the lines were initially composed of partially inbred individuals (offspring of the generation 2 families) (Fig. 4-1A). At generation 4 individuals were randomly mated within lines at which time the population consisted mainly of outbreds (mating between generation 3 offspring) and resulted in an increase in the population size of each line. Individual selection was resumed at generation 5 and continued until there was no longer any change in the phenotypic trait mean.

It is possible that artificial selection on consumption, conversion efficiency, dispersal or olfaction might be opposed by natural selection acting on these traits, or some other linked traits, in the direction opposite of the artificial selection. If this is the case we would expect the phenotypic response observed in the selection lines would have been lost when selection was relaxed. To test this possibility, selection was relaxed after the generation in which the selection

response was 0. This was generation six for all traits with the exception of consumption in which selection was relaxed at generation seven. After selection was relaxed these lines were maintained by collecting fifty to sixty offspring from each line in the same manner described in the selection experiment. Levels of consumption, conversion efficiency, dispersal and olfaction were measured after 10-12 generations of relaxed selection and within line random mating at which time we tested 40-50 adult female *P. persimilis* from each selection line.

Selection Lines – II For those traits in which selection appeared to be stable after selection was relaxed we conducted a second replicate of selection: high consumption, high conversion efficiency and high dispersal response. The selection lines in the second replicate were initiated from a source population of a different cohort from the Koppert source population. Predator conditions and age of predators were identical to those in the first replicate of the selection experiment. Selection was initiated by phenotyping 80-100 adult female predators from the source population for each trait. Selection was imposed as before by utilizing the breeding individuals that made up the 20% tail of the base population distribution (Fig. 4-1B). Individual based mass selection was used for each selection event. However, because of the difficulties encountered in the maintenance of sufficient population sizes during the first replicate, in the second replicate we only selected every other generation until no further change in the trait was observed (Fig. 4-1B). Similar to selection replicate I, an unselected control was maintained for the high dispersal line. We did not initiate a relaxation experiment in the second replicate.

Correlated Responses to Selection

Foraging Traits After selection plateaued in the first replicate of selection, we examined correlated responses in consumption, conversion efficiency, dispersal and olfactory response for

all lines subjected to selection regime I. The test populations were started by randomly choosing adult female predators from each selection line. Each foraging phenotype was then measured using previously described bioassays (see Phenotypic Bioassay section).

Life-History Traits We developed a life table to estimate life-history parameters and genetic correlations between life history traits and selected traits in each selection line of replicate I. A life table was also developed for the unselected control or base population from which the first replicate of selection lines was initiated. To estimate the life table of each line it is essential to have a cohort of age-synchronized individuals. Thus we used ten to fifteen adult female predators to produce a cohort of offspring from each selection line. These females were placed on whole leaves set abaxial side up on water-saturated cotton wool in 90-cm diam plastic petri dish. The adult female predators were allowed to oviposit for 24 h. The cohort upon which the life-history traits were measured was initiated by collecting thirty to forty one-day-old predator eggs from each line and placing them individually on a 2.2 cm diam leaf disk which was inserted into small glass vial. The vial was sealed with parafilm and maintained in an environmental chamber at 24$\pm$1°C, 60-70% relative humidity, and 16:8 h L: D photoperiod. The vials were inspected and prey eggs were provided as food daily. Once nymphs reached adulthood, adult females were placed as a group in a single vial for 4-8 h under the environmental conditions mentioned above to allow random mating. Ten mated adult females were then placed individually in vials under similar environmental conditions as described above. The vials were checked daily and prey eggs were provided as food until < 50% of the population were alive. The life-history traits measured were hatching time (time to emerge from egg), hatching percent, development time (time from nymph to adult ecdysis), survivorship from egg to adult of individual adult females.

Based on the complete life-table, we calculated the intrinsic rate of natural increase, r_m for-each selection line assayed in the test population. The intrinsic rate of increase can be computed as a solution to: $1 = \Sigma l_x m_x \, exp\ (-r_m x)$ where $l_x m_x$, is the net female productivity, l_x, is the fraction of females alive at age x, and m_x, is the average number of female offspring produced by each female at age x. This equation was iterated for r_m until a value of one was obtained. This value of r_m is the maximum exponential rate of increase by a population growing within defined physical conditions (Birch 1948; Carey 1993). Estimates of standard errors for these demographic growth parameters were generated by jackknife analysis of $l_x m_x$ life-table data. The jackknife method removes one observation (i.e., a single individual) at a time from the original data set and recalculates the statistic of interest from the truncated data set. These new estimates, or pseudovalues, form a set of jackknife estimates upon which summary statistics (means and variances) for r_m can be estimated (Shao and Tu 1985; Meyer et al. 1986). The jackknife method of resampling is commonly used for estimating variance for population growth statistics (Meyer et al. 1986).

Statistical Analysis

Analyses were conducted using the statistical program SAS v 9.1 (SAS Institute 2002). To measure the response to selection a one-way Analysis of Variance (ANOVA) using PROC GLM was performed to identify direct responses to selection between the high- and low-selection lines for consumption and conversion efficiency in replicate I. A one-way ANOVA was done to determine direct responses to selection between the selection lines and control for dispersal and olfactory response. Because the high- and low-dispersal and olfactory response lines were selected under different environmental conditions, separate controls for the high and low lines were maintained for the respective foraging trait. The model tested for differences in

the mean phenotypic values each generation between selection lines and the unselected control. The mean phenotypic value of the high- and low lines post-relaxation of selection was compared with the unselected control using a one-way ANOVA. For the dispersal and olfactory response lines, relaxation effects were examined using a one-way ANOVA between level of trait post-relaxation and the control line. To confirm that responses observed in selection replicate I were consistent, a second temporally distinct replicate was initiated on stable phenotypes obtained in selection regime I. A univariate GLM analysis was performed between selection lines of replicate I and II for the stable phenotypes. Based on results of selection regime I and II (Fig. 4-1A, B), realized heritability (h^2) for each selection line was calculated by regressing the cumulative selection differential (s) on the cumulative selection response (R). The selection response and the selection differential were calculated for each generation in which selection was applied (in generations where selection was relaxed the s = 0; Fig. 4-1A, B) (Falconer and Mackay 1996). The selection differential (s) was calculated each generation as the difference between the phenotypic mean of selected parental population relative to the mean of the entire population. The response to selection (R) was calculated as the difference between the phenotypic mean of the progeny and the phenotypic mean of the previous generation (Falconer and Mackay 1996). The realized heritabilities (h^2) and associated standard errors were calculated in PROC GLM by regressing the Σs on ΣR. The slope of this relationship represents the line-specific estimate of the heritability (Falconer and Mackay 1996).

The following analyses were performed to measure correlated responses to selection in replicate I. A one-way ANOVA (PROC GLM) was used to measure correlated responses in consumption rate and conversion efficiency for the high and low lines and unselected base population of each foraging trait. Correlated response to dispersal was calculated using a two-

way ANOVA with effects of selection line and prey density in the model. Because the high- and low-dispersal lines were selected under different prey density conditions (5 prey for low line and 40 prey for the high line) prey density was included in the model. The correlated responses to olfactory response were also calculated using a two-way ANOVA with effects of selection line and volatile level in the model. To differentiate between random movement and olfactory sensitivity, we had two volatile test conditions: infested volatiles and clean volatiles. Hence, volatile level was included in the model. A one-way ANOVA (PROC GLM) was used to test for correlated responses to selection in the different life-history traits (i.e., hatching time, hatching percent, development time and adult survival). Mean jackknife estimates of intrinsic rate of increase (r_m) were compared between high- and low lines and control for each foraging trait using a one-way ANOVA.

Results

Response to Selection, Stability and Heritability of Phenotypes

Consumption Selection regime I significantly affected mean prey egg consumption in the high and low lines in generation 1 ($F_{1,156}$ = 78.25, P < 0.0001, Fig. 4-2). The high and low consumption lines was differentiated at the end of the 7-generation period ($F_{1,23}$ =801.22, P < 0.0001, Fig. 4-2). Prey consumption rate responded rapidly to selection with an asymmetrical response; it was stronger in the high line than in the low line (mean prey consumption rate ± se, high line: 42.00 ± 1.05; low line: 17.20 ± 1.41; base: 25.95 ± 0.91, Fig. 4-2).

There were significant differences among the high- and low consumption lines than the unselected control after relaxation of selection (measured in selection regime I only, $F_{2,120}$ =131.99, P < 0.0001). The high consumption line remained at high levels despite relaxation of selection, but in the low line the prey consumption rate increased significantly when selection

was discontinued so that it was no longer different than the base (mean prey consumption rate ± se, high line: 40.76 ± 0.63; low line: 28.90 ± 0.58; base: 27.16 ± 0.68).

To confirm that the lines were in fact responding to selection and not simply diverging because of random genetic drift, we performed a second replicate of selection for the stable phenotypes (high consumption). The prey consumption rate was not significantly different in the high lines between selection regimes at the end pf the experiment ($F_{1,55}$ = 1.13, P = 0.29, Fig. 4-2, mean consumption ± SE, high line selection regime I: 42.00 ± 1.71; high line selection regime II: 39.91 ± 0.98). The selection response was more rapid in selection regime I than selection regime II because in the former selection was imposed every generation (except generation 3 and 4) whereas selection was imposed every other generation in selection regime II (Fig. 4-1A, B).

Realized heritabilities for consumption were estimated by regressing the cumulative response to selection (ΣR) on the cumulative selection differential (Σs) for each selection line. Heritability estimates of the high and low lines were significant and greater than zero (Table 4-1). Realized heritabilities for high consumption lines were comparable between the two selection regimes (Table 4-1).

Conversion Efficiency There was significant differentiation between the high- and low-conversion lines by generation 1 ($F_{1,146}$ = 144.48, P < 0.0001, Fig 4-3) which continued until the end of the selection experiment ($F_{1,101}$ =75.80, P < 0.0001, Fig 4-3).

Two months after selection was relaxed, the high conversion efficiency line remained significantly higher than the low line and control whereas the low conversion efficiency line was comparable to the base population (measured in selection regime I only, $F_{2,111}$=131.99, P=0.008; mean conversion efficiency ± se, high line: 0.18 ± 0.013; low line: 0.11 ± 0.014; base: 0.13 ± 0.014).

The second replicate of the high conversion efficiency line was not significantly different from selection replicate I at the end of the experiment ($F_{1,78} = 0.07$, $P = 0.79$, Fig. 4-3, mean conversion efficiency ± SE, high line selection regime I: 0.17 ± 0.007, high line selection regime II: 0.17 ± 0.01).

Heritability estimates from the high and low conversion lines was significant (Table 4-1). Realized heritabilities for the high conversion efficiency lines were comparable between the two selection regimes (Table 4-1).

Dispersal Response As mentioned previously, the high and low dispersal lines were selected under different environmental test conditions so unselected controls were maintained under each environmental test condition. After the first generation of selection, the high dispersal lines were differentiated from the base population ($F_{1,183} = 52.29$, $P < 0.0001$, Fig. 4-4A) and continued to be higher through the end of selection ($F_{1,99} = 84.47$, $P < 0.0001$, Fig. 4-4A). The response to selection reached a plateau at generation 2 which suggests that the dispersal response of *P. persimilis* has a lower potential for selection than other foraging traits that have higher levels of variation. There was significant differentiation between the low dispersal line and the unselected control by generation 1 ($F_{1,146} = 5.48$, $P = 0.02$, Fig. 4-4B); but there were no differences in generation 2 ($F_{1,66} = 0.02$, $P = 0.89$). Differences were observed at generation 3 ($F_{1,102} = 5.13$, $P = 0.03$) and continued through the 6-generation period ($F_{1,113} = 8.19$, $P = 0.005$, Fig. 4-4B).

The relaxation experiment indicated that the high dispersal line had a higher dispersal rate than the base population ($F_{1,78} = 25.28$, $P < 0.0001$, mean time to disperse ± se, high line:10.22 ± 2.97; base: 40.49 ± 2.97). The low dispersal line did not show a loss in phenotypic

value of the trait compared to the base population after relaxation of selection ($F_{1,70}$=18.42, P <0.0001, mean time to dispersal ± se, low line: 22.66 ± 1.77; base: 9.45 ± 2.50).

Although, both the high- and low-dispersal lines were stable after relaxation of selection, we initiated a second temporally separate replicate only for the high dispersal lines. We were only interested in the stability of the high foraging phenotypes including consumption and conversion efficiency because we wanted to examine the impact of the high foraging phenotypes on predator-prey dynamics in the greenhouse. In the second replicate of selection, the high dispersal line was significantly different from the control in generation 1 ($F_{1,98}$=9.97, P=0.0003, Fig. 4-4A) and continued through the experiment ($F_{1,79}$=48.92, P<0.0001, Fig. 4-4A). The response to selection in the upward direction plateaued in generation 2 for both selection regimes (Fig. 4-4A). Further, the second replicate of the high dispersal line was not significantly different from selection replicate I ($F_{1,118}$ = 2.61, P = 0.10, Fig. 4-4A, mean time to disperse ± SE, high line selection regime I: 10.20 ± 0.47, high line selection regime II: 11.38 ± 0.57).

The heritability estimates were significant for both the high- and low-dispersal lines. In contrast to other foraging traits, heritability was greater in the low line than the high line (Table 4-1). Realized heritabilities for high dispersal lines were comparable between the two selection regimes (Table 4-1).

Olfactory Response Similar to the protocol for dispersal selection lines, the high- and low-olfactory response lines were selected under different test conditions. We maintained controls for both test conditions where predator response to clean volatiles was assayed to differentiate between random movement in the presence of clean volatiles and olfactory sensitivity in the presence of prey-infested volatiles. There was no significant differentiation between the high olfaction line and the unselected control by generation 1 ($F_{1,16}$ = 2.62, P =0.13,

Fig. 4-5A). However, differences were observed in generation 2 ($F_{1,14}$=5.22, P =0.04) until the end of the 6-generation period ($F_{1,11}$ =12.96, P =0.004, Fig. 4-5A). There was significant differentiation between the low olfaction line and the unselected control in generation 1 ($F_{1,13}$= 7.02, P =0.02, Fig. 4-5B); but no significant differences were observed at the end of the selection experiment ($F_{1,7}$ =3.04, P =0.13, Fig. 4-5B). These results indicate that there is little or no genetic variation in the low-olfactory response or the environmental component of the phenotype masks the genetic component.

The high olfactory response line reverted back to pre-selection levels after relaxation of selection ($F_{1,7}$= 2.01, P =0.19, mean percentage response ± se, high line: 25.00 ± 2.40; base: 18.00 ± 2.17). The low-olfactory response line was not different from the base population after relaxation of selection ($F_{1,6}$= 3.43, P =0.11); low line: 37.50 ± 3.81; base: 47.50 ± 3.81). Hence selection was not imposed a second time on the high- and low-olfactory response lines.

The heritability estimates were much lower for the olfactory response lines than the other foraging traits, indicating that most of the variability in the olfactory response resulted from factors other than additive genetic variance (Table 4-1). Heritability estimates for the low olfactory response line were not significant (Table 4-1).

Correlated Responses to Selection

Foraging Traits

Consumption Bidirectional selection did not the affect prey consumption rate of the conversion efficiency ($F_{2,25}$ = 0.00, P = 0.99), dispersal ($F_{2,23}$ = 0.06, P = 0.94) or olfactory response ($F_{2,25}$= 0.22, P = 0.814) lines compared to the base population. The average prey consumption rate of the base population was 25.20 ± 0.93 eggs per 24 h.

Conversion Efficiency A negative correlation was detected between the low consumption line and conversion efficiency ($F_{2,24}$= 7.34, P = 0.003). The low-consumption line had higher conversion efficiency than the high consumption line and base population (mean conversion efficiency ± se, high line: 0.11 ± 0.05; low line: 0.14 ± 0.05; base population: 0.12 ± 0.005). Selection did not affect the conversion efficiency of the dispersal lines ($F_{2,23}$ = 0.13, P = 0.87) and olfactory response lines ($F_{2,25}$= 3.61, P = 0.06).

Dispersal Response In contrast to the consumption and conversion efficiency selection lines, the dispersal lines were selected under different test (prey density) conditions: 5 prey for the low line and 40 prey for the high line. Hence, the correlated response to dispersal was calculated using a two-way ANOVA with effects of selection line and prey density in the model. The average leaving time of the base population in the presence of 5 eggs was 25.00 ± 5.08 and 40 prey eggs was 55.55 ± 5.61.

Consumption was positively correlated with dispersal ($F_{2,55}$ = 5.86, P = 0.005). That is the high consumption line left the prey patch sooner, and the low line stayed longer on the leaf disk than the unselected control (Fig. 4-6A). The dispersal response was slower in the presence of 40 prey eggs than 5 eggs ($F_{1,55}$ = 41.38, P < 0.0001, Fig. 4-6A).

Conversion efficiency was not correlated with dispersal response ($F_{2,54}$= 1.41, P = 0.25, Fig. 4-6B). However, dispersal response of high- and low conversion efficiency lines was much faster with 5 prey eggs than 40 eggs ($F_{1,54}$= 54.65, P < 0.0001, Fig. 4-6B).

Olfactory response was positively correlated with dispersal response ($F_{2,61}$= 10.61, P =0.0002, Fig. 4-6C). The high olfactory response line left the prey patch sooner than the low line and unselected control (P<0.0001), and the low line stayed slightly longer on the leaf disk than the unselected control (P=0.05). Similar to the consumption and conversion lines, the

olfactory response lines also dispersed faster in the presence of 5 eggs than 40 eggs ($F_{1, 61}$ = 38.23, $P < 0.0001$, Fig. 4-6C). There was a significant two-way interaction between selection and prey density on the dispersal response of the olfactory lines than the control ($F_{2, 61} = 5.07$, $P = 0.009$).

Olfactory Response The olfactory response bioassay was conducted under two test conditions (high- and low-level of volatiles). We maintained a control where predator's response was assayed in response to clean volatiles to differentiate between random movement in the presence of clean volatiles and olfactory sensitivity in the presence of prey-infested volatiles. A two-way ANOVA with selection regime and type of volatiles in the model was used to test for correlated responses in olfaction. The mean percentage response of the base population in the presence of infested volatiles was 42.00 ± 4.28 and in the presence of clean volatiles was 16.00 ± 4.28.

The high consumption line was positively correlated with olfactory response ($F_{1,24}$ = 19.90, $P < 0.0001$, Fig. 4-7A). The low line was comparable to the unselected control. For all lines the olfactory response increased significantly in the presence of infested volatiles compared to clean volatiles ($F_{2,24} = 70.4$, $P < 0.0001$, Fig. 4-7A). There was a significant two-way interaction between selection regime and volatile level on the olfactory response of the consumption lines ($F_{2,24} = 6.63$, $P = 0.006$, Fig. 4-7A).

The high conversion efficiency line was also positively correlated with olfactory response ($F_{2, 24} = 136.52$, $P < 0.0001$, Fig. 4-7A). The high line had higher olfactory sensitivity compared to the low line and base population. Again, the olfactory sensitivity of mites increased in the presence of volatiles but not to clean volatiles ($F_{1, 24} = 26.00$, $P < 0.0001$, Fig. 4-7B). There was

a significant effect of interaction ($F_{2, 24}$ = 17.48, P< 0.0001) between selection and volatile level on the olfactory response (Fig. 4-7B).

Similar to other high foraging phenotypes, the high dispersal line also showed positive correlation with olfactory response ($F_{2, 18}$= 9.85, P = 0.0013, 4-7C). The low dispersal line had diminished olfactory response compared to the high line and base population (Fig. 4-7C). The lines showed an increased olfactory response in the presence of volatiles compared to when they were absent ($F_{1,18}$= 44.52, P <0.0001, Fig. 4-7C). There was a significant selection x volatile interaction ($F_{2,18}$ = 7.83, P = 0.0036) on the olfactory response of the dispersal lines compared to the unselected control (Fig. 4-7C).

Life-history Traits and Intrinsic Rate of Increase

Hatching Time and Percent Selection regime had no significant effect on the hatching time (days) of the high- and low-consumption ($F_{2,102}$ = 0.28, P = 0.75), conversion efficiency ($F_{2,111}$ = 1.05, P = 0.35), dispersal ($F_{2,107}$ = 1.95 P = 0.14) or olfactory response ($F_{2,104}$ = 1.00, P = 0.37) lines compared to the unselected control. The average hatching time in the base population was 1.21 ± 0.08 days.

Hatching percent did not differ in the high- and low-consumption ($F_{2,102}$ = 1.11, P = 0.33), conversion efficiency ($F_{2,111}$ = 2.38, P = 0.09), dispersal ($F_{2,107}$ = 1.01 P = 0.37) or olfactory response ($F_{2,104}$= 1.02, P = 0.36) lines compared to the unselected control. The average hatching percent in the unselected base population was 94.73 ± 3.59.

Development Time Selection regime had a significant effect on the development time (days) from nymph to adult ecdysis in the consumption lines ($F_{2,101}$ = 7.12, P = 0.001). The low consumption line had a slightly longer development time compared to high consumption line and unselected control (mean development time ± se, high line: 3.00 ± 0.03; low line: 3.16 ± .04;

base population: 3.00 ± 0.03). Bidirectional selection did not affect development time of the conversion efficiency ($F_{2,106}$ = 1.08, P = 0.45), dispersal ($F_{2,105}$= 1.98, P = 0.14) or olfactory response ($F_{2,103,}$ = 2.17, P = 0.11) lines compared to the unselected control population. The average development time in the base population was 3.00 ± 0.03 days.

Survivorship Bidirectional selection on foraging traits did not affect the survivorship of the high- and low-consumption ($F_{2,81}$ =0.29, P = 0.75), conversion efficiency ($F_{2,81}$ =0.83, P = 0.43), dispersal ($F_{2,81}$ =0.04, P = 0.96) or olfactory response ($F_{2,81}$ =0.49, P = 0.61) lines compared to the unselected base population. The percentage survivorship for a cohort of predatory mites from the base population was 68.57 ± 3.66.

Fecundity The high consumption line had a significantly higher fecundity than the low consumption line and the unselected control ($F_{2,66}$ =54.67, P <0.0001, mean fecundity ± se: high line: 3.58 ± 0.12; low line: 1.86 ± 0.12). Similar result was obtained for conversion efficiency lines ($F_{2,66}$ =98.18, P <0.0001, mean fecundity ± se: high line: 3.51 ± 0.08; low line: 1.94 ± 0.08). Selection on high- and low-dispersal did not affect daily fecundity of the lines ($F_{2,66}$ =0.85, P =0.43, mean fecundity ± se: high line: 2.34 ± 0.08; low line: 2.12 ± 0.08). Similarly, selection did not affect fecundity of the high- and low olfactory response lines ($F_{2,66}$ =2.54, P =0.08, mean fecundity ± se: high line: 2.12 ± 0.08; low line: 2.03± 0.08). The average daily fecundity in the base population was 2.27 eggs.

Intrinsic Rate of Increase Bidirectional selection significantly affected the intrinsic rate of increase (r_m) of the consumption lines ($F_{2,27}$ =854.39, P <0.0001, Table 4-2) and conversion efficiency lines ($F_{2,27}$ =569.43, P <0.0001, Table 4-2) compared to the unselected base population. The high consumption line had the highest intrinsic rate of increase and the low consumption line had the lowest. However, selection did not affect r_m of the dispersal lines

($F_{2,27}$ =2.88, P =0.07, Table 4-2) or olfactory response lines ($F_{2,27}$ =1.63, P =0.21, Table 4-2) compared to the unselected control line.

Discussion

Selection experiments are a powerful tool to estimate genetic variation and gain information about the genetic architecture of traits, including duration of response, asymmetry of response and selection limits. Artificial selection can be used to create foraging phenotypes that differ by a single trait to determine potential correlations in specific predator foraging traits and, hence, the adaptive significance of the manipulated traits. Our experiments demonstrate that all four foraging traits evaluated in *P. persimilis* -- prey consumption rate, conversion efficiency, dispersal and olfactory response -- are genetically variable and can evolve rapidly in response to selection. For all traits except olfactory response, there was a rapid response to selection and steady divergence of the high and low lines, which suggests that multiple genes probably affect these traits (Macnair 1990; Falconer and Mackay 1996; Orr 1998). Selection response in the foraging traits peaked after 3 or 4 generations for both high and low lines. For all traits we observed an asymmetrical response to selection, with selection for increased foraging behavior producing a faster response than selection for decreased foraging behaviors.

Previous studies on *P. persimilis* have demonstrated phenotypic variation in predator responsiveness to volatiles produced by *T. urticae*-infested bean plants (Margolies et al. 1997; Margolies 1999; Jia et al. 2002). Maeda (2006) also found genetic variation in dispersal tendency, olfactory response, prey consumption and fecundity in another predatory mite, *Neoseiulus womersleyi* (Shicha). The existence of natural genetic variation in dispersal rate, and its impact on the local predator-prey interaction, was suggested by Pels and Sabelis (1999). They tested two isofemale lines of *P. persimilis*, each derived from a different geographically

isolated population, and found consistent differences in prey-dependent dispersal; one line dispersed only after all prey were eliminated, while in the other some females began dispersing while prey were still present. To our knowledge these are the only studies that have focused on the genetic variation in foraging traits in the evolution of prey-finding by predators in a tritrophic system.

The realized heritabilities for foraging traits obtained from the selection experiments were much larger than expected for most behavioral traits in animals (Plomin 1990). The strong response to selection and high heritability estimates confirms the magnitude of genetic influence on the foraging traits. Heritability estimates from the present study for consumption and conversion efficiency were larger than those estimated for the dispersal and olfactory response. A previous study in *P. persimilis* showed that broad sense heritability estimates for consumption and oviposition rate estimated from isofemale lines were 0.88 ± 0.09 and 0.18 ± 0.04, respectively (Jia et al. 2002). The realized heritabilities estimated for dispersal and olfactory response in *P. persimilis* was less than 0.5 (except for low dispersal line). Heritability estimates for olfactory response were below the range 0.44–0.82 of those estimated for olfactory response in Margolies et al. (1997). This means that most of the variability in olfactory response cannot be attributed to additive genetic variance. In addition, heritabilities for the high consumption, high conversion efficiency and high dispersal response were comparable under the two selection regimes. This confirms that the patterns observed in the initial selection responses could be replicated, thus confirming that the lines were in fact responding to selection and not simply diverging because of random genetic drift. Laboratory estimates of heritability are thought to overestimate natural heritabilities due to reduced environmental variability compared to a field population (Riska et al. 1989). However, some studies show that laboratory estimates provide

reasonable estimations of magnitude and significance of heritabilities in the wild (Riska et al. 1989; Weigensberg and Roff 1996).

The only trait that did not show a response to selection was the low olfactory response, which was not different from the unselected base population even after 3-4 generations of selections. Empirical evidence for the depletion of genetic variance in single traits by selection is diverse. Limits were initially thought to be due to the exhaustion of standing variation in populations. However, theoretical work (Lande 1975) showed that mutation could maintain genetic variance in large populations and this could contribute to selection responses, as validated empirically (Frankham 1980; Mackay et al. 1996; Hill and Mbaga 1998). Nevertheless, natural selection can affect the level of genetic variation in natural populations of considerable size (Merila et al. 2001). Low-olfactory response may have been under strong and continuing directional selection, which may have resulted in the fixation of genetic variation. This might explain the lack of heritability in the low-olfactory response line; hence, there appears to be little genetic variance available for direct selection. Another hypothesis is that mechanistic or physiological constraints make it unlikely that genetic variation in one direction will be generated by mutation (Blows and Hoffman 2005). In predatory mites, the size of the mite puts constraints on the elaborateness of the sensory system (peripheral olfactory system) and the size of the neuronal circuits that process chemical cues. This may likely limit evolutionary divergence in olfactory response of mites.

We were also interested in examining the limits to the selection response. Selection limits may be imposed on a population either because of constraints by correlated traits or because all the alleles affecting the trait are either fixed or lost. It is also possible that artificial selection on dispersal is opposed by natural selection on dispersal or some correlated traits. We examined this possibility by relaxing artificial selection on all foraging phenotypes to see if natural

selection acting alone would reverse the changes obtained by direct selection on the foraging traits. All high foraging phenotypes were stable for 10-12 generations (approximately 2 months) after relaxation of selection except the high olfaction line. The low foraging phenotypes reverted back to pre-selection levels except in the low-dispersal line. In unpredictable environments, populations are expected to exhibit polymorphism for foraging traits (Southwood 1977). In fact, Jia et al. (2002) showed that there was a continuous distribution of foraging behaviors including prey consumption, fecundity, dispersal and olfactory response in *P. persimilis*. The persistence of the high foraging phenotypes and decline in the low phenotypes (with one exception) indicates that the low foraging phenotypes can be lost under certain environmental conditions unless specific selection for these traits occurs. All selection lines were reared on abundant prey resources in the relaxation study, which suggests that different genotypes may be maintained under different environments. For example, the low consumption line might be successful during fluctuating prey resources, whereas the high consumption line is maintained only under abundant prey resources. Both theoretical (Barton and Turelli 1989; Goldstein and Holsinger 1992) and empirical (Denno et al. 1991) studies suggest that if different genotypes exist and are favored by different environments, genetic variation can be maintained by spatially fluctuating environments. Temporally fluctuating environments also may maintain genetic variation (Mackay 1981; Gillespie and Turelli 1989) and this may be accomplished by opposing selection on the trait in question.

In theory, foraging behaviors, including consumption, conversion efficiency, dispersal and olfactory response, should be correlated with the ability to persist in a new habitat (Lewontin 1965; Simberloff 1981; Safriel and Ritte 1983). If life-history traits have evolved to function together to enhance survival and reproduction (Stearns 1992), then the phenotypic associations

predicted in theory should be reflected in genetic and phenotypic correlations between foraging behaviors and life-history traits because of their involvement in colonization and reproduction (Safriel and Ritte 1980; Parsons 1983). Such correlations have been observed in many insect species (Palmer and Dingle 1986; Dingle et al. 1988; Gu and Danthanarayana 1992; Mackay et al. 1996). However, studies on foraging behaviors in predatory arthropods and parasitoids provide no evidence of such correlations (Li and Margolies 1993, 1994; Wang et al. 2003; Maeda 2005, 2006). It may be that the foraging behaviors show low genetic correlations with fitness traits because the number of loci affecting foraging behaviors is low compared to the number of loci affecting total fitness (Mackay et al. 1996). However, conclusions about correlations must be made with caution because we might not find trade-offs in practice because of: variation in acquisition and allocation processes, genotype-environment interaction or variation in third traits in complex multivariate systems (e.g., Van Noordwijk and De Jong 1986; Pease and Bull 1988; Reznick et al. 2000; Blows and Hoffmann 2005). Nevertheless, artificial selection has proven to be a reliable and informative method to detect correlations or trade-offs (Maynard-Smith et al. 1985; Hill and Caballero 1992; Stearns 1992).

We detected a significant negative correlation between consumption and conversion efficiency; the low consumption line had higher conversion efficiency. By having higher conversion efficiency, the low consumption phenotypes may be able to compensate for low intake of food. The absence of such a mechanism might not allow the persistence of low consumption phenotypes in the field. Selection did not affect the prey consumption rate of the conversion efficiency, dispersal and olfactory response phenotypes. The same result was true for the conversion efficiency of the consumption, dispersal and olfactory response phenotypes. In contrast, Jia et al. (2002) showed that patch residence (converse of dispersal response) of *P.*

persimilis in the presence of prey-infested volatiles was negatively related with prey consumption rate; i.e., lines that dispersed sooner had lower consumption rates (Jia et al., 2002). However, in the absence of prey-infested volatiles, such as in the present study, we found no genetic relationship between dispersal and consumption rate. A previous study conducted using isofemale inbred lines of the predatory mite, *Neoseiulus womersleyi* (Shicha), also showed that prey eggs consumed did not differ in dispersal and olfactory response (Maeda 2005, 2006).

There was a positive genetic correlation between high consumption and dispersal and, conversely, a positive correlation between low consumption and dispersal response in the presence of abundant prey. Previous work by Jia et al. (2002) also demonstrated a negative relationship between residence time and prey consumption of *P. persimilis*; i.e., those mites that consumed more prey tended to leave sooner on single plants infested with *T. urticae* eggs. We also detected a positive correlation between olfactory response and dispersal; the high olfaction line had a faster leaving rate than the low line and base population in the presence of abundant prey. These results suggest that some of the genes that contribute to variation in consumption rate and olfactory response have pleiotrophic effects on the dispersal response of *P. persimilis*.

For all traits considered, the high foraging phenotypes showed a positive correlation with olfactory response. It seems that olfactory sensitivity increases with foraging levels of the phenotype. The presence of prey-infested plant volatiles is critical for foraging success of *P. persimilis* in patchy heterogeneous prey habitats. These predators locate and remain in prey patches in response to cues associated with prey density, including direct cues such as exuviae, feces, webbing, and eggs (Sabelis and van de Baan, 1983), and important indirect cues such as prey-induced plant volatiles (Maeda et al. 1998; Mayland et al. 2000). At long range, volatiles attract predators to prey-infested plants or cause them to search more intensively around a prey-

infested plant (Janssen 1999). Once a predator is on a plant, the same volatiles that attract predators are also important in local arrestment (Sabelis et al. 1984). Foraging phenotypes with high levels of consumption, conversion efficiency and dispersal must also have olfactory sensitivity in order to locate and stay in a prey patch. Hence, habitat heterogeneity play a major role in the maintenance of genetic variation in its olfactory response, as was suggested in studies of odor-guided behavior of *Drosophila melanogaster* Meigen (Mackay et al. 1996), *Cotesia glomerata* (L.) (Wang et al. 2003).

Genetic analysis of dispersal and olfactory response in arthropods indicate presence (Margolies et al. 1997; Jia et al. 2002; Wang et al. 2003; Maeda 2005) or absence of correlations (Maeda 2006). When herbivore-induced plant volatiles originate outside a prey patch containing predatory mites, a positive correlation between olfactory response and dispersal tendency would be expected because the residence time of predatory mites is affected by their responsiveness to herbivore-induced volatiles (Maeda and Takabayashi 2001; Jia et al. 2002). A statistical model of the effects of travel costs on dispersal tendency of predators predicted that it is adaptive to disperse early to maximize foraging efficiency when the travel cost is small (Bernstein et al. 1991). Because a sensitive olfactory response to prey-induced plant volatiles would decrease the travel cost (for reviews, see Vet and Dicke 1992; Dicke 1994; Takabayashi and Dicke 1996), predators with strong olfactory sensitivity should also exhibit high dispersal tendency. But when the travel cost is high, predators are expected to be more sedentary (Bernstein et al. 1991). Therefore, if predators had low olfactory sensitivity, a low dispersal tendency would also be expected. If the olfactory response and the dispersal tendency were genetically unrelated, the predatory mites may be able to adopt different foraging strategies (e.g., high olfactory sensitivity and low dispersal tendency) as an adaptation to different foraging conditions. Although we

could not test these predictions in natural populations of *P. persimilis,* Maeda (2005) showed that no natural population of *N. womersleyi* had a high olfactory sensitivity combined with a low dispersal tendency, and no natural population had a low olfactory sensitivity combined with a high dispersal tendency. The absence of such combinations of the two behavioral traits in natural populations suggests that natural selection would favor specific combinations of the two behavioral traits (i.e., a foraging strategy comprising both olfactory response and dispersal tendency).

Potential differences in the acquisition and allocation of energy seem to be of particular relevance in explaining these results (van Noordwijk and de Jong 1986; Reznick et al. 2000). In our study, the high consumption line and the high conversion efficiency line had a stronger olfactory response. This result may be attributed to the genetic variation in resource allocation. That is, well-fed individuals or individuals that are more efficient in converting prey into offspring may allocate more resources to all aspects of their foraging behavior, such as olfactory sensitivity. Further no negative correlations with life-history traits were detected for the high consumption and conversion efficiency phenotypes. On the other hand, some genotypes such as the high dispersal line have a better ability to acquire resources and, hence, have more resources to allocate to other aspects of their life-history (Reznick et al. 2000). Additionally, the high dispersal phenotype showed no evidence of trade-offs with other foraging traits (consumption, conversion efficiency and olfactory response) suggesting that genetic variation in resource acquisition might result in the positive correlation between dispersal response and foraging traits. However, there is a cost for acquisition that is required for this variation to exist which is thought to be maintained via temporal and spatial variability of resources or prey. *P. persimilis* forages in heterogeneous environments with patchy distributions of its prey, *T. urticae*; improved

acquisition of resources in environments with ample prey might trade off with environments with insufficient prey.

Interestingly, we detected asymmetry in the correlated responses in foraging traits of each selection line. For all traits considered, significant positive correlations with foraging behaviors were detected in the high lines compared to the low lines. For example, the high consumption line also had high dispersal and, conversely, the low lines had lower dispersal ability. The same was true for correlations in olfactory response of the foraging phenotypes. These results indicate that components of foraging behaviors are partly independent. Hence, future responses to selection may or may not be constrained by the underlying correlations.

We found no genetic correlations among foraging traits and life-history traits including hatching time (time to emerge from egg), hatching percent, development time (time from nymph to adult ecdysis), or daily survivorship to bidirectional selection with one exception; there was a negative correlation between low consumption and development time. The low-consumption line had a statistically longer development time (3.16 d) compared to the high consumption line and base population; but this might not translate to significant biological differences over the lifespan of the organism. Lack of correlations between key life-history traits and foraging traits suggest that habitat heterogeneity of *P. persimilis* may play a role in the maintenance of genetic variation of specific predator foraging traits. Strong genetic correlations can inhibit rapid responses to selection when they are acting on a multitude of traits simultaneously (Cheverud 1984). The lack of genetic correlation and rapid response to selection in 3 of the 4 foraging traits suggest that there may be a small number of loci with large phenotypic effects controlling the traits (Macnair 1990; Falconer and Mackay 1996; Orr 1998). Our experiment was carried under beneficial conditions when trade-offs may be masked (e.g., Van Noordwijk and De Jong 1986;

Reznick et al. 2000; Messina and Fry 2003). Nevertheless, our analyses identified no major patterns of correlations among key foraging traits in the predatory mite.

High foraging phenotypes would contribute to a high reproductive success (Vet 2001), and natural selection should favor these genotypes and, hence, eliminate the additive genetic variance (Bulmer 1976). However, the existence of genetic variation and correlations among foraging traits of predatory mites suggests that predatory mites must be able to adopt different foraging strategies in a tritrophic system. *Phytoseiulus persimilis* must deal with the potential conflicts that arise in allocating time and energy to different foraging demands, especially when resources become scarce. In tritrophic systems in which herbivores-induced plant volatiles attract natural enemies of tetranychid mites, natural selection might be expected to favor predator genotypes that employ plant volatiles more effectively to find and exploit their prey. That is, predatory mites that are more sensitive to chemical volatiles are more likely to efficiently locate new prey patches and may be at a selective advantage, especially when food becomes scarce. Although selection imposed on a population in nature is usually far from obvious, in the absence of other forces the additive genetic variance of foraging behaviors in predatory mites is expected to be reduced over time. Thus, finding a substantial amount of genetic variation in foraging behaviors of predatory mites is in conflict with this expectation, suggesting that the selection may not be directional or consistent. The advantage of certain genotypes with low consumption may be compensated for by having high conversion efficiency. In this way, natural selection imposed on the population may vary spatially and temporally and both genotypes may have similar fitness in nature. It is also possible that traits such as olfactory response may be influenced by variation in prey numbers as well as by phenotypic variability of the plants, which may contribute to the natural variation in foraging phenotypes.

Finally, we assessed fitness estimates or intrinsic rate of increase (r_m) for each foraging phenotype. The intrinsic rate of increase can be defined as the rate of increase per individual under specified physical conditions, in an unlimited environment where the effects of increasing density do not need to be considered (Birch 1948). There were significant differences in the intrinsic rate of increase (r_m) between the consumption lines and the unselected base population. The high consumption line had a higher r_m than the low and control lines, which was expected because the reproductive potential of the high consumption line is much greater than the low and control lines. The high conversion efficiency line also had higher r_m than the low line and base population owing to the higher fecundity of the high conversion line than the low and control lines. There was no difference in the r_m of the high- and low-dispersal and olfactory response lines compared to the base population because these lines did not differ in survivorship or fecundity. For a phenotype to be successful in a given environment it may need a certain minimum value for its intrinsic rate of natural increase, r_m. It does not necessarily follow that the higher the intrinsic rate of increase the more successful will the phenotype be, or that phenotypes with lower intrinsic rate of increase will cease to exist. Natural selection may operate to select phenotypes with an r_m high enough to enable them to compete successfully with other phenotypes but small enough to prevent a rate of multiplication which would exhaust the food supply in the environment (Birch 1948). Any given value of r_m may be attained by several routes because r_m has a number of component variables: the length of development of the immature stages, the survival rate of the immature stages, the adult survival and the age-specific fecundity schedule (Birch 1948).

An important question thus arises: Under what foraging conditions will *P. persimilis* exhibit a foraging strategy based on a strong or weak foraging response in consumption, conversion

efficiency, dispersal and olfactory response? Because *P. persimilis* preys specifically on tetranychid mite species, such as *T. urticae* – a highly polyphagous species, the predators confront many plant-prey combinations. Therefore, the foraging conditions for *P. persimilis* would differ depending on the quantity and quality of herbivore-induced plant volatiles (for reviews, see Takabayashi and Dicke 1996; Dicke 1999), as well as in terms of prey abundance and prey distribution patterns. In addition, *P. persimilis* can also survive on alternative foods such as pollen (Ashihara et al. 1978) and are also known to cannibalize egg and nymphal stages; but they cannot reproduce without tetranychid species (Polis 1981; Elgar and Crespi 1992). To reveal the factors that determine the foraging strategies of *P. persimilis* it will be necessary to systematically examine the effect of specific foraging traits under different conditions of prey abundance and distribution.

Genetic variation in the prey-consumption rate, conversion efficiency, dispersal and olfactory response, i.e., traits related to foraging efficiency, has clear practical, ecological, and evolutionary implications. Increasing the efficiency of natural enemies is a key concern in biological control (Lewis and Nordlund 1985). Good searching ability is an important component of successful control of pests by natural enemies (van Lenteren and Woets 1988), and predators that use prey-related volatile cues to search for prey may be more effective at locating prey patches (Rosen and Huffaker 1983), especially over a relatively long distance. Bearing this in mind, several scientists have proposed breeding plants that produce higher levels of prey-induced plant volatiles to attract natural enemies to infested plants (Dicke et al. 1990; Lewis and Martin 1990; Vet and Dicke 1992). The results of the present study suggest that it may be possible to select and breed predatory mites that have a strong olfactory response, strong dispersal, a high fecundity, and a high prey consumption rate. However, it remains unclear how

genetic variation in the foraging traits will influence the predator's search efficiency and predator-prey population dynamics (Jia et al. 2002). We will examine the role and impact of each of these traits on the predator-prey interaction at scales ranging from individuals, at which level we can examine issues relevant to fitness, to populations, at which level we can examine issues relevant to biological control.

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Figures and Tables

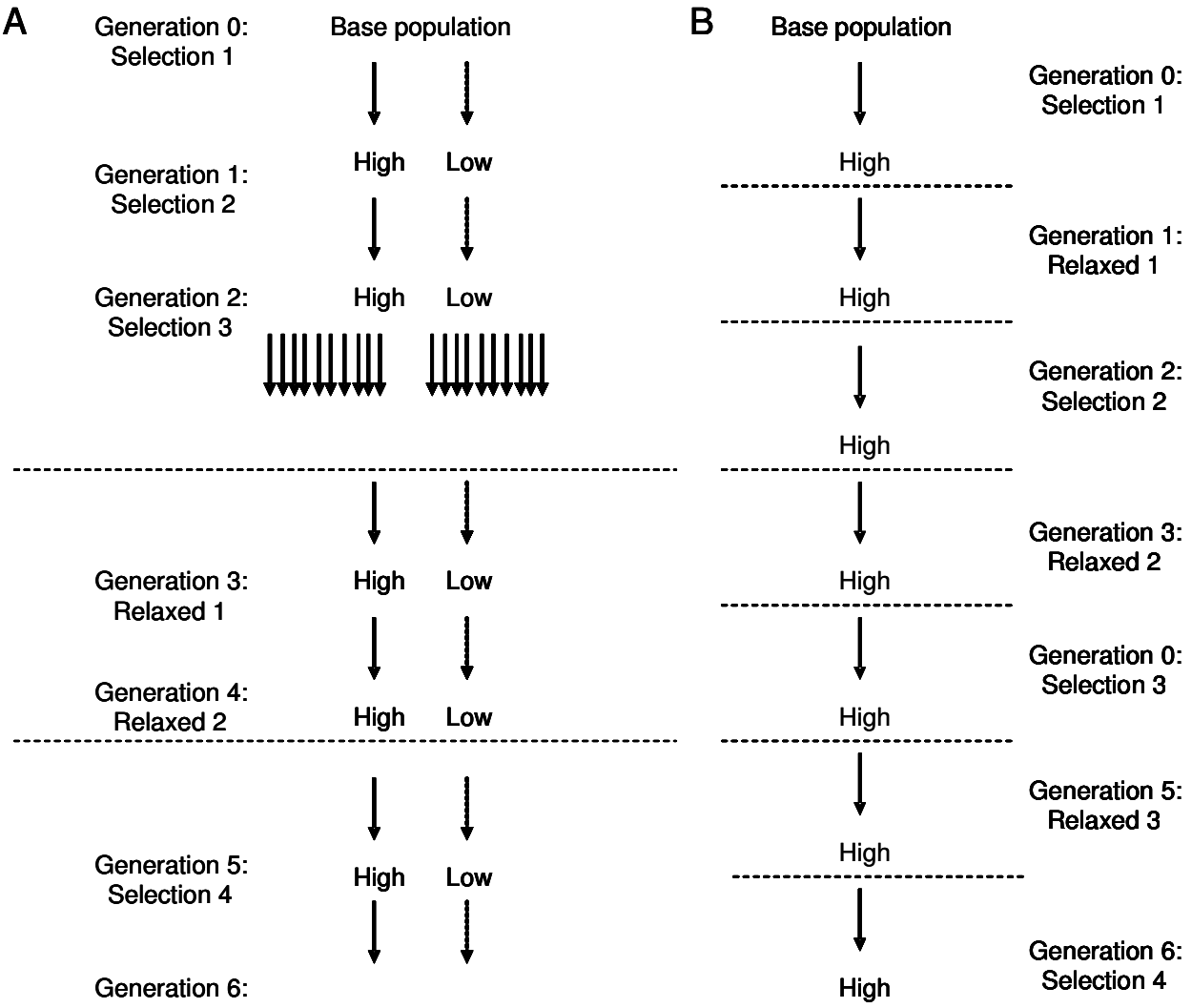


Figure 4-1 Diagram of the selection regime of two replicates A) bidirectional selection, B) alternating selection. For all traits the high and the low line were selected simultaneously. An unselected control line (not shown in diagram) was maintained under laboratory conditions. Arrows indicate selection lines for each trait.

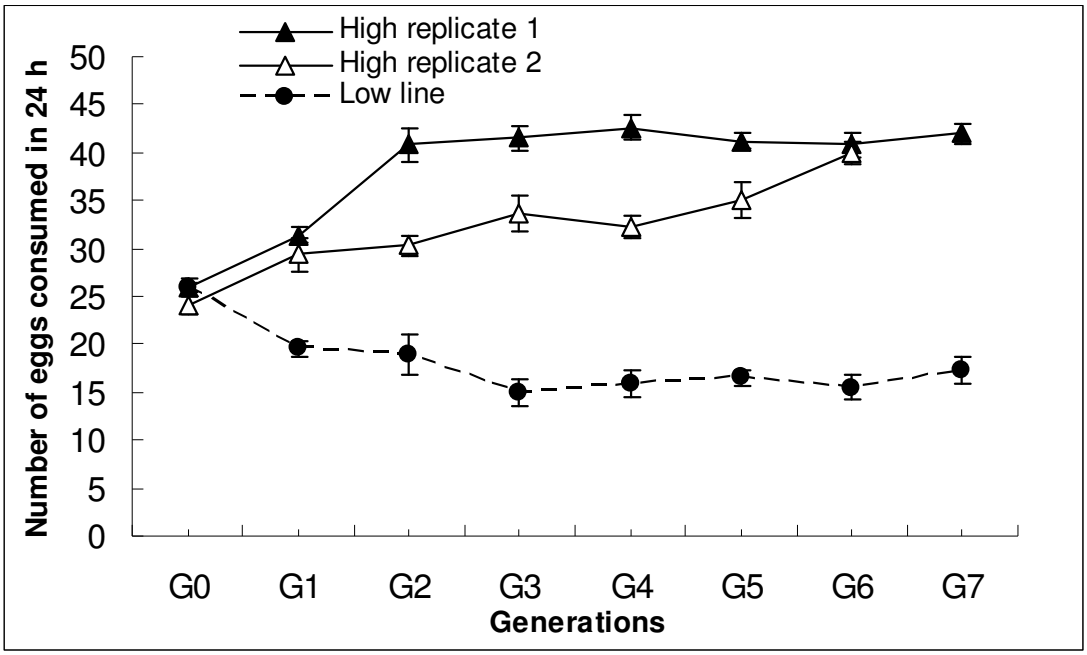


Figure 4-2 Mean ± SE prey consumption rate per generation for *P. persimilis* to different selection regimes.

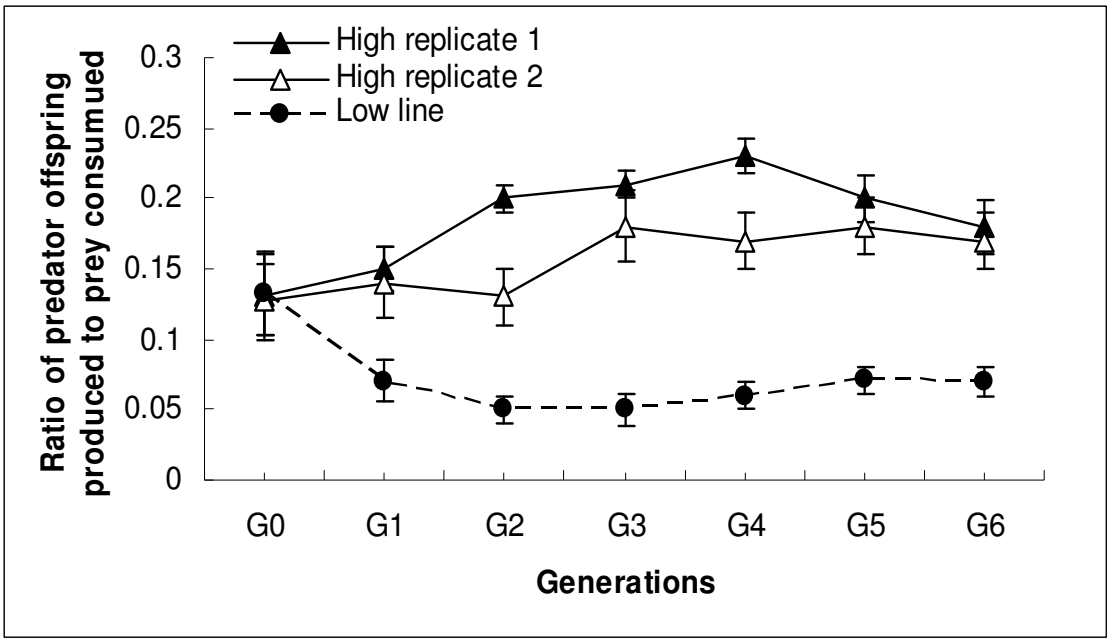


Figure 4-3 Mean ± SE conversion efficiency per generation for *P. persimilis* to different selection regimes.

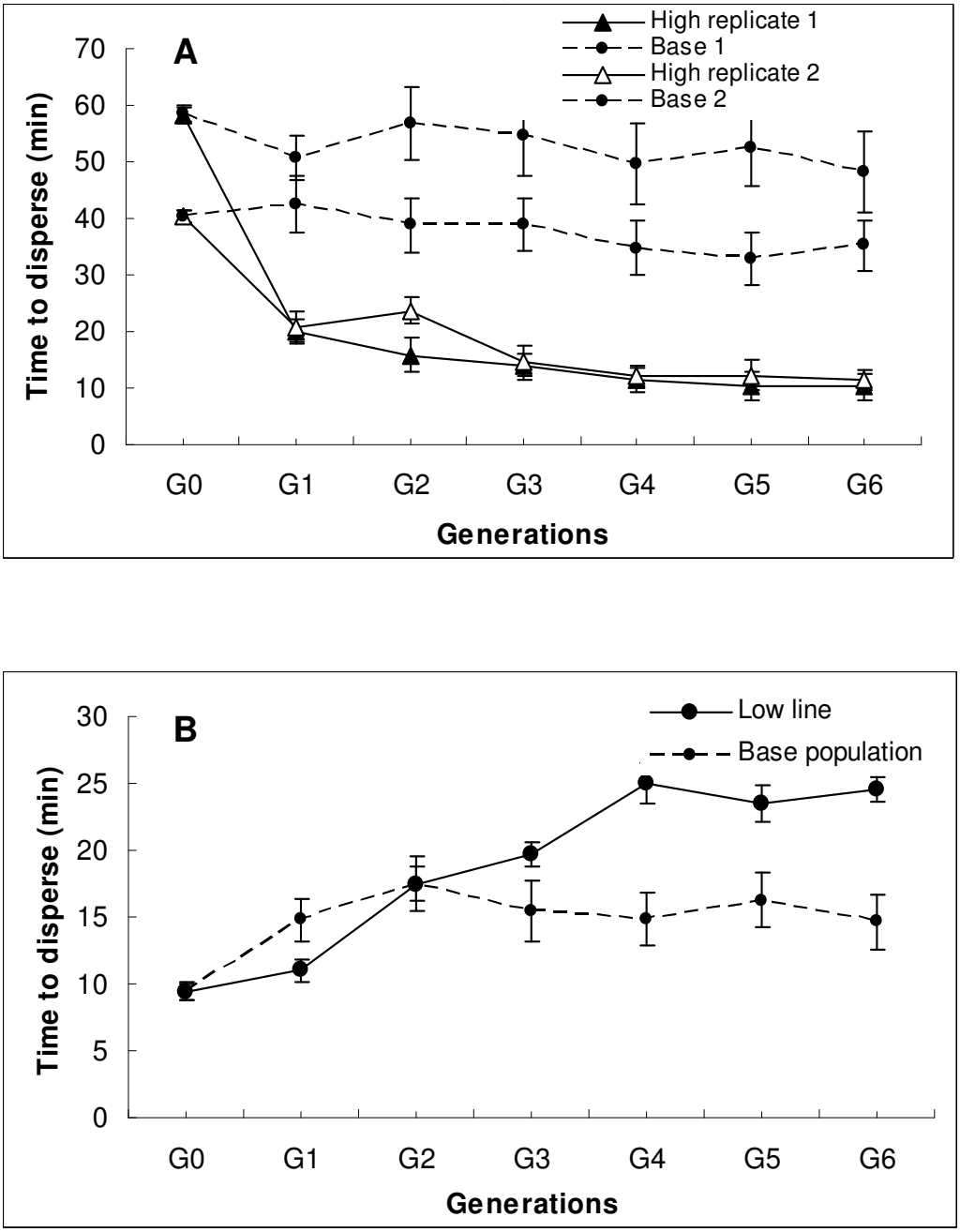
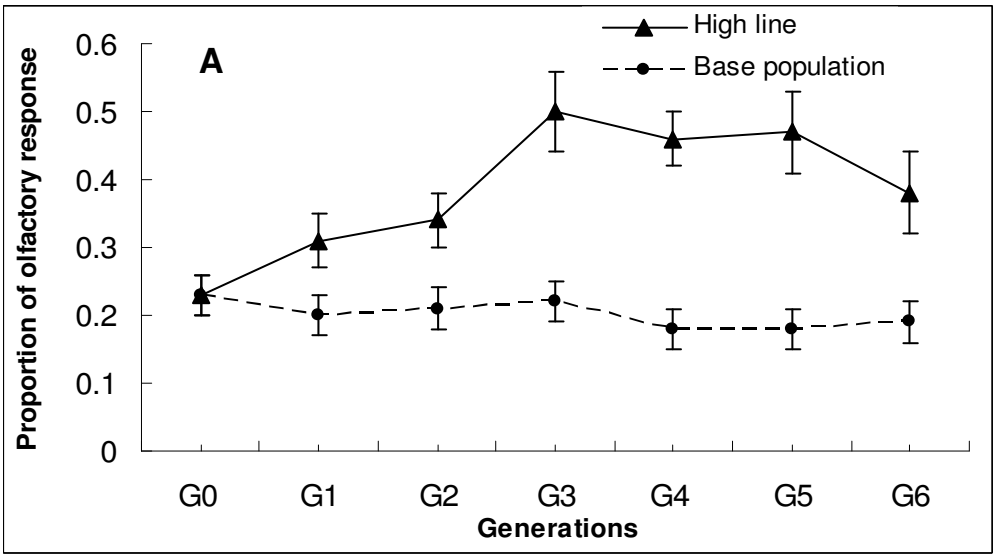


Figure 4-4 Mean ± SE dispersal response per generation for A) high lines and B) low line in *P. persimilis* to different selection regimes.



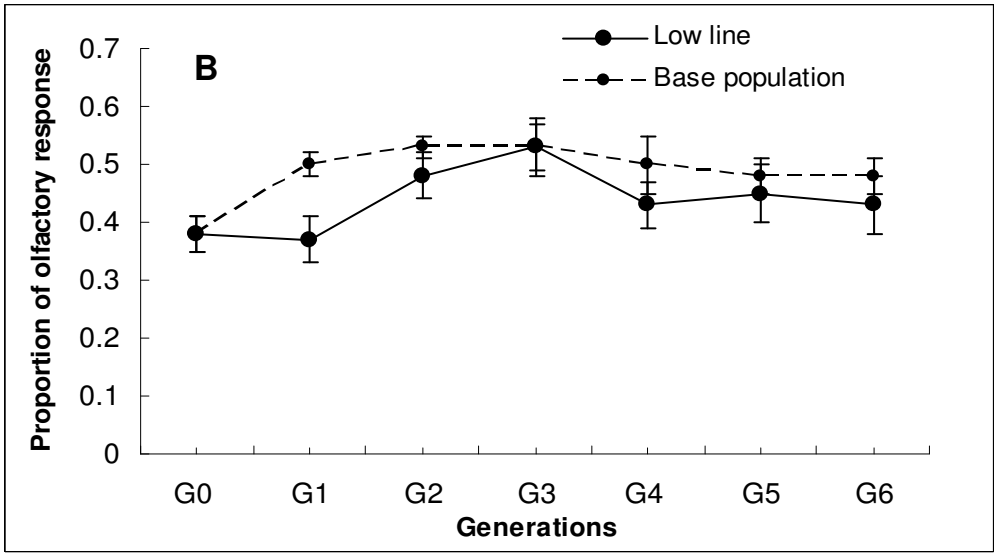
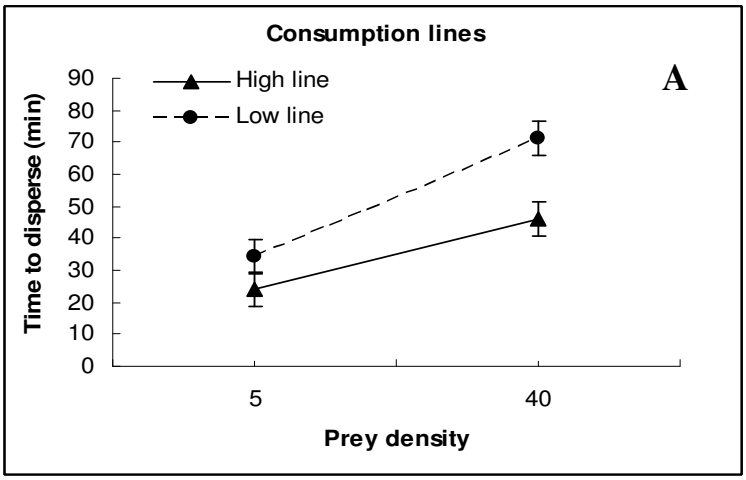
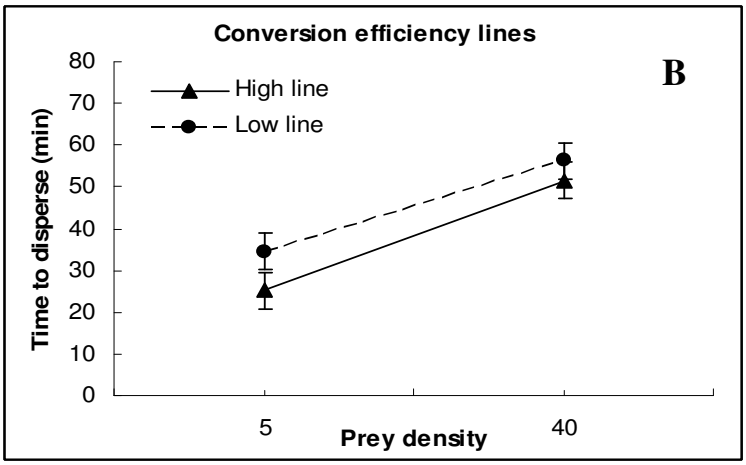


Figure 4-5 Mean ± SE olfactory response per generation for A) high line and B) low line in *P. persimilis* to different selection regimes.





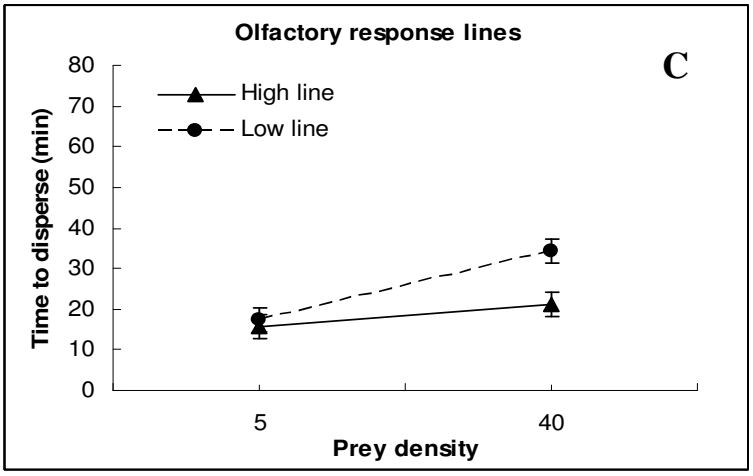


Figure 4-6 Correlated response in the dispersal ability of A) consumption lines, B) conversion efficiency lines and C) olfactory lines in the presence of 5 or 40 prey eggs. Phenotypic means ± SE are indicated for each line.

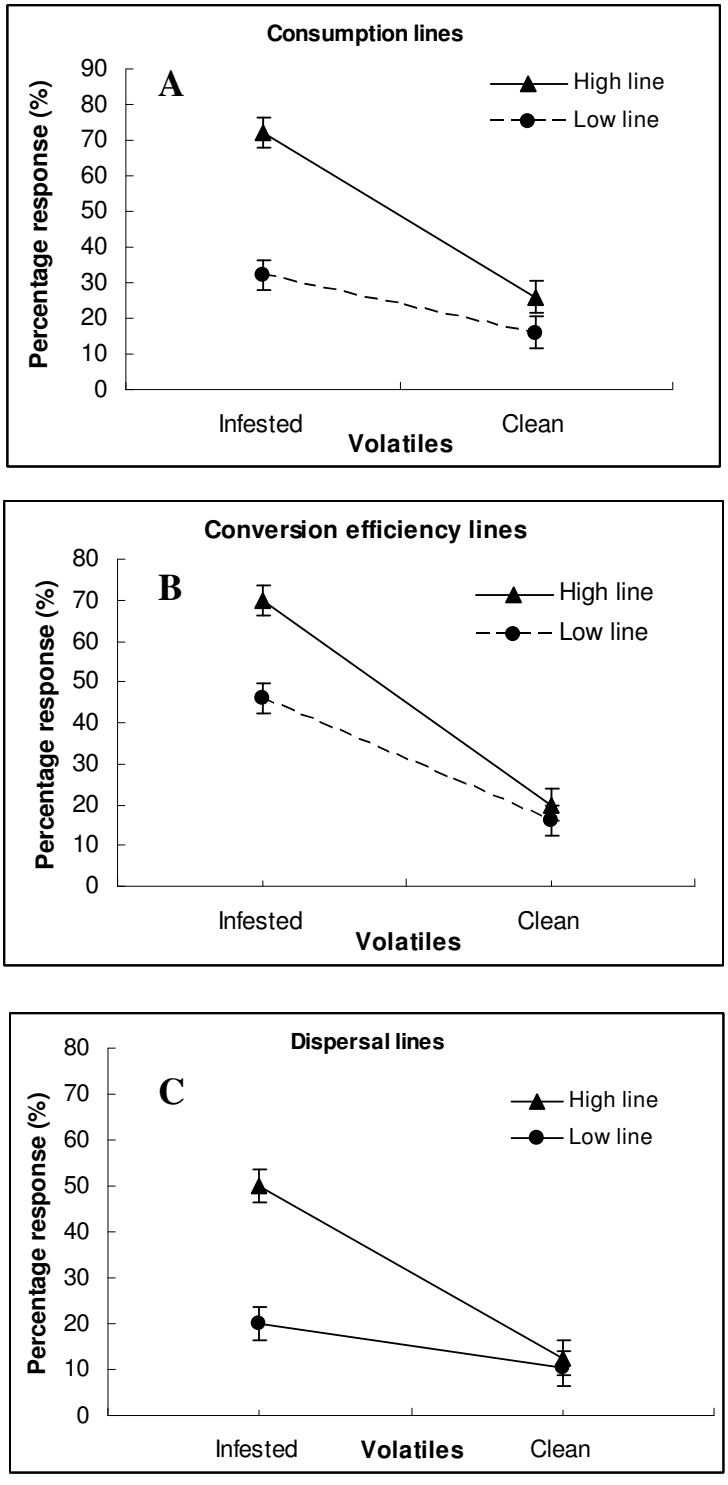


Figure 4-7 Correlated response in the olfactory response of A) consumption lines, B) conversion efficiency lines and C) dispersal lines to infested or clean plant volatiles. Phenotypic means ± SE are indicated for each line.

Trait	Line	Heritability ± SE	*P*
Consumption	High line 1	0.48 ± 0.11	0.008
	High line 2	0.42 ± 0.003	<0.0001
	Low line	0.26 ± 0.13	0.05
Conversion efficiency	High line 1	0.44 ± 0.16	0.05
	High line 2	0.56 ± 0.15	0.02
	Low line	0.20 ± 0.02	0.002
Dispersal response	High line 1	0.29 ± 0.02	<0.0001
	High line 2	0.28 ± 0.009	<0.0001
	Low line	0.64 ± 0.11	0.005
Olfactory response	High line	0.08 ± 0.02	0.023
	Low line	0.01 ± 0.04	0.83

Table 4-1 Realized heritability estimates of foraging traits in *P. persimilis*.

Trait	r_m
Consumption high line	0.429 ± 0.003
Consumption low line	0.298 ± 0.002
Conversion efficiency high line	0.418 ± 0.002
Conversion efficiency low line	0.307 ± 0.003
Dispersal response high line	0.367 ± 0.002
Dispersal response low line	0.369 ± 0.002
Olfactory response high line	0.380 ± 0.002
Olfactory response low line	0.374 ± 0.004
Unselected control	0.375 ± 0.002

Table 4-2 Intrinsic rate of increase (r_m) ± SE generated from jackknifes $l_x m_x$ data for cohorts of *P. persimilis* selection lines.

CHAPTER 5- Ecological Consequences of Genetic Variation in Foraging Behaviors of a Predatory Mite: Spatio-Temporal Dynamics of a Predatory Mite and its Prey

Abstract

Behavior underlies the ability of all animals to acquire essential resources. Thus, behavior provides a critical link to population dynamics, especially in complex or changing environments. To integrate behavior in the analyses of predator-prey population dynamics in heterogeneous landscapes, we conducted a greenhouse study to evaluate the role of several foraging-related traits on the dynamic interaction between the predatory mite, *Phytoseiulus persimilis*, and its prey, the twospotted spider mite, *Tetranychus urticae*, in a patchy environment. Through artificial selection, we created predator lines with high levels of either prey consumption, prey-to-predator conversion efficiency, or predator dispersal response. Using these lines we examined the impact of these predator foraging traits in a two-patch system under different predator-prey population ratios. We found significant differences in predator-prey densities and plant damage among the foraging traits. All foraging traits were comparable in predator-prey densities, whereas the control population had the lowest predator densities and the highest prey and plant damage. The initial predator release ratio did not affect predator numbers; however prey and plant damage differed depending on the ratio (1:10 or 1:30). Spatial analysis showed that the adult predator and prey distribution was aggregated for most of the experiment. Spatial association and correlation analysis confirmed the impact of foraging traits on predator-prey coincidence. The high conversion efficiency and dispersal lines had significant spatial

association and correlation with prey, whereas the consumption and unselected control were comparably lower. We hypothesize that prey patchiness may have reduced the feeding rate of the high consumption line and the control because these lines were less efficienct in locating distant prey patches. In contrast, the high dispersal and conversion efficiency lines exhibited a positive aggregative response wherein the majority of predators clustered in prey patches, thereby reducing prey and increasing reproductive output. Overall, we observed a positive spatial association between predator and prey, which changed over time. Our results indicate that foraging behaviors of the predatory mite affect its ability to locate patchily-distributed prey, thereby influencing foraging efficiency and predator-prey population dynamics. In addition, it appears that there may be multiple effective strategies for exploiting prey in this simple patch system.

Introduction

How animals forage for food is a core issue in ecology. This process forms the basis of trophic interactions and plays a fundamental role in shaping population dynamics, food webs, and communities (Begon et al. 1996). Thus, foraging behavior provides a critical link to understanding population dynamics, especially in complex or changing environments. Despite its importance, the gap between studies of predator/parasitoid foraging behavior and population dynamics is growing (Ives 1995; Roitberg and Mangel 1997; Morales and Ellner 2002). Instead of focusing on the impact of foraging behavior on population dynamics, many ecologists have attempted to explain observed variability by examining with ever increasing detail the evolutionary and mechanistic processes that underlie predator and parasitoid dynamics. Likewise, studies of population dynamic have centered on finding general rules that determine when natural enemies will aggregate or disperse, and how these might stabilize population

dynamics models (Hassell and May 1973, 1974; Murdoch and Oaten 1975; Gurney and Nisbet 1978; May 1978; Comins and Hassell 1979). By attempting to generalize the effects of spatial heterogeneity on population dynamics, these studies have drawn the discourse further from questions of behavior.

To bridge the gap, an important question to answer is how does variation in foraging behavior affect foraging efficiency and, thus, predator-prey/parasitoid-host interactions in spatially-heterogeneous environments? (Ives 1995). Spatial heterogeneity can be described in terms of the distribution of prey or hosts among patches and is important to understanding predator-prey/host-parasitoid interactions and dynamics for several reasons. First, patchily distributed prey present a foraging challenge for predators or parasitoids. Second, the stability of predator-prey or parasitoid-host interactions, both theoretically and empirically, is increased when prey and hosts both have a heterogeneous distribution (e.g., Bailey et al. 1962; Hassell and May 1973, 1974; Murdoch and Oaten 1975; Gurney and Nisbet 1978; May 1978; Comins and Hassell 1979). For example, the pattern of parasitism depends on the spatial distribution of the host which stabilizes the dynamics (Nicholson and Bailey 1935; Wright 1940; Huffaker et al. 1963; Pimentel et al. 1963; Hassell et al. 1991). Third, the pattern of predation or parasitism among patches of prey influences population dynamics (Ellner et al. 2001).

Foraging behavior is the expression of a complex phenotype. At a genetic level there may be tremendous variation in foraging traits among individuals of a species owing to the interaction of many genes (Sokolowski 2001). In addition, ecological factors not directly related to foraging, such as variation in life history traits, may also affect foraging success (Roitberg et al. 1992). Furthermore, the foraging success of an individual is influenced by factors such as the spatial and temporal distribution and suitability of resources, and the risks associated with

searching for food (Stephens and Krebs 1986). Together, the genetic variation, the life history, and the landscape produce wide variation in foraging phenotypes. Theoretical treatments (e.g., Hassell and May 1985; Pels et al. 2002) and empirical evidence (e.g., Murdoch et al. 1996; Hanski et al. 2004) suggest that even subtle differences in predator foraging, whether due to differences in phenotype or landscape structure, can greatly alter predator-prey population dynamics and prey suppression.

The question then arises, "Which attributes of predator foraging behavior are likely to have a large impact on predator-prey population dynamics?" The rate at which predators consume prey and the efficiency with which predators convert their food (i.e., prey) into offspring, determine the predator's impact on the local predator-prey dynamics, as described generally by the functional and numerical response. These two variables, consumption and conversion efficiency, reflect our understanding of the basic link between predator foraging and population dynamics assuming prey are always available. Within a local prey patch, which can be considered a homogeneous resource, the rate at which predators consume prey, and the efficiency with which predators convert their prey into offspring determine predator impact on local predator-prey dynamics. In heterogeneous or patchy landscapes, local (within patch) consumption rate and conversion efficiency affect regional as well as local dynamics because, by affecting local per capita prey availability, they affect the leaving rate of predators. In turn, when predators disperse from a patch they reduce the local predator population size (and the local predator-to-prey ratio) while at the same time increasing colonization of other prey patches and the predator-to-prey ratios in them thereby increasing global predator productivity (van Baalen and Sabelis 1995). Thus, traits that affect predator movement from and between patches are equally important to both local and global (i.e., among patch) dynamics (Hassell 1978;

Berryman and Gutierrez 1999). These traits will interact to affect the predator-to-prey ratio in each local patch, which in turn affects the stability of the interaction (Hassell 1978; Berryman 1999).

In homogeneous environments of predators and prey, individual predators should maximize their immediate benefits at the expense of long-term yields (Rosenzweig and MacArthur 1963; Maynard Smith 1982). Thus, natural selection favors predators with the highest consumption and population growth rate, and this will often cause predator-prey dynamics to become unstable (May 1972). When spatial structure prevents the populations from being well mixed, such predators may have a selective disadvantage because they do not make full use of the prey's growth capacity and, hence, produce fewer offspring. Most models on prey exploitation consider only strategies that differ in the predation rate (Slobodkin 1974; Gilpin 1975). Alternatives to these strategies include conversion efficiency and rate of emigration from a local population as argued by van Baalen and Sabelis (1995) and Pels et al. (2002). All of these strategies affect the population growth rate of the predator and thereby the predation pressure on the prey population. Low consumption or conversion rates and dispersal rates during the interaction will allow the local prey population to represent a larger resource in the future, which in turn may benefit the final size of the local predator population. In contrast, high consumption or conversion and dispersal rates during the interaction will cause the predators to have a higher impact on the local prey population, thereby giving up opportunities to exploit the full growth capacity of the prey population. However, it is not known which strategy would be most likely to be successful. The best strategy would depend on the degree to which predators can monopolize the exploitation of local prey populations, which in turn depends on the spatial

structure, the number of migrants, and, in particular, the stochastic nature of the colonization process (Pels et al. 2002).

In trying to understand population dynamics of predators and prey on the whole, very little quantitative information is available concerning the interrelations between population densities, spatial distributions and coincidence between predators and prey in time and space. Recently, spatial autocorrelation and variance among the various components in ecological systems has been more often treated as a source of useful information due to developments in geographic information systems and spatial statistics (Legendre 1993; Horne and Schneider 1995).

Within ecology there is currently interest in many forms of spatial studies, including the effects of scale, metapopulation dynamics, spatio-temporal dynamics, spatially-explicit modelling and spatial synchrony. Ecologists study spatial pattern to infer the existence of underlying processes, such as movement or responses to environmental heterogeneity. Spatial structure may indicate intraspecific and interspecific interactions such as competition, predation, and reproduction, or be driven by environmental heterogeneity of variables such as resource availability (Perry 1998). However, care is required in inferring causation, since many different processes may generate the same spatial pattern. Methods for analyzing spatial pattern have been developed in a wide variety of disciplines. The spatial pattern of sampled counts of any species may be regular, random or clustered, regardless of the properties of the frequency distribution of the counts. For two species, whatever the spatial pattern of the counts of the individual species, the two populations may display positive spatial association, as with diseased plants and their pathogen, dissociation (negative spatial association), as with an insect host in refuge from its parasitoid attacker (e.g., Reeve and Murdoch 1986), or randomness with respect

to one another. Traditionally, patterns for a single species have been measured using the relationship between variance and mean (e.g., Taylor 1961; Clark and Perry 1994), and association between two species has been measured by the correlation coefficient (Murchie et al. 1999). But in both of these approaches the information concerning the locations of the counts is discarded. We used the SADIE (Spatial Analysis by Distance Indices (SADIE) methodology, developed explicitly for the spatial analysis of ecological data in the form of spatially referenced counts (Perry et al. 1999). This system provides a biologically more intuitive index than traditional mathematically-based ratios involving sample variance and mean, and increased power due to the greater use of the spatial information in the sample. The SADIE technique provides a means to measure overall spatial pattern for a single set of data (Perry 1998) and spatial association for two sets of data (Perry 1998). It also provides a measure and map of local association and that quantifies the degree to which each unit contributes to an overall measure of spatial association (Winder et al. 2001).

The present study examined the functions and impacts of three specific predator foraging traits including consumption, conversion efficiency and dispersal response in an acarine predator-prey interaction that occurs in spatially complex landscapes. Specifically, our aim was to investigate the spatial and temporal dynamics of a predatory mite, *Phytoseiulus persimilis* Athias-Henriot and its herbiovorous prey, the twospotted spider mite, *Tetranychus urticae* Koch under different predator-prey release ratios. Through artificial selection we developed lines of *P. persimilis* that exhibit high levels of three traits that should affect the spatial interaction of predators with their prey: consumption rate, efficiency of conversion of prey eaten into predator offspring, and dispersal in response to prey density (Margolies et al. 1997; Margolies 1999; Jia et al. 2002; Nachappa et al. 2008). By selectively manipulating levels of individual predator

foraging traits (keeping others constant), we had the unique opportunity to address the question of the importance of individual response to population processes in landscapes (Ives 1995; Lima and Zollner 1996; Roitberg and Mangel 1997), thereby helping to link behavior and predator-prey population dynamics. Deciphering the impact of individual foraging behavior on a predator-prey system should also address the adaptive nature of specific phenotypes in an ecological context (Brakefield 2003).

We predicted different dynamics between selection lines and prey depending on predator-prey release ratios. We hypothesized that at the release ratio of 1:10 (one predator per 10 prey), high levels of consumption, conversion efficiency and dispersal response would lead to better prey suppression of the prey population owing to spatial and temporal synchrony between predator and prey. Studies on greenhouse ornamentals have shown successful control of spider mite numbers and plant damage at a predator-prey ratio of 1:10 (Markkula and Tiittanen 1976). At predator-prey ratio of 1:30, we predicted that the specific predator foraging traits will have different spatial and temporal distribution patterns with respect to prey. A predator–prey ratio of 1:30 is less than optimum for reduction of spider mite numbers and damage (Hamlen and Lindquist 198; Opit et al. 2004); so we expected to observe differences in the improved selection lines. We hypothesized that the consumption line will reduce spider mite numbers and damage locally and be positive correlated with the prey. However, they would not be successful in locating distant prey patches as they would continue to feed at local prey patches until prey extinction. We predicted that the conversion efficiency line would be positively associated, both locally and regionally, with prey causing reduction in prey numbers. Predators with a high dispersal response should be negatively correlated with prey initially, but disperse to distant prey patches resulting in overall positive association regionally with prey.

Materials and Methods

Study Organisms

The prey in our system, the twospotted spider mite, *Tetranychus urticae* Koch (Acari: Prostigmata: Tetranychidae), is a generalist herbivore that feeds on over 180 plant species, including over 100 cultivated species (van de Vrie et al. 1972). This spider mite is widely distributed throughout the world. Mites pass through five stages of development: egg, larva, protonymph, deutonymph, and adult. The population goes through a generation every 7 to 21 days, depending on the ambient temperatures in their environment. *Tetranychus urticae* mainly colonize the underside of leaves where mites produce webbing in which all stages live and most activity (e.g., feeding, mating, oviposition) takes place. Adult females deposit eggs close to where they feed, and immatures do not move very far from where they hatch (Suski and Naegele 1968; Kondo and Takafuji 1985); in this way, clusters, or patches, of spider mites develop. As mite feeding destroys leaf tissue within a patch, mites move to new, uninfested parts of a plant. As plants deteriorate spider mites disperse either by walking or as aerial plankton. The twospotted spider mites we used in our experiments were from a laboratory colony maintained on lima bean plants (*Phaseolus lunatus* cv. 'Sieva') at 24°C, 60-70% relative humidity, 16:8 h (L: D) photoperiod.

The predatory mite, *Phytoseiulus persimilis* Athias-Henriot (Acari: Mesostigmata: Phytoseiidae), is a specialist predator on tetranychids and the most frequently-used biological control agent for spider mites, especially in greenhouses (van Lenteren and Woets 1988). The predatory mite was introduced into The Netherlands from Chile in 1958 (Dosse 1958) and subsequently shipped to other parts of the world including the United States. *Phytoseiulus persimilis* are extremely small and are orange to bright reddish in color. Phytoseiid mites

reproduce by pseudoarrhenotoky, which is characterized by obligate fertilization of all eggs followed by a loss and/or heterochromatization of the paternal chromosomes in embryos that develop into males, resulting in a haploid condition of the males (Hoy 1979, Schulten 1985, Perrot-Minnot et al. 2000). Under normal conditions the sex ratio is female-biased, usually close to 0.83 (Helle and Sabelis 1985) and each female can produce 60 eggs in her lifetime (McMurty and Rodriguez 1987). *Phytoseiulus persimilis* has 5 developmental stages: egg, non-feeding larva, protonymph, deutonymph and adult (Sabelis 1981). All motile stages feed on spider mites. When predatory mites invade a spider mite-infested plant, the predator population is likely to deplete the local spider mite population (Chant 1961; Takafuji et al. 1983). Although this means that the local predator-prey interaction is limited and ephemeral, the interaction may persist on a regional scale due to repeated dispersal from and colonization of patches by both species (Diekmann et al. 1988; Nachman 1987, 1988, 1991; Sabelis et al. 1991; Walde 1991, 1994; Jansen and Sabelis 1992). As prey density drops to zero, *P. persimilis* will leave (Takafuji 1977; Bernstein 1984; Zhang and Sanderson 1993) and seek other patches.

The *P. persimilis* population from which we initiated selection was purchased from Koppert Biological Systems, Inc. (Romulus, Michigan), a commercial supplier of beneficial arthropods. *Phytoseiulus persimilis* were reared on twospotted spider mites in the laboratory for one generation under 24°C, 60-70% relative humidity, 16:8 h (L: D) photoperiod to allow the predators to acclimate to laboratory conditions. Selection lines were maintained in 1.89 l. mason jars with the metal lids removed and replaced with fine mesh screen to allow air exchange. *T. urticae*-infested bean plants were added to the jars every other day. Every week the bottom layers, consisting of dry leaves with few spider mites or predators were discarded.

Foraging Traits

Artificial selection was imposed to create lines that exhibited high levels of each of three ecologically-relevant foraging traits: consumption, conversion efficiency and dispersal response. Consumption and conversion efficiency were measured in a bioassay developed by Jia et al. (2002). Individual *P. persimilis* were presented with 40-50 one-day old *T. urticae* eggs for 24 h, after which the number of prey eggs left and the number of predator eggs generated were counted. Consumption rate was defined as the number of prey eggs consumed by a predatory mite within 24 h and conversion efficiency was the ratio of the number of prey eggs consumed to the number of predator eggs laid in that time. The dispersal response of *P. persimilis* was measured in a Petri dish bioassay modified from Maeda and Takabayashi (2001) and Nachappa et al. (2006a). Five *P. persimilis* adult females were placed on a leaf disk containing 40 prey eggs. After a 30 min acclimation period, we placed one end of a 30 x 5 mm parafilm strip on the leaf disk and counted as dispersers those predators that walked out to the mid-point of the strip. The high dispersal line was composed of those individuals that dispersed from the leaf disk in the presence of 40 eggs.

Selection on each trait was conducted once for the entire experiment following Nachappa et al. (2008). Seven to 10 day old adult female predators were used for all experiments. After selection plateaued, we measured all three traits in each line to make sure that only the trait of interest had changed. Three or four isofemale lines were started from each selected line to maintain the level of the trait in the line (Hopper et al. 1993; Jia et al. 2002). These isofemale lines were maintained throughout the experiment. One to two months before starting each replicate, females from the isofemale lines for each trait were combined so lines could interbreed for two generations, at which time they were phenotyped to ensure they exhibited the desired

level of the traits. Predators were collected from the arrays at the end of each replicate and again phenotyped to assess any change in the level of the trait during the course of the experiment.

Greenhouse Experimental Design

We conducted three time-replicated experiments in 69.4 m^2 greenhouses at the Throckmorton Plant Sciences Center at Kansas State University, Manhattan, KS, USA from Spring 2007 through Spring 2008. Temperature and relative humidity data were automatically collected every hour in each greenhouse with two HOBO™ environmental monitors (Onset Computer Corporation, Bourne, MA). The average daily temperature (º C) for each of the greenhouse experiment were (replicate 1: 24.25 ± 3.27, replicate 2: 23.89 ± 4.19, replicate 3: 25.79 ± 6.66; mean ± SE) and relative humidity (%) (Replicate 1: 52.17 ± 15.89, replicate 2: 40.36 ± 14. 12, replicate 3: 42.26 ± 12.27; mean ± SE). The average length of day and night (light: dark) during the experiment was approximately 16:8 (L: D) h. To minimize aerial movement of predator and prey we used a fine mesh screen on the fans to reduce air velocity to 2 m/s. Prior tests have shown that this air speed does not allow aerial movement of mites. Air velocity recorded at the front of the greenhouse was 1-1.34 m/s, 1-1.14 m/s in the middle and 0.4-0.8 m/s in the back of the greenhouse.

The experimental unit consisted of 24 plants set in 8 x 3 arrays based on a design used by Takafuji (1977) to study the effect of dispersal on this predator-prey interaction. Plants within an array were packed together as closely as possible so mites could move directly from plant to plant or pot to pot. To isolate the arrays from each other, two arrays were set on each greenhouse bench with a minimum of 10m between them. Further, each array was provided with a moat-system (Opit et al. 2004) to prevent mites from leaving the arrays.

The experiment was designed so that all units started with a similar number of spider mites in the same location. We created two prey patches at opposite ends of the long axis of each array using a single prey-infested as a patch. To create a patch, individual plants at the trifoliate-leaf stage were inoculated with spider mites prior to grouping plants into arrays. Spider mites were left for 10 d to become established, after which time infested and uninfested plants were assembled into the array and predators were introduced onto one of the infested plants at either a 1:10 or 1:30 predator-prey ratio based on pre-release counts of prey. The number of spider mites was estimated by counting adult spider mites, after which we released the predators to achieve the appropriate predator:prey ratio.

Population Counts

Numbers of adult prey and predators were counted on each plant once every 6 days for 24 days. Plant damage was also assessed every 6 days using the Leaf Damage Index (LDI) modified from Hussey and Parr (1963). The symptoms were ranked according to an ordinal scale as follows: 0, no damage; 1, incipient damage, one or two small feeding patches; 2, feeding patches tending to coalesce, but only 2/3 of leaf affected; 3, 2/3 of leaf with feeding marks as chlorotic patches; 4, dense feeding marks over entire leaf but appearance still green; 5, as 4, but leaf blanched and beginning to shrivel. LDI was calculated as an average of 24 plants per treatment combination. Additionally, at the end of each experiment we collected predators and tested to see if there was any loss in phenotypic value of the trait.

Spatial Distribution and Association

To determine the distribution patterns of predatory mites and spider mites, we used SADIE (Spatial Association using Distance IndicEs; Perry 1998; Perry et al. 1999). The program for performing this analysis is available as a free download at

www.rothamsted.bbsrc.ac.uk/pie/sadie/SADIE_home_page_1.htm. SADIE analyzes the geo-referenced data to measure the degree of clustering in counts. A cluster can have two forms: a patch or a gap. A patch is a region of relatively large counts close to one another, and a gap is a region of relatively small counts close to one another (Perry 1995). To quantify the degree of clustering, SADIE calculates the distance to regularity (D), defined as the minimum total distance that individuals in an observed arrangement would need to move to produce a uniform or regular spatial distribution (Perry 1998). The higher the value of D, the more the observed arrangement of counts is spatially aggregated. The degree of non-randomness was quantified by comparing the observed D with the mean expected distance to regularity (E_a) of randomization results for rearrangements in which the sampled counts first were randomly redistributed among the sampling locations (Perry 1995; 1998). The overall aggregation index, I_a , was calculated as $I_a = D/E_a$. A value of $I_a = 1$ suggests a spatially random pattern, $I_a > 1$ suggests a more aggregated pattern, and $I_a < 1$ suggests a more regular pattern (Perry et al. 1999). The associated probability (P_a) was calculated from the formal randomization tests (Perry et al. 1999; Perry and Dixon 2002) under the null hypothesis that observed counts were arranged randomly among the given sample locations. In addition, SADIE quantifies the contribution of each plant count at each sample location to a patch or a gap with unitless clustering indices. The clustering indices v_i and v_j measure the degree to which a sampling unit contributes to clustering as a member of a patch and a gap, respectively (Perry1998; Perry et al. 1999); v_i or v_j equals 1 for a random distribution of counts, $v_i > 1$ for a unit that belongs to a patch and $v_j < -1$ for a unit that belongs to a gap. All SADIE statistics were generated with SADIESHELL version 1.5.3 (Rothamsted Experimental Station, Harpenden, Herts, UK).

SADIE was also used to analyze spatial association (Perry et al. 1999; Perry and Dixon 2002) that compared the cluster indices for spider mites and predatory mites on a single location or plant. SADIE quantifies the contribution of counts at each sample location to a patch and a gap (Perry 1998; Perry et al. 1999). Positive association was indicated by the coincidence of a patch for one data set with a patch for the other, or by the coincidence of two gaps; negative association was indicated by a patch coinciding with a gap. The measure of spatial association was represented by a SADIE index, X, the linear relationship between the clustering indices of the two sets: $X>0$ for positively associated populations, $X \approx 0$ for populations positioned at random with respect to one another, and $X<0$ for negatively associated populations. The randomization method (Perry et al. 1999; Perry and Dixon 2002) was used to construct a formal test of significance in spatial association. The null hypothesis tested was that the spatial arrangement of predator adults is random with respect to those of the prey (i.e., no spatial association). Spatial association analysis was used to measure the temporal change of spatial distributions of predator and prey populations every 6 days up to 24 days. Sigma plot (Systat Software, Inc. Chicago, IL, USA) was used to map the patches and gaps. All SADIE statistics were generated with SADIESHELL version 1.5.3 (Rothamsted Experimental Station, Harpenden, Herts, UK).

Statistical Analysis

The experimental design was a repeated measures 4 x 2 factorial with 4 foraging behaviors (high consumption, high conversion efficiency, high dispersal response and unselected control) released at 2 predator ratios (1:10 and 1:30 predator: prey). Further, there were 4 sampling periods: days 6, 12, 18 and 24. Response variables from each array were: 1) total number of prey; 2) total number of predators; 3) average damage index; 4) SADIE Aggregation

Index for prey and 5) for predators; 6) SADIE gap index for prey and 7) for predators; 8) SADIE Patch Index for prey and 9) for predators; 10) spatial correlation coefficient; and 11) SADIE Association Index. Data were analyzed in SAS PROC MIXED (SAS Institute 2002) as a completely randomized design using foraging trait, ratio, time and their interaction as fixed effects, and replicate as random effects. Time was also a repeated measures factor. Models were fit assuming numerous standard structures for the serial correlation, and the best-fitting model was selected using Akaike's Information Criterion (Littell et al. 1996; Guerin and Stroup 2000). F-tests for fixed effects and t-tests for pairwise comparisons were performed based on the chosen correlation structure (Littell et al. 1996). Within each experimental unit we also examined the simple correlation (SAS Institute 2002) between the number of predator and prey on each plant at each sampling time to assess the degree of spatial association between predator and prey density.

Results

Foraging Traits

We successfully selected for lines that exhibited high levels of the three foraging traits: consumption, conversion efficiency and dispersal (Nachappa et al. 2008) (Table 5-1). In every case only the targeted trait changed (Nachappa et al. 2008). We did not detect any significant change in the phenotypic level of the traits prior to release and after termination of each greenhouse experiment (Table 5-2). There was one exception, the conversion efficiency was reduced at the end of the experiment in Rep 1 ($P = 0.01$); but it was different from the unselected control (Table 5-1).

Population Counts

Predators. Type of foraging trait (selected lines and unselected population) and the duration of the predator-prey interaction (time) had significant individual effects on predator numbers (Table 5-3). There was also a significant interaction between foraging trait and time (Table 5-3). Predator populations increased over time, but there were significant differences in the pattern of population growth and final predator densities among the high consumption, conversion efficiency, dispersal lines and the unselected control (Fig. 5-1). There were no differences in predator densities at day 6 ($t_{158} = 0.20$, $P = 0.84$) or day 12 ($t_{158} = 0.80$, $P = 0.43$). However, lines differed at day 18 ($t_{158} = 3.27$, $P = 0.0013$) and day 24 ($t_{158} = 11.67$, $P = 0.0013$). Overall, the high conversion efficiency line had the highest predator densities (8.41 ± 1.65; mean predator number ± SE) and the unselected control had the lowest predator densities (4.13 ± 1.65) (Fig. 5-1).

Prey. Foraging trait, predator-prey ratio, and time predators and prey interacted all had a significant effect on prey populations (Fig. 5-2A, B). In addition, there was a significant three-way interaction among these factors on prey numbers (Table 5-3). The greatest prey densities at either ratio were observed in the unselected population (1:10: 54.29 ± 17.19 and 1:30: 114.17 ± 17.19; mean prey number ± SE) (Fig. 5-2A, B), whereas the lowest prey numbers were detected in the conversion efficiency line (1:10: 38.78 ± 17.19 and 1:30: 56.94 ± 17.19) (Fig. 5-2A, B). Time had a significant effect on prey population growth rate. There were no differences in prey numbers at day 6 ($t_{158} = 1.26$, $P=0.21$); but differences were observed at day 12 ($t_{158} = 2.51$, $P=0.01$), day 18 ($t_{158} = 4.59$, $P<0.0001$) and day 24 ($t_{158} = 7.29$, $P<0.0001$) (Fig. 5-2A, B). All two-way interactions between main factors were significant or nearly significant for prey numbers (Table 5-3). At all times, prey numbers were much lower at the predator release ratio

of 1:10 (43.08 ± 15.18) ($t_{158} = 5.51$, P=0.005) than at 1:30 (74.06 ± 15.1817) ($t_{158} = 2.84$, P<0.0001) (Fig. 5-2).

Plant Damage. Foraging trait, predator-prey ratio, and time predators and prey interacted had a significant effect on plant damage. There were also significant two-way interactions between foraging trait and time of interaction and between predator release ratio and time of interaction (Table 5-3). The average plant damage ratings corresponded well with mean prey densities for the respective foraging traits over time (cf. Figs. 5-2A, B, 5-3). There were significant differences among selected lines and the control with respect to plant damage, with the unselected control having the greatest plant damage (Fig. 5-3). Plant damage also increased over the course of the experiment and significant differences were detected at day 6 ($t_{158} = 2.44$, P=0.02), day 12 ($t_{158} = 6.52$, P<0.0001), day 18 ($t_{158} = 14.16$, P<0.0001) and day 24 ($t_{158} = 20.65$, P<0.0001). Plant damage was much lower at the 1:10 predator release ratio (1.57 ± 0.17; mean damage ± SE) (P<0.0001) than at the 1:30 ratio (2.01 ± 0.17) ($t_{158} = -3.66$, P<0.0001).

Spatial Distribution of Predators

Aggregation Index. Foraging trait, predator-prey ratio, and time of interaction significantly affected predator aggregation. There was also a significant interaction between foraging trait and time with respect to aggregation patterns of predator populations (Table 5-4). Predator spatial distributions were significantly aggregated (I_a >1) for all foraging traits and for the unselected control (Consumption: 1.76 ± 0.09, Conversion: 1.64 ± 0.09, Dispersal: 1.68 ± 0.09 and Unselected control: 1.83 ± 0.09; mean aggregation index ± SE) (all P<0.0001). Further significant differences were only observed between conversion efficiency and the unselected control (P=0.01) and dispersal ability and the unselected control (P=0.05). Aggregation indices were significant for all sampling periods with an increasing trend from day 6 to 24 (Day 6: 1.48

± 0.11, Day 12: 1.74 ± 0.11, Day 18: 1.80 ± 0.11 and Day 24: 1.87 ± 0.11) (all P<0.0001). Spatial distributions only differed between day 6 and day 18 (P=0.003) and day 6 and 24 (P=0.004). Overall, spatial distributions for predators were aggregated (I_a >1) and no uniform (I_a <1) or random (I_a =1) distributions were observed for all foraging traits.

Gap Index. The gap index (v_j) was significantly affected by foraging trait, predator-prey ratio, and time of interaction. There was a significant two-way interaction between foraging trait and time (Table 5-4). Gap indices (v_j) for all lines were less than -1, indicating group of small adult predator counts that are close to one another (Consumption: -1.71 ± 0.07, Conversion: -1.60 ± 0.07, Dispersal: -1.62 ± 0.07 and Unselected control: -1.78 ± 0.07; mean gap index ± SE) (all P<0.0001). Significant differences in gap indices were detected between conversion efficiency and control (P=0.01) and between dispersal and control (P=0.02) which was similar to the result obtained for aggregation index. The gap index for predator populations at the sampling periods were significantly different (Day 6: -1.45 ± 0.10, Day 12: -1.75 ± 0.10, Day 18: -1.76 ± 0.10 and Day 24: -1.75 ± 0.10) (all P<0.0001). The gap index shows an increasing trend from day 6 through day 24. The gap indices were significantly different between day 6 and 12 (P=0.001), 6 and 18 (P=0.001) and 6 and 24 (P=0.001).

Patch Index. Only the main effects of time of interaction and predator-prey ratio were significant with respect to patch index (v_i) of predators (Table 5-4). The patch indices were significantly greater than 1 indicating grouping of large adult predator counts (Day 6: 1.23 ± 0.12, Day 12: 1.77 ± 0.12, Day 18: 1.78 ± 0.12 and Day 24: 1.84 ± 0.12; mean patch index ± SE) (all P<0.0001). The patch index for predators shows a growing trend from day 6 through day 24. Similar to the patterns obtained for gap indices, the patch indices were only different between day 6 and 12 (P=0.004), 6 and 18 (P=0.0004) and 6 and 24 (P<0.0001). This indicates that

clusters of large counts (patches) are prevalent initially, but as populations grow small counts (gaps) become more predominant. Overall, patch indices were significantly different at predator-prey ratios of 1:10 (1.54 ± 0.09) and 1:30 (1.76 ± 0.09). Although foraging trait did not influence patch index, the indices were (Consumption: 1.70 ± 0.11, Conversion: 1.50± 0.11, Dispersal: 1.67 ± 0.11 and Unselected control: 1.73 ± 0.11).

Spatial Distribution of Prey

Aggregation Index. Only time of predator-prey interaction had a significant main effect on aggregation of prey populations (Table 5-4). Prey populations were significantly aggregated (I_a >1) at all sampling period and showed an increasing pattern (Day 6: 1.18 ± 0.11, Day 12: 1.34 ± 0.11, Day 18: 1.43 ± 0.11 and Day 24: 1.63 ± 0.11 mean aggregation index ± SE) (all P<0.0001). Aggregation indices were significantly different among the selected lines and the unselected control for all days except between day 6 and 12 (P=0.17) and day 12 and 18 (P=0.32). The spatial distribution of prey adults for a specific foraging trait and the control also showed aggregated patterns (Consumption: 1.43 ± 0.12, Conversion: 1.51 ± 0.12, Dispersal: 1.32 ± 0.12 and Unselected control: 1.31 ± 0.12). Aggregation indices for prey were more aggregated than uniform (I_a <1) and no random patterns (I_a =1) were observed. Interestingly, uniform or regular distributions were observed in at day 18 and 24.

Gap Index. There was a significant main effect of time on gap index of prey populations (Table 5-4). The gap indices for prey populations at the different sampling periods were significantly different among selected lines and control and showed an increasing trend as well (Day 6: -1.17 ± 0.10, Day 12: -1.25 ± 0.10, Day 18: -1.41 ± 0.10 and Day 24: -1.543 ± 0.10; mean gap index ± SE) (all P<0.0001). Gap indices were significantly different among selected lines between day 6 and 18 (P=0.01), day 6 and 24 (P=0.0002) and day 12 and 24 (P=0.004).

The gap indices for specific foraging traits were (Consumption: -1.38 ± 0.11, Conversion: -1.46 ± 0.11, Dispersal: -1.29 ± 0.11 and Unselected control: -1.25 ± 0.11).

Patch Index. There was only a significant main effect of time on patch index of prey populations which was similar to results obtained for aggregation and gap indices of prey populations (Table 5-4). The patch indices for prey populations at the sampling periods were significantly different (Day 6: 1.06 ± 0.11, Day 12: 1.28 ± 0.11, Day 18: 1.35 ± 0.11 and Day 24: 1.60 ± 0.11; mean patch index ± SE) (all $P<0.0001$). The patch index also shows an increasing trend from day 6 through day 24 similar to that observed for aggregation index. Patch indices were significantly different between all sampling periods except day 6 and 12 ($P=0.11$), day 12 and 18 ($P=0.57$). Although non-significant, patch indices for specific foraging traits were greater than 1 (Consumption: 1.36 ± 0.13, Conversion: 1.41± 0.13, Dispersal: 1.28 ± 0.13 and Unselected control: 1.25 ± 0.13).

Spatial Association between Predator and Prey

Foraging trait and time of predator-prey interaction had a significant effect on the spatial association index, X. However, there were no significant interactions among main effects (Table 5-3). Spatial association between predator and prey was positive for all selected lines and the control (Consumption: 0.03 ± 0.08, Conversion: 0.20 ± 0.08, Dispersal: 0.29 ± 0.08 and Unselected control: 0.05 ± 0.08 mean association index ± SE) (Fig. 5-4A, B, C, D). However the association index was significant only for conversion efficiency ($P=0.01$) and dispersal lines (P=0.0003) and they were not different from each other ($P=0.38$) (Table 5-3) (Fig. 5-4A, B, C, D). Spatial analysis indicated no significant differences between consumption and control ($P=0.83$), conversion efficiency and control ($P=0.18$), or consumption and conversion efficiency ($P=0.12$) (Fig. 5-4). The spatial association patterns between predator and prey were

significantly different between dispersal and control (P=0.03) and dispersal and consumption (P=0.02) (Fig. 5-4A, B, D).

Spatial association between predator and prey was positive and significant at all times except day 18 (Day 6: 0.31 ± 0.08, Day 12: 0.16 ± 0.08, Day 18: -0.11 ± 0.08 and Day 24: 0.22 ± 0.08) (Fig. 5-4A, B, C, D). There were no significant differences in the spatial association index between day 6 and 12 (P= 0.17), day 6 and 24 (P= 0.38) or day 12 and 24 (P=0.61).

Correlation between Predator and Prey Densities

There were no significant interactions among the main effects (Table 5-3). However, the density distributions of predator and prey were positively correlated for the specific foraging trait and unselected control (Consumption= 0.23 ± 0.04, Conversion: 0.33 ± 0.04, Dispersal: 0.33 ± 0.04 and the Unselected control: 0.16 ± 0.04; mean correlation coefficient, r ± SE) (all P<0.0001 except control P=0.0001). The highest correlation coefficient was observed for the high conversion efficiency and the lowest for the unselected control. The high conversion efficiency was not different from dispersal line (P=0.98) but was different from the unselected control (P= 0.0011) and the high consumption line (P= 0.04). The high dispersal lines was different from the control (P= 0.0012) and the high consumption line (P=0.05).

The predator-prey numbers were positively correlated for all time periods except day 18, where no correlation was found (Day 6: 0.37 ± 0.04, Day 12: 0.29± 0.04, Day 18: 0.10 ± 0.04 and Day 24: 0.36 ± 0.04) (all P<0.0001 except day 18, P=0.12). There was no significant difference between day 6 and 12 (P= 0.35), day 6 and 24 (P= 0.42) or day 12 and 24 (P=0.90). We detected strong positive correlations initially (day 6 and 12), random distribution of predator and prey at day 18 and strong correlations at day 24. Further there were significant differences

in correlation coefficients between days 6 and 18 (P=0.01), and marginally significant differences between days 12 and 18 (P=0.08) and days 18 and 24 (P=0.06).

Discussion

There has been a call for better integration of behavior in analyses of predator-prey/host-parasitoid population dynamics (Ives 1995; Lima and Zollner 1996; Roitberg and Mangel 1997; Morales and Ellner 2002). In particular, how movement behavior of predators (and prey), when one or both occur in spatially-complex (i.e., patchy) distributions, affects predator foraging efficiency and predator-prey dynamics has not been adequately investigated. In fact, we know of no comprehensive experimental study of how spatial heterogeneity affects predator foraging efficiency and population dynamics. Therefore, current models – evolutionary or mechanistic – cannot predict predator foraging behavior. In contrast, several studies have shown the effects of spatial heterogeneity on the foraging efficiency of parasitoids (Madden and Pimental 1965; Cheke 1974), including how spatially distributed hosts influence foraging efficiency (Kareiva 1986; Kareiva and Odell 1987; Kareiva and Sahakian 1990). Spatial heterogeneity such as plant architecture affects predator foraging efficiency and behavior indirectly by mediating prey availability, density, abundance and distribution (Pimentel 1961; Lawton 1983; Freese 1995; Clark and Messina 1998).

To explicitly link predator foraging behavior with predator-prey population dynamics, an obvious question to ask is: how does spatial heterogeneity affect the efficiency of predators foraging for prey? (Ives 1995). In the present study we established a patchy prey distribution of the twospotted mite, *T. urticae*, and compared foraging efficiency of the acarine predator, *P. persimilis* (in terms of both prey number and plant damage), and predator-prey spatial dynamics based on differences in predator foraging traits and predator-prey release ratios. Results

supported our prediction that depending on the initial predator:prey ratio, the high levels of the three foraging traits -- consumption, conversion efficiency and dispersal selection -- would alter predator-prey population growth rates and associated plant damage compared to the unselected control. At either predator:prey ratios (1:10 or 1:30), the foraging traits were comparable to the unselected control in their ability to suppress prey. This result was also true for plant damage. However, initial predator: prey ratio did not influence predator densities. Because the high conversion line had the lowest prey densities and prey damage, it is not surprising that it had the highest predator populations. As expected, in the high conversion efficiency line predators had a higher reproductive output per prey consumed than in the high consumption line. Additionally, there is evidence that predator offspring dispersed more quickly than those in the high consumption line and, thus, were able to locate distant prey patches better. In essence, the conversion efficiency line exhibited attributes of both the high consumption and high dispersal line, which might make it more successful for locating prey patches and for maximizing reproductive output.

Unexpectedly, the high consumption line was not as effective in reducing prey populations as the other selected lines. In fact, besides more prey consumed, this line had a reproductive output similar to that found in the dispersal line. Several models and experiments have shown that variability in prey consumption depends on prey distribution (e.g., Cappuccino 1987; Kareiva 1990; Hastings et al. 1997; Yasuda and Ishikawa 1999; Bohan et al. 2000). We believe that prey patchiness may have reduced the overall feeding rate of the high consumption line, and would continue to do so unless predators were able to compensate by adopting a non-random searching behavior presumably in response to prey-induced plant volatiles (Janssen 1999). In contrast, the high dispersal and conversion efficiency lines have mechanisms that lead

to a positive aggregative response which leads to a high local predator-prey ratio in the most profitable prey patches, thereby reducing prey and increasing reproductive output.

The initial predator-to-prey ratio is a major factor that determines predator-prey interactions (Pels et al. 2002). Thus, we hypothesized that the predator-prey interaction for *P. persimilis* and *T. urticae* would differ depending on the initial predator-prey ratio. But this ratio did not affect predator numbers in our study. Because the reproductive output of predators depends primarily on prey availability, and because there were ample prey available at both the 1:10 and 1:30 ratios, this may explain why we did not detect differences in predator reproductive output. For example, there were sufficient prey locally for the high consumption line to maximize its output; conversely, the high dispersal line was able to locate distant prey patches, feed and also maximize its reproductive potential.

We did detect differences in prey numbers and plant damage depending on the ratio of predators to prey. Differences among selected lines and the control were marginal at a predator release ratio of 1:10, but they were greater at 1:30. This finding supports our prediction that selected lines would differ in their ability to impact predator-prey population growth rate depending on the initial predator-prey ratio and, more specifically, that all lines of predators would be effective at the higher release ratio. A release ratio for *P. persimilis* of 1:10 has been shown to be successful in controlling spider mite numbers and preventing plant damage (Markkula and Tiittanen, 1976). On the other hand, a predator-prey ratio of 1:30 does not protect plants from spider mites and damage (Hamlen and Lindquist 1981, Opit et al. 2004).

Among selected lines, differences in predator and prey populations were detected at day 18 and day 12, respectively. Both the predator and prey go through one generation every 7-10

days; hence, differences in population growth occurred after a minimum of two generations. Prey damage to leaves, however, was significantly different at all times.

There was a significant interaction between foraging traits and time for predator, prey and prey damage, suggesting that changes in predator and prey populations and plant damage occur differently over time for different foraging traits. The significant interaction between predator-prey ratio and time with respect to prey numbers and plant damage indicates that the influence of predator numbers on prey populations and associated damage develops at different rates. In general, plant damage was much lower at the 1:10 ratio than at 1:30. This result is expected because relatively more predators were present at the 1:10 ratio.

Our study showed that adult predator and prey distribution was largely aggregated over the course of the experiment with an aggregation index, $I_a > 1$. Further we did not detect random distributions for either predator or prey. However, uniform or regular ($I_a < 1$) distributions were observed occasionally for adult prey in all selected lines and in the control population at days 18 and 24. We believe that the uniform pattern of distribution of prey is probably the outcome of predation pressure. High predation pressure reduced prey numbers at which time it would be advantageous for prey to be evenly distributed when at low density as indicated in our study and Nachman (2006) and switch to a more patchy distribution when density increases (Nachman 2006). If the degree of prey aggregation is high, the predators would be able to achieve a higher predation rate than they would obtain if the prey had been evenly distributed and low (Nachman 2006). At high prey densities, prey are aggregated and relatively large part of the predator population will waste time by searching patches with prey densities below average; whereas the remaining part spends time in patches with high prey density. Owing to satiation of the predators staying in the most profitable patches, the mean predation rates, averaged over all

patches, will thus be lower than if all predators had been exposed to the mean prey density (Nachman 2006). This may explain why prey and predator densities were comparable among selected lines in our study.

Spatial association and correlation analysis confirms the impact of foraging traits on predator-prey coincidence by correlating densities or by clustering indices, respectively. Given that *P. persimilis* is a specialist predator on tetranychid mites, *T. urticae* (van Lenteren and Woets 1988), it is not surprising that we found spatial and temporal with prey items that forms the bulk of its diet. A study on strawberries also showed significant association between *P. persimilis* immature stages and *T. urticae* eggs and immatures and *P. persimilis* eggs and adults with *T. urticae* eggs and adults. This indicates that *P. persimilis* adults were laying eggs within developing colonies of *T. urticae* and then moving on to new colonies leaving prey available for the immature stages (Fitzgerald et al. 2008) which is consistent with the "parent-offspring" conflict theory. In the current study we did not measure association between different life stages of predator and prey. However, we detected a higher aggregation index for predators than prey, which may be indicate that adult female predators might lay eggs in a prey patch with sufficient prey and then leave to find other patches.

Predators from the high conversion efficiency and dispersal lines showed significant spatial association and correlation with prey, whereas those from the consumption line and the unselected control population had comparably lower spatial associations. Lines with high dispersal ability (adults tend to leave prey patch sooner) and conversion efficiency (adults leave more offspring locally which also disperse) were better able to locate the distant prey patch. In contrast, predators from the high consumption line and unselected control apparently had a reduced leaving rate, which may explain the low coincidence with prey. Overall, the spatial

association between predators and prey were positive initially (local patch) but then showed dynamic patterns depending on the foraging strategy of the individual predator.

It is interesting to note that the spatial association was not significant at day 18. In the present study, the association index and correlation analysis reverted to positive and were significant at day 24. There may be several reasons for a negative association between predator and prey on day 18. Aggregation indices showed that predator and prey were initially aggregated in one prey patch (I_a of >1). As predator populations increased, they reducing prey densities at which time prey adopt an even distribution among palnts (aggregation index I_a of <1 at day 18). Predators however, are aggregated (I_a of >1) in some prey patches and cannot efficiently "track" prey in all plants and causing spatial decorrelation with prey. This causes a delay in predator's ability to find prey patches consequenlty prey densities increase and they become aggregated once again. It is well known that effective natural enemies can cause arthropod populations to adopt an even or uniform distribution (Wilson et al. 1984) at low population densities through predation (Wilson et al. 1984) or through induced predator-avoidance behavior (Onzo et al. 2003).

Two hypotheses have been put forward to explain why different strategies for exploiting prey persist in nature despite selection on predators. First, the evolution of "super" predators is prevented by constraints on the predators (MacArthur and Levins 1967). Second, the evolution of super predators is counteracted by the evolution of antipredator traits in the prey (Red Queen hypothesis; Van Valen 1973). Pels et al. (2002) performed simulations using a metapopulation model with different exploitation strategies such as conversion efficiency, consumption, and immigration to determine which of the predator's exploitation strategies are evolutionarily stable and whether these strategies minimize the overall density of prey. Under selection for

conversion efficiency they found that the predator-prey system always goes globally extinct yet persists under selection for consumption or emigration rates, and that the evolutionarily stable exploitation strategies reduces local prey population growth rates.

Our experimental study confirms Pels et al. (2002) results in that all three exploitation strategies of interest were effective in reducing prey density. This result is interesting in that previous research (Nachappa et al. 2008) showed that fitness estimates (intrinsic rates of increase, r_m) (Birch 1948) associated with different *P. persimilis* foraging traits were significantly different. In particular, the high consumption and conversion line had the highest fitness and high dispersal line was comparable to the unselected control. On the basis of these findings one would expect that the high consumption line would be most favored by natural selection. Our study was conducted under a limited spatial distribution of prey -- two isolated patches per landscape or plant array -- which may not have been sufficiently heterogeneous for predators to manifest their full potential of its foraging strategies. We might also expect different predator-prey dynamics had we continued the experiment for longer periods or during declining prey populations.

Whether in natural or managed ecosystems, natural enemies must interact with their herbivorous prey in spatially heterogeneous landscapes in which the location and abundance of the two species may not be consistently correlated. However, for biological control to be effective the spatial coincidence of natural enemies and pests is important (Beddington et al. 1978; Murdoch and Oaten 1989). Their spatial coincidence depends in large part on the way in which natural enemies respond to pest density and distribution in terms of dispersal, prey consumption, and reproduction. The mechanisms underlying these factors determine the local and global abundances of both species, as well as the efficacy of biological control. For

example, the fact that prey aggregation benefits the predators at low densities may also have implications for biological control because it slows down the growth rate of the prey and helps the predators to survive during periods of prey scarcity (Murdoch and Briggs 1996). The knowledge of the spatio-temporal dynamics of prey and predator distributions can potentially provide valuable information on when and where to release natural enemies in augmentative biological control programs.

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Figures and Tables

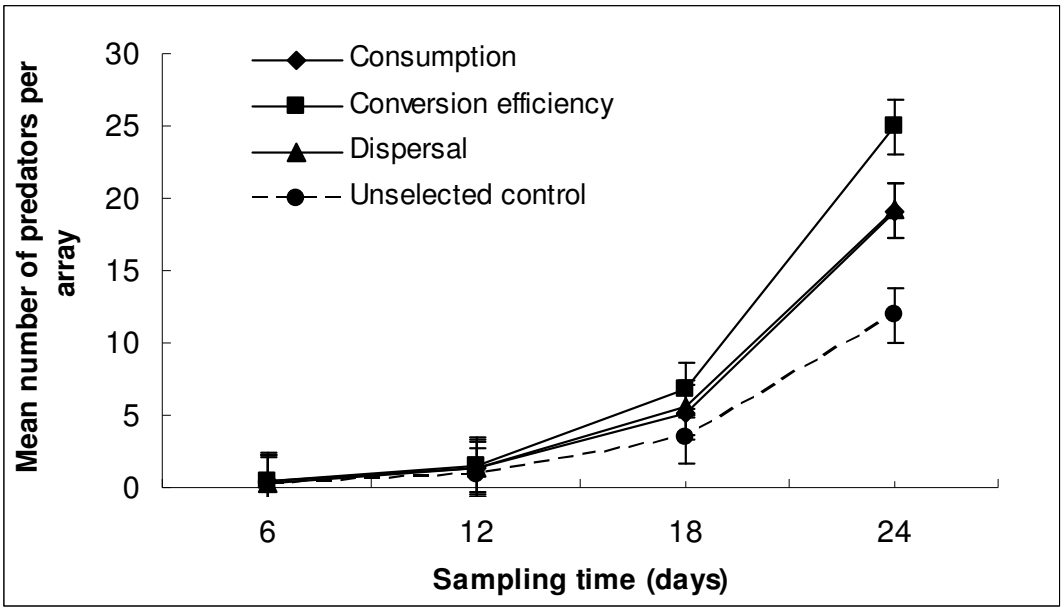

Figure 5-1 Mean predator numbers per array at four sampling periods. Vertical bars indicate ± SE for the experiment.

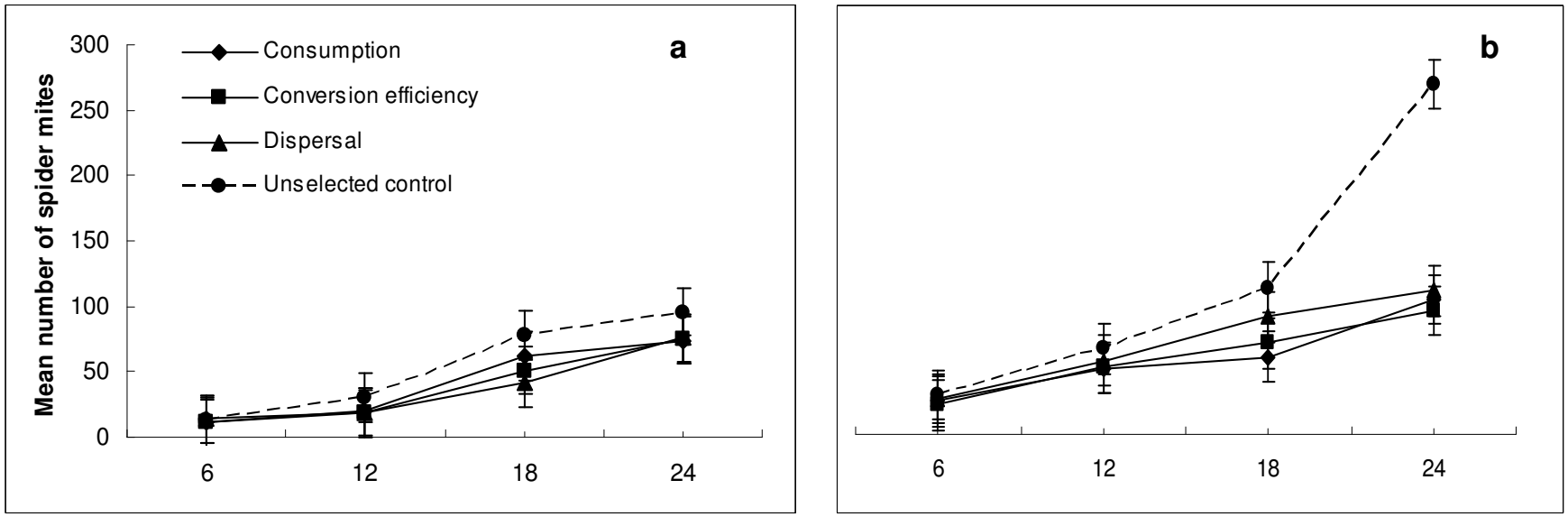

Figure 5-2 Mean prey numbers per array at predator release ratios of A) 1:10 and B) 1:30 sampled at four time periods. Vertical bars indicate ± SE for the experiment.

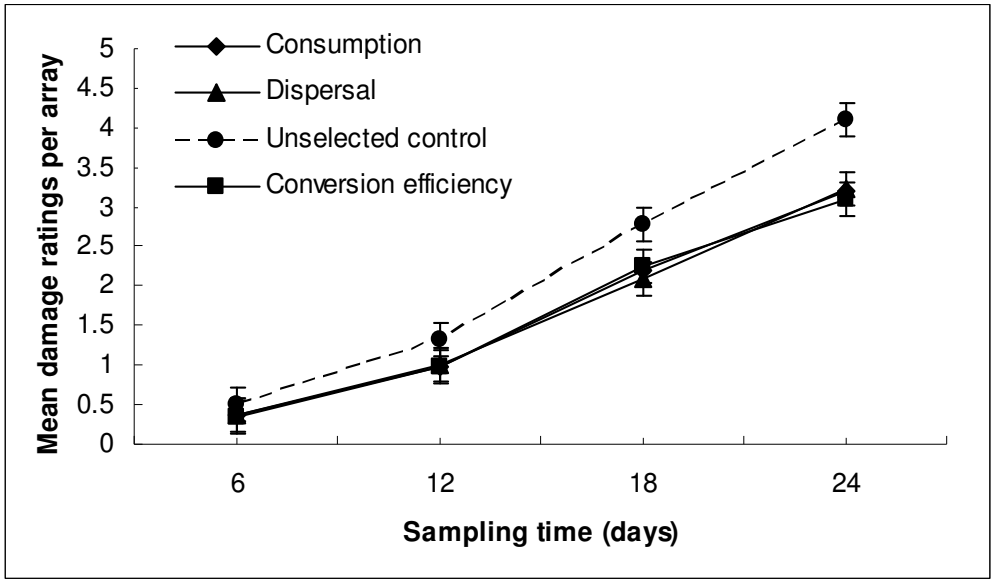

Figure 5-3 Mean plant damage ratings per array at four sampling periods. Vertical bars indicate ± SE for the experiment.

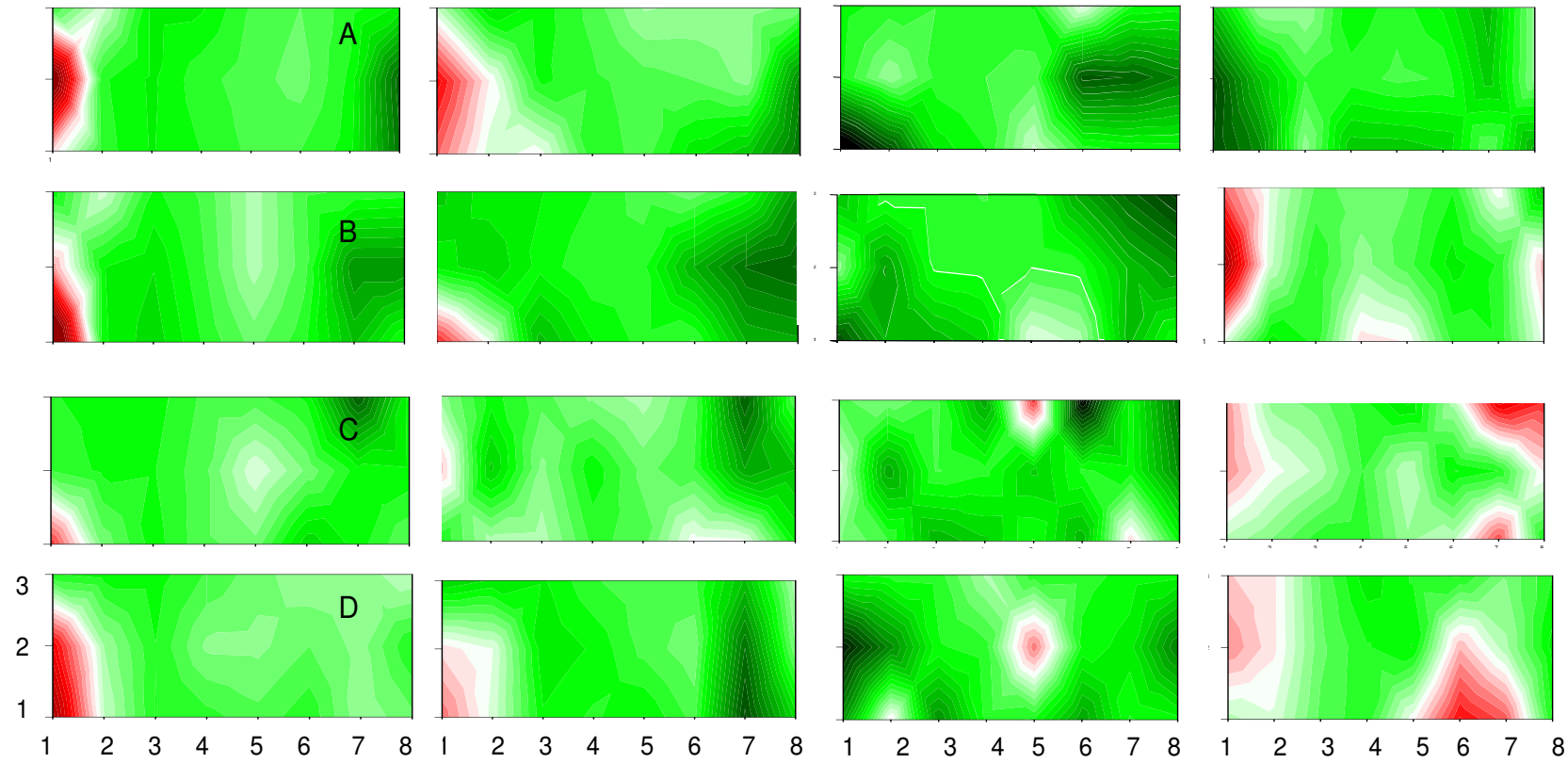

Figure 5-4 Example maps of spatial association patterns of predator and prey populations per array during the course of the experimental period. A) unselected control, B) consumption, C) conversion efficiency and D) dispersal response. Red color indicates spatial association index, X>0, positive association between predator and prey, green color indicates spatial

association index, X<0, negative association or dissociation between predator and prey, white color indicates spatial association index, X=0, random pattern of predator and prey.

Selected Line	Response		
	Prey consumed in 24h	Ratio of offspring produced to prey consumed in 24 h	Time to leave prey patch (min)
Consumption	39.91 ± 1.17 a	0.11 ± 0.05 b	46.30 ± 5.33 b
Conversion efficiency	27.88 ± 1.98 b	0.17 ± 0.008 a	51.50 ± 4.35 b
Dispersal	23.97 ± 2.37 b	0.12 ± 0.01 b	11.38 ± 1.67 a
Unselected control	24.08 ± 3.91 b	0.12 ± 0.005 b	55.55 ± 3.20 b

Table 5-1 Levels of response in specific predator foraging traits and the unselected control after selection plateaued. Means within columns followed by the same letter are not statistically different at P<0.0001.

Effect	Replicate 1		Replicate 2		Replicate 3	
	Before	After	Before	After	Before	After
Consumption	35.57 ± 0.89	35.43 ± 0.54	36.42 ± 1.23	34.59 ± 0.73	37.43 ± 1.41	34.00 ± 0.65
Conversion efficiency	0.18 ± 0.03	0.15 ± 0.01	0.16 ± 0.02	0.15 ± 0.02	0.18 ± 0.01	0.15 ± 0.01
Dispersal	7.60 ± 1.27	7.54 ± 0.90	11.23 ± 1.43	10.31 ± 0.98	13.52 ± 1.76	9.42 ± 1.61

Table 5-2 Levels of response in specific predator foraging traits immediately before and after greenhouse experiments.

Effect	Predators	Prey	Plant damage	Correlation coefficient (r)	Spatial association index (X)
Foraging trait	**0.0004**	**0.0002**	**0.006**	**0.002**	**0.05**
Ratio	0.44	**<0.0001**	**0.0003**	0.69	0.86
Foraging trait x ratio	0.16	0.07	0.75	0.52	0.82
Time	**<0.0001**	**<0.0001**	**<0.0001**	**0.05**	**0.0016**
Foraging trait x time	**<0.0001**	**<0.0001**	**0.003**	0.55	0.10
Time x ratio	0.92	**<0.0001**	**0.002**	0.30	0.57
Foraging trait x time x ratio	0.37	**<0.0001**	0.47	0.90	0.97

Table 5-3 Influence of type of foraging trait, predator release ratio and time of interaction on the number of predators, prey and associated plant damage. P-values highlighted in bold highlight are significant.

Effect	Aggregation index (I_a)		Gap index, V_j		Patch index, V_i	
	Predators	Prey	Predator	Prey	Predators	Prey
Foraging trait	**0.05**	0.39	**0.04**	0.32	0.13	0.69
Ratio	**0.04**	0.53	**0.03**	0.28	**0.004**	0.98
Foraging trait x ratio	0.25	0.42	0.22	0.43	0.54	0.49
Time	**0.002**	**0.0009**	**0.01**	**0.001**	**0.0002**	**0.0014**
Foraging trait x time	**0.02**	0.62	**0.03**	0.65	0.26	0.63
Time x ratio	0.07	0.60	0.13	0.54	0.11	0.68
Foraging trait x time x ratio	0.80	0.65	0.62	0.44	0.71	0.90

Table 5-4 Influence of type of foraging trait, predator release ratio and time of interaction on spatial distribution indices: aggregation (I_a), gap (V_j) and patch (V_i). P-values highlighted in bold are significant.

CHAPTER 6- Conclusions

Knowledge of the population impact of predator foraging is critical for understanding how behavioral responses affect predator-prey interactions under different environments, and to impose deliberate manipulations of predators in response to different environmental conditions, as might commonly occur in biological control. One way to link foraging behavior and population dynamics is to focus on the influence of specific predator foraging traits affecting both natural enemy fitness and pest suppression. My dissertation research addressed the role of four foraging traits in the predatory mite, *Phytoseiulus persimilis* Athias-Henriot (Acari: Phytoseiidae), and their impact on its interaction with its prey, the twospotted spider mite, *Tetranychus urticae* Koch (Acari: Tetranychidae). Results of my dissertation research, which identified the role and impact of predator foraging traits on natural enemy fitness and population consequences of the traits relevant to biological control, help to unify these areas of research.

In Chapter 2, I showed that the dispersal response of predatory mites was modified based on prey density in a patch and levels of external volatile cues related to their prey. The dispersal response decreased with increasing levels of prey in a patch irrespective of external volatile levels or feeding experience. Knowledge of environmental factors that affect predator giving-up time has applications for pest management because the timing of natural enemy dispersal can affect the ratio of natural enemies to pests, both within a patch and throughout a region. In turn, this affects pest suppression. With more specific information on the role and relative importance of external and internal cues available to predators, it may be possible to manipulate these cues to increase the efficiency of *P. persimilis* and other biological control agents.

In Chapter 3, I showed that the olfactory response of the predatory mite to prey-infested plants varies in direct relation to the population growth pattern of prey on the plant. The predator's response can be quantified as a function of mite-days, which is a cumulative measure of the standing adult female mite population sampled and summed over time. That is, response to volatiles increased with increasing numbers of prey per plant, or with the length of time the plant was infested by prey. Knowledge of the role of plant volatiles, in combination with other factors that underlie variation in predator behavioral response, will contribute to a better understanding of how *P. persimilis* forages for *T. urticae*. It may also lead to a greater ability to manipulate plant volatiles to increase the effciency of this biological control agent in a variety of ways. Some of these ideas include: 1) application of natural enemy-attracting volatiles, or other chemicals (e.g., jasmonic acid) which induce such volatiles, to crop fields; 2) breeding plants for increased production of these volatiles; and 3) genetically engineering plants for increased production of attractants. The bioassays and protocols developed in Chapters 2 and 3 were applied to artificial selection experiments on the dispersal and olfactory responses of *P. persimilis*, respectively.

In chapter 4, I examined the genetic components of phenotypic variation in ecologically-relevant foraging traits of the predatory mite: consumption rate, conversion efficiency, dispersal response and olfactory response to prey-induced plant volatiles using artificial selection regimes. I detected significant additive genetic variance in both directions of selection for nearly all of the foraging traits, the single exception being the low-olfactory response. The high foraging phenotypes were stable after relaxation of selection, whereas their low counterparts were not. There were significant genetic correlations between some foraging traits that were used in the selection treatments. For example, the high consumption line had a faster dispersal response

than the low line. There was no correlation among foraging traits and life-history traits such as hatching time (time to emerge from egg), hatching percent, development time (time from nymph to adult ecdysiast), fecundity and survivorship from egg to adult. Further, foraging traits differed in their intrinsic rate of increase (r_m) which reflects their potential success under natural conditions. Thus, finding a substantial amount of genetic variation in foraging behaviors of predatory mites and a lack of trade-offs with life-history traits suggests that correlations may not maintain the genetic variation in these traits. There may be other mechanisms that maintain genetic variation in foraging traits such as habitat heterogeneity. Future experiments may include testing the foraging traits in different environments to determine whether habitat heterogeneity maintains genetic variation in the foraging traits. A Quantitative Trait Loci (QTL) analysis can be done to help map regions of the predatory mite genome that contain genes involved in specifying the foraging trait.

Chapter 5 examined the impact of high, stable foraging phenotypes - consumption rate, conversion efficiency and dispersal response - on the predator-prey interaction under different conditions of prey density and distribution. In multiple-plant greenhouse experiments, I found significant differences between selected foraging phenotypes and the unselected control line in terms of predator-prey densities and plant damage. All foraging traits were comparable in predator-prey densities and plant damage, whereas the control population had the lowest predator densities and the highest prey numbers and damage. Spatial association and correlation analysis further confirmed the impact of foraging traits on predator-prey coincidence by correlating densities or by clustering indices, respectively. Certain foraging traits such as dispersal and conversion efficiency were more strongly correlated or associated with prey than were the consumption and unselected control line. I believe that prey patchiness may have reduced the

feeding rate of predators from the high consumption line because they were not efficient in locating distant prey patches. This study supports my contention that variability in foraging traits of the predatory mite, *P. persimilis*, affects its ability to locate patchily-distributed prey, thereby influencing foraging efficiency and population dynamics. Results of my dissertation demonstrates that the expression of foraging behaviors in response to ecological conditions is dependent on phenotypic variation, which is controlled in part by heritable genetic variation and genetic correlations with other phenotypes, and that this variation has consequences for individual's fitness. This work indicates that in a simple landscape structure with two spatially-separated prey patches and abundant prey, all behavioral variants maximize relative fitness (reproductive potential) and prey suppression. Certain foraging traits were concentrated in local prey patches, whereas others moved among prey patches. Results of this study suggest that future studies on foraging behaviors should examine predator fitness and prey suppression in landscapes with different levels of prey and distribution.

Implications for Biological Control

Knowledge of the genetic and ecological effects of predator foraging traits has implications for augmentative biological control. Increasing natural enemy efficiency remains a high priority for researchers, but identifying traits that affect efficiency is difficult. My results indicate that several predator foraging traits are heritable and amenable for breeding programs to improve the efficiency of *P. persimilis*. In addition, the high foraging phenotypes, including high consumption, conversion efficiency and dispersal, were stable after relaxation of selection for up to two months, which potentially reduces the labor costs that would be associated with repeated selection of predators in a rearing facility. Stability of foraging traits also makes them reliable and suitable for field releases. Absence of pleiotropic effects with other foraging and

life-history traits further confirms the suitability of these foraging phenotypes for augmentative biological control programs.

I am of the opinion that the high conversion efficiency line would have the greatest potential for mass rearing and would also be the most efficient for field release. From the commercial producer's point of view, the high conversion efficiency line may be the most feasible for breeding programs because it has a high reproductive potential per prey consumed, which may reduce the cost of rearing in terms of prey supply. Greenhouse experiments suggest that the high conversion efficiency line would have the highest spatial correlation with prey. Thus, it is reasonable to assume that releasing predators from this line may result in the lowest prey densities and highest predator numbers.

Data obtained from genetic studies may enable future pest management efforts to be fine-tuned according to the structure of a particular landscape. The ability of predators to locate resources in a landscape is influenced not only by the pattern of prey patches, but also by the amount of habitat fragmentation, i.e., the size of habitat patches, and the distance between them. There are several factors that can be varied to determine population dynamics of the foraging traits with prey. The spatial scale of the experiment can be varied; increasing the scale (such as a commercial greenhouse) will provide information about global population dynamic processes that occur. In contrast, decreasing the scale will provide information on the mechanistic aspects of predator-prey dynamics. Use of different prey patches (uniform to fragmented), more patches, or altering the inter-patch distance will help to differentiate the effectiveness of the foraging traits. For example, the high dispersal line may be more efficient in exploiting distant prey patches irrespective of prey patch distribution. Increasing prey density per patch may also distinguish the high consumption line from the high conversion efficiency and dispersal lines.

Distribution of predators can also be varied, from fine- to coarsely-grained. The duration of the predator-prey interaction is a key determinant of success of both short-term and long-term biological control programs. For the latter, the stability of the interaction is an important factor. By varying the duration of the experiment and the environmental components of the landscape, we may be able to assess which combination of traits, time and environmental conditions provides short- or long-term prey suppression. Other areas of research to be considered for future augmentative release programs are: releasing predators selected for composite traits. For example, high conversion efficiency with dispersal, or high consumption, high dispersal and high development might prove to be an effective suite of traits. Mixed releases of multiple predator lines selected for different foraging traits might also be a viable option for effective long-term pest management. With this information it may be possible to modify augmentation programs (e.g., change predator release patterns or predator: prey ratio) or conservation programs (e.g., by changing environmental conditions for specific predator lines) to increase the efficiency of biological control.

Appendix A - Chapter 2

SAS CODES

1) The effect of prey egg density, volatiles and feeding experience on giving-up time (GUT) of satiated and starved *P. persimilis* was analyzed using PROC MIXED.

```
Proc mixed method=Type3;
Class prey volatiles status run;
Model RI=prey|volatiles|status/DDFM=KR;
Random Run (Status*volatiles);
LSMeans prey volatiles status/Diff;
run;
```

2) The number of *T. urticae* prey eggs consumed by satiated and starved predators at each prey egg density and volatile condition was analyzed the by analysis of variance using PROC GLM in SAS (SAS Institute 2002).

```
proc glm;
Class status volatiles;
model tsmc= status| volatiles;
lsmeans status |volatiles /pdiff;
run;
```

3) The same criteria was used to conduct a life test analysis (PROC LIFETEST) to compare leaving rates among single predator and five predators at each prey density per petri dish using log-rank test (SAS Institute 2002).

```
proc lifetest;
time survday*censor(0);
strata predator status density volatiles;
run;
proc lifetest;
time survday*censor(0);
run;
```

Appendix B - Chapter 3

SAS CODES

1) A mixed-model analysis was conducted using treatment, time (days after inoculation), and their interaction as fixed effects, and experiment as random effects. Time was also a repeated measures factor. Models were fit assuming numerous standard structures for the serial correlation, and the best-fitting model was selected using Akaike's Information Criterion (Littell et al. 1996; Guerin and Stroup 2000). F-tests for fixed effects and t-tests for pairwise comparisons were performed based on the chosen correlation structure (Littell et al. 1996). All tests used a 0.05 type I error rate.

```
proc sort;
  by trt expt set;
run;

proc print;
run;

Proc Mixed CL;
Class expt set trt time;
Model time= trt time trt*time;
Random expt set(expt) expt*trt;
Repeated time/subject=trt*set(expt) Type=cs;
RUN;

Proc Mixed CL;
Class expt set trt time;
Model time= trt time trt*time;
Random expt set(expt) expt*trt;
Repeated time/subject=trt*set(expt) Type=ar(1);
RUN;

Proc Mixed CL;
Class expt set trt time;
Model time = trt time trt*time;
Random expt set(expt) expt*trt;
Repeated time/subject=trt*set(expt) Type=csh;
RUN;

Proc Mixed CL;
Class expt set trt time;
Model time = trt time trt*time;
```

```
Random expt set(expt) expt*trt;
Repeated time/subject=trt*set(expt) Type=arh(1);
RUN;

Proc Mixed CL;
Class expt set trt time;
Model time = trt time trt*time;
Random expt set(expt) expt*trt;
Repeated time/subject=trt*set(expt) Type=toep;
RUN;

Proc Mixed CL;
Class expt set trt time;
Model time = trt time trt*time;
Random expt set(expt) expt*trt;
Repeated time/subject=trt*set(expt) Type=toeph;
RUN;

Proc Mixed CL;
Class expt set trt time;
Model time = trt time trt*time;
Random expt set(expt) expt*trt;
Repeated time/subject=trt*set(expt) Type=ante(1);
RUN;

title1 'The chosen model is Unstructured correlation';

Proc Mixed CL;
Class expt set trt time;
Model time = trt time trt*time / ddfm=kr;
Random expt set(expt) expt*trt;
Repeated time/subject=trt*set(expt) Type=unr;
parms .03 .0027 .034 .039 .043 .265 .195 .512 .362 .105
      -.63 -.13 -.24 .11 -.42 .51 .33 -.51 .59 .53 .31 .35 .04 -.10 .25 .25 -
.19 .63 .57 .51 .22;
lsmeans trt trt*time / diff;
ods output lsmeans=lsm;
ods output diffs=diffs;
RUN;

title2 'Comparisons of TRTs 1 and 2';

proc print data=diffs;
  where trt=1 and _trt=2;
run;

title2 'Comparisons of all TRTs at each point in time';

proc print data=diffs;
  where time = _time;
run;

title2 'Plot of LSMeans against time for each TRT';

proc gplot data=lsm;
  plot estimate*time=trt;
ru
```

Appendix C - Chapter 4

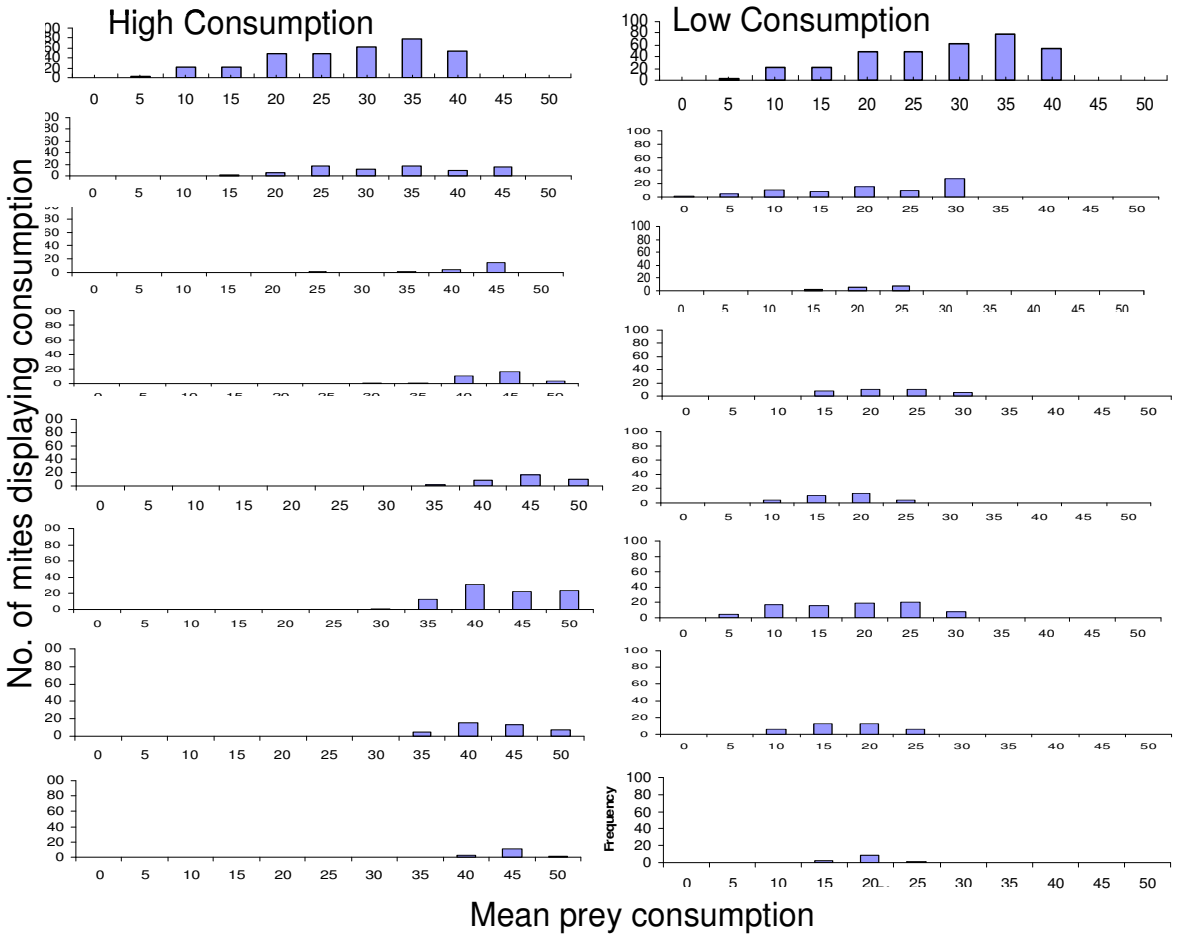

Figure A-1 Frequency distribution of consumption phenotypes in *P. persimilis* per generation.

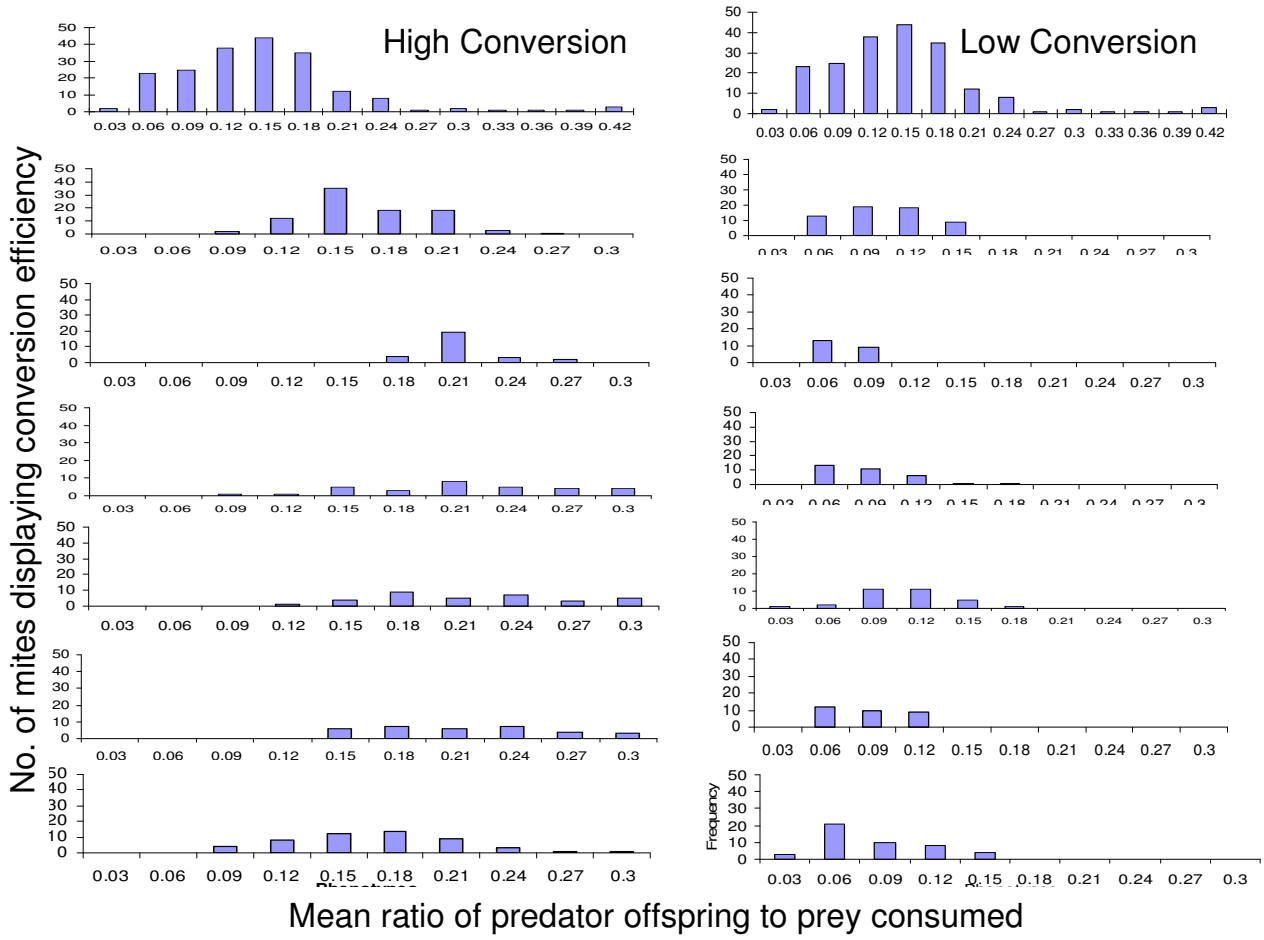

Figure A-2 Frequency distribution of conversion efficiency phenotypes in *P. persimilis* per generation.

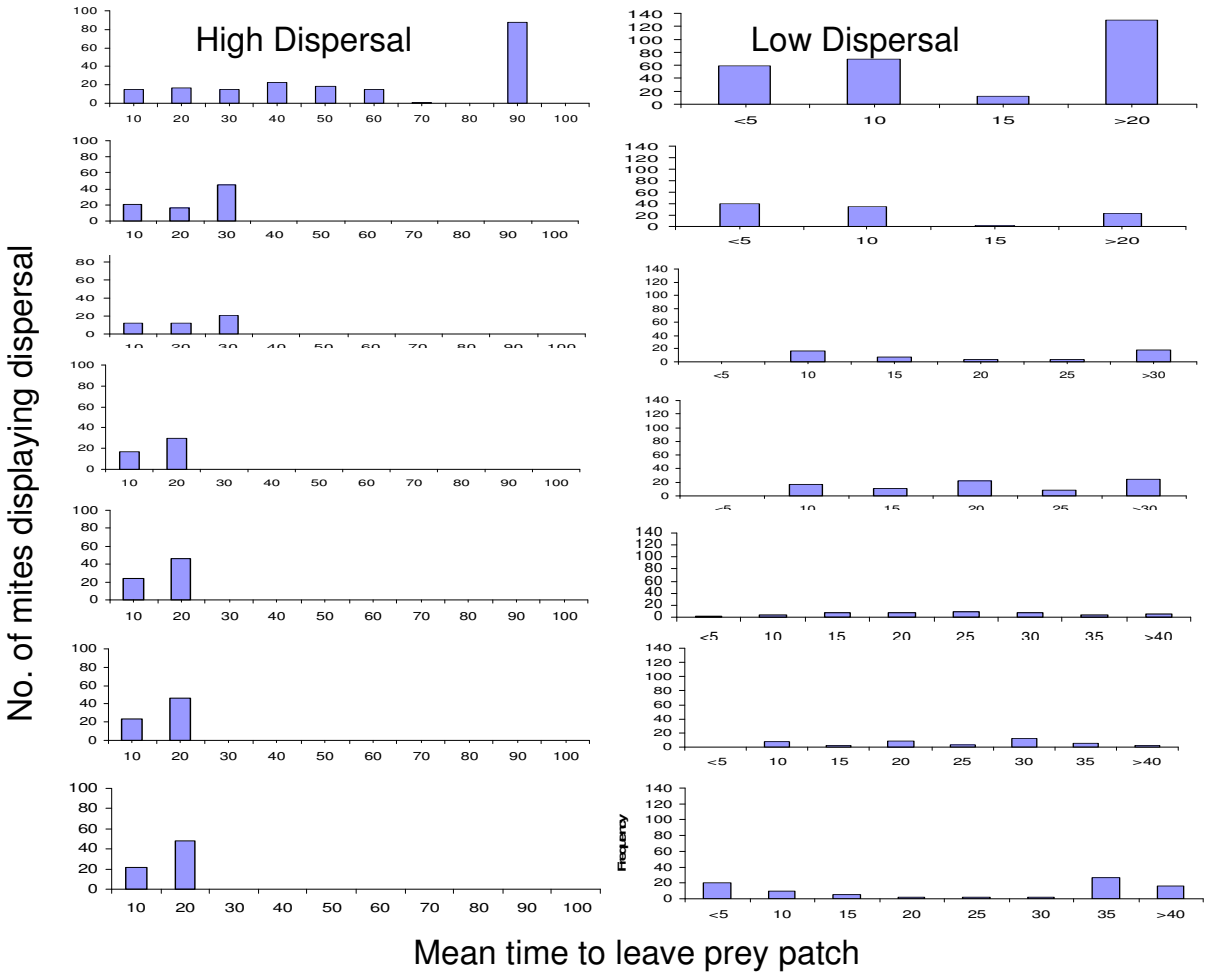

Figure A-3 Frequency distribution of dispersal response phenotypes in *P. persimilis* per generation.

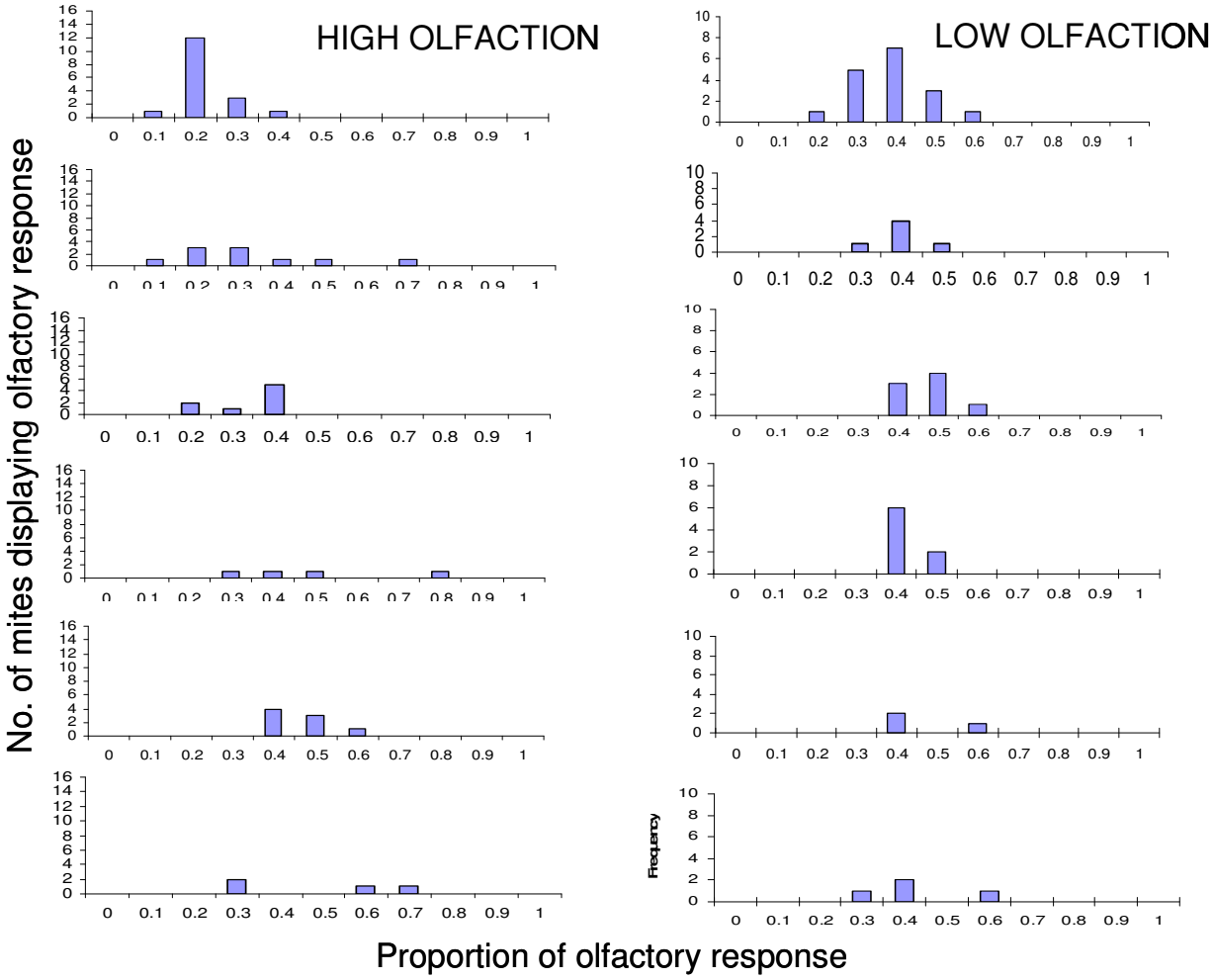

Figure A-4 Frequency distribution of olfactory response phenotypes in *P. persimilis* per generation.

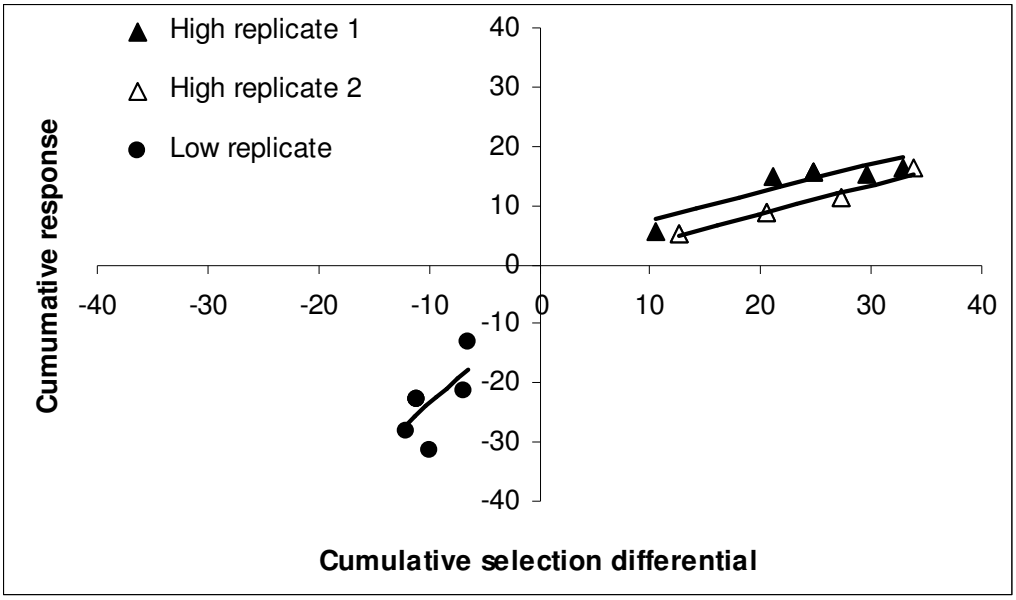

Figure A-5 Response of prey consumption rate to selection in *P. persimilis* relative to the cumulative selection differential for both high and low lines. The linear regression for high replicate 1: $r^2 = 0.78$, $F_{1,5} = 17.22$, $P = 0.01$; high replicate 2: $r^2 = 0.99$, $F_{1,5} = 14072.8$, $P < 0.0001$ and low line: $r^2 = 0.44$, $F_{1,2} = 3.89$, $P = 0.11$).

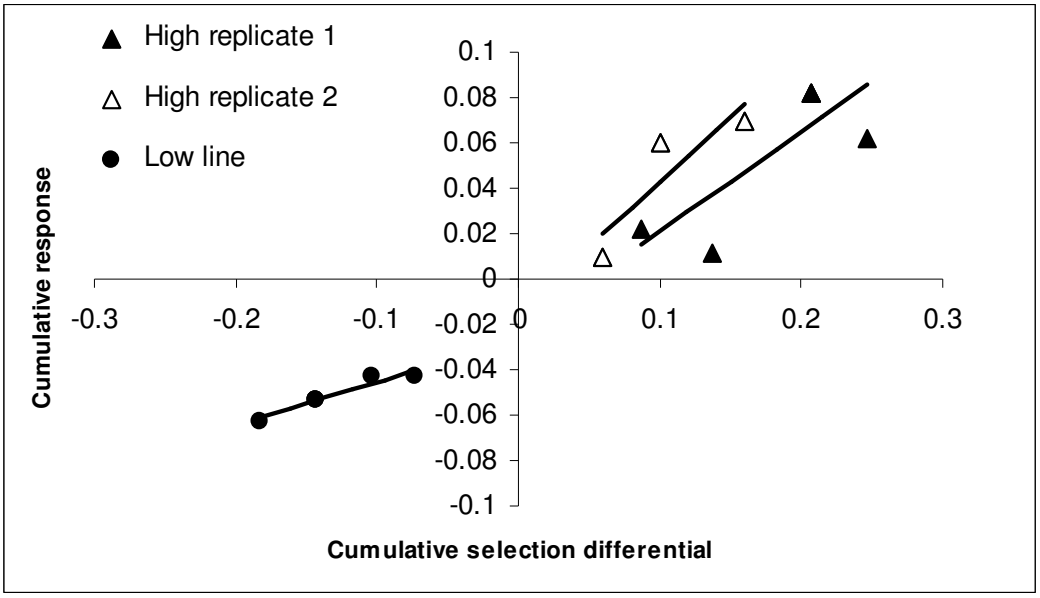

Figure A-6 Response of conversion efficiency to selection in *P. persimilis* relative to the cumulative selection differential for both high and low lines. The linear regression for high replicate 1: $r^2 = 0.64$, $F_{1,4} = 7.28$, $P = 0.05$; high replicate 2: $r^2 = 0.78$, $F_{1,4} = 14.59$, $P = 0.02$ and low line: $r^2 = 0.37$, $F_{1,4} = 2.24$, $P = 0.21$).

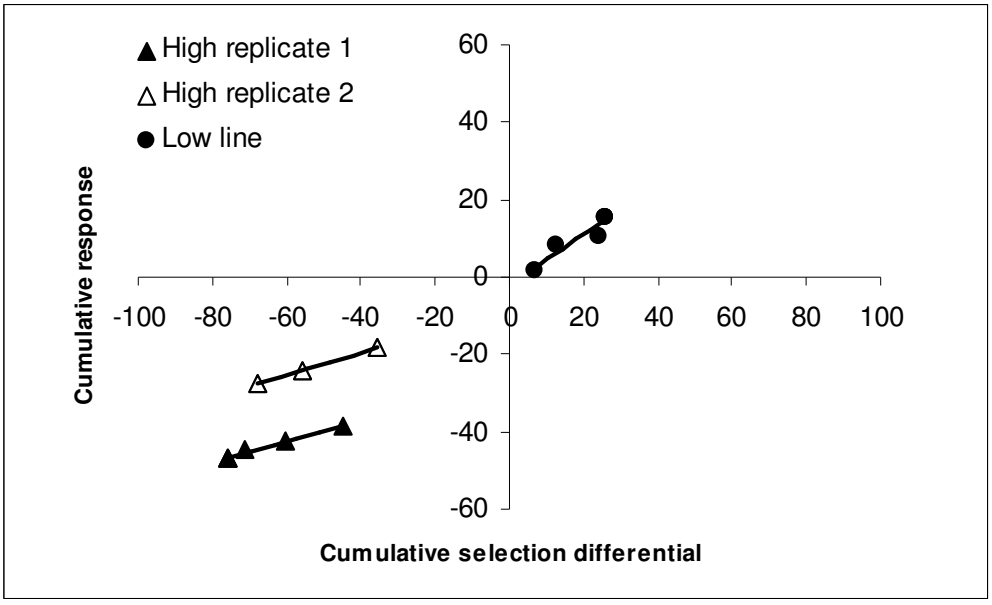

Figure A-7 Response of dispersal to selection in in *P. persimilis* relative to the cumulative selection differential for both high and low lines. The linear regression for high replicate 1: r^2 =0.98, $F_{1,4}$ =235.90, *P* <0.0001 and high replicate 2: r^2 = 0.99, $F_{1,4}$ =850.01, *P* <0.0001 and low line: r^2 =0.89, $F_{1,4}$ =30.39, *P* =0.005.

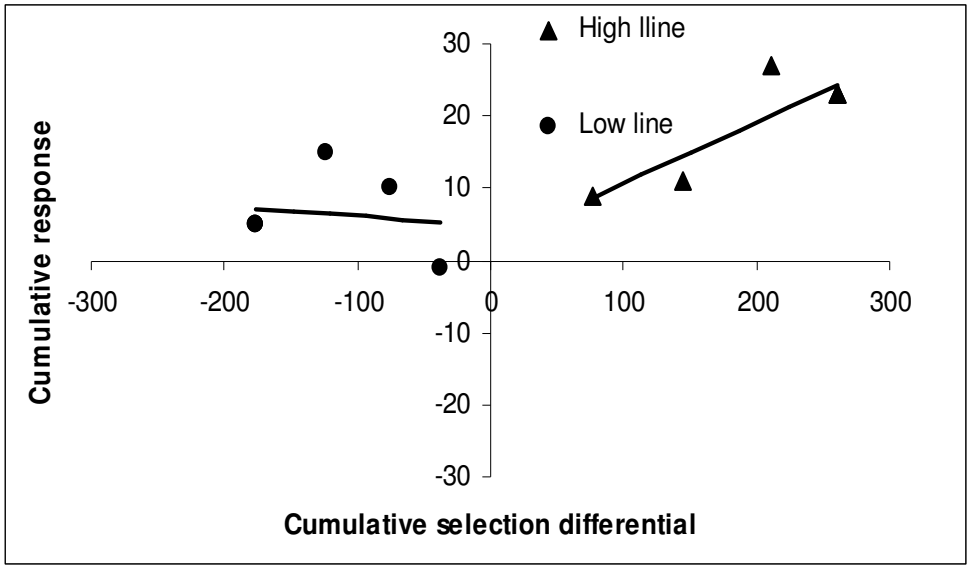

Figure A-8 Response of olfaction to selection in *P. persimilis* relative to the cumulative selection differential for both high and low lines. The linear regression for high line: r^2 =0.76, $F_{1,4}$ =12.86, P =0.02; low line 2: r^2 = 0.02, $F_{1,4}$ = 0.08, P =0.78.

SAS CODES

1. To measure the response to selection a one-way Analysis of Variance (ANOVA) using PROC GLM was performed to identify direct responses to selection between the high- and low-selection lines:

```
PROC GLM;
Class rep line;
Model variable= line;
lsmeans generation/ stderr pdiff;
run;
```

2. A one-way ANOVA was done to determine direct responses to selection between the selection lines and control.

```
PROC GLM;
Class line gen;
Model variable = line;
lsmeans line/ stderr pdiff;
run;
```

3. Responses of foraging traits prior to- and post-relaxation of selection were examined using a one-way ANOVA.

```
PROC GLM;
Class line;
Model variable= line;
lsmeans line/ stderr pdiff;
run;
```

4. A univariate GLM analysis was performed between selection lines of replicate I and II for the stable phenotypes.

```
PROC GLM;
Class rep line gen;
Model variable= line;
lsmeans line|gen/ stderr pdiff;
run;
```

5. The realized heritabilities (h^2) and associated standard errors were calculated in PROC GLM by regressing the Σs on ΣR.

```
Proc reg;
model r=s/ clm cli alpha=0.05;
plot r*s;
plot student.*predicted.;
output out=new student=sres;
proc univariate data=new normal plot;
var sres;
run;
```

6. A one-way ANOVA (PROC GLM) was used to measure correlated responses in consumption rate and conversion efficiency for the high and low lines and unselected base population of each foraging trait.

```
PROC GLM;
Class line;
Model variable= line;
means line/ lsd tukey lines;
run;
```

7. Correlated response to dispersal and olfaction was calculated using a two-way ANOVA with effects of selection line and prey density in the model.

```
PROC GLM;
Class line density;
Model variable= density or volatile|line;
lsmeans line|density or volatile/stderr pdiff;
run;
```

8. A one-way ANOVA (PROC GLM) was used to test for correlated responses to selection in the different life-history traits (i.e., hatching time, hatching percent, development time and adult survival).

```
PROC GLM;
Class line;
Model variable= line;
lsmeans line/ stderr pdiff;
run;
```

9. Mean jackknife estimates of intrinsic rate of increase (r_m) were compared between selection lines and control for each foraging trait using a one-way ANOVA.

```
PROC GLM;
Class line;
Model rm= line;
lsmeans line/stderr pdiff;
run;
```

Appendix D - Chapter 5

	Response		
Selected Line	Prey consumed in 24h	Ratio of offspring produced to prey consumed in 24 h	Time to leave prey patch (min)
Consumption Conversion efficiency Dispersal Unselected control	$F_{3,215}$= 29.36, P<0.0001	$F_{3,164}$= 11.84, P<0.0001	$F_{3,75}$= 105.81, P<0.0001

Table A-1 ANOVA table to determine the levels of response in specific predator foraging traits and the unselected control after selection plateaued.

Effect	Predators	Prey	Plant damage	Correlation coefficient (r)	Spatial association index (X)
Foraging trait	$F_{3,158} = 6.50$	$F_{3,158} = 6.84$	$F_{3,158} = 4.34$	$F_{3,62} = 5.58$	$F_{3,62} = 2.67$
Ratio	$F_{1,158} = 0.61$	$F_{1,158} = 22.09$	$F_{1,158} = 13.36$	$F_{1,62} = 0.16$	$F_{1,62} = 0.03$
Foraging trait x ratio	$F_{3,158} = 1.77$	$F_{3,158} = 2.39$	$F_{3,158} = 0.40$	$F_{3,62} = 0.76$	$F_{3,62} = 0.30$
Time	$F_{3,158} = 226.43$	$F_{3,158} = 249.48$	$F_{3,158} = 731.62$	$F_{3,62} = 2.60$	$F_{3,62} = 5.72$
Foraging trait x time	$F_{9,158} = 4.70$	$F_{9,158} = 15.35$	$F_{9,158} = 3.00$	$F_{9,62} = 0.88$	$F_{9,62} = 1.73$
Time x ratio	$F_{3,158} = 0.17$	$F_{3,158} = 15.35$	$F_{3,158} = 5.36$	$F_{3,62} = 1.26$	$F_{3,62} = 0.68$
Foraging trait x time x ratio	$F_{9,158} = 1.11$	$F_{9,158} = 11.99$	$F_{9,158} = 0.97$	$F_{9,62} = 0.46$	$F_{9,62} = 0.29$

Table A-2 ANOVA table to determine the effect of foraging behavior, predator release ratio and time on the number of predator, prey and associated prey damage.

Effect	Aggregation index (I_a)		Gap index, V_j		Patch index, V_i	
	Predators	Prey	Predator	Prey	Predators	Prey
Foraging trait	$F_{3,62} = 2.51$	$F_{3,62} = 1.03$	$F_{3,62} = 2.87$	$F_{3,62} = 1.19$	$F_{3,62} = 1.95$	$F_{3,62} = 0.50$
Ratio	$F_{1,62} = 4.42$	$F_{1,62} = 0.39$	$F_{1,62} = 5.10$	$F_{1,62} = 1.18$	$F_{1,62} = 8.81$	$F_{1,62} = 0.00$
Foraging trait x ratio	$F_{3,62} = 1.39$	$F_{3,62} = 0.95$	$F_{3,62} = 1.51$	$F_{3,62} = 0.94$	$F_{3,62} = 0.73$	$F_{3,62} = 0.81$
Time	$F_{3,62} = 5.38$	$F_{3,62} = 6.21$	$F_{3,62} = 3.79$	$F_{3,62} = 6.08$	$F_{3,62} = 7.66$	$F_{3,62} = 5.84$
Foraging trait x time	$F_{9,62} = 2.40$	$F_{9,62} = 0.80$	$F_{9,62} = 2.27$	$F_{9,62} = 0.76$	$F_{9,62} = 1.29$	$F_{9,62} = 0.79$
Time x ratio	$F_{3,62} = 2.51$	$F_{3,62} = 0.63$	$F_{3,62} = 1.92$	$F_{3,62} = 0.73$	$F_{3,62} = 2.11$	$F_{3,62} = 0.51$
Foraging trait x time x ratio	$F_{9,62} = 0.59$	$F_{9,62} = 0.76$	$F_{9,62} = 0.80$	$F_{9,62} = 1.01$	$F_{9,62} = 0.70$	$F_{9,62} = 0.46$

Table A-3 ANOVA table to determine the effect of foraging trait, predator release ratio and time on spatial distribution parameters including aggregation (I_a), gap (V_j) and patch (V_i) indices.

SAS CODES

1. Data were analyzed in SAS PROC MIXED (SAS Institute 2002) as a completely randomized design using foraging trait, ratio, time and their interaction as fixed effects, and replicate as random effects. Time was also a repeated measures factor.

The variables analyzed were 1) total number of prey; 2) total number of predators; 3) average damage index; 4) SADIE Aggregation Index for prey and 5) for predators; 6) SADIE gap index for prey and 7) for predators; 8) SADIE Patch Index for prey and 9) for predators; 10) spatial correlation coefficient; and 11) SADIE Association Index.

```
Proc Mixed;
Class unit rep trait time ratio;
Model variable= trait|ratio|time;
Repeated time/subject=unit Type=cs;
Random rep;
lsmeans trait|time|ratio/pdiff;
RUN;
```

2. Within each experimental unit we also examined the simple correlation (SAS Institute 2002) between the number of predator and prey on each plant at each sampling time to assess the degree of spatial correlation between predator and prey density.

```
proc corr data =corr_multiarray;
var tsm predators;
run;
```

3. A one-way ANOVA to determine the levels of response in specific predator foraging traits and the unselected control after selection plateaued.

```
 PROC GLM;
Class line;
Model variable= line;
lsmeans line/ stderr pdiff;
run;
```

4. A one-way ANOVA to determine the levels of response in each predator foraging traits immediately before and after greenhouse experiments

```
PROC GLM;
Class line;
Model variable= line;
means line/lsd tukey lines;
run
```