THE EFFECTS OF TWO FORAGING TRAITS ON WITHIN-PLANT FORAGING EFFICIENCY OF *PHYTOSEIULUS PERSIMILIS* (ACARI: PHYTOSEIIDAE)

by

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Abstract

Many crops grown in greenhouses are damaged by the twospotted spider mite, *Tetranychus urticae*. The predatory mite, *Phytoseiulus persimilis*, is a commercially-available predator that is commonly used to control twospotted spider mites on greenhouse crops; but its efficacy varies among crops, and it is generally ineffective at low prey densities. In general, predator foraging efficiency depends on how well predators find prey patches, the length of stay in prey patches, and consumption of prey while in prey patches. With respect to *P. persimilis*, I asked how this predator responds to different prey distributions, as might be encountered at different stages of spider mite infestations. I also asked how components of foraging, namely consumption rate and dispersal tendency, affected predator efficiency. To examine the former, I established *T. urticae* eggs on 6-leafed cucumber plants in two distributions. To examine the latter, I imposed artificial selection on a population of *P. persimilis* to create a line that exhibited extremely high consumption and one that demonstrated a greater tendency for dispersal. Subsequently, foraging efficiency was assessed by observing predator oviposition and consumption of twospotted mite eggs on individual leaves of 6-leafed cucumber plants. The number of eggs laid by predators corresponded to the number of prey consumed regardless of predator line. In addition, predators from both lines distributed their eggs proportional to where they fed. However, prey consumption differed between selected lines in response to prey distribution. Predators selected for high consumption fed more on the basal leaf where they were released; whereas prey consumption by the high dispersal and control lines were more evenly distributed throughout the plant. These

results contribute to a better understanding of how foraging behavior is modified in plant landscapes under different levels of expression of foraging traits. They also indicate that predator release strategies likely would need to modified in accordance with the kind of foraging trait(s) used in artificial selection programs. In general, my research, when combined with future studies at a broader landscape level, will facilitate decisions by biological control practitioners about whether changes in foraging efficiency resulting from artificial selection justify the cost investment of producing selected lines of *P. persimilis*

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Dedication

I would like to dedicate this thesis to my family and friends. I also would like to dedicate this thesis to any young person who has dreams and aspirations to pursue higher education.

Chapter 1 - INTRODUCTION AND LITERATURE REVIEW

Twospotted Spider Mite

The twospotted spider mite (TSSM), *Tetranychus urticae* Koch, is a highly polyphagous acarine herbivore (Zhang and Sanderson, 1997; Krips et al., 1999). Its known host plant range comprises more than 200 species, including over 30 economically-important crops such as corn, cotton, cucumbers, peanuts, sorghum, beans, melons, strawberries and a variety of greenhouse ornamentals (Van de Vrie et al., 1972; Hoffmann and Frodsham, 1993). *Tetranychus urticae* is a geographically widespread species, occurring across the United States and throughout much of the world.

Adult TSSM are minute (<0.05 mm) and have a green to yellowish to orange body color in addition to a pair of large dark spots (Hoffmann and Frodsham, 1993). The life cycle has five developmental stages: egg, larva, two nymphs (protonymph and deutonymph) and adult. Each nymphal stage consists of an active feeding phase and a quiescent (chrysalis) phase. Eggs and other pre-adult stages are colorless. Complete development (egg-adult) may take 5-20 days depending on temperature. Adult males emerge slightly before females, and mating begins shortly after females emerge. The mode of reproduction with respect to sex determination is haplodiploidy. Males are haploid, developing from unfertilized eggs; females are diploid and develop from fertilized eggs. TSSM lay about 19 eggs per day and a female is capable of laying over 100 eggs in her lifetime, which is usually 3-4 weeks.

Tetranychus urticae feed by piercing individual epidermal cells of leaves and withdrawing the liquid (Carey, 1984). This pattern of feeding causes chlorotic (yellow) spots to form at feeding sites. As populations grow, chlorotic patches coalesce into large

clumps that may span many leaves or even many plants. The damage caused by TSSM can be severe and, if not controlled, can limit production and reduce profits. A colony is founded when a female oviposits, usually on the lower leaf surface. She also deposits webbing in which eggs hatch and immatures feed (Zhang and Sanderson, 1997). As progeny become adults, new colonies are formed close to the parental colony. In greenhouses, as in other habitats, *T. urticae* may colonize different areas, thus creating a patchy distribution (Zhang and Sanderson, 1997).

Predatory Mite

Phytoseiulus persimilis Athias Henriot (Acari: Phytoseiidae), is a predatory mite that specializes on tetranychid mites as prey. In fact, reproduction and complete development only occur on mite species within the subfamily Tetranychinae (Hoffmann and Frodsham, 1993). It is considered to be a highly effective predator of *T. urticae* on many crops (Oatman and McMurtry, 1966; Opit et al., 2004) and has been used more frequently than any other predator in biological control programs against TSSM (Van Lenteren and Woets, 1988). It was introduced into Germany from Chili in 1958 and was subsequently shipped to other parts of the world (Hoffmann and Frodsham, 1993).

Phytoseiulus persimilis is tiny (~0.5 mm), fast-moving, and has a shiny orange to bright reddish color that is particularly pronounced in adults. As with *T. urticae, P. persimilis* has five developmental stages: egg, larva, protonymph, deutonymph, and adult (Chant, 1985). Eggs are oval to round and twice as large as those of *T. urticae*. Newly-laid eggs are clear, later becoming straw-colored prior to hatching. Larvae and nymphs are a salmon to light orange color. The life cycle (egg-adult) ranges from 5-25 days depending on temperature (Hoffmann and Frodsham, 1993).

Like other phytoseiids, *P. persimilis* determine the sex of progeny by a process called pseudo-arrhenotoky, whereby haploid males are produced after the paternal set of chromosomes are deleted from fertilized eggs, and diploid females develop from fertilized eggs that retain both sets of chromosomes (Wysoki and Swirski, 1968; Schulten et al., 1978). Between 71-81˚F, females lay an average of 60 eggs within a lifespan of 50 days (Laing, 1968; Sabelis, 1981). Eggs are deposited close to where they feed, typically on top of leaf hairs (trichomes) or in prey webbing. Immatures do not move far from where eggs hatch (Kondo and Takafuji, 1985). The larval stage does not feed, but subsequent nymphs and adults feed on all stages of prey (eggs, nymphs and adults). However, eggs are preferred (Sabelis, 1981; Blackwood et al., 2001). *Phytoseiulus persimilis* can consume 5-20 eggs per day depending on temperature and prey availability (Sabelis, 1981). Predators aggregate and search intensively within patches that have high prey densities. This strategy is believed to maximize foraging efficiency (Zhang and Sanderson, 1997). However, *P. persimilis* will leave patches when prey are not abundant, or when they receive volatile cues (known as herbivore-induced prey volatiles) of prey presence elsewhere (Maeda et al., 1998; Mayland et al., 2000; Maeda and Takabayashi, 2001). Thus, population survival and success depends on its movement in accordance with its prey, and the ability to forage in complex landscapes.

Predator-Prey Interaction

Spider mites create patchy infestations which expand until the host plant is exhausted as a quality food source or until invaded by predators (Chant, 1961; Takafuji et al., 1983). Spider mites are considered a transient food source for predators because prey populations build-up and crash, then new prey patches arise nearby. Prey populations terminate because they overexploit host plant resources and, as a result, undergo intense intraspecific competition leading to dispersal and/or high mortality (Overmeer, 1985). Prey patches also go extinct because of predation. Once the predatory mites have located a prey patch, they have the ability to decrease prey colonies rapidly, because of their fast development and high prey consumption rate, which facilitates their population growth. However, once prey populations have been reduced to low densities, food becomes scarce and predators must disperse or face starvation. Survival requires more than just the ability to disperse; *P. persimilis* also must be able to locate new prey patches. Moreover, to be effective as a biological control agent, predatory mites not only must move in accordance with their prey, but they must do so at a rate great enough to prevent prey populations from building to intolerable levels (Huffaker, 1958).

P. persimilis searches for spider mite prey at different spatial scales: intermediate to large patches within the habitat; prey colonies within a patch; and individual prey within a colony (Helle and Sabelis, 1985). As they search, predatory mites use environmental cues to help locate and evaluate prey patches (Nachappa et al., 2006).

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; Nachappa et al., 2010).

Therefore, predator-prey ratios in each patch will fluctuate, which affects the stability of the predator-prey interaction (Hassell, 1978; Berryman and Gutierrez, 1999) and effectiveness of biological control.

Foraging Behavior

Predators must be able to forage efficiently for food and shelter for their own survival and for that of their offspring. However, foraging efficiency of small arthropods such as *P. persimilis* is influenced not only by intrinsic traits, but also by extrinsic factors such as the characteristics of the plants on which their prey feed, including plant structure, plant architecture (Grevstad and Klepetka, 1992) and habitat quality (Carter and Dixon, 1984). Arthropod predators must also be able to find prey populations that are patchily-distributed in the environment (Waage, 1979). When foraging for prey/hosts, insects must make critical decisions that may determine whether they starve or not. The decision-making comes into play when predators/parasitoids have to make a choice between prey/host patches. Understanding how predators view prey patches is important in understanding how patches are perceived. For example, a prey patch can be perceived as part of a leaf or even a whole plant.

A detailed knowledge of predator foraging behavior, when combined with an adequate understanding of factors affecting population growth of a predator and prey, allows better predictions of the dynamics of predator-prey interactions. Furthermore, because extrinsic factors often have profoundly different effects on predator and prey, investigating these effects is essential for making meaningful predictions. Host plants, on which herbivorous arthropods feed and/or live, are the most influential extrinsic factor

when studying the interactions between herbivorous arthropods and their natural enemies (Price, 1986).

Patch-Choice and Patch-Departure

A prey patch is defined by how an organism views the environment. When it comes to foraging, there are two important decisions: (1) patch selection (which patch to choose) and (2) patch residence time (how long to stay in that particular patch) (Charnov, 1976; Waage, 1979). To make this decision optimally, predatory mites need to evaluate the resource levels of the currently-inhabited patch as well as those in other patches in their habitat (Stephens and Krebs, 1986).

Once in a patch, predators tend to exterminate prey, and therefore must determine when to disperse from the patch (Maeda and Takabayashi, 2001). Predator residence time is known to be affected by conditions in the current patch, such as density of both prey and competitors (e.g., Takafuji, 1977; Bernstein, 1984) and contact chemicals associated with exuviae, feces and webbing (e.g., see Sabelis and Dicke, 1985). Vanas et al. (2006) suggest that *P. persimilis* females are able to integrate information about the number of eggs laid and the number of spider mite eggs available for patch-leaving decisions. An animal may leave a patch because of information gained, resource depletion, or both (Pyke, 1984). Classical optimal foraging theory (e.g., Marginal Value Theorem [Charnov, 1976]) states that a forager should leave a patch once its net energy gain per time equals the average rate of energy gain over all patches in the entire habitat. Therefore, when there is high prey density, the average rate is high, which implies predators should only leave when prey density is low. In addition, there are some factors affecting residence time, such as foraging experience and level of starvation (Maeda,

2006), prey products and prey-infested plant volatiles (Maeda et al., 1998; Mayland et al., 2000; Maeda, 2006), and prey density (Bernstein, 1984; Tenhumberg et al., 2001). In the parasitoid, *Cotesia rubecula,* leaving tendency from hosts increased with high oviposition rates, suggesting that egg load may influence foraging decisions (Tenhumberg et al., 2001).

Enhancing Predator Efficiency

The ability of prey to distribute themselves in patches throughout the environment creates a problem for a predator with limited locomotion. To be effective in controlling pests, predators must have traits that enable them to move and locate prey (Huffaker, 1958). In addition, once a prey patch is located, predators must be able to deplete the prey population. Therefore, the capacity for both high consumption and high dispersal are important adaptive traits and also contribute to effective biological control.

One way to enhance predator performance is through artificial selection. For *P. persimilis*, previous work has documented significant additive genetic variation in several foraging traits (Jia et al., 2002; Nachappa et al., 2010), such that selection on these traits is possible (Margolies et al., 1997; Nachappa et al., 2010). Furthermore, selection on one trait is independent of other traits, and for certain traits, such as high consumption, it is relatively stable (Nachappa et al., 2010). *Phytoseiulus persimilis* nymphs and adults feed preferentially on eggs of tetranychid mites, including *T. urticae* (Sabelis, 1981). When prey are abundant, adults will consume an average of 24 prey eggs per day (Sabelis, 1981). By comparison, lines selected for high consumption will consume an average of 40 prey eggs. Predatory mites usually disperse from occupied patches when prey density approaches zero (Takafuji, 1977; Sabelis, 1981; Bernstein, 1984; Zhang and Sanderson,

1991). However, after selection for high dispersal, the majority of *P. persimilis* adult females leave a patch when a significant number of prey is still available. In single and multi-plant trials, Nachappa et al. (2010) showed that these genetically-selected predators performed better than the control predator population.

RATIONALE

To evaluate how different foraging traits influence the performance of *P. persimilis*, including its potential as a biological control agent of *T. urticae* in greenhouses and other protected environments, foraging needs to be assessed under conditions in which predators must search for prey in a natural context. The outcome of this kind of research can be used to make more meaningful fundamental predictions about predator-prey interactions in complex environments. From a practical perspective, understanding how predator foraging traits interact with environmental complexity (e.g., prey distribution) will help to determine whether genetically-selected predators can be used to improve biological control and, if so, which trait(s) to exploit. Findings also may result in adjustments to predator-prey release ratios so that desired levels and rates of pest suppression are achieved. Previous research with *T. urticae* and *P. persimilis* indicates that prey distribution affects predator efficiency (Gontijo et al., 2010). Thus, it may be possible to enhance the efficiency of *P. persimilis* by releasing more predators or by changing where they are released. Alternatively, one could consider using predators that exhibit different foraging strategies. I was interested in the latter option – specifically, to use artificial selection to increase selected foraging traits that might enhance the effectiveness of *P. persimilis*. In general, previous research has shown the potential for using artificial selection on natural enemy traits to improve biological control (Grafton-

Cardwell and Hoy, 1986; Rosenheim and Hoy, 1988; van Houten et al., 1995). More directly, Nachappa et al. (2010) showed that it was possible to artificially select *P. persimilis* for enhanced levels of several foraging traits. Furthermore, they demonstrated that the selected traits remained stable over multiple generations. Therefore, my thesis uses as a starting point findings from Gontijo et al. (2010) and Nachappa et al. (2010), but takes the research a step further by asking the question: Is the foraging efficiency of the predatory mite, *P. persimilis*, affected by different foraging traits and prey distributions on plants? My study focused on small-scale (within-plant) foraging in which *P. persimilis* selected for high consumption or high dispersal searched for *T. urticae* that occupied patches on different leaves of cucumber plants. Prey consumption and predator oviposition on plants with multiple prey patches were compared with those on which prey were available on the source leaf only (i.e., the leaf on which predators were initially placed).

OBJECTIVES AND HYPOTHESES

The specific objectives of this study were to:

1) measure the effects of prey distribution on the foraging efficiency of selected lines of the predatory mite, *P. persimilis*.

2) assess how predators/parasitoids utilize prey/host, once inside a prey patch.

The general hypothesis was that predators with selected traits would perform differently with respect to prey consumption and reproduction on single plants with multiple prey patches than the control line and from each other;

Specific hypotheses were:

1) *P. persimilis* selected for high dispersal would find and consume prey in more patches than predators selected for high consumption or those for which no selection was imposed, but because of the movement between patches will not consume as much as the high consumption trait.
2) Predators with the high consumption trait will consume more prey and lay more eggs in the initial prey patch than predators with other traits, but not use many prey patches.

Chapter 2 - THE EFFECT OF SELECTION FOR ENHANCED FORAGING TRAITS ON WITHIN-PLANT EFFICIENCY OF THE PREDATORY MITE, *PHYTOSEIULUS PERSIMILIS* (ACARI: PHYTOSEIIDAE)

Introduction

The twospotted spider mite, *Tetranychus urticae* Koch, is a generalist herbivore. It feeds on over 200 species of plants, including over 30 economically-important crops such as corn, cotton, cucumbers, peanuts, sorghum, beans, melons, strawberries and a variety of greenhouse ornamentals. Twospotted spider mites are widely-distributed in the United States and throughout the world. Because of the explosive growth potential of this pest (Sabelis, 1981), populations can rapidly infest and kill entire plants. The ability to disperse provides a means of infesting new areas. Like other spider mites, *T. urticae* create patchy infestations that expand until the host plant is exhausted as a quality food source, or until invaded by their predators.

The predatory mite, *Phytoseiulus persimilis* Athias-Henriot, is the most efficient biological control agent of *T. urticae* (Helle and Sabelis, 1985). This predator is capable of rapidly reducing prey colonies, in part, due to its short developmental time, but also because of its ability to feed and develop exclusively on mites in the subfamily Tetranychinae, which includes *T. urticae* (Hoffmann and Frodsham, 1993). The larvae do not feed; but nymphs and adults prey on all life stages of *T. urticae*, with preference shown for eggs. Spider mites are considered a transient food source for the *P. persimilis* because prey populations build up and crash locally, then new prey patches arise nearby.

The survival of the predator populations therefore depends on their ability to track temporal and spatial patterns in prey populations, which requires efficient searching in complex landscapes to locate prey.

Foraging efficiency can be defined as the ability to acquire hosts or prey; but it also includes the rate at which hosts/prey are consumed. In predators, prey consumption affects development, survival and reproduction and, thus, the numerical response of predators and parasitoids. However, the numerical response also has a spatial component which depends on dispersal ability. Therefore, foraging efficiency has a key influence on predator-prey interactions and population dynamics. One of the major extrinsic factors that affect foraging efficiency is prey distribution (Yasuda and Ishikawa, 1999). Because prey are typically distributed in patches throughout the environment, this creates a problem for predators with limited locomotion. To be an effective predator, traits that enable them to move and locate prey must be present (Huffaker, 1958). However, to be an effective biological control agent, dispersal among prey patches must be balanced by prey consumption within patches so that local prey (pest) populations are maintained at low levels globally. Therefore, the capacity for both consumption and dispersal are important fitness traits and also contribute to effective biological control.

My study compared lines of *P. persimilis* that were selected to exhibit high levels of one of two important components of foraging, namely the rate of consumption (how many eggs consumed in a 24-h period) and of dispersal (time it takes to leave a prey patch with abundant prey), with a line exhibiting normal consumption and dispersal. In order to evaluate the importance of each of these traits on foraging efficiency under different levels of prey distribution, including situations typically encountered by *P.*

persimilis, predators were allowed to forage on 6-leafed plants that contained either a single prey patch of *T. urticae* eggs or multiple patches distributed over all leaves. My hypotheses were: 1) predators selected for high consumption will consume most of the prey in the patch where they are placed, but have a difficult time finding new prey patches; and 2) predators exhibiting the high dispersal trait will locate more prey patches, but because of the movement between patches will not consume as many prey as predators with the high consumption trait.

Materials and Methods

Tetranychus urticae Koch

Twospotted spider mites were reared on lima bean plants (*Phaseolus lunatus* L.) in the laboratory (25 ± 2°C, 16:8 L:D, 35-40% RH). Prior to infestation, seeds (Willhite Seed Company, Poolville, TX) were sown into 0.3 x 0.6 m plastic flats containing a FAFARD® growth media (Conrad Fafard, Inc., Agawam, 76 MA, USA) at a rate of 21 seeds per flat and maintained in the greenhouse at (27.3 ± 6.3°C, 16:8 L:D, and 35.6 ± 13.8% RH). Flats were watered when media was dry to the touch to a depth of 1.25 cm. Fertilizer (Scotts Peters General Fertilizer, Hummert International, Earth City, MO) was applied weekly. Two weeks after seeding, flats were moved into screened cages (to prevent contamination) containing older infested plants. New plants were inoculated with spider mites by clipping and placing infested leaves from the older plants onto the canopy of new plants. Bean plants were replaced every other day; older plants were removed when new ones were added.

Phytoseiulus persimilis

The predators used in our experiments were obtained from Koppert Inc. (Romulus, MI), a commercial producer of natural enemies for biological control. The *P. persimilis* colony was maintained in 1.89 l Mason jars in the laboratory (25 ± 2°C, 16:8 L:D, 35-40% RH) that contained lima bean plants infested with mixed life stages of *T. urticae*. To continuously culture the predatory mites, a cup containing two lima bean plants was placed in each jar three times a week and then the leaves of older infested plants were cut over the top of the new plants. In this way both the *T. urticae* and *P. persimilis* colonies were propagated. To prevent predators or twospotted spider mites from escaping, and contaminants from entering the jars, each jar was covered with a fine mesh top. At the time experiments began, the laboratory colony of *P. persimilis* had undergone approximately 2 to 3 generations.

Bioassays. Consumption was 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 $\pm$ 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.

The dispersal response of *P. persimilis* was measured in a Petri dish bioassay modified from Maeda and Takayashi (2001) and Nachappa et al. (2006). 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* 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 a 30 x 5 mm Parafilm bridge was connected 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. Previous research showed 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., 2006).

Selected lines. Using these bioassays, I imposed artificial selection on the *P. persimilis* colony, following procedures outlined in Nachappa et al. (2010), to create lines of predators which exhibited high levels of either prey consumption or dispersal. During selection, I took 50 mites from each population and observed consumption and dispersal for each individual. If the levels for consumption or dispersal were below desired levels, I selected the top 10% from the original 50 mites. I repeated this process until the desired level was obtained, which normally took 2-3 generations. Predators selected for high consumption consumed, on average, 40 *T. urticae* eggs per day compared to 20-25 eggs for the control colony. Predators selected for high dispersal left a prey patch within about 7-10 minutes compared to about 26-30 minutes for colony females. Selection for one trait did not affect the other trait (Nachappa et al. 2010); therefore, female predators selected for high consumption or high dispersal exhibited the other trait at the same level as predators in the control colony. In addition, I used similar methods to select a control

line that exhibited the same consumption and dispersal rates as the base colony; this served to control for the process of selection and to reduce variation from the standard *P. persimilis* colony. The lines were checked every month to ensure that females used in experiments were consuming and dispersing at expected levels. Selection was re-imposed, as needed, to maintain traits at desired levels (see Appendix D). Samples of the standard colony and all selected lines were collected and stored as Sample Voucher #213 in the Kansas State University Museum of Entomological and Prairie Arthropod Research.

Cucumber propagation

Experiments were conducted using potted cucumber plants (*Cucumis sativus* L. cv. 'Cumlaude'). Plants were grown in the greenhouse at (27.3 ± 6.3°C, 16:8 L:D, and 35.6 ± 13.7% RH) from seed purchased from Hydro-Gardens (Colorado Springs, CO). Seeds were sown in 0.3 x 0.6 m plastic flats that contained a FAFARD® growth media. Watering was done daily, as needed. After one week, when seedlings had produced a fully-developed true leaf, they were transplanted individually to 6.35-sq. cm (2.5-inch) pots. A 20-10-20 fertilizer solution was applied weekly. After approximately 40 days when plants had 6 completely developed leaves, they were transplanted to 10.1-cm (4-inch) pots and fertilization was done with each watering.

Experimental procedures

The experiment was conducted in a 7.6 x 7.6 m greenhouse at Kansas State University, Manhattan, KS, from March to October, 2010. A HOBO data logger (Onset Computer Corporation, Bourne, MA) recorded hourly temperature and relative humidity

data throughout the experiment (temperature: 27.3 ± 6.3°C.; relative humidity: 35.6 ± 13.7% [mean ± SD]).

The experimental unit was a cucumber plant. At the time the experiment began, plants had 6 true leaves and the approximate plant height was 13.1 cm. The experiment had a 3 x 3 factorial treatment structure, with 3 types of predators (control, high consumption line, and high dispersal line) and 3 levels of prey distribution (all 6 leaves infested with *T. urticae* eggs, only the basal leaf infested, and the basal leaf infested but enclosed with a plastic wrap to prevent predators from leaving the leaf). The levels of infestation represent what one would see during an early infestation (one leaf infested) or during an established infestation (all six leaves infested). Each infested leaf contained 30 prey eggs. The experimental design was a randomized complete block (RCB) with time as the block and the 9 treatment combinations randomly assigned to a greenhouse location each time the experiment was run.

To infest plants, ten adult female *T. urticae* were placed directly on cucumber leaves (depending on the distribution) with a fine brush and left for 24-h after which they were removed. This resulted in approximately 150-200 eggs per leaf as well as webbing, frass, and leaf damage, all of which provided cues for predator foraging. The number of prey was then adjusted by removing excess eggs so that each leaf designated as a prey patch contained 30 eggs. Subsequently, a single *P. persimilis* female (1-2 week old) was released into the prey patch on the basal leaf and allowed to forage for 24 h. The plant was then inspected and the location of the predator noted before being removed. If an adult female predator was not found, the plant was discarded because the time spent foraging could not be determined and may have been less than 24 h. All leaves were

numbered, with "1" representing the basal leaf and "6" the uppermost leaf. Leaves were then placed individually in plastic Ziploc bags and stored in the freezer until they could be examined. For each leaf position the number of prey eggs consumed and the number of predator eggs found were recorded.

The experiment was replicated in 12 time blocks. The original experimental design was a randomly complete block. However, because the adult female predator could not be recovered from one or more treatments in most trials, this resulted in an unequal numbers of replicates (7 to 11 depending on specific treatment) and, thus, an unbalanced experimental design. Therefore, the data were subjected to ANOVA using the GLIMMIX procedure in SAS 9.2 (SAS Institute, 2002), which is designed to handle such data. To avoid Type I errors in making multiple comparisons, a Bonferroni correction was applied. Because of the high degree of variability in the response data and the unequal and relatively low number of replications, an alpha level of 0.1 was used instead of the conventional 0.05. In addition, to evaluate if there was a correlation between prey consumption and predator oviposition, I used the Pearson's Coefficient procedure in SAS 9.1 (SAS Institute).

Results

Prey consumption

When prey consumption was compared among *P. persimilis* lines on plants in which all 6 leaves were infested with *T. urticae* eggs, there was a highly-significant main effect due to predator foraging trait ($P < 0.0001$, $F_{2, 26} = 21.2$). Significantly more prey eggs were consumed on the entire plant by adult female predators from the control colony than from either of the selected lines; the fewest prey were consumed by females from

the high dispersal line (Figure 2.1). On plants with only the basal leaf infested, more eggs were consumed by predators selected for high consumption and the fewest prey were consumed by females from the high dispersal line.

A comparison of prey consumption on the basal leaf only showed highly-significant effects due to prey distribution treatment ($P = 0.0001$, $F_{2, 67} = 42.07$) and foraging trait ($P = 0.0001$, $F_{2, 67} = 44.87$). There was also a highly-significant trait by treatment interaction ($P = 0.0003$, $F_{4, 67} = 6.16$). On basal leaves of plants in which only that leaf was infested and predators could disperse, significantly fewer prey eggs were consumed by the high dispersal line (mean = 11.61 [90% C.I. = 9.0, 14.5]) than the high consumption line (18.3 [15.5, 20.9]) ($P = 0.0012$, $t = 4.44$, $df = 67$). Differences between the high dispersal and control lines were not significant ($P = 0.1605$, $t = 2.94$, $df = 67$) and there was no difference in prey consumption between the high consumption and control lines ($P = 1.000$, $t = -1.49$, $df = 67$) (Figure 2.2). There were no differences in prey consumption on the basal leaves of plants with all leaves infested versus only the basal leaf infested for the control or high consumption lines ($P = 1.000$, $t = -0.08$, $df = 67$ and $P = 0.4632$, $t = -2.56$, $df = 67$, respectively). However, females from the high dispersal line consumed significantly fewer prey on the basal leaf when other leaves were infested (5.48 [4.0, 7.4]) compared to when only the basal leaf was infested (11.61 [9.0, 14.5]) ($P = 0.0001$, $t = -5.09$, $df = 67$). Females from the high dispersal and control lines consumed significantly more prey on basal leaves in which predators were confined (i.e., they could not disperse) compared to open leaves ($P = 0.0446$, $t = -3.37$, $df = 67$ and $P = 0.0586$, $t = -3.28$, $df = 67$, respectively). However, in the high consumption line, there was

no significant difference in prey consumed between confined and open leaves (P = 1.00, t = - 0.94, df = 67) (Figure 2.3).

Predators from the high dispersal and control lines consumed more prey on plants in which all six leaves were infested compared to those with only the basal leaf infested (P = 0.0747, t = 1.82, df = 46 and P = <0.0001, t = 5.31, df = 46, respectively). In contrast, prey consumption by females from the high consumption line was similar for both prey distributions (P = 0. 6451, t = 0. 46, df = 46) (Figure 2.4).

On plants with all six leaves infested, prey consumption on the basal leaf versus all other leaves differed among predator lines. Females from the high consumption line consumed significantly more prey on the basal leaf (P = < 0.0001, t = 5.26, df = 49). Whereas prey consumption between the basal and upper leaves was more evenly distributed for predators from the high dispersal and control lines (P = 0.2965, t = - 1.08, df = 49 and P = 0. 2077, t = 1.28, df = 49, respectively) (Figure 2.5).

Predator oviposition

A comparison of predator oviposition on the basal leaf showed a highly-significant effect due to prey distribution (P = 0.003, $F_{2, 67}$ = 6.22), and a significant effect from foraging trait (P = 0.064, $F_{2, 67}$ = 2.86); there was no significant trait by treatment interaction (P = 0.850, $F_{4, 67}$ = 0.34). Pooled over all prey distributions, females from the high dispersal line produced significantly fewer eggs (1.14 [0.80, 1.6]) than those from the control colony (1.95 [1.5, 2.6]) (P = 0.092, t = 2.21, df = 67). High dispersers produced marginally fewer eggs than high consumers (1.14 [0.80, 1.6]) vs. 1.89 [1.4, 2.5]) (P = 0.1228, t = 2.08, df = 67), and there was no significant difference between the high consumption and control lines (P = 1.00, t = 0.15, df =67).

When foraging trait data were combined, predator oviposition on the basal leaf was also influenced by prey distribution. Significantly more eggs were laid on the confined basal leaf (2.42 [1.9, 3.2]) than on the basal leaf of plants with all leaves infested (1.16 [0.9, 1.6]) ($P = 0.0039$, $t = -3.36$, $df = 67$). Oviposition on the confined leaf was not different from the singly-infested basal leaf (1.50 [1.1, 2.1]) ($P = 0.1089$, $t = -2.14$, $df = 67$). However, there was no significant difference in numbers of predator eggs laid between the confined and open basal leaf of plants with only one leaf infested ($P = 0.9290$, $t = -1.02$, $df = 67$).

Number of predator eggs laid on the entire plant was not influenced by the number of infested leaves (prey patches) ($P = 0.1057$, $F_{1,46} = 2.72$), but there was a tendency for more eggs to be laid on plants with all leaves infested versus only the basal leaf. Predator trait did not affect oviposition ($P = 0.1831$, $F_{2, 46} = 1.76$), nor was there a significant interaction between prey distribution and foraging trait ($P = 0.4505$, $F_{2, 46} = 0.81$) (Figure 2.6). However, there were strong correlations between where the predators fed and where they laid their eggs, with the predators selected for high consumption having the strongest correlation and the control line having the weakest correlation, although all were significant [high consumption: $R^2 = 0.995$ ($P = 0.0001$); high dispersal: $R^2 = 0.935$ ($P = 0.0062$); and control: $R^2 = 0.860$ ($P = 0.0282$)], using Pearson's Correlation coefficients.

Discussion

Foraging efficiency was influenced by the spatial pattern of prey and by selection on the two foraging traits. On plants with all six leaves infested, females from the control line consumed significantly more prey eggs than females from either selected line. High

dispersers consumed the fewest prey. However, on plants with only the basal leaf infested, high consumption females consumed significantly more prey than the high dispersal line, and there were no differences between the control and either selected line (intermediate level of prey consumption). In addition, comparing prey consumption on the basal leaf with and without other leaves infested, the high dispersal line consumed relatively fewer prey when other prey patches were available than when prey were only present on the basal leaf; whereas there was no difference in prey consumption between prey distributions for the high consumption or control lines. Collectively, these findings suggest that high dispersers leave the basal leaf sooner than other predators. It is possible that on plants on which multiple leaves were infested, high dispersers may have perceived other prey on distant leaves by means of volatile cues, which may have contributed to their tendency to leave the basal leaf. However, data do not support this hypothesis because on plants with only one leaf infested, the high dispersers tended to leave the basal leaf. However, it still may be accurate to say the high dispersers tend to leave because of volatile cues on adjacent leaves, but this research showed no difference in dispersal tendency when one leaf was infested versus multiple leaves infested. A more likely explanation is that high dispersers left the basal leaf because of their inherent tendency to disperse and did not return because prey were available on upper leaves. This interpretation is supported by previous research (Jia and Margolies, 2002; Nachappa et al., 2010) which indicates that selection for high dispersal in *P. persimilis* influences the tendency to leave, but is not based on attraction to extrinsic cues. To support the idea that the high dispersal line has the tendency to leave prey patches, I compared prey consumption by predators on plants with the basal leaf infested, but under two conditions:

unrestricted movement and restricted movement (caged basal leaf). I found that in the high dispersal and control lines, predators consumed more *T. urticae* eggs on the caged basal leaf than on the one in which their movement was unrestricted. These differences in prey consumption might be predicted in that predators typically disperse even when there is a surplus of food (Nachappa et al. 2010). On the other hand, high consumers fed equally on the basal leaf with and without confinement, suggesting that selection for increased prey consumption also increases their residence time in a prey patch. This is further supported by a comparison of foraging on plants with only the basal patch infested versus all leaves infested. For high consumers, there was no difference in prey consumption on plants with single or multiple prey patches. In contrast, females selected for high dispersal or from the control line consumed more prey when multiple patches were available. This indicates that high dispersers and control females left the initial prey patch sooner than high consumers and, when other prey patches were available, could consume additional prey. On plants with all six leaves infested, a comparison of prey consumption on the basal leaf versus all other leaves provides additional support that predators from the high consumption line remain longer on the basal leaf; significantly more prey were consumed there than on the upper five leaves combined. On the other hand, the control and high dispersal females fed equally from prey patches on the basal and upper leaves.

Overall, predator oviposition was highest for females in the control line and lowest in the high dispersal line. Likely, this relates to differences in total prey consumption, which was lowest for high dispersers. In addition, the high dispersal line may be exerting more time and energy when dispersing, thereby reducing their ability to

produce and lay eggs. The number of predator eggs seems to match the number of prey consumed, no matter what treatments were compared. In fact, for each selected trait there was a high correlation between predator oviposition and prey consumption among infested leaves. This applied both to plants with all six leaves infested and with only the basal leaf infested.

To persist, predators must exhibit foraging strategies that enable them to find and consume prey that are patchily distributed in space and time. There are some trade-offs associated with decisions to leave a prey patch or stay. For instance, predators risk starvation and predation when they decide to leave in search of other prey patches. For adult female predators such as *P. persimilis*, decisions of how long to remain in a prey patch are determined not only by the food available to adult females, but also for their offspring (Vanas et al., 2006), thus posing a possible trade-off between parental and offspring survival. Assuming that natural selection maintains levels of various foraging traits that provide the best balance for long-term success, altering prey consumption and/or predator dispersal through artificial selection would be expected to reduce predator population persistence by destabilizing predator-prey dynamics. On the other hand, the goal of a short-term augmentative biological control program for *T. urticae* is different in that the ability of predators to respond quickly to a pest population throughout the entire crop is of critical importance because tolerance thresholds for plant damage typically are extremely low. Selection for enhanced foraging traits may lead to greater efficiency and effectiveness of biological control, but to achieve this goal may require an adjustment in the predator release strategy to match the behavioral responses of the selected predator foraging trait.

My findings at the single-plant level in cucumbers suggest that selection for enhanced prey consumption and/or predator dispersal may improve the efficiency of biological control programs for *T. urticae* using *P. persimilis*. However, selection for either trait would likely involve a trade-off in foraging efficiency within and among prey patches at the single-plant level. For example, the high dispersal line may find *T. urticae* in more patches, and sooner, than the high consumption line. However, high dispersers consume fewer prey and leave fewer offspring than high consumers. In the high consumption line, females would be expected to consume most of the prey in the source patch and lay more eggs before dispersing, thus efficiently controlling local pest populations; but their offspring would have fewer prey on which to feed, and this could depress the numerical response in the next generation if progeny mortality were high. In addition, adult females may not find other prey patches before pest populations become unacceptably large.

This research was conducted on individual plants using single adult female predators which foraged for only a short period. For this reason it is difficult to predict how each foraging trait would perform on the larger scale in which commercial greenhouse crops are grown. However, some general assumptions can be made. In a short-term biological control program, the high consumption trait may be of greater value because of the ability of predators to suppress prey populations. However, because of reduced dispersal, *P. persimilis* adults would need to be released directly into infested areas, which would require careful scouting, or else distributed uniformly throughout the crop to prevent pest outbreaks. High dispersers could also be effective in a short-term program, but numbers released would need to be high enough to reduce prey quickly

within patches where they are released. With the tendency for faster dispersal, releases could be targeted to parts of the crop where twospotted spider mites are detectable with the expectation that predators would move to other areas of the greenhouse where pests are at low, undetectable densities. For long-term crops, the high dispersal trait would likely result in the most effective level of biological control, including requiring fewer releases, because they may be able to persist in greenhouses by tracking the movement of *T. urticae* as they colonize new plants, or to offset new pest invasions.

Because the cost of selecting and maintaining lines of predators with enhanced foraging traits would be higher than using the standard colonies of *P. persimilis* that are commercially available, a question for future investigation is: do predators selected for increased consumption or dispersal confer a great enough advantage over a control colony of *P. persimilis* to justify the investment? In my short-term experiment on individual cucumber plants, overall prey consumption was highest in predators from the control colony. Moreover, they dispersed equally well as high dispersers in some cases. However, control colonies of *P. persimilis* tend to exhibit greater variability for foraging traits than selected lines. Therefore, overall population performance may be more variable, leading to greater unpredictability with respect to biological control. Risk is one of the most serious obstacles preventing growers from adopting biological control into their pest management programs.

In conclusion, my study contributes broadly to understanding how consumer arthropods respond to the distribution of its resources at different levels of landscape complexity. In addition, this research provides guidelines for future investigation to compare the efficiency and effectiveness of genetically-selected predatory mites as

biological control agents under different pest distributions on greenhouse food and ornamental crops.

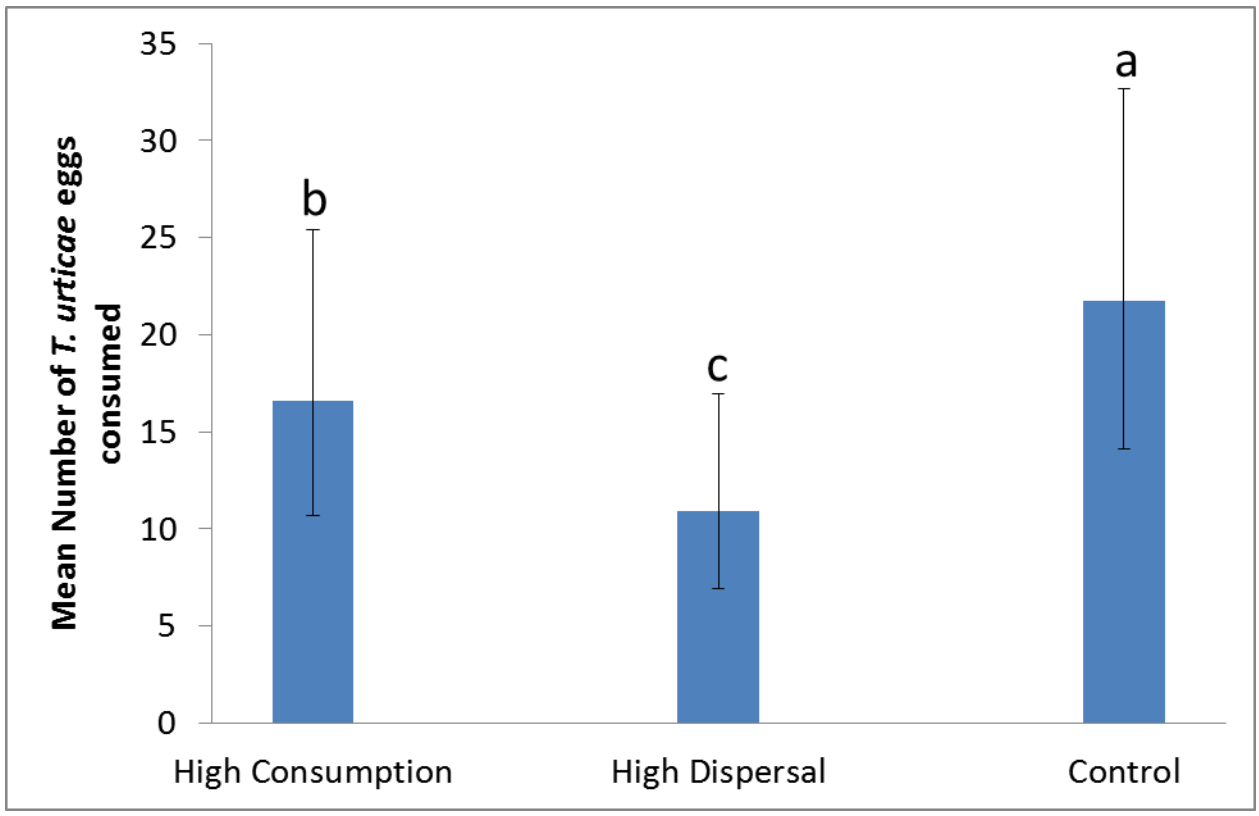

Figure 2.1 Mean (± 90% C.I.) number of *T. urticae* eggs consumed by adult female *P. persimilis* from selected lines and from the control on plants where all six leaves were infested. Different letters indicate significance at alpha = 0.10. The number of replications ranged from 8 to 11 depending on the treatment.

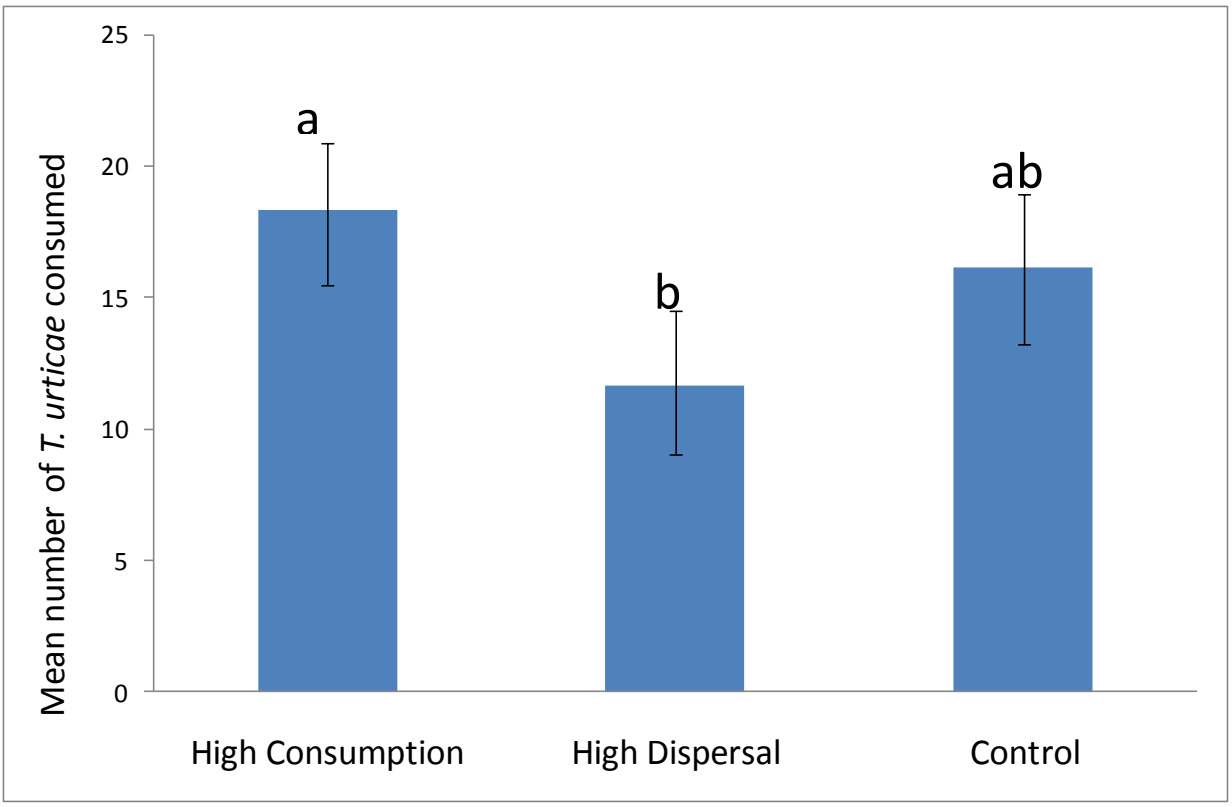

Figure 2.2 Mean (± 90% C.I.) number of *T. urticae* eggs consumed on the basal leaf by adult female *P. persimilis* from selected lines and from the control on plants with only the basal leaf infested. Different letters indicate significance at alpha = 0.10. The number of replications ranged from 7 to 8 depending on the treatment.

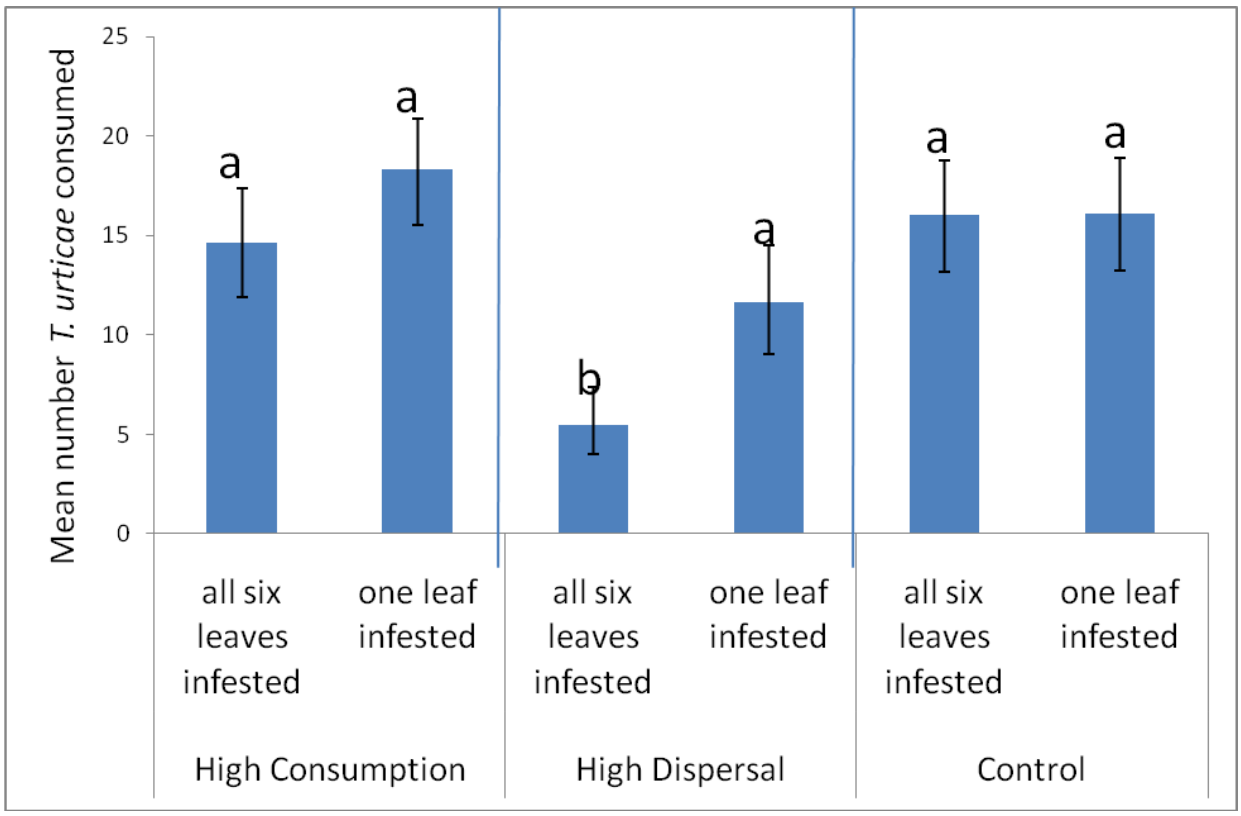

Figure 2.3 Mean (± 90% C.I.) number of *T. urticae* eggs consumed on the basal leaf by adult female *P. persimilis* from selected lines and from the control on plants with all six leaves infested vs. only the basal leaf infested. Different letters indicate significance at alpha = 0.10. The number of replications ranged from 7 to 11 depending on the treatment.

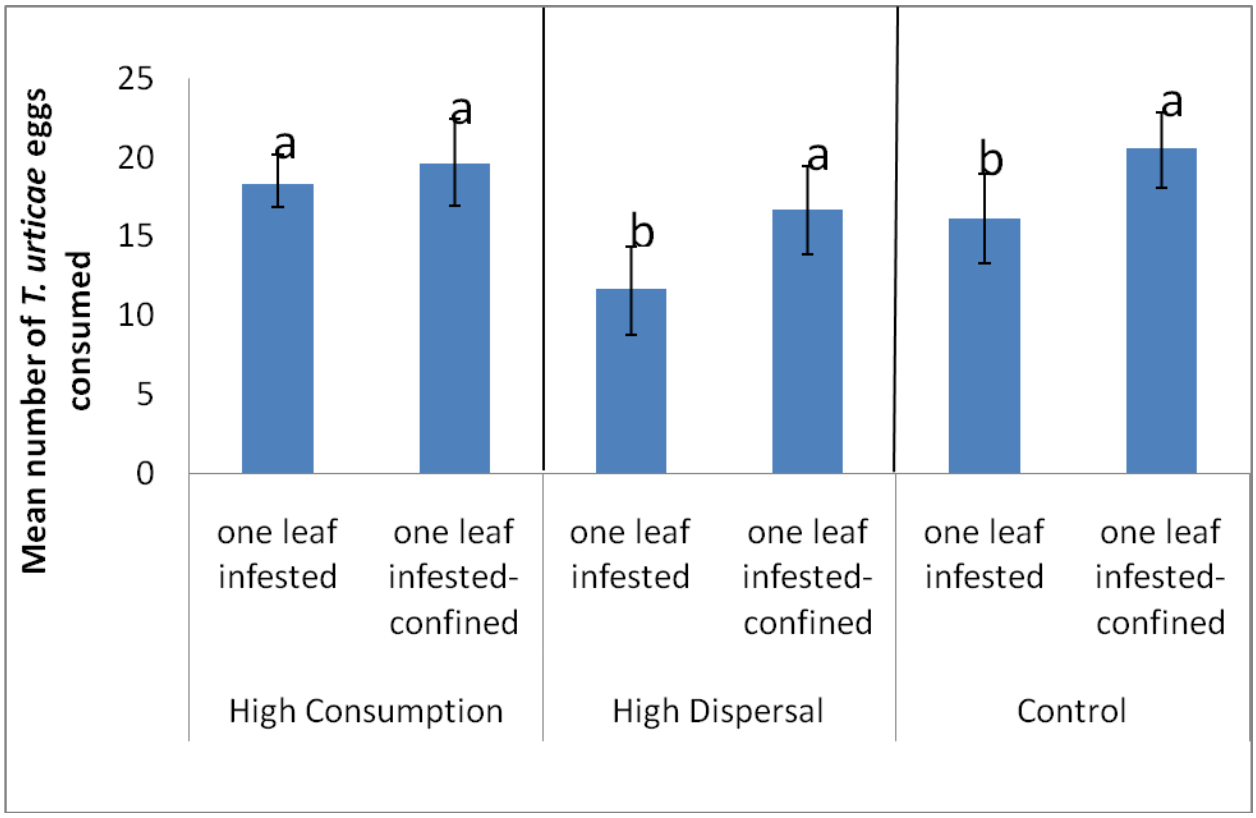

Figure 2.4 Mean (± 90% C.I.) number of *T. urticae* eggs consumed by adult female *P. persimilis* from selected lines and from the control on plants with the basal leaf infested, and with the basal leaf infested with restricted movement. Different letters indicate significance at alpha = 0.10. The number of replications ranged from 7 to 11 depending on the treatment.

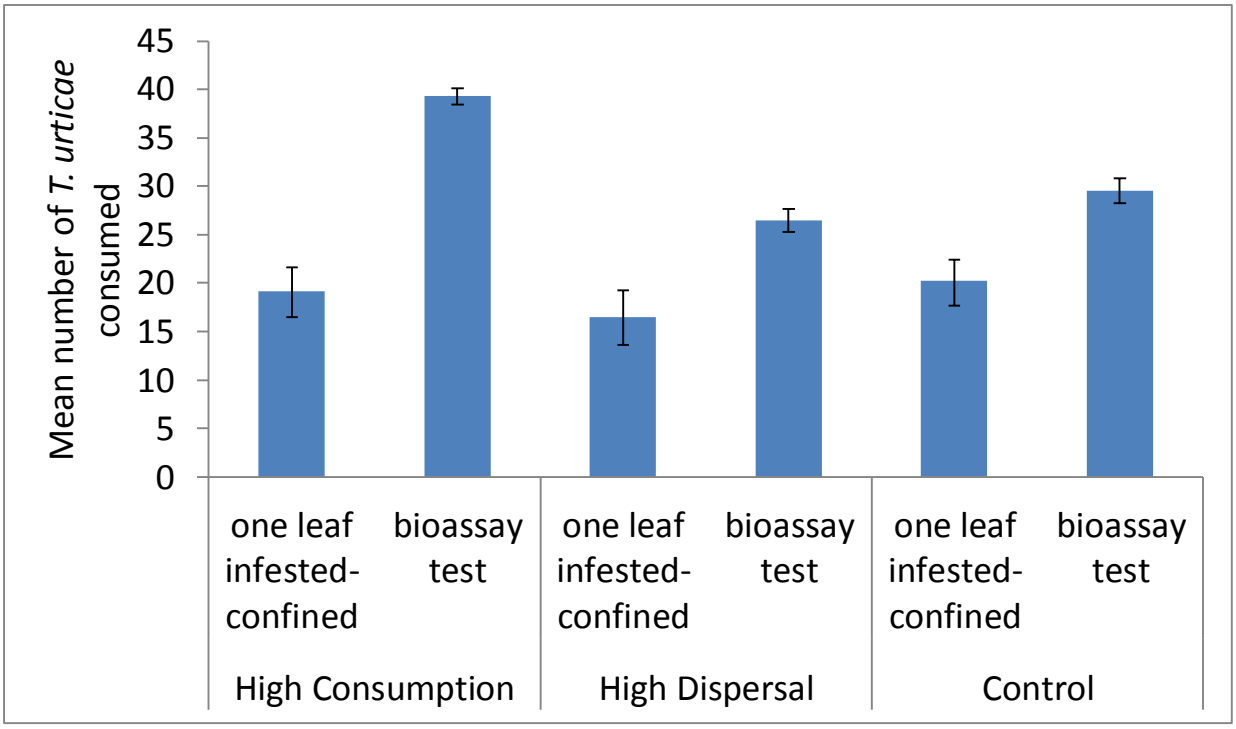

Figure 2.5 Mean number of *T. urticae* eggs consumed by adult female *P. persimilis* from selected lines and from the control on plants with only one leaf infested compared to the bioassay test. Different letters indicate significance at alpha = 0.10. The number of replications ranged from 7 to 11 depending on the treatment.

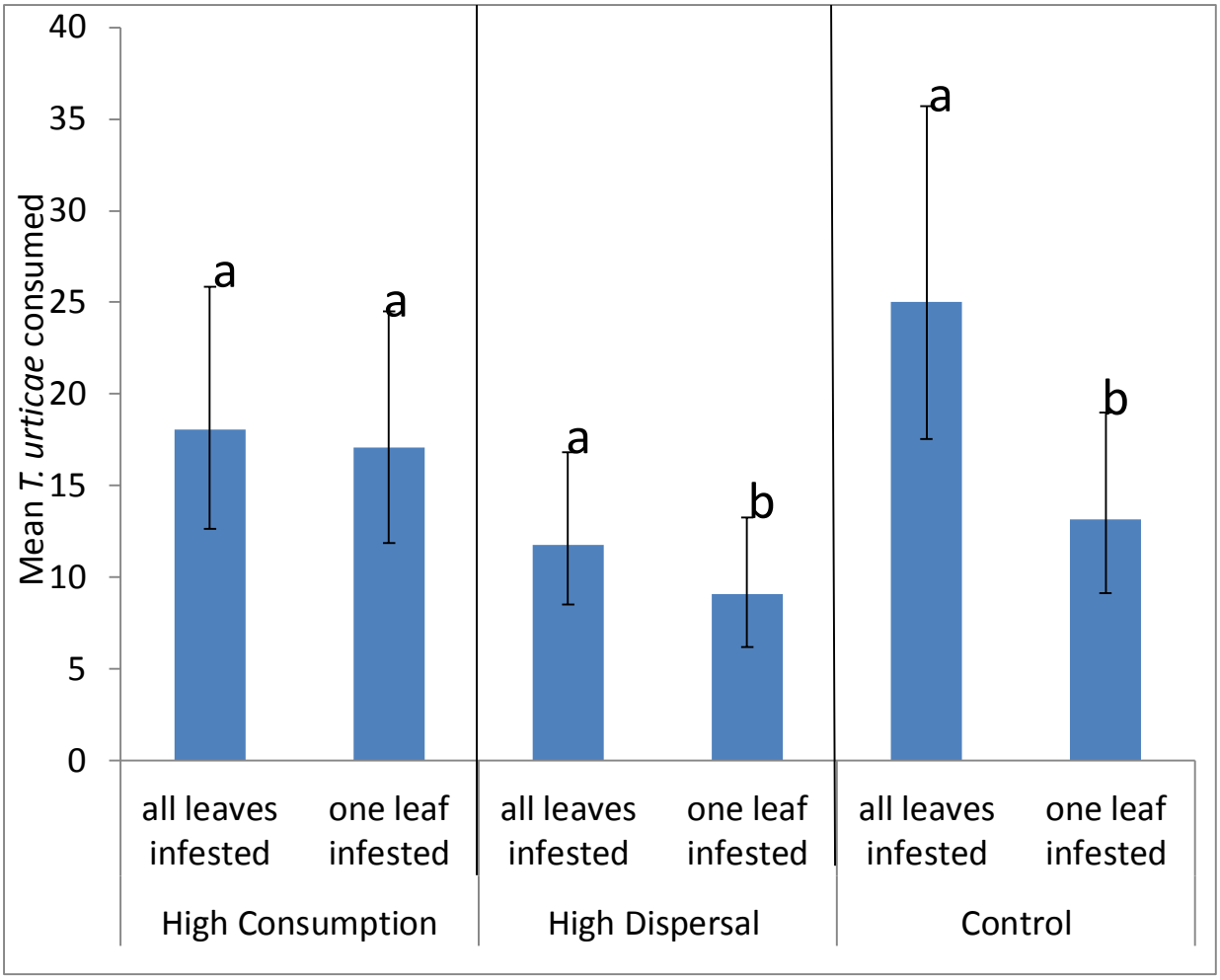

Figure 2.6 Mean (± 90% C.I.) number of *T. urticae* eggs consumed by adult female *P. persimilis* from selected lines and from the control on plants with all six leaves infested compared to plants with only the basal leaf infested. Different letters indicate significance at alpha = 0.10. The number of replications ranged from 7 to 11 depending on the treatment.

Table 2.1 Average number of *T. urticae* eggs consumed per leaf by adult female *P. persimilis* from lines selected for enhanced foraging traits and from the control colony on plants with all six leaves infested compared to plants with only the basal leaf infested.

Foraging Trait	Basal Leaf Infested	All Six Leaves Infested (1-6)						
		1	2	3	4	5	6	total
High Consumption								
	18.3	16.3	2.6	2	4.4	0	0	25.3
High Dispersal								
	11.6	7.9	3.1	0	4.4	.6	0	16.0
Control								
	16.1	16.3	3.8	1.3	4.5	2.9	.3	29.1

The number of replications and the individual data for each treatment combination are shown in Appendix C.

Table 2.2 Average number of *P. persimilis* eggs laid per leaf from lines selected for enhanced foraging traits and from the control colony on plants with all six leaves infested compared to plants with only the basal leaf infested.

Foraging Trait	Basal Leaf Infested	All Six Leaves Infested (1-6)						
		1	2	3	4	5	6	total
High Consumption								
	1.8	1.8	0.1	0.1	0.4	0	0	2.4
High Dispersal								
	1	0.8	0.4	0	0.8	0.1	0	2.1
Control								
	1.9	1.5	1.1	0.1	0.5	0.1	0	3.3

The number of replications and the individual data for each treatment combination are shown in Appendix C.

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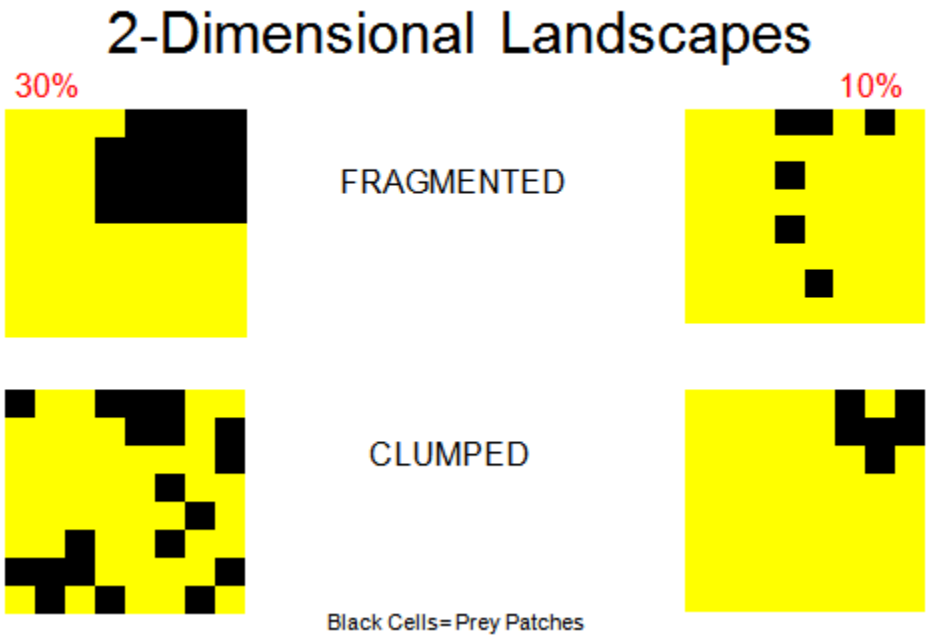
APPENDIX A - The effect of selection for enhanced foraging traits on the efficiency of the predatory mite, *Phytoseiulus persimilis* (Acari: Phytoseiidae), on a two-dimensional landscape.

An experiment was designed to assess the effects of prey density and prey distribution on the foraging efficiency of the predatory mite, *Phytoseiulus persimilis*. The prey species was the twospotted spider mite, *Tetranychus urticae*. The landscape on which predators foraged was 8 cm x 8 cm and consisted of a grid of 64 overlapping lima beans leaves, some of which were infested with *T. urticae* eggs. Four landscapes treatments were established, each consisting of a combination one of two prey densities (10 or 30% of the leaves infested) and one of two prey distributions: clumped (one large patch of infested leaves) or fragmented (5 to 10 smaller patches for the 10 and 30% prey density levels, respectively, scattered randomly throughout the landscape) (see diagram below). The distribution of prey patches in the landscape was generated using the RULE software program.



To infest leaves, thus creating patches of prey eggs, I released adult female *T. urticae* and allowed them to oviposit. Resulting egg numbers were adjusted by removal so that each leaf had 20 prey eggs. Infested leaves were than arrayed among un-infested leaves to achieve the prescribed pattern for each treatment.

For each prey density-prey distribution treatment combination, I released 5 adult female *P. persimilis* representing each of three foraging lines. Two lines were artificially selected for enhanced predator foraging traits – prey consumption and tendency for dispersal. The third line was a control colony. In all tests, predators were released at the center of the landscape and allowed to forage for 24 h, after which leaves were inspected. For each leaf in the landscape, numbers of prey consumed and predator eggs laid were counted. The number of adult predators recovered was also tallied.

Unfortunately, the predators were not successful at locating the prey patches when placed at the center of the landscape and allowed to forage. Therefore, we modified the design and released one predator inside one of the prey patches. Unfortunately, the data collected were unusable because the adult predators were not recovered at the end of the experiment. The inability to locate the predators created a problem analyzing the data because the length of time the predators were present on the landscape was unknown.

APPENDIX B – Statistical analysis codes (SAS) organized by table number and corresponding subanalysis.

```
*Ian Smith SAS code, 07Oct10;
*SAS code assuming data is placed inside program;
*RCBD with Date=block and with missing plant combinations;
data one;
  input date $ Trait $ plant LfInf Conf Leaf
      BladeL Internode PreyEggsCons PredEggsLd;
                TotPreyEggs=30;
                if LfInf=6 then Trt=1;
                if LfInf=1 and Conf=1 then Trt=3;
                if LfInf=1 and Conf=0 then Trt=2;
cards;
data here
;
*************************************************************;
*"BY LEAF" ANALYSES;
```

Subanalysis 1 – Figures 2.2, 2.3, 2.4, 2.5

```
*"BY LEAF" ANALYSES;
*Subanalysis 1, only Leaf 1=Basal leaf, all 3 trts;
* Response=PredEggsLd=Poisson (counts per leaf);
* Responses=PreyEggsCons/30=Binomial;
data SubA1; set one;
if Leaf=1;

proc sort data=SubA1; by leaf;
proc glimmix data=SubA1;
by leaf;
class date trait trt;
model predEggsLd = Trait|Trt/ddfm=satterth dist=poisson link=log;
random date;
lsmeans Trait|Trt/cl ilink;
title1 'SubAnalysis 1: leaf=1, All 3 Trts, y=Predator Eggs Laid ';

proc glimmix data=SubA1;
by leaf;
class date trait trt;
model preyEggsCons/TotPreyEggs = Trait|Trt/ddfm=satterth dist=binomial link=logit;
random date;
lsmeans Trait|Trt/cl ilink;
title1 'SubAnalysis 1: leaf=1, All 3 Trts, y=Proportion of prey eggs consumed';
```

Subanalysis 2 – Not enough data for statistical analysis

```
*Subanalysis 2, BY LEAF, Leaves 2-6, Trts 1 and 2;
* Response=PredEggsLd=Poisson (counts per leaf);
data SubA2; set one;

    if Trt=3 then delete;
 if Leaf=1 then delete;

proc sort data=SubA2; by Leaf;

proc glimmix data=SubA2;
by Leaf;
class date trait trt;
model predEggsLd = Trait|Trt/ddfm=satterth dist=poisson link=log;
random date;
lsmeans Trait|Trt/cl ilink;
title1 'SubAnalysis 2: By leaf, leaves 2-6, Trts 1 & 2, y=Predator Eggs Laid ';
```

Subanalysis 3 – Not enough data for statistical analysis

```
*Subanalysis 3, BY LEAF, Leaves 2-6, Trt 1;
* Responses=PreyEggsCons/30=Binomial;
data SubA3; set one;

    if Trt=1;
 if Leaf=1 then delete;

proc sort data=SubA3; by Leaf;

proc glimmix data=SubA3;
by Leaf;
class date trait;
model preyEggsCons/TotPreyEggs = Trait/ddfm=satterth dist=binomial link=logit;
random date;
lsmeans Trait/cl ilink;
title1 'SubAnalysis 3: By Leaf, Leaves 2-6, Trt 1, y=Proportion of prey eggs consumed';
```

Subanalysis 4 – Table 2.2

```
*LEAVES AS A FACTOR IN THE ANALYSES;
*Subanalysis 4, COMPARING LEAVES, Leaves 1-6, Trts 1 and 2;
* Response=PredEggsLd=Poisson (counts per leaf);
data SubA4; set one;
```

```
   if Trt=3 then delete;

proc glimmix data=SubA4;
class date trait trt leaf;
model predEggsLd = Trait|Trt|Leaf/ddfm=satterth dist=poisson link=log;
random date date*Trait*Trt;
lsmeans Trait|Trt|Leaf/cl ilink pdiff alpha=.10;
title1 'SubAnalysis 4: COMPARING LEAVES, leaves 1-6, Trts 1 & 2, y=Predator Eggs
Laid ';
```

Subanalysis 5 – Table 2.1

```
*Subanalysis 5, COMPARING LEAVES, Leaves 1-6, Trt 1;
* Responses=PreyEggsCons/30=Binomial;
data SubA5; set one;

   if Trt=1;

proc glimmix data=SubA5;
class date trait leaf;
model preyEggsCons/TotPreyEggs = Trait|Leaf/ddfm=satterth dist=binomial link=logit;
random date date*Trait;
lsmeans Trait|Leaf/cl ilink pdiff alpha=.10;
title1 'SubAnalysis 5: Comparing Leaves, Leaves 1-6, Trt 1, y=Proportion of prey eggs
consumed';

run;
quit;

*POOLING ALL LEAVES--ONE MEASUREMENT PER PLANT;
proc sort data=one;
by date trait trt plant;
proc means data=one sum noprint;
by date trait trt plant;
var PreyEggsCons PredEggsLd;
output out=sums sum=SPreyEggsCons SPredEggsLd;
proc print data=sums;
title1 'Counts of preyEggsConsumed and PredEggsLaid for whole plant';
```

Subanalysis 6 – Table 2.2

```
*Subanalysis 6, Trts 1 and 2;
* Response=SPredEggsLd=Poisson (counts per plant);
data SubA6; set sums;
```

```
   if Trt=3 then delete;

proc glimmix data=SubA6;
class date trait trt;
model SpredEggsLd = Trait|Trt/ddfm=satterth dist=poisson link=log;
random date ;
lsmeans Trait|Trt/cl ilink pdiff alpha=.10;
title1 'SubAnalysis 6: Pooling leaves, Trts 1 & 2, y=Predator Eggs Laid';
```

Subanalysis 7 – Figure 2.1

```
*Subanalysis 7, Trt 1;
* Response=PreyEggsCons/180=Binomial;
data SubA7; set sums;

   if Trt=1;
 TotPreyEggs=180;

proc glimmix data=SubA7;
class date trait;
model SpreyEggsCons/TotPreyEggs = Trait/ddfm=satterth dist=binomial link=logit;
random date ;
lsmeans Trait/cl ilink pdiff alpha=.10;
title1 'SubAnalysis 7: Pooling leaves, Trt 1, y=Proportion of prey eggs consumed';

run;
quit;

*POOLING ALL LEAVES--ONE MEASUREMENT PER PLANT;
proc sort data=one;
by date trait trt plant;
proc means data=one sum noprint;
by date trait trt plant;
var PreyEggsCons PredEggsLd;
output out=sums sum=SPreyEggsCons SPredEggsLd;
*proc print data=sums;
* title1 'Counts of preyEggsConsumed and PredEggsLaid for whole plant';
```

Subanalysis 8 – Figure 2.6

```
*Subanalysis 8, Trt 1 and Trt 2;
* Response=PreyEggsCons/180=Binomial;
data SubA7; set sums;

   if Trt=3 then delete;
 if Trt=1 then TotPreyEggs=180;
```

```
 if Trt=2 then TotPreyEggs=30;
/*
proc glimmix data=SubA7;
class date trait trt;
model SpreyEggsCons/TotPreyEggs = Trait|Trt/ddfm=satterth dist=binomial link=logit;
random date ;
lsmeans Trait|Trt/cl ilink pdiff alpha=.10;
title1 'SubAnalysis 8: Pooling leaves, Trt 1 & 2, y=Proportion of prey eggs consumed';
*/

proc glimmix data=SubA7;
class date trait trt;
model SpreyEggsCons= Trait|Trt/ddfm=satterth dist=poisson link=log;
random date ;
lsmeans Trait|Trt/cl ilink pdiff alpha=.10;
title1 'SubAnalysis 8: Pooling leaves, Trt 1 & 2, y=PNUMBER of prey eggs consumed';
run;
quit;
```

APPENDIX C – Prey consumption and predator oviposition data by trial for each prey-infested leaf on plants with all six leaves infested and with only the basal leaf infested.

Prey consumption by predators selected for high consumption for each trial, comparing plants with one leaf infested and all six leaves infested (leaf-by-leaf)

		Six Leaves Infested (By Leaf Number and 6-Leaf Total)						
Trial Number	One Leaf Infested	1	2	3	4	5	6	Total
1	27	0	0	0	0	0	0	0
2	0	10	11	0	0	0	0	21
3	0	30	10	0	0	0	0	40
4	23	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0
6	15	0	0	20	0	0	0	20
7	26	25	0	0	0	0	0	25
8	14	10	0	0	15	0	0	25
9	0	10	0	16	0	0	0	26
10	14	0	0	0	0	0	0	0
11	17	10	0	0	0	0	0	10
12	19	20	0	0	0	0	0	20

Predator oviposition by predators selected for high consumption for each trial, comparing plants with one leaf infested and all six leaves infested (leaf-by-leaf)

Trial Number	One Leaf Infested	Six Leaves Infested (By Leaf Number and 6-Leaf Total)						
		1	2	3	4	5	6	Total
1	3	0	0	0	0	0	0	0
2	0	1	1	0	0	0	0	2
3	0	4	0	0	0	0	0	4
4	3	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0
6	0	0	0	0	1	0	0	1
7	3	4	0	0	0	0	0	4
8	1	0	0	0	2	0	0	2
9	0	1	0	1	0	0	0	2
10	1	0	0	0	0	0	0	0
11	2	2	0	0	0	0	0	2
12	2	2	0	0	0	0	0	2

Prey Consumption by predators selected for high dispersal for each trial, comparing plants with one leaf infested and all six leaves infested (leaf-by-leaf)

		Six Leaves Infested (By Leaf Number and 6-Leaf Total)						
Trial Number	One Leaf Infested	1	2	3	4	5	6	Total
1	7	7	0	0	0	0	0	7
2	12	8	10	0	0	0	0	18
3	0	10	0	0	0	0	0	10
4	0	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0
6	0	12	0	0	6	5	0	23
7	0	0	0	0	0	0	0	0
8	8	0	0	0	21	0	0	21
9	13	5	16	0	0	0	0	21
10	15	9	0	0	17	0	0	26
11	11	16	5	0	0	0	0	21
12	13	12	0	0	0	0	0	12

Predator oviposition by predators selected for high dispersal for each trial, comparing plants with one leaf infested and all six leaves (leaf-by-leaf)

		Six Leaves Infested (By Leaf Number and 6-Leaf Total)						
Trial Number	One Leaf Infested	1	2	3	4	5	6	Total
1	1	1	0	0	0	0	0	1
2	1	1	1	0	0	0	0	2
3	0	2	0	0	0	0	0	2
4	0	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0
6	0	1	0	0	1	1	0	3
7	0	0	0	0	0	0	0	0
8	0	0	0	0	5	0	0	5
9	0	0	2	0	0	0	0	2
10	1	1	0	0	2	0	0	3
11	2	0	1	0	0	0	0	1
12	2	2	0	0	0	0	0	2

Prey Consumption by the control colony for each trial, comparing plants with one leaf infested and all six leaves infested (leaf-by-leaf)

		Six Leaves Infested (By Leaf Number and 6-Leaf Total)						
Trial Number	One Leaf Infested	1	2	3	4	5	6	Total
1	0	23	10	0	0	0	0	33
2	0	10	0	0	21	0	0	31
3	15	12	0	0	0	0	0	12
4	15	0	0	0	0	0	0	0
5	0	0	0	0	0	0	8	8
6	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0
8	15	17	20	0	0	0	0	37
9	18	0	0	0	0	0	0	0
10	19	17	0	0	15	13	0	45
11	18	21	0	0	0	0	0	21
12	13	20	0	10	0	0	0	30

Predator oviposition by the control colony for each trial, comparing plants with one leaf infested and all six leaves (leaf-by-leaf)

		Six Leaves Infested (By Leaf Number and 6-Leaf Total)						
Trial Number	One Leaf Infested	1	2	3	4	5	6	total
1	0	3	1	0	0	0	0	4
2	0	1	0	0	3	0	0	4
3	3	1	0	0	0	0	0	1
4	1	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0
6	0	1	0	0	0	0	0	1
7	0	0	0	0	0	0	0	0
8	1	0	0	3	0	0	0	3
9	3	0	0	0	0	0	0	0
10	1	1	0	0	1	1	0	3
11	3	4	0	0	0	0	0	4
12	1	2	0	1	0	0	0	3

APPENDIX D –Consumption and oviposition rates (per 24 h) of *Phytoseiulus persimilis* lines after selection for high consumption or dispersal. Data are shown for each selection date and with the corresponding trial number(s).

Date:	Trait	Consumption	Oviposition	Trial Number
2/16/10	high consumption	42.17	5.35	1-4
2/16/10	high dispersal	28.18	3.56	1-4
2/16/10	control	36.17	4.69	1-4
6/2/10	high consumption	37.30	4.72	5
6/2/10	high dispersal	25.16	2.97	5
6/2/10	control	28	3.72	5
7/10/10	high consumption	38.52	5.07	6-8
7/10/10	high dispersal	28.77	3.63	6-8
7/10/10	control	26.78	3.72	6-8
8/26/10	high consumption	40.11	5.43	9-10
8/26/10	high dispersal	24.97	3.49	9-10
8/26/10	control	28.76	4.09	9-10
10/2/10	high consumption	37.91	5.31	11-12
10/2/10	high dispersal	25.75	4.00	11-12
10/2/10	control	26.80	4.03	11-12

If when tested, the selected traits consumption and oviposition was not at the desired levels, selection was re-imposed. The selection process entailed testing 50 individual predators for each selected trait. Then take the top 10% from the 50 individuals tested and start a colony with those individuals. This process was repeated until the desired levels for each trait was met. For each selected trait, it took 2-3 generations to reach the desired levels.

e.g. Levels of traits after selection in preliminary tests. These levels served as targets for selection imposed during experiments.

Trait values of predator lines

MEASURED VARIABLES	PREDATOR LINE		
	HIGH CONSUMPTION (Mean ± S.E.)	HIGH DISPERSAL (Mean ± S.E.)	CONTROL (Mean ± S.E.)
CONSUMPTION (# prey / 24 h)	39.3 ± 0.5	26.6 ± 0.7	29.5 ± 0.7
DISPERSAL (min.)	28.1 ± 3.2	8.1 ±1.0	17.0 ± 2.1
FECUNDITY (# eggs / 24 h)	5.2 ± 0.1	3.5 ± 0.1	4.1 ± 0.1