THE SEARCHING BEHAVIOUR OF THE PREDATORY MIDGE LARVA, *Feltiella acarisuga* VALLOT (DIPTERA: CECIDOMYIIDAE), IN RESPONSE TO THE DENSITY AND DISTRIBUTION OF ITS PREY, *Tetranychus urticae* KOCH (ACARI: TETRANYCHIDAE)

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ABSTRACT

Searching efficiency is one of the criteria used to evaluate natural enemies for biological control potential in greenhouses. The searching behaviour of a predatory gall midge larva (*Feltiella acarisuga*) was examined at high and low prey (*Tetranychus urticae*) density (10 and 5 *T. urticae* eggs / cm^2) on the underside of tomato leaflets. Larvae significantly increased number of feeds, residence time and turning rate and decreased speed in response to higher prey density. Immediately after a feeding episode, "local search" behaviour, characterized by a significant reduction in speed and a significant increase in turning rate, was triggered. Speed and turning rate then gradually increased and decreased respectively, returning to "ranging" levels after about 15 min if more prey were not encountered and consumed. Larvae usually followed a forward-moving noisy loop after consuming a prey item.

The ability to alter search behaviour in response to prey density becomes more advantageous as prey become more aggregated in distribution. A survey of *T. urticae* density and distribution within greenhouse tomato plants in a commercial greenhouse found that at the within-leaflet level, *T. urticae* eggs were very aggregated ($s^2/m = 2.53$) while adults and juveniles were moderately aggregated ($s^2/m = 1.22$). Egg aggregation was found to increase with egg density at the within-leaflet level. The survey also found that adults and juveniles were most dense in the highest stratum of plants (1.39 / cm^2) and less dense in the middle and lowest strata (1.27 / cm^2 and 1.11 / cm^2 respectively). Eggs were most densely distributed in the middle stratum (7.24 / cm^2), less dense in the upper stratum (4.89 / cm^2) and least dense (1.11 / cm^2) in the lower stratum of the tomato plant.

The combined results of the search behaviour experiment and the *T. urticae* survey suggest that *F. acarisuga* larvae employ a search strategy that is highly efficient. It allows them to increase consumption rate and increases their chances of being able to pupate on a single leaflet, thus avoiding the glandular hairs on the stems and leaf petioles of tomato

plants. The results also suggest that the predator will show a strong aggregative response to their prey. The results of this study are being used to estimate some of the biological parameters that are needed to construct a simulation model of *F. acarisuga* - *T. urticae* population dynamics.

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CHAPTER I

INTRODUCTION

A. The problem

Two-spotted spider mites (TSSM) *Tetranychus urticae* Koch (Acari: Tetranychidae), are major pests of British Columbia greenhouse crops including tomatoes, sweet peppers and long English cucumbers (B. C. Ministry of Agriculture, Fisheries and Food, 1996). They feed on the underside of leaves, sucking cell fluids and causing the foliage to become pale and mottled in appearance. Damaged leaves become brittle and are eventually covered with TSSM webbing (B. C. Ministry of Agriculture, Fisheries and Food, 1996). Extensive yield loss occurs as a result of wilting of the leaves, reduced fruit size and number, and sun-scalding of the fruit due to loss of shading (McKinlay *et al.*, 1992). If left uncontrolled, TSSM are capable of completely destroying large numbers of their host plants (personal observation, 1997).

While adequate control of TSSM on sweet peppers and long English cucumbers has been achieved, primarily through the use of the predatory mite *Phytoseiulus persimilis* Athias-Henriot (Acari: Phytoseiidae), control of TSSM by chemical or biological means on greenhouse tomatoes remains problematic.

Biological control of TSSM by *P. persimilis* is successful on a wide range of greenhouse crops throughout the world (van Lenteren and Woets, 1988) but has proven unsatisfactory on tomato (Ravensburg *et al.*, 1987). This is due to the entrapment of *P. persimilis* on the glandular hairs on the stems and leaf petioles of tomato plants (van Haren *et al.*, 1987) and to the direct or indirect (through ingestion of TSSM) exposure to

toxic and repellent chemicals (for example 2-tridecanone) present in the glandular hairs and on the leaves of tomato (Farrar and Kennedy, 1991). This slows down the movement of *P. persimilis* between leaves, making control less effective (B. C. Ministry of Agriculture, Fisheries and Food, 1992).

Chemical control of TSSM is also problematic. In addition to the usual drawbacks of chemical control (health of greenhouse workers and adjacent environment, risk of evolving highly resistant populations of pests, phytotoxicity-induced yield reductions, the health of naturally occurring predators, parasites and competitors of pests), chemical control of TSSM on greenhouse tomato causes specific problems. Most B. C. vegetable greenhouses are located in the Fraser Valley area, in proximity to large urban centers. The products of Fraser Valley vegetable greenhouses are graded, packaged, marketed and sold by B. C. Hot House Foods Inc. Environmental and health consciousness has increased substantially throughout the past two decades. Therefore it is now possible to market Integrated Pest Management (IPM) products and ask a slightly higher price for them. B. C. Hot House Foods Inc. market their vegetables in B. C. and throughout the world as being herbicide free and pesticide reduced (N. Garland, 1996, personal communication). Therefore vendex (fenbutatin-oxide), a highly effective miticide registered for the control of TSSM on tomato in Canada, can only be used as a last resort by B. C. greenhouse tomato growers. In addition residues of vendex on tomatoes are not tolerated in the U.S.A. (L. Gilkeson, 1996, personal communication) because vendex is not registered for use on tomatoes there. About 80% of B. C. Hot House tomatoes are exported to the U.S.A. (N. Garland, 1996, personal communication). This limits the use of vendex considerably.

The number of other chemical options available for the control of TSSM are limited because they have to be compatible with the parasitoid *Encarsia formosa* Gahan (used to control the greenhouse whitefly, *Trialeurodes vaporarium* Westwood) and other beneficial insects that are released into the greenhouse (including *Aphidoletes aphidimyza*

Rondani for aphids, *Amblyseius cucumeris* Oudemans and *Orius insidiosus* Say for western flower thrips and *Trichogramma* spp. for caterpillars). Broad-spectrum insecticides are deleterious to *T. vaporarium* and other beneficial insects (see Table 1, B.C. Ministry of Agriculture, Fisheries and Food, 1992) and therefore cannot be used extensively to control TSSM on tomato.

The need to find an alternative solution for controlling TSSM on tomato recently led to a survey of naturally occurring enemies of TSSM in the Fraser Valley (Gillespie *et al.*, 1994). A predatory gall midge, *Feltiella acarisuga* Vallot (Diptera: Cecidomyiidae), was the most abundant predator throughout the 1992 and 1993 seasons, occurring at all three sites (Abbotsford, Surrey and Agassiz) and in all months of the survey (May to September). Recently, attention has been focused on *F. acarisuga* as a potential biological control agent of TSSM on tomato (Gillespie *et al.*, 1994; Shaddick, 1995). The larva is very small (1.7 mm long and 0.4 mm wide when fully developed; Roberti, 1954) and may be able to pupate on a single leaflet, depending on prey density (larvae require between 40 and 130 TSSM eggs to pupate; N. Sawyer, 1997, personal communication). This would allow the predator to avoid the glandular hairs on the stem and leaf petioles of the tomato plants, since the main dispersal stage is the winged adult.

B. Life history of *Feltiella acarisuga*

The life history of *F. acarisuga* was described in detail by Gillespie *et al.* (1994). The following is a brief summary. *Feltiella acarisuga* is a specialist predator of TSSM. Females are able to locate spider mite colonies from a distance and lay cylindrical shaped eggs on leaves that are infested with TSSM, on or near the colony. Larvae feed on both sexes and all stages of TSSM, after which they pupate on a leaflet, usually near a major vein. Males emerge shortly before females and the sex ratio is usually 1:1. Development

from egg to pupa requires about 15 days at 20° C and 10 days at 27° C. Larval development ceases at about 8° C, and temperatures above 35° C are lethal to larval development. Larval predatory activity is strongly influenced by relative humidity (RH), increasing rapidly in the range from 70% to 90% RH (Opit. 1995). Adults live for about 6 days at 25° C and 90% RH. Oviposition data is still uncertain, but evidence suggests that females usually begin laying eggs 24 h to 48 h after eclosion and are capable of laying more than 30 eggs in their lifetime.

C. Selecting, evaluating and improving the efficiency of natural enemies

van Lenteren and Woets (1988) proposed the following criteria for the preintroductory evaluation of natural enemies for biological control in greenhouses:

1. The natural enemy should be able to develop to the adult stage in or by feeding on the host. Furthermore, natural enemy development should be synchronous with that of the pest to prevent cyclical outbreaks.
2. The natural enemy should be able to develop, reproduce and disperse in the climatic conditions under which it is to be used.
3. The natural enemy should not attack other beneficial organisms in the same environment or non-pest organisms of importance in the area where it is to be introduced. In addition, other predators and parasites in the environment should not attack the natural enemy.
4. Mass production of the natural enemy should be inexpensive and efficient. Mass production should not alter the characteristics of the natural enemy.
5. Efficient natural enemies should have a pest kill rate equal to or greater than the potential maximum rate of population increase (r_m) of the pest species.

6. Good searching efficiency is also thought to be important. A high pest kill rate is not by itself sufficient for effectiveness, because at lower pest densities the full reproductive and predatory potential of the natural enemy may not be realized. Natural enemies should be able to locate and reduce pest populations before they have crossed economic threshold densities.

The sixth criterion is the focus of this thesis. The searching behaviour of *F. acarisuga* larvae for TSSM prey will be investigated. The theoretical importance of search efficiency and the aggregation of natural enemies in areas of high host or prey density has been the subject of argument (Murdoch and Stewart-Oaten, 1989). A number of theoretical models have been developed to tackle the issue. Hassell and May (1974) incorporated aggregation into a Nicholson-Bailey type model for parasitoids. They found that as aggregation increases, the number of sparse patches left unchecked increases, so pest numbers as a whole increase. This stabilizes parasitoid-host population dynamics but results in an increased density of hosts when the equilibrium is reached. Murdoch and Stewart-Oaten (1989) incorporated within-generation dynamics into a Lotka-Volterra type model for parasitoids and found the opposite. In this model the parasitoid is always efficient, even at low densities because it can continuously re-arrange its spatial distribution in response to host density. As aggregation increases, efficiency increases and therefore mean pest population densities decrease. However the stability of population dynamics also decreases because the host population may be wiped out entirely, which results in the extinction of the parasitoid, leaving the system subject to reinvasion by the pest.

Murdoch and Stewart-Oaten (1989) argue that when pest populations are in fact an ensemble of sub-populations, stability in each sub-population is not important. What matters is global stability of the ensemble and a mean pest density below the economic threshold.

In greenhouse biological control long-term stability is not important because either inundative or seasonal inoculative release methods are generally used. What really matters is pest suppression below the economic threshold. If *F. acarisuga* larvae are able to search for prey on tomato leaflets efficiently this should enhance biological control of the pest in two ways. First of all, a larger number of prey will be consumed per unit time because the larva will spend less time searching in less profitable areas of the leaflet. Second, the larva is more likely to find enough prey to pupate, within a single leaflet, allowing it to avoid the glandular hairs on the petioles and stems of tomato plants.

Basic research may also provide insight into how biological control works. Biological parameters estimated from basic research may be used to develop simulation models that predict predator-prey population dynamics under a variety of different conditions (Minkenberg *et al.*, 1986; Noldus *et al.*, 1987; Sabelis *et al.*, 1981). Information about how a predator searches for their prey in relation to their density and distribution is one of the parameters needed to construct simulation models of population dynamics. These simulation models may become increasingly important tools for fine-tuning biological control programs. They may be used for estimating the effect of changes in crop variety or greenhouse climate on the biological control capabilities of specific natural enemies, or for predicting the best method, timing and numbers of natural enemies to be introduced (International Organization for Biological Control / Western Palearctic Regional Section, 1983; Kole *et al.*, 1985).

Basic research may also play a vital role when attempting to develop efficient mass rearing, storage and shipping procedures. Knowledge of larval searching behaviour in relation to TSSM density and distribution may suggest better ways (e.g. that increase encounter rate with prey) to rear the natural enemy.

CHAPTER II

SEARCH BEHAVIOUR OF *Feltiella acarisuga* LARVAE AT TWO PREY DENSITIES

A. Introduction

Searching behaviour can be defined as an active movement by which insects seek resources such as food, mates, oviposition and nesting sites, and refugia (Bell, 1990). Since these resources are crucial to survival and reproduction, it follows that efficient searching mechanisms are likely to have evolved. Searching behaviour also incurs costs such as predation risk and time and energy taken away from other activities. Natural selection would be expected to favor searching behaviours that maximize costs - benefits and reduce risks incurred while searching.

The searching behaviour of a specific insect at any given time and place results from the convergence of three types of factors (Bell, 1990): (i) external environmental factors such as the type and distribution of resources and the risks inherent in their quest, (ii) the internal state of the insect such as hunger, sexual receptivity or age which determine what a particular individual needs at a particular time; and (iii) the biological capacities of the insect including innate search patterns, the ability to perceive sensory information and the ability to learn.

Understanding the way an insect perceives its environment and the distribution of resources within it is a difficult task. Hassell and Southwood (1978) suggest that an insect's perception may resemble a hierarchy with resource items, patches (aggregations of resource items or spatial subunits of the foraging area in which aggregations of resource items occur) and habitats (clusters of patches). Resource items are easy to define but the

concepts of patches and habitats present more difficulties and seem to be in part dependent on the spatial scales used in a particular study. Nevertheless, many aspects of the searching behaviour of insects are consistent with a hierarchical nature of the spatial distribution of resources (Roitberg *et al.*, 1982). In particular, movements within and between resource aggregations (patches) can be distinguished (e.g. Ives *et al.*, 1993; Li, 1992; Nakamuta, 1985). Movements within patches can usually be characterized as mechanisms for restricting search to the patch. Movements between patches can usually be characterized by more linear movements and the utilization of gross cues designed to find other patches within a habitat or to migrate to another habitat. The term *local search* or *area concentrated search* applies to movements and scanning within a patch. When an insect leaves a patch to search for others, the term *ranging* (Jander, 1975) or *extensive search* applies (Ferran *et al.*, 1994).

Insects can use a variety of mechanisms to restrict their searching to profitable patches (local search). Looping or spiraling local search occurs when an insect maintains a turn bias in a particular direction (left or right) or makes zigzag patterns in which the animal alternately moves to the left and right. This usually results in an overall increase in turning rate and tends to restrict an insects search path to within a patch.

Scanning refers to a set of mechanisms by which insects move their bodies, appendages or receptors so as to capture information from the environment efficiently. Usually it involves movements to the left and right of their search path, increasing the chance of contacting (physical, visual, chemical or auditory contact) a resource. Most insects scan for resources periodically while searching (e.g. Chandler, 1969; McCoy, 1984). Scanning cannot be performed while in movement (Bell, 1990) . An increase in scanning and therefore decrease in speed is often associated with local search.

These mechanisms are usually specifically designed for finding other resources after a first one has been found and are triggered after the finding and utilization of the first resource. Local search triggered by resource utilization is referred to as *success*

motivated search. (Vinson, 1977). However local search may also be triggered by other cues which indicate the presence of nearby resources. These cues may be physical (Nakamuta, 1985), visual (Harris and Miller, 1982), chemical (Shonouda, 1996) or auditory (Schmitz *et al.*, 1982). These cues may originate directly from the resource or they may originate from the environment in which resources are likely to be found. Other mechanisms for local search include turning back into a patch when the edge of the patch is detected (Havukkala and Kennedy, 1984).

As an insect consumes the resources within a patch encounter rates will drop to the point where costs of searching (time, energy and risks) exceed benefits (rate of utilization of resources). When it is no longer profitable to search in a particular patch (before the point of diminishing returns) we would expect insects to switch to ranging in order to leave the current patch and seek out more profitable ones. The simplest mechanism to achieve this is to gradually decrease turning rate and turning bias and gradually decrease scanning (increasing speed) after consuming each resource. An insect will then leave the patch after a certain amount of time (giving up time) or distance traveled (giving up distance) if another resource is not found. This strategy is used by many insects (e.g. Carter and Dixon, 1982; Fromm and Bell, 1987). Alternatively insects may be expected to switch to ranging when the encounter rate drops below the expected encounter rate for a particular patch or habitat. The expectation may be learned by experience or be genetically based (Waage, 1979).

Given that encountering prey, or perceiving stimuli that suggest the presence of nearby prey, may trigger local search behaviour, one would expect that predators in areas of higher prey densities will spend more time searching that specific area or patch. The residence time of predators in patches of high prey densities should therefore increase. This response should result in the aggregation of predators in areas of high prey density described by Kareiva and Odell (1987). Female two-spotted lady bird beetles increase local search behaviour and decrease ranging at higher prey (the pea aphid) densities, but

males of the same species do not show this response (Hemptinne *et al.*, 1996). The authors suggest that this may be due to the increased energy requirements of females. The carabid beetle *Pterostichus cupreus* shows a similar response to higher prey (the cereal aphid *Rhopalosiphum padi*) densities but another cereal aphid predator, the carabid beetle, *Bembidion lampros* does not show this response (Chiverton, 1988). The latter species did show local search behaviour after encountering prey, but consistently encountered small numbers of prey, even at high prey densities. An increase in residence time in response to increases in prey density has been observed for some but not all predaceous mites. *P. persimilis* shows an increased residence time at higher TSSM densities (Bernstein, 1984). *P. persimilis* is oligophagus, with a preference for TSSM. In contrast, the more generalist predators *Amblyseius degenerans* and *Amblyseius andersoni* did not alter residence time at higher TSSM densities (Eveleigh and Chant, 1982; Zhang and Sanderson, 1993).

The objective of this study is to examine the search behaviour of *F. acarisuga* larvae at low and high TSSM egg density. The following questions were addressed: (1) Do larvae alter their search behavior at high prey density by increasing the amount of time spent in local search behaviour and hence residence time? (2) Are changes in search behaviour induced by individual feeding episodes? (3) What are the specific locomotory aspects associated with larval local search?

B. Methods

(i) Rearing four-day-old *Feltiella. acarisuga* larvae

Feltiella acarisuga eggs were received once a week on TSSM infested tomato (trust cultivar) leaflets from the Agriculture Canada Research Station in Agassiz, British Columbia. Half of the batch (Group B) was stored inside a plastic container at 7° C for 24 h. This delayed hatching by 24 h. The other half of the batch (Group A) was kept in a

Styrofoam container with a transparent cover at 25° C, 16 h: 8 h (light: dark) photoperiod and 85-90% humidity.

Group A hatched the following morning. These larvae were kept on their original leaflets and fed *ad lib.* on the available TSSM (eggs, juveniles and adults). Two days later these larvae were transferred to fresh, *T. urticae* infested, tomato (trust cultivar) leaflets. All transfers of larvae were done under a microscope at 25x magnification using a very fine 5/0 wet paintbrush. Here they fed *ad lib.* on the available *T. urticae* (eggs, juveniles and adults).

Twenty-four h after transfer, 20 three-day-old larvae were removed from the leaflets. They were starved in small sealed Nalgene vials with a 1 cm^2 piece of tomato leaflet to maintain high humidity. Ten of them (AM group) were starved at 10:30 AM for 24 h. The other 10 (PM group) were starved at 01:30 PM for 24 h.

Group B larvae hatched two days after arrival and followed the same schedule as Group A, with each step delayed by one day.

This method allowed me to prepare 4 batches of *F. acarisuga* larvae of the same age and hunger level. Group A (AM) and Group A (PM) larvae were used for experiments on day 5 after arrival at 10:30 AM and 01:30 PM respectively. Group B (AM) and Group B (PM) larvae were used for experiments on day 6 after arrival at 10:30 AM and 01:30 PM respectively.

(ii)*Feltiella acarisuga* search behaviour at two prey densities

The search behaviour of *F. acarisuga* larvae was observed at two prey densities: 5 and 10 TSSM eggs/cm^2, uniformly distributed. Four -day-old larvae were chosen because they were large enough to allow clear visibility but presumably not old enough to be influenced by pre-pupation behaviour.

The experimental arena consisted of a fresh, flat tomato (trust cultivar) leaflet with the prey distributed on the lower surface of the leaflet. The leaflets varied in size between

13 and 16.5 cm^2. Pilot experiments suggested that behaviour would vary significantly at these two prey densities. The eggs were uniformly distributed covering the entire surface of the leaflet. The experimental leaflets were prepared (using a microscope at 25x) on the same day or the night before the trials using fresh (clear translucent colour) TSSM eggs in order to minimize the chance of eggs hatching. The leaflet was placed, with the lower surface facing upwards, on a wet piece of circular filter paper, within a covered transparent Pyrex Petri dish. This kept the relative humidity between 85-90%. This is the optimal RH for *F. acarisuga* activity (Gillespie *et al.*, 1994). Observations occurred at 25° C under well lit conditions. Cold light was used.

An apparently healthy larva (some mortality occurred during starvation) was transferred from a vial to the arena. The larva usually reacted to this disturbance with what appeared to be an escape response. It traveled at high speed following a straight line towards the edge of the patch. If the larva left the patch during this pre-observation period, it was transferred back to the arena. If damage occurred to the larva during this process, a new one was taken from the starvation vials and transferred onto the arena. This process was continued until a healthy larva encountered and began feeding on an egg. This usually occurred within 15 min of the first transfer. Observation of search behavior began after consumption of the first egg, and was continued for 2 h or until the larva left the arena. Ten trials at each prey density were performed. At each prey density, trials were planned so that Group A and B larvae were used equally and so that half of the trials were AM and half of them were PM.

(iii) Videotaping specifications

A video camera (Panasonic wv-cd 110) was placed directly above the arena (Figure 1) at maximum possible magnification; this was 10x. One mm of tomato leaflet appeared as 1 cm on the screen of the monitor. This was large enough for a good view of the larva but not large enough for an absolutely positive identification of TSSM eggs.

Therefore, to be absolutely sure that a larva was not moving because it was feeding, the arena was briefly inspected under a microscope at 50x every time the larva remained immobile for 1 min.

(iv) Interpretation of search paths from the videotapes

The search paths were manually mapped onto a grid with each square corresponding to 1 mm^2 of tomato leaflet. As the larva moved its position was mapped according to the square in which most of its body resided. Tick marks were used to record the travel path at 30 sec intervals. The starting position, ending position (position after 2 h or last position on the arena) and feeding sites were all recorded.

The following variables were extracted from the search paths: The number of feeds, residence time (sec), feeding time (sec), travel time (sec), distance traveled (mm) and the number of turns of 90° or greater. In addition for each trial, the leaf area, taping period (AM/PM) and the group of larvae used (A/B) were recorded. Residence time was the total amount of time spent on the leaflet. If the larva did not leave the leaflet within 2 h, residence time was recorded as 2 h. Feeding time was the total amount of time spent immobile. After feeding, larvae occasionally would not move for a long period of time (>10 min). Presumably they had already finished feeding and were performing some sort of metabolic function (perhaps excretion). This period was included in feeding time because it was not possible to discern accurately between resting and feeding. Travel time (residence time - feeding time) was the total amount of time the larva spent moving on the leaflet. The average speed (mm/sec) throughout each trial was calculated by dividing the distance traveled by the travel time. The average turning rate (# of turns/mm) throughout each trial was calculated by dividing the total number of turns by the distance traveled.

B. Results

(i). Differences in search behaviour at high and low prey density

Table 1 and Figures 2a, 2b, 2c, 2d and 2e summarize the search behaviour at the two prey densities. ANCOVA's of the dependent variables speed, turning rate, distance traveled, residence time and number of feeds were performed with prey density and other independent variables (Appendix I). These were leaf area, rearing group (A or B) and time of experiment (AM or PM).

On average, larvae at low prey density traveled 113.72 mm (SD=42.8, N=10) at a speed of 0.106 mm/sec (SD=0.017, N=10) and turned at a rate of 0.190 turns/mm (SD=0.063, N=10). They fed 0.5 times (SD=0.97, N=10) and resided in the arena for 21 min and 18 sec (SD=11 min and 49 sec, N=10). On average, larvae at high prey density traveled 286.32 mm (SD=96.2, N=10) at a speed of 0.073 mm/sec (SD =0.012, N=10) and turned at a rate of 0.380 turns /mm (SD=0.032, N=10). They fed 9.5 times and in all cases resided in the arena for the full 2 h duration of the trial (SD=0, N=10). The differences in speed, turning rate, distance traveled, number of feeds and residence time were all highly significant ($p < 0.001$, N=10) when prey density was used as the independent variable in the ANCOVA.

With one exception there were no significant differences in speed, turning rate, distance traveled, number of feeds and residence time due to leaf area rearing group or time of experiment. The one exception was speed which was significantly higher (p=0.034, N=10) amongst Group B larvae.

In summary, at the higher prey density larvae, on average, traveled slower, turned more often, and spent more time on the arena consuming more prey and covering more distance. Figure 3 shows representative samples of search paths at low and high prey density.

(ii) Changes in search behaviour induced by individual feeding episodes (at high prey density)

Speed and turning rate before and after individual feeds in high prey density trials were compared. Feeding episodes in which there was at least a 10 minute interval between the previous feed and the feed in question were used. This reduced the effect of previous feeds as much as possible. However it also reduced the sample size to 13 feeding episodes, since in many cases larvae found new prey at intervals shorter than 10 min. The sample size had to be further reduced to six feeding episodes since of the 13 episodes many occurred during the same trial (pertained to the same individual) and therefore could not be used in a non-parametric paired sample test.

Speed and turning rate 2 min before and 2 min after these six feeding episodes (Table 2 and Figures 4a, 4b) were compared with a sign test (non-parametric paired sample test). This was used instead of a paired t-test because of the very low sample size. Mean speeds before and after feeding episodes were 0.113 mm/sec (SD=0.058, N=6) and 0.054 mm/sec (SD=0.022, N=6) respectively. Mean turning rates before and after feeding episodes were 0.259 turns/mm (SD=0.104, N=10) and 0.588 turns/mm (SD=0.257, N=10) respectively. The differences were both significant ($p=0.016$, $N=6$).

(iii) Specific locomotory patterns associated with larval local search behaviour

The speed and turning rate of the larvae was tracked after each feed at high prey density. The values were calculated in 2 min intervals immediately after completion of a feeding episode. It was observed that these values began to stabilize about 15 min after a feed. Only after 4 feeding episodes did the larvae search for more than 15 min before consuming another prey item (Figure 5). These episodes were used to graph the progress of the larva after a feed. Second order polynomial equations were found to fit the data best (Figure 6: speed $R^2=0.42$, $N=4$, $P<0.05$ and turning rate $R^2=0.60$, $N=4$, $P<0.02$). After a

feed, the larva's turning rate increases dramatically, then slowly drops and begins to level off after 15 min at around 0.2 turns/mm. The larva's speed on the other hand decreases dramatically and then gradually increases leveling off around 0.12 mm/sec after 15 min.

Immediately after a feeding episode the larvae tend to search making a full circle and move from the consumed prey item in approximately the same direction they were traveling when they encountered it. This is known as forward looping (Bell, 1985). The direction of the larva and whether or not it made a circle after a feeding episode was recorded. Only paths greater than or equal to 5 min in length were used in order to allow the larva to display the behaviour (N=49). Complete circling occurred 83% of the time. Circles were almost completed (came within 1.4 mm of closing off the circle) 93.8% of the time. The larvae left at about the same angle of encounter (between 0° and 90° turn) 92.1 % of the time and left in a different direction (between 90° and 180° turn) 7.2% of the time.

D. Discussion

The results show that *F. acarisuga* larvae do alter their searching behaviour at higher prey densities. At higher prey density there is an overall increase in turning rate and decrease in speed. This leads to an increase in residence time in the patch. The results also show that one of the cues that triggers local search is prey consumption. Immediately after a feeding episode speed declines and turning rate increases. Speed and turning rate gradually increase after a feeding episode, and reach ranging levels after about 15 min if more prey are not encountered and consumed.

Feltiella acarisuga tend to follow a rather specific spatial search pattern after a feed. After feeding they tend to leave in approximately the same direction that they arrived in, and tend to complete a circle or loop within the following 5 min. This is similar to the

forward-moving noisy loop described by Fromm and Bell (1986) for the housefly *Musca domestica* searching for sucrose droplets. Even though scanning was not actually quantified scanning behaviour appeared to increase markedly after feeding (personal observation). This was associated with decreased speeds. This behaviour is reported for other larval predators (e.g. Syrphidae; Chandler, 1969).

To improve foraging efficiency larvae search in areas of high prey density where encounter rates are high and consumption rates are limited only by some metabolic function. Low speed and a high turning rate result in the continuous search of the same area of the tomato leaflet. At low prey density, when consumption rate is severely limited by prey encounter rate, larvae increase their speed and decrease their turning rate. By doing this, larvae reach the edge of the leaflet rapidly and may choose to leave the lower surface of the leaflet and search for prey elsewhere. Thus the search tactic of larvae insures that they will leave the patch before search in the patch becomes energetically unprofitable. This is consistent with theoretical models of optimal foraging (Hassell and May, 1974; Murdoch and Oaten, 1975; Charnov, 1976).

Benhamou (1992) investigated the theoretical efficiency of local search by a terrestrial predator within a continuous patchy environment (resource patches have no perceptible boundaries and can only be defined as areas of higher resource density). He compared a strategy that involved a continuous high speed and low turning rate to a strategy that involved a switch to a lower speed and a higher turning rate after consuming a prey followed by a gradual return to high speed and low turning rate. He found that the latter strategy resulted in encounter rates two to three times greater than the former strategy and that efficiency increased with environmental heterogeneity. This suggests that terrestrial predators ultimately search efficiently for clustered prey items by using simple proximate mechanisms.

The results showed that prey consumption triggered local search by *F. acarisuga* larvae. However, other stimuli that indicate the presence of nearby TSSM may trigger the

same response. These include prey encounter rate, TSSM webbing, exoskeletons and waste material, TSSM induced vibrations of the leaflet and volatile chemicals emitted by TSSM and possibly injured plants. Further work is needed to examine the effects of these factors on larval search behaviour.

CHAPTER III

SURVEY OF TSSM DENSITY AND DISTRIBUTION WITHIN TOMATO PLANTS

A. Introduction

Surveys of TSSM density and distribution on crop plants are usually performed at the within-greenhouse or within-field level (interplant distribution: Nihoul, 1993; Jones, 1990;), and more rarely at the within-plant level (intraplant distribution: Kasak *et al.*, 1995; Perring *et al.*, 1987). Detailed surveys of TSSM density and distribution within tomato leaflets are not available in the literature. However, *F. acarisuga* larvae alter searching behaviour based on TSSM density within tomato leaflets (see Chapter II). Since the search tactic of *F. acarisuga* is presumably most efficient when prey are clumped, one would expect TSSM to be aggregated at the within leaflet level in a natural ecosystem.

A survey of TSSM density and distribution (in a tomato greenhouse) at the within-leaflet level was conducted to test this hypothesis. The survey examined TSSM density and distribution within a leaflet, but also assessed TSSM density and distribution at the within-plant level. The within-plant data can be used to generate descriptive functions (Mangel, 1994) for use in the construction of theoretical models of predator-prey population dynamics.

B. Methods

Samples were taken from a tomato greenhouse at the Agriculture Canada research center in Agassiz, British Columbia. The trust cultivar was being grown on rockwool, using standard temperature and irrigation (B.C. Ministry of Agriculture, Fisheries and Food, 1996). Supplementary lighting started early in September, supplying 14 h of daylight in total. The plants were 12 weeks old. The greenhouse contained 96 plants divided into 4 rows. The greenhouse being sampled had previously been inoculated with TSSM. Sampling took place between 11 AM and 3 PM on 23 September 1994. The temperature was approximately 25° C and the RH was approximately 60 %.

Four plants were chosen at random within the greenhouse. Each plant was divided into 4 strata:

1. Tip of plant to first flower
2. First flower to first fruit.
3. First fruit to last fruit.
4. Last fruit to last leaf.

Two leaflets were selected at random from the first three strata. The fourth stratum had very few mites because most of the leaves were old and unhealthy. These were not used in the survey. Sticky traps were used to collect samples. A 17 cm x 10 cm piece of Scotch Book Tape was securely fastened (with regular Scotch Tape) onto a 20.3 cm x 12.7 cm cue card. The sticky side of the Book Tape faced upwards. The selected leaflet was removed from the plant. The lower surface of the leaflet was then pressed onto the sticky side of the Book Tape and the outline of the leaflet was drawn around the leaflet on the Book Tape with a permanent waterproof marker. After ensuring that each area of the leaflet had been firmly pressed onto the Book Tape, the leaflet was removed and discarded. This method allowed 100% transfer of all live TSSM stages from the leaflet to the Book Tape. The samples were then stored in sealed Styrofoam containers at 5° C.

The distribution and density of TSSM on the leaflets was determined by using a 0.25 cm^2 grid placed between the non-sticky side of the Book Tape and the cue card. The

number of eggs and all mobile stages of TSSM in each square were counted. Many of the adults and juveniles were severely damaged by the sampling process. It was clear that they were single individuals, but it was not clear whether they were a juvenile or adult. For this reason all adults and juveniles were counted together in the same group (mobiles) to distinguish them from the eggs (immobiles).

C. Results

A three-way analysis of variance was used to investigate differences in TSSM density between tomato leaflet samples. The dependent variable was TSSM density. The three factors were TSSM stage (mobiles vs. immobile stages), plant# (4 plants sampled) and stratum of plant that was sampled (top 3 strata used). Bonferroni adjusted t-tests were used to pinpoint significant differences within the ANOVA.

The mean density of all the samples of TSSM eggs and mobile stages was 5.028/cm^2 (SD=3.716, N=24) and 1.256/cm^2 (SD=0.756, N=24) respectively (see Table 3). The difference was highly significant ($p < 0.001$, N=24).

Mean TSSM densities within different plants and plant strata are summarized in Table 4. Differences in TSSM density were significant amongst the four sampled plants ($p=0.025$). Plant 3 had a significantly lower TSSM density relative to plant 2 ($p=0.045$). This was largely due to a large difference in mean immobile density (2.588/cm^2 ,SD=1.488, N=6 and 6.864/cm^2, SD=5.728, N=6 respectively) between the two plants. There was no significant difference in total TSSM density between the top two strata but stratum 3 was significantly less dense than stratum 2 ($p = 0.010$). The interaction between TSSM stage and stratum was also significant ($p = 0.020$). This means that TSSM stages are distributed differently along the length of the plant. Mobile stages are more dense in the first stratum (1.392/cm^2, SD=1.14, N=8) and less dense in the second and third

stratum (1. 268/cm^2, SD=0.604, N=8 and 1.108/cm^2, SD=0.416, N=8 respectively). The immobile stage was most densely distributed in the second stratum (7.244/cm^2, SD=4.832, N=8), less dense in the first stratum (4.888/cm^2, SD=2.656, N=8) and least dense in the third stratum (2.948/cm^2, SD=2.1, N=8).

Figure 7 shows representative samples of within-leaflet TSSM density and distribution. Clumping at the within-leaflet-level was measured simply by using the variance to mean ratio (s^2/m). A s^2/m ratio of one would imply that TSSM distribution was random. A s^2/m ratio of less than or more than one would suggest a more uniform or more clumped distribution respectively Eggs were found to be very clumped (mean leaflet s^2/m=2.533, SD=1.566, N=24) while mobile stages were only moderately clumped (mean leaflet s^2/m=1.217, SD=0.275, N=24). Degree of aggregation can also be visualized and quantified by plotting mean TSSM density / 0.25 cm^2 vs. the within leaflet variance (Taylor's power law; Taylor, 1961). Eggs were found to have a slope far greater than 1 (slope = 6.81, R^2= 0.84) meaning that that they are very clumped (Figure 8). Mobile stages were found to have a slope only slightly greater than 1 (slope = 1.36, R^2= 0.93) meaning that mobile stages are only slightly aggregated in distribution (Figure 9).

A plot of within-leaf aggregation index (s^2/m) against within-leaf TSSM egg density (Figure 10) revealed that aggregation increased with TSSM egg density (R^2=0.667, p <0.001). This was not true for mobile stages (R^2 = 0.009, p = 0.668, Figure 11).

D. Discussion

The results show that TSSM egg distribution is very aggregated at the within leaflet level, while TSSM adult and juvenile distribution is only moderately aggregated. This makes intuitive sense because eggs are laid by females in proximity to each other,

while adults and juveniles are mobile and can therefore move around the leaflet and the plant. TSSM mobile stages are not randomly distributed though, because they do show some degree of aggregation. This may be due to many factors, including preferred feeding sites within a leaflet. The results also show that as within-leaflet TSSM egg density increases, eggs become more aggregated in their distribution. There may be preferred oviposition sites within a leaflet such as beneath or in webbing (Sabelis, 1985) or at the convergence of two leaf veins (personal observation). These sites may provide enhanced protection from predators and/or the abiotic environment. At high TSSM densities these sites may become very full, resulting in a higher degree of aggregation.

These results have implications that shed more light on the searching behaviour of *F. acarisuga*. Since TSSM distribution is clumped, *F. acarisuga* employs an efficient search strategy by switching between local search and ranging in areas of higher and lower TSSM density within leaflets. This allows the predator to increase the number of prey consumed per unit time, as well as increasing the chances that a larva will be able to pupate without moving to other leaflets. Since this kind of search strategy becomes theoretically more efficient as aggregation increases (Benhamou, 1992), *F. acarisuga* are probably more efficient when searching for eggs than for mobile stages.

The survey also shed light on within-plant distribution of TSSM. Mobile stages are more densely distributed near the top of the tomato canopy, becoming less dense further down. Eggs are most abundant immediately below the top segment of the plants, moderately abundant in the top segment, and least abundant in the lower section of the canopy. The results are consistent with Hussey and Parr's (1963) description of the dispersal of TSSM within greenhouse plants. Females migrate to fresh leaves higher up in the host plant throughout the growing season. Virtually all TSSM movement between leaves is upwards. This explains why mobile stages are most densely distributed in the upper parts of the canopy and why eggs are most dense immediately below them. The distribution of TSSM and other mite species within plants also varies with time and type of

crop. The within-plant distribution of TSSM on hops varies throughout the season, at times being greater in the upper areas of the canopy and at others, being greater in the lower areas of the canopy (Kazak *et al.*, 1995). *Tetranychus cinnabarinus* were most aggregated in the upper third of greenhouse-grown ornamental plants (Chandler and Corcoran, 1981). However, Banks grass mites (*Oligonychus pratensis*) aggregate in the lower canopy of corn plants (Gilstrap *et al.*, 1980) and *T. cinnabarinus* aggregate in the middle portion of cotton plants (Carey, 1982).

It must be noted that the survey took place on one day only, in September 1994. It is possible that degree of aggregation at the within-leaflet level, and the overall distribution of TSSM within the tomato plant, change significantly over the course of the year. This must be taken into consideration when drawing conclusions from this survey.

CHAPTER IV

CONCLUSIONS

Feltiella spp. occur naturally as TSSM predators in many parts of the world, in both greenhouses and field crops. *Feltiella acarisuga* contributed to TSSM control in banana greenhouses in Italy (Colombo *et al.*, 1995) and was also a significant naturally occurring predator of TSSM in Italian field bean crops (Roberti, 1954). It has also been found in Japanese grape greenhouses (Akitsu Branch, Fruit Tree Research Station, 1992) and Japanese watermelon fields (Morishita *et al.*, 1994).

The lack of adequate control measures for TSSM in B. C. greenhouse tomatoes has led to the search of natural enemies of TSSM with biological control potential. *Feltiella acarisuga* is currently under investigation as a possible candidate. This predator is already commercially available in British Columbia (B. C. Ministry of Agriculture, Fisheries and Food, 1996) and in the United Kingdom (Shaddick, 1995). Releases in B. C. tomato greenhouses have shown that *F. acarisuga* can establish on tomato plants, and can contribute to limiting TSSM populations (Gillespie *et al.*, 1994). However establishment and control are not always successful, and the reasons for this are not fully understood (Gillespie *et al.*, 1994).

The success or failure of a biological control in a specific pest control program is probably largely dependent on the specific characteristics of the pest, crop and growing environment. However, van Lenteren and Woets (1988) criteria may serve as useful guidelines for the preintroductory evaluation of the potential of natural enemies for biological control in greenhouses

Recent studies of *F. acarisuga* biology (including this one) have yielded results which relate to van Lenteren and Woets (1988) six criteria:

1. *Feltiella acarisuga* develop fully to the adult stage by feeding on TSSM, and the development of predators and prey is approximately synchronous (Gillespie, 1994).

2. Studies of the effect of climatic conditions on *F. acarisuga* (Gillespie, 1994) have shown that *F. acarisuga* develops and consumes TSSM at temperatures well within greenhouse temperature ranges. RH was found to limit larval activity and adult lifespan considerably. *Feltiella acarisuga* is most effective at high RH's (between 70% and 90%). Typical greenhouse RH may be somewhat lower (see Chapter III, methods). This may be a factor that limits the efficacy of *F. acarisuga* in greenhouses. However greenhouse RH may vary within the greenhouse, and RH is probably higher when measured at the leaf surface because moisture trapped in the tomato canopy keeps the relative humidity at the leaf surface much higher than that of the general environment (Opit, 1995).

3. J. Rogers (personal communication, 1997) is currently examining interspecific competition between *F. acarisuga* and *P. persimilis*. The results suggest that the two predators feed on each others' eggs occasionally, but *F. acarisuga* will only feed on *P. persimilis* eggs in the absence of TSSM. However, *P. persimilis* will feed on *F. acarisuga* even in the presence of TSSM. This may present problems in greenhouses when the two predators are being used together and TSSM numbers are low. However, further work has shown that there is no significant reduction in TSSM consumption when the predators are used in combination. *Feltiella acarisuga* is parasitized by a small parasitic wasp: *Aphanogmus floridanus* Ashmead, (Hymenoptera: Cerafronidae) (Roberti, 1956). Parasitization rates as high as 90% have been reported (Oatman, 1985 for *Feltiella acarivora*; Gillespie *et al.*, 1994). This endoparasite may be a substantial mortality factor affecting *F. acarisuga* populations, thus severely limiting TSSM control. Further work is

needed to investigate how *A. floridanus* affects biological control of TSSM by *F. acarisuga*.

4. Gillespie and Quiring (1995) described a system for rearing *F. acarisuga* based on a staged rearing concept. The authors believe that the predator can be reared in sufficient quantities to satisfy demand from the greenhouse industry and that the system would allow insectary companies to produce the insect at a cost that is affordable to growers and that will also allow for some profit by the producing company. Further work is needed to determine if and how mass rearing may alter *F. acarisuga* characteristics.

5. Opit *et al.* (1997) investigated the functional response of *F. acarisuga* to adult TSSM. A strong type II functional response was reported suggesting that the predator kills more prey as prey density increases and that the predator kills more prey than it needs to complete development. In a 24 h period, TSSM females can produce an average of 3.5 offspring on tomato (Robertson *et al.*, in press); in the same period of time, *F. acarisuga* can kill 15 TSSM females. *Feltiella acarisuga* was found to have a higher attack rate and a lower handling time than *P. persimilis*, suggesting that it could be an effective predator of TSSM in greenhouse crops.

A good searching efficiency is the sixth criterion suggested by van Lanteren and Woets (1988). Search efficiency of both larvae (for TSSM prey) and adults (for TSSM infestations to oviposit around) must be considered. E. Basalayga (personal communication, 1997) found that *F. acarisuga* adults lay significantly more eggs on tomato leaflets with higher TSSM densities. This suggests that adults are able to discriminate between low and high TSSM density leaflets at close range, but it does not tell us if adults are able to locate TSSM infestations from a distance or how adults

disperse within a greenhouse once released. Further work is needed to investigate adult dispersal at the within-greenhouse level.

This study focused on the searching efficiency of larvae for TSSM prey at the within-leaflet level. *Feltiella acarisuga* larvae were found to use a search strategy that is efficient, leading to in ancrease in consumption rate of prey, if their distribution is aggregated within a tomato leaflet. This strategy involves switching from high traveling speed and a low turning rate (ranging) to low speed and high turning rate (local search) after consuming prey. Speed and turning rate then gradually increase and return to ranging levels after about 15 min if more prey are not encountered and consumed. The overall effect of this is that larvae will spend more time searching in areas of high prey density (where prey encounter and consumption rates are high) and less time searching in areas of low prey density (where prey encounter and consumption rates are low). Prey consumption was shown to be one stimulus that elicits local search but there may be others.

A survey of within-leaflet and within plant TSSM density and distribution in a tomato greenhouse showed that within-leaflet distribution of TSSM is aggregated. Eggs were found to be very aggregated and adult stages were found to be moderately aggregated. Egg aggregation increased with egg density within leaflets. Within-plant data showed that TSSM egg density is highest immediately below the upper portion of tomato plants and that juvenile and adult TSSM density is highest in the top part of the plant and declines further down the plant.

The combined results of the search behaviour experiment and the TSSM density and distribution survey suggest that *F. acarisuga* employ a search strategy that is efficient for the environment in which they search for prey. It allows them to increase consumption rate and increases their chances of being able to pupate without moving to other leaflets. These characteristics may allow larvae to avoid the glandular hairs on the stem and leaf petioles of tomato plants, which slow down *P. persimilis* reducing the efficiency of this

TSSM predator on tomato. In addition, the results suggest that *F. acarisuga* will show a strong aggregative response to TSSM prey. Even though the importance of predator aggregation is still in debate, it is still generally considered an important quality of natural enemies (Beddington *et al.*, 1978; Murdoch, 1990).

The results of this study (both search behaviour and TSSM density and distribution) will be used to estimate some of the biological parameters that are needed to construct a simulation model of *F. acarisuga* - TSSM population dynamics. This model may be able to predict population dynamics under different environmental circumstances and shed light on why *F. acarisuga* seems to work in some situations but not in others (D. Gillespie, personal communication, 1997). In addition, this model may suggest more efficient release methods, rates and locations and more efficient mass rearing programs of *F. acarisuga*.

REFERENCES

Akitsu Branch, Fruit Tree Research Station. 1992. *Bulletin of the Fruit Tree Research Station*. 22:109-130.

B.C. Ministry of Agriculture, Fisheries, and Food. 1996. *Greenhouse Vegetable Production Guide for Commercial Growers, 1996/97 edition* (J. Portree ed.). 120pp. B.C. Ministry of Agriculture, Fisheries and Food,Victoria.

B.C. Ministry of Agriculture, Fisheries, and Food. 1992. *Integrated Control of Greenhouse Pests* (R. A. Costello, D. P. Elliot and D. R. Gillespie eds.).19 pp. B.C. Ministry of Agriculture, Fisheries and Food,Victoria.

Beddington, J. R., C. A. Free and J. H. Lawton. 1978. Modeling biological control: on the characteristics of a successful natural enemy. *Nature* 273: 513-519.

Bell, W. J. 1990. Searching behaviour patterns in insects. *Annual Review of Entomology* 15: 9-16.

Benhamou, S. 1992. Efficiency of area-concentrated searching behaviour in a continuous patchy environment. *Journal of Theoretical Biology* 159: 67-81.

Carey, J. R. 1982. Within-plant distribution of tetranychid mites on cotton. *Environmental Entomology* 11:796-800.

Carter, M. C. and A. F. G. Dixon. 1982. Habitat quality and the foraging behaviour of coccinellid larvae. *Journal of Animal Ecology* 51: 865-878.

Chandler, A. E. F. 1969. Locomotory behaviour of first instar larvae of Aphidophagous syrphidae (Diptera) after contact with pea aphids. *Animal Behaviour* 17: 673-678.

Chandler, L. D. and S. M. Corcoran. 1981. Distribution densities of Tetranychus cinnabarinus on greenhouse-grown Codiaeum variegatum. *Environmental Entomology* 10: 721-723.

Charnov, E. L. 1976. Optimal foraging, the marginal value theorem. *Theoretical Population Biology* 9: 129-136.

Chiverton, P. A. 1988. Searching behaviour and cereal aphid consumption by Bembidion lampros and Pterostichus cupreus, in relation to temperature and prey density. *Entomologia Experimentalis et Applicata* 47:173-182.

Colombo, A., Campo, G. and M. Calabro. 1993. Controllo di Tetranychus urticae su banano in serra per mezzo di predatori. *Informatore Fitopatologico* 43(12): 56-61.

Eveleigh, E. S., and D. A. Chant 1982. The searching behaviour of two species of phytoseiid mites, Phytoselius persimilis Athias-Henriot and Amblyseius degenerans (Berlese), in relation to the density and distribution of prey in a homogenous area (Acarina: Phytoseiidae). *Canadian Journal of Zoology* 60:648-658.

Ferran, A., Ettifouri, M., Clement, P. and W. J. Bell.1985. Sources of variability in the transition from extensive to intensive search in Coccinellid Predators (Homoptera: Coccinellidae). *Journal of Insect Behaviour* 7(5): 633-647.

Farrar, R. R. Jr. and G. Kennedy. 1991. Insect and mite resistance in tomato. In *Monographs on theoretical and applied genetics: Genetic Improvement in tomato* (G. Kaloo ed.). pp 121-142. Springer-Verlag, Berlin.

Fromm, J. E. and W. J. Bell. 1987. Search orientation of *Musca domestica* in patches of sucrose drops.*Physiological Entomology* 12:297-307.

Gillespie, D. R. and D. J. M. Quiring. 1995. Rearing the predatory gall midge Feltiella acarisuga (Vallot) (Diptera: Cecidomyiidae). *Pacific Agriculture Research Centre.Technical Report* # 118.

Gillespie, D. R., D. M. J. Quiring, G. Opit and M. Greenwood. 1994. Biological control of twospotted spider mites on greenhouse tomato.*Pacific Agriculture Research Centre.Technical Report* # 105.

Gilstrap, F. E., K. R. Summy, L. D. Chandler, T. L. Archer and C. R. Ward. 1980. Within-plant distribution of Banks grass mite on corn in West Texas. *Environmental Entomology* 9:546-548

Harris, M. O. and J. R. Miller. 1982. Synergism of visual and chemical stimuli in the oviposition behaviour of Delia antiqua (Meigen) (Diptera: Anthomyiidae). *Proceedings of the 5th International Symposium on Insect-Plant Relationships*. Pudoc, Wageningen.

Hassell, M. P. and R. M. May. 1973. Stability in insect host-parasite models. *Journal of Animal Ecology* 52: 889-904.

Hassell, M. P. and T. R. E. Southwood. 1978. Foraging strategies of insects.*Annual Review of Ecological Systems* 9: 75-98.

Havukkala, I. and J. S. Kennedy. 1984. A program of self-steered turns as a humidity response in *Tenebrio*, and the problem of categorizing spatial maneuvers. *Physiological Entomology* 9:157-164

Hemptinne, J. L., A. F. G. Dixon and G. Lognay. 1996. Searching behaviour and mate recognition by males of the two-spot ladybird beetle, *Adalia bipunctata*.. *Ecological Entomology* 21: 165-170.

Hussey, N. W. and W. J. Parr.1963. Dispersal of the glasshouse red spider mite*Tetranychus urticae* Koch (Acarina: Tetranychidae). *Entomologia Experimentalis et Applicata* 6: 207-214.

International Organization for Biological Control/Western Palearctic Regional Section. 1983. Proceedings of the Meeting of the Work Group on Integrated Control in Glasshouses. *Bulletin IOBC/WPRS* VI/3, Darmstadt.

Ives, A. R. , Kareiva, P. and R. Perry. 1993. Response of a predator to variation in prey density at three hierarchical scales: lady beetles feeding on aphids. *Ecology* 74(7): 1929-1938.

Jander, R. 1975. Ecological aspects of spatial orientation. *Annual Review of Ecologycal Systems*. 6: 171-188.

Jones, V. P. 1990. Developing sampling plans for spider mites (Acari; Tetranychidae): Those who don't remember the past may have to repeat it. *Journal of Economic Entomology* 83(5): 1656-1664.

Kareiva, P. and G. Odell. 1987. Swarms of predators exhibit 'preytaxis' if individual predators use area-restricted search. *American Naturalist* 130: 233-270.

Kasak, C. W. C. Wyatt and L. C. Wright. 1995. The vertical distribution of mites and aphids on hops in southcentral Washington during the summer of 1993. *Journal of the Entomological Society of British Columbia* 92: 91-95.

Li, C. 1993. The foraging behaviour of a parasitoid wasp, *Aphelinus asychis*: a modeling approach. *PhD thesis.* Simon Fraser University, Burnaby.

Mangel, M. 1994. Spatial patterning in resource exploitation and conservation. Philosophical Transactions of the Royal Society of London B 343: 93-98.

McCoy, M. M. 1984. Antennal movements of the American cockroach *Periplaneta americana*. *PhD thesis.* University of Kansas, Lawrence.

McKinley R. G., A. M. Spaul and R. W. Straub. 1992. Pests of Solanaceous Crops. In *Vegetable Crop Pests* (R. G. McKinlay ed.).MacMillan Press Ltd, London.

Morishita, M., S. Yano and K. Azuma. 1994. Seasonal incidence of tetranychid mites, the cotton aphid, *Aphis gossypi* Glover and their predators. *Proceedings of the Kansai Plant Protection Society* 36: 7-11.

Murdoch, W. W. 1990.The relevance of pest-enemy models to biological control. In *Critical Issues in Biological Control* (M. Mackauer, L. E. Ehler and J. Roland eds.). pp 1-24. Intercept, Andover.

Murdoch, W. W. and A. Oaten. 1975. Predation and population stability. *Advances in Ecological Research* 9: 1-131.

Murdoch, W. W. and A. Stewart-Oaten. 1989. Aggregation by parasitoids and predators: effects on equilibrium and stability. 134: 288-310. *American Naturalist* 134: 288-310.

Nakamuta, K. 1985. Mechanism of the switchover from extensive to area concentrated search behaviour of the ladybird beetle *Coccinella septempunctata bruckii. Journal of Insect Physiology* 31: 849-856.

Nihoul, P. 1993. Asynchronous populations of Phytoselius persimilis Athias-Henriot and effective control of Tetranychus urticae Koch on tomatoes under glass. *Journal of HorticulturalScience* 68(4): 581-588.

Oatman, E. R. 1985. *Aphanogmus floridanus*, a primary parasite of *Feltiella acarivora*, a predator of spider mites on strawberry (Hymenoptera: Ceraphronidae; Diptera; Cecidomyiidae). *Proceedings of the Entomological Society of Washington* 87(4): 714-716.

Opit, G. 1995. Predation of two-spotted spider mites, *Tetranychus urticae* Koch (Acari: Tetranychidae) by the predatory midge, *Feltiella minuta* Felt (Diptera: Cecidomyiidae). *PhD thesis*. Simon Fraser University, Burnaby.

Opit, G. P., B. Roitberg and D. R. Gillespie. 1997. The functional response and prey preference of *Feltiella acarisuga* (Vallot) (Diptera: Cecidomyiidae) for two of its prey: male and female two-spotted spider mites, *Tetranychus urticae* Koch (Acari: Tetranychidae). *The Canadian Entomologist* 129: 221-227.

Perring, T. M., C. A. Farrar and R. N. Royalty. 1987. Intraplant distribution and sampling of spider mites (Acari: Tetranychidae) on cantalope. *Journal of Economic Entomolgy* 80: 96-101

Ravensburg, W. J., J. C. van Lenteren and J. Woets. 1982. Developments in application of biological control in greenhouse vegetables in the Netherlands since 1970. *International Organization for Biological Control, West Palearctic Regional Section Bulletin* VI/3: 36-48.

Roberti, D. 1954. I simbionti degli acari fitofagi. I. *Therodiplosis persicae* Kieffer. *Bollettino del Laboratorio di Entomologia Agraria "Filippo Slivestri"* 13: 285-301.

Roitberg, B. D., J. C. van Lenteren, J. J. M. van Alphen, F. Galis and R. J. Prokopy 1982. Foraging behaviour of *Rhagoletis pomonella*, a parasite of Hawthorn (*Crataegus viridis*) in nature. *Journal of Animal Ecology* 51: 307-325.

Schmitz, B., H. Scharstein and G. Wendler. 1982. Phonotaxis in Grillus campstris L. (Orthoptera: Gryllidae) I. Mechanism of acoustic orientation in intact female crickets. *Journal of Comparitive Physiology* 148: 431-444.

Shaddick, C. 1995. Midge versus mite. *Grower* 9/3/95: 13-17.

Shonouda, M. L. 1996. Crude aqueous extract (kairomone) from *Aphis fabae* Scop. (Hom., Aphidae) and its effect on the behaviour of the predator *Metasyrphus corollae* Fabr. (Dipt., Syrphidae) female. *Journal of Applied Entomology* 120: 489-492.

van Lenteren, J, C. and J. Woets. 1988. Biological and integrated control in greenhouses. *Annual Review of Entomology* 33: 239-269.

Vinson, S. B. 1977. Behavioural chemicals in the augmentation of natural enemies. In *Biological Control by Augmentation of Natural Enemies.* (R. L. Ridgeway, S. B. Vinson eds.). pp 237-239. Plenum, New York.

Waage, J. K. 1979. Foraging for patchily-distributed hosts by the parasitoid *Nemeritis canescens*. *Journal of Animal Ecology* 48: 353-371.

Zhang, Z. and J. P. Sanderson 1995. Two-spotted spider mite (Acari: Tetranychidae) and *Phytoselius persimilis* (Acari: Phytoseiidae) on greenhouse roses: spatial distribution and predator efficiency. Journal of Economic Entomology 88(2): 352-357.

Table 1 a. Summary of search behaviour of *F. acarisuga* results at high and low prey (*T. urticae* eggs) density. Ten trials at both prey densities were performed. Leaf area,rearing group and taping time were kept consistent for trials at both prey densities. Residence time and number of feeds at the two prey densities are shown.

	Prey Density eggs/cm²	Travel Time sec	Distance Travelled mm	Turns #	Speed mm/sec	Turning Rate #/mm
	5	870	109.4	23	0.126	0.210
	5	1950	175.2	55	0.090	0.314
	5	1230	136.6	17	0.111	0.124
	5	780	95.4	15	0.122	0.157
	5	1110	81.6	18	0.073	0.221
	5	1410	173.2	34	0.123	0.196
	5	810	83.8	21	0.103	0.251
	5	780	86.4	10	0.111	0.116
	5	1620	148.4	18	0.092	0.121
	5	420	47.2	9	0.112	0.191
Mean			113.0		0.106	0.190
SD			42.8		0.017	0.063
	10	3120	204.2	80	0.065	0.392
	10	3450	228.0	91	0.066	0.399
	10	5130	494.6	161	0.096	0.325
	10	3690	304.4	109	0.082	0.358
	10	4260	364.8	143	0.086	0.392
	10	2880	209.6	72	0.072	0.343
	10	4950	306.4	134	0.062	0.437
	10	4350	342.2	136	0.079	0.397
	10	3690	220.4	83	0.060	0.377
	10	3000	188.6	71	0.062	0.376
Mean			286.3		0.073	0.38
SD			96.2		0.012	0.032

Table 1 b. Summary of search behaviour of *F. acarisuga* results at high and low prey (*T. urticae* eggs) density. Ten trials at both prey densities were performed. Travel time, distance traveled, number of turns, speed and turning rate at both prey densities are shown.

	Prey Density eggs/cm²	Leaf Area cm²	Group A/B	Taping Time AM/PM	Residence Time sec	Feeds #
	5	14.8	B	AM	1470	1
	5	15.5	A	PM	3000	3
	5	13.0	A	PM	1230	0
	5	16.5	B	AM	780	0
	5	16.5	A	AM	1110	0
	5	13.8	B	PM	1410	0
	5	13.5	A	PM	960	1
	5	15.0	B	AM	780	0
	5	14.5	A	AM	1620	0
	5	16.0	B	PM	420	0
Mean		14.9			1278	0.5
SD		1.2			707	0.97
	10	14.0	A	PM	7200	10
	10	16.5	B	AM	7200	8
	10	13.5	A	AM	7200	5
	10	15.0	B	PM	7200	11
	10	15.5	A	PM	7200	12
	10	14.0	B	AM	7200	12
	10	14.8	A	AM	7200	12
	10	14.8	B	PM	7200	6
	10	14.5	A	PM	7200	7
	10	14.5	B	AM	7200	12
Mean		14.7			7200	9.5
SD		0.9			0	2.75

Table 2. Speeds and turning rates of *F. acarisuga* 2 min before and 2 min after a feeding episode (on *T. urticae* eggs). Only 6 episodes could be used to make valid independent comparisons.

Trial #, Feed #	Pre-feed Speed (mm/sec)	Post-feed Speed (mm/sec)	Pre-feed Turning rate (# turns/mm)	Post-feed Turning rate (# turns/mm)
3,2	0.068	0.045	0.400	0.555
4,3	0.190	0.080	0.175	0.208
5,2	0.183	0.083	0.272	0.600
7,9	0.062	0.025	0.270	1.000
8,2	0.075	0.042	0.111	0.667
9,4	0.102	0.050	0.327	0.500
Mean	0.113	0.054	0.259	0.588
SD	0.058	0.022	0.104	0.257

Table 3 a. Densities, variances and variance to mean ratios (aggregation indices) of *T. urticae* eggs on tomato leaflets in a commercial greenhouse. Two samples were taken from the top three strata of four plants.

Mobiles

Plant	Stratum	Density #/0.25cm²	Variance	Variance/ Mean
1	1	0.264	0.263	0.997
	1	1.000	1.309	1.309
	2	0.414	0.381	0.919
	2	0.421	0.594	1.410
	3	0.266	0.248	0.934
	3	0.230	0.230	0.998
2	1	0.169	0.354	2.098
	1	0.478	0.638	1.334
	2	0.254	0.358	1.413
	2	0.252	0.222	0.881
	3	0.252	0.291	1.158
	3	0.188	0.243	1.292
3	1	0.160	0.201	1.256
	1	0.188	0.200	1.063
	2	0.145	0.171	1.179
	2	0.142	0.159	1.127
	3	0.123	0.190	1.544
	3	0.347	0.447	1.291
4	1	0.338	0.343	1.031
	1	0.186	0.155	0.834
	2	0.323	0.373	1.155
	2	0.585	0.884	1.51
	3	0.36	0.384	1.067
	3	0.447	0.632	1.413
Mean		0.314	0.386	1.217
SD		0.189	0.268	0.275

Table 3 b. Densities, variances and variance to mean ratios (aggregation indices) of *T. urticae* mobile stages (adults and juveniles) on tomato leaflets in a commercial greenhouse. Two samples were taken from the top three strata of four plants.

Immobiles

Plant	Stratum	Density #/0.25cm²	Variance	Variance/ Mean
1	1	1.231	2.424	1.969
	1	2.582	13.443	5.206
	2	1.897	3.679	1.939
	2	2.317	7.350	3.172
	3	0.646	1.202	1.860
	3	0.461	0.538	1.168
2	1	1.242	4.183	3.369
	1	0.731	1.570	2.146
	2	2.282	13.160	5.767
	2	4.336	32.274	7.442
	3	0.412	0.618	1.499
	3	1.295	3.815	2.945
3	1	0.244	0.386	1.581
	1	1.129	1.972	1.746
	2	0.702	2.460	3.504
	2	0.821	1.468	1.788
	3	0.822	1.955	2.378
	3	0.165	0.280	1.696
4	1	1.406	2.332	1.658
	1	1.209	1.55	1.282
	2	0.946	1.334	1.41
	2	1.186	1.922	1.619
	3	1.717	3.108	1.81
	3	0.377	0.69	1.831
Mean		1.257	4.321	2.533
SD		0.929	6.906	1.566

Table 4. Mean density of *T. urticae* eggs and mobile stages (adults and juveniles) on tomato leaflets in a commercial greenhouse. Mean density of eggs and immobiles within each plant and within each stratum are shown.

	Mean Density (#/0.25cm²)		
	Immobile stages Mean (SD), N	Mobile stages Mean (SD), N	Combined Mean (SD), N
Plant			
1	1.522 (0.880) ,6	0.433 (0.290), 6	0.977 (0.845), 12
2	1.716 (1.432), 6	0.266 (0.110), 6	0.991 (1.230), 12
3	0.647 (0.372), 6	0.184 (0.083), 6	0.416 (0.353), 12
4	1.140 (0.434), 6	0.373 (0.134), 6	0.757 (0.512), 12
Stratum			
1	1.222 (0.604), 8	0.348 (0.285), 8	0.785 (0.669), 16
2	1.811 (1.208), 8	0.317 (0.151), 8	1.064 (1.134), 16
3	0.737 (0.525), 8	0.277 (0.104), 8	0.507 (0.406), 16

Figure 1. Video camera set-up used to observe and measure aspects of the search behaviour of *F. acarisuga* larvae for prey (*T. urticae* eggs) at high and low prey density (not to scale).

LEGEND

a . Petri dish with experimental arena

b. Video camera

c. VCR

d. Monitor

e. Grid with larva

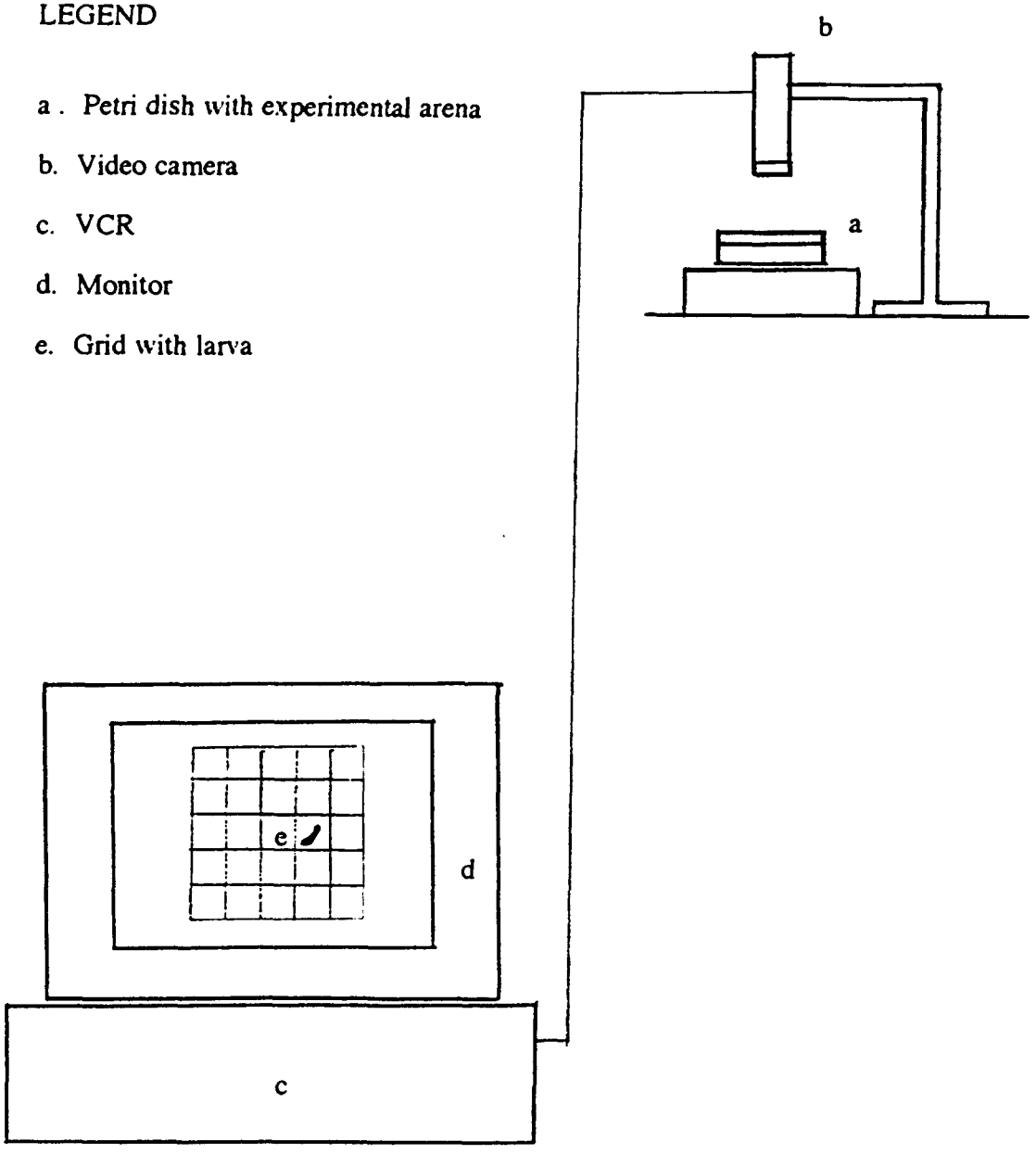


Figure 2 a. Distance travelled by *F. acarisuga* larvae at high and low prey (*T. urticae* eggs) density. The difference was significant ($p<0.001$, N=10).

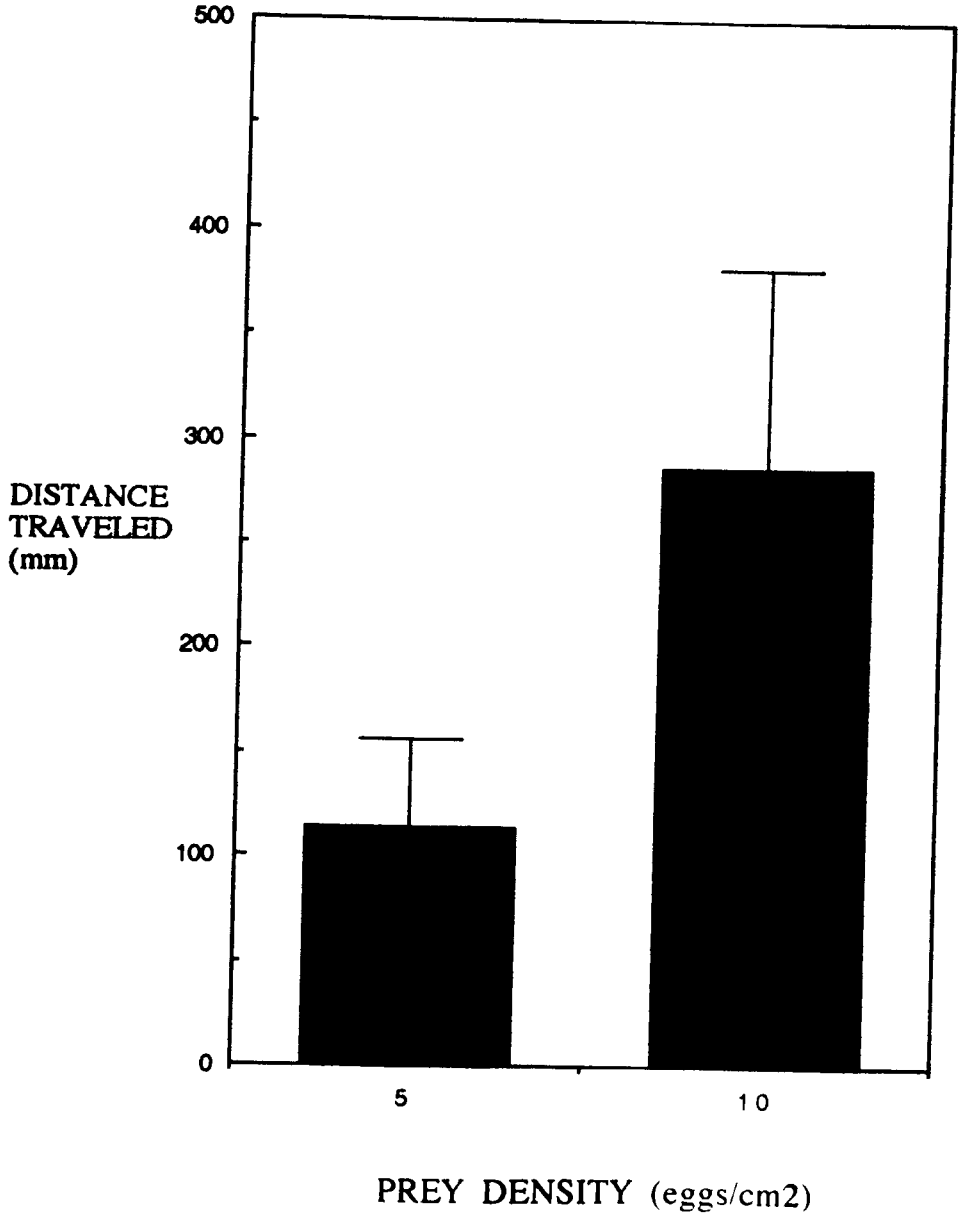

500
400
300
200
100
0
DISTANCE TRAVELED (mm)
5
10
PREY DENSITY (eggs/cm2)

Figure 2 b. Residence time of *F. acarisuga* larvae at high and low prey (*T. urticae* eggs) density. The difference was significant ($p<0.001$, N=10).

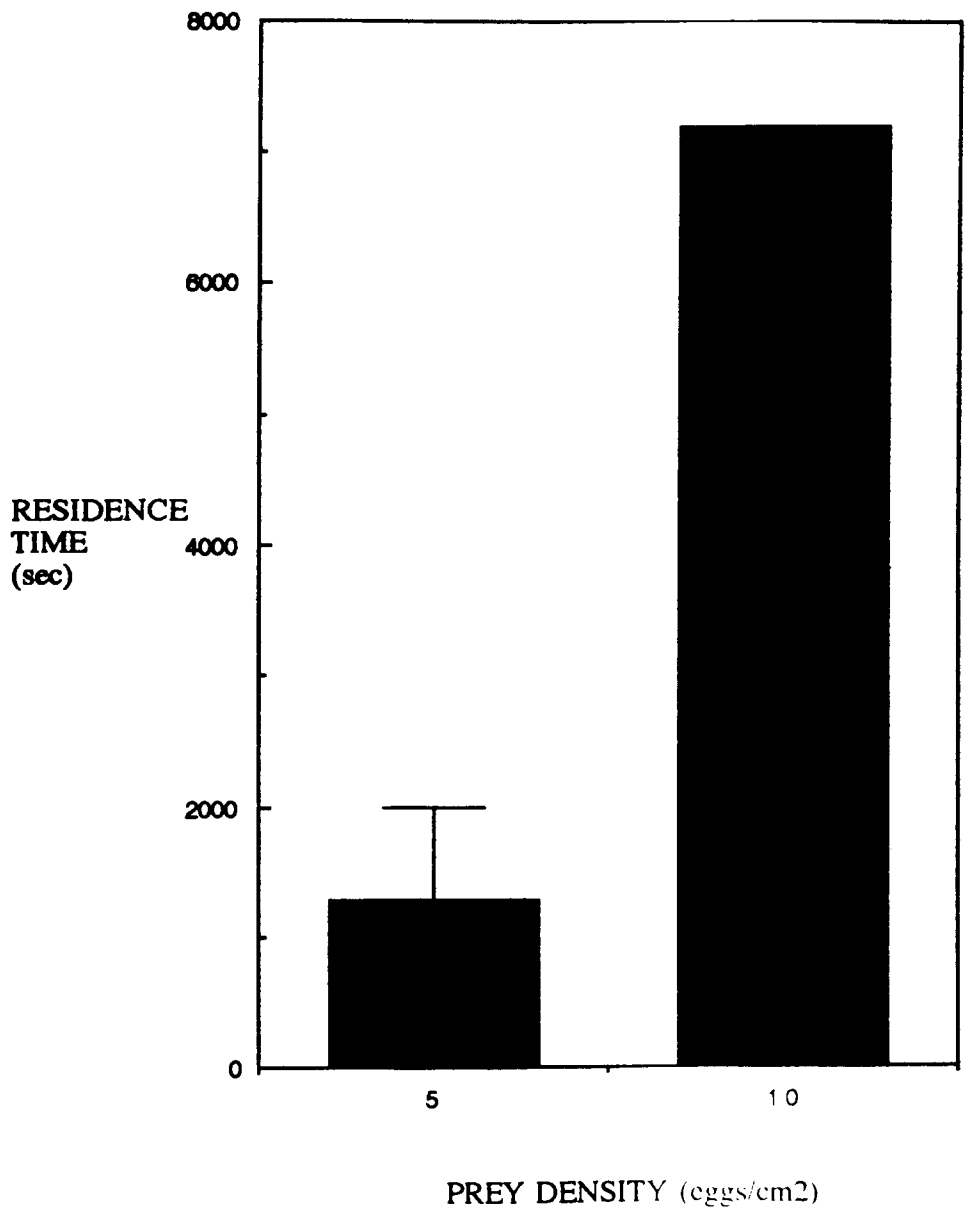

8000
6000
4000
2000
0
RESIDENCE TIME (sec)
5
10
PREY DENSITY (eggs/cm2)

Figure 2 c. Number of feeding episodes of *F. acarisuga* larvae at high and low prey (*T. urticae* eggs) density. The difference was significant ($p<0.001$, N=10).

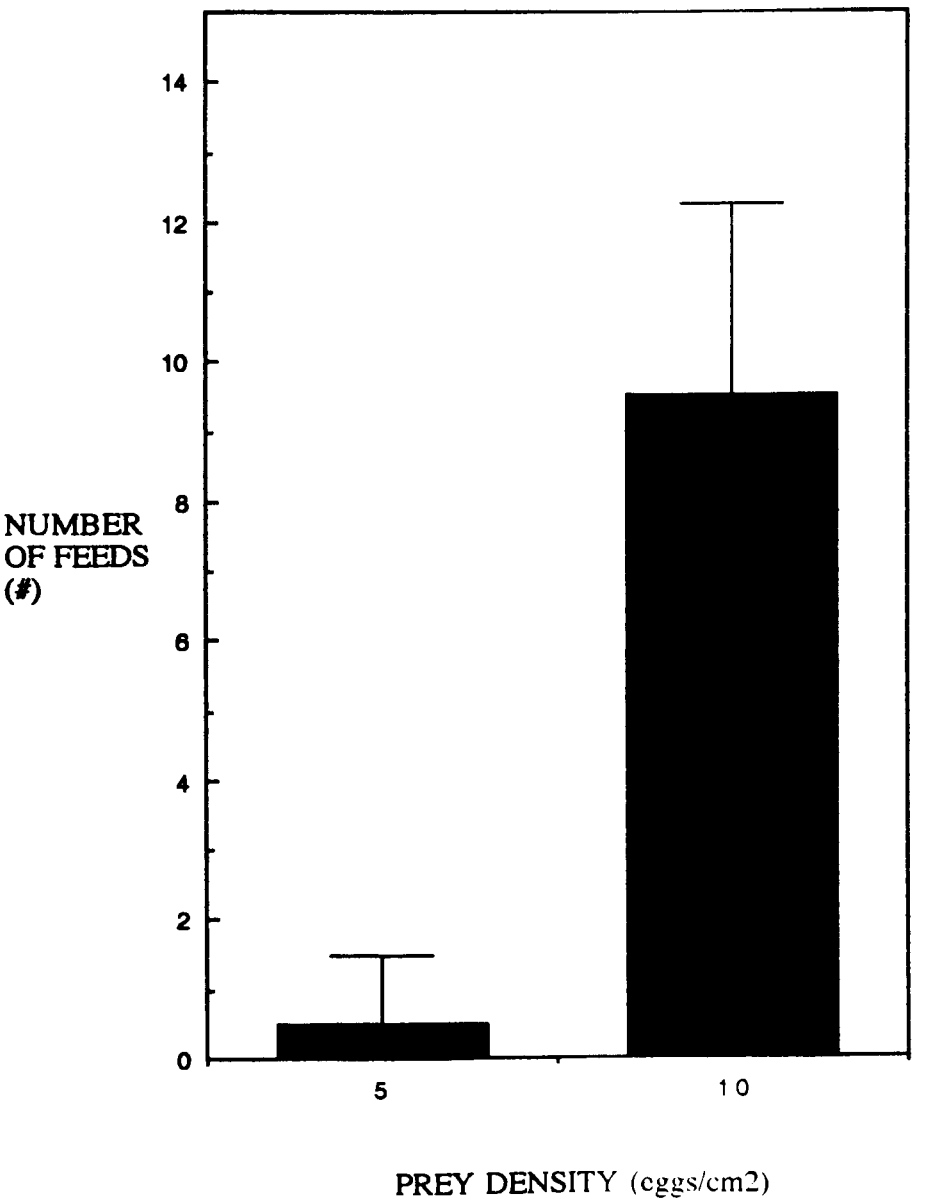

14
12
10
8
6
4
2
0
NUMBER OF FEEDS (#)
5
10
PREY DENSITY (eggs/cm2)

Figure 2 d. Mean speed of *F. acarisuga* larvae at high and low prey (*T. urticae* eggs) density. The difference was significant ($p<0.001$, N=10).

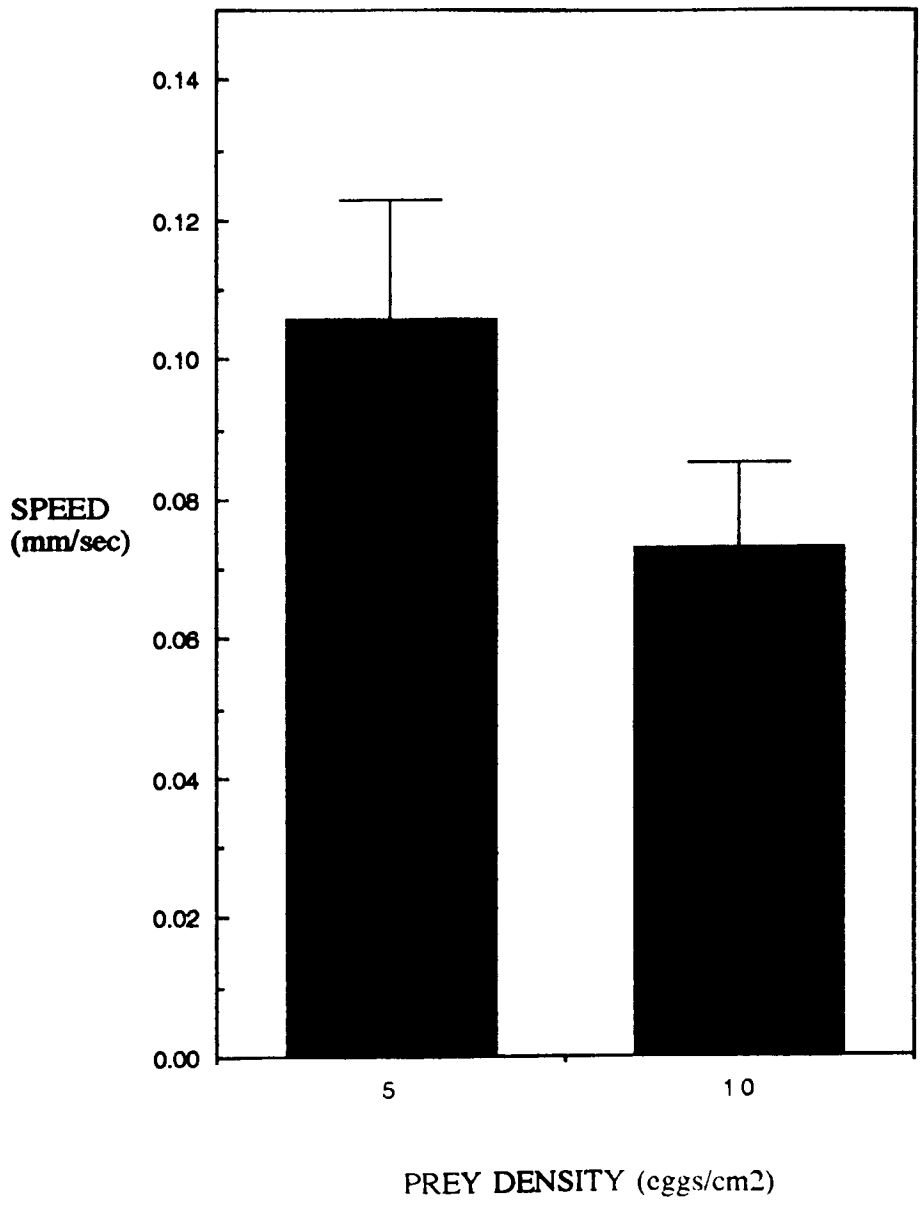

0.14
0.12
0.10
0.08
0.06
0.04
0.02
0.00
SPEED
(mm/sec)
5
10
PREY DENSITY (eggs/cm2)

Figure 2 e. Mean turning rate of *F. acarisuga* larvae at high and low prey (*T. urticae* eggs) density. The difference was significant ($p<0.001$, N=10).

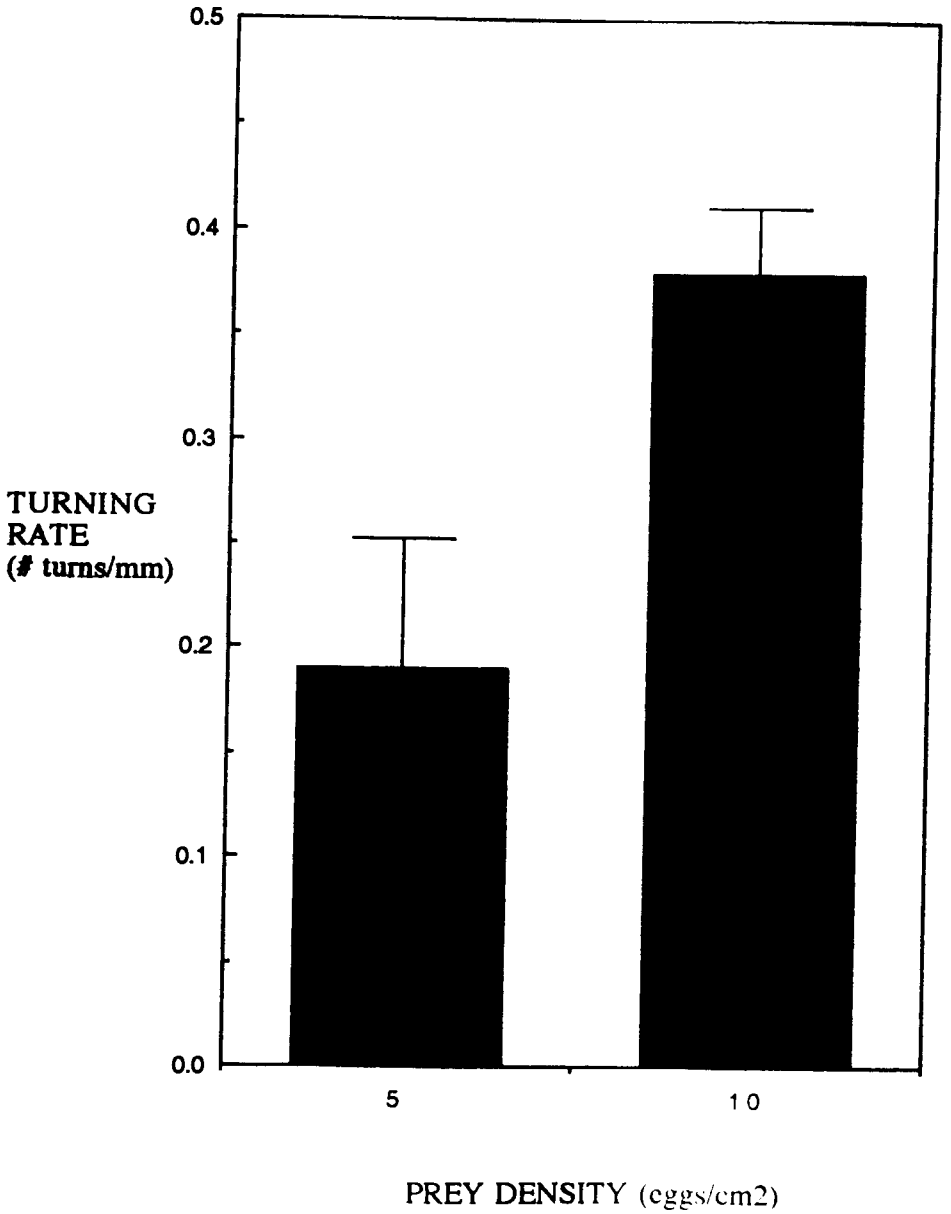
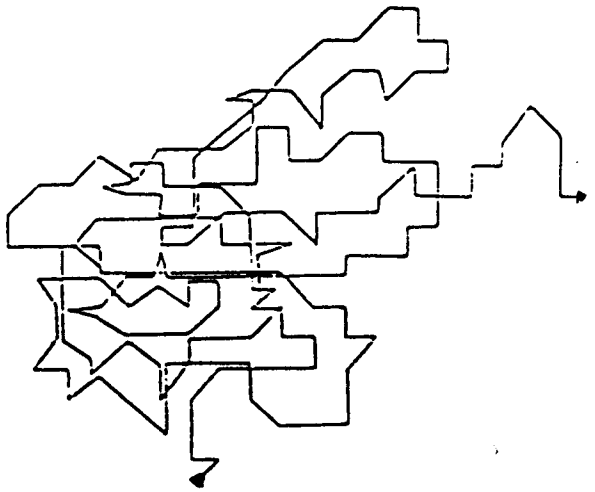

0.5
0.4
0.3
0.2
0.1
0.0
TURNING
RATE
(# turns/mm)
5
10
PREY DENSITY (eggs/cm2)

Figure 3. Representative samples of search paths of *F. acarisuga* larvae for prey (*T. urticae* eggs) at high (a) and low (b) prey density (not to scale).

a



b

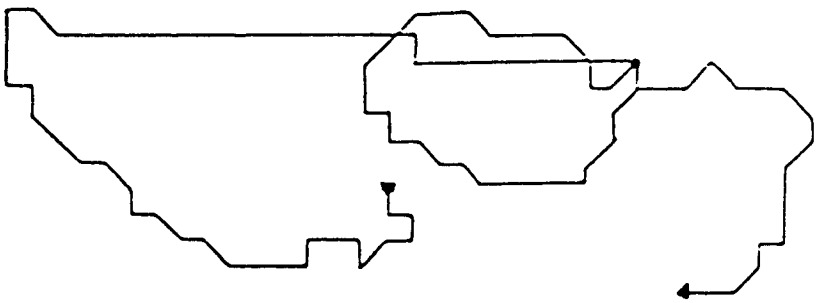


Figure 4 a. Speed of *F. acarisuga* larvae 2 min before and 2 min after a feeding episode (on *T. urticae* eggs). The difference was significant (p=0.016, N=6).

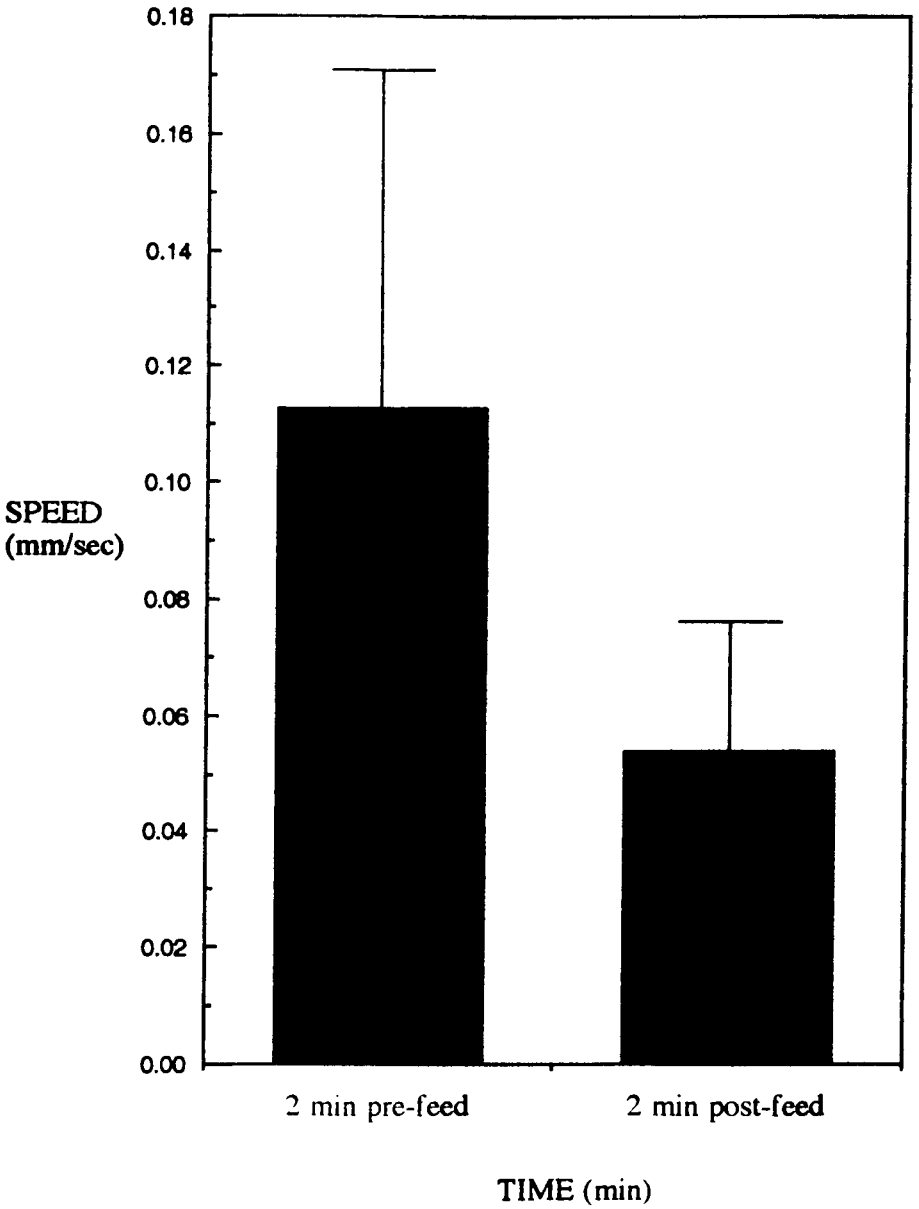

0.18
0.16
0.14
0.12
0.10
0.08
0.06
0.04
0.02
0.00
SPEED
(mm/sec)
2 min pre-feed
2 min post-feed
TIME (min)

Figure 4 b. Turning rate of *F. acarisuga* larvae 2 min before and 2 min after a feeding episode (on *T. urticae* eggs). The difference was significant (p=0.016, N=6).

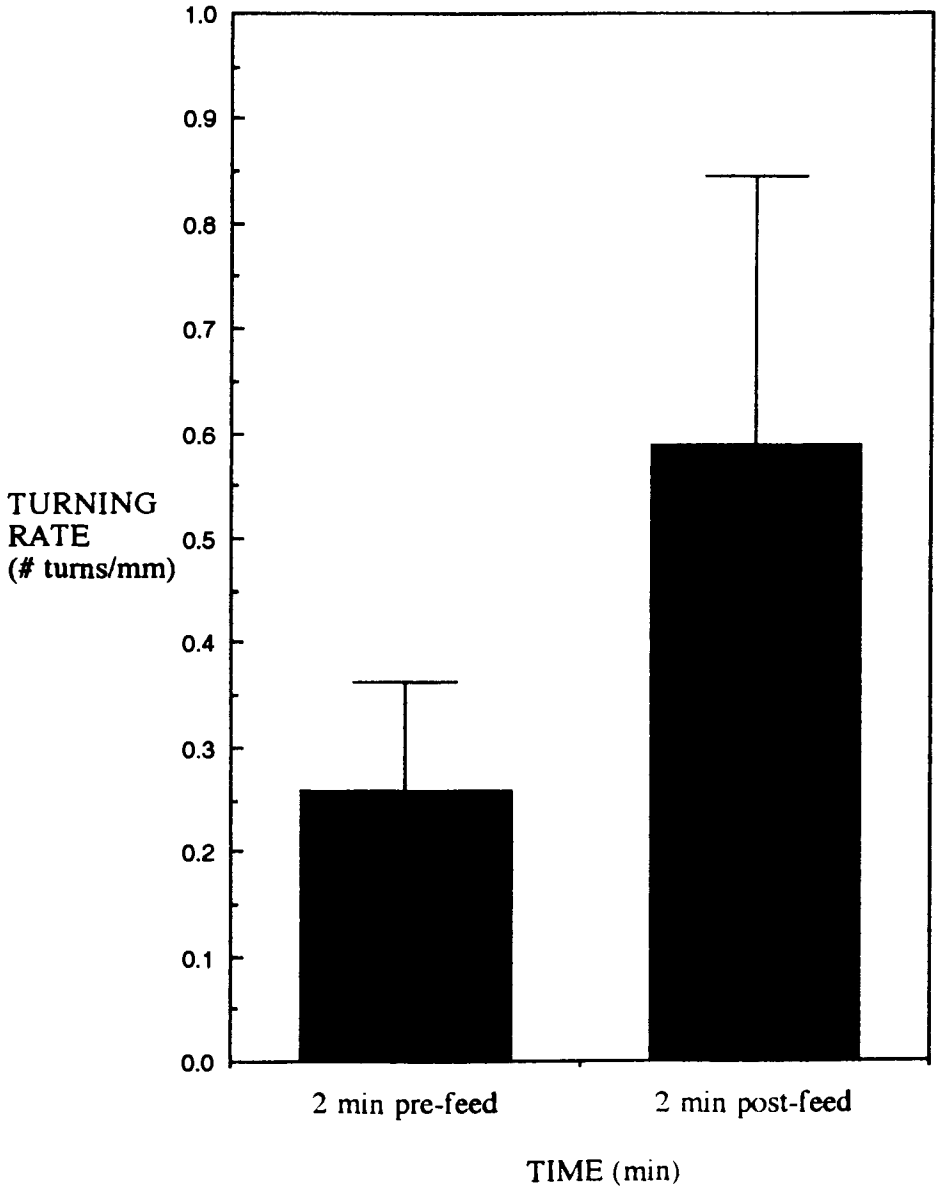
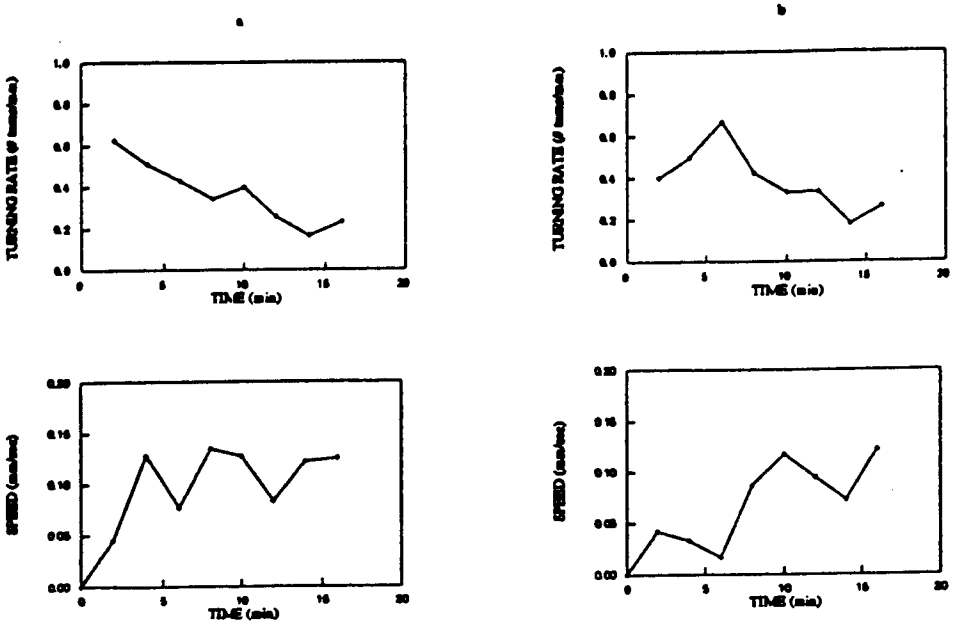

1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
TURNING RATE (# turns/mm)
2 min pre-feed
2 min post-feed
TIME (min)

Figure 5. Gradual change in speed and turning rate of *F. acarisuga* following a feeding episode (on *T. urticae* eggs). Only after four episodes did larvae search longer than 15 min before finding another prey item. These episodes are shown (a,b,c and d) Both speed and turning rate change gradually and return to pre-feeding levels after 15 min.


a
b
TURNING RATE (# transitions)
SPEED (cm/sec)
TIME (min)

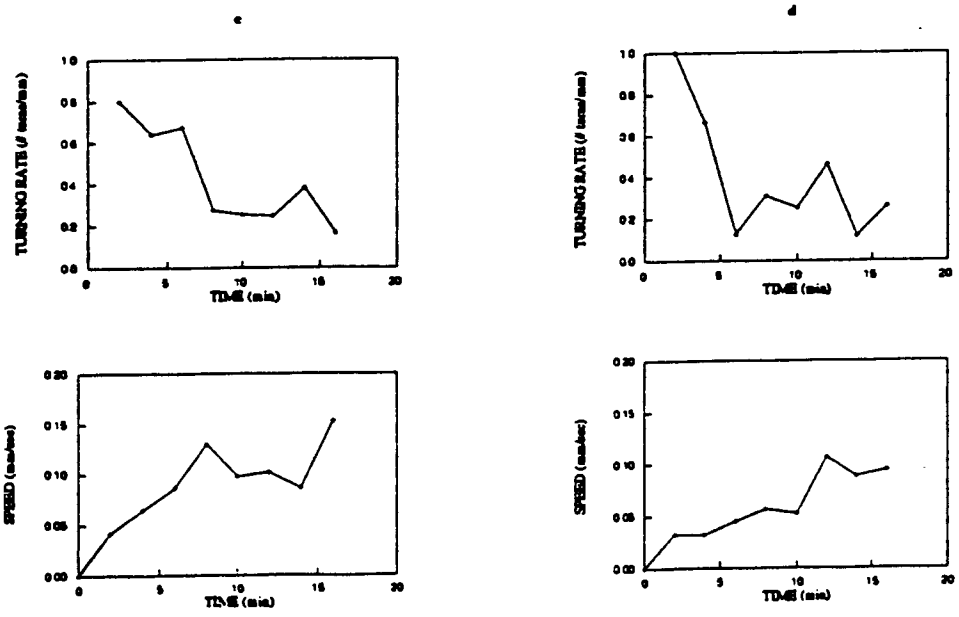
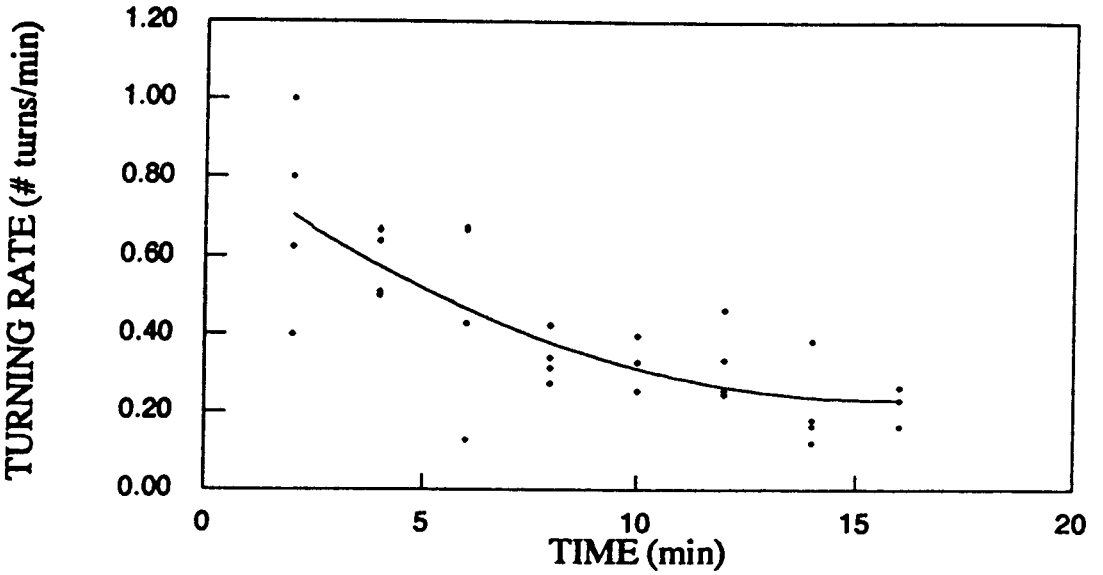

c
d
TURNING RATE (# transitions)
SPEED (cm/sec)
TIME (min)

Figure 6. Polynomial equations describing the gradual changes in speed and turning rate of *F. acarisuga* after feeding on a *T. urticae* egg. Turning rate (a) decreases gradually and is best described by the equation: $Y = 0.85 - 0.08*x + 0.0026*x^2$ ($R^2 = 0.6$, $p<0.02$, N=4). Speed (b) increases gradually and is best described by the equation: $Y = 0.025 + 0.0093*x - 0.00024*x^2$ ($R^2=0.42$, $p<0.05$, N=4).

a


TURNING RATE (# turns/min)
1.20
1.00
0.80
0.60
0.40
0.20
0.00
0
5
10
15
20
TIME (min)

b

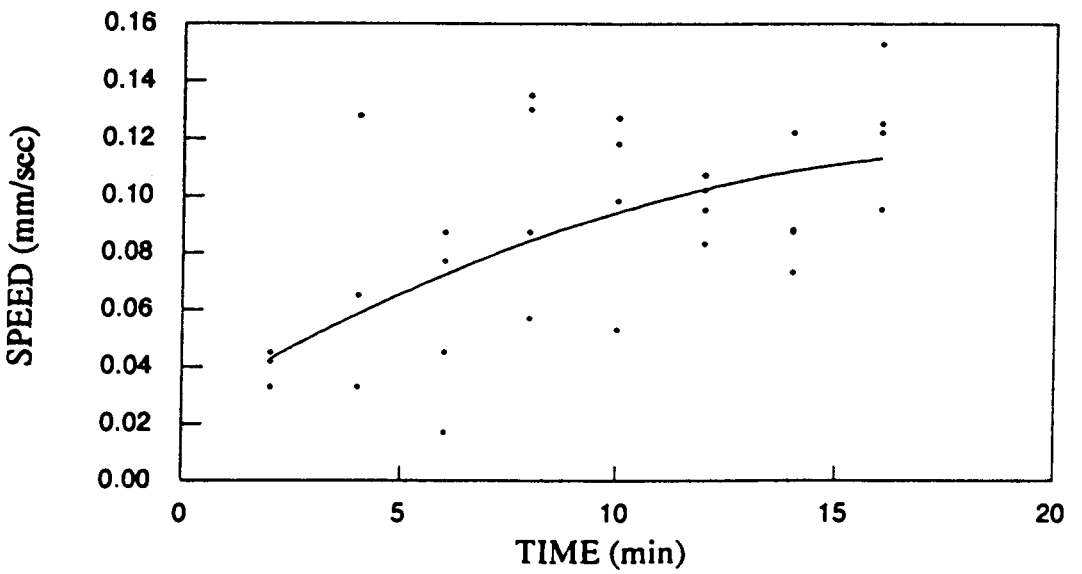

SPEED (mm/scc)
0.16
0.14
0.12
0.10
0.08
0.06
0.04
0.02
0.00
0
5
10
15
20
TIME (min)

Figure 7. Two representative samples (actual size) showing the distribution of *T. urticae* on tomato leaflets within a commercial greenhouse. The number in the top right corner of each $0.25cm^2$ cell refers to the number of mobile (adult and juvenile) *T. urticae* within the cell, while the number in the bottom left corner refers to the number of immobile (eggs) *T. urticae* within the cell.

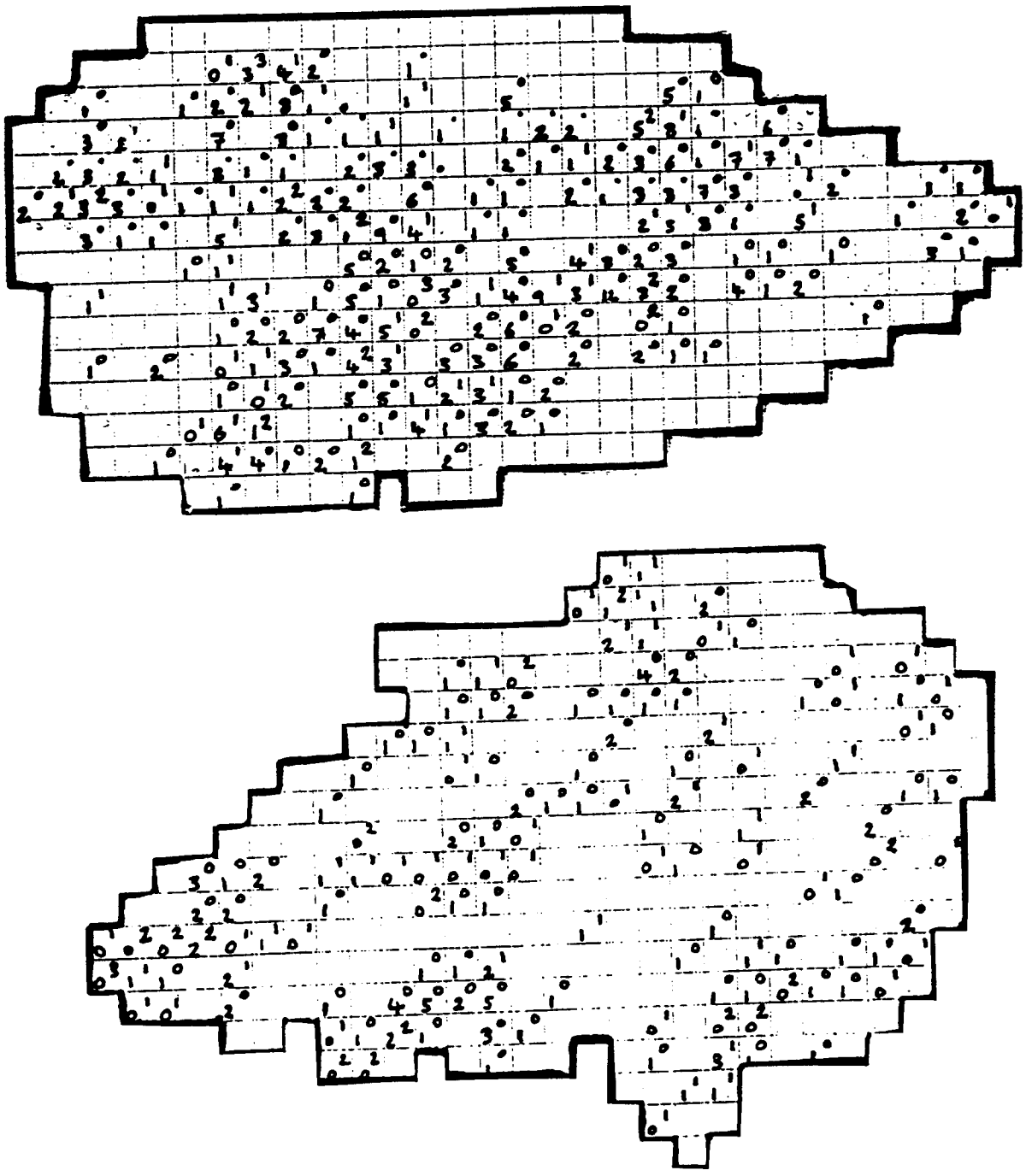


Figure 8. Plot of mean density vs. variance of *T. urticae* eggs on tomato leaflets within a commercial greenhouse. A slope of 6.81 was found meaning that the eggs are very aggregated at the within-leaflet level (Taylor's power law; Taylor, 1961).

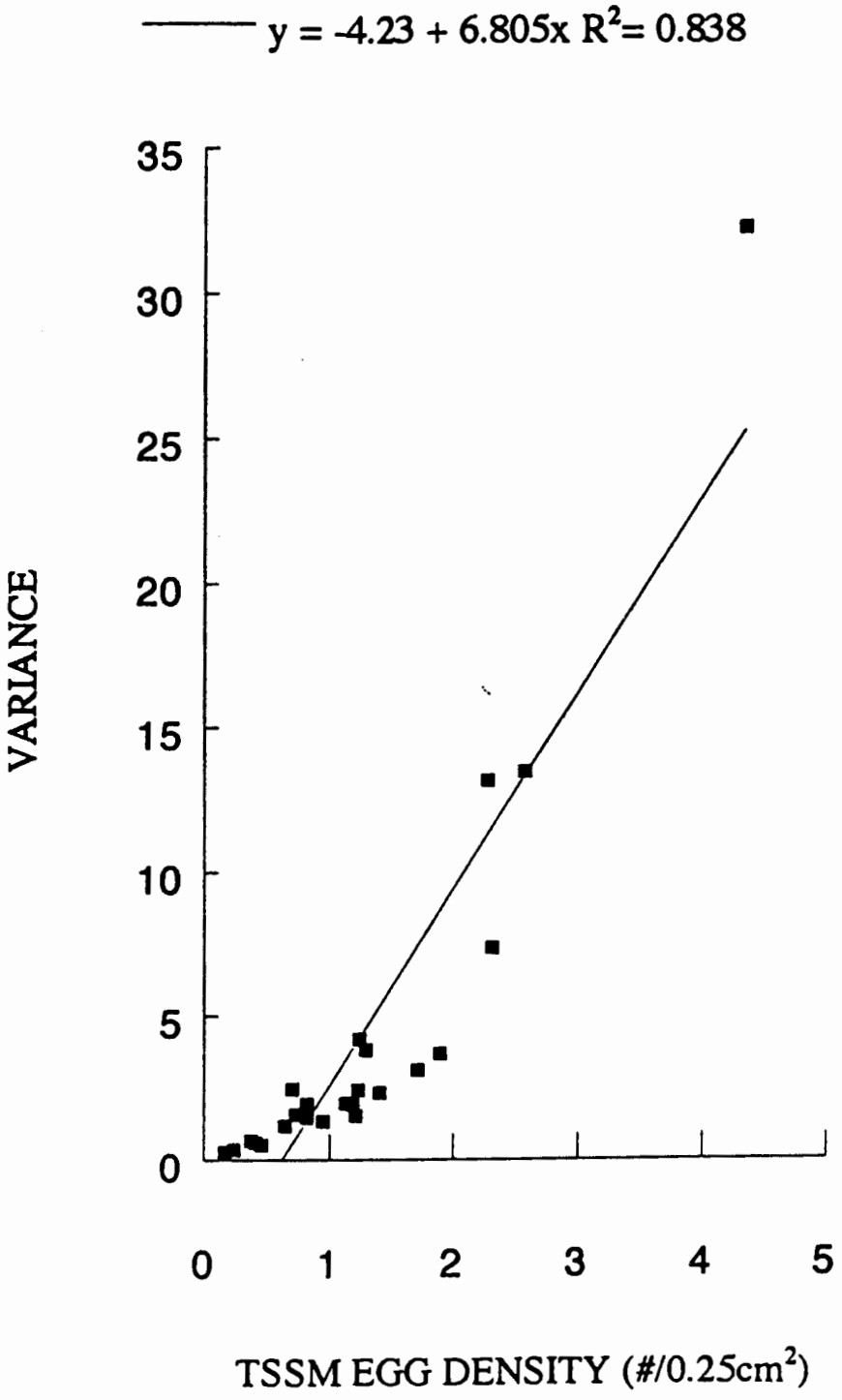

y = -4.23 + 6.805x R²= 0.838
VARIANCE
35
30
25
20
15
10
5
0
0
1
2
3
4
5
TSSM EGG DENSITY (#/0.25cm²)

Figure 9. Plot of mean density vs. variance of *T. urticae* mobile stages (adults and juveniles) on tomato leaflets within a commercial greenhouse. A slope of 1.37 was found meaning that adults and juveniles are slightly aggregated at the within-leaflet level (Taylor's power law; Taylor, 1961).

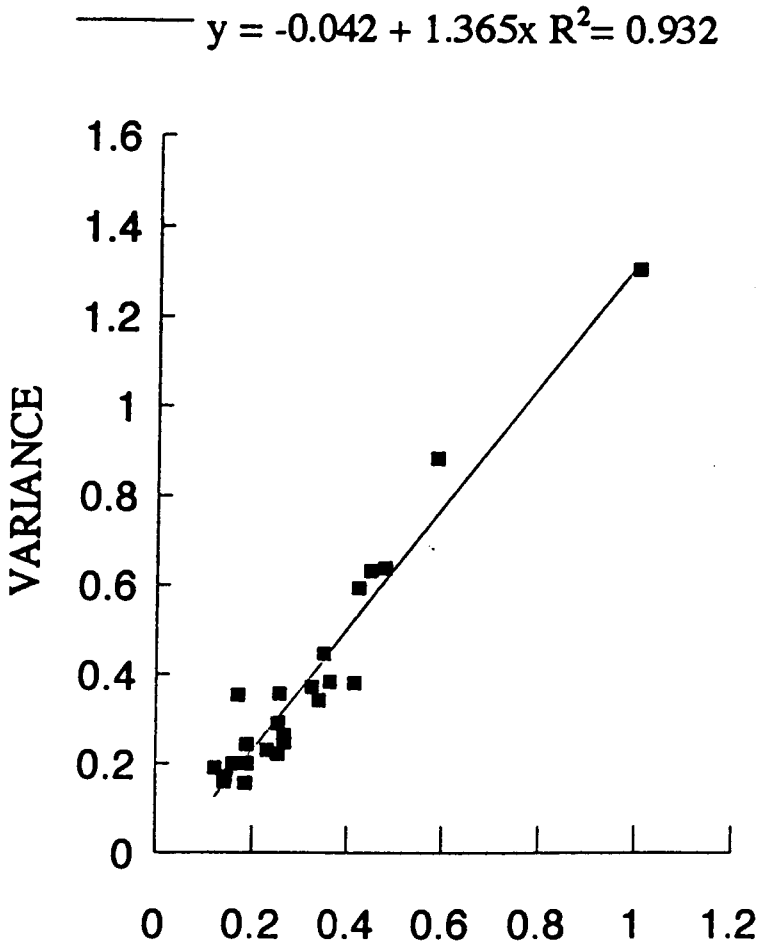

y = -0.042 + 1.365x R²= 0.932
VARIANCE
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
0 0.2 0.4 0.6 0.8 1 1.2
TSSM MOBILE STAGES DENSITY (#/0.25cm²)

Figure 10. Plot of mean density vs. agregation index of *T. urticae* eggs on tomato leaflets within a commercial greenhouse. Aggregation increases with mean density at the within-leaflet level (R^2=0.667, $p<0.001$).

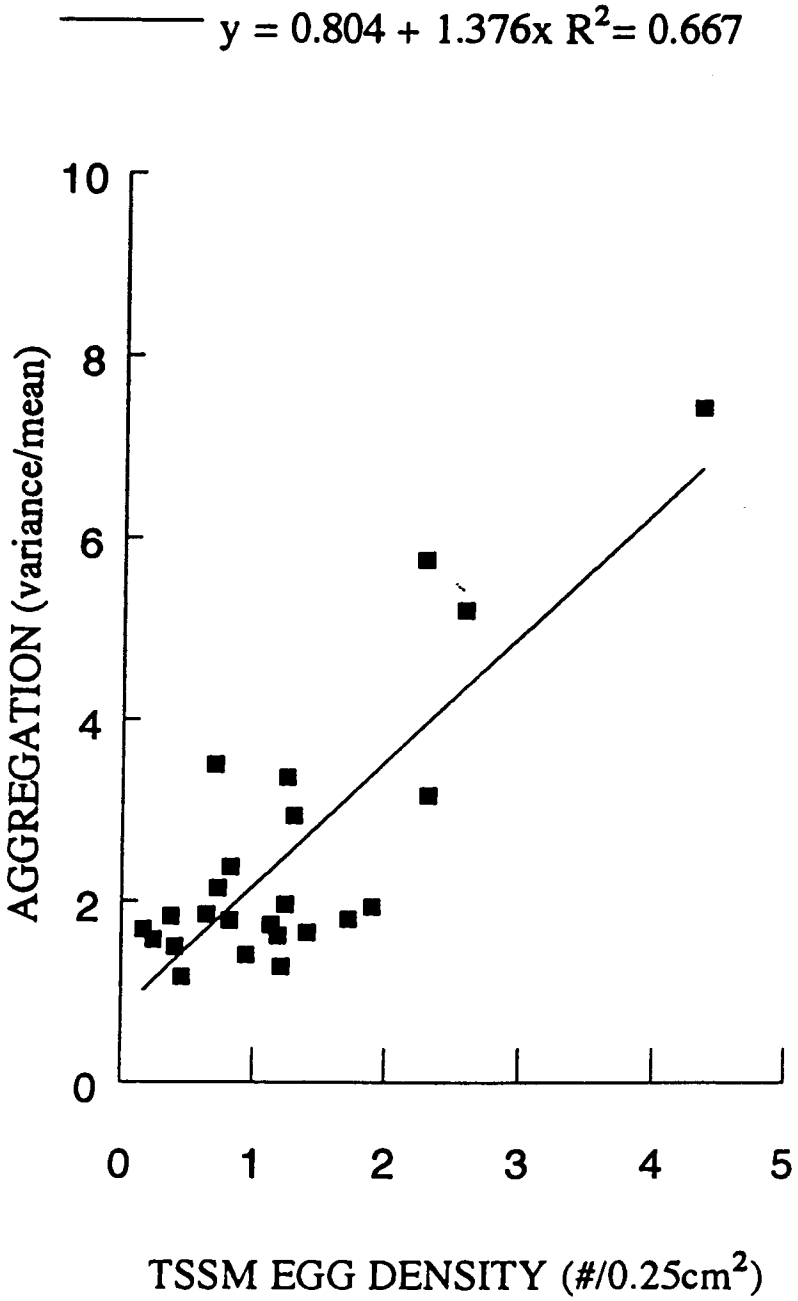
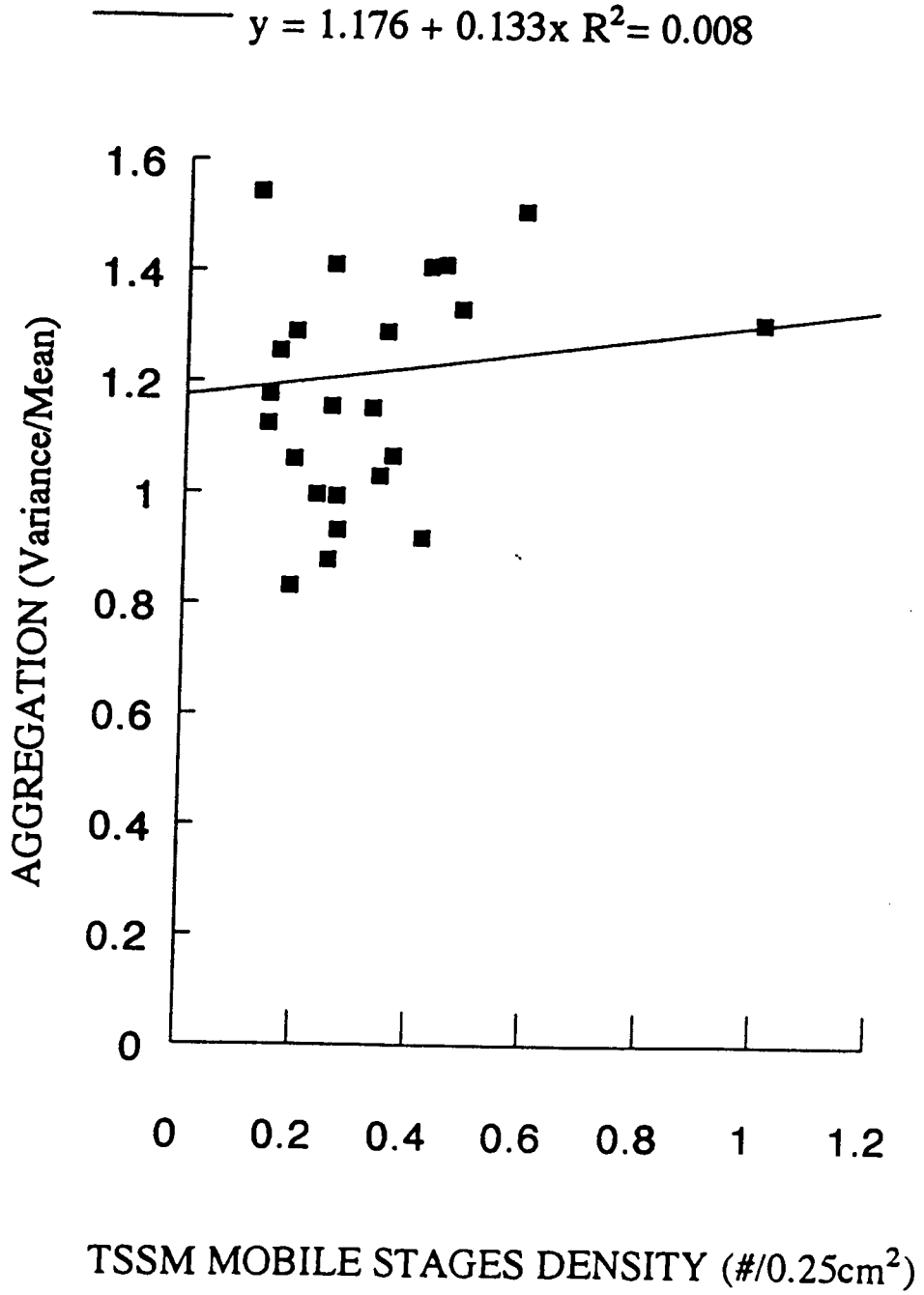

y = 0.804 + 1.376x R²= 0.667
AGGREGATION (variance/mean)
10
8
6
4
2
0
0
1
2
3
4
5
TSSM EGG DENSITY (#/0.25cm²)

Figure 11. Plot of mean density vs. agregation index of *T. urticae* e mobile stages (adults and juveniles) on tomato leaflets within a commercial greenhouse. Aggregation does not change with mean density at the within- leaflet level (R^2=0.009, p=0.668).


y = 1.176 + 0.133x R²= 0.008
AGGREGATION (Variance/Mean)
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
0
0.2
0.4
0.6
0.8
1
1.2
TSSM MOBILE STAGES DENSITY (#/0.25cm²)

APPENDIX I. ANCOVA showing the effect of changes in prey density, leaf area, rearing group and taping time on the speed, turning rate, distance traveled, residence time and number of feeds of *F. acarisuga* larvae.

DEP VAR:SPEED (mm/sec) N:20 MULTIPLE R:0.849 MULTIPLE R^2:0.721

ANALYSIS OF VARIANCE

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
PREY DENSITY	0.006	1	0.006	30.840	0.000
LEAF AREA	0.000	1	0.000	2.389	0.145
REARING GROUP	0.001	1	0.001	5.509	0.034
TAPING TIME	0.000	1	0.000	0.285	0.602
REARING GROUP * TAPING TIME	0.000	1	0.000	0.014	0.908
ERROR	0.003	14	0.000		

DEP VAR:TURNING RATE (#/mm) N:20 MULTIPLE R:0.925 MULTIPLE R^2:0.855

ANALYSIS OF VARIANCE

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
PREY DENSITY	0.185	1	0.185	79.707	0.000
LEAF AREA	0.007	1	0.007	3.088	0.101
REARING GROUP	0.003	1	0.003	1.257	0.281
TAPING TIME	0.005	1	0.005	2.238	0.157
REARING GROUP * TAPING TIME	0.000	1	0.000	0.142	0.712
ERROR	0.033	14	0.002		

DEP VAR:DISTANCE (mm) N:20 MULTIPLE R:0.851 MULTIPLE R^2:0.724

ANALYSIS OF VARIANCE

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
PREY DENSITY	142745.980	1	142745.980	29.068	0.000
LEAF AREA	3252.943	1	3252.943	0.662	0.429
REARING GROUP	6034.194	1	6034.194	1.229	0.286
TAPING TIME	62.032	1	62.032	0.013	0.912
REARING GROUP * TAPING TIME	19043.693	1	19043.693	3.878	0.069
ERROR	68750.797	14	4910.771		

DEP VAR:RESIDENCE TIME (sec) N:20 MULTIPLE R:0.989 MULTIPLE R^2:0.978

ANALYSIS OF VARIANCE

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
PREY DENSITY	.173550E+09	1	.173550E+09	615.978	0.000
LEAF AREA	2376.737	1	2376.737	0.008	0.928
REARING GROUP	402291.340	1	402291.340	1.428	0.252
TAPING TIME	23948.129	1	23948.129	0.085	0.775
REARING GROUP * TAPING TIME	64318.870	1	64318.870	0.228	0.640
ERROR	3944453.263	14	281746.662		

DEP VAR:NUMBER OF FEEDS (#) N:20 MULTIPLE R:0.926 MULTIPLE R^2:0.857

ANALYSIS OF VARIANCE

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
PREY DENSITY	404.201	1	404.201	82.321	0.000
LEAF AREA	0.759	1	0.759	0.155	0.700
REARING GROUP	0.042	1	0.042	0.009	0.927
TAPING TIME	0.032	1	0.032	0.007	0.937
REARING GROUP * TAPING TIME	7.670	1	7.670	1.562	0.232
ERROR	68.741	14	4.910		