THE EFFECT OF HOST PLANT

ON THE BIOLOGICAL CONTROL OF WESTERN FLOWER THRIPS

BY THE PREDATORY MITE, Amblyseius cucumeris

by

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BSc, University of British Columbia, 1984

PROFESSIONAL PAPER SUBMITTED IN PARTIAL FULFILLMENT OF

THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF PEST MANAGEMENT

in the Department

of

Biological Sciences

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SIMON FRASER UNIVERSITY

April, 1990

APPROVAL

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Degree: Master of Pest Management

Title of Professional Paper:

THE EFFECT OF HOST PLANT ON THE BIOLOGICAL CONTROL OF WESTERN FLOWER THRIPS
            BY THE PREDATORY MITE, AMBLYSEIUS CUCUMERIS

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The effect of host plant on the biological control
of western flower thrips, Frankliniella occidentalis,
by the predatory mite, Amblyseius cucumeris.

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ABSTRACT

The physical characteristics of host plants may affect
the success of biological control of western flower thrips,
Frankliniella occidentalis (Pergande), by influencing the
search behavior and predation rate of its natural enemies.
The objectives of this study were to characterize the search
path and behavior of the phytoseiid mite, *Amblyseius
cucumeris* (Oudemans), and determine the influence of crop
type and leaf surface characteristics on foraging behavior
and predation success.

The activity budget of A. *cucumeris* was composed of
56.3 ± 3.6% exploring, 24.0 ± 4.4% grooming, 11.0 ± 1.5%
drumming and 8.8 ± 2.1% walking. Mites travelled an average
speed of .56 ± .04 mm/second and tended to make 1.2 ± .4
turns/cm.

Contact with thrips leaf damage resulted in arrestment
of foraging mites. Subsequent searching was slower and
characterized by an increased turning rate. As a result,
mites searched damaged areas of leaves more intensely than
other areas, increasing their chance of encountering prey.

A. *cucumeris* allocated 10% more time to exploring, 13%
less time to grooming, travelled 60% further and was less
likely to retrace its path on pepper leaves than on cucumber
leaves. Such a foraging strategy resulted in an increased
encounter rate with prey and accounted for the observed

difference in predation rates. Mites ate an average of 70.7 ± 5.5% of the available thrips on pepper leaves, but only 44.7 ± 6.0% on cucumber leaves.

A. cucumeris also demonstrated more efficient foraging and a higher predation rate on glabrous cucumber leaves than on hairy cucumber leaves. A. cucumeris consumed an average of 48.7 ± .43% of available thrips on smooth leaves but, only 28.4 ± .38% of available thrips on hairy leaves. The presence of leaf hairs appeared to block the search path of mites and may have caused the increase in grooming and reduction in exploring observed on hairy leaves.

I conclude that the presence of hairs on cucumber leaves inhibit searching and reduce predation by A. cucumeris. Commercial use of a less-hairy cucumber variety would be expected to improve biological control provided that these plants were not also a better quality host plant for the pest.

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INTRODUCTION

A. Western flower thrips

Until recently, the range of the western flower thrips,
Frankliniella occidentalis (Pergande), appeared to be
restricted to western North America from British Columbia to
Mexico (Bailey 1933, Bryan and Smith 1956). By 1987 *F.
occidentalis* had spread eastward and was well established in
greenhouses in Ontario and Nova Scotia and collected from
field crops in Ontario and Québec (Broadbent et. al. 1987).
Frankliniella occidentalis now has a worldwide distribution
and has been found throughout the Americas and Europe, as
well as, in New Zealand and Japan (Bartlett 1988). This
rapid expansion of the distribution of western flower thrips
most likely resulted from the movement of infested plant
material.

Frankliniella occidentalis is polyphagous and has been
collected from over 139 plant species representing 45
families and 23 orders (Bryan and Smith 1956). It is
considered a pest of economic significance on many crops
including greenhouse vegetables and ornamentals (Mantel and
van de Vrie 1988). The ineffectiveness of chemical control
has focussed attention on developing better methods for
managing western flower thrips in greenhouses.

Western flower thrips females insert their eggs into

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the leaf tissue of host plants. Eggs hatch after four days at 26°C (Bryan and Smith 1956). There are two nymphal stages, the first lasting one or two days and the second lasting about three days at 26°C (Bryan and Smith 1956, Bournier and Bournier 1987). Nymphs then drop to the ground, or crawl to a protected crevice on the plant (Bailey 1938, Broadbent 1986) and moult into the pseudopupal stage, which lasts 4-5 days. Adults emerge from the soil and move to the host plant (Bailey 1938).

Adult female western flower thrips lay between 25 and 100 eggs and live for four to eight weeks, depending on temperature (Lublinkhof and Foster 1977, Krause 1987). They are pale to dark brown, about 1-2 mm long and have fringed wings. Adult thrips are very active and, although not strong fliers, are capable of efficient dispersal on the wind (Lewis 1959). During summer months they may migrate from neighbouring fields or surrounding weeds into greenhouses (Krause 1987).

Nymphs and adults feed by puncturing the epidermis and draining the contents of the cells (Borden 1915, Bournier and Bournier 1987). Such damage gives leaves a characteristic silver sheen due to air filling the emptied cell cavities. In addition, the damaged surfaces may be flecked by black droplets of frass.

Adults spend much of their time within flowers (Krause 1987). The flowers provide shelter and a source of pollen

and nectar. Trichilo and Leigh (1988) found that, although pollen was not required by *F. occidentalis*, the development time from egg to adult was reduced, fecundity increased and longevity improved when pollen was available.

Feeding by *F. occidentalis* in the flowers or on the developing fruitlets, often results in fruits that are deformed in shape and marked with silver flecks (Ramakers and van Lieburg 1982). Such damage is particularly severe in cucumber crops where distorted fruits are pruned out at an early stage by the grower because they will be either downgraded or completely unmarketable.

Furthermore, western flower thrips can act as vectors for viral, bacterial and fungal diseases (Bailey 1935). Tomato spotted wilt virus (TSWV) is vectored by thrips species (Paliwal 1974, 1976, Broadbent et al. 1987). As a result, there is a low tolerance for thrips in susceptible crops such as greenhouse tomatoes, peppers and many ornamentals when TSWV is common. Cucumbers, which are not susceptible to TSWV, can support relatively high thrips populations with less risk of economic loss.

Current recommendations for the chemical control of thrips in British Columbia greenhouses include broad spectrum insecticides such as nicotine sulfate smokes or Dibrom (Anonymous 1988), or application of either Diazinon or Thiodan to the floor of the greenhouse in order to kill the pseudopupal stage (Steiner and Elliott 1983, Costello

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et al. 1984, Anonymous 1988). While these measures are generally effective against the onion thrips, *Thrips tabaci* Lindeman, they have little impact on infestations of western flower thrips (Gillespie 1989). There are currently no pesticides registered for use in Canada on greenhouse vegetables that give adequate control of this pest (Gillespie 1989).

In addition, insecticides which are used in an attempt to control western flower thrips tend to be harmful to many beneficial insects. Many are also phytotoxic, burning the leaves of young plants and causing the abortion of flowers and immature fruits. Finally, the necessary interval between applying a chemical insecticide and harvesting is generally three days, or more. This may interfere with picking, particularly in cucumbers where fruits are harvested at least three times per week. (van Lenteren et. al. 1980b)

The ineffectiveness of available chemical control methods and, to a lesser extent, the problems associated with chemical insecticides have promoted the development and application of a biological control program for western flower thrips in greenhouse systems.

B. Biological control of western flower thrips

Biological control of pest insects and mites in greenhouse vegetable culture is used extensively throughout the world (van Lenteren and Woets 1988). Natural enemies are available for the control of whiteflies, mites, aphids and thrips (Hussey and Bravenboer 1971, van Lenteren et al. 1980b, van Lenteren and Woets 1988, Costello et al. 1984). The phytoseiid mite, *Amblyseius cucumeris* (Oudemans), is currently used as a biological control agent for western flower thrips in cucumber and sweet pepper greenhouses in British Columbia.

Amblyseius cucumeris passes through five stages: egg, larva, protonymph, deutonymph and adult. Eggs are white, oval in shape and are often attached to plant hairs (Hussey and Scopes 1985). They hatch in two to three days to non-feeding larvae (Gillespie and Ramey 1988). The larval stage generally lasts only one day at 25°C and is followed by protonymph and deutonymph stages that last about two days each at 25°C (Gillespie and Ramey 1988). Females lay an average of 1.5 eggs per day (Gillespie and Ramey 1988) for up to 40 days (El-Badry and Zaher 1961, Chant and Hansell 1971).

Both the nymphal stages and the adult *A. cucumeris* feed on a large variety of foods including pollen (Ramakers 1983, Tognina 1988) and several species of mites (Muma 1971, Jeppson et al. 1975, Ramakers 1983). Their preferred prey

in vegetable greenhouses seem to be thrips (de Klerk and Ramakers 1986), and they may consume five to six thrips per day (MacGill 1939). *Amblyseius cucumeris* generally feeds on first-instar and small second-instar thrips nymphs; it is not particularly successful at capturing large second-instars or adults (Kajita 1986, Bakker and Sabelis 1986, 1989). This means that western flower thrips are vulnerable to predation by A. cucumeris for only one or two days in their lifecycle.

When A. cucumeris comes into contact with potential prey, it attempts to capture them with its first pair of legs and chelicerae. Although the predatory mite appears to initiate attacks indiscriminantly on all stages of thrips (Bakker and Sabelis 1989), larger thrips can effectively defend themselves. When attacked, they jerk their abdomen and release a droplet of rectal fluid (Kajita 1986, Bakker and Sabelis 1989). After successfully seizing prey, the mite uses its mouthparts to puncture and extract the contents of the prey's body.

Eveleigh and Chant (1981b) described the foraging behavior of two other species of phytoseiid mite, *Phytoseiulus persimilis* and A. *degerans*. Their descriptions of feeding mites agree with my observations of A. *cucumeris*.

Amblyseius cucumeris has had mixed success as a biological control agent. It has provided excellent control of western flower thrips on some crops but poor to variable

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control on others (van Lenteren and Woets 1988, Lindhagen and Nedstam 1988, Gillespie pers. comm.). It has been used commercially in British Columbia sweet pepper greenhouses since 1985. Biological control in these greenhouses has been so successful that thrips damage is usually negligible. Consequently, in peppers, there has been a rapid increase in the use of biological control.

Commercial biological control of western flower thrips on cucumber crops began in British Columbia in 1986 and has not been as successful, or as predictable, as that on peppers (Bakker and Sabelis 1986, van Lenteren and Woets 1988). The use of chemical insecticides for western flower thrips precludes the use of biological control for other pest insects. The negative impact on beneficial insects can be minimized by applying insecticides, often mixed with polybutene (eg. Thripstick ®) to the plastic floor of greenhouses to kill thrips pseudopupae (Hussey and Scopes 1985, Krause 1987, van Lenteren and Woets 1988). Nonetheless, in cucumber greenhouse culture, economic losses due to western flower thrips have been significant (D. Gillespie pers. comm.).

The observed difference in the success of A. *cucumeris* as a biological control agent of western flower thrips might be due to the effect of the host plant on the predatory mite. Host plants can influence the natural enemies of insect pests in two ways, either indirectly or directly

(Bergman and Tingey 1979, Price et al. 1980, Price 1986).

Indirect plant effects are those mediated through the host plant such as the nutritional state of the prey, altered prey behavior or reduced prey population growth. Direct plant effects on natural enemies include both the physical and chemical characteristics of the host plant itself. This leads to two potential explanations for the differential success of A. cucumeris as a biological control agent of western flower thrips on cucumber and pepper crops.

First, the host plant may influence A. cucumeris indirectly, by affecting its prey. Cucumbers may be such a good host plant for F. occidentalis that its population growth is too rapid for A. cucumeris to control. The predatory mite may have better success as a biological control agent on peppers because they are a lower quality host plant for western flower thrips.

Woets and van Lenteren (1976) demonstrated that populations of greenhouse whitefly Trialeurodes vaporariorum (Westwood) develop at different rates on different host plant species. These differences in population development partly explain why biological control of whitefly is difficult on some plant species and rather easy on others.

Second, cucumbers may have a direct negative impact on A. cucumeris relative to peppers. This may be reflected in terms of differences in the ability of A. cucumeris to orient toward prey, or in its behavior or mobility on the

two crops. Plant characteristics which would be expected to vary among host plants and which might impact natural enemies include: alternate food sources, plant exudates, plant volatiles and foliage morphology.

Several studies have shown that the physical characteristics of a host plant affect the search behavior and ultimately, the predation rate of natural enemies. Rabb and Bradley (1968) reported that the glandular trichomes of tobacco interfered with the searching pattern of two hymenopterous egg parasites. Elsey (1974) found that the searching speed of two predators decreased with an increase in the density of glandular trichomes on tobacco. Evans (1976) found that the search patterns of anthocorid predators are influenced by the topography of plant leaves. Finally, Hulspas-Jordaan and van Lenteren (1978) demonstrated that leaf hairiness affected the walking speed and parasitization rate of the greenhouse whitefly parasitoid, *Encarsia formosa* Gahan.

It seems quite likely that the foraging success of A. *cucumeris* is similarly affected by the leaf surface morphology of different host plants. Relatively few studies have examined the effect of the host plant on the foraging success of entomophagous insects. Yet, studies of tritrophic systems are essential if we are to understand what role plants play in determining the success of biological control. Such an approach would not only help

explain the differential success of biological control on different crops, but would also indicate which plant characteristics most influence natural enemies and provide invaluable information for planning plant breeding programs.

C. Objectives

The objectives of this study were to characterize the search behavior of *A. cucumeris* and determine the influence of crop type and leaf surface characteristics on the foraging behavior and predation rate of this predatory mite.

CHAPTER II

FORAGING BEHAVIOR OF *Amblyseius cucumeris*

A. Introduction

The assessment of the effectiveness of natural enemies has, in the past, been based largely on information reflecting their ability to attack prey; their life history in relation to that of their prey; and their environmental tolerance (Murdoch 1973). Despite the obvious importance of these characters it is very important that another character, the searching capacity of the natural enemy, also be considered (Doutt 1964, Huffaker et al. 1970). Searching capacity, the ability of a predator to find prey when prey are scarce (Doutt 1964), is critical because it determines the ability of predators to locate prey and to maintain their numbers at various prey densities.

The search behavior of a predator can be separated into three steps: prey habitat location, prey location, and prey capture (Doutt 1964, Vinson 1976). Prey habitat location is probably of reduced significance in determining the search capacity of a natural enemy in greenhouses since greenhouses generally contain a single crop, and biological control agents are released directly onto the infested plants. In greenhouse biological control the ability of the natural enemy to locate and capture prey within the prey habitat are the most important components of search behavior.

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A predator searching within a habitat for its prey
makes several decisions including: where to search and how
much time to allocate to particular behaviors, such as
searching or resting. Virtually all predators search more
thoroughly for prey in some areas than they do in others
(Bonde 1989). This uneven searching effort may result in
higher predation rates in areas where prey are most abundant
(Rogers 1972, Hassel 1966).

A general finding of studies on the search behavior of
predators and parasites has been that the rate of predator
movement decreases and that the turning rate increases after
capture of a prey item (Smith 1973). Such non-random, or
"area restricted search", is the tendency of predators to
restrict their foraging to the vicinity of recent prey
captures before continuing on a wider-ranging exploration
(Kareiva and Odell 1987). This type of search behavior is
most efficient when prey are distributed non-uniformly
within the habitat.

The distribution of western flower thrips on a leaf
surface is nearly random with a tendency toward clumping
(grid size=2.5 cm, mean=1.42, variance-to-mean ratio=1.50,
X^2=19.2, p<.10) (Brower and Zar 1981). Thrips predators,
such as A. *cucumeris*, ought to exhibit area restricted
searching if natural selection has acted to maximize prey
encounter rates.

In addition, because western flower thrips are

relatively sedentary, they gradually become surrounded by damaged leaf tissue. Since fresh leaf damage is a reliable cue for the presence of thrips, A. cucumeris would be expected to change its behavior in response to contact with thrips damage.

This chapter describes the search behavior of A. cucumeris and reports the results of an experiment designed to determine the effects of the presence of thrips damage on searching.

B. Methods

Amblyseius cucumeris were obtained from D. Gillespie (Agriculture Canada Research Station, Agassiz, B.C.) and Applied Bionomics Ltd. (Sidney, B.C.). They were reared in the laboratory in one-liter containers of bran with the grain mite, Acarus siro L., and a mold mite, Tyrophagus sp., as prey. An aquarium pump was used to blow humidified air through the bran. This method, which is described by Ramakers and van Lieburg (1982), allows vast numbers of A. cucumeris to be produced in the laboratory.

Initial colonies of western flower thrips and rearing methods were obtained from D. Gillespie (Agriculture Canada Research Station, Agassiz, B.C.). Thrips were raised in one-quart canning jar cages in the laboratory. The solid lid was replaced by a round piece of filter paper and secured with a screwtop ring. The bottom of the cage was

filled with a 1.5 - 2 cm layer of peat moss to provide a pupation site for the thrips. Thrips were reared on cuttings from lima bean plants. The cuttings were placed in small water-filled containers inside the cages. These containers had lids with small holes in them for the stems of the cuttings to fit through. Cotton was used to plug the gaps around the stems to prevent thrips from falling into the water. Fresh cuttings were put in the cages every 5-7 days.

Experiments were carried out on leaf arenas consisting of a mature lima bean leaf with an area of about 200 cm², placed, dorsal surface up, on top of water-soaked cotton in a petri dish. The wet cotton prevented test mites from leaving the upper surface of the leaf arenas. All leaves were washed with distilled water prior to use.

Amblyseius cucumeris from the laboratory colony were placed on bean leaves infested with first-instar western flower thrips nymphs in a ratio of six thrips to one mite to allow mites an opportunity to feed on western flower thrips. After 24 hours these mites were isolated on small, 1.5 cm diameter, lima bean leaf disks and deprived of food for another 24 hours before the start of the experiment. Hunger level has been reported to affect the foraging of phytoseiid mites (Mori and Chant 1966, Sandness and McMurtry 1972). In this experiment mites were subjected to a 24 hour starvation period prior to testing, to ensure a consistent level of

energy demand.

Only gravid female mites were used in all experiments because of their high rate of energy demand (Bakker and Sabelis 1989). Mated females can be readily distinguished from males and unmated females. They have reddish streaks on their dorsal surface and are clearly pear-shaped with a vaulted posterior end caused by the presence of one or two large eggs in their oviduct (Bonde 1989).

Fifteen replicates were conducted for each of two leaf treatments: leaves that had been previously-infested with western flower thrips, and leaves that had not. Previously-infested leaf arenas each had ten thrips placed on them for the 24 hour period prior to the start of the experiment. Before the start of each trial the thrips were removed. These arenas were visibly marked with thrips damage. Uninfested leaves did not have thrips introduced to them and had no visible leaf damage.

At the start of each trial a mite was transferred to either a previously-infested arena, with thrips damage, or an uninfested leaf arena, with no thrips damage. A fresh arena was used for each test mite. Observations began 30 seconds after introducing a mite to an arena. Video equipment was used to record all mite activities for a ten minute period. The search path of each mite was mapped and their location and behavior at five-second intervals was recorded from the videotapes.

Variables recorded included the proportion of time
allocated to different behaviors, the speed of travel, the
distance travelled and the number of turns greater than 90°.
In order to account for differences in the walking speeds
of mites, the number of turns was divided by the distance
travelled. The resulting 'turning rate' data were used in
analyses.

The search path was also differentiated into three
qualitatively perceived trail types: 'tortuous walk',
'straight walk' and 'still'. A five-second time interval
was scored as tortuous if it contained one or more turns of
greater than 90°, and as straight if it contained none
(Sabelis et al. 1984, Dicke 1986). If a mite did not change
its location between two five-second surveys it was scored
as still.

The search path and behavior of mites on previously-
infested leaf arenas were expected to differ from those of
mites on uninfested leaf arenas. More specifically, I
hypothesized that the mites would allocate more time to
exploring and walking on previously-infested leaves than on
uninfested leaves. In addition, mites on previously-
infested leaves should turn more and travel more slowly than
mites on uninfested leaves. Differences in these parameters
would lead to more thorough searching of damaged leaves.

Data were tested for normality and proportional data
were transformed using arcsine($\sqrt{X}$). Values reported are the

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Mean ± Standard Error of untransformed data. One-tailed t-tests were used to test whether mites from the two leaf treatments differed significantly, and in the predicted direction, in their search paths or their allocation of time to different behaviors.

C. Results

Five different behaviors were identified in this experiment: explore, walk, drum, groom and rest.

An exploring mite is defined as one which moves slowly, less than 1.5mm per second. As it moves over the leaf surface it holds its first pair of legs, which are longer than the others, in front of its body and taps them from side-to-side on the substrate. These front legs are equipped with chemo-receptors, and possibly with mechano-receptors (Jackson 1974), and seem to be of primary importance in exploring the habitat and detecting prey.

A walking mite is defined as one which travels more than 1.5mm, or three body lengths, per second. The 'walk' behavior can also be distinguished from the 'explore' behavior in that the mite does not tap its front legs on the leaf surface, but holds them up in the air as it moves.

Drumming occurs when a mite taps its front legs on the leaf surface, but does not travel. This behavior often occured when a mite encountered an area of thrips leaf damage, or where there was some foreign object on the leaf,

such as a cotton fibre.

Grooming involves no travel and no tapping of front legs. The mite grooms itself by rubbing its legs over other parts of its body, or against each other. Resting, in this study, is defined as inactivity. It has been grouped with grooming because it is not always possible to differentiate the two. Even with this difficulty, it is clear that grooming is the predominant of the two behaviors. It was clearly distinguished from resting in more than 90% of the observations.

Pooling all data showed that exploring made up the largest portion (56.3 ± 3.6%) of the total activity budget. The rest of the time was spent grooming (24.0 ± 4.4%), drumming (11.0 ± 1.5%) and walking (8.8 ± 2.1%). The search paths of the mites were comprised of an average of 41.0 ± 2.1% straight walk, 26.8 ± 1.8% tortuous walk, and 32.2 ± 3.4% still. Mites travelled an average speed of .56 ± .04 mm/second.

Mites allocated significantly more time to exploring on leaves with thrips damage than on those without damage (t=2.13, p<.05). No other single behavior was significantly different between the two leaf treatments, although there was a corresponding increase in the combined time allocated to walking, grooming and drumming on uninfested leaves compared to previously-infested leaves (t=1.74, p<.05). (Figure 1)

Figure 1. The allocation of time to different behaviors by A. *cucumeris* on uninfested and previously-infested bean leaves.

Behaviors
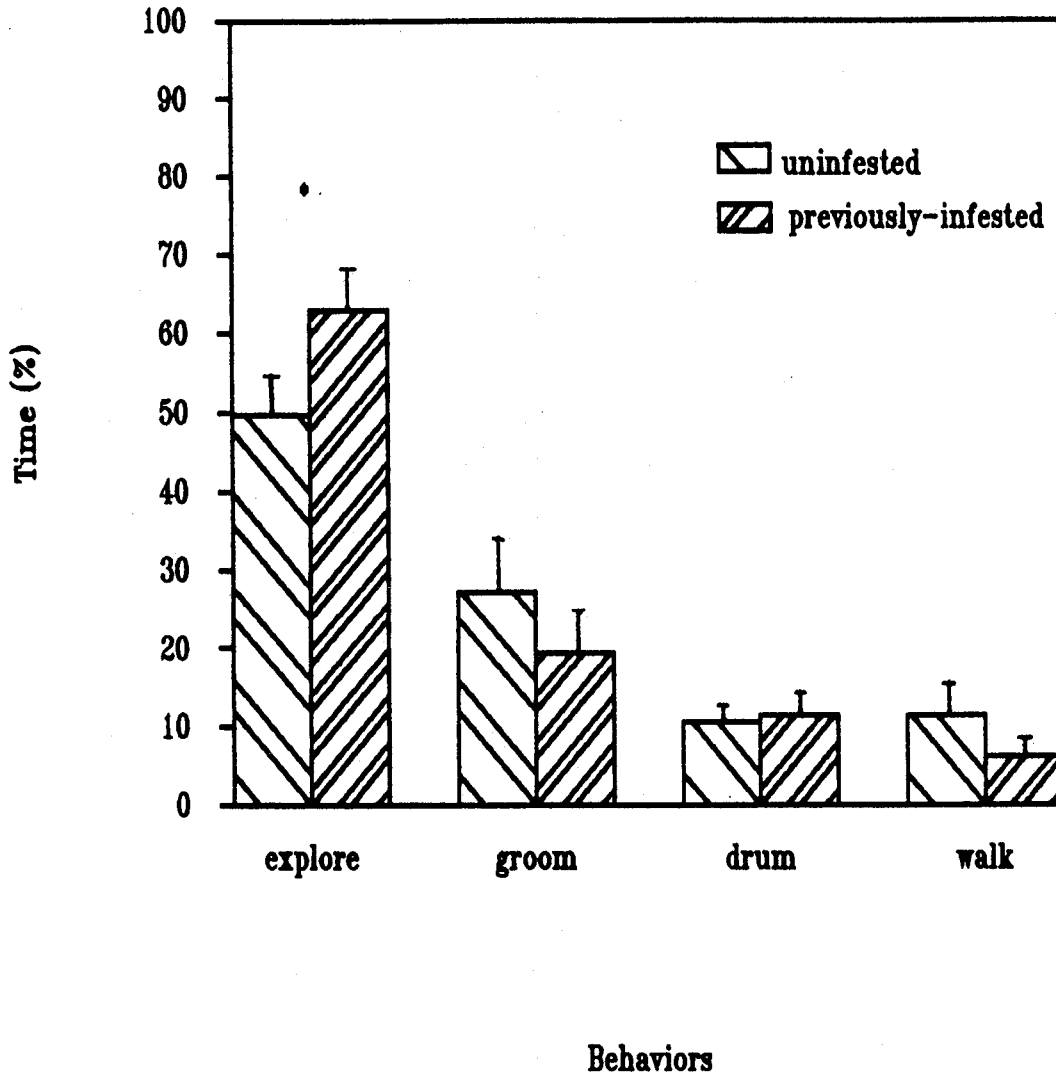
* one-tailed, p<0.05

Contrary to predictions, there were no significant differences in the search paths of mites on uninfested and previously-infested leaves (one-tailed t, p>.05, Table 1).

The large amount of variation in the search paths of individual mites may have masked the response of A. cucumeris to the two leaf treatments. For instance, two out of the fifteen mites tested on previously-infested arenas did not encounter any visible leaf damage during the entire observation period. Elimination of these trials from the analysis did not change the results (t<1.70, p>.05).

Individual mites tested on previously-infested arenas appeared to change their behavior and search path in response to contact with patches of leaf damage (Figure 2). The data were reanalyzed using only those from previously-infested arenas, and dividing the behavior and search path data into two groups: before and after the first encounter with leaf damage. Data were weighted with respect to the amount of time that passed before, or after, the mite encountered its first damage patch and analyzed using paired t-tests.

The amount of time required for a mite to find its first patch of thrips damage averaged 155 ± 55 seconds. After contacting thrips damage mites decreased the proportion of time that they allocated to walking five-fold (t=3.78, p<.01). This decrease in walking was accompanied by a corresponding increase in the amount of time spent

Table 1. Characteristics of the search path of _A. cucumeris_ on uninfested and previously-infested bean leaves.

		distance (mm)	#turns/distance	speed (mm/sec)	% straight	% tortuous	% still
Uninfested n=15	Mean=	260.60	.19	.06	41.88	25.17	33.04
	SE=	37.90	.02	.10	3.15	2.49	5.06
Previously-infested n=15	Mean=	250.20	.06	.18	40.19	28.31	31.50
	SE=	25.20	.07	.01	2.82	2.55	4.59
Transformation		(X)	(X)	(X)	asin($\sqrt{X}$)	asin($\sqrt{X}$)	asin($\sqrt{X}$)
t=		.23	1.63	1.09	.41	.89	.24

t-values of transformed data one-tailed, critical t=1.70, p=.05

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Figure 2. Typical search paths of A. *cucumeris* on
uninfested and previously-infested bean leaf
disks for five minutes. Cross-hatches
indicate five-second intervals. Arrow shows
contact with first thrips damage.
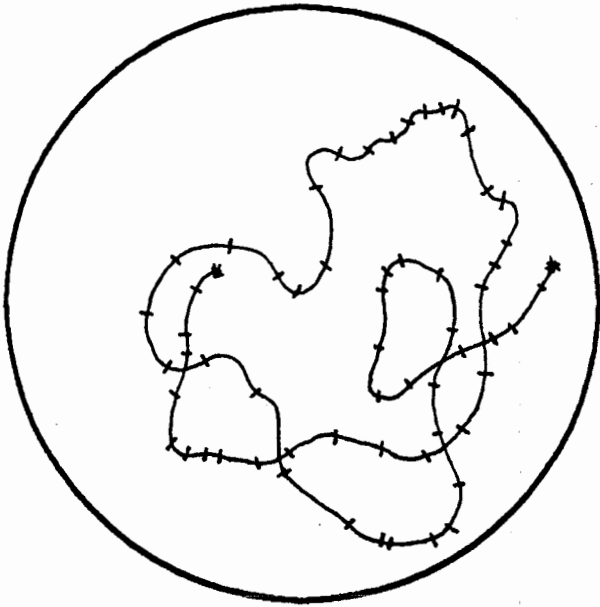
Uninfested

Previously-infested

22
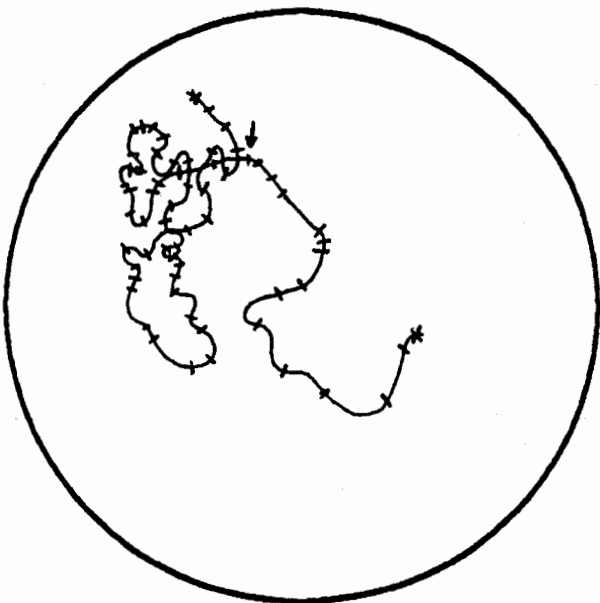
drumming (t=2.17, p<.05) and the amount of time spent grooming (t=2.19, p<.05). There was no change in the explore behavior after encountering leaf damage (t=.97, p>.05). (Figure 3)

Mites reduced their speed of travel (t=3.34, p<.01) and the distance travelled (t=3.07, p<.01) after contacting thrips damage. The search path contained less straight walk (t=4.07, p<.01) and more still (t=2.33, p<.05) after encountering damage than before. After contacting thrips damage mites were less likely to change position between successive 5-second intervals and when they did travel their path contained less straight walk. The tortuousness of the search path tended to increase after encountering damage, but not significantly (t=1.43, p>.05). (Table 2)

It is unclear whether these changes in foraging behavior and search path were the result of contact with damage patches or a function of some other factor such as the length of time since arriving on a leaf. In order to address this problem the data from mites tested on uninfested arenas were also divided into two groups, the first 155 seconds and the last 445 seconds. The cut-off time of 155 seconds corresponded to the mean time at which mites encountered their first damage patch on previously-infested arenas. Variables were weighted with respect to time.

Paired t-tests showed no significant difference in any

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Figure 3. The allocation of time to different behaviors by
A. cucumeris before and after encountering thrips
leaf damage.
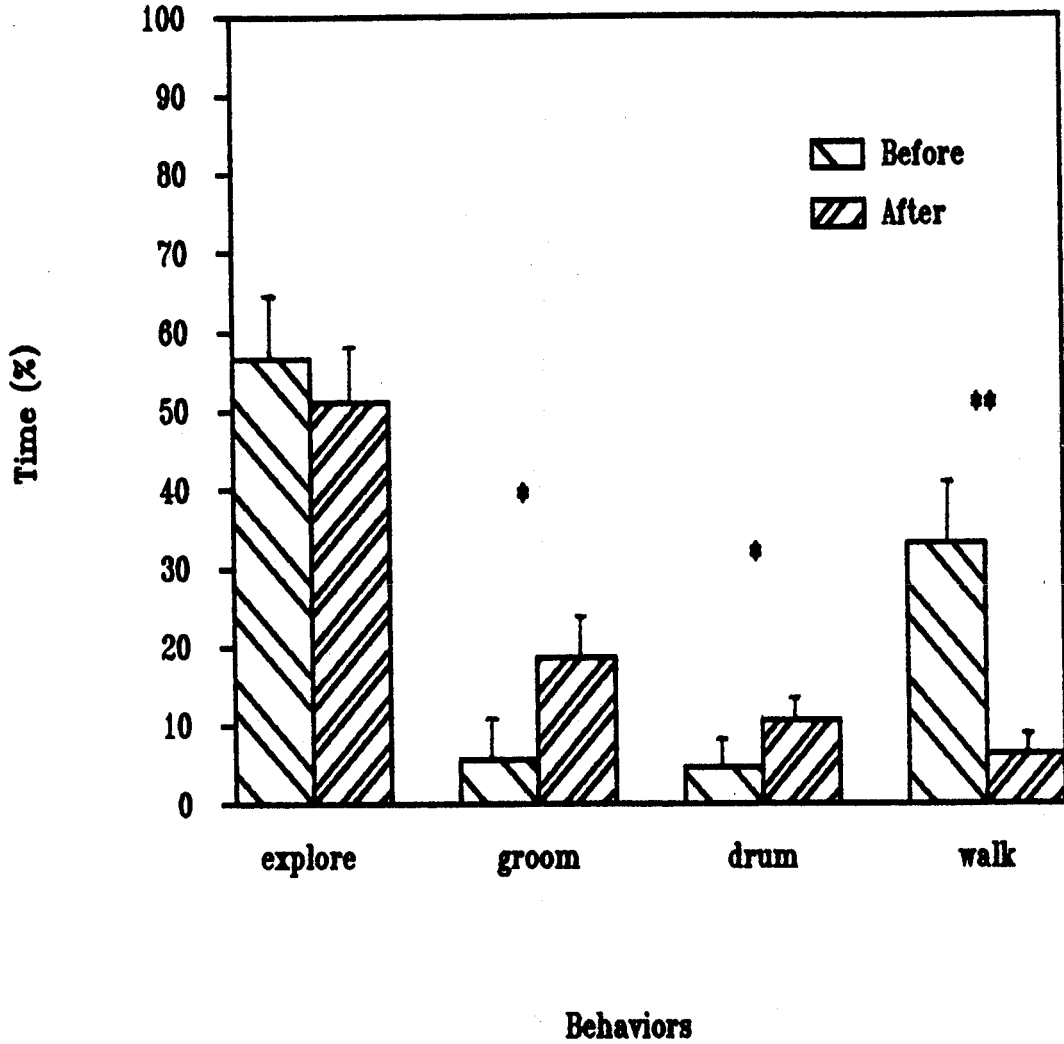
* two-tailed, p<.05
** two-tailed, p<.01

Table 2. Characteristics of the search path of A. cucumeris before and after encountering thrips leaf damage.

		distance (mm)	#turns/ distance	speed (mm/sec)	% straight	% tortuous	% still
Before n=15	Mean=	58.30	.15	.67	57.17	34.31	8.51
	SE=	10.40	.02	.09	5.46	5.36	4.75
After n=15	Mean=	27.29	.17	.39	35.30	24.89	26.17
	SE=	4.26	.02	.06	4.41	3.92	5.00
Transformation=		(X)	(X)	(X)	asin($\sqrt{X}$)	asin($\sqrt{X}$)	asin($\sqrt{X}$)
	t=	3.07 **	.92	3.34 **	4.07 **	1.43	2.33 *

t-values of transformed data

* two-tailed, p<.05
** two-tailed, p<.01

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of the behavior (p>.05, Figure 4) or search path (p>.05,
Table 3) parameters indicating that foraging did not change
over time on uninfested leaves. The observed changes in the
behavior and search path of mites on previously-infested
arenas was a result of contact with thrips damage rather
than a function of the time since arriving on a leaf.

T-tests were used to compare the search path and
behavior of mites before contacting leaf damage on
previously-infested leaves and mites in the first 155
seconds of arriving on uninfested leaves. There were no
significant differences in the behavior of mites form the
two treatments. The search path differed only in its
tortuosity. Mites walked more tortuously on the clean
uninfested leaves than they did on the previously-infested
leaves before encountering thrips damage.

D. Discussion

The foraging strategy used by A. cucumeris is well
suited to its life history as a non-visual predator.
Exploring and drumming were the two most important behaviors
involved in searching. These two behaviors alternated so
that the predatory mite homed in on areas of high thrips
activity. Exploring allowed mites to search leaves and find
patches of leaf damage. Contact with leaf damage resulted
in arrestment and drumming. Subsequent exploring was
characterized by a slower speed of travel and an increased

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Figure 4. The allocation of time to different behaviors by
A. cucumeris in the first 155 seconds and the
last 445 seconds of arriving on uninfested leaf
disks.
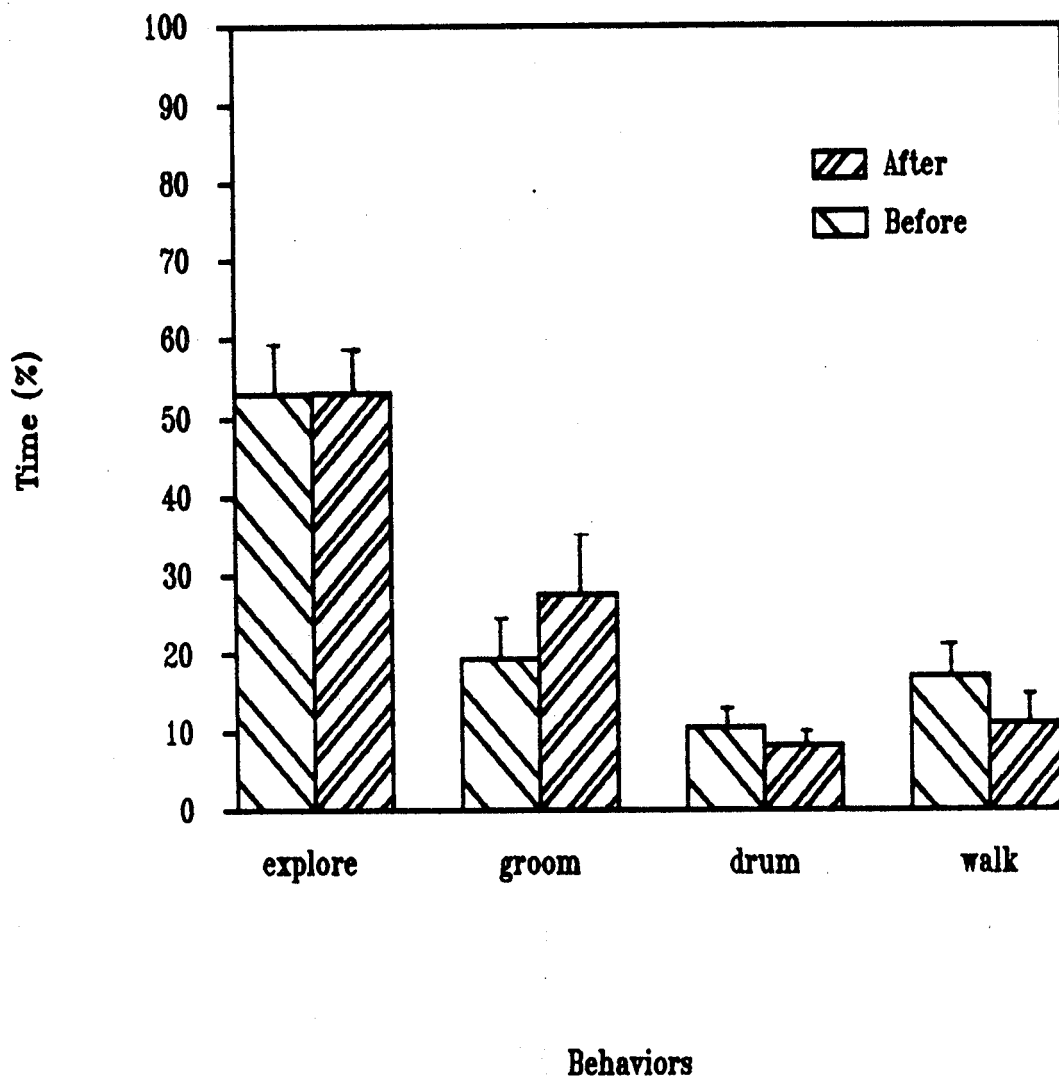
Table 3.   Characteristics of the search path of A. cucumeris in the first 155
seconds and the last 445 seconds of arriving on uninfested leaves.

		distance (mm)	#turns/ distance	speed (mm/sec)	% straight	% tortuous	% still
Before n=15	Mean=	44.12	.20	.55	48.82	28.04	23.13
	SE=	6.16	.02	.07	5.06	3.72	5.12
After n=15	Mean=	38.84	.20	.51	41.97	24.29	33.59
	SE=	7.19	.03	.07	4.36	3.08	6.89
Transformation=		(X)	(X)	(X)	asin(√X)	asin(√X)	asin(√X)
	t=	.87	.03	.56	.96	.91	1.3

t-values of transformed data
two-tailed, critical t=2.14, p=.05

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turning rate.

The proportion of time allocated to exploring was significantly higher on previously-infested leaves than on uninfested leaves, yet it did not change after contact with leaf damage. *Amblyseius cucumeris* seems to be able to evaluate leaf quality, in terms of the presence of prey, by some cue other than leaf damage. Exploring is probably triggered by a relatively long-distance cue, such as a volatile kairomone, which mites are able to detect soon after arriving on previously-infested leaves.

In contrast, the allocation of time to drumming increased after contacting leaf damage, but did not differ between uninfested and previously-infested leaves. Drumming is a relatively infrequent behavior that occurs only after physical contact with a patch of damage or foreign object on the surface of the leaf. Since damage patches have a loosely clumped distribution over the leaf surface (grid size=2.5 cm, mean=1.86, variance-to-mean ratio=1.48, X^2=19.22, p<.10), a mite that has found one damage patch is more likely to find additional ones.

The variables that best described the search path of the predatory mite were the number of turns per distance travelled and the speed of travel. Mites increased the amount of time that they spent in areas with leaf damage by reducing their speed of travel, travelling less frequently and turning more after encountering thrips leaf damage.

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This type of response to thrips damage would likely increase the encounter rate of A. *cucumeris* with its thrips prey.

Tortuosity, a qualitative description of the 5-second segments which made up the search path, was not as sensitive a measure of changes in the search path in this experiment. This was probably a result of the large variation within the search path of individual mites. After encountering leaf damage, mites were less likely to change location and tended to reduce the amount of straight walk.

Because A. *cucumeris* responded to thrips damage on leaves further experiments used leaves with thrips damage rather than actual thrips in order to assay the search capacity of A. cucumeris. This method eliminated complicating factors such as prey catchability, prey acceptance, and prey handling time, which depend, to some extent, on characteristics of individual thrips and make it difficult to isolate the effect of habitat on the predator.

From the results of this experiment I conclude that A. *cucumeris* exhibits area restricted search in response to contact with damage caused by western flower thrips. This search strategy is likely to increase its encounter rate with prey since thrips tend to be loosely clumped over the leaf surface.

CHAPTER III

EFFECT OF FOOD EXPERIENCE ON FORAGING

A. Introduction

Amblyseius cucumeris is a general predator. It has been reported to feed on various species of tetranychid mites (Muma 1971, Jeppson et.al 1975), thrips (Ramakers 1978), grain mites (Ramakers and van Lieburg 1982) and pollen (Ramakers 1983, Tognina 1988). Although thrips appear to be the preferred prey of *A. cucumeris* (de Klerk and Ramakers 1986, Gillespie and Ramey 1988) mites can develop and reproduce having fed only on pollen (Tognina 1988).

The ability of predaceous mites to utilize foods other than the pest they are meant to control should be beneficial to biological control since it would enable mites to survive periods of prey scarcity (Huffaker and Kennett 1956, Putman and Hearne 1964). Ramakers (1983) reported that A. *cucumeris* maintained low, but well spread populations in greenhouses even after thrips had been reduced to very low levels and suggested that the ability of *A. cucumeris* to prey on alternate hosts probably explained this phenomenon.

Commercial varieties of greenhouse cucumber and sweet pepper crops differ in the provision of alternate food sources, particularly pollen. Pepper flowers contain both male and female reproductive parts and produce pollen. The

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varieties of cucumber that are grown in greenhouses are parthenocarpic, that is, fruits develop without sexual fertilization and are seedless. All the flowers in a cucumber crop are female. Male flowers occur only rarely and are pruned off if seen. As a result, cucumbers produce virtually no pollen. If pollen is an important food source for A. cucumeris its presence in peppers and its absence in cucumbers may help to explain the observed difference in biological control on the two crops.

Several studies have reported that pollen and honeydew, when eaten in conjunction with prey, increase the fecundity and reduce the development time of phytoseiid mites (Putman 1962, McMurtry and Scriven 1964, 1966). Nutrition has also been observed to effect diapause induction, response to volatile kairomones and food utilization (Dicke et al. 1989). It is important to evaluate the effect of experience with different food sources on the subsequent foraging behavior.

This chapter reports on the results of experiments designed to test the effect of feeding on pollen, grain mites, or western flower thrips on subsequent foraging behavior and predation success. For logistic reasons it was preferable to use A. cucumeris directly from the laboratory colony in experiments. However, these mites were reared in bran with grain mites as substitute prey and then tested on leaves for their searching capacity for western flower

thrips.

The primary objective of this experiment was to determine if mites from the colony could be used directly in further experiments without first being provided with experience feeding on western flower thrips. It was also important to evaluate the effect of particular prey types on subsequent predator performance so that the results of this study could be extrapolated to the greenhouse situation where the availability of alternate food sources may vary.

B. Methods

This experiment was conducted in the same arenas as described in Chapter 2. Mites were exposed to one of three food treatments prior to testing: ten first-instar western flower thrips nymphs, ten grain mites, or a small brush load of bee pollen. After 24 hours each mite was transferred to a fresh leaf disk and deprived of food for another 24 hours.

In this experiment, mites were tested only on leaf arenas that had been infested with western flower thrips nymphs for the 24 hour period preceding the start of the experiment. All thrips were removed just prior to the start of each trial. Trials were videotaped for a period of five minutes each.

The search path of each mite was mapped and their location and behavior at 5-second intervals was recorded from the videotapes. Variables recorded include the

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behavior, the speed of travel, the distance travelled, the number of turns greater than 90°, the time required to contact the first patch of thrips damage and the proportion of all damage patches visited and the proportion of the search path that was classified as straight, tortuous and still.

I hypothesized that if experience was important in determining subsequent search behavior and predation success, then mites that had previously fed on either thrips, grain mites, or pollen should differ in their search path, behavior, and predation success.

After videotaping, a single first-instar thrips nymph was placed on each test arena to assay the effect of the three experience treatments on subsequent predatory ability and physiological condition. The number of eggs laid by each mite and the total number of thrips eaten during the 24 hour test period were recorded. This information was used as an indication of the effect of grain mites, thrips and pollen on subsequent predation rates and fecundity.

Each of the three treatments was replicated 16 times. Differences in the tortuosity of the search paths and the behavior of mites from the different experience treatments were tested using Kruskal-Wallis tests. Other search path variables were transformed by arcsine(X) or log(X) and analyzed using ANOVA. Predation and egg-laying data were analyzed using Chi-square tests with the null hypothesis of

no significant difference between the proportion of mites from each treatment to lay eggs, or to feed on thrips.

C. Results

Statistical analysis indicated that there were no significant differences in the amount of time allocated to different behaviors (Kruskal-Wallis, $X^2 < 5.99$, $p > .05$, Figure 5), the proportion of the search path classified as tortuous, straight and still (Kruskal-Wallis, $X^2 < 5.99$, $p > .05$, Table 4), or the search path ($F < 3.25$, $p > .05$, Table 4) of mites with experience feeding on either grain mites, western flower thrips, or pollen prior to testing. There was also no significant difference in the subsequent predation success of mites from the three experience treatments ($X^2 = .73$, $p > .05$, Table 5).

There was a significant difference in the number of mites from each of the three experience treatments to lay one, or more, eggs in the 24 hour period following videotaping ($X^2 = 11.40$, $p < .01$). A far greater proportion of the mites that had experience feeding on thrips laid eggs (.75), than mites that had previously fed on grain mites (.25), or on pollen (.06). (Table 5)

Figure 5. The allocation of time to different behaviors by
A. cucumeris as a function of food experience.
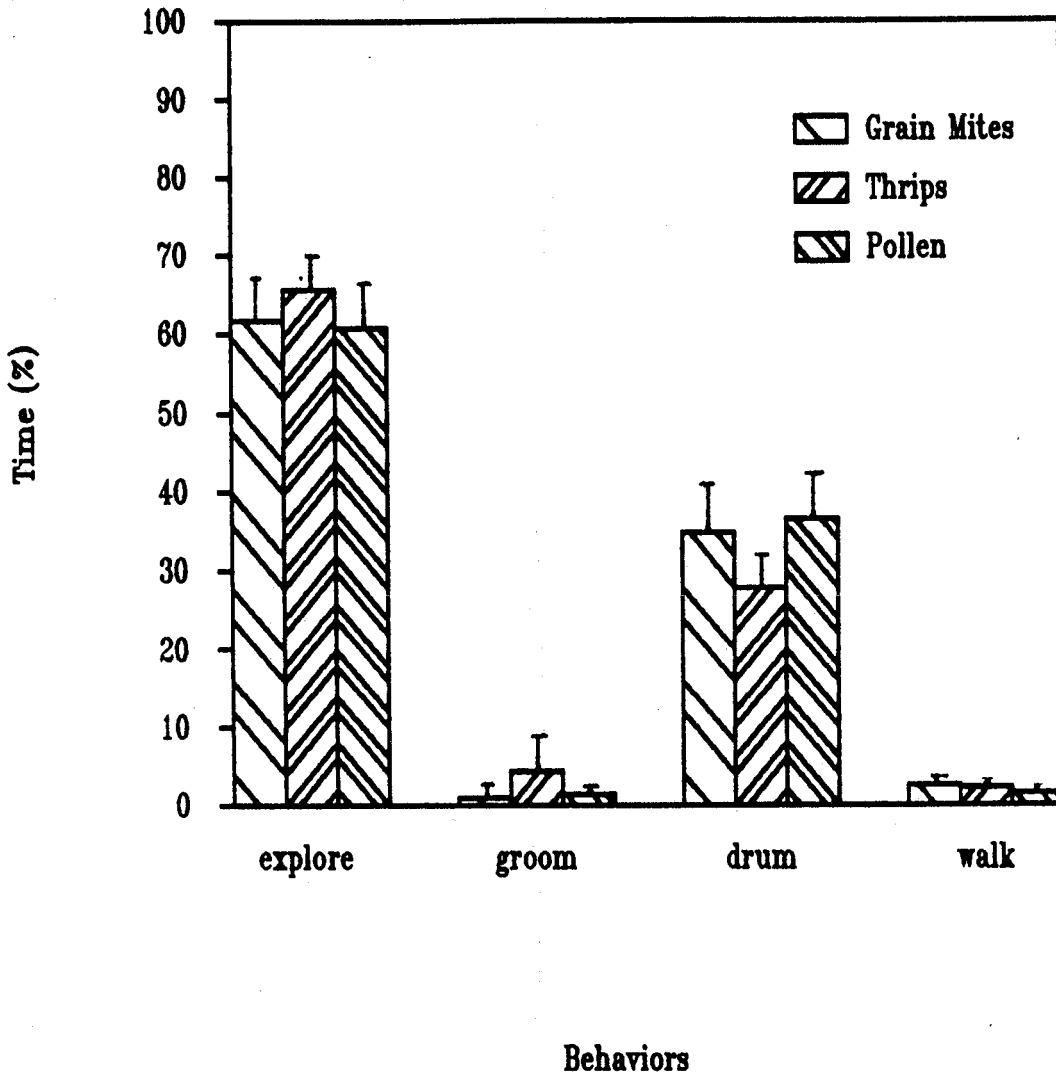
Table 4. Characteristics of the search path of _A. cucumeris_, as a function of experience feeding on grain mites, western flower thrips or pollen.

		distance (mm)	#turns/ distance	speed (mm/sec)	time to 1st damage (sec)	% damage found	% straight	% tortuous	% still
Grain Mites n=16	Mean=	119.40	.24	.62	114.70	23.19	45.94	32.81	21.36
	SE=	12.70	.02	.05	34.30	3.48	4.49	3.26	5.52
Thrips n=16	Mean=	132.00	.20	.66	64.40	22.62	43.96	35.42	20.62
	SE=	10.60	.01	.02	22.20	4.01	2.93	3.29	4.53
Pollen n=16	Mean=	111.60	.25	.61	69.50	16.25	39.69	33.96	26.35
	SE=	13.20	.03	.06	21.00	2.11	80.00	3.64	5.61
Transformation=		(X)	log(X)	log(X)	log(X)	asin($\sqrt{X}$)	asin($\sqrt{X}$)	asin($\sqrt{X}$)	asin($\sqrt{X}$)
	F=	.71	.85	.96	1.89	1.39	.86	.19	.97
	Chi²=								

F-values of transformed data
critical $F_{(2,45)} = 3.25$, p=.05

Table 5. Predation and egg laying by A. cucumeris as
a function of food experience.

	% mites to eat a thrips	% mites to lay 1+ eggs
Mites n=16	37.5	25.0
Thrips n=16	50.0	75.0
Pollen n=16	31.3	6.3
Chi-square=	.73	11.40 **

** Chi-square, p<.01

D. Discussion

The search path and behavior of mites with experience feeding on either grain mites, thrips or pollen were not significantly different. The reasonably large sample size (n=16) and the fact that Kruskal-Wallis is a very robust statistical test, 95% as powerful as ANOVA (Zar 1974), lend confidence to these findings. In further experiments mites were used directly from the colony without first providing them with experience preying on thrips.

There was also no significant difference in the predation rates of mites that had been exposed to the three experience treatments. Differences in predation success would have been better assayed if more thrips had been used. Unfortunately, the large number of first-instar thrips nymphs that would have been required for this was prohibitive, particularly since the main focus of this study was on search behavior.

Mites which were allowed to feed on thrips for 24 hours prior to the start of this experiment also laid the most eggs. Grain mites, which are adequate as a substitute host for mass-rearing are the second best food with respect to egg-laying. Pollen, which has been reported to increase the fecundity of phytoseiid mites when consumed in conjunction with prey (Putman 1962, McMurtry and Scriven 1964, 1966), appeared to be a poor food source by itself. However, pollen may be very important source of nutrition capable of

maintaining mite populations when other food sources are scarce (McMurtry and Scriven 1966, Ramakers 1983).

Pollen is also an important food source for western flower thrips (Kirk 1984, 1985). Trichilo and Leigh (1988) reported that access to pollen reduced the development time, increased the fecundity and improved the longevity of *F. occidentalis*.

Both western flower thrips and *A. cucumeris* consume pollen. However, it seems likely that pollen is a more important food source for thrips than it is for mites, since mites are relatively uncommon in pepper and cucumber flowers while adult thrips are frequently found there in high numbers.

Western flower thrips, grain mites and pollen were not equally nutritious to *A. cucumeris*. The physiological condition of mites, as indicated by fecundity, differed depending on their food in the 24 hours preceding the experiment. Although this difference did not have any significant influence on predation success in the short-term, it would probably have a long-term effect on mite population growth.

CHAPTER IV

FORAGING ON PEPPER AND CUCUMBER LEAVES

A. Introduction

Perhaps the simplest model to describe the dynamics of a population is: $N_{(t+1)} = N_{(t)} * e^{(b-d)}$. For western flower thrips, this states that the population of thrips at time (t+1) is equal to the population at time (t) multiplied by a function of the birth rate minus the death rate. As long as the birth rate exceeds the death rate the thrips population will grow.

The birth rate and death rate of thrips could be influenced by any number of environmental conditions including: temperature, humidity, photoperiod and host plant. Since the success of biological control of western flower thrips has been observed to vary on different crop species (van Lenteren and Woets 1988, Lindhagen and Nedstam 1988) it seems likely that the host plant plays an important role in regulating thrips populations.

Host plants could influence thrips populations by affecting the birth rate and death rate of thrips directly, or by affecting the death rate of thrips indirectly via the abundance or efficiency of natural enemies. This leads to two potential explanations for the difference in the success of A. cucumeris as a biological control agent on pepper and cucumber crops.

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First, cucumber plants may be a higher quality host for western flower thrips and provide a better source of nutrition or shelter, or a more favorable microclimate than pepper plants. If so, thrips would be expected to have a higher birth rate and survivorship on cucumbers than on peppers. If the resulting population growth of thrips on peppers were too high, relative to that of *A. cucumeris*, the predatory mite would not be able to keep thrips numbers below the level causing economic damage. *Amblyseius cucumeris* may have better success as a biological control agent on plant species which are a lower quality host for thrips.

Alternatively, *A. cucumeris* may not be as abundant or as effective a predator on cucumber plants as it is on pepper plants. The host plant may affect predation by *A. cucumeris*, indirectly, by affecting the availability or quality of its prey, or directly, via the physical and chemical characteristics of the host plant itself.

Plant characteristics which might directly impact natural enemies include: the availability of alternate food sources, the presence of plant exudates or plant volatiles, plant morphology and leaf surface characteristics. Differences in the ability of the predatory mite to find alternate food sources, orient toward its prey, travel or allocate time to searching would influence prey encounter rates, predation rates and mite population levels on the two

crops.

This chapter reports on the results of two experiments.
The first experiment was designed to determine if the
differential success of A. cucumeris as a biological control
agent on pepper and cucumber crops could be explained by
differences in the predation rate on the two species of host
plant. The objective of the second experiment was to
compare the search path and behavior of A. *cucumeris* on
pepper and cucumber leaves and determine if there were
differences which could influence prey encounter rates and
thus, predation rates on the two crops.

B. Experiment 1: Predation rates
(i) Methods

This experiment was carried out on pepper and cucumber
leaf disk arenas. An arena consisted of a 10 cm² leaf disk
placed, dorsal surface up, on wet cotton in a petri dish.
Cucumber and pepper leaves were obtained from D. Gillespie
(Agriculture Canada Research Station, Agassiz, B.C.).
Leaves were picked from the mid-canopy layer in greenhouses
with very low thrips populations. Only mature leaves with
no sign of thrips damage were used.

0, 1, or 10 thrips, giving densities of 0, .1, and 1.0
thrips per cm², were placed on either pepper or cucumber
leaf disks 24 hours prior to the start of the experiment.
This allowed the thrips to settle on the leaf and begin

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feeding. At the end of 24 hours a single mite was placed on each leaf disk.

Mites were starved for the 24 hour period prior to the start of a trial on either a cucumber or a pepper leaf disk. Each mite was later tested on the same type of leaf as it was starved on. This allowed mites to adjust to walking on one of the two leaf treatments.

A common problem with conducting predation experiments is trying to mimic the kinds of conditions under which insects make decisions in the real world. If a predator does not have the option of leaving a leaf then artificially high predation rates will result, particularly at low prey densities (Roitberg et al. 1982). The problem was resolved in this experiment by providing predators with the option of staying on, or leaving, a particular leaf.

Each arena was provided with a one-way escape route which gave mites the option of leaving the test arena. These escape routes were designed to be about the same width as a leaf petiole; the main path by which A. cucumeris moves from leaf-to-leaf on a plant. Escape routes were cut from the lids of plastic yogurt containers. The effectiveness of several designs was tested by placing a mite on the end of the escape route furthest from the leaf and observing whether it returned to the leaf.

The best escape route was a balloon-shaped platform with walls that were angled to guide an escaping mite

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through a narrow opening (Figure 6). Return was unlikely since mites rarely found the opening from the far side. In addition, the walls were coated in "Sticky Stuff" to prevent the mite from climbing over them. After 12 hours only 15% (n=20) of mites placed on the far end returned to the leaf, indicating that the routes provided pretty much a one-way path.

Each of the six treatments: three prey densities and two host plants was replicated 20 times. Mites were observed each hour for 12 hours and then again at the end of 24 hours. Variables recorded included the residence time, or the time at which a mite left the leaf disk, and the number of thrips eaten each hour. If a mite was still on *were prey replaced* the leaf disk after 24 hours it was scored as 24 hours.

Data were analyzed for crop and density effects. Residence time data were tested for normality and homogeneity of variances and then analyzed using two-way ANOVA. Predation rate data were analyzed using non-parametric Kruskal-Wallis tests (Bradley 1968).

If the host plant is important in determining the success of *A. cucumeris* as a biological control agent of western flower thrips, then the predation rate of mites on pepper leaves should be higher than on cucumber leaves. This difference may be moderated by prey density, since efficient searching is less important at high prey densities. Finally, this experiment will indicate whether *A. cucumeris*

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Figure 6. Leaf disk arena and escape route used in predation experiments.

petri dish (9 cm dia.)

leaf disk (3.5 cm dia.)

water-soaked cotton

escape route

walls coated with "sticky stuff"

gate

2cm   2mm↑   1mm→

platform

5mm   1.5 cm

4.5 cm

Escape route
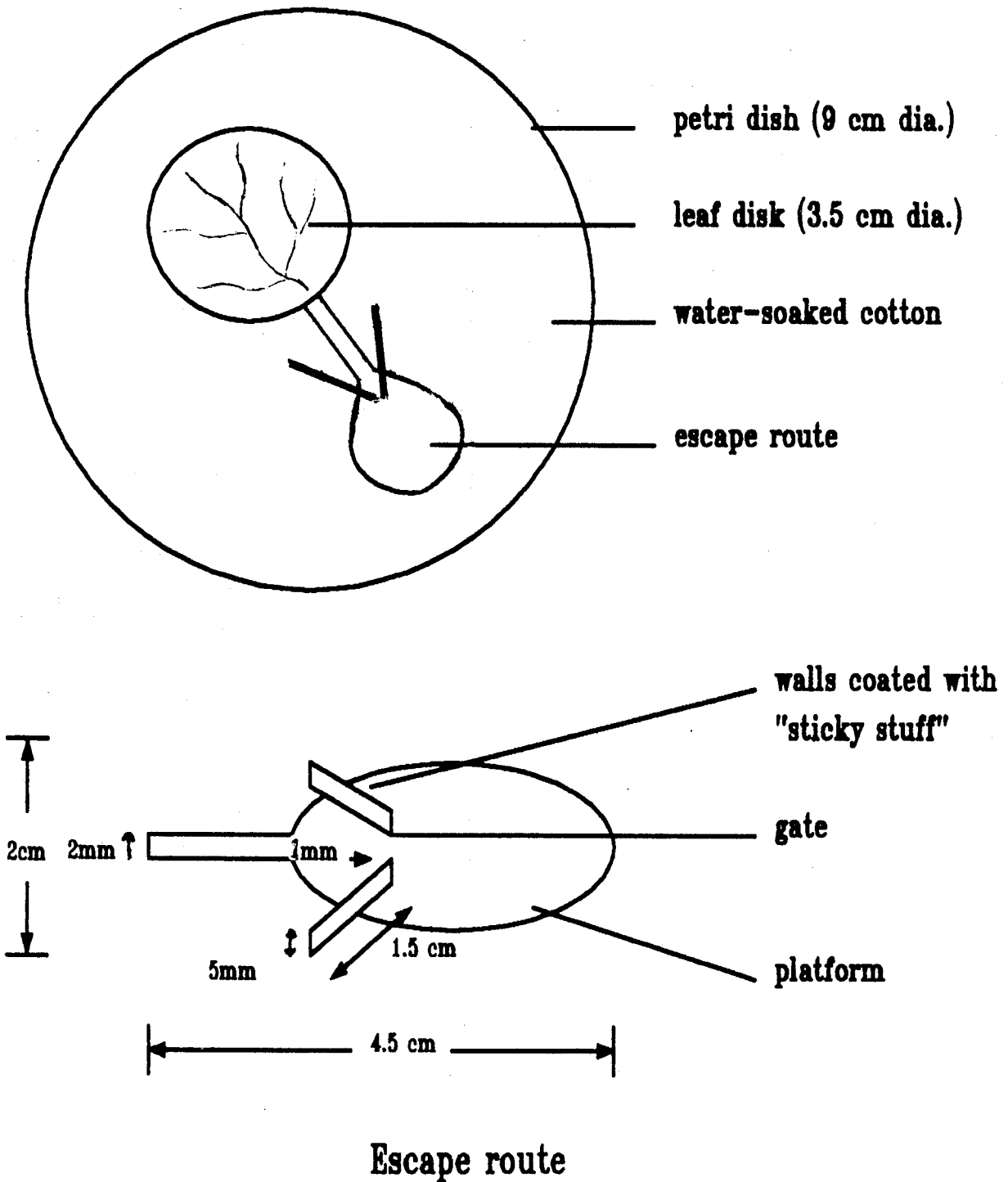
exhibits density dependent foraging over the densities tested.

(ii) Results

Amblyseius cucumeris was a more successful predator of western flower thrips on pepper leaves than on cucumber leaves. When mites were presented with ten thrips each they consumed an average of 6.65 ± .48 thrips on the pepper arenas, but only 3.95 ± .39 thrips on the cucumber arenas (t=4.39, p<.001). When presented with one thrips, mites successfully captured an average of .75 ± .10 thrips on pepper leaves and .50 ± .11 thrips on cucumber leaves (t=1.65, p<.05).

Mites feeding on the high prey density arenas could potentially eat from zero to ten thrips. Mites on the low thrips density arenas either ate the one available thrips, or did not. As a result of this difference, numerical computations of data across densities were biased. Data were converted to the proportion of available thrips eaten and the effect of leaf type and density were determined using a two-way Kruskal-Wallis test (Bradley 1968). Non-parametric statistics were used because data from the low prey density treatment were not normally distributed.

The proportion of thrips eaten did not differ between the two prey densities (X^2=-4.63, p>.05). *Amblyseius cucumeris* consumed a larger proportion of the available prey

on pepper leaves than on cucumber leaves (X^2=16.06, p<.01).
They ate an average of 70.7 ± 5.5% of the available thrips
on pepper leaves, but only 44.7 ± 6.0% on cucumber leaves,
regardless of thrips density. The interaction between crop
and density was not significant (X^2=3.65, p>.05, Table 6).

   Amblyseius cucumeris stayed significantly longer on
cucumber leaves than on pepper leaves (F=9.44, p<.01). The
length of time that the predatory mites remained on both
pepper and cucumber leaf disks increased with increasing
prey density (F=33.54, p<.01, Table 6) and varied with its
predation success. There was a strong correlation (r=.82,
t=6.05, p<.001, Figure 7) between the number of thrips eaten
and the residence time of mites on peppers at the high
thrips density. On cucumbers this relationship did not hold
(r=.27, t=1.20, p>.05, Figure 8).

   Mites on both pepper and cucumber arenas were more
likely to remain on arenas for 12 hours if they ate a
thrips, than if they did not (Fisher's exact probability
test, p<.01, Table 7). The average residence time for all
mites that did not consume a thrips was 1.76 ± .32 hours.

C. Experiment 2: Search path and behavior
(i) Methods

   This experiment was conducted on 10 cm² pepper and
cucumber leaf disks placed, dorsal surface up, on top of
water-soaked cotton in a petri dish. Half of the pepper

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Table 6. Predation rates and residence times of A. cucumeris as a function of prey density on cucumber and pepper leaves.

Crop and prey density		# eaten	proportion eaten	residence time (hours)
Cucumber				
0 thrips/cm2	Mean=	----	----	7.02
n=16	SE=			1.58
.1 thrips/cm2	Mean=	.50	.50	11.27
n=16	SE=	.12	.12	2.29
1.0 thrips/cm2	Mean=	3.95	.40	22.32
n=16	SE=	.39	.04	1.16
Pepper				
0 thrips/cm2	Mean=	----	----	5.16
n=16	SE=			1.63
.1 thrips/cm2	Mean=	.75	.75	6.79
n=16	SE=	.10	.10	1.32
1.0 thrips/cm2	Mean=	6.65	.67	16.05
n=16	SE=	.48	.05	1.85
	crop	Chi^2= 16.06 **		F= 9.44 **
	density	-4.63		33.54 **
	inter.	3.65		.87

** $p < .01$

Figure 7. Relationship between residence time and predation rate of A. *cucumeris* on pepper leaves. (Y=-.15+.67X, r=.82, n=19, p<.01)

Thrips Eaten

Leaving time (hours)
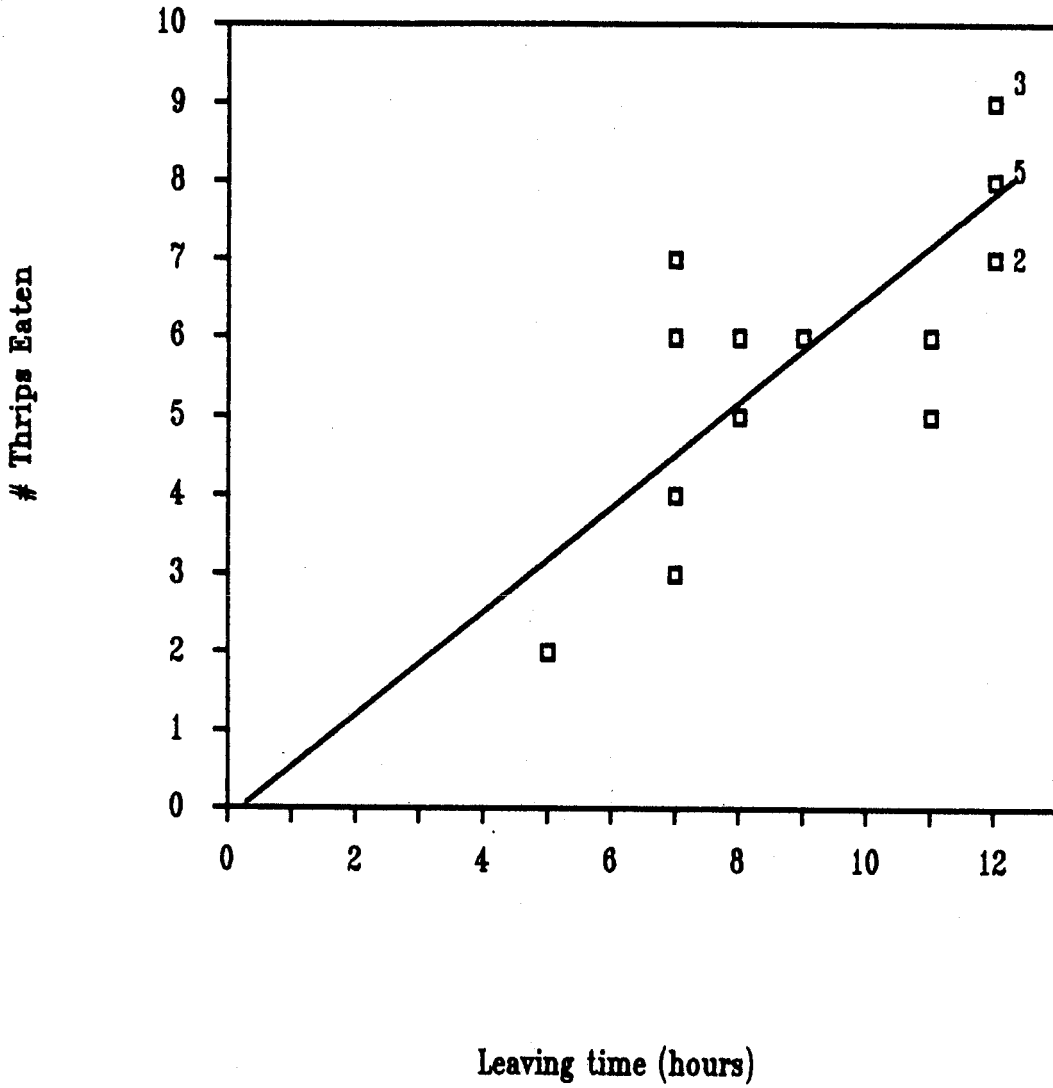
Figure 8. Relationship between residence time and predation rate of *A. cucumeris* on cucumber leaves. (r=.27, n=19, p>.05)
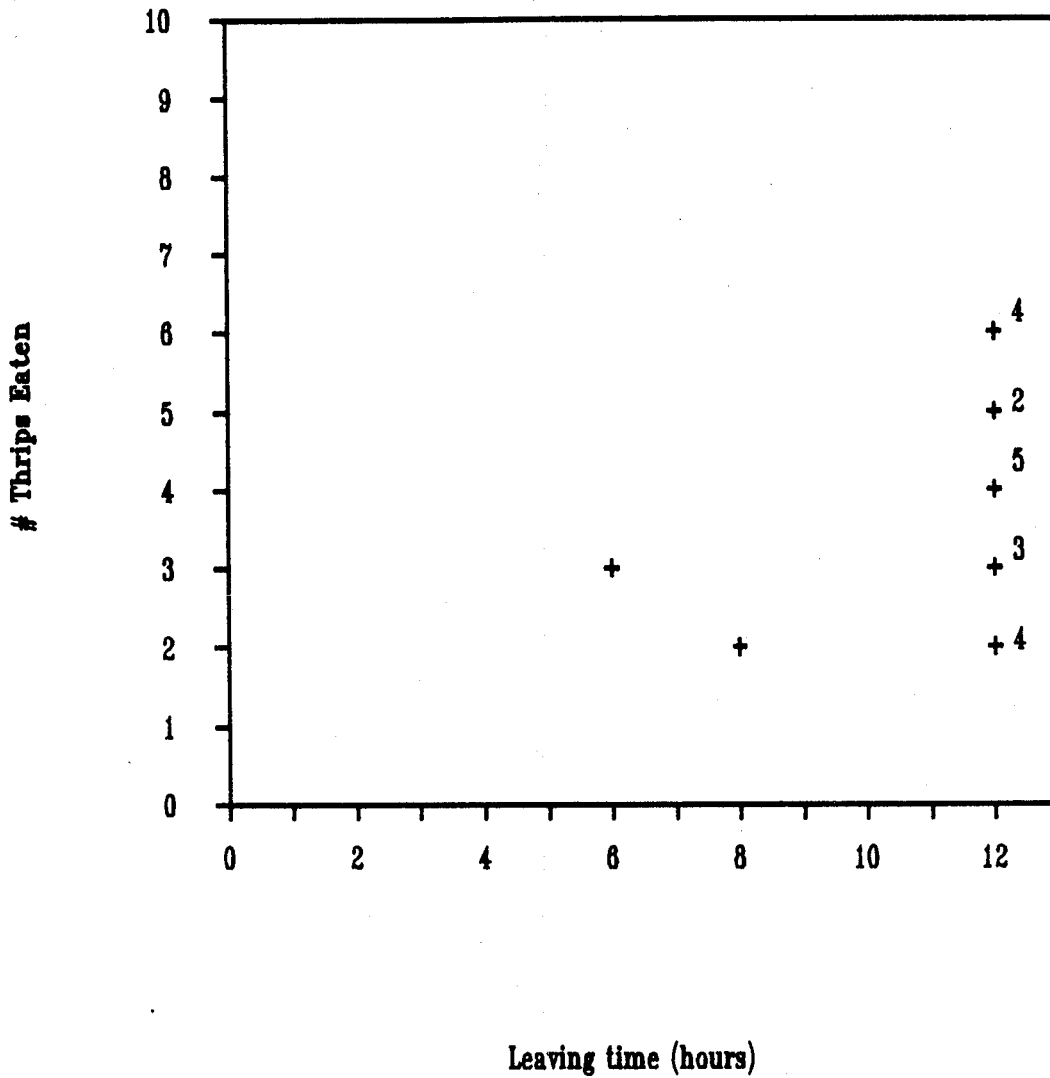
Table 7. The number of _A. cucumeris_ to remain on leaf disks as a function of predation success.

Pepper

	Leave within 12 hours	Remain 12 hours or longer
Eat	1	8
Do not eat	9	3

Fisher's exact probability test, p=.009

Cucumber

	Leave within 12 hours	Remain 12 hours or longer
Eat	2	9
Do not eat	8	1

Fisher's exact probability test, p=.003

arenas and half of the cucumber arenas were infested with
ten early-instar thrips nymphs each for 24 hours preceding
the experiment. The remaining arenas were left uninfested.
All thrips were removed prior to the start of each trial.

Mites were isolated on either pepper or cucumber leaf
disks, which determined the plant disk on which they would
later be tested on, and starved for 24 hours prior to the
start of the experiment. This allowed mites some time to
become accustomed to travelling on either pepper or cucumber
leaves.

Each of the four leaf treatments: uninfested cucumber,
previously-infested cucumber, uninfested pepper and
previously-infested pepper was replicated 19 times.

At the start of each trial a mite was transferred to
one of the four treatment arenas. A fresh arena was used
for each test mite. Observations began 30 seconds after
introducing a mite to an arena. Video equipment was used to
record all mite activities for a five minute period. The
search path of each mite was mapped and its location and
behavior at five-second intervals was recorded from the
videotapes.

Search path variables included: the speed of travel,
the distance travelled, the number of turns greater than 90°
and the proportion of the search path classified as either
straight, tortuous and still. In addition, the amount of
time allocated to exploring, grooming, drumming and walking

were recorded. Kruskal-Wallis tests were used to analyze the effect of crop species and the presence or absence of thrips damage on mite behavior and search path tortuosity. Other search path variables were analyzed by ANOVA after being transformed to meet the assumptions of normality and homogeneity of variances.

The previous experiment demonstrated that the predation rate of A. *cucumeris* was influenced by the species of the host plant. Mites were more successful predators of thrips on pepper leaves than on cucumber leaves. This difference in predation success should be accounted for by the search path and behavior of the predatory mites on the two crops.

Mites on pepper leaves should have a more efficient search path than mites on cucumber leaves. This would be expected to result in a higher encounter rate with prey on pepper leaves than on cucumber leaves. In addition, mites on previously-infested leaves were expected to travel more slowly and turn more frequently than mites on uninfested leaves.

(ii) Results

There were no significant differences in the behavior (Kruskal-Wallis, $X^2 < 5.99$, Figure 9), the proportion of the search path classified as tortuous, straight and still (Kruskal-Wallis, $X^2 < 5.99$, Table 8), or the search path (ANOVA, $F < 4.0$, $p > .05$, Table 8) of mites on uninfested and

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Figure 9. The allocation of time to different behaviors by A. cucumeris on uninfested (UI) and previously-infested (PI) cucumber and pepper leaves. (Bars topped by the same letter are not signigicantly different.)
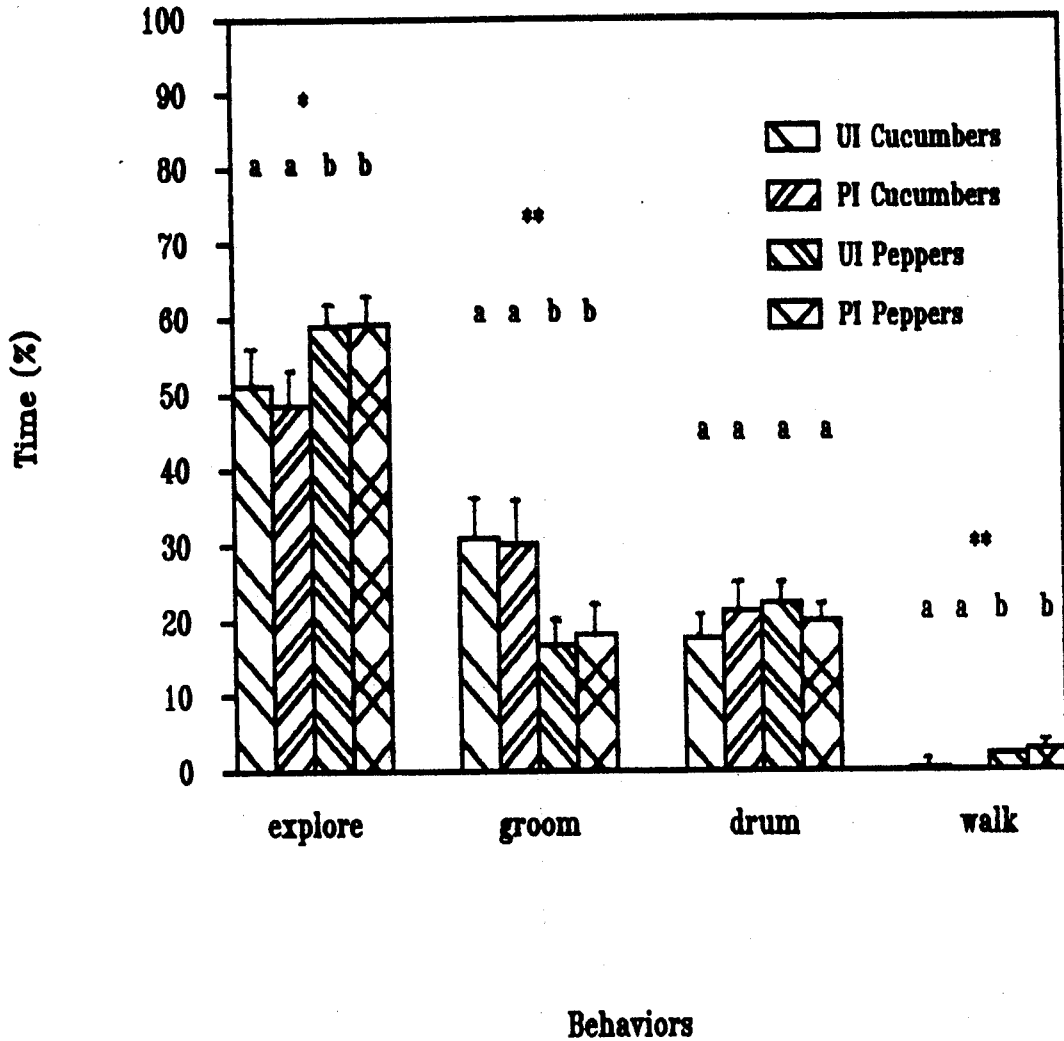
Table 8. Characterisitics of the search path of A. cucumeris on uninfested (UI) and previously-infested (PI) cucumber and pepper leaves.

		distance (mm)	turns/ distance	speed (mm/sec)	% straight	% tortuous	% still
Cucumber							
Uninfested n=19	Mean=	81.60	.28	.45	30.09	29.82	40.09
	SE=	10.40	.02	.03	2.57	3.22	4.76
Previously- infested n=19	Mean=	68.29	.30	.41	32.81	24.04	43.16
	SE=	8.00	.02	.03	2.78	2.39	4.55
Pepper							
Uninfested n=19	Mean=	181.70	.16	.78	45.44	32.37	23.95
	SE=	15.60	.01	.05	2.77	2.72	3.36
Previously- infested n=19	Mean=	178.80	.20	.76	38.42	36.84	24.82
	SE=	26.40	.02	.08	2.96	3.20	4.36
Transformation=		log(X)	(√X)	log(X)	(X)	(X)	(X)
F-values:	crop	39.70**	54.65**	65.11**			
	UI-PI	.23	3.98	1.41			
	inter.	.10	.53	.11			
Chi²:	crop				9.79**	8.89*	16.13**
	UI-PI				-.01	-.04	-.04
	inter.				2.78	2.82	.07

F-values of transformed data

* p<.05
** p<.01

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previously-infested leaf arenas. The lack of difference between mites on uninfested and previously-infested leaves is probably a result of the large amount of variation in the foraging of individual mites.

Amblyseius cucumeris allocated a larger proportion of time to exploring ($X^2=6.40$, $p<.05$) and walking ($X^2=11.01$, $p<.01$) on pepper arenas than on cucumber arenas, but spent more time grooming ($X^2=11.00$, $p<.01$) on cucumbers than on peppers (Figure 9). The large amount of time allocated to grooming on cucumber leaves may reflect the reduced activity level of mites on this crop. Alternatively, it may indicate the presence of some sticky, or irritating substance on the surface of cucumber leaves. There were no significant differences in the allocation of time to drumming on pepper and cucumber leaves ($X^2=.74$, $p>.05$, Figure 9).

The search path of the predatory mite varied considerably between pepper and cucumber leaves (Table 8). Amblyseius cucumeris travelled further, faster, and made fewer turns per distance travelled on pepper leaves than on cucumber leaves (ANOVA, $p<.01$). The search path of mites on pepper leaves was made up of a significantly larger proportion of both straight ($X^2=9.79$, $p<.01$) and tortuous walk ($X^2=8.89$, $p<.05$), while the search path of mites on cucumber leaves had a large portion of still ($X^2=16.13$, $p<.01$).

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D. Discussion

The length of time that a predator chooses to stay on a leaf is important in determining its efficiency as a biological control agent. The longer a predator stays the more likely it is to find prey, when prey are there. But, when there are no prey, it might be a better strategy to move to another leaf. This implies that efficient predators assess the quality of a particular leaf in terms of its prey density and modify their behavior accordingly. They spend more time searching in areas of high prey density and move to new areas when prey are depleted.

Amblyseius cucumeris stayed longer on leaves with a high density of thrips than on leaves with a low density of thrips. In addition, mites stayed longer if they successfully captured a prey than if they did not. If a mite did not capture a thrips within two hours of being placed on a leaf disk it was likely to leave.

Leaf residence time was also dependent on crop type. *Amblyseius cucumeris* remained on cucumber leaves significantly longer than on pepper leaves. On pepper leaves the predation rate and residence time were strongly correlated, indicating that A. cucumeris stayed longer on pepper leaves where they had already successfully captured prey than on pepper leaves where they had not captured prey. In contrast, A. cucumeris appeared to stay on cucumber

leaves regardless of predation success. Perhaps the predatory mite was less likely to find the escape route or less able to assess thrips density on cucumber leaves than on pepper leaves.

All the variation in the search path and the behavior of *A. cucumeris* was accounted for by the host plant at the thrips densities tested. Mites on uninfested and previously-infested leaf arenas did not forage differently.

The foraging behavior of mites on pepper leaves was characterized by a large portion of time allocated to exploring and a very small portion of time allocated to grooming. The search path of mites on peppers contained much more tortuous and straight walk than on cucumbers. In addition, *A. cucumeris* travelled faster and further on pepper leaves than on cucumber leaves. Mites also made few turns per distance travelled resulting in a broadly curving search path.

Foraging by *A. cucumeris* on cucumber arenas was characterized by the allocation of a large portion of time to grooming and much less time to exploring and walking than on pepper leaves. Mites also travelled more slowly and covered less distance during the five minute observation period. The search path of mites on cucumber leaves contained a large proportion of 'still'. Mites were less likely to change their location between successive five-

second intervals on cucumbers than on peppers. The higher turning rate on cucumbers resulted in mites frequently travelling through areas they had previously visited.

On pepper leaves mites travelled over a larger leaf area per unit time and were less likely to retrace their path than on cucumber leaves. The search path of A. cucumeris appeared to be more efficient on pepper leaves than on cucumber leaves (Figure 10) and should have resulted in a high encounter rate with prey and an increased predation rate on this crop.

The relationship between an individual's predation rate and food density is known as the functional response of the predator (Solomon 1949). The experiment conducted here is different from traditional functional response experiments in that predation was measured over an extended period of time and prey were not replaced after they were eaten. This means that the density of prey declined over the course of the experiment. But, this design probably mimics the situation faced by A. cucumeris preying on a leaf with a depleting prey population, particularly since the vulnerable first-instar thrips seem to be far less mobile than the mites.

As expected, the greater the density of prey the more thrips the mites ate. However, the proportion of available thrips eaten did not change with increasing prey density.

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Figure 10. Typical search paths of A. *cucumeris* on
previously-infested cucumber and pepper leaf
disks for five minutes. Cross-hatches
indicate five-second intervals.

Cucumber

Pepper

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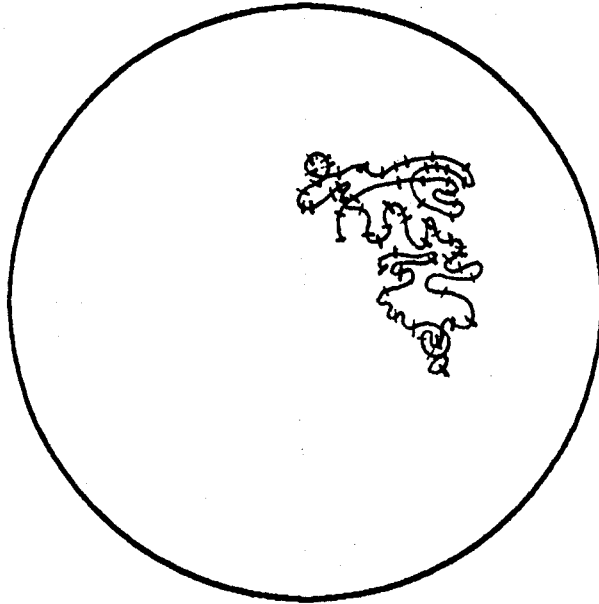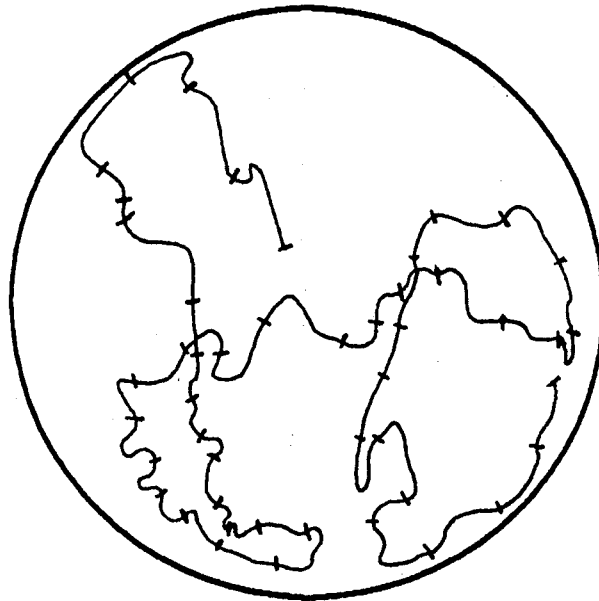
Therefore, A. *cucumeris* exhibited density independent foraging, as defined in the literature (Hassel 1966, Murdoch 1973), over the prey densities used in this experiment.

Not only did A. *cucumeris* have a lower predation rate on cucumber leaves than on pepper leaves, but it also remained longer and allocated less time to exploring. The results of the experiment outlined in Chapter 2 indicate that A. *cucumeris* may detect some cue, perhaps a volatile kairomone, in the presence of thrips damage and that this triggers an increase in the explore behavior. The results of this experiment could be explained if kairomones produced on cucumber leaves were less attractive or harder to detect than those on pepper leaves.

Amblyseius cucumeris differed significantly in its allocation of time to exploring and grooming and its search path efficiency on pepper and cucumber leaves. These differences in foraging likely influenced prey encounter rates and accounted for the observed difference in predation rates on the two crops.

The differential success of A. *cucumeris* as a biological control agent of western flower thrips on cucumber and pepper crops can be explained, at least in part, by differences in its predation rate on leaves from the two crops. The superior ability of A. *cucumeris* to control thrips on peppers is a result of its efficient

foraging strategy which likely results in a high encounter rate with prey. This is not to say that predation success is the only factor. Differences in the population growth rate of thrips on the two crops have not been thoroughly investigated and may contribute to the explanation for the differential success of biological control.

CHAPTER V

EFFECT OF LEAF SURFACES ON FORAGING

A. Introduction

The experiments outlined in Chapter 4 demonstrated that
A. cucumeris differed in its predation rate, behavior and
search path on pepper and cucumber leaves. Mites had
greater success preying on western flower thrips on pepper
leaves than on cucumber leaves. The higher predation rate
was probably accounted for by differences in the behavior
and search path of *A. cucumeris* which increased the
likelihood of encountering prey on pepper leaves.

Several studies have shown that the physical
characteristics of the host plant may influence predator and
parasite performance (Rabb and Bradley 1968, Elsey 1974,
Evans 1976, Hulspas-Jordaan and van Lenteren 1978, Bergman
and Tingey 1979, Obrycki 1986, Price 1986, Li et al. 1987).

In a detailed study of the foraging behavior of the
greenhouse whitefly parasitoid, *E. formosa*, Hulspas-Jordaan
and van Lenteren (1978) demonstrated that the
parasitization rate was strongly influenced by the leaf
structure of the plant. They looked at six plant species
with varying densities of leaf hairs. Cucumber and gherkin
both have large stiff hairs, tomato and gerbera have much
smaller hairs, eggplant has relatively few hairs, and sweet
pepper has no hairs at all. They found that both the

walking speed and the rate of parasitization were highest on smooth leaves and inversely proportional to leaf hairiness. (van Lenteren et. al. 1980a, van Lenteren and de Ponti 1989)

Amblyseius cucumeris may be similarly affected by plant morphology. The leaf surfaces of peppers and cucumbers differ markedly from each other. Whereas pepper leaves are smooth and waxy, cucumber leaves are covered with hairs. Cucumber hairs are unicellular, stellate and about .40 mm long (van Lenteren and de Ponti 1989). The hairs are non-glandular and not known to produce plant exudates, although they may trap irritating or sticky substances, such as the honeydew produced by aphids, scales or whiteflies.

The previous experiment suggested two ways in which the presence of hairs on cucumber leaves may have affected the foraging of A. cucumeris. First, the hairs may have physically interfered with the search path of the mites. *Amblyseius cucumeris* was frequently observed bumping into the hairs on cucumber leaves and then changing its direction of travel. As a result, mites frequently searched areas of the leaf that they had already visited. Second, the hairs may have been associated with some irritating or sticky substance which caused an increase in grooming behavior and a reduction in exploring.

De Ponti (1980) obtained a hairless cucumber mutant, Cucumis sativus L. cv IVT No. 761077 Mayak, from the U.S.S.R.. I received seeds from this hairless cucumber

variety from Dr. J. van Lenteren and Dr. L. Vet (Wageningen Agricultural University, The Netherlands). Plants were grown in the greenhouses of the Agriculture Canada Research Station in Agassiz, B.C.

Leaves from hairy, commercial cucumber varieties and the glabrous cucumber variety were assumed to be identical, except for the presence or absence of hairs, in this experiment. In fact, the two leaf types appeared similar in every other way including size, venation and cuticle texture.

If the presence of hairs on normal cucumber leaves adversely affected the foraging success of A. *cucumeris* then mites on smooth, cucumber leaves should have a higher predation rate, allocate more time to exploring, allocate less time to grooming and have a more efficient search path than mites on hairy cucumber leaves.

This chapter reports on the results of two experiments which were designed to test the influence of leaf hairiness on the predation rate, search path and behavior of A. *cucumeris*.

B. Experiment 1: Predation rates

(i) Methods

This experiment was conducted in a similar manner to Experiment 1 outlined in Chapter 4. Only the high prey density treatment of 1.0 thrips per cm^2, or ten thrips per

leaf disk, was used. Leaves from hairy and smooth cucumber varieties were used in the place of pepper and cucumber leaves.

Variables recorded included the number of thrips eaten and the residence time of mites. One-way t-tests were used to test for differences in the predation rate and leaving time of mites on smooth and hairy cucumber leaves.

If the presence of hairs on cucumber leaves is an important factor in determining the predation success of A. cucumeris then predation rates should be higher on the hairless cucumber variety than on the hairy cucumber variety. In addition, residence time was expected to be dependent on predation success on hairless leaves.

(ii) Results

The predation rate of A. cucumeris was substantially higher on smooth leaves than on hairy leaves (t=3.14, p<.01). Amblyseius cucumeris consumed an average of 4.70 ± .43 thrips on smooth leaves but, only 2.84 ± .38 thrips on hairy leaves (Table 9).

There was no significant difference in the amount of time that A. cucumeris remained on smooth and hairy leaves (t=.94, p>.05, Table 9). However, the length of time that A. cucumeris remained on smooth leaf disks depended on its predation success. There was a strong correlation (r=.88, t=7.93, p<.001, Figure 11) between the number of thrips

Table 9. Predation rates and residence times of A. cucumeris on hairy and smooth cucumber leaves with a prey density of 1.0 thrips per cm^2.

		# thrips eaten	proportion of thrips eaten	residence time (hours)
Hairy n=19	Mean= SE=	2.84 .38	.28 .04	14.42 2.02
Smooth n=20	Mean= SE=	4.70 .43	.47 .04	17.20 1.99
	t=	3.14**	3.14**	.94

** one-tailed, p<.01

Figure 11. Relationship between residence time and predation rate of *A. cucumeris* on smooth cucumber leaves. ($Y = .36 + .45X$, $r = .88$, $n = 19$, $p < .01$)
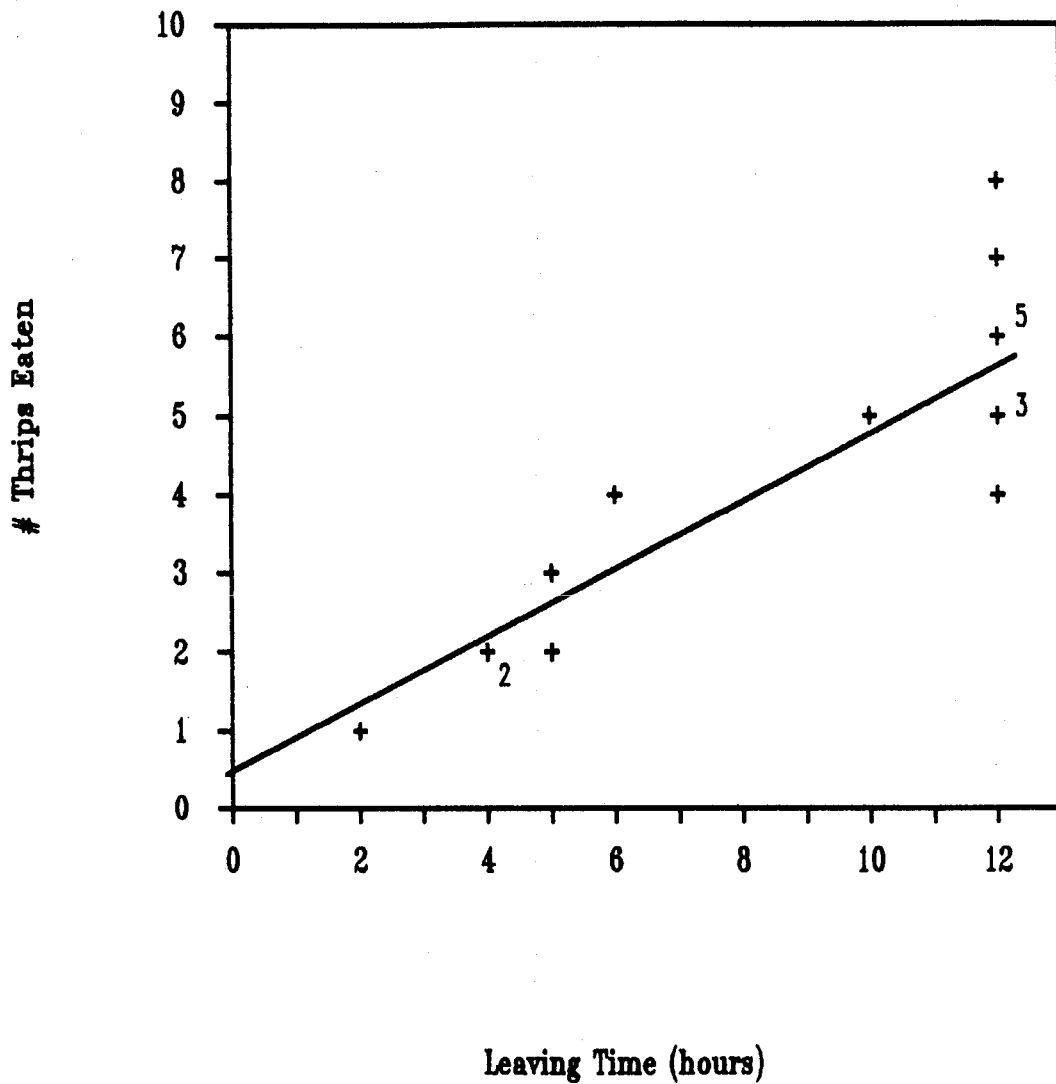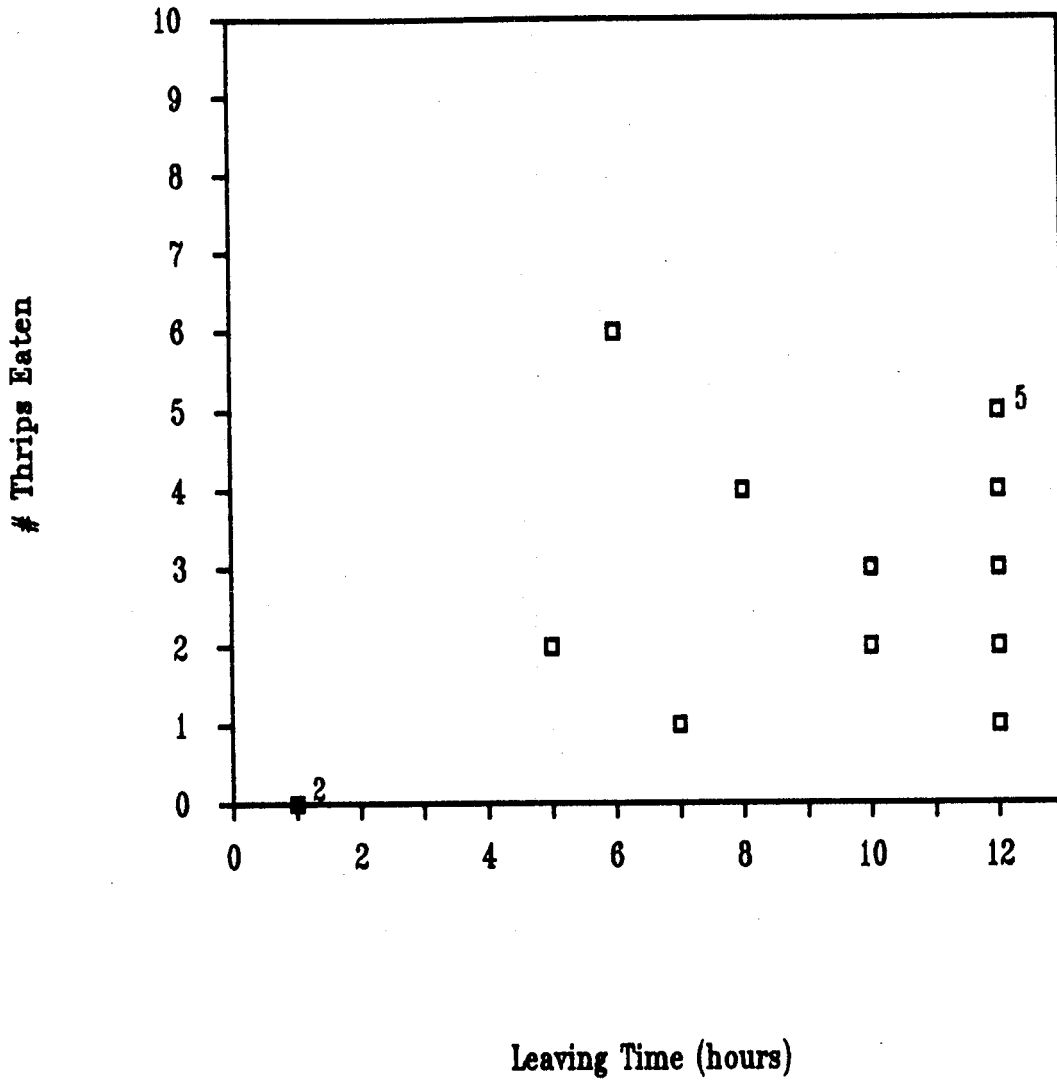

Thrips Eaten

Leaving Time (hours)

Figure 12. Relationship between residence time and
            predation rate of A. *cucumeris* on hairy
            cucumber leaves. (r=.43, n=19, p>.05)

eaten and the residence time of mites on smooth leaves. On hairy leaves this relationship did not hold (r=.43, t=2.05, p>.05, Figure 12).

Mites on smooth cucumber leaves showed a higher predation rate, but did not remain on test arenas longer than mites on hairy cucumber leaves. The residence time of mites on smooth leaves was correlated with predation success. In contrast, mites seemed to remain on hairy cucumber leaves regardless of predation success.

C. Experiment 2: Search path and behavior

(i) Methods

This experiment was conducted in a manner similar to Experiment 2 outlined in Chapter 4, but used only uninfested leaves. Leaves from hairy and smooth cucumber varieties were used in the place of pepper and cucumber leaves.

The search paths of the mites were mapped and their location and behavior at 5-second intervals were recorded. Variables included: the allocation of time to exploring, grooming, drumming and walking; the distance travelled; the turning rate; the speed of travel and the proportion of the search path classified as straight, tortuous and still. T-tests were used to identify differences in these parameters between mites on hairy and smooth cucumber leaves.

This experiment was designed to determine the effect of leaf hairs on the search path and behavior of A. cucumeris.

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I predicted that mites on smooth leaves would: allocate more time to exploring, allocate less time to grooming and have a more efficient search path than mites on hairy cucumber leaves. Such a foraging strategy would likely result in a higher encounter rate with prey on smooth leaves than on hairy leaves and would explain the higher predation rate that was observed on the hairy variety in the previous experiment.

(ii) Results

There were significant differences in the allocation of time by A. cucumeris to exploring (t=2.20, p<.01) and grooming (t=2.60, p<.01), but not to walking (t=.28, p>.05) and drumming (t=1.66, p>.05) on smooth leaves and hairy leaves (Figure 13). Amblyseius cucumeris spent 69.75 ± 2.88% of its total activity budget exploring on smooth leaves and only 58.33 ± 4.23% on hairy leaves. As predicted, the amount of time allocated to grooming was significantly higher on hairy leaves than on smooth leaves. It is unclear whether the increased grooming on hairy leaves reflects the reduced activity level of the mite or the presence of some sticky or irritating substance trapped in the leaf hairs.

Figure 14 shows typical search paths of A. cucumeris on hairy and smooth leaves for a five minute period. Amblyseius cucumeris tended to travel further (t=4.24, p<.01) and faster (t=4.66, p<.01) on smooth leaves than on

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Figure 13. The allocation of time to different behaviors by *A. cucumeris* on hairy and smooth cucumber leaves.
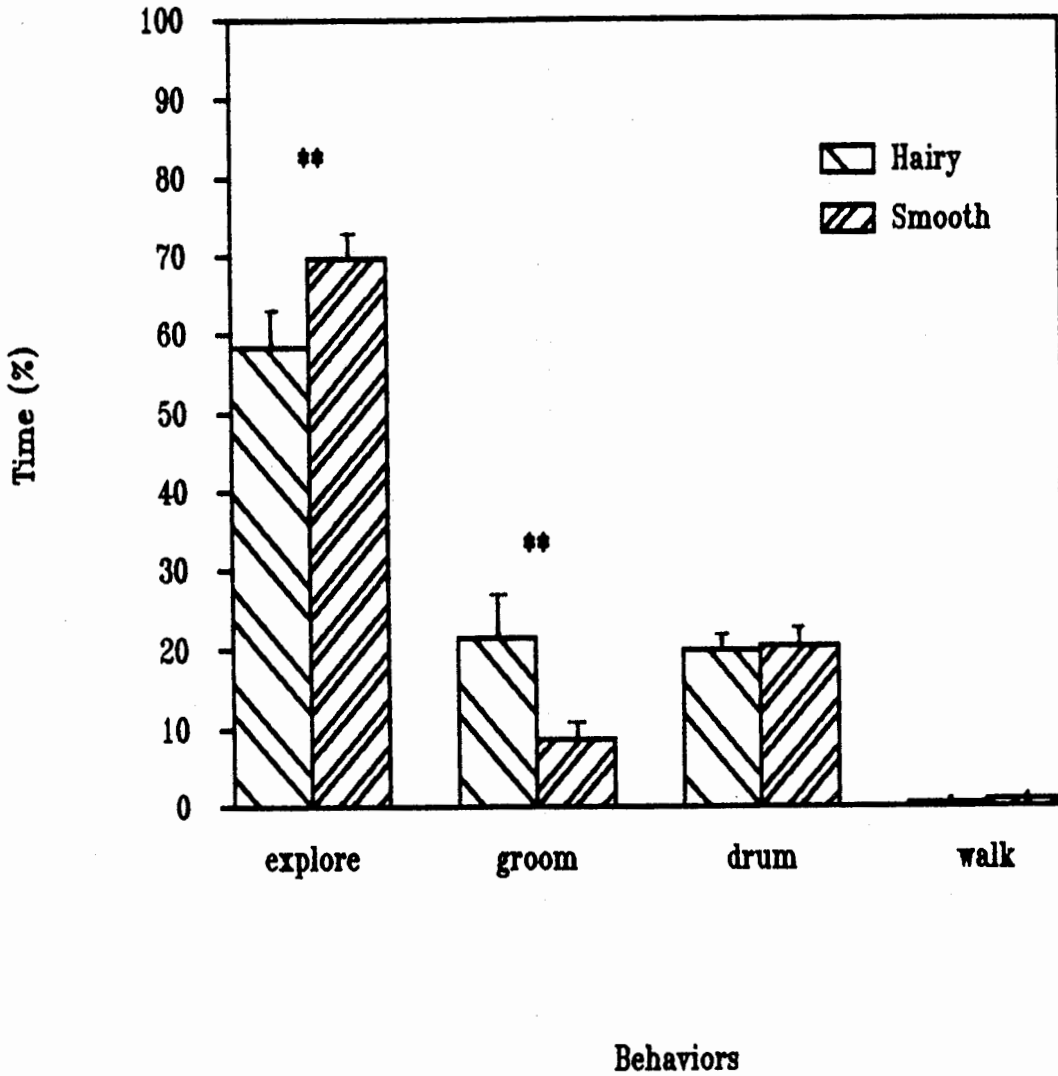
Figure 14. Typical search paths of A. *cucumeris* on hairy and smooth cucumber leaf disks for five minutes. Cross-hatches indicate five-second intervals.
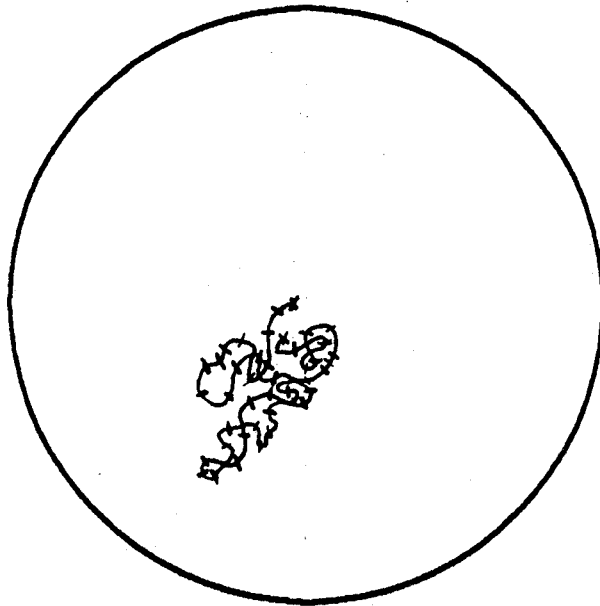
Hairy
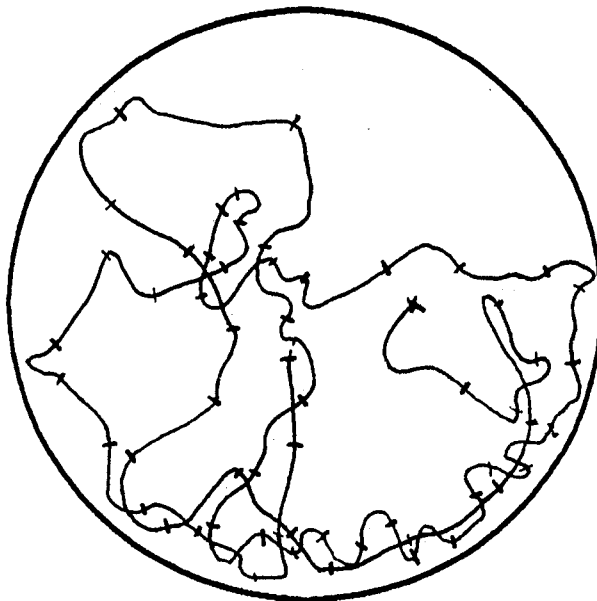
Smooth

Table 10. Characteristics of the search path of A. cucumeris on hairy and smooth cucumber leaves.

		distance (mm)	# turns/ distance	speed (mm/sec)	% straight	% tortuous	% still
Hairy n=20	Mean=	118.90	.30	.77	41.92	29.00	29.08
	SE=	13.10	.08	.04	4.14	2.68	5.52
Smooth n=20	Mean=	223.30	.20	1.11	40.92	44.75	14.33
	SE=	20.80	.06	.06	2.66	3.38	2.76
Transformation=		(X)	log(X)	(X)	asin(√X)	asin(√X)	asin(√X)
t=		4.24 **	2.16 **	4.66 **	.20	3.65 **	2.39 **

t-values of transformed data

** one-tailed, p<.01

hairy leaves (Table 10). In addition, mites turned more per distance travelled on hairy leaves than on smooth leaves (t=2.16, p<.01). As a result mites made broad turns on smooth leaves, whereas on hairy leaves they frequently turned and searched previously visited parts of the leaf.

Mites spent more time still on hairy leaves than on smooth leaves (t=2.39, p<.01). The search path of mites on smooth leaves contained a larger proportion of tortuous walk than that of mites on hairy leaves (t=3.65, p<.01). There was no significant difference in the amount of straight walk in the search path of mites on hairy and smooth cucumber leaves (Table 10).

As predicted, mites appeared to search smooth leaves more efficiently than hairy leaves. Mites should encounter more prey on smooth leaves since they travel over a larger leaf area per unit time and are less likely to retrace their path than on hairy leaves.

D. Discussion

As predicted, there were significant differences in the amount of time allocated to exploring and grooming, and in the search path efficiency of A. cucumeris on hairy and smooth cucumber leaves. These differences would be expected to affect prey encounter rates and account for the observed difference in predation rates on the two cucumber varieties.

Cucumber leaf hairs could have affected A. cucumeris in

several ways in these experiments. Leaf hairs may have interfered with the movement of mites by physical intervention or by trapping sticky substances, such as honeydew produced by Homopteran insects. The presence of irritating or sticky materials may have resulted in more time being allocated to grooming. Hairs may also have reduced the ability of the predatory mite to detect plant volatiles or kairomones and interfered with its ability to orient toward prey. In addition, the presence of leaf hairs may have affected A. cucumeris by affecting the temperature and humidity on the leaf surface.

The success of A. cucumeris as a biological control agent of western flower thrips seems to be strongly affected by the leaf surface characteristics of the host plant. In this experiment, the presence of hairs on the leaves of commercial cucumber varieties reduced the amount of time allocated to searching, interfered with the mobility of the mite and resulted in a reduced predation rate. The commercial use of a hairless cucumber variety would be expected to enhance the action of A. cucumeris as a biological control of western flower thrips.

CHAPTER VI

CONCLUSIONS

Relatively few studies have examined the effect of the
host plant on the foraging success of entomophagous insects.
Studies of tritrophic systems are essential if we are to
understand what role plants play in determining the success
of biological control. Such an approach would not only help
explain the differential success of biological control on
different crops, but would also indicate which plant
characteristics most influence natural enemies.

This study has provided one explanation for the
observed difference in the success of A. cucumeris as a
biological control agent of western flower thrips on
greenhouse pepper and cucumber crops. The predatory mite
differed in its predation rate on pepper and cucumber
leaves. Therefore, the superior ability of the predatory
mite to control thrips on peppers may be accounted for, at
least in part, by a higher predation rate on this crop.

The performance of A. cucumeris as a predator is
influenced by the physical characteristics of the host
plant. The presence of hairs on the leaves of commercial
cucumber varieties reduced the amount of time allocated to
searching and interfered with the mobility of the mite. As
a result, the prey encounter rate of A. cucumeris was
probably reduced on hairy cucumber leaves, accounting for

the lower predation rate observed on hairy compared to smooth leaves.

Hulspas-Jordaan and van Lenteren (1978), conducted a detailed study of the searching behavior and parasitization rate of the greenhouse whitefly parasitoid, *E. formosa*, on several host plants. They demonstrated that the highest rate of parasitization occurred on hairless plants such as sweet pepper and the lowest on densely-haired plants such as cucumber. In addition, the rate of parasitization and the walking speed of *E. formosa* were highest on smooth leaves and inversely proportional to leaf hairiness (van Lenteren et. al. 1980a, van Lenteren and de Ponti 1989).

E. formosa travelled 3.5 times as fast on leaves from glabrous cucumber mutants than on normal, hairy leaves (Hulspas-Jordaan and van Lenteren 1978, de Ponti 1980). The problem on these completely smooth leaves was that the parasitoids walked so fast that they walked over whitefly larvae without noticing them (van Lenteren 1989). In addition, because hairlessness and bitterness are genetically linked, the hairless cucumber varieties are not suitable for commercial production (van Lenteren pers. comm.).

A breeding program has been set up to develop hybrids between hairy and hairless cucumber varieties which are intermediate in hairiness. The aim is to produce a cucumber

variety which is favorable to the control of greenhouse whitefly by *E. formosa* and suitable for commercial cucumber production.

Commercial use of a less hairy cucumber variety would likely influence the biological control of western flower thrips by *A. cucumeris*. I would expect *A. cucumeris* to provide better thrips control on this variety than it does on the cucumber varieties currently grown. The foraging behavior and predation rate should be intermediate to those observed on smooth and hairy cucumber leaves in Chapter 5.

Another important aspect to the success of thrips biological control is whether hairless cucumbers, normally-haired cucumbers and intermediate hybrids are the same quality of host plant for western flower thrips. Host plant acceptance, the rate of development from egg to adult, mortality and fecundity could vary on the different leaf types. The relative effect of resistant crop varieties on the pest and its natural enemies must be evaluated.

It is generally recognized that breeding plants resistant to insect attack is compatible with biological control yet, few studies have taken a tritrophic level approach (Bergman and Tingey 1979, Price 1986, van Lenteren and de Ponti 1989). Breeding for insect resistance changes plant quality and this will have an impact on both the pest species and its natural enemies. Only by understanding the

interaction between the three trophic levels can we hope to manipulate plant characteristics so as to produce resistant plant varieties, which also promote natural enemies and biological control.

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