PREDATION OF TWO-SPOTTED SPIDER MITES,
*Tetranycus urticae* KOCH (ACARI: TETRANYCHIIDAE)
BY THE PREDATORY MIDGE, *Feltiella minuta* FELT
(DIPTERA: CECIDOMYIIDAE).

by

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B.Sc. (Hons.) Makerere University, 1986

THESIS 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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Title of Thesis/Project/Extended Essay
PREDATION OF TWO-SPOTTED SPIDER MITES, TETRANYCHUS URTICAE

Koch (Acari: Tetranychidae) by the Predatory Midge,

Feltiella Minuta Felt (Diptera: Cecidomyiidae)

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Predator - prey relationships are often influenced by factors such as the functional response and prey preference of a predator and hygrothermal conditions. In this study, the aforementioned factors were examined for the predatory midge, *Feltiella minuta* Felt, a predator of *Tetranychus urticae* Koch (two-spotted spider mites).

The functional response of *F. minuta* to increases in density of adult male and female two spotted spider mites followed a Holling type-II functional response. The rate of successful search and the handling time predicted by the Holling disc equation for male mites were 1.11 h$^{-1}$ and 0.28 h respectively. The predicted rate of successful search and handling time for female mites were 1.59 h$^{-1}$ and 1.74 h respectively. Doubling the size of the experimental arena from 2 cm$^2$ to 4 cm$^2$ had no significant effect on the functional response of *F. minuta*.

Preference of *F. minuta* for adult male and female mites was evaluated using functional response models. Analyses suggest *Feltiella minuta* exhibited a preference for female mites. A preference index of 0.69 was calculated using the ratio of rates of successful search (males:females).

The effects of temperature and humidity on mite consumption by *F. minuta* were investigated. The number of two-spotted spider mites eaten at relative humidities of 35, 60, 70, 80 and 90% were determined at a temperature of 27°C. Prey
consumption was significantly higher at relative humidities of 80 and 90%. The number of prey eaten at temperatures of 15, 20, 27 and 32°C were determined at a relative humidity of 90%. The highest number of prey were consumed at 27°C.

The type-II response exhibited by F. minuta indicates that it can not stabilize predator - prey population dynamics on its own; implying this predator may be unable to effectively control spider mites. Results also indicated that biological control of spider mites using F. minuta may be enhanced by manipulating the hygrothermal environment.
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CHAPTER 1

INTRODUCTION

A. Background information

Two-spotted spider mites (TSSM) Tetranychus urticae Koch (Acarina: Tetranychiidae) currently pose a serious threat to the British Columbia (B.C) greenhouse tomato industry. Tetranychus urticae feed mainly on the underside of tomato leaves where they destroy chloroplasts and cause the foliage to develop a yellow mottling and to become brittle and parchment-like (British Columbia Ministry of Agriculture and Fisheries 1990, Sabelis 1981). The TSSM threat is due to the following:

(1) The predatory mite Phytoseiulus persimilis Athias-Henriot (Acari: Phytoseiidae), the biological control agent currently used for the control of TSSM, has failed due to the high density of glandular trichomes on the stems of tomato plants. Glandular trichomes trap and kill predatory mites as they migrate from leaf to leaf via the stem in search of TSSM (Van Haren et al. 1987). Because of the limited efficacy of P. persimilis, greenhouse tomato growers in B.C spend very large amounts of money on introductions of this predator (Gillespie 1992 - personal communication).

(2) Fenbutatin-oxide (vendex), a highly effective miticide
registered for the control of TSSM on tomatoes in Canada, can only be used by B.C greenhouse tomato growers as a last resort. This is because a high percentage of the tomatoes produced in B.C are exported to the United States of America (U.S.A) where residues of vendex on tomatoes are not tolerated (Gillespie 1992 - personal communication); vendex is not registered for use in U.S.A.

(3) The number of options available for control of TSSM are limited because any strategy adopted for TSSM on tomatoes must also be compatible with the use of the parasitoid, Encarsia formosa, for biological control of greenhouse whitefly, Trialeurodes vaporariorum. Given the harmful effects of broad spectrum chemical insecticides on E. formosa, finding another biological control agent to take the place of P. persimilis seems like the only logical solution to the problem.

The scenario discussed above, recently led to a survey of natural enemies of TSSM in the Fraser Valley in an attempt to find a native replacement for the predatory mite, P. persimilis. This was done in the summer of 1992 and the predatory midge, Feltiella minuta Felt (Diptera: Cecidomyiidae), was identified as the most common natural enemy that was encountered (Gillespie et al. 1994). The larvae of this gall midge feed on all developmental stages of TSSM (Gillespie et al. 1994). To understand how F. minuta interacts with TSSM, models describing the predator-prey relationships between F. minuta and T. urticae should be developed.
Because of the recent taxonomic revision of Tetranychid (Acarina) mite predators of genus Feltiella, the new name for *F. minuta* is *Feltiella acarisuga* Vallot (Gagne 1995).

In the past, use of natural enemies to control pest populations was almost always based on observations or experiment and not theory. Natural enemies were chosen on the basis of what was known about their general life history, their tendency to attack the pest, whether they existed at the same time with the pest, physiological adaptation to the pest's climate and other characteristics deemed important for a predator to possess (Murdoch 1973). No effort was made to explain the way in which predation operated for successful and unsuccessful natural enemies, and lack of financial support was always blamed for this trial and error approach (Murdoch 1973). In the 1960's the situation started to change with a great deal of emphasis put on understanding how predators work by the use of techniques like modelling of entire pest situations (Murdoch 1973). Such models contain the necessary information about predator - prey dynamics, and therefore help us understand the significant interactions in the real world; this is crucial for the development of a sound pest management strategy (Ruesink 1976).

To predict the performance of *F. minuta* as a biological control agent, it is absolutely important that mathematical models describing *F. minuta* - *T. urticae* relationships be established. The construction of such models involves
documenting and explaining the behaviour of \textit{F. minuta}, in the hope of arriving at well corroborated general relationships; and incorporating these general relationships into mathematical models and exploring their implications for the behaviour of \textit{F. minuta} - \textit{T. urticae} at the population level (Hassel et al. 1976).

The amount of information available on \textit{F. minuta} is limited and does not exist in a form that can be used to construct models describing the behaviour of this predator.

My study was designed to document and explain aspects of the predatory behaviour of \textit{F. minuta} needed for the establishment of a general relationship between this predator and \textit{T. urticae}.

Predator response to prey density (functional response) was given much attention in my study because it is vital for the formation of the basic framework used in the mathematical modelling of predator-prey population dynamics (Hassel et al. 1976).

\textbf{B. Functional response theory}

Functional response describes the rate at which a predator kills its prey relative to the density of that prey (Solomon 1949). Functional response curves are useful in identifying the density at which a pest would escape control by the predator, the inference of basic mechanisms underlying predator-prey interactions and the improvement of practical
predictive powers for biological control (Houck and Strauss 1985, O'Neil 1990). Improving the predictive powers for biological control often involves assessing the contribution of a predator to the dynamics of a pest population (O'Neil 1990).

When an insect predator species is exposed to different densities of a single prey species in the same environment, the likely outcome is that the number of prey killed per unit time increases at a decelerating rate (Holling 1959b). Assuming *F. minuta* larvae show this type of functional response, the following equation describes this response (Holling 1959b):

\[
\frac{N_P}{P} = \frac{(a N T)}{(1 + a N T_h)} \quad (1)
\]

where \(\frac{N_P}{P}\) = Number of successful attacks (\(N_e\)) per predator.

\(N\) = Initial prey density.

\(T\) = Total time.

\(a\) = The predator's rate of successful search - the probability of capture for each prey while the predator is searching.

\(T_h\) = Handling time per prey item.

Equation 1 is essentially a deterministic instantaneous model which assumes that the predator searches without conscious choice at the same speed for randomly distributed
prey, with a constant handling time for all predators and prey items (Houck and Strauss 1985). The model assumes the likelihood of prey encounter is fixed and does not allow for the effect of prey depletion; i.e., the model is applicable only when the population size of prey remains essentially constant (Houck and Strauss 1985). This means that the prey density must be kept constant during functional response experiments because a description of the instantaneous feeding rate at each density is what is needed (Murdoch and Oaten 1975). This can be achieved by having experimental designs in which prey are continuously replaced as they are eaten (Houck and Strauss 1985, Murdoch and Oaten 1975).

Using Equation 1, Holling (1959a) examined the predator-prey interaction as a system of behavioural components that could be divided into parts and applied to predictive mathematical modelling. This equation is appropriate for a predator-prey system in which all available time is spent by the predator either in searching for prey or handling prey (Houck and Strauss 1985), and this means events will often occur in the following order:

(a) Prey are searched for until encountered.
(b) Encountered prey are pursued until caught.
(c) Captured prey are subdued.
(d) Subdued prey are eaten.
(e) A digestive pause follows the meal, and then searching resumes.
The predators rate of successful search is comprised of the following subcomponents: (i) the speed of pursuit of the predator, (ii) the speed of escape of the prey, (iii) capture success of the predator once the prey is encountered, (iv) the distance at which the predators can detect the prey, and (v) the ability of the prey to detect the predator (Holling 1966).

Handling time is comprised of subcomponents such as the time spent pursuing, subduing, and eating each prey, plus the time spent in a digestive pause before the next prey is attacked (Holling 1966).

When handling time is not negligible, the equation describes a functional response in which the per capita rate at which prey are killed decreases as prey density increases (Houck and Strauss 1985).

The rate of successful search determines the rate at which the curve approaches the upper asymptote and handling time is used to define the maximum number of prey that can be eaten, $T/T_h$ (Sabelis 1985, Hassel 1978).

According to Livdahl and Stiven (1983), a linear transformation of Hollings disc equation for use in regression analysis can be obtained by reciprocating both sides of equation (1) to give:

$$\frac{P}{N_s} = \frac{1}{(aTN + T_h)} \text{------------------- (2)}$$

This means data are plotted as reciprocals ($1/N_s$ and $1/N$).
The reciprocal of attack rate \( a \) will be equal to the slope of the line fitted by least squares, and the time of exposure multiplied by the \( y \)-intercept produces the handling time \( T_h \) (Livdahl and Stiven 1983). The rate of successful search and handling time are assumed to be constants for any given species of predator (Hassel 1978). Despite this assumption often being violated, considering \( a \) and \( T_h \) as constants remains adequate (Hassel 1978). In a functional response where the per capita rate at which prey are killed decreases with prey density, \( a \) and \( T_h \) are used in the construction of models describing predator-prey population dynamics.

Estimates of \( a \) and \( T_h \) should normally come from a standard non-linear least squares technique that is applied directly to the untransformed data (Hassel 1978). However, I used a linear regression applied to transformed data because it is not complicated (Livdahl and Stiven 1983). The problem with this approach is that it is filled with statistical problems and hence more likely to yield biased estimates of the parameters (Hassal 1978).

Estimates of \( T_h \) obtained by the Livdahl and Stiven method are normally much higher than those obtained from direct observation because the estimated values include periods of non-searching activity caused by factors such as satiation (Hassel 1978).

Obtaining single values of \( a \) and \( T_h \) for \( F. \) minuta is difficult because there are several larval instars which feed
on the male, female, immature and egg stages of TSSM. Values for both of these parameters are likely to be highly variable. This aspect should be incorporated into *F. minuta* - *T. urticae* models.

It is important to note that because functional response generally describes a short term behavioural phenomenon, functional response experiments should, therefore, take place in an interval that is short relative to the predator's life span (Murdoch and Oaten 1975). This ensures that the functional response reflects changes in the attack rate of a predator whose characteristics (age and size) remain basically constant during the interval (Murdoch and Oaten 1975).

In functional response experiments, different predators should be presented with different prey densities because this ensures each datum is statistically independent and eliminates any effect of the predator's "remembering" having fed at a previous feeding densities (Murdoch and Oaten 1985). The experiments can be likened to a predator exposed to prey whose density varies over time, on condition that there is no "memory" effect (Murdoch and Oaten 1975).

Functional response experiments conducted on a wide range of animals have revealed several kinds of curves from which three main types have been recognized (Holling 1959a).

**Type I.**

This type of curve represents an increasing linear
relationship (a linear rise to a plateau). This means prey are killed at a constant rate; i.e., the searching efficiency, \( N_s/N \), is constant. This type of response is found in filter feeders such as crustacean predators which consume plankton in direct proportion to its availability in the surrounding environment (Hassel 1978). The plateau of the curve occurs when the animal is satiated (Hassel 1978).

**Type II.**

In this type of response a predator species given varying densities of a single prey species eats more prey at higher prey densities, but does so at a decelerating rate. The searching efficiency is, therefore, an inverse function of prey density. This response produces a decelerating curve. This type of response has been found in a wide variety of predators including predatory insects (Holling 1966).

According to Murdoch and Oaten (1975) and Murdoch (1973), three factors are responsible for this type of response:

1. The initial rise in the curve is determined by contacts with prey increasing with prey density.
2. Because some time is spent handling each prey caught, the amount of time available for searching decreases with prey density.
3. A predator may reduce its hunting rate as it becomes more satiated, and it is likely to be more satiated more of the time at high prey densities than at low prey.
densities. This means its average hunting rate will decline with prey density.

The linear type-I response can be considered as a special case of the type-II response in which handling time is zero (Hassel 1978, O'Neil 1990). For both type-I and type-II responses, predation is not density dependent, i.e. the predation rate or predation efficiency, does not increase with prey density. This lack of density dependence, in addition to the inherent time-lag between an attack and the production of predator offspring results in these two types of response failing to stabilize predator - prey dynamics on their own; they cause instability in models (Hassel 1978).

**Type III.**

This type of functional response produces a sigmoid curve, whose upper asymptote is due to the effects of handling time; i.e. at high prey densities, predators spend all their available time handling prey (O'Neil 1990). The rate at which prey are killed increases with increasing prey density, but only over a portion of the range of prey density (O'Neil 1990). This results in a partly density-dependent prey mortality. This type of response is found in some parasitoids like *Encarsia formosa* (Burnett 1964). Despite being density dependent up to some threshold of prey density, a type-III functional response can not by itself stabilize predator - prey dynamics because of the time-lag in the production of
offspring resulting from the capture of prey (Hassel 1978). If
time delays are ignored, then predator-prey models based on
this type of response become stable (Hassel 1978). This is why
type-III functional response is wrongly believed to greatly
contribute to the stability of predator-prey population
dynamics.

Stability of predator-prey models is emphasized because it
is an important characteristic of effective biological control
(Hassel 1978).

According to Murdoch (1973) and Murdoch and Oaten (1975),
this type of response may arise for two reasons:

(1) The predator may not receive enough stimuli from the
prey at low prey densities to make it hunt intensively.

(2) In the field it is quite possible that a small number of
refuges offering security for prey exist so that as the
prey density is increased a greater proportion would be
vulnerable to attack.

Holling (1959a) considered the type-III response to be
characteristic of vertebrate predators, because of their
ability to learn. Learning leads to increase in handling
efficiency and searching efficiency, which means handling time
decreases while the rate of successful search increases. Some
insect predators have, however, shown this type of response.

The naiads of the damselfly Anomalagrion hastatum exhibit a
type-III response to Daphnia and Semicephalus when alternate
prey are present (Akre and Johnson 1979).
O'Neil (1990) suggests that the basis of a type-III response is that the predators are able to discern prey density and adjust their searching effort accordingly.
CHAPTER II

GENERAL METHODS

A. Introduction

Throughout this study a single method was used for the production of all experimental arenas - quadrangular tomato leaf surfaces. All the 3-day-old starved *F. minuta* larvae used in this study were also reared using a single method. All of the predation experiments were conducted under fluorescent light.

This chapter is devoted to describing the production of experimental arenas, rearing of 3-day-old starved larvae and evaluation of whether performing predation experiments under fluorescent light had an effect on *F. minuta* larvae. The effect of fluorescent light on predation had to be investigated because *F. minuta* larvae have been seen to forage primarily under low light conditions.

B. Experimental arenas

The experimental arenas used in this study were made from tomato plant leaves, *Lycopersicon esculentum* (cultivar Trust). To ensure a constant supply of high quality experimental arenas throughout the 4 month study period, three tomato crops, each consisting of 20 plants, were planted in a greenhouse. The planting times for the three crops were: (i)
three weeks before the study, (ii) one month after the study commenced and, (iii) two and a half months after the study commenced.

Harvesting the leaves involved picking two or three of the largest leaves from some of the plants 1-2 h before the experiment commenced, putting them in a plastic bag containing water to maintain their quality and storing them in a refrigerator at 10 °C. These leaves were later removed from their storage bags and cut into 1 cm by 1 cm or 1 cm by 2 cm arenas with their petioles intact. Because F. minuta and TSSM use both the top and bottom of the leaves, 1 cm by 1 cm and 1 cm by 2 cm arenas were considered as 2 cm² and 4 cm² of tomato leaf surface respectively. A drawing of an experimental arena is shown in Figure 1.

C. Preparation of experimental subjects

Predators employed in functional response experiments should be the same age and level of satiation. To accomplish this, three day old larvae that had been starved for 24 h were used for all experiments.

(i) Materials and Methods

The materials and methods described below are for the production of a single batch of 3-day-old starved F. minuta larvae.

One TSSM infested cucumber plant growing on sponge was put
on a small plastic plate which was half filled with water. It was then transferred to a cage containing about 120 *F. minuta* adults [male and female]. After 24 h the plant was shaken for 1 minute to remove any adults from the foliage and was transferred to a growth chamber maintained at 25 °C and 50% relative humidity. There was constant fluorescent light in the chamber. Water was added to the plastic plate every 12 h.

The eggs of *F. minuta* require 1-2 days to hatch and larvae mature to pupae in 4-6 days at 25 °C (Gillespie et al. 1994). Based on this information, the plant was removed from the growth chamber after 3.5 days and the larvae found on it were approximately 2 days old. Larvae were removed and placed in clean tomato leaf discs within easy grip culture dishes. Ten to 15 larvae were put into each dish. Dishes were then closed with tight fitting lids and taken to the same growth chamber that the rearing cucumber plant was in and left for 24 h. The products of this procedure were 3-day-old larvae that had been equally starved for 24 h.

There may be variability in larvae obtained from different plants. To minimize this variation, larvae obtained from one plant were used to perform experiments over the whole range of different treatments involved; i.e. blocking for variability that may exist in different larval batches. This meant that each time an experiment was conducted, 2 or 3 replicates of each treatment were performed using larvae from a single plant. This ensured that whatever variability existed was
shared by all treatments involved.
Figure 1. A drawing of the experimental arena. The water filled vial was required to prevent the arena from withering [decline in quality]. Experimental arenas used in the study were of two types that had the following dimensions: 1 cm x 1 cm and 1 cm x 2 cm.
WATER FILLED VIAL

LEAF PETIOLE

COTTON WOOL

EXPERIMENTAL ARENA
D. Effect of fluorescent light on predation

Larvae used throughout this study were reared in bright light, and experiments were also conducted under bright light. Given that F. minuta larvae often forage under low light conditions, it was therefore, important to determine if the bright light conditions that existed during rearing had any effect on consumption of TSSM by F. minuta larvae.

(i) Materials and method

Three-day-old starved larvae were used. Adult male TSSM used as prey were obtained from infested Pinto beans kept in the TSSM rearing chamber. The experiment was conducted in a well lit growth chamber maintained at 27°C; fluorescent bulbs provided the light. Each experimental arena consisted of a 2 cm² excised clean tomato leaf with a petiole.

The leaf petiole was placed in water in a small vial stoppered with cotton, and this was placed on a vial holder attached to a styrofoam box. Two types of boxes were used, one type had a lid made of transparent polythene material and the other was completely covered with black polythene material (including the lid). One litre of water was added to each box to keep the relative humidity at 90%.

The number of mites killed was determined by putting 25 prey and a single larva on each experimental arena for 8 h and counting the number of TSSM killed. Eleven replicates for each treatment were performed. Data were analysed using a t-test to
determine if the two treatment means differed significantly.

(ii) Results

The mean numbers of mites eaten in light and darkness were 9.40 +/- 1.17 [SE] and 11.45 +/- 1.16 [SE] respectively. There was no significant difference between the mean number of mites eaten (t-test, t=1.23; df=20; P>0.1). If the true difference between the mean number of mites eaten in darkness and those eaten in light is 2, the probability of falsely accepting the null hypothesis is 0.18, i.e the value of the type II error in this case is 0.18. If the true difference between the two means is 3, then the value of the type II error in this case is 0.06.

The results of this experiment show that rearing and conducting experiments with F. minuta under fluorescent light had no effect on the number of TSSM eaten.
CHAPTER III

FUNCTIONAL RESPONSE OF Feltiella minuta

A. Introduction

Predator response to prey density (functional response), to predator density and to prey distribution form the essential basis for the mathematical modelling of predator-prey population dynamics (Hassel et al. 1976). For a population dynamics model of F. minuta and T. urticae to be developed, it is vital to obtain information on these three aspects of predator-prey relationship. In my study, the functional response of F. minuta was examined. Presently there is no quantitative information on predation of TSSM by F. minuta. I did not find any published reports on the functional response of F. minuta feeding on TSSM in the literature. The objective of performing the functional response experiments described in this chapter was to provide quantitative information on the consumption of adult male and female TSSM by F. minuta. This information can be used in the construction of a F. minuta - T. urticae population dynamics model.

B. Adult males as prey

(i) Materials and methods

Three-day-old starved larvae were used for these
experiments. The prey, adult male TSSM, were obtained from infested Pinto beans which were kept in the mite rearing chamber. The experiments were conducted in well lit chambers maintained at a temperature of 27°C. Each experimental arena consisted of 2 cm² of excised clean tomato leaf surface. The tomato leaf petiole was placed in water in a small vial stoppered with cotton. This was then placed in a vial holder attached to a styrofoam box with a lid made of transparent polythene paper. One litre of water was poured into the styrofoam box to maintain the relative humidity inside at 90%.

Two-spotted spider mites were obtained from infested pinto beans. Mites obtained from pinto beans may not readily feed on tomato leaf arenas and could then spend more more time moving around. The effect of this could be an increased rate of encounter with *F. minuta* larvae hence slightly increasing the number of mites that are eaten. It was assumed that this change in feeding behaviour of the mites would not significantly alter results. Adult TSSM on a tomato leaf surface can easily be counted with the aid of a dissecting microscope.

*Feltiella minuta* functional response when feeding on adult male TSSM was determined by presenting the larvae with 3, 6, 12, 24 and 30 mites on an experimental arena. One larva was placed on each experimental arena. Five replicates at each density were performed. The experimental arenas were checked every 2 h to count and remove TSSM cadavers, and also to
replace these with an equal number of mites. The Total time for each experiment was 8 h. I assumed that the total number of cadavers at the end of 8 h represented the total number of mites killed by *F. minuta* larvae.

**(ii) Results**

The results of this experiment were tabulated (Table 1). The data approached a type-II functional response (Figure 2). The data were also plotted as reciprocals, and the equation of the regression line fitted by least squares was determined (Figure 3). The estimated rate of successful search, \(a\), and handling time, \(T_h\), were calculated from this equation as 1.11 h\(^{-1}\) and 0.28 h respectively. The estimated maximum possible number of prey, \(N_{\text{max}}\), that could be eaten in 8 hours, \(T/T_h\), was 28.57.
Table 1. Functional response of *F. minuta* feeding on adult male TSSM on a 2 cm$^2$ experimental arena. Prey densities used were 3, 6, 12, 24 and 30. Five replicates were performed at each density. Because killed prey were replaced, it is possible to get $N_s$ that is larger than $N$. The decline in searching efficiency with density is characteristic of a type-II functional response.
<table>
<thead>
<tr>
<th>Non-depleting Number of Prey Available (N)</th>
<th>Average Number of Prey Eaten (N̄)</th>
<th>Standard Error (SE)</th>
<th>Searching Efficiency (N̄/N)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>3</td>
<td>6</td>
<td>12</td>
</tr>
<tr>
<td></td>
<td>3.40</td>
<td>7.20</td>
<td>12.60</td>
</tr>
<tr>
<td></td>
<td>0.67</td>
<td>0.66</td>
<td>0.52</td>
</tr>
<tr>
<td></td>
<td>1.13</td>
<td>1.20</td>
<td>0.77</td>
</tr>
</tbody>
</table>
Figure 2. Functional response of *F. minuta* feeding on adult male TSSM on a 2 cm\(^2\) experimental arena. Prey numbers presented were 3, 6, 12, 24 and 30 and the experiment lasted 8 h. The curve follows a Holling type-II functional response. Each point in the curve is the mean +/− SE of 5 replicates.
NUMBER OF PREY KILLED (Na)

NUMBER OF PREY AVAILABLE (N)
Figure 3. Linear transformation and regression analysis of the functional response curve of *F. minuta* feeding on adult male TSSM on a 2 cm² experimental arena. Analysis is accomplished by plotting the data as reciprocals. The equation of the regression line drawn is $y = 0.035 + 0.905x$. ($n=25$; $r^2=0.71$; $P=0.0001$). From this equation $a$ and $T_h$ were calculated as 1.11 h⁻¹ and 0.28 h respectively. Because some points overlap on the graph, less than 6 replicates may appear per treatment.
C. Adult female TSSM as prey

(i) Materials and methods

The materials and method were quite similar to those used in the determination of functional response of F. minuta feeding on adult male TSSM, except for the following differences:

(1) Functional response in this case was determined by presenting larvae with 3, 6, 9 and 12 mites on an experimental arena. Large numbers of prey were not made available in this case because female mites are much larger (Appendix I) and the number that can be killed by a single larva is small.

(2) Eggs laid by mites were removed every two hours to ensure there was only one type of prey available to the larva in each experimental arena.

(3) Six replicates were performed at each prey density.

(ii) Results

The results of this experiment were tabulated (Table 2) and approached a type-II functional response (Figure 4). The data were plotted as reciprocals and the equation of the line fitted by least squares was determined (Figure 5).

In this case the two parameters were estimated as, \( a = 1.59 \text{ h}^{-1} \) and \( T_h = 1.74 \text{ h} \). The estimated maximum number of prey, \( N_{\text{max}} \), that could be killed in 8 hours, \( T/T_h \), was 4.6.
Table 2. Functional response of *F. minuta* feeding on adult female TSSM on a 2 cm\(^2\) experimental arena. Prey numbers presented were 3, 6, 9 and 12. Six replicates were performed at each density. The decline in searching efficiency with increase in prey density is characteristic of a type-II functional response.
<table>
<thead>
<tr>
<th>NON-DEPLETING NUMBER OF PREY AVAILABLE</th>
<th>SEARCHING EFFICIENCY $(N/N_a)$</th>
<th>STANDARD ERROR $(SE)$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$W$</td>
<td>3</td>
<td>2.29</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>3.40</td>
</tr>
<tr>
<td></td>
<td>9</td>
<td>3.83</td>
</tr>
<tr>
<td></td>
<td>12</td>
<td>4.44</td>
</tr>
</tbody>
</table>
Figure 4. Functional response of *F. minuta* feeding on adult female TSSM on a 2 cm$^2$ experimental arena. Prey numbers presented were 3, 6, 9 and 12 and the experiment lasted 8 h. The curve follows a Holling type-II functional response. Each point in the curve is the mean +/- SE of 6 replicates.
NUMBER OF PREY AVAILABLE (N)

NUMBER OF PREY KILLED (Na)
Figure 5. Linear transformation and regression analysis of the functional response curve of *F. minuta* feeding on adult female TSSM on a 2 cm² experimental arena (data in Table 2). This is done by plotting the data as reciprocals. The equation of the regression line drawn is $y = 0.218 + 0.631x$. ($n=36; r^2=0.25; P=0.0142$). From this equation $a$ and $T_h$ were calculated as 1.59 h and 4.60 h respectively. Because some points overlap on the graph, less than 6 replicates may appear per treatment.
**D. Discussion**

These functional response experiments show that *F. Minuta* has a type-II functional response when feeding on both adult male and female TSSM. Factors responsible for these decelerating curves that are characteristic to a type-II response have already been discussed.

The functional response curve has an upper asymptote of $N_{max} = T/T_h$, because, as the rate of prey capture increases with increasing density, the predator spends an ever greater proportion of its time handling prey with resulting decrease in the proportion of time available for searching (Houck and Strauss 1985).

Estimated handling time for females was much longer than that for males (1.74 versus 0.28 h⁻¹). The longer estimated handling time for female TSSM may be due to their larger biomass (size). The length and width measurements for male and female TSSM were determined during this study (Appendix I). Using these measurements and the assumption that mites are cylindrical, the estimated average volumes for male and female TSSM were calculated as $7.24 \times 10^{-9}$ mm³ and $2.98 \times 10^{-8}$ mm³ respectively; thus the volume of females is six times that of males. Flinn et al. (1985), also showed that the handling time is proportional to size of prey because the predator takes a longer time to kill larger prey.

The maximum number of prey consumed can be estimated by dividing the total time of the functional response experiment...
by the estimated handling time. The estimates for the maximum number of male and female TSSM consumed by a single *F. minuta* larva during a 24 hour period are 85.7 and 13.8 respectively. However, it is very likely that predators would become satiated before consumption rates reach these levels.

Estimates of instantaneous search rates for females and males were $1.11 \text{ h}^{-1}$ and $1.59 \text{ h}^{-1}$ respectively. Based on these estimates, females are encountered more frequently than males and some of the factors that could be responsible for this have been discussed in section D of this chapter. Research needs to be done to explain the difference in the rate of encounter that appears to exist between males and females.

Because a type-II functional response causes instability in predator-prey models, *F. minuta* on its own may not be an effective biological control agent for TSSM (Hassel 1978).

Determination of functional response of predators [natural enemies] in the laboratory has been seriously criticized. In most functional response experiments using arenas of limited size or high prey densities, attack rates will be limited by feeding behaviours like handling time (Weidenmann and O'Neil 1991). Arenas used in the study of functional response are sufficiently small and simple that search time is negligible, and this means attack rates at the highest prey density (or densities) are limited by the ratio $T/T_h$ (Weidenmann and O'Neil 1991). This is a problem because unrealistically large numbers of prey would get eaten in the laboratory. The work of
Wiedenmann and O'Neil (1991) and O'Neil (1988) illustrates this point. Their findings were that, *Podisus maculiventris* in the laboratory fed on up to 15 Mexican bean beetles (*Epilachna varivestis*) per day, and in the field it fed on up to 2 Mexican bean beetles per day even at high prey densities. The only explanation that could be given for the low rate of predation observed in the field was that the predator was limited in its ability to find prey in the expanse of the bean canopy (O'Neil and Stimac 1988). The large number of prey eaten in the laboratory can be explained by the fact that attack rates in the laboratory increased in a simple type-II response, giving the impression that handling time was the factor limiting attack rates, and secondly, the number of prey provided to predators in the laboratory greatly exceed those found in the field (O'Neil 1989). Relying on large numbers of prey consumed by a predator in the laboratory may bias our view on the contribution of some aspects of predator biology to predator-prey population dynamics and eventually our attempts to use predators to control pest outbreaks (O'Neil 1989). The value for the estimated number of male mites killed by *F. minuta* in the lab in 24 hrs is, for example, so large and may lead to the impression that this predator is an excellent natural enemy when this may not be the case. In the field, the functional response is more complex in that the shape of the curve is a function of prey density and searching by predators (Wiedenmann and O'Neil 1991). Wiedenmann and
O’Neil (1991) suggest that any study of functional response that ignores the limitations caused by searching may be both inaccurate and inappropriate, and results should be viewed with caution.

To address the problems discussed above, the functional response of *F. minuta* should be measured in the greenhouse as well as the lab to determine whether differences exist. Wrongly assuming that *F. minuta* would have a type-II response in the greenhouse could lead to the use of an inappropriate model (Equation 1) for evaluating *F. minuta - T. urticae* population dynamics. This would have the effect of wrongly associating particular aspects of predator behaviour with functional response, and largely ignoring the importance of plant growth form and the predator search behaviour in this system (O’Neil 1990).

Another problem usually encountered when conducting predation experiments is trying to imitate the conditions in which insects make decisions in the real world. If *F. minuta* is not allowed to leave the experimental arena then artificially high predation rates will result, especially at low prey densities (Roitberg et al. 1982). The problem was resolved in my study by giving each predator the option of staying on, or leaving an experimental arena. Results were taken for only those cases where the predator had stayed in the experimental arena for the whole duration of the experiment; in some cases the predator left the arena and the
E. EXPERIMENTAL ARENA SIZE AND FUNCTIONAL RESPONSE

(i) Introduction

O'Neil (1989) suggested that the large size of areas that predators search to find prey greatly limits their ability to find prey in the field. The experiment described below was done to determine the effect of increasing the size of the experimental arena from 2 to 4 cm$^2$ on the functional response of $F. minuta$.

(ii) Materials and methods

This experiment involved two functional response experiments. Part of the results of the functional response experiment with male TSSM in chapter III were used here - the result of 30 mites presented to the predator was excluded for the purpose of data analysis [case 1]. The materials and method for the functional response experiment done here were similar to those described earlier (chapter III, section B). In case 2, 4 cm$^2$ leaf arenas were used and 6, 12, 24 and 48 adult male mites were presented to predators. Six replicates were performed at each density. If density was defined in terms of mites per unit area of experimental arena, then for these experimental arenas of two different sizes [2 and 4 cm$^2$], the densities dealt with would be the same i.e 1.5, 3,
The linear transformation method of Lividahl and Stiven (1983) was then used to determine handling time and rate of successful search in both cases. An analysis of covariance was also performed to compare the two linear regressions.

(iii) Results

The results for case 1 are in Table I. The data approached a type-II functional response (Figure 6). The data were plotted as reciprocals, and the equation of the line fitted by least squares was determined (Figure 7).

The results of case 2 were tabulated (Table 3). The data approached a type-II functional response (Figure 8). The data were plotted as reciprocals, and the equation of the line fitted by least squares was determined (Figure 9).

In case 1, the estimates for $a$ and $T_h$ were 1.97 and 0.83, respectively. In case 2, $a$ and $T_h$ were 0.83 and 0.48, respectively.

Analysis of covariance showed that there was no significant difference between the two regression lines ($df=1; F=2.81; P=0.10$). Increasing the size of the arena from 2 to 4cm$^2$ had no significant effect on prey consumption ($df=1; F=0.91; P=0.35$). The only factor which affected prey consumption in this case was prey density ($df=1; F=61.37; P=0.0001$).
Figure 6. Functional response of *F. minuta* feeding on adult male TSSM on a 2 cm² experimental arena. Prey numbers presented were 3, 6, 12 and 24. The experiment lasted 8 hours. The curve follows a Holling type-II functional response. Each point on the curve is the mean +/- SE of 5 replicates.
NUMBER OF PREY AVAILABLE (N)
Figure 7. Linear transformation and regression analysis of the functional response curve of *F. minuta* feeding on adult male TSSM on a 2 cm$^2$ experimental arena. This is done by plotting the data as reciprocals. The equation of the regression line drawn is $y = 0.104 + 0.509x$. $(n=20; r^2=0.2; P=0.0001)$. From this equation $a$ and $T_h$ were calculated as 1.96 h$^{-1}$ and 0.83 h respectively. Because some points overlap on the graph, less than 6 replicates may appear per treatment.
Table 3. Results of the experiment on functional response of *F. minuta* feeding on adult male TSSM on a 4 cm² experimental arena. Prey numbers presented were 6, 12, 24 and 48. Six replicates were performed at each density.
<table>
<thead>
<tr>
<th>NON-DEPLETING NUMBER OF PREY AVAILABLE ( (N) )</th>
<th>AVERAGE NUMBER OF PREY EATEN ( (N_a) )</th>
<th>STANDARD ERROR ( (SE) )</th>
<th>SEARCHING EFFICIENCY ( (N_a/N) )</th>
</tr>
</thead>
<tbody>
<tr>
<td>6</td>
<td>3.66</td>
<td>0.71</td>
<td>0.61</td>
</tr>
<tr>
<td>12</td>
<td>5.57</td>
<td>1.7</td>
<td>0.46</td>
</tr>
<tr>
<td>24</td>
<td>8.71</td>
<td>0.73</td>
<td>0.36</td>
</tr>
<tr>
<td>48</td>
<td>15.50</td>
<td>1.63</td>
<td>0.32</td>
</tr>
</tbody>
</table>
Figure 8. Functional response of *F. minuta* feeding on adult male TSSM on a 4 cm² experimental arena. Prey numbers presented were 6, 12, 24 and 48. The experiment lasted 8 h. The curve follows a Holling type-II functional response. Each point on the curve is the mean +/- SE of 6 replicates.
NUMBER OF PREY AVAILABLE (N)

NUMBER OF PREY KILLED (Na).

0 10 20 30 40 50

0 2 4 6 8 10 12 14 16 18
Figure 9. Linear transformation and regression analysis of the functional response curve of *F. minuta* feeding on adult male TSSM on a 4 cm² experimental arena. This is done by plotting the data as reciprocals. The equation of the regression line drawn is $y = 0.060 + 1.215x$. ($n=24; r^2=0.57; P=0.0001$). From this equation $a$ and $T_h$ were calculated as $0.83 \text{ h}^{-1}$ and $0.48 \text{ h}$ respectively. Because some points overlap on the graph, less than six replicates may appear per treatment.
(iv) Discussion

In this experiment the number of TSSM eaten did not change significantly despite the increase in size of the experimental arena. These results do not support the findings of O'Neil and Stimac (1988), and Wiedenmann and O'Neil (1991) which show that even with the same density of prey, predators became more limited in their ability to find prey as the search area increased. The results also appear to indicate that large areas which predators search in the field may not be an important factor limiting their ability to find prey.

The results of this experiment may be attributed to the fact that the increase in size of the experimental arena was not large enough to cause a significant difference in the functional response of *F. minuta*.

I recommend that studies be done using much larger arenas than 4 cm² to determine if functional response still remains significantly unchanged.

E. Prey preference

(ii) Introduction

Prey preference can be defined as the disproportionate selection of one type of prey, relative to the proportions of prey available in the environment (Flinn et al. 1985). Predators often show a preference for one type of prey when offered a choice between 2 or more prey types. This leads to
more of that prey type getting eaten than would otherwise be expected (Cock 1978).

The purpose of doing the following experiment was to determine whether *F. minuta* showed preference for adult male or female TSSM. Prey preference can greatly affect the effective rate of increase of prey population per generation. Preference for female mites by *F. minuta* would, for example, remove the reproductive units from the prey population much faster than when no selectivity is exhibited. Preference for females reduces the rate of prey population increase. Prey preference is known to influence the intrinsic rate of increase of host populations; a factor that is important in the construction of predator-prey population dynamics models (Wrensch 1985).

Adult male and female TSSM were chosen to represent two different prey types because the differences that exist between them are striking and enhance the chance of a predator showing preference for one of them. Some of these differences are:

1. Adult female TSSM are much larger than the males. This difference could mean that females are much harder to subdue hence more males would be eaten. Alternatively the small size of the males may make them more evasive because they can easily escape when approached by *F. minuta*.

2. Given that females are heavier than males (have more
biomass/unit of body length), this may make them less mobile and thus experience more difficulty running away when confronted by predators than males.

(3) Differences exist in the nutritional quality of these two types of prey. Females are nutritionally superior to males because of the eggs they carry, therefore, *F. minuta* may be more likely to accept them (Houck 1986).

Cock (1978), suggested the use of functional response models to predict prey preference. This method is useful in that it predicts predation preference over a range of prey densities and proportions (Cock 1978). Four steps are involved in the process:

(1) Performing functional response experiments for each prey type separately.

(2) Estimating the instantaneous search rate and handling time using Hollings type II model for each prey type:

\[ N_s = \frac{(a.N.T)}{(1 + aT_h.N)} \]

where,

- \( N_s \) is number of prey consumed
- \( N \) is prey density
- \( T \) is total time
- \( a \) is the rate of successful search
- \( T_h \) is handling time.

(3) Using a combination of the two functional response
equations to describe the two-prey interaction:

\[ N_a = \frac{(aNT)}{(1 + aT_hN)} + (a'T_h'N') \] \[ N_a' = \frac{(a'N'T)}{(1 + a'T_h'N')} + (aT_hN') \]

where the variables are the same as previously defined except the terms with and without primes indicate male and female mite parameters respectively.

(4) Predation is examined over a range of the two prey types together and compared with the predicted numbers of prey eaten.

The null hypothesis in this method assumes that the predator shows no preference for any of the two types of prey - the predators response remains the same in the presence of either prey type, individually or together (Cock 1978). Parameters for male and female functional responses are used to predict predation, and hence preference when both prey types are present. If the predator shows preference for one of the prey types, then there will be statistical differences between experimental results and model predictions (Foglar et al).

(ii) Materials and methods

The predators functional response for each prey type when availability was 3, 6, 12, 24 and 30, and 3, 6, 9 and 12 for
adult male and female mites respectively had been determined earlier. These functional response experiments were all conducted on a 2 cm² leaf surface. Both of these experiments were used for the determination of handling time and rate of successful search for the two types of prey, and these parameters were then used to predict predation with both types of prey present.

Predator preference was tested with a prey availability range of 0/20 to 20/0 male/female, holding the total prey constant at 20. Numbers of males and females made available were 0, 5, 10, 15 and 20 and 20, 15, 10, 5 and 0 respectively in each treatment. Each of the 5 male/female combinations was replicated 7 times. In the course of the experiments, mites eaten were counted and replaced as required at 2 h intervals. Eggs laid by females were removed. The experiment lasted 8 h.

Results were used to draw a graph of proportion of males of 20 total prey versus proportion of males killed as a proportion of total prey killed [number of males killed/total number of both males and females killed]. A slope of 1 would indicate no preference while a concave or convex line would indicate negative preference for males or positive preference for males respectively.

Results were also subjected to a chi-square goodness of fit test to determine if a statistical difference existed between experimental results and model predictions.
(iii) Results

The results of this experiment were tabulated (Table 4). The concave line obtained when the proportion of males of 20 total prey was plotted against proportion of males eaten as a proportion of total prey consumed indicates preference for adult female TSSM (Figure 10).

There was strong evidence for the existence of a difference between experimental results and model predictions ($X^2=94.7; df=4; P<0.005$). The results of this experiment indicate preference by *F. minuta* for adult female TSSM.
Table 4. Results of the experiment to test *F. minuta* preference for male or female TSSM over a range of prey densities from 0/20 to 20/0 male/female, holding the total prey constant at 20. The numbers of male and female TSSM available were 0, 5, 10, 15 and 20 and 20, 15, 10, 5 and 0 respectively in each treatment. Any prey eaten were replaced in order to keep the total available number of prey constant. The experiment lasted 8 h.
<table>
<thead>
<tr>
<th>PROPORTION OF MALE TSSM IN THE EXPERIMENTAL ARENA</th>
<th>MEAN PROPORTION OF MALE TSSM EATEN +/- SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>0.25</td>
<td>0.20 +/- 0.02</td>
</tr>
<tr>
<td>0.50</td>
<td>0.28 +/- 0.04</td>
</tr>
<tr>
<td>0.75</td>
<td>0.66 +/- 0.03</td>
</tr>
<tr>
<td>1.00</td>
<td>1.00 +/- 0.00</td>
</tr>
</tbody>
</table>
Figure 10. The proportion of males of 20 total prey versus proportion of males killed as a proportion of total prey killed. Twenty prey were available in the arena. A concave line is obtained from observed predation. A line with a slope of 1 represents expected predation where no preference exists and prey are assumed to be killed in direct relation to their proportion in the experimental arena. Each male/female combination was replicated 7 times.
PROPORTION OF MALES OF 20 TOTAL PREY

PROPORTION OF MALES EATEN

0 0.2 0.4 0.6 0.8 1 1.2

0 0.2 0.4 0.6 0.8 1 1.2
(iv) Discussion

The results above indicate the searching behaviour of *F. minuta* does not remain constant in the presence of females alone, males alone, or both together. This change in searching behaviour leads to the preference for females that was observed.

Results of the functional response experiments for male and female TSSM alone can be used to predict whether *F. minuta* shows preference for male or female TSSM (Murdoch 1973). This is done by calculating the prey preference index for these two types of *F. minuta* prey as shown below (Murdoch 1973).

Using the disc equation of Holling (1959b):

\[ N_s = \frac{(aNT)}{(1 + aT_hN)} \]

where the variables are the same as previously defined.

The number of male or female TSSM that are eaten when both are present together can be predicted using equations 2 and 3. Dividing the equation 2 by equation 3 gives:

\[ \frac{N_e}{N_a} = \frac{aN}{a'N'} \]

Rearranging the equation gives:

\[ \frac{a}{a'} = \frac{N_e/N_a}{N'/N_a} \]
Given that searching efficiency is equal to the number of prey eaten divided by the number initially present,

\[ \frac{a}{a'} = \text{searching efficiency for females} / \text{searching efficiency for males} \]

The ratio \( \frac{a}{a'} \), called the prey preference index, is the ratio of searching efficiency for females:searching efficiency for males. What is discussed here is true only if exploitation is negligible or mites are replaced as they are eaten. From the results of the functional response experiments for male and female TSSM, the ratio of a for male TSSM:a for female TSSM was 0.69 – indicating a preference for female TSSM. A preference index of 0.69 means approximately 7 male TSSM will be eaten for every 10 females when both prey are present in equal proportion.

This preference for females shown by \( F. \) minuta may be an important factor in \( F. \) minuta - \( T. \) urticae population dynamics because females are the reproductive units. Preference for females will most likely have an effect on the net rate of increase of prey per generation; an important factor in the construction of predator-prey models (Hassel 1978, Wreensch 1985). The \( F. \) minuta - \( T. \) urticae model population dynamics model should, therefore, consider this preference for adult female mites.

Studies should be conducted to determine whether the
aforementioned differences between male and female mites contribute to preference for females, and whether preference for adult females exists even in cases where TSSM eggs and juveniles are presented as additional prey types.
CHAPTER IV

EFFECTS OF ABIOTIC FACTORS ON PREDATION BY F. minuta.

A. Introduction

Microenvironment exerts a significant influence upon the behaviour and population dynamics of arthropods (Bursell 1974a). Microclimatic factors that usually influence the relationship between terrestrial arthropods and their environment are air temperature, microhabitat temperature, wind speed, humidity and radiation (Ferro et al. 1979). The most important of the aforementioned factors are temperature and humidity; hence arthropod population dynamics models usually include functions depending on temperature and humidity, (Ruesink 1976, Ferro et al. 1979). Environmental humidity and temperature are of great importance in the lives of insects because: (i) water forms a large percentage of the insect tissues and survival depends on the ability to maintain the balance of water in the body (Chapman 1969); and (ii) enzymes function efficiently only within a limited temperature range (Chapman 1969). Ferro et al (1979), for example, found that humidity and temperature were the most important environmental factors regulating the population dynamics of the European red mite, Panonychus ulmi, and one of its predators, Amblyseius fallacis.
Temperature and humidity regulate arthropod population dynamics by influencing the rate of reproduction, rate of development and rate of death (Bursell 1974a, 1974b). These factors may also affect arthropod survival (Shipp and Gillespie 1993, Gillespie et al. 1994). Shipp and Gillespie (1993) found that the survival of Frankliniella occidentalis was reduced by exposure to conditions of high temperature and vapour pressure deficit.

To obtain a full understanding of the role of temperature and humidity on the population dynamics of a given insect species, it is important to elucidate the effects of these factors on all activities of the organism eg. prey consumption (Ruesink 1976). Therefore, I examined the effects of humidity and temperature on the consumption of TSSM by F. minuta.

B. Effect of temperature

(i) Materials and methods

The experiment was conducted in well lit growth chambers maintained at 15, 20, 27 and 32 °C. Each experimental arena consisted of a 2 cm² excised clean tomato leaf with a petiole. The leaf petiole was placed in a water filled vial stoppered with cotton. This was then placed in a styrofoam box with a lid made of transparent polythene. One litre of water was added to each box to maintain the relative humidity at 90%.

The number of prey consumed at each temperature was
determined by using 25 prey and 1 larva in each experimental arena. The experiment lasted 8 h, at the end of which the number of prey killed was determined. Prey density was not kept constant. Seven replicates were performed at each temperature.

Analysis of variance (ANOVA) was used to test whether differences existed in the mean number of TSSM eaten at the 4 temperatures, and means were separated using the Student-Newman-Keuls (SNK) multiple comparison procedure.

(ii) Results

The results of this experiment were tabulated (Table 5) and analysis of variance revealed that there was a significant temperature effect on the number of TSSM eaten by *F. minuta* (F=13.70; n=7; df=3,19; P=0.0001). The results were also displayed in graphical form (Figure 11). The results of the SNK multiple comparison procedure show which means were significantly different (SNK summary 1) means. There were no significant differences among the mean number of TSSM eaten at 15, 20 and 32 °C. The mean number of TSSM eaten at 27 °C was the largest, and was significantly different from the rest of the treatments.

(iii) Discussion

The results of this experiment indicate that prey consumption was highest at 27 °C, and significantly lower at
15, 20, and 32°C.

*Feltiella minuta* is ectothermic and therefore, its body temperature depends on environmental temperature. This means environmental temperature is going to determine how actively larvae consume TSSM, how rapidly this insect grows and how rapidly it reproduces (Jordan 1977, Chapman 1969). Because insects are ectothermic, their body temperature approximates and varies with ambient temperature; however, body temperature probably affects insect behaviour more than ambient temperature since it influences the nervous system and enzyme activity directly (Chapman 1969). Because the action of the nervous system and metabolic rate increase with temperature, insects are, therefore, more active at higher temperature (Chapman 1969). Ultimately, environmental temperature plays an important role in determining whether *F. minuta* can control TSSM of greenhouse tomatoes (Jordan 1977).

**Physiological explanation of results.**

At 15°C the lowest number of mites were killed. The reason for this could be that at temperatures below its preferred range, *F. minuta* larvae become increasingly less active until finally they are unable to move or do so only with difficulty - due to decline in nervous action and the metabolic rate (Chapman 1969). At 20°C significantly more mites were killed than at 15°C, and at 27°C the highest number of mites were killed; however, the number of mites killed at 32°C is
Table 5. The effect of temperature on TSSM consumption by *F. minuta*. Temperatures used were 15, 20, 27 and 32°C. Seven replicates were performed at each temperature.
<table>
<thead>
<tr>
<th>TEMPERATURE (°C)</th>
<th>AVERAGE NUMBER OF PREY KILLED</th>
<th>STANDARD ERROR (SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>15</td>
<td>6.50</td>
<td>0.57</td>
</tr>
<tr>
<td>20</td>
<td>8.33</td>
<td>0.80</td>
</tr>
<tr>
<td>27</td>
<td>10.50</td>
<td>0.53</td>
</tr>
<tr>
<td>32</td>
<td>7.67</td>
<td>0.53</td>
</tr>
</tbody>
</table>
Figure 11. The effect of temperature on consumption of TSSM by *F. minuta*. Temperatures used were 15, 20, 27 and 32°C. The graph indicates that the optimum temperature for foraging larvae is approximately 27°C. Seven replicates were performed at each temperature.
TEMPERATURE
(DEGREES CENTIGRADE)
SNK summary 1. There was no significant difference in the mean number of mites killed at 20 and 32°C, and 15 and 32°C. The mean number of mites killed at 27°C was significantly higher than the mean numbers of mites killed at other temperatures.
### SNK SUMMARY 1. TEMPERATURE

<table>
<thead>
<tr>
<th>SNK GROUPING</th>
<th>MEAN NUMBER OF PREY EATEN</th>
<th>NUMBER OF REPLICATES</th>
<th>TEMPERATURE (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>10.50</td>
<td>7</td>
<td>27</td>
</tr>
<tr>
<td>B</td>
<td>8.33</td>
<td>7</td>
<td>20</td>
</tr>
<tr>
<td>C B</td>
<td>7.67</td>
<td>7</td>
<td>32</td>
</tr>
<tr>
<td>C</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>6.50</td>
<td>7</td>
<td>15</td>
</tr>
</tbody>
</table>

Means with the same letter are not significantly different.
significantly lower than that at 27°C. The reason for this could be that increase in temperature increases the metabolic rate, but at 32°C [a temperature approaching the upper lethal limit of 35°C], the metabolic rate declines (Chapman 1969). According to Chapman (1969), at temperatures much higher than the preferred temperature, insects succumb to heat stupor—they lose the ability to move and hence eventually die.

Results explained in relation to functional response.

Because frequency with which prey are encountered [instantaneous search rate] and handling time are the two main factors influencing the number of prey that are eaten at each of the four temperatures, the results of this experiment should, therefore, be explained in context to these two factors.

Thompson (1978), examined the effect of temperature on the functional response of Ischnura elegans feeding on Daphnia magna. He found that the instantaneous search rate increased in a sigmoid manner with temperature while the handling time declined logarithmically. Everson (1980) found that the instantaneous search rate for Phytoseiulus persimilis feeding on Tetranychus urticae increased linearly with temperature while the handling time decreased exponentially. In general, for predators such as F. minuta, there is an inverse relationship between handling time and the rate of successful search (Thompson 1978).
The differences between prey consumption at the two lowest temperatures [15°C & 20°C] and 27°C can, therefore, be attributed to the inverse relationship that exists between handling time and the instantaneous search rate under conditions of changing temperature.

To completely understand the cause of this inverse relationship, handling time and the instantaneous search rate have to be examined in terms of changes to their subsidiary components in response to temperature. The relationship between the relative rate of gut emptying and temperature may explain the effect of temperature on searching efficiency (Sabelis 1981). According to Everson (1980), increased temperature results in increased energy demand which translates behaviourally to hunger. Increased energy demand or hunger may then affect the subsidiary components of handling time in the following manner. Starved *F. minuta* are more active than satiated ones, therefore, the time spent in pursuit of each TSSM should decline with increase in temperature (Everson 1980). Two-spotted spider mites on a tomato leaf surface are inactive at all temperatures [because they are involved in feeding] hence the time spent by *F. minuta* to subdue a single TSSM should be constant with TSSM providing equal resistance to capture at all temperatures (Everson 1980). According to Sandness and McMurtry (1972), less time is spent feeding on each successive prey in the hunger phase of the hunger-satiation cycle; i.e. the hungrier
the predator, the greater the amount of time spent feeding on a given prey. The digestive pause between each TSSM will decrease because the speed at which the gut empties will increase with the metabolic rate of *F. minuta* which in turn increases with temperature (Nakamara 1977). Sandness and McMurtry (1972) found that digestive pause constituted a large part of the total handling time of the phytoseiid predator *Amblyseius largoensis*. This means a significant reduction in digestive pause markedly reduces handling time. It appears that of the four subsidiary components of handling time, the digestive pause is affected most by temperature (Everson 1980).

The components of the rate of successful search may change with temperature in the following way. The speed of the *F. minuta* will increase with hunger (Sandness and McMurtry 1972) and temperature, while the speed of TSSM is negligible because they are inactive while feeding on the tomato leaf. Although the searching behaviour of *F. minuta* is probably influenced by TSSM, its reactive distance is most likely small and independent of hunger. Because of the increase in speed that takes place in *F. minuta*, the rate of successful capture of TSSM will increase with hunger and would approach 100% at a temperature of 27 °C (Sandness and McMurtry 1972). According to Sabelis (1981), it is very likely that the effect of temperature on searching behaviour shows one consistent tendency - temperature will not have a positive effect on one
behavioural component and a negative effect on another.

The way various components of handling time and the rate of successful search have been discussed here in relation to temperature requires testing in a *F. minuta - T. urticae* system to determine if each component behaves in the manner suggested.

The prey consumption at 32°C is significantly lower than for 27°C. This could be attributed to a decline in the rate of successful search - the frequency with which TSSM are encountered drops. According to Holling (1959a) a reduction in the instantaneous search rate may indicate that certain factors are operating to reduce the frequency of prey encounter; for example *F. minuta* may be in a state of greater heat stress at 32°C and therefore finds it more difficult to locate prey. Alternatively an additional time consuming behaviour by *F. minuta* may be operating causing a reduction in the amount of time available for searching (Holling 1959a).

Thirty two degrees centigrade is exceptionally warm and may be outside the normal range of temperatures experienced by *F. minuta* in the field even on a hot summer day. Under these conditions *F. minuta* may, most likely, get involved in some time consuming behaviour in order to offset high body temperature. Insects have little physiological control of body temperature; behavioural adaptations tend to maintain the temperature as near the optimum for metabolic activity as environmental conditions can allow (Chapman 1969).
(1991) notes that one of the ways insects avoid inhospitable habitats is by entering quiescence, i.e. slowing down. *Feltiella minuta* may engage in this behaviour as temperatures get beyond its normal range. It is also possible that *F. minuta* may spend more time searching for a cooler microclimate (Chapman 1969). According to Chapman (1969) the reduced activity [and death] experienced at high temperature could also be due to one or a combination of the following factors: (i) proteins may be denatured (Jordan 1977, Dingley and Smith 1968); (ii) the balance of metabolic processes may be disturbed so toxic products accumulate; (iii) food reserves may become exhausted; and (iv) desiccation which may cause death. According to Jordan (1977), most predators of common houseplant pests would start dying when their body temperature reaches 37.8°C. In my experiment the larvae were exposed to 32°C [air temperature], which is quite close to the upper temperature limit of *F. minuta* [35°C] (Gillespie et al. 1994). It is, therefore, possible that the larvae slowed down due to one or more of the above factors. The aforementioned reasons for the reduction in prey consumption at 32°C, need testing.

In a greenhouse situation, at high relative humidities, it is likely that prey consumption is significantly higher at a canopy temperature of 27°C than at 15, 20 and 32°C. Because the temperature of the microhabitat is what arthropods are exposed to, studies relating microclimatic temperature to standard meteorological temperature and prey...
consumption by *F. minuta* should be conducted. Without these studies, any model relating temperature to TSSM consumption will be dependent on a correlation rather than a cause-effect relationship.

C. Effect of humidity

(i) Materials and method

The experiment was conducted in well lit growth chambers maintained at 27°C. Each experimental arena consisted of a 2 cm² excised clean tomato leaf with a petiole. The petiole of each experimental arena was put into a water-filled vial stoppered with cotton. This was then put in a vial holder attached to a styrofoam box that had a transparent polythene paper lid. The cotton used in the vials was covered using parafilm to keep the water soaked cotton from causing changes in the relative humidity inside the box.

To four different Styrofoam boxes were added solutions of calcium chloride at different concentrations so that relative humidities of 35, 60, 70 and 80% were created inside the various boxes.

Two hundred cubic centimeters of solution were poured into each of these boxes. In the fifth box, 200 cm² of water was added to create a relative humidity of 90%. Before the experiment was started, digital humidity sensors were placed into each of these boxes and left in the experimental growth
chamber for 12 hours to ensure that the relative humidities mentioned above stayed at the expected level.

The number of mites consumed at each relative humidity level was determined by using 25 adult males and one starved larva in each experimental arena. Six replicates were performed for each relative humidity level. The experiment lasted 8 hours, at the end of which the number of mites killed was noted. Prey density was not kept constant.

Analysis of variance (ANOVA) was used to test whether differences existed in the mean number of TSSM eaten at the 5 different relative humidities, and the means were separated using the Student-Newman-Keuls (SNK) multiple comparison procedure.

(ii) Results

Results of this experiment were tabulated (Table 6). The results were also displayed in graphical form (Figure 12). The results of the SNK multiple comparison procedure show which means differed significantly (SNK summary 2). There was a significant humidity effect on the number of TSSM eaten by F. minuta (Table 6; n=6; F=20.22; df=4,25; P=0.0001). There was no significant difference in the mean number of prey eaten at 35, 60 and 70% relative humidity, and these means were significantly less than the means for 80 and 90% relative humidity. There was a significant difference in the mean number of TSSM eaten at 80 and 90% relative humidity, with the
most mites eaten at the latter humidity. Figure 8 indicates that more TSSM are eaten at higher relative humidities.

(iii) Discussion

The results of this experiment indicate that *F. minuta* consumes significantly more TSSM at high relative humidities (80 and 90%) than at intermediate (60 and 70%) and low relative humidities (35%).

The lack of a significant difference in the number of mites eaten at relative humidities of 35, 60 and 70% indicates that the increase in relative humidity from 35 to 70% was not enough to create a significant change in prey consumption by *F. minuta* larvae. This indicates *F. minuta* shows its best performance at high relative humidities only. In the course of my study I observed that *F. minuta* larvae always became motionless or nearly so when they were removed from leaves of the cucumber plants they were reared on and placed on a tomato leaf surface in an open petri dish in the laboratory. Closing the petri dish resulted in larvae becoming active again. The humidity in the *F. minuta* rearing room was always kept high using humidifiers and it varied from 65% when the room was warm to 85-90% when it became cool in the early morning hours. The humidity on the surface of cucumber leaves, where *F. minuta* larvae spend much of their time, is higher than that of the surroundings (Jordan 1977). The difference between the relative humidity underneath a cucumber leaf in the rearing
room and the environment of the laboratory may explain the inactivity observed in the larvae in the open petri dish. This observation and the results of this experiment indicate the importance of high relative humidity in keeping *F. minuta* active.

*Feltiella minuta* larvae are very small organisms and it is easy for them to lose a significant proportion of their body water, because small organisms have a higher surface to volume ratio compared to larger organisms. Because water is lost from all parts of the surface of an organism, a *F. minuta* larva with its large surface area compared to its small volume will suffer great evaporation stress if it finds itself in an environment that facilitates water loss (Jordan 1977).
Table 6. The effect of relative humidity on TSSM consumption by *F. minuta*. The relative humidities used were 35, 60, 70, 80 and 90%. Six replicates were performed at each relative humidity.
<table>
<thead>
<tr>
<th>Relative Humidity (%)</th>
<th>Average Number of Prey Killed</th>
<th>Standard Error (SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>35</td>
<td>0.50</td>
<td>0.34</td>
</tr>
<tr>
<td>60</td>
<td>2.67</td>
<td>0.62</td>
</tr>
<tr>
<td>70</td>
<td>2.50</td>
<td>0.56</td>
</tr>
<tr>
<td>80</td>
<td>5.67</td>
<td>0.92</td>
</tr>
<tr>
<td>90</td>
<td>9.00</td>
<td>1.03</td>
</tr>
</tbody>
</table>
Figure 12. The effect of humidity on consumption of TSSM by F. minuta. Relative humidities used were 35, 60, 70, 80 and 90%. The graph indicates foraging larvae require high humidity levels (80 and 90%) to kill large numbers of prey. Six replicates were performed at each humidity.
Number of prey killed vs. relative humidity (%).
SNK summary 2. The mean number of prey killed at 90% relative humidity was significantly higher than all the other means. The mean number of prey killed at 80% relative humidity was significantly higher than the mean numbers for 35, 60 and 70% relative humidity. No significant differences were found among the mean numbers of prey killed at relative humidities of 35, 60 and 70%.
SNK SUMMARY 2. RELATIVE HUMIDITY

<table>
<thead>
<tr>
<th>SNK GROUPING</th>
<th>MEAN NUMBER OF PREY EATEN</th>
<th>NUMBER OF REPLICATES</th>
<th>RELATIVE HUMIDITY (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>9.00</td>
<td>6</td>
<td>90</td>
</tr>
<tr>
<td>B</td>
<td>5.67</td>
<td>6</td>
<td>80</td>
</tr>
<tr>
<td>C</td>
<td>2.67</td>
<td>6</td>
<td>70</td>
</tr>
<tr>
<td>C</td>
<td>2.50</td>
<td>6</td>
<td>60</td>
</tr>
<tr>
<td>C</td>
<td>0.50</td>
<td>6</td>
<td>35</td>
</tr>
</tbody>
</table>

Means with the same letter are not significantly different.
At relatively high temperatures (e.g. 27°C) and low humidities this surface-volume relationship is important, because hot dry air draws out body moisture (Jordan 1977). This means that at high temperatures and low humidities, evaporation stress is bound to be more severe than at low temperatures and high humidities. Evaporation stress will most likely have a negative effect on prey consumption by *F. minuta* - an inverse relationship between evaporation stress and mite consumption likely exists and could account for the differences in mite consumption observed at the 5 different humidities. The aforementioned inactivity of larvae when exposed to the low humidity environment in the lab may be a response to evaporation stress. A high evaporation stress means the water content of the larvae is low, therefore, the metabolic rate is low [a high water content means a high metabolic rate] (Chapman 1969). The aforementioned inactivity may be due to depressed metabolic activity.

One of the ways in which insects avoid inhospitable environments is by entering quiescence (Wellso 1991). Quiescence is a state of being motionless or inert. In this experiment, relative humidities between 35 and 70% can be considered unfavourable and to cause inactivity in *F. minuta*; great evaporation stress may have existed at these relative humidities. Inactivity by *F. minuta* larvae means few or no TSSM get eaten.

In a greenhouse situation, this inactivity may be rare, even
when the relative humidity of the general environment is low, because the tomato canopy traps water vapour and creates conditions of high relative humidity within the canopy. According to Jordan (1977), the relative humidity in the vicinity of the leaf or stem where insects live may be 85%, even if the humidity is 50% in the general environment of the plant, and this is especially true if the plants are well watered.

Studies should be conducted to determine how the different components of rate of successful search and handling time change in response to changes humidity. Research should be done to determine the relationship between boundary layer humidity and TSSM consumption by *F. minuta*. This important because humidity of the ambient air is lower than that in the boundary layer where the larvae live and feed (Jordan 1977). Presently there is no practical method for measuring humidity within the leaf boundary layer (Ferro et al. 1979). Boundary layer humidity can, nevertheless, be calculated if the leaf temperature, air temperature and humidity within the tree canopy are known (Ferro et al. 1979). This is the only way of determining the cause-effect relationship that exists between humidity and mite consumption.

From the results of my experiment it can be concluded that *F. minuta* can kill large numbers of TSSM only when the relative humidity is high [80% and above].
CHAPTER V

CONCLUSIONS

Very few studies have focused on documenting and explaining the behaviour of *F. minuta*. Studies in this area are essential if we are to understand how *F. minuta* consumes TSSM. Information obtained from studies on this topic would facilitate the development of mathematical models describing the *F. minuta* - *T. urticae* relationships. The models could then be used to predict the performance of this predator as a biological control agent of TSSM in greenhouse tomatoes, and also permit the prediction of appropriate release rates under different TSSM densities (Gillespie et al. 1994).

My study has documented and explained some aspects of the predatory behaviour of *F. minuta*.

*Feltiella minuta* shows a type II functional response when feeding on both male and female TSSM on a 2 cm² experimental arena, under laboratory conditions. A predator is considered to have a "strong" functional response if the number of prey it kills increases with prey density - it kills more prey than it needs to complete development (Gillespie et al 1994). The functional response with adult male TSSM as prey is described by the random predator equation with parameters $a=1.11 \ h^{-1}$ and $T_h=0.28 \ h$. The functional response with adult females as prey has the parameters $a=1.59 \ h^{-1}$ and $T_h=1.74 \ h$. Based on these handling times, *F.minuta* can theoretically kill 28.6 and 4.6
TSSM respectively in 8 hours. *Feltiella minuta* larvae, therefore, showed a much "stronger" functional response to male mites than to female mites. Based on the "strength" of its functional response, *F. minuta* may be considered capable of regulating populations of spider mites (Gillespie et al.). However, my discussion in Chapter III cautions against this conclusion. *Phytoseiulus persimilis* feeding on adult female TSSM, on a bean leaf, has a type II functional response with the parameters $a=0.19 \text{ h}^{-1}$ and $T_h=10.34 \text{ h}$ (Everson 1979). *Feltiella minuta*, with a much higher value for $a$ and a smaller $T_h$, can kill six times more female mites than *P. persimilis*. Another characteristic of good a biological control agent that *F. minuta* has is a high search rate - this promotes a low equilibrium host population (Hassel 1978). Because of its high search rate and small handling time, *F. minuta* may therefore, be a more efficient biological control agent of TSSM than *P. persimilis*. Other members of family Cecidomyiidae also appear to possess a "strong" functional response. *Arthrocnodax occidentalis* Felt, for example, can kill 380 mites in 17 days (Chazeau 1985).

If conclusions were to be drawn based solely on the type of functional response shown by *F. minuta*, then one would say that this predator can not on its own be an effective biological control for TSSM. This conclusion is based on the fact that a type II response causes instability in predator-prey population dynamics (Murdoch and Oaten 1975, Hassel
This instability arises from the fact that a type II response is not density dependent and also due to the inherent time lag between an attack and the production of predator offspring (Hassel 1978 and Murdoch and Oaten 1975). The assessment of predator performance based on functional response alone may be considered rather simplistic. Other factors such as the existence or absence of refuges for prey, an invulnerable class of prey, spatial heterogeneity and predator aggregation play an important role in determining the level of stability of predator-prey population dynamics; and therefore the level of successful biological control (Murdoch and Oaten 1975, Hassel 1978, Beddington et al. 1978). Beddington et al. (1978), for example, found that the aggregation of predators in areas of high prey density can be of vital importance to stability. According to Hassel (1978), aggregation of predators when low equilibrium host populations have been established is important because it ensures stability. Host aggregation may be present in *F. minuta* because eggs are only laid on spider mite webbing; which happens to be where colonies of TSSM are often found (Gillespie et al. 1994). Two-spotted spider mites have a clumped distribution, therefore, *F. minuta* larvae will develop at sites where mite colonies exist (Sabelis and Dicke 1985). According to Hassel (1978), the standard for judging biological control agents should be whether or not they have high search rates and on
their ability to aggregate in patches of high host density; these are characteristics of ideal biological control agents. This idea is supported by Beddington et al. (1978) who suggest that spatial heterogeneity, patchy distribution of the host and the differential exploitation of these patches by natural enemies are vital for successful biological control. If we are to predict the performance of F. minuta, then all of the aforementioned factors for the assessment of a biological control agent should be considered and not the functional response alone.

The ability of F. minuta larvae to locate and kill TSSM when the size of the experimental arena doubled from 2 cm² to 4 cm² did not change significantly. This may be because increase in complexity did not accompany the change in size of arena hence no significant changes occurred in a and $T_h$ in the 2 types of arena. Studies should be done using 4 cm² arenas that are more complex and arenas much larger than 4 cm² to determine if functional response still remains unaffected.

The prey preference experiment that I conducted revealed that Feltiella minuta shows preference for female TSSM when males are present as a second prey type. The ratio $a$ for males:$a$ for females, the prey preference index, was calculated as 0.69 and this also indicated that female TSSM were the preferred prey when presented in equal proportion with male mites - 7 males will be eaten for every 10 females. This preference for females, if it exists in a greenhouse tomato
crop, could greatly influence the *F. minuta* - *T. urticae* population dynamics because females are the reproductive units (Wrensch 1985). By consuming more female mites, *F. minuta* has a better chance of keeping the TSSM population under control. Two factors may be responsible for the preference for females:

1. The female mites are of much higher nutritional quality than males because of the eggs they carry. Mite eggs are rich in lipids and proteins and may thus best satisfy the nutritional needs of *F. minuta* (Houck 1991). Optimal foraging theory predicts that a predator will prefer those prey which provide the best return on investment of handling time (Charnov 1976). The preference for female mites that I observed appears to support this theory.

2. Free from the task of laying eggs, male mites may be relatively more mobile than the females. Male mites are also smaller in size. This mobility, coupled with small size, reduces the probability of random confrontation with the predator (Houck 1991).

My study has also demonstrated that *F. minuta* requires high relative humidity (80 and 90%) to kill large numbers of TSSM. It appears that intermediate (60 and 70%) and low (35%) relative humidities leads to inactivity (inert behaviour) in *F. minuta*, hence low numbers of TSSM are eaten. This inactivity of *F. minuta* may be caused by evaporation stress, and appears to be more pronounced at relative humidities below 70% (Jordan 1977). Inert behaviour by *F. minuta* in a greenhouse with an established tomato crop ought to be rare as
the moisture trapped in the tomato canopy keeps the relative humidity at the leaf surface much higher than that of the general environment, and also because there are many high humidity microclimates within the tomato canopy (Jordan 1977). A model relating boundary layer humidity to consumption of TSSM should be developed.

The rate at which F. minuta kills prey does not appear to be directly related to temperature over the 15-32°C range; this relationship appeared to exist in the 15-27°C range. Based on my study, the optimum temperature for predation is approximately 27°C. The possible causes of the aforementioned direct relationship between temperature and number of prey killed, in the 15-32°C range, have already been discussed (chapter IV). According to Gillespie et al. (1994), temperatures beyond 35°C are lethal and no development occurs in F. minuta; it is, therefore, likely that at 32°C the larvae are suffering from temperature induced stress which interferes with mite consumption. This may explain the reduction in prey consumption. Using these results to predict how different greenhouse temperatures affect mite consumption, without including correction factors, is inappropriate because of the differences that exist between air temperature and the temperature at the leaf surface where F. minuta live and feed.

The following 2 observations highlight the differences that often exist between the temperature at the leaf surface and the ambient conditions: (1) In a tomato greenhouse, on a cool
day with clear skies, the temperature at the leaf surface may be 10°C higher than that of the ambient conditions - the leaf actively absorbs incident radiation and because it is not under any heat stress, little heat is lost through evaporative cooling (Ferro et al. 1979); (2) On a warm overcast day (a characteristic summer day), the temperature at the leaf surface is much lower than that of the ambient conditions (Ferro et al. 1979). These observations show the need to build models for the prediction of leaf surface temperature from air temperatures. Without this, predator - prey models may give misleading results.

Hot and dry conditions are conducive to rapid development and population increase in spider mites (Crocker 1985, Boudreaux 1958). Optimum temperature range for most rapid development is 24-29°C (Boudreaux 1958). Spider mites take in a lot more plant sap under dry conditions to avoid desiccation (Boudreaux 1958). High humidities reduce the rate of water loss, therefore, nutrient intake declines and causes the rate of reproduction and development to drop (Boudreaux 1958). Given that *F. minuta* thrives at high humidities and spider mites do not, the hygrothermal environment of the greenhouse could be manipulated in order to increase the effectiveness of *F. minuta* in controlling spider mites. The manipulation of hygrothermal conditions is not a problem because greenhouses are plant production systems where critical control of the environmental parameters is possible (Shipp and Gillespie
1993).

*Feltiella minuta*, despite exhibiting a type-II response in the laboratory, appears to have some characteristics that contribute to the stability of predator-prey population dynamics. *Feltiella minuta* may be capable of controlling TSSM, but more research needs to be done to provide information to support this notion and to improve our understanding of its behaviour in relation to its host. This information could then be used to improve biological control of TSSM in greenhouse tomatoes.
In this study, functional response experiments were conducted for both male and female TSSM. According to Flinn et al. (1985), size of prey (which is often proportional to biomass) greatly influences the rate of successful search and handling time of predator for a given prey item.

To explain possible differences in the functional response for these two types of prey, which could be due to differences in size, it was important to establish that a difference size exists between male and female TSSM. Visually, female TSSM appear much larger than males.

The assessment was done in the following manner: Two spotted spider mites were obtained from a colony reared on tomato plants at Simon Fraser University. One leaf that was heavily infested with mites was excised and placed in a petri dish. A piece of paper towel soaked in 95% ethanol was placed into the petri dish and the lid was then replaced. The ethanol soaked paper towel was left in the petri dish for 10 minutes. The purpose of the ethanol was to immobilize the TSSM to facilitate measurement of their body length and width. Body length was defined as the distance between the front of the chelicerea and the tip of the abdomen, and body width was defined as the distance between the sides of the abdomen at the widest point.
A dissecting microscope was used for the identification of male and female TSSM and to facilitate the transfer of mites from the leaf to a microscope slide.

An ocular micrometer, inserted into the eyepiece lens, was used to take measurements of mite width and length on a compound microscope. It had been determined using an objective micrometer, at a magnification of 40 [eyepiece = 12.5 and objective = 3.2], that 32 ocular micrometer markings were equivalent to 0.01 mm [the total length of all markings on the objective micrometer].

Mites were then transferred from the tomato leaf to the slide one at a time and the ocular micrometer readings that corresponded to the length and width for each mite were noted. Ten replicates were completed for male mites and the same number of replicates were done for the females. Since 32 ocular micrometer readings equal 0.01 mm, the real length and width values were then calculated using this information.

The results were analysed using a t-test to determine if differences existed in width or length for these two sexes of adult TSSM.

The mean width for male TSSM was found to be 0.0016 \( \pm \) 1.6x10^{-8} mm and for females 0.0059 \( \pm \) 2.56x10^{-8} mm. There was a significant difference in mean width between the sexes (t-test; n=10; P<0.005). The mean length for male TSSM was found to be 0.0036 \( \pm \) 7.2x10^{-8} mm and for females 0.0055 \( \pm \) 8.95x10^{-8} mm. There was a significant difference found in the
mean length (t-test; n=10; P<0.0005). The results show that female mites are larger in size than male mites.
LITERATURE CITED


