SPATIAL DISTRIBUTION AND REPRODUCTIVE BIOLOGY OF WESTERN FLOWER THRIPS, *FRANKLINIELLA OCCIDENTALIS* (PERGANDE) (THYSANOPTERA: THRIPIDAE)

By

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ABSTRACT

Western flower thrips (WFT), *Frankliniella occidentalis* (Pergande), are haplodiploids. Virgin females produce sons parthenogenetically but must be mated to produce daughters. As a result, primary and secondary (adult) sex ratios can diverge from the 1:1 ratio commonly observed in diploid systems. Field studies were conducted to examine the spatial distribution of WFT on two greenhouse crops, Bell peppers, *Capsicum annuum* (Linn.) and Long English cucumbers, *Cucumis sativus* (Linn.) to determine if there was a correlation between sex ratio and density. Leaf and flower samples were taken weekly. All adult and immature WFT were counted and sex of adults determined. Yellow sticky traps were used to monitor density and sex ratio of the dispersing adult population. Lab studies were also done to investigate if male availability affected the sex ratio and number of offspring produced by individual females. Laboratory experiments were done to assess the effects of sperm availability and maternal age on sex ratio of progeny produced.

On both crops, 84 to 95 % of adult WFT in flowers were females and most larvae (> 85 %) were found on leaves. Male WFT were rare on all plant parts even when caught in high numbers on traps. Approximately 75 % of females found on plants in the greenhouse were mated. Most (70 - 90 %) WFT on traps at low densities (< 200 individuals/trap) were males. This suggests that WFT populations are initiated by virgin females that likely overwintered as pseudopupae in the greenhouse. These females initially produce only sons, and may have to wait for these to emerge before they mate and produce daughters. As WFT density within a greenhouse increases, females are probably mated soon after emergence. Sex ratio of adults on traps becomes more female biased as density increases within a greenhouse. Heavily female biased (> 65 %) sex ratios were found on traps at high population densities (> 200 individuals/trap). Sex ratio

of adults on traps remained male biased in the pepper greenhouse (WL) where the population density of WFT remained low. Information regarding within-plant distribution of thrips is essential for population monitoring and control. Used together, regular examination of flowers and counts of adults on sticky traps allow quick detection of potential "hot spots" of WFT density. Sex ratio and density are highly correlated. Sex ratio of the dispersing adult population is a good predictor of outbreak potential of the extant WFT population.

Two WFT predators found in greenhouses were also monitored to document their effects on WFT population density and sex ratio. Mass introductions of the predatory mite, *Amblysieus cucumeris*, did not successfully control WFT in most greenhouses monitored. A natural infestation of pirate bugs, *Orius tristicolor* occurred in the only pepper house monitored. WFT density remained low throughout the growing season. *O. tristicolor* shows promise for future use in integrated pest management programs designed to control *F. occidentalis* in commercial greenhouses.

Lab studies showed that sex ratio of offspring produced by mated females was influenced by sperm supply and maternal age. Mated females produced sons and daughters which suggests that females control sex of offspring produced through selective fertilization. Once mated, two-thirds of offspring produced are females. Older females produced fewer daughters than younger females.

A principle conclusion from this study is that sex ratio of the WFT population within a greenhouse can be used to predict future population dynamics. Male availability may be the most important factor affecting the number of daughters produced by individual females which in turn may determine the potential of WFT populations to increase.

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Chapter 1

GENERAL INTRODUCTION

Frankliniella occidentalis (Pergande) (Thysanoptera: Thripidae), the western flower thrips (WFT), are distributed throughout North America (Lublinkhof and Foster 1977). In the last five years WFT have become a major pest in commercial floral and vegetable greenhouses in British Columbia (Vernon and Gillespie 1990). WFT damage crops directly because of their feeding and indirectly as vectors of tomato spotted wilt virus on ornamentals and some vegetable crops. WFT outbreaks in greenhouses are characterized by extremely rapid population growth and a devastating impact on the crop.

Use of the predatory mite, *Amblyseius cucumeris* (Oudemans), to control WFT in commercial cucumber and pepper greenhouses has become widespread in British Columbia since 1986 (Gilkeson et al. 1990). Successful control with these mites has been unpredictable and generally, growers still resort to insecticides to reduce rapidly growing WFT populations. Insecticides registered for use in British Columbia do not eradicate WFT in the greenhouses. Use of insecticides disrupts the establishment of naturally occurring predators and biological agents introduced for thrips and other pests within the greenhouse. A dependable biological control agent has not yet been found that can control WFT in vegetable greenhouses throughout the growing season.

The minute pirate bug, *Orius tristicolor* (White), has long been recognized as an important thrips predator on commercial vegetable and cotton crops in the United States (Bailey 1933, van den Bosch and Hagen 1966, Salaz-Aguilar and Ehler 1977, Stolz and Stern 1978, Letourneau and Altieri 1983). *O. tristicolor* preys on larval and adult stages of WFT and therefore is likely a much more effective WFT predator than *A. cucumeris*.

However it is not yet commercially available as a biological control agent in Canada. It is difficult to mass produce because of its voracious, cannibalistic nature.

Despite the ubiquitous nature of WFT and its reputation as a devastating horticultural and agricultural pest, little is known about WFT population dynamics and mating biology. Most of the work to date has focused on finding potential biological control agents and, how abiotic parameters within a greenhouse affect development time and fecundity of WFT (Bryan and Smith 1956, Lublinkhof and Foster 1977, Gillespie 1989, Gilkeson et al. 1990). WFT females insert their eggs into plant tissues. Females lay several eggs a day, one at a time continuously throughout their lifetime. There are two larval, feeding stages and two pseudopupae nonfeeding stages. Most researchers presume that pseudopupae drop off the plant and spend the remainder of the development period in the soil or litter surrounding the plants. Development time is 12 to 14 days in the lab at 21 ^{o}C and 70 % RH. Both adults are winged and capable of flight. Females can be distinguished from males because they are larger and darker than males and have black bands around their abdomen. Females live from 40 to 50 days in the lab; males live approximately half as long (personal observation).

A unique feature of this insect is its reproductive biology. WFT are haplodiploids. Females are diploid and males are haploid. Virgin females produce sons parthenogenetically, but must be mated to produce daughters. It is not known if mated females regulate sex ratio of progeny produced in response to local environmental conditions.

The main objective of this research was to examine the spatial distribution and mating biology of WFT on two commercial greenhouse crops; Bell peppers, *Capsicum annuum* (Linn.) and Long English cucumbers, Cucumis sativus (Linn.) variety anglicus

(Bailey) and laboratory. This study has three main components. The first examines the spatial distribution of WFT and two of its predators in these two crops. Predators also had to be monitored in case they had an affect on WFT population density or sex ratio. Mass introductions of the predatory mite, *A. cucumeris*, were made in all greenhouses monitored. *O. tristicolor* occurred naturally in one of the greenhouses monitored, House WL. The second part of this study examines changes in the temporal and spatial dynamics of WFT. Population density and sex ratio of adults were monitored in greenhouses using yellow sticky traps. I wanted to determine if there was a correlation between population density and sex ratio. Thirdly, lab experiments were conducted to examine a couple possible mechanisms responsible for the observed changes in sex ratio and density found in greenhouses. Experimental manipulations of female and male density were done in the laboratory to assess the affects of sperm availability and maternal age on sex ratio.

Chapter 2

SPATIAL DISTRIBUTION AND POPULATION DYNAMICS OF WESTERN FLOWER THRIPS ON TWO GREENHOUSE CROPS

INTRODUCTION

Western flower thrips (WFT), *Frankliniella occidentalis* (Pergande), are prevalent pests in commercially grown vegetables and flower crops in North America and Europe (Broadbent 1986, Yudin et al. 1986, Ramakers 1988, Yudin et al. 1988, Brodsgaard 1989). Although native to south coastal British Columbia, WFT have become established as major pests in commercial B.C. greenhouses only in the last five years (Vernon and Gillespie 1990a). It is not known if the strain that is responsible for damaging greenhouse crops is native or was introduced on plant material from other countries. WFT are of particular concern in greenhouses because (1) they are vectors of tomato spotted wilt virus (Sakimura 1962), (2) they are not readily controlled by commercially available biological control agents and (3) use of insecticides on WFT disrupts the establishment of naturally occurring predators and biological control programs for other greenhouse pests such as aphids, spider mites and white fly (Gillespie 1989).

The phytoseiid mite, *Amblysieus cucumeris* (Oudemans), is commercially mass produced and has been used extensively as a biological control agent for WFT in commercial vegetable greenhouses in B.C. since 1986. However, success with these predatory mites is unpredictable among greenhouses. The minute pirate bug, *Orius tristicolor* (White), occurs on many commercial vegetable and cotton crops grown in the USA and is recognized as an important predator of thrips (Bailey 1933, van den Bosch and Hagan 1966, Salas-Aguilar and Ehler 1977, Yokoyama 1978, Letourneau and Altieri

and Hagan 1966, Salas-Aguilar and Ehler 1977, Yokoyama 1978, Letourneau and Altieri 1983). *O. tristicolor* is primarily a western species, but occurs across the northern United States and Canada, and through Mexico into Central and South America (Herring 1966). In British Columbia, *O. tristicolor* is not yet commercially available for use as a biological control agent on greenhouse crops. However, occasionally it invades a greenhouse and becomes established. *O. tristicolor* may be more effective at controlling WFT because they consume adult and immature WFT (Salas-Aguilar and Ehler 1977, Stoltz and Stern, 1978) whereas the mite, *A. cucumeris*, feeds predominantly on the first and early second larval instars (Beglyarov and Suchalkin 1983, Bajita 1986, Bakker and Sabelis 1986). Therefore WFT may be susceptible to predation by *A. cucumeris* for a shorter period of time than to predation by *Orius*. There is still little understanding of the quantitative impact these predators have on the population dynamics of *F. occidentalis*.

The purpose of this portion of the study was to monitor seasonal population changes of WFT, and examine the spatial distribution of WFT adults and immatures on Long English cucumbers, *Cucumis sativus* (Linn.) variety anglicus (Bailey) and bell peppers, *Capsicum annuum* (Linn.). I also wanted to assess the relationship between WFT numbers in flower and leaves and those caught by sticky traps to ascertain which monitoring techniques would best predict future thrips densities. Population densities of *A. cucumeris* and *O. tristicolor* (when present) were monitored to assess the impact of these thrips predators on WFT population dynamics.

METHODS AND MATERIALS

Two of the greenhouses monitored were in Maple Ridge, British Columbia (CD and A15); the other two were in Langley, British Columbia (WL and GS). All

greenhouses were constructed of glass. Computer run systems monitored and maintained temperature and humidity levels within a greenhouse. Seeds were generally sown in early October. In mid-December plants in rockwool cubes were outplanted in rows into bags of sawdust, and grown under hydroponic conditions in standard sawdust growth medium (Adamson and Maas 1981, Anon., 1985). In all greenhouses, average temperatures ranged from 22 - 24 ^{o}C; average humidities ranged between 70 - 80 % (Table 1). In House GS in 1988, crops were outplanted relatively late, in January, because construction of the greenhouse was not completed. The propagation plants used in this greenhouse were obtained from another greenhouse; many of these plants were infested with WFT.

One Bell pepper and two Long English cucumber greenhouses were monitored from June to September in 1988, and February to August 1989. Only one pepper house was monitored because other local pepper houses had a higher percentage of other thrips species, mainly onion thrips *Thrips tabaci*, or the parasitoid, *Aphidius matricariae* (Haliday), which had been introduced to control aphids. This parasitoid is attracted in large numbers to yellow sticky traps used to monitor WFT (pers. observ.) so monitoring in these houses could potentially reduce the effectiveness of these biological control agents (Gilkeson pers. comm.). The pepper house (WL) and one of the cucumber houses (GS) were monitored for two years. The other cucumber houses (CD) and (AL5) were monitored for one year, 1988 and 1989 respectively. In 1988, crops were in full production by the time monitoring started. In 1989 greenhouses were monitored from the very beginning of the growing season, when plants were young and not yet producing fruit. Greenhouses were monitored until the WFT population had decreased to very low numbers or insecticides were used regularly to control the WFT population.

Table 1. Greenhouse Conditions. All greenhouses had an average temperature of approximately 22 - 24 ^{o}C and relative humidity of 70 - 80 %. Temperature and relative humidity ranges cover the extremes found throughout the growing season (*GH = Greenhouse. **cultivars grown in 1989.)

GH*	Crop	Cultivar	Size (m^2)	Temp (^{o}C) Range	Rel. Hum. Range	Plants per m^2
WL	Bell Peppers	Luteus Ariane Mauras Bruma Delphin Type 400**	16800	14-31	55-90 %	2.6
GS	Cucumbers	Carona Farona Mustang**	9290	17-30	72-85 %	1.4
CD	Cucumbers	Farona	4181	18-32	50-90 %	1.1
AL5	Cucumbers	Carona Mustang**	3840	24-29	74-80 %	1.4

Monitoring procedures

Monitoring was done in commercial greenhouses in which *F. occidentalis* was the predominant thrips species (>95% of thrips caught on traps). Monitoring was discontinued at a greenhouse when pesticides were used regularly to suppress the WFT population. Traps were checked and changed weekly. Plant samples were also taken weekly.

Yellow, opaque, vinyl plastic cards (12.7cm x 7.6cm; Cadillac Plastics, Vancouver British, Columbia) were used in 1989 to monitor changes in adult WFT and *Orius tristicolor* population densities. Cards were coated on both sides with an insect adhesive (Stikem Special, Seabright Enterprises, Emeryville, CA). Spectral reflectance at 0 - 650 nm was 81 to 83% (maximum at 580nm) with reflectance decreasing outside of range indicated. Percent reflectance was measured relative to a white magnesium oxide standard (= 100%) with a Cary 17 recording spectrophotometer. In 1988 commercially available plastic yellow cards, coated with the same glue, were used (Monagrow Inc., Vancouver, British Columbia). They were the same size as traps used in 1989 but the spectral reflectance was found to be lower (maximum reflectance intensity of 76% at 550nm). Vernon and Gillespie (1990a) found that greenhouse glass transmitted from 90 to 97% of incident wavelengths between 350 - 700nm and concluded that trap colour intensity was not affected by greenhouse glass. The lower reflectance intensity of traps used in 1988 should not have caused significantly different trap catches from that found in 1989. Vernon and Gillespie (1990a, 1990b) found yellow to be an effective WFT attractant when reflectance intensity at 550nm was 60 to 80+ percent and reflectance intensities of wavelengths at 350 and 440nm were low. Traps used in both years of this study met these qualifications. Although some blue colour traps catch more WFT than yellow, the proportion of male and female WFT caught does not differ significantly between these two colours (Brodsgaard 1989, Vernon and Gillespie 1990a). Yellow was

chosen for this study because adult WFT are much easier to sex, count and identify on yellow than on blue traps. Yellow is the most common trap colour used in commercial vegetable greenhouses and is the best general pest attractant for thrips and other greenhouse pests (specifically white fly) (Vernon and Gillespie 1990b).

Traps were attached with wooden clothespins to wires that supported the plants. These could easily be moved up the wires as plants grew. Traps were hung just above or at the top of the crop canopy because this is where the greatest number of dispersing adult WFT are caught (Gillespie and Vernon 1990) generally facing north/south. The number of traps used differed between greenhouses (Table 2) depending on size of the greenhouse and WFT density. Weekly counts were made of all adult WFT and pirate bugs caught on the traps. Adult WFT were also sexed. Adults can be sexed without magnification. Female WFT are much larger than males and have black band on their abdomen. Male are small and pale in comparison. Traps were changed weekly, and replaced at the same location. Mean number of WFT and predators per trap and standard errors were calculated for each sampling date, for every greenhouse. Rows were chosen systematically so that traps were distributed uniformly throughout the house, a systematic rather than a random sample. When a systematic sample is drawn from a random population, then estimates of means and variances are approximately equal to those achieved by random sampling (Scheaffer et al. 1979). I assumed that traps caught a random sample of flying WFT adults.

Trapping schedule

In the pepper greenhouse (WL), 1988, only 10 rows of plants (out of more than 270 rows) contained traps (one per row). Traps were placed randomly throughout the greenhouse in the middle of arbitrarily chosen rows. House WL was the largest greenhouse monitored (Table 1) and presented sampling and trapping problems not

Table 2. Trap numbers counted weekly in greenhouses monitored in 1988 and 1989.

House	Total No. of Traps	No. per Row	Julian Date
1988			
WL	10	1	
GS	38	3	< 199
	21	2	> 199
CD	42	3	< 223
	35-16	2-1	> 223
1989			
WL	22	2	
GS	47	3	< 71
	32	2	> 71
AL5	24	3	

encountered in other greenhouses. Most of these problems were overcome by using more traps in 1989. In 1988, plant samples were randomly taken throughout the entire house; in 1989 samples were taken from only one section of the greenhouse (28 rows of plants). In 1989, this section of the greenhouse was trapped more intensively than the rest of the house (6 rows had traps as opposed to 2 - 4 rows in every other section of the house). In 1989, 22 traps were counted weekly (one per row). In 1988, at house GS, 38 $\pm$ 1 traps were counted weekly (3 per row; placed approximately in the front, middle and back) (Table 2). The number of traps was reduced to 21 $\pm$ 1 for the last two sampling dates because trap catches of WFT were very high (> 500 per trap). In 1989, 47 $\pm$ 2 traps were initially counted in House GS. This was reduced to 32 traps at day 72. Monitoring of House GS was terminated before that in other greenhouses because the grower resorted to insecticides to suppress the WFT population. In House CD (1988), 42 traps were counted each week until day 222. On the last 5 sampling dates the number of traps counted were reduced from 35 to 16 because densities of WFT were greater than 500 per trap (Table 2). In House AL5 (1989), 24 traps were used throughout the monitoring period (3 per row). When a greenhouse became "saturated" with WFT (500 - 1000 WFT per trap), trap counting became very labour intensive and the number of traps per row within a greenhouse was decreased. It is difficult to count and sex all adults when trap catch is around 1000. At these high densities thrips numbers may be underestimated. For trap catches between 500 and 1000, adults only on the right or left half of each side was counted. The half of each face counted was chosen randomly. This total was multiplied by 2 to obtain the total WFT density per trap.

Plant samples

Plant parts were sampled weekly to determine the distribution of adult and immature WFT and predators on the crop, and also for an independent assessment of temporal changes in WFT population dynamics on a smaller scale. In the pepper

greenhouse (WL) only, plant samples were taken biweekly during August in 1989 because the WFT population had decreased to very low densities. Flower and leaf samples were taken throughout the greenhouse from the surface of the upper strata of the plant canopy. This is where the majority of WFT occur on the plants (Kirk 1985a, Gillespie 1989). The location (row number and position; front, middle or back) of the flower and leaf samples were chosen randomly prior to the sampling date using computer generated truncated random numbers. The range depended on the number of rows within the greenhouse. This was done to eliminate any sampling bias that may have occurred by knowing the density of thrips on traps within the greenhouse on the sampling day. In House WL, flower and leaf samples were taken from only one large section of the greenhouse in 1989. This was necessary to minimize the variance among flower and leaf samples and the number of samples taken weekly in this large house. The section chosen in 1989 initially had the highest WFT catch per trap within the house.

In 1988, the number of flower samples taken from each greenhouse varied weekly and no leaf samples were taken. In 1988, plant samples were randomly taken throughout House WL; in 1989 samples were taken from only one section of the greenhouse (28 rows of plants). In the pepper house (WL) in 1988, the number of flower samples ranged from 15 to 50. At the start of the sampling period, very few thrips were found in the flowers so sample numbers were increased to determine if they were being missed. In cucumber houses (GS and CD) monitored in 1988, 25 to 30 flower samples were taken each week. In House WL (1989) 10 flower and 10 leaf samples were taken until day 100, after which 20 flower and 20 leaf samples were taken. In 1989, leaf and flower samples were taken weekly in this house until day 150, after which samples were taken biweekly because the WFT population was so low. In both cucumber houses monitored in 1989 (GS and AL5), 30 flower and 20 leaf samples were taken weekly. Samples were processed immediately upon return to the lab. All adult and immature WFT were

visually counted and the sex of adults determined. Predators (*O. tristicolor* and *A. cucumeris*) occurring on traps or plant samples were counted only in 1989.

A. Flower samples

Flowers were placed individually into 25 ml. plastic vials immediately after picking. This is important to ensure that all stages of thrips in flowers are captured. WFT have a habit of freezing before flying when disturbed; it is unlikely that thrips inside or on the outside of the flowers escaped capture. As soon as the flower was placed in the vial, it was filled with 70% ethanol, and sealed. Only mature flowers were sampled; no buds were taken. At the laboratory, contents of the vials were individually filtered through a Buchner funnel lined with Whatman No. 1 filter paper to separate the flower specimen and the captured WFT from the alcohol. The filter paper, with the flower and thrips, was then placed into a petri dish and examined under a dissecting microscope. Flowers were thoroughly dissected and all WFT (adults and immatures) and predators counted.

B. Leaf samples

Leaf samples were taken only in 1989. Only upper canopy leaves were sampled despite the fact that these leaves may be more variable in age than leaves lower down on the plant. On mature plants most WFT are found on leaves in the upper canopy (Steiner 1990). Plastic bags (27 x 28 cm, Ziploc^{R}) were pulled over the entire leaf, the stem broken and the bag sealed quickly. Each leaf was put into a separate bag and kept in a cooler until examined at the lab. Individual adult and immature WFT and predators can be counted easily under a dissecting microscope. All areas of the leaf surface were visually scanned on both sides in a dissecting tray. First adults found on the leaf were removed, sexed and counted. After larvae had been counted, the bag was rinsed with water and the washing poured through a 100-mesh (149μm) sieve to collect individuals

caught inside the bag. Immature WFT and predators were rarely found in this washing. Most adult and immature WFT and predators (> 90 %) tended to remain on the leaf.

Predators

In both years, predatory mites were introduced by growers throughout all greenhouses to control the WFT population. The number of mites introduced depended on the number of plants per meter square, and density of the thrips population. Although each greenhouse likely contained different densities of predatory mites, growers generally followed the same set of arbitary application guidelines based on counts of thrips and predatory mites on leaf samples. There no data on how trap and plant sample densities of thrips represent actual population densities and spatial distribution. Growers generally started introducing predatory mites in mid-February. Predatory mites were obtained by most local growers from Applied Bionomics, Sidney B.C. In cucumber houses, applications were made weekly until the last couple of months of the growing season (July - September) or until the number of leaves with predators equaled the number of leaves with thrips only (L. Gilkeson, Applied Bionomics, pers. comm.). Growers were advised to introduce 100 - 200 per plant per week. Pepper growers made fewer, smaller introductions of *A. cucumeris*. Most growers made only two introductions of 10 - 25 mites per plant in a growing season (L. Gilkeson, pers. comm.). In pepper houses, fewer *A. cucumeris* per plant are necessary to control thrips because they are more efficient at searching for and finding WFT on pepper leaves (Peterson 1990).

A natural infestation of *O. tristicolor* occurred in 1988 and 1989 only in the pepper house (WL). Two ad hoc introductions of a few *O. tristicolor* adults (less than 100 adults each time (D. Gillespie pers. comm.) were made into House AL5 in 1989 (one in January and one in March) to examine their success of establishment. No *Orius* were found in houses CD and GS.

Data analysis

Spearman rank correlations were used to determine how densities of adults and immatures on the plants fluctuated with trap counts. For flower samples, paired-sample *t* tests, on arcsine squareroot transformed data, were used to compare numbers of adults and immatures for each sampling date within a greenhouse. Data from different greenhouses were not compared because of inherent natural differences. All statistical tests were performed using SYSTAT (Wilkinson, 1989).

RESULTS

Population growth of thrips -- Trap catch

Population densities of *F. occidentalis* for each of the greenhouses monitored in 1988 and 1989 are shown in Figure 1. Sampling started late in the growing season of 1988 (June). By this time, WFT had already reached high densities in one greenhouse (Figure 1a). Peak mean trap catches differed greatly among the cucumber and pepper houses (Figure 1a and 1b). In 1988, peak trap catch reached 900 in the cucumber houses (GS and CD) and 200 in the pepper house (WL). In 1989 the cucumber houses had peak densities that ranged between 1000 (GS) and 500 (AL5) WFT/trap. Trap catch in the pepper house (WL) never exceeded 200 WFT/trap in 1989 (Figure 1b). In 1988, the number of WFT per trap was initially lower in House CD than House WL because the crop had been replanted just prior to monitoring. Prior to day 150, the initial planting was pulled and destroyed because the crop had been badly damaged by a high WFT infestation. At day 170, plants were young and not yet producing fruit. Trap catch of adult WFT increased rapidly each week to densities similar to that found in house GS. After day 258 the grower resorted to insecticides to control thrips, and monitoring was terminated. In both years, trap catches of WFT were significantly lower at the end of the

monitoring period in House WL than in the other greenhouses. The large standard error associated with trap catch in House WL in 1988 may be attributed to the relatively small number of traps (n = 10) used per week to monitor WFT and predator populations throughout this huge house. In 1989, the number of traps used per week was doubled, n = 22, which appeared to decrease the variance for each sampling date (Figure 1b and 2b).

Total number of WFT per trap increased throughout the monitoring period in all cucumber greenhouses (Figure 1a and 1b). In House GS, the WFT population was very high relative to the other houses at the start of the monitoring period in both years. In 1989, trap catch in House GS may have reached peak densities, similar to those found in 1988, earlier because the propagation plants were infested with WFT (G. Schlact, pers. comm.). In House AL5, trap counts were significantly lower than in other greenhouses at the start of the monitoring period (Figure 1b). Trap counts increased to densities similar to those in House WL until day 165, after which they became significantly higher. After day 234 insecticides were used and field monitoring ended. In House AL5 trap catch of WFT decreased from approximately day 100 to day 152. Trap catch of WFT also decreased after day 100 in House WL. In both these houses the decrease in numbers of WFT found on traps was likely caused by predators (mites in House AL5, mites and pirate bugs in House WL). In 1989, pirate bugs were rarely found on the traps (total = 6 before August, n = 504 traps) or on the plants until the last month of sampling (total = 33 in month of August, n = 96 traps).

House WL

House WL was much larger than any of the cucumber greenhouses monitored. In 1988 I had a very difficult time deciding the number of traps necessary to get a representative sample of the dispersing WFT population and how many flower samples and from where they should be taken to examine the spatial distribution of WFT on

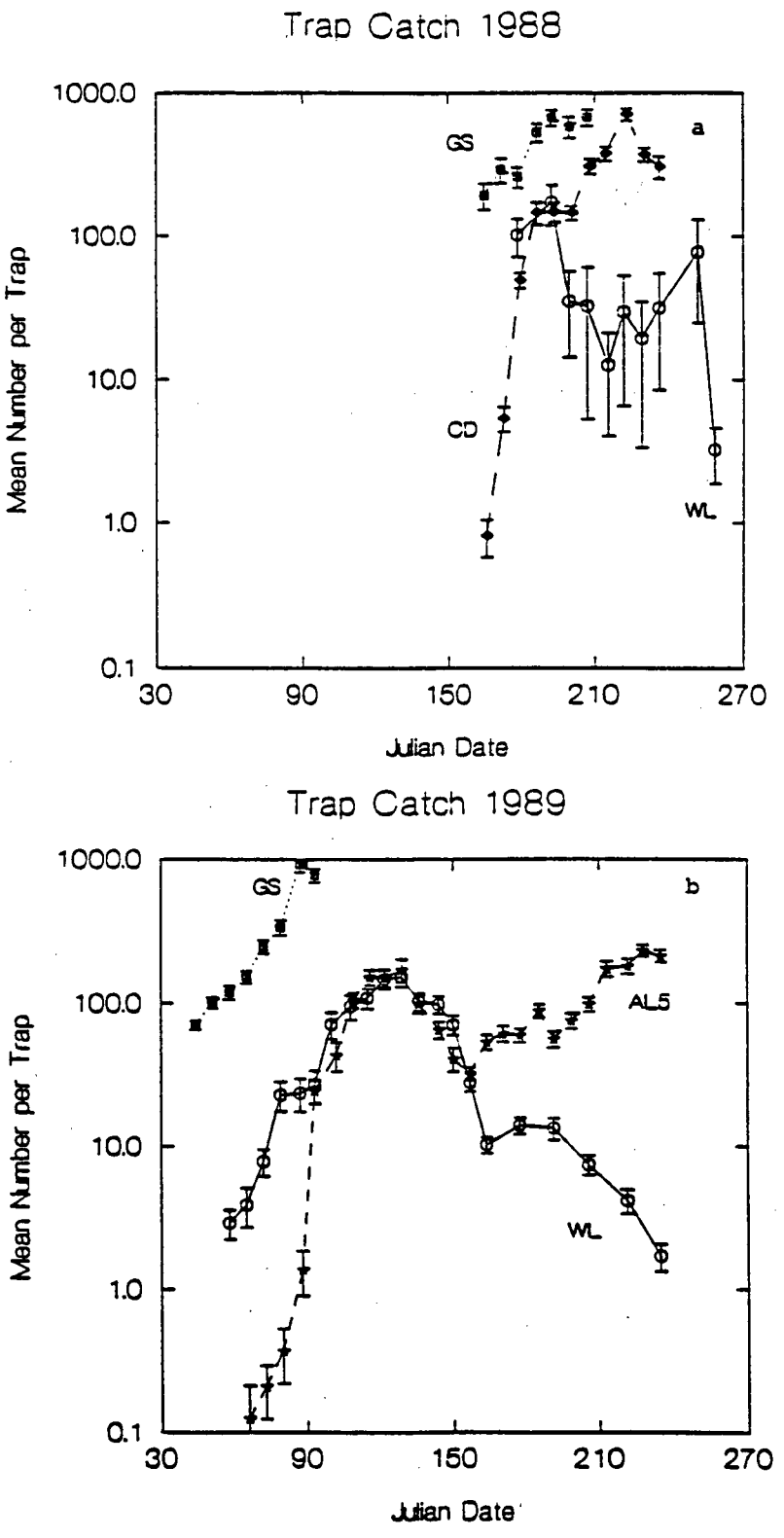

Figure 1. a) Mean number of adult WFT per trap (± SE) for each date sampled in 1988. WL = Pepper House. CD and GS = Cucumber Houses. b) Mean number of adult WFT per trap (± SE) for each date sampled in 1989. WL = Pepper House. GS and AL5 = Cucumber Houses.

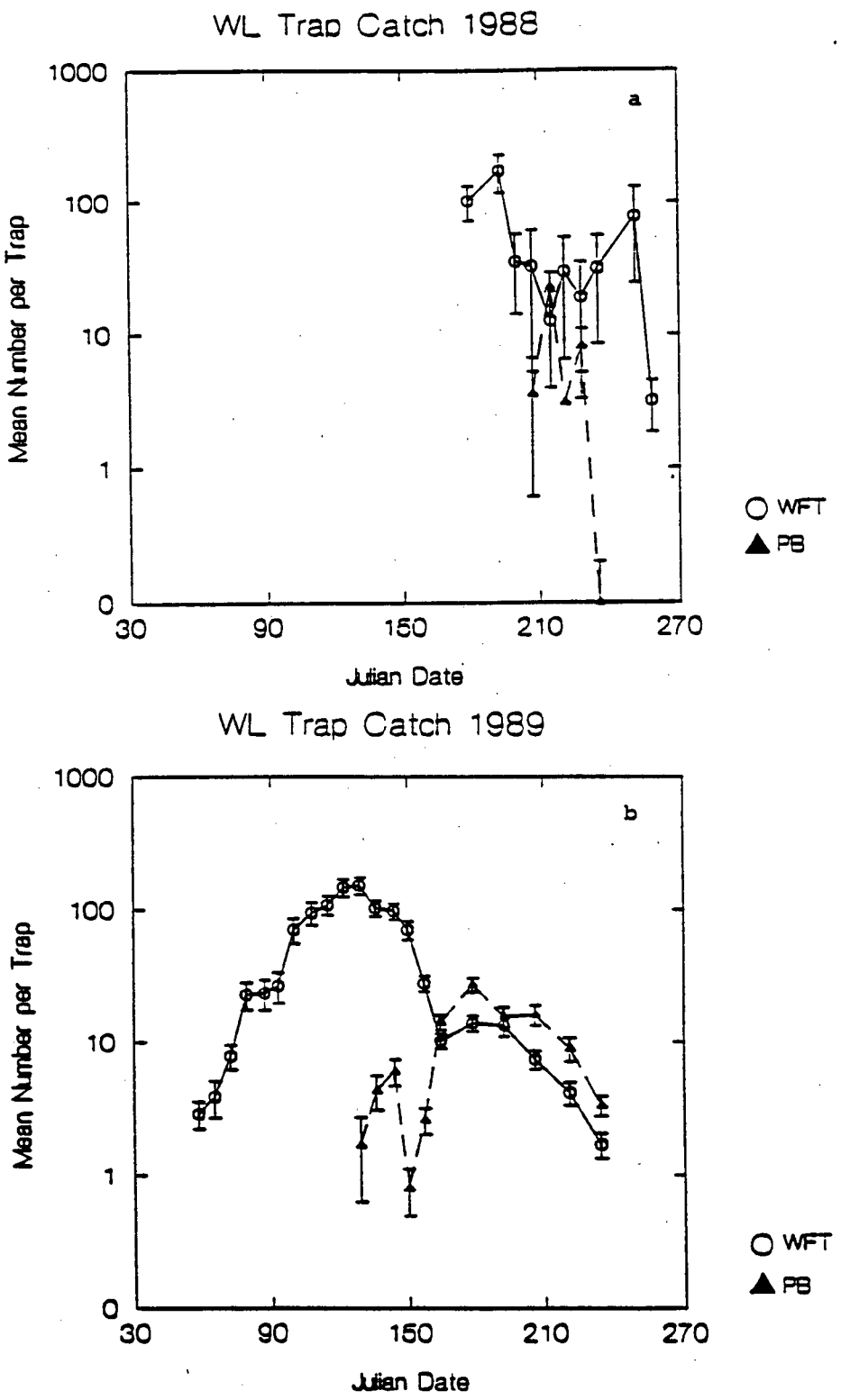

Figure 2. a) Mean number of WFT and *O. tristicolor* (PB) per trap (± SE) in 1988 (N = 10 traps/week) at Pepper House (WL) in 1988. Pirate bugs were not monitored prior to date 150. b) Mean number of WFT and *O. tristicolor* (PB) per trap (± SE) in 1989 (N = 22 traps/week) at Pepper House (WL) in 1989. No pirate bugs were seen on traps until after day 100.

pepper plants. In 1989 I believe I sorted these sampling problems out. This was also the only greenhouse monitored that had a natural infestation of *O. tristicolor*. In both years, similar peak WFT densities were reached. In 1988 there appeared to be no correlation between numbers of *Orius* and WFT on traps (Figure 2a). This may have been due to the small number of traps used in this hugh greenhouse to monitor pest and predator density or to the late start of field monitoring. Also, in 1988 *Orius* was not monitored until after day 150. However in 1989, there was a very good correlation in numbers of *Orius* and WFT found on traps (Figure 2b). As numbers of WFT increased, numbers of *Orius* found on traps also increased. As the density of WFT decreased, density of *Orius* also decreased. In 1989 *O. tristicolor* was not found on the traps until after day 100. The WFT population was reduced from >100 per trap to <10 per trap by the end of the monitoring period in both years. By the end of the monitoring period in 1989, more *Orius* than WFT were caught on traps.

Distribution of WFT on plants

As trap catch increased, the number of WFT found on plant samples also increased. Only WFT adults and the first two instars were found on plant samples; pseudopupae were not found. In 1988, the number of females and immatures found in flowers were not significantly correlated to density of adults on traps ($p > 0.05$, Table 3). However in 1989, number of female and immature WFT in flowers and immatures on leaves were all significantly correlated to total numbers of adults caught on traps ($p < 0.05$, Table 3). In 1989, in greenhouses with high numbers of *A. cucumeris* (Houses WL and AL5), numbers of females WFT in flowers were more strongly correlated to trap catch (males + females) than were numbers of immature WFT on leaves were. In House GS the difference was negligible. Female numbers in flowers were significantly correlated with numbers of immatures on leaves and in flowers. In both years, House

WL had significantly lower population densities of female and immature WFT, on both flower and leaf samples, than other greenhouses except AL5.

Males were rarely found on plants. More males were found in flowers (2% to 12%) than on leaves (1% to 3%) (Table 4). Mean number of males per flower or leaf are not represented in the histograms (Figures 3, 4, 5) because they represented a small proportion of WFT found. Females and immatures accounted for greater than 87% of the WFT in flowers. Adult female WFT represented greater than 55% of the WFT found in cucumber flowers. In the pepper house, House WL, adult females made up only 29% of WFT found in flowers, immatures represented the majority of WFT in pepper flowers. Active immatures (first and second instars) composed the greatest proportion (> 85%) of WFT on leaves (Table 4) in the pepper and all cucumber greenhouses.

A. Flower samples

Significantly ($p < 0.01$) more females than immatures were found in flowers from cucumber Houses GS and CD on most sampling dates (Figures 3 and 4). In House AL5, significantly more females than immatures were generally found in flowers during the final weeks of sampling (Figure 4). In the pepper house (WL), the numbers of immatures and females did not differ significantly on most sampling dates, although in both years immature WFT always outnumbered females (Figure 3 and 4). In both years, the mean number of female and immature WFT in flowers was significantly greater on the last sampling date than on the first in all cucumber greenhouses, but not the pepper house (WL). Numbers of female and immature WFT in flowers reached similar peak densities in cucumber houses CD and AL5.

In both years, density of females and immatures in flower samples were lower in the pepper house (WL) than in any of the cucumber greenhouses monitored. In both

Table 3. Spearman rank correlations were done to examine the relationship between mean trap catch (MTOT = adult males and females) and mean number of female and immature WFT in flowers (MFEMF and MIMM respectively) and immatures on leaves (MIMML). All correlations were not significant in 1988 ($p > 0.05$). All correlations were significant in 1989 ($p < 0.05$).

Year	No. observ.	HOUSE		MFEMF	MIMMF	MIMML
1988	7	WL	MTOT	.429	.643	
			MFEMF		.357	
	6	GS	MTOT	.543	.714	
			MFEMF		.600	
	10	CD	MTOT	.406	.455	
			MFEMF		-0.055	
1989	15	WL	MTOT	.805	.862	.715
			MFEMF		.874	.717
	7	GS	MTOT	.964	.929	.929
			MFEMF		.964	.893
	24	AL5	MTOT	.896	.589	.589
			MFEMF		.638	.679

Table 4. Distribution of WFT males, females and immatures (percent of total WFT found for each plant part) on flower and leaf samples taken from each greenhouse. GS, CD, AL5 = Cucumber Houses. WL*** = Pepper House. (n* = total number of samples taken. Samples were taken from June to September in 1988, and February to August in 1989. Imm.** = first and second instars).

Year	n*	Greenhouse	% Males	% Females	% Imm.**
FLOWERS					
1988	193	WL***	4	29	67
1988	219	GS	12	69	19
1988	278	CD	11	65	24
1989	270	WL***	2	30	68
1989	249	GS	6	55	39
1989	681	AL5	12	62	26
LEAVES					
1989	299	WL***	3	7	90
1989	195	GS	2	4	94
1989	490	AL5	1	14	85

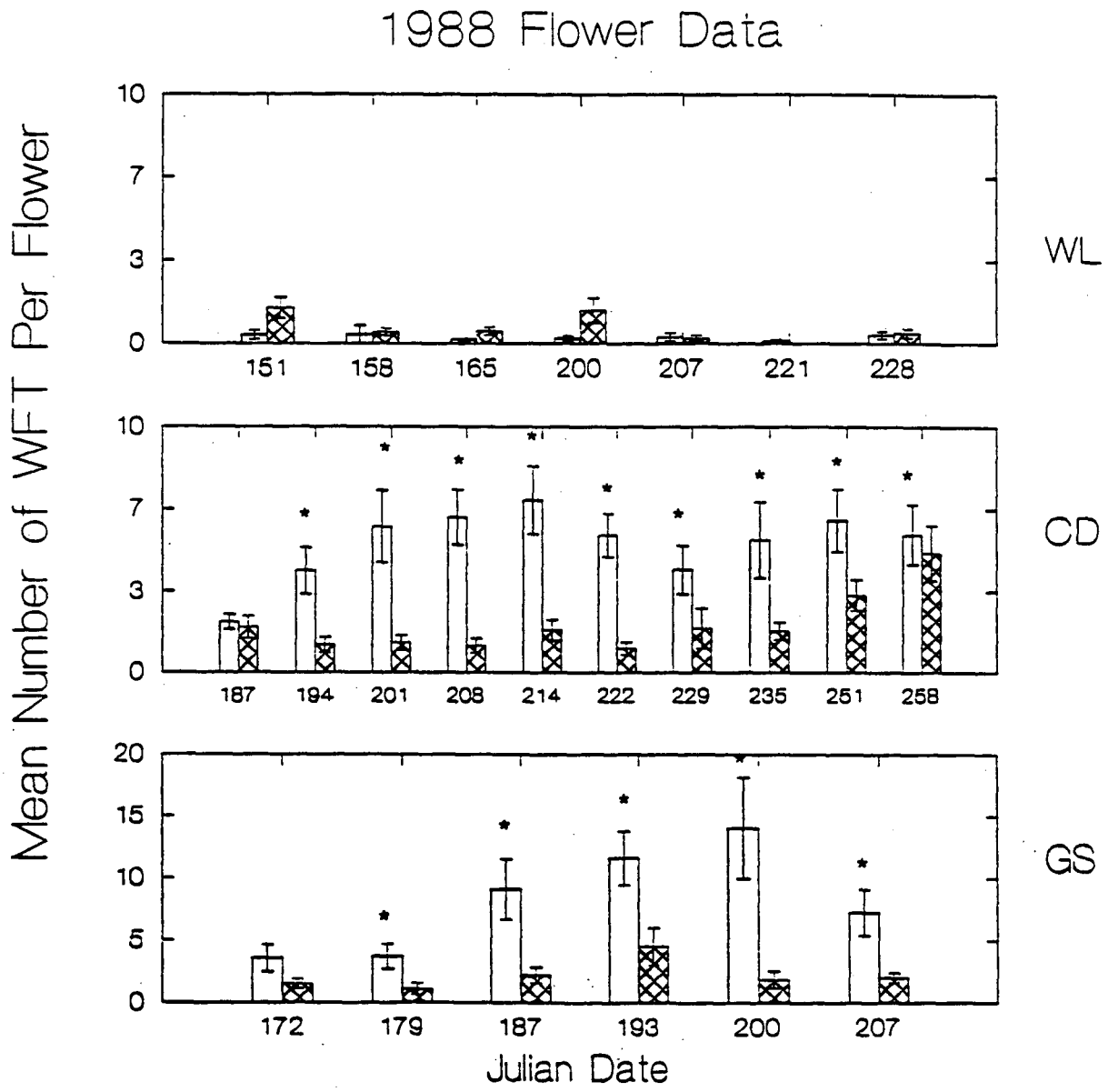

Figure 3. Mean number of female ☐ and immature ☒ WFT (± SE) per flower on each sampling date in 1988. WL = Pepper House. CD and GS = Cucumber Houses. Note different x-axes and y-axis for House GS. * denotes significant difference ($p < 0.01$, paired sample *t* test).

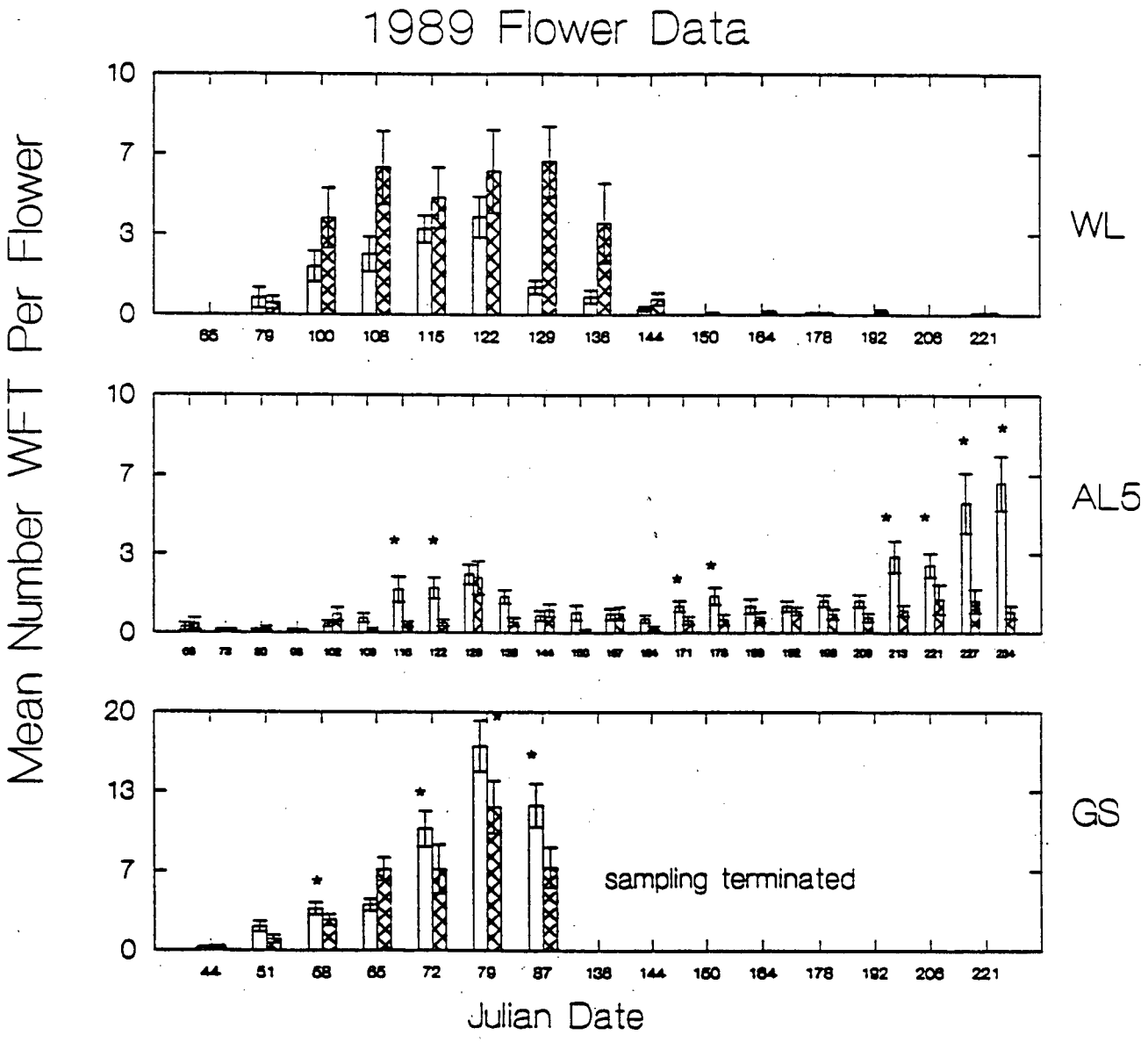

Figure 4. Mean number of female ☐ and immature ☒ WFT (± SE) per flower for each sampling date in 1989. WL = Pepper House. AL5 and GS = Cucumber Houses. Note different y-axis for House GS. * denotes significant difference ($p < 0.01$, paired sample *t* test).

years, House GS had higher numbers of adult and immature WFT in flowers than the other cucumber houses monitored (Figure 3 and 4). In House WL, WFT density in flowers were initially higher in 1989 than in 1988, but eventually decreased to densities similar to 1988. In House WL in 1989, females were first found in flower samples beginning in late March but by the end of May, females were not found here. Immature WFT density dropped from an average high of 6 per flower to less than 1 per flower over the same period. This decrease in numbers of thrips did not occur in any of the cucumber greenhouses monitored. *O. tristicolor* and *A. cucumeris* found on plant samples were counted only in 1989. More *A. cucumeris* were found in pepper flowers (House WL, total = 57) than in cucumber flowers (House GS, total = 8; House AL5, total = 41). In all greenhouses, the majority of *A. cucumeris* were found on leaves. Pirate bugs were rare. Two *O. tristicolor* nymphs were found in the final 4 weeks of sampling in the cucumber house AL5. In the pepper house (WL), very few *Orius* were observed on the plants in 1988. In 1989, although pirate bugs were frequently seen in random inspections of flowers throughout this greenhouse, very few were found in flower samples. A total of 6 *O. tristicolor* adults and 2 nymphs were found. This may have been because very few *Orius* occurred in the section of the greenhouse where the flower and leaf samples were taken, or because they flew away. In 1988, although application of insecticides was minimal in House WL, they were occasionally spot sprayed to suppress several pests (spider mites, aphids, loopers, and WFT). In 1989 no pesticides were used. This may be responsible for the increased length of *Orius* residence and number per trap in 1989.

B. Leaf samples

Immature WFT (first and second instars) were the dominant life history stage on leaf samples, accounting for at least 85% of the WFT (Table 2) in both cucumber and pepper greenhouses. At peak WFT densities, the number of immature WFT per leaf varied. The number of larvae found per leaf was lower in the pepper house (< 1 in House

WL) than in cucumber houses monitored (69 in House GS) (Figure 5). Most *A. cucumeris* were also found on leaves; very few were found in flower samples on both crops. A few *Orius* were found on leaf samples. In the pepper house (WL), 2 adults and 1 nymph were found; in the cucumber house AL5, 10 nymphs and 4 adults were found after day 171.

In all greenhouses monitored *A. cucumeris*, were introduced in large numbers throughout most of the growing season. The mites appeared to have become established in large numbers only in Houses WL and AL5. In House WL, from April 10 (day 100) to the end of the monitoring period *A. cucumeris* outnumbered immature WFT on leaf samples (Figure 5). Mean number of immature WFT remained below 1 per leaf; after day 150 no immatures were found. In House AL5, *A. cucumeris* appeared to maintain numbers of immature WFT below 10 per leaf until day 178, at which point WFT started to outnumber mites (Figure 5). During the remainder of the monitoring period as the number of immature WFT per leaf began to increase, numbers of predatory mites decreased. In House GS, although *A. cucumeris* was introduced, none were found on leaf samples. Numbers of immature WFT increased rapidly in House GS, starting in February, by late March (day 87) a mean of 70 per leaf was found (Figure 5). On leaves with many thrips, the youngest stages can be difficult to see because their colour is very similar to leaf tissue. Thus at high densities, their numbers may be under represented.

DISCUSSION

Trap catch and density of WFT on plants

Common pest management practices rely on sticky traps to monitor and estimate abundance of pests and predators over time. Several studies, outside and in greenhouses,

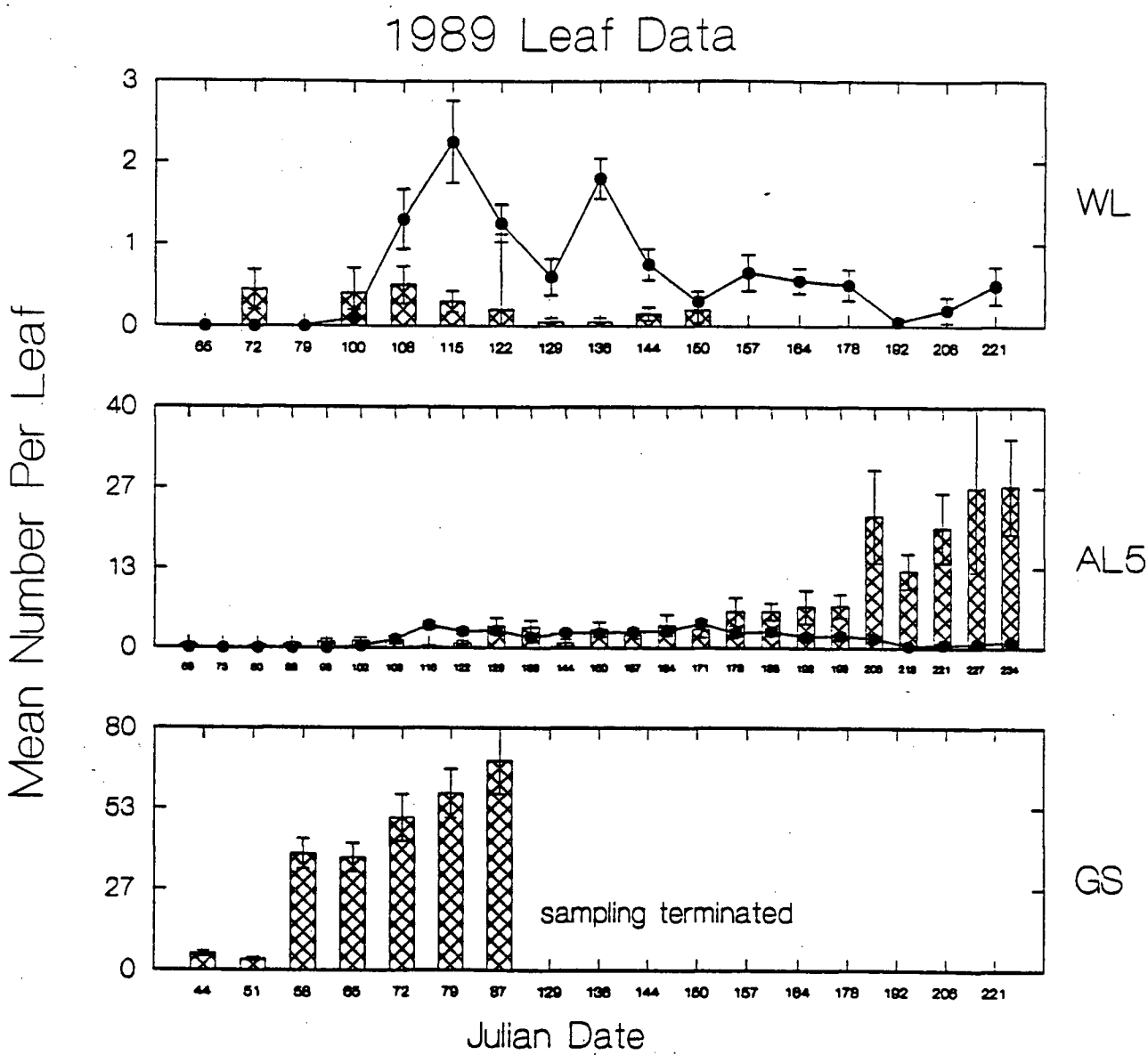

Figure 5. Mean number of immature WFT ⊠ and *A. cucumeris* ● (± SE) per leaf. No mites were found on leaf samples from House GS. WL = Pepper House. AL5 and GS = Cucumber houses. Note different y-axes.

examined adult *F. occidentalis* responses to trap placement and colour (Moffitt 1964, Yudin et al. 1987, Brodsgaard 1989, Gillespie and Vernon 1990, Vernon and Gillespie 1990a, 1990b). However, no studies have demonstrated how trap catch is related to the density of adults and immatures on plants. Steiner (1990) used mean number of WFT per leaf to estimate population density within a greenhouse but did use sticky traps for comparison. Knowledge of this relationship is necessary for a grower to make management decisions based on qualitative information of how trap catch is related to numbers on the plants. I found increased numbers of *F. occidentalis* adults and immatures on plants as adult trap catch increased. Trap catch increased throughout the growing season, peaking at different times in each greenhouse. Numbers of WFT found on traps decreased for a short period of time in House AL5 and continuously in House WL until very few were found on the traps. In both these cases this reduction was probably caused by predators. Peak densities of WFT differed between greenhouses. The reproductive rate of *F. occidentalis* may vary between greenhouses in response to house-specific abiotic and biotic conditions. Peak thrips density reached 500 to 1000 WFT per trap before growers resorted to chemical control.

Population dynamics of WFT can not be directly compared between cucumber and pepper greenhouses because of inherent differences in the two crops. Pepper leaves and flowers differ greatly from those of cucumber plants. Pepper leaves are about half the size of large cucumber leaves and have a waxy surface; the flowers contain pollen. Cucumber leaves on the other hand are hairy, and flowers do not contain pollen, only nectar. In addition, cucumber flowers are larger than pepper flowers. One must exercise caution however when interpretating how population dynamics of WFT differ between greenhouses containing different crops. On cucumber crops, large numbers of adult females and immatures were found in flowers (Table 4). The vast majority of adult WFT were found in flowers ($\bar{x}$ = 73 %) and immatures on leaves (> 85 %). Pickett et al.

(1988) found 68% of WFT adults in cotton flowers. For several plant species, others have found that flowers are readily colonized by *F. occidentalis*, the majority of which were adults (Yokoyama 1977, 1978, Yudin et al. 1986, 1987, Krause 1987, Pickett et al. 1988). Chemical and visual cues attract adults and immatures to these nutrient rich resources (Mulligan and Kevan 1973, Kirk 1984c). Floral nectar and pollen are utilized by several species of flower thrips (Yokoyama 1978, Kirk 1984a, 1984b, 1985a, 1987). Females may go to flowers to obtain nutrients for growth and reproduction. Pollen is rich in protein (Todd and Bretherick 1942) and may affect thrips fertility (Bournier et al. 1979, Kirk 1985a), egg production (Murai and Ishii 1982, Kirk 1985a) and larval growth (Murai and Ishii 1982). Trichilo and Leigh (1988) found that the addition of pollen to the diet of *F. occidentalis* reduced the development time from egg to adult, and increased adult longevity and fecundity.

Few studies of thrips have examined the sex of adults found in flowers. In the present study, females represented 84 - 95% of adults found in flowers of bell peppers and Long English cucumbers. Immature WFT (first and second instars) composed the greatest proportion of the population on the foliage (Table 4) although increasing numbers were found in the flowers as WFT density within a greenhouse increased. For two species of thrips *Thrips fuscipennis* and *T. major*, Kirk (1985b) found mostly adults in the flower *Calystegia sepium*s. Very few larvae were found. In these flowers, female *T. fuscipennis* greatly outnumbered males whereas for *T. major*, males outnumbered females (Kirk 1985b). Kirk (1985b) does not suggest why the sex ratio of adults should be so different in these two thrips species. Kirk (1985b) observed mating thrips in flowers and found that movement of males and females was affected by density; both sexes spent more time moving in and between densely occupied flowers. Very few males were found in flowers or on leaves. Pseudopupae were not found in flowers or on leaf samples. Pseudopupae are believed to drop off the plant onto the soil below to

complete development. Peak densities of adults and immatures found on plants varied between greenhouses and occurred when traps were catching peak numbers of adults on traps.

Male WFT were rare on all plant parts sampled even when caught in high numbers on traps. The reason for this is unclear. Perhaps males spend most of their time in flight during the day, and remain in flowers only long enough to copulate with available females. Thus, males may be more susceptible to being trapped than females. If this is true, males found in flower samples may only be incidental catches. Kirk (1984a) found that female *T. imaginis* tended to remain in the recesses of flowers during the day. In greenhouses however, high population densities of WFT may lead to crowding on the plants which may increase the tendency for females to move among plants. As density of the WFT population within a greenhouse increased, more females than males were caught on traps. Increased rates of departure at high densities have been reported for other species of thrips (Gopinathan et al. 1981, Kirk 1985b). At low densities within flowers, females tended to remain in one spot (Kirk 1985b). I do not believe however, that increased female movement within a greenhouse was totally responsible for the change in sex ratio on traps. As population density within a house increases, a greater proportion of females are mated. Once mated females produce mostly daughters (Chapter 3), and females make up a greater percentage of the adult WFT population (Chapter 2).

Flowers that are short-lived, relative to how long it takes for WFT eggs to hatch (2 - 4 days for WFT eggs to hatch at 22 ^{o}C in the lab) or for larvae to development to occur, would be used mostly by adults. Adults can fly from flower to flower whereas juvenile WFT must crawl. This niche separation between larvae and adults may break down in longer-lived flowers. Long English cucumber flowers senesce after

approximately 3 days, pepper flowers last for 4 - 6 days under average greenhouse conditions (B. Mauza, pers. comm.). This may explain why some females and the majority of larvae were found on leaves. Johnson (1986) found a majority (90%) of immature *T. palmi* on leaves. On both cucumbers and peppers, females may feed in flowers, but probably lay most of their eggs on leaves because of the epheremal nature of the flowers. Females and immatures probably remain in a flower until it starts to senesce at which point they most likely move to other flowers or leaves. Most immatures found in flowers probably moved there from nearby leaves to gain access to pollen (in peppers) or floral nectar (cucumbers). Kirk (1984a) found that 85% of the eggs laid by *T. imaginis* were outside flowers. More field observations are needed to ascertain where on pepper and cucumber plants female WFT oviposit. Immature WFT were more common in pepper flowers than in cucumber flowers for several possible reasons: 1) they may take advantage of the availability of pollen in pepper flowers, 2) female thrips have higher fecundity may be higher on peppers and therefore produce more offspring, 3) pepper flowers last longer (3 to 6 days compared with 2 to 4 days for cucumber flowers). Therefore immature thirps may have a longer period to accumulate in pepper flowers, 4) *O. tristicolor* may prey preferentially on WFT adults, so immature WFT are more common than adults.

Information regarding within-plant distribution of thrips is essential for population monitoring and control. Decreased plant vigor and damage to flowers and leaves due to feeding result in crop losses that make early detection and continual monitoring of *F. occidentalis* important. Steiner (1990) found that it was difficult to relate WFT density to the amount of fruit damage. Sometimes there was high numbers of WFT and a low amount of damage, other times there were few thrips and severe fruit damage. This may perhaps be explained by examination of the sex of thrips on traps. When traps are catching high numbers of males, very little damage may occur to the

crop. When traps are catching mostly females, severe fruit damage may occur because this is the sex that was found mainly in flowers. On greenhouse Long English cucumber and Bell pepper crops, female WFT are responsible for the majority of feeding damage in flowers. Females were found in flower samples before they were found on leaves. I suggest that for early detection of female WFT, flowers provide a good sampling unit and should be examined regularily. Used together, sticky traps and flower monitoring allow quick detection of potential hot spots of thrips activity and assessment of future WFT population dynamics. In houses where predatory mites have been introduced and established in large numbers, counts of immature WFT on leaves are not correlated as well to trap catch as are counts of females in flowers. It appears that *A. cucumeris* do most of their feeding on leaves and therefore have the greatest impact on immature WFT. Very few predatory mites were in cucumber flowers. Thus a more precise description of the WFT population in a greenhouse can be obtain from trap counts and female density in flowers.

Interactions of predators and WFT

A. cucumeris were more common in pepper flowers than in cucumber flowers. This may have been because predatory mites were established in higher numbers in House WL (the pepper house) than all of the cucumber greenhouses monitored except House AL5. *A. cucumeris* may use pollen (McMurty et al. 1970, Ramakers 1988) as an alternative food resource when thrips densities are low. Cucumber flowers do not contain pollen. Therefore more mites may have been found in flowers from the pepper greenhouse (WL) because of the additional food source offered by pollen. *A. cucumeris* feeds predominately on first instar larvae (Bakker and Sabelis 1989). Therefore when this prey stage is scarce, these mites may only be sustained by alternative food sources (Bakker and Sabelis 1989) such as pollen.

Gillespie (1989) found that *A. cucumeris* successfully controlled WFT on greenhouse cucumbers. This was not the case in most of the greenhouses I monitored. Hansen (1989) found that suppression of *Thrips tabaci* by *A. bakeri* on cucumbers differed among houses that had similar peak thrips densities and distribution of predators. In House GS, although large numbers of *A. cucumeris* were introduced, they were rarely found on leaf and flower samples. In House AL5, *A. cucumeris* was found on leaf samples, and appeared to be controlling the WFT population until day 171. The number of immature WFT per leaf remained below 10 which is considered a desirable level of control in greenhouses (Hansen 1989). Predatory mites were introduced into this greenhouse before traps were catching many thrips which may have resulted in excellent control of WFT initially. Later on in the growing season the rapid increase of WFT in flowers, leaves and on traps in House AL5 may be the result of mass immigration of WFT from outside into the greenhouse. This rapid increase in WFT density may overwhelm the ability of predators to control the population (Chant 1961). In addition, *A. cucumeris* enters diapause when daylength is less than eight hours, and night temperatures in the greenhouse fall below 21 ^{o}C at night; pirate bugs are apparently still effective at reducing the WFT population in late fall (Gilkeson et al. 1990).

High numbers of predatory mites must be established for control of the WFT population to be successful (Hansen 1988, 1989, Gillespie 1989). This is costly to the grower and there is still no guarantee that predatory mites will be effective at suppression of the WFT population. Several macro and micro, abiotic and biotic (Rasmy et al. 1984) parameters may affect continued establishment and success of these biological control agents (Rasmy et al. 1984, Hansen 1989). Such factors affect the predatory capabilities which consequently are responsible for regulating prey populations. The success of predatory mites may depend on the rate of increase of the thrips population (Hansen 1989), the crop/cultivar grown (Rasmy et al. 1984, Peterson 1990) and the distribution of

thrips within a greenhouse. *A. cucumeris* feeds mainly on first instar larvae; adult WFT are very difficult for them to kill (Beglyarov and Suchalkin 1983, Bakker and Sabelis 19860. Peterson (1990) found that *A. cucumeris* was a more efficient WFT predator on smooth pepper leaves than hairy cucumber leaves. Another species of predatory mite, *Typhlodromus mangiferus* consumed higher numbers of prey on smooth mango leaves than hairy *Lantana* leaves (Rasmy et al. 1984). More work needs to be done to ascertain why success with *A. cucumeris* is so unpredictable from year to year and between greenhouses.

The pepper house (WL) had the lowest WFT density on traps and on plant samples in both years of monitoring but the highest ratio of immatures to adults. The high production of immatures suggests that peppers are suitable hosts for WFT and others have found high WFT trap catches in pepper greenhouses when predatory mites have not become established in high numbers (B. Peterson, pers. comm.). Pepper flowers last longer than cucumber flowers which may allow immature WFT to accumulate. However pepper plants appear to react to WFT ovipostion by producing small craters around the eggs which may affect egg survivorship (Krause 1987). Lower densities of WFT in this pepper greenhouse (WL) compared to all other cucumber houses monitored may have resulted plants reaction to oviposition and the establishment of large numbers of *O. tristicolor* and *A. cucumeris*. Control of WFT was not achieved in most of the cucumber greenhouses monitored even though large numbers of predatory mites were introduced throughout the growing season. In all greenhouses, most predatory mites were found on leaves, very few were found in flowers. Unlike *A. cucumeris*, adult stages of the genus *Orius* are able to kill adult thrips (Bailey 1933, Ramakers 1978, Isenhour and Yeargan 1981). The excellent control of WFT in House WL may have resulted from the combined efforts of both predators: *O. tristicolor* feeding on adults and immatures on flowers and leaves, and *A. cucumeris* also feeding on immatures WFT on leaves.

Because very few *O. tristicolor* were caught in flower and leaf samples, their association with different life history stages of WFT on Bell peppers and Long English cucumbers could not be quantified. Salas-Aguilar and Ehler (1977) found adults and nymphs of *O. tristicolor* feeding on WFT in flowers of 32 species of plants.

It is difficult to say how attractive yellow traps are to *O. tristicolor* because the response of these predators to different colours has not been determined. The high numbers found on traps in this study may be the result of high *Orius* numbers and low thrips density. Low prey density may be responsible for increased movement of pirate bugs making them more susceptible to being caught by traps than when high numbers of thrips can be found on plants. During initial stage of establishment in a greenhouse very few may be caught on traps because of low numbers and little movement. However, *O. tristicolor* establishment and increase may be better on pepper crops because of the abundance of pollen. Pollen and floral nectar may serve as alternative food sources when prey populations are low (Salas-Aguilar and Ehler 1977, Yokoyama 1978).

Predator foraging behaviour and efficacy is important from an applied perspective. Nevertheless, few studies attempt to link foraging behaviour with field observations of predator and prey spatial patterns and relate these to the temporal dynamics of the predator prey system. *A. cucumeris* are the principle biocontrol agents currently introduced to control WFT in greenhouses. However, *O. tristicolor* may be more effective thrips predators than *A. cucumeris* for several reasons. *A. cucumeris* occurs mainly on leaves and feeds predominately on immature WFT (Kajita 1986, Beglyarov and Suchalkin 1983). They are not successful at capturing large second instars and adult WFT (Bakker and Sabilis 1989). *O. tristicolor* were observed in flowers more often than predatory mites, and eat adult as well as immature WFT (Salas-Aguilar and Ehler 1977, Isenhour and Yeargan 1981). Thus, WFT are vulnerable to predation by

A. cucumeris for a smaller portion of their lifetime. Morphological features of the plant affect the searching capacity of *A. cucumeris*. Peterson (1990) found that *A. cucumeris* was more efficient at finding WFT on pepper leaves than on cucumber leaves because hairs on cucumber leaves interrupted the mites search pattern. More work needs to be done to quantify the spatial distribution of *O. tristicolor* to understand its temporal dynamics and those of its prey, WFT, on these two greenhouse crops.

From this study, it appears that between 10 to 50 *O. tristicolor* per trap must be present before control of WFT is assured. However, the number of predators required likely depends on WFT density. Other studies have found that introduction and colonization of *Orius* sp. lowered population density of thrips (Salas-Aguilar and Ehler 1977, Stoltz and Stern 1978, Isenhour and Yeargan 1981, Letournear and Altieri 1983, Nagai et al. 1988). Nagai et al. (1988) found that intoduction of *Orius* into screenhouses reduced population density of *T. palmi* from 60 to 0.3 per leaf. Letourneau and Altieri (1983) demonstrated the ability of *O. tristicolor* to control *F. occidentalis* using predator inclusion-exclusion cage experiments on outdoor squash cultures. The efficacy of *Orius* predation may increase as WFT density increases, which would make them very effective at reducing WFT at high densities. In the lab, Isenhour and Yeargan (1981) found that adult *O. insidious* attacked and killed adult soyabean thrips past satiation when exposed to high prey densities in a small predation arena. If this behaviour also occurs in the field, *Orius* predation would be capable of reducing high thrips densities quickly.

Trap catch data revealed that increases in the number of *Orius tristicolor* occurred just after thrips density peaked. However it is difficult to specify what was responsible for the increase in *Orius* numbers. Very few nymphs or adults were found on plant samples. A predator population may respond immediately to changes in prey populations via immigration or may show a delayed response due to increased reproduction. Stoltz

and Stern (1978) found that the number of *Orius* and thrips were highly correlated in the field; increased thrips density led to subsequent increases in the *Orius* population. On other crops however *Orius* numbers did not increase when thrips density increased (Yokoyama 1978). Yokoyama (1978) suggested that the omnivorous feeding behaviour of *Orius* was responsible for the lack of a numerical response.

Data were collected from commercial greenhouses and so experimental manipulations involving the density of WFT or predators were not permitted. Lab and field experiments are necessary before the efficacy of pirate bug predation on reduction of WFT population density can be known. Chemical control of pests can be detrimental to beneficial insects. To ensure widespread occurrence of predators in the greenhouse, use of insecticides must be minimized. WFT eggs and pupae appear to be relatively resistant to most registered pesticides and adult females are difficult to reach with sprays because they hide in flowers. Although my results do not unequivocally demonstrate that *O. tristicolor* suppressed and maintained *F. occidentalis* at low densities, their ability to find and feed efficiently on WFT make them potentially important WFT predators in agroecosystems. The relatively short life cycle of *F. occidentalis* coupled with their high reproductive potential generates ideal conditions for population outbreak. High colonization rates and predator mobility may be important characteristics for predators to control rapidly growing pest populations in these highly disturbed temporary systems (Ehler and Miller 1978). In the future *O. tristicolor* should be integrated into pest management programs designed to control *F. occidentalis* in commercial greenhouses.

Chapter 3

SEX RATIO PATTERNS AND POPULATION DYNAMICS OF WESTERN FLOWER THRIPS

INTRODUCTION

Western flower thrips (WFT), *Frankliniella occidentalis* (Pergande), are pests on many commercial vegetable and flower crops so most research has focused on pest management measures. Little attention has been directed specifically to the biology and population dynamics of this system. Very little is known about WFT reproductive biology, mating behaviour or factors that may affect sex ratio. WFT are haplodiploids; females are always diploid and males haploid (Bryan and Smith 1956). Virgin females can only produce sons parthenogentically; production of daughters requires sperm. Males can be distinguished from females because they are smaller and pale in colouration; females also have dark bands around their abdomens. Both sexes are winged and capable of flight. It is not known when or where mating takes place. For most flower thrips it is assumed that mating takes place after dispersal (Crespi 1990); mating has been observed in flowers (Morison 1946-48, Kirk 1985). Lewis (1973) claims that adults mate within two or three days of emergence, although there is no experimental evidence that demonstrates this. Depending on temperature, adult females live from 40 to 50 days in the lab; males live approximately half as long (pers. observ.).

Despite the large literature devoted to the subject of sex allocation, starting with W.D. Hamilton (1967) and reviewed by Charnov (1982) and Karlin and Lessard (1986), sex allocation remains one of the most enigmatic aspects of life history theory. Most research has focused on how local mate competition (LMC) and resource or host quality affect sex allocation in fig wasps which are haplodiploid parasitoids (Hamilton 1967, .

Jones 1982, Assem 1971, Assem et al. 1984, Werren 1980, 1983, 1984). Female fig wasps lay batches of eggs inside a host; males are generally wingless. Males do not disperse; development, mating and resource competition between offspring occurs at the natal patch. Little attention has been directed towards determining if predictions and assumptions from sex allocation models, based on parasitoid life history strategies, can be extended to non-parasitoid haplodiploids in which both sexes are capable of dispersal.

The objective of this study was to monitor temporal and spatial changes in population density and sex ratio of adult WFT within several vegetable greenhouses to determine if there was a correlation between these two parameters. It has not been determined if WFT females alter sex ratio of offspring produced in response to environmental condtions. Both adult, or secondary, and primary sex ratio are of interest. However only adult sex ratios were examined. Trap catch was used to monitor how adult sex ratio changed with density. Implications of changes in density and sex ratio, with respect to WFT population analysis and management, are discussed. Experimental manipulations of WFT density were not possible because field work was done in commercial greenhouses.

METHODS AND MATERIALS

Monitoring period, procedures and localities

See Chapter 1.

Data analysis

Means were computed for each sampling date to minimize possible effects due spatial autocorrelation in trap catch among traps within a greenhouse. Analysis of

covariance was used to examine the relationship between density and adult sex ratio on traps among greenhouses. Separate regressions were used to graphically describe the above relationship for all greenhouses except House WL in 1988. The proportion of females was transformed using the arcsine squareroot transformation (MAPFEM). All statistical tests were performed using SYSTAT (Wilkinson, 1989).

RESULTS

Changes in sex ratio occurred at different densities in different greenhouses. Changes in sex ratio of adults on traps lagged slightly behind changes in density. The highest proportion of females found on traps occurred slightly after peak population densities within a greenhouse (Figures 1 and 2). In all houses, males composed 80 - 100% of the actively dispersing adult population at relatively low densities: ie. generally at trap catches below 200 individuals per trap (Figures 1 and 2). As density increased within a house, sex ratio of the dispersing WFT population became increasingly female biased. At high densities, trap catches above 200 individuals, 60 - 90% of adults on traps were female WFT. There was a significant greenhouse*density interaction in 1989, but not 1988 (whether or not House WL was included in analyses) (Table 1). However, density and sex ratio were significantly ($p < 0.01$) correlated in all greenhouses except House WL in 1988. In 1988 there was no significant relationship between density and proportion of females found on traps when House WL was included in the analyses (Table 1). However, when House WL (1988) was excluded from the 1988 trap catch, there was a significant correlation ($p = 0.001$) between the proportion of females (MAPFEM) and the total density (MTOT = total number of adults; males and females) found on traps. This relationship was also significant ($p = 0.0001$) for 1989 trap catch. A significant interaction between greenhouse and density was found only in 1989.

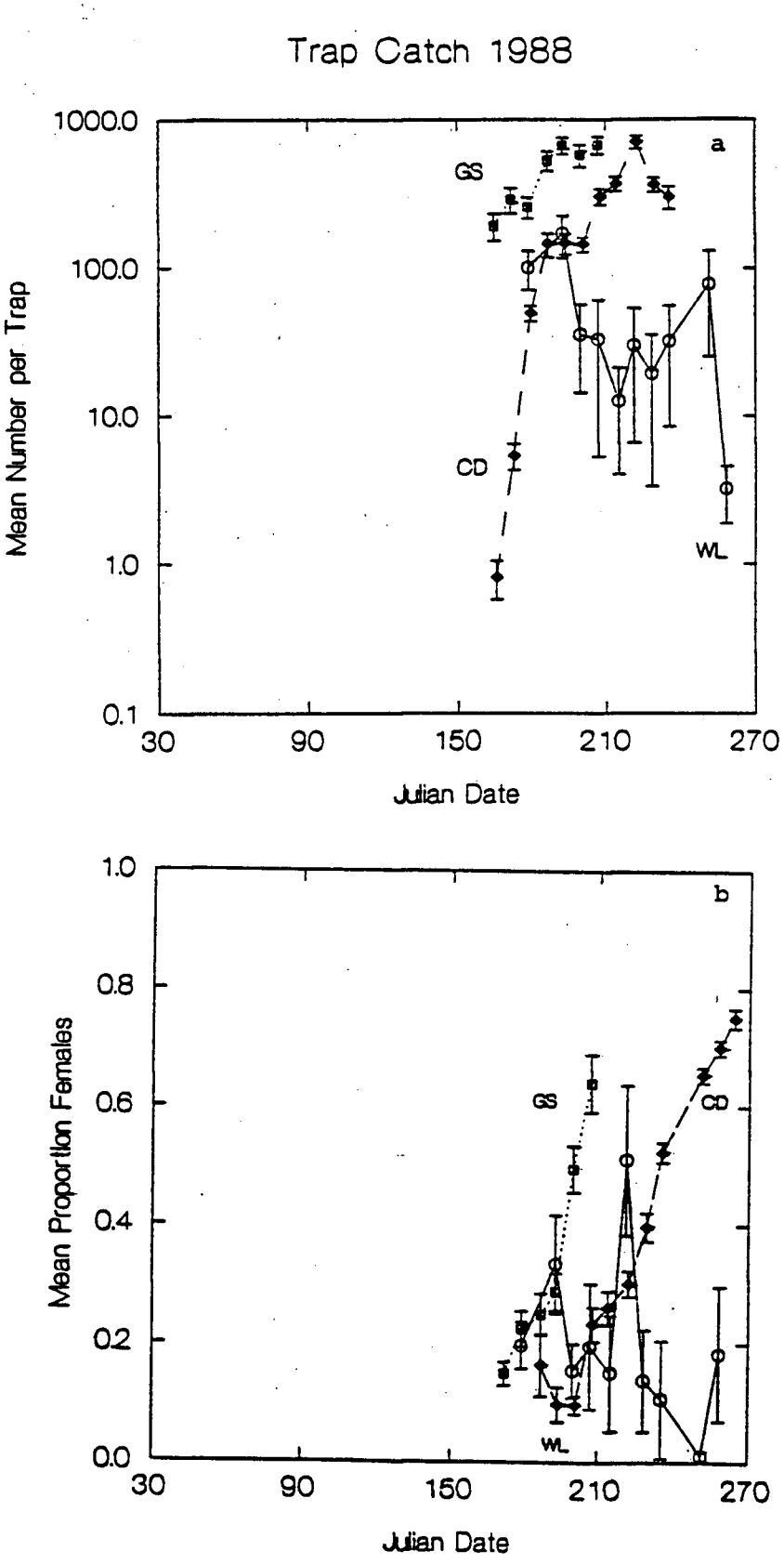

Figure 1. a) Mean number (± SE) of adult WFT (males + females) found on traps in 1988. b) Mean proportion of adult females found on traps. Monitoring was not started until after day 150. WL = Pepper House, GS and CD = Cucumber Houses.

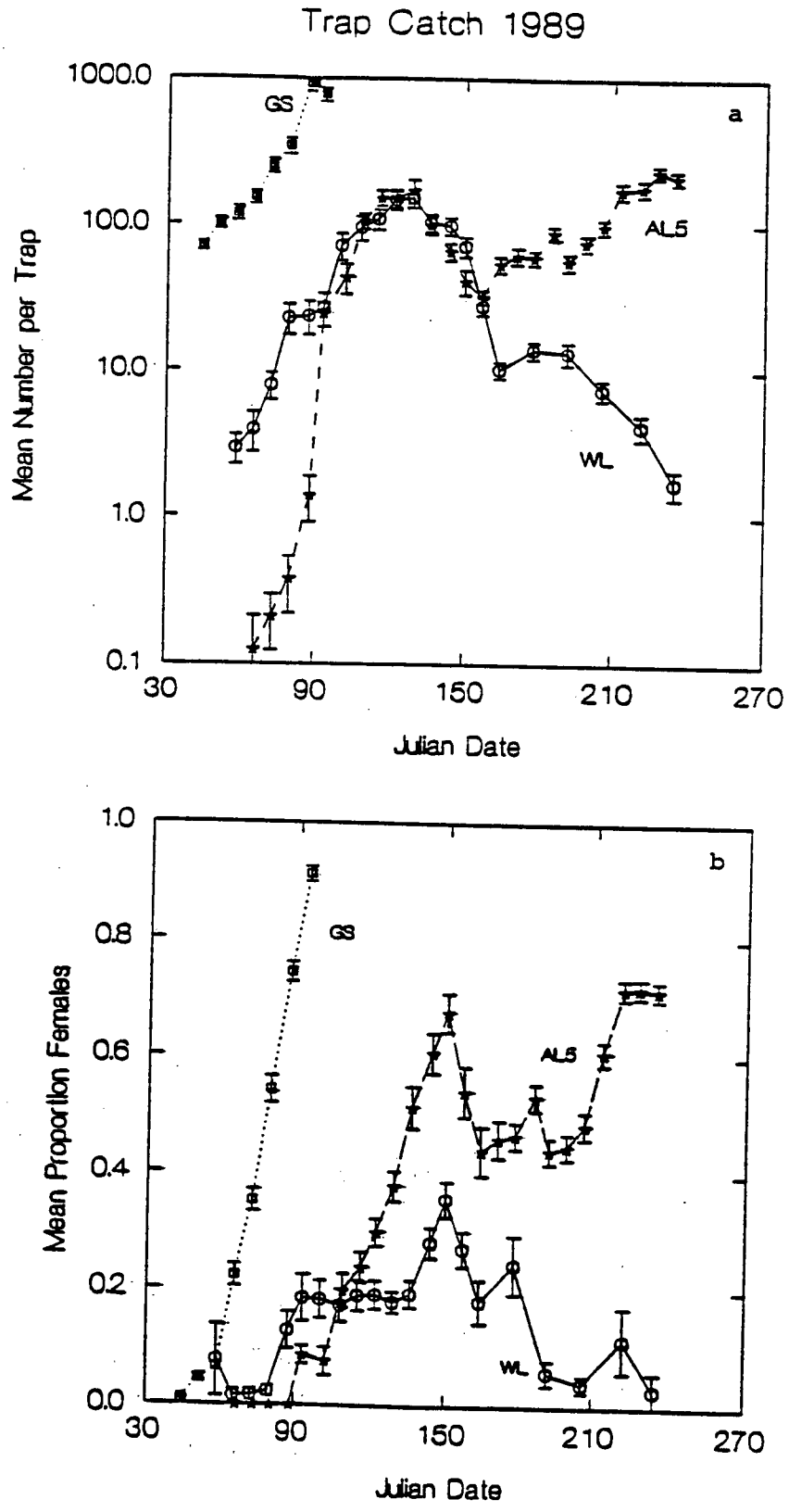

Figure 2. a) Mean number (± SE) of adults (males + females) on traps in 1989. b) Mean proportion of adult females on traps. WL = Pepper House, GS and AL5 = Cucumber Houses.

Table 1. Analysis of Covariance for 1988 and 1989. Model used:
MAPFEM = GH + MTOT + GH * MTOT (MAPFEM = arc-sine squareroot transformed proportion of females on traps; GH = greenhouse; MTOT = mean number of adults on a trap, males + females). For 1988 trap data P*, N*, R^{2*} are those values obtained from Analysis of Covariance when pepper greenhouse (WL) was excluded.

1988 $R^2 = 0.441$ $N^* = 21$ $R^{2*} = 0.489$

SOURCE	SS	DF	MSR	F-RATIO	P	P^*
GH	0.009	2	0.005	0.109	0.897	0.635
MTOT	0.052	1	0.052	1.225	0.279	0.001
GH* MTOT	0.095	2	0.048	1.114	0.344	0.149
ERROR	1.066	25	0.043			

1989 $R^2 = 0.622$

SOURCE	SS	DF	MSR	F-RATIO	P
GH	0.139	2	0.070	1.419	0.252
MTOT	1.638	1	1.638	33.347	0.0001
GH* MTOT	0.440	2	0.220	4.475	0.017
ERROR	2.357	48	0.049		

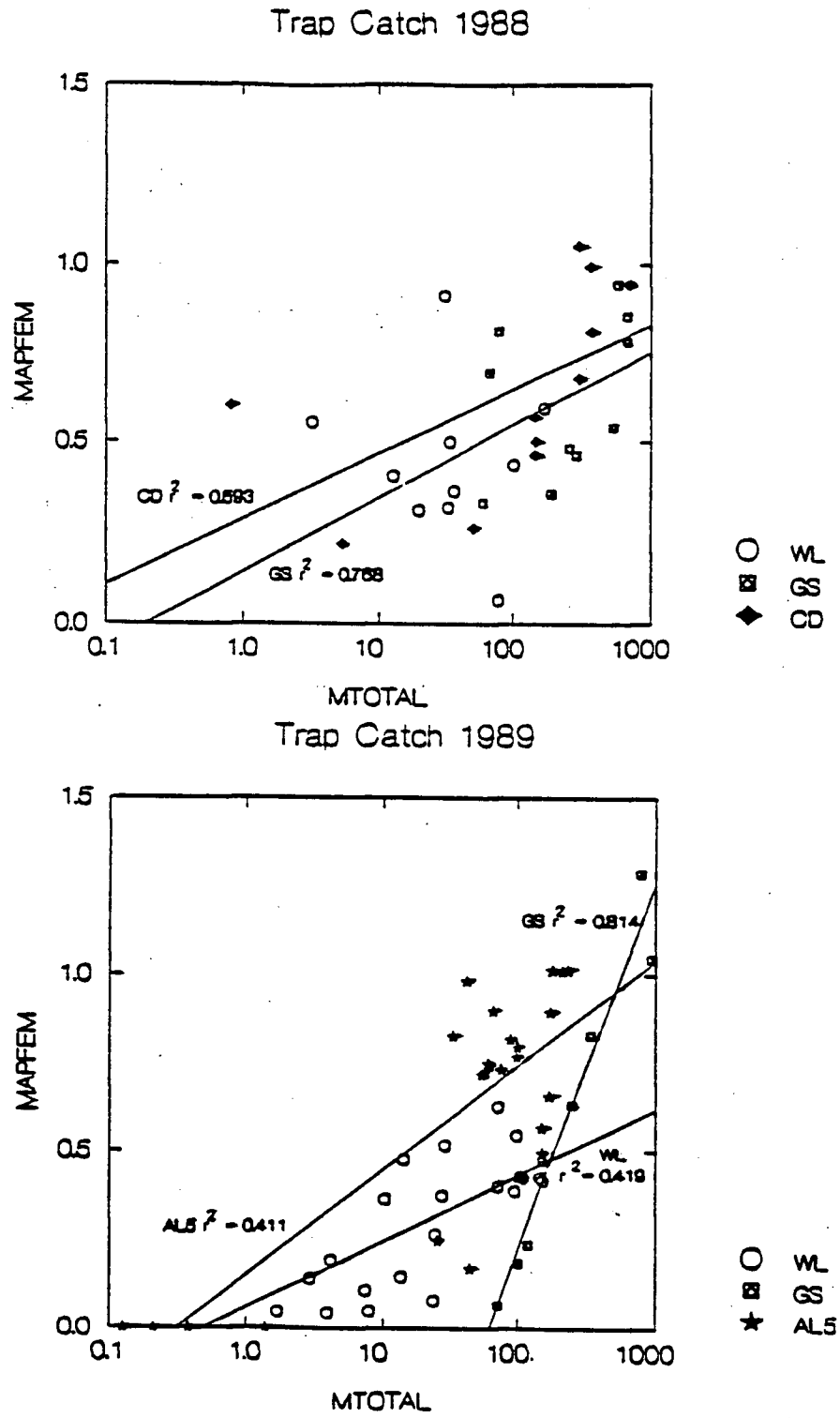

Figure 3. a) Regression of mean proportion of females (arc-sine square root transformed) (MAPFEM) and total density of adults (males + females) (MTOTAL) found on traps for a) 1988. Model for House GS: Y = 0.190 + 0.001x. Model for House CD: Y = 0.401 + 0.001x. and b) 1989. Model for House GS: Y = 0.186 + 0.001x. Model for House WL: Y = 0.180 + 0.002x. Model for House AL5: Y = 0.330 + 0.003x. All regressions of sex ratio and density were significant ($p < 0.01$) except House WL (1988) not shown.

Changes in adult sex ratio were similar in cucumber greenhouses monitored in 1988 (Figure 3). Similar peak densities of WFT were reached in both houses (GS and CD). Changes in the proportion of females with density were very different between greenhouses in 1989. In 1989, the proportion of females increased more rapidly in cucumber greenhouses than in the pepper house (WL) monitored. The pepper house had much lower densities of WFT per trap than in either of the cucumber houses (AL5 or GS).

DISCUSSION

Male biased trap catch at the start of the growing season suggests that WFT populations are initiated by virgin females that possibly overwintered as pseudopupae in the greenhouse. Shull (1914) and Eddy and Livingstone (1931) also found that only females overwintered in other species of thrips. However they did not specify if the overwintering forms were adults or psuedopupae. Eddy and Livingstone (1931) also found that females mated with sons produced parthenogenetically. Adult sex ratio of *Frankliniella occidentalis* within a greenhouse changed from a male bias (> 60%) at low densities to a heavily female biased (> 65%) population at high population density in all greenhouses except the pepper house (WL). The population density of WFT in this greenhouse never reached high numbers. These results agree with what Lewis (1973) noted for several other species of thrips and Krause (1987) found for a field population of WFT. Lewis (1973) and Krause (1987) found that females often predominate and that there are generally four times as many females as males. Female biased sex ratios lagged behind peak trap catches in all cucumber houses monitored. This would be expected if only female pseudopupae overwintered. Adult females that emerged can produce only sons, and must wait for these to mature before they mated and produced daughters. As

WFT density within a greenhouse increases, females are probably mated soon after emerging. These females can start producing daughters immediately.

Population densities of WFT were lower in House WL than in other houses monitored both years, and sex ratio did not shift. WFT dynamics in this greenhouse differed from all other greenhouses monitored perhaps for two main reasons: 1) this was the only pepper greenhouse monitored, all other greenhouses grew Long English cucumbers, and 2) large numbers of predatory mites and pirate bugs (Chapter 1) occurred in this house. There was a significant relationship between density and sex ratio of adult WFT on traps when House WL was excluded from the analysis of 1988 data and whether or not House WL was included in 1989 (Table 1).

Several factors may be invoked to explain the observed shift in sex ratio from a male to female bias with increasing density. From the population perspective, sex differential mortality may be the cause of female biased sex ratio observed later in the growing season. Adult sex ratio may bear no relationship to the primary sex ratio produced by females. Alternatively, the adult sex ratio observed may be the result of individual female strategies whereby females assess and respond to current environmental conditions. Males develop from unfertilized eggs and females from fertilized eggs. Control of insemination may therefore control sex ratio via regulation of release of sperm from the spermatheca. Alternatively, females may tend to produce more females once mated because they have little control over fertilization. Once mated all eggs may be fertilized until all the sperm has been used. However this does not appear to be true for WFT. My lab studies done to investigate this have shown that once mated females produced 64 - 69 % daughters (Chapter 3). Some sons are always produced. Females produce mostly daughters as long as they have enough sperm (Chapter 3).

Trichilo and Leigh (1988) found that female WFT brought back to the lab from the field produced 67 % daughters.

Sex differential mortality

Although sex of first-instars can be determined in some thrips species (Priesner 1960, Crespi 1987), in this study population sex ratios within greenhouses were derived from counts of adults on traps. Sex ratios obtained by sampling of adults in the field may differ from those produced by individual females because of differential larval mortality or differences in adult behaviour. Variations in sex and age specific survivorship should be known before other hypotheses can be used to explain variations in sex ratio. There is no information on larval mortality, and therefore no way of eliminating sex differential mortality as a factor contributing to the shift in sex ratio from male to female bias with density through time. Overwintering mortality may be a major factor determining the sex ratio of the initial population within a greenhouse and the resultant following dynamics. Haploid males in general are thought to be more vulnerable than females to deleterious mutations (Smith and Shaw 1980) and environmental stress during embryonic and larval stages. Adult sex ratios may be poor indicators of primary sex allocation. Female WFT live approximately twice as long, 40 to 50 day in the lab at 20 ^{o}C, as males. Therefore, one would expect twice as many females as males when the population reaches an equilibrium or stable age distribution. The shorter lifespan of adult male WFT would further enhance the proportion of females found on traps later on in the growing season. Greater production of daughters, longer lifespan of females, and sex differential mortality may account for the heavily female biased sex ratio (90 %) found in House GS.

Sex differences in migration (or mobility) may also affect sex ratio of WFT found on traps in greenhouses. Males may always be more susceptible to trapping than females. Males were rarely found on plant samples taken during the day (Chapter 1) or

night (unpublished data). Males may fly continuously during the day searching for females. Males probably mate with females that are locally available and then depart in search of other females. As density increases, crowding may increase movement of adults within greenhouses.

Lastly, the sex ratio observed may be a "hardwired" strategy triggered by daylength or other abiotic factors. Although I can not statistically uncouple effects of time and density on sex ratio, different greenhouses had different densities and sex ratios at the same time of year (Figure 1 and 2). Thus changes in sex ratio appear not to be "hardwired" or seasonally triggered. The significant greenhouse and density interaction found in 1989 (Table 3) may be attributed to differences in abiotic or biotic parameters influencing WFT and predator population growth.

Spatial structure of the WFT population within a greenhouse

The dispersion pattern of an organism is an important aspect of its population structure, resulting from interactions between individuals of a species and their habitat (Salifu and Hodgson 1987). Crespi (1990) found that in many *Haplothrips* and gall forming thrips, relatedness levels affect sex allocation patterns. He argues that dispersal patterns and distribution of a population can determine the fate of alleles that bias sex ratio. Similar explanations may be responsible for the shift in sex ratio as density increases and a greenhouse becomes "saturated". At low densities, the WFT population within a greenhouse may be subdivided into temporary, local mating groups possibly composed of the progeny of very few females. When relatedness within "isolated" breeding groups is high the sex ratio is expected to be female biased. Local mate competition (LMC) theory predicts that when mating takes place at the natal site, isolated females should produce primarily daughters with only enough sons to inseminate those daughters (Hamilton 1967). If she produces more sons than are required to inseminate

her daughters, sons will be competing among themselves for mates and she will have wasted energy that could be used to produce more daughters. As WFT density within a greenhouse increases, isolation between the mating groups may break down and result in a greater probability of outcrossing. When several females are present within a local patch, females should produce equal numbers of sons and daughters. These males will no longer compete only with sibs, but with non-sibling males as well. If this is true, LMC may contribute to female biased sex ratios until isolation between the mating patches breaks down, which may result in decreased relatedness within a patch. Curiously, as density increases within a greenhouse the sex ratio of adults found on traps remains female biased and does not stablize at a more equal sex ratio. Perhaps, resource quality is decreasing as the house becomes saturated and females are produced because they are more effective colonizers than males.

Fisher (1930) predicted that natural selection should favour a 1:1 sex ratio, generally selecting parents that invest equally in sons and daughters. One factor not included in Fisher's arguement was the role of spatial structure of a population. Selection can favour temporary overproduction of one or the other sex when populations are highly subdivided at the time of mating (Hamilton 1967, Nunney and Luck 1988), when generations overlap and when temporal changes in fitness expectations for the two sexes differ and parents have the ability to vary the sex ratio (Werren and Charnov 1978) and if mating occurs prior to dispersal sib-matings may occur. As a result, the population may exhibit some inbreeding which can result in production of female biased broods (Nunney and Luck 1988). Selection can also favour seasonal shifts in sex ratio if males and females experience different fitness payoffs seasonally, because of overlapping generations, those born at different times compete with more of their sex for relative reproductive success. This creates a situation where a parent may "derive" greater fitness by shifting the sex ratio towards offspring of the sex with the higher reproductive

success. However, when the WFT population is at peak densities, "saturation", the population may be at sex ratio equilibrium. When this is the case, a mother may achieve the same fitness returns through production of sons or daughters, and there is no disadvantage to being unmated (Godfray and Grafen 1988). Initially the precence of unmated, ovipositing females will lead to a male bias in the population sex ratio. This may then lead to selection on mated females to produce a female biased sex ratio in their progeny, which will tend to restore the sex ratio to an equilibrium of 50:50. Selection pressure on females may change over the growing season, as WFT population densities increase. Fisherian sex ratios may be produced by females once the population has increased and isolation between mating groups has been eliminated or reduced. LMC theory predicts that individual females should increase production of males in response to in local population densities. Females probably can not assess these changing conditions perfectly which may offer a plausible explanation for the lag in sex ratio with density. Because it is not known when or where WFT mate, it is difficult to identify which, if any, of these hypotheses are operating in this system.

One must be careful with interpretation and conclusions drawn from trends in sex ratio found on traps within a greenhouse. It is likely that trap catch in sections of a greenhouse are correlated in space and time. There are generally higher numbers of WFT on traps in some areas and lower densities in other areas of the greenhouse. This may be the result of initial settlement patterns of females which result in the formation of "hot spots" of population growth leading to aggregations in space and time. Many of the basic statistical methods used in ecological studies are impaired by autocorrelated data (Legendre and Fortin 1989). I have tried to eliminate these potential effects of spatial correlation among traps located next to each other within a greenhouse, by using mean trap catch and sex ratio for each date instead of using each trap separately for statistical

analyses. To examine the distribution and invasion patterns of WFT within a greenhouse, spatial structure maps and functions must be used.

Most data on sex allocation come from laboratory studies. This is one of the few attempts to examine sex allocation of haplodiploids under field conditions. Population density, sex ratio of offspring produced, resource quality, sex differential mortality and movement can all influence sex ratios of adult WFT in greenhouses. Nothing is known movement of WFT males and females within a greenhouses. Both sexes are winged and capable of flight. Examination of changes in sex ratio and density within greenhouses generated more questions than answers: In nature how many times can males mate before they run out of sperm? How many times do females mate and do they run out of sperm under natural condtions? Are males ever limiting? Are differences in offspring sex ratio a result of differential mortality or female oviposition behaviour? Lab studies are needed to determine mechanisms causing changes in sex ratio observed in the field. Knowledge of the spatial distribution pattern and sex ratio will provide a more dependable basis for estimation of thrips densitites to be used for future pest management decisions.

Knowing what factors influence offspring sex ratios is important for developing and testing sex ratio theories as well as for practical applications in biological control. Influences of extrinsic factors on population increase and development such as temperature and humidity are well documented (Bryan and Smith 1956, Lublinkhof and Foster 1977). However, effects of intrinsic factors, such as physiological condition and age of female, on developmental rate, population density and sex ratio are not well known. Although the mechanisms causing the shift in sex ratio have not been unequivocally determined, adult sex ratios may be used as a predictor of future WFT population dynamics within a greenhouse. The production of twice as many daughters

by mated females is probably responsible for WFT outbreaks within a greenhouse. Because feeding, ovipositing females cause the greatest damage to the crop, sex ratio reflects the potential impact of a population on the crop.

Chapter 4

POTENTIAL EFFECTS OF MALE AVAILABILITY ON THE SEX RATIO OF OFFSPRING PRODUCED BY *Frankliniella occidentalis*

INTRODUCTION

The sex ratio of adult WFT in vegetable greenhouses has been observed to change from a male to female bias as population density increases (Chapter 3). The proportion of females found in flowers is always high (Chapter 2) and those caught on traps increase to greater than 50 % once population densities are higher than 200 individuals per trap. At extremely high densities, close to 1000 per trap, 80 to 90 % of adults found on traps may be females. At population densities below 100 individuals per trap, the adult sex ratio generally remains at 10 to 20 % females (Chapter 3).

Factors that could influence adult sex ratios are: 1) sex differential mortality during embryonic or larval stages 2) differences in mobility between males and females which would influence their trappability 3) sex differences in lifespan and 4) differential production of sons and daughters by females. It is known female WFT live approximately twice as long as males in the lab (pers. obser.). Therefore, when a stable age distribution is reached (ie. at peak densities), twice as many females as males should be observed if both sexes are equally trappable.

Nothing is known about mortality during development or movement of WFT adult males and females within greenhouses. It is known that many more females than males are found in flowers and on leaves (Chapter 2). If males are constantly moving throughout the greenhouse, males should be more suseptible to being caught on traps than females. This should bias trap catch toward males.

Very little is known about proportions of virgin and mated females in wild populations of haplodiploids. To estimate this, female WFT were collected from leaves and flowers and brought back to the lab to determine the number and sex ratio of progeny produced. The proportion of virgins and mated females in a population will influence the sex ratio of subsequent adults within a greenhouse. WFT are haplodiploids. Unmated females produce sons parthenogenetically but females must be mated to produce daughters. Therefore, the sex ratio of wild populations will be influenced by the proportion of females that are not mated and the production of sons and daughters by mated females. Sex ratio of the adult population has important consequences with respect to outbreak potential of the population (Chapter 3) and damage to the crop (Chapter 2).

The effect of male and female density on sex ratio of offspring produced by mated female WFT is unknown. It is not known if females run out of sperm if not remated. In this case, sex ratio produced by mated females may be constrained by male availability. To study the influence of male availability on sex of offspring produced, the density of males and females was manipulated in the lab.

METHODS AND MATERIALS

WFT females used to start lab colonies were collected from commercial vegetable greenhouses. All experiments were done inside a walk-in growth chamber at the University of British Columbia. Temperature was maintained at $21 \pm 1\ ^{o}C$ and humidity at 70 ± 5 % RH. A photoperiod of 12 hours of light was used. These conditions are similar to average environmental conditions found in commercial greenhouses throughout the growing season. WFT colonies were maintained in 1-litre glass Mason

canning jars and reared on excised pinto bean leaves. Plastic specimen containers (128 ml.), filled with water, were placed inside the glass jars. Small holes, just large enough for bean leaf petioles, were burnt into the plastic lids of these containers and petioles were placed in water through the holes in the lids of the plastic containers. Leaves were changed every two to three days to maintain resource quality. All leaves used were approximately the same size and ranged from 12 to 15 days old (from germination). Two to three inches of peat moss lined the bottom of the glass jars providing a substrate for pseudopupae to complete development in. To allow air circulation within the jars, 9.0 cm. Whatman^{R} #1 filter papers were used as lids. Metal canning rings held the filter papers in place. Lab manipulations were done using these jars as mating and egg laying arenas. Adult progeny were sexed and removed daily once they started to emerge. Primary sex ratios were not examined.

Sex ratios produced by females collected from flower and leaf samples

To examine the sex ratio produced by adult females from greenhouses, females found in flower and on leaf samples were arbitrarily collected and brought back to the lab. These females were collected at moderately high, but not peak WFT densities. When population densities of WFT in a greenhouse are very low, it is difficult to find females in flowers or on leaves. Each female was put into a jar and left for one week. Females were transferred weekly to new jars until they died. If they were not found after seven days, they were presumed dead. I did not know the age or previous mating history of females collected from greenhouses. I wanted to determine 1) if there were more virgins in flowers than on leaves and 2) if females found in flowers produced a different sex ratio than those found on leaves.

Manipulation of male density

Manipulation experiments were performed to determine if the number of males a female mated with influenced her fecundity and the sex ratio of offspring produced. All females used in these experiments were virgins. Four experimental treatments were examined; individual females of a similar age were placed inside jars containing 0, 1, 5 or 10 males. I wanted to determine if females housed with 5 or 10 males produced more daughters than those housed with one male. Females without males (virgins) were used as controls. This experiment was done twice. In Experiment 1, females 7 to 8 days old were used the first experiment; each treatment was replicated 8 to 9 times. Males used ranged from 10 to 15 days old. Only offspring produced during this first week were examined. Females were removed and not transferred after one week. In Experiment 2, females were 1, 3, 6, 8, 10, 13, 15 days old; each treatment was replicated 7 to 8 times. This age range was necessary to obtain sufficient numbers of females for each treatment. Males were 14 to 16 days old. In both experiments, density of adults within jars differed only during the first week when males and females were present. Females had access to males only during the first seven days of the experiment. After one week males were removed and destroyed; females were transferred and housed individually in jars for oviposition. Females were transferred to new jars weekly until death. This prevented them from mating with their sons. The number of females in each treatment decreased over time because of death. In all experiments, daily sex ratios of offspring produced by individual females were recorded as adults emerged. Records were kept for 14 days after females were removed from the jar. Few progeny were found after 14 days. F1 adults were removed daily when they started to emerge to eliminate sib-matings resulting in production of F2. When more than one male was available, it was not known how many males the female mated with or how many times individual males mated. Data from the two experiments were not pooled. Each experiment was analyzed separately.

Manipulation of density of virgin females

For another set of experiments, the number of virgin females per jar was varied. There were two treatments; 1 female and 1 male, 3 females and 1 male. This experiment was done twice. The number of females per jar differed only during the first week, Time = 1. In the Experiment 3, females were 0, 2, 7, 9 days old at the start of the experiment. Females that are 0 days old were born on the day the experiment was started. Each treatment was replicated ten times. Males used were 2 days old. After Time = 1, the number of replicates of three females per jar increased because females were separated and put into individual jars. In experiment 4, females used were 0, 2, 4, 7 days old. Males used were 7 days old. There were 7 replicates of 1 female per jar, and 4 replicates of 3 females per jar at Time = 1. After one week, the number of replicates of the three females per group treatment increased because females were separated and housed in separate jars until death. Females were allowed access to males only during the first seven days of the experiment and density of adults within treatments differed only during this time. After 7 days, males were removed and destroyed; females were transferred and housed individually in jars. Females were transferred to new jars every seven days until they died or were not found and presumed dead. This experiment was also repeated twice. In the three female treatment group, I did not know if all females had equal access to the male or how many times each female mated. Progeny were sexed and removed as they emerged as adults. Data from experiments 3 and 4 were analyzed separately.

Data analysis

A two factor analysis of variance was used to examine the sex ratio of progney produced over time by females collected from greenhouses. This was done to take into account the affect of female and time. Kruskal-Wallis tests were done to examine the differences in sex ratio (proportion of daughters) produced by females mated with different number of males for every week (Experiments 1 and 2). In experiments 3 and 4

where female density was manipulated Mann-Whitney tests were used compare the proportion of daughters produced by individual females for each time period. All statistical tests were performed using SYSTAT (Wilkinson 1989). Jars in which females did not produce any offspring were excluded from all analyses.

RESULTS

The sex ratio (mean proportion of females, pfem $\pm$ SE) of progeny produced by females found in flowers (n = 45, pfem = 0.65 $\pm$ 0.04) was the same as that produced by females found on leaves (n = 43, pfem = 0.69 $\pm$ 0.05). Twenty-one to twenty-four percent of females found on both plant parts were virgins. Thus, most females found on the plants within a greenhouse had mated. Females mated with sons and produced offspring (males and females) when left in jars. There was no evidence that male progeny developed faster than females. Both sexes started to emerge at the same time; 12 to 14 days after the mother was first put into the jar.

Once mated, females produced both daughters and sons. A female biased sex ratio was produced by these females. The proportion of daughters produced decreased over time (Figure 1). For females (n = 29) that lasted both transfers, (three weeks after start of experiment) the number of daughters produced and brood size decreased. Virgin females were not included. The number of daughters differed significantly between weeks ($p = 0.001$, DF = 2) although there was also a significant difference in the sex ratio of offspring produced by individual females ($p < 0.001$, DF = 28). The number of sons produced by females remained relatively constant over time.

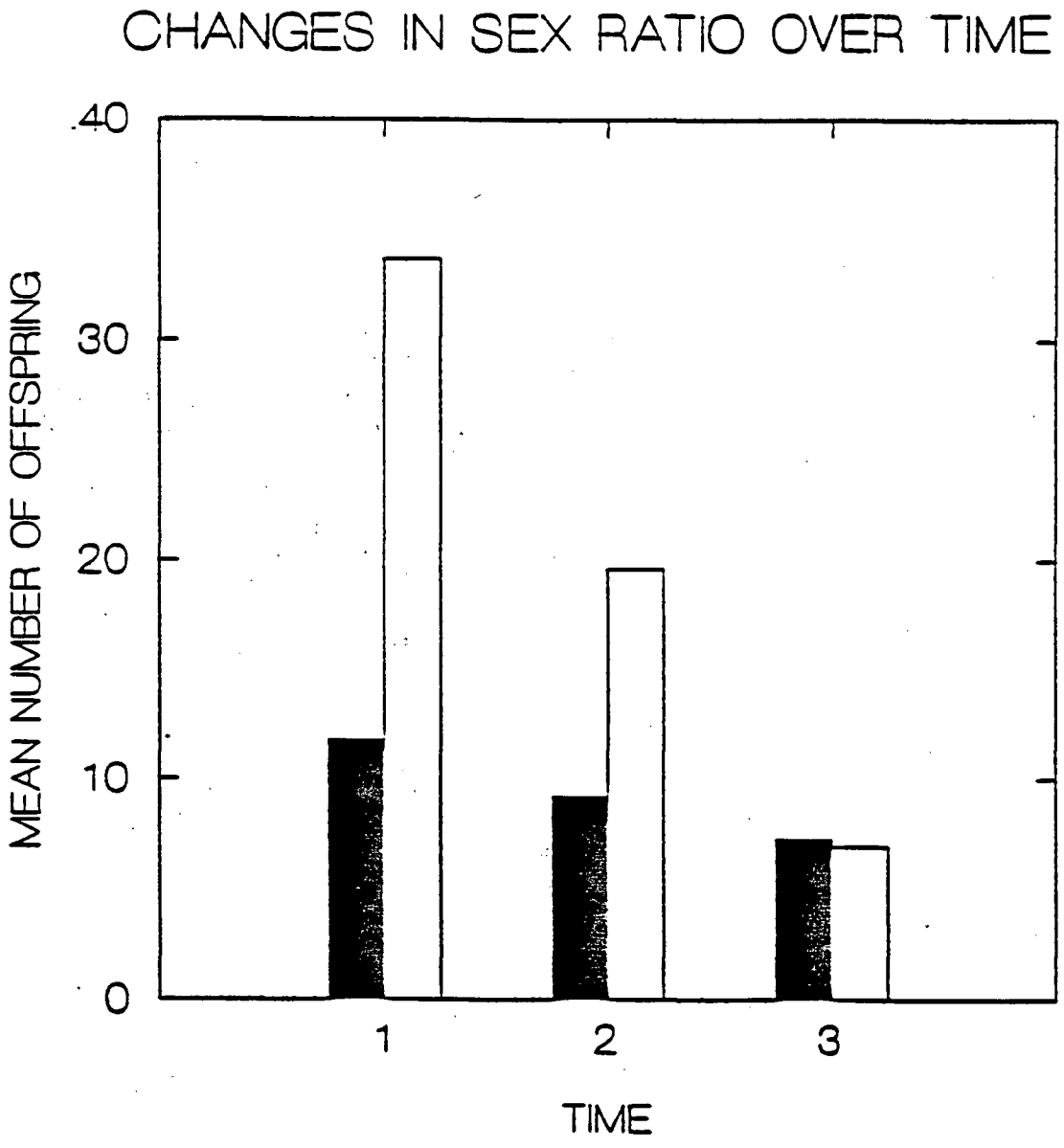

Figure 1. Mean number of daughters ☐ and sons ■ produced per female by females found in flower samples. Virgin females are not included. Time 1 = after 7 days, Time 2 = after 14 days, Time 3 = after 21 days.

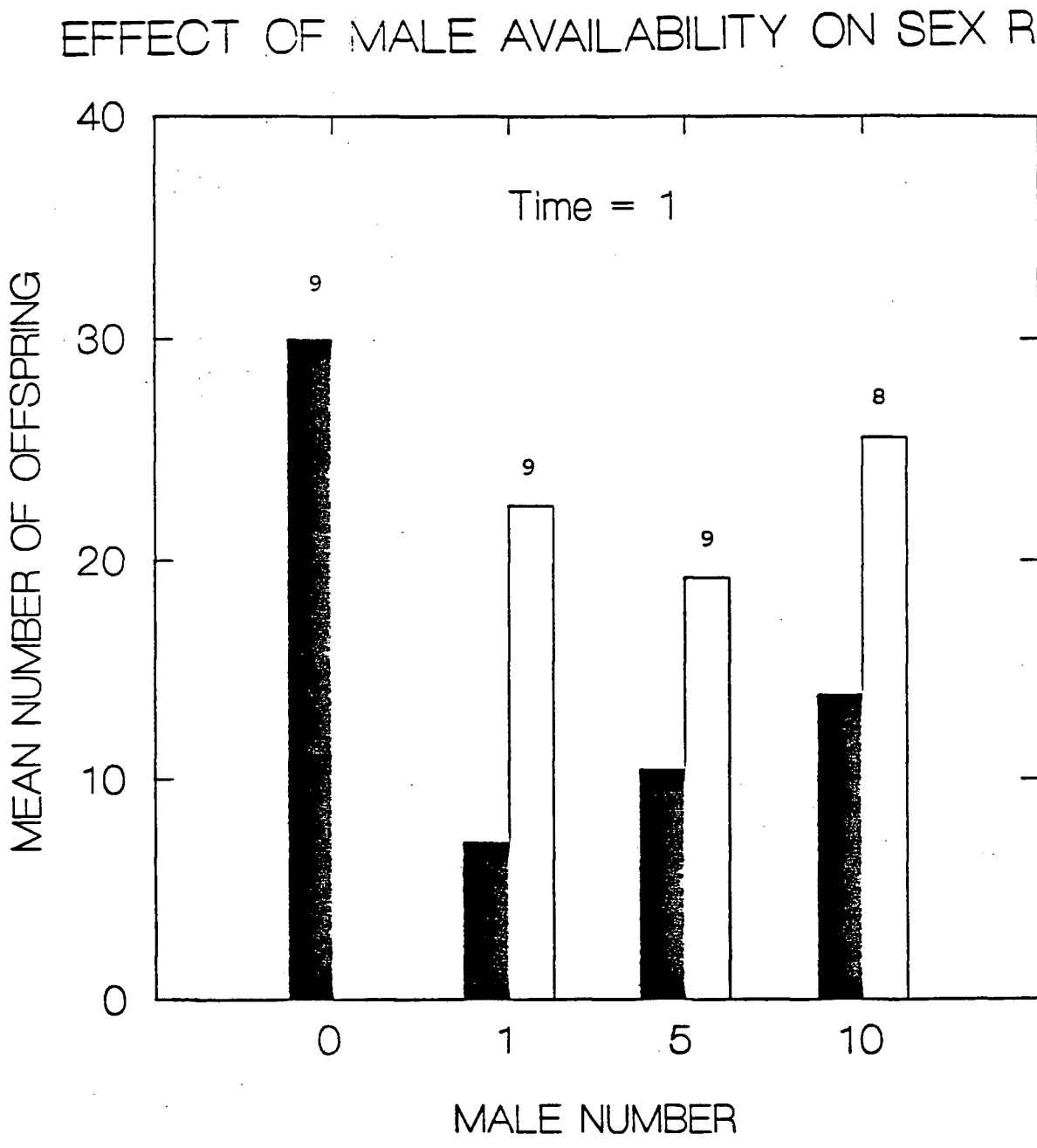

Figure 2. Experiment 1. Effect of male availability on the number of daughters ☐ and sons ■ produced per female. Time 1 = after 7 days of oviposition. Females were not transferred. The number of females in each treatment is shown on the top of the bars.

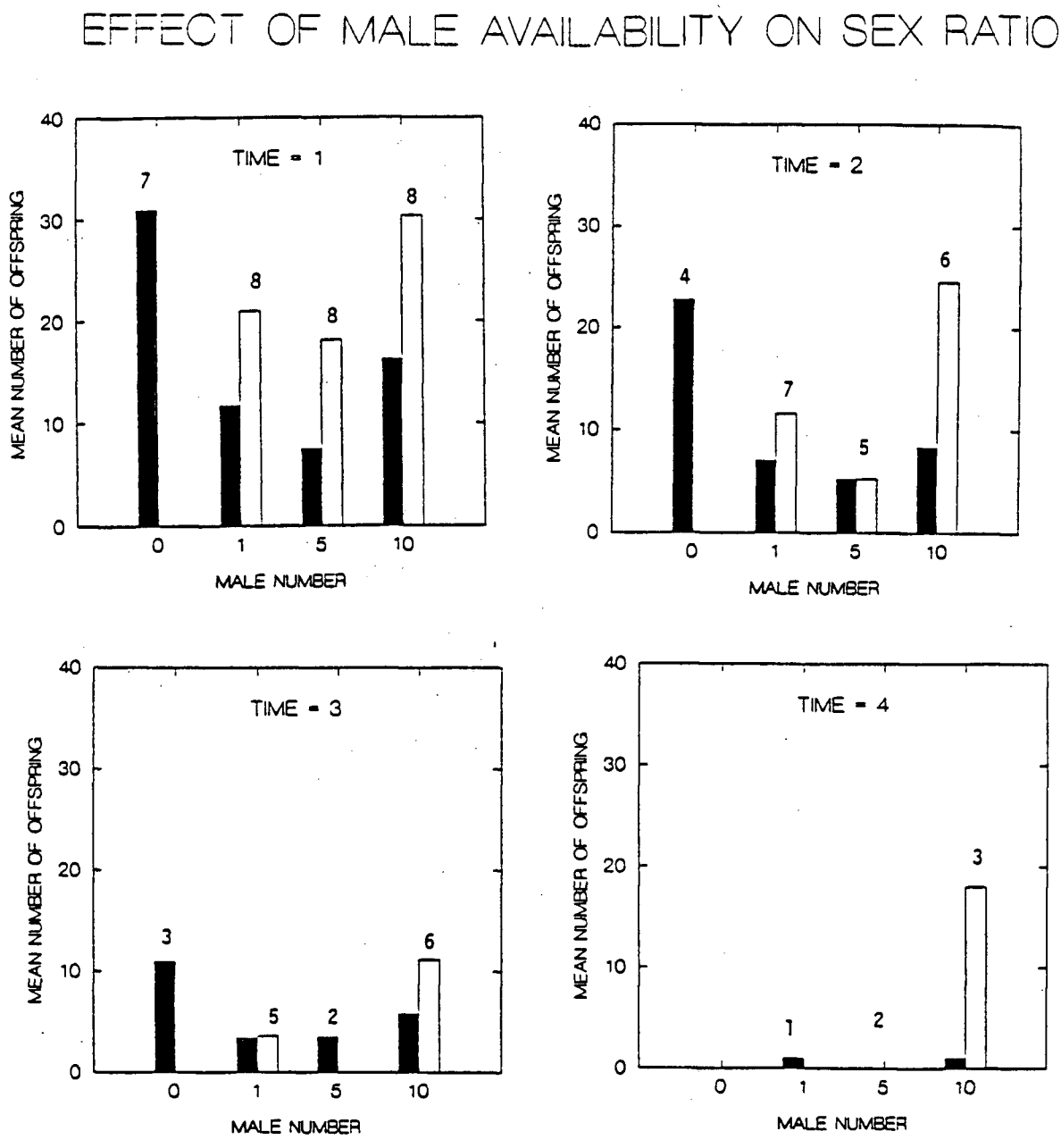

Figure 3. Experiment 2. Effect of male availabililty on the number of daughters □ and ■ sons produced per female. Time 1 = after 7 days of oviposition, Time 2 = after 14 days, Time 3 = after 21 days, Time 4 after 28 days. The number of females in each treatment is shown at the top of bars.

There was a no significant difference ($p > 0.05$) in experiments 1 and 2 in the proportion of daughters produced by females that had different numbers of males available to mate with (Figures 2 and 3). The lack of significance is likely due to the variability among females in age and numbers and sex ratio of offspring produced. However, only those females that had the potential to mate with 10 males produced daughters after four weeks. Brood size and the number of daughters produced decreased weekly. Mated females produced slightly more offspring in their lifetime than virgins (Figure 2). Virgin females (male number = 0) produced only sons. The numbers and proportion of sons and daughters produced by females in Experiments 1 and 2 were almost identical at Time = 1 (after one week) even though females used in Experiment 1 were on average younger than those used when this experiment was repeated (Experiment 2).

In experiments 3 and 4, all females were mated. The proportion of daughters produced weekly by females in groups of 3 per male and 1 per male did not differ significantly ($p > 0.05$). Small sample sizes and variability among females in sex ratio and number of progeny produced may be the cause of this. Time = 1 was excluded from analysis because three females were ovipositing in one jar during the first week. I could not determine how many progeny or the sex ratio produced by individual females during this time. Females in the 1 female treatment group produced more daughters at Time = 1 in experiments 3 and 4 (Figure 4 and 5 respectively). Both brood size and the number of daughters produced decreased over time; the number of sons produced by females in the two treatment groups did not change over time. All females produced on average less than 5 sons per week (Figures 4 and 5). Females from jars containing no other females (at Time = 1) produced more daughter during the first week than females that had to "share" male with other females. As for previous experiments, females were not allowed access to males after the first week. Adult females that differed in age from 0 (those born

on the day of the experiment) to 9 days old (those females that were born 9 days before the experiment) were tested. Nine day old females had already laid some male eggs. I did not count the number of males produced prior to the start of the experiment. All females initially produced female biased sex ratios. Although the numbers of daughters produced by females of different ages did not differ significantly ($p > 0.05$), brood size and the proportion of daughters produced decreases as females age (Figures 6). Thus females used for all of the experiments that were born before the start of experiment may have already produced on 15 to 10 sons a week, depending on their age.

DISCUSSION

Most females collected from flower and leaf samples produced female biased sex ratios, only 20% of females found were virgins. Mated females produced 65 - 69 % daughters irrespective of the plant part they were collected from. These females were collected when densities of WFT within a greenhouse were relatively high, around 100 individuals per trap. This may partially explain why most females found had already mated. Trichilo and Leigh (1988) found that WFT females collected from the field produced 67% daughters. It is very difficult to find adult females on the plant parts at low WFT densities. Many flower and leaf samples would be required which in a commercial setting is costly to the grower. Females need to be collected from greenhouses when WFT densities are very low to determine if most females found then are virgins. Very little is known about the level of unmatedness in natural populations of haplodiploids. Only one other study to date has examined the prevelance of virginity in wild populations. Godfray (1988) found that 23% of female *Apocrypta*, a parasitic wasp, were unmated, a value very similar to that found here.

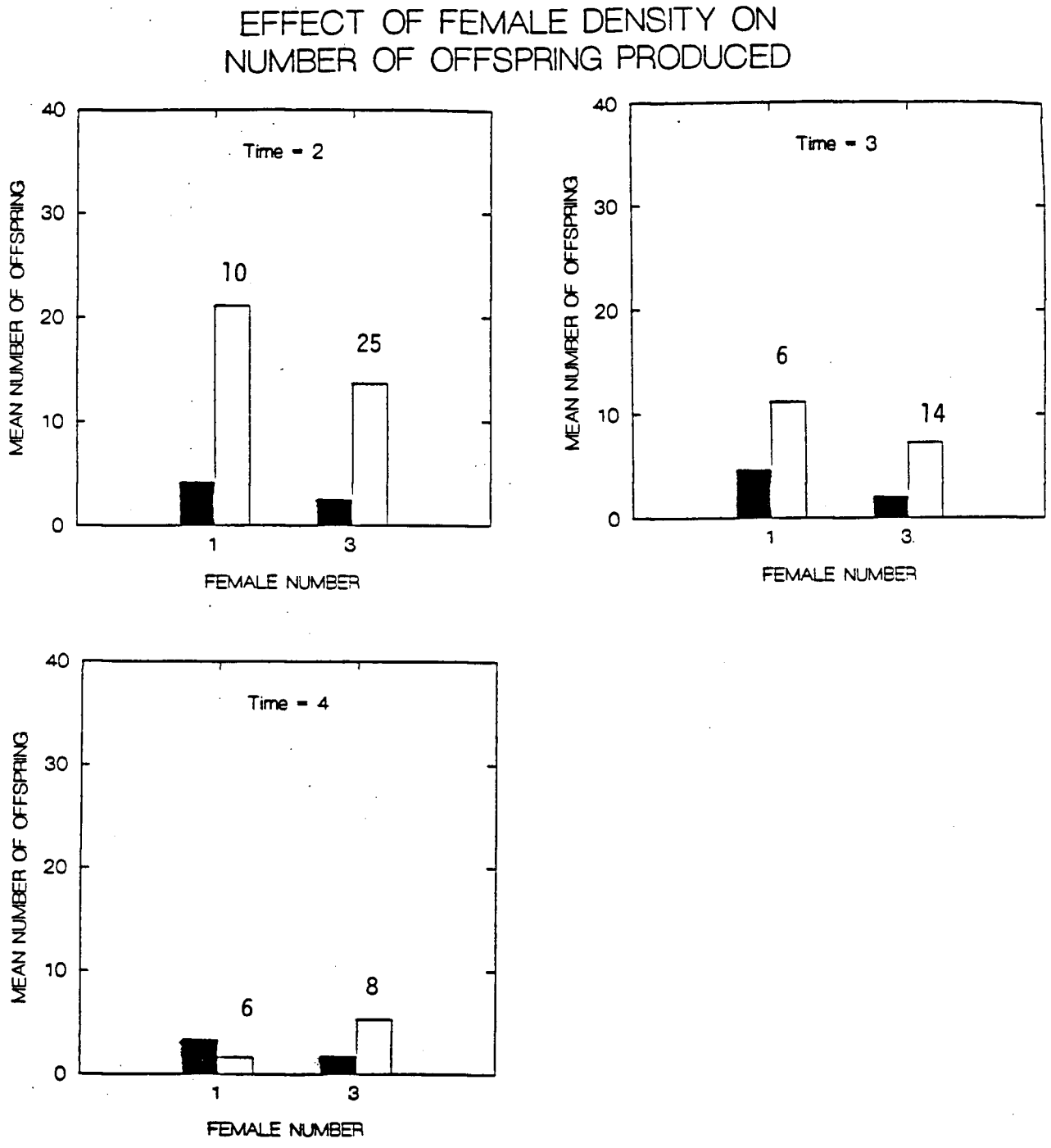

Figure 4. Experiment 3. Effect of mate "sharing" on the number of daughters □ and ■ sons produced per female. Two treatments were examined: 1 female/male, and 3 females/male. Time = 1 after 7 days of oviposition (not shown), Time 2 after 14, Time 3 after 21 and Time 4 after 28. After Time = 1 females in the 3 female/male treatment group were put into separate jars. The number of females in each treatment is shown at the top of the bars.

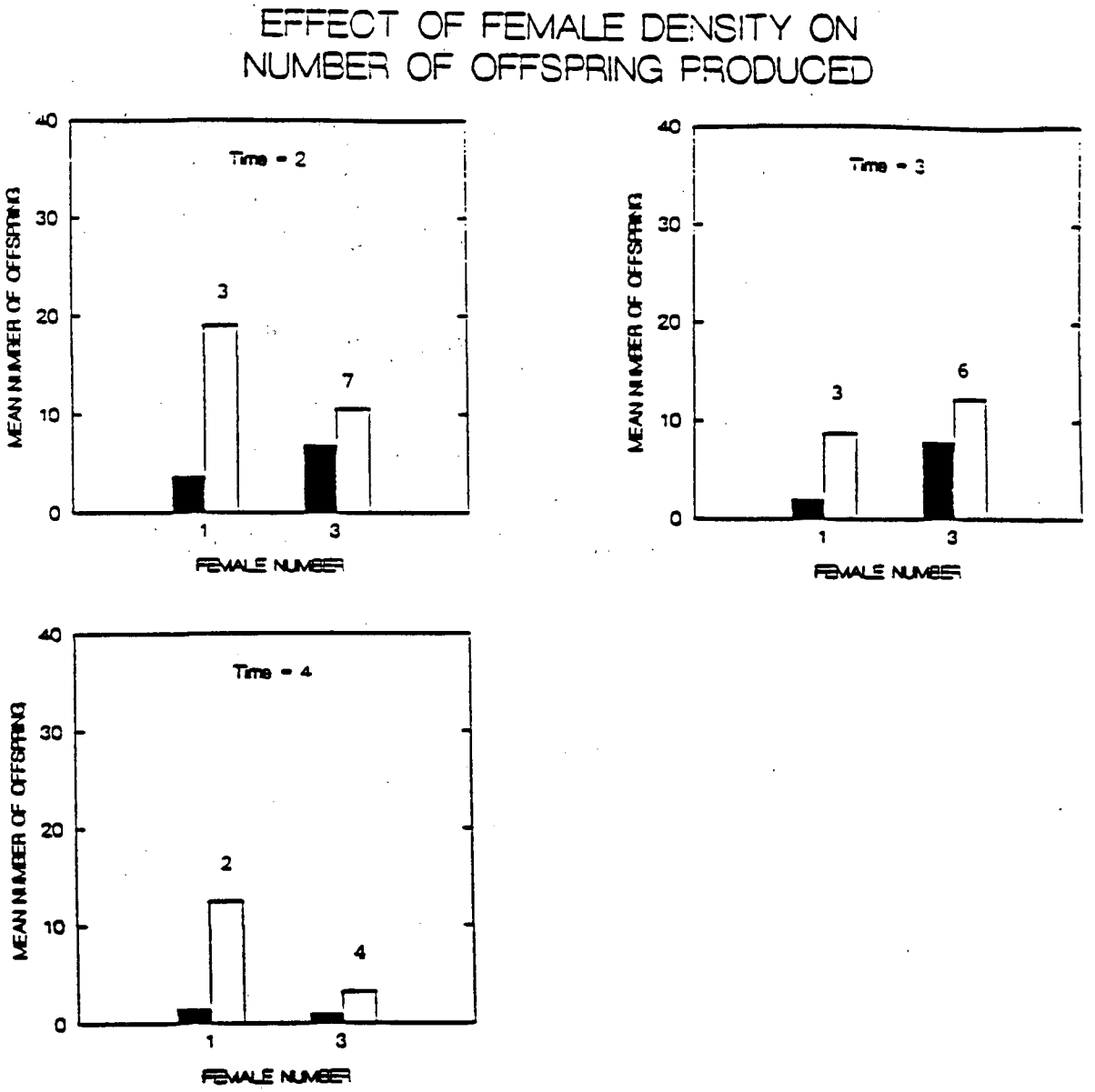

Figure 5. Experiment 4. Effect of mate "sharing" on the number of ☐ daughters and ■ sons produced. Two treatments were examined; 1 female/male, and 3 females/male. After Time = 1 females from 3 female/male treatment group were each put into separate jars. Time 2 after 14 days of oviposition, Time 3 after 21, Time 4 after 28. The number of females in each treatment is shown at the top of the bars.

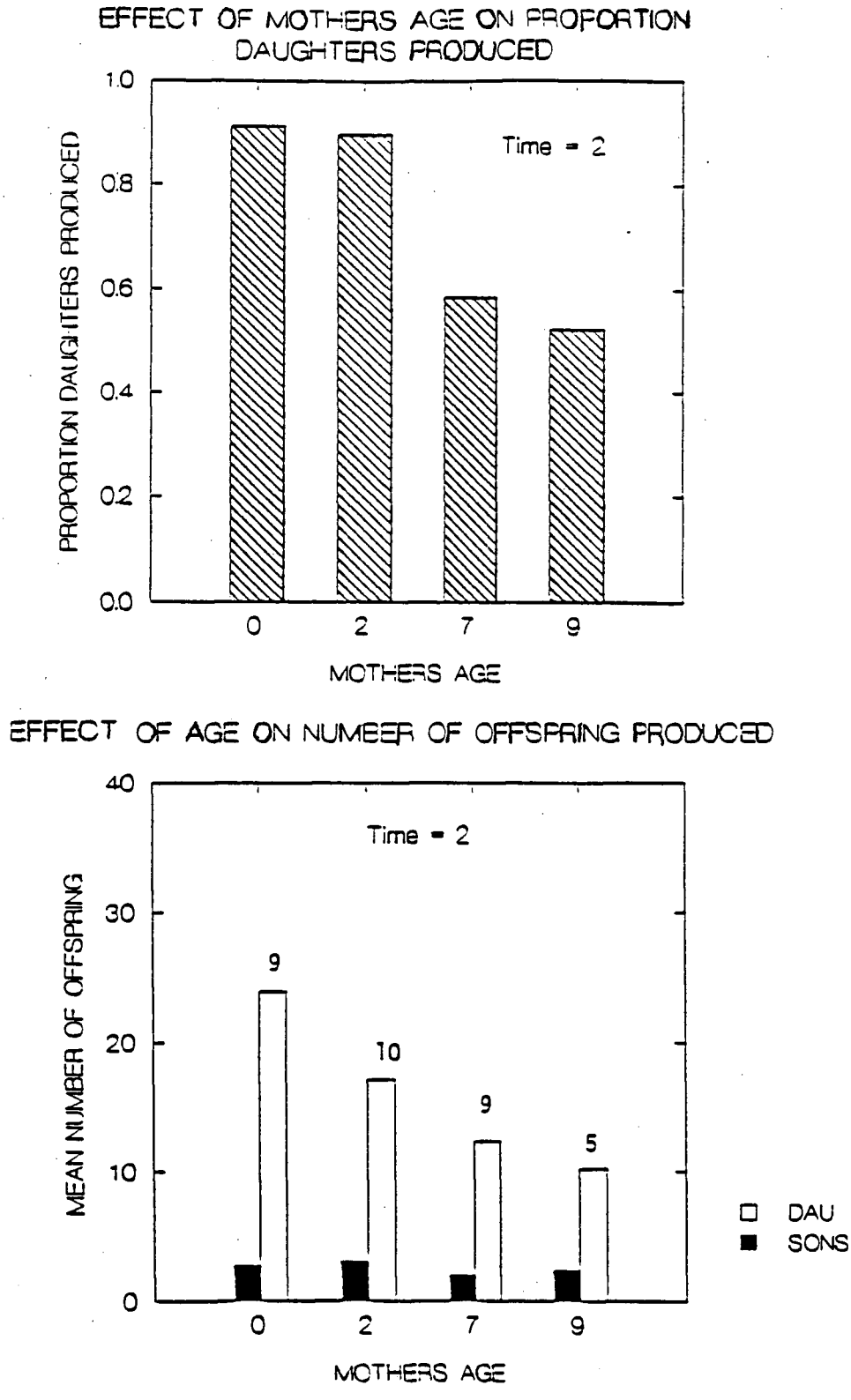

Figure 6. Effect of mother's age on the a) proportion of daughters produced and b) the number of offspring produced per female. Numbers at the top of bars represent the number of females in each age group.

In all lab studies, sex ratios of mated females were skewed toward the production of daughters. Sex specific differences in mortality may be responsible for observed sex ratios produced by mated females in the lab. Unfortunatley, I can not eliminate this factor as a possible mechanism because adult and not primary sex ratios were used. The sex of immatures was not determined. However, dead immatures were never found in jars. The total number of offspring produced by son producing virgins and mated females that produced both sons and daughters was similar. More work needs to be done that examines how primary and secondary or adult sex ratios are related.

The number of offspring produced is crucial to a population's ability to increase. The total number of eggs laid by other species of thrips ranges from 30 to 300, depending on the individual and the amount and quality of food (Lewis 1973). In WFT, oviposition begins within 72 hours of emergence and continues intermittently throughout almost all adulthood (Bryan and Smith 1956). Many of the factors influencing variation in fecundity in WFT have not been identified. For many species of thrips, protein availability enhances egg production. Temperature has little effect on total egg production but can influence the rate of ovipostion in other thrips species (Lewis 1973). Female WFT lay 4 to 6 eggs per day in the lab. The number of offspring produced per day decreases as females age. The longevity of an adult female WFT ranges between 40 to 50 days under laboratory conditions, males live approximately half that long (pers. observ.). Bryan and Smith (1956) found that development from egg to adult required 21.8 days at 20 ^{o}C. I found that development from egg to adult required 12 to 14 days at 21 $\pm$ 1 ^{o}C. Lublinkhof and Foster (1977) found similar development rates and longevity of adult WFT females in their lab experiments. All life stages develop more rapidly as temperatures increase from 15 to 30 ^{o}C (Lublinkhof and Foster 1977). However, longevity decreases as temperature increases from 15 to 30 ^{o}C (Lublinkhof and Foster 1977).

Factors influencing sex ratio are important because sex ratio determines the number of females, which contribute to the population's ability to "outbreak". The sex ratio of the WFT population within a greenhouse reflects the potential impact of the population to the crop (Chapter 3). These lab studies indicate that sex allocation in WFT is affected by sperm depletion and maternal age. Reproductive effort in mated female WFT was biased towards production of daughters. This supports the changes in adult sex ratio with density in found in commercial vegetable greenhouses (Chapter 3). Virgin females did not produce more offspring than mated females. Production of offspring is highest during the first week of an adult females life and decreases gradually thereafter. It appears that as long as sperm are available, approximately 2/3 of offspring produced are females. Only at low densities would females possibly run out of sperm in the field. This is not likely at high WFT densities. Only sex ratios produced at Time = 1 likely represent field conditions. At low WFT densities, females would have to produce sons and wait for these to develop before they mated and produced daughters. By this time, females will have aged and are not as proficient at producing daughters as those females mated immediately after emergence.

Sex ratio of a population depends not only on environmentally induced variation but also on secondary factors such as the rate of egg deposition, depletion of stored sperm and the amount of differential mortality during development (Flanders 1965). As females age, their eggs may change in some way that makes them less susceptible to fertilization. In *Rhodnius prolixus* Beament (1946) found fewer numbers of micropiles in older eggs than younger eggs which decreases their ability to be fertilized. King (1961) suggested that even for *Nasonia vitripennis*, the micropyle may be obscured by chance 25% of the time when passing down the oviduct disallowing fertilization.

The number of daughters produced each day by individual females varied greatly and may depend on the number of times she mated. This may partially explain why the number of daughters produced in a given week does not differ significantly between treatments in all manipulation experiments. For all lab experiments, I did not know how many times a female copulated with available male(s) in one week. In experiments which there was more than one male available, females may have been more choosy in the male they mated with. Virgin females produce 100% sons, mated females always produce some sons. This may be to ensure that their daughters are mated soon after emergence. Control of insemination may therefore control sex ratio which likely involves regulating the release of sperm from the spermathecae. Mated females always produced more offspring than unmated or virgin females although the difference was not significant. Females may be obtaining a nutritional contribution from the sperm. The number of daughters produced by individual females decreases as sperm is depleted and females age. There was no indication from these lab studies that virgin females delayed oviposititon until they were mated. Sons produced by virgin females started to emerge at the same time sons and daughters from mated females were first seen. Over time the number of daughters produced declined to a greater degree than the number of sons produced (Figure 1). In *Caliothrips fasciatus* females which have mated only once, lay unfertilized eggs towards the end of their lives (Bailey 1933). Bailey (1933) suggested that sperm became depleted or inactive as time progressed. In expanding WFT populations the age structure may be composed of younger females that produce mainly daughters.

Tetranychid spider mites also have female biased sex ratio. Most populations contain three times as many females as males (Krainacker and Carey 1988). Several studies on haplodiploid spider mites show that the proportion of sons produced increases as females age (Shih 1979, Hamilton et al. 1986, Krainacker and Carey 1988). As female

T. urticae aged, the proportion of male eggs laid by females increased until only males were produced (Hamilton et al. 1986). Only the first mating in female mites is effective (Krainacker and Carey 1990) even though they will mate more than once. In mites the primary sex ratio has been shown to be affected by maternal age, number of matings and paternal age (Krainacker and Carey 1990). When female spider mites were not allowed to remate, the proportion of sons produced increased as females aged. In the spider mite, *Tetranychus urticae*, young females produced mostly daughters whereas old females produced mostly sons (Carey and Krainacker 1988). Hamilton et al. (1986) also found this to be the case when females were inhibited from remating. My lab studies on sex ratio of progeny produced over time by female WFT also found that younger females produced more daughters than older females per unit time. If primary sex ratio depends on maternal age, then adult sex ratio in the population may be determined not only by sex-specific survival but also by population growth rate. Thus in growing populations, the age structure may be skewed towards younger females that produce mainly daughters. Highly biased production of daughters by mated females is likely in part responsible for WFT outbreaks within a greenhouse.

Boudreaux (1963) suggested that sex ratio of progeny for spider mites depended on the quantity of sperm the female received at mating and that the number of fertilized eggs would decrease as the mother aged due to sperm depletion. Potter and Wrensch (1978) found few sperm in the seminal receptacle of older female mites. Shih (1979) suggested that this resulted from sperm depletion. Shih (1979) found that sperm was depleted within 15 days when female spider mite *T. kanzawai* were only allowed to mate once. Paternal age can also affect the proportion of daughters produced if sperm quanity and quality decrease with the number of matings and age of the male respectively. Takafuji (1986) found that sex ratio by female spider mites depended primarily on the amount of sperm transferred to the female. Krainacker and Carey (1990) found that male

spider mites ran out of sperm after four to five matings in one day and that they required about four days before sperm stores were completely restored. Factors affecting sperm depletion in male spider mites may also affect sperm supply and utilization in male WFT. Paternal age and the number of time he has copulated may inturn affect sex of offspring produced by female WFT. These factors may determine offspring sex ratios through female manipulating fertilization. Nothing is known about changes in sperm viability or effects of multiple mating on sperm supply of male WFT. These effects were not examined in my lab studies and should be addressed in future studies.

In all lab experiments, female age and sperm quantity changed simultaneously. It is not known if the sex ratio of offspring produced by females was due to sperm depletion or age affects. Females were not allowed to remate after the first week. It appears that females that had the potential to mate with several males (10) within the first week, obtained enough sperm to last their lifetime (Figure 3). To separate sperm depletion effects on sex ratio from maternal age effects, lab experiments in which females are allowed to remate as they age must be done. From my lab studies it appears that both sperm availablity and maternal age can affect the number of daughters a female produces in her lifetime.

In conclusion it is difficult to assert that female WFT adjust the sex ratio of offspring produced in response to population density. There is no indication from these lab studies that females actively manipulate sex of offspring produced in response to changing evironmental conditions. However, it is possible that the range of conditions tested in these studies did not perturb the system enough to ellicit a response. Once mated females produce sons and daughters. Two-thirds of offspring produced by mated females are females; approximately the same number of sons are produced over time while the number of daughters decline. This suggests that females have control over sex

of offspring produced. When females are not allowed to remate, the proportion of daughters produced decreases and the proportion of sons increases over time. Sex ratio of progeny produced may not only be a function of sperm supply but also of maternal age. Increased production of males may result from sperm depletion and or reduced sperm viability. However, male availablity may be the most important factor affecting the number of daughters produced by individual females which in turn may determine the potential of WFT to outbreak within greenhouses.

Chapter 5

GENERAL CONCLUSIONS

Lack of control of WFT in the past can be attributed to two main factors, ill-adapted biocontrol agents and a lack of understanding of WFT mating biology. The predatory mite, *Amblyseius cucumeris*, is an inefficient biological control agent, whose predatory performance is hampered on cucumber crops (Peterson 1990), and that may diapause if temperatures drop below 20 ^{o}C in the greenhouse (Gilkeson et al. 1990). Low temperatures can occur during the early months of the growing season when western flower thrips females are initially becoming established in a greenhouse and during the later months of the growing season when high populations of WFT generally exist in the houses. These predatory mites may diapause while WFT populations are still increasing. A lack of knowledge regarding WFT mating behaviour, reproductive biology and distribution on crops in greenhouses has retarded the improvement of monitoring programs and interpretation of the effectiveness of biological control agents. This thesis makes a contribution to both these areas.

In chapter 2 I demonstrated that most females are found in flowers. Flowers should be monitored regularly to locate places of initial population growth within a greenhouse. Density of predatory mites should be increased as soon as females are seen in the majority of flowers examined in an area of the greenhouse or throughout the house. In chapter 3 I found a significant correlation between density of adults on traps and sex ratio. At low densities, traps catch mostly males; as population density of WFT within a greenhouse increases a greater proportion of individuals on traps are females. As soon as the number of females per trap starts to increase, the number of biological control agents should be increased, either in an area or throughout the greenhouse. At high densities,

greater than 500 thrips a trap, more than 70 to 90 % of adults on traps may be females. Examination of flowers and use of sex ratio on sticky traps provides growers with an efficient and precise means of monitoring the WFT population in commercial greenhouses. In chapter 4 I found that production of daughters by females can be affected by sperm availability and maternal age. Therefore maintainance of WFT at low densities through use of biological control agents or pesticides can limit the availablity of males, postponing production of daughters by females at an older age. Older females produce a smaller proportion of daughters per unit time than younger females.

Sex ratio

Two unique aspects this study examines are the prevalence of virginity and sex ratio in a field population of haplodiploids. It appears that populations of WFT within greenhouse are initiated by virgin females that probably overwinter as pseudopupae in the greenhouse. These females are capable of producing only sons and must wait for these to emerge before they can mate and produce daughters. By this time females are 12 to 14 days older. Increased male production occurs with age which may result from maternal affects, sperm depletion and/or reduced sperm viability. At high densities, it is likely that females encounter males and mate earlier in their life than females emerge and initially invade a greenhouse.

Even at moderate densities, 25 % of WFT females collected from flowers and leaves were virgins. The production of only sons by these females may be compensated by the production of mostly daughters (67 %) by mated females which will result in a nearly balanced sex ratio within the population. This fits Fisher's (1930) model which predicts that in panmictic (randomly mating) populations, investment in the production of males and females should be equal. Given equal investment in both sexes, sex ratios other than 0.5 may arise among adults for several reasons: 1) sex differential mortality,

2) sex differences in lifespan, 3) differential dispersal and lastly 4) female control of fertilization and differential production of sexes. All of these factors likely contribute to adult sex ratios found on traps over time. Females live twice as long as males in the lab. It is likely this is true also for field populations; therefore later in the growing season one may expect to see twice as many females as males. This coupled to overproduction of daughters by mated females are likely the two main factors responsible for highly female biased sex ratios found in greenhouses when densities of both males and females are high.

Sperm availability and maternal age affect the proportion of daughters produced by individual females in their lifetime. In field populations it is not likely that sperm becomes limiting. Nevertheless, suppression of greenhouse populations of WFT with biological control agents or pesticides can delay production of daughters by females. This in turn would restrict the potential of a WFT population to outbreak.

Future studies

Future studies need to address whether shifts in sex ratio from male to female bias recorded in the field are due to a combination of sex differential mortality and differences lifespan of males and females or female ovipositional behaviour. Lab experiments need to be done that determine the relationship between primary and resultant adult or secondary sex ratios, the effect of paternal age and mating history on sperm supply and viability. Dissections of the spermatheca of females mated to differing number of males and over time would reveal if sex ratio of offspring produced was the result of sperm availability, maternal age or a combination of the two. Experimental manipulations of the density of female and male WFT, and predators in smaller greenhouses need to be done to see if sex ratio of the adult population affected. Nothing is known about the movement of male and female WFT within a greenhouse. Sex differences in movement

within a greenhouses may affect trappability. Air samples should be taken regularly along with plant samples, and trap catch to determine how trap catch relates to movement of males and females within a greenhouse.

It appears from trap catch data that initially the WFT population is subdivided into isolated mating groups. Most of the matings in these isolated groups would be between mothers and sons. As population density increases, isolation between these mating groups likely breaks down and random mating occurs. Therefore more matings would occur between nonrelatives. The distribution of WFT in a greenhouse may change from random to aggregate to uniform as density increases. In the future I hope to show that there is a correlation between density, spatial distribution and sex ratio.

More research needs to examine the mating biology of WFT in the field. Future studies must ascertain if mating occurs on the plant in localized mating groups, or randomly on the soil where pseudopupae complete development. Pheromones may also be involved in the attraction of males to females in flowers. Females need to be collected from greenhouses at very low densities to determine how the proportion of unmated to mated female WFT changes as density within a greenhouse increases. Knowing the factors that affect offspring production has important theoretical and practical implications. These factors can be used for testing sex ratio theories as well as development of effective pest management programs.

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