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EFFECT OF ELEVATION AND HOST AVAILABILITY ON DISTRIBUTION OF STERILE AND WILD MEDITERRANEAN FRUIT FLIES (DIPTERA: TEPHRITIDAE)

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ABSTRACT

Effects of elevation and host fruit availability on the distribution of the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), were evaluated with cylindrical traps baited with a female-biased food-based synthetic lure. Tests were conducted in the Santa María valley, Guatemala during a sterile male release program. Traps were placed in or near host trees (primarily coffee and citrus) and in non-host trees when no hosts were available. Trap locations were grouped according to elevation every 170 m. Elevation group midpoints were 1103, 1273, 1443, and 1613 m above sea level. The spatial distributions of sterile males, wild males, and females were clumped throughout the 13 wk of sampling. More wild female flies were captured in coffee in the 1273 m elevation and on non-host trees in the 1103 m elevation. The number of wild males was directly related to the number of wild females captured, and the sex ratio (female: male) was highest at the 1443 and 1613 m elevation ranges. There was no relationship between the number of sterile males and number of wild females in the traps at any elevation. At all elevation ranges, an inverse relationship was observed between the numbers of wild females and males with the mean numbers of sterile males per trap. Wild *C. capitata* populations appeared to decrease when 40 sterile males were captured per trap with wild females per week. The results indicated that, during the sampling period evaluated, coffee appeared to be the main host plant for the wild population, *C. capitata* were more abundant at the 1273 m elevation range than at other elevations. Additional or alternative host species may harbor the female population at other times.

Key Words: *Ceratitis capitata*, fruit fly host plant, elevation, sterile insect technique, fruit fly spatial distribution.

RESUMEN

Plantas hospederas y elevación preferencial por la mosca Mediterránea de la fruta, *Ceratitis capitata* (Wiedemann), fueron evaluadas con trampas cilíndricas con cebo sintético que atrae hembras. Experimentos fueron realizados en Guatemala durante el programa de liberación de machos estériles. Trampas fueron colocadas en o cerca de árboles hospederos (principalmente café y cítricos) y en otros árboles no hospederos). Las trampas fueron agrupadas de acuerdo a su elevación cada 170 m, en los rangos de elevación 1103, 1273, 1443, y 1613 m por encima del nivel del mar. La distribución espacial de los machos estériles, hembras y machos fértiles y salvajes fue agrupada a través de las 13 semanas de muestreo. Las hembras salvajes fueron capturadas sólo en café (más en el rango de elevación 1273) y en las plantas no identificadas (más en el rango de elevación 1103). El número de machos salvajes fue proporcional al de hembras salvajes y el radio sexual (hembra: macho) fue mayor en los rangos de elevación 1443 y 1613. El número de machos estériles no fue afectado por el incremento de hembras salvajes en las trampas. En todos los rangos de elevación, se encontró una relación inversa entre el número promedio de hembras y machos salvajes con el número promedio de machos estériles. La población salvaje de la mosca del mediterráneo decreció cuando los machos estériles llegaron a ser 40 por trampa con hembras salvajes por semana. Los resultados indicaron que el café pareció ser la planta hospedera principal de la población salvaje durante el período de muestreo, y que durante este, las moscas del Mediterráneo fueron más abundantes en el rango de elevación de 1273 m que en otros rangos de elevación. Otras plantas hospederas alternativas podrían acarrear a la población de hembras salvajes en otros momentos.

Translation provided by the authors.

Ceratitis capitata (Wiedemann), the Mediterranean fruit fly, is considered the most destructive agricultural pest in the world. Even though it is not established in the continental U.S., its potential impact on the California and stone fruit industry has been projected to be about $0.5-1 million in agricultural losses per year (Siebert & Pradhan 1990). It has been reported to attack more than 260 species of fruits and vegetables world-wide (Liquido et al. 1991; Ovruski et al. 2003). Adult females damage fruit by depositing their eggs in holes made under the skin of the fruit. Availability of host plants suitable for oviposition is a key factor for understanding the population dynamics of the fruit fly and its distribution over space and time. This information can be used for planning management strategies for this pest. If the plants are not in fruit or have only low quality fruit, mature females either arrive in low numbers or emigrate rapidly and fly considerable distances before finding host plants with acceptable fruits (Prokopy & Roitberg 1989). Therefore, availability of host plants is considered a key factor in the temporal pattern of fruit fly abundance (Bess et al. 1963; Newel & Haramoto 1968; Malavasi & Morgante 1981; Vargas et al. 1983).

Successful eradication of the Mediterranean fruit fly has been obtained by the sterile insect technique (SIT) in combination with bait sprays in Mexico, and in the U.S. in California and Florida (Vargas 1989). Endemic populations of *C. capitata* occur in Guatemala, where efforts to suppress fruit fly populations in large portions of the country are occurring through the Programa Moscamed, a trilateral effort of the governments of the U.S., Mexico, and Guatemala (Linares & Valenzuela 1993). The primary effort in Guatemala is to maintain a barrier to prevent movement of *C. capitata* into Mexico and the U.S. The areas under SIT activity include a fly free area (57% of area, located in the northwest, closest to the border with Mexico), an infested area (33.8% of area, located in the southeast, where high populations of *C. capitata* are present) and a control area (9.2% of area, located between the free area and the infested area) (Linares & Valenzuela 1993). Traps are placed throughout this area and are monitored by Moscamed, and trapping data indicate that up to 98% of the region is under successful control, with no wild flies captured. However, localized isolated populations or "hot spots" of wild flies still persist in the infested area, and identification of the factors responsible for the hot spots is critical to the success of the eradication effort. The Santa María area of Guatemala is located close to the southeast edge of the infested area, and contains isolated populations of *C. capitata*. A study was initiated to evaluate the spatial distribution of endemic wild and released sterile *C. capitata* in this area and to identify effects due to elevation and host plant availability.

Materials and Methods

Traps and Lures

Cylindrical open-bottom dry traps (OBD; Heath et al. 1996) were baited with a three component lure consisting of ammonium acetate, putrescine, and trimethylamine, formulated as three separate patches backed with adhesive for securing inside the trap (Suterra, Inc., Bend, OR). The OBD trap (9 cm diam by 15 cm tall) is made from opaque green waxed cardboard and has three holes (2 cm diam) evenly spaced around the midline of the trap body. A yellow sticky insert (7.6 by 12.7 cm; Suterra LLC, Bend, OR) was hung inside the center of the trap to retain flies. Sticky inserts were replaced weekly, the three component synthetic lures were replaced every 4 wk, and traps were replaced when the cardboard deteriorated.

Fly Release

The sterile male-only *tsl* strain of *C. capitata* (Vienna-7) used in this study was produced by gamma irradiating pupae with 10Krad (100 gray) at the Moscamed rearing facility, Guatemala. Irradiated pupae were treated with 4g/liter of pupae with powdered florescent dye (Dayglo Color Corporation, Cleveland, OH) to mark the adults on emergence. *C. capitata* adults were kept at 23°C and fed a mixture of 15% sugar and 84.99% water thickened by 0.01% agar. At three to four days of age, flies were chilled to near 0°C, loaded into chilled-fly release machines (K&K Aircraft, Bridgewater, VA) installed in a Cessna Caravan, and released at an average rate of 3,600 flies per ha over the test area from an altitude of 2500 to 3000 m above sea level.

Protocol for Field Trial

The study was conducted in a geographically diverse area of Guatemala under SIT activity. The field site was approximately 20 km^2 and was centered at longitude -91.53° and latitude 14.71° in the Santa María valley between the Santa María and Santo Tomas volcanoes in the province of Quetzaltenango. Fifty-one traps were deployed throughout the valley at different elevations and host plants to monitor the presence of the wild populations and the sterile males released in the area. Trap sites were determined by generating a grid of potential trap locations based on a point in the center of the valley and spaced evenly 500 m apart. Traps were then placed as close to these potential trap locations as possible with GPS (Garmin International, Inc., Olathe, KS, GPS III Plus). A potential trap location was one that had road access, where the terrain (rivers, mountain, etc.) did not interfere with trap deployment, with

a known history of detection of *C. capitata* or where attack was likely due to phenology of known hosts or presence of wild alternative hosts. Potential trap locations were eliminated if they were inaccessible to the trappers, if they were bare of trees or structures to support a trap, or if permission for access was not granted. Traps were placed primarily in or near host trees, including coffee (*Coffea arabica* L.), or trees within a coffee grove, sweet orange (*Citrus sinensis* Osbeck), nispero (*Manilakara zapata* [L.] P. Royen), guava (*Psidium guajava* L.), mango (*Mangifera indica* L.), apple (*Malus pumila* P. Mill), melon (*Cucurbita melo* L.), and loquat (*Eriobatyra japonica* Lindl.). If no host trees were near the prospective location, a trap was placed in a non-host tree. Elevation of the traps varied from approximately 1,000-1,700 meters above sea level, and this range was divided into four equal groups of 170 m to determine elevation groups. Elevations (elevation ranges) were designated by their midpoint, and considered as 1103 m (1017-1187), 1273 m (1187.1-1357), 1443 m (1357.1-1527), and 1613 m (1527.1-1697).

The traps were sampled weekly for 13 wk from June to October 2002 (recorded as wk 26-38 out of 52 wk per year). During this time only a few hosts such as guava, citrus, and coffee were fruiting and available for *C. capitata* colonization. All flies captured were taken to the Moscamed laboratory in Mazatenango, Guatemala, examined to determine sex and sterility status following standard protocols (Anonymous 1983), and number of sterile males, wild males, and females were recorded. Meteorological data was not available.

Host Fruit Availability

Information on host fruit availability in the Santa María valley was obtained from records maintained by Moscamed. As part of the Moscamed protocol, fruit sampling is carried out in an extensive way to complement trapping (Linares & Valenzuela 1993), and host fruits are obtained from all places including urban, rural, wild, agricultural, and cultivated areas. Sampling routes are determined according to location of fruit trees inside private properties, access areas, and roads. Fruits were collected directly from trees when they were mature but still with solid (or firm) consistency. Sampling numbers varied according to fruit: 30-60 coffee or cherries, and 4-6 for other fruit trees. If pest levels are low, only fruits susceptible to the *C. capitata* attack with circular yellow or necrotic spots are collected. If many trees are present, samples are taken from different trees as long as they are not separated by more than 100 m. If fruits are scarce, they are collected from known hosts or from those that had higher probability of infestation, i.e., from the sunny side of the host plant at different heights. Historical data on collection dates and number of mature fruit sampled per collection date were used to estimate pattern of host fruit availability in trees used for trap placement in this study. Infestation levels were not recorded.

Data Analysis

Data were checked for homocedasticity prior to statistical analysis. To normalize the data and stabilize the variance, numbers of fruit flies captured per trap per week were square root-transformed ($x + 0.5$) and a repeated measure ANOVA was used to detect effects of sampling date and elevation range on female-male ratio. To detect differences in trap captures among different hosts and elevations, and to compare female:male ratio among elevation ranges, a Kruskal-Wallis ANOVA was used followed by a non-parametric multiple comparison procedure (Siegel & Castellan 1988) when no transformation normalized the data (SAS Institute 1998). The variance to mean ratio of the numbers of fruit flies captured each week sampled, for each fruit fly type (wild female, wild male, and sterile male) was used to determine the fruit fly spatial distribution (Southwood 1978).

Results and Discussion

Number of traps was variable at each elevation range and host plant. Traps were deployed on 25 non-host species, 24 coffee trees, one loquat and one orange tree (*Citrus* spp.). On coffee, 4, 14, 3, and 3 traps were deployed at the 1103, 1273, 1443, and 1613 m elevation ranges, respectively. On non-host species, 2, 4, 10, and 6 traps were deployed at the 1103, 1273, 1443, and 1613 m elevation ranges, respectively. In the 13 wks of sampling, wild females were captured in 5, 68, 6, and 9 traps on coffee and in 3, 1, 6, and 3 traps on non-host species at the 1103, 1273, 1443, and 1613 m elevation ranges, respectively. Five traps also were deployed above 1697 m, but no wild or sterile flies were ever captured in those traps. Therefore, these five traps were not considered in the analyses.

Because the wild females are the target for control and zero values confounded the results (no statistical differences were detected among elevations, plant species or between wild females or males, and sterile males), only traps that captured wild females were used in the analyses. The only traps that captured wild females were those traps deployed on coffee and non-host species. Table 1 shows the number of traps for each sampling date and for the 13 wks of sampling, and the average number of wild females, wild males, and sterile males captured at different elevations and host plants. The highest percentage of traps with wild females was found on coffee at the 1273 m elevation range, representing 41% of the traps that

TABLE 1. PERCENT OF SAMPLES WITH WILD FEMALES (OUT OF TOTAL NUMBER OF TRAPS TIMES NUMBER OF SAMPLES (13 WEEKS)) IN EACH ELEVATION GROUP AND IN EACH HOST GROUP, AND NUMBER OF *C. CAPITATA* CAPTURED IN TRAPS PLACED IN COFFEE. TESTS WERE CONDUCTED FROM JUNE TO OCTOBER 2002, IN SANTA MARIA, GUATEMALA.

Elevation range (m)	Coffee	*n*	Non-host species	*n*	Average (±SE) number of flies per trap per week		
					Wild females	Wild males	Sterile males
1103	10.4% (52)	4	12.5% (26)	2	1.0 ± 0.0 b	0.5 ± 0.2 b	10.8 ± 4.8 a
1273	40.5% (182)	14	2.1% (52)	4	5.4 ± 1.1 a	3.8 ± 0.9 a	26.1 ± 3.3 a
1443	16.7% (39)	3	5.0% (130)	10	3.0 ± 0.7 ab	0.6 ± 0.3 ab	16.2 ± 3.8 a
1613	25.0% (39)	3	4.2% (78)	6	1.9 ± 0.6 ab	0.5 ± 0.2 b	10.8 ± 1.9 a

Means in the same column followed by the same letters are not different (Kruskal-Wallis ANOVA, $P < 0.05$); *n* represents the total number of traps deployed on each host at each elevation range.

captured females. Captures of wild females at this elevation range were not significantly different than those captures at the 1443 and 1613 m elevation ranges but were higher than those at the 1103 m elevation range. Similar results were obtained for the wild males. The mean number of sterile males in traps with wild females on coffee was not significantly different among elevation ranges (Table 1). On the non-host trees, the highest percentage of traps with wild females was found at the 1103 m elevation range but this effect of elevation was not significant (Table 1, $H = 0.241$; $df = 3$, $P = 0.9708$). Findings of sterile males in comparable numbers at all elevation ranges may indicate that the sterile release program was successful in distributing the flies adequately to pursue an effective control of the wild female populations.

The peak of maturation for all the host plants available for *C. capitata* colonization was in mid May, and maturation rapidly decreased by the end of the summer. During late June, when this experiment began, host plants such as caimito (*Chrysophyllum cainito* L. (syn. *Achras caimito* Ruiz & Pavon)), mango, and mandarin (*Citrus reticulata* L.) only had a few mature fruits left on the trees. Coffee, sweet orange, sour orange (*Citrus aurantium* L.), and guava trees had the highest numbers of ripe fruits among the host plants evaluated at the end of June and throughout the experiment. Only guava, citrus (*Citrus* spp.), and coffee were fruiting and available for *C. capitata* colonization during the sampling period. No information was collected on the phenology of the trees where the traps were deployed. Therefore, we cannot infer the relation between host availability and trap captures.

The spatial distributions of sterile males, wild males, and wild females were clumped throughout the sampling period as indicated by the variance to mean ratio (Table 2), except on wk 38 when the sterile males appeared to be distributed at random. However, the overall spatial distribution of the sterile males was clumped. Previous studies also found a patchy distribution of the Mediterranean fruit fly under low population densities (Bateman 1972; Vargas et al. 1983; Nishida et al. 1985; Harris & Lee 1986, 1987; Harris et al. 1993; Papadopoulos et al. 1996; Prokopy et al. 1996; Israely et al. 1997; Katsoyannos et al. 1998; Papadopoulos et al. 2001).

Figure 1 presents the population dynamics of the wild females at the four elevation ranges on coffee and on the non-host trees. Even though the wild females appeared on both host and non-host trees at the beginning of the study (wk 26-30), they disappeared from the non-host trees after wk 32 and increased on coffee at all elevations. This observation might be an indication that while coffee and non-host trees are flowering or ripening, *C. capitata* populations use both tree species, but when ripening of coffee occurs on wk 33 and no other fruits or flower plants are available at this time, the female flies move to the

TABLE 2. MEAN/VARIANCE RATIO TO DETERMINE THE SPATIAL DISTRIBUTION OF *CERATITIS CAPITATA* CAPTURED IN CYLINDRICAL TRAPS BAITED WITH A FOOD-BASED SYNTHETIC ATTRACTANT IN SANTA MARIA, GUATEMALA.

Week	Wild females	Wild Males	Sterile males
26	0.02	0.03	0.04
27	0.09	0.00	0.02
28	0.10	0.37	0.21
29	0.42	0.61	0.01
30	0.24	0.29	0.01
31	0.46	0.80	0.02
32	0.11	0.12	0.03
33	0.06	0.09	0.03
34	0.10	0.08	0.03
35	0.31	0.16	0.15
36	0.61	0.49	0.81
37	0.22	0.50	0.52
38	0.45	0.57	1.04
Total	0.05	0.06	0.02

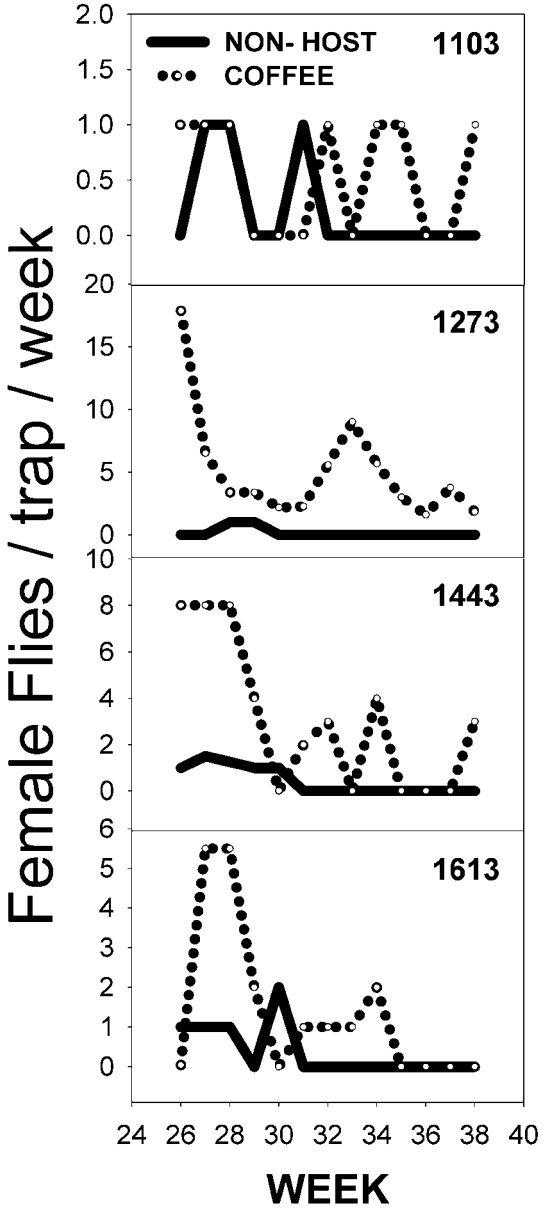

Fig. 1. Population dynamics of wild female *C. capitata* captured in cylindrical traps baited with food-based synthetic attractant during 12 weeks of sampling at different elevation ranges on coffee (dotted line) and non-host trees (solid line) in Santa María, Guatemala.

coffee areas in search of better feeding and oviposition sites. This observation agrees with Papadopoulos et al. (2003) findings that the Mediterranean fruit fly females aggregate in space in response to the changing phenology of host trees and to the sequential availability of ripe or semi-ripe fruits in an orchard. Moreover, *C. capitata* are known to adjust their foraging behavior in response to the changes in the spatial, temporal, and seasonal distribution of food and other resources (Hendrichs et al. 1991).

Because captures in traps on non-host trees were less than two females per trap per week for most of the study, only data from traps in coffee were used in the remaining analyses. A direct relationship between the mean number of wild females and males was found at different elevation ranges on coffee (Fig. 2). The number of wild males was directly proportional to the number of wild females, but the female:male ratio varied among elevation ranges ($F = 22.809$; $df = 1, 47$; $P < 0.001$). The highest female:male ratios were 4.0

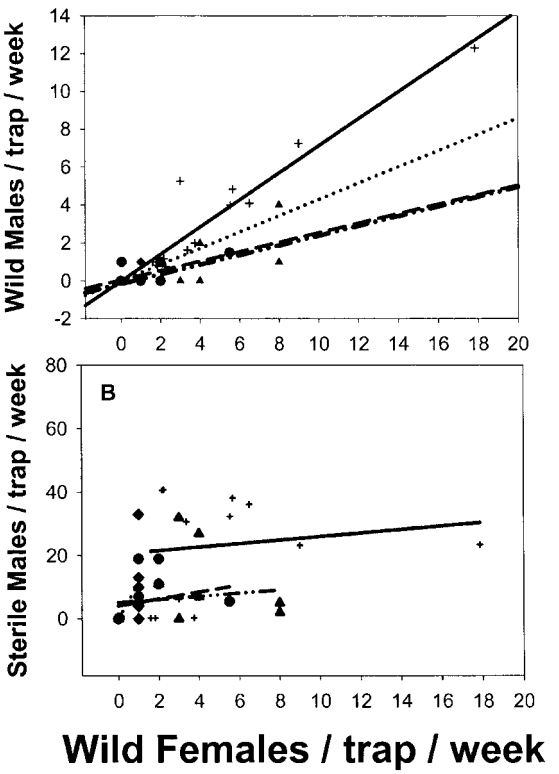

Fig. 2. Relationship between (A) mean number of wild female and male *C. capitata* and (B) mean number of wild female and sterile male *C. capitata* captured in cylindrical traps baited with food-based synthetic attractant and placed in coffee trees at different elevation ranges (◆:1103 m, +:1273 m, ▲:1443 m, •:1613 m above sea level) in Santa María, Guatemala. Lines indicate regression lines for 1103 m (– – –), 1273 m (——), 1443 m (– · · –), and 1613 m (· · ·). For wild-males/trap/week vs wild females/trap/week: $y = 0 + 0.43x$ ($r^2 = 0.26$, for 1103 m); $y = -0.19 + 0.71x$ ($r^2 = 0.89$ for 1273 m); $y = -0.17 + 0.26x$ ($r^2 = 0.47$, for 1443); $y = 0.04 + 0.25x$ ($r^2 = 0.63$, for 1613 m). For sterile males/trap/week vs wild females/trap/week $y = 11.14 + 0.36x$ ($r^2 = 0.37$, for 1103 m); $y = 20.50 + 0.56x$ ($r^2 = 0.02$, for 1273 m); $y = 5.08 + 0.50x$ ($r^2 = 0.02$, for 1443 m) and $y = 4.03 + 1.10x$ ($r^2 = 0.10$, for 1613 m).

± 2.0 and 2.3 ± 0.6 (mean ± SE) at the 1443 and 1613 m elevations, respectively. No relationship was detected between the number of wild females captured and the number of sterile males captured when all the elevations were considered (ANOVA, $F = 1.763$; $df = 1, 47$; $P = 0.1671$). However, after separating the sterile male and wild female captures by elevation range (Fig. 3.) an inverse relationship was observed between the numbers of wild females and sterile males per trap at the 1273 m elevation range. This is an additional indication that the sterile releases were successful in controlling the wild female populations. When the sterile males reached 40 per trap with-wild-females per week, a corresponding reduction was observed in the wild population of females (Fig. 3). A successful SIT program requires releasing enough sterile flies so that at least an overflooding ratio of 100 sterile males is reached for each wild fly captured (Garcia et al. 1999; Barry et al. 2003). This evaluation is averaged over all traps, also including those that do not capture any wild females. Furthermore, it is based on fly captures on Jackson traps that target only male flies. In this study, OBD traps were used for the analyses. Therefore, the discrepancy in numbers (40 versus 100) may be due to the exclusion of traps with zero-wild-females, and to the use of female biased traps resulting in an overflooding ratio below the required average. Because the wild female populations decreased at 40 sterile males per traps-with-wild-females, this may be an indication that the required overflooding ratio of 100 sterile males per wild female per trap captured was reached. Additional studies are required to adjust the over-flooding ratio based on OBD traps. Elevation effects have been observed with other tephritid species. For example, the melon fly, *Bactrocera cucurbitae* (Coquillet), is found mostly at low and medium altitudes in Reunion Island where it competes with the Ethiopian cucurbit fly, *Dacus ciliatus* Loew, both competing with the Indian Ocean cucurbit fly, *Dacus (Dacus) demerezi* (Bezzi) that occupies high altitude areas (Etienne 1972; Vayssieres & Carel 1999).

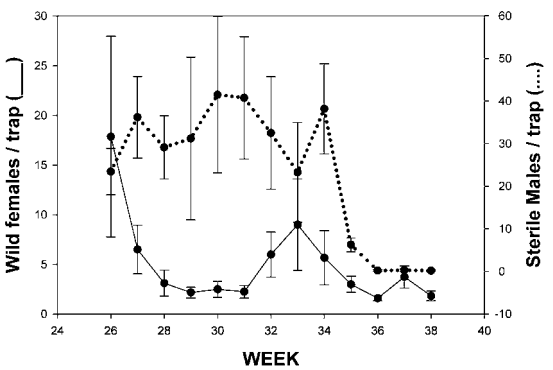

Fig. 3. Mean number of sterile males per week in traps with wild females (•••), and sterile male *C. capitata* (——) per week at the 1273 m elevation range.

After wk 32, numbers of sterile males decreased in all traps and the numbers of females began to increase at all elevation ranges. On wk 34, a decrease of the sterile males in the traps was observed, and an increase of the wild females occurred by wk 37. The inverse relationship of the sterile males and the wild populations of *C. capitata* is an indication that the aerial releases of sterile *C. capitata* were successful in reducing the wild populations in Santa María, Guatemala. This result reiterates previous eradication efforts of this pest at the Mexico-Guatemala border, which prevented the northward spread of the fly into Mexican territory (Orozco et al. 1994).

Data from this study support the hypothesis that elevation and host fruit availability affect the distribution of wild flies in the habitat of this valley. Wild male and female fruit flies were more abundant at the 1273 m elevation range on coffee throughout the sampling period. Even though higher mating success of sterile males was reported at low elevation sites (700 m) in Guatemala (Shelly et al. 2003), it is important to direct *C. capitata* control efforts with SIT to those areas where the wild populations persist as "hot spots" at higher elevations. Micro-environmental differences in humidity and temperature, as well as host fruit maturity, may have contributed to creating the favorable conditions for wild fruit flies. Microclimatic environmental parameters that regulate clumped distribution of the wild fruit flies remain to be identified.

Because the number of samples was unbalanced among elevation ranges, a balanced sampling scheme on coffee and other host plants among elevation ranges is needed to identify other possible host plant preferences by *C. capitata* wild populations. Furthermore, detailed information of fruiting phenology needs to be recorded to determine which host plants play a key role in the *C. capitata* population increases (Ovruski et al. 2003). We hypothesize that different available hosts harbor populations of different sexes, as reported by Papadopoulos et al. (2003), and also that different micro-environmental conditions (Eskafi & Kolbe 1990) may favor the survivorship of different fruit fly sexes. Because several factors may be interacting and affecting the spatial distribution of *C. capitata* in this area, micro-environmental conditions and fruit availability at different elevation ranges are needed to test these hypotheses that may explain the variation in sex ratios at different elevation ranges. Although coffee appeared to be the main host plant for the wild population during the sampling period reported herein, additional or alternative host species may harbor the female population at other times.

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