Recapture of Sterile Mediterranean Fruit Flies (Diptera: Tephritidae) in California's Preventative Release Program

JAMES D. BARRY,[1] TODD BLESSINGER,[2] AND JOSEPH G. MORSE

Department of Entomology, University of California, Riverside, CA 92521

J. Econ. Entomol. 97(5): 1554–1562 (2004)

ABSTRACT In southern California, the sterile insect technique has been used since 1994 to prevent establishment of the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann). This method involves the continual mass release of sterile flies, which suppress or eliminate any introduced wild fly populations. In addition, Jackson traps baited with trimedlure are deployed throughout the preventative release region for the dual purpose of detecting wild flies and monitoring released sterile flies. Sterile fly recapture data for a 3-yr period was compared with climate and to host plant (in which traps were placed). Precipitation was negatively correlated; and temperature and relative humidity were positively correlated with fly recapture levels. The highest numbers of flies were recaptured during trapping periods associated with intermediate relative humidity and temperature, and low precipitation. Flies were recaptured throughout the entire year, in traps that had been frequently relocated to host plants with fruit. This finding suggests that these flies were capable of locating acceptable fruit in a variety of abiotic conditions. However, these data do not necessarily suggest that measurements unimportant in explaining sterile fly recapture are not of value in determining other outcomes important to the goals of sterile release programs, such as reducing the likelihood of establishment of an introduced wild Mediterranean fruit fly population. Future research might build on these results in developing more precise models useful in predicting recapture of sterile flies.

KEY WORDS *Ceratitis capitata*, sterile insect technique, trapping, temperature, precipitation

THE STERILE INSECT TECHNIQUE (SIT) is used as a preventive measure to protect against establishment of the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), in many areas of the world. The success of SIT depends on sterile males mating with wild females (when present) to produce infertile eggs. In July 1996, the Preventative Release Program (PRP) was created to prevent the establishment of Mediterranean fruit flies in southern California (CDFA 2001a). The USDA/CDFA Cooperative Mediterranean fruit fly PRP is involved with receiving puparia, adult rearing, releasing sterile flies, trapping and monitoring programs, and maintaining fly quality control at an annual cost of ≈$18.6 million. Permanent establishment of Mediterranean fruit flies in California could cost commercial agriculture $1.3–1.9 billion (Siebert and Pradhan 1991, Siebert and Cooper 1995, Siebert 1999, CDFA 2001a).

Releases occur daily in the PRP, with exceptions on a few holidays, and in the presence of rain. Factors such as climate, fly quality, and host plant (location of Jackson trap) obviously could impact the fate of sterile flies; however, these conditions are not always predictable and there is a need to maintain high sterile fly densities over an area of 6,466 km^2 (CDFA 2001a). A greater understanding of the impact of climate on SIT may allow better predictions regarding field performance of sterile flies.

In areas where Mediterranean fruit flies are established, the pattern of fly population dynamics is seasonal and the effects of climate and host fruit often are difficult to separate. Harris and Lee (1989) found Mediterranean fruit fly populations in Hawaii to be influenced directly by host plants present and to be influenced indirectly by climate (as a result of differential survivorship on various host plant species depending on season). Examining field populations in Greece, Katsoyannos et al. (1998) came to a similar conclusion regarding the impacts of host plant composition and availability on the number of flies captured in traps. Although host plant composition is obviously important, Mediterranean fruit fly densities were generally the highest and most consistent during the dry season in Hawaii (Harris and Lee 1989, Harris et al. 1993), Nicaragua (Borge and Basedow 1997), and Costa Rica (Hedstrom 1993). The availability of host fruit played a key role in understanding Mediterranean fruit fly phenology in studies in Greece, Brazil (Aguiar-Menezes and Menezes 1996), Guatemala (Es-

[1] Current Address: Center for Blueberry and Cranberry Research and Extension, Rutgers University, 125A Lake Oswego Rd., Chatsworth, NJ 08019 (e-mail: jamesbarry@aesop.rutgers.edu).

[2] Department of Statistics, University of California, Riverside, CA 92521.

kafi and Kolbe 1990), and Hawaii (Nishida et al. 1985, Harris and Lee 1986). Agarwal and Kumar (1999) determined that natural population levels of the fruit fly *Bactrocera zonata* (Saunders) were positively correlated with maximum and minimum temperatures and rainfall and were negatively correlated with relative humidity.

Approximately 10,000 traps are inspected for flies every 2 wk in the PRP area (CDFA 2001a). Traps are frequently relocated to ensure that they are hung in host plants containing mature fruit. Several researchers have investigated the relationship between host plant and fly recapture. Using bait attractants, Wong et al. (1985) found higher Mediterranean fruit fly recapture rates in host plants than in nonhost plants, and identified the primary fly attractant to be the host tree, whereas bait attractant was secondary. Buyckx (1994) found that Mediterranean fruit fly distribution was better explained by host plant distribution than by prevailing wind patterns in northwestern Africa. If sterile flies are assumed to behave in a similar manner as their wild counterparts, then after mass release, sterile male flies should ultimately search for suitable host plants, perhaps after finding adequate shelter and food sources.

The objective of this study was to determine how climate and host plants with fruit (in which traps were placed) relate to the number of sterile Mediterranean fruit flies recaptured in traps. The results may provide information that can be used to develop models useful in predicting the fate of released SIT flies. The importance of host plants with acceptable fruit is discussed in relation to the use of trap deployment patterns to delineate future infestations of introduced Mediterranean fruit flies.

Materials and Methods

Between September 1998 and August 2001, sterile flies were released in southern California at a density of 96,528 flies per km^2 per wk over an area of 6,446 km^2 (CDFA 2001a). Sterile flies were chilled, loaded into an aerial release box, and released from a twin engine Beech aircraft, which flew 260 km/h at an altitude of 600 m, by using a computerized navigation guidance system based on a global positioning system. Ten trapping locations (2.59 km^2 each) were selected for analysis. These locations were all within a 40-km^2 area (Pomona, Glendale, and Claremont, Los Angeles County, CA).

Data Collection. Trapping records were obtained from the Los Angeles County Agricultural Commissioner's Field Office in Irwindale, CA. Jackson traps baited with trimedlure (Magnet 70-0 plug, 2 g of active material; Agrisense, Decatur, IL; plugs changed every 3 wk) were used to monitor flies. Each trapping area contained five traps (except one area that contained four) that were checked at 2-wk intervals and were relocated at 6 wk intervals. Each trap examined that contained at least one fly was assigned to one of five fly recapture levels (1, 1–14 flies caught; 2, 15–41; 3, 42–100; 4, 101–199; and 5, 200+; $n = 3{,}177$). To simplify the statistical analyses, traps containing no flies (≈0.5% of traps) were not included in the data set. Data were obtained from the South Coastal District Field Office for the USDA/CDFA Cooperative Preventative Release Program in Bell, CA.

The following assumptions were made: 1) flies were distributed frequently and randomly over all trapping areas for the duration of the study so that the total numbers of flies released did not differ between trapping periods; and 2) flies released on different days were comparable in quality (i.e., survivorship and flight ability).

Fly Recapture and Climate. Daily data for four climate variables: precipitation, maximum temperature, average relative humidity, and average solar radiation, were obtained from the California Irrigation Management Information System (CIMIS) weather station #78 in Pomona, Los Angeles County, CA, and were averaged over each trapping period (the backup station used for missing data was #82 in Claremont, Los Angeles County, CA) (CIMIS 2001).

The model of choice for data analysis of all four climatic variables (temperature, precipitation, relative humidity, and solar radiation) was ordinal logistic regression, because the number of flies recaptured was recorded as an ordinal variable (SAS Institute 1999). Ordinal logistic regression relates the probabilities $\gamma_k = P(Y \geq k)$ to the independent variables $X = (X_1, X_2, \ldots X_p)$ via the relation $\ln(\gamma_k/1 - \gamma_k)) = \beta_{0k} + \beta_1 * X_1 + \ldots \beta_p * X_p$ (McCullagh and Nelder 1989). The function on the left side of the equation is the logit function applied to γ_k. Note that the equation requires that the slope parameters β_j be constant across $_k$, and only the intercept β_{0k} is allowed to change.

A binary variable, Y, represented different groupings of the five ordinal recapture levels (i.e., 1–5). The proportion of data points for each interval was determined, with $Y = 1$ when the recapture level was ≥2 (and $Y = 0$ when recapture level <2) and was plotted versus the midpoint of the interval, for all the days on which the average daily maximum temperature or precipitation was within that interval (S-PLUS, Insightful Corp., Seattle, WA). These analyses also were performed with $Y = 1$ when the recapture level was ≥3, 4, and 5 for both temperature and precipitation. A total of 3,177 trap records with the associated temperature and precipitation data were included in each analysis. Logit plots of $\ln(\gamma_1/(1 - \gamma_1))$ and $\ln(\gamma_4/(1 - \gamma_4))$ versus temperature were generated that corresponded to the lowest and highest proportional trap recapture plots of temperature.

Two of the four climatic variables, precipitation and temperature, were chosen for separate analyses versus recapture levels to determine what limitations, if any, were present in the data set. Average daily precipitation values, corresponding with the interval a trap was deployed, were grouped into eleven 0.04-cm intervals, ranging from 0 to 0.44 cm, and average maximum temperature data were grouped into twelve 2°C intervals, ranging from 13 to 37°C.

The relationships between climate variables (precipitation, maximum temperature, average relative

Table 1. Analysis of climate max likelihood estimates for the logistic regression

Parameter	df	Estimate	SE	χ^2	Pr > χ^2
Intercept	1	0.1903	0.4518	0.1774	0.6736
Intercept2	1	1.6127	0.4507	12.8038	0.0003
Intercept3	1	2.9847	0.4533	43.3542	<0.0001
Intercept4	1	4.1117	0.4562	81.237	<0.0001
Maximum temp	1	−0.0483	0.0123	15.3233	<0.0001
Relative humidity	1	−0.0212	0.00503	17.8311	<0.0001
Precipitation	1	2.8199	0.2939	92.0476	<0.0001
Solar radiation	1	0.000235	0.000375	0.3910	0.5318

n = 3,177.

humidity, and average solar radiation) were analyzed using a correlation test to determine the Pearson product moment correlation coefficient (n = 1,096) (Minitab Inc. 2000).

Fly Recapture and Host Plant. A logistic regression was not used for analysis, because the independent variable (host plant) was categorical and instead, analysis was performed using a χ^2 contingency table. Analysis was conducted on a subset of the trapping records (n = 2,829). Excluded were hosts used less frequently ($n < 50$) and unknown hosts (n = 348). The following hosts were included in analyses: apple, *Malus sylvestris* Mill.; apricot, *Prunus armeniaca* L.; calamondin, *Citrofortunella mitis* (Blanco); fig, *Ficus carica* L.; guava, *Psidium guajava* L.; kumquat, *Fortunella* spp.; loquat, *Eriobotrya japonica* (Thunb.); nectarine, *Prunus persica* (L.) cultivar *nectarina;* orange, *Citrus sinensis* (L.); peach, *Prunus persica* (L.); persimmon, *Diospryos decandra* Lour.; and tangerine, *Citrus reticulata* Blanco. It was recognized that host plants were not randomly used with respect to time of year (CDFA 2001b), so significance could be a result of the environment, environment–host interaction, or host.

Results

Fly Recapture and Climate. The model for climate had a significant likelihood ratio (χ^2 = 243.91, df = 4, Pr > χ^2 = < 0.0001). Precipitation, maximum temperature, and relative humidity significantly affected fly recapture (Table 1). Intermediate temperatures (Fig. 1), intermediate relative humidity (Fig. 2), and lower amounts of precipitation (Fig. 3) were associated with higher recapture levels. Solar radiation did not significantly affect trap recapture, even though a direct relationship was suggested (Fig. 4).

The relationship between recapture levels and precipitation seemed to be similar in each comparison of recapture levels, with the suggestion of a general linear relationship (Fig. 5). The proportions and precipitation seemed negatively related, indicating that the number of flies recaptured decreased as precipitation increased. Proportions were equal to zero for several intervals of precipitation, 0.28–0.32 and 0.36–0.40 cm, because there were no trap records with those conditions. Above the 0.28-cm interval there were only two 2-wk trapping periods that had an average precipitation reading above 0.28 cm, with trap counts at five locations for both time periods. The average precipitation for these trapping periods was 0.34 and 0.41 cm. These two readings did not support the decreasing trend (Fig. 5d).

The relationship between recapture levels and temperature was not uniform in each comparison, but overall as temperature increased, the proportion also increased (Fig. 6). The relationship between temperature and recapture varied from exponential (Fig. 6a), to polynomial-like (Fig. 6b and c), and even quartic

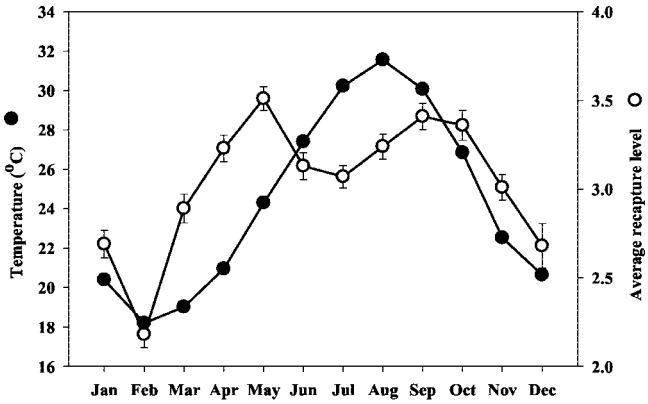

Fig. 1. Temperature (average daily high for each month) and average fly recapture level (per trapping interval) for all host plants (mean ± SE) by month for September 1998 to August 2001 (fly recapture levels: 1, 1–14 flies caught; 2, 15–41; 3, 42–100; 4, 101–199; and 5, 200+) (temperature, n = 1,096; fly recapture, n = 2,829).

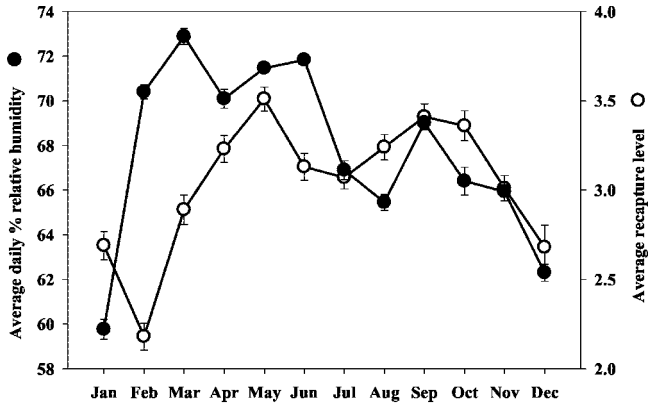

Fig. 2. Percentage of relative humidity (average daily value for each month) and average fly recapture level (per trapping interval) for all host plants (mean ± SE) by month for September 1998 to August 2001 (fly recapture levels: 1, 1–14 flies caught; 2, 15–41; 3, 42–100; 4, 101–199; and 5, 200+) (percentage of relative humidity, n = 1,096; fly recapture, n = 2,829).

(Fig. 6d). Logit plots of $\ln(\gamma_1/(1-\gamma_1))$ and $\ln(\gamma_4/(1-\gamma_4))$ versus temperature, resulted in plots that seemed quadratic and quartic (Fig. 7a and b, respectively; compare with Fig. 6a and d).

The four climatic predictors were all significantly correlated to each other (Table 2). Temperature was negatively correlated with relative humidity and precipitation and positively correlated with solar radiation; relative humidity was negatively correlated with solar radiation and positively correlated with precipitation; and precipitation was negatively correlated with solar radiation.

Fly Recapture and Host Plant. Placement of traps in different types of host plants, which were not used equally throughout the year, had a significant effect on the number of flies recaptured (χ^2 = 204.87, df = 44, $P < 0.0001$). Jackson traps were placed in 12 types of plants with $n > 50$. The host plants with the three highest average recapture levels were fig, nectarine, and loquat; and the three lowest were orange, kumquat, and calamondin. The usage patterns of different host plants for trap placement varied throughout the year, based on the presence of suitable fruit (Table 3).

Discussion

The number of flies recaptured after a sterile fly release was influenced by climate and the type of fruiting host plants that were present. Results of this study are not immediately comparable with many other studies using traps to assess tephritids, because in the current study flies were released continuously. This is an important distinction. In addition, none of the released flies were adapted to the environment into which they were released. One would expect to make recapture predictions, better than at random, if critical factors affecting fly quality and environmental conditions were known. Further discussion may help explain some of the observed results; others are left to speculation.

Climate. In general, higher temperatures were associated with higher fly recaptures. However, during the summer, when temperatures were highest, lower recapture levels were observed (Fig. 1), and this is likely the result of higher fly mortality (at this time of the year) (J.D.B., unpublished data). In other studies, elevated temperatures resulted in reduced fly activity

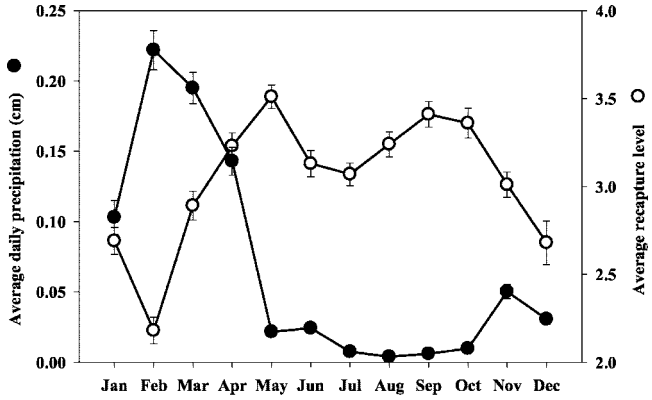

Fig. 3. Precipitation (average daily value for each month) and average fly recapture level (per trapping interval) for all host plants (mean ± SE) by month for September 1998 to August 2001 (fly recapture levels: 1, 1–14 flies caught; 2, 15–41; 3, 42–100; 4, 101–199; and 5, 200+) (precipitation, n = 36; fly recapture, n = 2,829).

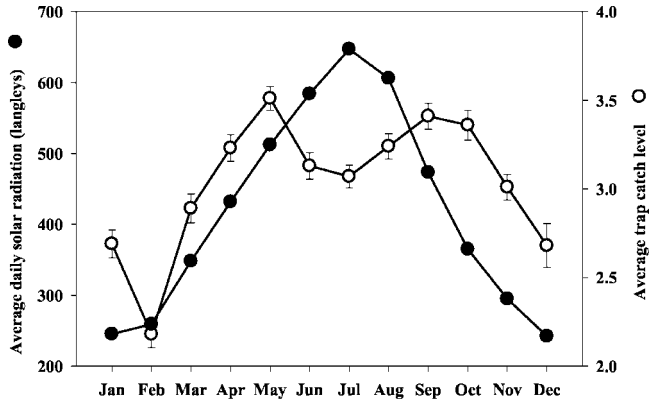

Fig. 4. Solar radiation (average daily value for each month) and average fly recapture level (per trapping interval) for all host plants (mean ± SE) by month for September 1998 to August 2001 (fly recapture levels: 1, 1–14 flies caught; 2, 15–41; 3, 42–100; 4, 101–199; and 5, 200+) (solar radiation, n = 1,096; fly recapture, n = 2,829).

(Prokopy et al. 1987), with flies shifting activity to cooler areas (Hendrichs and Hendrichs 1990) and periods during the day (Cayol 1996). In addition to fly mortality, the observed relationship between recapture and climate could be the result of changes in fly behavior to the trap attractant. Fitt (1981) found that *Dacus opiliae* Drew & Hardy responded differently to the same traps at different times of the year; relative humidity was suggested as a possible key influence, because three times as many males responded to traps in the wetter months compared with dryer months. Furthermore, the release rate of trimedlure would likely vary with relative humidity and temperature. For example, at lower temperatures, reduced recap-

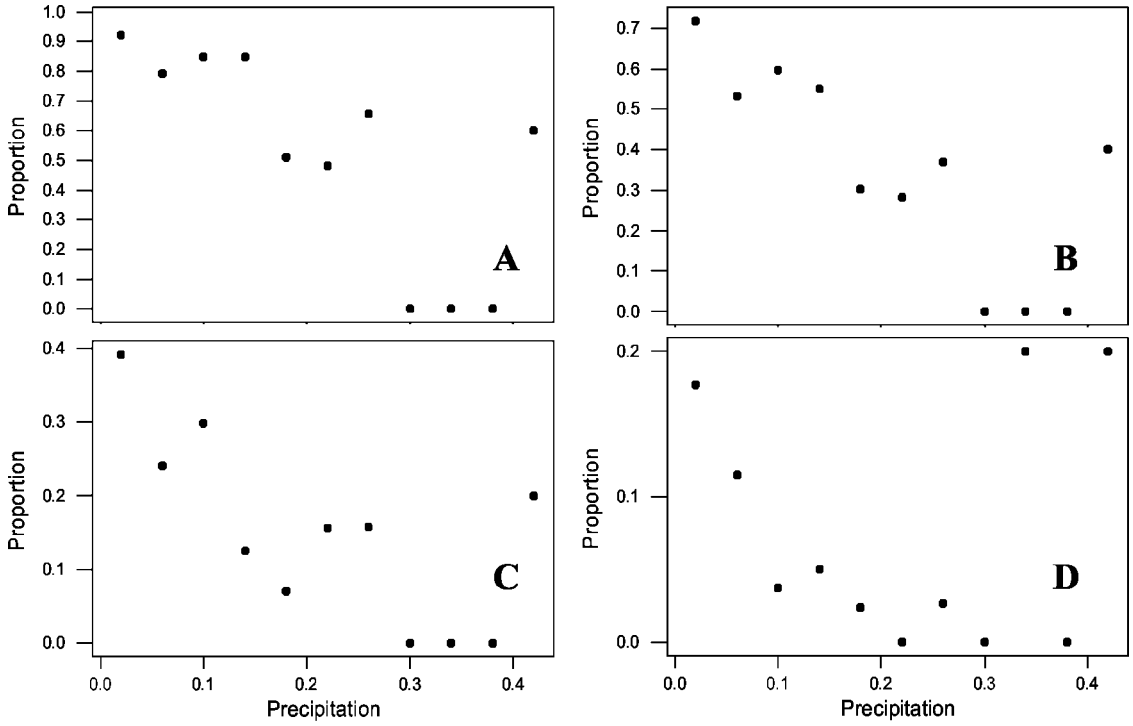

Fig. 5. Relationship between fly recapture and temperature is displayed as a proportion. Figures were constructed using a binary variable, Y, representing five ordinal recapture levels: 1, 1–14 flies; 2, 15–41; 3, 42–100; 4, 101–199; and 5, 200+. (a) Y was equal to 1 when the recapture level was ≥2 (i.e., when it was 2, 3, 4, or 5), and Y was equal to 0 when the recapture level was <2 (i.e., when it was 1). Likewise, in b, c, and d, Y was equal to 1 when the recapture level was ≥3, 4, and 5, respectively. In total, 3,177 recapture records were used to construct the figures.

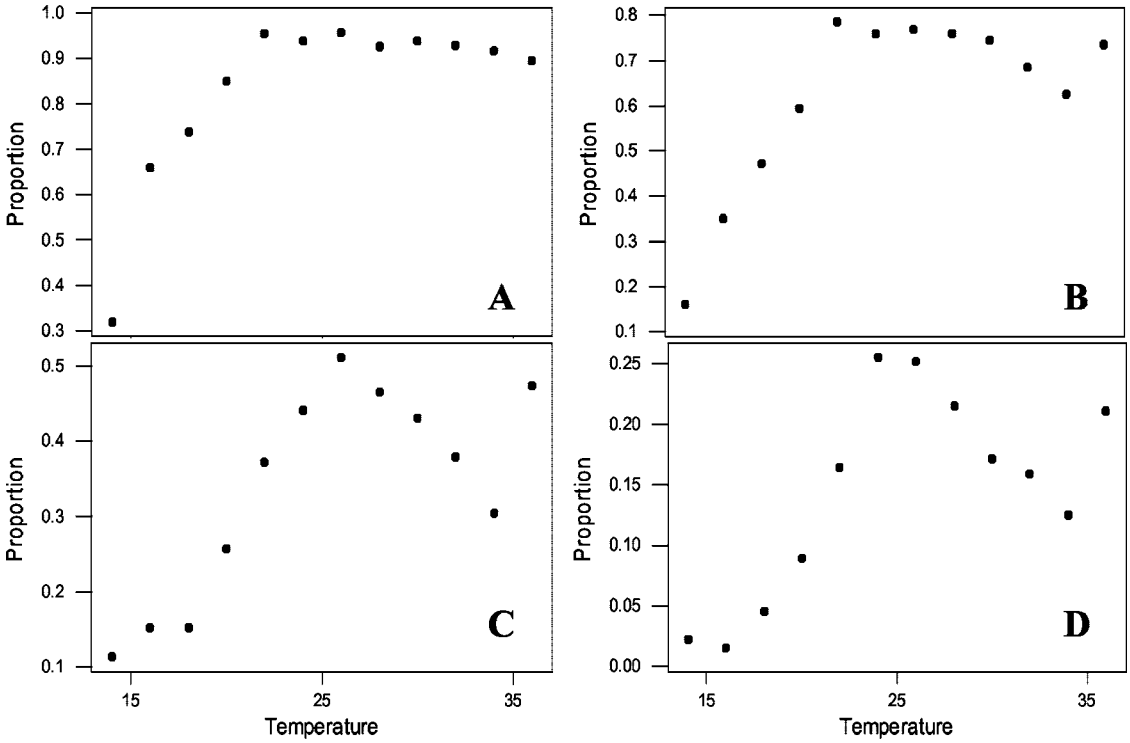

Fig. 6. Relationship between fly recapture and precipitation is displayed as a proportion. Figures were constructed using a binary variable, *Y*, representing five ordinal recapture levels: 1, 1–14 flies; 2, 15–41; 3, 42–100; 4, 101–199; and 5, 200+. (a) *Y* was equal to 1 when the recapture level was ≥2 (i.e., when it was 2, 3, or 4), and *Y* was equal to 0 when the recapture level was <2 (i.e., when it was 1). Likewise, in b, c, and d, *Y* was equal to 1 when the recapture level was ≥3, 4, and 5, respectively. In total, 3,177 recapture records were used to construct the figures.

ture may be associated with a lower release rate of trimedlure, whereas at higher temperatures the release rate may be higher than is optimal.

The proportions plotted in Fig. 5 are estimates of $\gamma 1 - \gamma 4$, at their respective temperatures. To perform an ordinal logistic regression on these data, $\ln(\gamma k/(1 - \gamma k))$ should behave similarly for each *k*, except at the intercepts (McCullagh and Nelder 1989). The logit plots (Fig. 7a and b) differ from each other in the same way that the corresponding proportion plots (Fig. 5a and d) differ from each other. (This was expected, because $\ln(x/(1 - x))$ is an increasing function of *x*.) The differences were less severe for the logit case; however, the assumption of constant slope parameters is not valid, and thus ordinal logistic regression is an implausible model.

Fly recapture could be treated as nominal, with a binary logistic regression performed for each category against a base category. However, it is important to include other variables (i.e., precipitation, solar radiation, and relative humidity) in an analysis, because they may have a significant affect on fly recapture. In addition, there could likely be significant correlation between variables. Future experimentation might use a response variable that was either quantitative or one with more ordinal categories. A normal regression analysis on the data could be performed if there were sufficient categories (i.e., 10–15) to allow recapture to be treated as a quantitative variable.

There may be confounding factors that increased the effect of precipitation on recapture. Although infrequent, precipitation often delayed aerial releases and as a result, flights in the affected trapping area were often missed for several days. Higher populations of wild Mediterranean fruit flies have been associated with dry weather periods (Hedstrom 1993), and this

Table 2. Correlation between climatic variables used in this analysis

Effect entered[a]	Precipitation	Temperature (max)	Relative humidity
Solar radiation	−0.243, $P < 0.0001$	0.745, $P < 0.0001$	−0.206, $P < 0.0001$
Relative humidity	0.229, $P < 0.0001$	−0.452, $P < 0.0001$	
Temperature (max)	−0.295, $P < 0.0001$		

[a] n = 1,096 for each variable [data are from CIMIS (2001) for Sept. 1998 to August 2001].

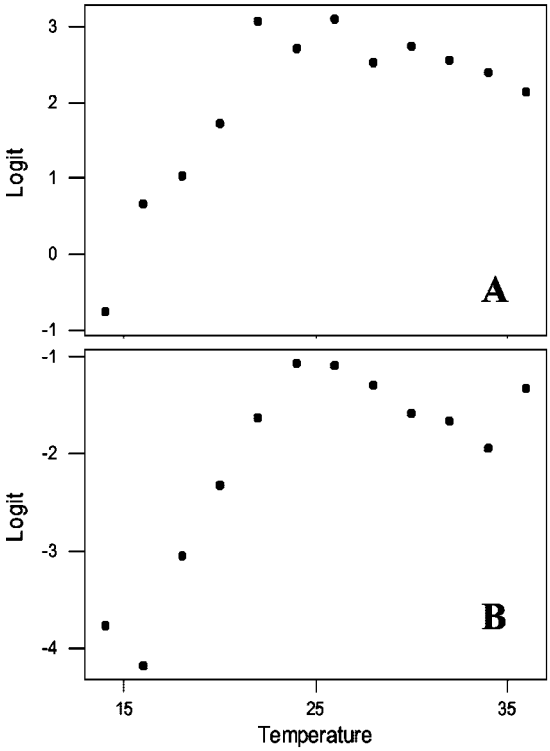

Fig. 7. Relationship between fly recapture and temperature is displayed as the logit or the log of the proportion. Figures were constructed using a binary variable, *Y*, representing five ordinal recapture levels: 1, 1–14 flies; 2, 15–41; 3, 42–100; 4, 101–199; and 5, 200+. (a) *Y* was equal to 1 when the recapture level was ≥2 and in b, *Y* was equal to 1 when the recapture level was ≥5. a and b correspond to the logit of Fig. 6a and d, respectively. In total, 3,177 recapture records were used to construct the figures.

species is known to prefer drier climates (Harris and Lee 1987, Harris and Lee 1989, Harris et al. 1993, Borge and Basedow 1997). Baker and van der Valk (1992) did not find that precipitation depressed fly recapture levels in an SIT program near Tapachula, Mexico. Data from the current study suggested that lower recapture rates could be the result of decreased fly activity. Although precipitation was an important factor, it is uncommon during most of the year in southern California and thus, other factors must play an importance role in determining fly recapture levels.

Solar radiation did not show a significant effect in this study, even though a positive correlation with fly recapture was suggested (Fig. 4) and solar radiation was highly correlated with temperature (Table 2), which did have a significant effect. The inclusion of solar radiation in the logistic regression may not have resulted in significance because of the inclusion of temperature in the model. Within a season, periods with higher sunlight (or lower cloud cover) are associated with higher amounts of solar radiation. Sunlight has been found to influence lek formation location (Whittier et al. 1992, Kaspi and Yuval 1999) and feeding activity (Hendrichs and Hendrichs 1990).

Future research should investigate which variables to include in future model iterations and whether some variables should be excluded for certain periods (i.e., perhaps precipitation should be excluded as a predictor during the summer).

Host Plant Species. It is difficult to separate the effects of host plant and recapture in this study, because plants were used only when fruit known to be attractive to the Mediterranean fruit fly were present (with the dual and perhaps more critical objective of maximizing the potential for trapping any wild flies that were present). The importance of suitable host fruit has been used to effectively explain population dynamics of Mediterranean fruit flies (Israely et al. 1997), *Anastrepha* spp. (Celedonio-Hurtado et al. 1995), and *Dacus* spp. (Drew et al. 1984). However, in our study, the recaptured flies had been released into the area and were not adapted to the host plant cycles as was the case in the studies with wild flies. Thus, it

Table 3. Frequency of host plant use by month

Host plant	Month of study[a]												No. traps
	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	
Apple	5.9	2.4	0.0	0.0	0.0	0.0	2.4	16.5	31.8	29.4	9.4	2.4	85
Apricot	0.0	0.0	0.0	5.6	32.0	46.6	14.1	0.9	0.6	0.3	0.0	0.0	341
Calamondin	30.2	24.5	13.2	1.9	3.8	0.0	0.0	0.0	0.0	1.9	11.3	13.2	53
Fig	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.7	35.8	41.5	17.0	0.0	53
Guava	8.5	3.6	0.9	0.9	0.4	0.0	0.0	0.4	4.5	25.0	42.9	12.9	224
Kumquat	19.2	23.8	16.2	10.8	3.8	0.8	0.0	0.0	5.4	7.7	7.7	4.6	130
Loquat	0.0	0.3	12.4	41.9	38.1	6.3	0.0	0.0	0.0	0.3	0.6	0.0	315
Nectarine	2.3	1.1	2.3	1.1	4.5	13.6	36.4	31.8	6.8	0.0	0.0	0.0	88
Orange	19.3	21.2	22.2	12.1	3.0	0.6	0.6	0.8	1.5	2.3	7.6	8.9	528
Peach	0.0	0.0	0.0	0.5	2.7	8.8	29.1	27.9	23.8	5.6	1.4	0.1	735
Persimmon	1.4	0.0	0.0	0.0	0.0	0.0	0.0	1.4	15.7	48.6	30.0	2.9	70
Tangerine	25.6	25.1	16.9	15.0	3.9	1.4	0.0	1.0	0.5	0.5	4.3	5.8	85
Misc.	10.3	12.1	8.0	8.0	2.6	4.6	4.9	6.6	13.2	12.4	11.8	5.5	348
No. traps	259	262	251	296	294	279	316	284	312	247	252	125	3,177

Traps collected before the eighth day of a month were grouped with the previous month. Trapping information included in this table was from traps deployed during September 1998 to August 2001. Five traps were placed in each of ten 2.59-km^2 trapping areas (except one with four traps), located within an area of 40 km^2 in Pomona, Glendale, and Claremont, Los Angeles County, CA.

[a] Values for all months within a row sum to 100%.

was not expected a priori that a strong relationship would be found between host plant and recapture. Host plants that were used were assumed to be the best location for a trap at that given time, even if they were located in a less preferred host plant. However, Mediterranean fruit flies are polyphagous and opportunistic pests, and these data suggest that at times when there were few preferred host plants present that were acceptable, flies were able to locate less preferred host plants that contained a trap.

The above-mentioned finding has several implications for delineating infestations. After a wild fly has been located, delimitation traps are placed to determine the extent of the infestation. To increase trap efficiency, Mangel et al. (1984) suggested placing traps along an outer border or in a cross pattern, instead of spacing traps evenly on a grid. Our results suggest that traps should be placed in host plants with acceptable fruit. Therefore, an optimized trap placement pattern may involve scouting for plants with suitable host fruit and then determining whether to use a border or cross trap pattern or placement. In some instances, the location of host fruit may result in favoring an alternative trap pattern.

A number of variables that could influence fly recapture were not known and thus were not included in the analysis (i.e., the trap inspector who chose trap location; location of the trap within the host plant, including height, foliage cover, and proximity to fruit; information about the host plant: size, quality of fruit present, proximity to other fruit trees). Israely et al. (1997) showed that trap orientation within a tree and the degree of canopy cover associated with the trap did not significantly affect fly capture. Factors that were not observed to be significant in this study are not necessarily of lower value to the overall PRP program, because they may be indicative of other conditions or qualities (i.e., mating success, activity, and survivorship) important in understanding potential SIT–wild Mediterranean fruit fly interactions. Given the massive size of the current database, which continues to grow daily, a future study of this magnitude may not occur soon; however, when it does, in the results of this study may assist in such an analysis.

Acknowledgments

We thank the late David Rumsey, Eileen Smith, Kevin Hoffman, Robert Dowell, Rufino Santos, Bob Garagliano, David Falcon, Eddie Serrato, Charlie Bernhardt, Ian McKellan, Mary Nolan, and many other personnel from the USDA/CDFA Cooperative Mediterranean fruit fly Preventative Release Program for valuable assistance, resources, support, and access to physical facilities in Los Alamitos, and Bell, CA; and R. D. Goeden and T. M. Perring for reviewing an earlier version of this manuscript. This research was funded in part by the California Citrus Research Board and by the California Department of Food and Agriculture and forms part of the Ph.D. dissertation of J.D.B.

References Cited

Agarwal, M. L., and P. Kumar. 1999. Effect of weather parameters on population dynamics of peach fruit fly, *Bactrocera zonata* (Saunders). Entomon 24: 81–84.

Aguiar-Menezes, E. L., and E. B. Menezes. 1996. Population fluctuation of the fruit flies and its relationship to host availability in Itaguai, RJ. Ann. Soc. Entomol. Brasil 25: 223–232.

Baker, P. S., and H. van der Valk. 1992. Distribution and behaviour of sterile Mediterranean fruit flies in a host tree. J. Appl. Entomol. 114: 67–76.

Borge, M. N., and T. Basedow. 1997. A survey on the occurrence and flight periods of fruit fly species (Diptera: Tephritidae) in a fruit growing area in southwest Nicaragua, 1994/95. Bull. Entomol. Res. 87: 405–412.

Buyckx, E. J. 1994. Bioclimatic effects on the distribution of the Mediterranean fruit fly (Diptera: Tephritidae) in the Maghreb, pp. 139–164. *In* P. Liedo [ed.], Fruit flies and the sterile insect technique. CRC, Boca Raton, FL.

Cayol, J. P. 1996. Box thorn, key early season host of the Mediterranean fruit fly. Int. J. Pest Manage. 42: 325–329.

[CDFA] California Department of Food and Agriculture. 2001a. Mediterranean fruit fly preventative release program: report to the legislature. Calif. Dep. of Food & Agriculture: Plant Health & Pest Prevention Services, Sacramento, CA.

[CDFA] California Department of Food and Agriculture. 2001b. CDFA trapping manual. Calif. Dep. of Food & Agriculture: Plant Health & Pest Prevention Services, Sacramento, CA.

Celedonio-Hurtado, H., M. Aluja, and P. Liedo. 1995. Adult population fluctuations of *Anastrepha* species (Diptera: Tephritidae) in tropical orchard habitats of Chiapas, Mexico. Environ. Entomol. 24: 861–869.

[CIMIS] California Irrigation Management Information System. 2001. California irrigation management information system. Calif. Dep. of Water Resources, Office of Water Use Efficiency, Sacramento, CA.

Drew, R.A.I., M. P. Zalucki, and G.H.S. Hooper. 1984. Ecological studies of eastern Australian fruit flies (Diptera: Tephritidae) in their endemic habitat. I. Temporal variation in abundance. Oecologia (Berl.). 64: 267–272.

Eskafi, F. M., and M. E. Kolbe. 1990. Infestation patterns of commonly cultivated, edible fruit species by *Ceratitis capitata* and *Anastrepha* spp. (Diptera: Tephritidae) in Guatemala and their relationship to environmental factors. Environ. Entomol. 19: 1371–1380.

Fitt, G. P. 1981. Ecology of Northern Australian Dacinae (Diptera; Tephritidae). II. Seasonal fluctuation in trap catches of *Dacus opiliae* and *D. tenufascia* and their relationship to host phenology and climatic factors. Austr. J. Zool. 29: 885–894.

Harris, E. J., and C.Y.L. Lee. 1986. Seasonal and annual occurrence of Mediterranean fruit flies [*Ceratitis capitata*] (Diptera: Tephritidae) in Makaha and Waianae Valleys, Oahu, Hawaii. Environ. Entomol. 15: 507–512.

Harris, E. J., and C.Y.L. Lee. 1987. Seasonal and annual distribution of the Mediterranean fruit fly (Diptera: Tephritidae) in Honolulu and suburban areas of Oahu Hawaii. Environ. Entomol. 16: 1273–1282.

Harris, E. J., and C. Y. Lee. 1989. Development of *Ceratitis capitata* (Diptera: Tephritidae) in coffee in wet and dry habitats. Environ. Entomol. 18: 1042–1049.

Harris, E. J., R. I. Vargas, and J. E. Gilmore. 1993. Seasonality in occurrence and distribution of Mediterranean fruit fly (Diptera: Tephritidae) in upland and lowland areas on Kauai, Hawaii. Environ. Entomol. 22: 404–410.

Hedstrom, I. 1993. Population dynamics and host relationships of neotropical fruit flies (Diptera: Tephritidae) in seasonal and non-seasonal environments. Int. J. Pest Manage. 39: 400–410.

Hendrichs, J., and M. A. Hendrichs. 1990. Mediterranean fruit fly (Diptera: Tephritidae) in nature: location and diel pattern of feeding and other activities on fruiting and nonfruiting hosts and nonhosts. Ann. Entomol. Soc. Am. 83: 632–641.

Israely, N., B. Yuval, U. Kitron, and D. Nestel. 1997. Population fluctuations of adult Mediterranean fruit flies (Diptera: Tephritidae) in a Mediterranean heterogeneous agricultural region. Environ. Entomol. 26: 1263–1269.

Kaspi, R., and B. Yuval. 1999. Mediterranean fruit fly leks: factors affecting male location. Funct. Ecol. 13: 539–545.

Katsoyannos, B. I., N. A. Kouloussis, and J. R. Carey. 1998. Seasonal and annual occurrence of Mediterranean fruit flies (Diptera: Tephritidae) on Chios Island, Greece: differences between two neighboring citrus orchards. Ann. Entomol. Soc. Am. 91: 43–51.

Mangel, M., R. E. Plant, and J. R. Carey. 1984. Rapid delimiting of pest infestations: a case study of the Mediterranean fruit fly. J. Appl. Ecol. 21: 563–579.

McCullagh, P., and J. A. Nelder. 1989. Generalized linear models, 2nd ed. CRC, Boca Raton, FL.

Minitab Inc. 2000. Minitab statistical software, version 13. Minitab Inc., State College, PA.

Nishida, T., E. J. Harris, R. I. Vargas, and T.T.Y. Wong. 1985. Distributional loci and host fruit utilization patterns of the Mediterranean fruit fly, *Ceratitis capitata* (Diptera: Tephritidae), in Hawaii. Environ. Entomol. 14: 602–606.

Prokopy, R. J., D. R. Papaj, S. B. Opp, and T.T.Y. Wong. 1987. Intra-tree foraging behavior of *Ceratitis capitata* flies in relation to host fruit density and quality. Entomol. Exp. Appl. 45: 251–258.

SAS Institute. 1999. User's manual, version 8.0. SAS Institute, Cary, NC.

Siebert, J. B. 1999. Update on the economic impact of the Mediterranean fruit fly on California Agriculture. Univ. of California Report, Oakland, CA.

Siebert, J. B., and V. Pradhan. 1991. The potential impact of the Mediterranean fruit fly, *Ceratitis captitata* (Wied.), upon establishment in California: an update. Univ. California Dep. of Agriculture & Resource Economics, Berkeley, CA.

Siebert, J. B., and T. Cooper. 1995. Embargo on California produce would cause revenue, job loss. Calif. Agric. 49: 7–12.

Whittier, T. S., K. Y. Kaneshiro, and L. D. Prescott. 1992. Mating behavior of Mediterranean fruit flies (Diptera: Tephritidae) in a natural environment. Ann. Entomol. Soc. Am. 85: 214–218.

Wong, T.T.Y., D. O. McInnis, R. M. Kobayashi, and J. I. Nishimoto. 1985. Distribution and seasonal abundance of adult male Mediterranean fruit flies (*Ceratitis capitata*) (Diptera: Tephritidae) in Kula, Maui, Hawaii. J. Econ. Entomol. 78: 552–557.

Received 11 November 2003; accepted 28 April 2004.