Release-Recapture of Sterile Male Mediterranean Fruit Flies (Diptera: Tephritidae) in Southern California

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Abstract. A key determinant to the success of the Sterile Insect Technique (SIT) against the Mediterranean fruit fly (medfly), *Ceratitis capitata* (Wiedemann), is an even spatial distribution of sterile males following their release. While numerous studies have measured medfly dispersal, these almost always involve ground releases, whereas large-scale SIT programs release sterile males from small aircraft. The objective of the present study was to describe dispersal of sterile *C. capitata* males following aerial release in an urban area of southern California included in an ongoing SIT program. At present, adjacent flight paths are spaced 268 m apart (six flight lanes per 1.61 km [1 mi]), but in the face of potential budget cuts, flights may be reduced, which could result in increased distances between adjacent flight paths. We undertook this study to assess whether flight reduction might jeopardize the SIT program's ability to achieve adequate ground coverage by sterile males. Dispersal of sterile males was monitored following four release flights made along a single 96.6 km east-west path between June 2011 and February 2012. Data were gathered using traps located along six transects established perpendicularly to the flight path as well as detection traps routinely monitored as part of the management program. Data showed that (i) most males were captured within 268 m of the release line, although some males traveled > 1 km, (ii) there was a higher number of captures north of the release line, (iii) most males were captured within 3 d of release, although, compared to other studies, a large proportion (15%) were captured ≥ 7 d after release. We discuss the implications of these findings and conclude that four flight lanes per 1.61 km would allow adequate coverage in the southern California SIT program.

Key words: Sterile Insect Technique, Preventative Release Program, pest management, invasive fruit flies

Introduction

The Sterile Insect Technique (SIT) is widely used to suppress or eradicate invasive populations of the Mediterranean fruit fly (medfly), *Ceratitis capitata* (Wiedemann), a polyphagous pest that attacks a great diversity of agricultural crops (Enkerlin 2005). An environmentally benign management tool, SIT involves the mass production, sterilization, and release of medfly males into the environment, with the aim of achieving sterile male by wild female matings. The eggs resulting from such crosses do not hatch, which leads to a reduced growth rate of the invading population. The success of medfly SIT hinges on several key components, including the sexual competitiveness and the vitality or survivorship of the released males (Caceres et al. 2007).

Another important element involves the spatial distribution of sterile *C. capitata* males following release. The maximum effectiveness of the SIT is presumably realized when sterile males are distributed evenly in the environment, and no areas are completely devoid of released flies (Meats and Edgerton 2008). Obviously, the release method is a key determinant, and given the relatively low dispersal of male medflies (see below), roving ground releases (Cunningham et al. 1980, Salvato et al. 2003) or aerial releases result in a more even distribution than do point releases (Nadel et al. 1967, Howell et al. 1975). In addition, the inherent tendency for movement displayed by *C. capitata* males influences their post-release spacing. Numerous studies (Wong et al. 1982, Cunningham and Couey 1986, Baker et al. 1986, Baker and Chan 1991, Plant and Cunningham 1991, Lance and Gates 1994, Barry et al. 2002, Meats and Smallridge 2007, Paranhos et al. 2010, Gavriel et al. 2011) have measured the dispersal capability of sterile male medflies following ground releases, and these typically show most males travel relatively short distances (< 400 m) with a small proportion traveling as far as several km. For example, working in southern California, Barry et al. (2002) reported that approximately 70% of ground released sterile males were captured within 100 m of their release point and only about 3% were found over 300 m from the release point. A second common finding of these studies is that the great majority of recaptures occur within several days of release, typically within 3–5 d of release. Again, Barry et al.'s (2002) results are typical: nearly 90% of released sterile medfly males were found within the first 3 d of release, and < 10% were recovered > 7 d after release.

As noted, the aforementioned studies involved ground releases, and in contrast very little data exist regarding dispersal of sterile *C. capitata* males following release from aircraft. To our knowledge, only Vargas et al. (1995) have gathered such data. In their main experiment, sterile medflies were released in a Hawaiian coffee field from a low-flying (30 m altitude) helicopter, and their dispersal was monitored by capturing males in trimedlure-baited traps placed in lines perpendicular to the release axis. Trimedlure (TML hereafter) is a male-specific attractant for *Ceratitis* spp. (Mwatawala et al. 2012). Traps were placed 50 m apart to a distance of 300 m on either side of the release path. Results showed that (i) the great majority (> 90%) of sterile *C. capitata* males were found within 100 m of the release path, (ii) few males dispersed more than 300 m, and (iii) very few males (< 10%) were captured ≥ 5 d after release. In an ancillary project, Vargas et al. (1995) compared medfly dispersion following release from a helicopter versus a small airplane and found that flies dropped from the airplane dispersed farther than those dropped from the helicopter, though most airplane-released males were still found within 200 m of the release line. The authors attribute this difference in dispersal to the greater release altitude used for the airplane (120 m), which increased the effect of wind on "fly drift" after release. A second study (Shelly et al. 2006) involving aerial release (small airplane, release altitude 600–800 m) of sterile male medflies in Florida similarly found that most recaptures were made within 5 d of release (no data on dispersal distance were reported in this study).

The objective of the present study was to describe dispersal of sterile *C. capitata* males upon release from airplanes in an urban area of southern California included in an ongoing SIT program. Since 1996, the California Department of Food and Agriculture (CDFA) has continually operated a Preventative Release Program (PRP) against the medfly in the Los Angeles Basin and surrounding areas (Dowell et al. 2000). Currently, releases are made over an area of approximately 6,400 km^2 (2,500 mi^2), which is divided into 2.6 km^2 grids (1 mi^2) (IPRFFSP 2006). At present, a particular grid receives two releases per week (approximately 62,500 males per grid per week) along six flight paths spaced 268 m apart (i.e., 1.61 km/6 or 1 mi/6 = 880 ft), with the successive (within-week) releases alternated between adjacent flight paths (i.e., release 1 along paths 1, 3, and 5, and release 2 along paths 2, 4, and 6). In the face of potential budget cuts, however, the PRP may need to reduce the number of release flights per grid, which could result in increased distances between adjacent flight paths. As a result, we undertook this study to assess whether a proposed flight reduction to 4/mi (402 m between adjacent flight paths) might jeopardize the program's ability to achieve adequate ground coverage by sterile males.

Materials and Methods

Insect production and handling. Details associated with rearing, shipping, and handling the sterile male medflies are provided in Andress et al. (2012), and only a brief summary is provided here. Data regarding post-release dispersal and longevity were obtained exclusively for sterile males produced at the CDFA's Fruit Fly Rearing Facility, Waimanalo, Hawaii, which continuously supplies sterile males of a genetic sexing strain (Franz et al. 1996) to the PRP operating in southern California. The flies were shipped as pupae, which were first coated with fluorescent dye, packed in plastic bags, and irradiated under hypoxia at 2 d prior to emergence at the USDA-APHIS Irradiation Facility in Waimanalo. Application of dye is standard protocol for SIT programs, and dye particles retained on the retracted ptilinum or the body of emerged adults allow differentiation between released and wild flies. For routine releases, the sterile pupae are dyed pink, while the flies used for dispersal/longevity measurements, which were a subset of regular daily shipments, were dyed blue to permit their identification. Following irradiation, the pupae were transported via commercial airlines to Los Angeles, where CDFA personnel collected and transported them to Los Alamitos, CA, which serves as the administrative and operational center of the PRP. The test flies were thus handled and shipped in the same way as flies used in the PRP.

Upon arrival at Los Alamitos, the pupae were loaded into eclosion towers (consisting of 50–60 horizontally stacked screen trays with sugar blocks provided as food) that were held in climate controlled rooms for 4 d, with peak adult emergence occurring 2 d after pupal placement. Towers were then wheeled into a refrigerated trailer (4°C), where they were chilled for 45–80 min. Towers were then disassembled tray by tray, and dislodged flies were taken to aircraft for release. In all aspects relating to eclosion, maintenance, and chilling, the test flies were treated in the same manner as flies used in the PRP.

Release protocol. Flies were released on three different dates in 2011 and one date in 2012 from a Beechcraft model 90 "King Air" aircraft flying west-to-east along a single 96.6 km (60 mi) long transect between Hollywood and Fontana (Table 1). Releases were made between 0845–1000 hrs, with the aircraft traveling at 274 km/h. The target release altitude in the PRP is 610 m above ground, and test flies were released at this altitude on all dates, except June 11, 2011, when a cloud filled inversion layer required higher release altitudes (763–966 m). With the exception of this date, winds

Table 1. Dates and environmental parameters for the four releases of sterile males along a 96.6 km (60 mi) west-east transect between Hollywood and Fontana, CA.

Date	Wind speed km/h / direction[a]	Air temperature (°C) Minimum	Maximum[b]	General sky conditions
June 11, 2011	0–5/S	15.0	29.4	Cloudy, inversion layer
Sept 12, 2011	10–27/E	17.8	32.2	Clear, sunny
Oct 17, 2011	10–24/SW	12.8	26.7	Clear, sunny
Feb 6, 2012	34–35/SW	7.2	18.3	Hazy

[a]Wind conditions at release altitude as measured by aircraft's recorders; wind speed at ground level was 2–3 km/h on all release dates.
[b]Near-ground temperature data recorded at La Verne, CA (weather.com), located near the mid-point of the flight line.

were quite strong with variable direction at the release altitude. Winds were calm at ground level on all dates. Near-ground temperatures and general sky conditions were variable among the release dates (Table 1).

Estimates of the number of flies released were made following standard operating procedures used by CDFA for all release flights made in the PRP. The total weight of test flies was measured and divided by the average weight of an individual fly. This value was then adjusted (downward) to account for non- or only partially-emerged flies and non-fliers, with these parameters measured as part of standard quality control practices (FAO/IAEA/USDA 2003).

Trapping protocol. Two sets of traps were operated. The first set was established specifically for this experiment and consisted of six trapping transects spaced irregularly along the flight line in locations that could be serviced easily (these traps will hereafter be referred to as transect traps). With the west end of the flight line considered 0 km, the transects were located at 22, 39, 40, 42, 58, and 63 km, i.e., they were located primarily in the western and central portions of the flight line. Each transect was perpendicular to the flight line and extended 4.8 km (3 mi) on either side of it, except for the February release when the transect extended only 1.6 km (1 mi) on either side of the flight line owing to limited manpower. We placed Jackson traps baited with TML (2 g plugs; IAEA 2003) at intervals of 268 m (1/6 mi) along each transect for a total of 37 traps per transect (total includes trap placed directly beneath line of flight), except February where each transect (reduced to 1.6 km on either side of the flight line) had 13 traps in total. Baited traps were set out several days prior to a release, and the sticky inserts were replaced 1, 3, 5, 7, 9, and 11 d after the release, with the exception of the October release for which traps were first serviced 3 d after the release.

The second set of traps included the TML-baited Jackson traps operated as part of the routine fruit fly monitoring program of the PRP (these traps will hereafter be referred to as PRP traps). Much of Southern California is divided into 2.59 km^2 (1 mi^2) grids, and most (but not all) of these grids contain five medfly traps that are continuously operated and generally serviced biweekly. The sticky inserts from all traps were taken to CDFA's Insect Identification Section for examination and scoring.

Data analysis. For each release date, a capture or recovery rate (number of test flies captured/number of test flies released) was computed for data pooled over all transect and PRP traps. Capture rates were compared among release dates using a χ^2 test.

Variation in trap captures among transect and PRP traps, respectively, was analyzed in two ways. First, we used linear mixed models with Restricted Maximum Likelihood (REML) algorithms based on capture rates observed for individual traps. In no tests were the underlying assumptions of normality and homoscedasticity met. However, we included these analyses, because (i) the results of ANOVA are considered robust even with large deviations from normality and constant variance (Zar 1996 and references therein), (ii) inclusion of numerical values (the capture rates) allowed finer resolution of dispersal trends than use of binary data (i.e., presence/absence of released flies) for individuals traps, and (iii) the number of flies released varied among the four release dates, and the use of capture rates (proportions) controlled for this variation, whereas use of only presence/absence information for traps would not (i.e, the number of traps with one or more captures would likely vary directly with the number of flies released). Nonetheless, to circumvent potential misinterpretation arising from these models, we also conducted binomial logistic regressions based on presence/absence data for both transect and PRP traps.

Transect traps. Because the numbers of flies released and captured varied among release dates (see below), analyses using linear mixed models were based on capture rates (arc sine transformed values; to increase readability, the term captures is used hereafter as short-hand for recovery rates or relative numbers of captures). Two models were constructed. In the first, release date and transect number were treated as random effects, and trap position was a fixed effect. This latter parameter included both distance from the flight line as well as direction, with positions north of the flight line labeled as +1, +2, …+18 (with increasing numbers indicating increasing distance from the flight line) and those south of the flight line as –1, –2, …–18 (for February, trap positions were +1…+12 and –1…–12). Transect traps along the line of flight were assigned position 0. In this first model, capture data were pooled over the different days on which traps were serviced, i.e., post-release time of capture was not considered. The Tukey test was used to identify significant differences in pair wise comparisons between trap positions. This and subsequent statistical analyses were performed using JMP 8 (SAS, Cary, NC).

The second model focused specifically on the effect of post-release interval on variation in transect trap capture. Release date and transect number were again considered random effects, and trap distance from the flight line (independent of direction) and days after release (based on alternate-day servicing of the transect traps, i.e., 1, 3, 5, 7, 9 or 11 d) were treated as fixed effects. While trap position was included in the preceding analysis, its inclusion here allowed for examination of the interaction between trap position and days post-release to determine whether an outward movement of flies from the flight path was detectable. As noted above, trap servicing of transect traps was incomplete for October 2011, and consequently data from this release were excluded from analysis. The Tukey test was used to identify significant differences among individual levels within a factor.

The binomial logistic regression was run using presence/absence as the dependent variable and distance and direction from the flight line or release line as independent variables. Although transect traps occurred at discrete intervals, distance was treated as a continuous variable as this generated equations for curves expressed in meters that were more easily compared with comparable curves describing data from the PRP traps. Data were included only for traps located within 1.6 km (1 mi) on either side of the flight line as few captures were made in the more distant traps.

PRP traps. The distances of PRP traps from the flight line were obtained by geocoding the exact location of the individual traps and then measuring the distance to the release line using Google Earth.

For the linear mixed model approach, trap distances were grouped into 134 m-wide bands (1/12 mi) to a distance of 3.2 km on either side of the flight line (i.e., 24 bands each in north and south directions from the flight line). Following the procedure adopted above, in direction-dependent descriptions of PRP trap data, bands were designated as + or – designating north and south of the flight line, respectively. Where direction was not considered, band 1 (± sign absent) included bands +1 and –1, band 2 included bands +2 and –2, and so on. Variation in trap capture was analyzed with a single model in which release date was considered a random effect and trap position (coded for distance and direction as described above) was the fixed effect. As noted above, PRP traps were serviced relatively infrequently and asynchronously with the experimental releases. As a result, they yielded no useful data on the time elapsed between release and capture, and no analysis on this relationship was performed.

As with the transect traps, binomial logistic regression was performed using data from PRP traps located within 1.6 km (1 mi) of the release line (n = 432 traps per release date), and the analysis was run as described above for the transect traps.

All statistical analyses were completed using JMP 10 (SAS Institute).

Results

Release numbers and captures. Roughly 650,000–970,000 test flies were released per date (Table 2), and over these dates capture rates varied between approximately 0.01%–0.03% for transect traps and 0.08%–0.16% for the PRP traps. The greater proportions noted collectively for the PRP traps reflect the greater number of PRP traps in the environment relative to transect traps. A total of 222 transect traps (6 transects each with 37 traps) were operating during any one release (with only 78 operating for the February release, six transects each with 13 traps). In contrast, approximately 1,400 PRP traps were located within 4.8 km (3 mi) of either side of the flight path. Based on data pooled over both sets of traps, capture rates varied between approximately 0.09%–0.19% over all releases, and this variation was significantly greater than expected by chance alone ($\chi^2 = 360.3$, df = 3, $P < 0.001$). Computed over both trap types, recovery rates were greatest for September, which also had the highest air temperatures among the release dates, and lowest for June, when flies were released at a higher altitude owing to weather conditions, and February, which had the lowest air temperatures among the release dates. As noted above, the transects were shortened in February relative to all other releases (1.6 km vs. 4.8 km on either side of the flight line), but this alone did not appear to account for the low capture rate. In proportional terms, the transect traps,

Table 2. Estimated release numbers of test flies on the four release dates with numbers of captured flies in transect and PRP traps. For a particular release, captures were summed across all post-release dates on which traps were serviced.

	Estimated	Captures					
	Release	Transect		PRP		Total	
Release date	Number	Number	%	Number	%	Number	%
June 11 2011	877,394	104	0.0119	698	0.0796	796	0.0914
Sept. 12 2011	907,195	287	0.0316	1,413	0.1558	1,690	0.1874
Oct. 17 2011	966,424	240	0.0248	1,108	0.1146	1,336	0.1395
Feb. 6 2012	645,295	143	0.0222	521	0.0807	664	0.1029

despite their lower numbers, actually captured a higher proportion of released flies in February than in June, and the PRP traps (whose number remained unchanged across releases dates) accounted for a smaller proportion of captures in February than any other release. Thus, a factor(s) other than reduced transect length was likely responsible for the low recovery rate observed in February.

Transect traps. *Analyses based on capture rates*. Not surprisingly, the majority of captures for all releases were either along the flight line or immediately adjacent to it (Fig. 1). Over all release dates, captures from trap positions 0 and 1 (independent of direction) comprised 78%–93% of the total captures of test flies, and captures from trap positions 0 - 2 (independent of direction) comprised 86%–95% of the total captures of test flies. With the exception of the October 2011 release, more captures were made in trap position 0 than in trap position 1. As examined in more detail below, captures exhibited a pronounced directionality, and transect traps north of the flight line captured, in relative terms, 1.7–11.5 times as many flies as traps south of the flight line (Fig. 2).

Statistical analysis revealed that release date and transect number accounted for 14% and 0.5% of the total variation in trap captures, respectively. While release date had a relatively small effect on total trap capture, there was some indication that travel distances of sterile males varied slightly among release dates. Comparing the numbers of captures in trap positions 0 and 1 relative to trap positions > 1 revealed significant variation among the release dates. Captures in trap positions 0 and 1 accounted for 93% of all captures in February 2012 compared to 78%–86% among the other release dates ($\chi^2 = 13.2$, df = 3, P = 0.004).

Consistent with the data presented in Figs. 1 and 2, trap position (a composite parameter including both distance and direction from flight line) had a highly significant effect on trap capture (F = 44.2, P < 0.0001). The Tukey test showed that captures along the flight line (trap position 0) were significantly greater than those at any other trap position (0 position: % total captures over all release dates = 51%). A

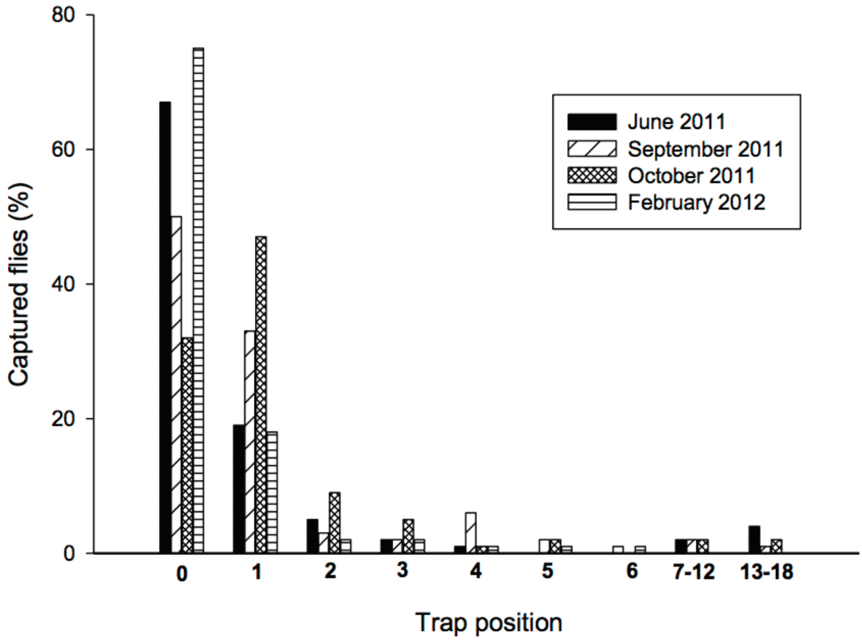


Figure 1. Capture of aerially released sterile male medflies as a function of the distance from the flight line for the four release dates. Ordinal values represent the proportion of the total captures in transect traps recorded at different positions, where trap position 0 indicates traps beneath the flight path, and higher trap positions represent increasing distances (by increments of 268 m between adjacent positions) along transects perpendicular to the flight line. For a given release date, data were pooled across the different transects, north and south directions (for positions ≥ 1), and the different post-release trap servicing dates. Numbers of captures for the different release dates are given in Table 2.

directional component was observed at trap position 1 as captures for position +1 (north of flight line) were significantly greater than those for position –1 (south of flight line; % total captures all release dates: +1 position = 24%, –1 position = 7%), with values for this latter position not significantly different from many more distant trap positions. No significant variation in captures was detected among trap positions 2–18 (both directions considered), in large part because relatively few flies were found in these more distant positions. To summarize, (i) most flies were captured at trap position 0, (ii) among flies captured away from the flight line, the majority was captured at trap position 1, and (iii) among these, significantly more flies were captured north of the flight line than south of the flight line. In other words, the overall directional pattern noted in Fig. 2 resulted primarily from the difference between captures at trap position +1 and trap position –1 and not to captures made at greater distances from the flight line.

The majority of flies were captured within 3 d of their release (Fig. 3). Over the three release dates included, 60%-65% of captured flies were caught on post-release days 1 and 3 compared to only 6%–21%

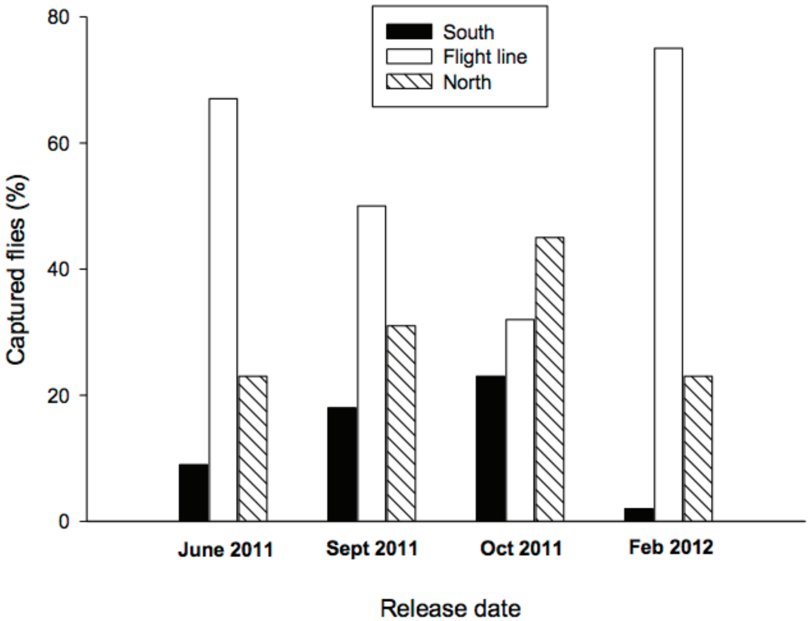


Figure 2. Capture of aerially released sterile male medflies as a function of the direction from the flight line for the four release dates. Ordinal values represent the proportion of the total captures in transect traps recorded south, north, or directly beneath the west-east oriented flight line. For a given release date, data were pooled across the different transects, different trap positions (for positions ≥ 1), and the different post-release trap servicing dates. Numbers of captures for the different release dates are given in Table 2.

on days 9 and 11 after release. Consistent with the preceding analysis, release date and transect number accounted for relatively small proportions (20% and 0.6%, respectively) of the total variation in trap captures. Analogous to the situation described above for distance traveled, there was some evidence that, while release date had a relatively small effect on captures, there was significant variation among dates in the frequency of captures made during different post-release intervals. Comparing the numbers of captures made between 1–3 d versus 5–11 d post-release intervals revealed no significant variation among the release dates ($\chi^2 = 0.6$, df = 2, P = 0.73). However, if the numbers of captures were compared between 1–5 d versus 7–11 d post-release intervals, significant variation was detected ($\chi^2 = 18.4$, df = 2, P < 0.001), reflecting primarily the fact that the proportion of captures made ≥ 7 d after release was much lower for February (10%) than for June 2011 (30%) or September 2011 (28%).

Days after release had a significant effect on captures (F = 144.8, P < 0.0001) as did trap distance from flight line (independent of direction; F = 46.0, P < 0.0001). The interaction term was also significant (F = 7.0, P < 0.0001). Based on the Tukey test, similar numbers of captures were recorded post-release days 1 and 3, and these values were significantly greater than captures on day 5 (Fig. 3). In turn, significantly more captures were recorded

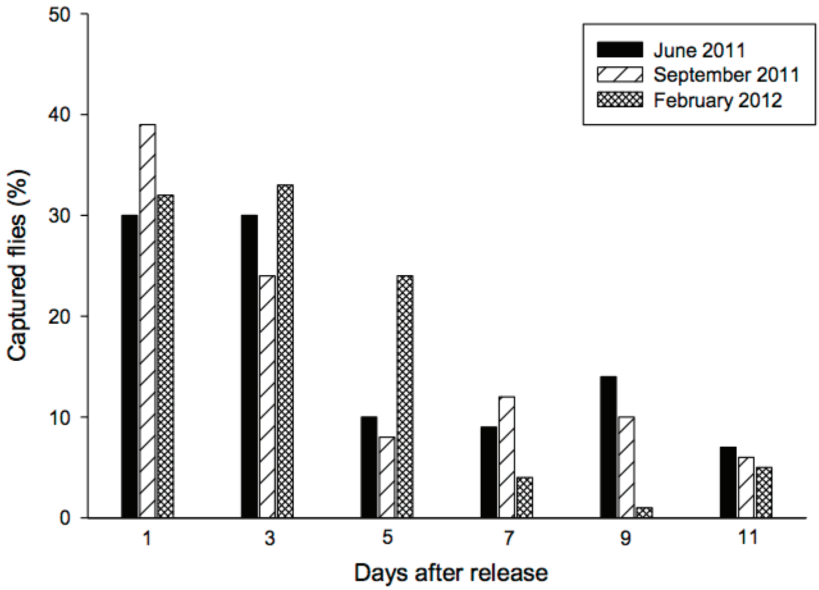


Figure 3. Capture of aerially released sterile male medflies as a function of days after release for three release dates (October 2011 was excluded owing to incomplete sampling). Ordinal values represent the proportion of the total recaptures in transect traps on alternate trap servicing days (1, 3, 5…11 d) after a release. For a given release date, data were pooled across the different transects and different trap positions. Numbers of captures for the different release dates are given in Table 2.

for post-release day 5 than days 7 and 9, which did not differ significantly from one another and were significantly greater than captures recorded for day 11.

The post-release timing of captures was also examined with respect to trap position to determine whether a time-course of fly movement away from the flight line could be detected. Captures at trap position 0 declined through time, while those at trap positions 1 and 2 increased through time, indicating dispersal over short distances away from the flight line (Fig. 4). Aside from the area adjacent to the flight line, however, there was little evidence of a "wave" of movement, i.e., increased fly captures at increasingly distant traps with increasing time since release. The only notable indication of long-range, outward movement was the occurrence of flies at trap positions ≥ 8 (2.1 km from flight line) only ≥ 7 d after release.

Analyses based on presence/absence. The logistic regression on presence/absence data confirmed two basic findings noted above (Fig 5). That is, both distance from the release line (χ^2 = 128.5, df = 1, P < 0.001) and direction (χ^2 = 19.8, df = 2, P < 0.0001) had significant effects on the probability that ≥ 1 fly was captured in a transect trap. Among transect traps, the probability of capturing at least 1 fly declined with increasing distance from the release line. For example, over all release dates, the odds that a transect trap beneath the release line captured at least 1 fly was 56% compared to only 24% and 13% for transect traps located 300 or 500 m from the flight line, respectively (independent of direction). Similarly, this analysis showed

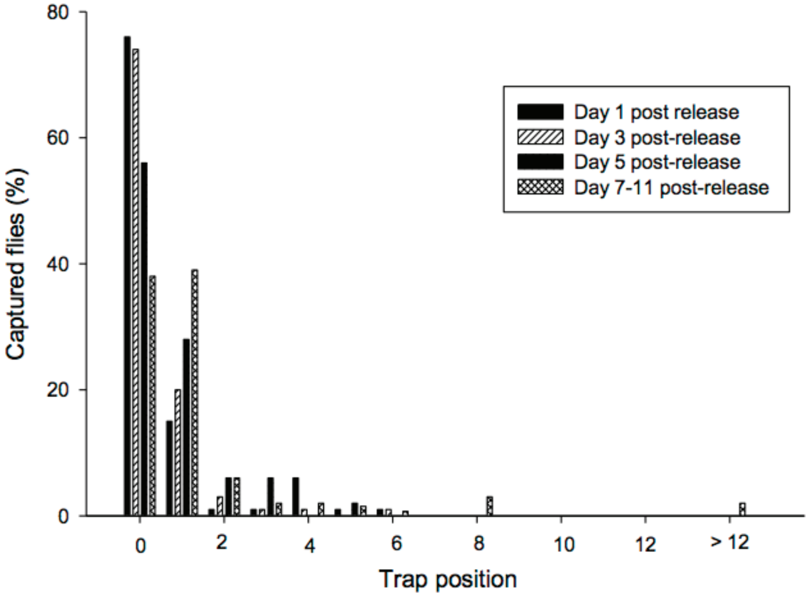
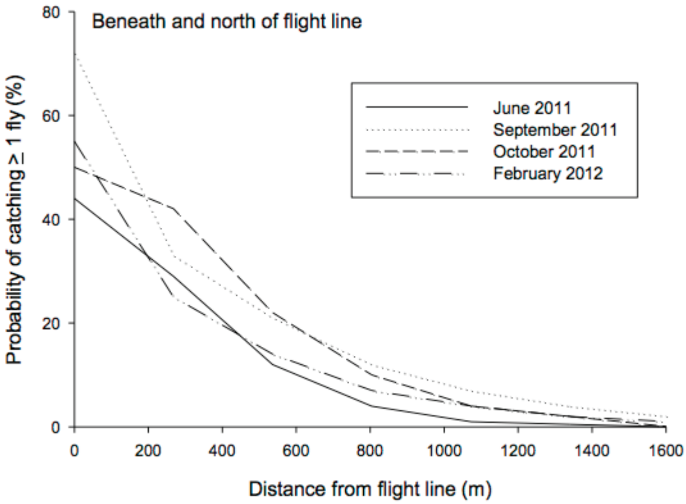


Figure 4. Capture of aerially released sterile male medflies at different trap positions for different trap servicing intervals following release (October 2011 was excluded owing to incomplete sampling). Ordinal values represent the proportion of the total captures in transect traps recorded at different positions on post-release days 1, 3, 5, and ≥ 7 d (i.e., 7, 9, and 11), where trap position 0 indicates traps beneath the flight path, and higher trap positions represent increasing distances (by increments of 268 m between adjacent positions) along transects perpendicular to the flight line. Capture data were pooled across release dates, transects, and directions; data for trap positions 13–18 were pooled and categorized as > 12. Numbers of captures for the different release dates are given in Table 2.

that, for a given distance, transect traps placed to the north of the release line had much higher probabilities of capturing ≥ 1 fly than those to the south of the line. For example, over all release dates, the odds that a trap 300 m north of the flight line captured at least 1 fly was 30% compared to only 17% for transect traps located 300 m south of the flight line.

In considering variation among the release dates, the binary data did not suggest noticeably lower dispersal in February as did the capture rate data. For the February release, the odds of a transect trap catching at least 1 released fly was 55%, which was lower than the value for September (72%) and only slightly above that recorded for October (50%). Also, north of the flight line (where the majority of captures was recorded), the likelihood that a transect trap 268 m distant from the flight line caught 1 or more released flies was actually lower in February (25%) than all other release dates (29%–42%).

PRP traps. *Analyses based on capture rates*. Consistent with the transect trap data, captures in the PRP traps decreased rapidly with increasing distance from the flight line (Fig. 6). Over all release dates, data pooled over north and south



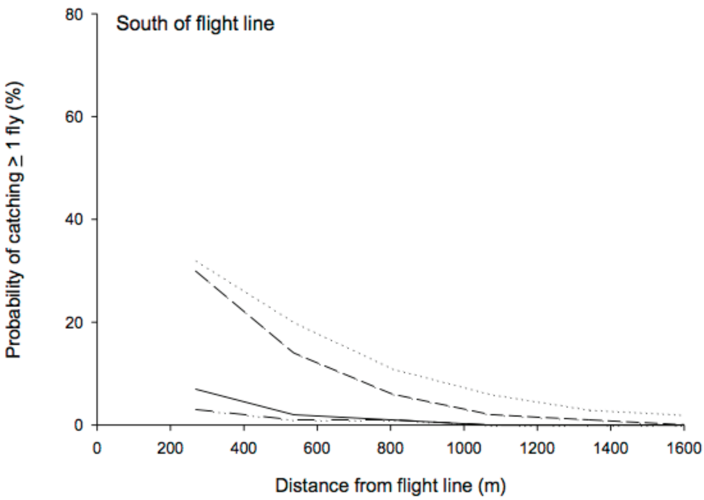


Figure 5. The probability of capturing ≥ 1 aerially released male medflies in transect traps as a function of distance from the east-west flight line located beneath or north of the flight line (top) or south of the flight line (bottom). North, over all dates: Y = 1/(1+e(–(–0.20766)–0.0028X+ 0.13053)); South, over all dates: Y = 1/(1+e(–(–0.20766)–0.0028X–0.58181).

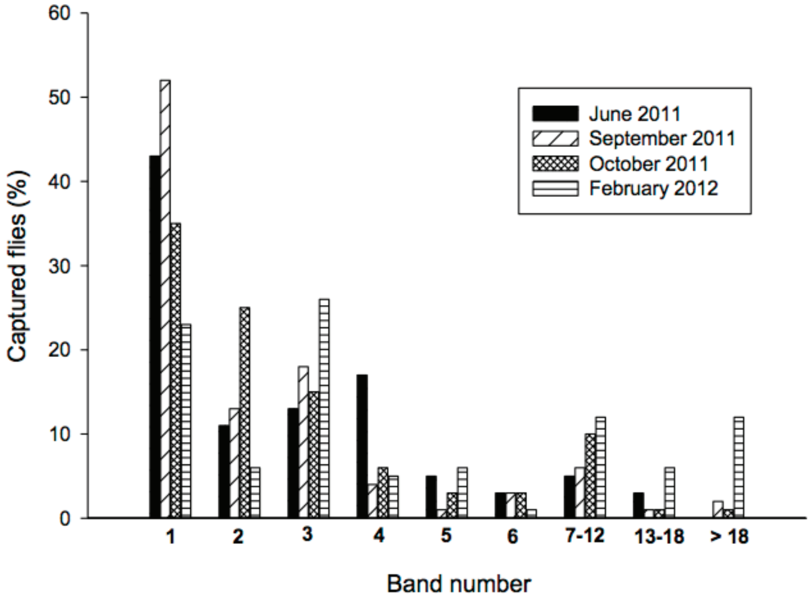


Figure 6. Capture of aerially released sterile male medflies in PRP traps in different bands parallel to the flight line. Ordinal values represent proportions of all captures in both north and south directions over all release dates in bands 134 m wide, where band 1 was centered on the flight line, band 2 extended 67 m on either side of band 1, and so on. Captures are depicted for PRP traps up to 3,216 m (2 mi; band 24) from the release line.

directions showed that 23%–53% of the total captures of flies occurred in band 1 (i.e., within 134 m on either side of the flight line), 30%–65% occurred in bands 1 and 2 (i.e., within 268 m of the flight line), and 67%–92% were recorded in bands 1–6 (i.e., within 804 m of the flight line). Nonetheless, some flies dispersed considerable distances: 11% of all captures were reported in bands 7–18 (i.e., between 938–2,412 m from the flight line), and 3% were found beyond band 24 (i.e., > 3,216 m from the release line). As with the transect data, captures in the PRP traps indicated differences in sterile male dispersal among the release dates, although the trend observed was opposite that noted for the transect trap data. Whereas the transect trap data suggested relatively low movement in February, the PRP trap data showed greater male dispersal in that month. In February, 20% of captures were reported in bands > 12 (more than 1.6 km from the flight line) compared to only 3% for each of the other release dates.

Statistical analysis revealed that release date accounted for only 1% of the variation observed in PRP trap captures and that trap position (a composite parameter including both distance and direction from the flight line) had a highly significant effect on trap captures ($F_{47, 192} = 6.9$, $P < 0.0001$). The multiple comparisons test revealed that trap captures for bands +1, +2, –1, and –2 differed from those of most other (more distant) bands. However, beyond this finding, there were few clear-cut differences detected between bands.

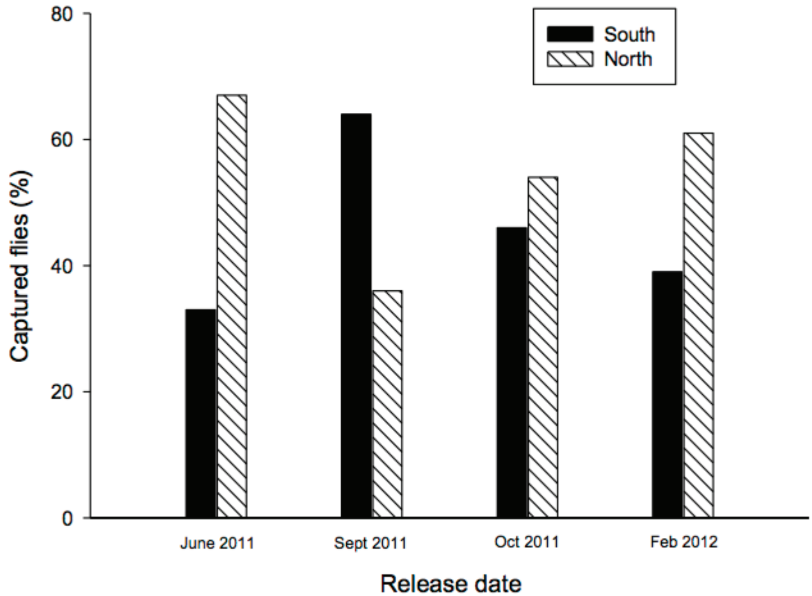


Figure 7. Capture of aerially released sterile male medflies in PRP traps as a function of the direction from the east-west oriented flight line. For a given release date, ordinal values represent the proportion of the total captures in PRP traps recorded north or south of the flight line.

Although captures were generally higher north of the flight line (Fig. 7), no significant differences were found between north and south bands that were equidistant from the flight line. Thus, unlike the situation described above for the transect traps (Fig. 2), the directional pattern noted for PRP traps was apparently the result of relatively small, and non-significant, differences between north and south bands. For example, over all release dates, the proportion of flies recorded from band +2 was approximately 8% compared to 5% for band –2, and the proportion of all captures from bands +3, +4, and +5 collectively was 19% compared to 9% for bands –3, –4, and –5.

Analyses based on presence/absence. The logistic regression on presence/absence data yielded results consistent with the above findings (Fig 8). That is, distance from the release line (χ^2 = 168.6, $P < 0.001$, df = 1) had a significant effect on the probability that ≥ 1 fly was captured in a PRP trap, while the direction from the flight line did not ($\chi^2 = 0.01$, $P = 0.90$, df = 2). Among PRP traps, the probability of capturing at least 1 fly declined with increasing distance from the release line. For example, over all release dates, the odds that a PRP trap beneath the release line captured at least 1 fly was 55% compared to only 41% and 33% for transect traps located 300 or 500 m from the flight line, respectively (independent of direction). Unlike the capture rate data, the presence/absence data did not suggest higher movement by flies in February: the odds that a PRP trap located 1,600 m from the flight line captured 1 or more released flies was similar between February (5%) and the remaining months (3%–9%).

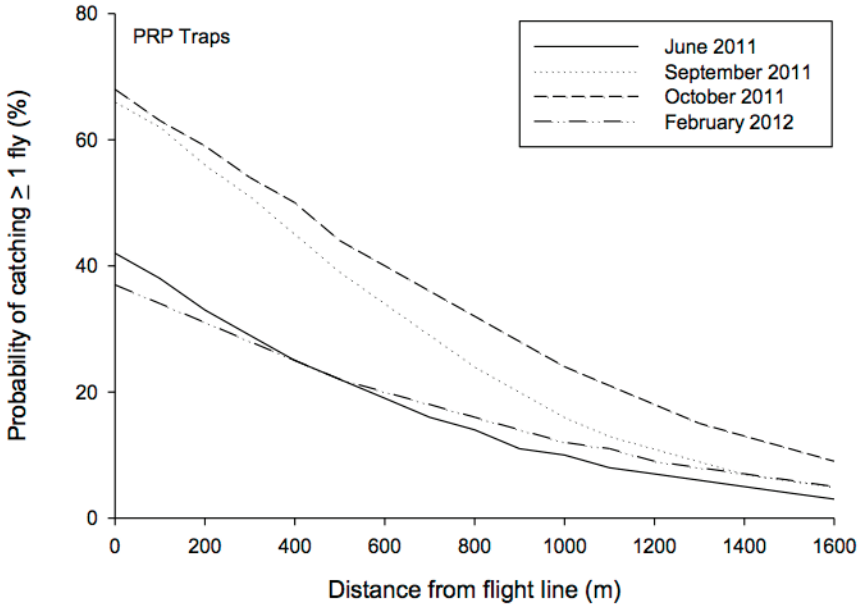


Figure 8. The probability of capturing ≥ 1 aerially released male medflies in PRP traps as a function of distance from the east-west flight line (independent of direction). Over all dates, Y = 1/(1+e(–(0.20768–0.00187X))).

Discussion

The present study presents a useful, albeit limited, characterization of the dispersal of aerially released sterile male medflies. A more complete description would have entailed more releases throughout the year, with multiple replicates in defined time intervals. In addition, releases ideally would have been made in different regions of southern California to include, for example, coastal and inland areas as well as rural and urban areas. Unfortunately, resources were not available for a more comprehensive study, and consequently the interpretation and robustness of the present results are constrained. Nonetheless, given the near-absence of similar published findings, the present study furnishes some insight into several key questions regarding SIT procedures used in medfly control. These questions include:

Do recovery rates of sterile males vary among releases? Significant variation was detected in recovery rates among release dates. While replication is lacking, it is interesting that the lowest recovery was observed for the release made in the coolest conditions (February 2012), and the highest was observed for the release made in the warmest conditions (September 2011). This finding agrees, in general, with Barry et al. (2002), who examined the relationship between PRP trap catch data and climatic data in a section of Los Angeles County and found lowest capture in the coldest months of January-March and highest capture in the hotter (but not the hottest) months of May, September, and October. Different temperature-dependent parameters, such as fly mortality and activity and lure volatility, likely affected capture rates, but identifying the relative importance of each of these is not possible at present.

How far do sterile males fly from the release path, and does dispersion vary among release dates? Not surprisingly, most captures were made near the flight line, although some long distance movement (> 1.61 km [1 mi]) was detected as well. Estimates of fly movement varied between the transect and PRP traps, with the latter indicating greater movement than the former. For example, transect trap positions 0 and 1 included the same area as PRP bands 1 and 2 (i.e., 268 m on either side of the flight line), and the proportion of the total flies captured over all releases was 85% for transect trap positions 0 and 1 compared to 52% for PRP bands 1 and 2. Similarly, the proportion of the total flies captured over all releases captured beyond 1,072 m (2/3 mi) was 11% for the PRP traps (> band 8) compared to 7% for the transect traps (> trap position 4). Not surprisingly, in the analysis based on simple presence/absence of released flies, data from the more numerous PRP traps indicated much greater dispersion than did the transect traps. For example, among PRP traps located > 1,000 m from the flight line, the odds of catching 1 or more released fly were between 6%–24% over the four release dates compared to 0%–7% among the transect traps.

As noted above, a chief goal of this study was to assess whether reducing release flights from 6/1.61 km to 4/1.61 km would preclude adequate distribution of sterile medflies. Such a reduction would increase the distance between adjacent flight lanes from 268 m to 402 m and thus require adequate fly movement approximately 200 m from a flight line (i.e., midway between adjacent lines). While the definition of "adequate" is arbitrary, the present data suggest that reasonable coverage could be achieved even with reduced flights. Position 1 of the transect traps was 268 m from the flight line and as shown traps at this position captured an average of 29% of recovered flies. Similarly, and more conservatively, band 3 of the PRP traps spanned the area 268–402 m from the release line, and traps in this band captured an average of 18% of the recovered flies. Presence/absence data also suggested adequate dispersal of released flies. Over all dates and independent of direction, the probability that a transect trap placed 268 m from the flight line caught at least 1 released fly was 24%, while the corresponding odds for a PRP trap located 200 m from the flight line was 45%. As above, the greater value obtained for PRP traps reflects the greater number of PRP traps deployed in the area.

Examination of temporal variation in male dispersion did not identify any clear trends. Based on capture rate data, the transect and PRP trap data suggested different patterns of variation, with the former indicating lowest dispersion in February and the latter indicating the opposite. Lower dispersion in February is consistent with the relatively cool temperatures as well as the low recovery rate observed in that month. However, the PRP trap data included a much larger sample of traps and a correspondingly larger sample of captured flies. In contrast, analyses based on presence/absence data did not reveal any clear-cut trends for either transect or PRP traps. Consequently, a more definitive characterization of seasonal dispersal is not possible at present and requires additional measurements.

Do released sterile males disperse evenly on either side of a flight line? In all likelihood, prevailing wind direction is the prime determinant of male distribution following release (Severin and Hartung 1912). In the present study, winds at the release altitude were blowing from a southerly or southwestern direction on three of the four release dates, and both transect and PRP traps to the north of the east-west oriented release line captured more males than traps to the south of this line.

How long do sterile males live after release? As noted above, sterile males appear to have low survivorship following release, a fact that necessitates frequent releases of large numbers of males over the same area (Lance and McInnis 2005). We also observed a steep temporal decline in the number of trapped males: nearly 66% of all captures were made within 3 d of release. Nonetheless, the number of captures made ≥ 7 d post-release in the present study was quite large relative to those reported in several other studies. The proportion of captures recorded ≥ 7 d after release was 15% in the present study (average of three release dates considered) compared to approximately 0.1% in Israel (Gavriel et al. 2011), 5% in Brazil (Paranhos et al. 2010), and 10% in Hawaii (Vargas et al. 1995). The 15% estimate noted here is also much greater than that reported by Barry et al. (2002), who, as noted above, also worked in southern California and observed less than 10% of captures ≥ 7 d post release.

In conclusion, research on SIT has, in general, focused more on rearing issues and field cage studies than post-release, "open field" questions, such as food and mate foraging, dispersal, and survival. Moreover, as noted above, most studies on post-release biology rely on ground releases of sterile male medflies, often in areas that are not part of an ongoing SIT program. Consequently, the applicability of these data to actual field operations is questionable. We urge study of dispersal and survival as an integral component of ongoing SIT programs to furnish information, not only on the biological performance of the released flies, but also on the cost effectiveness of the release protocol as spatial and temporal variability in fly movement and longevity may argue for flexibility in release rates in different areas of coverage and/or different times of the year.

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Literature Cited

Andress, E., E. Jones, M. War, and **T. Shelly.** 2012. Effects of pre-release chilling on the flight ability of sterile males of the Mediterranean fruit fly (Diptera: Tephritidae). Fla. Entomol. 95: 587–592.

Baker, P.S., and **A.S.T. Chan.** 1991. Appetitive dispersal of sterile fruit flies: aspects of the methodology and analysis of trapping studies. J. Appl. Entomol. 112: 263–273.

Baker, P.S., A.S.T. Chan, and **M.A. Jimeno Zavala.** 1986. Dispersal and orientation of sterile *Ceratitis capitata* and *Anastrepha ludens* (Tephritidae) in Chiapas, Mexcio. J. Appl. Ecol. 23: 27–38.

Barry, J.D., R.V. Dowell, and **J.G. Morse.** 2002. Comparison of two sterile Mediterranean fruit fly (Diptera: Tephritidae) strains released in California's preventative release program. J. Econ. Entomol. 95: 936–944.

Caceres, C., D. McInnis, T. Shelly, E. Jang, A. Robinson, and **J. Hendrichs.** 2007. Quality management systems for fruit fly (Diptera: Tephritidae) sterile insect technique. Fla. Entomol. 90: 1–9.

Cunningham, R.T., and **H.M. Couey.** 1986. Mediterranean fruit fly (Diptera: Tephritidae): distance/response curves to trimedlure to measure trapping efficiency. Environ. Entomol. 15: 71–74.

Cunningham, R.T., W. Routhier, E.J. Harris, G. Cunningham, L. Johnson, W. Edwards, R. Rosander, and **W.G. Vettel.**

1980. Eradication of medfly by sterile male release. Citrograph 65: 63–69.

Dowell, R.V., I.A. Siddiqui, F. Meyer, and **E.L. Spaugy.** 2000. Mediterranean fruit fly preventative release programme in southern California. p. 369–375 *In* K.H. Tan (ed.), Area-wide control of fruit flies and other insect pests. Penerbit Universiti Sains Malaysia, Pulau Pinang, Malaysia.

Enkerlin, W.R. 2005. Impact of fruit fly control programmes using the sterile insect technique. p. 651–676 *In* V.A. Dyck, J. Hendrichs, and A.S. Robinson (eds.), Sterile insect technique: principles and practice in area-wide integrated pest management. Springer, Dordrecht, The Netherlands.

[FAO/IAEA/USDA]. Food and Agriculture Organization/International Atomic Energy Agency/United States Department of Agriculture. 2003. Manual for product quality control and shipping procedures for sterile mass-reared tephritid fruit flies. Version 5.0. IAEA, Vienna, Austria.

Franz, G., P. Kerremans, P. Rendon, and **J. Hendrichs.** 1996. Development and application of genetic sexing systems for the Mediterranean fruit fly based on a temperature sensitive lethal. P. 185–191 *In* B.A. McPheron and G.J. Steck (eds.), Fruit fly pests: a world assessment of their biology and management. St. Lucie Press, Delray Beach, Florida.

Gavriel, S., Y. Gazit, A. Leach, J. Mumford, and **B. Yuval.** 2011. Spatial patterns of sterile Mediterranean fruit fly dispersal. Entomol. Exp. Appl. 142: 17–26.

Howell, J.F., M. Cheikh, H. Ben Salah, P. Crnjanski, W. Pils, and **E.J. Harris.** 1975. Suppression of Mediterranean fruit fly in Tunisia: a new method for aerial distribution of sterile flies from fixed wing aircraft. J. Econ. Entomol. 68: 244–246.

[IAEA] International Atomic Energy Agency. 2003. Trapping guidelines for area-wide fruit fly programmes. IAEA, Vienna, Austria.

[IPRFFSP] International Panel for Review of Fruit Fly Surveillance Programs. 2006. Review of fruit fly surveillance programs in the United States. USDA/APHIS/PPQ/Fruit Fly Program, Riverdale, MD.

Lance, D.R., and **D.B. Gates.** 2004. Sensitivity of detection trapping systems for Mediterranean fruit flies (Diptera: Tephritidae) in southern California. J. Econ. Entomol. 87: 1377–1383.

Lance, D.R., and **D.O. McInnis.** 2005. Biological basis of the sterile insect technique. p. 69–94 *In* V.A. Dyck, J. Hendrichs, and A.S. Robinson (eds.), Sterile insect technique: principles and practice in area-wide integrated pest management. Springer, Dordrecht, The Netherlands.

Meats, A., and **J.E. Edgerton.** 2008. Short- and long-range dispersal of the Queensland fruit fly, *Bactrocera tryoni* and its relevance to invasive potential, sterile insect technique and surveillance trapping. Aust. J. Exp. Agric. 48: 1237–1245.

Meats, A., and **C.J. Smallridge.** 2007. Short- and long-range dispersal of medfly, *Ceratitis capitata* (Dipt., Tephritidae), and its invasive potential. J. Appl. Entomol. 131: 518–523.

Mwatawala, M., M. Virgilio, S. Quilici, M. Dominic, and **M. De Meyer.** 2102. Field evaluation of the relative attractiveness of enriched ginger root oil (EGO)lure and trimedlure for African *Ceratitis* species (Diptera: Tephritidae). J. Appl. Entomol. doi: 10.1111/j.1439-0418.2012.01744.x

Nadel, D.J., J. Monro, B.A. Peleg, and **H.C.F. Figdor.** 1967. A method of releasing sterile Mediterranean fruit fly adults from aircraft. J. Econ. Entomol. 60: 899–902.

Paranhos, B.J., N.T. Papadopoulos, D. McInnis, C. Gava, F.S.C. Lopes, R. Morelli, and **A. Malavasi.** 2010. Field dispersal and survival of sterile medfly males aromatically treated with ginger root oil. Environ. Entomol. 39: 570–575.

Plant, R.E., and **R.T. Cunningham.** 1991. Analyses of the dispersal of sterile Mediterranean fruit flies (Diptera: Tephritidae) released from a point source. Environ. Entomol. 20: 1493–1503.

Salvato, M., G. Hart, T. Holler, and **T. Roland.** 2003. Release of sterile Mediterranean fruit flies, *Ceratitis capitata* (Diptera: Tephritidae), using an automated ground release vehicle. Biocontrol Sci. Technol. 13: 111–117.

Severin, H.H.P., and **J.W. Hartung.** 1912. The flight of two thousand marked male Mediterranean fruit flies (*Ceratitis capitata* Wied.). Ann. Entomol. Soc. Am. 5: 400–409.

Shelly, T.E., T.C. Holler, and **J.L. Stewart.** 2006. Mating competitiveness of mass-reared males of the Mediterranean fruit fly (Diptera: Tephritidae) from eclosion towers. Florida Entomol. 89: 380–387.

Vargas, R.I., L. Whitehand, W.A. Walsh, J.P. Spencer, and **C.L. Hsu.** 1995. Aerial releases of sterile Mediterranean fruit fly (Diptera: Tephritidae) by helicopter: dispersal, recovery, and population suppression. J. Econ. Entomol. 88: 1279–1287.

Wong, T.T.Y., L.C. Whitehand, R.M. Kobayashi, K. Ohinata, N. Tanaka, and **E.J. Harris.** 1982. Mediterranean fruit fly: dispersal of wild and irradiated and untreated laboratory-reared males. Environ. Entomol. 11: 339–343.

Zar, J.H. 1996. Biostatistical Analysis. 3rd ed. Prentice Hall, Upper Saddle River, New Jersey.