

# Analyses of the Dispersal of Sterile Mediterranean Fruit Flies (Diptera: Tephritidae) Released from a Point Source

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**ABSTRACT** One of the most common methods of studying insect dispersal is the recapture of members of a population released at a single time from a single location. This procedure especially lends itself to quantitative analysis. Quantitative studies of the dispersal of insects released in this manner may be divided into the following three general categories: (1) statistical studies in which certain dispersal parameters such as average distance flown are estimated without assuming any particular model; (2) curve fits to an empirical model having a predetermined functional form, such as an exponential; and (3) fits to a fundamental biological model such as a diffusion-based model. Each of these methods of analysis serves a purpose. For example, the first and second methods are often useful in developing control strategies for invasive pest species, whereas the third is useful for understanding the biological process driving dispersal. The article presents a quantitative analysis of the dispersal of irradiated Mediterranean fruit flies, *Ceratitidis capitata* (Wiedemann) in a macadamia nut orchard near Hilo, Hawaii. All three of the methods described above are used in the analysis. The article had three primary objectives. The first was to review and contrast the three methods of analyzing data on the dispersal of insects from a point source. The second was to illustrate how these methods may be applied to insect recapture data using the example of released Mediterranean fruit flies. The third was to use the quantitative analysis to compare the results of the present release study with other studies on related species and to draw general conclusions about the nature of the dispersal of released sterile Mediterranean fruit flies. Results indicated that a population of irradiated flies released from a single point dispersed in a manner that may be modeled as if the population consisted of two subpopulations, one of which was dispersing in a diffusionlike pattern and the other was not dispersing, and that the fraction of the population in the nondispersing subpopulation increased. The dispersal pattern appeared to be little influenced by prevailing wind and to remain centered near the release point. The pattern had almost complete circular symmetry.

**KEY WORDS** Insecta, *Ceratitidis capitata*, dispersal, modeling

ONE OF THE MOST COMMON methods of studying insect dispersal is the recapture of members of a population released from a single point at a single time. This method has the advantage of quickly making apparent any directional component of the dispersal pattern, such as might be caused, for example, by prevailing winds or by spatial anisotropy. Moreover, the directional component may be sufficiently small that it can be neglected or, if it cannot be neglected, it may be removed from the analysis by some means such as considering only a directional average distribution or using a moving coordinate system. In this case, the only spatial variable is distance from the point of release. This simple one-dimensional spatial form invites the construction of a mathematical representation of the distribution.

The dispersal of irradiated Mediterranean fruit flies, *Ceratitidis capitata* (Wiedemann), is of interest

from an applied as well as a basic perspective. One of the principal methods of eradication of invasive populations is the sterile insect technique (Knippling 1955), which involves the mass release of laboratory-reared populations that have been sterilized by irradiation. The males of the released population mate with the wild females, causing these females to lay infertile eggs. An understanding of the quantitative dispersal properties of irradiated flies is crucial to the successful application of this technique.

In the present paper we present a quantitative study of the dispersal of irradiated, laboratory-reared Mediterranean fruit flies. Beginning with the work of Severin & Hartung (1912), there have been numerous studies that included a component on the dispersal behavior of released unirradiated or irradiated medflies (e.g., Christiansen & Foote 1960, Soria & Cline 1962, Steiner et al. 1962, Nadel & Guerrieri 1969, Hafez et al. 1973, Serghiou & Symmons 1974, Wong et al. 1982). These studies

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provide the following description of the dispersal behavior of released Mediterranean fruit fly populations. The vast majority of the population does not disperse very far. Serghiou & Symmons (1974) cite a study by Katiyar & Valerio (1963) in which 87.5% of the flies recaptured were caught within 200 m of the release point. The studies of Nadel & Guerrieri (1969), Soria & Cline (1962), and Serghiou & Symmons (1974) also found the vast majority of the flies to be recaptured within a few hundred meters of the release point. A small fraction of the population, apparently borne by the wind (Christiansen & Foote 1960) may be recaptured at distances of several kilometers from the release point (Steiner et al. 1962, Hafez et al. 1973, Wong et al. 1982).

Because it is a relatively weak disperser, the Mediterranean fruit fly provides an ideal source of data for quantitative analysis. Traps laid out in a reasonably small area provide data in which virtually none of the captured flies are at the boundary of the trapping region. Although it cannot be guaranteed that the entire released population has stayed within this region, the data at least provide an excellent representation of an important subset of this population. Our investigation takes advantage of this dispersal property by undertaking a very thorough quantitative study on a set of data gathered from experiments in which populations of irradiated flies were released from a central location in a grid of traps, and the recapture of members of that population in the traps was recorded over time. The article has the following three primary objectives: (1) to provide a comparative review of methods for analyzing data on dispersal of insect populations from a point source, (2) to apply each of the methods discussed to data on the recapture of released Mediterranean fruit flies and thereby permit a comparison of the methods, and (3) to use the quantitative analysis to compare the results of our release study with other studies on related species and to draw general conclusions about the nature of the dispersal of released sterile flies.

There is an extensive literature on theoretical methods for performing this analysis. In our review, we subdivide the methods discussed in this literature into three categories. The first category is a statistical analysis in which the properties of the frequency distribution of captured insects is analyzed without reference to any particular model. The second and third categories base the analysis on one of two types of models: empirical and fundamental (cf. France & Thornley 1984). Empirical models assume a particular functional form for the data; for example, that trap catch declines according to an exponential or normal curve as a function of distance from the release point. Fundamental models, which usually consist of a system of differential equations, attempt to represent assumptions about the biological properties underlying the observed behavior.

The intellectual roots of the quantitative analysis of insect population dispersal can to a large extent be traced to studies by Dobzhansky & Wright (1943, 1974). Working with marked *Drosophila pseudoobscura* (Frolova), Dobzhansky & Wright (1943) released the flies from the base of an oak tree at the center of a cross-shaped trap pattern. For a period of a week or so, they recorded the number of marked flies recaptured as well as the number of wild *Drosophila* captured. Dobzhansky & Wright initially postulated that the flies might disperse according to a simple brownian (random) motion, in which case at any time after release they would be normally distributed, with the variance of the normal distribution proportional to the time from release. The data indicated, however, that the distribution of the population was not normal but instead was significantly leptokurtic. Moreover, the kurtosis of the distribution declined with time toward the value 3, which is the kurtosis of the normal distribution.

Because the marked population consisted of laboratory-reared flies, Dobzhansky & Wright proposed that this population consisted of two subpopulations, one more vigorous than the other. A failure of the less vigorous subpopulation to disperse rapidly coupled with a higher mortality rate for this subpopulation would explain the nonnormal observation. This hypothesis received some support from their subsequent study (Dobzhansky & Wright 1974), in which wild flies were released from the same site. The results of this experiment did not show the same initial leptokurtosis. The variance of the distribution, however, changed in time in a way not predicted by the simple brownian motion model.

A purely statistical analysis of insect dispersal avoids postulating any explicit model for the dispersal process; rather, it concentrates on the estimation of statistical parameters describing the dispersal pattern when the data is considered as a frequency distribution. Based on a histogram of fraction of the recaptured population versus distance from the point of release, one can compute the mean distance flown, the variance of the distribution associated with the histogram, and other statistics. Fletcher (1974) examined the distribution of Queensland fruit flies, *Dacus tryoni* (Froggatt) in this way, and Fletcher & Economopoulos (1976) used similar methods to compare the dispersal of irradiated and nonirradiated olive flies, *Dacus oleae* (Gmelin). Baker et al. (1986) used circular statistics (Batschelet 1981) to describe the dispersal of Mediterranean fruit flies and Mexican fruit flies, *Anastrepha ludens* (Loew).

Empirical models for insect population dispersal attempt to fit the data with a curve. The curve of Dobzhansky & Wright had the form  $\phi(r) = \alpha \exp[(-r/\beta t)^2]$ , where  $r$  is the radial distance from the point of release and  $t$  is time since release, to the insect population density data. Subsequent quantitative studies of insect dispersal have con-

sidered more general functions  $\phi(r)$ . Hawkes (1972) and Finch & Skinner (1975), studying the dispersal of *Erioischia brassicae* (Bouche'), tried functions of the form  $\phi = \alpha \exp(r/\beta)^k$  and  $\phi = \alpha \exp(r/\beta)$ . They reported that the former provides a better fit to the data. These models do not explicitly include time, so the value of  $\beta$  may be considered time-dependent. Taylor (1978, 1980) also made a comparative study of a variety of models. He simplified the form of the models by fitting the curve  $\ln \phi(r)$  rather than  $\phi(r)$  directly (Freeman [1977] used this transformation also). Taylor also considered a general family of models of the form  $\ln \phi(r) = \alpha + (r/\beta)^\gamma$ . He fit this equation to dispersal data from several sources. Freeman (1977) studied a variety of dispersal models in which time is explicitly represented.

Studies using the fundamental approach to the modeling of insect dispersal have focused on the physical and biological interpretation of the model. Dobzhansky & Wright's interpretation of their data in terms of two subpopulations has already been mentioned. Aikman & Hewitt (1972) applied the diffusion model to the dispersal of the grasshopper *Myrmeleotettix maculatus* (Thunb). Kareiva (1982) presented a detailed study from several physically based points of view of the combined walking and flying dispersal of the flea beetles *Phyllotreta cruciferae* Goeze and *P. striolata* (Fabricius). Kareiva (1983) and Rudd & Gandour (1985) discussed the physical derivation of the diffusion model for insect dispersal and compared this model with data from several sources. Banks & Kareiva (1983) and Banks et al. (1983) extended the diffusion model to include a time-varying diffusion coefficient, and Zia (1986) further extended the model to include convection and settling. These latter papers provide mathematically sophisticated methods for estimating the parameters of the model.

### Materials and Methods

Jackson traps (Harris et al. 1971) baited with trimedlure (Beroza et al. 1961) were hung in a square grid-shaped pattern in a large macadamia nut orchard near Hilo on the island of Hawaii. The traps were baited with  $\approx 0.6$  g of trimedlure in a commercial extender formulation (Capilure). The prevailing daytime winds were from the northeast. Eighty-one traps were evenly spaced in a 9 by 9 grid with a spacing of 129.5 m between traps. At the start of each replication, undyed, laboratory-reared sterile flies (Tanaka et al. 1970) were released from the center of the grid. Approximately 20,000 flies were released in each replication. A 1:1 sex ratio was assumed, so that each release was estimated to include  $\approx 10,000$  males. Twelve replications were conducted over a period of  $\approx 6$  mo. One of the replications showed almost total mortality in the 1st d after release and was not included in the analysis, which left 11 replications that were analyzed. The duration of a single replication was

3–10 d, depending on the time of year. The flies experienced severe mortality during certain seasons. More than 20 yr of experience releasing flies in this orchard indicates that high mortality is associated with periods when the trees are not flowering. This may imply that flowers provide a food source for the released population. The average duration of an experiment was  $\approx 8$  d. This is approximately the same duration as is typically reported in the literature (Serghiou & Symmons 1974). Each release was monitored until the population had been reduced to an essentially undetectable level.

During each replication, the traps were installed and removed on a daily basis (except on weekends). Traps were placed in the orchard in the predetermined grid pattern in the morning and removed 2 h later. This short exposure time was an attempt to ensure that the traps themselves would not bias the movements of the flies. Each trap was installed and removed sequentially in the same order so that all traps were exposed for 2 h. The number of flies captured in each trap during each 2-h exposure period was recorded. Each trap was inspected at approximately the same time each day.

### Results

We assume in our analysis that each trap attracts insects only from within the interior of a square region centered at the trap and having a side length equal to the trap spacing. That is, the trapping region may be visualized as a checkerboard, with a trap at the center of each square and with each square containing the area of attraction of the trap. Because all squares have equal area, the fraction of the total population contained within a square may be estimated by the fraction of the total trapped population that is trapped in that square. Fig. 1 shows a summary of the trap catch data for days 1, 3, and 7. The upper values represent the mean number of flies counted in each trap on that particular day. The lower values are generated by the fundamental model and are discussed below.

Qualitatively, the data indicate that the trapped population tends to remain in a roughly symmetric dispersal pattern centered about a point that drifts slightly from the point of release in the direction of the prevailing wind. The bulk of the trapped population remains well inside the trapping region for the duration of the experiment. We subdivide our analyses of the model into three distinct subsections, one for each type of analysis.

**Statistical Analysis.** The data set consists of a total of 11 releases, with recapture data for up to 10 d following release. Our statistical study uses data averaged over releases. To avoid problems with differential recapture rates among releases and with mortality, we studied spatial frequency of the population rather than population density as a function of time.

Dist from rel pt (m)	-518.0	-388.5	-259.0	-129.5	0.0	129.5	259.0	388.5	518.0	A
518.0	<b>0.4</b> 0.0	<b>0.2</b> 0.0	<b>0.2</b> 0.0	<b>0.6</b> 0.0	<b>0.5</b> 0.0	<b>0.0</b> 0.0	<b>0.0</b> 0.0	<b>0.0</b> 0.0	<b>0.0</b> 0.0	
388.5	<b>0.1</b> 0.0	<b>0.2</b> 0.0	<b>0.6</b> 0.0	<b>0.5</b> 0.1	<b>2.7</b> 0.1	<b>1.1</b> 0.0	<b>0.9</b> 0.0	<b>0.6</b> 0.0	<b>0.2</b> 0.0	
259.0	<b>0.0</b> 0.0	<b>0.6</b> 0.0	<b>2.3</b> 0.3	<b>7.4</b> 2.3	<b>8.3</b> 5.0	<b>6.4</b> 2.4	<b>1.5</b> 0.3	<b>0.6</b> 0.0	<b>0.5</b> 0.0	
129.5	<b>0.6</b> 0.0	<b>1.1</b> 0.1	<b>7.5</b> 2.3	<b>15.2</b> 22.9	<b>48.8</b> 53.4	<b>14.6</b> 23.2	<b>6.3</b> 2.4	<b>1.0</b> 0.1	<b>0.5</b> 0.0	
0.0	<b>0.1</b> 0.0	<b>1.1</b> 0.1	<b>4.1</b> 4.9	<b>40.6</b> 53.1	<b>228.1</b> 202.4	<b>28.8</b> 53.7	<b>8.4</b> 5.0	<b>2.8</b> 0.1	<b>4.9</b> 0.0	
-129.5	<b>0.8</b> 0.0	<b>1.3</b> 0.1	<b>1.4</b> 2.3	<b>6.8</b> 22.9	<b>23.6</b> 53.3	<b>17.5</b> 23.2	<b>1.7</b> 2.4	<b>0.5</b> 0.1	<b>0.1</b> 0.0	
-259.0	<b>0.0</b> 0.0	<b>0.3</b> 0.0	<b>1.0</b> 0.3	<b>0.7</b> 2.3	<b>1.6</b> 4.9	<b>0.6</b> 2.4	<b>0.5</b> 0.3	<b>0.3</b> 0.0	<b>0.4</b> 0.0	
-388.5	<b>0.0</b> 0.0	<b>0.1</b> 0.0	<b>0.2</b> 0.0	<b>0.5</b> 0.1	<b>0.3</b> 0.1	<b>0.2</b> 0.1	<b>0.4</b> 0.0	<b>0.1</b> 0.0	<b>0.1</b> 0.0	
-518.0	<b>0.1</b> 0.0	<b>0.0</b> 0.0	<b>0.2</b> 0.0	<b>0.1</b> 0.0	<b>0.5</b> 0.0	<b>0.1</b> 0.0	<b>0.0</b> 0.0	<b>0.1</b> 0.0	<b>0.0</b> 0.0	
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388.5	<b>0.1</b> 0.0	<b>0.0</b> 0.1	<b>0.1</b> 0.4	<b>1.0</b> 1.0	<b>3.0</b> 1.3	<b>0.9</b> 1.0	<b>1.4</b> 0.7	<b>0.5</b> 0.2	<b>0.0</b> 0.0	
259.0	<b>0.1</b> 0.1	<b>0.6</b> 0.4	<b>2.0</b> 1.7	<b>5.4</b> 4.1	<b>3.4</b> 5.8	<b>2.5</b> 4.2	<b>0.8</b> 1.7	<b>0.8</b> 0.5	<b>0.1</b> 0.1	
129.5	<b>0.1</b> 0.2	<b>0.6</b> 1.0	<b>3.2</b> 4.1	<b>5.0</b> 12.8	<b>17.8</b> 23.3	<b>10.0</b> 13.0	<b>1.8</b> 4.2	<b>0.8</b> 1.0	<b>0.2</b> 0.2	
0.0	<b>0.4</b> 0.2	<b>1.2</b> 1.3	<b>1.7</b> 5.7	<b>14.7</b> 3.2	<b>98.2</b> 93.0	<b>18.9</b> 23.5	<b>4.5</b> 5.8	<b>1.4</b> 1.3	<b>0.4</b> 0.2	
-129.5	<b>0.0</b> 0.2	<b>0.7</b> 1.0	<b>0.9</b> 4.1	<b>2.7</b> 12.8	<b>10.8</b> 23.3	<b>6.9</b> 13.0	<b>2.2</b> 4.2	<b>0.3</b> 1.0	<b>0.2</b> 0.2	
-259.0	<b>0.3</b> 0.1	<b>0.7</b> 0.4	<b>0.7</b> 1.7	<b>1.9</b> 4.1	<b>3.2</b> 5.8	<b>2.6</b> 4.2	<b>2.1</b> 1.7	<b>0.3</b> 0.5	<b>0.0</b> 0.1	
-388.5	<b>0.0</b> 0.0	<b>0.3</b> 0.1	<b>0.2</b> 0.4	<b>0.2</b> 1.0	<b>0.7</b> 1.3	<b>0.5</b> 1.0	<b>0.5</b> 0.5	<b>0.1</b> 0.1	<b>0.2</b> 0.0	
-518.0	<b>0.0</b> 0.0	<b>0.0</b> 0.0	<b>0.0</b> 0.1	<b>0.3</b> 0.2	<b>0.4</b> 0.2	<b>0.3</b> 0.2	<b>0.4</b> 0.1	<b>0.4</b> 0.0	<b>0.0</b> 0.0	
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518.0	<b>0.5</b> 0.0	<b>0.3</b> 0.0	<b>0.2</b> 0.1	<b>0.2</b> 0.1	<b>0.3</b> 0.2	<b>0.8</b> 0.1	<b>0.3</b> 0.1	<b>0.0</b> 0.0	<b>0.2</b> 0.0	
388.5	<b>0.0</b> 0.0	<b>0.0</b> 0.1	<b>0.0</b> 0.3	<b>0.3</b> 0.5	<b>1.5</b> 0.6	<b>2.0</b> 0.5	<b>1.8</b> 0.3	<b>0.7</b> 0.1	<b>0.5</b> 0.0	
259.0	<b>0.2</b> 0.1	<b>0.2</b> 0.3	<b>1.0</b> 0.7	<b>3.3</b> 1.4	<b>1.7</b> 1.9	<b>2.0</b> 1.4	<b>1.0</b> 0.7	<b>2.2</b> 0.3	<b>0.3</b> 0.1	
129.5	<b>0.3</b> 0.1	<b>0.8</b> 0.4	<b>0.8</b> 1.4	<b>4.5</b> 4.0	<b>3.5</b> 7.4	<b>6.7</b> 4.0	<b>1.5</b> 1.4	<b>0.2</b> 0.5	<b>0.2</b> 0.1	
0.0	<b>0.0</b> 0.2	<b>0.5</b> 0.5	<b>1.5</b> 1.8	<b>3.8</b> 7.3	<b>17.0</b> 30.9	<b>5.3</b> 7.4	<b>1.5</b> 1.9	<b>0.3</b> 0.6	<b>0.0</b> 0.2	
-129.5	<b>0.0</b> 0.1	<b>0.7</b> 0.3	<b>1.7</b> 0.7	<b>1.7</b> 4.0	<b>2.3</b> 7.3	<b>2.5</b> 4.0	<b>0.2</b> 1.4	<b>0.7</b> 0.5	<b>0.8</b> 0.1	
-259.0	<b>0.0</b> 0.0	<b>0.5</b> 0.3	<b>1.7</b> 0.6	<b>0.3</b> 1.3	<b>0.3</b> 1.8	<b>1.0</b> 1.3	<b>0.5</b> 0.6	<b>1.0</b> 0.3	<b>0.8</b> 0.1	
-388.5	<b>0.2</b> 0.0	<b>0.5</b> 0.1	<b>0.0</b> 0.3	<b>0.3</b> 0.4	<b>0.3</b> 0.5	<b>0.3</b> 0.3	<b>0.2</b> 0.3	<b>0.8</b> 0.1	<b>0.0</b> 0.0	
-518.0	<b>0.0</b> 0.0	<b>0.0</b> 0.1	<b>0.7</b> 0.3	<b>0.2</b> 0.4	<b>0.0</b> 0.5	<b>0.5</b> 0.5	<b>0.3</b> 0.3	<b>0.0</b> 0.1	<b>0.0</b> 0.0	

Fig. 1. Comparison of results of the fundamental model with normalized average data values. Values in bold represent average number of insects found in the trap at that location following release of irradiated *C. capitata* in a macadamia nut orchard. Values in plain type represent corresponding model values. A, 1 day after release; B, 3 days after release; C, 7 days after release.

There are two ways one could average frequency data over the releases. One is, for each day, to simply add all of the trap catch data for each trap for that day, and to add all the sums for each trap into a grand sum. The frequency for each trap would then be the trap sum divided by the grand sum. Mathematically this can be expressed as follows. For a given day, let  $n_{ij}$  be the number caught in trap  $i$  in release  $j$ . Let  $N_i$  be the trap sum for trap  $i$ , so  $N_i = \sum_j n_{ij}$ , the sum being taken over all releases for which there is data for that day. Let the grand sum be denoted  $T$ , then

$$T = \sum_{i=0}^n s_{ij} n_{ij}$$

If  $U_i$  denotes the average frequency in trap  $i$ , then  $U_i = N_i/T$ .

A second method is to convert the individual data for the given day for each release into frequencies, then average over releases. Mathematically, using the same notation as in the previous paragraph, let  $T_j$  denote the total trap catch for a given day for release  $j$ , then  $T_j = \sum_i n_{ij}$ . Let  $u_{ij}$  denote the frequency at trap  $i$  in release  $j$ , so that  $u_{ij} = n_{ij}/T_j$ . Then the average trap frequency  $U_i$  for trap  $i$  is  $U_i = \sum_j u_{ij}/R$ , where  $R$  is the number of days for which there is recapture data. It is a simple matter to show that the frequencies  $U_i$  obtained by this method are truly frequencies; that is, that they satisfy  $\sum_i U_i = 1$ .

Spatial frequencies obtained by the first of the two methods given above give greater weight to releases with higher trap catches, whereas frequencies obtained by the second method weight all releases equally. One might argue on this basis in favor of either method. The second method has the advantage that statistical properties of the frequencies, such as their variance, can be readily obtained. We examined our data using each of the two methods and found very little difference in the results. Only results obtained from the second method are given here, as those from the first method are virtually identical.

Table 1 summarizes the results of the analysis. The contents of the table include kurtosis, circular statistics, and mean distance flown, as functions of the number of days since release. The third column of the table gives the kurtosis of the average frequencies by day from release. The kurtosis of a frequency distribution is defined as  $\kappa = \mu^4/\sigma^2$ , where  $\sigma^2$  is the variance of the distribution and  $\mu^4$  is the fourth central moment (Okubo, 1980). For a population dispersing by random, brownian motion, the kurtosis of the frequency distribution is that of the Gaussian normal probability density, which is 3. It is evident from the table that the population initially is distributed in a highly leptokurtic manner and that the kurtosis generally tends to decline with time from day of release. As has already been mentioned, this pattern was observed by Dobzhansky & Wright (1943), and it has since been

Table 1. Basic statistical properties of the compiled data as a function of elapsed time since release of irradiated *C. capitata* in a macadamia nut orchard

No. elapsed d	No. replications	Kurtosis	$\chi^2$ statistic	Location of standard ellipse			Mean distance flown, m
				Center	Major axis	Minimum axis	
1	11	17.47	7.85	27.9	136.6	134.8	113.8
2	11	15.73	8.73	34.7	130.4	128.3	126.6
3	10	13.74	10.34	45.5	143.3	132.8	156.5
4	10	9.74	10.25	55.6	179.2	167.0	192.0
7	6	4.84	12.10	62.9	214.0	208.2	248.5
8	8	6.85	18.48	76.3	208.8	196.1	246.1
9	6	7.25	6.77	61.1	228.2	175.7	240.0
10	5	6.47	6.20	66.9	235.5	200.3	260.3

observed by other workers (e.g., Aikman & Hewitt 1972).

The fourth column in Table 1 gives an indication of the circular symmetry of the frequency distribution. The data were grouped by angular position from the release point into eight groups, each of angular size  $\pi/8$ . The  $\chi^2$  statistic was then computed for the test of randomness of the distribution. A value of the  $\chi^2$  statistic  $<14.07$  in the table indicates that the hypothesis of radial symmetry cannot be rejected at the 0.05 level of significance for the distribution data for that day. The fifth, sixth, and seventh columns of Table 1 give circular statistics (Batschelet 1981) of the population spatial frequency distributions. These may be compared with the data of Baker et al. (1986). The columns give the values of the center, half-length of the major axis, and half-length of the minor axis, respectively, of the standard ellipse of the distribution. These are computed from equation 7.27 of Batschelet (1981).

The last column in Table 1 gives the mean distance in meters flown by a member of the population. This is similar to the statistic computed by Fletcher (1974) and Fletcher & Economopoulos (1976), although it is not computed in the same way. The two papers mentioned above compute the mean flight distance by dividing their test region into annuli. We compute our mean distance by averaging over the grid in the following way: Let  $r_i$  denote the distance from the release point to trap  $i$ , and let  $f_i$  denote the fraction of the population caught in that trap. Then the mean distance  $d$  flown by a member of the population is

$$d = \sum_i r_i f_i$$

Several points may be noted immediately from inspection of Table 1. One is that the mean distance flown and the variance in distance flown are sufficiently small that the assumption that the entire distribution stays within the trapping region during the course of the trapping period is a reasonable one. A second is that the distributions, for the most

**Table 2.** Parameter values and fit ( $R^2$ ) of the model  $\phi(r) = \alpha \exp(r/\beta)^{-\gamma}$  for released irradiated *C. capitata* in a macadamia nut orchard

Day	$\gamma$ Fixed at 1		$\gamma$ Fixed at 2		$\gamma$ Free		
	$\beta$	$R^2$	$\beta$	$R^2$	$\beta$	$\gamma$	$R^2$
1	45.56	0.980	88.76	0.958	3.16	0.423	0.992
2	48.82	0.973	93.43	0.943	3.11	0.416	0.991
3	55.09	0.944	102.2	0.889	2.07	0.378	0.979
4	73.07	0.894	132.4	0.761	4.98	0.422	0.951
7	114.1	0.761	224.3	0.625	32.43	0.587	0.796
8	103.7	0.823	197.5	0.676	28.82	0.581	0.859
9	84.68	0.808	158.0	0.594	1.87	0.349	0.934
10	106.3	0.715	219.1	0.500	4.78	0.394	0.831

part, do not significantly depart from circularity. This, combined with the fact that the center of the standard ellipse stays near the release point and that the major and minor axes of the standard ellipse are nearly equal, indicates that the frequency distribution is almost radially symmetric. In these aspects, particularly the relative stability of the center of the population distribution, our results are quite different from those of Baker et al. (1986), who found that the center of their population distribution moved in an erratic manner. A final point is that the average distance flown and the size of the standard ellipse expands very rapidly in the first few days after the release of the population but does not expand very much after that. This indicates that the population disperses rapidly at first, but slowly after a few days. Mortality imposes a spatially uniform reduction on the dispersing population that is not reflected in the frequency statistics.

**Empirical Models.** One of the simplest ways to characterize the spatial distribution of a population is to fit the frequency distribution (i.e., the proportion of the population) to some curve such as an exponential. If the distribution of the population is assumed to be radially symmetric, then the frequency  $\phi(r)$  at a distance  $r$  from the center is defined by saying that the fraction of the population located at a distance between  $r$  and  $r + dr$  from the center is  $\phi(r)dr$ . In this section, we construct models for the population frequency distribution by fitting the data to curves of the form

$$\phi(r) = \alpha \exp[-(r/\beta)^\gamma].$$

This function generalizes the normal distribution, which is obtained if  $\gamma = 2$ , and the exponential distribution, which is obtained if  $\gamma = 1$ . Time is not explicitly included but is implicitly included by making the parameters vary with time. In the normal distribution, the variance of the distribution is  $\beta/2$ ; in the exponential distribution the variance is  $1/\beta$ . Because  $\phi(r)$  is a spatial frequency distribution, it must integrate to unity. This constrains the value of  $\alpha$  to be

$$\alpha = \frac{\gamma}{2\pi\beta^2\Gamma(2/\gamma)}$$

(Taylor 1980), where  $\Gamma$  is the gamma function

(Abramowitz & Stegun 1964). Therefore, fitting data to the curve in the general case involves selecting the two parameters  $\beta$  and  $\gamma$ . If  $\gamma$  is held fixed, there is only one free parameter, which is  $\beta$ . The parameters of the curves  $\phi(r)$  were obtained by nonlinear least squares regression. Two regression methods were tested; one is more complex and, in principle, more exact, whereas the other is a simple approximate method suitable for field analysis with a hand-held calculator. The first method considers the fraction  $F_i$  of the population contained in checkerboard square  $i$  as given by

$$F_i = \int_{x_{i-1}}^{x_i} \int_{y_{i-1}}^{y_i} \phi(x^2 + y^2) dy dx$$

where  $x_{i-1}$ ,  $x_i$ ,  $y_{i-1}$ , and  $y_i$  are the coordinates of the corners of the square. Let  $f_i$  be the average fraction of insects caught in trap  $i$ , and let  $F_i$  be as defined above. Then in this method, the parameters  $\beta$  and  $\gamma$  are estimated by making  $f_i$  as close to  $F_i$  as possible; i.e., by iteratively computing the sum of squares  $\Sigma (F_i - f_i)^2$  until this sum is minimized. We used a nonlinear minimization method to minimize the sum of squares. For the case in which the value of  $\gamma$  is fixed, the golden section search method was used to find the best value of  $\beta$ . For the case in which  $\gamma$  is free, we used the Nelder-Mead method. Both methods are described by Avriel (1976).

In the second method the value of the function  $\phi(x_i^2 + y_i^2)$  was used in place of the fraction  $F_i$ , described above. This method, which mathematically is a rectangular approximation to the integral given above, is simple because the integrals do not need to be computed. It is primarily useful as a field method for rapid development of curve fits using only a hand calculator. For this reason, values were computed only for the simplest case (when  $\gamma$  was fixed at 1).

We mention in passing that an alternative approach to ours is to transform the data using logarithms and to do a regression on  $\ln \phi(r)$  in a manner similar to that of Taylor (1980). Although the regression in this case is simpler, we found that for our data, this method biased the weights of the data points to such an extent that it gave considerably different results from those presented here.

Table 2 shows the results of the regression analysis. The table shows regressions for the cases in which  $\gamma$  is fixed at  $\gamma = 1$ , fixed at  $\gamma = 2$ , and set free, respectively, for the first method. As expected, the best  $R^2$  values are obtained when  $\gamma$  is free. In this case, the optimal value of  $\gamma$  is consistently near one-half. This is very similar to the results of Finch & Skinner (1975) and Taylor (1978).

The regression results for the second, simpler method were only tested for  $\gamma$  fixed at  $\gamma = 1$ . For this case the computed values of  $\beta$  were  $\beta = 61.6$  m for day 1 and  $\beta = 108.9$  m for day 7. Comparison with the corresponding values in Table 2 indicates that the simpler method provides reasonably ac-

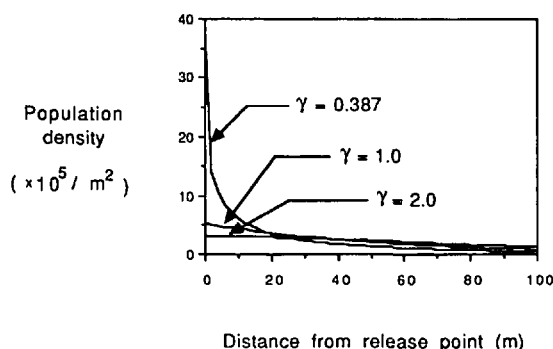


Fig. 2. Plots of curves of the form  $\phi(r) = \alpha \exp(\beta r)$ ,  $\phi(r) = \alpha \exp(\beta r^2)$ , and  $\phi(r) = \alpha \exp(\beta r^3)$  to the average spatial frequency data for the released populations of irradiated *C. capitata* on the third day after release. Crosses represent the actual data.

curate results. Fig. 2 shows plots of the three curves obtained by fitting curves to data from trap catches on the 3rd d after release. The difference between the function  $\phi(r)$  with  $\gamma$  free and the other two functions is quite striking, particularly given the similarity of the computed  $R^2$  values shown in Table 2. A second way to present the data, which has some relevance to sterile insect release programs, is to plot the fraction  $v(r)$  of the population within a given distance  $r$  from the release point. This fraction is given by

$$v(r) = 2\pi \int_0^r \phi(\rho) d\rho$$

where  $\phi$  is the spatial frequency function. This method of presenting the information also is the most useful means of comparison of the curves with the actual data. Fig. 3 shows plots of the function  $v(r)$  for day 3 together with the actual average population values for this day. It is again evident that the function  $\phi(r)$  with  $\gamma$  free represents the data most closely.

**Fundamental Model.** In this section, we develop a model for the dispersal of sterile medflies based on the diffusion equation. This model must be formulated in terms of the population density, denoted  $n(x, y, t)$  at location  $(x, y)$  and time  $(t)$ , rather than the spatial frequency as in the curve fit model. For this reason mortality is explicitly included. The simplest diffusion-based model incorporating mortality would be written

$$\frac{\partial n}{\partial t} = D \left( \frac{\partial^2 n}{\partial x^2} + \frac{\partial^2 n}{\partial y^2} \right) - \mu n,$$

where  $D$  is a diffusion coefficient and  $\mu$  is the mortality rate. The use of this equation as a model for insect dispersal has been extensively discussed by Kareiva (1983) and Rudd & Gandour (1985). As was the case for Dobzhansky & Wright (1943, 1974), this simple model does not provide a very good representation of our data. In the first place, the

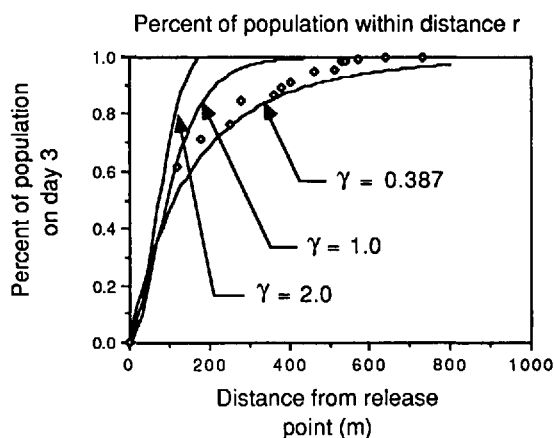


Fig. 3. Plots of the fraction  $v(r)$  of the population of released irradiated *C. capitata* located within a distance  $r$  from the point of release. Solid curves are integrals of the functions  $\phi(r) = \alpha \exp(\beta r)$ ,  $\phi(r) = \alpha \exp(\beta r^2)$ , and  $\phi(r) = \alpha \exp(\beta r^3)$ . Crosses represent actual data.

center of the dispersal pattern shown in Fig. 1 moves away from the release point as time progresses. Second, and more important, the rate of dispersal declines as the experiment progresses. It is therefore necessary to formulate a more complex model.

The movement of the center of the dispersal pattern is modeled by including a term representing convection, which may be caused by behaviorally directed dispersal or by prevailing winds or both. The decline in dispersal rate with time is modeled by assuming that, at any given time, the population behaves as if it consists of two groups, one that is actively dispersing at that time and one that is not. We refer to these two groups as the "unsettled" and "settled" populations and denote them by  $u(x, y, t)$  and  $s(x, y, t)$ , respectively. Thus we have  $n(x, y, t) = u(x, y, t) + s(x, y, t)$ . Population models similar to this have been studied by Okubo (1980) and by Zia (1986).

In our model, members of the population may move back and forth between the two groups, but there is a net tendency for the size of the "settled" group to increase. Thus after a time, most of the population is in the "settled" group, and the measured dispersal rate of the population is greatly reduced. It is important to note that we are not proposing that the actual fly population consists of two separate and distinct subpopulations; rather, we are saying that it can be described by a mathematical model consisting of two subpopulations. It is likely that the dispersal behavior of the actual insects is considerably more complex than this. In summary, our model comprises the following four separate effects: diffusion, which describes the tendency of the flies to disperse randomly; convection, which describes the tendency of the flies to disperse in a uniform direction; settling, which represents the tendency of the flies to cease dispersing for at

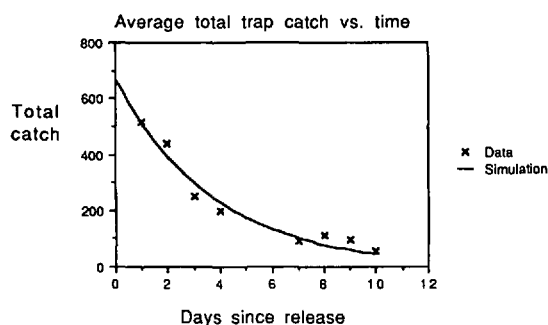


Fig. 4. Comparison of simulated total trap catches based on solutions of the differential equation model for dispersal with actual average trap catches.

least some of the time; and mortality, which is assumed in the model to be the same for "unsettled" and "settled" flies.

The model is formulated as follows. The "unsettled" flies are assumed to be diffusing with a fixed diffusion coefficient  $D$  and being convected at a fixed rate  $c$  in a direction with angle  $\theta$  to the  $x$  axis. At time  $t = 0$ , when an initial population  $N$  of flies is released, all of the flies are in the "unsettled" group. As  $t$  increases, the flies move between the "unsettled" and "settled" groups in such a way that the net rate of relative increase of the "settled" group has a fixed value denoted  $\sigma$ . Finally, both the "unsettled" and "settled" populations are subject to mortality at a relative rate  $\mu$ .

The differential equations describing the model together with their solution are

$$\frac{\partial u}{\partial t} + c \left( \frac{\partial u}{\partial x} \cos \theta + \frac{\partial u}{\partial y} \sin \theta \right) = D \left( \frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2} \right) - (\mu + \sigma)u$$

$$\frac{ds}{dt} = \sigma u - \mu s$$

subject to the initial conditions  $u(x, y, 0) = N_0 \delta(x, y)$  and  $s(x, y, 0) = 0$ . Here  $\delta(x, y)$  denotes the two-dimensional Dirac delta function. The boundary conditions are that  $u(x, y, t)$  and  $s(x, y, t)$  tend toward zero as the radial distance from the origin tends toward infinity. The solutions to these equations are

$$u(t, x, y) = \frac{N_0}{4\pi Dt} e^{-(\mu + \sigma)t} e^{-[(ct - x \cos \theta - y \sin \theta)^2 + (-x \sin \theta + y \cos \theta)^2]/4Dt}$$

$$s(t, x, y) = \int_0^t \sigma u(\tau, x, y) e^{-\mu(t-\tau)} d\tau.$$

There are six parameters in this model: the initial population  $N_0$ , the mortality rate  $\mu$ , the diffusion coefficient  $D$ , the net "settling" rate  $\sigma$ , the convection speed  $c$ , and the convection angle  $\theta$ . These parameters may be estimated using the trap catch data sets. The estimation procedure is as follows.

Table 3. Parameter values for the diffusion-convection-settling-mortality model for release of irradiated *C. capitata* in a macadamia nut orchard

Day	$D$	$\sigma$	$c$	$\theta$
1	16,071.9*	3.415*	1.510*	0.096*
2	6,732.7	0.898	0.603	0.058
3	5,253.0	0.563	18.140*	0.303*
4	5,253.0	0.387	0.774	0.056
7	5,389.4	0.165	0.548	0.062
8	7,412.7	0.289	0.279	0.029
9	4,417.8	0.148	0.786	0.061
10	6,152.7	0.119	0.393	0.052
Avg	5,792.7	0.367	0.563	0.053

Average parameter values were computed neglecting the values marked with an asterisk.

We first assume that the total number of flies caught on a given day in a given release is proportional to the total fly population with a fixed proportionality constant. If we let  $N(t)$  denote the total population at time  $t$ , then

$$N(t) = N_0 e^{-\mu t}$$

It follows from the assumptions of our model that  $N(t)$  declines exponentially with rate constant  $\mu$ . We may therefore estimate  $N_0$  and  $\mu$  by exponential regression of the total trap catch for a given release. By estimating our parameter  $N_0$  in this way, we are assuming that our model describes not the total population but rather a fraction of the population equal to the fractional trapping rate. As long as the fractional trapping rate is constant, this will not impose any inaccuracy in our estimation of the other parameters. The estimates obtained for  $N_0$  and  $\mu$ , averaged over all replications, are  $N_0 = 669.0$  and  $\mu = 0.268$ . Fig. 4 shows a plot of the function  $N(t)$  together with the average number of captures for each day.

Having estimated  $N_0$  and  $\mu$ , the remaining four parameters may be estimated by nonlinear regression similarly to the simple curve fit models  $\phi(r)$  already described. As a test of the model, we used the following procedure to obtain these estimates. For each day for which there were data, the average number of flies caught in each trap was computed. We then estimated the four parameters  $D$ ,  $\sigma$ ,  $c$ , and  $\theta$  for that day. The estimation method was to minimize the sum of the squares of the deviations using the Nelder-Mead method. If the model is a good one, then the values of the four parameters should be the same for each day. Table 3 shows these values for each day. The parameters change substantially from day 1 to day 2, but afterward are reasonably constant with one outlier. Table 3 also shows the average values of all the parameters of the model. These averages, which are the estimates of the population parameters, were computed without using the outlier values marked with an asterisk. Fig. 1 shows a comparison of the results of the fundamental model with the average data for days 1, 3, and 7. The qualitative fit of the model is good, including the convective



movement, the cessation of dispersal with increasing time, and the effect of mortality. The quantitative fit was tested by computing a linear regression of predicted against observed values for the nine central traps for all days (Fig. 5). The model tended to underestimate the population density near the release point and correspondingly overestimate it farther away. The null hypothesis that the data plotted in Fig. 5 can be fit with the line  $y = x$  is rejected ( $P < 0.01$ ).

The parameter values of the model may be interpreted as follows. The value of  $\mu = 0.268 \text{ d}^{-1}$  given above indicates that the population experienced an average mortality rate of  $(100\%)(1 - e^{-0.268}) = 24\%/d$ . The value of  $\sigma = 0.367 \text{ d}^{-1}$  indicates that the size of the settled group increased at a rate of  $(100\%)(1 - e^{-0.367}) = 44\%/d$ . The value of  $D$  (5,792.7) indicates that the area occupied by the unsettled group expanded  $\approx 6,000 \text{ m}^2/d$ , or  $\approx 0.006 \text{ km}^2/d$ . Given the high rate of growth of the settled group, the effective expansion of the population's area ceased after about 3 d. Finally, the low value of  $c$  (0.563 m/d) indicates that convection did not play a significant role in the dispersal of the population. The value of  $\theta$  (0.053) indicates that convection occurred in a west-north-westerly direction, approximately that of the prevailing wind.

### Discussion

Our results indicate that the overall dispersal patterns of the released sterile Mediterranean fruit flies are similar to those of other insect species that have been studied. The population distribution is initially leptokurtic, and the kurtosis of the distribution declines with time. The average kurtosis in our study actually ceased declining and even increased slightly at the end of the test. This may, however, be due to experimental error because the number of flies caught late in the test was often relatively small. The dispersal of the flies was not strongly dependent on angular position; the standard ellipses of the population were not very different from circles centered at the point of release. This indicates that convection played only a minor role in influencing dispersal, a conclusion reinforced by the results of the fundamental model.

Most of the dispersal of the populations occurred within the first 3 d after release. After that, the population settled down considerably. There are a number of possible explanations for this "settling" effect. One is that the flies respond to overcrowding by dispersal and that once this dispersal, together with mortality, has reduced the level of crowding, the dispersal ceases. A second potential explanation is that the more rapidly dispersing subpopulation leaves the experimental area altogether. Several studies (Christiansen & Foote 1960, Steiner et al. 1962, Hafez et al. 1973, Wong et al. 1982) have found a fraction of a released population of flies at a great distance from the release point. Our data

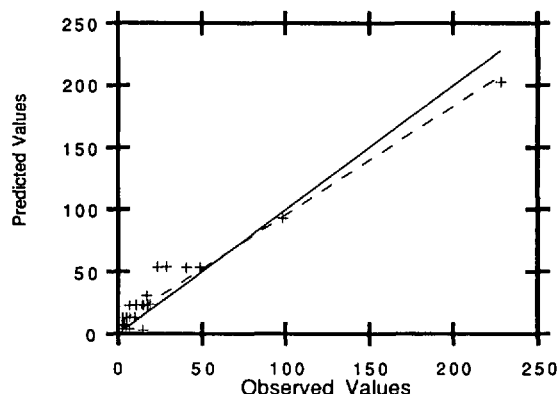


Fig. 5. Plot of predicted against observed values for the fundamental model. The dashed line shows the best least-squares fit, given by  $y = 8.48 + 0.87x$ .

argues against this second explanation, however, because if a substantial fraction of the population was leaving the trapping region, the number of flies trapped on the boundary of the region should have been larger. One could, in principle, use either the empirical or the fundamental model to estimate the fraction of the population at a great distance from the release site, but this would involve an extrapolation of the model to questions well beyond its validity of prediction. In any case, this information is not important for the management of released sterile populations because small populations of sterile insects have little effect on the wild population (Plant 1986).

The rate of dispersal of the populations was never very large. The average distance flown over the maximum life span of the cohort was  $<300 \text{ m}$ , and virtually the entire population remained within the  $1 \text{ km}^2$  test area. The average distance flown by the sterile flies was comparable to that of flies *D. oleae* reported by Fletcher & Economopoulos (1976) and the Mediterranean reported by Nadel & Guerrieri (1969) and Wong et al. (1982); it was considerably less than that of *D. tryoni* reported by Fletcher (1974).

One of our primary objectives was to present a constructive review of the methods available for the analysis of insect populations released from a single location, to show how these methods can complement and reinforce each other, and to permit comparison with other studies. For this reason, we provide considerable mathematical detail on the statistical and modeling techniques employed. The combined statistical and fundamental studies give an overall picture of a dispersal pattern consisting primarily of brownian motion. The population tends to remain in a pattern of circular symmetry about the release point. Our model displays the same decline in kurtosis observed in other studies but expands on the notion of two subpopulations, first introduced by Dobzhansky & Wright (1943), to include the movement of population

members from one subpopulation to the other rather than incorporating a differential mortality rate. The fundamental, diffusion-based modeling results indicate that under the conditions described here, a released population of sterile flies may be adequately described by a model that includes diffusion, convection, "settling," and mortality, and that of these, convection is the least important component. Each of the effects is described by a single constant parameter except for convection, which is described by two. Although the differential mortality rate model can account for the reduction in kurtosis of the population frequency distribution, it cannot account for the decline in dispersal rate as can a model incorporating differential dispersal rates. The fundamental model does not, however, provide a perfect fit to the data (Fig. 1 and 5). Although it predicts the values at the release point fairly well, it tends to predict a less rapid dispersal in the area immediately adjacent to the release point than actually observed.

The empirical and statistical analyses are useful from a more applied perspective. The Mediterranean fruit fly is a worldwide pest of major economic significance (Andrew et al. 1978). It is not at present established in the continental United States, although it is established in Hawaii and Central America and climatic considerations indicate that it could become established in a large portion of the continental United States (Gjullin 1931). Localized Mediterranean fruit fly infestations have occurred on numerous occasions in California and Florida, and on each occasion the population has been eradicated, often at great expense (Jackson & Lee 1985). One of the preferred eradication methods is the sterile insect technique (Cunningham et al. 1980). For this method to be successful, the entire spatial extent of the infestation must be inundated with sterile flies. Theoretical considerations and practical experience indicate that any localized failure to control the population will result in rapid and dramatic growth of the population in that area, soon overwhelming the capacity of the sterile insects to suppress the wild population in other areas (Plant 1986). For this reason it is important to know the dispersal characteristics of both the wild and the sterile populations (Wong et al. 1982). In particular, it is essential in planning release strategies to know the distance that the released sterile populations may be expected to disperse. Our study provides some information in this area. Based on the mortality rate shown in Fig. 4, less than half of the released population will survive beyond day 3. Data in Table 2 and Fig. 3 show that  $\approx 70\%$  of this surviving population will remain within 150 m of the point of release. Therefore, it is important in an efficient eradication program that the spacing between release points or lines be no more than 200–250 m to obtain thorough distribution. Of course, wider spacing of distribution lines could be compensated for by greatly increasing the numbers released at the sites but, given the

negative exponential nature of the survival and dispersal parameters, this is a highly inefficient approach. Experience in large-scale eradication programs such as in California in 1980–1982 and 1989–1990 shows that sterile fly supplies become an important limiting factor, so it is imperative that efficient use be made of such supplies.

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