# Dispersion theory and the sterile insect technique: application to two species of fruit fly

A. Meats[1]*, C.J. Smallridge[2] & B.C. Dominiak[3]

[1]*Fruit Fly Research Centre, School of Biological Sciences, University of Sydney A08, NSW 2006, Australia,* [2]*South Australian Research and Development Institute, Entomology Unit, Waite Precinct, GPO Box 397, Adelaide, SA 001, Australia,* [3]*Department of Primary Industries of New South Wales, 161 Kite Street, Orange, NSW 2800, Australia*

Accepted: 31 January 2006

*Key words: Ceratitis capitata*, *Bactrocera tryoni*, power law, negative binomial, Diptera, Tephritidae, SIT

**Abstract**

Dispersion theory is applied to the distribution of two kinds of sterile insect, Mediterranean fruit fly (Medfly), *Ceratitis capitata* (Wiedemann), and Queensland fruit fly (Qfly), *Bactrocera tryoni* (Froggatt) (Diptera: Tephritidae). Dispersion theories are an essential basis of sampling theory and sampling plans, but this paper looks at them from another direction and uses data from arrays of sterile insect technique (SIT) monitoring traps to compare the utility of different measures such as coefficient of variation (CV), the exponent b of Taylor's power law, and exponent k of the negative binomial distribution and also derives predictions pertaining to the density (and hence release rate) of sterile insects that would be required to achieve effective coverage of the target area. This is far more useful than reliance on just the mean values of trap catches because such reliance takes no account of the fact that sterile flies distribute themselves unevenly with many patches inadequately covered despite the impression given by the mean. Data were used from recapture rates following either 'roving releases' of Medfly or releases from fixed points of Qfly. The relation of recapture rate to CV indicated that a doubling of release rate in order to double average recapture rate from 150 per trap per week to a value of 300 would have very little effect in terms of reducing CV and that there appears to be no practical prospect of reducing CV to below unity with the current methods of release without incurring a manifold increase in cost. Similarly, models derived from the negative binomial equation indicated that a law of diminishing returns applies in terms of the increase in the amount of adequate coverage (such as the percentage of traps catching >50 flies per week) that can be obtained by increasing release rates.

## Introduction

Fruit flies tend to have contagious (clumped) distributions. Grosser patterns can be related to features of the habitat if the latter is variable (Zalucki et al., 1984; Vargas et al., 1990; Dimou et al., 2003; Papadopoulos et al., 2003). However, Plant & Cunningham (1991) released sterile Mediterranean fruit fly (Medfly), *Ceratitis capitata* (Wiedemann) (Diptera: Tephritidae), in an essentially homogeneous host-free plantation of Macadamia, and although mean recapture rate declined with the distance from the release point, there was also wide unexplained spatial variation in recapture rates in traps at any given distance. Likewise, releases of sterile Queensland fruit fly (Qfly), *Bactrocera tryoni* (Froggatt) (Diptera: Tephritidae), in 5 km$^2$ of citrus orchards resulted in a heterogeneous distribution, not all of which was obviously related to any variation in the habitat or distances from the release points (Horwood & Keenan, 1994). This should not be surprising because the history of sequential sampling plans has been essentially one of dealing with contagious distributions of pests in monocultures that would contain no obvious clues as to how to distribute sampling effort on a priori grounds; examples of these include pests in cotton (Kuehl & Fye, 1972), mites on citrus (Hall et al., 1997), aphids on Brussels sprouts (Wilson et al., 1983), borers in corn (Shelton et al., 1986), and leafhoppers on potatoes (Walgenbach et al., 1985) in rice (Kuno, 1963) and in Bermuda grass (Buntin, 1988). The causes of such distributions could be behavioural, due to intra- or interspecific interactions or some combination of these, but they are by no means obvious without closer investigation (Kuno, 1991; Southwood & Henderson, 2000).

*Correspondence: A. Meats, Fruit Fly Research Centre, School of Biological Sciences, University of Sydney A08, NSW 2006, Australia. E-mail: awm@bio.usyd.edu.au

 

An essential aim of sterile insect technique (SIT) (as with control using cover sprays of pesticide) is to treat all the individuals of the target pest within the target area. If this is not achieved, the pest may persist in localized patches or even increase locally to make control measures ineffective. It may not be necessary for treatment to reach all parts of the target area (for instance, if the target pest does not inhabit rocky outcrops or certain patches of vegetation), but the application of treatment should coincide with the distribution of the pest and in the absence of any detailed knowledge of that distribution, endeavours are made to spread sterile insects as evenly as possible in the areas in which the pest is likely to be. With released Medfly, a known cause of contagious distribution is the tendency of most of them to remain within a few hundred metres of where they are put, with relatively high concentrations staying around the point of release (Wong et al., 1982; Baker & Chan, 1991; Plant & Cunningham, 1991); with released Qfly, dispersal between 0.5 and 85 km has been recorded several times (review by Meats, 1998a), but few data are available for shorter distances although current models suggest that densities would be relatively far higher within 200 m of the point of release (Meats, 1996, 1998a,b).

Releases of sterile flies for SIT against infestations of Medfly are therefore designed to achieve a continuous (if not even) spatial distribution through aerial releases (Nadel et al., 1967; Howell et al., 1975; Vargas et al., 1995; Barry et al., 2004; Rendon et al., 2004) or 'roving' ground releases from moving vehicles (Cunningham et al., 1980), or both (Aruani et al., 1996). For the Qfly, SIT releases are at fixed points that are usually no further apart than 0.4 km and at the midpoints between the traps of the monitoring array (Meats, 1996; Meats et al., 2003).

The success of the release strategy in achieving an even distribution of sterile insects should be apparent from the distribution of recaptured sterile insects in the array of monitoring traps and in particular from the degree of dispersion. Measures of the spatial heterogeneity in density (degrees of dispersion) can be quantified in terms such as the coefficient of variation (CV) in density (Pacala & Hassell, 1991) or its spatial autocorrelation (Buntin, 1988; Clarke et al., 1997; Papadopoulos et al., 2003), the exponent of the negative binomial model (Pielou, 1960; Kuno, 1991; Nyrop & Binns, 1991; Clift & Meats, 1998; Southwood & Henderson, 2000), the exponent of Taylor's power law, or measures related to the latter (Buntin, 1988; Taylor & Woiwood, 1989; Nyrop & Binns, 1991; Southwood & Henderson, 2000).

Estimates of the degree of dispersion of a pest and its temporal variation can be utilized in strategies for its management (Clarke et al., 1997; Papadopoulos et al., 2003) especially to develop decision-making criteria for the initiation of control measures or to develop the most efficient sampling plan (in terms of accuracy of estimates obtained) for a given degree of effort (Kuno, 1991; Nyrop & Binns, 1991; Southwood & Henderson, 2000). However, some measures of dispersion are also of great significance to SIT because patterns of abundance of both sterile and target insects are of significance to its efficiency (Meats, 1983, 1996; Shiga, 1986). The most important factor in release strategies for SIT is the ratio of sterile to target insects (S : W ratio). The strategy could fail if the dispersion of sterile insects is such that there are patches of habitat where either there are no sterile flies or not enough of them to achieve a sufficiently effective S : W ratio should target flies be present as well. If a trap catches no sterile flies, the density of the latter in its vicinity is almost certain to be ineffective, especially if one or more target flies is trapped at the same time.

An effective density for sterile flies in a particular vicinity (as indicated by flies caught per week in the relevant trap) would depend upon the density of target flies (as indicated by the number of target flies caught in the same trap). Given that the density of target flies is usually reduced with a preliminary program of bait spraying (Villaseñor et al., 2000), it is most probable that the number of target flies to be found in a trap would be no more than 10 per week. Thus, we could deem the density of sterile flies to be potentially ineffective in a particular locality if 10 or fewer sterile flies per week were being caught in the relevant trap but probably effective if more than 50 sterile flies per week were trapped. It is difficult to be more precise at present because reports of effective ratios of sterile to wild flies are usually based on wide arrays of traps where many of the latter have ceased to catch target flies; in such circumstances, the S : W ratio appears to be very large whereas the true effective ratio should be based on the results of traps where target flies are still being caught (Meats, 1983, 1996).

It is the purpose of this paper to show that the relation of mean density to dispersion indices (particularly the exponent of the negative binomial distribution) can be used to determine the relation of the recapture rate (hence, by inference the release rate) of sterile Medfly or Qfly to the proportion of the target area that would be covered by an effective density of those insects. Specifically, it uses a model derived from the negative binomial equation to relate the mean of sterile flies recaptured per week to the percentage of traps with weekly recaptures of more than 0, 10, and 50 sterile flies.

## Materials and methods

### Releases of Medfly in Adelaide

'Roving' releases of sterile male Medfly were made in Adelaide (South Australia) from early spring to mid-summer of

2001 (September to December). Release of males only was possible through the use of a genetic sexing strain (Vienna 7 Mix 99) in which female eggs could be killed by exposure to a mild heat stress that did not affect males (Franz et al., 1996). The Western Australian Department of Agriculture in Perth produced the pupae, which were sterilized with 180 Gy gamma irradiation from a $^{60}$Co source. They were marked with fluorescent powders (Fiesta®, FEX Series, Swada, London, UK) and air freighted to Adelaide on a daily basis. Fourteen gram of pupae in paper bags were placed in 5-l cardboard tubs with 40 ml aqueous gel of Agar (0.6%) and sugar (18%), with the preservative methylparaben (0.01%). The tubs were held at 25 °C, 65% r.h., and L14:D10 until release 3 days later. The mean number of flies released per tub was 1200. The tubs were opened on the back of a moving vehicle every 160 m along a route that passed all the traps in the target area. Flies were recaptured in Lynfield (pot) traps that were baited with a mixture of 5 ml Capilure with 1% dichlorvos (Meats et al., 2002). The traps were deployed as an array with a spacing of 400 m. Catches were counted weekly after checking each fly for traces of marker powder in the ptilinal suture using a microscope illuminated with UV light. This paper uses the results from two suburbs, Salisbury and Millswood (which yielded the most extensive data), where the trap arrays had 74 and 143 traps, respectively.

#### Releases of Qfly in New South Wales

Sterile flies were produced at the facilities of NSW Agriculture in the Sydney region for use in SIT trials in several small inland towns (of areas up to 12 km$^2$) that were close to citrus production areas and in one production area of 8 km$^2$. The pupae of insects destined for release were mixed with fluorescent-marking powder (as described previously). Batches of pupae were produced on a weekly basis and gamma irradiated in Sydney at the Australian Nuclear, Scientific and Technical Organization (ANSTO) from a $^{60}$Co source with a dose of 71–73 Gy. They were then transported in thermally insulated boxes (by air for all releases except for the ones for the production area, which went by road) to an air-conditioned insectary near to the site of release. Two of these insectaries were in the Riverina district: (a) at Griffith (about 550 km, 50° W of Sydney) for releases at the Tharbogang production area, Hillston and Griffith; (b) at Narrandera (about 90 km, 67° E of Griffith) for releases at Leeton and Narrandera. The other insectary was located at Trangie (about 350 km, 45° W of Sydney) for releases at Gilgandra and Narromine.

Depending upon site and date, about 20,000–45,000 pupae were allocated to plastic bins (45 l capacity) with meshed lids or to mesh cages of similar size. The emerged flies were kept for 2 days and supplied with sugar and water. On any one occasion for any one trap array, equal numbers of flies were released at sites midway between the traps, which were spaced approximately 400 m apart (320 m at Tharbogang). At Hillston, pupae were distributed to release sites in lidded buckets that had exit holes in the sides so that emerging flies could escape. The number of traps was 50, 14, 75, 31, 30, 31, and 40 at Tharbogang, Hillston, Griffith, Leeton, Narrandera, Gilgandra, and Narromine, respectively. Flies were recaptured in Lynfield (pot) traps that were baited with 5 ml of a mixture of Cue lure and Malathion at a ratio of 8 : 1 (Meats et al., 2002). Counts of recaptured flies were made weekly, as for Medfly. Most of the trials took place from September to December 1999, but those at Tharbogang (Horwood & Keenan, 1994) and Gilgandra and Narromine (Meats et al., 2003) were conducted between 1994 and 1998.

#### Data and analyses

We intended to use data from short SIT trials to establish the relation between mean weekly recapture rate (m) and indices dispersion over a wide range of m. The Medfly trials in the Adelaide suburbs of Millswood and Salisbury yielded data of this kind as recapture rates (over 18 and 24 weeks, respectively) increased to high levels within a few weeks and declined after releases were discontinued. The Qfly trials intended for comparison (Griffith and Narrandera) did not yield very high recapture rates in any week of the 20-week period of trapping; these data were therefore augmented with recapture results from the weeks with the four highest catches at Leeton, and the three highest at the Hillston. For catches comparable with the highest ones for Medfly, we used the total catches for each trap at Tharbogang given by Horwood & Keenan (1994) and four and seven of the weeks of the highest catches at Narromine and Gilgandra, respectively (unpubl. from the trials reported by Meats et al., 2003).

For each week at each site (see previous text), the standard statistics calculated included mean catch per trap per week (m), its variance, standard deviation (SD), and CV (SD/m = CV). Taylor's power law (see Kuno, 1991; Nyrop & Binns, 1991; Southwood & Henderson, 2000) relates variance to mean (m) as variance = $am^b$. The constants of this relationship were calculated as the intercept $\log_{10}a$ and slope b, respectively, of the linear regression of $\log_{10}$variance on $\log_{10}$m, which has the form $\log_{10}\text{variance} = \log_{10}a + b \cdot \log_{10}m$. Linear regressions and the significance of differences between them were calculated in the standard way (Snedecor & Cochran, 1989), but calculations were restricted to data from catches when $m > 10$. The percentages of traps catching >0, >10, and >50 flies per week were found for each week at each site and related to m. These data were used for fitting negative binomial and linear regression

models (see succeeding text). In order to avoid too much random error, the model fitting was restricted to percentages greater than 100 $m^{-1}$.

#### Model expectations, fit, and predictions

Expected frequencies according to the negative binomial model for catches of a given number of flies (x) were calculated for any given value of k and mean trap catch (m) by

$$p_{x+1} = [(k + x)/(x + 1)] \cdot [m/(k + m)] \cdot p_x$$

where $x = 0, 1, 2 \ldots$
and $p_x$ is the probability of a trap catching x flies,
and the probability of no catch (x = 0) is

$$p_{x=0} = [(1 + (k/m))]^{-k}.$$

The percentage of traps expected to catch above a certain number of flies y was found by

$$\% > y = 100\,[1 - (p_{x=0} + p_{x=1} + p_{x=2} \ldots + p_{x=y})]$$

where the values of y of interest were 0, 10, and 50 for reasons given earlier.

The value of k giving the best fit (the highest percentage of variance explained) to a plot of % > y against mean catch per trap was found by trial and error using values of k spaced at intervals of 0.05 for values when the best fitting k appeared to have a value above 0.5 and intervals of 0.025 when it appeared to be below. Summary comparisons between the two species were made by calculating the mean expectations according to the negative binomial model for releases when the mean recapture rate per trap per week was 300.

Alternative comparisons were made from linear regressions of % > y against $\log_{10}$m the equation for which is of the form $\% > y = i + b \cdot \log_{10}m$. In this case, the model of best fit was obtained as part of the calculation of the regression equation and the percentage of variance explained was obtained from $100 \cdot r^2$ where r is the coefficient of correlation between the two variables (% > y and $\log_{10}$m). The prediction of % > y ± SE for m = 300 was made according to the method for calculating mean expectation for a given x value (Snedecor & Cochran, 1989).

## Results

#### Indices of dispersion

The Taylor's constants ($\log_{10}$a and b ± SE) were obtained from linear regressions of the form $\log_{10}\text{variance} = \log_{10}a + b \cdot \log_{10}m$. The values for Medfly were $\log_{10}a = 1.06$ (0.18) and b = 1.57 (0.1), and for Qfly were $\log_{10}a = 1.68$ (0.16) and b = 1.44 (0.09). The corresponding relationships between $\log_{10}$SD and $\log_{10}$m are given in Figure 1 where $\log_{10}$a and b have half the values given prevously. The two species do not significantly differ in terms of slope b (P = 0.34 and 0.17, respectively, in two- and one-tailed t-tests), but the Medfly regressions have significantly lower values for intercept, $\log_{10}$a (P = 0.014 and 0.007, respectively, in two- and one-tailed t-tests). This significant difference in terms of intercept means that for any given value of mean catch per trap per week, m, the variance and SD of m (and hence CV) is expected to be lower for Medfly releases than it would be for Qfly.

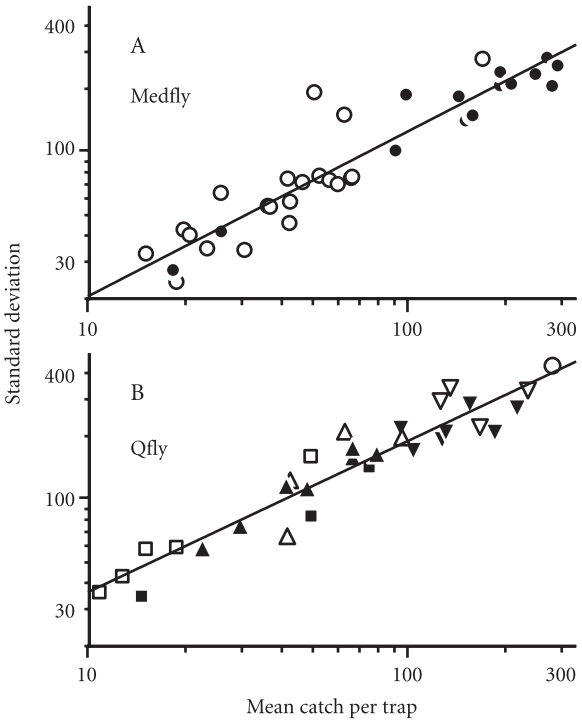


**Figure 1** The relation of $\log_{10}$SD of m to $\log_{10}$m where m = mean catch per trap per week. (A) Data from releases of Mediterranean fruit fly (Medfly), *Ceratitis capitata*, at suburban sites in Adelaide: Millswood (black discs) and Salisbury (white discs). (B) Data from releases of the Queensland fruit fly (Qfly), *Bactrocera tryoni*, at rural sites in NSW: Griffith (white squares), Hillston (black squares), Narrandera (black triangles), Leeton (white triangles), Gilgandra (inverted black triangles), Narromine (inverted white triangles), and Tharbogang (heavy circle).

The relation of $\log_{10}$ of the CV (CV = SD/m) to $\log_{10}$m was also linear. The values for intercept and slope ($\log_{10}$a and b ± SE) were, respectively, 0.53 (0.09) and −0.21 (0.05) for Medfly, and for Qfly they were 0.84 (0.08) and −0.28 (0.04). Each slope was negative because the corresponding slope of $\log_{10}$SD on $\log_{10}$m (Figure 1) was less than unity. However, the differences between the species in terms of $\log_{10}$a and b remained the same as did their statistical

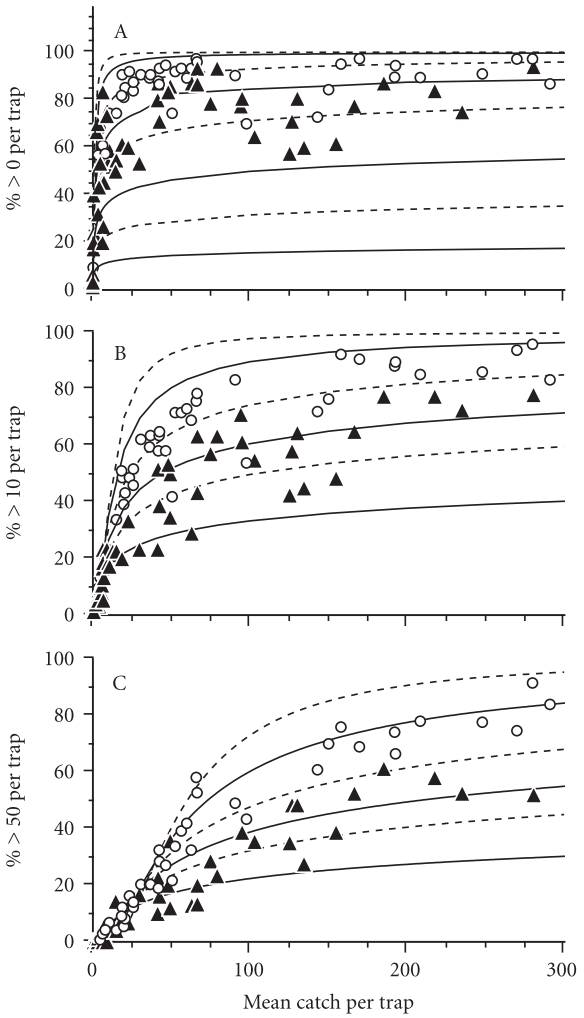


**Figure 2** The percentages of traps catching (A) >0, (B) >10, and (C) >50 flies per week related to mean catch per trap per week. The points are superimposed on curves denoting the theoretical predictions of the negative binomial model with specified values of k, which are (from top to bottom in each case) 2.0, 1.0, 0.5, 0.3, 0.2, 0.1, 0.05, and 0.02; the last two curves are omitted in the lower two graphs. Symbols: white circles, Mediterranean fruit fly; black triangles, Queensland fruit fly. Data for each species is from all releases given in the legend to Figure 1.

probabilities. The linear nature of the log–log plot infers that CV declines with m at an ever-decreasing rate.

#### Traps catching more than 0, 10, and 50 flies per week

The percentages of traps catching >0, >10, >50 flies per week (% > y) are related to mean catch per trap per week m in Figure 2. The points are superimposed on curves denoting the theoretical predictions of the negative binomial model with specified values of k. It can be noted that the theoretical negative binomial curves for % > 50 are not monotonic but tend to be sigmoid between values of m = 0–30 and in this region, curves for higher values of k can cross over those for lower values. Estimation of the values of k of the theoretical curves giving the best fit to the real data reveals that the latter appear to follow this sigmoid/cross over tendency.

Table 1 gives the k value yielding the best fit for each data set, together with the percentage of variance explained. The table also gives the amount of variance explained by an alternative type of model which is the regression of % > y on $\log_{10}$m. The percentages of variance explained by the regression models are also good but are mostly slightly lower than those obtained for the negative binomial model. Table 1 also gives the predictions of % > y (± SE) of both types of model for m = 300. The predictions are essentially similar, but the regression model is unfortunately capable of giving predicted percentages in excess of 100 if catches are very high.

#### Traps consistently catching fewer or more than 50 flies per week

The tendency of certain traps in an array to catch consistently either more or fewer than 50 flies per week was investigated in cases where mean catches were consistently at their highest. The ideal data to use would have been that where the weekly value of m was above 100 or 150 (i.e., the value of m above which the overall proportion of traps catching more than 50 is not expected to increase a great deal). With the Medfly data, the Millswood set met the criterion the most. There was an 8-week period at Millswood when the average value of m was 193; here, 47% of the traps caught >50 for 7–8 weeks and 5.4% trapped <50 for 7–8 weeks. In a 4-week period at Millswood (m averaging 214), 69% of traps caught >50 flies for 3–4 weeks and 16% trapped <50 over the same period. At Salisbury, trap catches were generally lower (average m for the highest 8- and 4-week periods being 77 and 93, respectively). In the 8-week period at Salisbury, 8% of traps caught >50 for 7–8 weeks and 27% trapped <50; in the 4-week period, 35% of traps caught >50 for 3–4 weeks and 29% trapped <50.

The Qfly data for Griffith and Narrandera did not meet the criterion given previously because m in these sets was usually <50. Despite this, there were some traps in each set that consistently trapped >50 in the few weeks when m was highest. In contrast, the large proportion consistently catching <50 was large, which is the overall expectation at such low values of m (see Figure 2). Thus, any consistency to catch <50 may have been largely due to this cause.

## Discussion

Many organisms are dispersed in such a way that the distribution of sample counts or trap catches is contagious

**Table 1** Predictions of negative binomial and regression models of percentage traps exceeding catch of y per week when mean catch per trap per week (m) is 300

| | Negative binomial model[2] | | | Regression model | |
|---|---|---|---|---|---|
| Species[1] and % > y | k | % var. expl.[3] | Prediction of % > y (± SE) for m = 300 | % var. expl. | Prediction of % > y (± SE) for m = 300 |
| Medfly % > 0 | 0.45 | 79 | 95 (1.2) | 62 | 101 (2.7) |
| Medfly % > 10 | 0.7 | 84 | 92 (1.5) | 89 | 96 (2.4) |
| Medfly % > 50 | 0.8 | 95 | 80 (1.6) | 90 | 80 (2.7) |
| Qfly % > 0 | 0.25 | 79 | 83 (1.8) | 78 | 89 (2.9) |
| Qfly % > 10 | 0.25 | 82 | 66 (1.5) | 86 | 72 (2.4) |
| Qfly % > 50 | 0.25 | 94 | 50 (1.3) | 80 | 50 (2.5) |

[1]Medfly = Mediterranean fruit fly, *Ceratitis capitata*; Qfly = Queensland fruit fly, *Bactrocera tryoni*.
[2]k = exponent of negative binomial model giving best fit to data.
[3]Percentage of variance in data explained by the model.

(clumped). Such distributions typically have both a Taylor's power law exponent b and a CV of greater than unity and may be fitted to a negative binomial model with a value of k below unity (Kuno, 1991; Southwood & Henderson, 2000). The causes of the clumping may be attributable to one or more of several causes including history (e.g., eggs laid in batches) or current behaviour (Kuno, 1991; Southwood & Henderson, 2000). The degree of clumping may decrease with increase in density (Southwood & Henderson, 2000), but this is not seen in the current data.

The dispersion characteristics of released sterile flies of the two species could not be distinguished from each other in terms of the value of b in Taylor's power equation where b is the slope of the regression $\log_{10}\text{variance} = \log_{10}a + b \cdot \log_{10}m$. The regressions differed with respect to their intercepts ($\log_{10}a$), but such differences are usually held to be attributable to non-specific factors such as sampling scale (Kuno, 1991; Southwood & Henderson, 2000). The present comparisons involved no difference in sampling scale, but it is possible that differences in intercept could have been due to differences in release technique (roving vs. static). From a practical point of view, the significant difference in terms of intercept implies that for any given value of mean catch per trap per week, m, the variance and SD of m (and hence CV), is expected to be lower for Medfly releases than it would be for Qfly. The two distributions can be also distinguished by the value of k giving the best fit to the negative binomial model. However, this could be due to differences in the method of release.

Regardless of any difference in release technique, the rate of change in CV with mean density and the fitting of the negative binomial model can both illuminate the limitations of the strategy of increasing the release rate of sterile flies in order to increase the proportion of the area that has sufficient sterile flies to control the wild population.

Coefficient of variation decreases in the current data with mean catch per trap (m), which is an index of density. However, it does so at a very slow and decreasing rate so that the regression model for Medfly indicates that, on average, CVs of 1.2 and 1.0 would be expected for m-values of 150 and 300, respectively. The corresponding values for Qfly are 1.7 and 1.4. Thus, it appears that the doubling of release rate in order to double average recapture rate from 150 per trap per week to a value of 300 would be expected to have very little effect in terms of reducing CV and that there is no practical prospect of reducing CV to below unity with the current methods of release without incurring a manifold increase in cost. In terms of the amount of benefit for extra flies released, the law of diminishing returns applies.

The same law applies to the strategy of increasing the percentage of traps catching more than 50 sterile flies. For Medfly, it appears that percentages of 66 and 80 would be expected on average for m-values of 150 and 300, respectively. The corresponding values for Qfly are 42 and 50.

The question remains as to how to overcome the lack of adequate coverage (up to 20% of the target area for Medfly and up to 50% for Qfly at the current highest levels of release). In such circumstances, it appears that although perhaps over half of the traps on a Medfly array would consistently catch >50 flies per week, there could be about 5% that would consistently catch less. Because Qfly data fit the predictions of a negative binomial model with a very low k-value (0.25 in contrast to 0.8 for Medfly), one would expect that a Qfly trapping array that trapped at the same average rate would have a considerably lower proportion of traps catching more than 50 flies per week and considerably more catching less than 50.

One way to improve coverage for Qfly SIT would be to change to the system of roving releases (or to aerial releases).

With Medfly, these strategies are already employed, thus further improvement may require the identification of consistently poorly performing traps. Some of such traps could be deemed to be in unsuitable habitat, but this would be doubtful if these traps also caught wild flies. Shiga (1986) found that in an SIT program involving releases of *B. cucurbitae* (Coquillett), a poor recapture rate of sterile flies was not necessarily associated with a capture rate of wild flies that was below the prevailing average and in fact the spatial correlation between wild and sterile trappings on the monitoring array was variable and often poor; similar observations have been made in the case of trial releases of sterile Qfly (A Meats, unpubl.). Thus, augmentative releases should be tried when there is apparently no good reason for low trapping rate, otherwise local eruption of wild flies may occur requiring even more of such releases (Shiga, 1986).

## Acknowledgements

The analytical work of this investigation was supported by the Australian Research Council grant LP 0562391. The Medfly SIT trials in Adelaide were supported by agencies of the State government of South Australia (PIRSA Plant Health and SARDI) and funding by Horticulture Australia (Project AH 01025). The Qfly trials were financed in part by the Horticultural Research and Development Corporation (Projects CT336, CT95027), and all were fully or partly supported by the New South Wales government (Department of Agriculture) and the Tristate Fruit Fly Organisation.

## References

Aruani R, Ceresa A, Granados JC, Taret G, Peruzzotti P & Ortiz G (1996) Advances in the national fruit fly control and eradication program in Argentina. Fruit Fly Pests: A World Assessment of Their Biology and Management (ed. by BA McPheron & GJ Steck), pp. 521–530. St Lucie Press, Delray Beach, FL, USA.

Baker PS & Chan ST (1991) Quantification of tephritid fruit fly dispersal. Guidelines for a sterile release programme. Journal of Applied Entomology 112: 410–421.

Barry JD, Blessinger T & Morse JG (2004) Recapture of sterile Mediterranean fruit flies (Diptera: Tephritidae) in California's preventative release program. Journal of Economic Entomology 97: 1554–1562.

Buntin GD (1988) Sampling techniques, population dispersion, and sampling plans for leafhoppers (Homoptera: Cicadellidae) in Bermuda grass. Environmental Entomology 17: 872–877.

Clarke AR, Zalucki MP, Madden JL, Patel VS & Paterson SC (1997) Local dispersion of the Eucalyptus leaf-beetle *Chrysophtharta bimaculata* (Coleoptera: Chrysomelidae), and implications for forest protection. Journal of Applied Ecology 34: 807–816.

Clift AD & Meats A (1998) The relation of 'percentage positive traps' to the negative binomial distribution and to progress in the eradication of *Bactrocera papayae* Drew and Hancock (Diptera: Tephritidae) in northern Queensland. General and Applied Entomology 28: 61–64.

Cunningham RT, Routhier W, Harris EJ, Cunningham G, Johnson L et al. (1980) Eradication of Medfly by sterile male release. Citrograph 65: 63–69.

Dimou I, Koutsikopoulos C, Economopoulos A & Lykakis J (2003) The distribution of olive fruit fly captures with McPhail traps within an olive orchard. Phytoparasitica 31: 124–131.

Franz G, Kerremans P, Rendon P & Hendrichs J (1996) Development and application of genetic sexing systems for the Mediterranean fruit fly based on a temperature sensitive lethal. Fruit Fly Pests: A World Assessment of Their Biology and Management (ed. by BA McPheron & GJ Steck), pp. 185–191. St Lucie Press, Delray Beach, FL, USA.

Hall DG, Childers CC, Eger JE & Allen JC (1997) Citrus rust mite (Acari: Eriophyidae) counts on fruit and the negative binomial distribution. Florida Entomologist 8: 1–10.

Horwood MA & Keenan PJ (1994) Eradication of the Queensland fruit fly. Report CT 336 to Horticulture Research & Development Corporation, NSW Agriculture, Orange, NSW, Australia.

Howell JF, Cheikh M, Salah HB, Crnjanski P, Pils W & Harris EJ (1975) Suppression of the Mediterranean fruit fly in Tunisia with released sterile insects. Journal of Economic Entomology 68: 244–246.

Kuehl RO & Fye RE (1972) An analysis of sampling distributions of cotton insects in Arizona. Journal of Economic Entomology 65: 855–860.

Kuno E (1963) A comparative analysis on the distribution of some nymphal populations of leaf- and planthoppers on rice plant. Researches in Population Ecology 5: 31–43.

Kuno E (1991) Sampling and analysis of insect populations. Annual Review of Entomology 36: 285–304.

Meats A (1983) Strategies for maximising the potential of the sterile insect release method: experiments with *Dacus tryoni*. Fruit Flies of Economic Importance (ed. by R Cavolloro), pp. 371–377. Balkema, Rotterdam, The Netherlands.

Meats A (1996) Demographic analysis of sterile insect trials with the Queensland fruit fly, *Bactrocera tryoni* (Froggatt) (Diptera: Tephritidae). General and Applied Entomology 27: 2–12.

Meats A (1998a) Predicting or interpreting trap catches resulting from natural propagules or releases of sterile fruit flies. An actuarial and dispersal model tested with data on *Bactrocera tryoni*. General and Applied Entomology 28: 29–38.

Meats A (1998b) The power of trapping grids for detecting and estimating the size of invading propagules of the Queensland fruit fly and risks of subsequent infestation. General and Applied Entomology 28: 47–55.

Meats A, Clift AD & Perepelicia N (2002) Performance of permanent and supplementary traps for Mediterranean and Queensland fruit flies in South Australia 1975–2001: comparison of male lure and food lure traps. General and Applied Entomology 32: 53–57.

Meats A, Duthie R, Clift AD & Dominiak BC (2003) Trials with variants of the sterile insect technique (SIT) for suppression of populations of the Queensland fruit fly in small towns neighbouring a quarantine (exclusion) zone. Australian Journal of Experimental Agriculture 43: 389–395.

Nadel DJ, Monro J, Peleg BA & Figdor HCF (1967) A method of releasing sterile Mediterranean fruit fly adults from aircraft. Journal of Economic Entomology 60: 899–902.

Nyrop JP & Binns M (1991) Quantitative methods for designing and analyzing sampling programs for use in pest management. Handbook of Pest Management in Agriculture, Vol. 2 (ed. by D Pimentel), pp. 67–132. CRC Press, Boca Raton, FL, USA.

Pacala SW & Hassell MP (1991) The persistence of host–parasitoid associations in patchy environments. II. Evaluation of field data. American Naturalist 138: 584–605.

Papadopoulos NT, Katsoyannos BI & Nestel D (2003) Spatial autocorrelation analysis of a *Ceratitis capitata* (Diptera: Tephritidae) adult population in a mixed deciduous fruit orchard in northern Greece. Environmental Entomology 32: 319–326.

Pielou DP (1960) Contagious distribution of the European red mite, *Panonychus ulmi* (Koch), and a method of grading population densities from a count of mite-free leaves. Canadian Journal of Zoology 38: 645–653.

Plant RE & Cunningham RT (1991) Analyses of the dispersal of sterile Mediterranean fruit flies (Diptera: Tephritidae) released from a point source. Environmental Entomology 20: 1493–1503.

Rendon P, McInnis D, Lance D & Stewart J (2004) Medfly (Diptera: Tephritidae) genetic sexing: large-scale field comparison of males-only and bisexual sterile fly releases in Guatemala. Journal of Economic Entomology 97: 1547–1553.

Shelton AM, Nyrop JP, Seaman A & Foster RE (1986) Distribution of European corn borer (Lepidoptera: Pyralidae) egg masses and larvae on sweet corn in New York. Environmental Entomology 15: 501–506.

Shiga M (1986) Analysis of spatial distribution in fruit fly eradication. Pest Control: Operations and Systems Analysis in Fruit Fly Management (ed. by M Mangel, JR Carey & RE Plant), pp. 387–398. Springer-Verlag, Berlin, Germany.

Snedecor GW & Cochran WG (1989) Statistical Methods, 8th edn. Iowa State University Press, IA, USA.

Southwood TRE & Henderson PA (2000) Ecological Methods, 3rd edn. Blackwell, Oxford, UK.

Taylor LR & Woiwood IP (1989) Temporal and spatial patterns in pheromone-trap catches of *Helicoverpa* spp. (Lepidoptera: Noctuidae) in cotton-growing areas of Australia. Bulletin of Entomological Research 79: 145–161.

Vargas RI, Stark JD & Nishida T (1990) Population dynamics, habitat preference, and seasonal distribution patterns of Oriental fruit fly and melon fly (Diptera: Tephritidae) in an agricultural area. Environmental Entomology 19: 1820–1828.

Vargas RI, Whitehand L, Walsh WA, Spencer JP & Hsu CL (1995) Aerial releases of sterile Mediterranean fruit fly (Diptera: Tephritidae) by helicopter: dispersal, recovery, and population suppression. Journal of Economic Entomology 88: 1279–1287.

Villaseñor A, Carrillo J, Zavalla J, Stewart J, Lira C & Reyes J (2000) Current progress in the Medfly program Mexico-Guatemala. Area-Wide Control of Fruit Flies and Other Insect Pests (ed. by KH Tan), pp. 497–508. USM Press, Penang, Malaysia.

Walgenbach JF, Wyman JA & Hogg DB (1985) Evaluation of sampling methods and development of sequential sampling plan for potato leafhopper (Homoptera: Cicadellidae) on potatoes. Environmental Entomology 14: 231–236.

Wilson LT, Pickel C, Mount RC & Zalom FG (1983) Presence-absence sequential sampling for cabbage aphid and green peach aphid (Homoptera: Aphididae) on Brussels sprouts. Journal of Economic Entomology 76: 476–479.

Wong TTY, Whitehand LC, Kobayashi RM, Ohinata K, Tanaka N & Harris EJ (1982) Mediterranean fruit fly: dispersal of wild and irradiated and untreated laboratory- reared males. Environmental Entomology 11: 339–343.

Zalucki MP, Drew RAI & Hooper GHS (1984) Ecological studies of eastern Australian fruit flies (Diptera: Tephritidae) in their endemic habitat. II. The spatial pattern of abundance. Oecologia 64: 273–279.