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Author: Meats, Alfie

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DISPERSION OF FRUIT FLIES (DIPTERA: TEPHRITIDAE) AT HIGH AND LOW DENSITIES AND CONSEQUENCES OF MISMATCHING DISPERSIONS OF WILD AND STERILE FLIES

ALFIE MEATS
Fruit Fly Research Centre, School of Biological Sciences, University of Sydney A08, NSW 2006, Australia

ABSTRACT

Both wild and released (sterile) *Bactrocera tryoni* (Froggatt) (Diptera: Tephritidae) and wild *Bactrocera papayae* (Drew and Hancock) in Australia had patchy distributions and comparisons with predictions of the negative binomial model indicated that the degree of clumping was sometimes very high, particularly at low densities during eradication. An increase of mean recapture rate of sterile *B. tryoni* on either of 2 trap arrays was not accompanied by a reduction in its coefficient of variation and when recapture rates were high, the percentage of traps catching zero decreased only slightly with increase in recapture rate, indicating that it is not practicable to decrease the heterogeneity of dispersion of sterile flies by increasing the number released. There was often a mismatch between the dispersion patterns of the wild and sterile flies, and the implications of this for the efficiency of the sterile insect technique (SIT) were investigated with a simulation study with the observed degrees of mismatch obtained from the monitoring data and assuming the overall ratio of sterile to wild flies to be 100:1. The simulation indicated that mismatches could result in the imposed rate of increase of wild flies being up to 3.5 times higher than that intended (i.e., 0.35 instead of 0.1). The effect of a mismatch always reduces the efficiency of SIT. The reason for this asymmetry is discussed and a comparison made with host-parasitoid and other systems. A release strategy to counter this effect is suggested.

Key Words: *Bactrocera tryoni*, *Bactrocera papayae*, patchiness, extinction, dispersion

RESUMEN

Las moscas naturales y liberadas (estériles) de *Bactrocera tryoni* (Froggatt) (Diptera: Tephritidae) y *Bactrocera papayae* (Drew and Hancock) en Australia tuvieron distribuciones en parches y sus compariciones con las predicciones de un modelo binomial negativo indicaron un nivel de agregación a veces fue muy alto, particularmente en las densidades bajas durante de eradicación. Un aumento en el promedio de la tasa de *B. tryoni* estériles recapturadas en las dos formas de trampas no fue acompañado por una reducción en su coeficiente de variación y cuando las tasas de moscas recapturadas fue alto, el porcentaje de las trampas que capturaron ninguna mosca bajó solo un poco con un aumento en la tasa de las moscas recapturadas, esto indicó que no es practicable bajar la heterogenicidad de dispersión de las moscas estériles por medio de un aumento el número de moscas liberadas. Muy a menudo se encontro un desajusto entre los patrones de dispersión de las moscas naturales y estériles, y las implicaciones de esto para la eficiencia de la técnica del insecto estéril (TIE) fueron investigadas en un estudio de simulación con los grados de desajustes observados obtenidos de los datos del monitoreo y se considero que la razón general del número de moscas estériles a moscas naturales fueron 100:1. La simulación indicó que los desajustes en los patrones de dispersión pueden resultar en una tasa impuesta sobre el aumento de las moscas naturales de hasta 3.5 veces mas alta que la tasa intentada (i.e., 0.35 en vez de 0.1). El efecto de un desajuste siempre reduce la eficiencia de TIS. Se discute la razón para esta asimetría y una comparición hecha con el sistema de hospedero-parasitoid y otros sistemas. Se sugiere una estrategia de liberación para contrarrestar este efecto.

Patchy dispersion patterns are widespread in ecological systems and may have fundamental significance to their stability on a number of scales (Huffaker et al. 1963; Hassell & Waage 1984; May 1978; Harrison 1991; Hassell et al. 1991; Pacala & Hassell 1991; Taylor 1991; Murdoch & Briggs 1996). Clumped dispersion patterns of pests have been related to patchiness of the natural or managed habitat (Zalucki et al. 1984; Vargas et al. 1989; Clarke et al. 1997; Papadopoulos et al. 2003) and knowledge of the spatial heterogeneity in the density of a pest and its temporal variation can be utilized in strategies for its management (Clarke et al. 1997; Papadopoulos et al. 2003). To do this, however, degrees of dispersion must be quantified in suitable terms such as the coefficient of variation 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; Southwood & Henderson 2000; Clift & Meats 1998), the exponent of Taylor's Power Law or measures related to the latter (Southwood & Henderson 2000; Zalucki et al. 1984; Taylor & Woiwood 1989).

Clumped dispersion has been reported for trap catches of adults of many fruit fly species (Diptera: Tephritidae) with examples in natural populations (Zalucki et al. 1984) and in an invading population subject to an eradication campaign (Clift & Meats 1998; Meats 1998) and in distributions of cohorts of released sterile flies (Teruya 1986; Plant & Cunningham 1991). During the outbreak stage of an exotic incursion of *Bactrocera papayae* Drew & Hancock (Diptera: Tephritidae) in northern Queensland (Australia), there was a gross pattern of localized distribution corresponding to discrete propagules of various sizes, and there was a further pattern of heterogeneous dispersion within them; a similar pattern was seen during the final stages of eradication of the incursion when the remnant populations were reduced to small isolated foci (Clift & Meats 1998; Meats1998).

Heterogeneous dispersion of fruit flies must be taken into account when control measures are deployed and their effectiveness assessed. When the sterile insect technique (SIT) is used against fruit flies, the wild population is reduced to foci (as above), whereas the distribution of sterile flies should be more widespread (Meats 1983, 1996; Meats et al. 1988). If mating competitiveness is measured directly in open field conditions, the apparent decline in its value (Iwahashi et al. 1983; Iwahashi 1996) may be an artifact of the use of the wrong value for the ratio of sterile to wild flies in the calculations. This can be due to the inclusion of areas without wild flies in censuses to establish the ratio with the result that a much higher value is used that is really the case in the areas where sterile and wild flies are actually present together; this in turn will lead to an underestimate of the value for mating competitiveness (Meats 1983, 1996; Meats et al. 1988).

There are, however, less striking mismatches in the distribution of sterile and wild flies and these have consequences for the efficiency of SIT and may apply at many stages of eradication (Shiga 1986). As with control with cover-sprays of pesticide, an essential aim is to treat all the individuals of the target pest within the target area. Thus, whereas it may not be necessary for the 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), the distribution of the treatment should coincide with the distribution of the pest. If it does not, the pest may persist in localized patches or even increase to make control measures ineffective.

It is the purpose of this paper to examine the dispersion of wild and sterile fruit flies and in particular the simultaneous dispersion patterns of wild and sterile *Bactrocera tryoni* (Froggatt) (Diptera: Tephritidae) that were observed during trials of release techniques (Meats et al. 2003a) and to calculate the consequences that would apply if those patterns were present during an SIT campaign when the overall ratio sterile to wild flies was 100:1.

Materials and Methods

General Analysis and Modelling

Because all of the investigations reported here involved real or simulated results from trapping arrays, there were many analytical and modeling methods in common as follows. Means (m) of catch per trap per week (or per 2 weeks for *B. papayae* data) on a monitoring array, their standard deviations and errors (SD and SEM), coefficients of variation (CV), correlations, linear regressions, and the statistical significance and any differences between them were calculated with standard formulas (Snedecor & Cochran 1989). Data were tested for conformity to Taylor's Power Law and negative binomial models for percentage of positive traps (traps with flies). Taylor's power law (Kuno 1991; Nyrop & Binns 1991; Southwood & Henderson 2000) relates variance (s^2) to mean (m) as $s^2 = am^b$. The constants of this relationship were calculated as the intercept ($\log_{10} a$) and slope (b), respectively, of the linear regression of $\log_{10} s^2$ on $\log_{10}(m)$, which has the form $(\log_{10} s^2) = \log_{10} a + b\ (\log_{10} m)$. The equivalent regressions with SD substituted for variance have values of $\log_{10} a$ and b at half the corresponding amounts.

The negative binomial expectations for the percentage of positive traps in an array (% trapping > 0 in a given week) were found by

$$(\% > 0) = 100(1 - p_0)$$

where p_0 is the zero term of the negative binomial distribution found by

$$p_0 = [1 + (m/k)]^{-k}$$

and k is a constant related to the amount to which the distribution is more clumped than random. A k value of infinity gives the same result as the zero term for the Poisson distribution, and values down to about five have a very similar effect. However, a k value of one or less is considered to indicate a significantly clumped distribution from an ecological perspective. If predators or parasitoids distribute their attacks on their prey or hosts in such a manner, a sufficiently large proportion of the latter will escape giving potential stability to the ecological relationship (May 1978).

Model predictions for percentage of positive traps over a range of values of mean catch per trap were generated, with k values of 2.0, 1.0, 0.5, 0.3, 0.1, 0.05, and 0.02 plotted on the relevant Fig.s so that the range within which real or simulated values fell could be seen.

Data from Sterile Releases at Gilgandra and Narromine

Trials of release techniques for sterile *B. tryoni* were carried out in a number of small towns in New South Wales, Australia, from Feb 1996 to Apr 1998 (Meats et al. 2003a). 'Conventional' releases of newly emerged sterile flies were made in Gilgandra and Narromine, which are about 75 km apart and about 350 km northwest of Sydney. Both towns are of similar size (5 km^2), have river frontage, a similar altitude (230-250 m), and are in a region that has an average annual rainfall of 500-600 mm. Both towns received marked sterile flies at an identical rate in any 1 week at weekly intervals during the study period. In a given week, equal numbers of flies were released at sites midway between the traps. It was estimated that the number of adults flown from the release sites varied from 48,000 to 115,000 males per km^2 per week but no flies were released in late autumn and winter period from mid Apr to mid Aug (Meats et al. 2003a).

Monitoring traps in each town were spaced at about 0.4 km from each other and cleared each week, and both the wild and sterile flies that were trapped by them were counted. The type of trap used was the Lynfield (pot) trap (Cowley et al. 1990). The wick of each trap was initially supplied with 4 mL of cue lure and 1 mL of malathion solution (50% in emulsifiable concentrate).

The sterile flies were produced at the facilities of NSW Agriculture (Meats et al. 2003a). The pupae were mixed with fluorescent marking powder from the 'FEX' series from Swada (London) Ltd. at a rate of 50 g per 100,000. The pupae (having completed about 75% of their development) were gamma-irradiated at the Australian Nuclear, Scientific and Technical Organization (ANSTO) from a ^{60}Co source with 71-73 Gy at a rate of 7.6-10.2 Gy per min (depending on the age of the source). They were transported in thermally insulated boxes by air to Dubbo and then by road to an air conditioned insectary at the Trangie Agricultural Research Centre. During the first 2 seasons, the sterile pupae were kept in modified plastic garbage bins (45 liter capacity, 30,000 pupae per bin) and these were transported to the release sites (on a trailer covered with a tarpaulin) after the adults had emerged (Dominiak et al. 1998). From Sep 1997, either small or large cages ($0.5 \times 0.5 \times 0.5$ m or $2.5 \times 1.7 \times 0.42$ m) with shade cloth mesh were used. The smaller cages could receive up to 16,000 pupae and the larger ones up to approximately 225,000. Adult flies were supplied with sucrose and water up to the time of release at which time they were 2-3 d old.

Limited Data Set for Towns under Sterile Releases

A restricted set of data from Gilgandra and Narromine was selected in order to avoid the statistical problem of non-independence between weekly catches when calculating the slopes and standard errors (SEM) of the regressions of the $\log_{10}$ values of s^2, SD or CV on $\log_{10}$ means of trap catches. The reason for the non-independence problem is that despite the fact that new flies were released each week, many flies from previous releases would be trapped as well. Unless analysis is restricted to catches that are months apart, this problem cannot be overcome completely for a fly that can survive as long as *B. tryoni*. However it is worth investigating how the problem can be reduced to reasonable proportions (say, with trap catches at different times having only around 5-10% or less of flies in common from the same set of releases).

Fletcher (1973) gives the results of 9 releases of *B. tryoni* made between Feb and Apr 1969, and from his data one can calculate that 50% of mature adults within about a 200 m radius leave the area in any week. Recent results have yielded estimates of between 47% and 85% per week (unpublished data). With the figure of 50%, one can estimate the percentage R of the set of release cohorts trapped on 1 occasion that would be trapped on a subsequent occasion n weeks later. When there are weekly releases of fresh flies, R would be found by

$$R = 100(0.5^n/(0.5^n + 0.5^{n-1} + 0.5^{n-n}))$$

Thus, the mean expectation would be that a given trap clearance would have only 6.7%, 3.2%, and 1.6% of flies with release dates in common with clearances that were, respectively, 3, 4, and 5 weeks later. It was arbitrarily decided that sufficient independence of census counts was obtained if they were 3 weeks or more apart.

Because there were breaks in the release program, the complete data set comprised weekly censuses with means that ranged from less than 1 to over 200. The restricted data set was limited to censuses that had mean rates of catch per trap of 50 or more in order for the results to be relevant to a real SIT program when large numbers of sterile flies would be recaptured.

Extinction of *B. papayae* at Cairns

An exotic incursion of *B. papayae* in and around Cairns (north Queensland, Australia) was eradicated by a campaign starting in Oct 1995 that used male annihilation with caneite blocks impregnated with methyl eugenol and malathion bait sprays comprising protein hydrolysate and malathion (Hancock et al. 2000). With 1 exception, the traps that caught the highest number of flies were on the original monitoring array in Cairns (spaced about 1 km apart). Thus, the use of the data from traps on that array yields information on dispersion pertinent to a wide range of wild fly densities during a trend to extinction.

Fortnightly totals were used because data in the form of weekly totals were not available.

Dispersion after Sterile Releases Stopped

Data on sterile fly recaptures from the full data set for Gilgandra were arbitrarily selected by choosing the first 4 censuses (in chronological order) that occurred with mean catch per trap in each of the ranges 80-61, 60-36, 35-21, 20-11, 10-1, and <1 (a total 24 censuses). For censuses with higher means, the set of 8 that was used for simulating the results of sterile release at Gilgandra (see below) was employed.

Simulated Extinction Trend

The set of 8 censuses that were used for simulating the results of sterile releases at Gilgandra (see below) was employed and 3 sets of simulated data were generated by dividing the catch data from that original set by 10, 100, and 500, respectively. There was a problem in simulating values for the percentage of positive traps by dividing the original catches as above. This was due to the fact that the dividing procedure could generate trap catches for low-scoring traps that were less than 1 and, moreover, if all these were deemed positive then the number of positive traps would never reduce (as it would with real data) when the mean number of flies trapped declined. Thus, for the purposes of the simulation, a trap was no longer deemed positive if the simulation resulted in there being 0.5 or less flies in it.

Similarity of Sterile and Wild Fly Dispersions

An index of dispersion similarity was found by calculating, for each census, the percentage of variation in wild flies among traps that was explained by the linear regression of wild flies in each trap with the number of sterile flies recaptured in the same trap (or alternatively, the value of $100r^2$ where r is the correlation coefficient). The index was calculated for the dates of the trap clearances used in the simulated SIT exercise (see below) and also for each of the 4 weekly clearances that preceded them.

Simulated SIT with Mismatched Dispersions

The efficiency of SIT with various dispersions of sterile and wild flies can be assessed by comparing the aggregate result of the locally imposed generational rates of increase (λ_{GIL}) of wild flies with that expected if the both sterile and wild flies were evenly spread (i.e., if the same imposed ratio of sterile to wild flies prevailed in all parts of the release area). In the case of the simulation used here, it is assumed that the mating competitiveness of the sterile flies is 0.5 and the overall ratio of sterile to wild flies is 100:1 and the natural generational rate of increase (λ_{GN}) of the wild flies is 5.0. Thus, if both kinds of fly were distributed evenly or their dispersions were identical (hence the sterile to wild ratio was the same in all parts) the imposed generational rate of increase both locally (λ_{GIL}) and overall (λ_{GIA}) would be 0.098. In this situation the imposed rate of increase is, as with all successful SIT, less than 1 indicating a decrease that in this case is just more than a tenfold reduction per generation. If dispersion patterns of the 2 fly types were different, then λ_{GIL} would vary from place to place with further consequences for the overall result (λ_{GIA}).

The simulated SIT calculations were based on real weekly censuses (trap clearances) selected from the data from Gilgandra and Narromine. Censuses with large numbers of sterile recaptures (mean recaptures per trap exceeding 100) were chosen in order to conform to a realistic semblance of a successful SIT operation. However, there were only 4 such censuses at Gilgandra (range of means, 103-218) and 3 from Narromine (range of means, 102-185) that satisfied this criterion and that were also spaced more than 2 weeks apart. Thus, to augment the data set, catches based on fortnightly totals were selected; this procedure made 4 more censuses available for Gilgandra and 1 more for Narromine (range of means, 87-185). The actual census dates used for Gilgandra were Mar 18 and 25 (1996), Dec 30 (1996), Mar 17 (1997), Apr 21 and 27 (1997), Sep 29 and Oct 6 (1997), Nov 10 (1997), Dec 29 (1997) and Jan 5 (1998), and Mar 16 (1998). For Narromine they were Mar 17 and 24 (1997), Mar 2 (1998), Mar 23 (1998), and Apr 20 (1998). It can be concluded, therefore, that less than 5% of flies in successive censuses came from the same release (see above) and virtually none did so in most cases.

For the SIT simulation, the dispersion of wild flies between traps was retained but the numbers for each trap were reduced by the same factor for any 1 census (trap clearance) date so that the overall sterile to wild ratio (i.e. the ratio pertaining to the recaptures of the whole trap set on that date) was 100:1. This was done by applying the following equation to the data for any given census date:

$$W_L = w_L\,(0.01 \cdot S_A / w_A)$$

where w_L is the unadjusted number of wild flies in a trap at the census date, W_L is the adjusted number, S_A is the total of sterile flies in all traps and w_A is the unadjusted total of wild flies in all traps.

For simulation of the effects of SIT with the given dispersions of sterile and wild flies on any one date, it was assumed that the natural rate of increase per generation (λ_{GN}) of the wild flies would have been 5 and the locally imposed rate of increase (λ_{GIL}) pertaining to the data from any 1 trap was calculated as follows:

$$\lambda_{GIL} = \lambda_{GN} /((CS_L/W_L)+1)$$

and the imposed rate of increase over the whole trap array (λ_{GIA}) was found by

$$\lambda_{GIA} = (\Sigma(\lambda_{GIL}W_L))/(\Sigma W_L)$$

where C is the mating competitiveness of the sterile flies, S_L is the number of sterile flies in the trap.

The relationship of various factors to the imposed rate of increase over the whole trap array (λ_{GIA}) was examined by means of correlation and regression analyses. The factors were as follows: the mean catch per trap of sterile flies and its SD, the percentages of positive traps with more than 0, 10, or 50 flies and the 'index of similarity' of the sterile and wild dispersion (see above).

Results

Complete Data for Gilgandra and Narromine

The relation between $\log_{10}$ standard deviation (SD) and $\log_{10}$ mean catch per trap (m) of *B. tryoni* appears to be linear. Both wild and sterile flies fit a common slope (b = 0.91) that explains 96.4% of the total variance, 91.3% of the variance of wild flies and 96.2% of that of sterile flies (Fig. 1). The slope for the analogous relation used by Taylor's Power Law (where variance replaces SD) is double of that in Fig. 1.

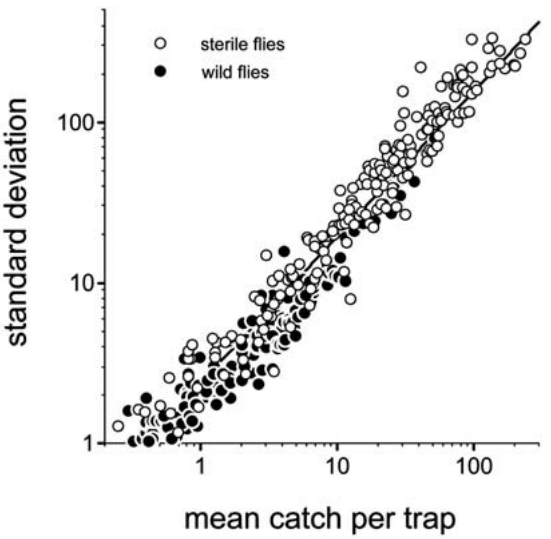

Fig. 1. The relation of standard deviation (SD) to mean (m) for weekly trap catches of wild and sterile *Bactrocera tryoni* at Gilgandra and Narromine. The common equation $\log_{10}$ SD = 0.37 + 0.91·($\log_{10}$ m) explains 91.3% of the variance of wild flies and 96.2% of that of sterile flies.

Limited Data Set for Towns under Sterile Releases

When restricted data sets were used for Gilgandra and Narromine in order to avoid non-independence between censuses, no significant differences between sterile and wild *B. tryoni* were found ($P > 0.05, n = 12$) for the slope of the regression of $\log_{10}$ SD (and therefore variance) on $\log_{10}$ mean catch per trap (Fig. 2a, Table 1). The regression slopes for $\log_{10}$ SD on $\log_{10}$ mean catch per trap did not differ significantly from unity ($P > 0.05, n = 12$) and this can be related to the finding that there were no significant relationships of

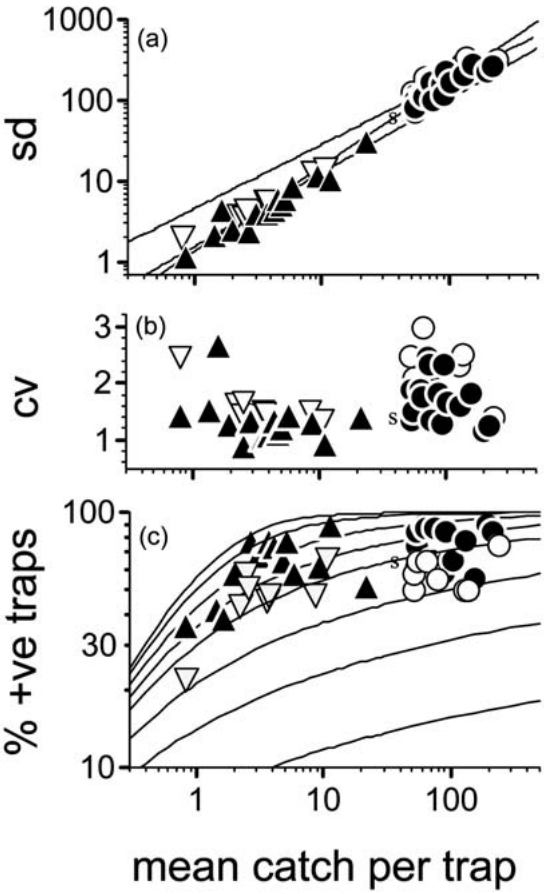

Fig. 2. The relation for wild and sterile *Bactrocera tryoni* of mean trap catch m to (a) its standard deviation, SD, (b) its coefficient of variation, CV, (c) the percentage of positive traps. Circular symbols, sterile flies, triangular symbols wild flies; black symbols, Gilgandra flies, white symbols, Narromine flies. In Fig. 2a the solid line is the common slope (b) of the regression $\log_{10}$ SD = a + b ($\log_{10}$ m). The upper and lower dashed lines are the equivalent slopes for sterile and wild flies respectively. In Fig. 2c, the alternating dashed and solid curves are the predictions of the negative binomial model with k values of respectively (top to bottom) 2, 1, 0.5, 0.3, 0.2, 0.1, 0.05, and 0.02.

TABLE 1. CONSTANTS OF TAYLOR'S POWER LAW[1] DETERMINED FROM REGRESSIONS PERTAINING TO *BACTROCERA TRYONI* AND *B. PAPAYAE* (DIPTERA: TEPHRITIDAE) IN AUSTRALIA.

Regression of form: $y = \log_{10} a + bx^2$	% var expl[3]	Intercept, a(± SEM)	Slope, b(± SEM)	Traps	Weeks
(a) Restricted range of trapping data at Gilgandra (wild *B. tryoni*)	94.0	0.26 (0.10)	1.92 (0.13)	31	16
(b) Restricted range of trapping data at Narromine (wild *B. tryoni*)	97.6	0.60 (0.06)	1.62 (0.10)	40	8
(c) Restricted range of trapping data at Gilgandra (sterile *B. tryoni*)	73.5	1.19 (0.51)	1.62 (0.26)	31	16
(d) Restricted range of trapping data at Narromine (sterile *B. tryoni*)	84.1	1.43 (0.56)	1.62 (0.29)	40	8
(e) Combined wild and sterile data (a-d)	97.7	0.26 (0.07)	2.11 (0.05)	n.a.	n.a.
(f) Cairns original grid (monitoring eradication of *B. papayae*)[4]	98.0	0.78 (0.08)	1.73 (0.08)	12	24[4]

[1]Mean (m) relates to variance (s^2) as $s^2 = am^b$
[2]$y = \log_{10}$ (*spatial variance*), $x = (\log_{10}$ *spatial mean*).
[3]Percentage of variance of $\log_{10}$ (*spatial variance*) explained by regression.
[4]Trap data based on fortnightly counts; all other rows based on weekly counts.
n.a. = not applicable.

coefficient of variation (SD/mean catch per trap) and mean catch per trap for either wild or sterile flies (Fig. 2b). The 3 regression lines shown in Fig. 2a pertain to the combined Gilgandra and Narromine data for sterile flies only (upper dashed line), wild flies only (lower dashed line), and wild and sterile flies combined (solid line). These regressions explain 71%, 93%, and 98% of the variance of the corresponding values of $\log_{10}$ SD. The common regression (solid line) explains 61% of the variance of sterile flies only and 90% of that of wild flies only.

The relationship between the percentage of positive traps and mean catch per trap (Fig. 2c) was variable but the values fell within the range predicted by negative binomial models for very clumped distributions having exponent (k) values in the range 0.1-1.0.

Extinction of *B. papayae* at Cairns

Data from the original monitoring grid at Cairns during the extinction of *B. papayae* are plotted on Fig. 3a-c in an analogous form to Fig. 2a-c. The slope of Fig. 3a appears to be similar to that of the slope for the combined data of Fig. 2a, but it is significantly lower than unity ($P < 0.01$, $n = 12$) with the consequence that the slope of $\log_{10}$ CV on $\log_{10}$ mean catch per trap (Fig. 3b) declines significantly with increasing mean ($P < 0.01$, $n = 12$). However, it can be argued that because these data come from successive trapping intervals, they are not strictly independent and conclusions as to statistical significance should be treated with caution. The relation between the percentage positive traps and mean catch per trap (Fig. 3c) fell within a similar range to that seen in Fig. 2c.

Dispersion after Sterile Releases Stopped

Fig. 4c enables the comparison to be made of the natural decline of sterile *B. tryoni* at Gilgandra and Narromine after releases stopped with the forced decline of *B. papaya*e at Cairns (above) that was due to male annihilation. Fig. 4c is very similar to Fig. 3c, with the percentage of positive traps falling within the predictions given by negative binomial models for very clumped distributions with k values in the range <0.05-1.0.

Simulated Extinction Trend

The results of the simulation of trends to extinction that were produced by manipulating data of sterile fly trapping at Gilgandra are shown in Figs. 4a-b. The original Gilgandra data are plotted on the right hand side of each graph. Three other sets of points are plotted which are the results of dividing the catch data from the original set by 10, 100, and 500, respectively.

The dashed lines in Fig. 4a illustrate how (because of the nature of the formula for SD) this process preserves, for each set of points, the original slope (b) of the regression $\log_{10}$ SD = $\log_{10} a + (b \log_{10} m)$. The value of the original b is 0.79 (± SEM, 0.20) for each set of points, not significantly different from unity ($P < 0.01$). The intercepts ($\log_{10} a$) are all different being (from right to left) 0.61, 0.40, 0.19, and 0.13. The common slope (solid line) has a slope (b = 0.996 ± SEM, 0.013) not significantly different from unity ($P << 0.01$).

The simulated values for percentage of positive traps (a trap ceasing to be deemed positive if the simulation results in there being 0.5 or less flies in it) show much less variation with decrease in mean

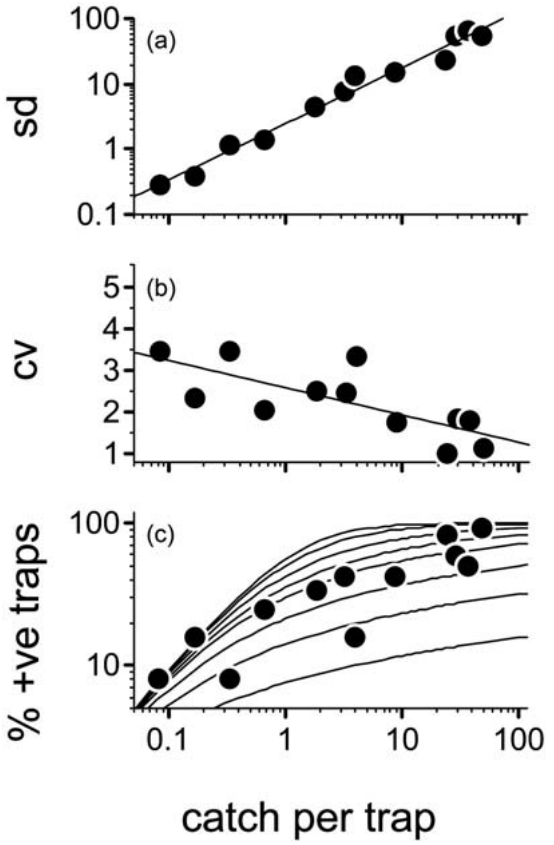

Fig. 3 The relation for wild *Bactrocera papayae* at Cairns of mean trap catch to (a) its standard deviation (b) its coefficient of variation (c) the percentage of positive traps. The alternating dashed and solid curves are the predictions of the negative binomial model with k values of respectively (top to bottom) 2, 1, 0.5, 0.3, 0.2, 0.1, 0.05, and 0.02.

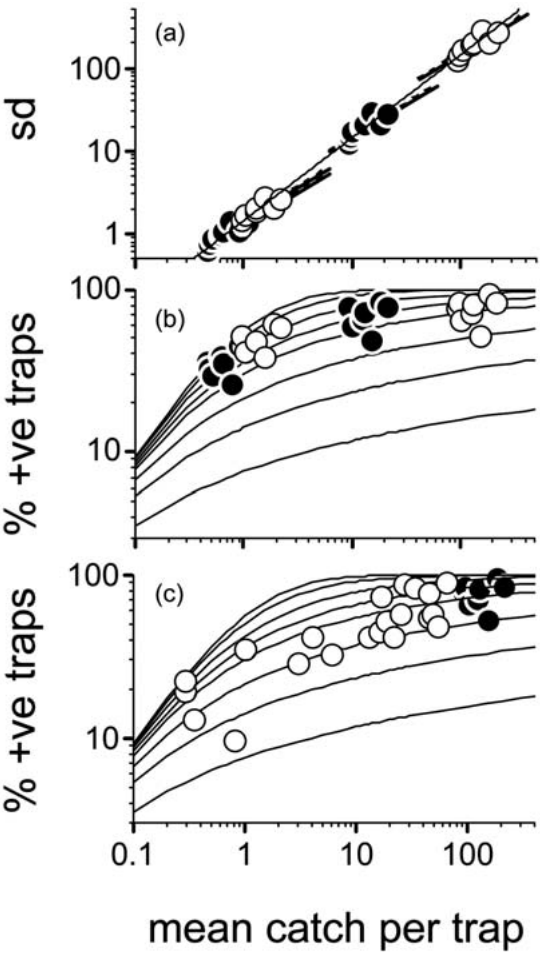

Fig. 4 Simulated decline in trap catches of sterile flies compared with a real range of high and low values for sterile flies at Gilgandra. The top graph (a) relates simulated mean catch per trap (m) to standard deviation (SD) as regressions of the form $\log_{10}$ SD = $\log_{10} a + (b \log_{10} m)$. The dashed lines are the regressions for each set of points; all have the same slope (b) of 0.79 but the intercepts ($\log_{10} a$) are all different being (from right to left) 0.61, 0.40, 0.19, and 0.13. The common regression (solid line) has a slope (b = 0.996). The middle graph (b) relates the percentage of positive traps to the mean catch (m). The alternating sets of white and black points pertain to (right to left) real data for Gilgandra sterile flies and the results of dividing the individual trap data for the latter by 10, 100, and 500, respectively. The lowest graph (c) relates real data for mean trap catches of Gilgandra flies to the percentage of positive traps. The black points are from the original set used in the upper 2 graphs and the white points are from weeks when the numbers of sterile flies decline due to cessation of releases. The alternating dashed and solid curves on (b) and (c) are the predictions of the negative binomial model with k values of respectively (top to bottom) 2, 1, 0.5, 0.3, 0.2, 0.1, 0.05, and 0.02.

catch per trap than is seen with real data from declining populations (compare Fig. 4b with Figs. 3c and 4c). With the simulated reductions, the original variation in percentage of positive traps appears to be almost exactly maintained. This is not consistent with Fig. 3c and 4c where the variation is encompassed by a wider range of negative binomial predictions when pertinent to lower mean catch rates.

Similarity of Sterile and Wild Fly Dispersions

Among the set of 8 sterile fly censuses used for the Gilgandra SIT simulation, there were only 3 instances of a significant correlation ($P < 0.05$) between immediately successive censuses (respectively 5, 6 and 10 weeks apart). For the 4 Narromine simulation SIT censuses, there were no significant correlations between successive censuses ($P > 0.05$). A similar lack of serial correlation applied to the wild flies trapped at each of the above dates. This is perhaps to be expected with such widely spaced dates.

When runs of 5 consecutive weekly censuses were compared (12 runs, each including weeks used for the SIT simulations) the correlation between dates was much stronger. The first census of any run was compared to the following 4 censuses with respect to both wild and sterile flies. For Gilgandra, the mean number of 'following censuses' (out of a possible maximum of 4) that was significantly correlated with the first ($P < 0.05$) was 3.1 for sterile flies and 3.4 for wild flies. The Narromine data had less sequential correlation, the equivalent Figures being 2 and 1, respectively. Indices of dispersion similarity of wild and sterile flies in any one week showed analogous results. Such an index is expressed as a percentage and is found by $100r^2$ where r is the correlation coefficient pertinent to numbers of wild and sterile flies in each trap in a given week. There was considerable consistency in the index at Gilgandra where, out of the 8 runs of 5 weeks, it stayed within a 10% band for 3 or more weeks for 6 of those runs. At Narromine, the similarity index was within a 10% band for never more than 2 weeks.

Simulated SIT with Mismatched Dispersions

The degree of mismatch between the distribution patterns of the wild and sterile flies varied over time. The imposed rate of increase (λ_{GIA}) varied from 0.13-0.35 despite the overall ratio of sterile to wild flies being one that should impose a value of 0.098 if the 2 types of fly were identically dispersed (see above). The mean catch per trap of sterile flies ranged from 87-218 and the associated SD values from 116-283. The percentages of the 3 categories of positive traps (those with >0, >10 and >100 sterile flies in) ranged from 52-90%, 23-53%, and 38-68%, respectively, whereas the index of dispersion similarity ranged from 23-73%.

Of the relationships between the imposed rate of increase and the various factors, only the 1 with the index of dispersion similarity (Fig. 5) was significant. The latter regression explained 60% of the variance of λ_{GIA}. Despite the rather low value of percentage variance explained, the regression line in Fig. 5 predicts a value of λ_{GIA} for 100% similarity in dispersion that is very close to the theoretical value of 0.098.

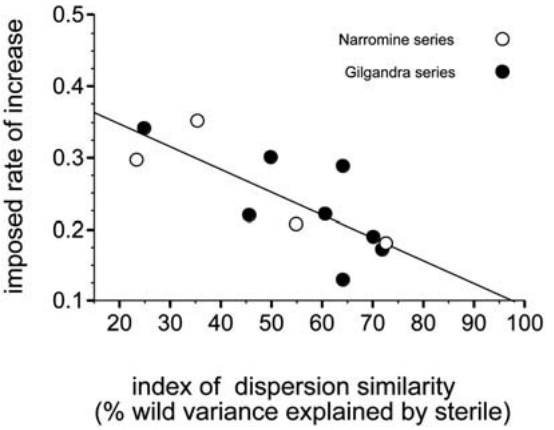

Fig. 5. Simulated results of SIT. The relation of degree of mismatch in dispersions of wild and sterile flies to imposed generational rate of increase when that value would be 0.098 if dispersions were perfectly matched and there was a ratio of sterile to wild flies of 100:1 in all parts of the treated area and the sterile flies had a mating competitiveness value of 0.5. The degree of mismatch is inversely related to the index of similarity, which is found by $100r^2$ where r is the correlation coefficient pertinent to the association of the numbers of wild and sterile flies in each trap in a given week. The dispersion patterns for both kinds of fly were based on data from actual distributions and Gilgandra and Narromine. The curve in the Fig. is a regression of the form $y = bx + a$ where y is imposed generational rate of increase, x is $100r^2$, r = coefficient of correlation between trap catches of wild and sterile flies, a = 0.41 (± 0.05, SEM) and b = -0.0032 (± 0.001, SEM).

DISCUSSION

Taylor's Power Law, SD and CV

The exponent (b) of Taylor's Power Law (slope of $\log_{10}$ variance of catch per trap on $\log_{10}$ of its mean) was found to be, in all cases, not significantly different from a value of 2. Zalucki et al. (1984) found that its value for *B. tryoni* in a natural area of coastal rainforest and open *Eucalyptus* woodland in south east Queensland (Australia) was significantly higher at 2.27 (SEM ± 0.07). The range of mean values was similar to those used here, but the area was over 10 times larger than the trap arrays at Gilgandra and Narromine and the traps were spaced by 1 km or more. Thus, the difference may be a matter of scale in sampling frequency, or size of sampled area (Southwood & Henderson 2000), but it is also possible that the town landscapes relevant to the present paper may be associated with a slightly less clumped distribution than a heterogeneous natural one. If the dispersal pattern of wild flies were the product of the distribution of favorable and unfavorable microhabitats and recent demographic history, then there is no reason for the Taylor exponent to be the same in all places. Sterile flies are initially distributed as evenly as possible and have no local demographic history thus their dispersion when trapped need not necessarily be the same as that of wild flies in the same area. Nevertheless, no significant differences were found between the Taylor exponent (b) of wild and sterile flies at Gilgandra and Narromine. However, the interpretation of regression slopes can depend on the range of values that are being used and this point will be developed in discussing the slopes of SD on mean.

The slopes for $\log_{10}$ SD on $\log_{10}$ mean are (inevitably) half the value of the Taylor exponent, and were not significantly different from unity in the case of *B. tryoni* and hence the CV of the same data did not decline with the mean. The equivalent slope for *B. papayae* was, in contrast, significantly lower than unity and hence the CV did decline with mean. The fact that CV did not decline with mean catch per trap in the case of sterile *B. tryoni* implies that a more even coverage in SIT will not necessarily be achieved by increasing the release rate. This is also supported by the relation of the percentage of positive traps to the mean (see later).

One of the problems of comparing regression slopes is that the greater the numerical range of the data series on abscissa, the steeper the slope of a significant relationship is likely to be. This is the result of the method of calculating the line with the method of 'least squares', which minimizes the squared deviations of the dependent variable from the line (Maelzer 1970; St. Amant 1970). Also, there is a similar effect on the measure of 'goodness of fit' as indicated by the percentage of variation of the dependent variable explained by the regression line. This is clearly illustrated by Fig. 2a where the common slope for sterile and wild flies (where the range of mean values is large) is compared with the slopes that pertain only to either the sterile or the wild flies (where the range of means is more restricted). The percentage of variance explained by the common slope is large (where the range of means is largest), the percentage explained by the 'wild only' slope is less (range of means of intermediate length) whereas the percentage explained by the 'sterile only' slope is least (the range of mean values of the sterile data being the least). Taking the case of the common slope versus either of the other 2 slopes, it is apparent that the fact that the variance explained by the former is greatest is an artifact of the process, whereby the mean of the dependent variables is roughly intermediate between the means of the wild and sterile variables taken separately. As a result, deviations of both kinds from the common means are much larger, whereas the deviations of either set from the common slope (the 'unexplained' deviations) are not much bigger than they are from their own specific slopes. A similar illustration can be seen in Fig. 4a for simulated extinction data, where the slopes of individual clusters of points can be compared with the common slope.

Relation to Negative Binomial Model

The relationship between the percentage of positive traps and mean catch per trap was variable in all cases, the values falling within the range predicted by negative binomial models for very clumped distributions having exponent (k) values in the range <0.05-1.0. The values of percentage of positive traps that are predicted by negative binomial models rise with decreasing slope as the mean increases. With such low values of k, they indicate a very poor return in terms of increasing the percentage of positive traps by increasing the number of flies released. For example, if k were 0.2, the model would predict a percentage of traps with positive values of 71% when catch per trap was 100 and this would rise only to 82% when the catch per trap was 1000.

Extinction Trends

Real extinction trends (of wild *B. papayae* at Cairns and of sterile *B. tryoni* when releases stopped) were very similar to the trend simulated by dividing the catch data from an original set by 10, 100, and 500, respectively. However, the scatter of points in the slopes of graphs of percentage of positive traps on mean catch per trap is smaller in the simulated data than it is in the real data. No attempt has been made to quantify this, but the data suggest that clumping can be more pronounced at lower densities in real situations that it is at higher ones. This is consistent with the model of patterns of outbreak and extinction (see Introduction) where colonization starts with discrete propagules and only remnant foci are left as extinction is approached.

SIT with Mismatched Dispersions

The imposed rate of increase (λ_{GIA}) varied from 0.13-0.35 despite the overall ratio of sterile to wild flies being of a value that should impose a rate of 0.098 if the 2 types of fly were identically dispersed. It is of interest that in no case did a mismatch result in an imposed rate of increase that was less than that expected from evenly matched dispersions. This was a consequence of the asymmetry of the effect of increasing the local density of sterile flies in one patch by decreasing it in another (as would happen with uneven dispersion with a given overall ratio of sterile to wild flies). This can be illustrated as follows by with the equation and competitiveness value (0.5) that were used in the simulations. Consider that 2 local patches have the same ratio of sterile to wild flies and that this ratio (100:1) imposed the same local rate of increase of 0.098. If the sterile flies were dispersed differently so that there were 170 sterile flies to every wild one in one patch and only 30 in the other then the rates of increase imposed on the wild flies would be 0.058 and 0.313, respectively, with the mean of the 2 patches taken together being 0.185 or about 1.9 times greater than would have been expected had the sterile flies been evenly dispersed. The effect is greater with greater mismatch and analogous results are obtained if the wild flies are varied instead of the sterile ones.

Such a phenomenon has analogies in the ecological model whereby sufficiently uneven distribution of attack rates by natural enemies (predators or parasitoids) on population patches of an organism can result in effective partial refuges for that organism that can facilitate the persistence of the relationship (Murdoch & Briggs 1996).

Implications for Release Strategy

It appears that the patchy distribution of released fruit flies is inevitable and that it is not practicable to decrease it by increasing the number released because the increase of mean recapture rate by an array of traps is not accompanied by a reduction in its coefficient of variation and with high recapture rates, the percentage of traps catching zero does not decrease appreciably with increase in recapture rate. It is probable that this would also apply to releases of other flying insects, whether for SIT or for inundative releases of natural enemies for augmentative biological control.

However, it appears from the simulation study that a clumped distribution would not be a problem if the target organism has a similar one (as could happen if patchiness of suitable micro-habitats was the sole cause). The problem arises when the dispersal patterns are mismatched. In that case, the reason is not likely to be environmental unsuitability because the target flies are present where the mismatch is adverse. Shiga (1986) described such a situation. He found that in an SIT program involving releases of *Bactrocera cucurbitae* (Coquillett), the spatial correlation between wild and sterile trappings on a monitoring array was variable and often poor over a period of three months, the index of similarity ranging from 1-41%. This compares with the range 23-73% reported in the present paper. The more extreme mismatches reported by Shiga (1986) were associated with resurgent foci or 'hot spots' of wild flies and these were treated with supplementary releases of sterile flies. Of course, in the case of Shiga's data one cannot tell whether the mismatches were the cause of the hotspots or vice versa. It would be highly likely that the more extreme mismatches were at least part of the cause of the hotspots if the mismatches preceded the eruptions and were also associated with locally low ratios of sterile to wild flies in the adjacent traps. In such circumstances, the population in the hot spots may have a rate of increase close to the natural one whereas the overall rate of increase pertaining to the whole trapping grid may still be below replacement rate ($\lambda < 1$). However, hotspots must be dealt with if eradication is to proceed to completion. It may be prudent, therefore, to avoid the occurrence of hot spots by identifying those traps where the mismatch produces an ineffective ratio of released to wild insects and augment areas surrounding the former with supplementary releases. This may be feasible because the degree of mismatch can be consistent for several weeks (as at Gilgandra).

When the numbers of wild insects become too low for reliable detection by traps, the problem of patchy coverage by wild flies is probably not serious, even in the vicinity of traps failing to recapture released sterile insects. This is because when population density is very low, the probability of persistence is also low (Meats et al. 2003b) However, continued monitoring would always be required for a given period after no target insects are trapped as a precaution against resurgence of the infestation (Shiga 1986; Clift & Meats 2004).

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