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RAPID DELIMITING OF PEST INFESTATIONS: A CASE STUDY OF THE MEDITERRANEAN FRUIT FLY*

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SUMMARY

We consider the problem of quickly determining extent of pest insect infestations, such as the Mediterranean fruit fly (*Ceratitis capitata* (Wied.)) infestation in California. We assume that trapping is the primary method of detection. Analytical techniques are used to provide a relationship between single trap performance as measured in the laboratory and the performance of groups of traps in the field. Monte Carlo simulation techniques are used to compare the efficiency of various trap placement patterns. Depending upon the objective adopted, the optimal choice of trap pattern may be a rectangle or a cross.

INTRODUCTION

An initial concern in most insect pest eradication programmes is determining the extent of the infestation. If the extent is overestimated then pesticide treatment, sterile insect release, and the establishment of quarantines may be applied to areas that are not infested. The consequences of underestimating the extent are more serious. The eradication program may fail or be seriously set back if infested areas go untreated. For example, Lindquist & Nadel (1981) suggest that one primary reason the sterile insect technique (SIT) failed to eradicate the Mediterranean fruit fly *Ceratitis capitata* (Wied.) in the 1980–82 Northern California campaign was that the extent of the infested area was not accurately defined. The original 'epicentre' of the infestation was selected because the first medfly in Santa Clara country was found at this point. The actual epicentre was later determined to be some distance away.

In this paper, we introduce a number of analytical and simulation techniques that can be used to determine the extent of a pest infestation, the location of the epicentre of the infestation, the efficacy of trapping patterns, and the value of information provided by trapping. Although our work was motivated by the medfly infestation, we believe that our techniques have general applicability and complement the existing literature on trapping (e.g. Cunningham & Couey 1983; Cunningham 1981; Dowell & Cherry 1981; Freeman 1977; Wolf, Kishoba & Toba 1971; McClendon *et al.* 1976; Hartsack *et al.* 1971). Bayesian methods provide a useful way to deal with the high levels of uncertainty present in most insect eradication programmes.

We assume that traps are the primary means of pest detection. After the first pest is trapped, new traps are placed near the infested region and all traps are inspected more frequently. In this paper we are primarily concerned with the placement of the extra traps. The placement of these traps may depend on the stage of the eradication campaign. During the initial stages, if the trap density (number of traps per square mile) is low, or if

* Dedicated to Joseph B. Keller on the occasion of his sixtieth birthday.

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the traps are inspected infrequently, information on the extent of the infestation may be quite poor. For example, during the initial stages of the Northern California medfly infestation in 1980 the trap density was less than one per square mile and the traps were inspected at infrequent intervals (R. Dowell personal communication). This may have contributed to the initial underestimate of the infestation.

During the later stages of the eradication campaign the boundaries of the infested region will be more precisely known. Satellite infestations may develop, however, and these infestations must be quickly delimited. It is likely that these satellite infestations will not become too extensive before they are detected. In this context, a satellite infestation may be a small infestation that arose from a larger one or it may be a separate infestation being detected at an earlier stage of development than the initial one.

A protocol was established for the placement of traps during the Northern California Medfly eradication campaign (Anon. 1982). We may summarize it as follows. Most potential infestation areas within 100 miles of the infestation had approximately ten traps per square mile; these traps were inspected weekly. Immediately after a medfly was found the inspection frequency was increased to daily in the 81 square miles around the point of detection. In addition, the density of traps was increased to fifty per square mile in a 9 square mile region surrounding the detection point, and to twenty-five traps per square mile in the 16 square mile perimeter of the central region. The additional traps were also inspected daily. Within 48 hours the central 9 square mile region was subjected to the aerial spraying of malathion bait.

This protocol, or one quite similar, will probably be used for trap placement in future eradication campaigns of the medfly or related pests in California. We therefore chose it as the basis for our study of the efficiency of trap placement strategies. Specifically we focus our attention on trap placement within a 9×9 mile square region centered at the point of first detection. The next section contains a brief survey of the biological aspects of medfly detection.

In the third section, we develop an analytical formalism for the study of trap placement. We base our approach on Bayesian estimation. The formalism allows us to relate properties of individual traps to the gain in information realized by placing traps at a given density in the region of interest.

In the fourth section we compare the effectiveness of various trap placement patterns using Monte Carlo simulation. We make this comparison for two cases. In the first case the infested area has a fixed large size. This corresponds to the initial discovery of the infestation when it may already be quite widespread. In the second case the infestation has a variable size. This corresponds to a satellite infestation, which is less likely to be widespread at the time of its detection.

The last section contains a discussion of our results and conclusions. We are able to make a few tentative recommendations based on our work. We also identify scientific questions whose answers would be especially useful in improving trap placement procedures, and we explain the operational usefulness of the answers to these questions.

MEDFLY DETECTION AND SPREAD—BIOLOGICAL OVERVIEW

Numerous devices have been used for medfly detection. These include kerosene-filled glass jars (Back & Pemberton 1918a; Bodenheimer 1951), invaginated glass traps with liquid protein lures (McPhail 1939) and plastic traps with Angelica seed oil lures (Steiner 1957a; Steiner, Miyashita & Christenson 1957b). The trap currently used most frequently in

Hawaii and California is the delta-type Jackson trap baited with trimedlure, a parapheromone. Trimedlure supercedes both siglure (Steiner *et al.* 1961) and medlure (Beroza *et al.* 1961) and is presently the most powerful attractant commercially available (Chambers 1977). The sex pheromone of the male medfly has been isolated (Jacobson *et al.* 1973) but is not available in commercial quantities.

The little work done on medfly dispersal is ambiguous. For example, using mark–recapture techniques Steiner, Mitchell & Baumhouer (1962) recorded a flight range for the medfly of over 20 km in Hawaii. Severin & Hartung (1912) reported it to be 2·5 km in Hawaii. Soria & Cline (1962) and Soria (1963) found its range to be less than 0·5 km in Tunisia. Katiyar & Valerio (1963), in Costa Rica, recorded a distance of 1·5 km, and Wakid & Shoukry (1976) found that its range was about 0·7 km. In short, there exists over a forty-fold difference in the estimated flight range of the medfly as reported in the experimental literature.

Cunningham & Couey (1983) recently measured the response of male medflies to trimedlure traps. They find that the fraction trapped declines exponentially with increasing distance from the trap of release point. The decline is such that virtually no medflies are trapped from release points over 800 feet from the trap.

ANALYTICAL AND SIMULATION METHODS

The objective of this section is to provide a framework for converting the performance of a single trap, as measured in a laboratory setting, with that of a set of traps in the field. In order to accomplish this, we must introduce several new concepts. We assume that the spatial distribution of host plants is uniform throughout the region of interest. This assumption could easily be relaxed in actual practice. We divide the region into a grid of 1-square-mile cells. The analytical framework is developed as follows. First we consider the epicentre of the infestation. We show how to calculate the probability that a medfly found in one cell is part of an infestation whose epicentre is in another cell. We use this probability to calculate 'prior' and 'posterior' probabilities, in the Bayesian sense, of finding a fly in one cell, given that a fly was found in another cell. The posterior probability incorporates the information about single trap performance and allows us to relate laboratory tests to field performance.

We begin by considering the epicentre. The notion of an epicentre of a pest infestation suggests that there is a point from which the pest infestation originates. We assume that the density of pests is highest at the epicentre and decreases in space as one moves away from the epicentre. Two models for such epicentres are shown in Fig. 1a,b. It could be that the density of pests is actually constant in space, as in Fig. 1c. In this case, the epicentre could be defined as the centre of gravity of the infestated area.

For the purpose of calculation, we assume that the infestation has the bell-shaped form shown in Fig. 1b. Consider the 9×9 mile grid with a pest found in the centre cell (Fig. 2a) before any human interference occurs. Assume that there is a parameter, σ, which we call the dispersal parameter, that characterizes the distance from the epicentre at which pests can be found. A technical description of σ is given in the Appendix. Although the dispersal parameter will change as the infestation spreads, for short enough periods we can assume that it is constant.

Our choice of the distributions shown in Fig. 1 implies assumptions such as a uniform distribution of hosts, a uniform acceptance of hosts, etc. These assumptions can be relaxed given appropriate data.

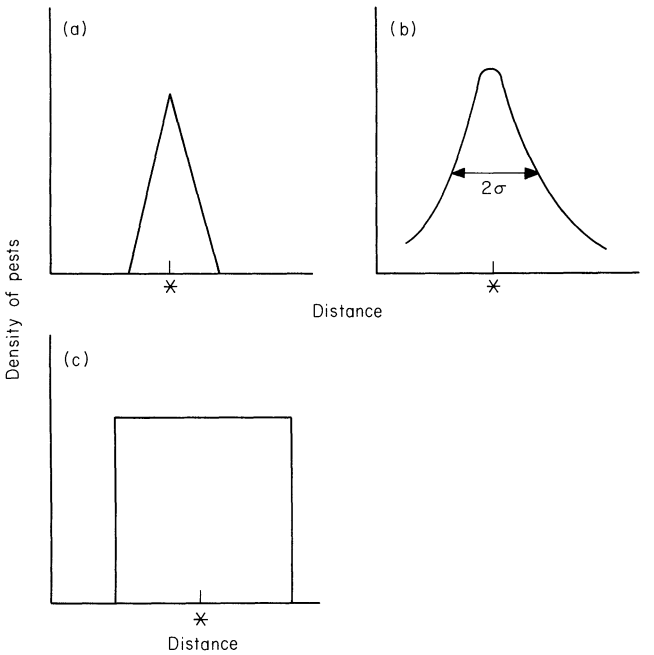


FIG. 1. Possible forms that an infestation might take. The asterisk denotes the infestation epicentre. (a) The pest population declines linearly from the epicentre. (b) The population forms a normal or bell-shaped curve. (c) The pest population is uniformly distributed over the infested region.

The fundamental observation is that finding a medfly in cell (0, 0) does not imply that the epicentre is that cell; if the dispersal parameter is large enough the epicentre could be cell (4, 4)—or even outside the 9 × 9 mile grid. The basic analytical question is then the relationship between dispersal parameter, trap radius, and the distance from the epicentre. In the Appendix, we discuss this relationship. We introduce numbers $e(i, j)$ defined by

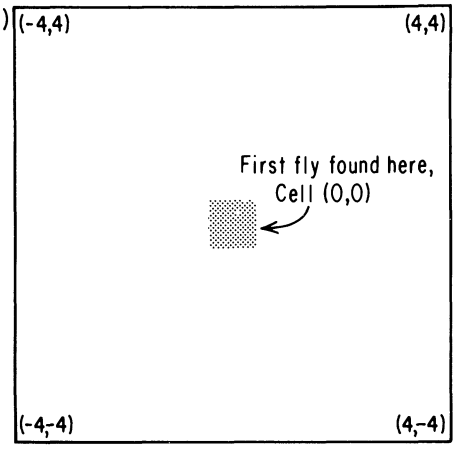
$$e(i, j) = \text{Probability that the epicentre is located in cell with coordinates (i, j) given that a medfly was found in cell (0, 0).} \quad (1)$$

In the Appendix we show how to calculate the $e(i, j)$. Figure 2b,c show the results obtained using a density similar to the one shown in Fig. 1b. We call these figures 'epicentre maps'. They provide a measure of the likelihood of the location of the epicentre. In Fig. 2b, for example $\sigma = 1$ mile is small enough that there is essentially no chance of the epicentre being located on the outer ring of cells. For $\sigma = 3$ mile, however (Fig. 2c), there is a chance that the epicentre is located in the outer ring of cells. In fact cell (4, 4) is 1/6 as likely as cell (0, 0) to contain the epicentre. For σ larger still, there is a greater chance that the epicentre is located outside of the 9 × 9 mile grid. Table 1 shows this probability as a function of σ.

Next, consider the calculation of prior and posterior probabilities of infestation. With a given dispersal parameter σ, the prior probability $p(i, j)$ is defined by

$$p(i, j) = \text{Probability that another medfly is in cell with coordinates (i, j), given that a medfly was found in cell (0, 0)}$$

(a)



(b)

0	0	0	0	0	0	0	0	0
0	0	2	10	17	10	2	0	0
0	2	29	130	215	130	29	2	0
0	10	130	585	965	585	130	10	0
0	17	215	965	1591	965	215	17	0
0	10	130	585	965	585	136	10	0
0	2	29	130	215	130	29	2	0
0	0	2	10	17	10	2	0	0
0	0	0	0	0	0	0	0	0

$e(i,j)\times 10^4$
$\sigma = 1$ mile

(c)

29	44	58	68	72	68	58	44	29
44	65	85	101	107	101	85	65	44
58	85	113	133	141	133	113	85	58
68	101	133	158	167	158	133	101	68
72	107	141	167	176	167	141	107	72
68	101	133	158	167	158	133	101	68
58	85	113	133	141	133	113	85	58
44	65	85	101	107	101	85	65	44
29	44	58	68	72	68	58	44	29

$e(i,j)\times 10^4$
$\sigma = 3$ miles

FIG. 2. (a) Schematic diagram of the region of investigation, which consists of a 9 × 9 mile square, divided into eighty-one cells, centred at the cell where the first fly was found. (b) An 'epicentre map' showing the likelihood that the epicentre is in a given cell when $\sigma = 1$ mile. (c) Same as (b) but with $\sigma = 3$ miles.

TABLE 1. Probability that the epicentre is outside the 9 mile square region

σ (mile)	Probability epicentre outside grid
1	~0
2	0·045
3	0·246
4	0·450
5	0·600

In the Appendix, we show how to calculate the $p(i, j)$ if σ is given. Figure 3(a), (b) show the $p(i, j)$ map obtained using $\sigma = 1$ mile and $\sigma = 3$ mile respectively.

We call $p(i, j)$ a 'prior probability' since it is the probability that pests are in a given cell before effort is made to gain information by trapping. The prior probability map can be used to determine the prior probability that the infestation has reached any given ring of cells. Of most interest is the outer ring of thirty-two cells, which we donote by R. The prior probability of pests in the ring of cell R can be computed from the formula

$$p(R) = \rho_c[1 - \prod_{i,j \,\varepsilon R} (1 - p(i, j))] + (1 - \rho_c) \max_{i,j \,\varepsilon R} p(i, j) \qquad (2)$$

(a)

0	0	0	1	2	1	0	0	0
0	1	14	63	104	63	14	1	0
0	14	181	816	1347	816	181	14	0
1	63	816	3677	6064	3677	816	63	1
2	104	1347	6064	9999	6064	1347	104	2
1	63	816	3677	6064	3677	816	63	1
0	14	181	816	1347	816	181	14	0
0	1	14	63	104	63	14	1	0
0	0	0	1	2	1	0	0	0

$p(i, j) \times 10^4$
$\sigma = 1$ mile

(b)

538	965	1456	1858	2014	1858	1456	965	538
965	1732	2613	3333	3613	3333	2613	1732	965
1456	2613	3941	5028	5450	5028	3941	2613	1456
1858	3333	5028	6414	6953	6414	5028	3333	1858
2014	3613	5450	6953	7537	6953	5450	3613	2014
1858	3333	5028	6414	6953	6414	5028	3333	1858
1456	2613	3941	5028	5450	5028	3941	2613	1456
965	1732	2613	3333	3613	3333	2613	1732	965
538	965	1456	1858	2014	1858	1456	965	538

$p(i, j) \times 10^4$
$\sigma = 3$ miles

FIG. 3. Prior probabilities of the spread of an infestation. The numbers represent the prior probability $p(i, j)$ that an infestation is in cell (i, j) given that a single fly was found in cell (0, 0). (a) $\sigma = 1$ mile; (b) $\sigma = 3$ miles.

In this equation $\prod_{i,j \in R}$ denotes multiplication over all cells with coordinates in R, and ρ_c is a measure of correlation between cells. If $\rho_c = 1$ then all cells are independent; if $\rho_c = 0$ then all cells are perfectly correlated so that if pests are in any cell in the ring, then they are in all cells on the ring. Table 2 shows $P(R)$ and ρ_c using the data from Fig. 3(b).

TABLE 2. Prior probability of pests in the outer ring ($\sigma = 3$ miles)

ρ_c	$P(R)$
0	0·201
0·1	0·280
0·2	0·360
0·3	0·439
0·4	0·518
0·5	0·597
0·6	0·676
0·7	0·755
0·8	0·834
0·9	0·913
1·0	0·992

In the case of complete independence of cells there is a 99% chance that pests are in the outer ring.

The goal of trapping is to provide information about the extent of the infestation. Again, we assume that the outer ring of cells is most important. If pests are found, then one knows that the infestation extends to that ring. Suppose however, that pests are not found at some density of n traps per cell. This does not necessarily mean that pests are absent from the outer ring. It is possible that they are present but were not trapped. To deal with this situation, we introduce a posterior probability $\hat{p}(i, j, n)$ defined by

$\hat{p}(i, j, n) =$ Probability that pests are present in cell with coordinate (i, j) given that there were n traps in this cell but no pests were trapped.

In the Appendix, we show how to calculate $\hat{p}(i, j, n)$. The calculation depends upon the *single trap efficiency*, α, which is the probability that a single trap captures a pest that is known to be present. In the Appendix we discuss how α can be calculated. We call $n\alpha$ the *total trap efficiency* (TTE). Corresponding to $\hat{p}(i, j, n)$ is a posterior probability $\hat{P}(R, n)$ that pests are in the ring R given a density of traps n per cell and no pests trapped. The amount of information provided by trapping can be estimated by considering Δ defined by

$$\Delta = \left[\frac{P(R) - \hat{P}(R, n)}{P(R)} \right] \times 100. \tag{3}$$

Thus, Δ is the percentage reduction in the prior probability caused by trapping.

In Fig. 4 we show typical plot of Δ against TTE, using a density similar to the one shown in Fig. 1(b) with $\sigma = 4$ mile, and a value $\rho_c = 0$. Curve (a) corresponds to linear trapping in which it is assumed that

Probability n traps capture a pest, given that at least one pest is present = Minimum $(1, n\alpha)$ (4a)

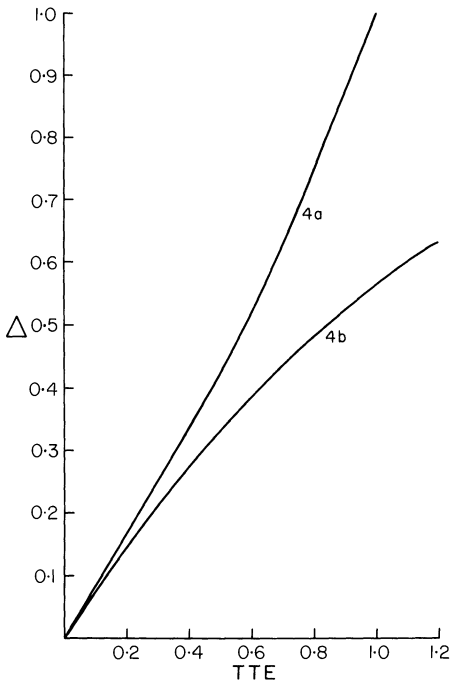


FIG. 4. Information gain Δ *v.* total trap efficient TTE. The upper curve corresponds to no diminishment in return (eqn 4a); the lower curve corresponds to diminishing returns (eqn 4b).

Curve (b) corresponds to diminishing returns trapping, in which it is assumed that

$$\text{Probability } n \text{ traps capture a pest, given that at least one pest is present} = 1\text{-}e^{-n\alpha} \tag{4b}$$

The case of linear trapping assumes complete independence of traps as the number of traps increases. For diminishing returns trapping, the increase in probability of detection decreases with increasing trap number.

There is a considerable difference in the two trapping models regarding the information provided by trapping. Different values of σ, ρ_c, and α will produce different values for the information provided by trapping.

The theory developed in this section is useful for relating individual trap performance to total trap efficiency per square mile. In principle, this theory could also be used to predict the performance of various trap placement patterns. In practice, however, the calculations are quite tedious. We therefore turn to Monte Carlo simulation techniques, which we describe in the next section.

MONTE CARLO SIMULATION OF INFESTATIONS

In order to examine the efficiency of various delimiting strategies we conducted Monte Carlo simulations. These were designed to simulate the events taking place during the first 48 hours after a medfly is detected. Within 48 hours of the detection of a medfly, protocol (Anon. 1982) calls for the aerial spraying of malathion bait. Aside from the obvious killing

of many flies, spraying distorts the infestation in complicated ways that are not clearly understood. We therefore restrict our considerations to the interval between the detection of the first medfly and the aerial spraying.

It is possible that in the future, the protocol will be different. For example, some strategies are:

(a) some longer period (say 7–10 days) before spraying;
(b) never spraying;
(c) spraying after a delimiting survey is conducted. The goal of such a survey is to determine the size, extent, and geographic distribution of the infestation.

We retain the assumption that all increased activity takes place in a 9 × 9 mile region centered at the detection point. Current protocol calls for the placement of 360 additional traps in a 9 square mile region surrounding the detection point during the first 48 hours. Our primary question was whether these 360 traps could be placed in a more efficient pattern.

We consider two situations. In the first, the infestation is already widespread before detection, as might be the case during the initial stages. This is simulated by fixing the infestation to cover a 15 × 15 mile square region as shown in Fig. 5. In the second situation, the infestation may or may not be widespread at the time of detection. This might be the case with satellite infestations. This situation is simulated by making the infested region a square, centred at (0, 0), whose perimeter is a randomly chosen odd number between 1 and 15 miles. In this case a new choice of perimeter is made with each simulation run.

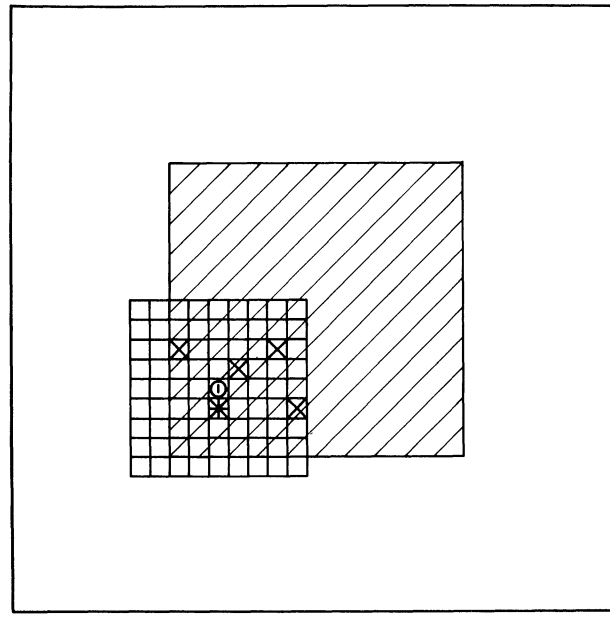


FIG. 5. Representation of a typical simulation run. The large shaded square is in the infested region. The first fly is found in the cell marked with an encircled '1'. A 9 × 9 inspection grid is centred at this cell. Note that many of the cells in the inspection region lie outside the infested region. Six additional flies are trapped, one each in four cells marked with an 'x', and two in the cell marked with a double 'x', just below the original cell.

The simulation runs for 100 units of time, so the time unit may be considered as 0·02 days. At each time unit a medfly becomes 'trappable' in one of the cells in the grid. We assume that the infestation is uniformly distributed so that at each time each cell is equally likely to contain the trappable fly. This assumption can easily be changed, if there is information to warrant it. The fly appearing at the first time unit is automatically caught. The cell in which the first fly is caught is the centre of a 9 × 9 grid which contains all the traps. We do not allow for the possibility of catching a fly outside the 9 × 9 grid; this corresponds to not inspecting traps outside this region during the two day interval. Within the 9 × 9 region traps are placed at a basic density of ten traps per cell and then 360 extra traps are added in some pattern. Note that not all of the eighty-one cells in the 9 × 9 region around the epicentre need be in the infested region. For example, in the case represented by Fig. 5, twenty-five cells (31%) are outside the infested region.

If a fly becomes 'trappable' in a given cell in the trapping region, the probability that it will actually be trapped is assumed to be 0·02 times the number of traps in the cell. Thus for example, the fly is always trapped if there are fifty traps in the cell, and is trapped with probability 0·4 if there are twenty traps. Recent data of Cunningham & Couey (1983) indicates that this assumption is reasonable at low trap densities, but somewhat optimistic at high densities. The number and location of the flies trapped in 100 time units is recorded and the simulation is repeated. Figure 5 shows a typical simulation run in which the density of traps in the nine cell centre region is fifty. Each simulation consists of 10 000 runs.

The parameters used here represent rough approximations chosen after discussion with the Medfly Task Force. The parameters of main interest are: the size of the infested area, the dispersal parameter, and the trapping radius. In the appendix, we show mathematically how these three parameters interact. In particular, we consider a trap of radius $L/\sqrt{2\pi}$ centred at the origin and an infestation with dispersal parameter σ centred h miles away from the origin. We show that if $L/\sqrt{2\pi}$ is much less than σ, then the probability of trapping a pest is approximately

$$p_d(h, r, \sigma) \approx \frac{2(L/\sqrt{\pi})^2}{\left(\frac{L}{\sqrt{\pi}}\right)^2 + 4\sigma^2} \exp\left\{\frac{-2h^2}{\left(\frac{L}{\sqrt{\pi}}\right)^2 + 4\sigma^2}\right\} \tag{5}$$

Four principal statistics are compiled during the simulation. The first is the average number N, of flies caught during the 100 unit time period. The second is the average detected extent, E, of the infestation, defined as follows. Let (i_0, j_0) be the co-ordinates of the centre cell of the trapping region during a given run. Let (i_n, j_n) be the co-ordinates of the cell in which a fly is trapped (if a fly is in fact trapped) in the nth time unit ($1 \leq n \leq 100$). Then

$$E_k = \max_n \{|i_n - i_0| + |j_n - j_0|\} \tag{6}$$

is the detected extent of the infestation in the kth run ($1 \leq k \leq 10\,000$). The average is

$$E = 10^{-4} \sum_{k=1}^{10^4} E_k. \tag{7}$$

Since $0 \leq E_k \leq 10$, the maximum possible value for E is 10. The third and fourth statistics are the coefficients of variation of N (denoted N_v) and E (denoted E_v).

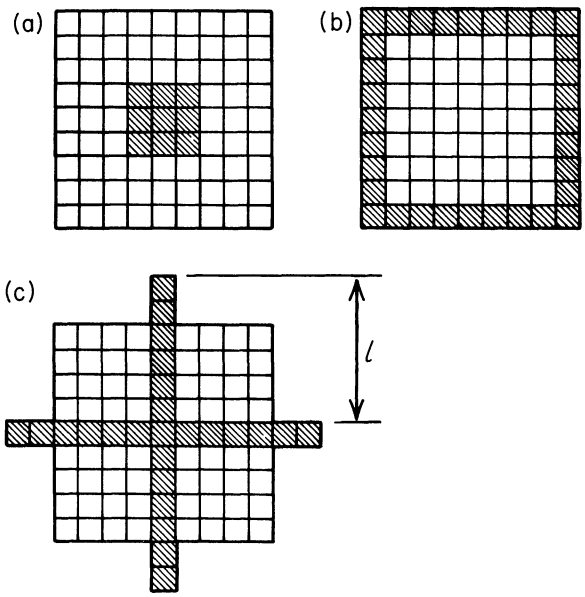


FIG. 6. Three of the five enhancement patterns tested. (a) The extra traps, placed in the centre cells, shown shaded. (b) The extra traps placed at the perimeter. (c) The extra traps placed in a cross with arm length l.

The values of N, E, N_v, and E_v for a given trap pattern should not be considered by themselves, but only in relation to values for other patterns. As a base line for comparison, we compute these values for the case in which no extra traps are added anywhere, i.e. each cell in the trapping region has ten traps. We will call this pattern 0. Pattern 1, shown in Fig. 6a, is that called for by the present protocol. It has a trap density of fifty per cell in the nine cells surrounding the centre. In pattern 2, 360 traps are placed uniformly throughout the region. Pattern 3 has traps at a density of twenty-one per cell in each of the thirty-two cells at the perimeter (Fig. 6b). Pattern 4, not shown, has traps placed at a density of thirty-three per square mile in the sixteen cells surrounding the 9 square mile central region. The motivation for this pattern is that it surrounds the region to be treated by aerial spraying. Pattern 5 consists of a cross-shaped region of extra traps as shown in Fig. 6c. The length of one arm of the cross is l. The density of traps is adjusted so that each pattern adds approximately 360 additional traps to the 810 (10 per square mile) present in pattern 0.

Table 3 shows the simulation results for the case of a fixed 15 × 15 mile infestation. A fifth statistic was collected for patterns 0, 2, and 3. This is P, the percentage of the runs in

TABLE 3. Simulation results with fixed size infestation

Pattern	N	N_v	E	E_v	P
0	6·3	0·44	5·8	0·29	57%
1	9·3	0·35	5·8	0·28	—
2	8·7	0·41	6·1	0·23	63%
3	7·7	0·44	6·4	0·24	79%
4	7·7	0·44	5·8	0·28	—
5	9·9	0·35	5·9	0·25	—

which a fly was detected somewhere in the perimeter of the trapping region. Table 4 shows the simulation results for the case of an infestation whose extent varies randomly from one run to the next.

TABLE 4. Simulation results with random size infestation

Pattern	N	N_v	E	E_v	P
0	4·4	0·68	3·7	0·76	29%
1	7·3	0·49	4·0	0·64	—
2	6·0	0·67	4·0	0·70	33%
3	5·2	0·72	4·0	0·75	41%
4	5·6	0·66	3·9	0·68	—
5	5·9	0·52	3·8	0·66	—

The results presented in Tables 3 and 4 may be interpreted as follows. The statistic N, the average number of flies trapped, gives an indication of the likelihood that the pattern will result in *some* flies being trapped in addition to the first one. The statistic E gives the average detected extent of the infestation. The statistic P, the percentage of time a fly is trapped at the perimeter, only has meaning for the case of widespread infestation; for this case it gives an indication of the ability of the pattern to indicate that the infestation actually is widespread. Table 3 corresponds to the case of a widespread infestation; for this case the success of the pattern in indicating that the infestation is widespread is probably more important than the average number of flies detected. Pattern 3, which places all the extra traps at the perimeter, performs best in this capacity. Pattern 5, the cross shape with $l = 4$, gives by far the highest value of N, but does not give a particularly high value of E. Table 4 corresponds to the case of an infestation in its initial stages, as, for example, a satellite infestation. In this case the most important statistic is probably N since this gives the likelihood of detecting the actual presence of an infestation. For this case pattern 1, in which all extra traps are concentrated near the centre, gives the best results.

DISCUSSION AND CONCLUSIONS

The recent experience of the Northern California medfly infestation of 1980–82 indicates that early delimiting of an infestation of a prolific pest such as the medfly is crucial to the successful eradication of the pest. In a climate such as that of Northern California the infesting population may double in 1 or 2 weeks, and more than 90% of the population may be in pre-adult stages (Carey 1982). In a rapidly growing population, accurate delimiting is essential for the effective use of the sterile insect technique, and in even the aerial application of malathion bait spray is of limited effectiveness against a population with such a small portion of adults.

One of the principal problems in delimiting by traps is the conversion of single trap properties as measured in the laboratory to the effectiveness of groups of traps in the field. Our results indicate that the results are driven by two main parameters: The dispersal parameter σ, the single trap efficiency α.

The parameter σ, which depends on the elapsed time since the start of the infestation, is a measure of the spatial extent of the infestation. In the third section we assume that the intensity of the infestation, when plotted against distance from the epicentre, forms a

bell-shaped or normal curve. This would be the case if the infestation were spreading by a process of simple diffusion as Wong *et al.* (1982) suggest. In this case σ has the usual interpretation as the standard deviation of the normal curve.

The parameter α represents the probability of a single trap capturing a single fly. In the Appendix we give a formula for calculating α in terms of the effective trap radius. There is a feeling among experienced field workers that as the density of traps is increased, there is a diminishing return on the number of traps (H. Cox personal communication, cf. discussion in Simon *et al.* 1975), but there is little experimental evidence to support this. From scientific perspective, then, our results indicate that the most important parameters to measure are the dispersal rate of the pest and the effective trap radius.

Our results show how the two biological parameters σ and α can be combined to give the operational parameter Δ, which measures the information provided by trapping. Δ can be used as an input by the operational decision maker, who must decide if a given increase in Δ is worth the cost of that information. Our results can be used to estimate Δ.

In the fourth section we use Monte Carlo simulation techniques to compare the effectiveness of various trap placement patterns. We assume that there is a basic uniform distribution of traps and study the placement of additional traps placed in the region surrounding the point of first detection of a pest.

Two points are worth noting. The first is that in this section we assume that the infestation has a uniform distribution similar to that of Fig. 1c. This is done for computational reasons. The second is that we assume a uniform distribution of host plants so that the number of traps per square mile is equal to the density of the traps. This is also done for computational simplicity, but it is important to remember that in all of our theoretical work the trap density, and not the number of traps in a square mile cell, is important. For example, in a square mile cell with a density of fifty traps per square mile, if half of the area of the cell is taken up by a lake then the appropriate number of traps for that cell is twenty-five.

Our results indicate that in the early stages of delimiting an infestation, when the infestation may already be quite widespread, it is most useful to put extra traps around a perimeter some distance from the presumed epicentre. At a minimum, we would recommend that as extra traps are added to a region, the trappers should start from the perimeter and work in.

In the delimiting of satellite infestations, when the infestation is less likely to be widespread, the placement of the extra traps near the centre appears to be most effective. Our results indicate, however, that the placement of extra traps in a cross shape centred at the point of first detection is an efficient pattern and deserves further investigation.

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MATHEMATICAL APPENDIX

We begin by considering the construction of the epicentre map. The starting point is the density $\rho(i, j, i', j', \sigma)$, presumed known, and defined by

$$\rho(i, j, i', j', \sigma) = \text{Probability of pests in cell with coordinate } (i, j) \text{ given that the epicentre is in cell with coordinates } (i', j') \tag{A1}$$

For the calculations shown in the text, we used

$$\rho(i, j, i', j', \sigma) = \exp\left[\frac{-(i - i')^2 - (j - j')^2}{2\sigma^2}\right] \tag{A2}$$

The choice of model in (A2) is an unnormalized Gaussian density. It has the property that if the epicentre is located in cell (i', j') then the probability that another pest is present is 1.

In order to find $e(i, j)$ we use Bayes' theorem from probability (e.g. Feller 1968). Then

$$e(i, j) = \text{Probability that the epicentre is located in cell } (i, j) \text{ given a pest found in cell } (0, 0) \tag{A3}$$

$$= \frac{\text{Probability that the epicentre is in cell } (i, j) \text{ and a pest found in cell } (0, 0)}{\text{Probability that a pest is found in cell } (0, 0)} \tag{A4}$$

$$= \frac{\rho(0, 0, i, j, \sigma)}{\Sigma \rho(0, 0, i', j', \sigma)} \tag{A5}$$

The summation in (A5) extends over all possible cells. For the model (A2), since the integral of the Gaussian density is $2\pi\sigma^2$, the summation in (A5) is replaced by $2\pi\sigma^2$. Equation (A5) was used to construct the epicentre maps shown in the text.

Once $e(i, j)$ is known, we can find the prior probability $p(i, j)$:

$$p(i, j) = \text{Probability another pest in cell } (i, j) \text{ given that a pest was found in cell } (0, 0) \tag{A6}$$

$$= \sum_{(i, j)} \{\text{Probability pest in cell } (i, j) \text{ given an epicentre at } (i', j')\} \times \text{Probability of an epicentre at } (i', j') \text{ given a fly found in cell } (0, 0) \tag{A7}$$

$$= \sum_{(i', j')} \rho(i, j, i', j', \sigma)\, e(i', j') \tag{A8}$$

Equation (A8) was used to calculate the prior probability maps shown in the text.

Next, consider the posterior probability $\hat{p}(i, j, n)$, assuming the single trap efficiency is known. Let $1\text{-}f_n(\alpha)$ be the probability that n traps of identical efficiency α catch a pest, given presence of the pest. Then

$$\hat{p}(i, j, n) = \text{Probability that the pest is present in cell } (i, j) \text{ given that } n \text{ traps did not catch a pest} \tag{A9}$$

$$= \frac{\text{Probability that the pest is present and n traps did not catch it}}{\text{Probability that } n \text{ traps did not catch the pest}} \tag{A10}$$

$$= \frac{p(\mathrm{i}, \mathrm{j}) \cdot \mathrm{f}_n(\alpha)}{1 - p(\mathrm{i}, \mathrm{j}) + p(\mathrm{i}, \mathrm{j})\, \mathrm{f}_n(\alpha)} \tag{A11}$$

The first term in the denominator is the probability that the pest is absent from cell (i, j); the second term is the probability that the pest is present but not trapped. The posterior probability $\hat{p}(\mathrm{R})$ of a ring of cells is obtained by using eq (A11) instead of $p(\mathrm{i}, \mathrm{j})$ in eqn (2) of the text.

Next consider the calculation of α, the single trap efficiency. Assume that M_{T} pests are uniformly distributed in a 1 mile square cell and that a fraction q of them are trappable. For example, for the medfly, q is apparently between 0·5% and 5%. Experimental evidence of Cunningham & Couey (1983) indicate that a single trap in a one square mile cell will trap approximately 4% of the medflies in that area. Cunningham & Couey also show that the effectiveness of trimedlure traps declines exponentially with distance. We may therefore assume that a trap has an effective area within which it is attractive.

If the effective area of a trap is L^2, then the probability that k of the M_{T} pests are trapped is given by the binomial formula

$$\binom{qM_{\mathrm{T}}}{k} (\mathrm{L}^2)^k (1 - \mathrm{L}^2)^{2M_{\mathrm{T}} - k} \tag{A12}$$

For large $q\mathrm{M}_{\mathrm{T}}$, small L^2, (A12) is well approximated by the Poisson process with parameter α given by

$$\alpha = q\mathrm{M}_{\mathrm{T}} L^2, \tag{A13}$$

which is identified as the single trap efficiency. Table A1 shows α as a function of L^2 for $q = 0{\cdot}5\%$, $\mathrm{M}_{\mathrm{T}} = 10^4$.

TABLE A. Single trap efficiency

L(ft)	α
5	0·000045
10	0·000179
15	0·000404
20	0·000717
25	0·001121
50	0·00448
100	0·0179
150	0·0404
200	0·0717
250	0·1121
300	0·1614
350	0·2197
400	0·2870
450	0·3632
500	0·4484

The final mathematical consideration involves the interaction between the trap radius and the dispersal parameter σ. If the effective area of a trap is L^2, then the effective trap radius r is

$$r = L/\sqrt{\pi} \tag{A14}$$

Consider a trap placed at the origin and an infestation centred h miles from the origin with

dispersal parameter σ. In particular, assume that the relative density of pests at the point (x, y) is

$$\rho(x, y) = \frac{1}{2\pi\sigma^2} \exp\left\{\frac{-(x - x_h)^2 - (y - y_h)^2}{2\sigma^2}\right\} \tag{A15}$$

Here (x_h, y_h) is the centre of the infestation, with $x_h^2 + y_h^2 = h^2$.

The probability that the trap at the origin traps a pest is then

$$p_D(h, r, \sigma) = \frac{1}{2\pi\sigma^2} \iint_{x^2+y^2 \le r^2} \exp\left\{\frac{-(x - x_h)^2 - (y - y_h)^2}{2\sigma^2}\right\} dx\, dy \tag{A16}$$

Dobbie (1959) shows that by converting this integral to polar coordinates it becomes the integral of a Bessel function. Expanding the Bessel function and integrating gives

$$p_D(h, r, \sigma) = 1 - \exp\left\{\frac{-h^2 - R^2}{2\sigma^2}\right\} \sum_{i=0}^{\infty} \frac{(h^2/2\sigma^2)^i}{i!} \sum_{j=1}^{i} \frac{(R^2/2\sigma^2)^j}{j!} \tag{A17}$$

For $r \ll \sigma$, which is the case of most interest here, (A17) is approximated by

$$p_D(h, r, \sigma) \approx \frac{2r^2}{r^2 + 4\sigma^2} \exp\left\{\frac{-2h^2}{r^2 + 4\sigma^2}\right\} \tag{A18}$$