THE POWER OF TRAPPING GRIDS FOR DETECTING AND ESTIMATING THE SIZE OF INVADING PROPAGULES OF THE QUEENSLAND FRUIT FLY AND RISKS OF SUBSEQUENT INFESTATION

A. Meats

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

Summary

A method is given for interpreting the trapping rates of cuelure traps. This is related to the catching power of grids of different sizes and densities. Results depend on where it is assumed that the invading propagule arose on the grid (at a trap site or between traps). Thus methods for highest and lowest estimates are given. The magnitude of the difference between the two gets larger the larger the grid spacing so that catches on grids of 5 and 10 km spacing are essentially uninterpretable. Using the highest estimates for grids of 0.4 and 1 km spacing, a method is given for assessing the risk of a continuing infestation from the number of flies caught. The assessments are based on our knowledge of the minimum density required for breeding. These estimates are compared with those assumed by the existing code of practice.

INTRODUCTION

Origin of new propagules and the risk of infestation

New propagules of fruit flies can arise in a hitherto fly-free area either because an immigrant gravid female arrives and lays eggs or because infested fruit is carried in and discarded inappropriately (say on a compost heap). In the isolated quarantined 'fly free' areas of Australia, it is most likely that all occurrences are due to the latter cause. Bateman (1977) pointed out that species such as the Queensland fruit fly (*Bactrocera tryoni* Froggatt) are relatively poor colonisers of new areas since emerging flies would spend up to 7–14 days dispersing before they mature and hence would have little chance of encountering potential mates. Thus the detection of flies at very low frequencies (especially on intense grids of cuelure traps) does not necessarily mean that females will be fertilised and infest fruit. It is the purpose of this paper to relate low detection rates to propagule size and infestation risk.

A STRATEGY FOR RISK ASSESSMENT

Meats (1998a) reviews field experiments with *B. tryoni* involving releases of various numbers of teneral flies at a point and their subsequent recapture when mature on arrays of traps extending to various distances. Risk assessment is thus possible along the following lines.

(a) Calculate the proportion of flies from a natural propagule emerging at a point that will be captured on a trapping grid. The model for this should apply to any size of grid and any density of traps.

(b) Estimate the original numbers of males in the propagule from the result of (a) multiplied by the number of flies actually caught on a particular grid.

(c) From estimates of how flies distribute themselves with time, calculate the chances of a fly from a propagule of any given size encountering a mate and thus continuing the infestation. This estimate multiplied by (b) will give the probable number of mated flies arising from a propagule of a given size.

Each of these steps in turn consists of a number of subsidiary steps as explained in the following account. Basically, the entire process depends on our knowledge of how flies survive and disperse after emergence and of how mating opportunity when mature depends on fly density.

THE DYNAMICS OF A NEW PROPAGULE

General phenomena

Fletcher (1973) established with a long series of trials that teneral flies, released at a point, would disperse quite rapidly so that at maturity only about 20% would remain within approximately 200 m of the release point and that, thereafter, the mature flies remaining within the 200 m radius would decrease at a rate of approximately 50% per week. Fletcher (1974a) related the recapture rate per trap (hence density) of mature flies to distance at various times after release as either teneral or mature cohorts. The relationship essentially conforms to an 'inverse

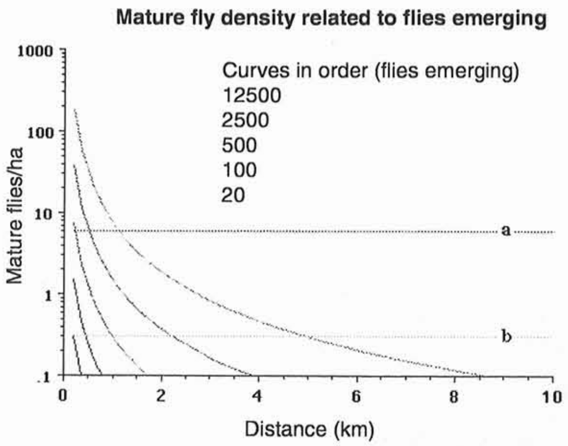

Figure 1. The density distribution of flies on reaching maturity after emerging at a point as propagules of sizes indicated. The horizontal lines (a, b) indicate density limits for breeding as discussed in the text.

square rule' whereby catch per trap declines as the reciprocal of the square of the distance.

The model of Meats (1998a) combines the information from Fletcher (1973, 1974a) to predict (for flies released as either teneral or mature cohorts) the recapture rate per trap in relation to time and distance. Since recapture rate can be related to density (Fletcher 1974b), the model can be used to predict the distribution of a cohort of flies that emerge naturally at a point (i.e. an invading propagule). Figure 1 shows the expected distribution of flies at the time they reach maturity. The curve for this figure was calculated using methods that are explained later involving equations (10a, b) for the densities within 200 m of emergence and the inverse square rule (equation 5) for densities beyond this radius.

It can be seen from figure 1 that, even with large cohorts, most maturing flies will disperse into a virtual void of low fly density in which there is little chance of mating encounters. Two minimum thresholds of density for mating are indicated on the figure and will be examined later in the paper.

A dispersal model and its application to **B. tryoni**

A full version of the model is given by Meats (1998a). The latter is used to calculate mean expectations and these are compared with the results of various release trials. For conformity, the mean expectations are adhered to in the present paper despite the fact that, at first sight, they give the illusion of undue precision. All predictions pertain to males only.

Basically, the 'inverse square rule' means that if we can predict the density of flies within a 200 m radius of the release (or emergence) point and we can estimate what the recapture rate would be with a notional trap at this point, then we can estimate the catch per real trap at any other distance.

We can use normal demographic notation for the calculations pertinent to the area of 200 m radius. The notation conventionally applies to survival rates (i.e. proportions remaining alive at different times). However, in our case the survival notation pertains to the proportion remaining alive that also remain within the 200 m radius (i.e. the others are not necessarily dead, they may be still alive but outside the 200 m radius). Fletcher's (1973) data are also in this form as it was not possible to distinguish between mortality and emigration rates. It is not necessary to do so for prediction of recapture rates.

If the daily survival rate of immature flies in the 200 m radius is p_{xI} and the rate for mature flies is p_{xA} then the proportion remaining when flies mature (i.e. when age (x) in days = D) is

$$l_D = \pi p_{xI} = 0.2 \quad (1a)$$

The proportion surviving to halfway through the first day of trapping is

$$l_T = l_D p_{xA}^{0.5} \quad (1b)$$

With a capture rate of 1% per day (Fletcher 1974b) the first day's catch is thus approximately

$$C_1 = l_D p_{xA}^{0.5} \cdot (1 - p_{xt}) \quad (2)$$

where $p_{xt} = 0.99$ = the proportion not trapped per day and p_{xA} is defined below.

The proportion remaining thereafter declines at approximately 50% per week, hence with additional mortality due to trapping, the daily adult survival rate within the 200 m radius is found by

$$p_{xA} = 0.5^{(1/7)} \cdot 0.99 = 0.8966 \quad (3)$$

The mean expectation of C_1 is thus 0.0018938 and l_T is 100 times this.

The accumulated proportion ($AP_{(0.2)}$) catchable in n days within the 200 m radius (0.2 km) is thus

$$AP_{(0.2)} = \sum_{D+1}^{D+n} C = C_1 \frac{\left(1 - p_{xA}^{\ n}\right)}{(1 - p_{xA})} \qquad (4)$$

When n is large (say, 49 d) the quantity in the first set of brackets is virtually equal to 1. Thus the mean expectation of $AP_{0.2}$ for such a long period is 0.01832.

The above gives the accumulated proportion of a cohort caught or catchable by a trap set at the point of emergence.

The proportion caught per trap at any other distance (d) is found by the 'inverse square rule' (Fletcher 1974a; Meats 1998a) as

$$AP_d = AP_{0.2} \cdot \left(\frac{0.2}{d}\right)^2 \qquad (5)$$

This relation also describes how density declines with distance and was used as such by substituting density for AP in calculating the curve in figure 1.

A capture model for standard grids

If we had a known number of traps at known distances we could predict the number of flies captured from a propagule of known size. This is a useful way of monitoring the success of releases of sterile flies for SIT (Meats 1998b). Conversely, of relevance to the present paper, we could estimate the numbers in the original propagule from the numbers caught on the grid.

Meats (1997b) gives a model that relates the catching power of standard grids to the recapture rate of either a real or a notional trap at the point of origin. The result for any particular grid configuration depends on whether flies originate at a real trap site or between real trap sites.

(a) Capture rate when flies emerge at the trap site

In this case, the catch at the trap at the point of origin will be the same as for the notional trap (see earlier). The accumulated catch at this trap (see earlier) is designated $AP_{(0.2)}$. The other traps on the grid can be regarded as being approximately arranged in rings around the central trap with mean annuli occurring at intervals of 1 trap spacing (S). Since catch per trap declines from the origin as $\left(\frac{0.2}{d}\right)^2$ and the density of traps with distance is constant then the catch per annulus will decline as $\left(\frac{0.2}{d}\right)$. The accumulated proportion caught at the first ring is thus

$$AP_{(R1)} = AP_{(0.2)} \cdot \left(\frac{0.2}{S}\right)^2 \cdot \left[\frac{2\pi S}{S}\right] \qquad (6)$$

$$= AP_{(0.2)} \cdot \left(\frac{0.2}{S}\right)^2 \cdot 2\pi$$

The accumulated catch on the grid (as a proportion of the emerging cohort) to radius n is thus

$$AP_{(grid)} = AP_{(0.2)} + AP_{(R1)}\left(1 + \frac{1}{2} + \frac{1}{3} + \frac{1}{4} \ldots \frac{1}{n}\right) \qquad (7)$$

(b) Capture rate when flies emerge between trap sites

The most extreme version of this is where flies emerge equidistant from four traps on a grid. There is no central trap but the catch for a notional trap in this position must be calculated in order to estimate the catch in the first ring. The first ring will be at a radius of *(0.5)S* and the other rings will be at radii of *(1.5)S*, *(2.5)S*, *(3.5)S ... (n - 0.5)S*.

The accumulated catch at the first ring will be

$$AP_{(R1)} = AP_{0.2} \cdot \left(\frac{0.2}{0.5S}\right)^2 \pi \qquad (8)$$

The accumulated catch to radius n is

$$AP_{(grid)} = AP_{(R1)}\left[1 + \frac{1}{3} + \frac{1}{5} + \frac{1}{7} \ldots \frac{1}{2n-1}\right] \qquad (9)$$

The capture rate for flies thus depends upon the place on the grid from which they emerge. For grids of 1 km spacing or more, the capture rate is much higher if flies emerge at a trap site. This trap will recapture a fraction approaching 2% for *B. tryoni* regardless of the spacing of the other traps, whereas if the nearest traps are at one half of the trap spacing away they will catch a relatively small proportion in total and the other traps will catch almost insignificant amounts.

The capture model given above yields an estimate of $AP_{(grid)}$, the expected proportion of flies emerging on a grid that are caught on the grid. It is possible to estimate the numbers that emerged on the grid from the reciprocal of this estimate multiplied by the number of flies actually caught. However, we never know quite where flies emerge on a grid relative to the nearest trap (this could range from right at a trap site to equidistant between four traps). The method above gives the two extreme estimates for $AP_{(grid)}$ one for the 'at trap' assumption and one for the 'between trap' assumption. These will give us the 'lowest' and 'highest' estimates in each case (see later).

The remainder of this section applies to either estimate of $AP_{(grid)}$. It can then be modified to apply to mature flies and (as explained in a later section) to partial catches where captures are made for only a week or two of the period in which flies are trappable.

Number of flies emerging

$AP_{(grid)}$ is the expected accumulated catch of the grid as a proportion of the number of flies that emerged. Hence the number of flies that emerged (N_E) is found by

$$N_E = \frac{n}{AP(grid)} \qquad (10a)$$

where n is the number of flies trapped.

Number of flies reaching maturity

The number of flies ($N_{M(0.2)}$) remaining within 200 m of the emergence site on reaching maturity is found by following equations (1a, b)

$$N_{M(0.2)} = N_E \cdot l_T \qquad (10b)$$

The density of flies reaching maturity in the 200 m radius (flies ha^{-1}) is thus found by dividing the result by 12.5664.

Many other flies will have dispersed to mature elsewhere. The total on the grid, $N_{M(grid)}$, can be calculated following equations (6) and (7).

$$N_{M(grid)} = N_{M(0.2)} + \left[N_{M(0.2)} \cdot \left(\frac{0.2}{S}\right)^2 \cdot 2\pi \cdot \left(1 + \frac{1}{2} + \frac{1}{3} \ldots \frac{1}{n}\right)\right] \qquad (10c)$$

Where n in this case is the number of trap spacings to the furthest ring of traps and S is the trap spacing in km.

Example with 0.4 km grid

The difference between 'highest' and 'lowest' estimates of $AP_{(grid)}$ (and hence 'highest' and 'lowest' estimates of propagule size) are larger the greater the trap spacing. The 'highest' estimates are approximately 18% and 70% higher than the lower ones for 0.4 km and 1 km grids respectively (Meats 1998b).

Figure 2 gives the 'lower' estimates of propagule size per fly trapped for grids of 0.4 km spacing and various diameters. The lowest curve pertains to grids that trap at least 49 d after flies mature (i.e. respond to traps). The upper two curves pertain to 'partial catches' (one week of trapping within the 49 d period) and will be discussed in the next section.

Figure 2 shows how the estimate of propagule size per fly caught varies with the radius of a 0.4 km grid. The estimate gets lower the bigger the radius of the grid because the proportion of the original cohort trapped will be larger on bigger grids and hence the reciprocal (propagule size per fly caught) will be smaller. However, this effect is quite small as the radius of the grid is increased beyond 3–4 km.

A SUBMODEL FOR PARTIAL CATCHES BY GRIDS

This submodel is necessary for two practical reasons. Firstly, one normally wants results quickly, i.e. after 7 or 14 days of trapping. Secondly, the grid (delimitation grid) may be installed late in response to a catch by a sentinel trap (detection trap)—thus not only would the grid have missed the initial period

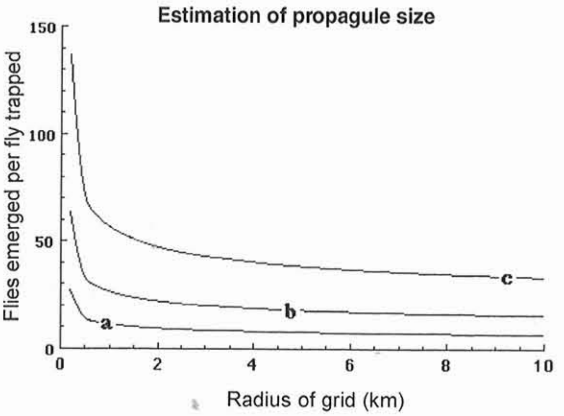

Figure 2. Estimates of propagule size from the trapping rate of a grid of 0.4 km spacing related to grid radius, Curve (a) pertains to 7 or more weeks of trapping. Curves (b) and (c) pertain to the first week of trapping if the grid is installed 2 days after detection of an infestation by a sentinel trap. Curve (b) assumes that the first fly entered the sentinel trap just before it was inspected (same day); curve (c) assumes the first fly was caught 7 days before the sentinel trap was inspected.

For maximum density of mature flies (flies/ha) within 200 m of origin, divide ordinate value by 66.36 following equation 10(b).

when flies would have been trappable, one would still want to interpret the first 7 or 14 days of trapping by the grid despite its late installation.

Equations (7) and (9) estimate the extremes of a range of values that could apply to the proportion of a propagule trapped by a grid. They both use an estimate for the accumulated catch by a trap at the point of origin (whether it is really there or not). The accumulated proportion caught by this trap is given by equation (4) and is designated $AP_{(0.2)}$.

Total proportion catchable by a grid

When a grid is in place before the first fly is caught, the accumulated catch to 7 weeks or beyond is virtually found by using in equations (7) and (9) for a value of $AP_{(1)}$ that is found by

$$AP_{(0.2)} = C_1\left[\frac{1}{1-p_{xA}}\right] \quad (11a)$$

where C_1 is (as given earlier) the first day's catch.

$AP_{(0.2)}$ for periods of 7 weeks or more has a mean expectation of 0.01832 as given earlier. Thus if equations (7) and (9) are used in this way they give estimates of the total proportion of a propagule catchable by the grid $AP_{(grid)}$ (total).

Partial proportion catchable (early result)

The partial accumulated catch from the first fly to d days later is found by following the logic of equation (4).

$$AP_{(grid)}(partial) = AP_{(grid)}(total)\left(1-p_{xA}^{d}\right) \quad (11b)$$

Thus the partial proportion caught for the first 7 and 14 days is lower than the total proportion by a factor of 0.5432 and 0.783 respectively. The lower curve of figure 2 (propagule size indicated per fly caught) would therefore be higher by a factor of 1.872 and 1.277 respectively (i.e. the reciprocals of the first two figures).

Partial proportion catchable (late installation)

The partial catch when the grid is put in place G days after the first fly is caught by a sentinel trap is

$$AP_{(grid)}(partial) = AP_{(grid)}(total) \cdot p_{xA}^{G} \quad (11c)$$

The partial catch when the grid is put in place after G days and is monitored d days later (say 7 or 14 days later) is

$$AP_{(grid)}(partial) = AP_{(grid)}(total) \cdot \left(p_{xA}^{G} - p_{xA}^{G+d}\right) \quad (11d)$$

Practical solutions to late installation

When a grid is installed or intensified in response to the detection of flies in a sentinel trap, the main problem is that we cannot tell precisely when the sentinel trap started catching the flies. There is a possibility of a 7 day error if traps are cleared weekly. Thus two estimates of partial catches must be made using maximum and minimum delays involved in grid installation.

The upper two curves of figure 2 give such estimates for flies trapped in the first week after installation after a delay between trap clearance and installation of $2d$. Thus following equation (11d) the values of G and $G+d$ are 9 and 16 respectively for the upper curve and 2 and 9 for the middle curve.

A MODEL FOR VERY LOW DETECTION RATES RELEVANT TO QUARANTINE ZONES

This method uses a more precise calculation made possible when very few (1–5) flies are trapped and very few traps (adjacent ones) catch the flies. It can be applied to grids of any intensity (even sentinel grids) but is more precise the smaller the spacing between the traps. In particular, it allows us to give some meaning to data from sentinel traps—e.g. what can one fly mean or what can 2 flies in two weeks mean?

Once again, the logic and mean expectations of the model of Meats (1998a) are used and we still have to calculate higher and lower estimates because the results depend on whether we assume flies emerge at a trap site or between trap sites.

Lowest estimates (general)

When only one or two flies are trapped in a hitherto fly-free area we can assume from the inverse square relationship (given earlier) that they emerged in the vicinity of the immediately adjacent traps. If they emerged actually at a trap site then the size of the original propagule can be estimated (per fly trapped) as the reciprocal of the proportion expected to be trapped.

Lowest estimates (trapping for 7 weeks from first fly)

If flies are trapped for at least 49 d after they first become mature then the accumulated proportion caught ($AP_{(0.2)}$) by a trap at the emergence site is given by equation (4) and has a mean expectation of 0.01832. Thus the mean expectation for the number of flies that emerged is $\frac{1}{0.01832}$ = 54.585 per fly caught. The number per hectare emerging in the 200 m radius is thus $\frac{54.585}{12.5664}$ = 4.3437 per fly caught.

How many flies would remain in the 200 m radius at maturity? The proportion is l_T and is found by equation (1b) with a mean expectation of 0.18938. Thus the above quantities for number and density of newly emerged flies are multiplied by 0.18938 to give the mean expectations per fly caught for newly emerged flies. These would therefore be 10.3373 within the 200 m radius or 0.82262 ha^{-1} per fly trapped.

Lowest estimates (limited trapping results)

The expected proportions trapped over a limited period are found as before (from equations (11a–d). Thus one week of trapping would catch only 53.42% of the expected total trapped and 2 weeks would catch 78.3%. Therefore the estimates for propagule size and numbers per hectare given above would be multiplied by $\frac{1}{0.5342}$ for 1 fly in 1 week and by $\frac{2}{0.783}$ for 2 flies in two weeks. Other adjustments for other periods can be calculated using equation (11d).

Highest estimates (general conversion factor)

If the propagule emerged between the traps then the inverse square rule indicates that the catch would represent much less than 1.832% catchable by a trap at the emergence site. Hence the reciprocal (i.e. the number of flies emerging per fly caught) would be much higher. The highest value for flies emerging is given if it is assumed that the propagule emerged equidistant from 4 traps on a sentinel grid. The catch per trap per fly caught would be ¼ of that for a single trap and the number of flies or number per hectare quoted above for the 'at trap' assumption should be multiplied by H where

$$H = \left(\frac{\frac{1}{2}S \cdot \sqrt{2}}{0.2}\right)^2 \cdot \frac{1}{4} \qquad (12)$$

Table 1. Interpretation of low frequency catches for quarantine thresholds. Estimates (per fly trapped) of original propagule size (flies emerging) and subsequent mature flies ha^{-1} within 200 m of origin.

Trap spacing (km)	Estimates of flies emerging		Estimates of maturing flies ha^{-1} near origin	
	lowest	highest	lowest	highest
0.4	27.29	54.59	0.412	0.823
1.0	54.59	170.6	0.823	2.571
5.0	54.59	4264	0.823	64.27
10.0	54.59	17,058	0.823	257.0

Numbers above apply to 1 fly caught per 7 wk period.
Multiply *pro rata* if more flies are caught.
For 1 fly in 1 week multiply by 1.872
For 2 flies in 2 weeks multiply by 2.554
For 0.4 km grid installed after detection at wider spacing use multipliers as in text.

This multiplier is 0.5, 3.125, 78.125 and 312.5 for spacings (S) of 0.4, 1, 5 and 10 km respectively. Table 1 summarises the results of sample calculations for various grid spacings.

Density and infestation risk

We can relate low frequency captures to numbers of mature flies per hectare. But what number of flies per hectare represents a risk of a female being mated and laying eggs? The only reliable answer can come from experience quantified by a risk analysis applied to real data relating flies caught to the incidence of first infestation or a subsequent generation. At present there is no proper risk analysis but a consensus that 2 flies in 2 weeks should trigger grid intensification to a spacing of 400 m, and the trapping of 5 flies or more should represent an unacceptable level of risk (Anon. 1997). Pending an empirical risk assessment, however, we can produce an estimate based on our current knowledge of the mating behaviour of *B. tryoni*.

Firstly, it appears from Tychsen (1977) that flies of both sexes must be in the same tree in the same dusk period. Thus assuming a maximum area of 5x5 m, a male fly must be in the same $^1/_{400}$ ha as a female fly. Thus the male in question has a $^1/_{400}$ chance of being in the right place at the right time if the density of male flies is 1 ha^{-1}. This conclusion is specific to *B. tryoni*. For species where attraction between sexes can occur over larger distances the value for 'maximum area' (above) must be suitably adjusted. The question as to whether the result would be affected by a non-random distribution is dealt with below.

Secondly, it appears from equation (4) that the mean number of days spent by a mature fly within 200 m (a circle of area 12.5664 ha) of the emergence site is $\frac{1}{1-p_{xA}}$ or approximately 10. Thus a fly will have on average approximately 10 chances of mating in the area of highest density. However, the presence of a male and a female in proximity does not guarantee that mating will occur. Even in small cages the probability is only about 0.8 (Fay and Meats 1983). In an area of 5x5 m the chances would be lower; unpublished observations suggest that the probability is less than 0.1. At lower densities it would be virtually zero.

Finally, we can calculate the probability of mating from the zero term of a frequency distribution. It really does not matter whether we choose a Poisson (random) distribution or a negative binomial one with $k<1$, (clumped distribution) because at very low frequencies the results converge (Clift and Meats 1998).

Using the zero term for the Poisson distribution we can estimate the number (N) of flies mating from a propagule as

$$N = 12.5664n[1 - exp-(\bar{x}_1 \cdot \bar{x}_2 \cdot \bar{x}_3)] \quad (13)$$

where

n = the number of male flies maturing ha^{-1} within a 200 m radius of the emergence site (area 12.5664 ha).

$\bar{x}_1$ = the mean probability of being in a 5 x 5 m area with a female fly = $\frac{n}{400}$

$\bar{x}_2$ = the mean probability of mating in a 5x5 area when there is a female present = 0.1

$\bar{x}_3$ = the mean number of dusks available = 10

The probability starts to exceed one fly mating when n exceeds 6 of each sex per hectare. Thus we can speculate that 6 males ha^{-1} indicates a trigger level for quarantine precautions. This roughly corresponds to the trapping of 2 flies in 2 weeks on a 1 km grid if the flies emerged equidistant between four traps (i.e. if the highest estimate of n were true). As shown earlier, the highest estimate of n for a 1 km grid is 3.125 times the lowest. Moreover, it should be noted that the estimate for $\bar{x}_3$ is probably too high. Thus the possibility of an infestation ensuing after 2 flies are trapped in 2 weeks is likely to be very small. Hence this kind of trapping rate should trigger grid intensification and only a higher number of flies should be taken to represent a risk of infestation.

Density limits at the edges of large propagules

When propagules are large (as in the upper curves of figure 1) or when a local infestation is well established (second or third generation) the risk of infestation may extend beyond the distance where fly density drops to 6 ha^{-1}. This is because flies will continue to diffuse out of the high density area and maintain the density at the fringe. There is also, with a continuing supply of new flies from the centre, the tendency for the clumping of the distribution to be significant so that a mean density of (say) 1 ha^{-1} would have local 'hot spots' of higher density. It is characteristic of fruit fly grids that the traps with the highest catches can have between 10 and 20 times the mean catch rate (Meats 1998c). Thus the lowest density for contagion for such circumstance is indicated on figure 1 as $\frac{6}{20}$ flies per hectare.

DISCUSSION OF CURRENT CODE OF PRACTICE

The current code of practice for fruit fly management (Anon. 1997) recommends trigger levels for grid intensification and 'outbreak declaration'. It recognises that three levels of trapping rate have a different significance. There is a very low level when no action is required, an 'intermediate' level when increased monitoring is required and a 'high' level when it is considered that there is such a risk of flies mating and infesting fruit that it warrants the declaration of an outbreak and the implementation of protocols for quarantine and eradication.

The code is couched in terms that would apply to areas with a sentinel grid of 1 km spacing although it can also be applied to 0.4 km grids which are common in urban areas within or near quarantine zones.

(a) If only 1 fly is trapped per two week period within a 1 km radius then no action is taken.

(b) If 2 flies are trapped within a 1 km radius of each other in 2 weeks (this usually means 2 flies in the same trap) then monitoring should be twice weekly and the grid intensified to a spacing of 0.4 km (16 traps around the perceived 'outbreak centre').

(c) If 5 flies are trapped within 1 km of each other within a 2 week period then an outbreak is declared and trapping intensified as in (b).

(d) If (b) happens first (at a single trap inspection date) then an outbreak is declared if 3 more flies are trapped on the intense grid within the next two weeks. Otherwise, rule (c) applies.

The above are only the extracts of the code relating to trapping (males) with cuelure (the subject of this paper). There are other triggers in the code relating to 'protein' traps for females and the results of fruit sampling. Discussion here is limited to comparing the results of this paper with aspects of the code relating to grids of cuelure traps.

Permanent (sentinel) grids of 1 km and 0.4 km spacing

When grids are permanently in place we can use equations (10a, b) to calculate the numbers of maturing flies per hectare within 200 m of the emergence site (the region expected to have the highest concentration). We can then estimate the infestation risk per fly caught if we take the earlier finding that 6 ha^{-1} is the lowest density for a continuing infestation.

Figure 3 gives estimates of maturing flies per hectare in relation to trapping rate. 'Highest' and 'lowest' estimates are given for each type of grid, based on 'at trap' and 'between trap' assumptions as explained earlier (equations 4 and 12). The code of practice does not distinguish between the two types of grid, yet the interpretation of trapping rates is quite different according to the models used in this paper. The significance of a fly caught on a 0.4 km grid can be much less than one caught on a 1 km grid because the density of traps is 6.25 times greater. Also, the differences between 'highest' and 'lowest' estimates of fly density are much wider in the case of a 1 km grid.

In the case of a 0.4 km grid it appears that 5 flies trapped in 2 weeks indicates a maturing fly density that is just below the level of infestation risk if the 'highest' estimate is used. In the case of a 1 km grid, the 'highest' estimate exceeds the infestation limit when 2 flies are trapped in 2 weeks. However, this is the worst possible interpretation as the 'highest' estimation assumes that flies emerge as far as possible (about 0.7 km) from the nearest traps. The real density of mating flies could be anywhere down to the level estimated by the 'lowest' estimate. Thus 2 flies in two weeks on a permanent 1 km grid should probably be regarded as a trigger for grid intensification to a spacing of 0.4 km so that a more accurate estimate can be obtained. The trapping of 5 flies in two weeks on a 1 km grid is unequivocally a sign that infestation is likely because even the 'lowest' estimate is close to the threshold level.

Grids intensified to 0.4 km

Again, 'lower' and 'higher' estimates apply. However, there is the added complication of not knowing exactly what the delay is between the first fly entering a sentinel trap and the installation of the intense grid. The bigger delay, the higher the significance of each trapped fly becomes (equations 11a–d).

Thus for figure 4, the highest estimates are adjusted assuming a 7 day delay (making the estimate even higher) and the lowest estimate is based on the assumption that there is no delay (i.e. assuming that the two 'trigger' flies entered the sentinel trap on the day of inspection and grid intensification was immediate).

The differences between the 'highest' and 'lowest' estimates are at their largest with these assumptions and (as above) we can take the 'highest' estimate to be the worst possible case and assume that the most probable case is somewhat less serious in terms of density of mature flies. Nevertheless, figure 4 would appear to disagree with the code of practice. Figure 4 suggests that the trigger for outbreak declaration should be when 2 flies are trapped in the two weeks after grid intensification whereas the code of practice has 3 flies as its trigger level in such circumstances.

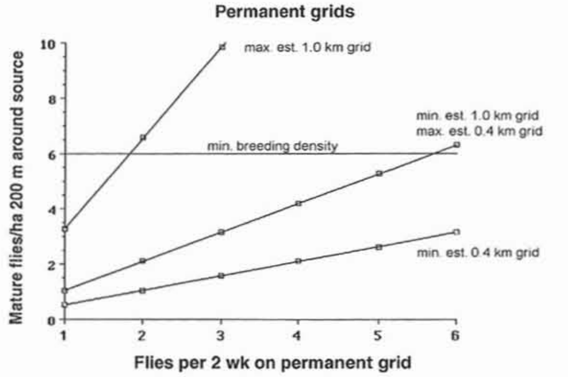

Figure 3. The interpretation of trapping rates on permanent grids. Abscissa relates to flies caught in the first two weeks of trapping. For the first 7 weeks of trapping, the estimates of the mature fly densities should be increased by 22.7%.

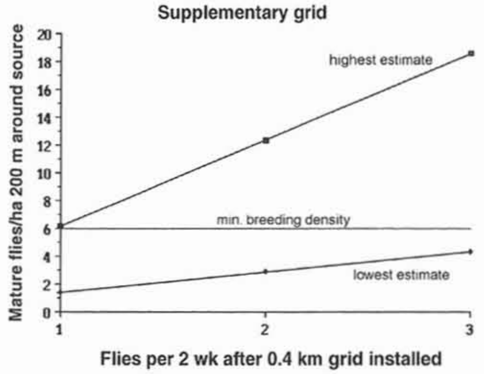

Figure 4. The interpretation of trapping rates on intensified grid after 2 flies have been already trapped on a sentinel grid. Abscissa relates to flies caught in the first two weeks of trapping on the intensified grid.

GENERAL DISCUSSION

Interpretation of fly catches is obviously not simple but depends on the grid density and the assumptions that can be made about the origin of the infestation. A method of estimating the origin of an infestation is given by Meats (1998c) but it is not suitable when flies are only trapped in ones and twos. Thus we must rely on upper and lower estimates—which are wider apart the greater the trap spacing. Catches on grids of spacing greater than 1 km are essentially uninterpretable since the upper and lower estimates are so wide apart. Sentinel traps of 5 and 10 km spacing in fact could be detecting an ongoing infestation of considerable magnitude even if only one fly is trapped. This may be acceptable or not depending on the perceived risks to fruit exports in the area in question.

Practical verification of the models given in this paper is required since although high and low estimates are given, they are in turn derived from mean expectations. Data is required from areas of low quarantine significance since any positive eradication response to fly catches required by prevailing protocols in quarantine areas would predetermine the results.

REFERENCES

Anon. (1997). *Code of Practice for Management of Queensland Fruit Fly.* Standing Committee on Agriculture and Resource Management, Department of Primary Industries, Canberra.

Bateman, M.A. (1977). Dispersal and species interaction as factors in the establishment and success of tropical fruit flies in new areas. *Proc. Ecol. Soc. Aust.* **10:** 106–112.

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

Fay, H.A.C. and Meats, A. (1983). The influence of age, ambient temperature, thermal history and mating history on mating frequency in males of the Queensland fruit fly, *Dacus tryoni, Entomol. Exp. Appl.* **34:** 273–276.

Fletcher, B.S. (1973). The ecology of a natural population of the Queensland Fruit Fly, *Dacus tryoni,* IV. The immigration and emigration of adults. *Aust. J. Zool.* **21:** 541–565.

Fletcher, B.S. (1974a). The ecology of a natural population of the Queensland Fruit Fly, *Dacus tryoni,* V. The dispersal of adults. *Aust. J. Zool.* **22:** 189–202.

Fletcher, B.S. (1974b). The ecology of a natural population of the Queensland Fruit Fly, *Dacus tryoni,* VI. Seasonal changes in fruit fly numbers in the areas surrounding the orchard. *Aust. J. Zool.* **22:** 353–363.

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*. *Gen. appl. Entomol.* **28:** 29–38.

Meats, A. (1998b). A quality assurance measure for field survival rates of released sterile flies based on recapture rates. *Gen. appl. Entomol.* **28:** 39–46.

Meats, A. (1998c). Cartesian methods of locating spot infestations of the Papaya Fruit Fly *Bactrocera papayae* Drew and Hancock, within the trapping grid at Mareeba, Queensland, Australia, *Gen. appl. Entomol.* **28:** 57–60.

Tychsen, P.H. (1977). Mating behaviour of the Queensland fruit fly, *Dacus tryoni* (Diptera : Tephritidae) in field cages. *J. Aust. Entomol. Soc.* **16:** 459–465.

This page left blank intentionally