

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*

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Summary

As with many insects, a batch of released (or naturally emerging) flies declines in density with time at the point of origin and declines in density at any time with distance from the origin. A generic model is presented that can be adapted for a variety of species and is tested with data on the Queensland fruit fly, *Bactrocera tryoni* (Froggatt). It requires prior estimation of parameters that are readily obtained for fruit flies and predicts proportions captured or recaptured in terms of catch per trap at any distance. It is therefore applicable to any number and disposition of traps of any type.

The model is sensitive to variations in mortality rates and development times. The example with sterile and fertile *B. tryoni* shows how this feature can be used to assess the quality of released sterile flies.

INTRODUCTION

Describing dispersal

When insects disperse from a point they achieve a distribution whereby density is greatest near to the point of origin and falls with distance according to a relationship that can vary with time, from case to case and from species to species (Mason *et al.* 1995; Mayer and Atzeni 1993; Baker and Chan 1991a,b; Banks *et al.* 1988; Taylor 1978, 1980). Most of these features are well illustrated by Baker and Chan (1991b). Initially the majority of the insects will be around the central point with density dropping to immeasurably low levels within a short distance; with time, the central density of insects drops exponentially, density still declines from the centre but insects are detected progressively further out. Thus the form of the distribution depends upon whether current, progressive or total catches are considered.

This has relevance to the way in which the first generation of an invading propagule of fruit flies can spread the infestation and to the way in which sterile fruit flies disperse after release and to the way in which release points must be spaced in order to achieve an adequate density of sterile flies over a wide area.

Of the simpler models for dispersal, Taylor (1978) proposed a general form:

$$N = \exp(a + bX^c)$$

where N is the density (or catch per trap) at distance X from the central point and a , b , and c are constants. All the constants are unknown so the equation must be fitted by iterative multiple regression.

According to this model, the number caught per trap at distance x as a proportion of those caught at a trap at the centre is

$$\frac{N_x}{N_o} = \exp[b(x^c - 1)]$$

Alternatively, if no central trap is used, the catch per trap at one ring of traps at distance (2) as a proportion of the catch per trap at a lesser distance (1), which could be the innermost ring, is

$$\frac{N_2}{N_1} = \exp\left[b\left(x_2^c - x_1^c\right)\right]$$

In practice, we can use an even simpler model. Beyond the central area, fruit flies and many other species will decline in density in some exponential manner so that catch per trap C at distance $d(2)$ will be related to catch per trap at a lesser distance $d(1)$ by

$$C_{d(2)} = C_{d(1)} \cdot \left(\frac{d(1)}{d(2)}\right)^n$$

When $n=2$, this amounts to the simple 'inverse square' relationship found by Fletcher (1974a) for the Queensland fruit fly, *Bactrocera tryoni* (Froggatt).

Unfortunately this cannot apply when $d(1)$ approaches zero, so some method is required to predict C at the first ring of traps rather than at the central point. In practice, this is necessary anyway

when one considers the general problems of detecting dispersal by means of traps with lures.

Detecting dispersal with lure traps

The use of baited traps has the advantage of catching more insects per unit of effort than other methods but it also creates a number of difficulties when it comes to interpreting the results. Firstly, each trap has a radius of influence (Cunningham and Couey 1986) which may be only a few metres when protein hydrolysate or trimedlure is used and may be well over 100 m in the case of traps with cuelure or methyl eugenol. If insects respond to traps immediately after release, all of them will be placed within the range of influence of a central trap and the lure itself may retard the dispersal of insects that do not enter the central trap.

Secondly, when the insects have a chance to disperse before becoming responsive to traps (or before traps are set) a central trap will sample the distribution within its radius of influence and the catching rate will not reflect the true density at the centre, but the mean density at some distance from it.

Thirdly, we must consider other trapping dynamics that apply regardless of where traps are set. Trapping rates are influenced by trap efficiency (the proportion of insects that are capable of responding that are actually caught per day). They are therefore also affected by maturation rate (governing time elapsing before the insects are old enough to respond to traps). Consequently they are also influenced by the rates of survival both before and after insects are old enough to respond to traps.

A STRATEGY FOR MODELLING AND TESTING

It is the purpose of this paper to provide a model for the above processes that predicts the catch per trap at any given distance after any given time. The model is empirical and its form is constrained by the type of information that is most readily obtained for tephritid fruit flies and which is already available in the case of the Queensland fruit fly, *Bactrocera tryoni*. The model is thus adaptable for use with other species and does not require estimation of the kind of parameters demanded by theoretical diffusion models (Banks *et al.* 1988; Mayer and Atzeni 1993) and it does not

require assumptions about form of the distribution in the immediate area of release.

Basic form of the model

The model calculates how many flies will remain each day within a small radius (r) of the site of release (or emergence), how fast they mature (become trappable) and how many would be caught per day by a notional trap at the point of origin that would relate to density at distance r . By using the inverse square law (or an analogous model) it can then give the expected total catch per trap at any distance. Hence data on rate of diffusion are not required unless one also wishes to calculate catch per trap on any given day or up to a given day during the total trapping period.

Essential data required—example of the Queensland fruit fly

Firstly, traps must be calibrated. This was first done for *B. tryoni* with cuelure traps in 1961 (Monro and Richardson 1969). Fletcher (1974b) refined the calibration technique for grids of 100 m and 400 m spacing so that it was free from bias due to dispersal and mortality.

Secondly, one must establish the relationship between recapture rate and distance with either a large grid or with lines of traps radiating from the point of origin to at least a distance where only a low percentage of the total catch is made (in the case of *B. tryoni* this would be about 20 km.) Fletcher (1974a) was able to establish an 'inverse square rule' that applied to the total catch per trap of *B. tryoni* (essentially flies caught up to 7 weeks after release). By using data for shorter periods Fletcher (1974a) could also determine means and variances of displacement rates for both immature and mature flies. However, the latter data are only useful for calculating distant catches early in the trapping period when the inverse square rule must be adjusted to account for travelling time (see later).

Thirdly, we require a direct estimate of the rate at which flies disperse from the immediate vicinity of the release (or emergence) site. Fletcher (1973) reports an extensive series of trials performed throughout the summer and autumn months involving weekly recaptures with hand nets of cohorts of both

immature and mature flies within 200 m of their release point.

Fourthly, we need some knowledge of the maturation rate of flies in various field conditions in order to estimate the time elapsing before flies can respond to traps (Meats 1981; O'Loughlin *et al.* 1984).

Finally, it is desirable to have an estimate of how survival rate varies with treatment, especially if sterile insects are being used (Fay and Meats 1987; Perepelicia and Bailey 1993).

Tests of the model

Following Meats (1981) it is desirable to test a model on sets of data that were not used in the elaboration of the model. Accordingly the test data used in this paper come from the following sources:

- (i) Release at Strathfield (NSW) by Monro and Richardson (1969).
- (ii) Releases at Wangaratta (Vic.) by MacFarlane *et al.* (1987).
- (iii) Release at Beckenham (Perth, WA) by Yeates (pers. comm.).
- (iv) Releases at Wilton (NSW) by Fletcher (1974b). This last data set is extensive and yielded the inverse square law and the displacement data, hence the only independent aspect of the model tested with Fletcher (1974b) is the actual level of the trap catches (which is governed by the disappearance rate from a 200 m radius).

BASIC COMPONENTS OF THE MODEL

Survival and dispersal from a 200 m radius

The probability of a fly remaining alive within a 200 m radius of the release (or emergence) point to any given day (x) is l_x . The probability of a fly remaining from any day for a further day ($x+1$) is p_x .

$$\text{Hence } p_x = \frac{l_{x+1}}{l_x}$$

$$\text{and } l_x = \prod_{y=0}^{y=x-1} p_y$$

In theory, we could distinguish between the various components of any p_x value

$$p_x = p_{x(1)} \cdot p_{x(2)} \cdot p_{x(3)} \cdots p_{x(n)}$$

In reality, some values cannot be factorized from available data and most are not necessary for modelling purposes. The present model uses four components of p_x where

$$p_x = p_{xi} \cdot p_{xm} \cdot p_{xs} \cdot p_{xt}$$

The component p_{xi} is the probability of an immature fly in a cohort remaining alive within the 200 m radius (i.e. not dying and not emigrating) in the interval $x, x+1$. When the cohort reaches maturity p_{xi} is set at 1.

The component p_{xm} is the analogous probability for a mature fly, being set at 1 when the cohort is immature.

Both p_{xi} and p_{xm} were identified and estimated by Bateman and Sonleitner (1967) and quantified in detail by Fletcher (1973) with a long series of release experiments. Each in turn was composed of the product $p_{x(emigration)} \cdot p_{x(survival)}$ the components of which could not be distinguished. However, the overwhelming component is likely to be $p_{x(emigration)}$ because field cage studies suggest that $p_{x(survival)}$ is in the range 0.98–0.99 (Sonleitner 1973; O'Loughlin *et al.* 1984). However, mortality in actual field conditions may be higher, hence $p_{x(survival)}$ may be lower than 0.98.

Despite the wealth of detail given by Bateman and Sonleitner (1967) and Fletcher (1973) the choice of p_{xi} for the model must be somewhat arbitrary since maturation times can only be estimated approximately. If the proportion remaining at maturity is 0.2 then p_{xi} is $0.2^{1/D}$ where D is maturation time (see later). It appears that the number of mature flies remaining, halves each week giving a value of p_{xm} of 0.9057.

The component p_{xs} takes account of the additional mortality expected if the flies have been sterilized. It is defined as

$$p_{xs} = \frac{P_{x(survival, sterile)}}{P_{x(survival, fertile)}}$$

This is likely to be very variable, depending upon the rigours of the sterilization process and the mode of packaging and transport both before and after that process. Optimal procedures that are possible with small batches can in fact have no effect on the subsequent emergence and survival rates, hence p_{xs}

can be as high as 1 (Fay and Meats 1987). However, with mass rearing, packaging and long transport times, low emergence and subsequent survival rates have been noted (Sproule *et al.* 1992; Perepelicia and Bailey 1993). An approximate value of $p_{xs} = 0.93$ is used in this paper.

The component p_{xt} is the survival rate from trapping. This obviously depends upon the density of traps and the lure used. In the case of *B. tryoni* it only applies to sexually mature flies as cue lure is used as the trap's lure. From Fletcher (1974b) we can take p_{xt} for a grid of 100 m spacing as 0.93. For a single trap operating in a 200 m radius p_{xt} will be 0.99. Hence trapping mortality due to traps spaced at 400 m or greater is trivial. However the value of $(1-p_{xt})$ is required for the proportion of flies that could be trapped per day by a notional trap at the centre of the 200 m radius.

Maturation date

This is the date (D) when p_{xm} substitutes for p_{xi} and p_{xt} begins to operate. Meats (1981) related temperature (T) to the number of weeks (G) from egg laying to first egg production by the next generation. Since maturation time in *B. tryoni* is one third of G , the number of days from emergence to sexual maturity is $2.333 G$. Various applications of this method can be found in O'Loughlin *et al.* (1984) and Sproule *et al.* (1992). Of course, if flies are released in a post-teneral state, the 'elapsed' development time must also be accounted for. A simpler method is available when using historical data because maturation date can be estimated from the date flies were first trapped.

OPERATION OF THE MODEL

Daily and accumulated catch rate within 200 m radius

These calculations are required so that catch per trap can be estimated for greater distances. Normally, the catch rate within 200 m of the release point is of no interest in dispersal studies because an intense grid would be required (i.e. a maximum spacing of 100 m). However, the Beckenham example used in this paper (Yeates, pers. comm.) used a 100 m grid. Hence we can thus use the trapping rate, expected from Fletcher (1974b) for a 100 m grid, to compare the model

directly with the Beckenham data pertaining to the 200 m radius. Thus the value of p_{xt} for Beckenham is 0.93.

With all the other examples, there is no '200 m radius' data to test, therefore we calculate the results expected for a notional trap at the release point which would catch (from Fletcher 1974b) 1% of the trappable flies per day in an area of that radius. The value of p_{xt} used is therefore 0.99.

The catch rate C on day x is a proportion of the original cohort of N flies since it is a proportion of the proportion remaining at that date. The latter proportion is calculated as a mid-interval survival rate because flies that would have been counted as caught on day x would have been trapped over the previous 24 h. Hence

$$C = 0.5(l_{x-1} + l_x)(1 - p_{xt})$$

The accumulated proportion of N flies caught to day x is therefore $\sum C$ or in terms of actual flies is $N \sum C$.

Catches beyond the 200 m radius

Extensive grids have spacings of 0.4 km or greater (Fletcher 1974a; MacFarlane *et al.* 1987). The total accumulated catch per trap (essentially catches up to 7 wk) can be calculated from the accumulated catch of the notional trap within the 200 m radius by using the 'inverse square' relation verified by Fletcher (1974a).

For Queensland fruit fly, the accumulated catch per trap (T) at one distance ($d(1)$) from the release point is related to the catch per trap at another distance ($d(2)$) by

$$T_{d(2)} = T_{d(1)} \left(\frac{d(1)}{d(2)} \right)^2$$

The value of $T_{d(1)}$ pertinent to the 200 m radius is found by the model as

$$T_{(0.2)} = N \sum C$$

Thus if, for example, $d(2)$ were 1 km, the catch per trap at this distance would be

$$T_{d(0.2)} \left(\frac{0.2}{1} \right)^2 = \frac{N \sum C}{25}$$

Accumulated catches to a given date

The basic model (above) is for the total catch per trap at either the 200 m radius or beyond. Accumulated

catch ($T_{d(0.2)(y)}$) to a given date (y) at the 200 m radius is found by summing the daily estimates to that date

$$T_{d(0.2)(y)} = N \sum_{x=0}^{x=y} C$$

For distant traps at any distance (d) this value obviously cannot be used to estimate catches to that date by simply using the inverse square rule because allowance must be made for travelling time or mean flight time (f), hence a possible prediction would be

$$T_{d(2)(y)} = T_{d(0.2)(y-f)} \left(\frac{0.2}{d} \right)^2$$

Unfortunately f can only be calculated from the distances at which flies are actually trapped over a given period (Fletcher 1974a). Thus the use of mean f would result in prediction of zero catches beyond the mean distance flown. There is, however, a way of using the above formula as a good approximation so long as f pertains only to a distance of 1 km and predictions are restricted to catches per trap at 1 km and beyond.

The mean distances flown, found by Fletcher (1974a), apply only to flies reaching his grid (i.e. to rings of traps extending approximately from 1 km to 20 km). The variance was very large and was reflected in the fact that the catch per trap for any period declined from the first ring according to an inverse square relationship. There is thus, apparently, a wide variation in speed and we can infer that there would be a wide variation in time to reach the first ring of traps. Some flies leaving the 200 m radius at given time would actually travel at the mean speed and would reach the traps after the mean delay expected for 1 km. Others would have yet to reach the 1 km mark at this time whereas others would have already passed it and travelled up to several km beyond. The corollary of this argument is that flies reaching the first ring in a given week would have left the 200 m radius at different times but the mean time could be found from the reciprocal of the mean speed.

Hence, we can still use the above equation to predict catch per trap at 1 km if y pertains to 1 km and d is taken as 1. It also serves to predict catch per trap at distances beyond 1 km since the inverse square rule applies beyond that distance. For predictions beyond

1 km therefore, y still pertains to the delay for 1 km but d pertains to the relevant distance.

We can find mean distance per day (d_f) from Fletcher (1974a). The time taken for 1 km is thus $\frac{1}{d_f} = y$. For flies released as immatures the values for d_f are respectively 0.198, 0.319 and 0.345 for 2, 3 and 4 weeks after release. For flies released when mature, the values are 0.727 and 0.501 for 1 and 2 weeks respectively. Note that the mean speeds are only *apparent* values revealed from the trapping results. These are not true speeds because traps are cleared once per week. However, it is trapping results that the model will predict, therefore these data are appropriate.

The effects of the delay due to flight time gets less with time after release as the model value for $T_{d(0.2)}$ accumulates at ever decreasing increments. Thus the difference between $T_{d(0.2)y}$ and $T_{d(0.2)(y-f)}$ becomes negligible after 3–4 weeks, hence the predictions for longer and total catching periods can be done by simply using the simple inverse square model given in the previous section.

QUICK COMPUTATION

The explicit version of the model, given above, can be simplified to one for the exponential decline in numbers (and hence flies recaptured) around the point of release and one for the decline in recapture rate per trap with distance. The example is for *B. tryoni* maturing 8 d after release (i.e. $D = 8$).

The proportion surviving up to D is l_D .

For fertile flies $l_D = \Pi p_{xi} = 0.2$

For sterile flies $l_D = \Pi p_{xi} \Pi p_{xs} = 0.2(0.93^D) = 0.1119$

The daily survival rate from D is p_{xA}

For fertile flies $p_{xA} = p_{xm} \cdot p_{xt} = 0.8966$

For sterile flies $p_{xA} = p_{xm} \cdot p_{xt} \cdot p_{xs} = 0.8339$

The proportion recaptured in the 200 m radius on the first day of trapping is thus

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

The accumulated proportion recaptured after n days is

$$\sum_{D+1}^{D+n} C = \frac{C_1 (1 - p_{xA}^n)}{(1 - p_{xA})}$$

When n is large (say over 49 days) this is virtually the same as the sum for an infinite series (i.e. total catch) hence

$$\sum C = C_1 \left(\frac{1}{1 - p_{xA}} \right)$$

For fertile flies $\sum C = 0.01832$

For sterile flies $\sum C = 0.006151$

Thus if N flies were released the number catchable by a central trap is $T_{(0.2)} = N \sum C$.

The proportion captured per trap at any other distance is calculated from the inverse square relationship as before, using 0.2 for the central trap (real or notional) and the distance of the other trap as d . For instance a trap 1 km from the release point

would be expected to recapture $100 \left(\frac{\sum C}{25} \right)$ percent of

the flies originally released. Table 1 gives the results of an example where there are rings of traps (at 8 traps per ring) at 1, 1½, 2, 3 and 4 km.

Table 1. Recapture rate (%) of rings of traps with 8 traps per ring.

Distance from release point (km)	¹ Released as fertile flies	² Released as sterile flies
1	0.5856	0.19683
1½	0.2602	0.08748
2	0.1464	0.04921
3	0.0651	0.02187
4	0.0366	0.01230
TOTAL	1.0939	0.3677

¹ Maturing 8 d after release.

² Maturing 8 d after release; for longer times the results are reduced by 0.93 for each extra day, hence total if $D=15$ is 0.22%.

RESULTS

Release at Beckenham

37,800 sterile male flies were released in a suburb of Perth in an unpublished trial (Yeates, pers comm.) that took place in Jan./Feb. 1990 at the start of the mass sterile fly release phase of the campaign to eradicate *B. tryoni* (Sproule *et al.* 1992). The experimental grid of 110 traps had a spacing of 100 m

and was surrounded by the Perth monitoring grid which at that time had a spacing interval of about 1 km. A total of 980 flies were caught by the 15 traps that were within 200 m of the release point. The traps between 100–200 m actually caught most per trap and the catching rate fell (as expected) further out and no flies were recaptured on the general monitoring grid. However, the trial took place just after the last intensive bait spraying had been done (Sproule *et al.* 1992) so the ability of the flies to survive beyond the trial area had been compromised.

We can however test the model against the accumulated catch in the 200 m radius. The mean maturation date (D) is taken to be 8 d. As the flies were sterile, both p_{xI} and p_{xS} are set at 0.93.

Figure 1 compares the observed results with those expected from the model. The total recapture rate within 200 m was 2.6% whereas the model expectation is 3.05 %.

Release at Strathfield

The pioneering work of Monro and Richardson (1969) involved the release of 367 fertile male flies of wild origin in a suburb of Sydney. They had a very small grid of 16 traps with a spacing interval of 400 m. Thus even the inner four traps were 83 m beyond the perimeter of the 200 m radius used by the model. The catch per trap at 283 m according to the inverse square relationship should be only half that of a notional trap sampling the 200 m perimeter. The maturation date was approximately 7 d as the flies were post-teneral at release after being marked with ³²P.

Figure 2 shows that the model provides a reasonable fit to the data on accumulated catch by the inner four traps despite the low number of flies involved. The inner 4 traps recaptured 3.54% of the flies whereas the model expectation was 2.49%. The outer ring of traps recaptured only 2 flies in total whereas the model expectation was 4.7.

Release at Wangaratta

MacFarlane *et al.* (1987) released four lots of newly emerged sterile flies. With two of these, the weather was too cold to expect any recaptures at maturity. With the other two releases the weather was warm enough to permit maturation in 15 d in both cases. We can thus combine the results for these two releases.

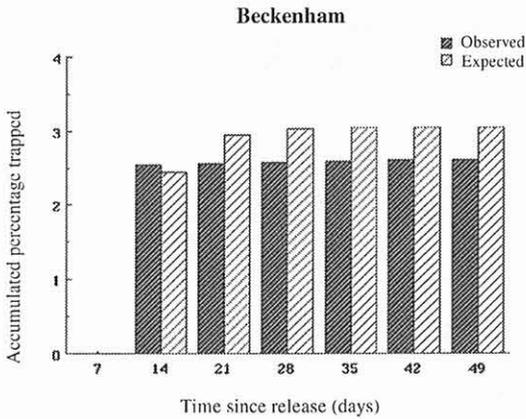


Figure 1. Percentage of sterile flies recaptured within 200 m of the release site at Beckenham compared to model prediction. Data from D.K. Yeates, unpubl.

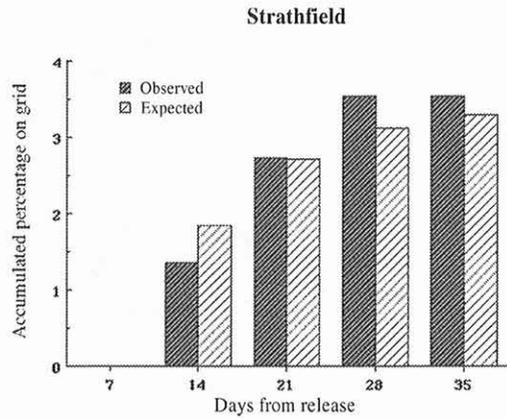


Figure 2. Percentage of wild flies recaptured after release at Strathfield compared to model prediction. Data from Monro and Richardson (1969).

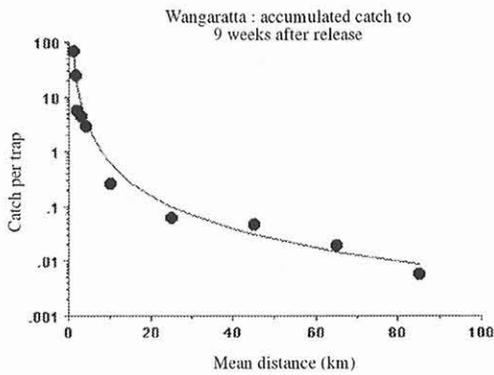


Figure 3. Numbers of sterile flies captured per trap after release at Wangaratta. Model prediction is shown by the curve. Data from MacFarlane *et al.* (1987).

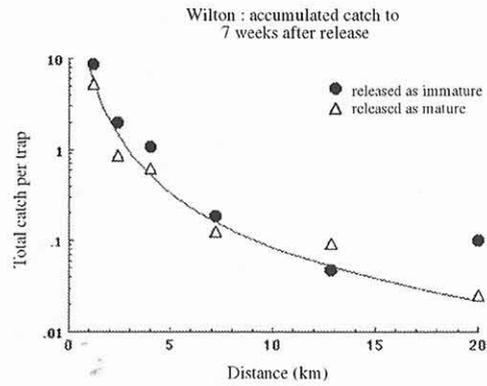


Figure 4. Numbers of wild flies accumulated per trap up to seven weeks after release at Wilton. Curve is model prediction. Data from Fletcher (1974).

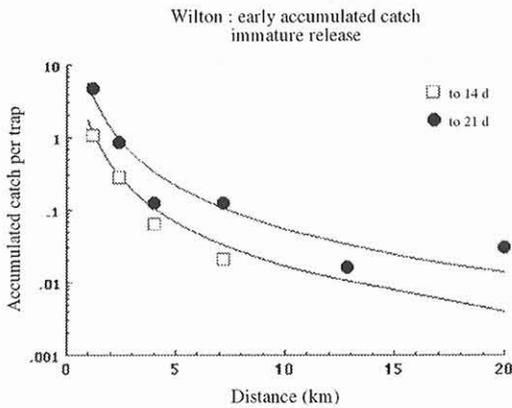


Figure 5. Partial trapping results at Wilton for flies released when immature. Numbers recaptured up to 14 and 21 days after release. Other details as figure 4.

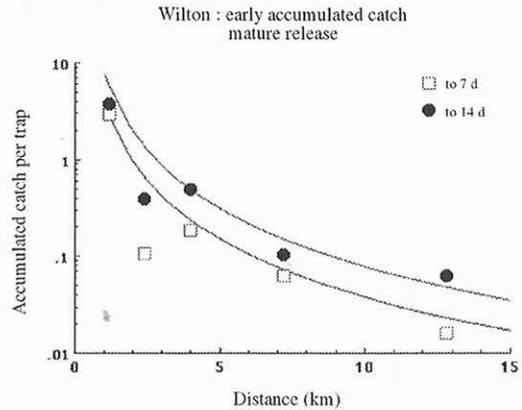


Figure 6. Partial trapping results at Wilton for flies released when mature. Numbers recaptured up to 7 and 14 days after release. Other details as figure 4.

Approximately 470,000 males were released and 0.23% were recaptured. A low rate of recapture is to be expected with a grid with traps spaced widely apart. The grid was essentially the Victorian monitoring grid (mean spacing of 5 km) augmented with rings of traps set at 1 to 6 km from the release point. Overall, the grid extended to 100 km in many directions but was truncated to the north by the state border so that the biggest complete annulus had a diameter of 35 km although the 45 km annulus was about 80% complete.

Figure 3 shows how the catch per trap at 1 km was successfully predicted by the model and that the inverse square relationship holds out to the 85–95 km group of annuli. It is also obvious from the model that the probability of recapture by even a large set of traps beyond 100 km is very low. For instance 160 traps at 100 km (approximately spaced at 5 km) would be expected to catch only 1 fly.

Releases at Wilton

Fletcher (1974a) gives details of the dispersal of wild, unirradiated flies from Wilton on to a grid extending 0.8–24 km from the release point. He analysed data in terms of the recaptures made in grouped annuli having mean distances of 1.18, 2.4, 4, 7.2, 12.8 and 20 km respectively. Flies released when immature were given marks of paint at the post teneral stage and mean time from release to maturity is estimated as 8 d. Another set of marked flies was released when mature.

Figure 4 shows the accumulated catch per trap (up to 7 weeks) for both sets of flies. The model expectation given is for the set released as immatures. The model curve for the mature flies is omitted for clarity as it is only slightly lower (by about the depth of a plot symbol).

We can also test the model against the accumulated recaptures to earlier dates. Observed and expected predictions are compared in figures 5 and 6 for immature and mature flies respectively. The success of the model in all three figures is due to its reasonable prediction of the recaptures at the first ring of traps; the expected recaptures further out are due to the application of the inverse square relationship that was discovered by Fletcher (1974a) from these very data.

DISCUSSION

General application

Practically any model that predicted an exponential decline with time and with distance at any time would give a reasonable picture of the fate of a batch of released flies (or an emerging propagule). The current model is based on readily measured parameters (which are species specific) and the predictions are in terms of catch per trap (distance specific). The model is therefore applicable to any disposition of traps and is not reliant on a given trap spacing, or to regular spacing or to a complete grid network.

Sensitivity and sterile fly quality

The model is sensitive to variations in (or errors in estimation of) mortality and development time. This is particularly the case with sterile flies where the lowered survival rate ($p_{xs} < 1$) associated with packaging, sterilization, transport and release method is hard to predict. It should also be noted that the residual effect of pre-release bait sprays or other fly reduction measures will also decrease p_{xs} .

Figure 7 shows the relationship between the recapture rate of sterile flies and a range of p_{xs} values. The relationship is given both for flies maturing in 8 d (about the earliest that can be expected) and in 14 d (about the latest). The recapture rate (as a proportion

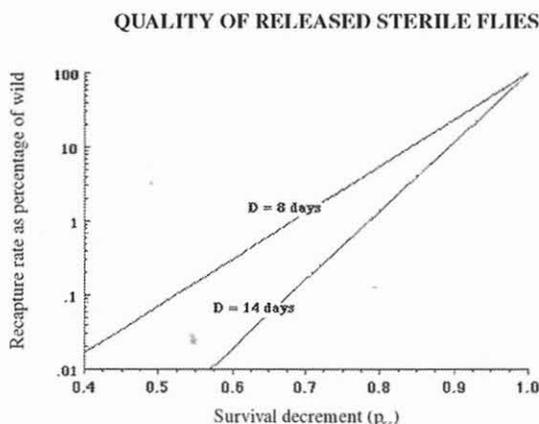


Figure 7. Sterile fly quality. The relation between recapture rate (as a percentage of that expected of wild flies) and daily survival decrement due to induction of sterility. The relationship is given for the shortest expected maturation time ($D = 8$ days) and the longest ($D = 14$ days) as discussed in the text.

expected when $p_{xs}=1$) drops dramatically with p_{xs} but even more so the longer the time (D) that elapses before maturity (when flies first become trappable). D would normally be expected to be 8 d in the warmest weather and 14 d in the coolest weather that would allow flies to be recaptured (Fletcher 1974a; MacFarlane *et al.* 1987).

When $p_{xs} = 0.93$, the recapture rate is about a third of the rate for $p_{xs} = 1$ if $D=8$ and is about one fifth if $D=14$. Where p_{xs} is 0.88 these fractions are $1/6$ and $1/13$ respectively.

The full relationship is given by $L = -b(1 - p_{xs})$ where L is \log_{10} of the proportion represented by the recapture rate for the sterile insects divided by that expected when $p_{xs} = 1$. The constant b is found by

$$b = 2.3 + 0.5 D.$$

Thus it is clear that by increasing the survival rate of sterile flies, we can increase the recapture rate (and hence the sterile:wild ratio) by many fold.

We can re-arrange the equation to estimate p_{xs} directly from the recapture rate.

$$p_{xs} = 1 + \left(\frac{L}{2.3 + 0.5D} \right)$$

If we can discount any effect of pre-release bait spraying (or other fly reduction measure) then our estimate of p_{xs} will give us a measure of the quality of the sterile flies at release in relation to their ability to survive. Thus we have a measure for monitoring any improvement in this aspect of sterile insect technology (Meats *et al.* 1988).

Capture rates of fertile flies and propagule size

Since we can estimate the recapture rate if we know the number released, then it follows that we can estimate the number of wild flies emerging in a hitherto fly free area from the trapping rate. The estimate depends on where it is assumed that flies emerged on the grid. This problem and methods of establishing highest and lowest estimates are given in a later paper (Meats 1998).

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REFERENCES

- Baker, P.S. and Chan, S.T. (1991a). Appetitive dispersal of sterile fruit flies: aspects of the methodology and analysis of trapping studies. *J. Appl. Entomol.* **112**: 263–273.
- Baker, P.S. and Chan, S.T. (1991b). Quantification of tephritid fruit fly dispersal. Guidelines for a sterile release programme. *J. Appl. Entomol.* **112**: 410–421.
- Banks, H.T., Kareiva, P.M. and Zia, L. (1988). Analyzing field studies of insect dispersal using two-dimensional transport equations. *Environ. Entomol.* **17**: 815–820.
- Bateman, M.A. and Sonleitner, F.J. (1967). The ecology of a natural population of the Queensland fruit fly (*Dacus tryoni*). I. The parameters of pupal and adult populations during a single season. *Aust. J. Zool.* **15**: 303–335.
- Cunningham, R.T. and Couey, H.M. (1986). Mediterranean fruit fly (Diptera: Tephritidae): distance/response curves to trimedlure to measure trapping efficiency. *Environ. Entomol.* **15**: 71–74.
- Fay, H.A.C. and Meats, A. (1987). Survival rates of the Queensland fruit fly, *Dacus tryoni*, in early spring: field-cage studies with cold-acclimated wild flies and irradiated, warm- or cold-acclimated, laboratory flies. *Aust. J. Zool.* **35**: 187–195.
- 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**: 541–515.
- 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.
- MacFarlane, J.R., East, R.W., Drew, R.A.I. and Betlinski, G.A. (1987). Dispersal of irradiated Queensland fruit flies, *Dacus tryoni* (Froggatt)(Diptera Tephritidae), in south-eastern Australia. *Aust. J. Zool.* **35**: 275–281.
- Mason, P.L., Nichols, R.A. and Hewitt, G.M. (1995). Philopatry in the alpine grasshopper *Podisma pedestris*: a novel experimental and analytical method. *Ecol. Entomol.* **20**: 137–145.
- Mayer, D.G. and Atzeni, M.G. (1993). Estimation of dispersal distances for *Cochliomyia hominivorax* (Diptera: Calliphoridae). *Environ. Entomol.* **22**: 368–374.
- Meats, A. (1981). The bioclimatic potential of the Queensland fruit fly, *Dacus tryoni*, in Australia. *Proc. Ecol. Soc. Aust.* **11**: 151–161.
- Meats, A., Fletcher, B.S. and Fay, H.A.C. (1988). Environmental assessment of the quality of mass-reared sterile insects. In *Fruit Flies of Economic Importance* (ed. Economopoulos, A.P.). Elsevier, Amsterdam. pp. 201–208.
- Meats, A. (1998). The power of trapping grids for detecting and estimating the size of invading propagules of the Queensland fruit fly and risks of subsequent infestation. *Gen. appl. Entomol.* **28**: 47–55.
- Monro, J. and Richardson, N.L. (1969). Traps, male lures, and a warning system for Queensland fruit fly, *Dacus tryoni* (Frogg.) (Diptera, Trypetidae). *Aust. J. Agric. Res.* **20**: 325–338.
- O'Loughlin, G.T., East, R.A. and Meats, A. (1984). Survival, development rates and generation times of the Queensland fruit fly, *Dacus tryoni*, in a marginally favourable climate: experiments in Victoria. *Aust. J. Zool.* **32**: 353–361.
- Perepelicia, N. and Bailey, P. (1993). *The integrated chemical and sterile release trial to eradicate the Queensland fruit fly at Ingle Farm, suburb of Adelaide*. Report of Primary Industries South Australia, Adelaide. 32 pp.

Sonleitner, F.J. (1973). Mark-recapture estimates of overwintering survival of the Queensland fruit fly, *Dacus tryoni*, in field cages. *Res. Popul. Ecol.* 14: 188-208.

Taylor, R.A.J. (1978). The relationship between density and distance of dispersing insects. *Ecol. Entomol.* 3: 63-70.

Taylor, R.A.J. (1980). A family of regression equations describing the density distribution of dispersing organisms. *Nature* 289: 53-55.