

A QUALITY ASSURANCE MEASURE FOR FIELD SURVIVAL RATES OF RELEASED STERILE FLIES BASED ON RECAPTURE RATES

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Summary

The quality of released sterile male insects used for population control with the sterile insect technique (SIT) is related to their ability to survive to mating age and to their subsequent rates of survival and mating competitiveness. The latter is usually expressed as a proportion, denoted here as C_M , being the overall mating success of the average sterile male relative to that of a wild male in encounters with wild females. If survival to mating is expressed with an analogous term C_S , this would be 'survival competitiveness' and the product $C_S C_M$ would be a measure of the total field competitiveness of released flies C_R .

This paper gives a method of estimating C_S from the recapture rate of the sterile males on the monitoring grid of traps that is used for SIT. The logical steps are as follows:

(a) A new demographic statistic is introduced, 'the expectation of mating life' (EML) that is derived from the conventional 'expectation of further life', e_x . This precisely relates survival to mean mating age, giving the mean number of mating days that a newly emerged fly can expect to have.

(b) C_S is defined in demographic terms as $C_S = \frac{(EML, \text{sterile})}{(EML, \text{wild})}$

(c) C_S is then related to recapture rate divided by the recapture rate expected of wild flies on an identical grid.

$$C_S = \frac{(\text{recapture rate, sterile})}{(\text{recapture rate, wild})}$$

(d) A recapture model is developed, based on previously obtained data from wild flies. This gives the expected recapture result for wild flies on a trapping grid of any size and trap spacing.

(e) Other quality assurance measures are derived from C_S such as the daily survival decrement p_{xs} associated with SIT.

The results of nine SIT campaigns with the Queensland fruit fly (*Bactrocera tryoni* Froggatt) are compared in terms of C_S and other measures of quality. In no case was the quality of SIT flies more than 21% of that expected of wild flies. In most cases the results were less than 5% of expectation. Thus a range of improvement from 5 to more than twenty fold is possible in terms of C_S which is the survival component of quality. Because C_S is a multiplier in the equation for total field quality, this has significant implications for the efficiency of SIT. Reasons for poor field survival in SIT are discussed.

INTRODUCTION

For the sterile insect technique (SIT) to work, sufficient male insects must be released so that, at maturity, they outnumber the mature wild males by a ratio that would ensure the rapid decline of the target population. In an ongoing program of regular releases, the target for any released batch is the population of newly emerged wild flies, because the latter will mature contemporaneously with the released flies and compete for mates. Thus the effectiveness (i.e. the quality) of the sterile flies depends both on how well they survive to maturity (when compared to wild flies) and how well they compete with wild males for wild females when they are mature. Any deficiency in these two qualities will dictate that the effective release rate of sterile flies must be higher than it would be otherwise. Of the two qualities, most attention has been paid to mating competitiveness, yet this would be of little avail in the field if only a low proportion of sterile flies actually

survive to mating age. What is needed is a measure of total field competitiveness that takes account of both survival and mating abilities and can be related to the results of the simple trapping program that always monitors the ratio of sterile to wild flies during any SIT campaign.

DEMOGRAPHY OF SIT

Basic relationships

Assuming that the released insects are completely sterile, the ratio required to reduce the rate of target female reproduction per female (R_0) to any desired level R'_0 is found by

$$\frac{S_R}{W_R} = \frac{\left[\left(\frac{R_0}{R'_0} \right) - 1 \right]}{C_R} \quad (1)$$

where C_R is total field competitiveness, S_R is the number of sterile flies at release and W_R is the number of target flies of equivalent age (i.e. teneral)

when the release is made. For regular releases, the target flies are considered to emerge over the last half of the previous inter-release interval and the first half of the present one. An approximate method of estimating this quantity is given by Meats *et al.* (1988).

Meats *et al.* (1988) were also able to calculate C_R more precisely from the rearranged equation

$$C_R = \frac{\left[\left(\frac{R_0}{R'_0} \right) - 1 \right]}{\frac{S_R}{W_R}} \quad (2)$$

However they were able to do this by using the results of field cage experiments where S_R and W_R were known precisely (since known numbers of teneral were put in cages) and the (R_0) value could be estimated from eggs hatched per wild female in the control cages (no sterile flies) and R'_0 could be estimated from eggs hatched per wild female when sterile flies were also present.

In field programs, we are unlikely to have such omniscience without a great deal of effort but we can estimate C_R in another way if mature males can mate as long as they live (Fay and Meats 1983).

$$C_R = \left[\frac{EML, \text{sterile}}{EML, \text{wild}} \right] \cdot C_M \quad (3a)$$

where EML is expectation of mature life (or mating life) at release and C_M is mating competitiveness as normally calculated for field conditions (Fay and Meats 1987b; Iwahashi 1996).

The quantity in the brackets is the survival component of C_R and is the outcome solely of the difference in survival rate between sterile and wild flies as explained later. We can call this component 'survival competitiveness' or C_S hence

$$C_S = \left[\frac{EML, \text{sterile}}{EML, \text{wild}} \right] \quad (3b)$$

and

$$C_R = C_S \cdot C_M \quad (3c)$$

Equations 3a-c assume that mating propensity is constant with age. Fay and Meats (1983) show that this is likely to be the case with *B. tryoni* for up to 8 weeks. In other cases, additional terms would be required, depending on how mating propensity declined with age. It should be noted however, that

the chief determinant of EML is always likely to be the survival rate—i.e. the decline in the number of flies with age (which determines EML) is likely to be much more important than any decline in the expression of a behavioural trait.

EXPECTATION OF MATURE OR MATING LIFE (EML) AND EXPECTATION OF RECAPTURE

The following account explains the precise meaning of EML and how it relates to survival rate. It also explains how the ratio of sterile to wild EML relates to the ratio of observed and expected recapture rates.

Releases made with mature flies

Flies are not normally released in the mature state with SIT but the concept of EML is best explained from this starting point. EML is a derivative of the conventional actuarial statistic, expectation of further life, e_x . The latter is the mean lifetime remaining for a cohort of age x . When x is taken as the age of attaining maturity, ($x=D$) then $e_{x(D)}$ is the expectation of mature (or mating) life, EML_D .

Thus if x were in days and a cohort of 1000 maturing wild male flies had a value of $e_{x(D)} = 40$, then this would be the equivalent of 40,000 'fly days'. If flies were trapped at 1% per day then the total of flies recaptured would be 400. However, if 1000 maturing sterile male flies had a value of $e_{x(D)} = 20$ then this would represent only 20,000 'fly days' and a total recaptured of only 200.

The mating opportunity for males is analogous to the trapping probability. With the above example, 1000 maturing sterile flies would represent only half the number of 'mating units' as 1000 maturing wild flies. Thus

$$\begin{aligned} & \frac{e_{x(D)}(\text{sterile})}{e_{x(D)}(\text{wild})} \\ &= \frac{EML_D(\text{sterile})}{EML_D(\text{wild})} \\ &= \frac{\text{recapture rate (sterile)}}{\text{recapture rate (wild)}} \end{aligned} \quad (4)$$

The assumption of this equation is analogous to that made for the previous ones—i.e. that the probability of capture is constant with age in any particular set of circumstances. Should response to traps vary with age then a modifying term would be required.

We would not normally want to release wild flies as part of a SIT program, thus the trapping ratio would be calculated from the actual recapture rate for the sterile flies and the rate expected of wild flies had they been released on an identical grid. The method for estimating the expected recapture rate of wild flies on a grid of any particular size or trap spacing is given in a later section using the data of Fletcher (1974a).

Releases made with teneral flies

We would normally want to release sterile flies in the teneral state, thus we would normally require an expression for *EML* that applied to newly emerged flies. This requires a precise explanation of how e_x is normally calculated.

The standard formula for expectation of further life (Carey 1989) is

$$e_x = \sum_{y=x}^{y=\max} l_y/l_x \quad (5)$$

where y is time (in days) from emergence; x is the value of y that l_x pertains to; l_x is the proportion surviving from emergence to that age and l_y is the proportion surviving from emergence to any age in the range indicated at the summation sign.

Thus if we are interested in mean expectation of life from emergence, $x=0$, $l_x=1$ and

$$e_x = \sum_{y=0}^{y=\max} l_y \quad (6)$$

If we are interested in the mean expectation of further life from maturity ($x=D$) then

$$e_{xD} = \sum_{y=D}^{y=\max} l_y/l_D \quad (7)$$

The mean expectation of mature life from age 0 is the above quantity discounted for the survival rate to maturity (i.e. multiplied by l_D), hence

$$EML_0 = \sum_{y=D}^{y=\max} l_y \quad (8)$$

If the daily survival rate of mature flies p_{xA} is assumed constant then Meats (1998) shows that the calculation of *EML* can be simplified to merely a multiple of the survival rate to halfway through the first day of maturity.

$$EML_0 = l_D \cdot p_{xA}^{0.5} \cdot \left[\frac{1}{(1-p_{xA})} \right] \quad (9)$$

EML and recapture ratio from teneral releases

The analogue of equation (4) is

$$\begin{aligned} & \frac{e_{x0}(\text{sterile})}{e_{x0}(\text{wild})} \\ &= \frac{EML_0(\text{sterile})}{EML_0(\text{wild})} \quad (10a) \\ &= \frac{\text{recapture rate (sterile)}}{\text{recapture rate (wild)}} \end{aligned}$$

where recapture rate is the number recaptured divided by the number released *as tenerals*. The above equation is formally

$$\frac{EML_0(\text{sterile})}{EML_0(\text{wild})} = \frac{T_{GS}}{T_{GW}} \quad (10b)$$

where T_{GS} is the recapture rate of the sterile flies and T_{GW} is the recapture rate expected had wild flies been used on a grid of similar size and trap spacing. The latter expectation is calculated from the recapture model given in a later section.

HOW *EML* IS AFFECTED BY SIT PROCEDURES

A glance at the equation (9) for *EML* reveals that it is entirely made up of survival terms. If SIT procedures affect survival then extensive repercussions for *EML* (i.e. quality) are to be expected.

The first term of the *EML* equation (survival rate to maturity) is the combined multiple of the daily immature survival rates (p_{xI}).

$$l_D = \prod_{x=1}^{x=D} p_{xI} \quad (11)$$

The other two terms are reliant on the daily survival rate for adults, (p_{xA}).

Meats (1998) illustrates how the p_x values are in turn multiples of other survival terms,

$$p_{xI} \text{ or } p_{xA} = p_{x(1)} \cdot p_{x(2)} \cdots p_{x(n)} \quad (12)$$

Sterile insects have an extra term p_{xS} in each case. This means that the daily survival rate in both the immature and mature stages is reduced by the multiplier p_{xS} .

Meats (1998) established the relationship between the value of p_{xS} and the proportion by which the expected recapture rate of sterile flies was lower than the expected recapture rate of wild flies. The relationship also has to incorporate maturation time since the longer the sterile flies take to mature the

fewer of them survive to maturity (i.e. become trappable). In demographic terms,

$$l_D(\text{sterile}) = l_D(\text{wild}) \cdot p_{xs}^D \quad (13)$$

The relationship from Meats (1998) is

$$L = -b(1 - p_{xs}) \quad (14)$$

$$\text{or } p_{xs} = 1 + \left(\frac{L}{b}\right) \quad (15)$$

$$\text{where } b \text{ for } B. \text{ tryoni} = 2.3 + 0.5D \quad (16)$$

$$L = \log_{10} \left(\frac{T_{GS}}{T_{GW}} \right) = \log_{10} \left(\frac{EML_0, \text{sterile}}{EML_0, \text{wild}} \right) \quad (17)$$

T_{GS} is the recapture rate of sterile flies on the trapping grid used in the SIT campaign and T_{GW} is the expected recapture rate for wild flies had they been released on the grid. The expected recapture rate for wild flies is calculated according to the recapture model (given later) which is based on the results of Fletcher (1974a) on wild *B. tryoni* flies and is applicable to any size of grid or trap spacing.

The estimation of the EML ratio at maturity for sterile flies released as teneral

Following equations (8) and (12)

$$EML_D = \frac{EML_0}{l_D}$$

Thus for flies released as tenerals the *EML* ratio of those surviving to mature is

$$\left(\frac{EML_D, \text{sterile}}{EML_D, \text{wild}} \right) = \frac{\left[\frac{T_{GS}}{l_{D(S)}} \right]}{\left[\frac{T_{GW}}{l_{D(W)}} \right]} = \frac{\left[\frac{T_{GS}}{T_{GW}} \right]}{p_{xs}^D} \quad (18)$$

The last step is possible because of the relation shown in equation (13).

THE POWER OF GRIDS FOR RECAPTURING RELEASED FLIES

Types of recapture models

Trapping grids of given densities can be calibrated to establish the percentage of the population caught per day (Fletcher 1974b). This is the best way of estimating the density of a natural population from trapping results since it can be assumed that the number of flies leaving the grid is balanced by the number of flies entering it. There will be some flies that leave and re-enter but there will be a net tendency for flies originally on the grid to leave and these will

be replaced by flies originating elsewhere. These assumptions are not valid when we are dealing with an invading propagule or with a batch of marked flies released in a restricted area.

When we are only interested in a marked batch of flies released on the grid we have to cope with the fact that there will be a net tendency to disperse beyond the grid. Thus the recapture rate of marked flies is dependent not only on grid density but also on the area of the grid.

The model of Meats (1998) is specifically designed for such circumstances and can cope with any grid configuration. It can be applied to releases from more than one point so long as they are made within the grid.

The basic recapture model

Full details are given by Meats (1998). Basically the model calculates the proportion remaining within a 200 m radius of the release site and calculates the proportion recaptured by a notional trap at the centre: The proportion recaptured by any real trap at any other distance is estimated (for *B. tryoni*) by the inverse square rule of Fletcher (1974a). This is a laborious procedure when there are many traps but it is possible to group traps with similar distances and use the radius of the mean annulus in each case. With regular grids, the procedure can be simplified further as explained below.

Note that this recapture model uses demographic terms that are applicable to the area within 200 m of the release site. Survival terms, therefore, have an emigration component (Meats 1998). The recapture rate for the area beyond 200 m is calculated with a submodel that accounts for the demographics of the emigrating flies.

Recapture model for regular grids

(a) Method one: release at trap site

In this case there is a real trap at the centre (instead of a notional one used for calculating catches at other distances). The daily catch at this trap (as a proportion of the original cohort) is calculated as in Meats (1998) and is basically 1% of the proportion remaining in the 200 m radius. The first day's catch (as a proportion of the original cohort emerging) is thus

$$C_1 = l_D \cdot p_{xA}^{0.5} \cdot (1 - p_{xt}) \quad (19)$$

The trapping survival rate is $p_{xt} = 0.99$; the other symbols are as before. This mean expectation for wild flies (consistent with the data of Fletcher 1974a) is 0.001894. The mean expectation for sterile flies with a p_x value of 0.93, maturing in 8 days is 0.001022.

The total accumulated catch with constant p_{xA} is

$$\sum C = C_1 \left[\frac{1}{(1 - p_{xA})} \right] \quad (20)$$

The mean expectations for wild and sterile flies (as above) are 0.01832 and 0.006152 respectively.

The accumulated catch up to a limited number of days (n) is

$$\sum_{D+1}^{D+n} C = C_1 \frac{(1 - p_{xA}^n)}{(1 - p_{xA})} \quad (21)$$

For the other traps we can use a radial approximation using trap spacing (S) for mean annuli and $(2\pi r/S)$ for the mean number of traps per annulus (where r is the radius of the annulus). We can also take advantage of the fact that, with a regular grid, although the mean catch per trap will fall as the square of r , the mean number of traps will increase as r thus the total catch per annulus will only fall as r .

The accumulated catch of the first ring of traps will be

$$T_{R1} = \sum C \cdot \left(\frac{0.2}{d} \right)^2 \cdot 2\pi \quad (22)$$

where $d = S$.

The accumulated catch on the grid to ring n is found by

$$T_G = \sum C + T_{R1} \left(1 + \frac{1}{2} + \frac{1}{3} + \frac{1}{4} \dots \frac{1}{n} \right) \quad (23)$$

Note that the first term is for the central trap, T_{R1} accounts for the first ring and the remainder accounts for all the others. The first term is thus the same for all grids, regardless of spacing and will represent the vast majority of the catch when spacing is large ($S \geq 1$ km).

(b) Method two: release between trap sites

In this case the central trap is only notional and the value of its 'catch' is not added to the result but only used to calculate the catches in the rings of traps. The first ring of traps is, for modelling purposes, at half a trap spacing from the central point. The catch in the first ring is therefore found by

$$T_{R1} = \sum C \cdot \left(\frac{0.2}{0.5S} \right)^2 \pi \quad (24a)$$

Subsequent rings will be at 3, 5, 7 ... n times $S/2$. Thus the total catch on the grid to ring n is

$$T_G = T_{R1} \left[1 + \frac{1}{3} + \frac{1}{5} + \frac{1}{7} \dots \frac{1}{(2n-1)} \right] \quad (24b)$$

Figure 1 shows the relationship between grid diameter and recapture rate for grids of traps spaced at 0.4, 1 and 5 km respectively (using method 2).

Comparison of the two methods

Releases are normally made between trap sites. When comparing the recapture rate during SIT with that expected from an equivalent number of wild flies it is immaterial which release method is used as long as the appropriate calculation is employed. There is little difference in expected recapture rate between the two methods when the grid has a spacing of 0.4 km. Method 2 will recapture 18, 16 and 13.4% more than method 1 for grid diameters approximately to 5, 10 and 50 km respectively.

When the grid spacing is 1 km, method 1 would obtain a higher recapture rate, chiefly due to the influence of the existence of a central trap and the fact that the nearest traps in method 2 are relatively far away from the release point. Method 1 therefore catches 59, 69 and 73% more than method 2 for grids of diameters approximating to 5, 10 and 50 km respectively.

When the grid spacing is 5 km the difference between the two methods is enormous because all the traps with method 2 will catch a trivial amount compared with the central trap used in method 1 which catches virtually all the trapped flies in the latter case.

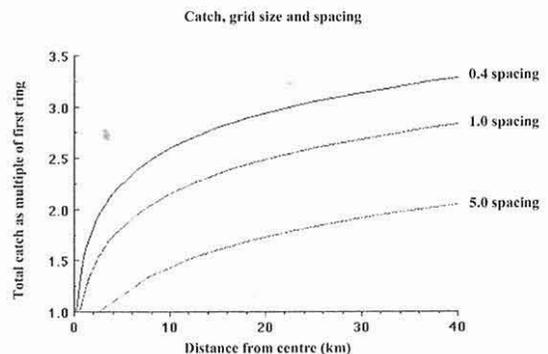


Figure 1. Catch, grid size and spacing.

RESULTS

Table 1 gives the results of the application of the recapture model (using method 2) to the recapture rates recorded in various SIT campaigns.

Mating expectations of teneral sterile flies at release

The mating expectation of newly emerged flies is given in the first column of table 1 expressed as a percentage of that expected of wild flies. It is defined

as $100 \frac{(EML_0, \text{sterile})}{(EML_0, \text{wild})}$ where the EML_0 values are

defined as in equation (8) and pertain to flies at emergence. The EML_0 values could not be estimated

directly but their ratio was obtained using equation

(10b) as $100 \left(\frac{T_{GS}}{T_{GW}} \right)$ where T_{GS} is the recapture rate of

the sterile insects and T_{GW} is the recapture rate expected had wild flies been used on a grid of identical size and trap spacing.

The EML_0 ratio is the survival component of total field competitiveness (i.e. the survival aspect of quality). As can be seen from the table, there was a wide variation in survival quality between the different SIT campaigns with the best ones only achieving values of about 20% of that of wild flies and the worst ones having values of less than 1%.

Mating expectation at maturity of sterile flies released as tenerals

The second column of table 1 gives analogous estimates for those sterile flies that actually survived to the age of maturity (D). The figures in column 2 are

thus found as $100 \frac{(EML_D, \text{sterile})}{(EML_D, \text{wild})}$ following equation

(18).

Since the result of equation (18) depends upon both the value of p_{xs} and D , the maximum likely range is given. As explained below, if D is low, p_{xs} is also low for a given recapture ratio and vice versa. Thus the range indicated in the second column of the table corresponds to the highest and lowest likely combinations of p_{xs} and D .

It is axiomatic that any EML_D will be higher than the corresponding EML_0 . However, it is significant

that the $\left(\frac{EML_D, \text{sterile}}{EML_D, \text{wild}} \right)$ ratio is much higher than the

corresponding ratio for EML_0 . The EML_D value of sterile flies is as high as 62% of the wild value for the best case and is no lower than 17% in the worst one (compare with 20% and <1% respectively for the EML_0 values). This shows how much the EML_0 of sterile flies is affected by a low survival rate before maturity. A higher EML at maturity (EML_D) is not much use if only a very few flies survive to maturity.

Table 1. Quality Assurance Measures for SIT flies

Campaign and Reference	Mating Expectation* at maturity (% of wild)	Mating Expectation† at maturity (% of wild)	Maturation time (D)	Daily survival decrement‡ (% of wild)
1. Wangaratta	20.6	62	15	93
2. Tharbogang (b)	19.3	51-59	8-14	89-92
3. Tharbogang (a)	8.0	40-49	8-14	83-88
4. Perth	5.0	35-45	8-14	29-86
5. Wagga Wagga	0.66	25-33	8-14	65-77
6. Cowra	0.25	22-29	8-14	59-72
7. Adelaide (c) (Glenside)	0.66	25-33	8-14	65-77
8. Adelaide (b) (Aldinga)	0.066	19-25	8-14	50-66
9. Adelaide (a) (Ingle Farm)	0.026	17-23	8-14	43-61

$$* 100 \frac{EML_0, \text{sterile}}{EML_0, \text{wild}} = 100 C_s$$

$$† 100 \frac{EML_D, \text{sterile}}{EML_D, \text{wild}}$$

$$‡ 100 p_{xs}$$

References:

- MacFarlane *et al.* 1987; 2 and 3, Horwood and Keenan 1994; 4, Sproule *et al.* 1992; 5, Dominiak *et al.* 1998;
- James 1992; 7, Jackman *et al.* 1996; 8, Perepelicia *et al.* 1994; 9, Perepelicia and Bailey 1993.

The daily survival rate decrement (p_{xs}) for sterile flies

The final column of table 1 gives the range of p_{xs} value associated with each SIT campaign. The values were calculated following equations (15)–(17) which are repeated below.

$$p_{xs} = 1 + \left(\frac{L}{b}\right) \quad (15)$$

$$\text{where } b = 2.3 = 0.5D \quad (16)$$

$$\text{and } L = \log_{10}\left(\frac{T_{GS}}{T_{GW}}\right) \quad (17)$$

For the Wangaratta data, D is known ($D=15$) thus a single estimate can be calculated since the recapture rate was 20.6% of that expected of wild flies, giving $L = -0.686$. In the other cases D is unknown and doubtless varied from release to release during each campaign due to seasonal variations in prevailing temperature.

In these cases, a maximum likely range of P_{xs} is given, using the maximum likely range of D which is 8–14 days. It is possible that in some cases D could fall outside this range (e.g. Wangaratta) but most if not all values (and certainly the mean) with a series of releases in the usual type of campaign will fall in the range 8–14. If D were greater than 15 the weather would be too cold to recapture flies (Fletcher 1974a) and SIT is usually suspended for the season (Sproule *et al.* 1992).

DISCUSSION

Relative importance of survival and mating competitiveness

The *EML* ratio is dramatically related to sterile fly quality and is the survival component of total field competitiveness. The *EML* ratio multiplied by mating competitiveness gives us the total quality (total field competitiveness) of the released flies.

Mating competitiveness values of *B. tryoni* in the range 0.8–1 are now commonly achieved so there is little room for improvement as a value of 1.0 indicates that a sterile fly is the equivalent of a wild fly in mating success. On the other hand, the survival aspect of quality has been a neglected area and there is much room for improvement (possibly up to a 5-fold improvement on the best results so far with the Queensland fruit fly). This is shown dramatically by

figure 2 which presents the pertinent data of table 1 in graphical form.

Possible causes of low survival rates with SIT

One possible cause may be the effect of mass production rather than sterilization, particularly because the breeding regime in factory conditions involves discarding flies when they are still young (Sproule *et al.* 1992). However, this seems unlikely because in many cases extreme longevity and high e_x values have been noted. O'Loughlin *et al.* (1984) record that the half life of cohorts of mass-reared flies in field cages in Melbourne averaged 100 d, corresponding to an $e_{x(o)}$ value (the mean span of adult life) of 144 d. Similarly from the field cage trials of Sonleitner (1973) we can estimate $e_{x(o)}$ as 50 d. These longevities are far higher than those seen in SIT campaigns. Liedo and Carey (1996) show that there is little difference in $e_{x(o)}$ for wild and laboratory strains of *Ceratitis capitata* (Wiedemann), *Anastrepha ludens* (Loew) and *A. suspensa* (Loew).

The low survival rate of SIT flies may be due to the sterilizing dose of gamma radiation (80–100 Gy). However, Fay and Meats (1987a,b) found that mass-reared sterile flies could survive as well as wild flies in large (tree containing) field cages provided that they were acclimated to the prevailing weather conditions in the late puparial stage. Thus the

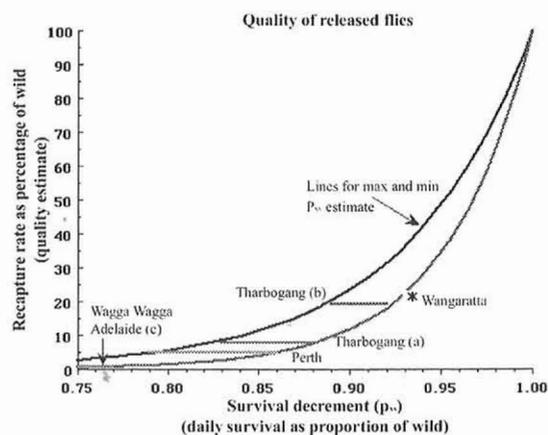


Figure 2. Quality of released flies. The relation between recapture rate (as a percentage of that expected of wild flies) and daily survival decrement due to induction by sterility. The upper and lower curves are for the shortest ($D=8$ days) and longest ($D=14$ days) maturation times normally expected during release campaigns. The horizontal lines plot the likely range of values for daily survival decrement for the campaigns listed in table 1.

sterilizing procedure itself is not necessarily deleterious.

A further possibility is that released flies that do not survive well are unsuitably acclimated. The experiments of Fay and Meats (1987a,b) were in early spring at Wilton (NSW). They found that unsuitably acclimated flies (transferred directly from the normal laboratory temperature of 25°C) survived badly when compared to wild flies. Most SIT is carried out in warm weather thus at first sight it is difficult to envisage that flies reared in a factory at around 25°C would be at a disadvantage. However, field conditions in Australia can be very much hotter than the normal laboratory environment in summer and sterile flies in transit and in field holding facilities may get overheated, and stressed rather than acclimated to the warmer conditions. Meats (1984) established that stress survived at one stage of a life history could affect survival ability at the next stage even if conditions had returned to optimal.

Dominiak *et al.* (1998) discuss the various methods of storage and release used in Australia and it appears likely that stress as revealed by low emergence rates could be responsible for the subsequent poor recapture rates.

The post-release environment may also affect survival if it is toxic due to residual bait sprays and lure blocks (Sproule *et al.* 1992). Also, the post-release environment may be naturally adverse and more data are required on the relation of recapture rates to prevailing weather conditions during individual campaigns where a series of releases are made.

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