CHAPTER 3.1.

ROLE OF POPULATION AND BEHAVIOURAL ECOLOGY IN THE STERILE INSECT TECHNIQUE

Y. ITÔ¹, K. YAMAMURA² AND N. C. MANOUKIS³

¹*Deceased*

²*Statistical Modeling Unit, Institute for Agro-Environmental Sciences,
NARO, Tsukuba 305-8604, Japan*

³*Tropical Crop and Commodity Protection Research Unit,
Daniel K. Inouye United States Pacific Basin Agricultural Research Center,
United States Department of Agriculture – Agricultural Research Service
Hilo, Hawaii 96720, USA
Email: Nicholas.Manoukis@ARS.USDA.GOV*

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SUMMARY

Important principles of population and behavioural ecology in relation to the application of the sterile insect technique (SIT) for the control of a pest are explained. These include: (1) a logistic population model for estimation of the population fluctuation of target animals and the number of sterile males to be released for successful eradication, (2) mark-recapture estimations of density and mortality rate of the target population, especially for remote areas, where repeated releases and recaptures are difficult, (3) models of dispersal to assess dispersal distance of target animals, and (4) equations for estimating the decrease of sexual competitiveness of mass-reared strains under field conditions. The method to estimate dispersal distance curves when attraction areas of traps are overlapping, and changes in mate-choice of wild females resulting from inadvertent selection when the SIT is applied, are explained. The necessity of field estimation of sexual competitiveness of released sterile males is also emphasized.

1. INTRODUCTION

In one of three seminal papers (Baumhover et al. 1955; Knipling 1955; Lindquist 1955) reporting the first success of the sterile insect technique (SIT) to eradicate insect pests, Knipling presented a table showing an example of model simulation for explaining the effect of sterile male releases. The model is

$$N_{g+1} = N_g R Q$$

where N_g and N_{g+1} are numbers of females at the g th and $(g+1)$ th generation, and R and Q are rates of change in the population size per generation and the proportion of normal females (females which can lay hatchable eggs), respectively. This early model shows that population ecology theory and models have been an integral part of the SIT from the outset (Barclay, this volume; Barclay et al., this volume).

The early success in eradicating the New World screwworm *Cochliomyia hominivorax* (Coquerel), in the area-wide integrated pest management (AW-IPM) programme in Florida in 1959, was not always replicated in subsequent AW-IPM programmes integrating the SIT (Krafsur 1998; Liebhold et al. 2016). In many cases this was because government officials thought about the SIT as an established technique consisting only of releasing sterile insects, with animal and plant health workers engaged in programmes releasing sterile insects without basic ecological and behavioural studies. Some early programmes did not include first estimating the number of wild females, simulating the process based on a population model incorporating the SIT, and evaluating in the field the mating competitiveness of the released sterile males. Thus, in some of those cases, many sterile males were released but eradication failed, and it was not possible to know the major reason for failure, in

spite of flooding the wild population with sterile males, e.g. ratios of the number of sterile to wild males were 112:1 in a Mediterranean fruit fly *Ceratitis capitata* (Wiedemann) programme in Nicaragua (Rhode et al. 1971), and 311:1 in another *C. capitata* programme in Procida Island (Cirio and de Murtas 1974). Without a full understanding of the population and behavioural ecology, the planning, implementation, and evaluation of programmes that release sterile insects become very difficult (FAO/IAEA 2016; Barclay, this volume; Barclay et al., this volume; Vreysen, this volume).

The goal of this chapter is to describe basic theory, models, and some mathematical techniques from population and behavioural ecology that are helpful for planning and executing the SIT component of an AW-SIT programme aimed at the control of pest insects – suppression, containment, prevention or eradication (Hendrichs, Vreysen et al., this volume).

2. THEORETICAL POPULATION DYNAMICS

2.1. Logistic Model

The most basic model of population increase is the Hale-Malthus model:

$$dN_t/dt = rN_t \quad (1)$$

or, integrating equation 1,

$$N_t = N_0 e^{rt} \quad (2)$$

where N_t , N_0 , r and e are number of individuals at time t , number at the beginning of increase, intrinsic rate of increase, and the base of natural logarithms (= 2.71828...), respectively. If population increase with discrete generations, as seen in many insects, is considered, equation 1 can be written as

$$N_{g+1} = N_g R \quad (3)$$

or

$$N_g = N_0 R^g \quad (4)$$

the equation used by Knipling (1955), where $\ln R = r$ (Begon and Mortimer 1981).

In equations 1 and 3, the population size increases indefinitely, but the large N_t or N_g may result in a smaller rate of increase, due to density-dependency, and the population may reach an upper limit. The most widely used model of density-dependent population increase is the logistic model,

$$dN_t/dt = N_t(r - hN_t) \quad (5)$$

where h is the suppressive effect of existence of an individual on the intrinsic rate of increase. Here r/h is the upper limit of increase, and writing $r/h = K$,

$$\frac{dN_t}{dt} = rN_t \frac{K - N_t}{K} \quad (6)$$

or by integration,

$$N_t = \frac{K}{1 + e^{a-rt}} \quad (7)$$

where a is a constant.

To establish a population model of the melon fly *Zeugodacus* (formerly *Bactrocera*) *cucurbitae* (Coquillett) under control by the SIT, Itô (1977) used a discrete expression of equation 7 to calculate generation-based increase of a logistic population (Fujita and Utida 1953). We have the following relation from equation 7 of g generation: $e^{a-rg} = (K/N_g) - 1$. By substituting this relation for equation 7 of $(g + 1)$ generation, we obtain

$$R_g = N_{g+1}/N_g = \frac{K}{1 + e^{a-rg}e^{-r}} / N_g = e^r / (1 + N_g B) \quad (8)$$

where $B = (e^r - 1)/K$. In place of Itô's procedure, we can use a logistic difference model, such as

$$N_{g+1} = \frac{N_g R}{(1 + cN_g)^b} \quad (9)$$

where b and c are constants (Hassell 1975; Begon et al. 1996), in place of equation 4 for constant increase. Fig. 1 shows examples of Hale-Malthusian (dashed) and logistic increase of density (N_g).

2.2. Dynamics of Populations under Control by the SIT

In equations 8 or 9, the population size of the next generation can be expressed as

$$N_{g+1} = N_g R_g \quad (10)$$

and when the SIT is applied

$$N_{g+1} = N_g R_g H_g \quad (11)$$

where H_g is the proportion of fertile (hatchable) eggs, and this value indicates the suppressive effect of sterile males on population increase. Thus, H_g is considered to be a function of the ratio of the number of sterile males, N_s , to fertile (normal) males, N_f in the field, that is,

$$H_g = f(N_s(g)/N_f(g)) \quad (12)$$

Figure 1. Exponential (A) and sigmoidal (B) increase in the population.
The equation giving a sigmoidal increase is the logistic model.

If the number of sterile males released in each generation is the same,

$$H_g = f(N_s/N_f(g)) \quad (12')$$

how can f be determined? To establish a model of the SIT process for the melon fly on Kume Island, Okinawa, Itô (1977) adopted a Poisson distribution (mean number of matings = 1.61) for the frequency of matings per wild female. The probability that a female would mate with normal and/or sterile males was approximated by the binomial distribution. Based on this Poisson-binomial model, a curve showing the relationship between the expected hatchability of eggs and the N_s/N_f ratio was obtained (Fig. 2). The H_g values read from this graph are incorporated into equation 11 where R_g is derived from equation 8.

For the melon fly on Kume Island, Itô used the following values: $N_0 = 125\,000$, $K = 2\,700\,000$, $r = 1.2$ (3.3 times increase per generation when N_0 is near 0), and $a = 3.971$. R_g changes in response to N_g , but based on the observed tendency that the number of melon flies decreases twice per year, in summer and winter in almost every year, Itô used the following R values for 4 months (assuming 12 generations per year): $R_4 = R_5 = 0.5$, $R_{10} = 0.2$ and $R_{11} = 0.238$. By these decreases the population returned to the minimum density (125 000). Calculation of N_g for the untreated period (before the SIT) gave a series of bimodal curves in which 125 000 and 2 621 568 were the annual minima and maxima, respectively (curve A of Fig. 3). H_g values estimated from Fig. 2, using N_g ($N_{f(g)}$ in equation 12) and a constant N_s , were used for simulation of the SIT process.

Figure 2. Relationship between the ratio of sterile to fertile males, and the ratio of fertile to sterile eggs, in a Poisson-binomial model (solid line). The broken line depicts the relationship when the insects mate only once. (Figure from Itô 1977, reproduced with permission.)

Curves B, C, and D of Fig. 3 are the results of simulation (initial ratios of sterile to normal males are shown in the legend). Fig. 3 indicates that, although eradication was not possible when the ratio of the number of sterile males released per month was one half of the minimum density of wild males ($N_0 = 125\,000$ and $N_s = 62\,500$), eradication can be attained only during 2 years when the number of released males is the same as the minimum density (curve C). Note that the ratio of sterile males to wild ones is less than unity when a decrease of wild insects has occurred.

Itô's published result was unexpected since it shows that if the sexual competitiveness (hereafter mating competitiveness + sperm competitiveness) of

released sterile males is the same as that of wild males, the release of much smaller numbers of sterile males than previously anticipated (e.g. 10/1 in Knipling 1955) can lead to success in an eradication programme. In the same year, using a similar logistic model for mosquito populations, Haile and Weidhaas (1977) obtained a similar result.

Once the curve of H_g against N_s/N_f is obtained, this curve can be used to estimate the sexual competitiveness of sterile males under field conditions. If the ratio of fertile eggs known from observation of eggs laid by wild females from the target population fell within the area above the curve in Fig. 2, this can be due to a reduction of sexual competitiveness of the released males.

The required ratio of sterile to wild males is a function of r or R . Itô and Kawamoto (1979) attempted to simulate the population processes based on Itô's model by substituting different values of r . Their results show that a ratio of 10 sterile males to 1 wild male could result in the eradication of the target species within only 12 generations even when the rate of increase per generation, R , was 20 ($r = 3$).

These results show that the quality (sexual competitiveness) of mass-reared and sterilized males is much more important than the overflooding ratio.

Barclay and Mackauer (1980), Barclay (1982), and Itô et al. (1989) provided detailed explanations of differential equation models of the SIT.

Figure 3. Fluctuations in the number of flies in the model population without the SIT (A) and populations with the SIT. The initial ratios of sterile to normal males are 0.5/1 (number of sterile males = 62 500) in B, 1/1 (number of sterile males = 125 000) in C, and 2/1 (number of sterile males = 250 000) in D, respectively. C' is the trend when winter mortality was halved in treatment C. Seasonal trends in the ratio of sterile to fertile (wild) males (N_s/N_f) are shown in the lower section of the figure. (Figure from Itô 1977, reproduced with permission.)

2.2. Spatial Considerations

The above description of population dynamics does not consider the effect of spatial differences on population dynamics under the SIT. For programs in locations such as Kume Island, with an area of around 60 km², this is entirely appropriate and effective. However, in many continental settings, or in contexts where there is a “pest free” area with a surrounding area where the pest is established, further development is helpful.

Hendrichs, Vreysen et al. (this volume) gave a useful starting point, defining a rectangular core area where the goal is to reduce or eliminate the pest. Surrounding this core on all sides is a larger buffer zone, where the aim is to kill target species transiting toward the core area. One important question is how wide this buffer zone must be to give a reasonable certainty that the targeted pest is not able to enter the core area. Barclay et al. (2011) worked thorough an example of how to apply this model, summarized below. A simple model for the population in the buffer zone has the density of the pest increasing closer to the outer edge. If the population in the buffer has births (β) and deaths (δ), and movement is modelled via simple diffusion (described in detail in section 4.1.) controlled by the diffusion coefficient D , then

$$\frac{dF(x,t)}{dt} = D\nabla^2 F(x,t) + \beta F(x,t) - \delta F(x,t) \quad (13)$$

Setting boundary conditions such that at the outside of the buffer area, $F(0,t) = F_0$, the density of insects is highest due to entry into the buffer of pests from the outer area, and at the inside edge of the buffer, $F(w,t)$, the density is a small proportion of F_0 , e.g. 10^{-6} . In this situation, almost all insects entering the buffer zone die before reaching the core area.

If either the survivorship or reproductive viability of insects in the buffer area are equal to the birth/entry rate, such that $\beta F - \delta F = 0$, then we have a simplified steady-state situation where only the space derivative is non-zero

$$D\nabla^2 F = (\delta - \beta)F \quad (14)$$

which has solutions proportional to $e^{[-(\delta-\beta)/D]x}$. Again, assuming the boundary conditions above (outer edge = F_0 ; $F_0 e^{[-(\delta-\beta)/D]x} = 10^{-6}$) taking logarithms, $\ln(10^{-6})=13.8$, and so the buffer width (w) is

$$w = \frac{13.8}{[(\delta-\beta)/D]^{1/2}} \quad (15)$$

Note that units need to be consistent: if β and δ are in time units per week, then the diffusion coefficient D also must be per week.

For the case of control in the buffer zone via the SIT with a release rate proportional to the ambient population, then δ can include both natural mortality and sterility from mating with a sterile male; the model is identical to the one above (Barclay, this volume).

Two other important spatial considerations are aggregation or “clumping”, and

whether the sterile insects distribute themselves similarly to the target pest. If the target is not randomly distributed, but the sterile insects generally are, then release rates might have to be increased to achieve control (FAO/IAEA 2016). A common way to assess clumping is to calculate the Coefficient of Dispersion (CD) (Southwood 1978) from the counts of insects found across samples (e.g. traps or fruit). CD is the ratio of the sample variance over the sample mean. A CD value of 1 (variance and mean are identical) suggests a random distribution in space; the sample is consistent with a Poisson distribution. A value above 1 suggests clumping or aggregation, while a value below 1 indicates a uniform distribution.

In practice, the CD statistic is less useful (has less power) if the population is sparse. An alternative is to use the negative binomial distribution. To assess clumping Barclay (1992) applied this approach (in the negative binomial distribution the parameter k with values approaching zero indicate increasing aggregation, while higher values indicate random distributions). He found that, for $k = 0.25$, about four times the release rate would be needed for the same effectiveness when compared with a uniformly distributed target population (Barclay, this volume). A related practical example with field data is given in Shiga (1986).

In at least two recent studies, where the distribution of wild and released sterile insects have been examined, the two were found to be similar (Vreysen et al. 2011; Gavriel et al. 2012). Despite this, spatial aggregation remains an important factor to be considered when determining parameters for application of the SIT. It should be assessed for each target population and location, especially in determining required release rates.

3. ESTIMATION OF POPULATION DENSITY AND MORTALITY BY MARK-RECAPTURE

The previous section indicated that the number of sterile males to be released must be the same as, or more than, the minimum number of males in the target locality. Thus the density of target populations must be estimated to determine the appropriate number of sterile males for release. Since direct counting is not applicable to adults that move freely, mark-and-recapture methods are the only way to estimate the population size of many species that are targets of the SIT. In this section, equations of mark-and-recapture methods are briefly explained. Krebs (1989) provided a detailed explanation of equations and ways of using them. Another comprehensive source on mark-recapture calculations is Service (1993).

3.1. Petersen Method

The Petersen method (also called the Lincoln Index) is the simplest way to use the mark-recapture method because it is based on a single episode of releasing marked animals and a second single episode of recapturing individuals. The equation is

$$\hat{N}_P = M_1 n_2 / m_2 \quad (16)$$

where $\hat{N}_P$, M_1 , n_2 and m_2 are the estimated total population, the number of individuals marked and released on the first day (day 1), the number of individuals caught on day 2, and the number of marked individuals recaptured on day 2, respectively. Variance of $\hat{N}_P$ can be estimated by

$$V(\hat{N}_P) = \frac{M_1(M_1 - m_2)n_2(n_2 - m_2)}{m_2^3} \quad (17)$$

In a release experiment to estimate population size for the SIT, usually laboratory-reared insects are released. This is especially necessary at the final stage of the SIT, because at this stage the number of wild males is small. The estimation of the number of wild individuals (unmarked individuals) is of greater interest than the total number of individuals. An estimate of the number of wild individuals, which is denoted by $\hat{U}_P$, can be obtained by

$$\hat{U}_P = M_1 u_2 / m_2 \quad (18)$$

where $u_2 = n_2 - m_2$. The variance is given by

$$V(\hat{U}_P) = \frac{\hat{U}_P(\hat{U}_P - u_2)(u_2 + m_2)}{u_2 m_2} \quad (19)$$

The following five assumptions are used for the Petersen method: (1) the population is closed, so the total number is constant, (2) all animals have the same chance of getting caught in the first sample, (3) marking individuals does not affect their catchability, (4) animals do not lose their marking(s) between the two sampling periods (Box 1), and (5) all marked individuals are reported on discovery in the second sample. Even when these assumptions hold, the Petersen method tends to overestimate the actual population, especially in small samples. For small samples (e.g. $m_2 < 10$), using the following two modified equations is recommended (for equations for variance, see Southwood 1978 and Itô and Murai 1978):

$$\text{A: } \hat{N}_{P'} = \left[\frac{(M_1 + 1)(n_2 + 1)}{m_2 + 1} \right] - 1 \quad (20)$$

$$\text{B: } \hat{N}_{P''} = \frac{M_1(n_2 + 1)}{m_2 + 1} \quad (21)$$

If estimated N_P is very large as compared with M_1 and n_2 (e.g. $N_P > 10M_1$ or $10n_2$), equation 21 is recommended, but if N_P is relatively small and/or n_2 animals are killed during sampling (e.g. by trapping), equation 20 is recommended (Itô and Murai 1978; Southwood 1978).

Box 1. Method to Estimate Loss of Marking(s)

The fourth assumption in the Petersen method, that animals do not lose marking, is a prerequisite for every model of mark-recapture estimation. Seber (1982) described a method to estimate the loss of marking.

Mark all the n_1 individuals in the first sample (or all the laboratory-reared animals released on day 1) in two ways, A and B (by two colours or two points on the body). Then

π_x = Probability that a marking of type x is lost by the time of the second sample ($x = A, B$),

π_{AB} = Probability that both markings are lost,

m_x = Number of marked animals caught on day 2, with mark x only,

m_{AB} = Number of marked animals on day 2 with both marks, and

m'_2 = True number of recaptures on day 2 ($m'_2 + u_2 = n_2$).

Then the maximum likelihood estimates of m'_2 , π_A and π_B are:

$$\pi_A = m_B / (m_B + m_{AB}),$$

$$\pi_B = m_A / (m_A + m_{AB}) \text{ and}$$

$$m'_2 = (m_A + m_{AB})(m_B + m_{AB}) / m_{AB} \\ = c(m_A + m_B + m_{AB})$$

This means that the observed recapture ($m_A + m_B + m_{AB} = m_2$) must be corrected by a factor $c [= 1 / (1 - \pi_A)(1 - \pi_B)]$ to give an estimate of the actual number of recaptures m'_2 .

For large samples,

$$\hat{N}' = n_1 n_2 / m'_2$$

and, if laboratory-reared animals are released,

$$\hat{N}' = n_1 u_2 / m'_2$$

with

$$\hat{V} = \frac{N^3}{n_1 n_2} \pi_A \pi_B \left[\frac{1}{(1 - \pi_A)(1 - \pi_B)} \right] \\ + \frac{N^3}{n_1 n_2} \left[1 + \frac{2N}{n_1 n_2} + 6 \left(\frac{N}{n_1 n_2} \right)^2 \right]$$

When $n_1 = 500$, $n_2 = 149$, $m_{AB} = 7$, $m_A = 1$ and $m_B = 2$,

$$\pi_A = 2 / (2 + 7) = 0.222, \quad \pi_B = 1 / (1 + 7) = 0.125$$

$$m'_2 = [(1+7) \times (2+7)] / 7 = 10.286$$

As $m_A + m_B + m_{AB} = 10$, $m'_2 - m_2 < 1$, suggesting that the rate of loss of marking is negligibly small.

Here

$$\hat{N}' = (500 \times 149) / 10 = 7450 \text{ and}$$

$$\hat{V} = 6869641, \text{ and s. d.} = 2621$$

The assumption of a closed population is usually not satisfied. For long-lived animals, mark and recapture during a short period may permit neglecting mortality, but the longevity of adult insects is often relatively short. However, Itô (1976) showed that the Petersen method gives the true population density on day 1 (before death) if only mortality exists, and gives the density on day 2 (after recruitment) if only recruitment exists. If both exist, the true density on day 1 is $Np/(1+B)$ or $Np/(1+B/S)$, where S and B are rates of survival and recruitment, respectively (Table 1). If there is no recruitment, the Petersen method gives a good estimate of density even when mortality and/or emigration exist. For a method to determine the existence of recruitment, see Seber (1982).

Table 1. Effects of mortality and/or emigration and dilution (emergence and/or immigration) on the Petersen estimates

	N_2	M_2	n_2	m_2	N_P
(1) Mortality/emigration occurs but no dilution	SN_1	$\frac{SM}{1}$	pSN_1	$\frac{pS}{M_1}$	$(pSN_1M_1)/(pSM_1) = N_1$
(2) Dilution occurs but no mortality/emigration	$N_1(1+B)$	M_1	$pN_1(1+B)$	$\frac{pM}{1}$	$[pN_1(1+B)M_1]/pM_1 = N_1(1+B)$
(3) Both mortality/emigration and dilution occur	$N_1(S+B)$	$\frac{SM}{1}$	$pN_1(S+B)$	$\frac{pS}{M_1}$	$[pN_1(S+B)M_1]/pSM_1 = N_1(1+B/S)$
(4) Same as in (3) but in reverse order	$SN_1(1+B)$	$\frac{SM}{1}$	$pSN_1(1+B)$	$\frac{pS}{M_1}$	$[pSN_1(1+B)M_1]/pSM_1 = N_1(1+B)$

N_2 , M_2 , n_2 and m_2 are the numbers of individuals living in the target area, those marked and released, individuals caught on day 2, and recaptured on day 2, respectively.

N_P , S , B and p are Petersen estimates (of day 1), rates of survival and dilution from day 1 to day 2, and rate of capture, respectively.

3.2. Yamamura Method

Although the Petersen method is the simplest method of estimation, the estimates are subject to large biases because the method ignores the mortality that must exist in the field. Yamamura et al. (1992) proposed a method that includes field mortality, where: (1) individuals reared in the laboratory are marked and released, and (2) traps are used for the recapture census, and all captured individuals are removed from the field population. This method requires one release procedure and two capture censuses.

Thus one more sampling census must be added to the Petersen method. There are four assumptions: (1) the wild population size is constant during the two consecutive sampling censuses (even if many wild individuals are lost by emigration from the

study area or by artificial removal, the wild population size returns to the original level through immigration from the surrounding area), and (2) the proportion of marked individuals that survive and remain in the population between the two successive censuses, i.e. the rate of remaining, is constant. The last two assumptions are the same as (3) and (4) of the Petersen method.

If the marked individuals are released on day 1, and recaptured on day 2 and day 3, then the maximum likelihood estimates of the survival rate, S_Y , and the wild population size, U_Y , are given by

$$\hat{S}_Y = \frac{u_2 m_3}{m_2 u_3} + \frac{m_2}{M_1} \quad (22)$$

$$\hat{U}_Y = \hat{S}_Y M_1 u_2 / m_2 \quad (23)$$

3.3. Jolly-Seber Method

Most populations are constantly changing in size because birth (emergence for adult populations), death, immigration, and emigration are not always balanced. Although the wild population is assumed to be nearly constant in two successive census periods in the Yamamura method, this is not always the case. The Jolly-Seber method is applicable to such a changing population. Two or more releases are required to apply the Jolly-Seber method. Recapture censuses are also required two or more times, the first recapture being conducted just before the second release. Estimates are obtained by using the following equations (for small samples, see Seber 1982 or Krebs 1989):

$$\begin{aligned} \hat{M}_i &= (R_i Z_i / r_i) + m_i & (i = 2, 3, \dots, s-2) \\ \hat{U}_{J(i)} &= \hat{M}_i u_i / m_i \\ \hat{N}_{J(i)} &= \hat{M}_i n_i / m_i \\ \hat{S}_{J(i)} &= \hat{M}_{i+1} / (\hat{M}_i - m_i + R_i) \\ \hat{B}_{J(i)} &= \hat{N}_{J(i+1)} - \hat{S}_{J(i)} (\hat{N}_{J(i)} - n_i + R_i) \end{aligned} \quad (24)$$

where

$\hat{M}_i$ = Estimated number of marked individuals living in the area just before the sample i .

$\hat{N}_{J(i)}$ = Total number of individuals just before the sampling at time i .

$\hat{U}_{J(i)}$ = Number of unmarked individuals just before the sampling at time i .

$\hat{S}_{J(i)}$ = Survival rate during i and $i+1$.

$\hat{B}_{J(i)}$ = Number of individuals that entered the population during i and $i+1$.

n_i = Total number of animals caught in sample i ($= m_i + u_i$).

m_i = Number of marked animals caught in sample i .

u_i = Number of unmarked animals caught in sample i .

R_i = Total number of animals released after sample i .

r_i = Number of the R_i individuals released at sample i and caught again in some later sample.

Z_i = Number of individuals marked *before* sample i , not caught in sample i , but caught in some sample after time i . Let m_{hj} be the number of marked animals caught in sample j last caught in sample h ($1 \leq h \leq j - 1$). Then we obtain

$$Z_i = \sum_{j=i+1}^s c_{i-1,j} \quad \text{where} \quad c_{i-1,j} = \sum_{h=1}^{i-1} m_{hj}$$

An example calculation is shown in Box 2. The method of calculation for larger samples, and special tables to be used for these, are shown in Seber (1982) using good numerical examples including a method to estimate variances. The variance formula for $\hat{U}_{J(i)}$ is given by Yamamura et al. (1992). Assumption (3) of the Petersen method is especially important for the Jolly-Seber method. Krebs (1989) described many methods to assess whether this assumption is satisfied or not.

3.4. Hamada Method (Modified Jackson Positive Method)

The above-mentioned methods were listed in ascending order of the required amount of work. The Petersen method requires one release and one capture census, the Yamamura method one release and two capture censuses, and the Jolly-Seber method two releases and two capture censuses. The difference in requirements between the Yamamura and the Jolly-Seber methods seems to be very large, since the addition of one more release usually requires more work than that of one more capture census. Since AW-IPM programmes releasing sterile insects are often carried out in remote areas, the addition of a release is especially laborious. Therefore in many cases one release is conducted, accompanied by three or more subsequent capture censuses, resulting in a series of regression estimates (see Jackson (1939) method).

Jackson (1939) presented equations to estimate the density and survival rate in an open population by a single release and multiple recapture censuses (Jackson positive method). As a first step an index y_i is calculated using the following equation:

$$y_i = 10^4 m_i / M_0 n_i \quad (25)$$

where M_0 is the number of individuals marked and released on the first day (day 0; here day 0 is used to show the first day in place of day 1 as in the preceding methods, for simplicity of explanation of the regression method), y_i is a standardized number of

marked insects to be recaptured on day i , assuming that 100 marked individuals are released on day 0 and 100 individuals are randomly caught on day i . Other symbols are the same as in the preceding equations. If total insect density is almost constant, and if marked individuals are returned to the field after being recaptured, by plotting y_i against i (Fig. 4) a survivorship curve of marked individuals in the field is obtained.

Box 2. Jolly-Seber Three-Point Method

As a special case of the Jolly-Seber method, an example of estimating population parameters based on two releases and two recaptures is shown. Let us consider a typical case of mass-marking experiment in which individuals reared in the laboratory are marked and released. All captured individuals are killed. On day 1, individuals are released with a red mark. On day 2, individuals are released with a blue mark. The following is the result of a release experiment of *Spodoptera litura* (F.) conducted by Wakamura et al. (1992).

Day	n_i	R_i	U_i	Number of recaptured individuals	
				Red marked	Blue marked
1		1934			
2	409	1968	26	383	
3	633		24	181	428

The Jolly-Seber method yields

$$\hat{M}_2 = R_2 Z_2 / r_2 + m_2 = (1968 \times 181 / 428) + 383 = 1215$$

$$\hat{S}_{J(1)} = \hat{M}_2 / R_1 = 1215 / 1934 = 0.63$$

$$\hat{U}_{J(2)} = \hat{M}_2 u_2 / m_2 = 1215 \times 26 / 383 = 83$$

For the Yamamura method, we obtain

$$\begin{aligned} \hat{S}_Y &= (u_2 m_3) / (m_2 u_3) + m_2 / M_1 \\ &= (26 \times 181) / (383 \times 24) + 383 / 1934 = 0.71 \end{aligned}$$

$$\hat{U}_Y = \hat{S}_Y M_1 u_2 / m_2 = 0.71 \times 1934 \times 26 / 383 = 93$$

For the Petersen method, we obtain

$$\hat{U}_P = M_1 u_2 / m_2 = 1934 \times 26 / 383 = 131$$

The estimate obtained by the Petersen method is much larger than that obtained by other methods. The Yamamura method generally yields results similar to those of the Jolly-Seber method if marked individuals are sufficiently mixed with wild individuals.

If the survival rate is constant, the survival rate can be estimated using a linear regression:

$$\log y_i = \log y_0 + i \log S \quad (26)$$

where S is the survival rate per unit time (as $0 \leq S \leq 1$, $\log S$ is always negative), y_0 is a constant representing the expected number of recaptures on the assumption that 100 marked individuals released on day 0 are instantaneously intermingled into the wild population, and that 100 specimens are randomly caught before either mortality or recruitment occurs. Then an estimate of the total number of individuals on day 0 using

$$\hat{N}_{J+} = 10^4 / y_0 \quad (27)$$

is obtained together with the survival rate S from the slope of the regression line.

In the Jackson positive method, recaptured individuals should be returned to the original population. Since, in programmes integrating the SIT, recaptures are made with traps, the survival rate decreases as the number of recaptures increases, resulting in an overestimated y_0 (Fig. 4). Thus N_{J+} will be underestimated. Itô (1973) devised a modified equation to reduce some of this bias by using a modified index y'_i , such that

$$y'_i = 10^4 m_i / M'_{0(i)} n_i \quad (28)$$

where

$$M'_{0(i)} = M_0 - \sum_{j=1}^{i-1} m_j$$

then $\log y'_i = \log y'_0 + i \log S$ and $\hat{N}_I = 10^4 / y'_0$

Figure 4. Comparison of Jackson positive and Itô methods using hypothetical values. Assuming no trapping mortality, change in y_i should parallel the survivorship curve of marked insects and, when daily survival rate is constant, the curve of $\log y_i$ should be linear against i (left). However, if there is trapping mortality, y_i should have smaller than expected values with time, and the linear regression should yield an overestimated value of $\log y_0$ (right), which in turn results in an underestimation of N_{J+} . (Figure adapted from Itô et al. 1989, reproduced with permission from Elsevier.)

Hamada (1976) found that the Itô method gives an overestimated value when the number of released laboratory-reared marked males is much larger than the wild population size. He showed that a direct estimation of the number of wild males with the following equation gives the least (but not zero) stable negative bias (usually below 20%):

$$z_i = 10^4 m_i / M'_{0(i)} u_i \quad \text{and} \quad \hat{U}_H = 10^4 / z'_0 \quad (29)$$

where $u_i = n_i - m_i$, and $\log z_i = \log z_0 + i \log \hat{S}$. The Hamada method has been applied widely to estimate the wild melon fly density in Okinawa. The Hamada method is based on a similar assumption as in the Yamamura method — the number of wild individuals is kept constant during the capture period. If the number of recapture censuses is two, the Yamamura method is preferable since it is the maximum likelihood estimate for this situation. Table 2 gives estimated densities and survival rates of male melon flies using the Petersen and Hamada methods, showing the relative stability of the estimated values.

Table 2. Comparison of estimates of the density of male melon flies with the Petersen and Hamada methods (data from Tanaka et al. 1978)

Station	Date of release	$\hat{U}_P$ /ha	$\hat{U}_H$ /ha	$\hat{S}$ /day ¹
1	June 28	136	85	0.81
	July 12	173	87	0.83
2	July 22	166	109	0.74
	August 9	251	180	0.77

$\hat{U}_P$ and $\hat{U}_H$ are the numbers of wild males estimated by the Petersen and Hamada methods, respectively. For the Petersen method, the numbers of males caught on the 4th (station 1) and 2nd (station 2) days after release are used as n_2 and m_2 (equation 16). Numbers of recaptures in the Hamada method are four in station 1, and five in station 2.

¹ Estimated by the Hamada method, using linear regression of $\log z_i$ and $\log \hat{S}$ in equation 26.

3.5. Jackson Negative Method

Jackson (1939) also presented another model (Jackson negative method) to estimate the population size based on multiple-release single-recapture data. Marked individuals are released on several occasions (on days $-i$, $(-i + 1), \dots$, -1) with different markings, and thereafter a single random catch is made on day 0. Here

$$y_{-i} = 10^4 m_{-i,0} / M_{-i} n_0 \quad (30)$$

where $m_{-i,0}$, the number of individuals released on day $-i$ and recaptured on day 0, is expected to increase with time. If the survival rate of marked individuals is constant, one can estimate y_0 by the linear regression of $\log y_{-i}$ on i , that is, $\log y_i = \log y_0 + i \log S$. Then, as in the positive method, N_{J-} is

$$N_{J-} = 10^4 / y_0 \quad (31)$$

When laboratory-reared individuals are released, the following equations are applicable:

$$y'_{-i} = 10^4 m_{-i,0} / M_{-i} u_0, \quad \text{and} \quad U_{J-} = 10^4 / y'_0 \quad (32)$$

Reisen et al. (1979) and Koyama et al. (1982) noted that the trapping mortality, which induces a negative bias in the Jackson positive method, does not cause bias in density estimates obtained by the negative method because recapture is made only once for any group of released individuals. This method was used to estimate melon fly density in mountainous parts of Okinawa. Multiple releases of marked flies were made from a helicopter, followed by a single recapture by the many persons who checked traps.

3.6. Fisher-Ford Method

The Fisher-Ford (1947) "trellis" method differs from the approaches described above in that it incorporates an arbitrary number of releases and recaptures (greater than one of each) to obtain an estimate of population size; it also requires an estimate of daily survivorship that is independently derived, and that each released marked cohort of individuals be individually identifiable. However, the requirement of a daily survivorship can be used to set a range on the population size estimate as shown in the worked example below (Box 3).

Fig. 5 shows the results of a mark-recapture study with mosquitoes in Mali, West Africa via a "triangular table" or "trellis diagram", originally introduced by Fisher and Ford (1947). In these tables the dates are arranged horizontally along the top. The total captured on a given date is shown at the end of the cells running to the lower left side of the diagram, while the total number released on that date is given along the lower right. The recaptures are given in the body of the table, with each intersecting cell representing the number of insects marked and released on date N that was recaptured in subsequent dates. For example: on July 3, 126 mosquitoes were released of a total of 160 captured. Following the left slanting diagonal, two mosquitoes marked on July 3 were recaptured on July 4, one was recaptured on July 5, and none after that. The distribution of release dates for recaptures on any given day is also apparent. For example: on March 19, three mosquitoes that had been released on March 18 were recaptured together with four from the release on March 17 and one from the release on March 16.

Box 3. Fisher-Ford Method

Calculation of the population size is described in terms of operations on a table, following the approach used with the introduction of this method by Fisher and Ford (1947). Here we follow this practice with data from Baber et al. (2010), presented in Table A using data from Fig. 5 with an assumed daily survivorship of 0.6.

The first column gives sampling dates in reverse chronological order, while the last column gives the row dates + 1. Columns to the left of the vertical line refer to the dates in the first column, those to the right refer to the dates in the last. Working left to right, we have the number of days from the end of the experiment in column 2, and the number of marked individuals released in column 3 (these can also be read in Fig. 5). Column 4 is the expected number of marked individuals recaptured, calculated as follows: sum of row values from the bottom of the table, each value is

$$E_m = \sum_{i=n}^l MS^d$$

where n is the current row, l is the last row of the table, M is the number of marked individuals released, and S^d is the estimated daily survivorship raised to the number of days from the end of the sampling (column 2).

Table A. Calculation of population size following the method of Fisher and Ford (1947) for mosquito data collected in Fourda, Mali, in 2008 by Baber et al. (2010), assuming a daily survivorship of 0.6

Date 1	d	M	E_m	R	C	P	Date 2
09 July	1	0	63.7	-	-	-	10 July
08 July	2	0	63.7	1	505	53 606	09 July
07 July	3	0	63.7	2	335	29 634	08 July
06 July	4	299	63.7	5	235	13 859	07 July
05 July	5	157	24.9	5	385	37 841	06 July
04 July	6	144	12.7	5	187	11 995	05 July
03 July	7	126	6.0	6	166	7550	04 July
02 July	8	148	2.5	7	160	4910	03 July

d : days from the end of experiment; M : number of individuals marked and released; E_m : number of marked individuals expected in the environment considering daily survival; R : number recaptured; C : number captured; P : estimated population size.

Values in columns 5–7 refer to dates in column 8 (“Date 2”). For each date j , the estimated population size P is calculated as follows:

$$P = \frac{E_m C}{S^d R}$$

Considering population size estimates with at least 3 releases (July 6 and later) yields an average population size estimate of 33 735 with an SE of 8284. Assuming a higher daily survivorship of 0.8 gives a mean population size estimate of 77 085 and an SE of 31 007.

4. ESTIMATION OF DISPERSAL DISTANCE BY MARK-RECAPTURE

The immigration of wild insects into an area treated with sterile insects is one of the most important causes of failure of some AW-IPM programmes integrating the SIT (Lance and McInnis, this volume). If wild males have sufficient dispersal ability, the male sterile:fertile ratio ($N_s/N_f(g)$ in equation 12') will decrease, causing higher fertility in wild females. Estimation of the dispersal range is also important for estimating the $N_s/N_f(g)$ ratio from field data. If the dispersal range is small, the $N_s/N_f(g)$ ratio should be estimated using samples obtained from the small area, whereas if the dispersal range is large, samples obtained from the large area should be combined. Furthermore, if the range of dispersal is known, an optimal spatial design for the release of sterile males can be constructed. If the dispersal range is small, sterile males should be released at many spatial points to increase uniformly the male sterile:fertile ratio. In this section several techniques to estimate the dispersal range of individuals are described.

4.1. Diffusion Equation

A two-dimensional simple diffusion equation will be the simplest theoretical model that can be applicable to the two-dimensional dispersal of marked individuals. Assuming that the movement of marked individuals is Brownian random motion (the rate of which is invariant in time and space), the number of marked individuals at time t at coordinate (x, y) , which is denoted by $m(x, y, t)$, is described by a partial differential equation (Okubo 1980, Shigesada and Kawasaki 1997):

$$\frac{\partial m(x, y, t)}{\partial t} = D \left(\frac{\partial^2 m}{\partial x^2} + \frac{\partial^2 m}{\partial y^2} \right) \quad (33)$$

where D is the diffusion coefficient that measures the dispersal rate with units (distance²/time). When M_0 individuals are released at time 0 from the origin $(0, 0)$, the solution is given by

$$m(x, y, t) = \frac{M_0}{4\pi Dt} \exp \left[-\frac{(x^2 + y^2)}{4Dt} \right] \quad (34)$$

which is a two-dimensional normal distribution with mean zero, correlation coefficient zero, and variance $2Dt$ in each dimension. If the distance from the origin is denoted by $r = \sqrt{x^2 + y^2}$, then equation 34 is rewritten in a simpler form

$$m(r, t) = \frac{M_0}{4\pi Dt} \exp\left[-\frac{r^2}{4Dt}\right] \quad (r \geq 0) \quad (35)$$

The proportion of individuals in a circle of radius d at time t , which is denoted by $F(d, t)$, is given by

$$F(d, t) = \frac{1}{M_0} \int_0^d 2\pi r \cdot m(r, t) dr = 1 - \exp\left[-\frac{d^2}{4Dt}\right] \quad (36)$$

Thus, the proportion of individuals in a circle of radius $\sqrt{4Dt}$ is $1 - \exp(-1) = 0.63$, and that in a circle of radius $2\sqrt{4Dt}$ is $1 - \exp(-4) = 0.98$. A rearrangement of the above equation yields

$$\log_e[1 - F(d, t)] = -d^2/(4Dt) \quad (37)$$

Therefore, if the distribution of marked individuals is observed at time t , an estimate of D can be obtained by plotting the observed $\log_e[1 - F(d, t)]$ against d^2 and by estimating the slope $-1/(4Dt)$ using a liner regression with intercept zero (Broadbent and Kendall 1953). If the relation is not linear, it can be judged that the dispersal is not a random diffusion with a constant D (e.g. Inoue 1978). The expectation of the square of the distance is given by

$$E[r^2] = \frac{1}{M_0} \int_0^\infty 2\pi r \cdot r^2 \cdot m(r, t) dr = 4Dt \quad (38)$$

Thus, the moment estimate of D is given by the observed mean square of the distance divided by $4t$. If estimates of the mean square distance for several t are available, the common D can be estimated by plotting the mean square distance against t and by estimating the slope $4D$ using the linear regression with intercept zero.

4.2. Random Correlated Walks

The diffusion model described above is useful in its simplicity and mathematical tractability. In terms of an organism moving in real space with discrete time-steps, diffusion can be understood as a random walk: at each time-step the organism moves a random step-length (with given range) in a randomly chosen direction. The step direction at time t is independent from the direction at $t-1$, all are equally likely including complete reversal. This “classical” random walk results in an average expected displacement of the entire population = 0, as indicated above.

Even in the absence of cues, this kind of motion is not realistic for most organisms. Forward bias is common, as are correlations between directions chosen in subsequent time-steps (Miller et al. 2015). A random correlated walk (Kitching 1971;

Kareiva and Shigesada 1983; Byers 2001) is an extension of a classical random walk (diffusion) that restricts the range of new directions after a given step, thus resulting in more realistic dispersal.

Kareiva and Shigesada (1983) derive the relationship between an organism's movement behaviour and its expected square displacement using a random correlated walk as follows: if each move m is a vector (x_m, y_m) then the total displacement after n moves, R_n , is

$$R_n = \sum_{m=1}^n (x_m, y_m) \quad (39)$$

the length of each move is the Euclidean distance; it and each turning angle θ_m are independent random variables with probability densities equal to $p(l)dl$ and $g(\theta)d\theta$, respectively. The expected values for these random variables are:

$$E(l) = \int_0^\infty l p(l)dl \quad (40)$$

$$E(l^2) = \int_0^\infty l^2 p(l)dl \quad (41)$$

$$c = E(\cos \theta) = \int_{-\pi}^{\pi} \cos \theta g(\theta)d(\theta) \quad (42)$$

$$s = E(\sin \theta) = \int_{-\pi}^{\pi} \sin \theta g(\theta)d(\theta) \quad (43)$$

Since a set of moves can be represented by independent random draws from $p(l)$ and $g(\theta)$, the process of movement in this model is a first-order Markov chain -- where a given draw is not influenced by the previous draw. However, the probability density of values can be non-uniform. Relating the distribution of values to biological movement is straightforward: if the distribution is uniform for angles between -180 and 180 then the movement pattern will follow classical diffusion (a random walk) as described above. If the probability density is 1 for an angle of 0 and 0 for all other angles in the range, then the movement pattern is a straight line (sometimes termed a "ballistic" disperser; Miller et al. 2015). If the distribution is intermediary, then the movement is considered a random correlated walk.

A useful result from Kareiva and Shigesada (1983) is the expected squared displacement. Assuming an equal probability of right or left turns, the following equation is derived:

$$E(R_n^2) = nE(l^2) + 2E(l)^2 \frac{c}{1-c} \left(n - \frac{1-c^n}{1-c} \right) \quad (44)$$

This model enables a direct relation between behavioural changes influencing $p(l)$ or $g(\theta)$ and consequent changes in the expected net displacement.

4.3. Distribution of Cumulative Recaptures

Traps are frequently used to capture marked individuals (FAO/IAEA 2018). If traps are set for a sufficiently short period around t , the observed distribution of captured individuals can be used for a sample distribution of dispersing individuals at time t . If traps are set for a longer period, the observed distribution cannot be used for a distribution at a specific time. A trap also performs some integration of density over space as well as over time. Such a spatial integration may cause some difficulties in the estimation of dispersal distance; one such difficulty is discussed in Box 4.

In several experiments, marked individuals have been trapped until most of them died or left the study area. In these cases estimates of the distribution of the cumulative number of recaptured individuals in each trap can be obtained. The theoretical distribution of the cumulative recaptures can be described by relatively simple equations under several assumptions. Let δ be instantaneous natural mortality (or disappearance rate), and α trap efficiency. Assuming that the number of recaptures is sufficiently small relative to the number of total release, M_0 , so that the mortality δ is not influenced by the mortality caused by trapping, then the cumulative number of recaptures at a trap placed at a distance r is given by

$$C(r) = \frac{\alpha M_0}{2\pi D} K_0 \left(\sqrt{\frac{\delta}{D}} r \right) \quad (45)$$

where K_0 is a zero-order modified Bessel function of the second kind (Broadbent and Kendall 1953; Williams 1961). Turchin and Thoeny (1993) used an approximation for equation 45

$$C(r) \approx \frac{A}{\sqrt{r}} \exp \left(-r \sqrt{\frac{\delta}{D}} \right) \quad (46)$$

where A is a constant. This equation can be described by a linear form,

$$\log_e[C(r)] + \frac{1}{2} \log_e(r) \approx \log_e(A) - r \sqrt{\frac{\delta}{D}} \quad (47)$$

therefore $\sqrt{\delta/D}$ can be estimated by plotting the observed $\log_e[C(r)] + \frac{1}{2} \log_e(r)$

against r , and by estimating the slope by using a linear regression method, although such an estimation procedure is not preferred from a statistical point of view. Like Inoue's (1978) method using equation 37, equation 47 can be used to judge the randomness of dispersal. If the relation is not linear, then dispersal is not a simple random diffusion with a constant D (Cronin et al. 2000). Note that δ and D cannot be estimated separately since the accumulation of recaptures eliminates information on the velocity of dispersal in this estimation procedure.

Box 4. Overlap of Attraction Areas of Traps

In a study of the dispersal of marked male sweetpotato weevils *Cylas formicarius* (F.), and using plastic funnel traps with 1 mg sex pheromone, Miyatake et al. (2000) placed traps in eight directions, and at distances of 10, 20, 50, 100, and 200 m, from the release point. However, Yasuda and Sugie (1990) estimated that the radius of the circular attraction area of a trap (area of 30% recapture) is about 50 m. According to Fig. 52 in Yasuda (1998), the radius of 60% recapture is less than 30 m. (The distribution of the attraction rate around a trap might be a normal distribution or a distribution with larger kurtosis. Therefore, how can the radius of the “attraction area” be determined?) If we use a trap site of 10 or 20 m from the release point, the attraction areas of traps placed by Miyatake et al. (2000) at sites near the release point are overlapping, and many males might be attracted by two or more traps. Thus such traps might attract more individuals when they are in an isolated place, leading to an overestimation of the dispersal range.

If traps were distributed in a lattice pattern, the effect of the overlap of traps can be reduced to a negligible level. If individually marked insects are released from many points of the lattice, reduction of the effect is better. Therefore it is recommended that a lattice-pattern arrangement of traps be used. However, since many data are taken if traps are arranged along four or eight directions to estimate the dispersal range, a method that reduces the effect of overlap of attraction areas is described hereafter.

Fig. A shows an example of the effect of overlap of attraction areas. Individuals in the striped area would be attracted to two traps. Therefore, we must calculate the area of half of the striped area (double stripes) and subtract this from the area of the circle. In Fig. A, the distance between the two traps, and the radius of the attraction area, are $2a$ and R , respectively. As $\theta = \cos^{-1}(a/R)$, θ can be calculated when R is known. The area of the triangle ABC of Fig. A is $[2\sqrt{R^2 - a^2} \times a]/2$. Then half of the striped area can be calculated by $[\pi R^2 \times 2\theta/(2\pi)] - [\sqrt{R^2 - a^2} \times a]$. This area must be subtracted from the attraction area of a trap, πR^2 , to obtain the true attraction area.

When this procedure is carried out for data from Miyatake et al. (2000), a smaller value for dispersal distance is obtained (Fig. B). Although Miyatake et al. (2000) set traps along eight directions on circles of which the radii were 10, 20, 50, 100, and 200 m from the single release point, data for 10 m are omitted because the attraction areas of three or more traps overlap at 10 m points.

Figure A. Method to estimate overlapping area (striped area) of attraction of two traps.

There is a dilemma in applying these models. If trap efficiency is high, these models cannot be applied since δ is influenced by the mortality caused by traps, whereas if trap efficiency is low, the spatial distribution cannot be estimated with sufficient precision. This dilemma can be solved by a uniform placement of traps. If traps are placed uniformly in a lattice pattern, the mortality caused by traps is constant, and hence δ will be kept constant irrespective of trap efficiency.

4.4. Empirical Distributions

The models described above, being based on clear assumptions such as random diffusion and constant mortality, do not always fit the data sufficiently well. The heterogeneity among individuals used to calculate the diffusion coefficient, along with the spatial and temporal heterogeneity, may be one of the causes of such discrepancy. A promising approach for incorporating the heterogeneity of the diffusion coefficient is to assume that the population consists of two groups with different D , as seen in Inoue (1978) and Cronin et al. (2000). An actual population may sometimes consist of many groups that have different tendencies of dispersal. At present, however, there is no simple theoretical model to describe such complicated situations. Therefore, in such cases, empirical equations will still be useful for

describing the dispersal of individuals.

Taylor (1980) and Turchin (1998) pointed out the usefulness of an empirical equation to describe the number of recaptures, $\phi(r)$, in a trap placed at a distance r :

$$\phi(r) = \lambda r^{-\varepsilon} \exp\left[-(r/\beta)^\gamma\right] \quad (48)$$

where β , λ , ε , and γ are constants. Several empirical equations are given by special cases of equation 48. If $\varepsilon = 0$ and $\gamma = 2$, we obtain a half-normal distribution (Itô and Miyashita 1965):

$$\log_e[\phi(r)] = a - br^2 \quad (49)$$

where $a = \log_e(\lambda)$ and $b = 1/\beta^2$. If $\varepsilon = 0$ and $\gamma = 1$, we obtain an exponential distribution (Kettle 1952):

$$\log_e[\phi(r)] = a - br \quad (50)$$

where $a = \log_e(\lambda)$ and $b = 1/\beta$. If $\varepsilon = 0$ and $\gamma = 0.5$, we obtain the equation used by Wallace (1966):

$$\log_e[\phi(r)] = a - b\sqrt{r} \quad (51)$$

where $a = \log_e(\lambda)$ and $b = 1/\sqrt{\beta}$. Several theoretical distributions are also described by equation 48. The instantaneous distribution of dispersing individuals, equation 35, corresponds to the case of $\gamma = 2$ and $\varepsilon = 0$. The cumulative distribution under random dispersal, equation 46, corresponds to the case of $\gamma = 1$ and $\varepsilon = 0.5$ of equation 48. Taylor (1978) compared the descriptive ability of these empirical equations, and showed that Wallace's equation (equation 51) is most preferred. Plant and Cunningham (1991), in analysing the dispersal of sterile Mediterranean fruit flies, also concluded that equation 51 is most preferred.

The parameters such as a or b of the above equations cannot readily be interpreted in biological terms. Several statistics will be more useful than the parameters themselves for describing the dispersal ability of individuals. Hawkes (1972) suggested that "mean dispersal distance" be used. For equation 48, the statistic is calculated by

$$\bar{r} = \frac{\int_0^{\infty} 2\pi r^2 \phi(r) dr}{\int_0^{\infty} 2\pi r \phi(r) dr} = \beta \Gamma\left(\frac{3-\varepsilon}{\gamma}\right) \bigg/ \Gamma\left(\frac{2-\varepsilon}{\gamma}\right) \quad (52)$$

where Γ indicates the gamma function. In the case of equation 51, for example, we obtain $\bar{r} = 20/b^2$ from equation 52. The median dispersal distance, $r_{0.5}$, i.e. the radius of a circle that encloses 50% of the individuals, will be another useful statistic for the description of the dispersal ability of individuals (Turchin and Thoeny 1993). This statistic is obtained by numerically solving the equation

$$\frac{\int_0^{r_{0.5}} 2\pi r \phi(r) dr}{\int_0^{\infty} 2\pi r \phi(r) dr} = 0.5 \quad (53)$$

Fig. 6 is an example of fitting equation 51 to data from male sweetpotato weevils. For simplicity, linear regression was used to estimate b , 0.342. Hence the estimate of mean dispersal distance is obtained by $20/0.342^2 = 171$ m. The median dispersal distance was estimated by a numerical calculation to be 115.2 m. The mean dispersal distance is much larger than the median dispersal distance, since the form of $\phi(r)$ is highly leptokurtic, i.e. L-shaped. In summarizing the characteristics of the dispersal curve, the median dispersal distance will generally be preferred over the mean dispersal distance.

5. BEHAVIOURAL ECOLOGY: SEXUAL COMPETITIVENESS OF RELEASED STERILE MALES IN THE FIELD

The quality of sterile males to be released is the most important element in the success of an AW-IPM programme integrating the SIT. Although quality includes survival rate, dispersal ability, and other aspects that relate to the vigour of released males, the most attention must be paid to the decline of sexual competitiveness (Parker, Vreysen et al., this volume; Lance and McInnis, this volume; Vreysen, this volume).

Even when the survival rate or dispersal ability of mass-reared and sterilized males is lower than those of wild males, an increase in the frequency of mass releases or the number of release points can compensate for these deficiencies. However, if long-term mass-rearing creates a strain in which released males have a different courtship behaviour (pattern of vibration, courtship sound, etc.) than that of the wild males and therefore are not accepted by wild females, an increase in the number of released sterile males cannot compensate for this deficiency.

Figure 6. Distance-density curve of number of marked adult sweetpotato weevils recaptured in traps. Equation 51 is fitted by linear regression. (Data from Miyatake et al. 2000.)

This is a subject of behavioural ecology or sociobiology. Although sexual behaviour and behavioural changes in mass-reared strains have been studied in several species that are targets of the SIT (e.g. Prokopy and Hendrichs 1979; Sivinski et al. 1989), probably the only AW-IPM programme releasing sterile insects, which incorporated behavioural ecology as an important aspect throughout implementation, has been the melon fly eradication programme in Okinawa, which was completely successful (Yamagishi et al. 1993).

5.1. Effects of Long-Term Mass-Rearing more Important than the Effects of Sterilization

The effects of sterilization, e.g. by X- or γ -radiation, are often regarded as an important source of the decline of vigour and/or sexual competitiveness of males (Bakri et al., this volume). However, experiences accumulated during the Okinawa melon fly programme suggest that changes in sexual behaviour of released males due to long-term mass-rearing are much more important than the effects of sterilization (Itô et al. 1993; Parker, Vreysen et al., this volume). The inadvertent selection of strains with rapid development and early fecundity produces reduced longevity and other genetic changes in the selected strain (Miyatake 1996, 1998; Shimizu et al. 1997). The high-density rearing of adults in small cages can lead to the selection of strains in which reared males do not perform the same sexual behaviours as wild males in the field.

5.2. Competitiveness must be Measured in the Field

In many AW-IPM programmes integrating the SIT, sexual competitiveness has been measured in the laboratory, e.g. observing wild females mating with marked wild males and mass-reared and/or sterilized males in a cage (Fried 1971; Parker, Vreysen et al., this volume). However, conditions in a laboratory cage are different from those in the field (Lance and McInnis, this volume; Vreysen, this volume). In a programme to eradicate the melon fly from Kume-zima, Okinawa (1973–1977), Iwahashi et al. (1983) measured sexual competitiveness in the field. They collected wild females from Kume-zima, the target area, and Okinawa-Hontô, the control (non-SIT) area, and examined the hatch rates of eggs laid by those females.

Haisch (1970) presented the following equation for the laboratory examination of competitiveness, c :

$$\hat{c} = \frac{H_n - H_c}{H_c - H_s} \cdot \frac{w}{1 - w} \quad (54)$$

where

w = proportion of males of wild strain among all males,

H_n = percentage egg hatch in matings between normal (wild) males and females of wild strain,

H_C = percentage egg hatch in competitive matings,

H_S = percentage egg hatch in matings between sterile males and normal females.

To use this equation in the field, Iwahashi et al. (1983) substituted percentage hatch of eggs laid by females collected in the target and control areas for H_n and H_C , respectively. H_S is 0 in the Okinawa melon fly programme. For comparison of c values while applying the SIT, or between two or more SIT areas, an estimation of variance is necessary. Iwahashi et al. (1983) presented an equation for estimating the variance of c (Box 5).

Box 5. Variance of Haisch Index of Sexual Competitiveness of Mass-Reared/Sterilized Males

In the final stage of an eradication programme that releases sterile insects, when most males collected are sterile males, $1 - w$ becomes near zero. In this stage, H_C may also become small. As c values become quite sensitive to small changes in $1 - w$ and H_C , estimation of variance is necessary. The following equation from Iwahashi et al. (1983) is recommended:

$$V(\hat{c}) = \left[\frac{w}{H_C(1-w)} \right]^2 \times \left[\frac{H_n(1-H_n)}{N_n} + \frac{H_n^2(1-H_C)}{H_C N_C} + \frac{(H_n - H_C)^2}{w(1-w)N_w} \right]$$

Here N_n and N_C are the numbers of eggs examined in the control area and the release area, respectively. N_w is the number of flies examined in the release area. For other symbols, see explanation of equation 54.

Release strain sexual competitiveness decreased from about 80% in the 5th generation after the beginning of mass-rearing to 20% in the 18th generation, during the final stage of the Kume-zima programme (Fig. 7, upper). Even at this time, high sexual competitiveness in laboratory cages was still observed (see closed triangles in Fig. 7, upper).

Soemori et al. (1980) described experiments that suggest an explanation for such a discrepancy between laboratory and field data. They released individually marked flies into cages or rooms of different sizes and recorded the mating performance. Fig. 7 (lower) shows the percentage of males that mated in relation to the volume of space available per male in the experimental area. Males of the wild strain could not mate well in a small space, whereas males of the laboratory strain performed best in these conditions.

Figure 7. Upper: Sexual competitiveness of mass-reared and sterilized male melon flies measured in the field (adapted from Iwahashi et al. 1983). Closed circles are for data from Kume-zima; the open circle is for data from another islet Kudaka-zima. Solid triangles are competitiveness values measured in laboratory cages. Vertical lines show standard deviations. (Box 5 shows the equation for variance.) Lower: Relationship between size of cage per fly and percentage of successful mating of males of mass-reared (open circles, 33–34 generations) and wild (closed circles) strains when caged together with mass-reared females. (Figure from Soemori et al. 1980, reproduced with permission.)

5.3. *Inadvertent Selection of Mate-Choice when the SIT is Applied*

In a field cage, Hibino and Iwahashi (1988) compared the mating success of males of wild and mass-reared strains. One of their results, using flies of a wild strain of Okinawa Hontô (O-males and O-females), is shown in Fig. 8 (upper). Firstly, even when courted by wild males, wild females accepted copulation in only 4 of 37 courtship trials, showing strong mate-choice by females. Secondly, O-females never accepted (0/46) courtship from mass-reared (R) males. Other experiments showed similar results (Itô et al. 1993). When Hibino and Iwahashi (1988) carried out these experiments, melon flies on Okinawa Hontô, as a result of the application of the SIT, were near extinction. Therefore O-females had been subjected to strong selection pressure by the released sterile males.

Hibino and Iwahashi (1991) carried out similar experiments using wild flies taken from Ishigaki-zima, where a programme releasing sterile insects had not yet begun. Fig. 8 (lower) shows that females of Ishigaki wild flies (I-females) accepted courtship from R-males (4/57) as well as from I-males (3/51).

There are two possible explanations for the difference in behaviour between flies on the two islands: (1) O-flies and I-flies had genetically different courtship and acceptance characters, and the courtship character of R-males was more similar to that of I-males, and (2) the "SIT-resistance hypothesis" — the wild female population was initially heterogeneous and contained individuals which accepted a broad range of male courtship characters (McInnis et al. 1996; Whitten and Mahon, this volume). However, females that accepted sterilized R-male courtship could not produce progeny. Thus, under strong selection pressure from the SIT, a female genotype that accepted the courtship of mass-reared males may have become extinct. Next Hibino and Iwahashi (1991) conducted an experiment on mate choice of O-females between O- and I-males. O-females then accepted courtship by I-males (1/19) as well as by O-males (1/14), indicating that the second explanation is correct, thus demonstrating for the first time the evolution of mate-choice in insects.

5.4. *How Can the Spread of an SIT-Resistant Strain be Overcome?*

How can the problem of an increase in the number of females that do not accept courtship from mass-reared males be overcome? Besides the obvious approach of establishing a new colony from the target population, and/or cryopreserving the embryos of recently colonized strains (Parker, Mamai et al., this volume; Whitten and Mahon, this volume), as well as improving the competitiveness of sterile males (Shelly and McInnis 2001; Pereira et al., this volume; Vreysen, this volume), an additional answer is provided by the development of the logistic population model (e.g. equation 8).

Tsubaki and Bunroongsook (1990) conducted a simulation experiment to estimate the effect of the change in mate-choice, using a logistic model (equation 8) incorporating two strains. They showed that the effect of a reduction in mating competitiveness of mass-reared and sterilized males is much more important than the effect of a change in female mate-choice. Their simulation also indicated that releases of two or three times more sterile males than would be released in a non-mate-choice

model can eradicate a target population that has a change in female mate-choice. In the Okinawa melon fly programme integrating the SIT, an increase in the number of released sterile males over that first planned for release (based on an estimate of the wild fly density) resulted in complete eradication of the population.

The incorporation of recent ideas in behavioural ecology, as well as in population ecology, into the SIT is indispensable for its success. It is recommended that Krebs and Davies (1993) be consulted on the basic concepts of this subject.

Figure 8. Upper (a): Mate-choice by wild female melon flies collected on Okinawa Hontô (O-females) for wild males (O-males) or males of mass-reared strain (R-males). Arrows indicate the direction in which the behavioural sequence proceeds. Upper numerals indicate the frequencies of the transitions when O-females encountered O-males, lower numerals indicate cases when O-females encountered R-males (adapted from Hibino and Iwahashi 1988). Lower (b): Mate-choice by wild female melon flies collected on a non-SIT island Ishigaki-zima (I-females) for Ishigaki wild males (I-males) or mass-reared males (R-males). (Figure from Hibino and Iwahashi 1991, reproduced with permission.)

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