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Determination of the sterile release rate for stopping growing age-structured populations

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ABSTRACT
A freely-growing age-structured population was modeled for growth and control by sterile male releases. Equilibrium populations yield critical sterile male release rates that would hold the population at equilibrium. It is shown here that these rates may be different from the release rates required to stop a growing population and bring it to an equilibrium. A computer simulation was constructed of this population and a parameter sensitivity analysis graphed the effects on the required sterile male release rate of fertility, mating delay in adult females, net juvenile survivorship, three adult survivorship curves, the time spent in the juvenile stages, and total life span. The adult survivorship curves had the greatest effect on the required sterile release rate for population elimination. The required release rate was also determined for *Ceratitis capitata* (Wiedemann) using survivorship and fertility data from a laboratory strain. The concepts of over-flooding ratio and release ratio were discussed and quantified for the cases above.

1. Introduction

The sterile insect technique (SIT) has been used successfully to control or eliminate a variety of insect pest species, mostly dipteran, for over half a century (Klassen and Curtis 2005). However, in the models of SIT the predicted sterile release rates required for eradication of a pest population (critical release rates) have often underestimated the release rates that were found to be necessary in control operations in the field (Knipling 1982), and the reasons for this have not always been apparent. Most of the models used for this have estimated necessary sterile release rates from equilibrium models, because critical release rates are easy to find at equilibrium (e.g., Klassen & Creech 1971; Miller & Weidhaas 1974; Prout 1978; Barclay & Mackauer 1980).

The derived statistic of most interest to the pest control manager is the critical sterile release rate (i.e., the release rate that maintains the pest population at an equilibrium) (Knipling 1979). There appear to be three cases to consider in determining the critical sterile release rate: one is for species that are univoltine and have one relatively short reproductive period each year and in which generations do not overlap; another is for populations at equilibrium as a result of density-dependent population regulation, in which generations may or may not overlap; the third is for multivoltine species that reproduce more or less continuously during the growing season and are not yet under strong density-dependent regulation. The distinction here is

that for univoltine species, the size of the existing sterile population following a single release is the size of the release, perhaps prorated by survivorship until mating, whereas in the case of continuous (or daily) growth, each daily (or periodic) release simply adds to the population of sterile males that are still alive from previous releases. This paper explores the latter situation in which growth is more or less continuous during the growing season and generations overlap.

Another statistic of major interest is the over-flooding ratio, which has long been a measure of the ratio of sterile males to wild males (e.g., Steiner et al. 1965) and is sometimes thought of as the size of sterile releases compared with the wild population, which is approximately valid in species with short reproductive seasons and non-overlapping generations. In species in which the reproductive period is protracted, often extending throughout the warm season in temperate climates, an ambient population of sterile males exists following several releases and the over-flooding ratio is not equal to the periodic release rate divided by the wild male population size and must be estimated by sampling or some other means. The over-flooding ratio is here called φ.

The other ratio to be defined is the release ratio, defined as the ratio between the periodic sterile male releases and the wild male sub-population, and it is here called ρ. In the case of species with one short reproductive period each year, the two (φ and ρ) are approximately equal. Simulations of such populations

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yield the same sterile release rate required to stop population growth and then hold the population at equilibrium as that predicted by the model at equilibrium (unpublished). In freely-growing populations with overlapping generations, the release ratio and the over-flooding ratio are not equal.

The paper of Barclay et al. (2014) derived critical control rates that are required to hold an age-structured population at an unstable equilibrium, thus separating success (if the control rate is increased above the critical rate) from failure (if the control rate is decreased below the critical rate). The present paper builds on the previous publication on control of age-structured populations and shows that the equilibrium statistics derived, while important, are not sufficient to allow calculation of the appropriate values of the sterile release rates and over-flooding ratios required to stop a growing age-structured population by the sterile release technique. The "required sterile release rate", r', is defined here to be the value of the sterile male release rate, r, necessary to stop a population growing freely in a stable-age distribution (i.e., the growth rate eventually becomes zero with $r = r'$). For clarity, and to establish an upper limit to r', only populations are considered that are undergoing density-independent growth, in which density-dependence has not yet started to influence the growth rate, as may be the case with many spot infestations.

The methods developed here are made specific in an example using Mediterranean fruit flies, *Ceratitis capitata* (Wiedemann) (Diptera: Tephritidae) and use four methods presented below to estimate the required sterile male release rate, r'. These four estimation methods emerge from a simulation of an age-structured population and involve five further ratios defined to summarize the results and simplify application of them to real pest populations.

The effects of two aspects of sterile male quality are considered on the critical release rate and the required release rate of sterile males. They are (1) unequal survivorship of wild and sterile males, and (2) unequal mating competitiveness of wild and sterile males. Both have been commonly observed in sterile release control programs (Calkins & Parker 2005) and continue to plague some programs in spite of improvements in rearing techniques. Both unequal survivorship and unequal mating competitiveness usually reduce the effectiveness of SIT and require increased numbers needed to be released (Barclay 2001; Calkins & Parker 2005; Barclay & Vreysen 2011).

2. Modeling approach

2.1. Development of the model

Barclay et al. (2014) modeled a population of a monogamous species with distinct egg, larval, pupal and adult stages, with a daily time step, survivorship that was age-specific and with no density-dependent population regulation. Eggs are assumed to take ke days from oviposition to hatch, and only eggs that eventually hatch are included, so there is no daily mortality tallied. The numbers of eggs in the ith age class at time t is $E_{i,t}$, and as there is no egg mortality, $E_{i+1,t+1} = E_{i,t}$ for $1 \leq i < ke$. Eggs of age ke hatch into larvae, so that $L_{1,t+1} = E_{ke,t}$.

Larvae require kl days for development and the number of larvae in the ith larval age class at time t is $L_{i,t}$ for $1 < i \leq kl$. Larvae survive from age i to age $i+1$ at a rate q_i, so that $L_{i+1,t+1} = q_i L_{i,t}$ for $1 \leq i < kl$. Similarly pupae require kp days for development and the number of pupae in the ith pupal age class at time t is $P_{i,t}$ for $1 \leq i \leq kp$. Pupae survive from age i to age $i+1$ at a rate u_i, so that $P_{i+1,t+1} = u_i P_{i,t}$ for $1 \leq i \leq kp$. Also, the first pupal age class is $P_{1,t+1} = q_{kl} L_{kl,t}$.

There are five categories of adults, also referred to as adult population components, as well as the three juvenile components, eggs, larvae and pupae. The five adult population components at age i and at time t are as follows: virgin females ($V_{i,t}$), females mated to fertile (wild) males ($F_{i,t}$), females mated to sterile males ($G_{i,t}$), wild males ($M_{i,t}$) and sterile males ($N_{i,t}$). The virgin adult females are assumed to become receptive to male mating advances at age τ days, and all of age τ mate on that day and immediately start ovipositing. Adult virgin females, fertile-mated females and sterile-mated females all survive at a rate w_i from female age i to age $i+1$, except that mated females start on their day 1 at survivorship $w_{1+\tau}$ because eclosion occurred τ days before. Wild males survive at a proportional rate y_i from age i to $i+1$ and sterile males correspondingly survive at a rate z_i. Thus, age classes i at time t survive as follows: $V_{i+1,t+1} = w_i V_{i,t}$; $F_{i+1,t+1} = w_{i+\tau} F_{i,t}$; $G_{i+1,t+1} = w_{i+\tau} G_{i,t}$; $M_{i+1,t+1} = y_i M_{i,t}$; $N_{i+1,t+1} = z_i N_{i,t}$. These equations are also given in the Appendix, and Table 1 gives a list of variable and parameter definitions.

In the absence of sterile male releases and with no density-dependent population regulation, the population will eventually assume a stable-age distribution with all population components increasing by a certain multiple (λ_1) every day. If sterile males are being released, then there is a release rate, r^*, at which the population will not increase further and a steady state (equilibrium) will be attained. This equilibrium is unstable in the absence of density-dependent regulation and it is of interest only inasmuch as it separates success (if the actual release rate, r, is greater than r^*) from failure (if the sterile release rate is less than r^*). This sterile male release rate, r^*, is called the critical release rate and it is what is calculated in standard models of SIT (e.g., Berryman 1967; Ito 1977; Barclay & Mackauer 1980; Barclay 2001; Barclay et al. 2014).

Table 1. List of parameters and variables of the model with definitions.

Parameters	Definition
ke	Number of days from oviposition to egg hatching
kl	Number of days from egg hatching until pupation
q_i	Survivorship of larvae from age i to age $i+1$.
kp	Number of days from pupation to adult eclosion
u_i	Survivorship of pupae from age i to age $i+1$.
jd	Number of days spent in the juvenile stages ($= ke + kl + kp$).
σ	Maximum longevity from oviposition to death of adults.
h_x	Hatchability of eggs from adults of age x.
l_x	Survivorship of adults from age x to age $x+1$.
m_x	Fecundity of adult females of age x.
r	Number of sterile males released each day (or time period).
r^*	Critical sterile release rate that establishes an equilibrium.
r'	Required sterile release rate that stops a growing population.
r_p^*	Provisional critical release rate, being r^* calculated at the onset of sterile male releases.
w_x	Survivorship of adult females from age x to age $x+1$.
y_x	Survivorship of wild adult males from age x to age $x+1$.
z_x	Survivorship of sterile adult males from age x to age $x+1$.
γ	Net juvenile survivorship from egg to adult.
μ	Mean daily fertility (mdf).
τ	Age of adult females at mating and first oviposition.
α	The index r' / r_p^*, the required sterile release rate / the provisional critical release rate.
β	The index r' / M_0, the required sterile release rate / initial value of M.
φ	"The number of sterile males in the wild" divided by "the number of wild males"
φ^*	Critical value of φ; $\varphi^* = N_e / M_{er}$.
ρ	The ratio of the sterile males released divided by the existing wild male population.
ρ^*	Critical value of ρ.

Variables	Definition
$E_{i,t}, L_{i,t}, P_{i,t}$	Values of eggs, larvae and pupae of age i and at time t.
F, G,	Fertile-mated and sterile-mated adult females
V	Virgin adult females
M, N	Fertile and sterile adult males
$F_{i,t}, G_{i,t}, V_{i,t}, M_{i,t}, N_{i,t}$	Values of F, G, V, M and N of age i at time t.
Fe, Ge, Ve, Me, Ne	Equilibrium values of F, G, V, M and N.
F_1, G_1, V_1, M_1 and N_1	Numbers in first age classes of F, G, V, M and N.
F_T, G_T, V_T, M_T, N_T	Total numbers of F, G, V, M and N ($=$ sum of age classes).
M_0, F_0	Total adult males and mated females just prior to the onset of sterile releases

Operators	
Σ_0^i	Sum of the subscripted expression from 0 to i.
Π_0^i	Product of the subscripted expression from 0 to i.

To derive the critical release rate, r^*, it will be assumed that the population is at its unstable equilibrium and that sterile males are being released at a rate $r = r^*$. Since all mortality is assumed to be independent of the density of any of the population components, net larval survivorship from age one to kl is obtained from the following equation: $L_{kl} = q_{kl-1} L_{kl-1} = q_{kl-1}$

$q_{kl-2} L_{kl-2} = \ldots = q_{kl-1} q_{kl-2} q_{kl-3} \cdots q_1 L_1 = \Pi_1^{kl-1} q_i L_1$, where $\Pi_1^{kl-1} q_i$ is the product of the larval survivorships from $i = 1$ to $kl - 1$, and thus represents net larval survivorship. Similarly, net pupal survivorship is $\Pi_1^{kp-1} u_i$. The net adult survivorships are as follows. For virgin females, there are only τ age classes before they mate, so the net survivorship is $\Pi_1^{\tau-1} w_{i \cdot i}$. For fertile-mated and sterile-mated females, the net survivorship is $\Pi_1^{kf-1} w_{i+\tau}$. For wild males, the net survivorship is $\Pi_1^{km-1} y_i$ and for sterile males it is $\Pi_1^{km-1} z_i$. By the same logic as above it can also be shown that the size of the jth adult age class at equilibrium is computable by replacing kf with j for mated females and by replacing km with j for males. Thus the jth age class of fertile-mated females is $F_j = F_1 \Pi_1^{j-1} w_{i+\tau}$, for wild males it is $M_j = M_1 \Pi_1^{j-1} y_i$, and for sterile males is $N_j = N_1 \Pi_1^{j-1} z_i$. This allows the calculation of totals for each adult population component as shown below.

The sum of the virgin adult females is $\Sigma_1^{\tau} V_i = V_1 + V_2 + \cdots + V_{\tau} = w_0 V_1 + w_1 V_1 + w_1 w_2 \quad V_1 + \cdots + \Pi_0^{\tau} w_i \ V_1 = \Sigma_1^{\tau} \Pi_0^i w_j \ V_1$, where j goes from 0 to i and i goes from 1 to τ and $w_0 = 1.0$. The sum of the fertile-mated females is $\Sigma_1^{kf} F_i = F_1 + F_2 + \cdots + F_{kf} = F_1 + w_{1+\tau} F_1 + w_{1+\tau} w_{2+\tau} F_1 + \cdots + \Pi_1^{kf-1} w_{i+\tau} \ F_1 = \Sigma_1^{kf} \Pi_0^i w_{i+\tau} F_1$ where j goes from 0 to i and i goes from 1 to kf. Similarly, the sum of the wild males is $= \Sigma_1^{km} M_i = \Sigma_1^{km} \Pi_0^i y_j M_1$ and the sum of the sterile males is $\Sigma_1^{km} N_i = \Sigma_1^{km} \Pi_0^i z_j \ N_1$.

Two derived statistics required for making a link between the adult components and the first egg age class and also in determining the critical release rate are the net survivorship from eggs to adult eclosion, γ, and the mean daily fertility (mdf), μ, (called "mean fertile eggs per fly-day" by Carey 1989):

$$\gamma = \left(\prod_1^{kl-1} q_i \right) \left(\prod_1^{kp-1} u_i \right) \tag{2.1}$$

$$\mu = \sum_1^{\infty} l_x \, m_x \, h_x \Big/ \sum_1^{\infty} l_x, \tag{2.2}$$

and where l_x, m_x and h_x are the survivorship and fecundity of fertile-mated females and hatchability of their eggs, respectively, from age x to age $x+1$ (Carey 1989). The equation for the critical sterile release rate, r^*, (Barclay et al. 2014) is then obtained by solving the five adult equations at equilibrium simultaneously for r in terms of Fe, the fertile-mated female subpopulation (see Appendix for equilibrium equations). In reality the equation for Ge can be ignored as it is simply a hitchhiker on the system of equations and can be predicted from the other four equations. Doing the appropriate substitutions and simplifying yields the critical

value of r, r^*

$$r^* = \gamma\mu \, Fe \left[\sum_0^{km-1} \prod_0^i y_j \right] \left\{ \gamma\mu \left[\sum_0^{kf-1} \prod_0^i w_j \right] \left(\prod_0^\tau w_j \right) - 1 \right\} \Big/ \left[\sum_0^{km-1} \prod_0^i z_j \right].$$
$$(2.3)$$

The product $\Pi_0^i w_j$ is the product of the adult survivorships (w_j) from $j = 0$ to i and the sum $[\Sigma_0^{km-1} \Pi_0^i y_j]$ is the sum from $i = 0$ to $km-1$ of the products of y_j from $j = 0$ to i, with w_0 and y_0 both equal 1.0. The sums and products in brackets in Equation (2.3) refer to the sums of survivorships of wild males, wild females and sterile males, respectively. An alternative formulation using the wild male equilibrium, Me, instead of Fe is given as

$$r^* = Me \left\{ \gamma\mu \left[\sum_0^{kf-1} \prod_0^i w_j \right] \left(\prod_0^\tau w_j \right) - 1 \right\} \Big/ \left[\sum_0^{km-1} \prod_0^i z_j \right]$$
$$(2.4)$$

using the equation for the wild male equilibrium, Me, given in Equation (A4), $Me = [\Sigma_0^{km-1}\Pi_0^i y_j]$ $[\gamma\mu \, Fe]$, and substituting it into (2.3). Using this formulation facilitates the calculation of a first approximation to r^*, called the provisional critical release rate, r_p^*, using the total males, M_T, called M_0, just prior to the onset of sterile male releases; this form is used because mated females may be difficult to distinguish from virgin females. This release rate, r_p^* will not be correct, because Me will not equal M_0 but it may suffice as a first approximation, later to be modified.

Using (2.4), the critical daily release ratio of sterile male releases to the equilibrium wild male population, $\rho^* = r^*/Me$, is

$$\rho^* = \left\{ \left[\sum_1^{kf-1} \prod_1^i w_j \right] \left(\prod_1^\tau w_j \right) \gamma\mu - 1 \right\} \Big/ \left[\sum_1^{km-1} \prod_1^i z_j \right].$$
$$(2.5)$$

In addition, the critical over-flooding ratio, $\varphi^* = Ne/Me$, is

$$\varphi^* = \left[\sum_1^{kf-1} \prod_1^i w_j \right] \left(\prod_1^\tau w_j \right) \gamma\mu - 1, \qquad (2.6)$$

where Ne is the equilibrium number of sterile males.

Note that the fraction that ρ^* is of φ^* is

$$\rho^*/\varphi^* = 1 \Big/ \left[\sum_1^{km-1} \prod_1^i z_j \right]. \qquad (2.7)$$

2.2. Simulation and sensitivity analysis using the population equations

In this section we dispense with the assumption that the population is at equilibrium. A simulation was developed to determine the sterile release rate required to stop a growing population and yield the equilibrium (i.e., zero growth). The equations to describe each daily time step in each life stage were programmed in FORTRAN. Control was started when the stable age distribution (SAD) of an increasing population was attained. To do this, the simulation was run for 2000 simulated days with no sterile releases, but with re-normalization of all life stages every 50 days to prevent computer overflow. Re-normalization was achieved by multiplying every age class of every population component ($E_T + L_T + P_T$ (= total juveniles), F_T (= total adult females mated to fertile males), V_T (= total virgin females), and M_T (= total fertile males)) by 1.0 / F_T. Thus, total fertile-mated females became 1.0 and all age classes of all other stages were multiples of this, so that elements in the population retained the same numerical relationships to each other.

The second part of the simulation was to initiate and maintain daily sterile male releases on this increasing population. Once sterile releases began, no further re-normalization was done. An initial (provisional) estimate was made of the critical release rate from (2.4) using M_0 instead of Me. The release rate, r, was then established in an iterative loop starting at zero and ending many times above the estimated critical rate. This was done 40,000 times in small steps to ensure accuracy. In each run two values of F_T were noted, one at 30 days after the start of sterile releases, F_{T1}, and the other at 200 days (F_{T2}). The criterion for having found a value close to the real value, r', was that the quotient of F_{T1} and F_{T2} from a run not differ proportionally by more than a small interval, usually between 0.9 and 1.1 between days 30 and 200 during the run (i.e., $0.9 < (F_{T1} / F_{T2}) < 1.1$). Each such determination resulted in one point on the output graphs. In some cases, instability of the model at equilibrium resulting from long durations of the juvenile or adult stages prevented such accurate determination and lesser accuracy had to be accepted.

A parameter sensitivity analysis was done on several life history features with the measured variable being required sterile release rate, r', to achieve equilibrium. Each of the parameters for the sensitivity analysis was iteratively varied keeping the other parameters constant at their default values. Unfortunately this procedure does not allow evaluation of interactions between parameters; however the number of cases would be prohibitively large if parameters were varied orthogonally. The features that were varied were as follows: (1) fecundity, f, per mated female; for this purpose all
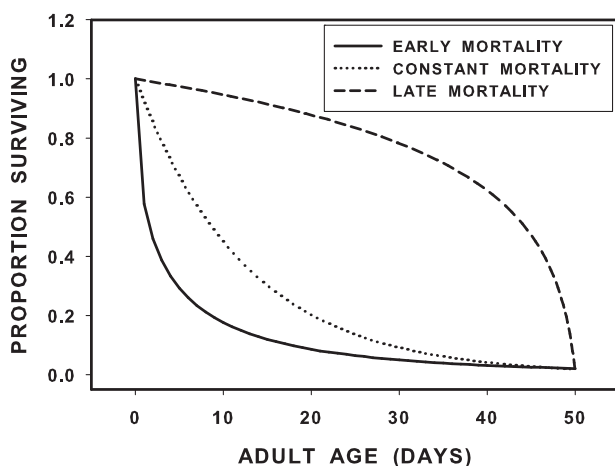
Figure 1. Three hypothetical adult survivorship curves (adapted from Slobodkin 1961) in which survivorship is high until late in adult life (top curve), survivorship is a constant proportion of those remaining alive (middle curve) and survivorship is low near the beginning of adult life (bottom curve). Reprinted with permission from the Annals of the Entomological Society of America.

mated females of all age classes had the same daily fecundity and mating occurred three days after adult emergence. Fecundity was varied from 2 to 20 in steps of 2. For all other features, a default value of $f = 10$ was used. (2) Delay in mating of emerged adult females (τ days). The 8 values of τ were 1 to 8; the default value of τ was 3. (3) Net juvenile survivorship, γ (values were 0.4, 0.6 and 0.8; the default was 0.6). (4) Adult survivorship curves (Figure 1), using an approximation to three of the four curves given by Slobodkin (1961). The default was curve 2, the exponential curve. (5) The duration, jd days, spent in the juvenile stages (using 100 days for the total life span). Values for jd were 20, 30, 40, 50; default was 40. (6) Total life span, σ. Values were 50, 75 and 100 days; the default was 100. The use of the SAD, with the initial growth period of 2000 days, can be seen as a null model. Any initial condition is arbitrary, but the SAD is an easily definable condition and is useful as a start. In many situations it might be a reasonable approximation to reality. Such may be the case in a spot infestation that goes unnoticed for several weeks or months or in a freely-growing established population that has been growing for some time.

2.3. The use of demographic data in sterile release programs and an example

As an example of the above methodology, the simulation was parameterized for a cohort life table study of the Mediterranean fruit fly, *C. capitata*. In a laboratory study of three tephritid species, Vargas et al. (1984) found that the total pre-adult mortality of eggs, larvae and pupae of *C. capitata* was 31% (i.e., $\gamma = 0.69$). The lengths of the egg, larval and pupal stages were about

2.3, 7.2 and 9.5 days long, totaling about 19 days ($ = jd$ of condition (v) above). The authors also gave a survivorship curve from day 1 (oviposition) to about day 95, when only 1% of the cohort was still alive. The greatest daily mortality was in the larval stage, followed by older adults after day 50. Fecundity and egg hatchability curves were given from day 28, when the first oviposition occurred by mated adults, until day 95, by which time oviposition had almost completely ceased. The fertility and survivorship data were derived from the graphs of Vargas et al. (1984). The mdf was computed with the sum being taken over all ages of all adult females, and l_x, m_x, and h_x are, respectively, the female survivorship to age class x, the fecundity of age-class-x adults and the hatchability of their eggs; the value calculated for mdf was $\mu = \Sigma_1^{kf} l_x \, h_x m_x / \Sigma_1^{kf} l_x = 7.78$ for *C. capitata* using the Vargas et al. (1984) data. The period between adult female emergence and the onset of oviposition, τ, was about eight days. The population was grown without sterile releases for 2000 days, by which time it had achieved a SAD, and then sterile males were released onto it.

2.4. Unequal quality of wild and sterile males

Calkins and Parker (2005) list 12 features affecting quality of factory-reared sterile male insects. These are all potentially important in causing differences in wild and sterile male performance, some of which can be grouped together and considered under single parameters. Two features are considered here: (1) unequal survivorship of wild and sterile males, and (2) unequal competitive mating ability of wild and sterile males.

(1) Unequal survivorship of wild and sterile males $z_i \neq y_i$

The daily survivorships of wild and sterile adult males are given as y_i and z_i, respectively, in Section 2.1 and these occur in Equation (2.3) defining r^*, the critical release rate. If $z_i = y_i$, then Equation (2.3) simplifies. The extent to which r^* differs if $z_i \neq y_i$ is given by the following quotient:

$$\eta = \left[\sum_1^{km-1} \prod_1^i y_j \right] \bigg/ \left[\sum_1^{km-1} \prod_1^i z_j \right]. \qquad (2.8)$$

If r_e^* is the value of r^* when $z_i = y_i$, and if r_u^* is the value of r^* when $z_i \neq y_i$, then

$$r_u^* = \eta r_e^*. \qquad (2.9)$$

(1) Unequal competitive mating ability of wild and sterile males

Unequal competitive mating ability is usually designated by the parameter c (Barclay 2005), and c is applied to the sterile male population size. As sterile males are usually less competitive, c is usually less than one. If we apply c to $N_{T,t}$ in the equations for $F_{T,t}$ and

$G_{T,t}$ in Equation (A4), we obtain an equation for $F_{T,t}$ of

$$F_{T,t} = \left[\sum_1^{kf-1} \prod_1^i w_j \right] \left\{ \left(\prod_1^\tau w_j \right) \gamma \mu \ F_T \left[M_{T,t}/(M_{T,t} + cN_{T,t}) \right] \right\}. \tag{2.10}$$

Substituting the expressions for $M_{T,t}$ and $N_{T,t}$ given in the appendix gives the value of r^* to be

$$r^* = \gamma \mu \ Fe \left[\sum_1^{km-1} \prod_1^i y_j \right] \left\{ \gamma \mu \left[\sum_1^{kf-1} \prod_1^i w_j \right] \left(\prod_1^\tau w_j \right) - 1 \right\} \Big/ c \left[\sum_1^{km-1} \prod_1^i z_j \right], \tag{2.11}$$

which is $1.0/c$ times the value given in Equation (2.3), so that the value of r^* is simply inflated by a value $1.0 / c$.

3. Modeling results

3.1. Numbers at the stable age distribution and the population equilibrium

The total numbers of the two population components (virgin females (V_T) and males (M_T)) in the SAD are shown in Figure 2, middle column of panels (panels B, E, H, K, N and R) with F_T, V_T, and M_T, having been divided by F_T. Daily growth rates (λ_1) are shown in the left-hand column of panels of Figure 2 (panels A, D, G, J, M and Q). Total population component numbers at equilibrium (referred to as "component equilibrium" in Figure 2), excluding sterile males, Ne, but including also sterile-mated females (Ge) which are part of the wild population, are shown in Figure 2, right-hand panels (panels C, F, I, L, P and S), with Fe again having been normalized to 1.0. The equilibrium ratios are very different from those in the SAD, with total males being usually less than 2.5 times the total mated females in the SAD examples shown, whereas total males ranged from above 15 to almost 250 times the total mated females for the corresponding equilibrium populations. This discrepancy is significant in comparing the value of r, r', required to stop a growing population with the provisional critical value of r, r_p^*, at any given value of F_T. From watching detailed output during some runs, it appears that once sterile male releases begin, F_T usually changes very little as increasing numbers of virgin females mate with sterile males and enter the G component, but the virgin females (V), the sterile-mated females (G) and the wild males (M) continue to increase for some time until the equilibrium configuration is achieved.

3.2. Release and over-flooding ratios

Five derived measures of sterile male release rates obtained from the parameter sensitivity analyses are given below.

(1) The ratio, α, of the required sterile release rate, r', divided by the initial estimate of the provisional critical release rate, r_p^*, ($\alpha = r'/r_p^*$) remained close to 0.5 for most of the six features considered above (Figure 3; there called R'/Rp^*) except for the adult survivorship curves; α was lowest with high early adult mortality and highest with low early adult mortality. If F_T can be accurately estimated during the increase prior to the onset of sterile releases, then r' can be adequately estimated from the graphs in Figure 3. While it may appear counter-intuitive that the required release rate is less than the provisional critical release rate, this is a result of the changes in numbers of virgin females, fertile-mated females, sterile-mated females, and wild males following the onset of daily sterile male releases, as well as the fact that r^* requires Fe, but F_0 (i.e., F_T just prior to the onset of sterile releases) was all that was available. The release of sterile males yielded sterile-mated females and these increased with successive releases up to their equilibrium; at the same time, the number of fertile-mated females actually decreased slightly as both the adult males and the sterile-mated females increased. This same pattern was observed for a variety of parameter values (Figure 3).

(2) The ratio, β, of r' divided by M_T (in this case called M_0) at the first sterile male release ($\beta = r'/M_0$) varied widely, so the logarithm (base 10) was used. Values of β typically ranged from less than 10 up to a few hundred with parameter variation for most of the parameters. This measure might be used when attempting to establish an over-flooding ratio for a target population, because sampling will establish the total population size, being twice the male component, and r^*/M_0 could be calculated from (2.4), as if the system were at equilibrium, and thence r'/M_0 could be estimated initially from that. The difficulty comes in precisely estimating M_0 in a growing population, but mark-recapture estimates coupled with applying the daily population growth rate (Figure 2, left-hand panels) might suffice.

(3) The ratio of r' divided by the value of M at equilibrium (Me) after the population has been stopped gives what is suggested by the equilibrium models (Barclay et al. 2014) to be the critical value of r/M (i.e., the critical value $\rho^* = r^*/Me$) once equilibrium has finally been established.

(4) The ratio Me/M_0 (where $Me/M_0 = \beta/\rho$) gives an idea of the extra initial over-flooding ratio required to stop a growing population over that required to hold a population at equilibrium when releases are started at the provisional critical release rate of r_p^*, and when the wild males were M_0 in number. This measure also varies with the parameter values in a way similar to that of r' and
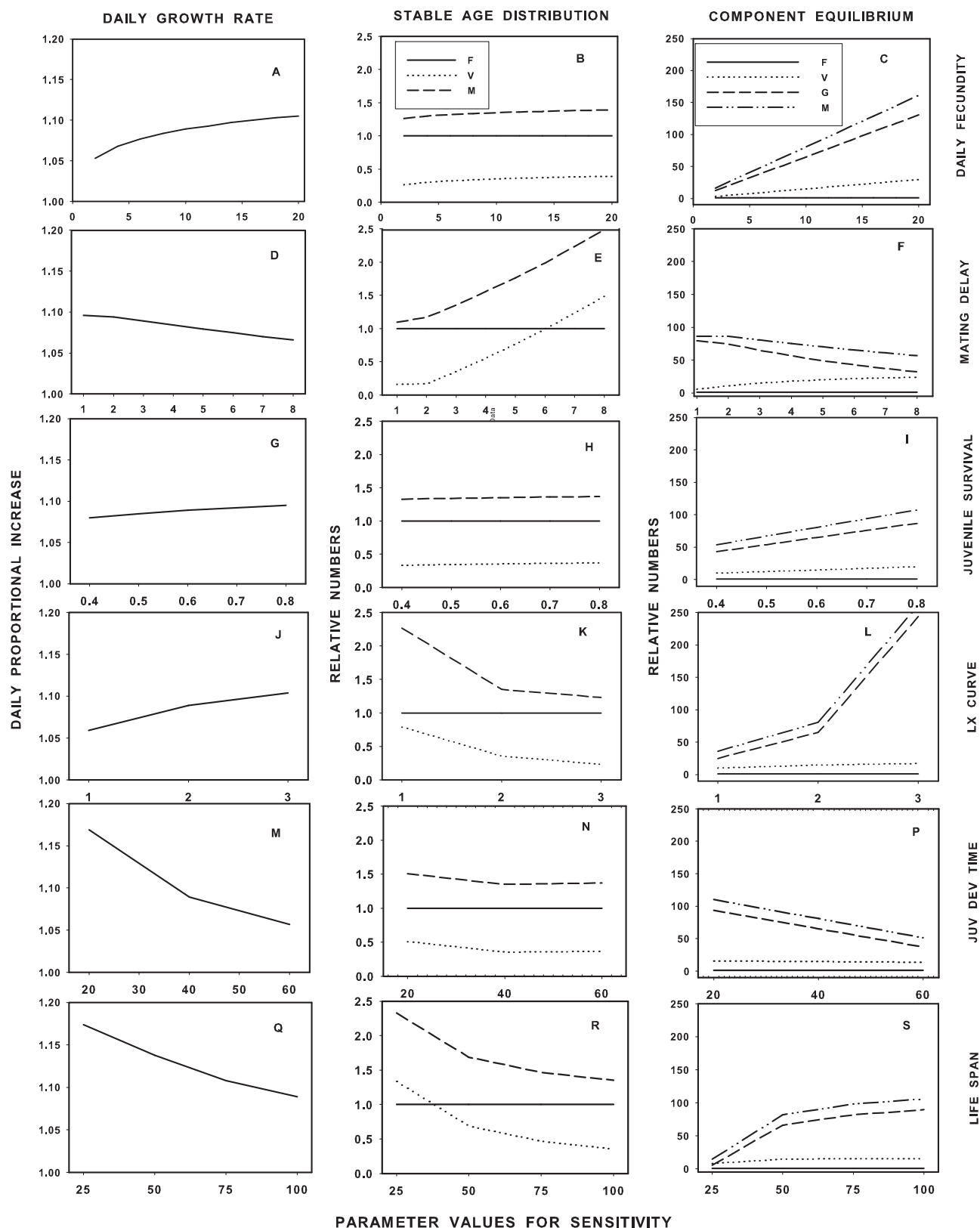
Figure 2. Graphs of the stable age distribution for the six parameters: (i) fecundity (*f*), (ii) mating delay (*τ*), (iii) net juvenile survivorship (*γ*), (iv) three adult survivorship curves, (v) the duration (days) that is spent in the juvenile stages, *jd*, and (vi) total life span (days), showing the daily growth rate (left-hand panels); virgin female (V_T), mated females (F_T) and male (M_T) numbers in a population that is increasing and in a stable age distribution with no sterile male releases (middle panels); and similar graphs of the equilibrium values of mated females (*Fe*), virgin females (*Ve*), sterile-mated females (*Ge*) and wild males (*Me*) for a population at equilibrium maintained by sterile releases at the critical rate, r^* (right-hand panels). In the middle and right-hand panels, all variables shown are standardized so that total fertile-mated females (*F*) equals 1.0. For the stable-age distributions the male numbers are between 1.0 and 2.5 times those of the fertile-mated females, whereas for the population at equilibrium the number of males is between 15 and 250 times the number of fertile-mated females, and in all cases the males are 50% of the total population. All panels within a column have the same figure legend. All panels within a row have the same parameter designation at the right of the right-hand column.
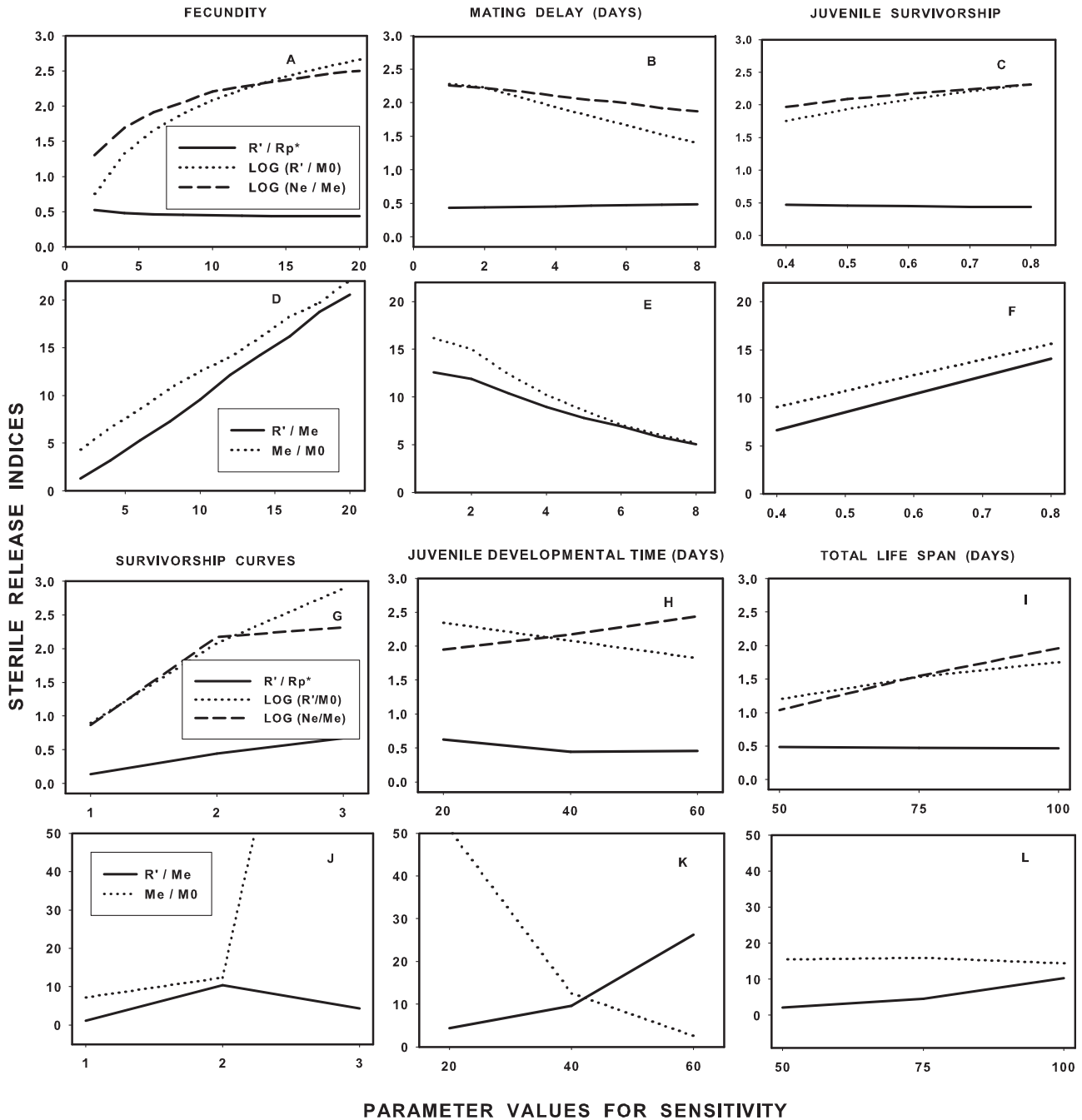
Figure 3. Sensitivity analysis showing the behavior of five derived statistics relating to sterile releases (r' / r_p^*, $\log(r' / M_0)$, r' / Me, Me / M_0, and $\log(Ne / Me)$) for each of the six features: (i) fecundity (f), (ii) mating delay (τ), (iii) net juvenile survivorship (γ), (iv) three adult survivorship curves, (v) the duration (days) that is spent in the juvenile stages, jd, and (vi) total life span, σ (days). The ranges of the parameters that were being incremented were: (i) fecundity: 2−20 eggs laid per fertile-mated female per day; (ii) mating delay: one to eight days after eclosion; (iii) net juvenile survivorship: 40%−80%; (iv) three adult survivorship curves: convex, exponential and concave; (v) the fraction that is spent in the juvenile stages: 20%, 40% and 60% of the total life span of 100 days; and (vi) total life span: 25, 50, 75 and 100 days. The default values of the parameters other than the one being incremented were: (i) fecundity: 10, (ii) mating delay: 3, (iii) net juvenile survivorship: 60%; (iv) adult survivorship curves: exponential; (v) the number of days spent in the juvenile stages: 40 and (vi) total life span: 100 days.

r^*, but the increase is extreme if the adult survivorship curve is convex upwards (the top curve in Figure 1). This curve is similar to the survivorship curve for *C. capitata* given by Vargas et al. (1984), although that survivorship curve was obtained under ideal laboratory conditions, and would likely be more like the second (exponential) survivorship curve for field populations.

(5) The ratio sterile males to fertile males, Ne / Me, both at equilibrium after the population has been stopped, is the critical over-flooding ratio, φ^*, to hold a population at the equilibrium values of the population components, and can be estimated entirely from the demographic parameters using Equations (2.4) and (A4). This ratio is what is desired to achieve when releasing sterile males
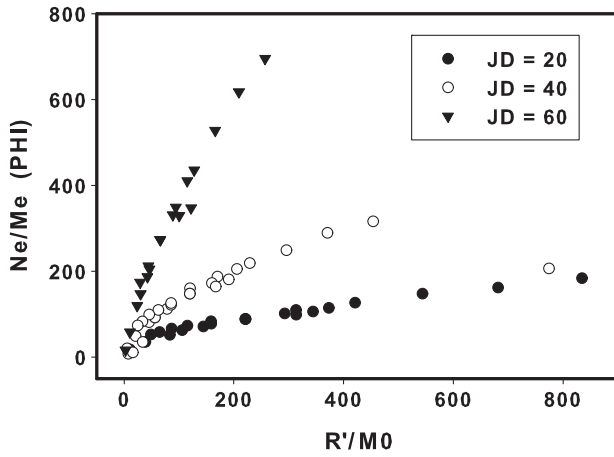
Figure 4. Values of the indices r'/M_0 (horizontal axis) and Ne/Me (vertical axis) showing strong associations for each of three values of the relative duration of the juvenile stages (juvenile developmental time (jd) of 20 days, 40 days and 60 days) out of the total life span of 100 days. The graphs were drawn using ten values of fecundity, eight values of mating delay and three values of juvenile survivorship for each of the three values of juvenile developmental time. Survivorship curves one and two fell near the lines but survivorship curve three (delayed mortality) was an outlier. Total life span was incompatible with the survivorship curves used for larval developmental time.

either daily or at some other interval. Fortunately, this ratio is usually known at the onset of sterile releases if the relevant demographic information is known. It is noticeable that the logarithms of the ratios Ne/Me are often very close to those of the ratio r'/M_0. Although logarithms are deceptive in comparing relative sizes, even the absolute sizes usually varied together. The absolute sizes of the ratios r'/M_0 and Ne/Me are shown in Figure 4 for three values of duration of the juvenile stages ($jd = 20$, 40 and 60 days); the two ratios follow fairly tight curved relationships, with the exception of one outlier: curve 3 with other parameters at default values. Curve 3 is unlikely to be realized often in the field, with all the attendant sources of mortality, such as weather and predation, so this anomaly may not be observed often. Thus, it appears that the ratio r'/M_0, once M_0 is estimated, could be used in conjunction with φ^* as an estimator or r'. The estimation of M_0 would be the main problem in that case.

The three data curves shown in Figure 4 were fitted to power functions by least squares and the resulting power functions are as follows:

$\varphi* = 6.22 \ u^{0.498}$ for $jd = 20$, giving

$$r'/M_0 = u = 10^{\{[\log(\varphi*) - \log(6.22)]/0.498\}}, \qquad (3.1a)$$

$\varphi* = 8.28 \ u^{0.599}$ for $jd = 40$, giving

$$r'/M_0 = u = 10^{\{[\log(\varphi*) - \log(8.28)]/0.599\}}, \qquad (3.1b)$$

$\varphi* = 13.1 \ u^{0.717}$ for $jd = 60$, giving

$$r'/M_0 = u = 10^{\{[\log(\varphi*) - \log(13.1)]/0.717\}}, \qquad (3.1c)$$

where $\varphi^* = Ne/Me$ and $u = r'/M_0$ (and u is β from 3.2b), and jd is the duration of the juvenile stages (for a total life span of 100 days). The parameter values here are likely only accurate for total life spans of 100 days, but the general form of the estimator should be similar for other life spans.

3.3. Estimation of the components of the above five indices

The estimation of the total males and total mated females requires the estimation of the total population on a given day and then the application of the daily rate of increase (Figure 2, left-hand column) to estimate the population size on the day of the first sterile release. Total males (M_T) and total mated females (F_T) can then be estimated using the SAD shown in Figure 2 (middle column), if the relevant demographic parameters are known.

The provisional estimation of r^*, r_p^*, requires detailed knowledge of the daily fecundity and age-specific adult survivorships as well as of total mated females (using (2.3)) or total males (using (2.4)). Total males will be easier, as they usually constitute one half of the total population.

The estimation of the required sterile release rate, r', can be done by measuring either F_T or M_T to obtain an initial estimate r_p^*; after that the relationships in Figure 3 (panels A, B, C, G, H and I) can be used to estimate r'.

The estimation of Fe and Me, the values of fertile-mated females and wild males at an equilibrium formed by sterile males being released daily at a rate r', can be estimated by assuming that r' in the growing population will equal r^* of the equilibrium population that is eventually achieved and then estimating Fe or Me by inverting (2.3) or (2.4), respectively.

The estimation of Ne can be found by assuming that r' of the growing population equals r^* of the equilibrium and then using the equation for Ne in A4.

3.4. Estimation of the over-flooding ratio from sampling data

Chains of estimation would likely start with the initial estimation of M_0 or F_T by sampling and then application of the relationships between r', Me and M_0 shown in Figure 3, to obtain r', Me and then eventually Ne. The daily critical release rate could then be estimated by inverting the equation for Ne in A4. The steps of four such chains could be as follows.

(i) Estimate M_0, then obtain $\varphi^* = Ne/Me$ from (2.6), then r'/M_0 from (3.1) and then obtain $\rho' = r'/M_0$. In symbols,

$$\varphi^* = Ne/Me \rightarrow \frac{r'}{M_0} \rightarrow \rho' \left(= \frac{r'}{M_0}\right). \quad (3.2a)$$

(ii) Estimate M_0, and then obtain r' via the relationship between $\log(r'/M_0)$ from Figure 3 (panels D, E, F, J, K, and L) and the six parameters, then obtain Me via the relationship between Me and M_0, then obtain r^* from (2.4), then form $\rho = r^*/Me$ or obtain Ne from r^* and then form $\varphi^* = Ne/Me$. In symbols, $M_0 \rightarrow \log(r'/M_0) \rightarrow \boldsymbol{r'}$; then

$$Me/M_0 \rightarrow Me \rightarrow r^*. \quad (3.2b)$$

(iii) Estimate M_0, then Me / M_0 from Figure 3 (panels D, E, F, J, K, and L), then form r'/M_0 from Figure 3 (the same panels), then $Ne/Me(=\varphi^*)$ then $r'/Me(=r^*/Me=\rho^*)$. In symbols,

$$M_0 \rightarrow Me/M_0 \rightarrow r'/Me \rightarrow r^*/Me \rightarrow \rho^*. \quad (3.2c)$$

(iv) Estimate M_0, then F_0 from fractions representing the relative heights of the curves for M and F in Figure 1, panels B, E, H, K, N and R. As there appears to be no good reason simply to multiply these fractions together, a geometric mean is calculated to obtain a conversion factor. Then estimate r_p^* using Equation (2.3), then r'/r_p^* from Figure 3, panels A, B, C, G, H and I, and thence r'. Me can also be estimated by computing φ^* and using $r'=r^*$ at equilibrium to get Fe and thence Me and ρ'. In symbols,

$$M_0 \rightarrow F_0 \rightarrow r_p^* \rightarrow r'/r_p^* \rightarrow r' \rightarrow \varphi^* \rightarrow Me \rightarrow \rho'. \quad (3.2d)$$

Various such estimation chains are possible and ideally one would use more than one chain and then compare the results for consistency. In estimating many of these, the relationships of the sterile index and all the parameters would need to be combined in some way. Two ways are suggested here. (1) The relationships shown in Figure 3 could be incorporated together for each of the five indices by assuming that the effects of the six factors are independent and forming multipliers from them, with 1.0 being the default and the values computed being proportions of the default values realized in the target species. (2) Since the effects of the six factors are likely not independent, then the catalogue of values contained in the supplementary material to this paper could be used instead, together with interpolation. This catalogue spans the range of parameter values used in Figure 3, combined orthogonally, but containing fewer

points and also does not include total life span, as the survivorship curves are not compatible with an orthogonal combination with the other five factors. However, it appears likely that life span is mostly a scaling parameter and might not interact much with the other five factors. For life spans other than 100 days, Figure 3 will provide a means of making tentative estimates. The following information would be useful in executing these chains of estimation: daily age-dependent survivorship (or mortality) for each population component, mean daily fertility (μ), and initial estimates of males (M_0) at the initiation of sterile releases.

3.5. Medfly example from laboratory survivorship data in simulation.

The value of daily sterile releases that stopped the growing population (the required release rate) was found by simulation to be 18711. The fertile female population at the start of sterile releases, F_0, was 15.61. The provisional critical sterile release value, r_p^*, was calculated from (2.3) using the value of F_0, and was 18,089; however, the corresponding wild male subpopulation was 38.16 at the start of sterile releases and 3823 at the equilibrium produced by the critical sterile release rate. The corresponding total population sizes were 76.3 and 7646, respectively. Thus, the calculated required over-flooding ratios were $18711/38.16 = 490$ near the start of sterile releases and $18{,}711/3823 = 4.89$ at equilibrium with sterile males being released at the required rate of 18711 per day. Thus, using the equilibrium critical over-flooding ratio at the onset of sterile releases based on M_0 would provide no control, as the ratio would be only about 1% of the required ratio.

As we do not have any information on the survivorship of sterile male adults, the same values have been used for both wild and sterile adult males. To illustrate the effects of reduced sterile male survivorship, assume that the survivorship of each age class of sterile male adults is a proportion 0.9 of that of the corresponding age class of wild males. Then using the survivorships shown in Figure 1 of Vargas et al. (1984), the sum $[\Sigma_0^{km-1}\Pi_0^i y_j] = 46.24$ and the sum $[\Sigma_0^{km-1}\Pi_0^i z_j] = [\Sigma_0^{km-1}\Pi_0^i 0.9\, y_j] = 8.52$. The reduction of effectiveness of sterile males is thus $46.24/8.52 = 5.43$, and a multiple of 5.43 must be applied to r^* (if it was calculated as if $z_i = y_i$ for all i). However, this inflation is already built into Equation (2.3) if the sterile survivorships, z_i, are known. It is apparent that if sterile male daily survivorships are much less than those of the wild males, then required release rates are prohibitively high with this shape of survivorship curve.

The situation with unequal mating competitive ability of sterile and wild males is even simpler. If the mating competitiveness of sterile males was a proportion

50

0.7 of that of wild males, then the value of r^* would be $18089/0.7 = 25841$ and the value of r' would be $18711/0.7 = 26730$. The corresponding release and over-flooding ratios would be similarly inflated.

3.6. Calculation of r′ using the chains of estimation and medfly survivorship data

For this we need some information from the medfly computations. We assume that an estimate of the total increasing population (half are males) has been made just prior to the start of sterile male releases, and since we have no other information, we assume that sterile male survivorship is the same as that of the wild males. From these, we compute the following: $M_0 = 38.16$; $F_0 = 15.61$; $\gamma = 0.69$; $\mu = 7.78$; $[\Sigma_0^{km-1}\Pi_0^i y_j] = 41.55$; $(\Pi_0^\tau w_j) = 0.971$; so $r^* = (0.69)(7.78)Fe[(0.69)\ (7.78)\ (41.55)(0.971) - 1]$; $r_p^* = 18089$; $r_p^*/M_0 = 474.0$, and r' from the simulation was 18,711.

(1) $\varphi^* = Ne\ /\ Me \rightarrow r'\ /\ M_0 \rightarrow \rho'\ (= r'/\ M_0)$

From (2.6), $\varphi^* = [\Sigma_1^{kf-1}\Pi_1^i w_j](\Pi_1^\tau w_j)\gamma\mu - 1 = (0.69)\ (7.78)(41.55)(0.971) - 1 = 215.6$.

From (3.1a), $u = r'/\ M_0 = 10^{\{(\log(215.6)\ -\ \log(6.22))/0.498\}} = 1237$.

Then $r' = (u)(M_0) = (1237)(38.16) = 47,206$.

The discrepancy between this estimate of r' and the measured value of 18711 (i.e., $47,206/18,711 = 2.52$ times as great) is probably caused by the value of u being outside the domain of the graph and the curve being nearly flat there, so a small error in φ^* would yield a large error in r'. In addition, the survivorship curve for medfly is not the same as the one that the relationships in Figure 3 were based on. Since the discrepancy is substantial, it is advisable to go no further in the chain of estimation.

(2) $M_0 \rightarrow \log(r'\ /\ M_0) \rightarrow r'$; then $Me\ /\ M_0 \rightarrow Me \rightarrow r^*$

M_0 was measured from the simulation to be 38.16; the value used in practice must be estimated from the growing population in the field.

From Figure 3, $\log(r'/M_0) = \log(r'/M_0) = (0.919)(0.711)(1.027)(1.333)(1.103)(1.00)[2.12] = 2.0917$

$$r'/M_0 = 10^{2.0917} = 125.49$$
$$r' = (38.16)(125.49) = 4788.6$$

The fractions in parentheses are the fractions that the six parameter values are of the default values; so, for example, 0.919 is the correction for using $\mu = 7.78$ instead of a fertility value of 10 throughout, as was done in the simulation. This is obtained by dividing the height of the curve for $\log(r'/\ M_0)$ at the realized value by the height at the default value in Figure 3, panel A. The other corrections are similarly obtained. These corrections are multiplied together and applied to the height (in brackets) of the curves at their default values (i.e., 2.12). The only curve not to have the same

default height was that for total life span, which was always at its default value in these calculations, so the correction factor was 1.00.

(3) $M_0 \rightarrow Me/M_0 \rightarrow r'\ /Me \rightarrow r^*/Me \rightarrow \rho^*$

Estimate of total population size $= 76.32$, so $M_0 = 38.16$.

Then estimate Me/M_0 from Figure 3 (panels D, E, F, J, K, and L), then form r'/M_0 from Figure 3 (the same panels).

$$Me/M_0 = (0.867)(0.40)(1.10)(13.76)(3.929)(1.00)$$
$$[12.5] = 258.25.$$

$$Me = (258.25)(38.16) = 9854.8.$$
$$r'\ /Me = (0.739)(0.480)(1.160)(0.60)(0.40)$$
$$(1.00)[10.0] = 0.9875.$$

$$r' = (9854.8)(0.9875) = 9765$$

Since the estimate is far from the value of r' obtained from the simulation, we go no further in this chain.

(4) $M_0 \rightarrow F_0 \rightarrow r_p^* \rightarrow r'\ /r_p^* \rightarrow r' \rightarrow \varphi^* \rightarrow Me \rightarrow \rho'$

Initial estimate of $M_0 = 38.16$

Then $F_0 = k_1\ M_0$ from Table 1, where

$$k_1 = [(0.75)(0.40)(0.72)(0.83)(0.68)(0.73)]^{0.167} = 0.6682$$

(i.e., k_1 is the geometric mean of the six ratios of F/M from Figure 1)

So $F_0 = (0.6682)(38.16) = 25.5$

$r_p^* = 29513$, using Equation (2.4)

$\varphi^* = 215.6$ (from Equation (2.6))

$r'/r_p^* = k2$ (from Figure 3) where k_2 is the correction factor to apply:

$$k_2 = (1.0)(1.1)(0.95)(1.4)(1.3)(1.0)[0.45] = 0.856$$
$$r' = (29513)(0.856) = 25259$$

This is to be compared with $r' = 18711$ from the simulation. We again don't go to any further estimations because of the discrepancy between the two estimates. The arithmetic mean of the four estimates is $(47206 + 4789) + 9765 + 25259)/4 = 21755$. This is fairly close to the value from the simulation (18711). This may be simply a coincidence or it may indicate that the mean of several independent estimates is likely to be more accurate than any single estimate by this method.

3.7. Calculation of r′ from exponential survivorship

Here an exponential survivorship curve is substituted for the one given by Vargas et al. (1984). This may bring the calculations one step closer to those of field

conditions. The only two of the six relevant panels that have changed here from the previous case are the fertility, which is now based on $\mu = 6.61$, and the survivorship curve, which is now based on curve 2. Here: $\gamma = 0.69$; $\mu = 6.61$; $[\Sigma_0^{(km-1)} \Pi_0^{(i)} y_j] = 22.00$; $\Pi_0^{(\tau)} w_j = 0.701$; $M_0 = 27.18$; r' from the simulation was 2147.2.

(1) $\varphi^* = Ne/Me \to r'/M_0 \to \rho' = r'/M_0$

From (2.6), $\varphi^* = (0.69)(6.61)(22.00)(0.701) - 1 = 70.4$.

From (3.1a), $u = r'/M_0 = 10^{\{(\log(70.4) - \log(6.22))/0.498\}} = 130.6$.

Then $r' = (u)(M_0) = (130.6)(27.18) = 3549.7$.

The discrepancy between this estimate of r' and the measured value of 2147.2 is much less (i.e., 3537.5/2147.2 = 1.65) than that with the laboratory survivorship, and the value of u is within the domain of Equation (3.1a) and the graph in Figure 4.

(2) $M_0 \to \log(r'/M_0) \to r'$; then
$Me/M_0 \to Me \to r^*$

M_0 was measured from the simulation to be 27.18.

From Figure 3,

$$\log(r'/M_0) = (0.784)(0.711)(1.027)(1.00)(1.103)$$
$$\times (1.00)[2.12] = 1.33865.$$

$$r'/M_0 = 10^{1.33865} = 21.81.$$
$$r' = (21.81)(27.18) = 592.8.$$

This estimate is considerably less than the measured value of 2147.2.

(3) $M_0 \to Me/M_0 \to r'/Me \to r^*/Me \to \rho^*$

Estimate of the total population size is 54.36, so $M_0 = 27.18$.

Then estimate Me/M_0 from Figure 3, then r'/M_0 from Figure 3,

$$Me/M_0 = (0.667)(0.40)(1.10)(1.00)(3.929)(1.00)$$
$$\times [12.5] = 14.41,$$

$$Me = (14.41)(27.18) = 391.8,$$
$$r'/Me = (0.50)(0.480)(1.160)(1.00)(0.40)(1.00)$$
$$\times [10.0] = 1.1136,$$
$$r' = (391.8)(1.1136) = 436.3.$$

Again the estimate falls far short of that from the simulation.

(4) $M_0 \to F_0 \to r_p^* \to r'/r_p^* \to r' \to \varphi^* \to Me \to \rho'$.

Initial estimate of $M_0 = 38.16$.

Then $F_0 = k_1 M_0$ from Table 1, where

$$k_1 = [(0.75)(0.40)(0.72)(0.76)(0.68)(0.73)]^{0.167}$$
$$= 0.6584$$

(i.e., k_1 is the geometric mean of the six ratios of F_0 / M_0 from Figure 1).

Hence, $F_0 = (0.6584)(27.18) = 17.90$,

$r_p^* = 5748$, using Equation (2.4)
$\varphi^* = 70.4$ (from Equation (2.6))
$r'/r_p^* = k2$, from Figure 3, where

$$k_2 = (1.0)(1.1)(0.95)(1.0)(1.3)(1.0)[0.45] = 0.61,$$

$$r' = (5748)(0.61) = 3506.3.$$

This is to be compared with $r' = 2147$ from the simulation, so again we don't go to any further estimations because of the discrepancy between the two estimates.

The arithmetic mean of the three estimates is $(3549.7 + 592.8 + 436.3 + 3506.3)/4.0 = 2021.3$. This compares favorably with the estimate obtained from the simulation and it is closer to the simulated value than any of the four individual values and thus reinforces the previous suggestion that the mean of several estimates is better than any single one.

4. Discussion

4.1. Implications of continuous growth

When using sterile releases against an increasing population, allowance must be made for the fact that the population is increasing. If the control method (e.g., spraying or trapping) is started at full strength and thus has no time lag once it is started, and if it has an action that is independent of pest density, then there is no discrepancy between the sterile release rate for holding a population at equilibrium, r^* and that for stopping a growing population, r'.

An implication for the use of SIT on populations with continuous growth is that populations will continue to grow for some time following the onset of sterile releases as a result of the existing juvenile sub-population at that time and also as a result of the fact that periodic releases will not immediately yield a large sterile population at equilibrium, as it takes time for such a population to build up. Thus, there are two time lags in the system that prevent immediate stopping of growth of the wild population, and the critical sterile male release rate calculated from equilibrium models will not usually give an appropriate value to stop the growth of a population. However, it is perhaps surprising that the total fertile-mated subpopulation (F_T) actually decreases once sterile male releases begin. This is partly because the growth of the fertile-mated population is decreased by the mating of virgin females with sterile males and partly because the fertile-mated female subpopulation, F_T is not an equilibrium value for F, and so the changes in F_T as it converges to the equilibrium value, Fe, are not as predictable as one might expect, and the provisional critical value of sterile male releases, r_p^*, bears little obvious relationship to the final critical value, r^*, when the equilibrium is

finally achieved, and even less relationship to the over-flooding ratio that must be used to stop a growing population. This illustrates the deceptive nature of only considering the critical sterile over-flooding ratio predicted by the equilibrium models when dealing with a growing population. It also illustrates the fact that the equilibrium configuration of population components is very different from the configuration of the SAD of a growing population. While the critical and required sterile male release rates may not differ greatly, the over-flooding ratios usually do.

There are at least three tactics that could usefully be employed in this situation when using SIT as the control agent: (1) do an initial knockdown with an aerial insecticide (Mangan 2005), (2) do a large initial sterile male release to bring the sterile population quickly up to its equilibrium, (3) use another control method, such as trapping, in combination with SIT to reduce the required sterile release rate and the over-flooding ratio to manageable levels (Knipling 1979; Hendrichs et al. 2005; Barclay et al. 2014). All three of these tactics may still leave a large juvenile population that will replenish the adult population once the juveniles emerge as adults, although the effects of the juveniles could be minimized by either several insecticidal knockdowns or by the judicious use of another control method in combination with SIT (Barclay 1987; Barclay & Vreysen 2011; Suckling et al. 2012; Barclay et al. 2013).

4.2. Utility of the sterile release indices

Five indices of sterile male releases were defined above. Each of these five measures gives some information on the management of control by SIT. However, all five are subject to errors of estimation. The question still remains regarding which ones will be most useful to the operational control manager.

The first of these five indices, r'/r_p^*, is nearly constant and since usually $r' < r^*$, a conservative approach would be to use r^* as the estimate of the required daily sterile male release rate. However, this necessitates estimating F_T, and the mated females would need to be distinguished from unmated adult females. If teneral females are exactly the same group as virgin females, then discrimination may be easy; if not, then one might use an even more conservative approach using total adult females, $F_T + V_T (= M_T)$, as the basis for estimating r_p^*.

The second of the five indices is r'/M_0, is a measure of the over-flooding ratio calculated from the value of M at the onset of sterile male releases. M_0 could be estimated just prior to the first sterile release, and unless the sex ratio is much different from one-to-one, it can be taken as simply half of the total adult population at that time. The trouble with this measure is that M_0 is highly sensitive to the parameters (Figure 3) and thus estimation of the indices may be subject to large errors.

The third index is r'/Me, which is the final over-flooding ratio and can be calculated once r' has been estimated and if the population growth parameters (μ, γ, etc.) are known. A conservative estimate would be r_p^*/Me, where r_p^* is calculated from the adult female sub-population just prior to the first sterile male release and Me is calculated from the appropriate value of r'/Me shown in Figure 3 or from (2.5) and (A4). This index is perhaps the closest to what most SIT workers are accustomed to, although it is also subject to errors in estimation in both r^* and Me and does not give a good indication of required initial release ratios, ρ'.

The fourth index is Me / M_0 and it gives a measure of the extent of the under-estimate of the age-structure effect arising from using values of variables in a growing population to estimate those in an equilibrium population. This value may be called the "growth effect" in estimating over-flooding ratios. Because this ratio depends on the accuracy of the estimate of M_0, it may yield a misleading value, although if both Me and M_0 are affected in the same direction by the errors, then these may tend to cancel and preserve the integrity of the estimate.

The fifth index is Ne/Me, which is the critical over-flooding ratio, φ^*, at equilibrium. The estimation of this must normally be done by calculation using the parameter values in (A4) and (2.6). However, if a conservative approach is used, and r' is taken to be r^*, which is greater than r', then (3.1) could also be used as a conservative estimate of the required over-flooding ratio to be employed in the control program.

4.3. Predictions for medfly

The predictions for medfly were done on data that were obtained from a laboratory study and are thus rather unrealistic from the beginning. They are shown mainly as an example of how to do the computations and what the results might look like. They also highlight some of the difficulties in applying these chains of estimations to real data sets from pest species in the field. All the chains are based on a total life span of 100 days, whereas in the field, few species will have a life span of near 100 days, and the estimation chains appear to be somewhat sensitive to longevity. Also, the form of the adult survivorship curve appears to affect the estimations rather strongly and interpolation between curves that are given here might be problematic. The exponential survivorship curve gave better results than the curve for late mortality, and it is more likely to be realized in the field, so the outlook for the estimators may be more optimistic than it appears at first sight. These above difficulties appear to affect the estimations in different ways, so that the calculation of four or more of them yields results that are closer to the measured value than any of the estimators taken singly.

4.4. Realism of the models and universality of the results

The models used in this paper are all density-independent age-structured models potentially applicable to a wide variety of species that experience an extended period of relatively free growth during the growing season. However, they exist in isolation as a single species with no outside influences. In reality, all species interact with other species with consequences for control that are varied. Field populations are subject to numerous influences, such as weather, parasitism, predation, human influences, density-dependence, etc. In particular, density-dependent population regulation would be expected to reduce the required sterile male release rate (Miller & Weidhaas 1974; Barclay & Mackauer 1980) and also dampen the instability of the population components that was observed in some of the simulations (May 1976). It would also likely alter the survivorship curve in ways that would reduce the growth effect. These outside influences would generally impose extra mortality on the pest population and thus make control easier (Barclay 1992).

The relationships shown in Figure 3 are a consequence of demographic processes and should indicate valid trends, but should not be applied indiscriminately to particular species without independent investigation of the behavior of the species population to be controlled. In this sense, the Medfly example is also only for illustrative purposes and it should be re-worked for a particular medfly population to be controlled, especially since the survivorship values obtained by Vargas et al. (1984) differ considerably from those obtained by Carey (1982), and likely also from those found in the wild; in the wild the survivorship curve would probably be closer to the middle curve (constant proportional mortality) in Figure 1 and the mating delay (τ) greater. However, a discrepancy in calculated over-flooding ratios (r'/M_0 vs r'/Me) for a growing population will likely occur under any feasible growing conditions.

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Appendix. The age-structured model

Juvenile Equations:

$$\text{Eggs}: E_{1,t+1} = \sum_1^{kf} F_{i,t}\, m_i h_i = \mu\left(\sum_{\tau}^{kf}\prod_0^i w_{j+\tau}\right) F_{1,t}$$
$$= \mu F_{T,t}; E_{i+1,t+1} = E_{i,t},$$

for $i = 1$ to ke,

$$\text{Larvae}: L_{1,t+1} = E_{ke,t}; L_{i+1,t+1} = q_i L_{i,t}, \qquad (A1)$$
$$\text{Pupae}: P_{1,t+1} = q_{kl} L_{kl,t}; P_{i+1,t+1} = w_i P_{i,t}.$$

Initial adult age classes:

$$V_{1,t} = w_{kp-1}\, P_{kp,t} = \gamma E_{1,t-kl-kp} = \gamma\mu F_{T,t},$$
$$F_{1,t} = w_\tau V_{\tau,t}\left[\sum_1^{kf} M_{i,t} / \left(\sum_1^{kf} M_{i,t} + \sum_1^{kf} N_{i,t}\right)\right]$$
$$= \left(\prod_0^{\tau-1} w_j\right)\gamma\mu F_{T,t}\left[M_{T,t}/\left(M_{T,t}+N_{T,t}\right)\right],$$
$$G_{1,t} = w_\tau V_{\tau,t}\left[\sum_1^{kf} N_{i,t} / \left(\sum_1^{kf} M_{i,t} + \sum_1^{kf} N_{i,t}\right)\right],$$

$$(A2)$$

$$M_1 = w_{kp-1}\, P_{kp,t} = \gamma E_{1,t-kl-kp} = \gamma\,\mu F_{T,t};$$
$$N_1 = r.$$

Adult survivorship equations:

$$F_{i+1,t+1} = w_i F_{i,t};\ \ G_{i+1.t+1} = w_i G_{i,t};\ \ V_{i+1,t+1} = w_i V_{i,t},$$
$$(A3)$$
$$M_{i+1,t+1} = y_i M_{i,t};\ \ N_{i+1,t+1} = z_i N_{i,t}.$$

Totals of each population component:

$$V_{T,t} = \left[\sum_0^{\tau-1}\prod_0^i w_j\right] V_{1,t} = \left[\sum_0^{\tau-1}\prod_0^i w_j\right]\gamma\mu F_{T,t},$$

$$F_{T,t} = \left[\sum_0^{kf-1}\prod_0^i w_j\right] F_1$$
$$= \left[\sum_0^{kf-1}\prod_0^i w_j\right]\left\{\left(\prod_0^\tau w_j\right)\gamma\mu F_T\left[M_{T,t}/\left(M_{T,t}+N_{T,t}\right)\right]\right\},$$

$$G_{T,t} = \left[\sum_0^{kf-1}\prod_0^i w_j\right]\left(\prod_0^\tau w_j\right)\gamma\mu F_T\left[N_{T,t}/\left(M_{T,t}+N_{T,t}\right)\right],$$

$$(A4)$$

$$M_{T,t} = M_{1,t}\left[\sum_0^{km-1}\prod_0^i y_j\right] = \left[\sum_0^{km-1}\prod_0^i y_j\right]\gamma\mu\left[F_{T,t}\right],$$

$$N_{T,t} = \left[\sum_0^{km-1}\prod_0^i z_j\right] r.$$

Component equilibria; adult totals:

$$Ve = \left[\sum_0^{\tau-1}\prod_0^i w_j\right]\gamma\mu Fe;\ \ Me = \left[\sum_0^{km-1}\prod_0^i y_j\right]\gamma\mu[Fe],$$

$$(A5)$$

$$Ge = \gamma\mu rFe\left(\sum_\tau^{kf-1}\prod_1^i w_j\right)\Big/(r+\gamma\mu rFe);$$

$$Ne = \left[\sum_0^{km-1}\prod_0^i z_j\right] r^*,$$

where the four components above are all given in terms of *Fe*, and *Fe* is usually assumed to be the equilibrium value of the fertilized female population to be measured.