

# Mass Rearing and Harvesting Based on an Age-Stage, Two-Sex Life Table: A Potato Tuberworm (Lepidoptera: Gelechiidae) Case Study

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Environ. Entomol. 17(1): 18-25 (1988)

**ABSTRACT** Traditional age-specific life table analysis does not take variable development rates into account and deals only with the female population. In this paper, rearing and harvesting of specific life stages are analyzed in the context of a general age-stage, two-sex life table. The question of selecting optimal harvest and discard strategies for the design of insect mass rearing facilities is discussed. The method is demonstrated using data collected from a culture of the potato tuberworm, *Phthorimaea operculella* (Zeller).

**KEY WORDS** Insecta, *Phthorimaea operculella*, life tables, reproduction

MASS REARING of insects is an important component of biological control and of sterile insect release programs. Several insect rearing handbooks are available (for example, King & Leppla 1984, Singh & Moore 1985) but, as evidenced by recent literature (Carey & Vargas 1985, Vargas et al. 1985, Whittlecraft et al. 1985, Plant 1986), more efficient rearing methods are always being sought. However, many problems remain to be solved. For example, excess production sometimes must be discarded to reduce the colony size, and at other times the colony is too small. A lack of proper planning in a rearing and harvesting program can result in wasted money, labor, and time, leading to failure of a research or control program.

In addition to specifying diet, rearing densities, and related rearing conditions, a properly designed rearing program must also specify the discard age and harvesting rates (e.g., Carey & Vargas 1985). Most of these components can be determined by conducting preliminary experiments for each life stage, but optimal discard age and harvesting rates are most easily determined with the assistance of an appropriate life-table model. Haile & Weidhaas (1984) and Carey & Vargas (1985) have published mass-rearing models based on age-specific life tables. However, as Chi & Liu (1985) point out, in using the age-specific life tables, variability in development rate among individuals is ignored and only the female population is accounted for. They concluded that the age-specific life table, either the Leslie matrix (Leslie 1945, 1948) or Birch's method (Birch 1948), is inappropriate for insect or mite species where significant variation in the rate of development occurs. Concerns about the two-sex problem or variable development rates have been addressed in some papers (Caswell & Weeks 1986,

Plant & Wilson 1986), but none of them has included variable development rates, stage differentiation, or both sexes in a single model.

Variation in development rates can result in a significant age-stage overlap. Chi & Liu (1985) developed a model to account for this variation in development rates, and the male population, by describing the population structure as a matrix of  $n$  rows and  $m$  columns (Fig. 1A), where  $n$  is the age-class number and  $m$  is the stage number, survival rates are considered to be a function of growth and development rates, both males and females are included, and both stage and age groupings are possible.

Our objective is to present a method for determining the optimal discard age and harvest rates using Chi and Liu's age-stage, two-sex, model. Our approach parallels the age-specific analysis presented by Carey & Vargas (1985). The method is demonstrated using life history data obtained from a laboratory culture of potato tuberworm, *Phthorimaea operculella* (Zeller) (details reported in Etzel 1985 and Chi 1988). The potato tuberworm is frequently used as a source of food for cultures of such predatory insects as lacewings and coccinellids.

## The Model

**Age-Specific Mass Rearing and Harvesting.** As discussed by Chi & Liu (1985), age-specific survival rates ( $l_x$ ) can be calculated without ignoring the variability in the development rate of the population. In age-specific mass rearing and harvesting, cohorts can be maintained as separate units despite the fact that at the "same" age, individuals may be in different life stages (Fig. 1B), resulting in a harvest of both life stages.

When harvesting age corresponds to a single stage, the length of time that each individual has

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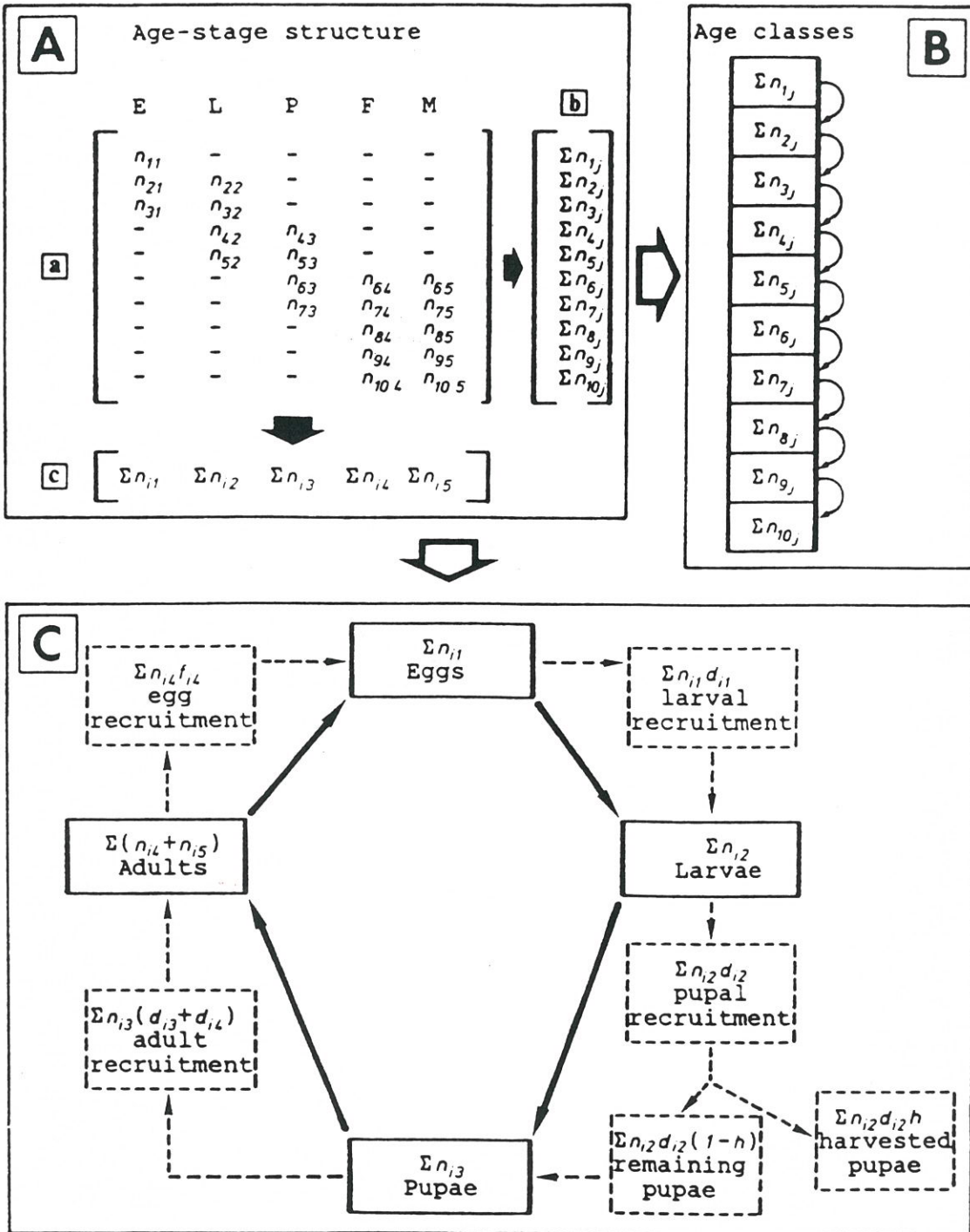


Fig. 1. (A) a, The age-stage structure; b, the age structure, and c, the stage structure of a population. (B) The age-specific mass rearing and harvesting model. The arrows represent the transitions including harvest and natural mortality rates. (C) The stage-specific mass rearing and harvesting model.

been in that stage will, in general, be different. In this case, the harvest rate can be calculated according to Carey & Vargas (1985). However, the raw data from a life-history study must be analyzed

using the two-sex, age-stage life table in order to obtain the proper  $l_x$  and  $m_x$  curves. Nevertheless, it is clear that a solely age-specific approach is applicable only if the differences in ages or stages

among harvested individuals are not critical to the desired purpose.

**Stage-Specific Mass Rearing and Harvesting.** For mass rearing and harvesting of most insect populations, it is preferred that the harvested individuals are of the same age in the target stage. Furthermore, to save space and utilize rearing equipment efficiently, it is also preferred that individuals in different stages, rather than ages, are maintained in separate units. Therefore, a stage-specific growth and harvesting model will be more appropriate for most mass rearing programs. As shown in the stage-specific harvesting model in Fig. 1C, the insects are grouped as eggs, larvae, pupae, and adults; the recruits to each stage (the dashed boxes) are transferred daily, a process common to most insectaries. According to Chi & Liu (1985), recruitment for larval, pupal, and adult stages can be described by  $\sum n_{i1}d_{i1}$ ,  $\sum n_{i2}d_{i2}$ , and  $\sum n_{i3}(d_{i3} + d_{i4})$ , respectively, where the  $d_{ij}$  are elements of an  $n \times m$  developmental matrix  $D$ . Since  $i$  is the age index and  $j$  is the stage index,  $d_{i3}$  and  $d_{i4}$  are the rates of development from the pupal stage to adult females and males, respectively. The number of eggs laid each day is

$$\sum_{i=1}^n \left( \sum_{j=1}^m n_{ij} f_{ij} \right),$$

where  $f_{ij}$  are elements of an  $n \times m$  fecundity matrix  $F$ . Assuming the harvest target stage is the pupa, we need to harvest the recruitment of pupae, which is mathematically equivalent to harvesting part of the developmental rate of the previous stage (the larval stage) ( $d_{i2}$ ). Let  $\alpha$  be the stage just prior to the target stage. If we remove, in each time period, a proportion  $h$  ( $0 \leq h \leq 1$ ) of the individuals moving from stage  $\alpha$  to  $\alpha + 1$ , then the new matrix of developmental rates will be  $D'$ , where  $d'_{ij} = d_{ij}$  except for  $j = \alpha$ , where  $d'_{i\alpha} = d_{i\alpha}(1 - h)$ . Note that  $h$  is the harvest rate per potential recruit to the target stage. A new age-stage specific survival matrix  $S'$  can then be calculated from  $D'$  and the  $n \times m$  growth matrix  $G$  as described in Chi & Liu (1985). Note that because  $d'_{i\alpha}$  depends on  $h$ , so do the elements of  $S'$ . It can then be shown (Chi & Liu 1985) that the harvest rate per laid egg ( $h_c$ ) is

$$h_c = \sum_{i=a}^b s'_{ia} d_{ia} h \tag{1}$$

where  $a$  and  $b$  are the youngest and oldest age classes in stage  $\alpha$ .

To maintain the colony at zero growth rate (intrinsic rate,  $r = 0$ ), we require that the rate of population growth  $R_0$  be unity. In the notation of Chi & Liu (1985) the probability of surviving to age  $i$  is

$$l_i = \sum_{j=1}^m s'_{ij}$$

or

$$R_0(h) = \sum_{i=1}^n \sum_{j=1}^m s'_{ij}(h) f_{ij}$$

and we need to solve for the value of  $h$  that satisfies

$$\sum_{i=1}^n \sum_{j=1}^m s'_{ij}(h) f_{ij} = 1 \tag{2}$$

The stable age-stage distribution matrix  $P'$  and the corresponding stable stage distribution can be calculated from  $G$ ,  $D'$ , and  $F$  as described in Chi & Liu (1985). If we build up a colony according to this stable age-stage distribution  $P'$ , then harvesting a proportion  $h$  of the new recruits to target stage  $\alpha + 1$  (or a proportion  $h_c$  per newly laid egg) will theoretically maintain the colony at constant population size. Furthermore, all harvested individuals are at the same developmental stage. The harvest rate  $h$  can be found by using numerical methods to solve Equation 1. The relationship between the daily production of newly laid eggs ( $Y_c$ ) and the daily harvested amount ( $Y$ ) of the target stage per new egg in this stable population is then

$$Y = Y_c h_c$$

or

$$Y = Y_c \sum_{i=a}^b s'_{ia} d_{ia} h \tag{3}$$

This formula can be used to calculate the number of newly laid eggs ( $Y_c$ ) needed to sustain a daily harvest rate (yield) of  $Y$ . The recruitment to each stage in this stable population is then

$$\begin{aligned} N_c &= Y_c \quad (\text{egg recruitment}) \\ N_1 &= Y_c \sum_{i=1}^n s'_{i1} d'_{i1} \quad (\text{larval recruitment}) \\ N_p &= Y_c \sum_{i=1}^n s'_{i2} d'_{i2} \quad (\text{pupal recruitment}) \\ N_a &= Y_c \sum_{i=1}^n s'_{i3} (d'_{i3} + d'_{i4}) \quad (\text{adult recruitment}) \end{aligned} \tag{4}$$

The total population size ( $T_t$ ) is then

$$T_t = Y_c / p'_{11}$$

where  $p'_{11}$  is the proportion of new eggs in the stable age-stage distribution. The number of individuals in the  $j$ th stage ( $T_j$ ) is then

$$T_j = \sum_{i=1}^n Y_c s'_{ij} \tag{5}$$

If the harvest rate per adult ( $h_a$ ) is preferred, it can be obtained from

$$h_a = p'_{11} h_c / \sum (p'_{i4} + p'_{i5}) \tag{6}$$

where  $p'_{11}$ ,  $p'_{i4}$ , and  $p'_{i5}$  are the elements of the stable

age-stage distribution (matrix  $P'$ ), and the sum in the denominator ranges over all possible adult age classes.

Based on the stable stage structure, the required space, food, labor, and other inputs can be calculated. The biomass of harvested individuals can also be calculated, because the increase of biomass during insect development is more or less stage-specific. If the harvested individuals are kept for  $t$  days before they are used, the mortality during this post-harvest period should be considered, and the actual yield ( $Y_a$ ) can be calculated as

$$Y_a = Y_c \sum_{i=1}^n \left( s'_{ia} d_{ia} h \prod_{k=i+1}^{i+t} g_{k\alpha+1} \right), \quad (7)$$

where  $g_{k\alpha+1}$  are the elements of the previously mentioned growth matrix  $G$ , representing the probability that an individual of age  $k$  and stage  $\alpha + 1$  will survive to age  $k + 1$  while remaining in stage  $\alpha + 1$ .

**The Discard Age.** In many insect species, older females lay few or no eggs, making it economical to discard those adults in order to save food, space, labor, and time. If  $\delta$  denotes the discard age (the last age class kept in colony), then the respective net reproduction rate  $R_0$  is a function of  $\delta$

$$R_0(\delta) = \sum_{i=1}^{\delta} \sum_{j=1}^m s_{ij} f_{ij}. \quad (8)$$

If  $\beta$  is the first egg-laying age, then it is clear for  $\delta \in [\beta, n]$  that:

$$R_0(n) \geq R_0(n - 1) \geq R_0(n - 2) \geq \dots \geq R_0(\beta) \quad (9)$$

because all the terms in  $R_0$  are positive. Equation 2 can be rewritten as:

$$\sum_{i=1}^n \sum_{j=1}^m s'_{ij}(h(\delta)) f_{ij} = 1 \quad (10)$$

The respective harvest rates  $h$  and  $h_c$  are also functions of  $\delta$  and have the same relationship

$$h(n) \geq h(n - 1) \geq h(n - 2) \geq \dots \geq h(\beta)$$

and

$$h_c(n) \geq h_c(n - 1) \geq h_c(n - 2) \geq \dots \geq h_c(\beta)$$

Thus, to obtain the maximal harvest per newly laid egg, we must keep all adults until they die. However, maintaining an adult colony that contains older, less fecund individuals may be uneconomical. Carey & Vargas (1985) used the optimal harvest per adult female to determine the discard age. In the stage-specific harvest, we can also use Equations 1, 6, and 10 to calculate  $h_a$  for different discard ages  $\delta$ , and then calculate the discard age that maximizes  $h_a$ . It is tedious, however, to recalculate Equations 1, 6, and 10 for all possible discard ages. A more direct approach is to use the original data in the fecundity and survival matrices  $F$  and  $S$  and calculate  $R_0(\delta)$ , the net reproduction rate, for various values of the discard age  $\delta$ . This can be

done rapidly by starting with  $R_0(\beta)$ , as given in Equation 9, and adding one term at a time to obtain  $R_0(\delta)$  for the next age category. To maintain colony equilibrium, we need to return one egg daily to the colony from the  $R_0(\delta)$  eggs produced per egg per day, and harvest the remaining ( $R_0(\delta) - 1$ ) eggs. The total number of adults in this equilibrium colony (see Equation 4) is

$$A(\delta) = \sum_{i=1}^{\delta} (s_{i4} + s_{i5})$$

and the reproduction rate per adult is

$$\epsilon(\delta) = R_0(\delta)/A(\delta) \quad (11)$$

The  $\delta$ , which gives the maximal  $\epsilon$ , will maximize  $h_a$  but will not necessarily maximize  $h$  or  $h_c$ . An optimal discard age policy, however, can be implemented only if the colony is separated into age-stage units so that the age of each adult is known. Such a rearing procedure would be very complicated. An alternative is to keep the daily recruits to the adult stages in separate units and maintain each unit for  $\delta - c + 1$  days, where  $\delta$  is the discard age and  $c$  is the youngest age class of adult (recall that slower developing individuals will be recruited at some age older than  $c$ ). The total number of adults in the colony then exceeds  $N_a(\delta)$ , as calculated using Equation 4, so that the daily recruitment of eggs exceeds the required  $Y_c$  (calculated using Equation 3). In this way, the adult population size is maintained at a value higher than the theoretical value, but not as high as if we ignored discarding.

**Setting Up and Stabilizing Colony.** As mentioned in the previous section, a mass rearing and harvesting program under equilibrium conditions is based on the stable age-stage distribution, where there are a constant number of individuals in each age-stage class, and each day we harvest a constant number of individuals entering the target stage. To establish a stable colony yielding a daily harvest rate  $Y$ , we need to input  $Y_c$  eggs per day from outside the colony until the population begins to oviposit, then supplement the number of oviposited eggs to total  $Y_c$  for  $\delta$  days, where  $\delta$  is the discard age. Note that harvesting begins as soon as the number of individuals recruited to stage  $\alpha + 1$  exceeds the number  $N_{\alpha+1}$  corresponding to the stable age-stage distribution (see Equation 4), and the surplus is harvested until the complete stable age-stage distribution is (theoretically) achieved on day  $\delta$ . In theory, after  $\delta$  days, no eggs are needed from outside the colony because egg production from the colony itself (that is,  $Y_c$ ) is sufficient for equilibrium. In practice, numbers will fluctuate due to variation in birth and survival rates. This fluctuation can be controlled by modifying the harvest rate and reducing or increasing  $Y$  as appropriate, so that  $N_{\alpha+1}$  is stabilized at the value given by Equation 4. This type of response to uncertainty is analogous to constant escapement policies found in fisheries management (Clark 1985).

Table 1. Population parameters and stable-stage distribution of the potato tuber worm with and without harvesting<sup>a</sup>

Harvesting	Population parameter				Stable stage distribution			
	$r$	$\lambda$	$R_0$	$T$	Egg	Larva	Pupa	Adult
Without (SE)	0.136 (0.007)	1.146 (0.008)	69.7 (15.0)	31.2 (0.4)	56.5	36.1	6.2	1.2
With	0	1	1	—	32.6	66.0	0.79	0.59

<sup>a</sup>  $r$ , intrinsic rate of increase ( $d^{-1}$ );  $\lambda$ , finite rate of increase ( $d^{-1}$ );  $R_0$ , net reproductive rate (offsprings per individual);  $T$ , mean generation time (d).

In summary, the objectives are to:

- Collect life history data and analyze it, using two-sex, age-stage life table analysis (that is, calculate matrices  $G$ ,  $D$ ,  $F$ ,  $S$ ,  $P$ ).
- Find the optimal discard age using Equation 11, then use Equations 1, 6, and 10 to find the respective harvest rates  $h$ ,  $h_a$ , and the optimal  $h_a$  which maintains the population at zero growth rate. Calculate the new survival matrix  $S'$ , the stable age-stage distribution matrix  $P'$ , the daily new eggs  $Y_c$  needed to obtain the expected yield  $Y$  from the target stage, and the stable proportion in each stage.
- Set up the stable colony, as described above, to be stabilized at day  $\delta$ .
- Beyond day  $\delta$ , monitor variations in  $N_a$  and adjust  $Y$  from its theoretical value so as to stabilize the number of after-harvest new recruits to the target stage  $\alpha + 1$  (that is,  $N_{\alpha+1}$ ) at its correct value.

**Potato Tuberworm Example.** The potato tuberworm has been reared in the Div. Biological

Control, Univ. Calif., Berkeley, since the 1940s and is used as a food source for lacewings and coccinellids. A detailed description of rearing methods is reported in Etzel (1985). The life history data were analyzed based on Chi & Liu's method (1985). The matrices of growth rates ( $G$ ), development rates ( $D$ ), and fecundity ( $F$ ) are reported elsewhere (Chi 1988). Variation in development rates and differential survivorship between the sexes, as indicated by these matrices, suggest that an age-stage, two-sex approach is more precise than the traditional age-specific "female life table" approach for modeling growth and harvesting in this insect. The population parameters obtained are given in Table 1 (note that  $T$  in this table is the mean generation time and  $\lambda$  is the finite rate of increase). These data are calculated with respect to the total population (both sexes together). The standard errors of these parameters are estimated, using a Jackknife technique (Sokal & Rohlf 1981).

Following the theory outlined in the previous section, a number of quantities were calculated.

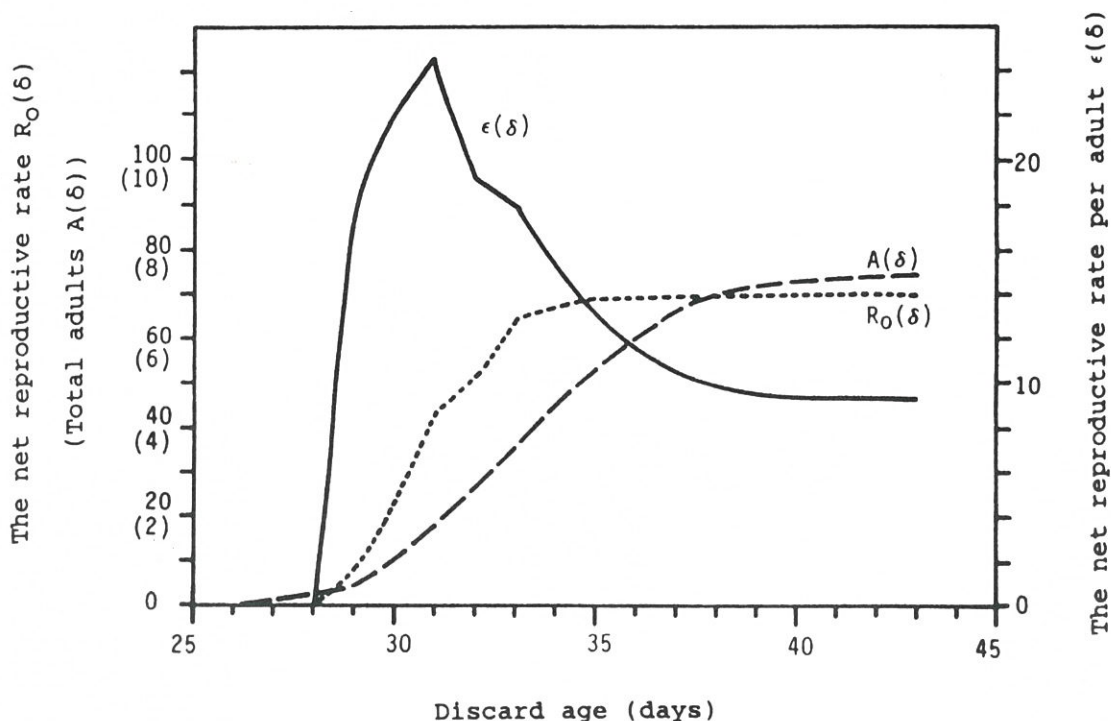


Fig. 2. The net reproductive rate  $R_0$  (eggs/egg), total adults ( $A$ ), and the ratio  $E = R_0/A$  at different discard ages.

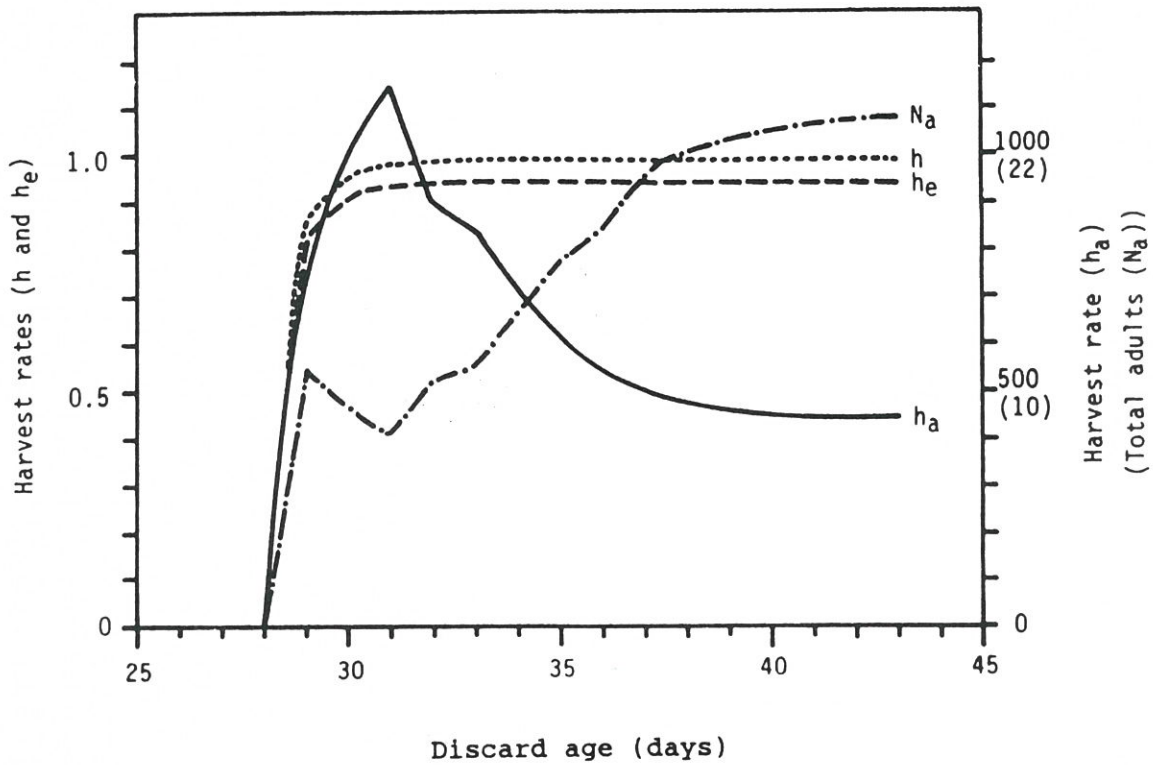


Fig. 3. Harvest rates [ $h$  (pupae/pupa),  $h_e$  (pupae/egg) and  $h_a$  (pupae/adult)] and the respective total adults ( $N_a$ ) at different discard ages.

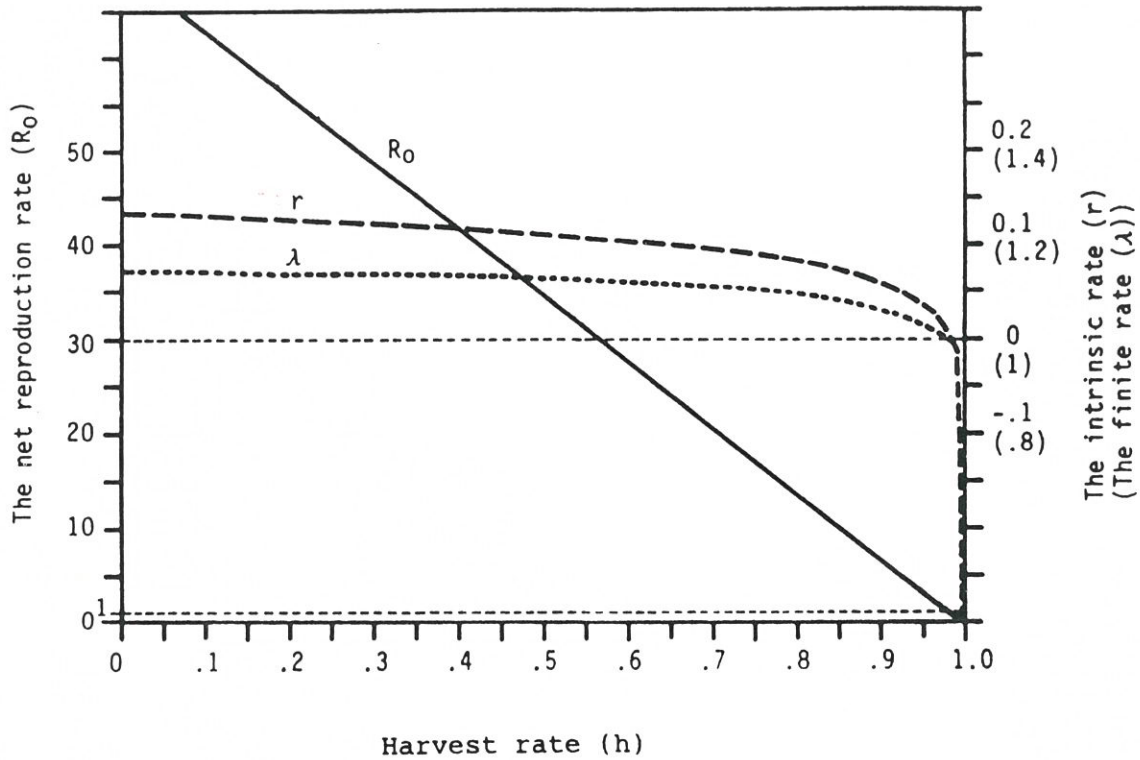


Fig. 4. The intrinsic rate  $r$  ( $d^{-1}$ ), finite rate  $\lambda$  ( $d^{-1}$ ), and net reproductive rate  $R_0$  (eggs/egg) as a function of harvest rate  $h$  (pupae/pupa).

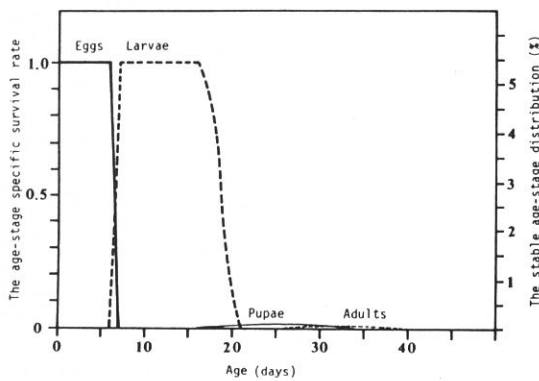


Fig. 5. The age-stage specific survival rate and the stable age-stage distribution.

The quantities  $R_0(\delta)$ ,  $A(\delta)$ , and  $\epsilon(\delta)$  as functions of the discard age  $\delta$  are displayed in Fig. 2, while  $h(\delta)$ ,  $h_c(\delta)$ ,  $h_a(\delta)$ , and total number of adults in the stable age-stage distribution as functions of  $\delta$  are shown in Fig. 3. From Fig. 2 and 3 we see that the optimal discard age for the potato tuberworm is 31 d, with corresponding  $h_a = 22.9$  pupae per adult, and  $h_c = 0.928$  pupae per new egg. This  $h_a$  is much higher than in the case where no adults are discarded ( $h_a = 8.70$  pupae per adult). However, this  $h_c$  is only slightly lower than the nondiscarded value  $h_c = 0.936$  pupa per new egg. These differences imply that, with a much lower adult population size, the harvest rate of recruits per new egg can still be kept relatively high. However, because the mean longevity of adults is relatively short (8.3 d) and adults do not need to be fed, keeping the older adults does not increase the cost. Therefore, discarding older adults does not reduce rearing costs in this case, unless the space is limited. The intrinsic growth rate  $r$ , finite rate  $\lambda$ , and the net reproductive rate  $R_0$ , as a function of the harvest rate  $h$ , are displayed in Fig. 4.

When pupae are the target stage and no adults are discarded, the equilibrium harvest rate of new pupae is 0.986 pupa per pupa. The harvest rate per new egg is 0.936 pupa per egg. The stable stage distribution under harvesting has the same form as the survival curves and is shown in Fig. 5. The population parameter and stable stage distribution before and after harvesting are given in Table 1. The daily recruits for each stage after harvesting and the actual number of each stage per 10,000 new eggs in the colony are listed in Table 2. The harvest rate based on any stage can be derived from the stable age-stage distribution (Equation 5).

### Conclusion

For most holometabolous insect species, a stage-specific mass rearing and harvesting analysis may be more appropriate than the traditional age-specific approach. For some hemimetabolous insects, the situation is complicated by unusual life histories

Table 2. The daily recruits for each stage (after removing the harvested part) and the actual number in each stage per 10,000 new eggs

	Egg	Larva	Pupa	Adult
Daily recruits	10,000	10,000	136	126
Stage number	60,000	121,500	1,456	1,076
Daily harvest	—	—	9,364	—

such as apterous and nonapterous aphid morphs. Adult mortality rates are often sex related, in which case a two-sex, life-table analysis should be used to obtain the proper age-specific survival rates and fecundity parameters. In cases where two stages are harvested (e.g., the harvest of eggs for egg parasites and larvae for predators), the use of the stage-specific harvest methods presented here may improve efficiency in rearing operations.

In most applications fecundity, development rates, and mortality rates may be quite variable between generations. This uncertainty can be reduced by keeping rearing conditions constant, continuously monitoring population levels, revising life table data, and adjusting harvest rates so that the size of the adult breeding population is stabilized. The regularly revised life-table data can also be used as an index for estimating the vigor and variability of the population. When the intrinsic growth rate decreases, the vigor of the laboratory culture declines. When the variability of population parameters decreases (decreased SE), the overall fitness of the population in the field might decrease. Because both of these problems can be resolved by introducing new wild individuals into the laboratory culture, a life-table approach that monitors variation in development may prove to be an invaluable tool for maintaining the genetic viability of laboratory cultures.

In theory, this model is applicable to most mass rearing problems. However, in practice the savings obtained by instituting the type of mass rearing program outlined here may be economically justifiable only for very large-scale operations.

### Acknowledgment

We are grateful to two anonymous referees for their valuable suggestions on revisions of this manuscript. This work was supported in part by NSF Grant DMS-8511717 to W.M.G. and an Alfred P. Sloan Foundation Award to W.M.G. and K. Wachter.

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Received for publication 2 September 1986; accepted 13 October 1987.