Periodic Mass Rearing and Harvesting Based on the Theories of Both the Age-Specific Life Table and the Age-Stage, Two-Sex Life Table

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ABSTRACT Periodic mass rearing and harvesting of specific life stages are analyzed based on the theories of both the age-specific life table and the age-stage, two-sex life table. Formulae for the calculations of the optimal discard age and harvest rate are derived. For practical applications, the use of thermal summation to manipulate the developmental time of specific life stage is suggested. The model is demonstrated using life table data of *Ostrinia furnacalis* (Guenée).

KEY WORDS *Ostrinia furnacalis*, life table, harvesting theory

ECONOMICALLY RATIONAL MASS rearing and harvesting are important to applied ecology, especially when resources are limited. In published papers, mass-rearing models with or without age-structure have been constructed. Haile & Weidhaas (1984) described a model with rough stage structure. Carey & Vargas (1985) constructed a mass-rearing model based on an age-specific life table (Birch 1948). To take both sexes and the variable developmental rate among individuals into account, Chi & Getz (1988) built the stage-specific mass-rearing and harvesting model based on an age-stage, two-sex life table. All of the above mentioned models assume continuous recruitment and harvesting at each time interval. Because a large time interval will result in having individuals of different stages in the same age class, a reasonably small time unit (e.g., day) should be used in life table studies and in construction of mass-rearing models to ensure the harvesting of specific life stages. Such a continuous rearing program is tedious, wasteful, and impractical for most purposes. However, most mass-rearing programs require periodic recruitment and harvest, e.g., the harvest and release of predators or parasitoids at specific time intervals. Therefore, before the construction of a periodic mass-rearing program, a life table study has to be carried out using small time units as age class; then a mass-rearing and harvesting model can be constructed for larger time intervals (week or month). Without theories of periodic mass rearing and harvesting, empirical methods will still play important roles in most rearing programs, however; research that is focused on rearing methods and diets generates only limited success. Therefore, detailed studies on the theory of periodic mass rearing and harvesting are necessary for the construction of a more applicable mass-rearing program. In this paper, periodic mass rearing and harvesting is analyzed based on the theories of both the age-specific life table and the age-stage, two-sex life table. Equations are derived for various rearing and harvesting strategies. Data on the Asian corn borer, *Ostrinia furnacalis* (Guenée), are used as examples.

Model

Harvesting the Egg Stage. *Age-specific Mass Rearing and Harvesting.* For species without stage differentiation, an age-specific life table can be used to construct the mass-rearing model. If Y_e newly laid eggs are input into the mass-rearing system at the beginning, the egg production rate at time t (Y_t) will be

$$Y_t = Y_e l_t m_t, \tag{1}$$

where l_t is the age-specific survival rate (the probability that a new-born individual will survive to age t) and m_t is the age-specific fecundity at age t (average number of offspring reproduced by individual of age t). Supposing all eggs laid at age t can be harvested for a certain purpose, the number of harvested eggs, Y_h, will be

$$Y_h = Y_t = Y_e l_t m_t. \tag{2}$$

However, if the colony has to be self-sustained at the time of harvest, the same number of eggs, Y_e, must be saved as recruits for the next generation. Then, the number of harvest eggs (Y_h) at time t will be

$$Y_h = Y_t - Y_e = Y_e(l_t m_t - 1). \tag{3}$$

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Because Y_h must be a positive number, it is necessary that $l_t m_t > 1$. Equations 2 and 3 describe the simplest cases of periodic harvesting of egg stage, where only eggs laid by females of a specific age t are harvested. In some cases, eggs within a certain age range are harvested and Y_h can be calculated as

$$Y_h = Y_e \sum_{x=t'}^{t} l_x m_x. \tag{4}$$

In other words, equation 4 gives the number of harvested eggs (Y_h) laid during the time interval t' to t. However, if Y_e eggs laid on a specific day u ($t' \le u \le t$) must be saved as recruits for the next generation, then the total number of harvested eggs Y_h is

$$Y_h = Y_e \cdot \left\{ \sum_{x=t'}^{t} l_x m_x - l_u m_u + (l_u m_u - 1) \right\}. \tag{5}$$

Mathematically, equation 5 can be rewritten as

$$Y_h = Y_e \cdot \left\{ \sum_{x=t'}^{t} l_x m_x - 1 \right\}. \tag{6}$$

However, equation 5 implies that the recruits are obtained from those eggs laid on day u, and the harvesting of Y_e eggs is possible if and only if $l_u m_u > 1$. Thus, equation 5 should not be replaced by equation 6.

Stage-specific Mass Rearing and Harvesting. For species with stage differentiation, an age-stage, two-sex life table is justified for constructing a rational mass-rearing model (Chi & Getz 1988). Assuming the harvest stage j is the female stage, the number of eggs Y_t laid in a single day t can be calculated as

$$Y_t = Y_e \, s_{tj} \, f_{tj}, \tag{7}$$

where s_{tj} is the element of the survival rate matrix **S**, representing the probability that an egg survives to age t while in the female stage, while f_{tj} is the element of the fecundity matrix **F**, representing the fecundity of a female individual of age t. If all eggs laid at time t can be harvested, the number of harvested eggs (Y_h) will be

$$Y_h = Y_t = Y_e \, s_{tj} \, f_{tj}. \tag{8}$$

However, in a self-sustained mass-rearing system, the same number of Y_e eggs laid on day t have to be used as the recruits to the colony, the number of harvested eggs Y_h can be calculated as

$$Y_h = Y_e \, s_{tj} \, f_{tj} - Y_e. \tag{9}$$

It can be rewritten as

$$Y_h = Y_e(s_{tj} \, f_{tj} - 1). \tag{10}$$

If eggs laid during time interval t' to t are harvested, then the total number of harvested eggs is given by

$$Y_h = Y_e \sum_{x=t'}^{t} s_{xj} \, f_{xj}. \tag{11}$$

Similarly, for a self-sustained colony where only those eggs laid on day u ($t' \le u \le t$) can be saved as recruits, the number of harvested eggs is given by

$$Y_h = Y_e \cdot \left\{ \sum_{x=t'}^{t} s_{xj} \, f_{xj} - s_{uj} \, f_{uj} + (s_{uj} \, f_{uj} - 1) \right\}. \tag{12}$$

Mathematically, Equation 12 can be rearranged as

$$Y_h = Y_e \cdot \left\{ \sum_{x=t'}^{t} s_{xj} \, f_{xj} - 1 \right\}. \tag{13}$$

Because $s_{uj} f_{uj} > 1$ (equation 12) is necessary for a positive harvest, equation 12 should not be replaced by equation 13.

Harvesting Other Life Stages

Age-specific Mass Rearing and Harvesting. If Y_e newly laid eggs are input into the mass-rearing system at the beginning, and after t days all individuals (aged t) developed from these eggs will be harvested, the harvested number Y_h can be calculated as

$$Y_h = Y_e l_t. \tag{14}$$

If the colony has to be self-sustained, some individuals have to be saved to produce eggs for the next generation. Thus, the harvested number Y_h must be less than $Y_e l_t$. It can be calculated from

$$Y_h = Y_e l_t h, \tag{15}$$

where h is the harvest rate ($0 < h < 1$). Moreover, if Y_d eggs from those eggs reproduced on day u ($u \ge t$) are used as recruits for the next generation, Y_d can be calculated from

$$Y_d = Y_e l_u m_u (1 - h). \tag{16}$$

If h is small, Y_h might be unable to meet the required harvest amount, while the remaining individuals produce excessive eggs for the next generation, that is $Y_d >> Y_e$. On the contrary, if h is too large, the remaining individuals will be unable to supply enough eggs for the next generation, or $Y_d << Y_e$. Obviously, for any u, that gives $l_u m_u > 1$, there will be one and only one h_{eq} (the equilibrious harvest rate) which gives $Y_d = Y_e$ and thus

$$l_u m_u (1 - h_{eq}) = 1. \tag{17}$$

Equation 17 can be used to calculate the h_{eq} at age t, which allows the mass-rearing system to be self-sustained with exact Y_e recruitment at age u. Thus, h_{eq} depends on u, while Y_h depends on both u and t.

Stage-specific Mass Rearing and Harvesting. Based on the age-stage, two-sex life table, if Y_e eggs are input into the mass-rearing system at the beginning and after t days all individuals newly developed to stage j will be harvested, the harvested number Y_h is then given by

$$Y_h = Y_e \, s_{t-1j-1} \, d_{t-1j-1}, \tag{18}$$

where d_{t-1j-1} is the element of the developmental rate matrix **D**, representing the probability that an individual of age $t-1$ and stage $j-1$ will develop to stage j and age t after one day. However, on day $t-1$ some individuals might already be in stage j; therefore, it is necessary to remove those individuals from the colony in order to apply equation 18 properly. Such a rearing procedure would be very complicated. If the age difference among individuals of the same stage is not important, a simpler procedure is to harvest all individuals of stage j on day t; then, the harvest number Y_h will be

$$Y_h = Y_e s_{tj}. \tag{19}$$

If the age difference among individuals of the same stage cannot be completely ignored and only individuals which developed to stage j during the period $t - a$ to t are harvested, the harvest number Y_h is

$$Y_h = Y_e \cdot \left\{ \sum_{x=t-a}^{t-1} \left[s_{x-1j-1} d_{x-1j-1} \prod_{y=x}^{t-1} g_{yj} \right] + s_{t-1j-1} d_{t-1j-1} \right\} \tag{20}$$

where g_{yj} are the elements of a growth matrix **G**, representing the probability that an individual of age y and stage j will survive to age $y + 1$ while remaining in stage j. In a two-sex population model, the male stage (k) is given in the last column of the population matrix (Chi & Liu 1985, Chi 1988). If the male adults are harvested, the following three equations must be used instead of equations 18, 19 and 20.

$$Y_h = Y_e s_{t-1k-2} d_{t-1k-1}, \tag{21}$$

$$Y_h = Y_e s_{tk}, \tag{22}$$

$$Y_h = Y_e \cdot \left\{ \sum_{x=t-a}^{t-1} \left[s_{x-1k-2} d_{x-1k-1} \prod_{y=x}^{t-1} g_{yk} \right] + s_{t-1k-2} d_{t-1k-1} \right\}, \tag{23}$$

where s_{t-1k-2} is the probability that an egg survives to age $t-1$ and is in the pupal stage and d_{t-1k-1} is the probability that a pupa of age $t-1$ will develop to the male stage (Chi 1988). Equation 21 gives the number of harvested individuals which developed to the male stage on day t. Equation 22 gives the total number of males harvested on day t, while Equation 23 gives the number of males within age range $t-a$ to t.

In a self-sustained rearing program, some individuals have to be saved as recruits. Assuming only the individuals newly developed to stage j will be harvested (equation 18) and h is the harvest rate, the harvest number Y_h on day t is then

$$Y_h = h \cdot Y_e s_{t-1j-1} d_{t-1j-1}. \tag{24}$$

Because the matrix **D** is influenced by harvesting, a new matrix of developmental rates **D′** should be calculated, where $d'_{ij} = d_{ij}$ except for $d'_{t-1j-1} = d_{t-1j-1}(1 - h)$. Consequently, a new survival matrix **S′** can then be calculated from **D′** and **G** as described by Chi & Liu (1985). The number of eggs laid on day u ($u \geq t$) will be

$$Y_d = Y_e \, s'_{uj}(h) \, f_{uj}. \tag{25}$$

In Equation 25, f_{uj} is the fecundity of a female at age u, $s'_{uj}(h)$ is the probability that an egg will survive to age u and be in the female stage when the harvest rate is h. An equilibrious harvest strategy is to have $Y_d = Y_e$, i.e.,

$$s'_{uj}(h_{eq}) f_{uj} = 1. \tag{26}$$

The equilibrious harvest rate h_{eq} can be obtained by solving equation 26 numerically.

The Discard Age. For a more economic rearing program, it is sometimes necessary to discard older individuals to save space and food. Carey & Vargas (1985) used the optimal harvest rate per adult female to determine the discard age. Based on the two-sex life table, Chi & Getz (1988) used the maximal reproduction rate per adult to determine the discard age. In a periodic mass-rearing model, the discard age may be quite variable with different criteria. In this section, the basic concept is described according to different harvest strategies.

Discard Age for Harvesting the Egg Stage. If c_y is used to represent the cost of keeping an individual of age y for one day, the production rate/cost ratio for Equation 4 will be

$$r(d) = \frac{Y_e \sum_{x=t'}^{d} l_x m_x}{Y_e \sum_{y=1}^{d} l_y c_y} = \frac{\sum_{x=t'}^{d} l_x m_x}{\sum_{y=1}^{d} l_y c_y} \tag{27}$$

where the denominator $\Sigma \, l_y c_y$ is the total cost of keeping an individual from birth to age d. The maximal $r(d)$ gives the last age d which should be kept in the mass-rearing colony for an optimal production rate/cost ratio. A similar equation can be formulated for equation 5.

If c_{xy} is used to represent the cost of keeping an individual of age x and stage y for one day, the production rate/cost ratio for the stage-specific harvesting (Equation 11) is

$$r(d) = \frac{Y_e \sum_{x=t'}^{d} s_{xj}\, f_{xj}}{Y_e \sum_{x=1}^{d} \sum_{y=1}^{j} s_{xy} c_{xy}} = \frac{\sum_{x=t'}^{d} s_{xj}\, f_{xj}}{\sum_{x=1}^{d} \sum_{y=1}^{j} s_{xy} c_{xy}} \qquad (28)$$

where the denominator $\Sigma\Sigma\, s_{xy}c_{xy}$ is the total cost of keeping an individual from birth to age d.

Discard Age for Harvesting Other Life Stages. For the age-specific mass-rearing model, equation 17 isused to determine the equilibrious harvest rate (h_{eq}) at age t which in turns allows the production of sustainable recruitments Y_e at age u ($u \geq t$ and $l_u m_u > 1$). Because h_{eq} is a function of u, it is denoted as $h_{eq}(u)$ in the following discussion. For a self-sustained mass rearing, the production rate/cost ratio is

$$r(t,u) = \frac{l_t h_{eq}(u)}{\sum_{y=1}^{t} l_y c_y + \sum_{y=t+1}^{u} l_y c_y [1 - h_{eq}(u)]}, \qquad (29)$$

The notation $r(t,u)$ points out that the production rate/cost ratio is a function of t and u. The maximal $r(t,u)$ gives the economically optimal discard age u_{opt} of the age-specific harvesting. In the stage-specific mass-rearing model, the production rate/cost ratio for equation 18 can be calculated as

$$r(t) = \frac{s_{t-1j-1}\, d_{t-1j-1}}{\sum_{x=1}^{t-1} \sum_{y=1}^{j-1} s_{xy} c_{xy}}. \qquad (30)$$

Because the equilibrious harvest rate h_{eq} is a function of u and Y_h is a function of t and u (equations 24, 25, and 26), the same notation $h_{eq}(u)$ and $r(t,u)$ are used in the self-sustained stage-specific harvesting. The production rate/cost ratio is given by

$$r(t,u) = \frac{s_{t-1j-1} d_{t-1j-1}\, h(u)}{\sum_{x=1}^{u} \sum_{y=1}^{j} s'_{xy} c_{xy}}. \qquad (31)$$

Similarly, the maximal $r(t,u)$ gives the economically optimal discard age u_{opt} of the stage-specific harvesting.

Use of Thermal Summation. Within a temperature range, the development rate of insects is a linear function of the temperature; in other words, a constant thermal summation is required to complete the development of a specific stage. This concept is usually described by the simple equation

$$D \cdot (T - T_0) = K \qquad (32)$$

where K is the thermal summation, T_0 is the base temperature (the lower developmental threshold), T is the ambient temperature, and D is the time required to complete the development at temperature T. Equation 33 is rearranged from equation 32 and can be used to calculate the required ambient temperature necessary for an insect to complete development by a specific time D

$$T = T_0 + K/D. \qquad (33)$$

Using this method, eggs laid on different days can be kept at different temperatures in order to have them complete development simultaneously. Thus, when harvesting the egg stage, equations 6 and 13 can be used instead of equations 5 and 12; furthermore, the restriction of $l_u m_u > 1$ and $s_{uj}\, f_{uj} > 1$ can be ignored. This gives a greater flexibility in planning the rearing facility. When harvesting any life stage (other than egg) in an age-specific model, the equilibrious solution can be calculated from

$$\sum_{x=a}^{t'} l_x m_x (1 - h_{eq}) = 1. \qquad (34)$$

Equation 34 is similar to that reported by Carey & Vargas (1985). However, equation 34 is true for a periodic mass-rearing and harvesting program based on an age-specific life table and incorporated with control of ambient temperature. The applicable range (a to t′) is usually smaller than that of a continuous mass-rearing program (Carey & Vargas 1985). For the stage-specific harvesting, the equilibrious harvest rate can be calculated from

$$\sum_{x=a}^{t'} s'_{xj}(h_{eq}) f_{xj} = 1. \qquad (35)$$

A Case of the Asian Corn Borer. The Asian corn borer, *Ostrinia furnacalis* (Guenée) (Lepidoptera: Pyralidae), is a common corn pest in Asia. Studies on rearing techniques and artificial diets have been published by Chou et al. (1980), Hirai & Legacion (1985), Hung et al. (1988), and Horng & Chu (1989). In this study, the artificial diet developed by Salama (1970) and slightly modified by Hung et al. (1988) was used. The Asian corn borer was collected from an experimental field at Taiwan Agricultural Research Institute, Taichung, Taiwan. The life history data were analyzed according to Chi's method (1988). The ma-

Table 1. Age-stage-specific growth rate for *O. furnacalis*

Age	Egg	Larva	Pupa	Female	Male
1	0.82	—	—	—	—
2	1.00	—	—	—	—
3	0.88	—	—	—	—
4	0.19	1.00	—	—	—
5	0.14	1.00	—	—	—
6	0.00	1.00	—	—	—
7	—	1.00	—	—	—
8	—	0.91	—	—	—
9	—	0.95	—	—	—
10	—	1.00	—	—	—
11	—	1.00	—	—	
12	—	1.00	—	—	—
13	—	1.00	—	—	—
14	—	1.00	—	—	—
15	—	1.00	—	—	—
16	—	0.97	—	—	—
17	—	0.99	—	—	—
18	—	0.97	—	—	—
19	—	0.91	1.00	—	—
20	—	0.90	1.00	—	—
21	—	0.76	1.00	—	—
22	—	0.83	1.00	—	—
23	—	0.74	1.00	—	—
24	—	0.80	1.00	—	—
25	—	0.75	0.98	—	—
26	—	0.73	0.94	—	1.00
27	—	0.82	0.92	1.00	1.00
28	—	0.67	0.86	1.00	1.00
29	—	0.83	0.83	1.00	1.00
30	—	1.00	0.67	1.00	1.00
31	—	0.40	0.69	1.00	0.96
32	—	1.00	0.86	1.00	0.92
33	—	1.00	0.78	1.00	0.96
34	—	0.00	0.71	0.95	0.92
35	—	—	0.83	1.00	0.96
36	—	—	0.80	0.96	0.96
37	—	—	0.75	0.96	0.88
38	—	—	0.83	0.92	0.83
39	—	—	0.60	0.96	0.95
40	—	—	1.00	0.92	0.89
41	—	—	1.00	0.82	1.00
42	—	—	0.67	0.83	0.94
43	—	—	0.00	0.88	0.67
44	—	—	—	0.80	0.73
45	—	—	—	0.83	0.38
46	—	—	—	0.80	0.67
47	—	—	—	0.63	1.00
48	—	—	—	1.00	1.00
49	—	—	—	0.40	0.50
50	—	—	—	0.00	1.00
51	—	—	—	—	1.00
52	—	—	—	—	1.00
53	—	—	—	—	1.00
54	—	—	—	—	1.00
55	—	—	—	—	1.00
56	—	—	—	—	1.00
57	—	—	—	—	1.00
58	—	—	—	—	1.00
59	—	—	—	—	1.00
60	—	—	—	—	1.00
61	—	—	—	—	1.00
62	—	—	—	—	0.00

Table 2. Age-stage-specific development rate for *O. furnacalis*

Age	Egg	Larva	P→F	P→M
1	0.00	—	—	—
2	0.00	—	—	—
3	0.12	—	—	—
4	0.81	0.00	—	—
5	0.86	0.00	—	—
6	1.00	0.00	—	—
7	—	0.00	—	—
8	—	0.00	—	—
9	—	0.00	—	—
10	—	0.00	—	—
11	—	0.00	—	—
12	—	0.00	—	—
13	—	0.00	—	—
14	—	0.00	—	—
15	—	0.00	—	—
16	—	0.00	—	—
17	—	0.00	—	—
18	—	0.03	—	—
19	—	0.09	0.00	0.00
20	—	0.10	0.00	0.00
21	—	0.22	0.00	0.00
22	—	0.17	0.00	0.00
23	—	0.26	0.00	0.00
24	—	0.20	0.00	0.00
25	—	0.25	0.00	0.02
26	—	0.27	0.04	0.02
27	—	0.18	0.00	0.08
28	—	0.33	0.06	0.08
29	—	0.17	0.02	0.15
30	—	0.00	0.15	0.18
31	—	0.60	0.19	0.12
32	—	0.00	0.10	0.05
33	—	0.00	0.17	0.06
34	—	1.00	0.21	0.07
35	—	—	0.08	0.08
36	—	—	0.10	0.10
37	—	—	0.00	0.25
38	—	—	0.17	0.00
39	—	—	0.40	0.00
40	—	—	0.00	0.00
41	—	—	0.00	0.00
42	—	—	0.33	0.00
43	—	—	0.50	0.50
44	—	—	—	—
45	—	—	—	—
46	—	—	—	—
47	—	—	—	—
48	—	—	—	—
49	—	—	—	—
50	—	—	—	—
51	—	—	—	—
52	—	—	—	—
53	—	—	—	—
54	—	—	—	—
55	—	—	—	—
56	—	—	—	—
57	—	—	—	—
58	—	—	—	—
59	—	—	—	—
60	—	—	—	—
61	—	—	—	—
62	—	—	—	—

trices of growth rates (**G**), development rates (**D**), fecundity (**F**) and survival rates (**S**) are given in Tables 1–4, respectively. Significant variation in development rates and differential survivorship can be observed in the stage frequency curve (Fig. 1). The age-specific survival rates and fecundity are also constructed (Fig. 2) and were used as an example of age-specific mass-rearing and harvesting model. However, as Chi & Getz (1988) pointed out the age-specific mass rearing model should only be applied to female populations without significant variations among indi-

Table 3. Age-stage-specific fecundity for *O. furnacalis*

Age	Egg	Larva	Pupa	Female
1	0	—	—	—
2	0	—	—	—
3	0	—	—	—
4	0	0	—	—
5	0	0	—	—
6	0	0	—	—
7	—	0	—	—
8	—	0	—	—
9	—	0	—	—
10	—	0	—	—
11	—	0	—	—
12	—	0	—	—
13	—	0	—	—
14	—	0	—	—
15	—	0	—	—
16	—	0	—	—
17	—	0	—	—
18	—	0	—	—
19	—	0	0	—
20	—	0	0	—
21	—	0	0	—
22	—	0	0	—
23	—	0	0	—
24	—	0	0	—
25	—	0	0	—
26	—	0	0	—
27	—	0	0	0
28	—	0	0	0
29	—	0	0	0
30	—	0	0	17.83
31	—	0	0	10.83
32	—	0	0	10.47
33	—	0	0	17.89
34	—	0	0	7.50
35	—	—	0	13.17
36	—	—	0	13.88
37	—	—	0	15.12
38	—	—	0	9.71
39	—	—	0	2.83
40	—	—	0	3.08
41	—	—	0	11.14
42	—	—	0	4.83
43	—	—	0	2.81
44	—	—	—	1.87
45	—	—	—	0
46	—	—	—	0
47	—	—	—	0
48	—	—	—	0
49	—	—	—	0
50	—	—	—	0
51	—	—	—	—
52	—	—	—	—
53	—	—	—	—
54	—	—	—	—
55	—	—	—	—
56	—	—	—	—
57	—	—	—	—
58	—	—	—	—
59	—	—	—	—
60	—	—	—	—
61	—	—	—	—
62	—	—	—	—

Table 4. Age-stage-specific survival rate for *O. furnacalis*

Age	Egg	Larva	Pupa	Female	Male
1	1.00	—	—	—	—
2	0.82	—	—	—	—
3	0.82	—	—	—	—
4	0.72	0.10	—	—	—
5	0.14	0.68	—	—	—
6	0.02	0.80	—	—	—
7	—	0.82	—	—	—
8	—	0.82	—	—	—
9	—	0.75	—	—	—
10	—	0.71	—	—	—
11	—	0.71	—	—	—
12	—	0.71	—	—	—
13	—	0.71	—	—	—
14	—	0.71	—	—	—
15	—	0.71	—	—	—
16	—	0.71	—	—	—
17	—	0.69	—	—	—
18	—	0.68	—	—	—
19	—	0.66	0.02	—	—
20	—	0.60	0.08	—	—
21	—	0.54	0.14	—	—
22	—	0.41	0.26	—	—
23	—	0.34	0.33	—	—
24	—	0.25	0.42	—	—
25	—	0.20	0.47	—	—
26	—	0.15	0.51	—	0.01
27	—	0.11	0.52	0.02	0.02
28	—	0.09	0.50	0.02	0.06
29	—	0.06	0.46	0.05	0.10
30	—	0.05	0.39	0.06	0.17
31	—	0.05	0.26	0.12	0.24
32	—	0.02	0.21	0.17	0.26
33	—	0.02	0.18	0.19	0.25
34	—	0.02	0.14	0.22	0.25
35	—	—	0.12	0.24	0.24
36	—	—	0.10	0.25	0.24
37	—	—	0.08	0.25	0.24
38	—	—	0.06	0.24	0.23
39	—	—	0.05	0.23	0.19
40	—	—	0.03	0.24	0.18
41	—	—	0.03	0.22	0.16
42	—	—	0.03	0.18	0.16
43	—	—	0.02	0.16	0.15
44	—	—	—	0.15	0.11
45	—	—	—	0.12	0.08
46	—	—	—	0.10	0.03
47	—	—	—	0.08	0.02
48	—	—	—	0.05	0.02
49	—	—	—	0.05	0.02
50	—	—	—	0.02	0.01
51	—	—	—	—	0.01
52	—	—	—	—	0.01
53	—	—	—	—	0.01
54	—	—	—	—	0.01
55	—	—	—	—	0.01
56	—	—	—	—	0.01
57	—	—	—	—	0.01
58	—	—	—	—	0.01
59	—	—	—	—	0.01
60	—	—	—	—	0.01
61	—	—	—	—	0.01
62	—	—	—	—	0.01

vidual development rate. As discussed in previous sections, periodic mass rearing can be manipulated case by case. A thorough numerical analysis would be unnecessary and impossible. In Table 5, several analytical results of harvesting the egg stage are listed. Because other criteria may be important, a greater harvest rate does not always mean a better rearing strategy. In this paper, theage-specific life table of the Asian corn borer is constructed using the two-sex life table; thus, the differences between age-specific and stage-specific harvesting are minor. For harvesting other life stages, the rearing program is com-

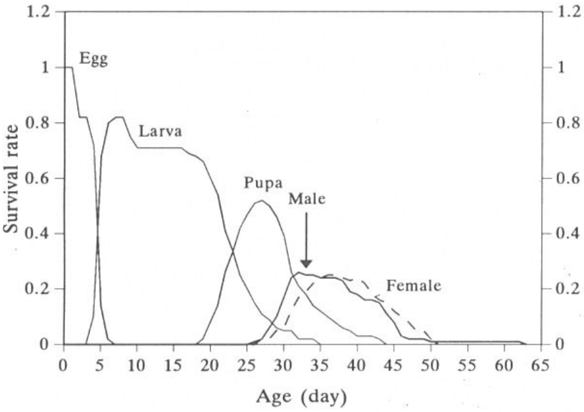

Fig. 1. Curves of age-stage specific survival rate of *O. furnacalis* at 26°C.

plicated especially when a self-sustained colony is to be maintained. Five cases are listed in Table 6. The major purpose of this paper is to report the theoretical aspect of periodic mass rearing and harvesting. Principle data given in Tables 1–4 can be used for further analysis.

Mass-rearing and harvesting of insect species is important not only to applied but also theoretical ecology. A continuous mass- rearing program can be designed according to the model developed by Chi & Getz (1988); however, it is economically justifiable only for very large-scale operations, such as state-wide or country-wide biological control. For most regional operations, a periodic mass-rearing program is more feasible. As described in this paper, periodic mass rearing is quite flexible and can be manipulated according to available facilities and required production rates. The use of thermal summation can increase the number of harvested individuals of specific stage. Based on the theoretical analysis of periodic mass rearing and harvesting, models can be constructed to satisfy specific requirements.

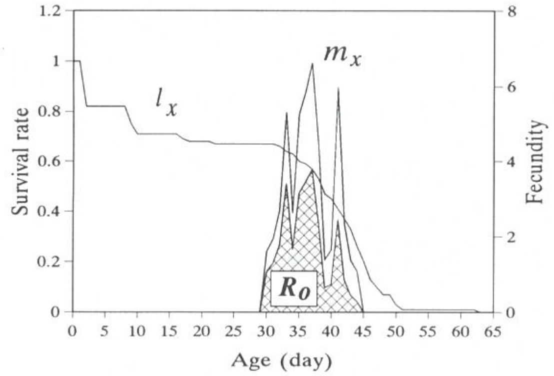

Fig. 2. Curves of age-specific survival rate (l_x) and fecundity (m_x) and the net reproductive rate (R_O) of *O. furnacalis* at 26°C.

Table 5. Number of eggs harvested by using different strategies ($Y_e = 1000, t = 35$)

Strategy	No. eggs (Y_h)	Equation
Age-specific	3,162	2
Age-specific, self-sustained	2,162	3
Age-specific (age range, 30–35)	12,360	4
Age-specific (age range, 30–35), self-sustained	11,360	5
Stage-specific	3,161	8
Stage-specific, self-sustained	2,161	9
Stage-specific (age range, 30–35)	12,359	11
Stage-specific (age range, 30–35), self-sustained	11,359	12

Table 6. Number of females harvested by using different strategies ($Y_e = 1000, t = 35$)

Strategy	No. females (Y_h)	Harvest rate (h or h_{eq})	Equation
Age-specific	600	1	14
Age-specific, self-sustained	410	0.684	15 and 17
Stage-specific	29	1	18
Stage-specific (all available females)	240	1	19
Stage-specific (females age range, 33 to 35)	78	1	20 ($a = 3$)

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