Life-Table Analysis Incorporating Both Sexes and Variable Development Rates Among Individuals

HSIN CHI[1]

Division of Biological Control, University of California, Berkeley,
Albany, California 94706

ABSTRACT Raw data analysis of an age-stage, two-sex life table, incorporating variable development rates among individuals, is described, using data obtained from rearing the potato tuberworm, *Phthorimaea operculella* (Zeller) (Lepidoptera: Gelechiidae). The intrinsic rate of increase is calculated with respect to both sexes. The stable age-stage distribution, stable age distribution, and the stable stage distribution are also calculated. Different results are obtained when the same data are analyzed using the traditional age-specific life table (Leslie matrix or Birch's method). These differences occur because the traditional age-specific life table deals only with female populations and does not take variable development rates among individuals into account. The relationship between the net reproduction rate and mean female fecundity in the age-stage, two-sex life table is described by a simple formula.

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

LIFE TABLE STUDIES are fundamental to not only demography but also to general biology. In such studies, development times and survival rates of each stage, longevity of adults, and the daily fecundity of females are recorded for every individual. Using elementary statistics, means and standard deviations can be calculated. In traditional life-table analysis, these means are used to calculate age-specific survival rates and age-specific fecundity using either the Leslie matrix (Leslie 1945) or Birch's method (Birch 1948). These procedures have been widely used by researchers in many different fields (Laing 1969, Shih et al. 1976, Cave & Gutierrez 1983, Vargas et al. 1984, Carey & Vargas 1985). However, variation in development rate is well known, even when a population is kept under constant laboratory conditions. The range of variation depends on many factors (for example, temperature and food). To assume that all individuals have the same development rate is biologically unrealistic and may be misleading. Therefore, ignorance of such variation when using either the Leslie matrix or Birch's method should be carefully considered. One method of incorporating this variation is the use of distributed delay theory in modeling (for example, Gutierrez et al. 1984, Plant & Wilson 1986). On the other hand, Chi & Liu (1985) developed an age-stage life table theory for both sexes, incorporating variable developmental rates among individuals. In comparison with the distributed delay models, Chi & Liu's model is different in that both sexes were included, and variation in development rates was integrated sequentially for all stages and expressed in the form of a stage distribution. The stage structure of a population can also be calculated in Chi & Liu's model. Furthermore, most life-table analyses have been concerned only with the "female" population. Most lepidopteran, coleopteran, and orthopteran pests are not parthenogenetic, however, and both males and females are economically important. Moreover, the development rate may differ between the sexes. Susceptibility to either chemical or biological control agents may be quite variable among stages and sexes. These and many other differences among stages and sexes explicitly point out the inadequacy of the female age-specific life table. In addition, whether to calculate the intrinsic rate of increase of a "female" population or of the population as a whole is a central question in ecology. In the theoretical model of Chi & Liu (1985), the population parameters are calculated with respect to both sexes and incorporating variable developmental rates among individuals. However, the major obstacle in taking the variable developmental rates and the male population into account is the difficult and tedious work of applying the age-stage, two-sex life table theory to the raw data analysis. The purpose of this paper is to describe a method for applying Chi & Liu's (1985) theory to the raw data collected from a life table study, using data obtained from potato tuberworm, and then to compare the results obtained by using Leslie matrix theory (Leslie 1945). The relationship between the primary sex ratio of a cohort and the net reproduction rate is derived. A simulation example is also given to illustrate the general features of results obtained in simulation work based on the age-stage two-sex life table.

Materials and Methods

Life History Study of Potato Tuberworm. A culture of the potato tuberworm, *Phthorimaea*

Table 1. Descriptive raw data of life history for individual potato tuberworms and the daily fecundity of each female

Day	1 M	2 F	3 F	4 F	5 M	6 F	7 M	8 F	9 F	10 M	11 M	12 F	13 F	14 M	15 F	16 F	17 M	18 F	19 N	20 N
1	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E
2	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E
3	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E
4	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E
5	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E
6	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E
7	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L
8	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L
9	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L
10	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L
11	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L
12	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L
13	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L
14	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L
15	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L
16	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L
17	L	P	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	—
18	P	P	P	L	L	L	L	P	L	L	L	L	L	L	L	L	L	L	L	—
19	P	P	P	P	P	P	L	P	P	P	P	P	L	L	L	L	L	L	L	—
20	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	L	L	P	—
21	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	—
22	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	—
23	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	—
24	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	—
25	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	—
26	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	—
27	P	P	P	P	P	P	P	0	P	P	P	P	P	P	P	P	P	P	P	—
28	P	0	0	P	P	P	P	0	P	P	P	P	P	P	P	P	P	P	—	—
29	P	124	22	0	P	P	P	0	P	P	P	P	P	P	P	P	P	P	—	—
30	A	12	74	97	A	0	A	26	67	A	P	P	2	P	P	P	P	P	—	—
31	A	0	13	28	A	61	A	36	37	A	A	75	90	A	P	100	A	P	—	—
32	A	4	0	1	A	11	A	9	10	A	A	48	5	A	44	17	A	9	—	—
33	A	2	1	4	A	7	A	6	5	A	A	12	12	A	53	45	A	111	—	—
34	A	0	0	0	A	15	A	2	1	A	A	4	0	A	11	8	A	27	—	—
35	A	0	0	0	—	15	A	0	0	A	A	1	0	A	15	0	A	4	—	—
36	—	0	0	—	—	2	A	0	0	—	A	0	0	A	2	0	A	0	—	—
37	—	0	0	—	—	3	A	0	0	—	A	0	0	A	0	0	A	0	—	—
38	—	—	—	—	—	4	—	—	0	—	—	0	0	A	0	0	—	—	—	—
39	—	—	—	—	—	0	—	—	—	—	—	—	0	—	0	0	—	—	—	—
40	—	—	—	—	—	0	—	—	—	—	—	—	—	—	0	—	—	—	—	—
41	—	—	—	—	—	0	—	—	—	—	—	—	—	—	0	—	—	—	—	—
42	—	—	—	—	—	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—
43	—	—	—	—	—	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—

[a] E, egg; L, larva; P, pupa; F, female; M, male; N, sex unknown.

operculella (Zeller) (Lepidoptera: Gelechiidae), was obtained from the insectary colony of the Division of Biological Control, University of California, Berkeley. One hundred eggs laid on paper towels during a 1-d period were collected. Each egg was put on a potato tuber (grade B russet potato) and kept in a glass jar (9 cm diameter, 15 cm height) containing 20 g of sand. After 10 d, tubers that did not have the normal black feces were dissected to assess larval mortality. When the larvae emerged from the tubers to pupate in the sand, each individual was placed in a separate plastic jar (4 cm diameter, 4 cm height). As the adults emerged, they were paired and kept in the same sized plastic jar covered with a piece of paper towel for egg laying. The daily survival of each adult and fecundity of females was then recorded. Rearings were conducted at 24°C.

The Raw Data and Basic Analysis. To simplify this discussion, only the descriptive raw data for 20 randomly selected potato tuberworms out of the original 100 individuals are listed in Table 1. The sex ratio of these 20 individuals was similar to the primary sex ratio of the original cohort. In Table 1 the daily history of all individuals from birth to death, including daily fecundity of females, is recorded. The developmental stages are listed as egg, larva, pupa, and adult. The sexes of individual adults were distinguished as male (M), female (F), or unknown (N, those that died before the adult stage). A dash is used to indicate a dead individual, and the numerals indicate the number of eggs deposited. The data in Table 1 are then reorganized for Table 2, the statistical summary table. In Table 2, the developmental time for each stage is summarized for each individual. The means of each stage,

Table 2. Quantitative raw data of life history for individual potato tuberworms

No.	Sex	Developmental stage (d)				Daily fecundity														
		Egg	Larva	Pupa	Adult	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	M	6	11	12	6														
2	F	6	10	11	10	0	124	12	0	4	2	0	0	0	0				
3	F	6	11	10	10	0	22	74	13	0	1	0	0	0	0				
4	F	6	12	10	7	0	97	28	1	4	0	0							
5	M	6	12	11	5														
6	F	6	12	11	14	0	61	11	7	15	15	2	3	4	0	0	0	0	0
7	M	6	13	10	8														
8	F	6	11	9	11	0	0	0	26	36	9	6	2	0	0	0			
9	F	6	12	11	9	67	37	10	5	1	0	0	0	0					
10	M	6	12	11	6														
11	M	6	12	12	7														
12	F	6	12	12	8	75	48	12	4	1	0	0	0						
13	F	6	13	10	10	2	90	5	12	0	0	0	0	0	0				
14	M	6	13	11	8														
15	F	6	13	12	10	44	53	11	15	2	0	0	0	0	0				
16	F	6	13	11	9	100	17	45	8	0	0	0	0	0					
17	M	6	14	10	6														
18	F	6	14	11	6	9	111	27	4	0	0								
19	N	6	13	8d[a]	—														
20	N	6	10d[a]	—	—														
Means	F	6	12.1	10.7	9.5	27	60	21	8.6	5.7	2.5	0.8	0.6	0.5	0	0	0	0	0
	M	6	12.4	11.0	6.6														

[a] d, death of individual during the stage.

as well as of the daily fecundity, are calculated. The range of maturation (total preadult period) is 26–31 d with a mean of 29.06 d. Assuming that all females emerged on the same day, the data in Table 2 are usually displayed in a figure with l_x and m_x curves (Fig. 1), or a table of l_x and m_x starting from the first egg-laying age. Because the traditional age-specific life table does not take stage differentiation into account, no proper way for stage grouping can be found. The simplest way is to use
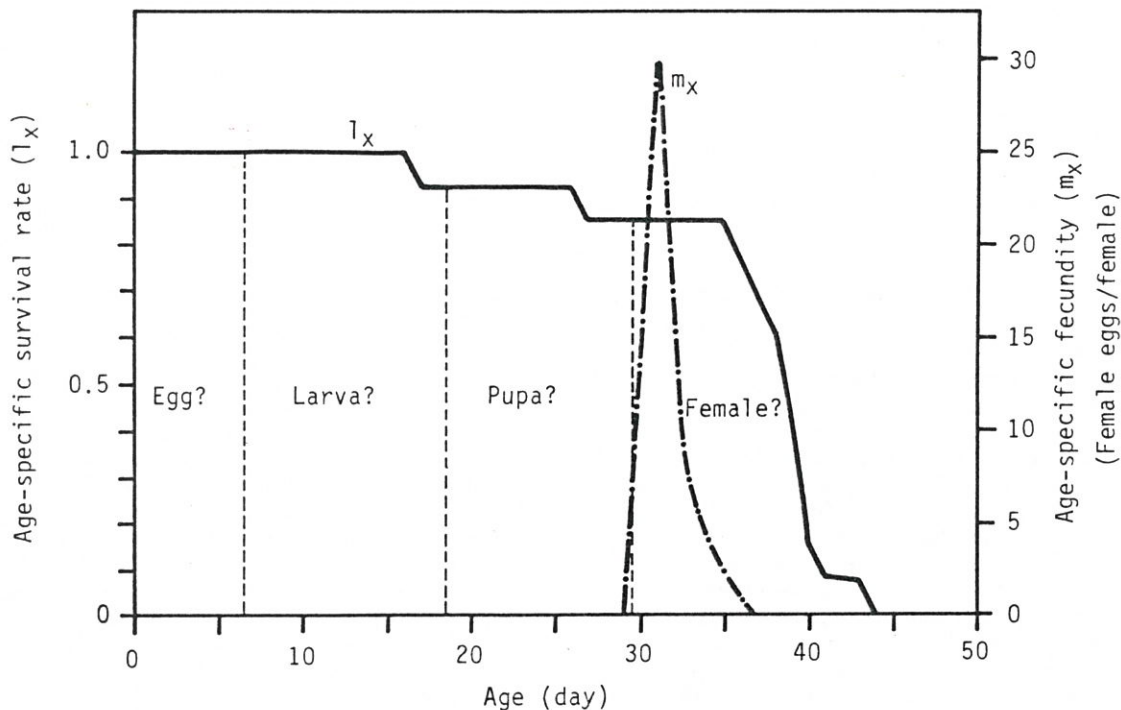

Fig. 1. The curves of age-specific survival and fecundity (m_x) rates of the potato tuberworm (female population only), constructed by using the means of developmental times (assuming that all females emerged at the same time). The stage grouping is questionable.
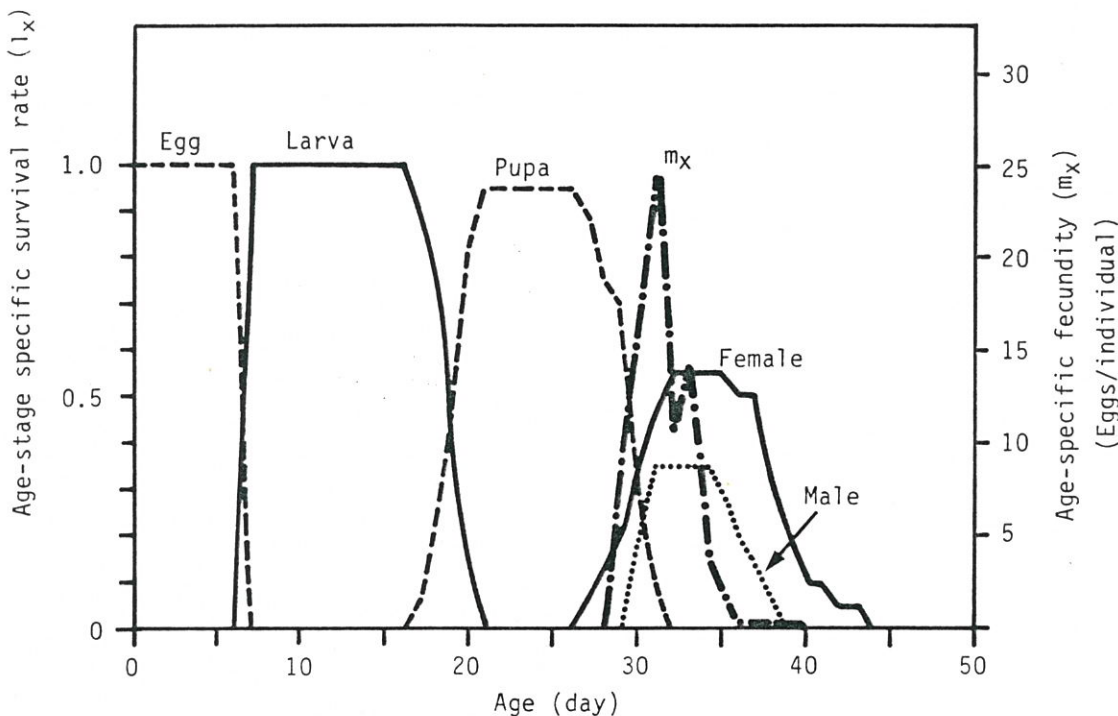
Fig. 2. The curves of age-stage specific survival rate and fecundity (m_x) of the potato tuberworm, constructed using a two-sex life-table analysis. Variable development rate is included without assuming all adults emerged on the same day. Both males and females are included.

the rounded means of each stage to divide the life span into stages. This method has been used by researchers (for example, Evans & Smith 1952, Carey 1982) and then cited in textbooks (for example, Fig. 5.4 of Pianka 1983, 109). However, the sum of the means of each preadult stage does not necessarily equal the mean of total preadult developmental period for all individuals. This inconsistency will result in problems with setting stage intervals on the time axis of the survival curve. This is one dilemma in using the traditional life table and also one of the reasons proper stage grouping is impossible in traditional age structure population theory. Many life tables based on the mean of preadult development time can be found in the literature (Laing 1969, Carey 1982, 1984a, b, Shih et al. 1976, Vargas et al. 1984). The most frequently cited references are Lewis (1942), Leslie (1945, 1948), Birch (1948), and Andrewartha & Birch (1954). Using the traditional age-specific life table, the intrinsic rate of increase, the net reproduction rate, and the mean generation time were calculated. These results are listed in Table 4 for comparison with the results of two-sex life table analysis.

However, if we follow the daily change in Table 1 and draw the numbers of each stage into curves, a clear overview can be obtained (Fig. 2). In Fig. 2, we can see the development of eggs to the subsequent stages, the emergence of males and females, and the reproductive curve of this popula-

tion. This figure illustrates the original features of development rate, survivorship, and fecundity of this population. If Fig. 1 and 2 are compared with the raw data in Table 1, obvious discrepancies can be noticed in fecundity and survival curves. In Fig. 1, where the mean of preadult developmental time was used, the females emerged and began to lay eggs on the 30th day; however, according to Table 1, the first female emerged on the 27th day and the first egg-laying began on the 29th day. Also, the shape of the fecundity curve in Fig. 1 is quite different than that in Fig. 2, where the age is counted from the egg and without assuming that all the females emerged on the same day. On the contrary, when calculating the daily mean fecundity in Table 2 and Fig. 1, we have added together the eggs laid by different individuals on different days. This is a questionable procedure. Furthermore, there are two other important differences in these figures. First, the survival curve in Fig. 1 refers only to the female population, whereas the survival curve in Fig. 2 refers to the total population. Second, because of the difficulty in distinguishing between the sexes during the preadult stages, the preadult mortality certainly contains both males and females. This mortality cannot be properly included if only the female population is considered. Based on the curves of the age-stage specific survival rate and fecundity (Fig. 2), the theoretical basis of two-sex life tables, incorporating variable development rates among individuals, was developed (Chi & Liu

Table 3. Change of number in each stage during the life history

Day	Stage					Daily total eggs	Eggs/♀ (f_{i4})
	Egg	Larva	Pupa	Female	Male		
1	20	—	—	—	—	—	—
2	20	—	—	—	—	—	—
3	20	—	—	—	—	—	—
4	20	—	—	—	—	—	—
5	20	—	—	—	—	—	—
6	20	—	—	—	—	—	—
7	—	20	—	—	—	—	—
8	—	20	—	—	—	—	—
9	—	20	—	—	—	—	—
10	—	20	—	—	—	—	—
11	—	20	—	—	—	—	—
12	—	20	—	—	—	—	—
13	—	20	—	—	—	—	—
14	—	20	—	—	—	—	—
15	—	20	—	—	—	—	—
16	—	20	—	—	—	—	—
17	—	18	1	—	—	—	—
18	—	15	4	—	—	—	—
19	—	8	11	—	—	—	—
20	—	2	17	—	—	—	—
21	—	—	19	—	—	—	—
22	—	—	19	—	—	—	—
23	—	—	19	—	—	—	—
24	—	—	19	—	—	—	—
25	—	—	19	—	—	—	—
26	—	—	19	—	—	—	—
27	—	—	18	1	—	0	0
28	—	—	15	3	—	0	0
29	—	—	14	4	—	146	36.50
30	—	—	7	7	4	278	39.71
31	—	—	2	9	7	440	48.89
32	—	—	—	11	7	158	14.36
33	—	—	—	11	7	258	23.45
34	—	—	—	11	7	68	6.18
35	—	—	—	11	6	35	3.18
36	—	—	—	10	4	4	0.40
37	—	—	—	10	3	3	0.30
38	—	—	—	6	1	4	0.67
39	—	—	—	4	—	0	0
40	—	—	—	2	—	0	0
41	—	—	—	2	—	0	0
42	—	—	—	1	—	0	0
43	—	—	—	1	—	0	0

Table 4. Population parameters of potato tuberworms calculated using a two-sex life-table analysis and the Leslie matrix approach

Parameter	Two-sex life table	Leslie matrix
Intrinsic rate (r)	0.136	0.127
Net reproduction rate (R_0)	69.7	53.6
Mean generation time (T)	31.2	31.3

stage-specific growth rate, g_{ij}), and the probability of developing to stage $j + 1$ at age $i + 1$ (the age-stage-specific developmental rate, d_{ij}). For example, there are 15 larvae and 4 pupae on the 18th day; according to Tables 1 and 3, 8 larvae from these 15 larvae have grown older in the larval stage, therefore $g_{18,2} = 8/15$ or 0.53. On the other hand, 7 larvae developed to the pupal stage, therefore $d_{18,2} = 7/15$ or 0.47. Obviously, $g_{18,3}$ equals 1. The pupal stage represents a special case. The pupae can either develop into males or females. The probability of a pupa (in this example, n_{i3}) developing into a female ($n_{i+1,4}$) is d_{i3}; the probability of a pupa (n_{i3}) developing into a male ($n_{i+1,5}$) is d_{i4}. For example, in Table 3 there are 14 pupae and 4 females on the 29th day. After 1 day, there are 7 pupae, 7 females, and 4 males. According to Tables 1 and 3, 3 of these 14 pupae developed into females and 4 into males. Therefore, $d_{29,3} = 3/14$ and $d_{29,4} = 4/14$, while $g_{29,3} = 7/14$ and $g_{29,4} = 1$. These elements of the matrices G and D are given in the Appendix. The age-stage-specific fecundity of females (f_{i4}) is calculated as the number of eggs per female and is listed in Table 3. All the remaining elements in the fecundity matrix (matrix F) are zero.

Based on matrices G, D, and F, the age-stage-specific survival rate matrix S (Appendix), as well as the population parameters, can be calculated by following the methods of Chi & Liu (1985).

Results and Discussion

Population Parameters. The intrinsic rate of increase, r, the net reproduction rate, R_0, and the mean generation time, T, are listed in Table 4. The stable age-stage distribution calculated as described in Chi & Liu (1985) is displayed in Fig. 3. The population parameters calculated using traditional age-specific life tables (Leslie matrix or Birch's method) showed obvious differences when compared with the results obtained from the age-stage, two-sex life table analysis. These differences arise because the Leslie matrix does not take the male population and variable development rates among individuals into account. As mentioned previously, the concept of a "female" life table is quite abstract for a bisexual population. There are many reasons to question the meaning of the intrinsic rate of increase of the "female" portion of a bisexual population, especially when males and females have different development rates and longevity.

Female Fecundity and Net Reproduction Rate.

1985). The detailed procedures for analyzing raw data are described below.

Two-Sex Life Table Analysis. According to Chi & Liu (1985), the population structure can be described by using an age-stage-matrix N with n rows and m columns (n is the number of age groups and m is the number of stage groups). In this model, the survival rate is considered as a composition of the growth (getting older in the same stage) and development rates (getting older and developing to the next stage). This concept is consistent with reality but makes the raw data analysis more difficult. The first step in the two-sex life table analysis is to reduce Table 1 to a stage frequency table (Table 3). In Table 3 the daily number of individuals in each stage is recorded from the birth to the death of this cohort. Then, using Tables 1 and 3, we can estimate the probability of an individual in age i and stage j growing to age $i + 1$ but remaining in stage j after one age interval (the age-

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1	20	—	—	—	—	—	—
2	20	—	—	—	—	—	—
3	20	—	—	—	—	—	—
4	20	—	—	—	—	—	—
5	20	—	—	—	—	—	—
6	20	—	—	—	—	—	—
7	—	20	—	—	—	—	—
8	—	20	—	—	—	—	—
9	—	20	—	—	—	—	—
10	—	20	—	—	—	—	—
11	—	20	—	—	—	—	—
12	—	20	—	—	—	—	—
13	—	20	—	—	—	—	—
14	—	20	—	—	—	—	—
15	—	20	—	—	—	—	—
16	—	20	—	—	—	—	—
17	—	18	1	—	—	—	—
18	—	15	4	—	—	—	—
19	—	8	11	—	—	—	—
20	—	2	17	—	—	—	—
21	—	—	19	—	—	—	—
22	—	—	19	—	—	—	—
23	—	—	19	—	—	—	—
24	—	—	19	—	—	—	—
25	—	—	19	—	—	—	—
26	—	—	19	—	—	—	—
27	—	—	18	1	—	0	0
28	—	—	15	3	—	0	0
29	—	—	14	4	—	146	36.50
30	—	—	7	7	4	278	39.71
31	—	—	2	9	7	440	48.89
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33	—	—	—	11	7	258	23.45
34	—	—	—	11	7	68	6.18
35	—	—	—	11	6	35	3.18
36	—	—	—	10	4	4	0.40
37	—	—	—	10	3	3	0.30
38	—	—	—	6	1	4	0.67
39	—	—	—	4	—	0	0
40	—	—	—	2	—	0	0
41	—	—	—	2	—	0	0
42	—	—	—	1	—	0	0
43	—	—	—	1	—	0	0

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Mean generation time (T)	31.2	31.3

stage-specific growth rate, g_{ij}), and the probability of developing to stage $j + 1$ at age $i + 1$ (the age-stage-specific developmental rate, d_{ij}). For example, there are 15 larvae and 4 pupae on the 18th day; according to Tables 1 and 3, 8 larvae from these 15 larvae have grown older in the larval stage, therefore $g_{18,2} = 8/15$ or 0.53. On the other hand, 7 larvae developed to the pupal stage, therefore $d_{18,2} = 7/15$ or 0.47. Obviously, $g_{18,3}$ equals 1. The pupal stage represents a special case. The pupae can either develop into males or females. The probability of a pupa (in this example, n_{i3}) developing into a female ($n_{i+1,4}$) is d_{i3}; the probability of a pupa (n_{i3}) developing into a male ($n_{i+1,5}$) is d_{i4}. For example, in Table 3 there are 14 pupae and 4 females on the 29th day. After 1 day, there are 7 pupae, 7 females, and 4 males. According to Tables 1 and 3, 3 of these 14 pupae developed into females and 4 into males. Therefore, $d_{29,3} = 3/14$ and $d_{29,4} = 4/14$, while $g_{29,3} = 7/14$ and $g_{29,4} = 1$. These elements of the matrices G and D are given in the Appendix. The age-stage-specific fecundity of females (f_{i4}) is calculated as the number of eggs per female and is listed in Table 3. All the remaining elements in the fecundity matrix (matrix F) are zero.

Based on matrices G, D, and F, the age-stage-specific survival rate matrix S (Appendix), as well as the population parameters, can be calculated by following the methods of Chi & Liu (1985).

Results and Discussion

Population Parameters. The intrinsic rate of increase, r, the net reproduction rate, R_0, and the mean generation time, T, are listed in Table 4. The stable age-stage distribution calculated as described in Chi & Liu (1985) is displayed in Fig. 3. The population parameters calculated using traditional age-specific life tables (Leslie matrix or Birch's method) showed obvious differences when compared with the results obtained from the age-stage, two-sex life table analysis. These differences arise because the Leslie matrix does not take the male population and variable development rates among individuals into account. As mentioned previously, the concept of a "female" life table is quite abstract for a bisexual population. There are many reasons to question the meaning of the intrinsic rate of increase of the "female" portion of a bisexual population, especially when males and females have different development rates and longevity.

Female Fecundity and Net Reproduction Rate.

1985). The detailed procedures for analyzing raw data are described below.

Two-Sex Life Table Analysis. According to Chi & Liu (1985), the population structure can be described by using an age-stage-matrix N with n rows and m columns (n is the number of age groups and m is the number of stage groups). In this model, the survival rate is considered as a composition of the growth (getting older in the same stage) and development rates (getting older and developing to the next stage). This concept is consistent with reality but makes the raw data analysis more difficult. The first step in the two-sex life table analysis is to reduce Table 1 to a stage frequency table (Table 3). In Table 3 the daily number of individuals in each stage is recorded from the birth to the death of this cohort. Then, using Tables 1 and 3, we can estimate the probability of an individual in age i and stage j growing to age $i + 1$ but remaining in stage j after one age interval (the age-

Appendix

Matrix G: Age-stage specific growth rate

Age	Egg	Larva	Pupa	Female	Male
1	1.00	—	—	—	—
2	1.00	—	—	—	—
3	1.00	—	—	—	—
4	1.00	—	—	—	—
5	1.00	—	—	—	—
6	0.00	—	—	—	—
7	—	1.00	—	—	—
8	—	1.00	—	—	—
9	—	1.00	—	—	—
10	—	1.00	—	—	—
11	—	1.00	—	—	—
12	—	1.00	—	—	—
13	—	1.00	—	—	—
14	—	1.00	—	—	—
15	—	1.00	—	—	—
16	—	0.90	—	—	—
17	—	0.83	1.00	—	—
18	—	0.53	1.00	—	—
19	—	0.25	1.00	—	—
20	—	0.00	1.00	—	—
21	—	—	1.00	—	—
22	—	—	1.00	—	—
23	—	—	1.00	—	—
24	—	—	1.00	—	—
25	—	—	1.00	—	—
26	—	—	0.95	—	—
27	—	—	0.83	1.00	—
28	—	—	0.93	1.00	—
29	—	—	0.50	1.00	—
30	—	—	0.29	1.00	1.00
31	—	—	0.00	1.00	1.00
32	—	—	—	1.00	1.00
33	—	—	—	1.00	1.00
34	—	—	—	1.00	0.86
35	—	—	—	0.91	0.67
36	—	—	—	1.00	0.75
37	—	—	—	0.60	0.33
38	—	—	—	0.67	0.00
39	—	—	—	0.50	—
40	—	—	—	1.00	—
41	—	—	—	0.50	—
42	—	—	—	1.00	—
43	—	—	—	0.00	—

Matrix D: Age-stage specific development rate

Age	Egg	Larva	Pupa	Female	Male
1	0.00	—	—	—	—
2	0.00	—	—	—	—
3	0.00	—	—	—	—
4	0.00	—	—	—	—
5	0.00	—	—	—	—
6	1.00	—	—	—	—
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	—	0.05	—	—	—
17	—	0.17	0.00	0.00	—
18	—	0.47	0.00	0.00	—
19	—	0.75	0.00	0.00	—
20	—	1.00	0.00	0.00	—
21	—	—	0.00	0.00	—
22	—	—	0.00	0.00	—
23	—	—	0.00	0.00	—
24	—	—	0.00	0.00	—
25	—	—	0.00	0.00	—
26	—	—	0.05	0.00	—
27	—	—	0.11	0.00	—
28	—	—	0.07	0.00	—
29	—	—	0.21	0.29	—
30	—	—	0.29	0.43	—
31	—	—	1.00	0.00	—
32	—	—	—	—	—
33	—	—	—	—	—
34	—	—	—	—	—
35	—	—	—	—	—
36	—	—	—	—	—
37	—	—	—	—	—
38	—	—	—	—	—
39	—	—	—	—	—
40	—	—	—	—	—
41	—	—	—	—	—
42	—	—	—	—	—
43	—	—	—	—	—

Female fecundity is usually defined as the mean number of eggs per female, while the net reproduction rate is defined as $R_0 = \Sigma l_x m_x$ (the number of female offspring per female). Obviously, both of them are calculated from the same data (Table 1). Is there any relationship between these two values? Table 5 lists some data from the literature. All these data were calculated using the Leslie matrix or Birch's method. The sex ratios are included when available. No relationship between the mean fecundity and the net reproductive rate is apparent. As only females are considered, one can calculate m_x by counting the eggs laid daily, rearing them to the adult stage, then counting the number of females. One can omit the last two steps by using the sex ratio of the parent population, or by assuming a 1:1 sex ratio. Although sex determination by the first method is very tedious and sometimes impossible, assuming a 1:1 sex ratio or using the sex ratio of the parent generation is a questionable procedure because of generation-to-generation variation.

However, in the two-sex life-table analysis, the relationship between these two values can be derived as follows. By starting with N eggs, the survival number to each age-stage class is $N \cdot s_{ij}$, and the total number of eggs laid by the adults emerged from these original N eggs is

$$\sum_{i=1}^{n} \sum_{j=1}^{m} N s_{ij} f_{ij} \qquad (1)$$

If N_f females emerged from these N eggs, then the mean fecundity (F) per female is

$$F = \left(\sum_{i=1}^{n} \sum_{j=1}^{m} N s_{ij} f_{ij} \right) / N_f \qquad (2)$$

In the two-sex life table, the net reproduction rate is defined as $R_0 = \Sigma\Sigma s_{ij} f_{ij}$. Therefore, the relationship between F and R_0 is from equations (1) and (2)

$$F = (N/N_f) \cdot R_0$$

This formula can be rewritten as $R_0 = F(N_f/N)$,

Matrix S: Survival rate to each age-stage interval

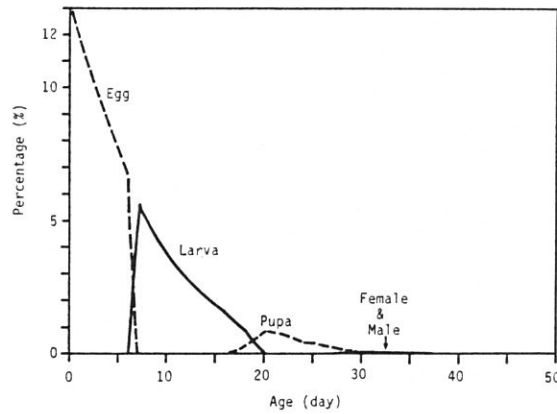| Age	Egg	Larva	Pupa	Female	Male
1	1.00	—	—	—	—
2	1.00	—	—	—	—
3	1.00	—	—	—	—
4	1.00	—	—	—	—
5	1.00	—	—	—	—
6	1.00	—	—	—	—
7	—	1.00	—	—	—
8	—	1.00	—	—	—
9	—	1.00	—	—	—
10	—	1.00	—	—	—
11	—	1.00	—	—	—
12	—	1.00	—	—	—
13	—	1.00	—	—	—
14	—	1.00	—	—	—
15	—	1.00	—	—	—
16	—	1.00	—	—	—
17	—	0.90	0.05	—	—
18	—	0.75	0.20	—	—
19	—	0.40	0.55	—	—
20	—	0.10	0.85	—	—
21	—	—	0.95	—	—
22	—	—	0.95	—	—
23	—	—	0.95	—	—
24	—	—	0.95	—	—
25	—	—	0.95	—	—
26	—	—	0.95	—	—
27	—	—	0.90	0.05	—
28	—	—	0.75	0.15	—
29	—	—	0.70	0.20	—
30	—	—	0.35	0.35	0.20
31	—	—	0.10	0.45	0.35
32	—	—	—	0.55	0.35
33	—	—	—	0.55	0.35
34	—	—	—	0.55	0.35
35	—	—	—	0.55	0.30
36	—	—	—	0.50	0.20
37	—	—	—	0.50	0.15
38	—	—	—	0.30	0.05
39	—	—	—	0.20	—
40	—	—	—	0.10	—
41	—	—	—	0.10	—
42	—	—	—	0.05	—
43	—	—	—	0.05	—

Fig. 3. The stable age-stage distribution of the potato tuberworm. Males and females comprise <1% of the stable population.

and the total number of individuals in stage j is

$$N_j = \sum_{i=1}^{n} n_{ij}$$

Therefore, in the simulation based on the age-stage, two-sex life table, the curves for each stage and for the total population can be obtained. In Fig. 4, unlimited population growth of the potato tuberworm is simulated starting with 100 eggs. The result gives a complete age-stage description for each time period.

Conclusions

Variation in development rate is a common phenomenon in biology, and ignoring this variation results in changes in the survival and fecundity curves. These changes, in turn, affect the precision of the life tables that are constructed. Two-sex life-table analysis offers the following advantages: since it takes variability in development rate among individuals into account, it is more realistic than those based only on the means of development times; it deals with the total population (male, female, and those that die before the adult stages); and in simulation studies it accounts for the complete age-stage distribution of the population. The last point is important because we sample only specific stages in field studies, different stages have different susceptibilities to insecticides, and there are very different behavioral patterns between stages.

Even in parthenogenetic populations, development rate varies. For precise data analysis, life-table studies of these populations should also be analyzed using the two-sex life table but ignoring the male column. For parthenogenetic populations, one can easily prove whether using the means to construct life tables will result in serious errors. By ignoring the stage differentiation and counting the age from the day the eggs were laid, then calculating the age-specific survival rate and fecundity,

where N_f/N is the proportion of these N eggs which develop into females. The F obtained by using the above formula gives the same value as that obtained by using routine statistics. The absence of a clear relationship between the values for R_0 and F (Table 5) obtained by using the Leslie matrix or Birch's method is a consequence of the assumption that all individuals have the same developmental rate, which results in the fecundity curve of each individual being moved to the same day.

Simulation of Population Growth. Without taking the male population and variable development rates into account, simulating population growth generally generates a single curve—the total female population without stage grouping. This is inconvenient for simulation work in both theoretical and applied research. Ignoring developmental variation may also result in inaccurate simulations. According to Chi & Liu (1985), the total population size N_t is given by

$$N_t = \sum_{i=1}^{n} \sum_{j=1}^{m} n_{ij}$$

Table 5. Data of mean fecundities (F), net reproduction rates (R_0), and sex ratio of some insects and mites species cited from the literature

Species	F	R_0	Sex ratio	Reference
Spodoptera litura	1,587	405.91	1:1	Chen & Hsiao (1984)
Spodoptera litura	1,218	262.62	1.78:1	Chen & Hsiao (1984)
Lygus hesperus	49.7	6.09	Unavailable	Cave & Gutierrez (1983)
Tetranychus urticae	37.9	30.93	2.9:1	Laing (1969)
Tetranychus urticae	103.3	74.84	16:8	Carey & Bradley (1982)
Tetranychus pacificus	78.9	44.65	15:9	Carey & Bradley (1982)
Tetranychus urticae	143.9	97.4	Unavailable	Shih et al. (1976)
Dacus cucurbitae	880.6	255.4	1:1	Vargas et al. (1984)
Dacus dorsalis	1,428.2	418.5	1:1	Vargas et al. (1984)
Ceratitis capitata	994.6	317.5	1:1	Vargas et al. (1984)
Hypoaspis aculeifer	87	36.1	4:1	Chi (1981)
Pediobius foveolatus	58.0	50.9	Unavailable	Kauffman & Flanders (1985)
Epilachna varivestis	621.4	76.4	Unavailable	Kauffman et al. (1985)

the population parameters obtained will be exactly the same as when using the two-sex life table. Furthermore, for any two-sex population, including the males as non-egg-laying females while ignoring the stage, the population parameters obtained are the same as when using the age-stage, two-sex life table. These results support the age-stage, two-sex life table theory. However, using the Leslie matrix or Birch's method, it is not possible to draw the stage curve. The difference between the results obtained using the age-stage, two-sex life table and a traditional age-specific life table depends on the variation in development rates and the primary sex ratio. Since the mean duration of preadult stages is always greater than the first adult emergence, the m_x curve in traditional age-specific life tables starts later than the true one. This results in a decrease in the intrinsic rate of increase. However, using the mean development times also moves the fecundity curves of each individual closer to the mean of the preadult stage. This generally results in a higher peak on the m_x curve and an increase in the intrinsic rate of increase. These effects are well known in demography (e.g., see Price 1984, chapter 10). Thus these two phenomena have a compensatory effect, decreasing the difference between the population parameters obtained using traditional life table and using the age-stage, two-

sex life table, especially when the primary sex ratio is close to 1:1. But many significant differences can be noted, some mentioned above. It is not possible to group stages properly using an age-specific life table. The true population can be described properly only when the male population is included—one should not assume that the size of the male population can be obtained by multiplying the number of females by a simple index (for example, sex ratio), as in many species the males have different developmental rates and longevity. Stage differentiation is not only a fascinating phenomenon in the biology of arthropods but also in quantitative population ecology. Differences in behavior, habitat, susceptibility to control agents, and many other factors illustrate the importance of information concerning the stage structure of a population. Stage structure will undoubtedly be an important part of proper timing of treatments in I.P.M.

For a two-sex, age-stage analysis of raw data, the author has developed a user-friendly computer program called LIFETABL, written in BASIC and implemented on an IBM–PC microcomputer. The output includes color graphics utilities. Interested readers should contact the author for further information.

Fig. 4. Simulation of the population growth of the potato tuberworm based on a two-sex life table.

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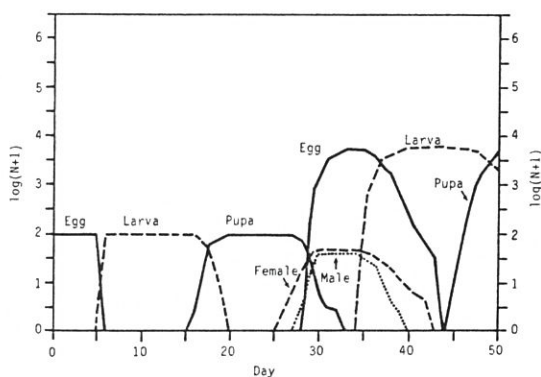Carey, J. R. 1982. Demography and population dynamics of the Mediterranean fruit fly. Ecol. Model. 16: 125–150.

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Hsin Chi
P.O. Box 17-25
Taichung, Taiwan 40098
Republic of China