Age-Stage, Two-Sex Life Tables of *Aphidius gifuensis* (Ashmead) (Hymenoptera: Braconidae) and Its Host *Myzus persicae* (Sulzer) (Homoptera: Aphididae) with Mathematical Proof of the Relationship Between Female Fecundity and the Net Reproductive Rate

HSIN CHI[1] AND HAW-YUAN SU

Laboratory of Theoretical Ecology, Department of Entomology, National Chung Hsing University, 400 Taichung, Taiwan, Republic of China

ABSTRACT Life history data for *Aphidius gifuensis* (Ashmead) and *Myzus persicae* (Sulzer) were collected in the laboratory. To consider both sexes and variable developmental rates among individuals, the raw data were analyzed using the age-stage, two-sex life table. The intrinsic rate of increase (r) for *A. gifuensis* is 0.264 d^{-1}. The mean parasitism rate is 92.3 aphids per female. The intrinsic rate of increase for *M. persicae* is 0.252 d^{-1}. For applying the female age-specific life table to a female population, we prove that the relationship between the mean female fecundity (F) and the net reproductive rate (R_0) is $R_0 = s_a F$, where s_a is the preadult survival rate. When the female age-specific life table is applied to two-sex populations, the relationship between F and R_0 is $R_0 = s_a w F$, where s_a is the preadult survival rate of females, and w is the female proportion in offspring. This is valid when w is a constant for the age-specific fecundity (m_x) of all ages. Because sexing preadult individuals is difficult, and obtaining a constant sex ratio in offspring is uncertain, determining preadult mortality of the individual sexes may be problematical. As a result, calculations of the age-specific survival rate (l_x) and fecundity and population parameters may be adversely affected. Moreover, if l_x and m_x are constructed based on adult age, they may also cause errors in population parameters. Because the application of female age-specific life table to stage-structured bisexual population results in inaccuracies, we recommend that the age-stage, two-sex life table should be used in insect demographic studies.

KEY WORDS life table, *Aphidius gifuensis* (Ashmead), *Myzus persicae* (Sulzer), parasitoid

Aphidius gifuensis (Ashmead) is one of the common parasitoids of the green peach aphid, *Myzus persicae* (Sulzer), in Taiwan (Tao 1972), China (Tang and Chen 1984), and Japan (Takada 1976, 2002, Nakata 1995). It has been studied as a biological control agent against *M. persicae* (e.g., Ohta et al. 2001, Wei et al. 2003). As a worldwide pest, *M. persicae* has been frequently studied (e.g., Cole 1997, Guldemond et al. 1998, Sauge et al. 1998). For quantitative analysis on mass rearing and practical application of insect natural enemies in biological control, it is crucial to know the development, the stage differentiation, the reproduction, and the predation rate of the target populations. Because a cohort life table gives the most comprehensive description of the growth, development, and reproduction of a population (Lotka 1907, Lewis 1942, Leslie 1945), its importance in the study of population dynamics has been realized for decades (van den Bosch et al. 1973). A comparative study of the cohort life tables of both predator and prey in the laboratory reveals their biological potential under controlled conditions and forms the basis for modeling of predator–prey or parasitoid–host dynamics. Although the development of age-structured population models has a long history (see Charlesworth 1994), the importance of incorporating the age structure in predation theory was recognized much later by Hassell (1978). However, because traditional age-specific life tables (e.g., Lotka 1907, Lewis 1942, Leslie 1945, Birch 1948) deal only with female individuals and ignore variation in the developmental rate among individuals, they are unable to take the predation rate of males and the variable predation rate of different stages into consideration. Still, the intrapopulation variations in developmental rate among individuals are important for a population to survive the natural selection of an environment with very unpredictable onset of harsh conditions (Istock 1981, Price 1997) and should be incorporated into the life table analysis. To take into account the variable developmental times among individuals, the stage differentiation, and both sexes, Chi

---

[1] Corresponding author: Box 17–25, Taichung 40098, Taiwan, Republic of China (e-mail: hsinchi@dragon.nchu.edu.tw).

and Liu (1985) and Chi (1988) developed the age-stage, two-sex life table theory and data analysis. Because variation in developmental rate among individuals and between sexes in a natural population is common, an age-stage structured model helps take the variation in the predation rate and the survival rate of individuals of the same age but different stage into consideration. Based on the age-stage, two-sex life table, Chi and Getz (1988) built a mass rearing and harvesting model. Chi (1990) simulated the timing of control based on the age-stage, two-sex life table. Chi and Yang (2003) reported the age-stage life table and predation rate of the predator *Propylaea japonica* Thunberg (Coleoptera: Coccinellidae) fed on *Myzus persicae.* In this paper, we use the age-stage, two-sex life table theory to analyze the life history data of the parasitoid *A. gifuensis* and its host *M. persicae*, as well as the parasitism rate of *A. gifuensis.* We define the curtailed intrinsic rate of increase to explore the effect of population survival on the intrinsic rate. We then show the inaccuracies inherent in life tables based solely on adult age. Furthermore, we give a theoretical proof on the relationship between the female mean fecundity and the net reproductive rate for the female age-specific life table.

Materials and Methods

Life Table Study. *Myzus persicae* (Sulzer) (Homoptera: Aphididae) were obtained by cutting aphid-infested portions from the leaves of 30 randomly selected kale plants (*Brassica oleracea* L. variety *alboglabra* Musil) growing in a vegetable plot on the campus of National Chung Hsing University, Taichung, Taiwan. To expand the aphid gene pool, no more than two aphids were selected from each leaf portion. Aphids were maintained separately in individual petri dishes. Parasitoids of *A. gifuensis* (Ashmead) (Hymenoptera: Braconidae) were collected by placing 20 potted kale plants with an abundance of *M. persicae* in the same vegetable field.

Life Table of *M. persicae.* Single seedlings of kale planted in plastic pots (9 cm in diameter, 7 cm in height) with commercial potting soil were used as rearing containers. A cylinder (8.8 cm in diameter, 10.5 cm in height) made of overhead projector film was placed on each individual pot. On the top of the cylinder, a reversed plastic cup (9 cm in diameter, 5.5 cm in height) was used as the cover. A 4-cm diameter hole was cut at the center of the cup bottom and covered with fine mesh cloth for ventilation. For the life table study, one female adult of *M. persicae* was placed on each of 52 kale seedlings and kept in a growth chamber ($25 \pm 1°C$, $65 \pm 5\%$ RH, and a photoperiod of 12:12 [L:D] h) for 12 h (using two 20-W fluorescent plant light bulbs and two 20-W regular fluorescent light bulbs). Subsequently, one newborn nymph was kept on each seedling, and the female adult and remaining nymphs were removed. A total number of 52 *M. persicae* were used for the life table study. The development, survival, and fecundity of individual aphids were recorded every 12 h until the

death of each individual. Life table data for *M. persicae* were collected during November and December 1993.

Life Table of *A. gifuensis.* The parasitoid was kept in a growth chamber under the same conditions as *M. persicae.* For the life table study, 10 rearing containers each with ≈ 100 *M. persicae* on kale and a small vial of 10% honey water were used. Three male and three female young adults (3–5 d old) of *A. gifuensis* were released into each container and removed after a 24-h period. The aphids on kale were observed daily for the formation of mummies. Mummies were collected into individual glass vials (1.4 cm in diameter and 5 cm in height) and observed daily for adult emergence. Adults were paired after emergence. Thirty pairs of *A. gifuensis* were used in the life table study. Each pair was kept in a kale seedling container with 35 aphids of mixed nymphal stage. Each day, the parasitoids were moved to a new container with another 35 aphids, while the aphids from the previous day were observed daily for mummies. Mummies from different days were recorded and kept separately until the emergence of the adult parasitoids. The date and sex of all emerged offspring were recorded. Life table data for *A. gifuensis* were collected during February and March 1994.

Life Table Analysis. The raw life history data of both *M. persicae* and *A. gifuensis* were analyzed based on the theory of age-stage, two-sex life table (Chi and Liu 1985, Chi 1988). The means and SEs of the life table parameters were estimated by using the Jackknife method (Sokal and Rohlf 1995). To facilitate raw data analysis, life table analysis, and the Jackknife method, a user-friendly computer program, TWOSEX-MS-Chart (Chi 2004), designed in Visual BASIC (Version 6.0 Service pack 6) for the Windows operating system, has been made available at http://140.120.197.173/Ecology/prod02.htm (Chung Hsing University) and http://nhsbig.inhs.uiuc.edu/wes/chi.html (Illinois Natural History Survey). The age-stage specific survival rate (s_{xj}; where x = age and j = stage), the age-stage specific fecundity (f_{xj}), the age-specific survival rate (l_x), the age-specific fecundity (m_x), and the population parameters (r, the intrinsic rate of increase; λ, the finite rate of increase, $\lambda = e^r$; R_0, the net reproductive rate; T, the mean generation time) were calculated accordingly. In this paper, the intrinsic rate of increase is estimated by using iterative bisection method from $\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1$ with age indexed from 0 (Goodman 1982). The bisection method can be found in most textbooks of numerical analysis (Burden and Faires 2005). The mean generation time is defined as the time length that a population needs to increase to R_0-fold of its size as the stable age distribution and the stable increase rate are reached. In other words, this means $e^{rT} = R_0$ or $\lambda^T = R_0$. The mean generation time is calculated as $T = (ln R_0)/r$. The gross reproductive rate (GRR) is calculated as $GRR = \Sigma m_x$. The Student's *t*-test was used to determine differences in population parameters between *A. gifuensis* and *M. persicae* (Zar 1999).

Table 1. Means ± SEM of developmental periods (days), adult longevity (days), effective fecundity (F; parasitoids successfully emerged from mummy, offspring/female), total parasitism rate (no. of M.persicae parasitized per female parasitoid), and parasitoid preadult mortality (parasitoids failed to emerge from mummy) of A. gifuensis

Statistics	n	Mean ± SEM
Preadult developmental periods	60	11.02 ± 0.14
Adult male longevity	30	9.73 ± 0.46
Adult female longevity	30	9.17 ± 0.72
Effective fecundity	30	92.0 ± 6.5
Female offspring	30	42.8 ± 4.6
Male offspring	30	49.2 ± 5.3
Total parasitism rate	30	92.3 ± 6.5
Parasitoid preadult mortality	30	0.3 ± 0.1

Two text files (Aphidius_lifetable.txt and Myzus_lifetable.txt) containing the raw life history data of *A. gifuensis* and *M. persicae* are also available at http://140.120.197.173/Ecology/prod02.htm.

Life Expectancy Analysis. Because variation in the developmental rate is a common phenomenon, overlapping of stages in the life history is observed in many insect and mite populations, and hence, individuals of the same age may be in different developmental stages. Consequently, individuals of the same age but different stage may have different life expectancies. Based on the age-stage, two-sex life table, we can calculate the life expectancy for individual of age x and stage y as

$$e_{xy} = \sum_{i=x}^{n} \sum_{j=y}^{m} s'_{ij} \qquad [1]$$

where n is the number of age groups and m is the number of stages. The s'_{ij} is the probability that an individual of age x and stage y will survive to age i and stage j and is calculated by assuming $s'_{xy} = 1$ and following the procedures described in Chi (1988). The calculation of life expectancy is included in the raw data analysis by TWOSEX-MSChart program.

Results

Life Tables. Because the preadult development of *A. gifuensis* (from egg to pupa) occurs in the body of the host aphid, we divided the life history of *A. gifuensis* into the preadult stage, the adult female, and the adult male. The developmental periods of *A. gifuensis* are given in Table 1. The survival rate s_{xj} gives the probability that a newborn egg will survive to age x while in stage j (Fig. 1). The l_x is the probability that a newborn egg will survive to age x; thus, the curve l_x (Fig. 1) is a simplified version of s_{xj}. Because of variation in the developmental rate among individuals, there is obvious stage overlapping in Fig. 1. The age-stage specific fecundity (f_{xj}; Fig. 2) gives the number of offspring produced by individual *A. gifuensis* at age x and stage j. Here only those offspring that successfully emerged from mummies were counted for effective fecundity. Because only females reproduce, there is only a single curve of f_{x2} in Fig. 2. The age-specific fecundity (m_x) and the age-specific maternity ($l_x m_x$) of *A. gifuensis* are also shown in Fig. 2. In Fig. 2, the cumulative reproductive rate to age x is calculated as

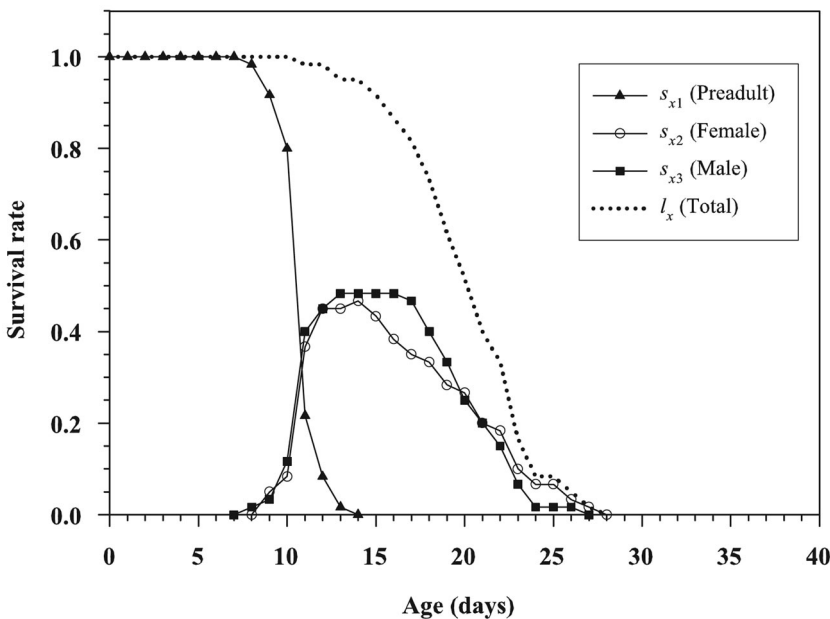$$R_x = \sum_{i=0}^{x} l_i m_i \qquad [2]$$

Fig. 1. The age-stage survival rates for each stage of *A. gifuensis* and the survival rate of total cohort (l_x).
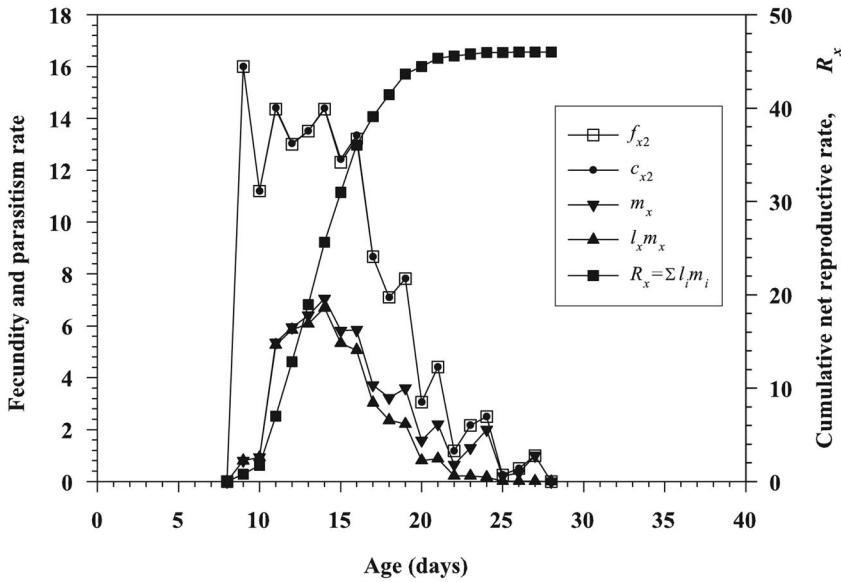
Fig. 2. The age-stage specific fecundity (f_{x2}) and parasitism rate (c_{x2}) of the female adult stage, the age-specific fecundity (m_x), the age-specific maternity ($l_x m_x$), and the cumulative reproductive rate (R_x) of *A. gifuensis*.

The maximum of the cumulative reproductive rate (R_x) is the net reproductive rate R_0, i.e., 46 offspring. Although reproduction ends at the age of 28 d, 95% of the net reproductive rate is completed at the age of 19 d.

The means of developmental periods, the adult longevity and fecundity of *M. persicae* are listed in Table 2. As mentioned above for *A. gifuensis*, the change of stage structure during the life history of *M. persicae* can be observed in the curves of the age-stage survival rate (s_{xj}; Fig. 3). Although the fecundity of *M. persicae* has a peak at the end of its life history (f_{x5} and m_x; Fig. 4) because of the low survival rate (l_x) at the end of its life history (Fig. 3), the contribution of those offspring to the net reproductive rate (R_0 = 29.5 offspring; Table 3) is minor. The 95% net reproductive rate is reached on age 24 d (R_x in Fig. 4). There are no significant differences in the intrinsic rate of increase, the finite rate of increase, and the gross reproductive rate between *A. gifuensis* and *M. persicae* (Table 3). However, significant differences in the net reproductive rate and the mean generation time between *A. gifuensis* and *M. persicae* were obtained according to Student's *t*-test.

Net Parasitism Rate. For a parasitoid, if it lays only one egg per host and all eggs can develop to the adult stage, the parasitism rate of this parasitoid will be equal to its fecundity. If some offspring of a parasitoid do kill their hosts but fail to emerge from the mummies, the parasitism rate will differ from the fecundity rate. We define the age-stage specific parasitism rate c_{xj} as the number of aphids parasitized and eventually killed by a parasitoid of age x and stage j. The parasitism rate of *A. gifuensis* on *M. persicae* is also plotted in Fig. 2. Because only females can oviposit in aphids, there is only a single curve of c_{x2} in Fig. 2. The mean parasitism rate is 92.3 aphids per female (Table 1). In our study, a preadult mortality of <1% is recorded by following the emergence of offspring from mummies. Because most parasitoids successfully emerged from mummies, the curve of parasitism rate (c_{x2}) is almost identical to the curve of fecundity (f_{x2}). By integrating the survivorship with the parasitism rate, we define the summation of the parasitism rate through the life span as the net parasitism rate (C_o). It can be calculated as

$$C_0 = \sum_{x=0}^{n} \sum_{j=1}^{m} c_{xj} s_{xj} \qquad [3]$$

where n is the number of age groups and m is the number of stage groups of the parasitoid. The net parasitism rate for *A. gifuensis* is 46.15 aphids per female. The net parasitism rate can be an indicator of the efficiency of a parasitoid based on life table.

Life Expectancy. The curves of the life expectancies of *A. gifuensis* and *M. persicae* are given in Figs. 5 and 6, respectively. By taking the variable developmental rate between sexes and among individuals into consideration, this method can be used not only to detect the differences in life expectancy between male and
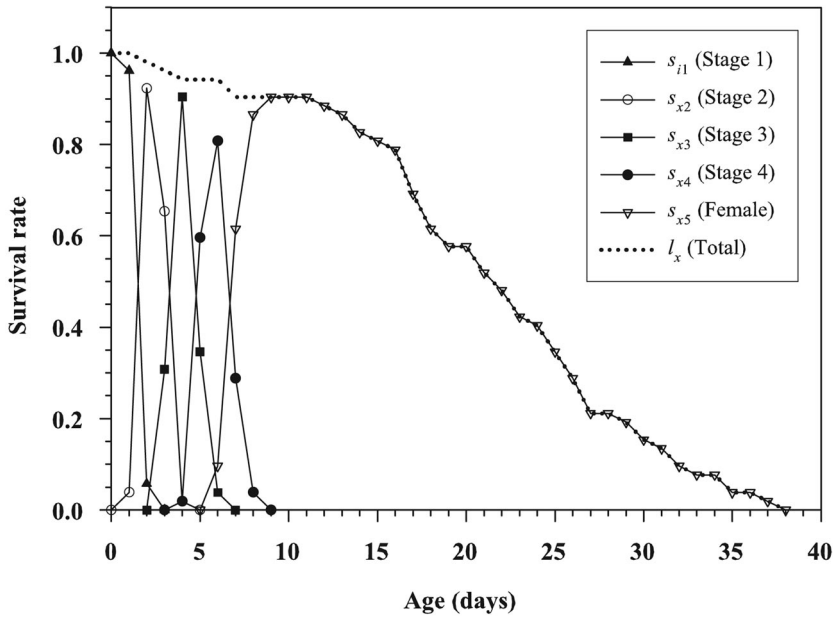
Table 2. Means ± SEM of developmental periods (days), adult longevity (days), and fecundity (*F*; offspring/female) of *M. persicae*

Statistics	*n*	Mean ± SEM
Developmental time		
N1	50	2.00 ± 0.04
N2	50	1.70 ± 0.07
N3	49	1.67 ± 0.07
N4	48	1.85 ± 0.06
N1–N4	48	7.25 ± 0.10
Adult longevity	48	15.85 ± 1.00
Fecundity	48	31.9 ± 2.3

Fig. 3. The age-stage survival rates for each stage of *M. persicae* and the survival rate of total cohort (l_x).

female but also among stages. Under controlled laboratory conditions, our results show that the life expectancy monotonously decreases with aging.

Curtailed Intrinsic Rate of Increase. To describe the effect of longevity and fecundity on the intrinsic rates of *A. gifuensis* and *M. persicae*, we define the curtailed intrinsic rate r_δ as the solution of

$$\sum_{x=0}^{\delta} e^{-r_\delta(x+1)} l_x m_x = 1 \qquad [4]$$

where r_δ is the intrinsic rate of the population by assuming that it survives only to age δ and discarding all l_x and m_x beyond age δ. The curve of r_δ for both *A. gifuensis* and *M. persicae* are plotted in Fig. 7. Because *M. persicae* began reproduction at an earlier age than *A. gifuensis*, the curve of r_δ for *M. persicae* preceded that for *A. gifuensis*. It shows that the *M. persicae* population has a better chance of survival than *A. gifuensis* does. In Fig. 7, the curves of cumulative contribution to the intrinsic rate of increase of *A.*
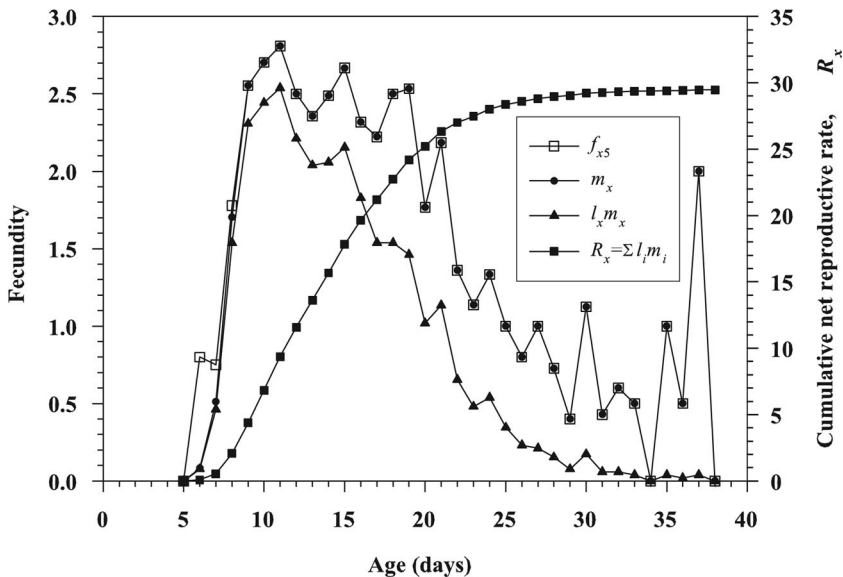

Fig. 4. The age-stage specific fecundity (f_{x5}) of the female adult stage, the age-specific fecundity (m_x), the age-specific maternity ($l_x m_x$), and the cumulative reproductive rate (R_x) of *M. persicae*.

Population parameter	A. gifuensis	M. persicae	t	df	P
r	0.264 ± 0.010	0.252 ± 0.007	0.912	110	0.3637 (>0.05)
λ	1.302 ± 0.014	1.287 ± 0.009	0.908	110	0.3658 (>0.05)
GRR	59.0 ± 8.7	49.8 ± 2.9	0.941	110	0.3489 (>0.05)
R_0	46.0 ± 6.8	29.5 ± 2.4	2.164	110	0.0326 (<0.05)
T	14.5 ± 0.2	13.4 ± 0.3	3.256	110	0.0015 (<0.05)

There are significant differences in R_0 and T between *A. gifuensis* and *M. persicae* according to Student's *t*-test.

r, intrinsic rate of increase (day^{-1}); λ, finite rate of increase (day^{-1}); GRR, gross reproductive rate (offspring per individual); R_0, net reproductive rate (offspring per individual); T, the mean length of a generation (days).

gifuensis and *M. persicae* are plotted. The calculation of r_δ is included in the TWOSEX-MSChart program.

The cumulative contribution (r_y) of age y is calculated as

$$r_y = r \cdot \sum_{x=0}^{y} e^{-r(x+1)} l_x m_x \qquad [5]$$

where r is 0.264 d^{-1} for *A. gifuensis* and 0.252 d^{-1} for *M. persicae*. Because all m_x are zeros before age 6 d for *M. persicae* and before age 9 d for *A. gifuensis*, the curves of r_δ and r_y start at age 6 d for *M. persicae* and at age 9 d for *A. gifuensis* (Fig. 7). It is obvious that the cumulative contribution r_y is not an intrinsic rate but is instead a descriptive value of the cumulative input of individuals surviving to age y to the intrinsic rate r. The curtailed intrinsic rate of increase r_δ, however, gives the actual intrinsic rate for a population surviving only to age δ. In Fig. 7, the r_y of *M. persicae* of age 6 and

7 d does positively contribute to the intrinsic rate of increase, but the curve r_δ shows that, if the population survives only to age 6 or 7 d, the intrinsic rate will be negative and the population will decrease. Therefore, the curtailed intrinsic rate is useful for describing the effect of reduction in survivorship on the intrinsic rate of increase.

Relationship Between F and R_0. As proven by Chi (1988) for two-sex life table, the relationship between the net reproductive rate R_0 and the mean female fecundity F is given as

$$R_0 = F\left(\frac{N_f}{N}\right) \qquad [6]$$

where N is the total number of individuals used for life table study and N_f is the number of female adults. For *A. gifuensis*, the data for N, N_f, F, and R_0 are 60, 30, 92, and 46.0, respectively. For *M. persicae*, they are 52, 48, 31.9, and 29.5, respectively. Obviously, data of both *A. gifuensis* and *M. persicae* show consistence with the relationship of equation 6, although the round-off effects during the calculation of R_0 resulted in negligible differences between R_0 and $F(N_f/N)$.

Relationship Between F and R_0: When the Age-specific Female Life Table Theory Is Applied to Female Parthenogenetic Populations. The mean fecundity of females (F) is a simple statistic and is generally calculated by summing fecundity data of all females and divided by the total number of females. For a traditional female age-specific life table, the net reproductive rate of a female population is defined as
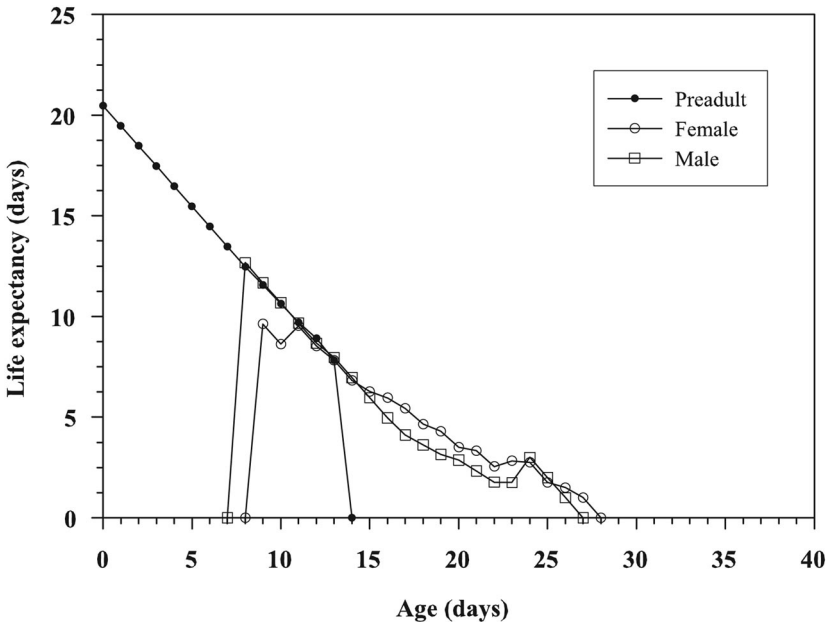
$$R_0 = \sum_{x=0}^{\infty} l_x m_x \qquad [7]$$

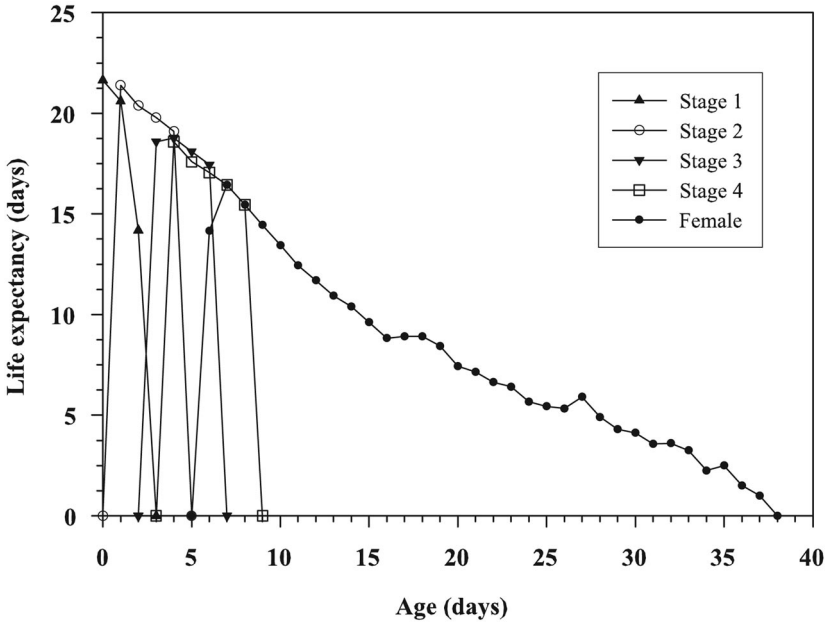Fig. 5. Age-stage life expectancy of *A. gifuensis*.

Fig. 6. Age-stage life expectancy of *M. persicae*.

If the total number of females at the beginning (birth) of the cohort is n_0 and b_{ix} is the fecundity of individual i at age x (where the age is counted from birth), the total fecundity of individual i is B_i and

The total fecundity summed over all individuals is F_{total} and

$$B_i = \sum_{x=0}^{\infty} b_{ix} \qquad [8]$$

$$F_{total} = \sum_{i=1}^{n_0} B_i = \sum_{i=1}^{n_0} \sum_{x=0}^{\infty} b_{ix} = \sum_{x=0}^{\infty} \sum_{i=1}^{n_1} b_{ix} \qquad [9]$$
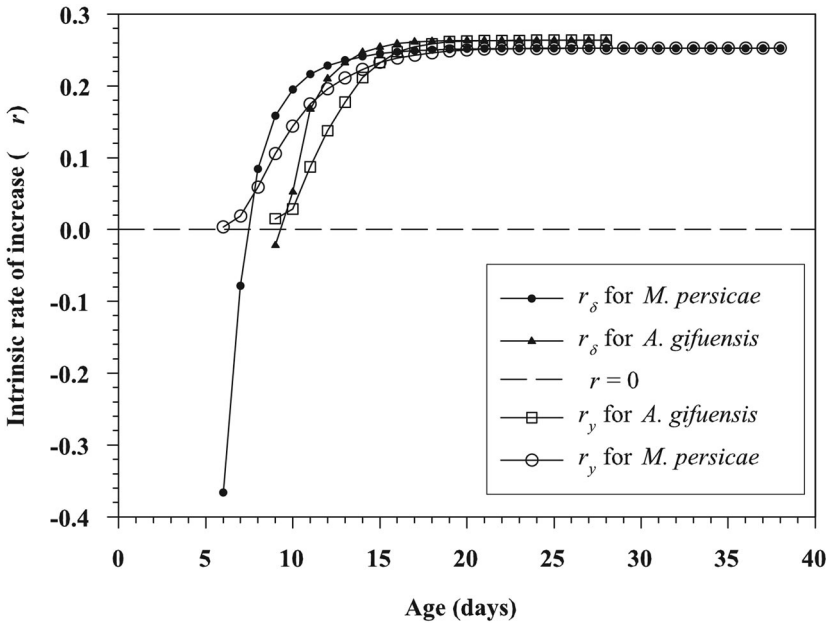

Fig. 7. Curtailed intrinsic rate of increase (r_δ) and cumulative contribution to intrinsic rate of increase (r_y) for *A. gifuensis* and *M. persicae* of different ages.

where n_x is the number of female surviving to age x. If all females successfully develop to the adult stage, i.e., there is no preadult mortality, the mean female fecundity (F) is calculated as

$$F = \frac{F_{total}}{n_0} = \frac{\sum\limits_{i=1}^{n_0} B_i}{n_0} = \frac{\sum\limits_{i=1}^{n_0}\sum\limits_{x=0}^{\infty} b_{ix}}{n_0} \quad [10]$$

Both B_i and b_{ix} are integers. The mean fecundity of female (F) is a simple statistic, and the only rounding-off takes place when the mean is calculated at the last step. If the same data are analyzed by using female age-specific life table, the age-specific fecundity (m_x) and survival rate (l_x) can be calculated as

$$m_x = \frac{\sum\limits_{i=1}^{n_x} b_{ix}}{n_x} \quad [11]$$

and

$$l_x = \frac{n_x}{n_0} \quad [12]$$

During the calculation of each m_x and l_x, rounding-off is an inevitable step to get required significant digits. The relationship between the net reproductive rate R_0 and the mean female fecundity F is

$$R_o = \sum\limits_{x=0}^{\infty} l_x m_x = \sum\limits_{x=0}^{\infty}\left(\frac{n_x}{n_0}\cdot\frac{\sum\limits_{i=1}^{n_x} b_{ix}}{n_x}\right) = \frac{\sum\limits_{x=0}^{\infty}\sum\limits_{i=1}^{n_x} b_{ix}}{n_0} = F$$

$$[13]$$

Hence, for the female age-specific life table, the net reproductive rate (R_0) equals the mean female fecundity (F), if and only if there is no preadult mortality in the female population and all offspring are female. However, if there is preadult mortality and only n_a females reached the adult stage ($n_a < n_0$), the mean female fecundity (F) is

$$F = \frac{\sum\limits_{i=1}^{n_a} B_i}{n_a} = \frac{\sum\limits_{i=1}^{n_a}\sum\limits_{x=0}^{\infty} b_{ix}}{n_a} = \frac{\sum\limits_{x=0}^{\infty}\sum\limits_{i=1}^{n_x} b_{ix}}{n_a} \quad [14]$$

In this case, the relationship between R_0 and F is given as

$$R_0 = \sum\limits_{x=0}^{\infty} l_x m_x = \frac{\sum\limits_{x=0}^{\infty}\sum\limits_{i=1}^{n_x} b_{ix}}{n_0} = \frac{n_a}{n_0}\cdot\frac{\sum\limits_{x=0}^{\infty}\sum\limits_{i=1}^{n_x} b_{ix}}{n_a}$$

$$= \left(\frac{n_a}{n_0}\right) F = s_a F \quad [15]$$

The s_a is the probability that a newborn offspring will survive to the adult stage in the female population.

In other words, it is the survival rate of the total preadult stages of the female population. It is clear that equation 13 is a special case of equation 15 with $n_a = n_0$. Because both the net reproductive rate (R_0) and the total fecundity (F) are calculated from the daily fecundity of all females, it is reasonable to expect that there is some relationship between them. The above proof (equations 7–15) shows that a concrete bond between R_0 and F does exist in the age-specific female life table as in two-sex life table (equation 6). Theoretically, the relationship between F and R_0 is exactly given as equation 6, 13, or 15. However, because all data of l_x and m_x are calculated inevitably by rounding-off to limited digits, a negligible difference may occur between F and R_0. Although equations 6 and 15 appear similar, they are actually different. In equation 6, N is the total number of individuals used for the life table study, and N_f is the number of female adults emerged from N. However, in equation 15, n_0 is the total number of females at the beginning of the cohort life table study, and n_a is the number of females which reached the adult stage.

Relationship Between F and R_0: When Age-Specific Female Life Table Theory Is Applied to Two-Sex Populations. If the total number of individuals at the beginning (birth) of the life table study is n_0, and there are f_0 females and u_0 males in n_0 (i.e., $n_0 = f_0 + u_0$), we can calculate the mean female fecundity as

$$F = \frac{\sum\limits_{i=1}^{f_a} B_i}{f_a} = \frac{\sum\limits_{i=1}^{f_a}\sum\limits_{x=0}^{\infty} b_{ix}}{f_a} = \frac{\sum\limits_{x=0}^{\infty}\sum\limits_{i=1}^{f_x} b_{ix}}{f_a} \quad [16]$$

where f_a is the number of females surviving to the adult stage and f_x is the number of females surviving to age x. Obviously, the preadult mortality for females is $1 - (f_a/f_0)$. The age-specific fecundity (m_x) and survival rate (l_x) are

$$m_x = \frac{\sum\limits_{i=1}^{f_x} b_{ix}\cdot w}{f_x} \quad [17]$$

and

$$l_x = \frac{f_x}{f_0} \quad [18]$$

where w is the proportion of female offspring ($0 \leq w \leq 1$). Here we assume w is a constant for all ages. With similar derivation of equations 11–15, the relationship between F and R_0 is

$$R_0 = \sum\limits_{x=0}^{\infty} l_x m_x = \frac{w\cdot\sum\limits_{x=0}^{\infty}\sum\limits_{i=1}^{f_x} b_{ix}}{f_0} = w\cdot\frac{f_a}{f_0}\cdot\frac{\sum\limits_{x=0}^{\infty}\sum\limits_{i=1}^{f_x} b_{ix}}{f_a}$$

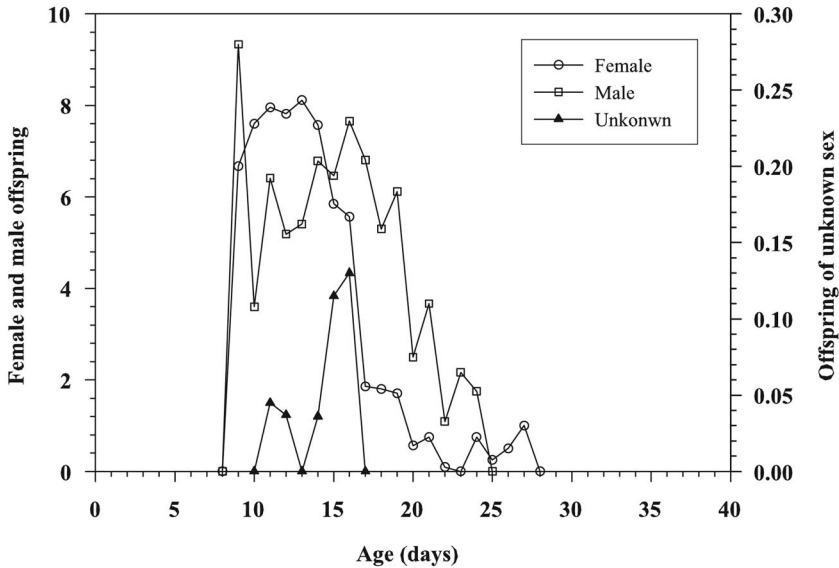$$= w\left(\frac{f_a}{f_0}\right) F = w s_a F \quad [19]$$

Fig. 8. The mean offspring number of different sexes produced by *A. gifuensis* at different age (unknown, offspring died in preadult stage).

where s_a is the preadult survival rate of females in a two-sex population. Equation 19 will be true, if and only if w is a constant for m_x of different ages. In the life table study for two-sex populations, we know the number of females surviving to the adult stage (i.e., f_a) and the daily fecundity of each female (i.e., b_{ix}). However, to apply equations 17–19 to a two-sex population with confidence, we need to know f_0 and w. Because life table studies are tremendously tedious and time-consuming, the sex ratios of offspring produced by females of different ages are seldom monitored, and usually a w of 0.5 is assumed. Moreover, because of the difficulty in distinguishing between the sexes during the preadult stage, an identical preadult mortality is usually assigned to both sexes. Under these assumptions, the relationship between F and R_0 for a two-sex population should be identical to equation 19 when the age-specific female life table theory is applied to two-sex populations. However, if we are not sure of these assumptions, we are likewise not sure of the analytical results as well as the population parameters.

For a clearer explanation, we can use the following numerical example. We begin a hypothetical life table study with 100 eggs. Thirty individuals die before the adult stage, whereas 36 males and 34 females emerge as adults. For a two-sex life table analysis, we know that $N = 100$ and $N_f = 34$ (equation 6). For an age-specific female life table, we are sure that 36 males should be excluded from analysis and $f_a = 34$ (equation 16). However, we are not sure about f_0, because we do not know how many females are among those 30 individuals that died in the preadult stage. If all 30 individuals are pooled with the 34 females for a female age-specific life table analysis, the survival rate (l_x), the net reproductive rate (R_0), and the intrinsic rate (r) are underestimated. However, if we exclude those 30 individuals and use only the 34 females for a life

table analysis, the survival rate (l_x), the net reproductive rate (R_0), and the intrinsic rate (r) are overestimated. This problem will always be there when the female age-specific life table theory is applied to a two-sex population.

Sex of Offspring. Because only female offspring of parasitoids can oviposit in aphids, it is helpful to detect the sex of their offspring. The offspring of different sexes of *A. gifuensis* is plotted in Fig. 8. Because only a small portion of offspring died in the preadult stage, a different scale on the right y-axis is used to make them visible.

Discussion

Life Tables. The net reproductive rate and the mean generation time of *A. gifuensis* were found to be significantly higher than that of *M. persicae* in our study. However, because the fecundity curves of *M. persicae* began 3 d earlier than *A. gifuensis*, there is no difference in the intrinsic rate of increase between the parasitoid and its host. The observed population parameters of both the host and its parasitoid are apparently the result of long-term coevolution. In this study, there is no difference in the *GRR* between the parasitoid and its host. Because the m_x is calculated based on the fecundity of all surviving females at the beginning of reproduction, whereas the m_x at older ages is calculated based on the fecundity of a few surviving females (sometimes even a single female), the m_x of the older ages contribute significantly less to the population. Because the *GRR* ignores the different weight of m_x of different ages, its ecological significance and the result of statistical comparison should be interpreted with caution.

Net Parasitism Rate. For a predator, the age-specific predation rate can be defined as the number of prey

killed by an individual predator of a specific age, whereas the age-specific fecundity is the offspring produced by an individual female predator of that age. Therefore, the predation rate of a predator usually differs from its fecundity (Chi and Yang 2003), in other words, $R_0 << C_0$. Chi and Yang (2003) used Q_p (the ratio of the net predation rate to the net reproductive rate, $Q_p = C_0/R_0$) to describe the transformation rate from prey population to predator offspring and obtained a Q_p of 17.7 for *Propylaea japonica* Thunberg (Coleoptera: Coccinellidae) fed on *M. persicae*. When a similar ratio is calculated for *A. gifuensis* reared on *M. persicae*, we obtain $Q_p = 1.0$. Ohta et al. (2001) showed that, at 25°C, the mummification rate of attacked aphids was 97.7% and the emergence rate from mummies was 96.4%. In that case, the Q_p will also be close to 1.0. However, if a female parasitoid lays more than one egg in its host, we can expect $Q_p < 1.0$. The Q_p gives a demographic estimation for the relationship between the reproductive rate and parasitism rate of a parasitoid.

Curtailed Intrinsic Rate of Increase. Cohen and Mackauer (1987) plotted the curve of cumulative contribution to the intrinsic rate of increase for *Ephedrus californicus* Baker (Hymenoptera: Aphidiidae) and concluded that females in older age classes contributed very little to the cohorts growth rate. In this study, we showed that the cumulative contribution r_y is not an intrinsic rate but is a descriptive value of the cumulative input of individuals surviving to age y to the intrinsic rate r. However, the curtailed intrinsic rate of increase r_δ gives a proper estimation of the effect of the survival rate on the intrinsic rate of increase. For risk assessment in conservation of endangered species, r_δ can be used to describe the effect of decrease in longevity on the survival probability of a population.

Relationship Between *F* and R_0. In this paper, our proof shows that R_0 is related to the total fecundity (equations 15 and 19). Using the age-specific female life table, Souissi and Le Rü (1997) studied the life tables of *Apoanagyrus lopezi* De Santis (Hymenoptera: Encyrtidae) and concluded that the R_0 was not related to the total fecundity. One of the major reasons that caused the erroneous explanation in the report of Souissi and Le Rü (1997) was the preadult mortality. Because of the difficulty in distinguishing between the sexes during the preadult stages and preadult mortality usually contains both males and females, this mortality cannot be properly included when only the females of a two-sex population is considered in the construction of a female life table. Because the preadult mortality cannot be properly included, an incorrect value may be obtained for f_a/f_0, and, consequently, an improper result regarding the relationship between R_0 and F will occur as well. It is also obvious that if the population parameters are estimated by using simplified equations (e.g., Cole 1997, Guldemond et al. 1998), the relationship between R_0 and F will be inconsistent with the proof discussed previously (equations 13, 15, and 19). Moreover, if the life table is constructed based on the adult age (e.g., Smith

1993, Liu and Stansly 1998, Headrick et al. 1999, Tang et al. 1999, Chabi-Olaye et al. 2001, Tsai and Wang 2001, Hentz and Nuessly 2004), the errors in survival rate (l_x) and the fecundity (m_x) will ultimately result in errors in R_0, and the relationship between R_0 and F will be inconsistent with the proof of this study (equations 13, 15, and 19). Because the net reproductive rate (R_0) takes the survival rate into consideration, the equation $R_0 \leq F$ will always apply. If there is preadult mortality, then certainly $R_0 < F$. The relationship between R_0 and F (equations 15 and 19 can be used to check the inconsistencies in R_0 in other published studies, provided R_0, F, w, and s_a are reported). Finally, if the preadult mortality is either incorrectly calculated or ignored, not only the survival rate (l_x) and the net reproductive rate (R_0) will be erroneously estimated, but also the intrinsic rate. Because n_0 and n_a are the basis for the calculation of survival rate and the net reproductive rate, we suggest that the data of n_0, n_a (or s_a), F, and R_0 should be explicitly specified when reporting the female life table for a female population. Similarly, the data of n_0, f_a, f_0 (or s_a), w, F, and R_0 should be specified when reporting the female life table for a two-sex population.

Sex of Offspring. López and Botto (1997) reported that the offspring sex ratio of *Eretmocerus* sp. (Hymenoptera: Aphelinidae) changed with female age. In our study, we also noticed the offspring sex ratio varies with female age. Although the cause of the variation in offspring sex ratio is unknown, the differences itself should be taken into consideration in parasitoid–host relationship studies and be integrated into the life table theory in the future.

Problems in Life Tables Based on Adult Age. Many researchers organize fecundity data based on "adult age" by assuming all adults emerged on the same day. However, ignoring the differences in preadult development results in errors in the survival and fecundity curves based on "adult age." Joyce et al. (1999) reported the preimaginal developmental time for *Amitus bennetti* Viggiani and Evans (Hymenoptera: Platygasteridae) ranged from 18 to 31 d. However, they calculated the daily fertility based on adult age and found the highest fecundity on the first day of adult age. Because the first reproduction days of individual females actually vary according to the range of the adult emergence (18–31 d), the fecundity curve based on adult age resulted in an overestimation of the fecundity rate and finally errors in the population parameters. If the life history raw data are organized according to the model of Caswell (1989), it will yield results similar to those obtained using "adult age," because the model of Caswell classifies individuals by age within stages. Liu and Stansly (1998) showed a variable developmental rate and stage overlappings in *Bemisia argentifolii* Bellows and Perring (Homoptera: Aleyrodidae) (Fig. 2 in Liu and Stansly 1998). However, they ignored the variable developmental rate among individuals and organized the oviposition and survivorship based on adult age (Fig. 3 in Liu and Stansly 1998). Van Steenis (1993) reported the intrinsic rate of increase of *Aphidius colemani* Viereck based

These parts points out the major problem with traditional female age-specific life table. You need to understand these sections.

on the adult age. His data of l_x were given with an age interval of 1 d as 13.71, 14.71, etc., which is apparently based on the mean of the female developmental period (12.7 ± 0.21 [SE] d) (Table 3 in van Steenis 1993). It resulted in an odd age interval of 0.71 d for the first age group (0 ≈ 0.71 d). The above examples show that if the age-specific life table is constructed based on the mean of developmental period, it is inappropriately assumed that all females emerged on the same day, and variation in the developmental time is ignored. It then results in the problem that the first age group has an odd age interval, which in turn, causes more difficulties when those l_x and m_x are used in simulation. A similar predicament can be seen in Abou-Setta et al. (1986). Chi (1988) and Chi and Yang (2003) discussed in detail the differences between the traditional female life table and the age-stage, two-sex life table and showed the inaccuracies of fecundity curve constructed using adult age or artificially constructed nonoverlapping stages.

In summary, age-stage life table studies at various conditions in both laboratory and field provide irreplaceably comprehensive data for modeling population dynamics and predator–prey dynamics. Because the parasitism rate of a parasitoid varies with its age, it is impossible to describe the parasitoid–host relationship by using models based only on the total population sizes of parasitoid and host. Although study of parasitism rate based on life tables is very tedious and difficult, it is the only reliable way to get a comprehensive and thorough understanding of the parasitoid–host relationship. Moreover, because of the variable susceptibility to pesticides and biological control agents of different pest stages, a stage-structured population model gives better prediction on the timing of control (Chi 1990).

We showed a number of possible errors that may occur when applying the female age-specific life table to a two-sex population. Ecologists may want to consider quantifying these errors. Because the error depends on the overlap between stages, sex ratio, and preadult mortality, a general quantification on the error is impractical. However, the inappropriate assumptions in applying the female age-specific life table theory to a two-sex population should be seriously taken into consideration. Using the age-stage, two-sex life table, both sexes are included, and stage differentiation existing in insect life history can properly be described. We recommend that the age-stage, two-sex life table should be used in insect demographic studies.

In this paper, we discussed the cohort life table data collected in the laboratory where the age and stage of every individual are known. However, when stage-structured data of a population are collected from field studies through sampling, it is difficult to determine the age of individuals. Manly (1990) discussed this problem. Whether the methods of Manly can be applied to the age-stage, two-sex life table needs further study.

With the increasing awareness of the shortage of resources, life table studies of interacting populations will certainly play an important role in ecosystem management and pest control for a sustainable agriculture. In theoretical ecology, life table studies incorporating age-stage specific predation and/or parasitism rate will surely play an important role in the elucidation of predator–prey and parasitoid–host relationships.

References Cited

Abou-Setta, M. M., R. W. Sorrell, and C. C. Childers. 1986. Life 48: a BASIC computer program to calculate life table parameters for an insect or mite species. Fla. Entomol. 69: 690–697.

Birch, L. C. 1948. The intrinsic rate of natural increase of an insect population. J. Anim. Ecol. 17: 15–26.

Burden, R. L., and J. D. Faires. 2005. Numerical analysis, 8th ed. Thomson, Belmont, CA.

Caswell, H. 1989. Matrix population models: construction, analysis, and interpretation. Sinauer, Sunderland, MA.

Chabi-Olaye, A., F. Schulthess, H. M. Poehling, and C. Borgemeister. 2001. Factors affecting the biology of *Telenomus isis* (Polaszek) (Hymenoptera: Scelionidae), an egg parasitoid of cereal stem borers in West Africa. Biol. Control. 21: 44–54.

Charlesworth, B. 1994. Evolution in age-structured populations, 2nd ed. Cambridge University Press, Cambridge, UK.

Chi, H. 1988. Life-table analysis incorporating both sexes and variable development rate among individuals. Environ. Entomol. 17: 26–34.

Chi, H. 1990. Timing of control based on the stage structure of pest population: a simulation approach. J. Econ. Entomol. 83: 1143–1150.

Chi, H. 2004. TWOSEX-MSChart: a computer program for the age-stage, two-sex life table analysis. http://140.120.197.173/Ecology/Download/Twosex-MSChart.zip.

Chi, H., and W. M. Getz. 1988. Mass rearing and harvesting based on an age-stage, two-sex life table: a potato tuber worm (Lepidoptera: Gelechiidae) case study. Environ. Entomol. 17: 18–25.

Chi, H., and H. Liu. 1985. Two new methods for the study of insect population ecology. Bull. Inst. Zool. Acad. Sinica. 24: 225–240.

Chi, H., and T. C. Yang. 2003. Two-sex life table and predation rate of *Propylaea japonica* Thunberg (Coleoptera: Coccinellidae) fed on *Myzus persicae* (Sulzer) (Homoptera: Aphididae). Environ. Entomol. 32: 327–333.

Cohen, M. B., and M. Mackauer. 1987. Intrinsic rate of increase and temperature coefficients of the aphid parasite *Ephedrus californicus* Baker (Hymenoptera: Aphidiidae). Can. Entomol. 119: 231–237.

Cole, R. A. 1997. The relative importance of glucosinolates and amino acids to the development of two aphid pests *Brevicoryne brassicae* and *Myzus persicae* on wild and cultivated Brassica species. Entomol. Exp. Appl. 85: 121–133.

Goodman, D. 1982. Optimal life histories, optimal notation, and the value of reproductive value. Am. Nat. 119: 803–823.

Guldemond, J. A., W. J. van den Brink, and E. den Belder. 1998. Methods of assessing population increase in aphids and the effect of growth stage of the host plant on population growth rates. Entomol. Exp. Appl. 86: 163–173.

Hassell, M. P. 1978. The dynamics of arthropod predator-prey systems. Princeton University Press, Princeton, NJ.

Headrick, D. H., T. S. Bellows, and T. M. Perring. 1999. Development and reproduction of a population of *Eretmocerus eremicus* (Homoptera: Aleyrodidae). Environ. Entomol. 28: 300–306.

Hentz, M., and G. Nuessly. 2004. Development, longevity, and fecundity of *Sipha flava* (Homoptera: Aphididae) feeding on *Sorghum bicolor.* Environ. Entomol 33: 546–553.

Istock, C. A. 1981. Natural selection and life history variation: theory plus lessons from a mosquito, pp. 113–127. *In* R. F. Denno and H. Dingle (eds.), Insect life history patterns: habitat and geographic variation. Springer, New York.

Joyce, A. L., T. S. Bellows, and D. H. Headrick. 1999. Reproductive biology and search behavior of *Amitus bennetti* (Hymenoptera: Platygasteridae), a parasitoid of *Bemisia argentifolii* (Homoptera: Aleyrodidae). Environ. Entomol. 28: 282–289.

Leslie, P. H. 1945. On the use of matrices in certain population mathematics. Biometrika. 33: 183–212.

Lewis, E. G. 1942. On the generation and growth of a population. Sankhya. 6: 93–96.

Liu, T. X., and P. A. Stansly. 1998. Life history of *Bemisia argentifolii* (Homoptera: Aleyrodidae) on *Hibiscus rosa-sinensis* (Malvaceae). Fla. Entomol. 81: 437–445.

López, S. N., and E. N. Botto. 1997. Biology of a South American population of *Eretmocerus* sp. (Hymenoptera: Aphelinidae) attacking the greenhouse whitefly. Biol. Control. 9: 1–5.

Lotka, A. J. 1907. Studies on the mode of growth of material aggregates. Am. J. Sci. 24: 199–216.

Manly, B.F.J. 1990. Stage-structured populations: sampling, analysis and simulation. Chapman & Hall, London, UK.

Nakata, T. 1995. Population fluctuations of aphids and their natural enemies on potato in Hokkaido, Japan. Appl. Entomol. Zool. 30: 129–138.

Ohta, I., K. Miura, and M. Kobayashi. 2001. Life history parameters during immature stage of *Aphidius gifuensis* Ashmead (Hymenoptera: Braconidae) on green peach aphid, *Myzus persicae* (Sulzer) (Homoptera: Aphididae). Appl. Entomol. Zool. 36: 103–109.

Price, P. W. 1997. Insect ecology, 3rd ed. Wiley, New York.

Sauge, M. H., J. Kervella, and T. Pascal. 1998. Settling behaviour and reproductive potential of the green peach aphid *Myzus persicae* on peach varieties and a related wild *Prunus.* Entomol. Exp. Appl. 89: 233–242.

Smith, L. 1993. Effect of humidity on life history characteristics of *Anisopteromalus calandrae* (Hymenoptera: Pteromalidae) parasitizing maize weevil (Coleoptera: Curculionidae) larvae in shelled corn. Environ. Entomol. 22: 618–624.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry, 3rd ed. W. H. Freeman, San Francisco, CA.

Souissi, R., and B. Le Rü. 1997. Comparative life table statistics of *Apoanagyrus lopezi* reared on the cassava mealybug *Phenacoccus manihoti* fed on four host plants. Entomol. Exp. Appl. 85: 113–119.

Takada, H. 1976. Studies of aphids and their parasites on cruciferous crops and potatoes. I. Parasite complex of aphids. Kontyû. 44: 234–253.

Takada, H. 2002. Parasitoids (Hymenoptera: Braconidae, Aphidiinae; Aphelinidae) of four principal pest aphids (Homoptera: Aphididae) on greenhouse vegetable crops in Japan. Appl. Entomol. Zool. 37: 237–249.

Tang, Y., and Z. Chen. 1984. Preliminary study on the biology and the ecology of *Aphidius gifuensis* (Ashmead). J. Fujian Agric. College. 13: 119–125.

Tang, Y. Q., S. L. Lapointe, L. G. Brown, and W. B. Hunter. 1999. Effects of host plant and temperature on the biology of *Toxoptera citricida* (Homoptera: Aphididae). Environ. Entomol. 28: 895–900.

Tao, C. C. 1972. Integrated control of cruciferous vegetable aphids in Taiwan. Taiwan Agric. Qtly. 8: 140–154.

Tsai, J. H., and J. J. Wang. 2001. Effects of host plants on biology and life table parameters of *Aphis spiraecola* (Homoptera: Aphididae). Environ. Entomol. 30: 44–50.

van den Bosch, R., P. S. Messenger, and A. P. Gutierrez. 1973. An introduction to biological control. Plenum, New York.

Van Steenis, M. J. 1993. Intrinsic rate of increase of *Aphidius colemani* Vier. (Hym., Braconidae), a parasitoid of *Aphis gossypii* Glov. (Hom., Aphididae), at different temperatures. J. Appl. Entomol. 116: 192–198.

Wei, J., T. Li, R. Kuang, Y. Wang, T. Yin, X. Wu, L. Zou, W. Zhao, J. Cao, and J. Deng. 2003. Mass rearing of *Aphidius gifuensis* (Hymenoptera: Aphidiidae) for biological control of *M. persicae* (Homoptera: Aphididae). Biocontrol Sci. Technol. 13: 87–97.

Zar, J. H. 1999. Biostatistical analysis, 4th ed. Prentice Hall, Upper Saddle River, NJ.