Two-Sex Life Table and Predation Rate of *Propylaea japonica* Thunberg (Coleoptera: Coccinellidae) Fed on *Myzus persicae* (Sulzer) (Homoptera: Aphididae)

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ABSTRACT The life history data of the predator *Propylaea japonica* Thunberg at 25°C fed on *Myzus persicae* (Sulzer) were collected in the laboratory. To take both sexes and the variable developmental rate among individuals into consideration, the raw data were analyzed based on the age-stage, two-sex life table. The intrinsic rate of increase for *P. japonica* is 0.1133 d^{-1}. The net reproductive rate is 67.6 offspring and the mean generation time is 37.7 days. To incorporate the age-stage variability of the predation rate with the two-sex life table, the daily predation rate of individual *P. japonica* of both sexes was collected for each predatory stage. The net predation rate for *P. japonica* is 1199.5 aphids.

KEY WORDS life table, predation rate, *Propylaea japonica* Thunberg

THE COHORT LIFE TABLE gives the most comprehensive description of the survivorship, development, and reproduction of a population, and, as such, is fundamental to both theoretical and applied population ecology. The collection of life table data for relevant species at different trophic levels in a food chain is a basic and important task for conservation (Bevill and Louda 1999) or pest management (Naranjo 2001). The theory and methodology of the life table are discussed in most ecology textbooks (e.g., Price 1984, Ricklefs and Miller 1999). In the predator-prey system, because the stage structure of a predator population changes from time to time and because there are nonpredatory stages (e.g., egg and pupal stages), the incorporation of both the life table and the stage-specific predation rate into the predator-prey model is worthy of study. It is also helpful in the practical application of predation theory to biological control.

Hassell (1978) pointed out that the inclusion of the predator and prey age structure is an important step in understanding predator-prey relationships. Most life tables, however, (Lewis 1942, Leslie 1945, Birch 1948, Caswell 1989, Carey 1993) deal only with the survival and the fecundity of the female population. They ignore the male population and the contribution of male predators to predation. The traditional age-specific life table does not take stage differentiation into consideration and no proper way for stage grouping can be found. The artificially constructed nonoverlapping stages cause many problems. For example, because the sum of the means of each preadult developmental stage does not necessarily equal the mean of total preadult developmental period for all individuals, this inconsistency results in problems in setting stage intervals on the age axis of the survival curve. Another problem is with age-specific fecundity. Because adults emerge at different ages and stage grouping is impossible in age-specific life table, many researchers have constructed the age-specific fecundity based on "adult age." When doing so, the fecundity data of each individual were artificially moved forward or backward by assuming that all adults emerged on the same day. In other words, the eggs laid by different individuals on different age (counted from birth) are summed to calculate the age-specific fecundity (or the adult age-specific fecundity). Because the first age of reproduction is crucial to the intrinsic rate of increase (e.g., Price 1984, p. 231), the artificial nonoverlapping stage curves and fecundity curve based on adult age will result in under- or overestimation of the population parameters. Furthermore, in life table studies, there is usually some individual mortality before the adult stage is reached. This mortality cannot be properly included when only the female population is considered. But those individuals do cause damage on host plants (if it is an herbivore), serve as food of predators (if it is a prey), or consume prey (if it is a predator). It is inappropriate to ignore their existence. Chi and Liu (1985) and Chi (1988) pointed out that age-specific life tables cannot properly describe the stage differentiation of insect and mite population and so developed an age-stage, two-sex life table. For a proper description of the variability of predation rate with age and stage, the daily predation rates during the whole life history of a predator population should be analyzed according to the age-stage structure of the life table. By using *Propylaea*

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japonica Thunberg as an example, we studied its predation on *Myzus persicae* (Sulzer) based on the age-stage, two-sex life table. For a quantitative description of the predation rate at population level, we calculated the net predation rate as a population parameter of predator by combining the survival rate and age-stage specific predation rate.

Materials and Methods

Life Table Study. *Propylaea japonica* Thunberg (Coleoptera: Coccinellidae) was collected on the campus of National Chung Hsing University (Taichung, Taiwan) and kept on potted *Brassica juncea* (L.) *foliosa* Bailey in an outdoor screened house. Excessive *Myzus persicae* (Sulzer) (Homoptera: Aphididae) were offered daily as food source for the *P. japonica.* For the life table study, *P. japonica* were kept in a growth chamber (25±1°C, 65±5% RH and a photoperiod of 12:12 [L:D] h) for two generations. Then 55 eggs laid by 15 pairs of *P. japonica* in 1 d were collected and kept in a growth chamber under the same conditions. After the eggs hatched, the first instars were moved to individual rearing containers. Single seedlings of *B. juncea* var. *foliosa* planted in plastic pots (9-cm diameter, 7-cm height) were used as rearing containers. A reversed plastic cup (9-cm diameter, 5.5-cm height) was used as a cover. At the center of the cup bottom, a 4-cm diameter hole was cut out and covered with fine mesh cloth for ventilation. The survival and development of *P. japonica* were recorded daily. Aphids of mixed stage were added to maintain the daily food supply at 50 to 60 *M. persicae* for each rearing container. After the emergence of adults, males and females were paired. Each pair of *P. japonica* was fed with approximately 100 *M. persicae* every day. The fecundity and survival were recorded daily until the death of each individual.

Predation Rate Study. To study the daily predation rate, 25 eggs laid by five pairs of *P. japonica* in 1 d were collected. The rearing method was the same as that used in the life table study. For quantification of the daily predation rate, 20 individuals of the third-instar *M. persicae* were supplied to the first- and the second-instar *P. japonica* per day. For the third- and the fourth-instar *P. japonica*, 30 and 50 individuals of the third-instar *M. persicae* were supplied, respectively. For paired male and female *P. japonica*, 100 individuals of third-instar *M. persicae* were supplied. Each day, the survivorship, fecundity, and predation rate of *P. japonica* were recorded and recruits of *M. persicae* were added to maintain the respectively daily food supply. Because each larva was kept in an individual rearing container during the larval stage, the daily predation rate could be recorded for each individual. However, because adult male and female were kept as pairs, we ignored the difference between sexes and one half of the daily predation rate of a pair was assigned to both male and female as long as both of them remained alive. If one sex of a pair died, the daily predation rate was assigned to the living one.

Life Table Analysis. The life history raw data of all 80 individuals of both studies were pooled and analyzed according to the age-stage, two-sex life table (Chi and Liu 1985) and the method described by Chi (1988). The means and standard errors of the population parameters were estimated by using the Jackknife method (Sokal and Rohlf 1981).

To avoid the tedious work of raw data analysis in the age-stage, two-sex life table study, a computer program TWOSEX (Chi 1997) designed in Visual BASIC for the Windows operating system is available at http://140.120.197.173/Ecology/prod02.htm (Chung Hsing University) and http://nhsbig.inhs.uiuc.edu.tw/wes/chi.html (Illinois Natural History Survey). TWOSEX groups the raw data and calculates all life table statistics. 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, λ, e^r, R_0, the net reproductive rate; T, the mean generation time) are calculated accordingly. The mean generation time is defined as the time length that a population needs to increase to R_0-fold of its size (i.e., $e^{rT} = R_0$ or $\lambda^T = R_0$) as the stable increase rate (the intrinsic rate r and the finite increase rate λ) is reached. The mean generation time is calculated as $T = \ln R_0/r$.

A text file (Propylaea_lifetable.txt) containing the raw data of life history of *P. japonica* is also available at http://140.120.197.173/Ecology/prod02.htm.

Predation Rate Analysis. To take the variable predation rate among stages into consideration, the raw data of predation rates for the 25 individuals in the predation study were grouped into a matrix **C** according to the age and the stage of the predator. The age-stage specific rate (c_{xj}) gives the mean number of third-instar *M. persicae* consumed by individual *P. japonica* of age x and stage j. In the age-stage, two-sex life table (Chi and Liu 1985), the age-specific survival rate (l_x), and the age-specific fecundity (m_x) for individual aged x are calculated as

$$l_x = \sum_{j=1}^{\beta} s_{xj} \qquad [1]$$

and

$$m_x = \frac{\sum_{j=1}^{\beta} s_{xj} f_{xj}}{\sum_{j=1}^{\beta} s_{xj}}, \qquad [2]$$

where β is the number of life stages and s_{xj} is the age-stage specific survival rate, i.e., the probability that a newborn survives to age x and stage j. The age-specific predation rate (k_x) is the mean number of prey consumed by *P. japonica* of age x and can be calculated as

$$k_x = \frac{\sum_{j=1}^{\beta} s_{xj} c_{xj}}{\sum_{j=1}^{\beta} s_{xj}} \qquad [3]$$

Taking the survival rate into consideration, the age-specific net predation rate (q_x) gives the weighted number of third-instar *M. persicae* consumed by predator of age x and is calculated as

$$q_x = k_x l_x. \qquad [4]$$

From equations 1, 3, and 4, it is obvious that

$$q_x = \sum_{j=1}^{\beta} s_{xj} c_{xj} \qquad [5]$$

We then define the net predation rate (C_0) as the summation of the q_x over all age groups giving

$$C_0 = \sum_{x=0}^{\delta} \sum_{j=1}^{\beta} s_{xj} c_{xj} = \sum_{x=0}^{\delta} k_x l_x, \qquad [6]$$

where δ is the last age of the population. Although the net reproduction rate R_0 represents the mean number of offspring reproduced by an individual during its life span, the parameter C_0 gives the mean number of prey consumed by an individual during its life span. It is a demographic parameter that represents the predation capacity of the predator population, including all individuals of both sexes and those that died before the adult stage. The ratio of the net predation rate to the net reproductive rate gives the transformation rate from prey population to predator offspring. We define this ratio (Q_p) as:

$$Q_p = \frac{C_0}{R_0} \qquad [7]$$

Q_p gives the number of prey needed for the production an offspring from a predator.

For the time-consuming work of the raw data analysis of predation rate, a computer program CONSUME (Chi 2001) is designed in Visual BASIC and is also available at the previously mentioned web sites. An example file containing the raw data of daily predation rate of individual *P. japonica* (file name: Propylaea_consume.txt) is also available at http://140.120.197.173/Ecology/prod02.htm.

Results and Discussion

The developmental periods and predation rates for each stage are given in Table 1. Because of the variable developmental rate among individuals, the survival curve of a cohort usually shows significant stage overlapping. The age-stage survival rate (s_{xj}) of *P. japonica* is given in Fig. 1. This gives the probability that a newborn will survive to age x and stage j. There are significant overlaps between curves of different stages. For any age x, a newborn can survive only to one of the stages, therefore, it is always true that $\sum_{j=1}^{\beta} s_{xj} \leq 1$ in Fig. 1. Some researchers have ignored the variable developmental rate and have used the rounded means of each stage to divide the life span into nonoverlapping stages (for example, Fig. 8.5 of Pianka 1994, 153; Tables 4-4, 4-5, 6-14, and 6-12 of Carey 1993). Chi (1988) discussed the problems and errors in ignoring stage overlapping. The age-stage fecundity (f_{xj}) gives the number of offspring reproduced by individual *P. japonica* of age x and stage j per day (Fig. 2). Because only female adults reproduce, there is only a single curve of f_{x4} in Fig. 2. The age-specific survival rate (l_x), the age-specific fecundity (m_x), and the age-specific maternity ($l_x m_x$) of *P. japonica* are also plotted in Fig. 2. If the same raw data were analyzed using traditional female age-specific life tables (Lewis 1942; Leslie 1945; Birch 1948), it would be impossible to view the changes of the stage structure, because traditional life tables ignore male individuals and the variable developmental rate among individuals (i.e., the stage differentiation). Many researchers organize the fecundity data based on adult age (for examples, Fig. 2 of Tsai 1998, Fig. 3 of Riudavets and Castañé 1998, Tsai and Wang 2001). However, ignoring the differences in preadult development results in errors in the fecundity curve. It is very easy to prove the errors accompanying the fecundity curve based on adult age or the artificially constructed nonoverlap-

Table 1. Means of developmental periods (d) and predation rate (number of *M. persicae*) of each stage of *P. japonica*

Stage	Developmental period (d)			Predation rate (no. of *M. persicae*)		
	n	Mean	SEM	n	Mean	SEM
Egg	73	3.0	0.1	23	–	–
Larva	58	6.9	0.1	20	97.4	6.9
Pupa	53	4.2	0.1	18	–	–
Adult female	24	52.7	5.6	9	1593	326
Adult male	29	54.7	4.4	9	1515	304

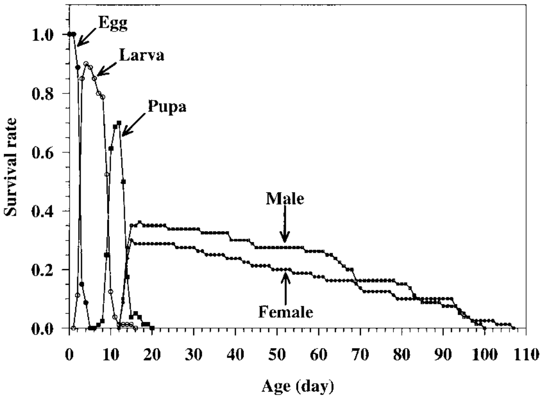

Fig. 1. The age-stage specific survival rate of *P. japonica*.

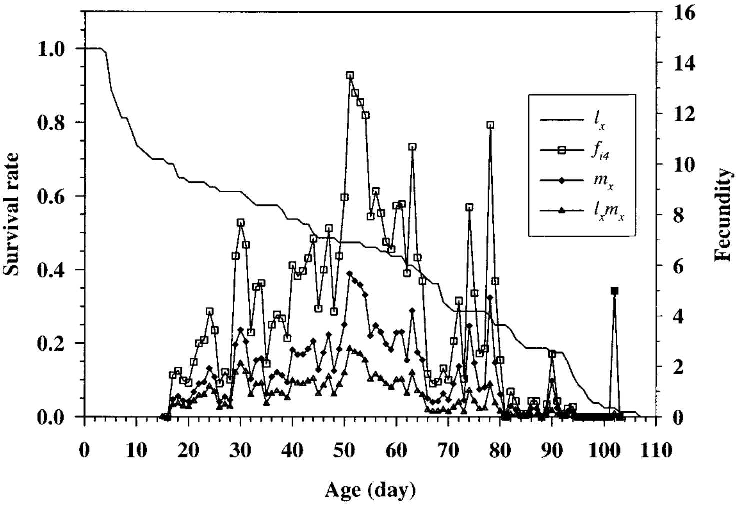

Fig. 2. The age-specific survival rate (l_x), the age-stage specific fecundity (f_{i4}) of the female adult stage, the age-specific fecundity (m_x), and the age-specific maternity (l_x m_x) of *P. japonica.*

ping stages. If we assume there is only one life stage and one sex, i.e., the age is counted from birth and all males and those died before the adult stage are assumed to be females with zero fecundity, we can construct the age-specific survival curve (we call it here l_y) and fecundity curve (we call it m_y), which take all individuals of the cohort into consideration and without assuming that all adult emerged on the same time. The age-specific survival curve (l_y) and fecundity curve (m_y) are the true life history of the cohort. They will be exactly the same as l_x and m_x in Fig. 2, which are based on the age-stage, two-sex life table. But the age-specific survival curve (l_y) and fecundity curve (m_y) cannot describe the stage differentiation and stage overlapping. Furthermore, we can calculate the intrinsic rate of increase using l_y and m_y, and this intrinsic rate will be exactly the same as what we get using two-sex life table in the following text. However, if the age-specific survival rate is constructed based on the means of nonoverlapping stages and the age-specific fecundity is constructed based on the adult stage, they will be different from the l_x and m_x in Fig. 2. If the life history raw data is organized according to the model of Caswell (1989, p. 83), it will result in the same problem as using adult age, because Caswell's model classifies individuals by age within stages. Chi (1988) discussed in detail the differences between the traditional female life table and the age-stage, two-sex life table.

When all 80 individuals are used to calculated the population parameters, the intrinsic rate of increase (r) is 0.1123 d^{-1}, the finite rate of increase (λ) is 1.119 d^{-1}, the net reproductive rate (R_0) is 67.6 offspring, and the mean generation time (T) is 37.5 d. Because the mean generation time is calculated using $T = \ln R_0 / r$, there is no discrepancy in the relationship among r, R_0, and T. However, if the means and standard errors of the population parameters were estimated by using the Jackknife method (Sokal and Rohlf 1981), the intrinsic rate of increase (r) of *P. japonica* is 0.1133 ± 0.0091 d^{-1} (mean ± SEM), the finite rate of increase (λ) is 1.118 ± 0.010 d^{-1}, the net reproductive rate of *P. japonica* (R_0) is 67.6 ± 17.0 offspring, and the mean generation time of *P. japonica* is 37.7 ± 2.0 d. It results in some degree of discrepancy between the estimated means and their definition. For example, according to the relationship between r and λ (i.e., $e^r = \lambda$), λ should be $e^{0.1133} = 1.11997$. But the estimated mean of λ by Jackknife method is 1.118. Moreover, according to $T = \ln R_0 / r$, T should be $\ln 67.6/0.1133 = 37.2$ d. However, the estimated mean of T by Jackknife method gives 37.7 d. A more detailed discussion concerning the general application of the Jackknife method can be found in statistical books (e.g., Sokal and Rohlf 1981). Discussion on specific application of the Jackknife method on the population parameters can be found in Meyer et al (1986).

The net predation rate C_0 for *P. japonica* is 1199.5 ± 212.3 aphids. The Q_p for *P. japonica* fed on *M. persicae* is 17.7. This means that it needs 17.7 prey for the reproduction of one predator egg. This Q_p gives an demographic estimation for the relationship between the reproduction rate and predation rate of predator. The age-stage specific predation rate (c_{xj}) of *P. japonica* are give in Fig. 3. In general, the daily predation rate of an adult is higher than that of a larva. However, the age-stage specific predation rate did not decrease with the aging of the adult. The curves of the age-specific predation rate (k_x) and the age-specific net predation rate (q_x) are given in Fig. 4. Because eggs and pupae of *P. japonica* do not consume prey, there are two obvious gaps in k_x and q_x (the two arrows in Fig. 4). When the survival rate is taken into consideration, the age-specific net predation rate (q_x) of the adults increases at first, then gradually decreases with the age-specific survival rate (l_x). The changes of predation rate with age and stage means that ignoring the age and stage structure of the predator population will

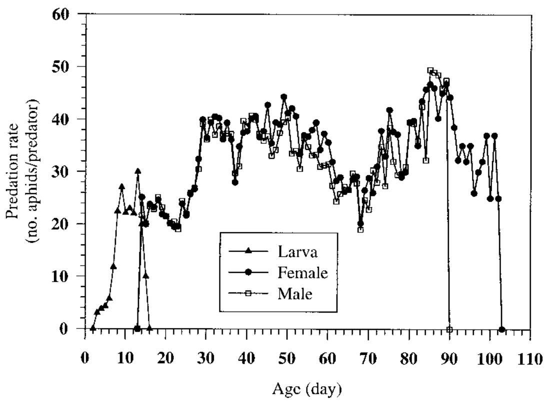

Fig. 3. The age-stage specific predation rate (c_{xj}) of *P. japonica* fed with the third nymphal stage of *M. persicae.*

result in significant errors in the predation model. As Getz and Haight (1989, p. 347) pointed out, if the sexes are split at an earlier life stage, then the equations can be modified accordingly in the age-stage, two-sex life table analysis. After the life table study is completed, it is possible to separate the sexes from the egg stage based on the raw data. This was not necessary for this work, because the larval period is relatively short compared to the adult stage.

The age-stage variability of predation rate of predator and that of vulnerability of prey have been observed in many studies. For example, Isenhour and Yeargan (1981) reported that adults of *Orius insidiosus* (Heteroptera: Anthocoridae) killed significantly more first-instar soybean thrips, *Sericothrips variabilis* (Thysanoptera: Thripidae), than adult thrips, and adult females killed more thrips than did adult males. Clements and Yeargan (1997) reported that all stages of *O. insidiosus* fed on eggs and first instars of the green cloverworm, *Plathypean scabra* (F.) (Lepidoptera: Noctuidae). Fourth instars and adults of *O. insidiosus* could prey upon second-instar caterpillars. However, no stage of *O. insidiosus* was able to feed upon third instars of the caterpillar. Hu and Frank (1997) compared the feeding rates of adults and larvae of five *Philonthus* species (Coleoptera: Staphylinidae) by measuring their consumption of eggs and larvae of the horn fly, *Haematobia irritans* (L.) (Diptera: Muscidae), and found that *P. longicornis* devoured more prey eggs than larvae, but *P. ventralis* devoured more larvae than eggs. Milne and Walter (1997) reported that second-instar larvae of *Frankliniella schultzei* Trybom (Thysanoptera: Thripidae) consumed significantly more eggs than any other life stage. McConnell and Kring (1990) observed significant differences between the number of nymphs and adults of aphids consumed by *Coccinella septempunctata* L. (Coleoptera: Coccinellidae). Schmaedick and Shelton (1999) reported that *Pieris rapae* (L.) (Lepidoptera: Pieridae) eggs and first instars suffer variable mortality from arthropod predators in cabbage fields. All of these facts about the stage-specific predation rate were not taken into consideration in simple predation models, e.g., the Lotka-Volterra predation model and its derivatives. Simple models are inappropriate for the study of the predator-prey relationship of age-structured populations. Therefore, it is safe to say, for age-structured or stage-structured populations, that it is impossible to build realistic predation models without the knowledge of the age-specific predation rate or age-stage predation rate.

Furthermore, many generally known facts point out the importance of a stage-structured population model and life table for studying predator-prey relationship. For example, Radwan and Lövei (1982, 1983) and Roy et al. (1999) reported the stage structure of

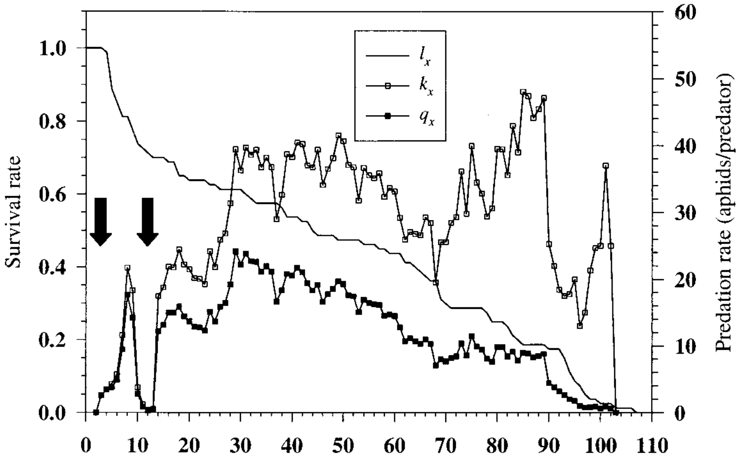

Fig. 4. The age-specific survival rate (l_x), the age-specific predation rate (k_x), and the age-specific net predation rate (q_x). The summation of all q_x (area under the q_x) gives the net predation rate (C_0). The two arrows points out the gaps in curves of k_x and q_x, because eggs and pupae of *P. japonica* don't consume prey.

both predator and prey changes with season. This very simple fact points out the necessity of using a stage-structured population model to study the predator-prey system in most communities. Shipp and Whitfield (1991) reported the stage-specific functional response for a variety of predators. To make optimal use of the stage-specific functional response, they should integrate life tables of predator and prey into the predator-prey system. Teixeira and Polavarapu (2001) showed the variability of emergence time of female blueberry maggot at different temperature. The results of their study and many others point out that the variability of developmental time within a population is a natural fact. If one constructs artificial nonoverlapping stages, it inevitably results in errors. Because pesticide susceptibility varies among pest and predator stages (Appel and Tanley 2000, Biddinger and Hull 1995, Elek and Beveridge 1999, Kjær et al. 1998, Li et al. 1995, Pons et al. 1999), the stage-specific susceptibility should be taken into consideration in biological control systems with pesticide applications. As a matter of fact, Stark and Wennergren (1995) evaluated the demographic toxicological analysis for the estimation of pesticide effectiveness on populations and suggested a stage-structured approach would improve the demographic method of toxicological analysis. Bellows et al. (1992) gave a general review on the life-table construction and analysis in the evaluation of natural enemies. The importance of the stage structure for the timing of control measures has been reported by Chi (1990). The mass rearing and harvesting of insect populations based on two-sex life table is discussed by Chi and Getz (1988). Because the survival, development, and reproduction of a predator is affected by prey (e.g., López-Arroyo et al. 1999), it is necessary to collect the lift table of predator fed on the target prey species. Heinz and Parrella (1994) reported that the cost of biological control of *Bemisia argentifolii* was higher than the insecticide-based management program. Therefore, for an ecological and economical pest management program, the stage-specific predation rate should be incorporated with the life tables of predator and prey to optimize the efficiency of biological control. These findings show that not only should the stage-specific predation rate of predator be considered, but also the stage-specific vulnerability of prey. All the papers cited above and many others show that predation theory based on stage-structured life table deserves further study in both theoretical and applied aspects. In this paper, we take the predation rate of both sexes into consideration and integrate the stage-specific predation rate into the age-stage, two-sex life table.

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