Life Table and Predation of *Lemnia biplagiata* (Coleoptera: Coccinellidae) Fed on *Aphis gossypii* (Homoptera: Aphididae) with a Proof on Relationship Among Gross Reproduction Rate, Net Reproduction Rate, and Preadult Survivorship

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ABSTRACT   The life history and predation rate of *Lemnia biplagiata* (Swartz) fed on *Aphis gossypii* Glover was studied at 25°C in the laboratory. The raw data were analyzed based on the age-stage, two-sex life table to take the variable developmental rate among individuals and both sexes into consideration. The intrinsic rate of increase (r) is 0.1570 d^{-1}, the finite rate of increase (λ) is 1.170 d^{-1}, the net reproduction rate (R_0) is 291.1 offspring per individual, the mean generation time (T) is 36.2 d, and the gross reproduction rate (GRR) is 604.8 offspring. *L. biplagiata* consumed 430 ± 42 aphids (mean ± SD) during the larval stage. The mean consumption rate for an adult during the first 25 d (aged 14–38 d from birth) is 1,548 ± 118 aphids. The mean consumption for an older adult (aged 60–119 d from birth) is 1,319 ± 1,259 aphids. When the survival rate is taken into account, the net consumption rate is 3,022 aphids per individual during the total life span. The transformation rate from prey population to predator offspring is 10.4. The relationship among GRR, R_0, and the preadult survival rate (l_a) is proven as $R_0 < l_a \cdot GRR < GRR$. However, when applying the female age-specific life table to a two-sex population, due to the difficulty in determining the preadult mortality of the females, the calculated age-specific survival rate and fecundity are possibly incorrect and consequently the relationship among GRR, R_0, and l_a also may be incorrect.

KEY WORDS   Life table, predation, *Lemnia biplagiata*, *Aphis gossypii*

Lemnia biplagiata (Swartz) (Coleoptera: Coccinellidae) is a common predatory ladybird in Taiwan and mainland China (Yao and Tao 1972). Its prey includes cotton aphid, *Aphis gossypii* (Glover); green peach aphid, *Myzus persicae* (Sulzer); and other Homoptera (Tao 1990). *L. biplagiata* has been studied as a biological control agent in India (Saharia 1980) and China (Deng et al. 1987). In the former USSR, it was imported from Vietnam for use in greenhouses to control *A. gossypii* on cucumber and *M. persicae* on peppers (Tverdyukov et al. 1993). The population ecology of *L. biplagiata*, however, remains largely unknown.

Life table studies are fundamental to population ecology. A life table gives the most comprehensive description of the survivorship, development, and reproduction of a population. The theory and methods of the life table are discussed in most ecology textbooks (Price 1997, Ricklefs and Miller 1999). The collection of life table data for related species at different trophic levels in a food chain is a basic and important task for conservation (Bevill and Louda 1999) and pest management (Naranjo 2001). Knowledge of the life table of both predator and prey is necessary for the mass rearing and practical application of a natural enemy to biological control systems (Chi and Getz 1988, Chi and Yang 2003). However, most of the traditional female age-specific life tables (Lewis 1942, Leslie 1945, Birch 1948) ignore the male population and the stage differentiation. They cannot take into account the variable predation rate among stages and the predation rate of the male. To take the variable developmental rates among individuals and both sexes into consideration, Chi and Liu (1985) and Chi (1988) developed an age-stage life table theory. Because variation in developmental rate among individuals and between sexes in a natural population is a normal occurrence (e.g., Fig. 2 of Chi 1988, Fig. 3 of Liu et al. 1997, and Fig. 2 of Liu and Stansly 1998), 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. By using the age-stage, two-sex life table, Chi and Yang (2003) described the life table and stage-specific predation rate of the predator *Propylaea japonica* Thunberg (Coleoptera: Coccinellidae) fed on *M. persicae*. In this article, we use the age-stage, two-sex life table theory to analyze the life history data and predation rate of *L. biplagiata* fed on *A. gossypii* to incorporate

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the variable developmental rates among individuals and the male population. Furthermore, we mathematically prove the relationship among gross reproduction rate, net reproduction rate, and preadult survivorship.

Materials and Methods

Life Table Study. *L. biplagiata* was originally collected in the guava orchard of Taiwan Agricultural Research Institute (Taichung, Taiwan) in 1996 and has subsequently been reared on *A. gossypii* on *Cucumis melo* L. in the laboratory for 39 generations. For the life table study, *L. biplagiata* were kept in a growth chamber (25 ± 1°C, 70 ± 10% RH and a photoperiod of 12:12 [L:D] h) for one generation. One hundred eggs laid by 20 pairs of adults within a 1-d period were collected in a plastic box (7 by 5 by 3 cm³, with a fine mesh nylon net covering for ventilation). The box was kept in a growth chamber under the same conditions. Hatched larvae were moved daily to individual rearing boxes, and 140–200 *A. gossypii* of mixed stages kept on a leaf of *C. melo* were supplied as food. When adults emerged, the females and males were paired, and >400 aphids of mixed stages on a leaf of *C. melo* were supplied. In the rearing box, two pieces of plastic tubes (≈1.2 cm in diameter, 3 cm in length, made from plastic pipette tubes) were offered for oviposition; small petri dishes (3 cm in diameter) with moistened cotton were used for water supply. The fecundity and survival were recorded daily until the death of each individual.

Predation Rate Study. To supply *L. biplagiata* with *A. gossypii* of the same age, 30 adults of *A. gossypii* were set on individual leaves of *C. melo.* After 1 d, adult aphids were removed. The newborn aphids were kept on the leaves for 3 d. Using this technique, 3-d old aphids were obtained for the predation study. Before a leaf was used in the predation study, the number of aphids was recorded. For the study of the predation rate by larvae, 30 larvae of *L. biplagiata* hatched on the same day, aged 3-d from birth, were moved into individual rearing boxes, and were given a leaf of *C. melo* with 140–200 aphids daily. After 24 h, the surviving aphids were counted, the predation rates recorded, and the larvae of *L. biplagiata* were transferred to new rearing boxes with another 140–200 aphids. This continued until all larvae pupated. When adults emerged, the sex of each individual was recorded. Because each larva was kept in an individual rearing case during the larval stages, the daily predation rate could be recorded for each individual. For the study of the predation rate by young adults, 15 pairs of newly emerged adults (aged 14 d from birth) were collected, paired, and put into individual rearing boxes. A leaf of *C. melo* with 300–400 aphids was supplied daily. The surviving *L. biplagiata* were transferred to new rearing boxes, and the survival and predation rates were recorded daily for the next 25 d. For the predation rate by older adults, we collected 15 pairs of 46-d-old adults, aged 60 d from birth, and paired them in rearing boxes with 3-d-old aphids. The survival and predation rates were

Table 1. Developmental time, adult longevity, and fecundity of *L. biplagiata* at 25°C

Parameter	Stage	n	Mean	SEM
Developmental time (d)	Egg	62	3.18	0.08
	First instar	60	1.97	0.02
	Second instar	55	1.15	0.05
	Third instar	55	1.73	0.06
	Fourth instar	54	2.09	0.07
	Pupa	54	4.02	0.02
	Total preadult	54	14.13	0.13
Adult longevity (d)	Adult male	23	105.6	6.50
	Adult female	31	105.7	3.54
Fecundity (*F*) (offspring)	Adult female	31	939.1	67.4

recorded until the death of all individuals. Because the adults 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 sexes remained alive. If one sex of a pair died, the daily predation rate was assigned to the surviving individual.

Life Table Analysis. The raw life history data of all individuals of this study 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 using the Jackknife method (Sokal and Rohlf 1981). To facilitate raw data analysis, life table analysis, and the Jackknife method, a user-friendly computer program, TWOSEX-MSChart (Chi 2004), was designed in Visual Basic for the Windows operating system. It is available at http://140.120.197.173/Ecology/download/TWOSEX-MSChart.zip (National Chung Hsing University, Taiwan) and http://nhsbig.inhs.uiuc.edu/wes/chi.html (Illinois Natural History Survey, Urbana, IL). The age-stage specific survival rate (s_{xj}) (where x is the age and j is the stage), age-stage specific fecundity (f_{xj}), age-specific survival rate (l_x), age-specific fecundity (m_x), and population parameters (r, intrinsic rate of increase; λ, finite rate of increase; R_0, net reproduction rate; and 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 $\lambda^T = R_0$) at the stable age-stage distribution. The mean generation time is calculated as $T = \ln R_0 / r$.

Results and Discussion

Of 100 eggs used at the beginning of the life table study, 62 eggs hatched successfully. There are four instars. The means of developmental periods for each developmental stage, longevities for adult male and female, and female fecundity of *L. biplagiata* are given in Table 1. The total developmental period for preadult stages was 14.1 d, whereas adults lived as long as 105.7 d. A maximal daily fecundity of 74 eggs was observed. For the total life span, a maximal fecundity of 1,711 eggs has been recorded for a single female. The mean female fecundity of *L. biplagiata* is 939.1 eggs.
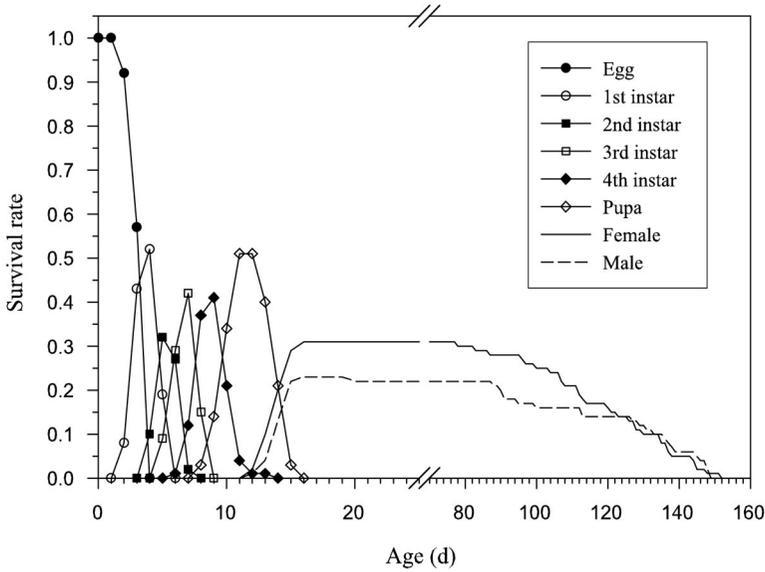
Fig. 1. Age-stage specific survival rate of *L. biplagiata* at 25°C.

The s_{xj} gives the probability that a newborn will survive to age x and stage j (Fig. 1). There are significant overlaps during the developmental period. Under controlled conditions, both male and female can survive long periods, and there is no decrease in survival rates for either male and female for ≈60 d post-emergence.

If the raw data were analyzed using a traditional female age-specific life table (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 dif-

ferentiation). Many researchers have ignored the variable developmental rate among individuals and have used the rounded means of each stage to divide the life span into nonoverlapping stages (e.g., Fig. 8.5 of Pianka 1994, 153; Table 4–4, 4–5, 6–14, and 6–12 of Carey 1993). These procedures inevitably result in errors in life table parameters. Chi (1988) gave a comprehensive discussion on the problems and errors due to ignoring stage overlapping.

The number of offspring produced by individual *L. biplagiata* of age x and stage j per day is shown with f_{xj} in Fig. 2. Because only females reproduce, there is only a single curve f_{x7} (i.e., female is the seventh life
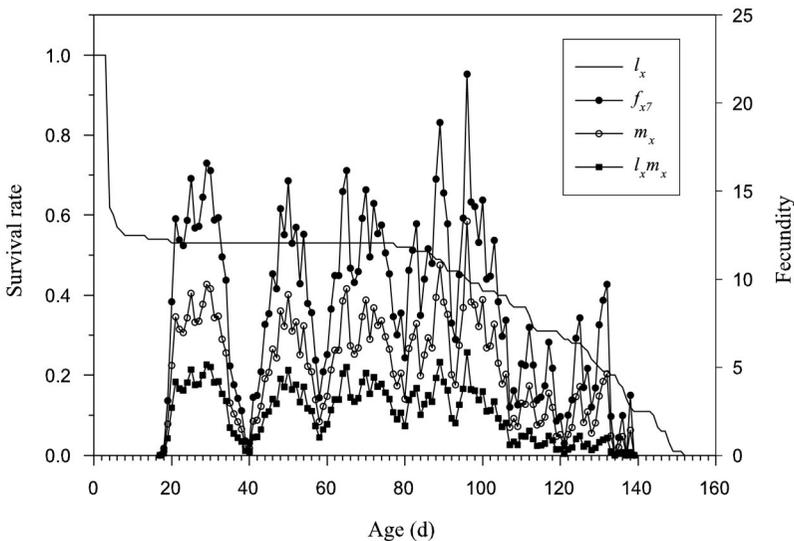

Fig. 2. Age-specific survival rate (l_x), age-stage specific fecundity (f_{x7}) of the female stage (the seventh life stage), age-specific fecundity (m_x), and the age-specific maternity ($l_x m_x$) of *L. biplagiata* at 25°C.

stage). The l_x, m_x, and age-specific maternity ($l_x m_x$) also are plotted in Fig. 2. It shows that there are periodic reproductive peaks approximately every 20 d, and these may be due to periodicity of the reproductive physiology. Abou Zied et al. (2003) found a periodic reproduction in the Australian sheep blowfly, *Lucilia cuprina* (Wiedemann) (Diptera: Calliphoridae).

Many researchers ignore the differences in preadult development among individuals and organize fecundity data based on adult age (Fig. 3 of Liu and Stansly 1998, Fig. 1 of Calvitti and Remotti 1998, Fig. 2 of Tsai 1998, Fig. 3 of Riudavets and Castañé 1998, Fig. 1 of Hansen et al. 1999, Fig. 4 of Joyce et al. 1999, Table 3 of Havelka and Zemek 1999, Fig. 1 of Abdel-Salam and Abdel-Baky 2001, Fig. 2 of Chabi-Olaye et al. 2001, Fig. 2 of Tsai and Wang 2001, Fig. 4 of Greenberg et al. 2003, and Stenseng et al. 2003). For example, Liu and Stansly (1998) observed a significant variation in the developmental rate among individuals of *Bemisia argentifolii* Bellows & Perring (Homoptera: Aleyrodidae) (Fig. 2 in their article) but ignored the variable developmental rate and organized the survivorship and fecundity based on adult age (Fig. 3 in their article). Headrick et al. (1999) reported the preimaginal developmental time for female *Eretmocerus eremicus* Rose & Zolnerowich (Hymenoptera: Aphelinidae) attacking *B. argentifolii* on cotton ranged from 16 to 27 d (Table 3 of Headrick et al. 1999). Their calculations of the daily oviposition, however, were based only on adult age. Because the first reproduction days of individual females actually vary according to the range of the adult emergence, ignoring the differences in preimaginal development results in errors in the fecundity curve, and, eventually, in errors in the population parameters. Thus, 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, the curves will be different from the l_x and m_x that are based on the age counted from the birth of the individual. If the life history raw data are 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 explicitly the differences between the traditional female life table and the age-stage, two-sex life table.

When data of all 100 individuals of *L. biplagiata* in this study are used to calculate the population parameters, the r is 0.1565 d^{-1}, λ is 1.1694 d^{-1}, R_0 is 291.1 offspring, mean generation time (T) is 36.3 d, and gross reproduction rate (*GRR*) is 604.8 offspring. We also estimated the means and standard errors of the population parameters by using the Jackknife method (Sokal and Rohlf 1981). The estimated r of *L. biplagiata* is 0.1570 ± 0.0069 d^{-1} (mean ± SEM), λ is 1.1700 ± 0.0080 d^{-1}, R_0 is 291.1 ± 48.3 offspring, T is 36.2 ± 1.0 d, and *GRR* is 604.8 ± 85.3 offspring. There are minor differences between the results estimated by using the Jackknife method and that calculated by pooling data of all individuals. Discussion concerning

the general application of the Jackknife method can be found in standard statistics books such as Sokal and Rohlf (1981). Discussion on specific applications of the Jackknife method on population parameters can be found in Meyer et al. (1986). Perdikis and Lykouressis (2002) reported r, R_0, and T of the predatory bug *Macrolophus pygmaeus* Rambur (Hemiptera: Miridae) at 27.5°C of 0.0981 d^{-1}, 49.94, and 46.62, respectively. According to life table theory, $T = \ln R_0 / r$. Because the results of Perdikis and Lykouressis (2002) showed that $T \neq \ln R_0 / r$, their data may be in error. Similar errors are found in Morales-Ramos and Cate (1992) and Urbaneja et al. (2001). As proven by Chi (1988) for the two-sex life table, the relationship between R_0 and mean female fecundity, F, is given as follows:

$$R_0 = F \cdot (N_f / N) \qquad [1]$$

where N is the total number of individuals used for life table study and N_f is the number of female adults. In this study, the value of N, N_f, F, and R_0 for *L. biplagiata* is 100, 31, 939.1, and 291.1, respectively. Their relationship is consistent with equation 1. Seal et al. (2002) studied the life table of *Catolaccus hunteri* (Hymenoptera: Pteromalidae). In their report, *GRR* was 291.60 and R_0 was 216.84 when reared on cowpea weevil, *Callosobruchus maculatus* (F.), at 25°C (Table 3 of Seal et al. 2002). In Lee and Ahn (2000), *GRR* and R_0 for *Amblyseius womersleyi* (Schicha) (Acari: Phytoseiidae) at 24°C are 20.42 and 12.48, respectively (Table 8 of Lee and Ahn 2000). For a clear understanding on the relationship between *GRR* and R_0, we give the following proof. In the female age-specific life table, the gross reproduction rate is defined as follows:

$$GRR = \sum_{x=0}^{\delta} m_x \qquad [2]$$

where δ is the last age of the cohort. The net reproduction rate is defined as follows:

$$R_0 = \sum_{x=0}^{\delta} l_x m_x \qquad [3]$$

Before the adult emergence, all m_x values are zero. Thus, if the adult emerged on age a, then

$$\sum_{x=0}^{a-1} l_x m_x = 0 \qquad [4]$$

$$R_0 = \sum_{x=a}^{\delta} l_x m_x \qquad [5]$$

and

$$GRR = \sum_{x=a}^{\delta} m_x \qquad [6]$$

Because l_x is a monotone decreasing sequence of age, it gives

$$1 \geq l_a \geq l_{a+1} \geq l_{a+2} \geq \ldots \geq l_\delta \qquad [7]$$

Therefore, it follows that

$$R_0 = \sum_{x=a}^{\delta} l_x m_x \leq \sum_{x=a}^{\delta} m_x = GRR \qquad [8]$$

The extreme case of $R_0 = GRR$ exists if and only if $l_x = 1$ when $m_x > 0$. Because l_x decreases with age and finally diminishes to zero, it is safe to expect that

$$R_0 < GRR \qquad [9]$$

and

$$\sum_{x=a}^{\delta} l_a m_x > \sum_{x=a}^{\delta} l_x m_x = R_0 \qquad [10]$$

Thus, if $l_a < 1$ (i.e., there is preadult mortality), it gives

$$R_0 = \sum_{x=a}^{\delta} l_x m_x < \sum_{x=a}^{\delta} l_a m_x = l_a \sum_{x=a}^{\delta} m_x < \sum_{x=a}^{\delta} m_x = GRR$$

$$[11]$$

Conclusively, the following relationship exists for both the age-stage, two-sex life table and the female age-specific life table:

$$R_0 < l_a \cdot GRR < GRR \qquad [12]$$

However, when applying the female age-specific life table to a two-sex population, due to the difficulty in determining the preadult mortality of the females, the calculated age-specific survival rate and fecundity are possibly incorrect and consequently the relationship among GRR, R_0, and l_a also may be incorrect. In the report of Seal et al. (2002), the age-specific survival rate at adult emergence is significantly <0.5 at 25°C, i.e., $l_a < 0.5$ (Fig. 1 of Seal et al. 2002). If $GRR = 291.60$, then the following relationship should exist:

$$R_0 < l_a \cdot GRR < 0.5 \times 291.60 = 145.8$$

Thus, if the GRR is 291.60 as reported in Seal et al. (2002), then R_0 must be <145.8. Their results, $R_0 = 216.84$ and $GRR = 291.60$, are noticeably inconsistent with the above-mentioned proof (equation 12). In the report of Lee and Ahn (2000), the mortality of the total immature stage of *A. womersleyi* is 60% at 24°C (Table 1 of Lee and Ahn 2000), i.e., $l_a = 1 - 0.6 = 0.4$. If the $GRR = 20.42$, then it must give

$$R_0 < l_a \cdot GRR = 0.4 \times 20.42 = 8.168$$

Obviously, R_0 must be <8.168. Therefore, their results, $R_0 = 12.48$ and $GRR = 20.42$, are apparently inconsistent with the above-mentioned proof (equation 12). The above-mentioned two examples demonstrate an additional problem that may result from the application of the age-specific female life table to stage-structured populations. Detailed discussions on the problems are given in Chi (1988) and Chi and Yang (2003). The GRR for *L. biplagiata* is 604.8. The R_0 is 291.1. The l_a is 0.54. Our results are consistent with the relationship as proven in equation 12. Lemos et al. (2003), who reported the GRR, R_0, and survival rate to adulthood for *Euborellia annulipes* (Lucas) (Dermaptera: Anisolabididae), also had results consistent with equation 12. In equation 2, GRR is a simple summation all m_x. At the beginning of reproduction, m_x is calculated based on the fecundity of all surviving females. However, at older ages, m_x is generally calculated based on the fecundity of a few surviving females, sometimes even a single female. Thus, m_x of the older ages contribute significantly less to the population. Because GRR ignores the different weight of m_x of different age, it should be interpreted with caution. Nevertheless, equation 12 can be certainly used as a criterion for double-checking the statistical results in life table studies.

The age-specific predation rate (k_x) during the larval stage of *L. biplagiata* is shown in Fig. 3. The age-specific predation rate is the mean number of aphids consumed by *L. biplagiata* of age x. By taking the survival rate into consideration, Chi and Yang (2003) defined the age-specific net predation rate (q_x) as the weighted number of prey consumed by predator of age x and it is calculated as follows:

$$q_x = l_x k_x$$

The q_x also is plotted in Fig. 3. The result shows that the larval predation rate increased significantly from age 3 to 8 d. Then, because some larvae entered the pupal stage, the predation rate decreased on age 9 d. During the entire larval stages, an individual of *L. biplagiata* consumed 430 ± 42 (mean ± SD) aphids. The age-specific predation rates and age-specific net predation rate during the first 25 d of the adult stage (aged 14 to 38 d from birth) are shown in Fig. 4. It increased significantly with the age for ≈15 d and then decreased for a few days. In comparison with the fecundity curve (Fig. 2), a similar periodic predation rate of 20 can be observed. The total average consumption rate during the first 25 d of the adult stage is 1,548 ± 118 aphids. The age-specific predation rates and age-specific net predation rate for older adults (aged 60 to 119 d counted from birth) are shown in Fig. 5. For older adults, the predation rate decreased with age and no obvious periodicity of predation rate is observed. The total consumption rate for an older adult is 1,319 ± 1,259 aphids with a coefficient of variation (CV) of 95%. The high CV value is due to the significant variation in survival in older adults. Because experiments on predation rate are very time-consuming, we did not collect data for the age interval from 39 to 59 d. Instead, we calculated the mean of the daily predation rate for the age intervals from 29 d to 38 d and from 60 d to 69 d (counted from birth), and then we used it as the estimated predation rate for the age interval from 39 to 59 d. Chi and Yang (2003) calculated the net predation rate (C_0) as follows:

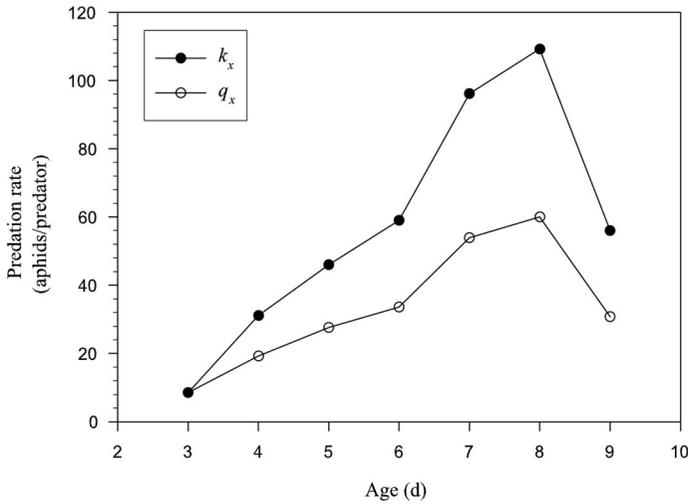$$C_0 = \sum_{x=0}^{\delta} k_x l_x$$

Fig. 3. Age-specific predation rate (k_x) and age-specific net predation rate (q_x) of larva of *L. biplagiata* at 25°C; the age is counted from birth.

where δ is the last age of the population and k_x is the age-specific predation rate. In this study, because the data on predation is recorded only to age 119 d, we obtained a net predation rate $C_0 = 3{,}022$ for $\delta = 119$. Chi and Yang (2003) showed that the contribution of older predators to the net predation rate is minor. Because of the low predation rate after age 120 d, we ignore the predation rate from age 120 to 152 d. Chi and Yang (2003) defined the transformation rate from prey population to predator offspring as follows:

$$Q_p = \frac{C_0}{R_0}.$$

The Q_p for *L. biplagiata* fed on *A. gossypii* is 10.4. This means that *L. biplagiata* needs 10.4 individuals of 3-d-old *A. gossypii* 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. Sahayaraj and Paulraj (2001) reported that the predation rate of *Rhynocoris marginatus* F. (Heteroptera: Reduviidae) on *Spodoptera litura* F. (Lepidoptera: Noctuidae) larvae increased with stage. Xia et al. (2003) studied the functional responses of *Coccinella septempunctata* L. (Coleoptera: Coccinellidae) fed on *A. gossypii* and found significant difference in predation rates among predator stages. The age-stage variability of predation of predator and that of vulnerability of prey have been observed by many researchers (Isenhour and Yeargan 1981, Clements and Yeargan 1997, Hu and Frank 1997, Chi and Yang 2003). All of these facts about stage-specific predation rates could not be taken into ac-
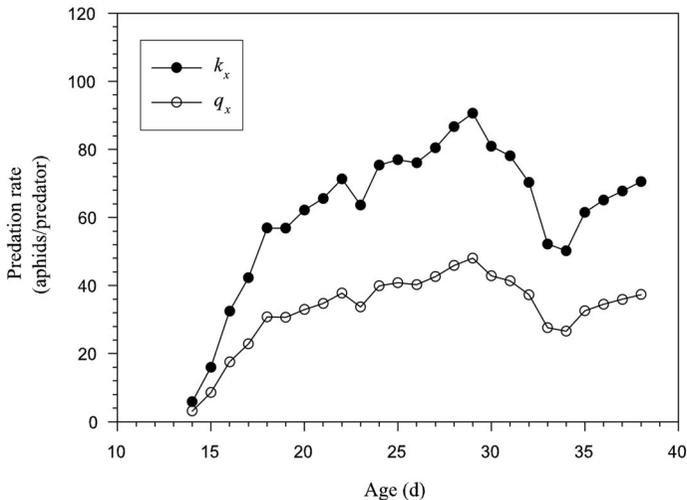

Fig. 4. Age-specific predation rate (k_x) and age-specific net predation rate (q_x) of young adult of *L. biplagiata* at 25°C; the age is counted from birth.
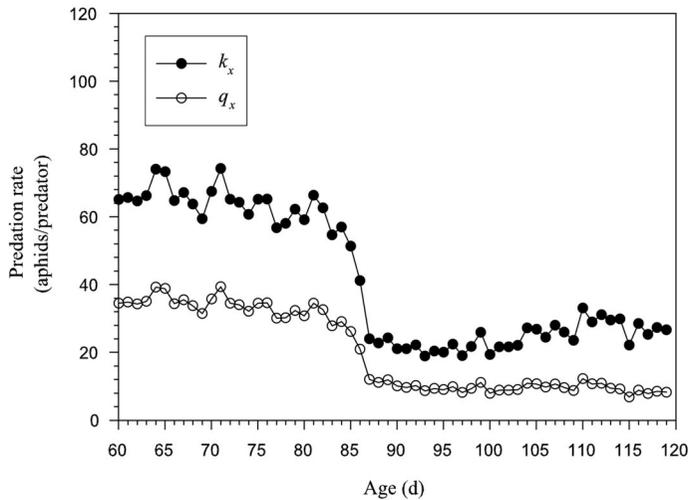
Fig. 5. Age-specific predation rate (k_x) and age-specific net predation rate (q_x) of older adult of *L. biplagiata* at 25°C; the age is counted from birth.

count in simple predation models without age or stage structure, e.g., Lotka–Volterra predation model and its derivatives. Actually, Hassell (1978) had pointed out that the inclusion of the predator and prey age structure is an important step in understanding predator–prey relationship. Because most animal species are age-structured or age-stage-structured, further accumulation of the knowledge of the stage-specific predation rate and stage-structured life table will be necessary for a proper modeling of predator–prey dynamics.

Acknowledgments

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