

# Linking Life Table and Predation Rate for Biological Control: A Comparative Study of *Eocanthecona furcellata* (Hemiptera: Pentatomidae) Fed on *Spodoptera litura* (Lepidoptera: Noctuidae) and *Plutella xylostella* (Lepidoptera: Plutellidae)

Shu-Jen Tuan,<sup>1</sup> Chih-Chun Yeh,<sup>1</sup> Remzi Atlihan,<sup>2</sup> and Hsin Chi<sup>1,3</sup>

<sup>1</sup>Department of Entomology, National Chung Hsing University, Taichung 402, Taiwan, Republic of China (sjtuan@dragon.nchu.edu.tw; yehsnake@yahoo.com.tw; hsinchi@dragon.nchu.edu.tw), <sup>2</sup>Department of Plant Protection, Faculty of Agriculture, University of Yuzuncu Yil, 65080 Van, Turkey (ratlihan@yyu.edu.tr), and <sup>3</sup>Corresponding author, e-mail: hsinchi@dragon.nchu.edu.tw

Received 25 July 2015; Accepted 17 August 2015

## Abstract

To better understand the predator–prey relationship and to compare predation rates, we studied the life table and predation rate of the predator *Eocanthecona furcellata* Wolff (Hemiptera: Pentatomidae) when reared on two major crucifer pests, *Spodoptera litura* (F.) (Lepidoptera: Noctuidae) and *Plutella xylostella* L. (Lepidoptera: Plutellidae). The net reproductive rate, intrinsic rate of increase, finite rate, and net predation rates of *E. furcellata* reared on *P. xylostella* were 292.4 offspring,  $0.1389\text{ d}^{-1}$ ,  $1.1490\text{ d}^{-1}$ , and 644.1 third instars of *P. xylostella*, respectively. These values are significantly higher than those reared on *S. litura*, i.e., 272.3 offspring,  $0.1220\text{ d}^{-1}$ ,  $1.1298\text{ d}^{-1}$ , and 863.1 third instars of *S. litura*. To evaluate the predation potential of *E. furcellata* fed on *P. xylostella* and *S. litura*, we combined both the growth rate and predation rate to calculate the finite predation rate ( $\omega$ ); our results showed that *E. furcellata* is an effective predator of both *S. litura* ( $\omega = 1.6029$ ) and *P. xylostella* ( $\omega = 1.4277$ ).

**Key words:** *Eocanthecona furcellata*, *Spodoptera litura*, *Plutella xylostella*, two-sex life table, predation rate

To precisely quantify predator–prey relationships, it is necessary to take the population growth and the predation rate of the predator into consideration. It is not justified to conclude that a predator is more efficient than another predator solely based on a faster population growth rate. Neither is it justified to conclude a predator is more efficient than another predator based solely on a higher predation rate. To improve the effectiveness of biological control procedures, we need to quantify the survival rate, stage differentiation, fecundity, as well as the predation rate of the predator from its birth to death, i.e., we have to collect not only the life table data but also the predation rate in the life table framework (Yu et al. 2013a).

The tobacco cutworm, *Spodoptera litura* (F.) (Lepidoptera: Noctuidae), is one of the most common and widespread insect pests in Asian countries (Ahmad et al. 2007), ranging from Pakistan and India through China, Japan, Australia, and Taiwan. Due to its diverse host range, high fecundity, and long-distance migration ability, it is an important pest in many countries (Ahmad et al. 2007, Tuan et al. 2014). In Taiwan, annual outbreaks of *S. litura* occur mainly in mid-summer and late fall despite the various management

strategies that have been adopted by local growers and government oversight agencies (Jiang et al. 2010).

The diamondback moth, *Plutella xylostella* L. (Lepidoptera: Plutellidae), is another widely distributed and important pest of cruciferous crops. Due to its rapid development, high fecundity, and insecticide resistance (Chapman et al. 2002, Furlong et al. 2013), it has been a serious pest for many decades. The annual cost for its global control is estimated at US\$ 4–5 billion per year (Talekar and Shelton 1993, Furlong et al. 2013).

For many decades now, biological control has been an increasingly popular alternative to traditional means of insect control, especially considering the current growing concern for environmental protection and food safety that exists today (De Clercq et al. 2003, Zanuncio et al. 2006). There has been, however, limited success in controlling greenhouse pests (Messelink et al. 2014). In order for a biological control program to succeed, a thorough understanding of the growth, stage structure, fecundity of both predator and prey, and the predation rate of the predator are essential (Farhadi et al. 2011, Yu et al. 2013a,b). Because only a life table offers a comprehensive understanding of the survival, development, and

reproduction of a species, it is a key component of successful biological control. The traditional female age-specific life tables (Lewis 1942, Leslie 1945, Birch 1948, Carey 1993), however, ignore the male populations and the effects they may have on the pest population. These tables are incapable of describing the stage structure that is critical to the calculation of predation capacity due to either the variable predation rate among stages or the presence of a nonpredatory stage. The practical application of these tables in biological control is limited. Chi and Liu (1985) and Chi (1988) developed the two-sex life table theory, which can advantageously take into consideration both the stage differentiation and the males' contribution. The two-sex life table has also been used in the study of predator-prey relationships (Yu et al. 2005, Chi and Su 2006, Farhadi et al. 2011, Huang and Chi 2012, Yu et al. 2013a, Khanamani et al. 2015) to include the variation in predation rate due to stage differentiation and the effect of male predators.

*Eocanthecona furcellata* Wolff (Hemiptera: Pentatomidae) is a common predatory stink bug in Southeast Asia, India, China, Taiwan, and Japan and has often been observed in cotton, chickpea, and vegetable fields (De Clercq 2000, Chang and Hsieh 2001, Nyunt 2008). Since 1996, *E. furcellata* has been mass-reared and used as a biological control agent in Taiwan against a few pests including *S. litura* and *P. xylostella* (Chang 2002). Kumar et al. (1996) also considered *E. furcellata* as a promising predator of *Craspedonta leayana* (Latr.) (Chrysomelidae: Coleoptera). Although a few studies reported the basic ecology and predation rate (Chu and Chu 1975b, Chang and Hsieh 2001), the life table and predation rate of this bug have not been studied. To demonstrate the advantage and necessity of predation rate studies incorporating life table data in biological control programs, we collected the age-stage, two-sex life table and predation rate data of *E. furcellata* preying on *S. litura* and *P. xylostella*. The information generated will be useful in various aspects of implementing a biological control program, including devising procedures for the mass rearing of natural enemies, calculating the number of individuals necessary per release, and determining the ideal timing of the release(s).

## Materials and Methods

### Insect Rearing

The population of *S. litura* was originally collected from cabbage and taro fields in the Wufeng District, Taichung, Taiwan. Insects were reared on artificial diets according to Tuan et al. (2014) in a walk-in chamber set at  $25 \pm 1^\circ\text{C}$ ,  $60 \pm 10\%$  RH, and a photoperiod of 12:12 (L:D) h. Larvae were mass reared from the first to third instars in plastic cups (9.5 cm in diameter, 5.5 cm in height). The fourth instars were isolated and reared in 30-well plastic plates until pupation. Ten to 12 pairs of newly emerged adults were kept in the mating containers (13.5 cm in diameter, 18.5 cm in height) lined with paper towel material for oviposition and provided with cotton balls soaked with 20% honey water as adult food. Egg masses were collected daily. To maintain genetic diversity, egg masses were field collected annually and intermixed with the laboratory colony.

The original colony of *P. xylostella* was provided by the Taiwan Agricultural Chemicals and Toxic Substances Research Institute. Larvae were reared on an artificial diet (Asano et al. 1993, Tuan et al. 1997) in a walk-in chamber set at the same conditions as above. Larvae were mass reared from the first to fourth instar in plastic cups (9.5 cm in diameter, 5.5 cm in height). Pupae were collected daily and transferred to the mating cage (44 cm in length, 30 cm in width, 22 cm in height). Newly emerged adults were

provided with cotton balls soaked with 20% honey water as food. A piece of aluminum foil (6 by 10 cm) dipped in cabbage leaf solution (130 g leaf tissue blended with water 500 ml) and air-dried was used as the substrate for oviposition by the diamondback moth.

The colony of *E. furcellata* was originally provided by the Miaoli District Agricultural Research and Extension Station, Council of Agriculture, Taiwan. The stink bugs were reared on larvae of *S. litura* in a walk-in chamber set to the same conditions as mentioned earlier. Nymphs were kept in groups (~50 nymphs) in plastic containers (22 cm in diameter, 6.5 cm in height). Ten to 15 pairs of emerged adults were placed in plastic cages (13.5 cm in diameter, 18.5 cm in height) with a sufficient number of prey and a paper towel lining provided for oviposition. Because newly hatched bugs, i.e., the first nymphal stage (hereafter abbreviated as N1), were nonfeeding, requiring only water, they were provided with cotton balls soaked with water. Second to fifth nymphal stage bugs (abbreviated as N2–N5) were supplied with prey of *P. xylostella* or *S. litura* in surplus.

### Host Plant

During the life table and predation study, *Brassica oleracea* L. was used as the host plant for both *P. xylostella* and *S. litura*. The cabbage seedlings were planted in 5-inch plastic pots (14.7 cm in diameter and 12.6 cm in height) using a mixture of sandy loam, loam, organic cultivating soil, and peat soil (Potgrond H, Klassmann-Deilmann GmbH, Geeste, Germany) in a greenhouse set at  $24 \pm 2^\circ\text{C}$ ,  $80 \pm 10\%$  RH, and a photoperiod of 12:12 (L:D) h maintained in supplemental light. During the experimental periods (October 2012 to February 2013), the fertilizer Compound-Fer 43 (N:P:K:Mg = 15:15:15:4, Taiwan Agricultural Biotechnology Co., Ltd., Taiwan) was applied once monthly during vegetative growth. Palm-sized middle leaves were collected for the experiments.

### Life Table Study and Predation Rate of *E. furcellata*

Ten pairs of newly emerged *E. furcellata* adults were kept in an oviposition container (13.5 cm in diameter; 18.5 cm in height). After 24 h, egg masses were collected from the containers. For the life table study, newly hatched nymphs were selected from different egg masses. In total, 81 and 82 nymphs of *E. furcellata* were used for the life table study on *P. xylostella* and *S. litura*, respectively. From N1 to N3, insects were reared in groups of  $\pm 10$  individuals. Beginning with the fourth nymphal stage, individual bugs were isolated in separate plastic containers (7 cm in diameter; 20 cm in height). As mentioned earlier, bugs of N1 were only provided with cotton balls soaked with water. In attempting to equalize prey size, only third instar larvae of *S. litura* or fourth instar larvae of *P. xylostella* (7.5–8.2 mm in length and 0.68–0.75 mm in width) were provided as food for *E. furcellata* in the life table study. Each individual N2–N5 of *E. furcellata*, was supplied with 10, 15, 20, and 25 larvae, respectively, of either *P. xylostella* or *S. litura* daily. Cabbage leaves were provided as a food source for the caterpillars in each container. A paper towel lining was used to collect eggs. The tops of the containers were covered with a fine mesh net for ventilation. A cotton ball soaked with water was suspended in the center as a water source for *E. furcellata*. After the adults emerged, male and female individuals were paired in a new container and supplied with 90 prey caterpillars (either the third instar of *S. litura* or the fourth instar of *P. xylostella*). The longevity, fecundity, and predation rate were recorded daily. Eggs laid by individual females at different ages were kept separately until the hatch rates were recorded. Because adults were kept

as pairs, the mean daily predation rate per adult was averaged for both sexes.

**Life Table Analysis**

The raw data of the developmental time, survivorship, and female daily fecundity of *E. furcellata* individuals were analyzed based on the age-stage, two-sex life table (Chi and Liu 1985, Chi 1988) using the computer program TWOSEX-MSChart (Chi 2015b). The age-stage specific survival rate ( $s_{xj}$ ), where  $x$  is the age and  $j$  is the stage; the age-specific survival rate ( $l_x$ ); the age-stage specific fecundity ( $f_{xj}$ ); the age-specific fecundity ( $m_x$ ) and the population parameters (the net reproductive rate,  $R_0$ ; the intrinsic rate of increase,  $r$ ; the finite rate,  $\lambda$ ; and the mean generation time,  $T$ ) were calculated in sequence. According to Chi and Liu (1985),  $s_{xj}$  is the age-stage specific survival rate, i.e., the probability that a newly hatched individual will survive to age  $x$  and stage  $j$ . The age-specific survival rate ( $l_x$ ) and the age-specific fecundity ( $m_x$ ) for individuals aged  $x$  are calculated as

$$l_x = \sum_{j=1}^{\beta} s_{xj} \tag{1}$$

and

$$m_x = \frac{\sum_{j=1}^{\beta} s_{xj} f_{xj}}{\sum_{j=1}^{\beta} s_{xj}} \tag{2}$$

where  $\beta$  is the number of life stages.

The net reproduction rate is defined as the mean number of offspring that an individual can produce during its lifetime and is calculated as

$$R_0 = \sum_{x=0}^{\infty} l_x m_x \tag{3}$$

The intrinsic rate of increase was estimated from the Euler-Lotka formula using the method of iterative bisection with the age indexed from 0 (Goodman 1982) as

$$\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1 \tag{4}$$

The finite rate ( $\lambda$ ) is calculated as

$$\lambda = e^r \tag{5}$$

The mean generation time is the time length that a population needs to increase to  $R_0$ -fold of its size as the population reaches the stable age-stage distribution and is calculated as

$$T = \frac{\ln R_0}{r} \tag{6}$$

The bootstrap method was used to estimate the standard errors of the developmental time, fecundity, longevity, and population parameters (Efron and Tibshirani 1993) using 200,000 bootstraps (Akca et al. 2015, Polat Akköprü et al. 2015). The results of treatments were compared using the paired bootstrap test based on the confidence interval of difference (Efron and Tibshirani 1993, Polat Akköprü et al. 2015).

**Predation Analysis**

The raw data for the daily predation rate of all individuals were analyzed according to the age-stage, two-sex life table using the computer program CONSUME-MSChart (Chi 2015a). The

age-specific predation rate ( $k_x$ ) is the mean number of prey consumed by a predator of age  $x$  and is calculated as

$$k_x = \frac{\sum_{j=1}^{\beta} s_{xj} c_{xj}}{\sum_{j=1}^{\beta} s_{xj}} \tag{7}$$

where  $c_{xj}$  is the age-stage-specific predation rate of individuals at age  $x$  and stage  $j$  (Chi and Yang 2003). The age-specific net predation rate  $q_x$  represents the number of prey consumed by the surviving *E. furcellata* at age  $x$ , and is calculated as

$$q_x = l_x k_x = \sum_{j=1}^{\beta} s_{xj} c_{xj} \tag{8}$$

Chi and Yang (2003) defined the net predation rate ( $C_0$ ) as the summation of  $q_x$  over all age groups

$$C_0 = \sum_{x=0}^{\infty} \sum_{j=0}^{\beta} s_{xj} c_{xj} = \sum_{x=0}^{\infty} k_x l_x \tag{9}$$

This represents the total number of prey killed by an average predator during its lifetime, including individuals that died in the preadult stages and adults of both sexes.

The ratio of the net predation rate  $C_0$  to the net reproductive rate  $R_0$  gives the transformation rate from prey population to predator offspring, and the ratio ( $Q_p$ ) is calculated as

$$Q_p = \frac{C_0}{R_0} \tag{10}$$

This value is the mean number of prey that a predator needs in order to produce a single viable egg.

To compare the predation capacity of a predator on different prey, Chi et al. (2011) and Yu et al. (2013a) defined the finite predation rate ( $\omega$ ) as

$$\omega = \lambda \psi = \lambda \sum_{x=0}^{\infty} \sum_{j=0}^{\beta} a_{xj} c_{xj} \tag{11}$$

where  $\lambda$  is the finite rate of the predator population;  $\psi$  is the stable predation rate;  $a_{xj}$  is the proportion of individuals belonging to age  $x$  and stage  $j$ ;  $c_{xj}$  is the age-stage specific predation rate as defined earlier. The variances and standard errors of  $C_0$ ,  $Q_p$ ,  $\psi$ , and  $\omega$  were estimated by using the same 200,000 bootstrap samples from the life table analysis. The bootstrap subroutine is included in the TWOSEX-MSChart (Chi 2015b) and CONSUME-MSChart (Chi 2015a) programs. Both programs are available without charge and may be downloaded at <http://140.120.197.173/Ecology/>.

**Population and Predation Projection**

The life table and predation rate data from the earlier studies were used to project the population growth and predation capacity of *E. furcellata* and *P. xylostella* using the program TIMING (Chi 2015c) using the method described in Tuan et al. (2014). The program TIMING is also available for downloading at the TWOSEX-MSChart site.

**Results**

**Life Table of *E. furcellata* Fed on *P. xylostella* and *S. litura***

Although nymphs of *E. furcellata* could develop to adults and produce offspring when fed on larvae of either *P. xylostella* or *S. litura*, significant differences in developmental times of N1–N3, N4, and total preadult periods were observed. The total preadult duration of *E. furcellata* fed on *S. litura* was 26.7 d. This was significantly longer

**Table 1.** Mean ( $\pm$  SE) of development time, adult longevity, total longevity, APOP, TPOP, and fecundity of *E. furcellata* fed on larvae of *P. xylostella* and *S. litura*

Statistics	Prey				P
	n	<i>P. xylostella</i>	N	<i>S. litura</i>	
Egg duration (day)	81	7.0 $\pm$ 0.0a	82	7.1 $\pm$ 0.1a	0.4343
N1–N3 duration (day)	76	9.6 $\pm$ 0.1b	82	10.6 $\pm$ 0.1a	<0.0001
N4 duration (day)	74	2.4 $\pm$ 0.1b	79	3.4 $\pm$ 0.1a	<0.0001
N5 duration (day)	72	5.6 $\pm$ 0.1a	77	5.6 $\pm$ 0.1a	0.5824
Total preadult (day)	72	24.5 $\pm$ 0.1b	77	26.7 $\pm$ 0.2a	<0.0001
Adult (female)	36	38.1 $\pm$ 2.3a	37	40.0 $\pm$ 2.4a	0.5637
Adult (male)	36	36.9 $\pm$ 2.7b	40	62.9 $\pm$ 5.1a	<0.0001
Total longevity (female)	36	62.8 $\pm$ 2.3a	37	67.1 $\pm$ 2.3a	0.1835
Total longevity (male)	36	61.3 $\pm$ 2.6b	40	89.6 $\pm$ 5.0a	<0.0001
APOP (day)	36	6.5 $\pm$ 0.2b	37	7.4 $\pm$ 0.2a	0.0035
TPOP (day)	36	31.2 $\pm$ 0.3b	37	34.5 $\pm$ 0.3a	<0.0001
Oviposition period (day)	36	18.3 $\pm$ 1.6a	37	17.7 $\pm$ 1.3a	0.7633
Fecundity (total eggs/female)	36	829.1 $\pm$ 66.3a	37	725.6 $\pm$ 53.5a	0.2246
Fecundity (viable eggs/female)	36	658 $\pm$ 62a	37	604 $\pm$ 50a	0.5000

Standard errors were estimated by using 200,000 bootstraps. Means followed by different letters are significantly different between two treatments using the paired bootstrap test at the 5% significance level.

than the average of 24.5 d when *E. furcellata* were fed on *P. xylostella*. When reared on *S. litura*, the male longevity of *E. furcellata* (89.6 d) was significantly longer in comparison to the 61.3 d found for those reared on *P. xylostella*. There were, however, no differences in the N5, female adult duration, total female longevity, oviposition period, and fecundity between the two prey species (Table 1).

The age-specific fecundity and the age-specific hatch rate varied with the prey species and maternal ages (Fig. 1). The total eggs laid per female *E. furcellata* reared on *P. xylostella* and *S. litura* were 829.1 and 725.6 eggs; while the total hatched eggs were 658 and 604 eggs, respectively (Table 1). The overall hatch rate was 79.4% when reared on *P. xylostella*, with the daily hatch rate ranging from 0 to 95.4%. When reared on *S. litura*, it was 83.2% ranging from 37.6 to 100.0%. There was no significant difference between the overall hatch rates of *E. furcellata* reared on the two prey species. Because the hatch rate varied with maternal age, using the total number of eggs would result in overestimating the population survival rate, fecundity, and population parameters (Chi et al. 2015, Mou et al. 2015). Accordingly, we included only the hatched eggs of the parent cohort and the hatched eggs of daily fecundity in the following analyses.

The age-stage survival rate ( $s_{xj}$ ) shows the probability that a newly hatched individual will survive to age  $x$  and stage  $j$  (Fig. 2). Because the variable developmental rates found among individuals were included in the age-stage, two-sex life table, the overlaps between different stages could be observed in Fig. 2. The age-specific survival rate ( $l_x$ ), the age-specific fecundity ( $m_x$ ), and the age-specific maternity ( $l_x m_x$ ) curves are plotted in Fig. 3. A maximal daily mean fecundity of 35 offspring per *E. furcellata* ( $f_{xj}$ ) was observed at age 47 d when reared on *S. litura*; when reared on *P. xylostella*, the maximal daily mean was 43.1 eggs at age 33 d.

Male *E. furcellata* adults reared on *S. litura* survived longer than males reared on *P. xylostella*. The adult preoviposition period (APOP), i.e., the time between the adult emergence and first oviposition, was 6.5 and 7.4 days, respectively, on *P. xylostella* and *S. litura* (Table 1). The total preoviposition period (TPOP), i.e., the time period from birth to first reproduction in females, was 31.2 and 34.5 days, respectively.

### Population Parameters

The standard errors of the population parameters were estimated using the bootstrap method with 200,000 resampling (Table 2). The intrinsic rate of increase ( $r$ ) and the finite rate of increase ( $\lambda$ ) of *E. furcellata* reared on *P. xylostella* (0.1389 d<sup>-1</sup> and 1.1490 d<sup>-1</sup>) were significantly higher than those reared on *S. litura* (0.1220 d<sup>-1</sup> and 1.1298 d<sup>-1</sup>). The net reproductive rate ( $R_0$ ) was also higher for those reared on *P. xylostella* (292.4 offspring) than on *S. litura* (272.3 offspring). The mean generation time ( $T$ ) was longer when *E. furcellata* fed on *S. litura* (46.0 d) than on *P. xylostella* (40.9 d).

### Predation Rate

The predation rates of female N2–N5 nymphs, and adults on *P. xylostella* were 13.5, 8.1, 60.6 and 670.0 larvae, respectively (Table 3). These rates were significantly higher than those of males with the exception of the N4 predation rate. By comparison, the predation rates of the female N2–N3, N4, and N5 nymphs fed on *S. litura* were 7.6, 19.3, and 57.1 larvae (Table 3). These values were higher than the corresponding male predation rates, but the male adults consumed an average of 938.0 larvae, which was significantly higher than the 730.1 larvae consumed by the adult females. The total number of prey consumed by adults was significantly higher than that of the total of the preadult stages due to the longer adult time period.

The age-stage consumption rates ( $c_{xj}$ ) of *E. furcellata* fed on *P. xylostella* and *S. litura* are plotted in Fig. 4. This represents the number of caterpillars consumed by *E. furcellata* at age  $x$  and stage  $j$ . Similar to the  $s_{xj}$  curves, there were overlaps of the age-stage consumption rates due to the variable developmental rates occurring among individuals. The age-specific predation rate ( $k_x$ ) and age-specific net predation rate ( $q_x$ ) are shown in Fig. 5. Because the eggs and N1 are incapable of prey consumption, significant predation gaps were found in the range from age 0 to 8 d on both prey species. N5 bugs preparing for their last molt ceased feeding, resulting in a significant drop of predation rate at approximately 22 and 25 d when reared on *P. xylostella* and *S. litura*, respectively. Incorporating the survival rate and predation rate, the net predation rates ( $C_0$ ) for *E. furcellata* fed on *P. xylostella* and *S. litura* were

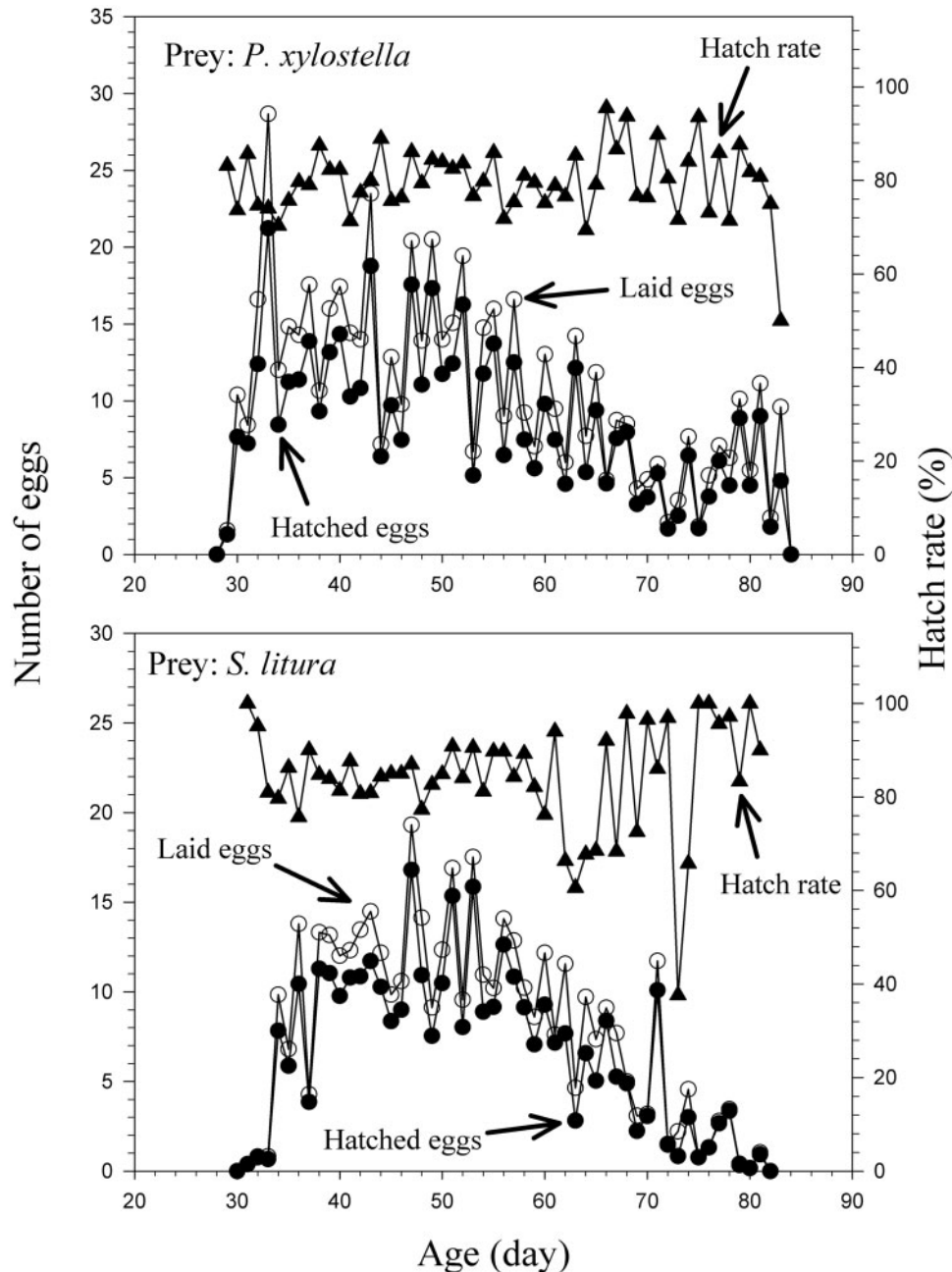


Fig. 1. Age-specific fecundity (total eggs and hatched eggs) and hatch rate of *E. furcellata* fed on *P. xylostella* and *S. litura* at 25°C.

644.1 and 863.1, respectively; representing the number of prey consumed during the lifetime of the predator. The transformation ( $Q_p$ ) for *E. furcellata* reared on *P. xylostella* and *S. litura* were 2.2 and 3.2, respectively (Table 4). According to Chi and Yang (2003), the value of  $Q_p$  showed that *E. furcellata* required 2.2 *P. xylostella* fourth instar larvae or 3.2 third instar *S. litura* larvae to produce each egg.

#### Population and Predation Projection

The population growth and the predation capacity of *E. furcellata* fed on *P. xylostella* and *S. litura* are shown in Fig. 6. The changes of stage structure of *E. furcellata* can be observed in Fig. 6A and C. Because *E. furcellata* is nonpredatory in the egg stage and the predation rate varies with age, values for the predation potential and total

population size did not increase proportionally and exhibited different degrees of fluctuation (Fig. 6B and D).

## Discussion

#### Age-Stage, Two-Sex Life Table

Chu and Chu (1975b) reported that they observed no differences in the nymphal developmental time of *E. furcellata* when reared on the larvae of *Chilo suppressalis*, *Pieris rapae*, *Pyrausta nubilalis*, *S. litura*, and *Galleria mellonella* at 28°C. In our study, the durations of the immature stages and adult longevity of *E. furcellata* reared on *P. xylostella* were shorter than those reared on *S. litura* at 25°C (Table 1). The developmental time of *E. furcellata* nymphs and adult longevity were affected by different prey densities. *E. furcellata*

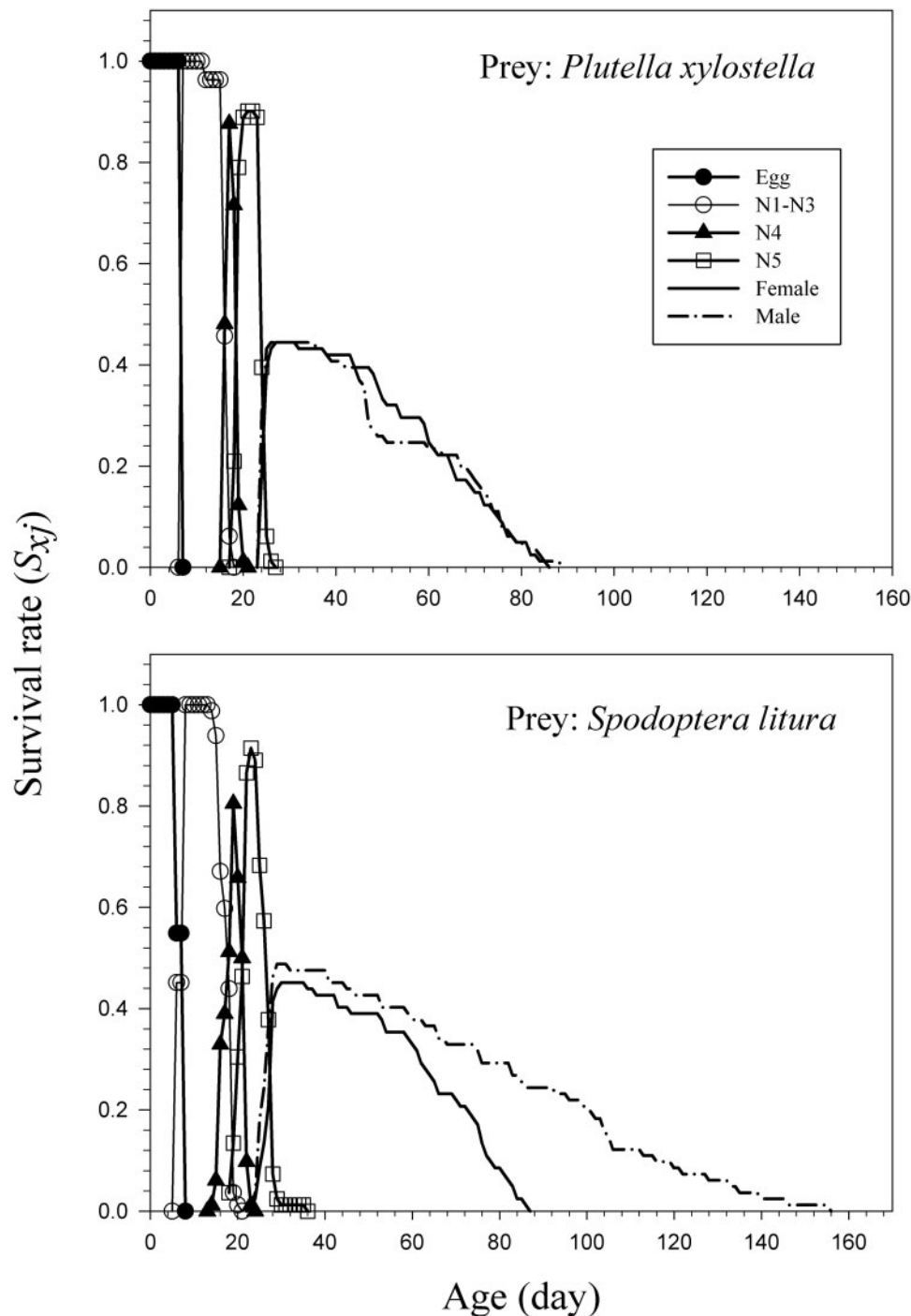


Fig. 2. Survival rate ( $s_{xj}$ ) of *E. furcellata* fed on *P. xylostella* and *S. litura* in the laboratory at 25°C.

nymphs developed more rapidly on 10 diamondback moth larvae than on only one larva per day (Nyunt 2008). The development times of all immature stages were much shorter than those reported by Nyunt (2008), because sufficient prey were provided daily at different life stages in this study. In Table 1, the male adults fed on *S. litura* larvae had longer longevity compared with the female adults; however, the life spans of both male and female *E. furcellata* were similar when reared on *P. xylostella*. Chu and Chu (1975b) reported a shorter longevity of both male and female *E. furcellata* when reared on *P. rapae* at 25°C. This may be a consequence of using a different host species.

The variable developmental rates that occurs among individuals resulted in the overlaps of  $s_{xj}$  (Fig. 1). Because traditional female age-specific life tables (Lewis 1942, Leslie 1945, Birch 1948, Carey 1993) are incapable in describing the stage differentiation and ignore the effects of the male population, these overlaps as well as the male survival rate would not be evident when female-only life tables are used. Huang and Chi (2012) discussed the problems accompanying the application of the female age-specific life table to a two-sex population and pointed out some of the resulting errors that are inherent in publications using these life tables. For example, Perumalsamy et al. (2009) reported a net reproductive rate

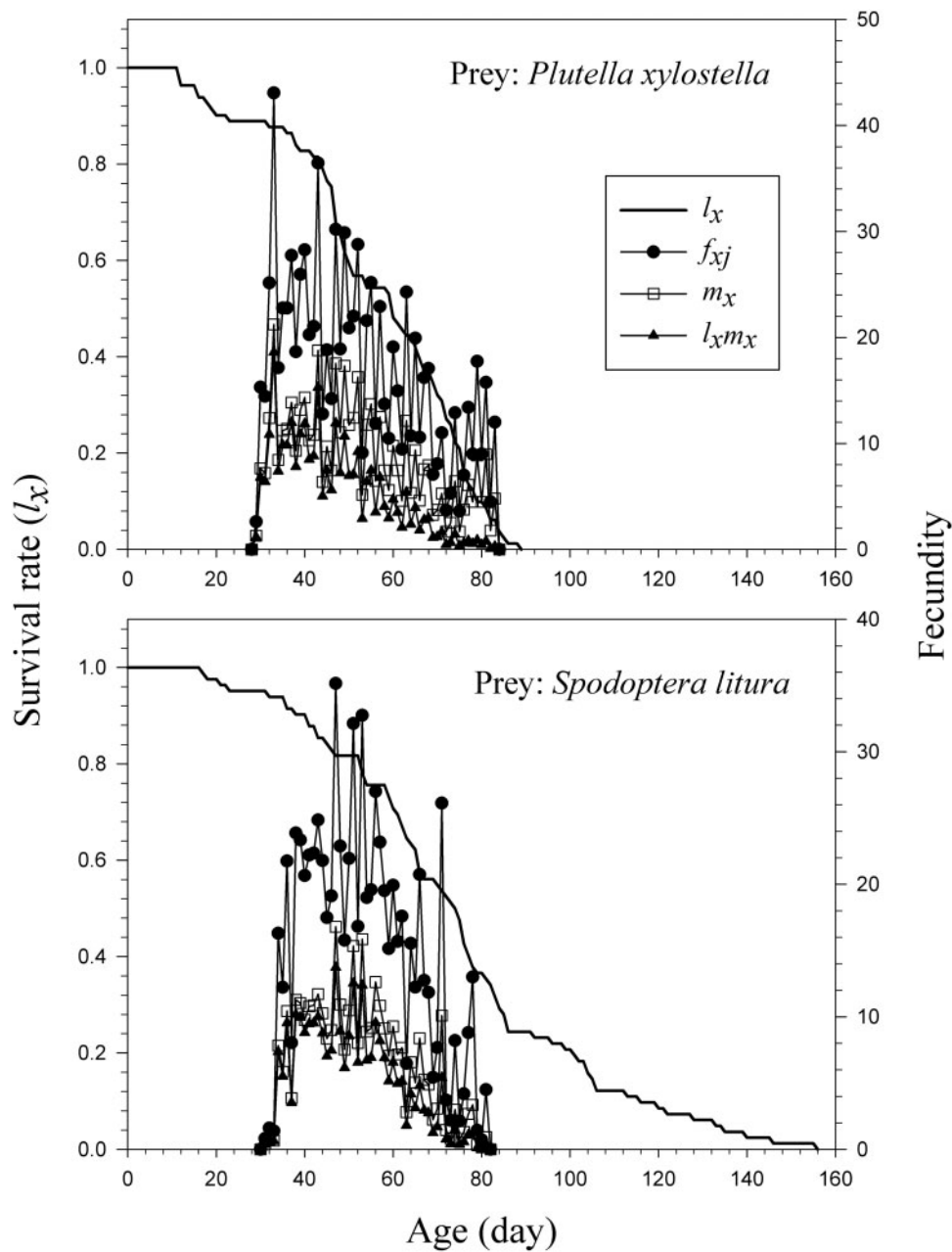


Fig. 3. Age-specific survival rate ( $l_x$ ), fecundity ( $m_x$ ), maternity ( $l_x m_x$ ), and female age-specific fecundity ( $f_{xj}$ ) of *E. furcellata* fed on *P. xylostella* and *S. litura* in the laboratory at 25°C.

Table 2. Population parameters (mean ± SE) of *E. furcellata* fed on larvae of *P. xylostella* and *S. litura*

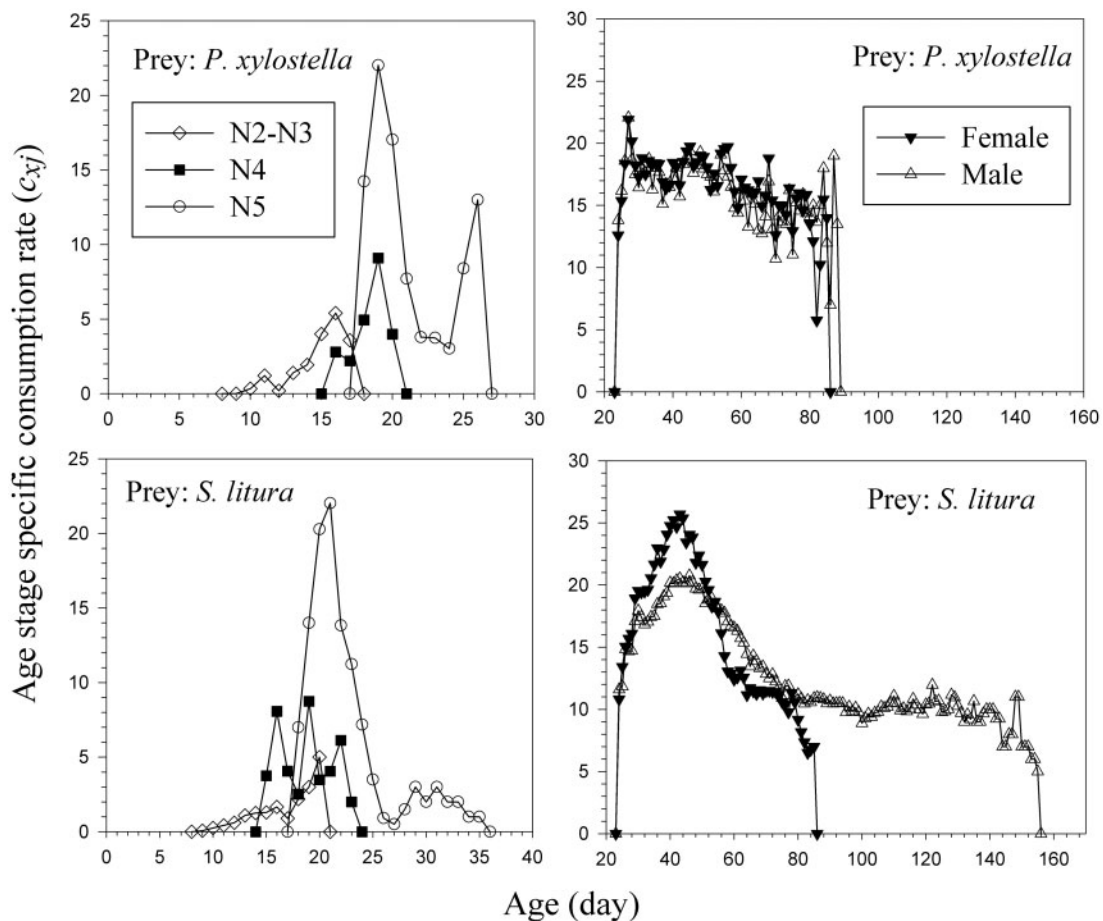
Population parameter	Prey		P
	<i>P. xylostella</i>	<i>S. litura</i>	
Intrinsic rate of increase, $r$ ( $d^{-1}$ )	0.1389 ± 0.0040a	0.1220 ± 0.0034b	0.0019
Finite rate of increase, $\lambda$ ( $d^{-1}$ )	1.1490 ± 0.0046a	1.1298 ± 0.0039b	0.0019
Net reproduction rate, $R_0$ (offspring)	292.4 ± 45.4a	272.3 ± 40.2a	0.7418
Mean generation time, $T$ (d)	40.9 ± 0.5b	46.0 ± 0.4a	<0.0001

Standard errors were estimated by using 200,000 bootstraps. Means followed by different letter are significantly different between two treatments using the paired bootstrap test at the 5% significance level.

**Table 3.** Predation rates (mean  $\pm$  SE) of different stages of *E. furcellata* fed on larvae of *P. xylostella* and *S. litura*

Stage	Predation rate (Preys/predator)								
	<i>P. xylostella</i>				<i>S. litura</i>				
	<i>n</i>	Female	<i>n</i>	Male	<i>n</i>	Female	<i>n</i>	Male	
Nymph stage	N2–N3	36	13.5 $\pm$ 0.5aA	36	11.4 $\pm$ 0.5bA	37	7.6 $\pm$ 0.3aB	40	7.9 $\pm$ 0.4aB
	N4	36	8.1 $\pm$ 0.8aB	36	8.0 $\pm$ 0.9aB	37	19.3 $\pm$ 1.3aA	40	16.7 $\pm$ 0.9aA
	N5	36	60.6 $\pm$ 2.3aA	36	53.1 $\pm$ 1.8bA	37	57.1 $\pm$ 2.1aA	40	49.6 $\pm$ 1.8bA
Total pre-adult	N2–N5	36	82.1 $\pm$ 2.1aA	36	72.4 $\pm$ 1.6bA	37	84.0 $\pm$ 2.4aA	40	74.1 $\pm$ 1.9bA
Adult		36	670.0 $\pm$ 49.4aA	36	645.1 $\pm$ 44.1aB	37	730.1 $\pm$ 38.1aA	40	938.0 $\pm$ 63.8bA

Standard errors were estimated by using 200,000 bootstraps. Means followed by different lower case letters represent significant difference between sexes in the same treatment, while a capital letter denotes a difference between the same sexes of different treatments using paired bootstrap test at the 5% significance level.

**Fig. 4.** Age-stage, two-sex consumption rate ( $c_{xj}$ ) of *E. furcellata* fed on *P. xylostella* and *S. litura* at 25°C.

( $R_0 = 243.693$ ) of *Oligota pygmaea* (Solier), which is only slightly different than the gross reproductive rate (GRR = 245.313). The huge gap occurring between the curves of  $l_x m_x$  and  $m_x$  (Fig. 3 in Perumalsamy et al. 2010) demonstrated, however, that there must be an error in either  $R_0$  or GRR. Yu et al. (2005) mathematically proved the relationship between GRR, net reproduction rate, and preadult survivorship. Dannon et al. (2010) reported a mean fecundity of 121.5 for *Maruca vitrata* reared at 20°C, which was lower than the net reproductive rate ( $R_0 = 139.5$ ). Because the net reproductive rate is calculated by taking the survival rate into account, it

is impossible that  $R_0 > F$  [as demonstrated by Chi (1988) and Chi and Su (2006)]. Since the earlier results found by Dannon et al. (2010) are mathematically impossible, there must be fundamental inaccuracies in their calculations and/or assumptions.

In Fig. 3, there are many peaks in the  $m_x$ ,  $l_x m_x$ , and  $f_{xj}$  curves. According to Chu and Chu (1975a,b), *E. furcellata* females oviposit egg masses consisting of a few to more than 100 eggs. Because *E. furcellata* generally produced egg masses at 2- to 3-d intervals, the raw data of daily egg production of individual females showed obvious periodicity in this study. However, due to the variable



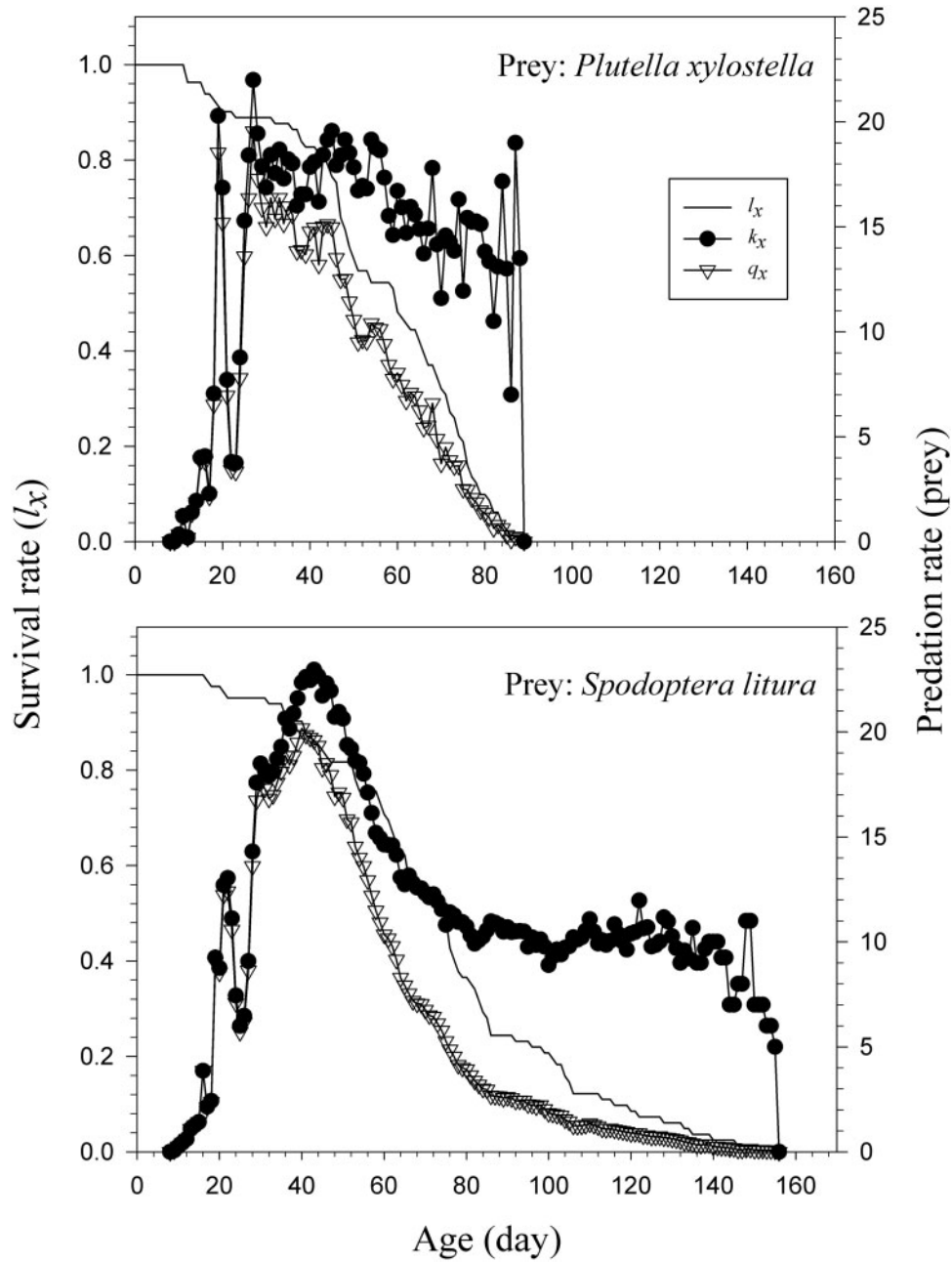


Fig. 5. Age-specific survival rate ( $l_x$ ), age-specific predation rate ( $k_x$ ), and age-specific net predation rate ( $q_x$ ) of total population of *E. furcellata* fed on *P. xylostella* and *S. litura* at 25°C.

**Table 4.** Mean ( $\pm$  SE) of net predation rate ( $C_0$ , no. preys), transformation rate ( $Q_p$ , no. preys per viable predator egg), stable predation rate ( $\psi$ , no. preys) and finite predation rate ( $\omega$ , preys/d) of different stages of *E. furcellata* fed on larvae of *P. xylostella* and *S. litura*

Parameter	Prey species				
	<i>n</i>	<i>P. xylostella</i>	<i>n</i>	<i>S. litura</i>	<i>P</i>
$C_0$	81	644.1 $\pm$ 38.3b	82	863.1 $\pm$ 43.6a	0.0002
$Q_p$	81	2.2024 $\pm$ 0.3230a	82	3.1694 $\pm$ 0.5193a	0.0992
$\psi$	81	1.2426 $\pm$ 0.0358b	82	1.4188 $\pm$ 0.0417a	0.0015
$\omega$	81	1.4277 $\pm$ 0.0423b	82	1.6029 $\pm$ 0.0476a	0.0066

Standard errors were estimated by using 200,000 bootstraps. Means followed by different letters are significantly different between two treatments by using paired bootstrap test at the 5% significance level.

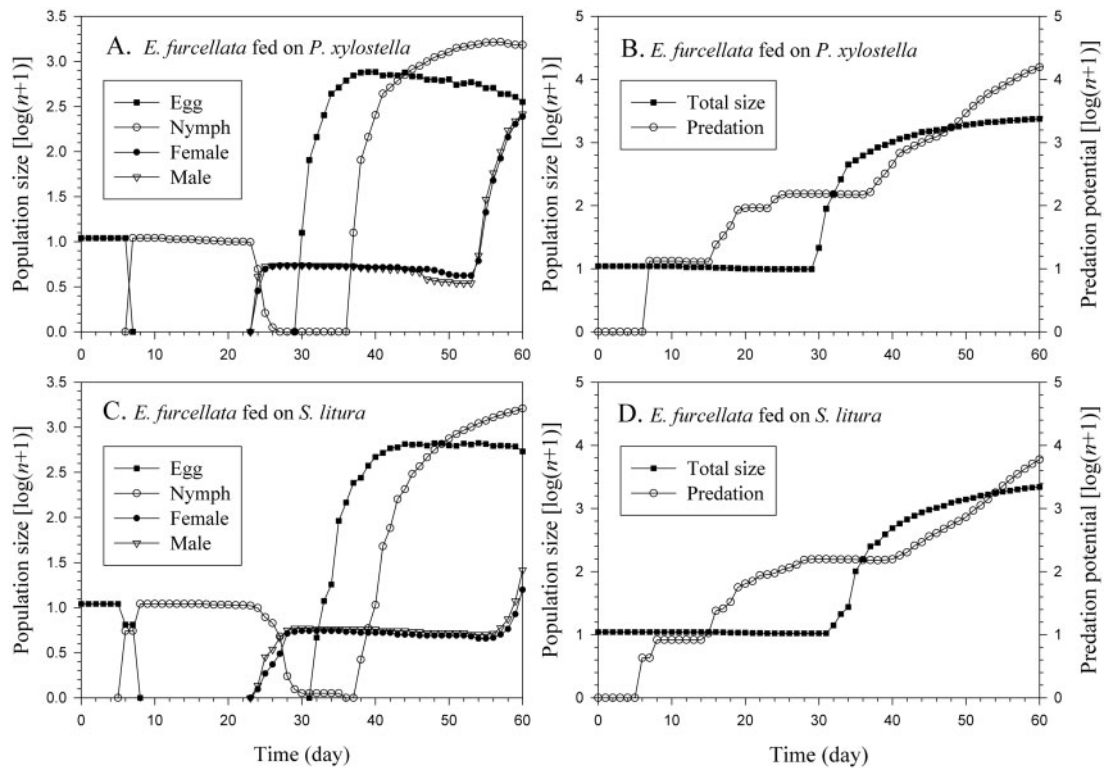


Fig. 6. Population and predation projection of *E. furcellata* fed on *P. xylostella* and *S. litura*.

developmental time and consequently the variable reproduction schedules among individuals, such periodicity became less obvious when the curves of all individuals were pooled together. The mean lifelong fecundity per female was 658 and 604 eggs for *E. furcellata* reared on *P. xylostella* and *S. litura*, respectively (Table 1). These values are higher than those ( $341 \pm 128.9$  eggs) reported by Tseng (1982) and Gupta et al. (2013) ( $173.5 \pm 10.59$  eggs) when rearing *E. furcellata* on *S. litura*.

#### Population Parameters

Chi (1988) demonstrated that the relationship between the mean fecundity ( $F$ ) and the net reproduction rate ( $R_0$ ) for two-sex life tables was

$$R_0 = F \times \frac{N_f}{N} \quad (12)$$

where  $N$  is the total number of eggs used at the beginning of the life table study and  $N_f$  is the number of female adults emerged from  $N$ . As in other previous studies based on the two-sex life table, our data on both *P. xylostella* and *S. litura* were completely consistent with Equation 12. The intrinsic rate of increase ( $r$ ), the finite rate of increase ( $\lambda$ ), and the net reproduction rate ( $R_0$ ) showed high growth potential of *E. furcellata* reared on both *P. xylostella* and *S. litura*.

#### Predation Rate

In our study, the predation rate of *E. furcellata* reared on *P. xylostella* was different than those individuals reared on *S. litura*. Adults males reared on *S. litura* were shown to have a longer longevity than females, and, accordingly, consumed more *S. litura* than females. The predation rate of individuals in the preadult stages generally increased with age, except for the fourth nymphal stage of specimens reared on *P. xylostella*. N5 individuals consumed more prey than

other preadult stages. Nyunt (2008) reported the daily consumption of diamondback moth larvae by the N2–N5 stages of *E. furcellata* nymphs was 4.1, 4.3, 6.0, and 8.5 larvae, respectively, of the 10 larvae provided. These values are much lower than our results. The predation rate of *E. furcellata* on the two prey species studied suggests that females require more prey than males in order to prepare for egg production in the adult stage (Table 3).

#### Population and Predation Projection

As demonstrated in Fig. 6A and C, changes in the stage structure can be easily depicted using a population projection extrapolated from the age-stage, two-sex life table data. Because traditional female age-specific life tables (Lewis 1942, Leslie 1945, Birch 1948, Carey 1993) are incapable of describing stage differentiation, depicting stage structure such as in Fig. 6A and C would not have been possible when they are used. Researchers who have used age-specific life tables and attempted to group life history into stages have inevitably made errors in their published results; for example, fecundity ( $m_x$ ) was reported during the immature stage by Kennedy et al. (1996, Table 2). Another important consideration is that traditional female age-specific life tables totally ignore the contribution of the male component of the population to the overall predation rate. This is particularly critical in predaceous species where the effects of the males may, in many cases, be equal to that of the females. We demonstrate the importance of linking the predation rate with the life table data to increase the efficacy of biological control programs.

#### Application of the Life Table Data to Biological Control and Rearing Programs

When evaluating the efficiency of a predator, it is inappropriate to make a judgment solely based on population growth potential

(the intrinsic rate or the finite rate) or the predation rate of the predator. A predator with a rapid growth rate may have a low predation rate, while another predator might have a higher predation rate but a slower growth rate. To demonstrate, the intrinsic rate of *E. furcellata* fed on *P. xylostella* was higher than those fed on *S. litura*, while the net predation rate of *E. furcellata* fed on *P. xylostella* was lower than those fed on *S. litura*. Chi et al. (2011) and Yu et al. (2013a) introduced the finite predation rate to include the finite rate ( $\lambda$ ), the stable age-stage distribution ( $a_{xj}$ ), and the age-stage predation rate ( $c_{xj}$ ). These rates represent the growth potential of a predator, the stable population structure, and the predation capacity at different ages and stages, respectively. In our study, the finite predation rate ( $\omega$ ) values were 1.4 and 1.6 prey/d on *P. xylostella* and *S. litura*, respectively (Table 4). These values show that *E. furcellata* is a more effective predator when preying on *S. litura* compared with preying on *P. xylostella*. This comparison, however, is based on a stable age-stage distribution. Before the populations reach a stable age-stage distribution, the predation capacity of *E. furcellata* fed on *P. xylostella* may be higher than those fed on *S. litura* as shown in Fig. 6B and D at 60 d. This comparison does not factor in the different damage potentials of the two pests. In the future, studies should include determining the damage potentials and the economic thresholds of the pest species and integrating these with the life table and predation rate data.

Hassell (1978) noted that including the predator and prey age structure is an important step in understanding predator-prey relationships. In our study, the basic data of survival rate, developmental time, stage differentiation, and fecundity of *E. furcellata* were collected and precisely described. Furthermore, as a result of our predation study, the predation rate of individuals of both sexes at different ages and stages could be evaluated in detail. This information is crucial to the study of predator-prey relationships and is certainly essential for the successful implementation of biological control programs. It has only been within the past few years, however, that a life table and the predation rate have been coordinated within a single study (Chi and Yang 2003, Yu et al. 2005, Chi and Su 2006, Farhadi et al. 2011, Yu et al. 2013a, Khanamani et al. 2015). This study demonstrates, once again, that a life table study incorporating age-stage predation rate is a promising and persuasive method for biological control.

## Acknowledgments

We appreciate Shu-Chen Peng for her supply of *E. furcellata* and help with rearing techniques and Ching-Chou Tzeng for supplying specimens of *P. xylostella*. This study is partly supported by MOST 102-2313-B-005-028 and MOST 103-2923-B-005-003.

## References Cited

- Ahmad, M., A. H. Sayyed, N. Crickmore, and M. A. Saleem. 2007. Genetics and mechanism of resistance to deltamethrin in a field population of *Spodoptera litura* (Lepidoptera: Noctuidae). *Pest Manag. Sci.* 63: 1002–1010.
- Akca, I., T. Ayvaz, E. Yazıcı, C. L. Smith, and H. Chi. 2015. Demography and population projection of *Aphis fabae* (Hemiptera: Aphididae): with Additional Comments on Life Table Research Criteria. *J. Econ. Entomol.* 108: 1466–1478.
- Asano, S., T. Maruyama, T. Ivasa, A. Seki, M. Takahashi, and G. R. Soares Jr. 1993. Evaluation of biological activity of *Bacillus thuringiensis* test samples using a diet incorporation method with diamondback moth, *Plutella xylostella* (Linnaeus) (Lepidoptera: Yponomeutidae). *Appl. Entomol. Zool.* 28: 513–524.

- Birch, L. C. 1948. The intrinsic rate of natural increase of an insect population. *J. Anim. Ecol.* 17: 15–26.
- Carey, J. R. 1993. Applied demography for biologists: with special emphasis on insects. Oxford University Press, New York.
- Chang, C. P. 2002. Mass rearing and utilization of the predatory stink bug, *Eocanthecona furcellata*. *Formosan Entomol. Spec. Pub.* 3: 175–181.
- Chang, C. P., and F. K. Hsieh. 2001. Predatory capacity of the predatory stink bug, *Eocanthecona furcellata* (Wolff) (Hemiptera: Pentatomidae) on various prey. *Formos. Entomol.* 21: 257–267.
- Chapman, J. W., D. R. Reynolds, A. D. Smith, J. R. Riley, D. E. Pedgley, and I. P. Woiwod. 2002. High-altitude migration of the diamondback moth *Plutella xylostella* to the U.K.: a study using radar, aerial netting, and ground trapping. *Ecol. Entomol.* 27: 641–650.
- Chi, H. 1988. Life table analysis incorporating both sexes and variable development rates among individuals. *Environ. Entomol.* 17: 26–34.
- Chi, H. 2015a. CONSUME-MSChart: a computer program for the age-stage, two-sex consumption rate analysis. National Chung Hsing University, Taichung, Taiwan. (<http://140.120.197.173/Ecology/>) (accessed 25 June 2015).
- Chi, H. 2015b. TWSEX-MSChart: a computer program for the age-stage, two-sex life table analysis. National Chung Hsing University, Taichung, Taiwan. (<http://140.120.197.173/Ecology/>) (accessed 25 June 2015).
- Chi, H. 2015c. Timing-MSChart: Computer program for population projection based on age-stage, two-sex life table. (<http://140.120.197.173/Ecology/>) (accessed 25 June 2015).
- Chi, H., and H. Liu. 1985. Two new methods for the study of insect population ecology. *Bull. Inst. Zool. Acad. Sin.* 24: 225–240.
- Chi, H., and H. Y. Su. 2006. 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. *Environ. Entomol.* 35: 10–21.
- Chi, H., and T. C. Yang. 2003. Two-sex life table and predation rate of *Prophyllaea japonica* Thunberg (Coleoptera: Coccinellidae) fed on *Myzus persicae* (Sulzer) (Homoptera: Aphididae). *Environ. Entomol.* 32: 327–333.
- Chi, H., Y. B. Huang, H. Allahyari, J. Z. Yu, D. F. Mou, T. C. Yang, R. Farhadi, M. Gholizadeh. 2011. Finite predation rate: a novel parameter for the quantitative measurement of predation potential of predator at population level. *In* *Natural Proceedings* (<http://proceedings.nature.com/documents/6651/version/1/files/npre20116651-1.pdf>) (accessed 25 June 2015).
- Chi, H., D. F. Mou, C. C. Lee, and C. L. Smith. 2015. Comments on the paper of Hernandez-Suarez et al. “Invariance of demographic parameters using total or viable eggs”. *J. Appl. Entomol.* doi: 10.1111/jen.12225.
- Chu, Y. L., and C. M. Chu. 1975a. Feeding habit of *Eocanthecona furcellata* (Wolff). *Plant Prot. Bull.* 17: 133–141.
- Chu, Y. L., and C. M. Chu. 1975b. Life history and the effect of temperature on the growth of *Eocanthecona furcellata* (Wolff). *Plant Prot. Bull.* 17: 99–114.
- Dannon, E. A., M. Tamò, A. van Huis, and M. Dicke. 2010. Functional response and life history parameters of *Apanteles taragamae*, a larval parasitoid of *Maruca vitrata*. *BioControl* 55: 363–378.
- De Clercq, P. 2000. Predaceous Stinkbugs (Pentatomidae: Asopinae), pp. 737–789. *In* C. W. Schaefer and A. R. Panizzi (eds.), *Heteroptera of economic importance*. CRC Press LLC, Boca Raton, FL.
- De Clercq, P., I. Peeters, G. Vergauwe, and O. Thas. 2003. Interaction between *Podisus maculiventris* and *Harmonia axyridis*, two predators used in augmentative biological control in greenhouse crops. *BioControl* 48: 39–55.
- Efron, B., and R. J. Tibshirani. 1993. *An introduction to the bootstrap*. Chapman & Hall, NY.
- Farhadi, R., H. Allahyari, and H. Chi. 2011. Life table and predation capacity of *Hippodamia variegata* (Coleoptera: Coccinellidae) feeding on *Aphis fabae* (Hemiptera: Aphididae). *Biol. Control* 59: 83–89.
- Furlong, M. J., D. J. Wright, and L. M. Dossall. 2013. Diamondback moth ecology and management: problems, progress, and prospects. *Annu. Rev. Entomol.* 58: 517–541.
- Goodman, D. 1982. Optimal life histories, optimal notation, and the value of reproductive value. *Am. Nat.* 119: 803–823.

- Gupta, R. K., M. Gani, P. Jasrotia, and K. Srivastava. 2013. Development of the predator *Eocanthecona furcellata* on different proportions of nucleopolyhedrovirus infected *Spodoptera litura* larvae and potential for predator dissemination of virus in the field. *BioControl* 58: 543–552.
- Hassell, M. P. 1978. The dynamics of arthropod predator-prey system. Princeton University Press, Princeton, NJ.
- Huang, Y. B., and H. Chi. 2012. Age-stage, two-sex life tables of *Bactrocera cucurbitae* (Coquillett) (Diptera: Tephritidae) with a discussion on the problem of applying female age-specific life tables to insect populations. *Insect Sci.* 19: 263–273.
- Jiang, M. Y., J. H. Gao, Y. B. Huang, and Y. S. Xie. 2010. The management of *Spodoptera litura* in green manure field. Technical services of TARI/COA 82: 19–22.
- Kennedy, J. S., G. Van Imp, Th. Hance, and Ph. Lebrun. 1996. Demecology of the false spider mite, *Brevipalpus phoenicis* (Geiiskes) (Acari, Tenuipalpidae). *J. Appl. Entomol.* 102: 493–499.
- Khanamani, M., Y. Fathipour, and H. Hajiqanbar. 2015. Assessing compatibility of the predatory mite *Typhlodromus bagdasarjani* (Acari: Phytoseiidae) and resistant eggplant cultivar in a tritrophic system. *Ann. Entomol. Soc. Am.* 108: 501–512.
- Kumar, M., A. N. Shylesha, and N. S. A. Thakur. 1996. *Eocanthecona furcellata* (Wolff) (Heteroptera: Pentatomidae): a promising predator of *Craspedonta leayana* (Latr.) (Chrysomelidae: Coleoptera) on *Gmelina arborea* in Meghalaya. *Insect Environ.* 2: 56–57.
- 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: Indian J. Stastics* 6: 93–96.
- Messelink, G. J., J. Bennisson, O. Alomar, B. L. Ingegno, L. Tavella, L. Shipp, E. Palevsky, and F. L. Wäckers. 2014. Approaches to conserving natural enemy populations in greenhouse crops: current methods and future prospects. *BioControl*. 59: 377–393.
- Mou, D. F., C. C. Lee, C. L. Smith, and H. Chi. 2015. Using viable eggs to accurately determine the demographic and predation potential of *Harmonia dimidiata* (Coleoptera: Coccinellidae). *J. Appl. Entomol.* 139: 579–591.
- Nyunt, K. T. 2008. Potential of the predatory pentatomid *Eocanthecona furcellata* (Wolff) as a biocontrol agent on American bollworm in cotton in Myanmar. Faculty of Agricultural Sciences Georg-August University Göttingen, Germany.
- Perumalsamy, K., R. Selvasundaram, A. Roobakkumar, V. J. Rahman, A. Babu, N. N. Muraleedharan. 2009. Life table and predation of *Oligota pygmaea* (Coleoptera: Staphylinidae) a major predator of the red spider mite, *Oligonychus coffeae* (Acarina: Tetranychidae) infesting tea. *Biol. Control* 51: 96–101.
- Polat Akköprü, E., R. Atlihan, H. Okut, and H. Chi. 2015. Demographic assessment of plant cultivar resistance to insect pests: a case study of the dusky-veined walnut aphid (Hemiptera: Callaphididae) on five walnut cultivars. *J. Econ. Entomol.* 108: 378–387.
- Talekar, N. S., and A. M. Shelton. 1993. Biology, ecology, and management of the diamondback moth. *Annu. Rev. Entomol.* 38: 275–301.
- Tseng, J. M. 1982. Comparative response of *Eocanthecona furcellata* (Wolff) and *Podisus maculiventris* (Say) to temperature and photoperiod and their relative potential as beneficial predators. Ph.D. dissertation, Entomology and Nematology, University of FL.
- Tuan, S. J., S. S. Kao, Y. C. Chao, and R. F. Hou. 1997. Investigation of pathogenicity AcMNPV to nine Lepidopteran pests in Taiwan. *Chin. J. Entomol.* 17: 209–225.
- Tuan, S. J., N. J. Li, C. C. Yeh, L. C. Tang, and H. Chi. 2014. Effects of green manure cover crops on *Spodoptera litura* (Lepidoptera: Noctuidae) populations. *J. Econ. Entomol.* 107: 897–905.
- Yu, J. Z., H. Chi, and B. H. Chen. 2005. 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. *Ann. Entomol. Soc. Am.* 98: 475–482.
- Yu, J. Z., H. Chi, and B. H. Chen. 2013a. Comparison of the life table and predation rates of *Harmonia dimidiata* (F.) (Coleoptera: Coccinellidae) fed on *Aphis gossypii* Glover (Hemiptera: Aphididae) at different temperatures. *Biol. Control* 64: 1–9.
- Yu, L. Y., Z. Z. Chen, F. Q. Zheng, A. J. Shi, T. T. Guo, B. H. Yeh, H. Chi, Y. Y. Xu. 2013b. Demographic analysis, a comparison of the jackknife and bootstrap methods, and predation projection: a case study of *Chrysopa pallens* (Neuroptera: Chrysopidae). *J. Econ. Entomol.* 106: 1–9.
- Zanuncio, J. C., W. P. Lemos, M. C. Lacerda, T. V. Zanuncio, J. E. Serrão, and E. Bauce. 2006. Age-dependent fecundity and fertility life tables of the predator *Brontocoris tabidus* (Heteroptera: Pentatomidae) under field conditions. *J. Econ. Entomol.* 99: 401–407.