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Life table and predation capacity of *Hippodamia variegata* (Coleoptera: Coccinellidae) feeding on *Aphis fabae* (Hemiptera: Aphididae)

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ABSTRACT

The life history and predation rate of variegated lady beetle, *Hippodamia variegata* (Goeze), fed on the black bean aphid, *Aphis fabae* Scopoli, were studied under laboratory conditions. Developmental, survival, fecundity, and predation rate data were analyzed using the age-stage, two-sex life table and the traditional age-specific female life table. Means and standard errors of population growth parameters were calculated using the jackknife method. Using the age-stage, two-sex life table, the intrinsic rate of increase (r), net reproductive rate (R_0), mean generation time (T) and finite rate of increase (λ) were 0.2031 d^{-1}, 389.0 offspring, 29.4 d, and 1.2252 d^{-1}, respectively. The population parameters r, R_0, T, and (λ) calculated using the female age-specific life table were 0.2045 d^{-1}, 387.6 offspring, 29.16 d, and 1.2269 d^{-1}, respectively. Although no statistically significant differences were found between population parameters of the two methods, the female age-specific life table could not include the male population and its contribution to predation, nor was it possible to describe the stage differentiation. The net predation rate (C_0) using the age-stage, two-sex life table was 1127.1 aphids, and 1503.1 aphids when using the female age-specific life table. The higher net predation obtained when using the female age-specific life table was an overestimation caused by ignoring the male population. Our results demonstrate that by using the age-stage, two-sex life table we can accurately describe the survival, development, and predation capacity of the predator.

1. Introduction

To achieve a successful biological control program, it is necessary to characterize the growth, stage structure, fecundity, and predation rate of the pest's predators. Proper data analysis of the life history and predation rates play essential roles in this process. A key component of this knowledge is the life table. Only life tables can provide a comprehensive description of the development, survival, and fecundity of a population. Southwood (1966) stated that the intrinsic rate of increase is the most useful life table parameter for comparing the population growth potential of different species under specific climatic and food conditions. By correlating studies on the predation rate and life table and by taking variations due to age, stage, and sex into consideration, the growth, stage differentiation, reproduction, as well as the predation rate can be effectively characterized (Chi and Yang, 2003).

The black bean aphid, *Aphis fabae* Scopoli, is one of the major aphid pests in Iran. One of its dominant coccinellid predators is *Hippodamia variegata* (Goeze), the variegated lady beetle. This coccinellid, an important aphidophagous predator in Europe (Hodek and Honek, 1996), is widely distributed in a large portion of the Palearctic region (Obrycki and Orr, 1990). In Australia, the beetle was recorded preying on 12 aphid species and one psyllid species feeding on various crops, weeds and ornamental plants (Franzmann, 2002). Jafari and Goldasteh (2009) reported the functional response of this ladybird on *A. fabae* in the laboratory. No information, however, is currently available on the efficiency of this species in controlling *A. fabae*.

The life history of many insects has been studied using the traditional female age-specific life table (for example: Hansen et al. 1999; Havelka and Zemek, 1999; Janssen and Sabelis, 1992; Ren et al., 2002; Russo et al., 2004; Zanuncio et al., 2006). In a female age-specific life table, only female individuals are taken into consideration and the variable developmental rate among individuals are ignored (e.g., Lewis 1942; Leslie 1945; Birch 1948). The life table parameters of *H. variegata* have been studied using traditional female age-specific life tables of individuals reared on several species of aphids including *Dysaphis craraegi*, *Aphis gossypii*, *Myzus persicae*, *Brevicoryne brassicae*, and *Rhopalosiphum padi* as prey on various crops under various environmental conditions (El Habi et al., 2000; El Hag and Zaitoon, 1996; Kontodimas and Stathas, 2005; Lanzoni et al., 2004; Mollashahi et al., 2004). Chi and Liu (1985) and Chi (1988) demonstrated that the traditional female

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age-specific life tables (e.g., Lewis, 1942; Leslie, 1945; Birch, 1948) ignore the males and the stage differentiation. Chi and Liu (1985) developed an age-stage, two-sex life table theory to take both sexes and variable developmental rates among individuals into consideration. Chi and Yang (2003) applied the age-stage, two-sex life table to the predators *Propylaea japonica* (Col.: Coccinellidae) and demonstrated it can properly include the variable predation rate of different predator stages. Yu et al. (2005) applied the same life table in studying the predation rate of *Lemnia biplagiata* (Col.: Coccinellidae) fed on *A. gossypii*. This method was also used in the study of the parasitoid wasp, *Aphidius gifuensis* (Hym.: Braconidae) (Chi and Su, 2006). These studies showed the advantages of incorporating the predation study into the age-stage, two-sex life table.

In this paper, we studied the life history and predation rate of *H. variegata* fed on *A. fabae*. We analyzed the data by using both the age-stage, two-sex life table and the traditional female age-specific life table.

2. Material and methods

2.1. Insect culture

More than 100 adult *H. variegata* (approximately 1:1 sex ratio) were collected from an alfalfa farm in Karaj region, Tehran Province, Iran in September 2007. The stock colony of *H. variegata* was reared on *A. fabae* and maintained in a growth chamber set at 25 ± 1° C, 70 ± 10% RH, and a photoperiod of 16:8 (L:D) for two generations before being used for life table study. To maintain genetic variability, 50 adult *H. variegata* were field collected and mixed with the stock colony every 6 months. Aphids were reared on broad bean plants, *Faba vulgaris*, under 21 ± 1 °C and 70 ± 10% RH, and a photoperiod of 16:8 (L:D). The broad bean plants were planted in pots filled with sawdust and fertilized with HORTI® micro and macro elements fertilizer (2% solution in water) every 4 days.

2.2. Life table study

Coccinellid eggs laid within a 6-h period were collected for the life table study. A total of 123 eggs was obtained from a random sample and kept in a growth chamber set at 23 ± 1 °C, 70 ± 10% RH, and a photoperiod of 16:8 (L:D). Newly emerged larvae were transferred to 6-cm Petri dishes containing 2% agar and reared individually on a broad bean leaf that had been placed upside down in the middle of each Petri dish. Petri dishes were kept in the incubator and *A. fabae* of third or fourth nymphal stage on a leaf of *F. vulgaris* were supplied daily as food. Based on preliminary tests, different numbers of aphids were supplied to different stages/sexes of *H. variegata*: 10 aphids for first instar; 15 aphids for second instar; 20 aphids for third instar; 75 aphids for fourth instar; 40 aphids for male adult and 120 aphids for an adult pair (male and female). Larval mortality and development were checked every 12-h until the adult stage. After the emergence of adults, males and females were paired and checked daily to record survival and number of eggs laid.

To determine the sex ratio of *H. variegata* offspring, 60 eggs or more were collected from females of different ages every third day after the beginning of oviposition. In total, 13 egg samples were collected. The hatch rate and sex ratio of these eggs were recorded.

2.3. Predation rate study

To study the predation rate, it was necessary to collect similar sized aphid nymphs to give to the beetles. Initially, 50 adults of *A. fabae* were placed on an individual *F. vulgaris* plant and allowed to produce progeny. After 2 days, the adult aphids were removed, and the newborn aphids kept under constant temperature (21 °C). At 3 days, all aphids are either in the third or fourth nymphal stage, and were then used in the predation study. As described in the previous section, different numbers of aphids were supplied to different stages/sexes of *H. variegata*. Petri dishes were checked daily and the number of consumed aphids was recorded and the pre-designated density of aphids (according to stage) was supplied to the different stages of *H. variegata*. After the emergence of adults, individual males and females were paired. Subsequently, each pair was given 120 aphids on a *F. vulgaris* leaf per day and the number of consumed aphids was recorded until the death of both beetles.

Previous study on the functional response of males and females of *H. variegata* to prey (Farhadi et al., 2010) showed that there is a significant difference between male and female maximum predation rates. To distinguish the predation rate of males from that of females, the predation rate of 20 males was studied under identical conditions. To calculate the female daily predation rate, the average male daily predation rate was subtracted from the average predation rate of the pairs. In this way, we calculated the daily predation rate of males and females separately. Dead males were replaced with live individuals (only during the first week of the experiment). Because natural mortality of the prey under the experimental condition was very low, the natural mortality of *A. fabae* was not deduced from the daily predation rate.

2.4. Data analysis

The data of life table and predation rate were analyzed using the age-stage, two-sex life table and the traditional female age-specific life table.

2.4.1. Age-stage, two-sex life table

Developmental time of all individuals, including males, females, and those dying before the adult stage, and female daily fecundity were analyzed according to the age-stage, two-sex life table (Chi and Liu, 1985; Chi, 1988). The age-stage specific survival rate (s_{xj}) (where x = age and j = stage), the age-stage specific fecundity (f_{xj}), the age-specific survival rate (l_x), the age-specific fecundity (m_x), and the population parameters (r, the intrinsic rate of increase; λ, the finite rate of increase, $\lambda = e^r$; R_0, the net reproductive rate; T, the mean generation time) are calculated accordingly. The age-specific survival rate includes both male and female, and is calculated according to Chi and Liu (1985) 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 β is the number of stages. In this paper, the intrinsic rate of increase is calculated by using the iterative bisection method from

$$\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1 \tag{3}$$

with age indexed from 0 (Goodman, 1982). The mean generation time is the time length that a population needs to increase to R_0-times of its size as the stable age distribution and the stable increase rate are reached, i.e., $e^{rT} = R_0$ or $\lambda^T = R_0$. Thus, it is calculated as $T = (\ln R_0)/r$. The gross reproductive rate (GRR) is calculated as

$GRR = \sum m_x$. Because life table studies are extremely time consuming and replication is impractical, we used the jackknife method (Sokal and Rohlf, 1995; Meyer et al., 1986) to calculate the means and standard errors of the life table parameters. Data analysis and population parameters (r, R_0, T, and λ) were calculated by using the TWOSEX-MSChart program (Chi, 2005). The TWOSEX-MSChart is available at http://140.120.197.173/Ecology/prod02.htm (Chung Hsing University) and http://nhsbig.inhs.uiuc.edu/wes/chi.html (Illinois Natural History Survey).

2.4.2. Predation rate analysis based on age-stage, two-sex life table

The daily consumption of all individuals, including males, females, and those dying before the adult stage, was used to calculate the age-stage specific consumption rate c_{xj}. This is the mean number of *A. fabae* consumed by individual *H. variegata* in age x and stage j. The age-specific predation rate (k_x) is the mean number of aphids consumed by *H. variegata* at age x and was calculated by the following formula proposed by Chi and Yang (2003):

$$k_x = \frac{\sum_{j=1}^{\beta} s_{xj} c_{xj}}{\sum_{j=1}^{\beta} s_{xj}} \tag{4}$$

According to Chi and Yang (2003), the net predation rate (C_0) gives the mean number of prey consumed by an average individual predator during its entire life span, and is calculated as

$$C_0 = \sum_{x=0}^{\infty} k_x l_x \tag{5}$$

The transformation rate from prey population to predator offspring (Q_p) is the ratio of the net predation rate to the net reproductive rate (Chi and Yang, 2003). It is calculated as:

$$Q_p = \frac{C_0}{R_0} \tag{6}$$

Predation rate data were analyzed using the computer program CONSUME-MSChart as designed by Chi (2005). Standard errors of predation parameters were also calculated using the jackknife resampling method. CONSUME-MSChart is also available for download at the websites mentioned in Section 2.4.1.

2.4.3. Female age-specific life table

Of the 123 eggs produced, 42 emerged as female adults, 39 as male adults, and 42 died in the preadult stage. Construction of a female age-specific life table involves two major inherent difficulties: sexing of preadult individuals is usually very difficult, and, therefore, incorporating preadult mortality into the life table is problematic. Second, because it is impossible to describe stage differentiation, there is the problem of stage grouping. To solve these problems, we constructed the age-specific female life table using the following manipulations and assumption. First, we assumed the sex ratio in the preadult mortality was the same as that found in the emerged adult males and females, i.e., ♀/(♀ + ♂) = 0.5185, then the number of females that died in preadult stage was rounded to an integer. In this way, the female age-specific life table was constructed based on 64 individuals, i.e., 42 surviving female adults plus 22 individuals that died in preadult stages. Second, we divided the life span into stages by using the mean developmental time of each stage. Third, we multiplied the daily fecundity with the same sex ratio to calculate the age-specific female offspring (m_x). These manipulations may affect the subsequent analysis and result in a number of miscalculations that will be considered in the Discussion section. The intrinsic rate of increase (r) was calculated by using Eq. (3), however, l_x is the female age-specific survival rate at age x and m_x is the age-specific female fecundity. Jackknife re-sampling methods were used to calculate the mean and standard error of population parameters.

2.4.4. Predation rate analysis based on female age-specific life table

Based on the same assumptions used in Section 2.4.3, we analyzed the female age-specific predation rate, k_x, and used Eq. (5) to calculate the net predation rate for the female population.

The Student t-test was used to determine differences between the results of the population parameters found for the age-stage, two-sex life table and the female age-specific life table (Zar 1999).

2.5. Population projection

We projected the population growth with an initial population of 10 eggs to reveal the growth and age-stage structure of *H. variegata*. The computer program: Timing-MSChart (Chi, 2008) is also available from the corresponding author and the above-mentioned website.

3. Results and Discussion

3.1. Age-stage, two-sex life table

Of the 123 eggs initially collected for the life table study, 96 hatched successfully, and, of these, 81 emerged as adults. Pre-adult mortality of *H. variegata* was 34.1%. The survival percentage in our study was higher than that reported by El Hag and Zaitoon (1996), Jafari et al. (2002), and Lanzoni et al. (2004). The total developmental time for all pre-adult stages was 16.3 d (Table 1). The developmental durations were close to those reported by Lanzoni et al. (2004), but longer than those reported by Mollashahi et al. (2004), and shorter than those of El Hag and Zaitoon (1996). El Habi et al. (2000) reported the total developmental time was temperature-dependent and ranged from 7 to 27.58 days.

Male adult *H. variegata* lived an average of 62.38 d, which was significantly longer than that of the female adults (44.93). El Hag and Zaitoon (1996) found no significant difference between the longevity of males and females of *H. variegata* fed on *B. brassicae* and *R. padi* at 25 °C. Mollashahi et al. (2004) reported an average longevity of 53.4 d at 26 °C. In our study, the first copulation took place within 24 h after emergence and was repeated several times during adult life. Mated females began ovipositing, on average, 3.4 d after emergence (pre-oviposition period). The total pre-oviposition period was 19.6 d. Gabre et al. (2005) pointed out that total pre-oviposition period is a more appropriate statistic from the point of view of demography, because it can reflect the effect of

Table 1
Development time (day) of different stages, adult longevity, fecundity, preovipositional period, total preovipositional period of *H. variegata* reared on black bean aphids at 23 °C.

Statistics	N	Mean	SEM
Developmental time			
Egg (d)	96	3.03	0.02
First instar (d)	90	2.09	0.06
Second instar (d)	87	1.87	0.04
Third instar (d)	85	2.07	0.04
Fourth instar (d)	83	2.90	0.06
Pupa (d)	81	4.40	0.08
Total pre-adult (d)	81	16.33	0.07
Adult longevity and fecundity			
Female adult longevity (d)	42	44.9	3.1
Male adult longevity (d)	39	62.4	5.7
Fecundity (F) (eggs/female)	42	1139.2	67.8
Preovipositional period (d)	42	3.4	0.16
Total preovipostional period (d)	42	19.6	0.15

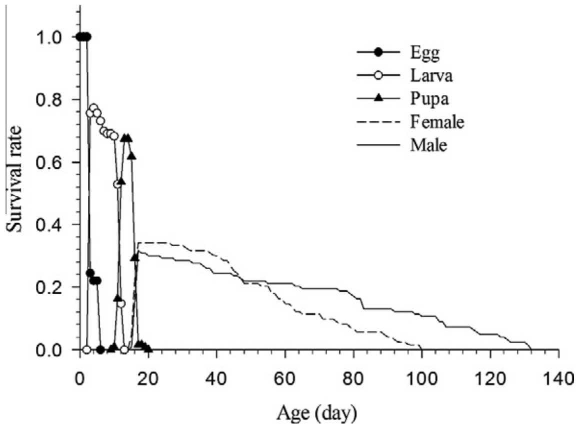

Fig. 1. Age-stage survival rate (s_{xj}) of *H. variegata* on *A. fabae* at 23 °C.

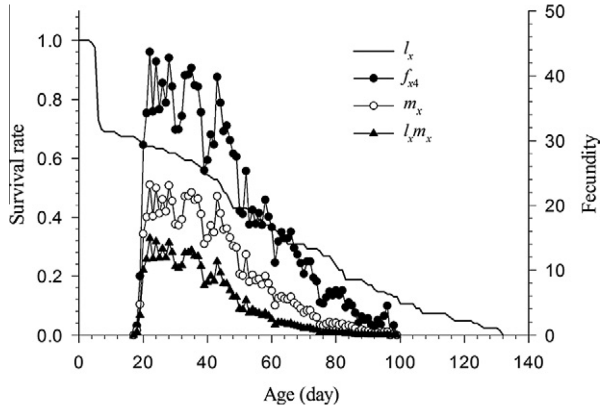

Fig. 2. Age-specifc survival rate (l_x) and age-stage fecundity of female (f_{x4}) (eggs/female), and age-specific fecundity (m_x) of *H. variegata* on *A. fabae* at 23 °C using the age-stage, two-sex life table.

the first reproduction on the population parameters. The mean fecundity per female was 1139.2 eggs (Table 1).

Fig. 1 illustrates the trends in age-stage specific survival rate (s_{xj}), i.e., the probability that a newborn will survive to age x and stage j. Because the variable developmental rate occuring among individuals was incorporated into the age-stage, two-sex life table, the survival curve of a cohort shows stage overlapping (Chi and Yang, 2003).

By using Eqs. (1) and (2), we calculated the age-specific survival rate (l_x) and fecundity rate (m_x), and display them in Fig. 2. The age-stage specific fecundity rate (f_{xj}) of female adult *H. variegata* is also plotted in Fig. 2. The curve of l_x is a simplified version of the age-stage survival rate (s_{xj}).

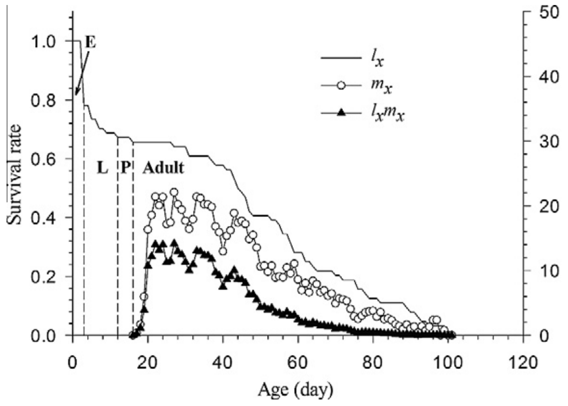

Fig. 3. Age-specific survival rate (l_x), and age-specific fecundity (m_x) of *H. variegata* on *A. fabae* at 23 °C using the female age-specific life table (E, egg; L, larva; P, pupa).

3.2. Female age-specific life table

To compare differences between the age-stage, two-sex life table and the traditional female age-specific life table, we constructed the l_x and m_x (Fig. 3) according to the procedures described in Section 2.4.3. The female age-specific life table deals only with the female population, therefore only a single survival rate, for females, was generated. Because the traditional female age-specific life table neglects the male population and the variable developmental rate among individuals, the stage overlapping and male survival curve could not be calculated.

3.3. Population parameters

In the Chi and Liu model (1985), the population parameters were calculated based on data of the entire cohort, i.e., both sexes and the variable developmental rates among individuals. Calculated parameter and standard errors of the intrinsic rate of increase (r), net reproductive rate (R_0), mean generation time (T), and the finite rate of increase (λ) obtained by using the age-specific model and age-stage specific model are shown in Table 2. Statistical analysis showed that there was no significant difference between r, R_0, λ, and T calculated by female age-specific life table and age-stage, two-sex life table when using the t-test at the 5% significance level (Table 2). Our results showed that the inclusion of males and the variable developmental rate has little effect on the population parameters for *H. variegata*. However, Fig. 1 contains significantly more comprehensive information on the cohort as a whole. Our results are close to the intrinsic rate of increase of *H. variegata* reported by Kontodimas and Stathas (2005), but differ from those of El Hag and Zaitoon (1996), Lanzoni et al. (2004) and Mollashahi et al. (2004), possibly as a result of using different prey species and data analysis method.

Chi (1988) demonstrated that the relationship between the mean female fecundity (F) and the net reproductive rate can be described as

Table 2

Population parameters (Means ± SEM) of *H. variegata* calculated by using the age-specific female life table and the age-stage, two-sex life table. R_0, net reproductive rate; *GRR*, gross reproductive rate; r, intrinsic rate of increase; λ, finite rate of increase; T, mean generation time; C_0, net predation rate.

Parameter	Age-stage, two-sex life table	Age-specific female life table	*T*	*P*
R_0 (offspring/individual)	389.0 ± 54.0	387.6 ± 42.2	0.0169	0.987
GRR (offspring)	745.1 ± 96.1	796.5 ± 36.2	0.378	0.706
r (d^{-1})	0.2031 ± 0.0054	0.2045 ± 0.0042	0.178	0.859
T (d)	29.4 ± 0.4	29.2 ± 0.4	0.413	0.680
λ (d^{-1})	1.2252 ± 0.0066	1.2269 ± 0.0052	0.178	0.859
C_0 (preys/predator)	1127.98 ± 98.4	1503.1 ± 159.6	2.102	0.037

Table 3
Mean number and standard error (SE) of black bean aphids eaten by different stage/sex of *Hippodamia variegata*.

Sex		1st instar	2nd instar	3rd instar	4th instar	Adult	All stage
Female	Mean	4.93	9.14	20.36	102.48	2140.62	2284.36
	SE	0.35	0.55	1.04	2.72	126.91	127.55
Male	Mean	4.56	8.82	20.38	81.21	970.10	1085.08
	SE	0.26	0.49	0.92	2.08	76.17	76.43

$$R_0 = \frac{N_f}{N} F \tag{7}$$

where N is the total number of individuals used at the beginning of the life table study (i.e., 123 eggs), and N_f is the number of female adults emerging from these N eggs. It also means $N_f \times F = R_0 \times N$. In other words, the total number of offspring produced by all females equals the net reproductive rate times the cohort size. In our results, $N_f \times F = 47{,}846.4$ and $R_0 \times N = 47{,}847$. This minor difference is due to rounding-off. This relationship shows the precision obtainable in the age-stage, two-sex life table analysis.

The difference between the results obtained using the age-stage, two-sex life table and the age-specific life table depends on the variation in development rates and primary sex ratio (Chi, 1988). Because the sex ratio is close to 1:1 and the stage overlapping is short in comparison to the entire life span, the artificial manipulation based on those assumptions does not cause a significant difference between population parameters. However, Fig. 1 and 2 accurately describe the survival, development, and reproduction of the cohort. Population projection based on the age-stage, two-sex life table can, therefore, give correct simulation of the growth and stage differentiation.

3.4. Predation rate

The numbers of black bean aphid prey consumed by different stages/sexes of *H. variegata* are listed in Table 3. It shows that the consumption rates increase from the first through the fourth instar for both sexes. Fourth instars consumed more total aphids than the other three instars combined, but fewer than the adults. Because the body size of females is bigger than the males and they require more energy for egg production, females consumed more than twice the number of aphids as the males.

The age-stage predation rate (c_{xj}) of *H. variegata* on black bean aphid is shown in Fig. 4. It illustrates the trend in age-stage specific predation rate, i.e., the mean number of aphids consumed by a predator of age x and stage j. Using Eqs. (4) and (5), we calculated the age-specific predation rate (k_x) and the net predation rate (C_0) of the cohort. The C_0, or average predation rate, was 1127.98 aphids per individual (based on the original 123 eggs). We combined all stages and plotted the age-specific predation rate (k_x) and age-specific net predation rate (l_xk_x) in Fig. 5. Because both sexes are taken into consideration in the age-stage, two-sex life table, the greater longevity of males has been taken into account in calculation of C_0 as shown in Figs. 4 and 5.

By using the same manipulations used in constructing the female life table, we calculated the predation rate for the female population (Fig. 6). The predation curve in Fig. 6 does not reflect the effects upon the predation rate contributed by the male portion of the cohort. Because the female age-specific life table considers only the female population and ignores the male predation rate, the net predation rate of 1503 aphids is higher than that of the two-sex life table. This is the average predation rate of an individual of the female population (64 individuals). Predation rate analysis using the female age-specific life table will result in

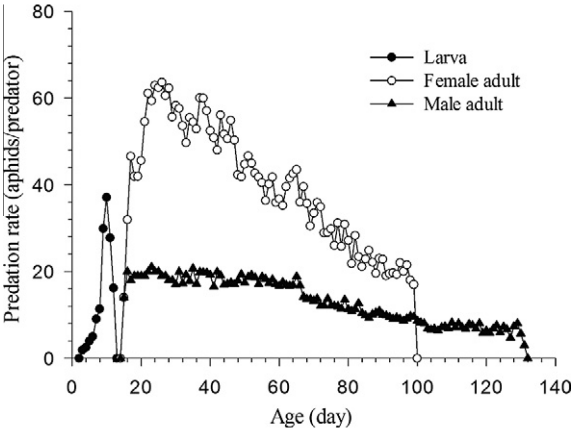

Fig. 4. Age-stage predation rate (c_{xj}) of *H. variegata* based on the age-stage, two-sex life table.

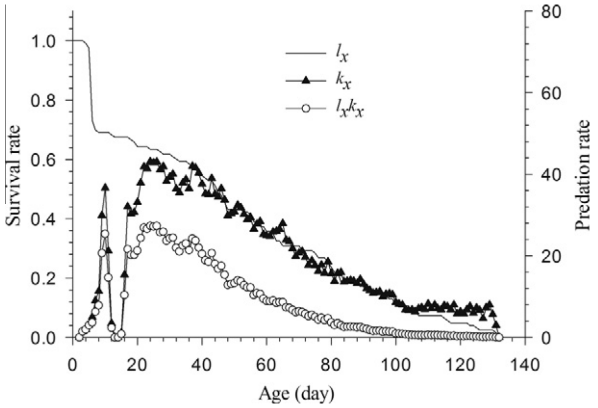

Fig. 5. Age-specific survival rate (l_x), predation rate (k_x), and age-specific net predation rate of *H. variegata* on black bean aphids using the age-stage, two-sex life table.

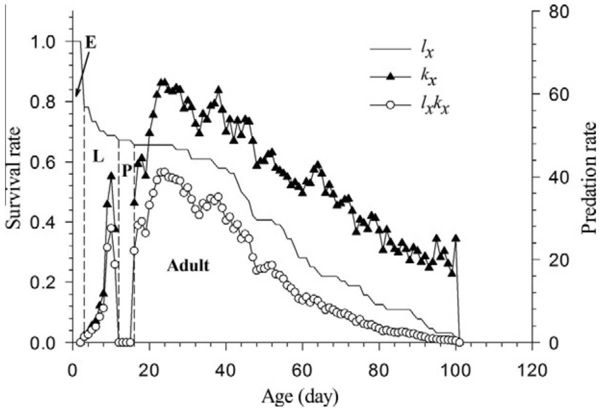

Fig. 6. Age-specific survival rate (l_x), predation rate (k_x), and age-specific net predation rate of *H. variegata* on black bean aphids using the female age-specific life table (E, egg; L, larva; P, pupa).

overestimating the predation rate, and can, therefore, adversely affect efforts in using female age-specific life tables in biological control programs.

In most previous studies, researchers have typically paired adults and then, ignoring potential differences in the predation rates of the two sexes, have arbitrarily divided the total daily predation rate equally between the two sexes (Chi and Yang, 2003; Yu et al., 2005; Mo and Liu, 2006; Mo and Liu, 2007). Preliminary tests indicated that male beetles consumed fewer prey than the females. If half of the daily predation total of each pair was arbitrarily assigned to males, this would result in an overestimation of the predation rate of males and an underestimation in the females. To distinguish the predation rate of the males from that of the females, the predation rate of 20 males were recorded in this study as described in Section 2.3. We then calculated the female daily predation rate by subtracting the average male daily predation rate from the total daily predation rate of the pairs.

Females, particularly during the oviposition period, feed more than males (Hodek and Honek, 1996). Our observations showed similar differences between the sexes. The predation rate was high in the first 30 days and then gradually decreased with age. The trend of predation rate corresponds to the female age-specific fecundity (See Fig. 2).

Isenhour and Yeargan (1981) reported that adult females of *Orius insidiosus* consumed more thrips than did adult males. Variations in predation rates during different ages and/or stages are common occurences. Ignoring the age and stage structure of a predator is a common mistake in estimating predation rates, and doing so often results in significant miscalculations (Chi and Yang, 2003). This effect is especially clear when the total predation rate is plotted against the cohort age (Fig. 7).

Predation rate parameters of *H. variegata* obtained by using the age-specific method and the age-stage specific method are compared in Table 2. The transformation rate from prey population to predator offspring (Q_p) was close to 3, meaning that *H. variegata* requires approximately three black bean aphids to produce a single egg. The transformation rates of *Lemnia biplagiata* on *A. gossypii* and *Propylaea japonica* on *Myzus persicae* were reported as 10.4 and 17.7, respectively (Yu et al., 2005; Chi and Yang, 2003).

Tommasini et al. (2004) studied life table and predation rate of four *Orius* species on eggs of *Ephestia kuehniella* (Zeller) and adults of *Frankliniella occidentalis* (Pergande). They defined the net consumption rate as

$$K_0 = \sum l_x K_x \tag{8}$$

where K_x was the age-specific predation rate. This equation is similar to Eq. (5) defined by Chi and Yang (2003) for the age-stage, two-sex life table. However, Eq. (8) considers only female individuals. Tommasini et al. (2004) calculated the predation-rate (k_m) as

$$k_m = \frac{\ln K_0}{T_k} \tag{9}$$

where T_k was calculated as

$$T_k = \frac{\sum l_x K_x x}{K_0} \tag{10}$$

Tommasini et al. (2004) borrowed these two equations originally used for the estimation of mean generation time and intrinsic rate from Birch (1948). In Eq. (10), however, the denominator K_0 is the net predation rate of the female predator (i.e., the average number of prey killed by a predator), while x is the age of the female predator, and l_x is the survival rate of the female predator at age x. Thus, the T_k calculated by using Eq. (10) gives the mean age of the female predator when a prey is killed. Instead of obtaining the predation rate as intended, using the above two equations produced an entirely unrelated result, thus invalidating their usage for this purpose. This shows Eqs. (9) and (10) are invalid.

Comparison of the two methods showed there were significant differences between both the survival and predation curves. However, the population parameters of *H. variegata* calculated by using the age-specific life table and age-stage, two-sex life table are not significantly different. Because the mean durations of each stage were used to construct the survival curve (l_x) and fecundity curve (m_x) (Fig. 3), the fecundity curves of individuals were moved toward the mean preadult duration. This shows that when the fecundity curves of some individuals are moved forwards, while others are moved backwards, these movements result in a compensation effect and diminish the differences between the population parameters calculated using female age-specific life table and the age-stage, two-sex life table. Our results indicate that the original cohort of 123 *H. variegata* individuals consumed a total of 138,741 aphids. Of these, 90,193 aphids were consumed by female adults, 37,834 by male adults, and, 10,714 during the larval stages of the predator. The 138,741 figure exactly equals the product of C_0 times the total number of individuals used for the life table study, i.e., 1127.98 × 123 = 138,741.54. The minor difference is due to rounding-off during calculation. This precise relationship demonstrates that the net predation rate C_0 (Chi and Yang, 2003) is a valid definition.

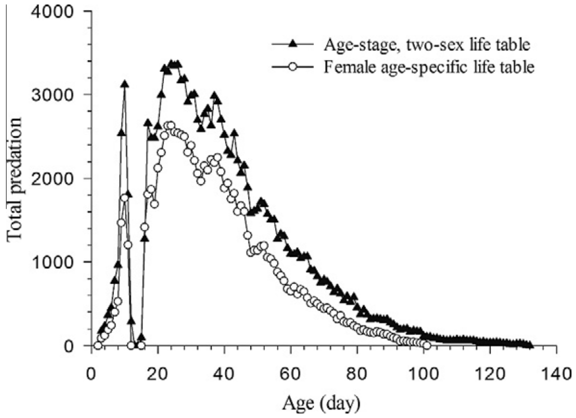

Fig. 7. Total predation rate of *H. variegata* calculated based on the age-stage, two-sex life table and the female age-specific life table.

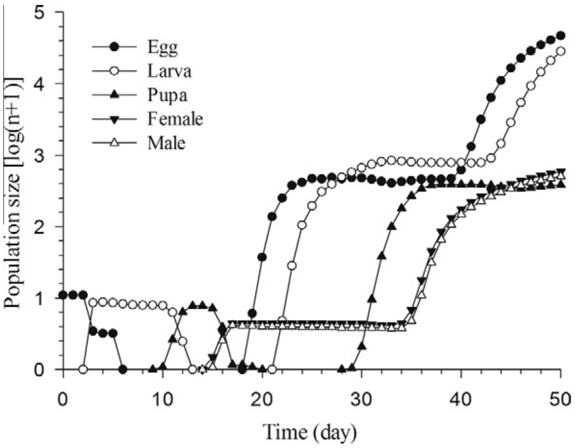

Fig. 8. Population projection showed the change of age-stage structure of *H. variegata* during population growth.

3.5. Application of life table data

There are two types of information in a life table study, i.e., the basic data and the derived parameters. The population parameters, i.e., intrinsic rate and the mean generation time, are the derived parameters. They are calculated based on the assumption that the environmental factors are constant and the population structure reaches a stable age-stage distribution as time approaches infinity. The intrinsic rate is a good parameter to reveal and compare the potential of insect populations under different treatments. Its practical application in pest management, however, is limited. The basic data, i.e., survival rate, developmental rate, and fecundity (Figs. 1 and 2), describe the life history and stage differentiation. These data can be used in population projections to predict growth trends, as well as the stage structure of a population in the short term or long-term future. In Fig. 8, we demonstrate the advantage of using the age-stage, two-sex life table in revealing the stage and sex structure when projecting a population.

4. Conclusion

Our results show that the age-stage, two-sex life table describes the predation rate precisely. The net predation rate based on a female age-specific life table will produce an overestimation of the control efficiency of the whole population. On the other hand, the two-sex life table provides the actual control efficiency of the entire population, i.e., both sexes are included. For further study, incorporating functional response with predation study based on life table will be worthy of pursuit.

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