Perspective

Comparison of the life tables and predation rates of *Harmonia dimidiata* (F.) (Coleoptera: Coccinellidae) fed on *Aphis gossypii* Glover (Hemiptera: Aphididae) at different temperatures

Jih-Zu Yu [a], Hsin Chi [b,*], Bing-Huei Chen [c]

[a] Applied Zoology Division, Taiwan Agricultural Research Institute, Wufeng, Taichung, Taiwan, ROC
[b] Laboratory of Theoretical and Applied Ecology, Department of Entomology, National Chung Hsing University, Taichung, Taiwan, ROC
[c] Council of Agriculture, Taipei, Taiwan, ROC

HIGHLIGHTS

► We studied the life history and predation of *Harmonia dimidiata* (F.) at different temperatures.
► We analyzed the raw data by using the age-stage, two-sex life table.
► We compared the jackknife and bootstrap techniques.
► We suggest that the jackknife technique should not be used for the estimation of R_0.
► We use the finite predation rate for the comparison of predation potential.

GRAPHICAL ABSTRACT

An accurate description of the survival, development, and predation capacity of a predator can be achieved using the age-stage, two-sex life table.
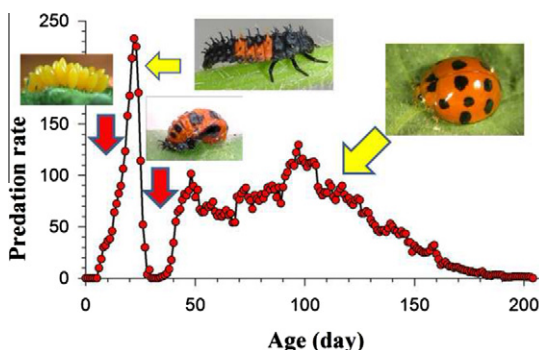
ARTICLE INFO

ABSTRACT

The life histories and predation rates of the ladybird beetle *Harmonia dimidiata* (F.) were compared among beetles kept at 15, 20, and 25 °C. The beetles were fed on *Aphis gossypii* Glover and were maintained at 70 ± 10% RH and a 14:10 (L:D) h photoperiod. According to the age-stage, two-sex life table, the net reproductive rates (R_0) were 147.4, 98.7, and 62.5 offspring for beetles kept at 15, 20, and 25 °C, respectively. Additionally, we employed both the jackknife and bootstrap techniques for estimating the means, variances, and standard errors of the population parameters. The sample means of R_0 and the other population parameters obtained using the bootstrap technique fit a normal distribution, but the jackknife technique generated biologically meaningless zero values for R_0. The net predation rates were 10963, 13050, and 7492 aphids for beetles kept at 15, 20, and 25 °C, respectively. For a comprehensive comparison of predation potential, we incorporated both the finite rate and the predation rate into the finite predation rate. When both the growth rate and the predation rate were considered, our results showed that *H. dimidiata* is a more efficient biological control agent for *A. gossypii* at 20 and 25 °C than at 15 °C.

1. Introduction

The melon aphid (*Aphis gossypii* Glover) is a global insect pest with a wide range of host plants, including the 84 species in 34

* Corresponding author. Address: P.O. Box 17–25, Taichung 40299, Taiwan, ROC.
Fax: +886 4 22875024.
E-mail address: hsinchi@dragon.nchu.edu.tw (H. Chi).

families that have been recorded in Taiwan (Tao, 1990). Infection by aphids causes the stunting or death of crops due to the sucking of sap, the secretion of honeydew that acts as a sooty mold medium, and the transmission of viral plant diseases (Chang et al., 1987; Escriu et al., 2000; Gildow et al., 2008).

According to Tao (1990), 34 arthropod species that are natural enemies of the melon aphid have been recorded in Taiwan. Among these, 17 species are ladybird beetles, with *Harmonia dimidiata* (F.) being a common example. Kuznetsov and Pang (2002) reported a daily predation rate of more than 200 *A. gossypii* for *H. dimidiata* (F.). They also observed that *H. dimidiata* (F.) can be kept in a refrigerator at 15 °C for 4 months without aphids and that approximately 90% of this population could survive on a 10% honey solution. *H. dimidiata*'s high voraciousness and ability to survive at low temperatures may make them a useful natural enemy for the purposes of biological control.

To successfully mass rear predatory natural enemies for biological control, it is necessary to determine their population characteristics, including growth rate, stage differentiation, fecundity, and predation rate. The key components for this type of evaluation are life table studies and assessments of predation rate. Only a life table can provide a comprehensive description of the species' development, survival, and fecundity. A proper assessment of predation potential should include the evaluation of a life table. For most insects, the developmental rates vary among individuals and between the sexes (Istock, 1981; Chi and Liu, 1985; Carey, 1993). Chi and Liu (1985) and Chi (1988) noted that neglecting the variable developmental rate and the male population may cause errors in calculating the age-specific survival rate and, consequently, result in errors in assessing the demographic parameters. Chi and Liu (1985) and Chi (1988) developed an age-stage, two-sex life table that takes stage differentiation and the male population into consideration. The age-stage, two-sex life table has been used to describe the population characteristics of many insect and mite species under the influence of a variety of physical conditions.

The influence of a key abiotic external factor, temperature, on insect development has been studied extensively. Improving our knowledge of the effects of temperature on insect development will be helpful in the mass rearing of insects and their application as natural predators of pests. Previous works (Kuznetsov and Pang, 2002; Agarwala et al., 2009) have indicated that in terms of developmental time, fecundity, and functional response, the most favorable temperature for culturing *H. dimidiata* on *A. gossypii* is 20–25 °C. However, there is a lack of experimental life table data regarding the effects of temperature. In the present study, data regarding the life histories and predation rates of *H. dimidiata* fed on *A. gossypii* at different constant temperatures will be collected and analyzed based on an age-stage, two-sex life table that considers the variations in development and the predation rates among individuals and between the sexes. For the comparison of predators, we will use the finite predation rate to compare the predation potential of predators living under different conditions.

2. Materials and methods

2.1. Aphid and ladybird beetle cultures

Melon aphids (*A. gossypii*) were mass cultured as the prey of *H. dimidiata* for more than 10 years, following the method of Yu and Chen (2001). The muskmelon (*Cucumis melo* L.), variety Autumn Favor (Known-You Seed Co., Ltd., Taiwan) was cultivated as the host plant for the rearing of *A. gossypii*. Pots of muskmelon were placed in a net case ($60 \times 90 \times 90$ cm^3), for the maintenance of an aphid stock in the laboratory, and in a rearing cage ($60 \times 90 \times 180$ cm^3), for the mass production of aphids in a green-

house. The *H. dimidiata* stock specimens were originally collected from Fu-Hsing Township, Taoyuan County, Taiwan, in 2003. They were cultured on melon aphids for many years in a laboratory of the Taiwan Agricultural Research Institute in Taichung, Taiwan. The rearing method utilized for *Lemnia biplagiata* (Swartz) by Yu and Chen (2001) was employed in this study. To maintain genetic diversity, *H. dimidiata* adults were collected from the field and added to the laboratory colony every few months.

2.2. Study of life tables and predation rates at different temperatures

Paired *H. dimidiata* adults were obtained from the stock population and cultured with melon aphids in plastic cups (5 cm in diameter and 7 cm height) covered with fine nylon netting for ventilation. Before initiating the life table study, cups were maintained at either 15, 20, 25, or 30 °C with a 70 ± 10% RH and a photoperiod of 14:10 (L:D) h for a generation. Afterwards, ten cups containing *H. dimidiata* pairs were prepared and kept in a growth chamber at each temperature for the collection of eggs for the life table. One hundred eggs laid within a 24 h period were collected and kept in growth chambers in the same conditions under which they were laid. Hatched larvae were moved to new cups for individual rearing. In addition, more than 400 *A. gossypii* of mixed ages were supplied every day as prey to the larvae on the melon leaves. The number of *A. gossypii* was counted before being fed to each ladybird beetle. The number of surviving aphids was also recorded for each group, and the larva of *H. dimidiata* was transferred to a new cup and supplied with new aphids. When the adults emerged, females and males were paired and kept together in rearing cups. A small Petri dish (3 cm in diameter) with moistened cotton wool was used as a water source. Two pieces of plastic tubing (1.2 cm in diameter, 3 cm in length, made from plastic pipette tubes) were supplied for oviposition. A sufficient number of aphids (more than 800) were counted and provided to each pair daily. The fecundity (or eggs produced) and the survival of the ladybird beetles and the number of aphids they killed were recorded daily until the deaths of all individuals. Because adult males and females were kept as pairs, we ignored differences between the sexes, and one half of the daily predation rate of a pair was assigned to each the male and the female, as long as both of them remained alive. If one member of a pair died, the full daily predation rate was then assigned to the living one. Because *H. dimidiata* could not reproduce at 30 °C, life table studies were conducted at 15, 20, and 25 °C in growth chambers.

2.3. Life table analysis

Raw data on the survivorship, longevity, and female daily fecundity of individuals of *H. dimidiata* were analyzed according to the age-stage, two-sex life table (Chi and Liu, 1985; Chi, 1988) using the computer program TWOSEX-MSChart (Chi, 2012a). Data on daily predation rates were analyzed with the computer program CONSUME-MSChart (Chi, 2012b). Following Chi and Liu (1985), the age-stage specific survival rate (s_{xj}), where x is 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); the net reproductive rate (R_0); the intrinsic rate of increase (r); the finite rate of increase (λ); and the mean generation time (T) were calculated. The net reproductive rate (R_0) was calculated as follows:

$$R_0 = \sum_{x=0}^{\infty} l_x m_x \qquad (1)$$

The intrinsic rate of increase (r) was estimated by using the iterative bisection method and the Euler–Lotka equation with the age indexed from 0 (Goodman, 1982):

$$\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1 \qquad (2)$$

The finite rate (λ) and the mean generation time (T) were calculated as follows:

$$\lambda = e^r \qquad (3)$$

$$T = \frac{\ln(R_0)}{r} \qquad (4)$$

2.4. Predation rate analysis

Following Chi and Yang (2003) and Yu et al. (2005), the age-specific predation rate (k_x) was calculated as follows:

$$k_x = \frac{\sum_{j=1}^{\beta} s_{xj} c_{xj}}{\sum_{j=1}^{\beta} s_{xj}} \qquad (5)$$

where β is the number representing the life stage and c_{xj} is the age-stage specific predation rate of individuals at age x and stage j. To account for the age-specific survival rate, the age-specific net predation rate (q_x) was calculated as follows:

$$q_x = l_x k_x \qquad (6)$$

The cumulative predation rate (C_y) is the number of prey killed by an average predator from birth to age y, while the net predation (C_0) is the total number of prey killed by an average individual during its life span. They were calculated as follows:

$$C_y = \sum_{x=0}^{y} l_x k_x \qquad (7)$$

$$C_0 = \sum_{x=0}^{\infty} l_x k_x \qquad (8)$$

The transformation rate from prey population to predator offspring (Q_p) was calculated as follows:

$$Q_p = \frac{C_0}{R_0} \qquad (9)$$

This rate represents the mean number of aphids a predator needs to consume to produce an offspring.

2.5. Statistical analysis

Both the jackknife (Sokal and Rohlf, 1995) and the bootstrap (Efron and Tibshirani, 1993) techniques were used to estimate the means, variances, and standard errors of the population parameters. The means, variances, and standard errors of the predation rates were estimated with the bootstrap technique. Because bootstrapping uses random resampling, a small number of replications will generate variable means and standard errors. To generate less variable results, we used 10000 replications in this study. We used the Tukey–Kramer procedure (Dunnett, 1980) to compare the difference among treatments.

3. Results

3.1. Age-stage, two-sex life table

Because *H. dimidiata* did not lay any eggs at 30 °C, only the data from the 15, 20, and 25 °C growth chambers are reported here. Out of the cohorts of 100 eggs of *H. dimidiata* collected at the beginning of the life table study, 87, 87, and 71 eggs hatched successfully at 15, 20, and 25 °C, respectively. The means of the developmental periods for each preadult stage, the longevity of the adults, and the female fecundity of *H. dimidiata* are given in Table 1. The longest preadult developmental period was 38.8 d at 15 °C, while the shortest was 18.4 d at 25 °C.

The maximal daily fecundities of *H. dimidiata* were higher at higher temperatures; however, the maximum lifetime fecundities showed the reverse trend. The highest fecundity was observed at 15 °C (409.5 eggs), followed by a recording at 25 °C (312.3 eggs).

The age-stage survival curve s_{xj} depicts the probability that a newborn will survive to age x and stage j. The overlaps between different stages during a development period demonstrate the variable developmental rates among individuals (Fig. 1).

The number of offspring produced by an individual *H. dimidiata* of age x and stage j is shown in Fig. 2. Because only females produce eggs, there is only a single curve, f_{x7}, that represents females in the seventh life stage. The parameters l_x, m_x, and age-specific maternity ($l_x m_x$) are also plotted in Fig. 2. At 20 and 25 °C, the curves of m_x and $l_x m_x$ show roughly periodic peaks in reproduction.

3.2. Population parameters

The means and standard errors of the population parameters that were estimated by employing the jackknife (Sokal and Rohlf,

Table 1
Developmental times, adult longevities and fecundities of *Harmonia dimidiata* at different temperatures.

Statistics	Temperature					
	15 °C		20 °C		25 °C	
	n	Mean ± SEM	n	Mean ± SEM	n	Mean ± SEM
Developmental time (d)						
Egg	87	6.0 ± 0.0	87	5.0 ± 0.0	71	4.0 ± 0.0
1st instar	82	3.9 ± 0.1	85	2.4 ± 0.1	71	2.0 ± 0.0
2nd instar	78	3.3 ± 0.1	85	2.2 ± 0.1	70	1.5 ± 0.1
3rd instar	74	4.2 ± 0.1	83	2.7 ± 0.1	63	1.8 ± 0.1
4th instar	67	10.0 ± 0.1	75	7.5 ± 0.1	34	5.6 ± 0.1
Larva	67	21.3 ± 0.2	75	14.9 ± 0.1	34	10.7 ± 0.1
Pupa	65	11.4 ± 0.2	75	7.6 ± 0.1	33	3.7 ± 0.1
Pre-adult	65	38.8 ± 0.3	75	27.5 ± 0.1	33	18.4 ± 0.1
Adult longevity (d)						
Female	36	91.4 ± 6.8	43	54.3 ± 4.1	20	59.6 ± 3.8
Male	29	98.9 ± 5.4	32	57.6 ± 4.2	13	63.5 ± 4.7
Fecundity (offspring)	36	409.5 ± 67.4	43	229.4 ± 63.1	20	312.3 ± 46.0
Daily maximum		54		75		81
Lifelong maximum		1699		1594		718
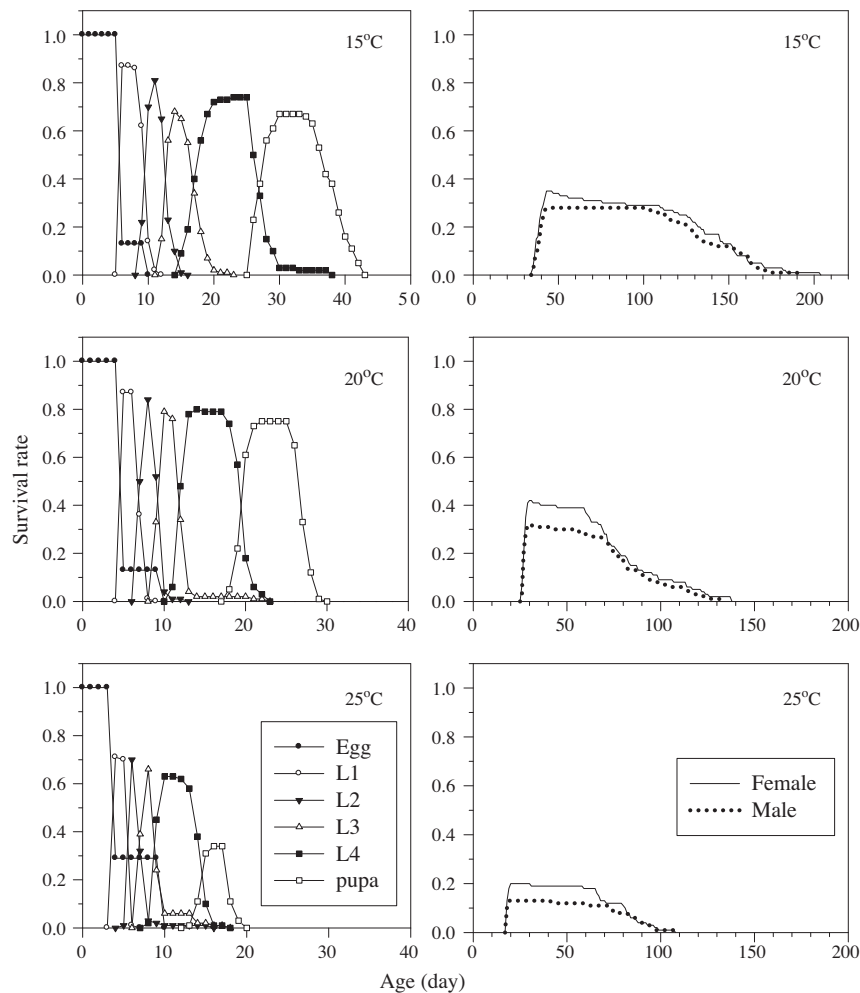
Fig. 1. Age-stage specific survival rates of *Harmonia dimidiata* at 3 constant temperatures. The first adults emerged at 34, 26, and 18 d and the survival rates were 0.69, 0.75, and 0.34 at 15, 20, and 25 °C, respectively.

1995) and the bootstrap techniques (Efron and Tibshirani, 1993) are listed in Table 2. The survival rate, as counted when the first adult emerged (l_a), was 0.65, 0.75, and 0.33 at 15, 20, and 25 °C, respectively. When the jackknife technique was employed, the estimated values of r and R_0 were close to those that were estimated employing the bootstrap technique.

3.3. Predation rate

At three temperatures, the total predation rates of the first to the fourth instar increased in an exponential way. The total numbers of aphids killed during the larval stage were 2877.3, 3081.9, and 1722.4 aphids per larva at 15, 20, and 25 °C, respectively (Table 3). At 15 and 25 °C, the maximum daily predation rate of *H. dimidiata* was higher in the larval stage than in the adult stage (Fig. 3). However, both female and male adults lived longer and consumed more aphids in total as adults than as larvae. A male adult could consume as many as 19690 aphids at 25 °C, while a female adult could consume 18355 aphids at the same temperature.

The age-specific predation rate (k_x) is the mean number of aphids consumed per *H. dimidiata* of age x (Fig. 3), while the age-specific net predation rate (q_x) is the weighted number of prey consumed by a predator of age x (Eq. (6)). Both k_x and q_x were calculated by considering sex differentiation and stage differentiation. The non-predatory stages, which included the eggs and pupae, formed two gaps in the predation rate.

When taking survival rates, predation rates, and longevities into consideration, the highest net predation rate, C_0, was 13050 aphids at 20 °C. The transformation rate Q_p provides a demographic estimation of the relationship between the reproduction rate and the predation rate of a predator (Chi and Yang, 2003). When the values of R_0 obtained from the bootstrap technique were used as denominators in Eq. (8), the value of Q_p indicates that *H. dimidiata* requires 131.8 *A. gossypii* of mixed ages for the production of each egg at 20 °C.

4. Discussions

4.1. Age-stage, two-sex life table

The durations of all preadult stages exhibit a temperature-dependent trend: shorter developmental durations observed at higher temperatures. Our results are similar to the results of Kuznetsov and Pang (2002) and Gillani et al. (2007). In our study, the male adults were longer-lived compared to the mean longevity of female adults (Table 1). Our results indicate shorter life spans than the 81.0 d for females and 73.0 d for males of *H. dimidiata* fed on *Brevicoryne brassicae* at 25 ± 2 °C reported by Gillani et al. (2007). Gillani et al. (2007) reported a larger mean lifetime fecundity of 422.31 eggs for *H. dimidiata* reared on *B. brassicae* at 25 ± 2 °C. Kuznetsov and Pang (2002) reported that the most favorable temperature for *H. dimidiata* was 20–25 °C. Our study
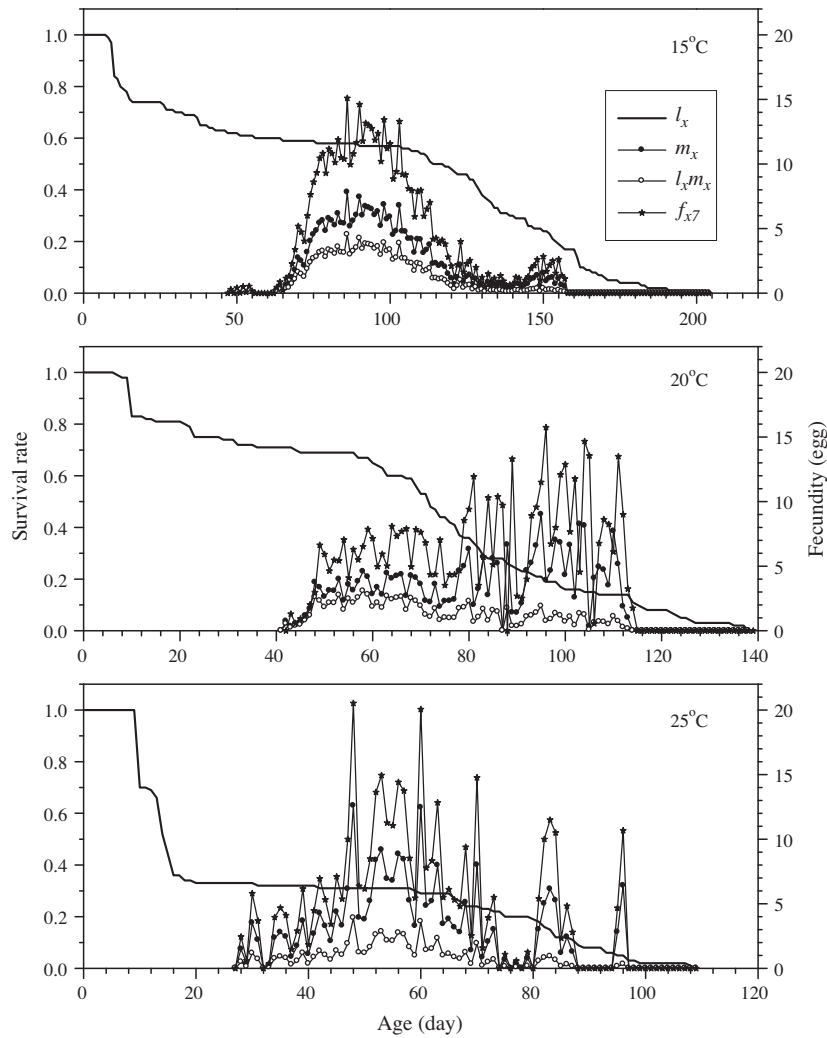
Fig. 2. Age specific survival rates (l_x), fecundities (m_x), maternities ($l_x m_x$) and age-stage specific fecundities (f_{x7}) of *Harmonia dimidiata* at 3 constant temperatures.

Table 2
Population parameters (with r as the intrinsic rate of increase, λ, the finite rate of increase, R_0, the net reproductive rate, and T, the mean generation time) and the standard errors (in parentheses) of *Harmonia dimidiata* at different temperatures, estimated by using all individuals and the jackknife and bootstrap techniques.

Parameters	Temperature (°C)								
	15 °C			20 °C			25 °C		
	All	Jackknife	Bootstrap	All	Jackknife	Bootstrap	All	Jackknife	Bootstrap
r	0.0559	0.0562a[a]	0.0557A	0.0720	0.0726b	0.0714B	0.0824	0.0832b	0.0816C
(d^{-1})		(0.0024)	(0.0024)		(0.0049)	(0.0050)		(0.0066)	(0.0066)
λ	1.0575	1.0578a	1.0573A	1.0746	1.0753b	1.0740B	1.0859	1.0867b	1.0850C
(d^{-1})		(0.0025)	(0.0025)		(0.0052)	(0.0054)		(0.0071)	(0.0071)
R_0	147.4	147.4a	147.5A	98.7	98.7ab	99.0B	62.5	62.5b	62.3B
(offspring)		(31.1)	(30.8)		(29.3)	(29.2)		(15.5)	(15.4)
T	89.3	89.3a	89.3A	63.8	63.9b	63.8B	50.2	50.0c	50.3C
(d)		(1.6)	(1.5)		(2.0)	(2.0)		(1.8)	(1.7)

[a] Data followed by a lower case letter are estimated using the jackknife technique. The same letter indicates no significant difference between temperatures based on the Tukey–Kramer procedure at a 5% significance level. Data followed by an upper case letter are estimated using the bootstrap technique. The same letter indicates no significant difference between temperatures.

has shown that *H. dimidiata* could not reproduce at a higher temperature (30 °C). These observations demonstrate that *H. dimidiata* is adapted to mild temperatures.

Traditional female age-specific life tables (Lewis, 1942; Leslie, 1945; Birch, 1948) ignore the variable developmental rate among individuals (i.e., stage differentiation), as well as the role of male individuals in a population. If traditional life tables had

been used in this study, the stage survival rates and overlaps would not have been observed. Comprehensive discussions on the problems of female age-specific life tables are included in Chi (1988), Yu et al. (2005), Chi and Su (2006) and Huang and Chi (2012a).

At 20 and 25 °C, the curves of m_x and $l_x m_x$ (Fig. 2) show roughly periodic peaks in reproduction that are similar to those exhibited

Table 3
Predation rates (mean ± SEM) of *Harmonia dimidiata* fed on *Aphis gossypii* at different temperatures.

Stage and statistics		Predation rate (aphids/predator)		
		15 °C	20 °C	25 °C
Larval stage	1st instar	99.4 ± 3.3	133.6 ± 5.9	101.0 ± 2.6
	2nd instar	169.0 ± 6.2	201.2 ± 9.7	128.6 ± 11.7
	3rd instar	435.1 ± 17.3	476.1 ± 14.7	347.5 ± 17.4
	4th instar	2175.4 ± 31.0	2271.5 ± 31.8	1179.2 ± 38.2
Total preadult	1st to 4th instar	2877.3 ± 37.1	3081.9 ± 30.8	1722.4 ± 35.2
Adult stage	Female	12960 ± 1,041	13665 ± 957	18355 ± 1144
	Male	14326 ± 881	14493 ± 981	19690 ± 1476
Total life span	Female	15860 ± 1042	16810 ± 956	20081 ± 1137
	Male	17176 ± 898	17491 ± 984	21408 ± 1473
Net predation rate C_0		10963 ± 881	13050 ± 876	7492 ± 973
Transformation rate Q_p		74.3	131.8	120.3
Stable predation rate		90.2	170.5	163.0
Finite predation rate		95.2	183.3	177.0
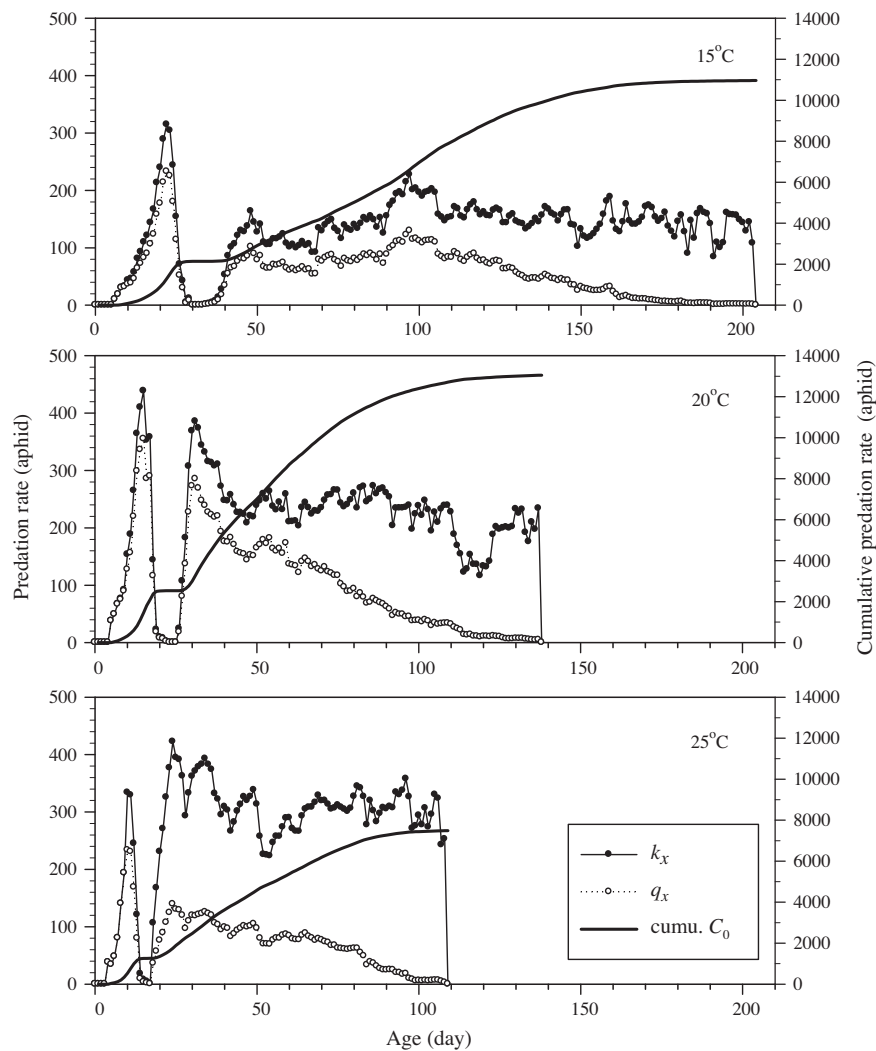
Fig. 3. Age-specific predation rates (k_x), age-specific net predation rates (q_x) and cumulative net predation rates of *Harmonia dimidiata* at different temperatures, with the age being counted from birth. The maximum value of q_x during the larval stage occurs at age 22, 15, and 10 d for individuals raised at 15, 20, and 25 °C, respectively.

by another predaceous ladybird beetle, *L. biplagiata*, in Yu et al. (2005). The periodic reproductive peaks are apparent in the raw data of the daily fecundity of individual females, in which reproductive peaks are separated by zeros, which represent periods of no reproduction. These peaks may be due to the periodicity of *H. dimidiata*'s reproductive physiology (Yu et al., 2005).

4.2. Population parameters

As proven by Chi (1988), based on the two-sex life table, the relationship between R_0 and mean female fecundity (F) is given as follows:

$$R_0 = F \times \frac{N_f}{N} \tag{10}$$

where N is the total number of individuals included at the beginning of the life table study and N_f is the number of female adults that resulted from N. Our data for N, N_f, F and R_0 (Tables 1 and 2) were consistent with Eq. (10), for which all individuals are included in the calculation of R_0. However, when the bootstrap technique was employed in the calculation of R_0, minor differences were apparent due to the application of the resampling technique. Chi and Yang (2003) also noticed that the application of a jackknife technique resulted in degrees of discrepancy between the estimated means and their definitions. Eq. (10) is valid for the age-stage, two-sex life table, as well as the traditional female age-specific life table. It shows a simple and robust relationship between the common statistics of mean fecundity and the net reproductive rate that was defined more than 100 years ago (Boeckh, 1890).

The temperature-dependent attributes of both the intrinsic rate of increase (r) and the finite rate of increase (λ) were clear. However, the net reproductive rate (R_0) was lower and the mean generation time (T) was shorter at higher temperatures.

Meyer et al. (1986) discussed the application of the jackknife and bootstrap techniques to population parameters. Based on results for cladoceran species, Meyer et al. (1986) suggested that the precision for reporting r values should be limited in most cases to two significant figures. According to the means and standard errors of our current and previous studies, we suggest that four significant figures are necessary to confirm the values' differences, precision, and variability. Moreover, the frequency distribution of the net reproductive rate that was estimated by employing the bootstrap technique met the assumptions of normality (Fig. 4), which is an important premise for further statistical analysis. However, zero pseudo values were obtained for R_0 by using the jackknife technique (Fig. 4). A R_0 of zero means that the population cannot reproduce offspring and that no intrinsic rate can be estimated. This results in a serious contradiction in the application of the jackknife technique to the estimation of population parameters. Huang and Chi (2012b) mathematically invalidated the use of the jackknife technique in estimating the net reproductive rate.

4.3. Predation rate

H. dimidiata larvae are very voracious. Although males consumed more aphids than females did, the difference was not significant ($P = 0.584$). A similar trend in feeding capacity was observed by Kuznetsov and Pang (2002). They observed a maximum of 200 *A. gossypii* killed per day by older *H. dimidiata* larvae at 22–25 °C. Devi et al. (2007) observed the predatory potential of *H. dimidiata* to be 75.80, 135.25, 340.60, and 653.25 *Cervaphis quercus* in instars I–IV, respectively. Gillani et al. (2007) reported that a *H. dimidiata* larva could consume 18.3–88.75 *B. brassicae* per day. This predation rate increased, beginning with the later instars and continuing into the adult stage, and resulted in an average of 11550.5 aphids consumed during the imago stage. Sharmila et al. (2010) reported a maximum of 92.13 ± 5.06 *Tuberculatus nervatus* eaten by fourth-instar *H. dimidiata*. The males were also more voracious than the females, although both showed temperature dependence.

The age-specific predation rate (k_x) is the mean number of aphids consumed per *H. dimidiata* of age x (Fig. 3). By considering the survival rate, Chi and Yang (2003) defined the age-specific net predation rate (q_x) as the weighted number of prey consumed by a predator of age x (Eq. (6)). Both k_x and q_x were calculated by taking sex differentiation and stage differentiation into consideration. The non-predatory stages, which included the eggs and pupae, formed two gaps in the predation rate that could be accurately depicted only by using the age-stage, two-sex life table. This demonstrates the importance and advantage of the age-stage, two-sex life table in biological control. Kuroda and Miura (2003) compared the effectiveness of two methods for releasing *Harmonia axyridis* (Pallas) to combat *A. gossypii* and suggested that the suppressive effect of several egg mass sheets released over time was higher than that of one release. However, they did not explain how to determine the proper releasing interval. The time intervals representing the non-predatory gaps that were identified by employing the age-stage, two-sex life table (Fig. 3) can be useful for determining the release interval in a biological control program.

By taking survival rates, predation rates, and longevities into consideration, higher net predation rates, C_0, were observed at 15 and 20, than at 25 °C. The transformation rate, Q_p, provides a demographic estimation of the relationship between the reproduction rate and the predation rate of the predator (Chi and Yang, 2003). The higher values of Q_p were observed at 20 and 25 °C. The almost doubled Q_p value at 20 °C (131.8), in comparison with the value of 74.3 at 15 °C, means that the predators killed more prey to produce an egg at 20 °C. Therefore, it can be interpreted
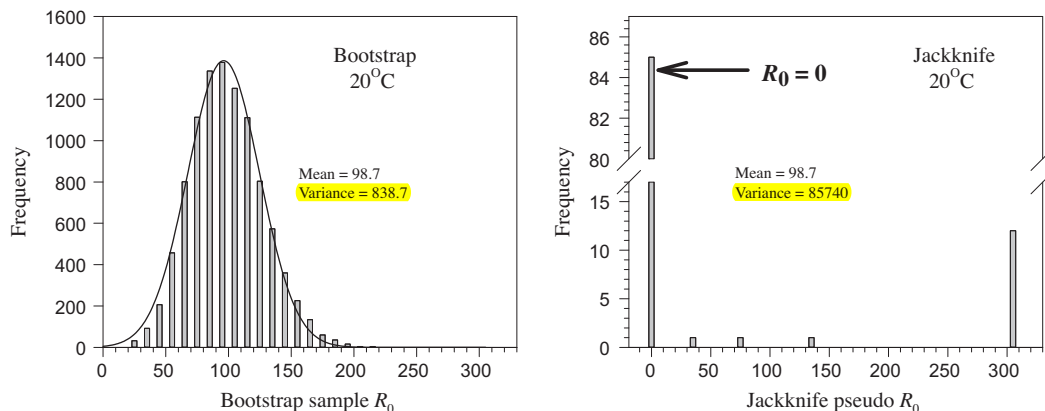

Fig. 4. Frequency distributions of the net reproductive rates estimated by employing the bootstrap and jackknife techniques. When the jackknife technique was employed, males, non-reproductive females, and those individuals that died in the immature stages generated zeros for the pseudo-R_0.

that *H. dimidiata* is more voracious and has greater control potential at 20 °C than at 15 °C.

Male *H. dimidiata* contributed significantly to the predation of aphids. However, the traditional female age-specific life tables ignore the male individuals and their contribution to predation and do not enable the proper description of stage differentiation. Consequently, the application of the traditional female age-specific life table in biological control programs is limited. Farhadi et al. (2011) demonstrated that the application of female age-specific life tables will result in an overestimation of the predation capacity of *Hippodamia variegata* (Coleoptera: Coccinellidae). In contrast, the age-stage, two-sex life table includes both sexes and stage differentiation for an accurate calculation of the predation capacity.

4.4. Application of life table data for biological control and rearing programs

In using a predaceous ladybird beetle for biological control, individuals in the larval stage are more effective control agents than the adults (Trouve et al., 1997), unless the adults are flightless (Kuroda and Miura, 2003; Seko et al., 2008). Inayat et al. (2011) reported that the overall larval feeding rate was twofold greater than that of the adult. In greenhouse conditions, Kuroda and Miura (2003) released *H. axyridis* egg sheets on cucumber plants, and the emerged larvae effectively decreased the density of *A. gossypii*. Furthermore, Kuznetsov and Pang (2002) indicated that *H. dimidiata* larvae do not leave plant leaves before total aphid extirpation. Therefore, the larval stage of *H. dimidiata* has the potential to be of use in biological control programs. The advantage of a predation study based on the age-stage, two-sex life table is evident in its proper stage grouping compared to the traditional female age-specific life table.

To assess the population growth potentials and the efficacies of insect rearing programs, different methods and parameters have been used. For example, Kalushkov (1998) concluded that *Encallipterus tillae* and *E. betulae* were the most suitable prey species, based on their larval development rates, larval mortality, adult fresh weight and abundance in the field. Atlihan and Kaydan (2002) suggested that *Scymnus apetzi*, *S. subvillosus*, and *Exochomus nigromaculatus* might be useful in IPM according to their life table parameters. Soroushmehr et al. (2008) compared the life table of a ladybird beetle (*Scymnus syriacus*) fed on *Aphis spiraecola* on different host plants. However, in comparing the efficiency of a predator, we have to consider not only the predator's population growth rate but also its predation rate. Although the net reproductive rate R_0 was highest at 15 °C, the highest intrinsic rate and the finite rate were at 25 °C when the effect of time, i.e., the reproductive age, was considered. A faster intrinsic rate of increase or finite rate does not necessarily represent an efficient predator. In the present study, *H. dimidiata* exhibited a higher net predation rate at 20 °C than at 25 °C. Chi et al. (2011) suggested using the finite predation rate to compare the predation potential of different predators fed on the same prey or of the same predator fed on different preys. The finite predation rate (ω) was calculated as follows:

$$\omega = \lambda\psi = \lambda\sum_{x=0}^{\infty}\sum_{j=1}^{m}a_{xj}c_{xj} \qquad (11)$$

where λ is the finite rate of a predator with a stable age-stage distribution, ψ is the stable predation rate ($\psi = \sum\sum a_{xj}c_{xj}$), and a_{xj} is the proportion of individuals belonging to age x and stage j in a stable age-stage distribution. Higher finite predation rates of *H. dimidiata* occurred at 20 and 25 °C. Our results demonstrate that *H. dimidiata* is a more powerful predator at 20 and 25 °C than at 15 °C, when both the predator's population growth rate and its predation rate were considered.

5. Conclusion

Although Hassell (1978) has already noted the importance of knowing a predator's stage-specific predation rates and life tables for the proper modeling of predator–prey dynamics a few decades ago, most biological control and pest management programs do not yet use this valuable life table tool. In this study, we demonstrate that an accurate description of the survival, development, and predation capacity of a predator can be achieved with the age-stage, two-sex life table.

Acknowledgments

References

Agarwala, B.K., Singh, T.K., Lokeshwari, R.K., Sharmila, M., 2009. Functional response and reproductive attributes of the aphidophagous ladybird beetle, *Harmonia dimidiata* (Fabricius) in oak trees of sericultural importance. Journal of Asia-Pacific Entomology 12, 179–182.

Atlihan, R., Kaydan, M.B., 2002. Development, survival and reproduction of three coccinellids feeding on *Hyalopterus pruni* (Geoffer) (Homoptera: Aphididae). Turkish Journal of Agriculture and Forestry 26, 119–124.

Birch, L.C., 1948. The intrinsic rate of natural increase of an insect population. Journal of Animal Ecology 17, 15–26.

Boeckh, J., 1890. Die statistische Messung der ehelichen Fruchtbarkeit. In: Bulletin de l'Institut International de Statistique, vol. 5, first section.

Carey, J.R., 1993. Applied Demography for Biologists with Special Emphasis on Insects. Oxford University Press, New York.

Chang, Y.M., Hsiao, C.H., Yang, W.Z., Hseu, S.H., Chao, Y.J., Huang, C.H., 1987. The occurrence and distribution of five cucurbit viruses on melon and watermelon in Taiwan. Journal of Agricultural Research China 36, 389–397.

Chi, H., 1988. Life-table analysis incorporating both sexes and variable development rates among individuals. Environmental Entomology 17, 26–34.

Chi, H., 2012a. TWOSEX-MSChart: computer program for age stage, two-sex life table analysis. Available from: <http://140.120.197.173/ecology/>.

Chi, H., 2012b. CONSUME-MSChart: computer program for consumption rate analysis based on the age stage, two-sex life table. Available from: <http://140.120.197.173/ecology/>.

Chi, H., Liu, H., 1985. Two new methods for the study of insect population ecology. Bulletin of the Institute of Zoology, Academia Sinica 24, 225–240.

Chi, H., Mou, D.F., Allahyari, H., Yu, J.Z., Huang, Y.B., Yang, T.C., Farhadi, R., Gholizadeh, M. 2011. Finite predation rate: a novel parameter for the quantitative measurement of predation potential of predator at population level. In: Nature Precedings. Available from: <http://hdl.handle.net/10101/npre.2011.6651.1>.

Chi, H., Su, H.Y., 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. Environmental Entomology 35, 10–21.

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

Devi, M.S., Bijaya, P., Agarwala, B.K., Singh, T.K., 2007. Seasonal abundance and feeding potential of *Harmonia dimidiata* (Fabricius) in relation to key sucking pest of oak. Biological control 21 (Special Issue), 1–105.

Dunnett, C.W., 1980. Pairwise multiple comparisons in the homogeneous variance, unequal sample size case. Journal of American Statistical Association 75, 789–795.

Efron, B., Tibshirani, R.J., 1993. An Introduction to the Bootstrap. Chapman and Hall, New York.

Escriu, F., Perry, K.L., García-Arenal, F., 2000. Transmissibility of *Cucumber mosaic virus* by *Aphis gossypii* correlates with viral accumulation. Virology 90, 1069–1072.

Farhadi, R., Allahyari, H., Chi, H., 2011. Life table and predation capacity of *Hippodamia variegata* (Coleoptera: Coccinellidae) feeding on *Aphis fabae* (Hemiptera: Aphididae). Biological Control 59, 83–89.

Gildow, F.E., Shah, D.A., Sackett, W.M., Butzler, T., Nault, B.A., Fleischer, S.J., 2008. Transmission efficiency of *Cucumber mosaic virus* by aphids associated with virus epidemics in snap bean. Virology 98, 1233–1241.

Gillani, W.A., Matin, M.A., Rafi, M.A., 2007. Bionomics of tropical coccinellid beetle *Harmonia* (*Leis*) *dimidiata* (F) (Coleoptera: Coccinellidae) under laboratory conditions. Pakistan Journal of Agricultural Research 20, 79–83.

Goodman, D., 1982. Optimal life histories, optimal notation, and the value of reproductive value. American Naturalist 119, 803–823.

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

Huang, Y.B., Chi, H., 2012a. 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. Journal of Insect Science 19, 263–273.

Huang, Y.B., Chi, H., 2012b. Life tables of *Bactrocera cucurbitae* (Diptera: Tephritidae): with an invalidation of the jackknife technique. Journal of Applied Entomology. http://dx.doi.org/10.1111/jen.12002.

Inayat, T.P., Rana, S.A., Rana, N., Ruby, T., Sadiqui, M.J.I., Abbas, M.N., 2011. Predation rate in selected coccinellid (coleoptera) predators on some major aphidid and cicadellid (hemipteran) pests. International Journal of Agriculture and Biology 13, 427–430.

Istock, C.A., 1981. Natural selection and life history variation: theory plus lessons from a mosquito. In: Denno, R.F., Dingle, H. (Eds.), Insect Life History Patterns: Habitat and Geographic Variation. Springer-Verlag, New York, pp. 113–127.

Kalushkov, P., 1998. Ten aphid species (Sternorrhyncha: Aphididae) as prey for *Adilia bipunctata* (Coleoptera: Coccinellidae). European Journal of Entomology 95, 343–349.

Kuroda, T., Miura, K., 2003. Comparison of the effectiveness of two methods for releasing *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) against *Aphis gossypii* Glover (Homoptera: Aphididae) on cucumbers in a greenhouse. Applied Entomology and Zoology 38, 271–274.

Kuznetsov, V.N., Pang, H., 2002. Employment of Chinese Coccinellidae in biological control of aphids in greenhouse in Primorye. Far Eastern Entomologist 119, 1–5.

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

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

Meyer, J.S., Ingersoll, C.G., McDonald, L.L., Boyce, M.S., 1986. Estimating uncertainty in population growth rates: jackknife vs. bootstrap techniques. Ecology 67, 1156–1166.

Seko, T., Yamashita, K., Miura, K., 2008. Residence period of a flightless strain of the ladybird beetle *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) in open fields. Biological Control 47, 194–198.

Sharmila, M., Devikarani, Kh., Singh, T.K., 2010. Seasonal incidence and predatory potential of *Harmonia dimidiata* (Fab.) in relation to *Tuberculatum nervatus* Chakrabarti and Raychaudhuri. Annals of Plant Protection Sciences 18, 340–343.

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

Soroushmehr, Z., Sahragard, A., Salehi, L., 2008. Comparative life table statistics for the ladybeetle *Scymnus syriacus* reared on the green citrus aphid, *Aphis spiraecola*, fed on two host plants. Journal of Entomological Science 11, 281–288.

Tao, C.C., 1990. *Aphis gossypii* Glover. In: Tao, C.C. (Ed.), Aphid-Fauna of Taiwan Province, China. Taiwan Museum, pp. 176–177.

Trouve, C., Ledee, S., Ferran, A., Brun, J., 1997. Biological control of the damson-hop aphid, *Phorodon humuli* (Hom.: Aphididae), using the ladybeetle *Harmonia axyridis*. Entomophaga 42, 57–62.

Yu, J.Z., Chen, B.H., 2001. Effect of concealment and rearing density on the development and survival of *Lemnia biplagiata* (Coleoptera: Coccinellidae). Journal of Agricultural Research China 50, 68–74.

Yu, J.Z., Chi, H., Chen, B.H., 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. Annals of the Entomological Society of America 98, 475–482.