The Life Table and Parasitism Rate of *Diadegma insulare* (Hymenoptera: Ichneumonidae) Reared on Larvae of *Plutella xylostella* (Lepidoptera: Plutellidae), With Special Reference to the Variable Sex Ratio of the Offspring and Comparison of Jackknife and Bootstrap Techniques

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ABSTRACT The life table and parasitism rate of *Diadegma insulare* (Cresson) (Hymenoptera: Ichneumonidae), a larval parasitoid of the diamondback moth *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), were studied at $25 \pm 1°C$, $65 \pm 10\%$ RH, and a photoperiod of 16:8 (L: D) h. The data were analyzed based on the age-stage, two-sex life table theory. Because the sex ratio of offspring varies with the age of the female parent, we used only female offspring to calculate the intrinsic rate of increase (r), finite rate of increase (λ), net reproductive rate (R_0), and mean generation time (T) by using the jackknife technique, the values of which were $0.18407 \, d^{-1}$, $1.2021 \, d^{-1}$, 17.94 offspring, and 15.69 d, respectively. We also calculated these parameters by using bootstrap technique. They were not significantly different from those estimated by using the jackknife technique. We included both male and female offspring in the calculation of the parasitism rate. The net parasitism rate (C_0) was 42.63 larvae. Moreover, population projection showed differences between simulated population based on total offspring and female offspring. Because both the offspring sex ratio and the parasitism rate depend on female age, it is necessary to use the age-stage, two-sex life table for a correct analysis. Frequency of the net reproductive rate estimated by using bootstrap technique fit normal distribution well, whereas frequency data estimated by using jackknife technique failed the normality test. We suggest that the jackknife technique should not be used for the estimation of population parameters.

چکیده: جدول زندگی و نرخ پارازیتیسم زنبور *Diadegma insulare* (Cresson) (Hymenoptera: Ichneumonidae) پارازیتوئید مرحله لاروی شب پره پشت الماسی *Plutella xylostella* (L.) (Lepidoptera: Plutellidae) در دمای C° ۱±۲۵، رطوبت نسبی ۱۰±۶۵ درصد و دوره نوری ۱۶ ساعت روشنایی و ۸ ساعت تاریکی مطالعه شدند. داده ها بر اساس تئوری جدول زندگی سن- مرحله، دو جنسی تجزیه و تحلیل شد. بدلیل تغییر نسبت جنسی نتاج با سن حشره مادر، تنها نتاج ماده برای محاسبه نرخ ذاتی افزایش جمعیت (r)، نرخ متناهی افزایش جمعیت (λ)، نرخ خالص تولید مثل (R0)، و میانگین طول نسل (T) با استفاده از روش جک نایف استفاده شدند. مقدار به دست آمده برای این پارامترها به ترتیب ۰/۱۸۴۰۷روز⁻¹، ۱/۲۰۲۱روز⁻¹، ۱۷/۹۴ زاده و ۱۵/۶۹ روز بود. این پارامترها با روش بوت استرپ نیز محاسبه شدند که اختلاف معنی داری با روش جک نایف دیده نشد. ما هر دو نوع نتاج نر و ماده را در محاسبه نرخ پارازیتیسم در نظر گرفتیم. نرخ خالص پارازیتیسم ۴۲/۶۳ شته بود. به علاوه پیش بینی جمعیت نشانگر اختلاف معنی دار بین جمعیت شبیه سازی شده بر اساس همه نتاج با جمعیت شبیه سازی شده تنها بر اساس نتاج ماده بود. چون نسبت جنسی نتاج و نرخ پارازیتیسم وابسته به سن حشره مادر می باشند، استفاده از جدول زندگی سن-مرحله، دوجنسی برای تجزیه و

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تحلیل و کاربرد درست نتایج در کنترل زیستی ضروری می باشد. فراوانی تخمین های محاسبه شده برای نرخ خالص تولید

مثل توسط روش بوت استرپ به خوبی با توزیع نرمال مطابق بود اما آزمون نرمال بودن برای داده های جک نایف رد شد.

ما پیشنهاد می کنیم روش جک نایف برای تخمین پارامترهای جمعیت استفاده نشود.

KEY WORDS   demography, parasitism rate, offspring sex ratio, jackknife, bootstrap

The diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), has been one of the most important pests of crucifer crops throughout the world for several decades, although all of its life stages are attacked by natural enemies (Talekar and Shelton 1993). For example, Harcourt (1969) reported that the larval parasitoid *Diadegma insulare* (Cresson) (Hymenoptera: Ichneumonidae) played an important role in regulating diamondback moth populations in cabbage (*Brassica oleracea* L.) fields. However, the biological control of the diamondback moth has not been successful and has not been widely adopted.

Diadegma insulare is a solitary larval parasitoid (Cordero et al. 2007). It parasitizes the first three instars of the diamondback moth, emerges from the prepupa and overwinters as a pupa, either within the pupa of the moth or among the remnants of the crop (Harcourt 1960). According to Idris and Grafius (1993), the larval mortality of the diamondback moth caused by *D. insulare* can be as high as 75%. The parasitoid shows an excellent search capacity and has been studied as a potential biological control agent in integrated management programs for the diamondback moth (Harcourt 1969, 1986).

Because life table studies best depict the details of survival, development, and reproduction, they facilitate the understanding of the dynamics of insect populations (Wittmeyer and Coudron 2001). They are thus an invaluable tool for conservation, pest management, and the timing of pest control (Amir-Maafi and Chi 2006, Eliopoulos and Stathas 2008, Talebi et al. 2008, Kavousi et al. 2009). If the study of the parasitism rate is incorporated in the analysis, life table studies show unprecedented advantages in the practical applications of integrated pest management and biological control (Chi and Yang 2003, Farhadi et al. 2011). However, traditional female age-specific life tables (i.e., Lotka 1907, Lewis 1942, Leslie 1945, Birch 1948) address only the survivorship and the fecundity of the female individuals. Moreover, they ignore stage differentiation, the male population, and the contribution of the species to predation (Chi and Su 2006, Farhadi et al. 2011). The applications of these traditional types of life tables to population ecology and pest management are therefore limited. To include these realistic biological considerations, e.g., the differentiation of stages and the two sexes, Chi and Liu (1985) and Chi (1988) developed the age-stage, two-sex life table theory and corresponding methods for data analysis. The overlap of stages and the two sexes could then be properly considered (Chi 1988, Yu et al. 2005). Chi and Getz (1988) constructed a mass rearing and harvesting model based on the age-stage, two-sex life table. The timing of control based on stage-specific pesticide susceptibility was simulated by Chi (1990). The applications of the age-stage, two-sex life table include a study of the predator–prey relationship between *Propylaea japonica* Thunberg (Coleoptera: Coccinellidae) and *Myzus persicae* (Sulzer) (Chi and Yang 2003).

Without the knowledge of both the life table and parasitism rate of a biological control agent, it is impossible to correctly describe the growth, the stage differentiation, and the reproduction of the natural enemy. Furthermore, it is impossible to define a quantitative mass-rearing plan or to time the release of the natural enemy. In this study, we collected raw data on the life history of *D. insulare* and its rate of parasitism on *P. xylostella.* We then analyzed these data with the age-stage, two-sex life table to incorporate both sexes and stage differentiation. Because only female offspring contribute to parasitism and because the offspring sex ratio of *D. insulare* varies with the age of the female parents, we specifically considered the variable sex ratio of the offspring. We also used population projection to demonstrate the importance of inclusion these findings in computer simulation. For the estimation of variances of population parameters, we used both jackknife and bootstrap techniques and compared the frequency distribution of estimated values.

Materials and Methods

The Insects. Pupae of the diamondback moth and *D. insulare* originally were collected from the cabbage fields of Karaj region (Alborz province, Iran) and transferred to a growth chamber maintained at $25 \pm 1°C$, $65 \pm 10\%$ RH, and a photoperiod of 16:8 (L:D) h. The diamondback moth pupae were maintained in glass cylinders (10 cm in diameter, 25 cm in height). The emerged adults were transferred to cages (10 by 40 by 60 cm) with fresh cabbage plants (Chinese cabbage, *Brassica pekinensis* (Lour.) Rupr.). A piece of cotton wool soaked with 20% honey solution was supplied as food to the adult diamondback moths. The cabbage plants were replaced daily. Cabbage plants with eggs were transferred to new cages daily. Using this method, we collected diamondback moth larvae of the ages required for the study.

Life Table Study of *D. insulare*. For the life table study of the parasitoid, a cabbage plant with ≈300 third instars of the diamondback moth was exposed to eight pairs of adult *D. insulare* in a cage (30 by 60 by 40 cm) to allow the parasitoids to lay eggs. After 24 h, each larva was transferred to an individual glass cylinder (6 cm in diameter, 5 cm in height) and observed

daily. Because the egg and larval stages of *D. insulare* developed inside the body of the diamondback moth larva, we combined these two stages as the egg–larva stage. When a parasitoid pupa was formed, the duration of the egg–larva stage was recorded. When the parasitoid adults emerged, they were sexed, paired, and kept in individual containers (6 cm in diameter, 5 cm in height) with a cabbage leaf and 20 third instars of the diamondback moth. A piece of cotton wool soaked with 20% honey solution was supplied as food to the adults. After 24 h, the parasitoids were transferred to a new container with another 20 third instars of the diamondback moth. Parasitoid pupae formed on different days were recorded daily and kept individually until the emergence of the adults. The pupal duration and the sex of all emerged parasitoids were recorded.

Life Table Analysis. The raw life history data for *D. insulare* were analyzed based on the theory of the age-stage, two-sex life table according to Chi and Liu (1985) and Chi (1988). The means and standard errors of the life table parameters were estimated with the Jackknife technique (Sokal and Rohlf 1995). To facilitate raw data analysis, life table analysis, and the jackknife and the bootstrap techniques, a user-friendly computer program, TWOSEX-MSChart (Chi 2012a), was used. Student's *t*-test at the 5% significance level was used to measure the differences in developmental times and longevity between the male and female parasitoids. 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) were calculated as specified by the following equations. According to Chi and Liu (1985), the age-specific survival rate for the two-sex life table is calculated as follows:

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

where k is the number of stages. The age-specific fecundity is calculated as

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

The intrinsic rate of increase can then be estimated with the iterative bisection method from the Euler–Lotka equation as follows:

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

with age indexed from 0 (Goodman 1982). The net reproductive rate is calculated as follows:

$$R_0 = \sum_{x=0}^{\infty} l_x m_x \qquad [4]$$

The mean generation time is defined as the length of time that a population needs to increase to R_0-fold of its original size (i.e., $e^{rT} = R_0$ or $\lambda^T = R_0$) as the stable rate of increase (the intrinsic rate r and the finite increase rate λ) is reached. The mean generation time is calculated as $T = \ln R_0/r$. The gross reproductive rate (*GRR*) is calculated as $\sum m_x$.

The method described by Chi and Su (2006) was used to calculate the age-stage life expectancy (e_{xj}), which is also included in the TWOSEX-MSChart program. Because differences in development time often occur among individuals, an overlap between stages in the life history is common in many insect and mite populations. Consequently, individuals of the same age may be in different developmental stages and have different life expectancies.

The net parasitism rate (C_0) is calculated according to Chi and Yang (2003) and Farhadi et al. (2011) as follows:

$$C_0 = \sum_{x=0}^{\infty} k_x l_x \qquad [5]$$

where k_x is the age-specific parasitism rate of the parasitoid. The mean and standard error of C_0 also were estimated with the jackknife and bootstrap techniques. We then calculated the ratio of the net parasitism rate to the net reproductive rate as

$$Q_p = \frac{C_0}{R_0} \qquad [6]$$

The parasitism rate was analyzed with the computer program CONSUME-MSChart designed by Chi (2012b) in Visual BASIC 6.0. This program is available for download at the websites specified above. To estimate the standard error of Q_p, we used each pseudo-value of the net parasitism obtained in jackknifing, the net parasitism rate obtained in bootstrapping, and net reproductive rate to calculate the mean value of Q_p and its standard error. Timing-MSChart program (Chi 2012c) was used for projection of population growth based on age-stage two-sex life table theory.

Results

Development Time and Survival Rate. There was no significant difference in the development time of the egg–larva between the male (5.6 d) and female (5.4 d) ($t = 0.655$, $P = 0.518$) (Table 1). Furthermore, no significant differences were found in the duration of the pupal stage ($t = 1.297$, $P = 0.205$) or the overall preadult development time ($t = 1.426$, $P = 0.164$). The total preadult development times were 13.9 and 13.4 d for males and females, respectively (Table 1). The female adults of *D. insulare* lived on average 6.4 d, a

Table 1. Developmental times, longevity, and fecundity (female and male offspring) of *D. insulare* reared on *P. xylostella* at 25 ± 1°C, 65 ± 10% RH, and a photoperiod of 16:8 (L:D) h

Duration and fecundity	Mean ± SE		t	P
	Male	Female		
Egg–larva	5.6 ± 0.2	5.4 ± 0.2	0.655	0.518
Pupa	8.3 ± 0.2	7.9 ± 0.1	1.297	0.205
Total preadult	13.9 ± 0.3	13.4 ± 0.2	1.426	0.164
Adult	6.3 ± 0.2	6.4 ± 0.2	0.210	0.835
Total longevity	20.2 ± 0.3	19.8 ± 0.3	0.919	0.370
TPOP (d)	-	13.4 ± 0.2	-	-
APOP (d)	-	0	-	-
Oviposition period (d)	-	5.4 ± 0.2	-	-
Fecundity (offspring) (F)	22.8 ± 1.0 (male offspring)	17.9 ± 0.9 (female offspring)		

value not significantly different from that of the male adults (6.3 d) ($t = 0.210$, $P = 0.835$). The total longevity from birth to death for the female (19.8 d) was not significantly different from that of the male (20.2 d) ($t = 0.910$, $P = 0.370$) (Table 1).

To illustrate the difference between male and female survival, the survival rates (s_{xj}) of both male and female individuals are shown in Fig. 1A and B, respectively. These curves show the probability that a newborn egg will survive to age x while in stage j. The means and standard errors are the summarized descriptive statistics (Table 1), whereas the survival curves depict the detailed survival and stage differentiation process of the cohort. The overlap of stages during the developmental period can also be observed in Fig. 1.
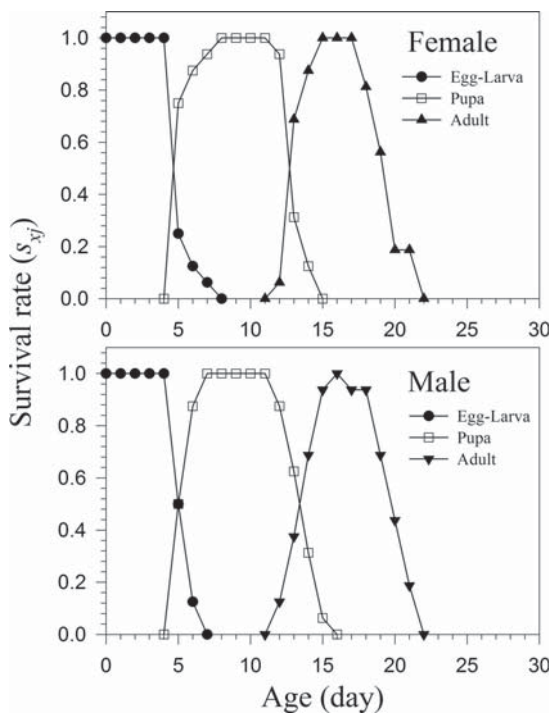

Fig. 1. Age-stage survival rates for each stage of female and male *D. insulare* reared on *P. xylostella*.

Fecundity and Offspring Sex Ratio. The adults of *D. insulare* mated after emergence, and the mated females began laying eggs on the same day. The oviposition period of the female was 5.4 d on average. Each female produced on average 17.9 female offspring ($F_{\female}$) and 22.8 male offspring ($F_{\male}$) (Table 1). During the entire life span, the cohort laid a total of 682 eggs. In total, 651 eggs, or 95.5% of the eggs laid, developed successfully to the adult stage. In total, 287 female adults and 364 male adults were produced. The sex ratio (female: male) of these 651 offspring was approximately $\female:\male$ = 1: 1.27. However, the sex ratio varied with age and ranged from 1: 0.857 to 1: 3.33. To partition the total fecundity into the production of female offspring ($F_{\female}$) and male offspring ($F_{\male}$), we calculated the number of female offspring and male offspring for each individual. Because only female parasitoids can lay eggs in the larvae of the diamondback moth, it is important to recognize such variation in the survival rate and the sex ratio of the offspring. To display this important information, we present these data in plots of the age-specific reproductive rates for both sexes and for those that died before the adult stage (Fig. 2). The cohort began the production of female offspring on day 12, reached a peak for 3 d (13–15 d), and ended on day 21. Because the females mated and parasitized hosts on the same day of emergence, the adult preoviposition period (APOP) was zero. However, if the preoviposition period was counted from birth, i.e., the total preoviposition period (TPOP), it was 13.4 d (Table 1). The l_x curve shows the age-specific probability that a newborn egg will survive to age x. Because the data shown represent a simplified version of s_{xj}, the overlap between stages cannot be observed in Fig. 2.

Life Expectancy. The life expectancy (e_{xj}) of each age-stage of *D. insulare* is plotted in Fig. 3. This figure shows the mean duration that individuals at age x and stage j are expected to survive. For both the female and the male, a newly laid egg is expected to live and develop through consecutive stages until an age of ≈20 d. This value is exactly equal to the mean longevity listed in Table 1. A first-day pupa can live ≈14.75 d longer on average, whereas a newly emerged adult female can live ≈7.75 d longer and an adult male ≈8.19 d longer.
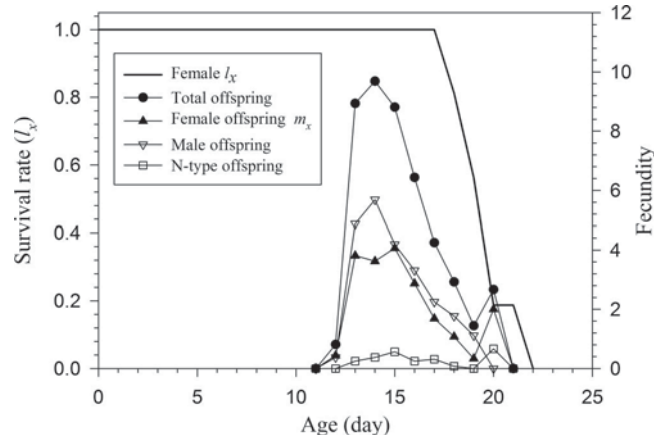
Fig. 2. Age-specific survival rate of females, total number of offspring, female offspring, male offspring, and offspring that died in an immature stage for *D. insulare* reared on *P. xylostella*.

Population Parameters and Reproductive Values. For the calculation of population parameters, we used only the age-specific fecundity of female offspring (m_x) in Fig. 2. The values of all major life table parameters are also shown in Table 2. By using the jackknife technique, the intrinsic rate of increase (r) of *D. insulare* is 0.18407 d^{-1}, the net reproductive rate (R_0) is 17.94 offspring, the gross reproductive rate ($GRR = \sum m_x$) is 19.91 offspring, the finite rate of increase (λ) is 1.2021 d^{-1}, and the mean generation time (T) is 15.69 d. These results are similar to those estimated by using bootstrap technique (Table 2). These results suggest that if the population reaches the stable age-stage distribution and if there are no mortality factors other than the physiological ones, *D.*

insulare population can increase 1.2-fold per day or at an exponential rate of 0.184 per day, and it can multiply 17.9 times every 15.7 d. According to the definition of Chi and Yang (2003), the parasitism-reproduction ratio (Q_p) was 2.402 by using jackknife technique and 2.381 by using bootstrap technique (Table 2). The difference is not significant.

The reproductive value (v_{xj}) is used to describe the expected contribution of individuals of *D. insulare* at age x and stage j to future offspring (Fig. 4). Although the age-specific fecundity at age 12 d was only 0.44 offspring per female (Fig. 2), a female individual at age 12 d had a peak reproductive rate of 19.3. The effect of age on the reproductive value can be clearly observed in the v_{xj} curves.

Population Projection. The results of population projection are shown in Fig. 5. If we use all offspring and ignore the variation in sex ratio and hatch rate of offspring because of female age, the population growth trend will be misleadingly faster (Fig. 5A) than that only the successfully hatched female offspring were included (Fig. 5B).

Jackknife and Bootstrap Technique. Frequency distribution of pseudo-values of the net reproductive rate ($R_{0-pseudo}$) and the net predation rate ($C_{0-pseudo}$) obtained by using jackknife technique are shown in Fig. 6. The distributions are different from those of the
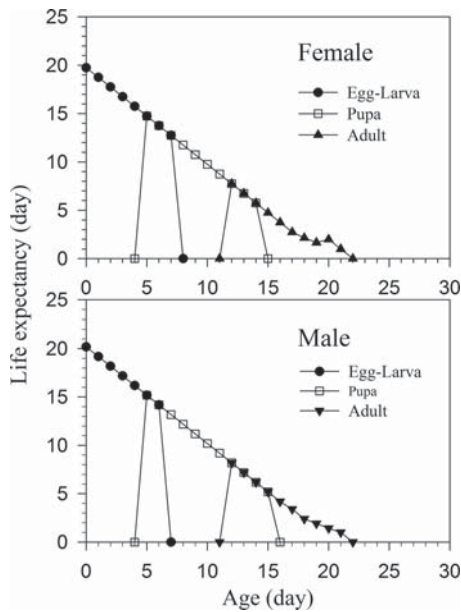

Fig. 3. Life expectancy (e_{xj}) of each age-stage of female and male *D. insulare* reared on *P. xylostella*.

Table 2. Means and standard errors of population statistics and life table parameters of *D. insulare* reared on *P. xylostella* at 25 ± 1°C, 65 ± 10% RH, and a photoperiod of 16:8 (L:D) h estimated by using jackknife and bootstrap (10,000 replicates) techniques

| Population statistics	Jackknife	Bootstrap
Net reproductive rate (R_0)	17.94 ± 0.90	17.96 ± 0.88
Intrinsic rate of increase (r)	0.18407 ± 0.00334	0.1839 ± 0.0033
Mean generation time (T)	15.69 ± 0.23	15.70 ± 0.22
Finite rate of increase (λ)	1.2021 ± 0.0040	1.2019 ± 0.0040
Gross reproductive rate (GRR)	19.91 ± 0.80	19.87 ± 0.89
Net parasitism rate (C_0)	42.63 ± 1.72	42.67 ± 1.68
Parasitism-reproductive ratio (Q_p)	2.402 ± 0.054	2.381 ± 0.151
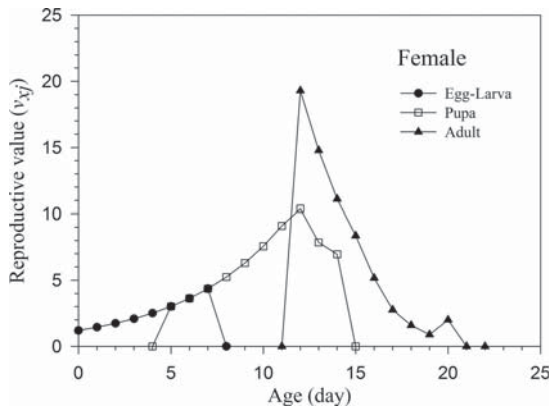
Fig. 4. Reproductive value (v_{xj}) of each stage of female *D. insulare*.

means of the net reproductive rate ($R_{0,B}$) and the net predation rate ($C_{0,B}$) of samples generated by using bootstrap technique (10,000 bootstraps). Bootstrapping gives high coefficients of determination (R^2).

Discussion

Development Time and Survival Rate. Based on our findings, there were no significant differences between the sexes in the development times of the egg–larva, pupa, preadult, and adult stages or in the total longevity. Golizadeh et al. (2008) reported that the development times of *D. anurum* on *P. xylostella* reared on cabbage were 5.57, 8.85, and 14.42 d for the

Fig. 5. Population projection by using total offspring and hatched female offspring.

egg–larva, the pupa, and the total preadult stage, respectively. Our results are similar to their findings. Their l_x curve was based on the female age-specific life table and ignored the variable developmental rates among individuals. In contrast to their single l_x curve, the curves of age-stage survival rates (s_{xj}) (Figure 1) demonstrated the advantageous ability of the age-stage, two-sex life table to reveal substantially more details about the life history, including the overlaps between stages and the parameter values for both sexes. The neglect of the variable developmental rate among individuals and the use of the adult age inevitably will result in errors in the life table parameters (Yu et al. 2005).

Fecundity and Offspring Sex Ratio. Our results showed that adult females started laying eggs immediately after emergence, a pattern observed also in *Aphidius gifuensis* (Ashmead) (Chi and Su 2006) and in many parasitoids. However, only the age-stage, two-sex life table can depict the stage differentiation correctly and precisely. The total preoviposition period (TPOP) is 13.4 d for *D. insulare* females (Table 2). It is close to the age of peak reproductive value at age 12 d (Fig. 4). Similar results have been reported in other studies based on the two-sex life table, e.g., *Chrysomya megacephala* (F.) (Diptera: Calliphoridae) (Gabre et al. 2005) and *H. hebetor* (Say) (Amir-Maafi and Chi 2006). Collectively, these results demonstrate that TPOP is a much more informative statistic than APOP.

Chi and Su (2006) reported that the offspring sex ratio of *Aphidius gifuensis* (Hymenoptera: Braconidae) changed with female age. In this study, we also found that the offspring sex ratio varies with female age (Fig. 2). This result is especially important for parasitoids because only female parasitoids can contribute to biological control. Moreover, because the adult female *D. insulare* survived only 6–7 d (Table 2), with a peak parasitism period of 3 d (Fig. 2), the field releases should be based on life table analysis to obtain precise timing and synchronization with the occurrence of the susceptible stages of the host (Getu et al. 2004). Moreover, these results demonstrated the importance of using the age-stage, two-sex life table method in the study of parasitoid–host relationships and biological control. To take the dependency of offspring sex ratio on female age into account, Huang and Chi (2011) developed a new model based on the age-stage, two-sex life table.

Life Expectancy. Chi and Su (2006) observed that the consideration of variation in the developmental rate between sexes and among individuals suggests that the life expectancy calculated from the age-stage, two-sex life table reveals more details than the value calculated from the traditional age-specific female life table. The overlap between the egg–larva and pupa stages is 2 d for the male, whereas the overlap is 3 d for the female. However, the overlap between the pupa and the adult is 4 d for the male and 3 d for the female. These details can also be observed in the survival curves (Fig. 1). Although no significant difference in life expectancy was found between male and female *D. insulare*, our analyses showed the advantages of the
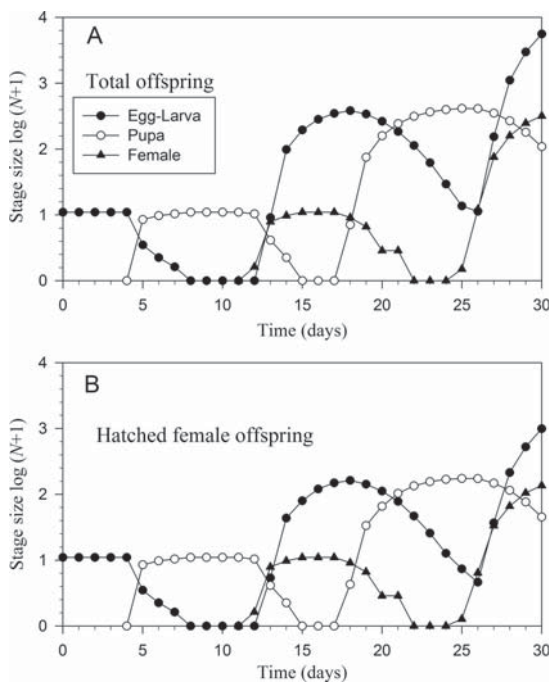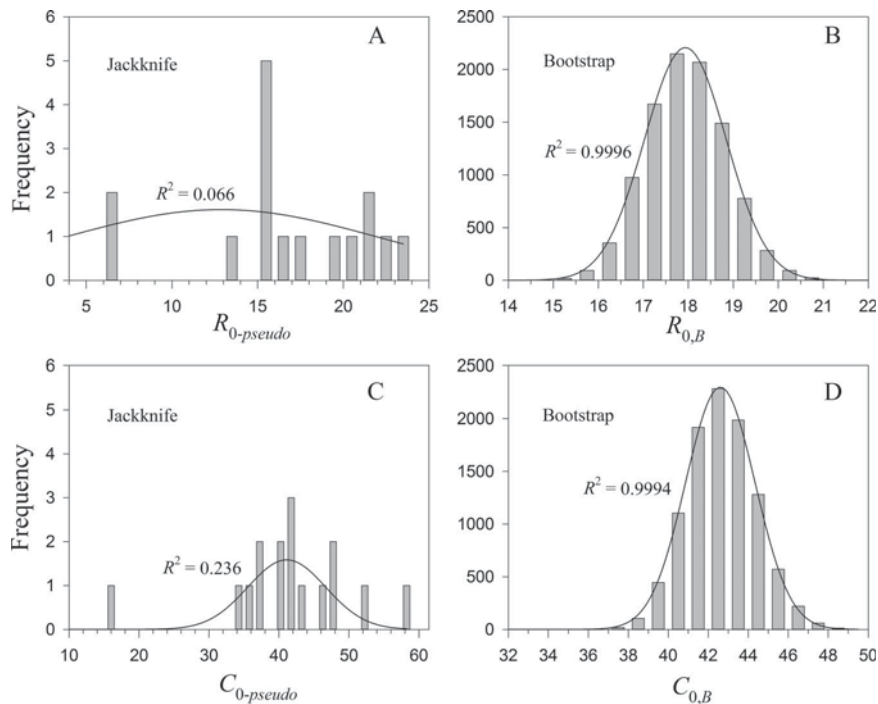
Fig. 6. Frequency distribution of the net predation rate and net reproductive rates estimated by using jackknife technique (A, C) and bootstrap technique (B, D).

two-sex life table for separating and revealing the details of the life history.

Population Parameters and Reproductive Value. With the age-stage, two-sex life table, we found that the net reproductive rate (R_0) was 17.9 offspring. The mean fecundity of the female offspring ($F_♀$) is 17.9 offspring. Our result is totally consistent with the proof of Yu et al. (2005), i.e., if there is no preadult mortality (or it is excluded), it is always the case that $R_0 = F$. At 25°C, Golizadeh et al. (2008) reported values of R_0, r, and T of *D. anurum* as 15.289 ♀ per ♀ per generation, 0.169 d^{-1}, and 16.083 d, respectively. We used their values of l_x and m_x (Fig. 2 of Golizadeh et al. 2008) to recalculate R_0. We found that the correct R_0 should be 20.7, not 15.289. This significant difference in R_0 might be caused by errors resulting from the use of adult age or by miscalculation. Chi (1988), Chi and Su (2006), Farhadi et al. (2011), and Huang and Chi (2012a) described the problems and errors associated with the application of the traditional age-specific female life table to a two-sex population. Yu et al. (2005) pointed out that if the life history data are organized according to the stage-specific model of Caswell (2001), it will result in the same problem as the use of adult age does because Caswell's model classifies individuals into different stages of life.

Mo and Liu (2006) observed that information about the intrinsic rate of increase (r) may help in selecting useful biological control agents. Golizadeh et al. (2008) claimed, "In theory, a parasitoid that has a population growth rate equal to or greater than its prey should efficiently regulate the population of its host." At 25°C, the intrinsic rate of increase of *D. anurum* is 0.169 d^{-1} (Golizadeh et al. 2008), whereas the intrinsic rate of increase of its host (the diamondback moth) ranged from 0.244 to 0.293 d^{-1} (Golizadeh et al. 2009); the intrinsic rates of increase of the diamondback moth are much higher than those of the parasitoid. Golizadeh et al. (2008) concluded, "*D. anurum* could be effective in biocontrol of diamondback moth integrated with other enemies or other compatible control methods." Although the intrinsic rate of natural increase (r) has indeed been used as a key demographic parameter to describe the population growth potential under environmental conditions (Andrewartha and Birch 1954), a high intrinsic rate of natural increase does not necessarily mean an efficient parasitism rate. To measure the efficiency of a natural enemy, we must consider not only its intrinsic increase rate but also its predation rate (parasitism rate). Chi and Su (2006) showed that the intrinsic increase rate of a parasitoid exceeds that of its host aphids because of the more rapid and adaptive development of the parasitoid inside its host.

Population Projection. The intrinsic rate of increase shows the potential of population growth, but it gives no information about the number of individuals in different developmental stages and sexes. The intrinsic rate of increase cannot be used to predict the growth of a population until it reaches stable age distribution. To show the detailed information we projected population growth by using TIMING-MSChart program (Chi 2012b). Because only the fe-

male individuals can kill their hosts, population projection using all offspring will overestimate the potential of this biological control agent (Fig. 5A). On the contrary, the results of population projection based on female offspring are more realistic (Fig. 5B). The parameters of population increase rate (r and λ) are the potential growth rate of a population at stable age distribution, which is generally not realized in fields. The population projection shows, however, the stage structure of a population without the assumption of stable age distribution and is therefore more realistic.

Jackknife and Bootstrap Technique. Both techniques have been used in the estimation of standard errors of population parameter (Meyer et al. 1986, Caswell 2001, Oyeyemi 2008). Oyeyemi (2008) compared the jackknife and bootstrap methods and conclude that the bootstrap underestimates the standard errors. In this study, we found that the standard errors estimated by both methods are very close. The frequency distribution of the estimated net reproductive rate showed, however, that bootstrap generated a normal distribution of estimated means. Although Meyer et al. (1986) and Oyeyemi (2008) claimed that jackknife is more cost-effective in computation time; with the fast advance of computer technology computation time is no more a problem. A bootstrap procedure with 10,000 replicates can be completed within seconds. Furthermore, normality is a more important criterion for further statistical test than computation time, and bootstrap technique is more advantageous in the respect. Huang and Chi (2012b) compared the use of jackknife and bootstrap techniques in demographic analysis. They suggested that jackknife technique should not be used for the analysis of gross reproductive rate either. Huang and Chi (2012c) mathematically proved that the application of the jackknife technique will result in biologically unrealistic $R_{0,i\text{-}pseudo}$ and consequently overestimation of the variance of R_0. They concluded that the jackknife technique should not be used for the estimation of variability of the net reproductive rate.

Conclusion. A rational biological control program must study the life tables of both pests and their natural enemies on different host plants to gain sufficient knowledge of the underlying ecology. It must also incorporate the stage-specific predation rate of predators or the parasitism rate of parasitoids in the life table of these natural enemies to schedule and quantify the mass rearing and release of these biological control agents (Chi and Yang 2003). To detect the real growth potential, we used only female offspring to calculate the population parameters in this paper. Because there are stage overlaps and the production of male offspring is an important part of the parasitism rate, the traditional female age-specific life table should not be used. The application of the age-stage, two-sex life table can properly include the stage differentiation and male population in both life table and predation rate analyses. Because density is an important factor of population growth and predation, we will take it into consideration in the construction of a realistic model.

Life table studies and computer simulation incorporating age-stage specific predation, the parasitism rate, or both, will surely play an important role in the explanation of predator–prey and parasitoid–host relationships and in pest management (Chi and Su 2006). The results of this laboratory study show the potential of *D. insulare* under ideal conditions in the absence of competitors, without pesticides, and in the absence of other detrimental factors. The effects of environmental conditions on the biological parameters of *D. insulare* should be precisely measured to construct a incremental and augmented release of this parasitoid. A more complete assessment of the potential of *D. insulare* as a biological control agent and its interaction with diamondback moth larvae requires additional information on its feeding and search behavior, including its functional responses to different densities of its host.

For the estimation of the standard error of the net reproductive rate and the net predation rate, the bootstrap gives a normal distribution that is advantageous for further statistical analysis and comparison.

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