Demographic Analysis, a Comparison of the Jackknife and Bootstrap Methods, and Predation Projection: A Case Study of *Chrysopa pallens* (Neuroptera: Chrysopidae)

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ABSTRACT The life table of the green lacewing, *Chrysopa pallens* (Rambur), was studied at 22°C, a photoperiod of 15:9 (L:D) h, and 80% relative humidity in the laboratory. The raw data were analyzed using the age-stage, two-sex life table. The intrinsic rate of increase (r), the finite rate of increase (λ), the net reproduction rate (R_0), and the mean generation time (T) of *Ch. pallens* were 0.1258 d^{-1}, 1.1340 d^{-1}, 241.4 offspring and 43.6 d, respectively. For the estimation of the means, variances, and SEs of the population parameters, we compared the jackknife and bootstrap techniques. Although similar values of the means and SEs were obtained with both techniques, significant differences were observed in the frequency distribution and variances of all parameters. The jackknife technique will result in a zero net reproductive rate upon the omission of a male, an immature death, or a nonreproductive female. This result represents, however, a contradiction because an intrinsic rate of increase exists in this situation. Therefore, we suggest that the jackknife technique should not be used for the estimation of population parameters. In predator-prey interactions, the nonpredatory egg and pupal stages of the predator are time refuges for the prey, and the pest population can grow during these times. In this study, a population projection based on the age-stage, two-sex life table is used to determine the optimal interval between releases to fill the predation gaps and maintain the predatory capacity of the control agent.

KEY WORDS life table, *Chrysopa pallens*, jackknife, bootstrap, population projection

The green lacewing, *Chrysopa pallens* (Rambur), is carnivorous in both the adult and larval stages and is an important natural enemy of many agricultural and forestry pests, for example, aphids, mites, whiteflies, and the eggs and young larvae of lepidopterous insects (Sterling et al. 1989). The species is known as a prospective indigenous biological control agent in the Palaearctic region, including China (Mu et al. 1980, Zhao 1988). *Ch. pallens* has long been valued in the natural environment by biological control workers, and its biological characteristics have been studied frequently for several decades (Zhao 1988, Canard and Volkovich 2001, Shi et al. 2008). However, ecological knowledge regarding *Ch. pallens*is still far from complete and is insufficient for the effective use of the species as a natural enemy in biological control programs.

Life table studies generate basic, detailed, and comprehensive ecological data, such as survivorship, development, and fecundity; these data are necessary for the efficient use of natural enemies in biological control. In a two-sex predator population such as the green lacewing, both male and female predators can kill aphids. Therefore, it is important to include the male individuals in considerations of biological control. Moreover, because the predation rate varies with age and stage and because certain life stages of the green lacewing, for example, the eggs and pupae, are not predatory, proper stage grouping is important for estimating the number of predators capable of predation and the total predatory capacity. However, traditional female age-specific life tables (Lotka 1907, Lewis 1942, Leslie 1945, Birch 1948) ignore the male individuals and the differentiation by stages; therefore, the application of these traditional approaches to ecological studies and biological control is limited and often causes errors (Huang and Chi 2012a). Chi and Liu (1985) and Chi (1988) developed the age-stage, two-sex life table, which includes both sexes as well as variable development rates among individuals. Because life table research is extremely time- and labor-

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consuming, replication is usually impractical. Without replication, the estimation of the variability of population parameters must rely on statistical resampling methods, primarily the jackknife and bootstrap methods. Comparisons and debates regarding these two methods have frequently appeared (Efron 1979, Meyer et al. 1986). In practical biological control, the multiple release of biological control agents is necessary. The determination of the optimal interval between releases is an important task. The advantages of the age-stage, two-sex life table for stage grouping have been demonstrated relative to the timing of control (Chi 1990) and the design of stage-specific harvesting (Chi and Getz 1988, Chi 1994). These advantages deserve to be investigated to facilitate the estimation of the optimal interval between releases.

To attain a comprehensive understanding of the life table of *Ch. pallens* as well as to facilitate the effective use of this species as a biological control agent, we collected life history data for *Ch. pallens* in this study. We then analyzed the raw data using the age-stage, two-sex life table. We compared the frequency distribution and biological meanings of the estimates obtained with the jackknife and bootstrap techniques. Finally, we used a population projection to find the optimal intervals between releases to minimize the effects because of the nonpredatory stages of the predator population.

Materials and Methods

Insects. The laboratory colony of *Ch. pallens* used in this study was collected in April 2010 from Tai-An (36° 15′ N, 116° 59′ E), Shandong, China. The lacewings were kept in plastic cylindrical containers (25 cm diameter, 15 cm height) and reared with *Aphis craccivora* Koch on broad bean, *Vicia faba* L., in an environmental chamber at 22°C, a photoperiod of 15:9 (L:D) h, and 60 ± 5% relative humidity (RH).

Life Table Study. Fifty-two lacewing eggs laid on broad bean leaves within 24 h were collected and transferred to a glass tube (2 cm diameter, 7 cm long) for the life table study. The hatched larvae were transferred to individual glass tubes within 24 h and reared on sufficient aphids until cocooning. The development of the larvae was recorded daily. The development periods for the prepupa and pupa and the adult emergence rate were also recorded. Adults were paired after emergence. Each pair was kept in a glass cylindrical container (10 cm diameter, 6 cm high) and fed with *A. craccivora.* The numbers of eggs produced were recorded daily until the death of the female adult.

Life Table Analysis. The raw data were analyzed using the age-stage, two-sex life table theory developed by Chi and Liu (Chi and Liu 1985, Chi 1988) and the method described by Chi (1988). The following parameters were calculated: age-stage specific survival rate (s_{xj}, where x = age and j = stage), age-stage specific fecundity (f_{xj}), age-specific survival rate (l_x), age-specific fecundity (m_x), age-stage life expectancy (e_{xj}), and reproductive value (v_{xj}), preoviposition period of female adult (APOP), and total preoviposition period of female counted from birth (TPOP). The population parameters (r, intrinsic rate of increase; λ, finite rate of increase; R_0, net reproduction rate; and T, the mean generation time) were also calculated. The intrinsic rate of increase was estimated with the iterative bisection method from the Euler–Lotka formula:

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

with age indexed from 0 (Goodman 1982). The life expectancy (e_{xj}) was calculated according to Chi and Su (2006). The mean generation time is defined as the period of time needed by a population to increase to R_0-fold of its size (i.e., $e^{rT} = R_0$ *or* $\lambda^T = R_0$) at the stable age-stage distribution and is calculated as $T = (\ln R_0)/r$, where $R_0 = \Sigma l_x m_x$, $\lambda = e^r$. The gross reproductive rate (*GRR*) is calculated as Σm_x. For the tedious and complicated calculations involved in the analyses of raw data and of the life table, a computer program (TWOSEX-MSChart) was used in this analysis (Chi 2012a). This program is written in Visual BASIC for the Windows operating system and is available at http://140.120.197.173/Ecology/Download/Twosex.rar and http://www.znu.ac.ir/agriculture/pages/plantprotection/software/index.htm.

Jackknife Technique. To estimate the means and SEs of the life table parameters, we used the jackknife technique (Sokal and Rohlf 1995) and bootstrap technique (Efron and Tibshirani 1993). To apply the jackknife technique, we first calculate the population parameter based on all n individuals of the cohort. For example, we calculate the intrinsic rate r_{all} based on all individuals according to equation 1. We then omit individual i and use the other n-1 individuals to calculate the jackknife value of r_{i-jack}. Next, we calculate $r_{i-pseudo}$ as

$$r_{i-pseudo} = n \cdot r_{all} - (n-1) \cdot r_{i-jack}. \qquad [2]$$

The jackknife estimates of the mean of the intrinsic rate (r_J), the variance (s_J^2), and the SE ($se(r_J)$) of the intrinsic rate of increase are calculated as

$$r_J = \frac{\sum_{i=1}^{n} r_{i-pseudo}}{n} \qquad [3]$$

$$s_J^2 = \frac{\sum_{i=1}^{n} (r_{i-pseudo} - r_J)^2}{n-1} \qquad [4]$$

$$\mathrm{se}(r_J) = \sqrt{\frac{s_J^2}{n}}. \qquad [5]$$

The same method is used for λ, R_0, T, and *GRR*.

Bootstrap Technique. In the bootstrap procedure, we randomly sample n individuals from the cohort with replacement and calculate the $r_{i\text{-}boot}$ for this boot-

Table 1. Developmental time (days), longevity (days), and fecundity (eggs/female) of *Chrysopa pallens* at 22°C and 80% RH

Parameter	Stage	*n*	Mean ± SE
Developmental time (days)	Egg	52	4.3 ± 0.1
	First instar	51	3.7 ± 0.1
	Second instar	49	2.7 ± 0.1
	Third instar	43	4.6 ± 0.1
	All instars	43	10.9 ± 0.2
	Prepupal	43	5.2 ± 0.1
	Pupa	39	7.4 ± 0.3
Adult longevity (days)	Male	20	33.7 ± 1.8
	Female	19	29.2 ± 3.0
Adult preoviposition period (APOP) (days)	Female	17	6.2 ± 0.4
Total preoviposition period (TPOP) (days)	Female	17	34.3 ± 0.5
Oviposition period (days)	Female	17	22.4 ± 0.5
Fecundity (*F*) (eggs/female)	Female	17	660.7 ± 69.0

strap sample according to equation 1, where n is usually the cohort size used at the beginning of the life table study. For each bootstrap sample i, lx, and m_x are calculated from the n individuals selected randomly with replacement. Thus, the data on the same individual are repeatedly selected. We repeat this procedure m times (m = 10,000) and compute the mean of these m bootstraps (r_B), variance (s_B^2), and SE (se(r_B)) as

$$r_B = \frac{\sum_{i=1}^{m} r_{i-boot}}{m} \quad [6]$$

$$s_B^2 = \frac{\sum_{i=1}^{m} (r_{i-boot} - r_B)^2}{m - 1} \quad [7]$$

$$\text{se}(r_B) = \sqrt{s_B^2} \quad [8]$$

The same method is used for other population parameters. Both the jackknife and the bootstrap methods are included in the computer program TWOSEX-MSChart.

Predation Projection. The computer program TIMING-MSChart (Chi 2012b) is used to project the population growth of *Ch. pallens* based on the life table data collected in this study. To consider the variable predation rate in the estimation of the predatory capacity of a predator population, we used the stage-specific predation rates of *Ch. pallens* collected by Li et al. (2009).

Results

The egg duration of *Ch. pallens* ranged from 4 to 5 d, with a mean of 4.3 d. The total larval developmental time was 10.9 ± 0.2 d (mean ± SE). Among the emerged adults, there were 20 males and 19 females (Table 1). The corresponding sex ratio (male:female) is 1:0.95. The preadult survival rate was 75%. The adult preoviposition period (APOP), that is, the time between adult emergence and first oviposition (ignoring the duration of the preadult stages), was 6.2 ± 0.4 d. If the preoviposition period is counted as the time from birth to first reproduction in females (the total preoviposition period, TPOP), it is 34.3 ± 0.5 d.

The age-stage specific survival rates (S_{xj}) of *Ch. pallens* are plotted in Fig. 1. This parameter is the probability that a newborn egg will survive to age x and stage j. In these curves, stage differentiation because of variable developmental rates among individuals can be observed. Because s_{xj} includes the variation among individuals in developmental rates, we can detect stage overlaps during the development of a cohort as well as the survival curves of males and females. For example, the probability of a newborn egg surviving to age 35 d in the male adult stage is 0.38. The corresponding probability in the female adult is 0.35. The horizontal survival curve of male adults showed no mortality during the age interval 28≈50 d. The mean longevity of the male and female adults was 33.7 and 29.2 d, respectively (Table 1). On average, a female

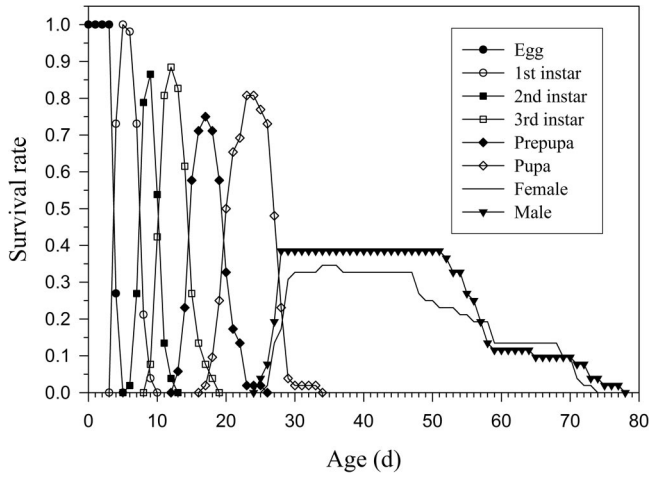

Fig. 1. Age-stage specific survival rate of *Chrysopa pallens* at 22°C and 80% RH.

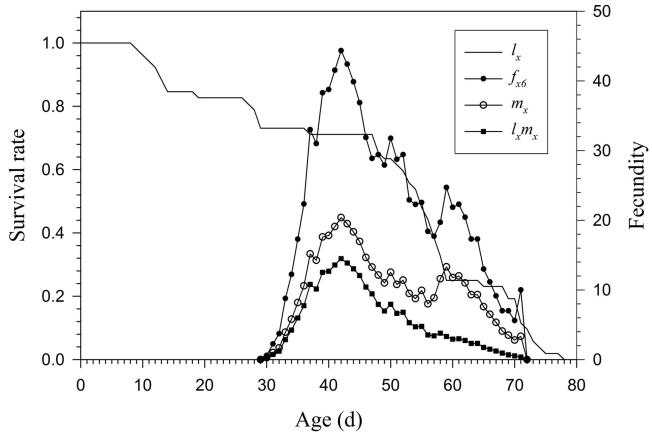

Fig. 2. Age-specific survival rate (l_x), age-stage specific fecundity (f_{x7}) of the female stage, age-specific fecundity (m_x), and age-specific maternity ($l_x m_x$) of *Chrysopa pallens* at 22°C and 80% RH.

adult *Ch. pallens* produced 660.7 eggs during an average oviposition period of 22.4 d (Table 1).

The age-specific survival rate (l_x), female age-specific fecundity (f_{x7}), age-specific fecundity of the total population (m_x), and age-specific maternity ($l_x m_x$) are illustrated in Fig. 2. The maximum lifetime fecundity of the female is 1,289 eggs, whereas the maximum age-specific mean fecundity of the female (f_{x7}) is 44.4 eggs at age 42 d.

If all individuals are included, the intrinsic rate of increase (r), the finite rate of increase (λ), the net reproduction rate (R_0), and the mean generation time (T) of *Ch. pallens* were 0.1258 d^{-1}, 1.1340 d^{-1}, 241.4 offspring and 43.6 d, respectively (Table 2). If the jackknife method is used with the Euler–Lotka equation, the means and SEs of r, λ, R_0, and T were 0.1264 ± 0.0056 d^{-1}, 1.1347 ± 0.0063 d^{-1}, 241.2 ± 55.1 offspring, and 43.6 ± 0.9 d, respectively. If the bootstrap method is used, the means and SEs of r, λ, R_0, and T were 0.1238 ± 0.0056 d^{-1}, 1.1318 ± 0.0063 d^{-1}, 234.1 ± 54.3 offspring, and 43.6 ± 0.9 d, respectively.

The life expectancy (e_{xj}) of each age-stage group of *Ch. pallens* is plotted in Fig. 3. The values (e_{xj}) are the times that individuals of age x and stage j are expected to live after age x. For example, the life expectancy of a newborn egg was 48.9 d, whereas a female adult of age 35 d is expected to live 24 more days. Because this study was conducted in the laboratory without the adverse effects of field conditions, the life expectancy decreased gradually with age.

Fisher (1930) defined the reproductive value as the contribution of an individual to the future population. The reproductive values (v_{xj}) of individuals at age x and stage j of *Ch. pallens* are presented in Fig. 4. A newborn egg had a value of 1.1340, which is the finite rate itself. Females near the peak of reproduction, however, contributed considerably more to the population than those at other ages and stages. For example, a newly emerged female (age 26 d) has a reproductive value of 74.2. In contrast, a 37-d-old female has a markedly higher reproductive value, 267.1.

To demonstrate the fundamental differences between the jackknife and bootstrap methods, we plot the frequency distribution of the intrinsic rate, the mean generation time, and the net reproductive rate in Fig. 5. Although the means and SEs estimated with these two methods are close, as shown in Table 2, their frequency distributions are markedly different. The bootstrap method generated normally distributed estimates and smaller variances; in contrast, the jackknife generated a nonnormal distribution and substantial variances.

The population growth of *Ch. pallens* was projected in a way similar to that used in Chi (1990) and Huang and Chi (2012a) with TIMING-MSChart (Chi 2012b). In the projection beginning with a single release of 10 eggs aged 3 d, the curve of the predatory capacity of *Ch. pallens* decreased after 10 d, when the larvae began to pupate. This feature corresponded to the time refuge formed by the nonpredatory prepupa and pupa stages. A 6-d gap with a predatory capacity of zero was obvious (Fig. 6A). The population projection with a second release on the 15th day could narrow the gap in the predatory capacity (Fig. 6B). If the second

Table 2. Population parameters of *Chrysopa pallens* at 22°C and 80% RH estimated with the whole-cohort method, jackknife technique, and bootstrap technique

Population parameter	Whole cohort	Jackknife technique	Bootstrap technique
		Mean ± SE	Mean ± SE
Intrinsic rate of increase r (d^{-1})	0.1258	0.1264 ± 0.0056	0.1238 ± 0.0056
Finite rate of increase λ (d^{-1})	1.1340	1.1347 ± 0.0063	1.1318 ± 0.0063
Net reproduction rate R_0 (offspring)	241.4	241.4 ± 55.1	234.1 ± 54.3
Mean generation time (T) (d)	43.6	43.6 ± 0.9	43.8 ± 0.9
Gross reproduction rate *GRR* (offspring)	432.6	432.6 ± 97.1	424.1 ± 94.5

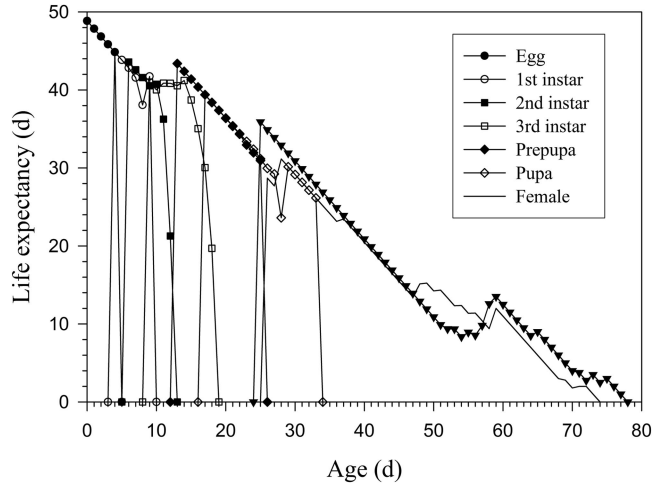

Fig. 3. Life expectancy of each age-stage group of *Chrysopa pallens* at 22°C and 80% RH.

release occurred on the 10th d, the time refuge virtually disappeared (Fig. 6C).

Discussion

The developmental times and population parameters of *Ch. pallens* obtained from our study are generally consistent with those found by previous studies. Mu et al. (1984) reported that the developmental duration for the preadult stages of the second generation (June to July) of *Ch. septempunctata* (synonym of *Ch. pallens*) in the field in Tai-An, China was 3.5, 10.6, 5.1, and 6.0 d for the egg, larva, pupa, and APOP, respectively. Zhao (1988) reported the mean developmental times of egg, larval, and pupal stage of *Ch. septempunctata* at 25°C reared on *Aphis craccivora* as 3.38, 11.01, and 13.26 d, respectively. Shi et al. (2008) reported that the total duration of the larval stage of *Ch. pallens* was 10.72 d at 22°C. In the current study, the total duration of the larval stage at 22°C was 10.9 d. This value is very similar to all the published data given above. If *Ch. pallens* was reared on *Bemisia tabaci* (Gennadius), the duration of the egg, first instar, second instar, third instar, and pupa was 7.0, 4.2, 6.2, 8.2, and 12.2 d, respectively (Khan and Wan 2008). These values are longer than those found for *Ch. pallens* reared on aphids. The differences between the findings of Khan and Wan (2008) and this study might result from the difference in prey species. A variety of factors have been reported to cause differences in the developmental time of predators. These factors include the host plants, temperature, rearing methods, and prey species (Campbell et al. 1974; Dixon 1977, 1987; Logan et al. 1976; Schowalter 2000; Kavousi et al. 2009; Nasreen et al. 2004).

Because the age-stage, two-sex life table incorporates variation among individuals in developmental rates, stage overlaps in the survival rate can be observed. At 25°C and 75% RH, Schneider et al. (2009) studied the effect of glyphosate on the development

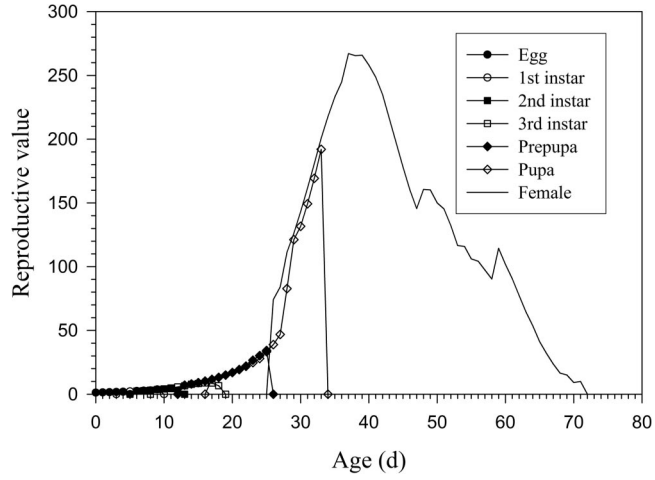

Fig. 4. Reproductive value of each age-stage group of *Chrysopa pallens* at 22°C and 80% RH.

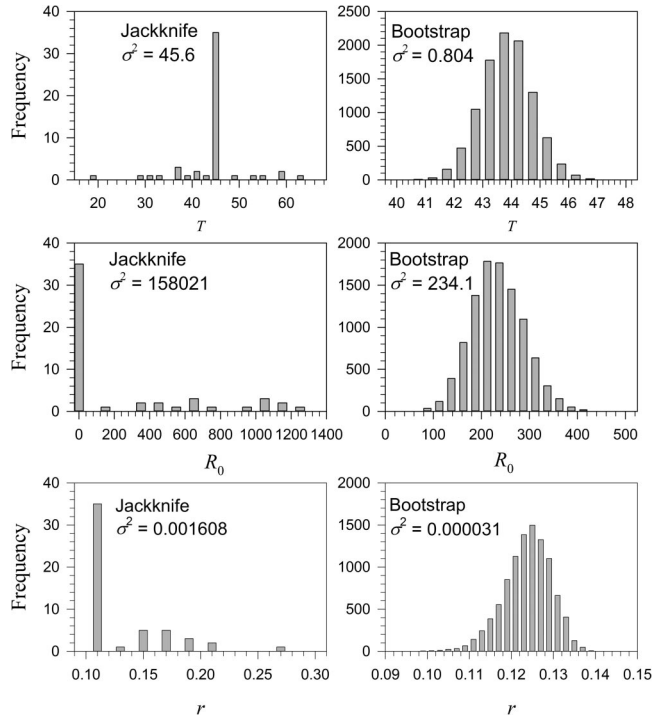

Fig. 5. Frequency distribution of estimated intrinsic rate of increase based on jackknife and bootstrap techniques.

and survival of *Chrysoperla externa* Hagen. The age-stage, two-sex life table successfully revealed the stage overlaps. In our study, significant overlaps could also be observed (Fig. 1). At ages 17 and 18 d, we observed third instars, prepupae, and pupae at the same time.

As Chi (1988) and Yu et al. (2005) observed, the calculation of survival rate and fecundity based only on the adult age assumes that all adults emerged on the same day. This approach ignores the differences in the preadult developmental times. Consequently, these manipulations and assumptions yield inaccurate survival and fecundity curves. For example, because the survival rate (l_x) must be a decreasing sequence of age, it must, by definition, be in the format

$$1 \geq l_1 \geq l_2 \geq l_3 \geq l_4 \geq l_5 \geq l_6 \ldots$$

Sandhu et al. (2010) constructed life tables based on adult ages. The survival curves (l_x) (Page 2028; Fig. 1h,i) showed errors of the form $l_{x+1} > l_x$. Similar errors can be found in papers using simplified methods for the estimation of the finite rate based on adult age (Muturi et al. 2011).

Chi and Su (2006) demonstrated that if an age-specific female life table is applied only to the female component of a population, the relationship between F and R_0 is $R_0 = l_a \times F$, where l_a is the preadult survival rate of females in a female population. If age-specific female life table theory is applied to a two-sex population, the relationship between F and R_0 is $R_0 = w \times s_a \times F$, where s_a is the preadult survival rate of females in a two-sex population and w is the female population of offspring; this equation will be true if and only if w is a constant for m_x at different ages. Again, an erroneous relationship between the mean fecundity and the net reproductive rate will be obtained if a life table is constructed based on adult age alone and ignores preadult mortality. Yu et al. (2005) and Chi and Su (2006) discussed this problem in detail.

Chi (1988) proved that the relationship between the net reproductive rate R_0 and the mean female fecundity F for two-sex life tables is $R_0 = F \times (N_f/N)$, where N is the total number of eggs used at the beginning of the life table study and N_f is the number of female adults emerged. In this study, $N = 52$, $N_f = 19$, $F = 660.7$, and $R_0 = 241.2$. Our data for R_0 and F are consistent with the previously demonstrated relationship $R_0 = F \times (N_f/N)$. The minor difference in the values is because of roundoff. Because the net reproductive rate (R_0) incorporates the survival rate, the equation $R_0 \leq F$ will always apply. If preadult mortality occurs, then certainly $R_0 < F$. Yu et al. (2005) showed that the relationship between the *GRR*, R_0, and preadult survivorship (l_a) is $GRR > l_a \cdot GRR > R_0$. Our results are consistent with this relationship. Chi (1988) and Chi and Yang (2003) discussed the differences between the traditional female age-specific life table and the age-stage, two-sex life table in detail and also stated that the survival and fecundity curves based solely on the adult age may be misconstrued.

The life expectancy based on the age-stage, two-sex life table reveals not only the differences among individuals of the same age but also the differences between stages and sexes (Fig. 3). Furthermore, because the life expectancy value is calculated using the

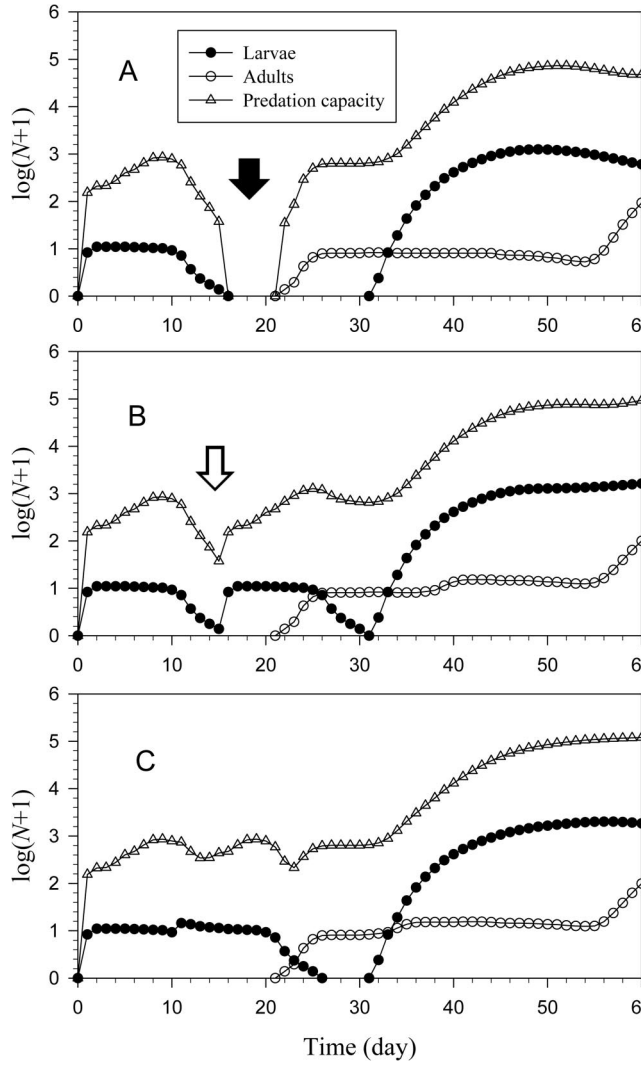

Fig. 6. Results of population projection: (A) single release; (B) two releases (with the second release on the 15th day); (C) two releases (with the second release on the 10th day). The single release included a time refuge that appeared when the predators were in the prepupa and pupa stage (the solid black arrow in A). If the second release was on the 15th day, the time refuge decreased significantly (the open arrow in B). If the second release was on the 10th day, the time refuge virtually disappeared.

age-stage survival rate (s_{xj}) without assuming that the population reaches a stable age-stage distribution, it can be used to predict the survival of a population without assuming a stable age-stage distribution (Yang and Chi 2006).

In this study, the peak reproductive value of *Ch. pallens* occurred at age 37 d (Fig. 4). This value falls between the mean TPOP (34.29 ± 0.51 d) for all *Ch. pallens* females (Table 1) and the peak of $l_x m_x$ in Fig. 2. The results suggest that when the females begin to reproduce, the reproductive value also increases. When most female individuals complete preadult development and begin to produce eggs, the cohort soon achieves its highest contribution to the population (Gabre et al. 2005). This peak is consistent with the peak of $l_x m_x$ in Fig. 2.

The basic and important differences in the frequency distributions of the intrinsic rate, the mean generation time, and the net reproductive rate estimated with the jackknife and bootstrap methods are demonstrated in the values of the variances (Fig. 5). The normality of the underlying distributions is an important basis for further statistical analysis. The highest bar in the frequency distributions of the jackknife estimates shows that the omission of any one male, any individual that died in the immature stage, or any nonreproductive female will all result in the same pseudo-value. This outcome will then cause the result of omitting a single individual to be weighed heavily. If the net reproductive rate is zero, no intrinsic rate of increase exists. When the jackknife is used, the omission of one individual may result in a zero net

reproductive rate. This result represents a contradiction, however, because an intrinsic rate of increase exists in this situation. Thus, the biologically meaningless zeros of the net reproductive rate obtained with the jackknife method present a serious theoretical problem. The bootstrap method generated normally distributed estimates and smaller variances. In contrast, the jackknife generated nonnormal distributions and substantial variances. If the bootstrap is used, the omission of any individual will not produce identical extreme values because the bootstrap is performed with random sampling with replacement. Although the jackknife method has been widely used in many demographic studies (e.g., Chi and Getz 1988, Tsai and Wang 2001, Huang and Chi 2012) during past several decades, according to the above discussion and the detailed mathematical invalidation of Huang and Chi (2013) we suggest that the jackknife technique not be used for the estimation of the variance of population parameters.

Chi (1990) and Huang and Chi (2012) demonstrated the effectiveness of population projection based on the age-stage, two-sex life table in revealing changes in stage structure during population growth. In this study, for a projection that began with a single *Ch. pallens* cohort of 10 eggs aged 3 d, the curve describing the predatory capacity decreased after 10 d, when the larvae began to pupate. This feature of the curve corresponded to the time refuge formed by the nonpredatory prepupa and pupa stages. A 6-d gap in which the predatory capacity was zero was obvious (Fig. 6A). A population projection with an extra release of 10 eggs aged 3 d on the 15th day could narrow the gap in the predatory capacity (Fig. 6B). Moreover, the time refuge virtually disappeared if the second release occurred on the 10th d (Fig. 6C).

Although insects are rarely subject to constant temperatures in nature, controlled laboratory studies can provide basic and valuable insights into the population dynamics of a particular species (Summers et al. 1984). The results obtained in this study provide information useful for predicting the population potential of *Ch. pallens* as a key agent in biological control programs, including the control of aphids and many other insect pest species. The use of the age-stage, two-sex life table method to study *Ch. pallens* yielded considerably more accurate and useful data than the data that would have been obtained using the female-only age-specific life table.

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