Comparison of Life Tables of *Cheilomenes sexmaculata* (Coleoptera: Coccinellidae) Under Laboratory and Greenhouse Conditions

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ABSTRACT The ladybird *Cheilomenes sexmaculata* (F.) is an important aphidophagous predator in Asia. In order to mass rear predators for biological control, it is valuable to identify the features of populations that are affected by variations in field conditions. Life tables can provide comprehensive descriptions of the development, survival, and fecundity of a population. However, there are few life table studies of *C. sexmaculata*. Studies of life history have been carried out in many arthropods using the traditional female age-specific life table, which takes only female individuals into consideration, while the variations in developmental rates amongst individuals are ignored. In this paper, we constructed life tables for *C. sexmaculata* fed on *Myzus persicae* (Sulzer) both at constant temperature in the laboratory and fluctuating temperature in the greenhouse, and analyzed the data using the age-stage, two-sex life table. The bootstrap technique was used to estimate the standard errors of the population parameters. The results showed that preadult *C. sexmaculata* developed more slowly and had lower survival and reproductive rates under greenhouse conditions, as indicated by the curves of age-stage survival rate (s_{xj}), age-stage-specific fecundity (f_{xj}) of the female stage, age-specific fecundity (m_x), and age-specific maternity (l_xm_x). Our results also showed that the intrinsic rate of increase (r), net reproductive rate (R_0), and finite rate of increase (λ) under laboratory and greenhouse conditions were $0.1668\,d^{-1}$ and $0.1027\,d^{-1}$, 192.1 and 53.0, and $1.1815\,d^{-1}$ and $1.1082\,d^{-1}$, respectively. Our results revealed significantly different life table parameters for *C. sexmaculata* under laboratory and greenhouse conditions. This information will be useful for developing a successful mass-rearing program for *C. sexmaculata* for use in biological control.

KEY WORDS *Cheilomenes sexmaculata*, life table, population parameter, bootstrap technique

The predacious ladybird *Cheilomenes* (*Menochilus*) *sexmaculata* (F.) (Coleoptera: Coccinellidae) is an important aphidophagous predator in Asia (Agarwala and Yasuda 2000). It has been recorded preying on a number of aphid species including *Aphis craccivora* (Koch) (Agarwala et al. 2001), *Aphis gossypii* (Glover), *Rhopalosiphum maidis* (Fitch), *Myzus persicae* (Sulzer), *Uroleucon compositae* (Theobald), *Lipaphis erysimi* (Kaltenbach), and *Aphis nerii* (Boyer de Fonscolombe) (Omkar and Bind 2004). Its voracity and tolerance of high temperatures may make it an efficacious biological control agent in high-temperature agroecosystems, including greenhouses (Wang et al. 2013). The biology of the ladybird has been studied for decades in the laboratory (Gautam 1989, Sugiura and Takada 1998, Rai et al. 2003). However, ecological knowledge of *C. sexmaculata* is incomplete, in particular regarding the effective use of this species as a natural enemy in biological control programs.

To successfully mass rear natural predators for biological control programs, it is helpful to determine certain population characteristics, such as growth rate, stage structure, and fecundity (Yu et al. 2013a). Proper quantitative analyses of the life history parameters of natural predators play an essential role in this process. A useful instrument in deriving such information is the life table, which can provide a comprehensive description of the development, survival, and fecundity of a population (Farhadi et al. 2011). Studies of life history have been carried out in many arthropods using the traditional female age-specific life table (e.g., Abdel-Salam and Abdel-Baky 2001, Lanzoni et al. 2004, Russo et al. 2004, Zanuncio et al. 2006). This takes only female individuals into consideration, and ignores the variations in developmental rates amongst individuals (Birch 1948). The application of this traditional approach to ecological and biological control studies is therefore limited and can even introduce errors (Huang and Chi 2012). Chi and Liu (1985) developed an age-stage, two-sex life table which takes both sexes into consideration as well as interindividual variation in developmental rates. The age-stage, two-sex life table has since been used to describe the population

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characteristics of many insect and mite species in a variety of environmental conditions (e.g., Farhadi et al. 2011, Yu and Chi 2012, Yu et al. 2013a).

Despite its potential use in biological control programs, there are few published studies on the life history and population parameters of the ladybird *C. sexmaculata* under variable environmental conditions, even though these play an important role in the successful mass rearing and release of coccinellids. Previous studies reported the effect of temperature and photoperiod on the development, reproduction, and predation activity of the ladybirds (Wang et al. 2013). However, life table data are lacking to estimate the population dynamics of *C. sexmaculata* in both mass rearing conditions and after release into the target environment. In this study, we set out to better understand the life table of *C. sexmaculata* in order to facilitate the effective use of this species as a biological control agent, by constructing life tables for *C. sexmaculata* fed on *M. persicae* both at constant temperature in the laboratory and at fluctuating temperature in the greenhouse, and analyzed the data using the age-stage, two-sex life table.

Materials and Methods

Ladybird Cultures. Adult *C. sexmaculata* were collected from Wuhan Botanic Garden, Chinese Academy of Sciences (Wuhan city, Hubei province, China) during July–August, 2011. In total, 260 adults (107 females and 153 males) were transported to the laboratory at Natural Enemy Research, Institute of Plant and Environment Protection, Beijing Academy of Agriculture and Forestry Sciences (Beijing, China) and reared using the aphid *M. persicae* as prey. The aphids were maintained on cultured eggplant seedlings in the laboratory under the same environmental conditions as *C. sexmaculata*. The ladybirds were reared in custom-made culture cages (45.0 by 50.0 by 50.0 cm^3, with aluminum alloy frames and 100-mesh plastic gauze) at a density of 80–100 adults or 130–150 larvae per cage. The culture environment was regulated using an automatic environmental management system (Sunauto, Beijing, China) at 25 ± 1°C, 70% relative humidity (RH), a photoperiod of 16:8 (L:D) h, and illumination intensity 1,200 Lux.

Laboratory Life Table Study. Pairs of *C. sexmaculata* adults were taken from the experimental population and cultured with the aphid *M. persicae* in plastic cups (8 cm in diameter and 12 cm height) covered with fine nylon net (45 mesh) for ventilation. Before starting the life table study, the cups were maintained at the same environmental conditions as the experimental population. Newly laid eggs were collected from 20 pairs of adult ladybirds (one pair per cup) within 24 h after mating. Ninety-eight eggs were collected and maintained at 25 ± 1°C, 70% RH, a photoperiod of 16:8 (L:D) h, and illumination intensity 1,200 Lux. Hatched first-instar larvae were moved to a new cup for individual rearing and supplied with aphids as above. The development and survival of each larva were recorded daily. When the adults emerged, a single female and male were paired in a new rearing cup. A sufficient number of aphids were provided to each pair daily. The fecundity (i.e., number of eggs produced) and the survival of each adult were recorded daily until death.

Greenhouse Caged Life Table Study. *C. sexmaculata* adults were released to control *M. persicae* on eggplants in the greenhouse. A total of 205 eggs laid within a 24-h period were collected from the eggplant leaves. Newly hatched first-instar larvae were transferred to the leaves, aphids were supplied, and the cages (10.0 by 6.0 by 25.0 cm^3) were enclosed with mesh (200 mesh) for individual rearing. The development and survival of the larvae were recorded daily. After emergence of the adults, males and females were paired and checked daily to record their survival and the number of eggs laid until the deaths of all individuals. The greenhouse caged life table study was conducted in June–August of 2013 in the Beijing Noah organic vegetable farm (40° 6' N, 116° 59' E), where the average temperature in the greenhouse was 24.1, 30.2, and 32.3°C, and the average relative humidity was 76, 75, and 81%, in each month respectively.

Life Table Analysis. The development time, survivorship, longevity of individuals, and female daily fecundity of *C. sexmaculata* were analyzed according to the age-stage, two-sex life table (Chi and Liu 1985, Chi 1988) using the computer program

TWOSEX-MSChart (Laboratory of Theoretical and Applied Ecology, Department of Entomology, National Chung Hsing University, Taiwan; Chi 2013). 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), the age-stage life expectancy (e_{xj}), the reproductive value (v_{xj}), the preoviposition period of female adults (APOP), the total preoviposition period of females from birth (TPOP), and the key population parameters (r, the intrinsic rate of increase; λ, the finite rate of increase; R_0, the net reproductive rate; T, the mean generation time) were calculated accordingly.

In this paper, the age-specific survival rate includes both males and females, and was calculated according to Chi and Liu (1985) as $l_x = \sum_{j=1}^{\beta} s_{xj}$ and $m_x = \frac{\sum_{j=1}^{\beta} s_{xj} f_{xj}}{\sum_{j=1}^{\beta} s_{xj}}$, where β is the number of stages. The intrinsic rate of increase was estimated using the iterative bisection method and the Euler–Lotka equation with the age indexed from 0: $\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1$. The life expectancy ($e_{xy} = \sum_{i=x}^{n} \sum_{j=y}^{\beta} s'_{ij}$) was calculated according to Chi and Su (2006). The mean generation time was 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 was calculated as $T = \frac{\ln R_0}{r}$, where $R_0 = \sum_{x=0}^{\infty} lxmx$. The finite rate was calculated as $\lambda = e^r$.

Table 1. Development time (d) of different stages, adult longevity, fecundity, preovipositional period, and total preovipositional period of *C. sexmaculata* under the laboratory and greenhouse conditions

Life history traits	Stage	Laboratory		Greenhouse		df	*F*	*P*
		n	Mean ± SE	*n*	Mean ± SE			
Developmental time (d)	Egg	98	2.5 ± 0.1	205	3.6 ± 0.1	301	0.310	<0.01
	L1	85	2.0 ± 0.1	149	3.2 ± 0.1	301	3.447	<0.01
	L2	78	1.9 ± 0.1	127	2.5 ± 0.1	232	11.103	<0.01
	L3	73	2.1 ± 0.1	108	3.0 ± 0.1	200	43.136	<0.01
	L4	69	2.8 ± 0.1	77	3.9 ± 0.1	179	15.099	<0.01
	Pupa	64	3.2 ± 0.1	70	4.6 ± 0.1	144	5.260	<0.01
	Preadult	64	14.2 ± 0.2	70	20.9 ± 0.3	132	14.571	<0.01
Adult longevity (d)	Female	29	35.4 ± 1.3	34	30.0 ± 1.4	61	0.882	<0.01
	Male	35	39.0 ± 1.7	36	28.2 ± 1.9	69	0.359	<0.01
Fecundity (F) (eggs/female)	Female	29	650 ± 39	34	318 ± 24	61	1.573	<0.01
Preoviposition period (APOP; d)	Female	29	8.8 ± 0.3	34	9.7 ± 0.4	61	9.729	>0.05
Total preoviposition period (TPOP; d)	Female	29	23.5 ± 0.4	34	30.1 ± 0.6	61	4.532	>0.05

The significant differences in life history traits in *C. sexmaculata* between the laboratory and greenhouse conditions were compared with *t*-tests at a 5% significance level using SPSS 17.0.

Statistical Analysis. The TWOSEX-MSChart computer program was used to estimate parameters (Chi 2013) and the bootstrap technique (Efron and Tibshirani 1993) was used to estimate the mean, variance, and standard error of the population parameters. Because bootstrapping uses random resampling, a small number of replications will generate variable means and standard errors. To generate less variable results, we used 10,000 replications in this study. Differences in life history traits in *C. sexmaculata* between the laboratory and greenhouse conditions were compared using *t*-tests at the 5% significance level using SPSS 17.0. Differences in population parameters between the laboratory and greenhouse conditions were compared using *t*-tests and the TWOSEX-MSChart computer program.

Results

Age-Stage, Two-Sex Life Table. Results are hereafter stated respectively for laboratory and greenhouse conditions. Of 98 and 205 eggs initially collected for the life table study, 85 and 149 eggs hatched successfully, of which 64 and 70 emerged as adults. The preadult survival rate was 65.3 and 34.1%. The mean developmental period for each stage, adult longevity, female fecundity, adult preovipositional period, and total preovipositional period of *C. sexmaculata* are given in Table 1. The developmental time for all preadult stages was 14.2 and 20.9 d, a notably longer developmental period under greenhouse conditions. Adult *C. sexmaculata* females and males in the laboratory lived an average of 35.4 and 39.0 d, which was significantly longer than adult longevity under greenhouse conditions (30.0 and 28.2 d, respectively). The adult preoviposition period (APOP, the time between adult emergence and first oviposition ignoring the duration of the preadult stages) was 8.8 and 9.7 d. If the preoviposition period is counted as the time from birth to first reproduction in females, TPOP (the total preoviposition period) was 23.5 and 30.1 d. However, the fecundity under laboratory conditions (650 eggs) was significantly higher than that in the greenhouse (318 eggs).

The age-stage-specific survival rate (s_{xj}) is the probability that a newborn egg will survive to age x and stage j (Fig. 1). A significant reduction in the survival of stage L2 to adult under greenhouse conditions can also be observed in the curves of s_{xj} (Fig. 1).

The age-specific survival rate (l_x) (A), and female age-stage-specific fecundity (f_x) and age-specific fecundity of the total population (m_x) (B), of *C. sexmaculata* under laboratory and greenhouse conditions are illustrated in Figure 2. The curve of l_x is a simplified version of s_{xj}. The curves of l_x, f_x, and m_x of *C. sexmaculata* generated under greenhouse conditions were lower than those found under laboratory conditions. Our results show that *C. sexmaculata* had lower survival and reproduction in the greenhouse. Under laboratory conditions, the maximum female age-stage-specific fecundity (f_x) was 38.5 eggs at 28 d, whereas the female age-stage-specific fecundity (f_x) was 21.2 eggs at 35 d under greenhouse conditions.

The life expectancy (e_{xy}) of *C. sexmaculata* under laboratory and greenhouse conditions is plotted in Figure 3. The values (e_{xy}) indicate the times that individuals of age x and stage y are expected to live after age x. For example, under laboratory conditions, the life expectancy of a newborn egg is 37.8 d, whereas adult females and males of age 18 d are expected to live 32.1 and 37.7 d more. However, under greenhouse conditions, the life expectancy of a newborn egg is 23.7 d, whereas adult females and males of age 18 d are expected to live 32.6 and 26.9 d more.

The contribution of an individual of age x and stage j to the future population is described by the age-stage reproductive value (v_{xj}; Fig. 4). A newborn egg under laboratory and greenhouse conditions had a reproductive value of 1.1821 and 1.1086, respectively, which was very close to the finite rate of increase (Table 2). Females near the peak of reproduction contributed considerably more to the population than those at other ages and stages. Under laboratory conditions, a 26-d-old female had a markedly higher reproductive value, 196.1, whereas a 35-d-old female under greenhouse conditions had the highest reproductive value of 128.7. The reproductive value of *C. sexmaculata* under greenhouse conditions was lower and more varied than that in the laboratory.

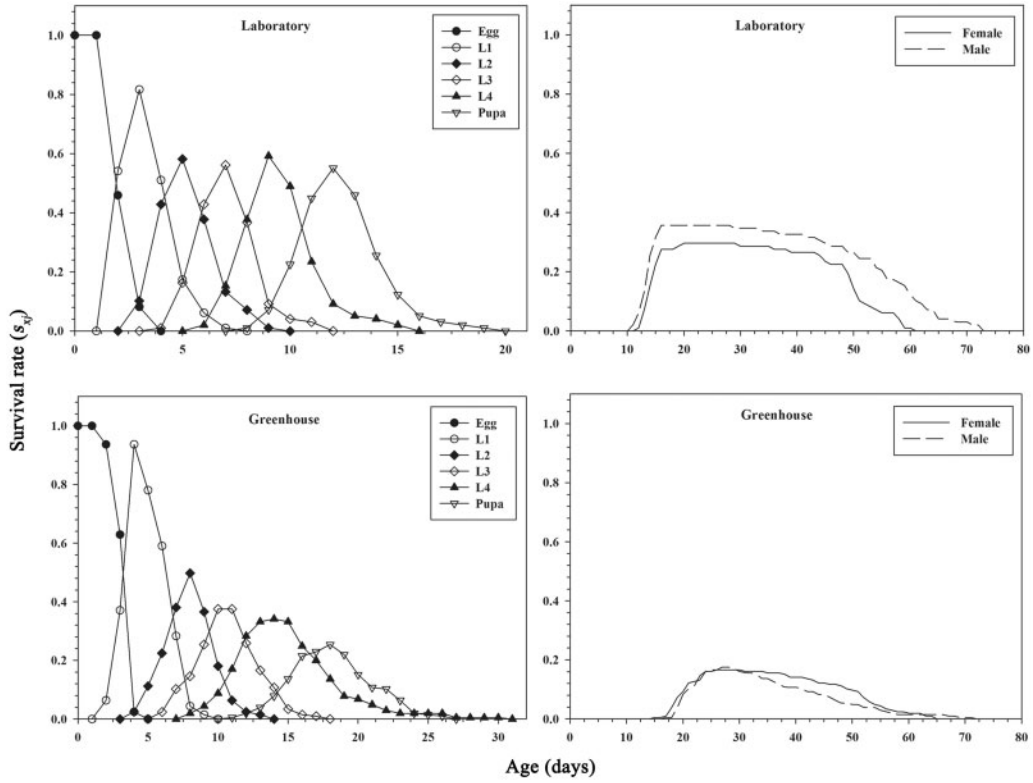

Fig. 1. Age-stage-specific survival rate (s_{xj}) of *C. sexmaculata* under laboratory and greenhouse conditions.

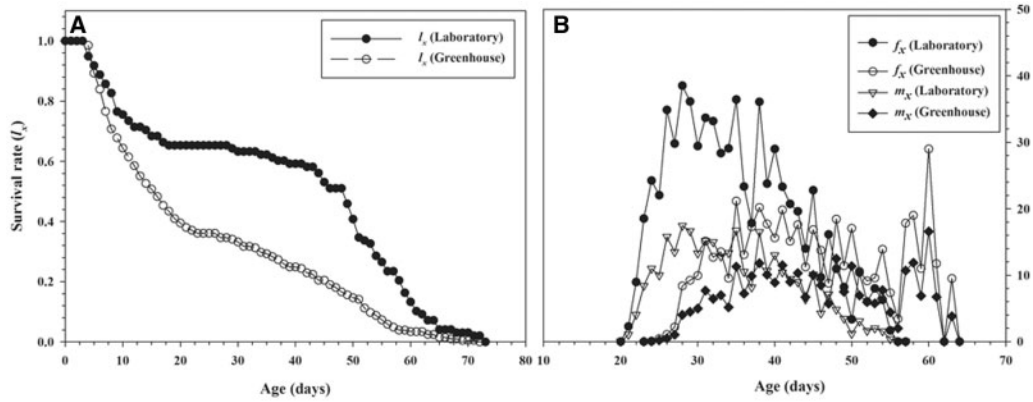

Fig. 2. Age-specific survival rate (l_x) (A), female age-stage-specific fecundity (f_x) and age-specific fecundity (m_x) (B) of *C. sexmaculata* under laboratory and greenhouse conditions.

Population Parameters. The mean and standard errors of the population parameters as estimated by the bootstrap technique (Efron and Tibshirani 1993) are listed in Table 2. The intrinsic rates of increase (r) were $0.1668\,d^{-1}$ and $0.1027\,d^{-1}$, the net reproductive rates (R_0) were 192.1 and 53.0 offspring, the finite rates of increase (λ) were $1.1815\,d^{-1}$ and $1.1082\,d^{-1}$, and the mean generation times (T) were 31.4 d and 38.5 d. The population parameters obtained in the laboratory were higher than those in the greenhouse, except for the mean generation time. Statistical analysis showed that there was a significant difference between r, R_0, λ, and T in the laboratory and the greenhouse (Table 2).

Discussion

Life Table of *C. sexmaculata*. Insects regularly experience the fluctuating thermal regimes that are typical of natural habitats. However, controlled laboratory studies can provide basic, valuable insights into the

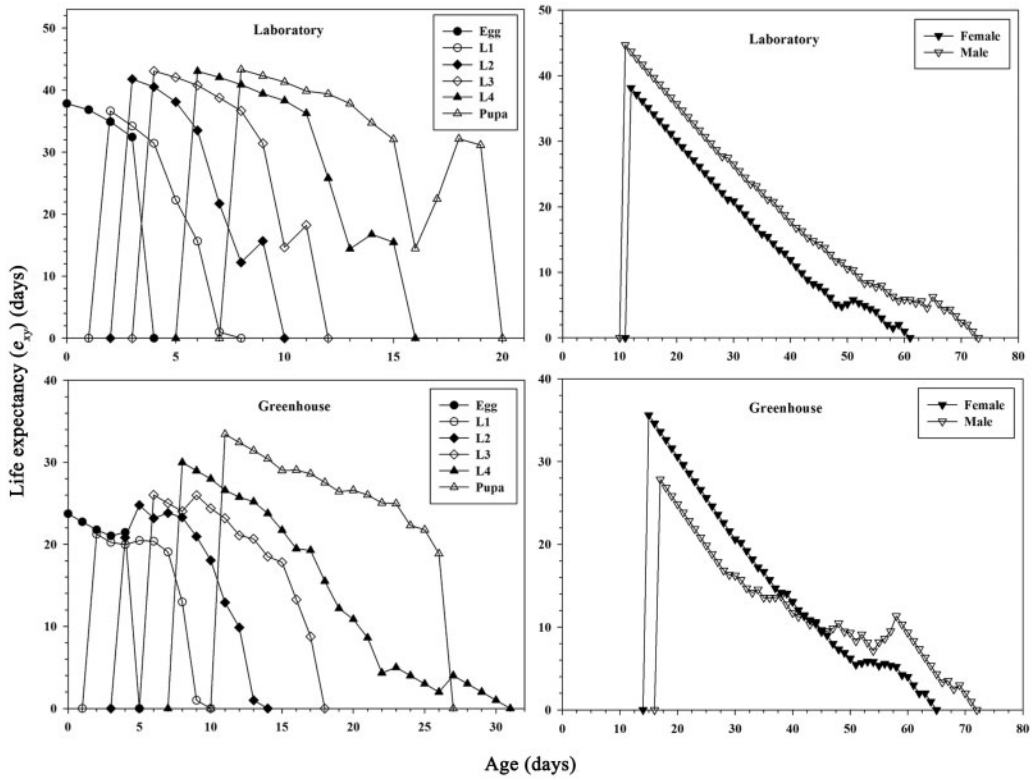

Fig. 3. Life expectancy (e_{xy}) of *C. sexmaculata* under laboratory and greenhouse conditions.

population dynamics of a species. In this study, the results accurately describe the survival, development, and reproductive trends in population development of *C. sexmaculata* shown in an age-stage, two-sex life table under laboratory and greenhouse conditions. The ladybirds under laboratory conditions developed more quickly in the preadult stage and were longer-lived, with higher fecundity, compared with those in the greenhouse. Moreover, significant reductions in survival and reproduction of *C. sexmaculata* under greenhouse conditions can be observed in the curves of s_{xj} (Fig. 1), f_x and m_x (Fig. 2). Several causative factors may be responsible for the differences in the life tables seen under laboratory and greenhouse conditions. We observed variable characteristics of *C. sexmaculata* within the greenhouse, where fluctuating temperature, higher humidity, photoperiod and light intensity, and variable quality of food (host plants and prey species) resulted in slower developmental rate, shorter longevity, and lower reproduction.

Overlap between developmental stages can be observed (Fig. 1) because variable developmental rate among individuals was incorporated into the age-stage, two-sex life table. If the survival curves were constructed based only on the means of each immature stage or adult life span, the stage overlap would not have been observed and would have resulted in less informative survival and fecundity curves. Liu (2005) noted overlap in the stages of *Delphastus catalinae* (Horn) (Coleoptera: Coccinellidae), but the variable developmental rate and inferred age-specific fecundity schedules based on adult age were not taken into account in that study. Yu et al. (2005) and Chi and Su (2006) provided detailed explanations and a mathematical proof to address the errors in life tables based on adult age.

Population Parameters. In Chi and Liu's model (1985), population parameters are calculated using an entire cohort, including both sexes and incorporating variable developmental rates among individuals. Because of the problems associated with the female age-specific life table (Huang and Chi 2012), we used the age-stage, two-sex life table to calculate the population parameters of *C. sexmaculata*. The net reproductive rate (R_0), the finite rate of increase (λ), and the intrinsic rate of increase (r) of *C. sexmaculata* in the laboratory were significantly higher than the corresponding rates under greenhouse conditions. The population parameters are the derived parameters in a life table study. They are calculated based on the assumption that the environmental factors are constant and the population structure reaches a stable age-stage distribution as time approaches infinity. Southwood (1966) stated that the intrinsic rate of increase is the most useful life table parameter for comparing population growth potential under different treatments. A shorter preoviposition period is expected to result in a higher intrinsic rate of increase (r) if fecundity remains

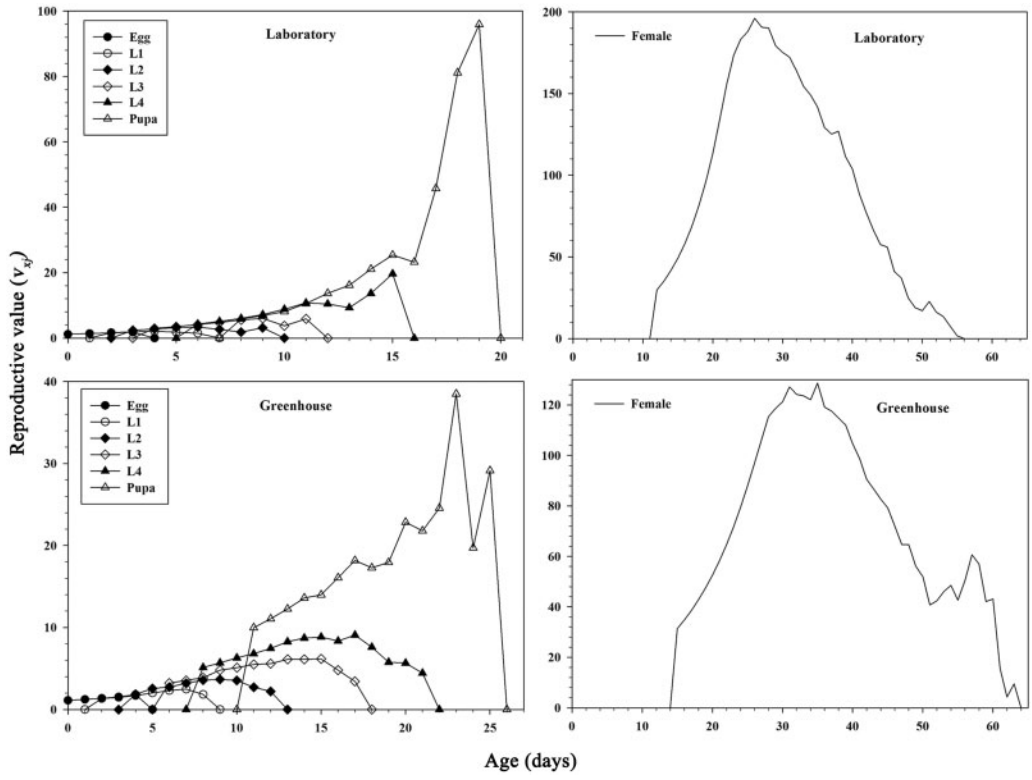

Fig. 4. Reproductive value (v_{xj}) of *C. sexmaculata* under laboratory and greenhouse conditions.

Table 2. Population parameters of *C. sexmaculata* in the laboratory and greenhouse

Population parameter	Estimated by using bootstrap method		df	*F*	*P*
	Laboratory	Greenhouse			
The intrinsic rate of increase r (d^{-1})	0.1668 ± 0.0062	0.1027 ± 0.0049	301	87.406	<0.001
The finite rate of increase λ (d^{-1})	1.1815 ± 0.0073	1.1082 ± 0.0054	301	50.433	<0.001
The net reproduction rate R_0 (offspring/individual)	192.1 ± 32.2	53.0 ± 9.2	301	41.616	<0.001
The mean generation time T (d)	31.4 ± 0.4	38.5 ± 0.7	301	99.729	<0.001

The TWOSEX-MSChart computer program was used to estimate parameters and the bootstrap technique was used to estimate the mean, variance, and standard error of the population parameters. The significant differences of population parameters between the laboratory and greenhouse conditions were compared with *t*-tests using the TWOSEX-MSChart computer program.

constant (Lewontin 1965). In this study, the TPOP of *C. sexmaculata* in the laboratory was shorter than that under greenhouse conditions.

At 25°C, the age-stage life expectancy gradually decreases with age since conditions in the laboratory are favorable. Under the variable environmental conditions of the greenhouse, the life expectancies were significantly shorter. Life expectancy is calculated using the age-stage-specific survival rate (s_{xj}) without assuming that the population reaches a stable age-stage distribution. Thus, it can be used to predict the survival of a population under those conditions. 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. Chi and Su (2006) discussed in detail on the differences between the traditional female age-specific life table and the age-stage, two-sex life table, and identified possible errors in the survival and fecundity curves based on adult age.

Fisher (1930) defined reproductive value as the contribution of an individual to the future population. The reproductive value significantly increases at the time of adult female emergence. In this study, the peak reproductive value of *C. sexmaculata* in the laboratory and greenhouse conditions occurred at 26 and 35 d of age, respectively (Fig. 4). When the females begin to reproduce, the reproductive value also increases.

Application of Life Table Data for Biological Control. In a life table study, the basic data, including survival rate, developmental rate, and fecundity, describe the life history and stage differentiation. These data can be used in population projections to predict growth trends, as well as the stage structure of a population in the short- or long-term future (Farhadi et al.

2011). The results revealed significant differences between the life tables of *C. sexmaculata* under laboratory and greenhouse conditions, differences in population characteristics that can be helpful in developing a successful mass rearing program of *C. sexmaculata* for biological control. Moreover, in comparing the efficiency of a predator, we have to consider not only the predator's population growth rate but also its predation rate which will produce an estimate of the control efficiency of the whole population. Chi and Yang (2003) applied the age-stage, two-sex life table to the predator *Propylaea japonica* and demonstrated that it can properly include the variable predation rate of different predator stages. The same life table for studying the predation rate was also used in studies of *Lemnia biplagiata* fed on *Aphisgossypii* (Yu et al. 2005), *Hippodamia variegate* fed on *Aphis fabae* (Farhadi et al. 2011) under laboratory conditions, and *Harmonia dimidiata* fed on *Aphis gossypii* at different temperatures (Yu et al. 2013b). In addition, this method was used in the study of the parasitoid wasp, *Aphidius gifuensis* (Chi and Su 2006). These studies showed the advantages of incorporating a predation study into the age-stage, two-sex life table. Further studies on the predation capacity of *C. sexmaculata* based on the age-stage two-sex life table would certainly be worthwhile.

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References Cited

Abdel-Salam, A. H., and N. F. Abdel-Baky. 2001. Life table and biological studies of *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) reared on the grain moth eggs of *Sitotroga cerealella* Olivier (Lep., Gelechiidae). J. Appl. Entomol.125: 455–462.

Agarwala, B. K., P. Bardhanroy, H. Yasuda, and T. Takizawa. 2001. Prey consumption and oviposition of the aphidophagous predator *menochilus sexmaculatus* (Coleoptera: Coccinellidae) in relation to prey density and adult size. Environ. Entomol. 30: 1182–1187.

Agarwala, B., and H. Yasuda. 2000. Competitive ability of ladybird predators of aphids: A reviewof *Cheilomenes sexmaculata* (Fabr.) (Coleoptera: Coccinellidae) with a worldwide checklist of preys. J. Aphidol. 14: 1–20.

Birch, L. C. 1948. The intrinsic rate of natural increase in an insect population. J. Anim. Ecol. 17: 15–26.

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

Chi, H. 2013. TWOSEX-MSChart: Computer program for age stage, two-sex life table analysis. Retrieved from: <http://140.120.197.173/ecology/>.

Chi, H., and H. Liu. 1985. Two new methods for the study of insect population ecology. Bull. Inst. Zool. Acad. Sin. 24: 225–240.

Chi, H., and H. Y. Su. 2006. Age-stage, two-sex life tables of *Aphidius gifuensis* (Ashmead) (Hymenoptera: Braconidae) and its host *Myzus persicae* (Sulzer) (Homoptera: Aphididae) with mathematical proof of the relationship between female fecundity and the net reproductive rate. Environ. Entomol. 35: 10–21.

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

Efron, B., and R. J. Tibshirani. 1993. An introduction to the bootstrap. Chapman and Hall, New York, NY.

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

Fisher, R. A. 1930. The genetical theory of natural selection. Clarendon Press, Oxford, United Kingdom.

Gautam, R. D. 1989. Influence of different hosts on the adults of *Menochilus sexmaculatus* (Fab). J. Biol. Control 3: 90–92.

Huang, Y. B., and H. Chi. 2012. Age-stage, two-sex life tables of *Bactrocera cucurbitae* (Coquillett) (Diptera: Tephritidae) with a discussion on the problem of applyingfemale age-specific life tables to insect populations. J. Insect Sci. 19: 263–273.

Lanzoni, A., G. Accinelli, G. G. Bazzocchi, and G. Burgio. 2004. Biological traits and life table of the exotic *Harmonia axyridis* compared with *Hippodamia variegata*, and *Adalia bipunctata* (Coleoptera: Coccinellidae). J. Appl. Entomol. 128: 298–306.

Lewontin, R. C. 1965. Selection for colonizing ability (pp. 77–94). *In* H. G. Baker and G. L. Stebbins (eds.), The genetic of colonizing species. Academic Press, San Diego, CA.

Liu, T. X. 2005. Life history and life table analysis of the whitefly predator *Delphastus catalinae* (Coleoptera: Coccinellidae) on collards. Insect Sci. 12: 129-135.

Omkar, O., and R. B. Bind. 2004. Prey quality dependent growth, development and reproduction of a biocontrol agent, *Cheilomenes sexmaculata* (Fabricius) (Coleoptera: Coccinellidae). Biocontrol Sci. Technol. 14: 665–673.

Rai, M. K., V. V. Ramamurthy, and P. K. Singh. 2003. Observations on the biology of the coccinellid predator, *Cheilomenes sexmaculata* (Fab) on *Aphis craccivora*. Ann. Plant Prot. Sci. 11: 7–10.

Russo, A., G. E. Cocuzza, and M. C. Vasta. 2004. Life tables of *Xylocoris flavipes* (Hemiptera: Anthocoridae) feeding on *Tribolium castaneum* (Coleoptera: Tenebrionidae). J. Stored Prod. Res. 40: 103–112.

Southwood, T. R. E. 1966. Ecological methods with particular reference to the study of insect populations. Methuen, London.

Sugiura, K., and H. Takada. 1998. Suitability of seven aphid species as prey of *Cheilomenes sexmaculata* (Fabricius) (Coleoptera: Coccinellidae). Jpn. J. Appl. Entomol. Zool. 42: 7–14.

Wang, S., X. L. Tan, X. J. Guo, and F. Zhang. 2013. Effect of temperature andphotoperiod on the development, reproduction, and predation of the predatory ladybird *Cheilomenessexmaculata* (Coleoptera: Coccinellidae). J. Econ. Entomol. 106: 1–9.

Yu, B. H., and H. Chi. 2012. Age-stage, two-sex life tables of *Bactrocera cucurbitae* (Coquillett) (Diptera: Tephritidae) with a discussion on the problem of applying female age-specific life tables to insect populations. Insect Sci. 19: 263–273.

Yu, J. Z., H. Chi, and B. H. Chen. 2005. Life table and predation of *Lemnia biplagiata* (Coleoptera: Coccinellidae) fed on *Aphis gossypii* (Homoptera: Aphididae) with a proof on relationship among gross reproduction rate, net reproduction rate and preadult survivorship. Ann. Entomol. Soci. Am. 98: 475–482.

Yu, J. Z., H. Chi, and B. H. Chen. 2013a. Comparison of the life tables and predation rates of *Harmonia dimidiate* (F.) (Coleoptera: Coccinellidae) fed on *Aphis gossypii* Glover (Hemiptera: Aphididae) at different temperatures. Biol. Control 64: 1–9.

Yu, L. Y., Z. Z. Chen, F. Q. Zheng, A. J. Shi, T. T. Guo, B. H. Yeh, H. Chi, and Y. Y. Xu. 2013b. Demographic analysis, a comparison of the Jackknife and Bootstrap methods, and predation projection: A case study of *Chrysopa pallens* (Neuroptera: Chrysopidae). J. Econ. Entomol. 106: 1–9.

Zanuncio, J. C., W. P. Lemos, M. C. Lacerda, T. V. Zanuncio, J. E. Serrao, and E. Bauce. 2006. Age-dependent fecundity and fertility life tables of the predator *Brontocoris tabidus* (Heteroptera: Pentatomidae) under field conditions. J. Econ. Entomol. 99: 401–407.

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