

Density-Dependent Demography and Mass-Rearing of *Carposina sasakii* (Lepidoptera: Carposinidae) Incorporating Life Table Variability

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Abstract

Carposina sasakii Matsumura is one of the most destructive fruit-boring pests of pome and stone fruit trees in eastern Asia. Because larvae complete their development inside a single fruit, larval density per fruit is a critical factor in their survival, development, and fecundity. The effect of larval density was examined to determine the ideal density for devising an economic and sustainable mass-rearing system for harvesting of *C. sasakii*. Mass production of insects of the same age of a specific stage is not only important in biological control, but also in pheromone extraction, culturing of entomopathogenic nematodes and fungi, etc. Life history data for six larval densities (1–5, 6–10, 11–15, 16–20, 21–30, and 31–40 larvae/apple) were collected at 25.5 ± 0.5°C, 75.0 ± 5.0% RH, and a photoperiod of 15:9 (L: D) h. Data were analyzed using the age-stage, two-sex life table. The results showed that the highest preadult survival rate (42.00%), fecundity (104.70 eggs), and population parameters (intrinsic rate of increase $r = 0.0718 \text{ d}^{-1}$, net reproductive rate $R_0 = 23.03$ eggs, and finite rate of increase $\lambda = 1.0744 \text{ d}^{-1}$) were observed at a density of 1–5 larvae/apple. However, when the rearing costs and production rate were considered, the density of 16–20 larvae/apple was the most economical for mass-rearing *C. sasakii* in order to achieve a daily harvest rate of 1,000 pupae (from 273 apples per day). To ensure the sustainability of the mass-rearing system, we included the life table variability in the harvesting strategy.

Key words: peach fruit moth, rearing technique, larval density, age-stage two-sex life table, sustainable harvesting

The peach fruit moth, *Carposina sasakii* Matsumura, is one of the most destructive fruit-boring pests of pome and stone fruit trees, including apple, pear, jujube, peach, apricot, hawthorn, etc. (Pei and Yuan 1996, Kim et al. 2001, Gong 2012, Wu and Huang 2014). The distribution of *C. sasakii* was originally restricted to eastern Asia, but with the development of international agricultural trade, the moth has now been introduced into the United States, Uruguay, and Australia (Liu et al. 1997, Han et al. 2000, Wang et al. 2014). The species is listed as a quarantine pest in the United States, Chile, Canada, South Africa, and Russia (Liu et al. 2010). In China, the larvae feed inside the fruits of jujube and apple. This has become especially commonplace in the Northern Taihang Mountain region of China where these fruits are plentiful. In some instances, the

infestation rate has exceeded 91% and resulted in heavy economic loss (Zhang et al. 2017), and the infestation rate can even reach 100% in poorly managed apple orchards (Hua et al. 1996). For many years, growers have mainly relied on broad-spectrum chemical insecticides to control *C. sasakii* (Quan et al. 2016).

With the improvement of living standards in China, fruit consumption has increased in recent years (Huang et al. 2017). As a result, the acreage of fruit orchards has increased substantially (Deng et al. 2018). Dwarfing and high-density planting patterns have been applied in apple and jujube orchards in northern China to increase production per acre, where many growers have become more attentive to orchard and pest management (Liu et al. 2015, Ding et al. 2017). The distribution and occurrence of fruit tree pests, including *C. sasakii*, have

increased accordingly with the increase in growing acreage. The rapid expansion of fruit tree planting has resulted in a striking increase in the amount of damage caused by *C. sasakii* and has drawn the attention of researchers (Li et al. 2012, Quan et al. 2017).

Although a few insecticides are known to be effective against this pest (so far), there will always be a need to screen new pesticides due to the phenomenon of pesticide resistance. Although the pheromones of this pest have been studied and tested in the field (Xue et al. 2010, Zhang et al. 2017), more studies are still needed in this area. It is critical to collect life table data because they contain data that are critical to thoroughly understanding the population ecology of a pest. In addition, when life table data are incorporated into the construction of a mass-rearing system, it greatly increases the effectiveness and efficiency of the mass-rearing system and supplements previous research that has been done on the species. Traditional female age-specific life tables (sensu Lewis 1942, Leslie 1945, Birch 1948, Carey 1993) are, however, incapable of offering accurate pest information, because they ignore the entire male population and are not designed to describe stage differentiation (Huang and Chi 2012a, b). In contrast, age-stage, two-sex life tables take both sexes and stage differentiation into account and have, therefore, been widely used in insect life table studies during the past two decades (Zhou et al. 2010, Bong et al. 2012, Núñez-Campero et al. 2014, Saadat et al. 2016, Ajvad et al. 2018).

Mass production of insects of the same age of a specific stage is not only important in biological control, but also necessary in pheromone extraction, culturing of entomopathogenic nematodes and fungi, toxicological studies, etc. Excess production often leads to wastage in the need to reduce the colony size, whereas at other times the size of the colony may be insufficient. Proper design of a rearing and harvesting system can avoid wasting money, labor, and time. To maximize rearing efficiency and minimize costs, Chi and Getz (1988) used the age-stage, two-sex life tables to devise an efficient and cost-effective mass-rearing system for the potato tuberworm. Therefore, life tables are not only important tools for population ecology and pest management, but they are also necessary tools for mass-rearing and harvesting insects for biological control, toxicity research, and pheromone extraction (Chi and Getz 1988).

Density is an important factor affecting the survival, development, and fecundity of insects (Varley and Gradwell 1970, Hassell 1975, Stiling 1988). However, different density scales have been used in research according to a particular insect's ecology and different rearing methods. Underwood (2010) studied the density-dependent growth of *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae) in individual tomato plants. Kong et al. (2011) studied the effect of larval density of *Loxostege sticticalis* L. (Lepidoptera: Pyralidae) in 650-ml glass jars. Wu et al. (2011) studied the density effect of *Bactrocera tau* (Walker) (Diptera: Tephritidae) on single 30-g pieces of fruit. Zhang and Wang (2015) used intact apples to study the larval density effect on the development and survival of *C. sasakii*. Due to the limited resources inherent in a single fruit, larval density is a critical factor to the survival and development of the larvae, and consequently the fecundity of the emerged adults in a variety of pest species (Sato and Yaginuma 1989). Therefore, studies on the effect of larval density on the survival, development, and fecundity and its consequence on the life table and population growth rate are important to understanding the population ecology and mass-rearing of *C. sasakii*. In this study, we collected life table data for *C. sasakii* with different initial densities of larvae per apple and analyzed the results by using an age-stage, two-sex life table to take the stage differentiation and both sexes into consideration (Chi and Liu 1985, Chi 1988). We then used the life table data to analyze the mass-rearing and harvesting system of *C. sasakii*. In addition, to

ensure the sustainability of the rearing system, we devised a means for including the life table uncertainty in calculating the harvest rate.

Materials and Methods

Insects

The colony of *C. sasakii* was established from infested apples collected from an apple orchard in Taigu County, Shanxi Province, China in the fall of 2012. Since then the colony has been maintained for over 20 generations in the Forest Conservation Laboratory, College of Forestry, Shanxi Agricultural University. Larvae of *C. sasakii* were reared on apples (*Malus pumila* Mill. 'Fuji') at $25.5 \pm 0.5^\circ\text{C}$, $75.0 \pm 5.0\%$ RH, and a photoperiod of 15:9 (L: D) h in an incubator (SPX-250B-G, Shanghai BoXun, China). After mature fifth-instar larvae emerged from infested apples, they were placed in a plastic box (18 cm in diameter and 10 cm in height) for pupation. The plastic box was filled with 350 g autoclaved sand, moistened with 45 g of double-distilled H₂O (dd H₂O) to maintain humidity. Individual pairs of newly emerged females and males were paired in a cylindrical glass container (40 cm in diameter and 50 cm in height) covered with gauze and supplied with a cotton-wool pad soaked with 10.0% honey water as adult food. The bottom of the cage was lined with a sheet of filter paper for egg deposition. Apples of similar size (70.0–80.0 mm in diameter) and weight (170.0–220.0 g) were used for *C. sasakii* rearing.

Life Table Study

Eggs laid on the filter paper within a 24-h period were collected for the life table study. Filter papers with eggs were cut into small triangular pieces and placed in a container (18 cm in diameter and 10 cm in height). A layer of cotton (5.5 g) humidified with 19.5-ml dd H₂O was placed at the bottom and covered with filter paper. Eggs were kept in the incubation chamber for 6 d until reaching the blackhead stage (Wang et al. 2010); at which time, the filter papers with eggs were removed and placed on the calyx of an apple (Chang et al. 1977). Five initial densities of eggs (5, 10, 20, 30, and 40 eggs per apple) were used for the life table study. Because all larval stages (first to fifth instars) feed entirely inside the apples, we grouped them into a single larval stage. Ten apples were used for each density. Egg hatching was examined at 18:00 every day, and all unhatched eggs were counted as egg mortality. After larvae bored into the apples, the fruit was checked daily for the emergence of mature fifth-instar larvae. When no larvae had emerged from the apples for five consecutive days, the apples were dissected to confirm the death of any larvae remaining inside the fruit (Zhang et al. 2014). Emerged mature larvae were placed individually inside a plastic container (11 cm in diameter and 5 cm in height, containing 150-g autoclaved sand and 19.5 ml of dd H₂O to maintain humidity) for pupation. We considered cocooning as pupating because *C. sasakii* develop into an encased pupa. Egg hatching, mature larva emergence, pupation, and adult emergence dates were recorded. Because we could not determine the egg and larval stage durations for each individual, it was impossible to match the egg hatching data with the fifth-instar emergence data. We could, however, determine the egg-larva period of each individual based on their larval emergence date. Using the procedure described by Chang et al. (1964), newly emerged adult moths were paired using a sex ratio of 1:2 (female: male) in a plastic container (10 cm in diameter and 18 cm in height). Because the number of males from the experimental adults was often insufficient for pairing, young male adults were recruited from the mass-rearing colony when necessary; these males, however, were excluded from the life table analysis. According to Li et al. (2010), effective mating is determined by the shape of the copulatory pouch and the existence of a spermatophore

within it under a Zeiss Stemi 2000 stereomicroscope. A cotton-wool pad soaked with 10.0% honey water was supplied as adult food. The number of eggs deposited by each female was recorded daily at 18:00, and the filter paper liner was replaced until female died.

Data Analysis

The raw life table data of all individuals were analyzed using the computer program TWOSEX-MSChart (Chi 2018) based on the age-stage, two-sex life table theory (Chi and Liu 1985, Chi 1988). The bootstrap technique (Efron and Tibshirani 1993, Huang and Chi 2012a, Polat-Akköprü et al. 2015) was used to estimate the variance and standard error of the population parameters with 100,000 bootstraps. Because the number of larvae that tunneled into an apple was the actual density, we grouped the data into six larval densities: 1–5, 6–10, 11–15, 16–20, 21–30, and 31–40 larvae/apple. The paired bootstrap method was used to analyze the differences between each of the six larval densities. The age-stage-specific survival rate (s_{xj} , where x = age and j = stage), age-specific survival rate (l_x), age-stage specific fecundity (f_{xj}), and age-specific fecundity (m_x) were calculated using the following equations:

$$s_{xj} = \frac{n_{xj}}{n_{01}}, \quad (1)$$

$$l_x = \sum_{j=1}^k s_{xj}, \quad (2)$$

$$f_{xj} = \frac{E_{xj}}{n_{xj}}, \quad (3)$$

$$m_x = \frac{\sum_{j=1}^k s_{xj} f_{xj}}{\sum_{j=1}^k s_{xj}}, \quad (4)$$

where n_{xj} is the number of individuals surviving to age x and stage j , n_{01} is the number of eggs used at the beginning of the life table study, k is the number of stages, and E_{xj} is the total number of eggs laid by surviving individuals at age x and stage j .

The net reproductive rate (R_0) was then calculated as follows:

$$R_0 = \sum_{x=0}^{\infty} l_x m_x. \quad (5)$$

The intrinsic rate of increase (r) and finite rate of increase (λ) were calculated as follows:

$$\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1, \quad (6)$$

$$\lambda = e^r, \quad (7)$$

with age indexed from zero (Goodman 1982). The mean generation time (T) was then calculated as follows:

$$T = \frac{\ln R_0}{r}. \quad (8)$$

The oviposition days (O_d) and eggs per oviposition day (E_d) were calculated based on daily fecundity of reproductive females, i.e., females actually producing eggs, according to Chen et al. (2018).

The life expectancy (e_{xj}) is the length of time that an individual of age x and stage j is expected to survive. It was calculated according to Chi and Su (2006) as follows:

$$e_{xj} = \sum_{i=x}^{\infty} \sum_{y=j}^k s'_{iy}, \quad (9)$$

where s'_{iy} is the probability that individuals of age x and stage j would survive to age i and stage y , calculated by assuming $s'_{xj} = 1$. The contribution of an individual of age x and stage j to the future population (v_{xj}) (Fisher 1993) was calculated according to Tuan et al. (2014a, b) as follows:

$$v_{xj} = \frac{e^{r(x+1)}}{s_{xj}} \sum_{i=x}^{\infty} e^{-r(i+1)} \sum_{y=j}^k s'_{iy} f_{iy}. \quad (10)$$

To construct a rearing system producing 1,000 *C. sasakii* pupae daily, we used the age-stage survival rate (s_{xj}) and fecundity (f_{xj}) to calculate the sustainable harvest rate h that maintains the net reproductive rate after harvest, i.e., $R_0(h) = 1$, according to Chi and Getz (1988):

$$R_0(h) = \sum_{x=0}^{\infty} \sum_{j=1}^k s_{xj} f_{xj} (1-h) = 1. \quad (11)$$

If $R_0 \leq 1$, no positive h can be obtained by using equation 11. This means that sustainable rearing systems are impossible under that rearing condition. If $2 > R_0 > 1$, sustainable mass rearing and harvesting are possible, but the harvestable portion is smaller than the population size in the rearing system. Therefore, to have a cost-effective rearing system, we need a rearing condition that results in $R_0 > 2$. Moreover, because equation 11 does not consider the variability of the survival rate, developmental rate, and fecundity, using the harvest rate h calculated from equation 11 may lead to insufficient harvesting or a collapse of the rearing system due to variations of population characteristics from one generation to another. To solve the problem, we used the following equations:

$$R_{0,0.1587}(h) = \sum_{x=0}^{\infty} \sum_{j=1}^k s_{xj} f_{xj} (1-h) = 1, \quad (12)$$

$$R_{0,0.025}(h) = \sum_{x=0}^{\infty} \sum_{j=1}^k s_{xj} f_{xj} (1-h) = 1, \quad (13)$$

where $R_{0,0.1587}$ and $R_{0,0.025}$ represent the 0.1587th and 0.025th percentile of R_0 . If the bootstrap results are normally distributed, $R_{0,0.1587}$ and $R_{0,0.025}$ are approximately $R_0 - SE(R_0)$ and $R_0 - 2 \times SE(R_0)$, respectively, where $SE(R_0)$ is the standard error of R_0 . According to Özgökçe et al. (2018), we sorted the 100,000 bootstrap R_0 values in ascending order to obtain the 0.025 and 0.1587 percentiles of R_0 . We then used equation 12 or 13 to calculate the conserved harvest rate. By using equations 12 and 13, the rearing system will produce a sustainable harvest, with a probability of system collapse being less than ca. 0.16 and 0.025, respectively. We then used the harvest rate (h) to calculate the number of daily new egg recruits (Y_d) necessary for a sustainable mass-rearing system capable of producing 1,000 pupae daily:

$$Y_e \times s_{EL} \times h = 1000. \quad (14)$$

where s_{EL} is the egg-larva survival rate. Finally, we used the method described by Chi and Getz (1988) to calculate the number of daily recruits to each stage (R_j), the total number of individuals in each stage (N_j), and the daily number of apples needed to maintain such a system.

Results

The age-stage specific survival rate (s_{xj}) provides a detailed description of not only the survival probability to age x and stage j of a

newly laid egg, but also the stage differentiation. Because s_{xj} takes the variation in developmental rates among individuals into account, we were able to depict stage overlap during the development of a population (Fig. 1). Increases in the variation in developmental rate among *C. sasakii* individuals are directly correlated with significant increases in stage overlapping. The egg-larva survival rate decreased significantly with increasing larval density (Fig. 1). The shortest egg-larval developmental periods (25.6 d) were observed at a density of 16–20 larvae/apple, whereas the longest egg-larva duration (30 d) was observed when density was 1–5 larvae/apple. There were no significant differences in pupal durations between the 11–15 and 16–20 larvae/apple treatments, whereas the pupal durations in other treatments were significantly longer than in these two treatments. The total preadult duration in the 1–5 larvae/apple treatment (41.3 d) was significantly longer than other treatments, whereas the shortest preadult duration (36.1 d) occurred in the 16–20 larvae/apple treatment (Table 1).

The egg-larva survival rate decreased significantly with increasing larval density (Fig. 1). The survival rate from egg-larva to pupa stage was the lowest (7.80%) at the highest density (31–40 larvae/apple) while the highest survival rate (48.67%) occurred at the lowest larval density (1–5 larvae/apple) (Table 1). In general, the overall preadult survival rate (s_a) decreased with increasing larval density, although there were no significant differences among the 6–10,

11–15, and 16–20 larvae/apple densities (Table 1). The proportion of emerged female adults in a cohort (N_f/N) was the highest (22.00%) at 1–5 larvae/apple, whereas the lowest (2.70%) was in the 31–40 larvae/apple density (Table 1). The longevity of female adults ranged from 4.5 to 5.1 d, whereas the males lived for 4.1–4.9 d.

When the survival rates of all stages are pooled together, the age-specific survival rate (l_x) corresponds to the probability that an egg will survive to age x (Fig. 2). The l_x curve declined earlier at higher densities. The age-specific fecundities of adult females (f_{x3} , adult female is the third life stage) are shown in Fig. 2. The maximum peak age-stage specific fecundity ($f_{xj} = 45.00$) occurred at the age of 52 d in the 11–15 larval density (Fig. 2). However, the age-specific net maternity ($l_x m_x = 3.74$) peak was at 41 d in the 1–5 larval density (Fig. 2). The highest female fecundity (F) occurred in the 1–5 larvae/apple density. Because all females in the 1–5 larvae/apple treatment produced offspring, the mean fecundity of reproductive females (F) is the same as F . In the 16–20, 21–30, and 31–40 larvae/apple densities, there were one, two, and one females, respectively, that did not lay eggs. Therefore, the F_r values in these treatments were slightly higher than F (Table 2).

No significant differences were observed in the *C. sasakii* adult preoviposition periods (APOP, the period between female adult emergence and first oviposition) among the different larval densities (Table 2). However, the total preoviposition period (TPOP, the

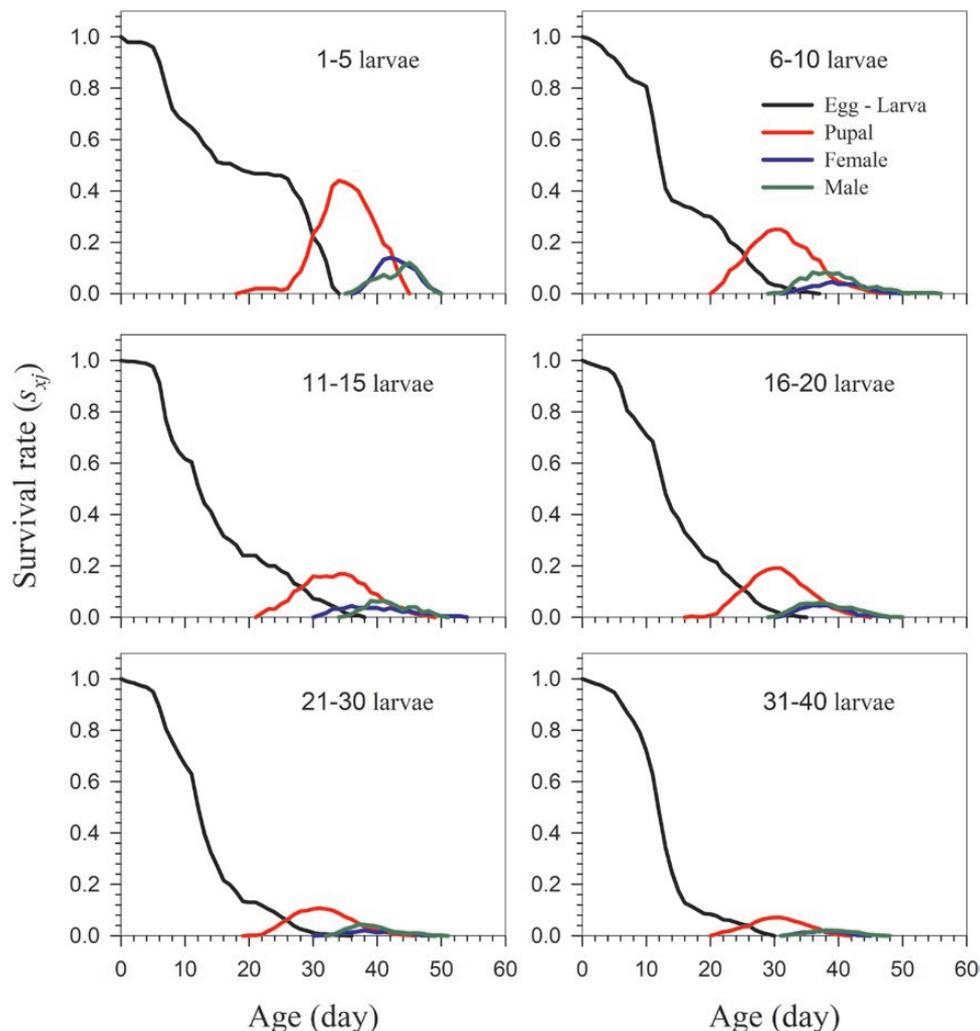
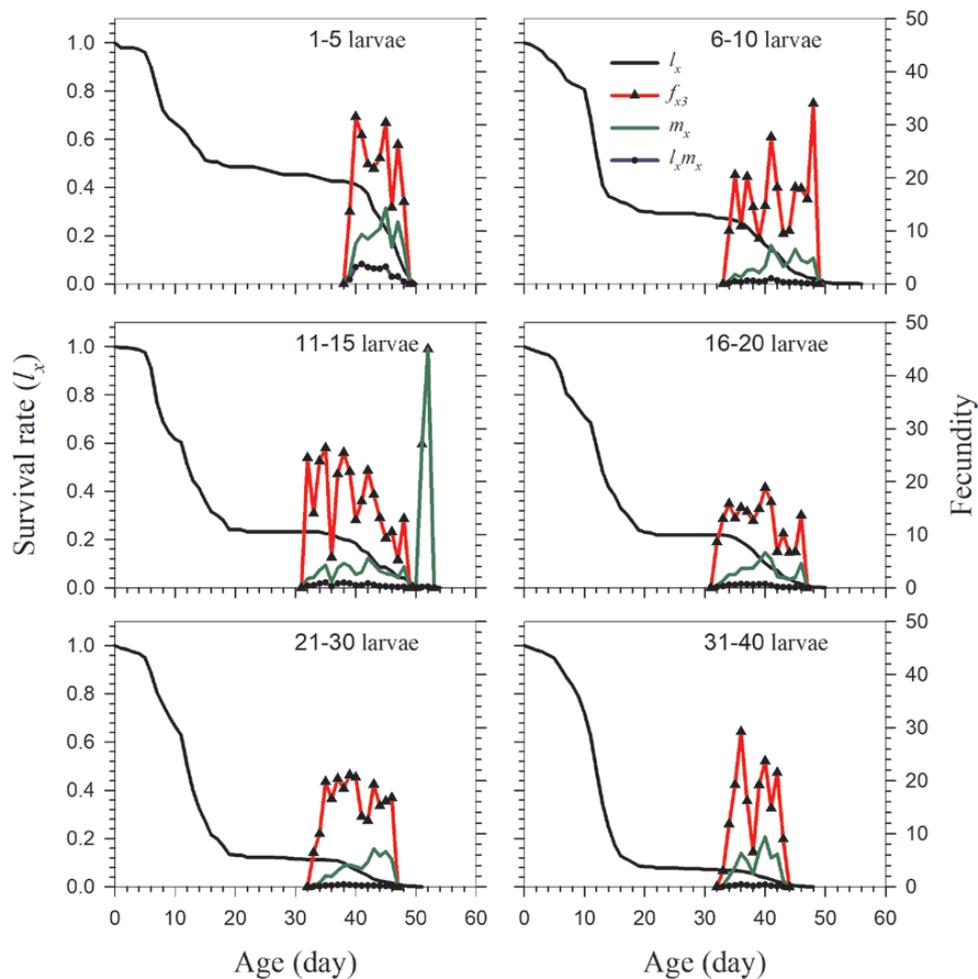


Fig. 1. The age-stage specific survival rate (s_{xj}) of *C. sasakii* at different larval densities per apple.

Table 1. Mean (\pm SE) of egg-larva duration (d), egg-larva mortality (%), pupal duration (d), pupation rate (%), pupal mortality (%), preadult survival rate (s_p), preadult duration (d), proportion of female adult N_f/N (%), and female and male adult longevity of *C. sasakii*

Parameter	Density (larvae/apple)					
	1–5	6–10	11–15	16–20	21–30	31–40
Egg-larva duration (d)	30.0 \pm 0.4a	26.2 \pm 0.4bc	29.0 \pm 0.7a	25.6 \pm 0.3c	26.6 \pm 0.3b	25.7 \pm 0.3bc
Egg-larva survival rate (%)	48.67 \pm 4.07a	29.33 \pm 2.63b	23.20 \pm 2.67bc	22.37 \pm 1.72cd	12.21 \pm 1.11e	7.80 \pm 0.85f
Pupal duration (d)	10.7 \pm 0.1bc	11.1 \pm 0.2a	10.1 \pm 0.1d	10.3 \pm 0.1d	10.9 \pm 0.1ab	10.6 \pm 0.1c
Pupal survival rate (%)	86.30 \pm 4.02c	88.4 \pm 3.38c	1.00 \pm 0.00a	97.73 \pm 1.31ab	90.48 \pm 2.86c	82.05 \pm 4.38c
Preadult survival s_p (%)	42.00 \pm 4.02a	26.00 \pm 2.53b	23.20 \pm 2.67b	21.86 \pm 1.70b	11.05 \pm 1.07c	6.40 \pm 0.78d
Preadult duration (d)	41.3 \pm 0.3a	37.4 \pm 0.5cd	39.1 \pm 0.6b	36.1 \pm 0.3e	37.5 \pm 0.3c	36.4 \pm 0.3de
N_f/N (%)	22.00 \pm 3.38a	8.00 \pm 1.56b	11.20 \pm 2.00b	8.98 \pm 1.17b	3.49 \pm 0.62c	2.70 \pm 0.51c
N_m/N (%)	22.00 \pm 3.38a	8.00 \pm 1.56b	11.20 \pm 2.00b	8.81 \pm 1.16b	3.36 \pm 0.60c	2.60 \pm 0.50c
Female adult longevity (d)	4.6 \pm 0.1cd	5.1 \pm 0.1a	4.6 \pm 0.2bcd	4.5 \pm 0.1d	5.0 \pm 0.2abc	5.1 \pm 0.2ab
Male adult longevity (d)	4.1 \pm 0.2c	4.9 \pm 0.1a	4.5 \pm 0.1bc	4.6 \pm 0.1b	4.5 \pm 0.1b	4.8 \pm 0.2ab
Mean longevity of all individuals (d)	26.1 \pm 1.5a	19.9 \pm 0.8b	18.6 \pm 0.9b	18.0 \pm 0.5b	15.1 \pm 0.4c	13.8 \pm 0.3d

Means followed by different letters in the same row are significantly different between treatments, determined by using the paired bootstrap test ($P < 0.05$). Standard errors were estimated by using 100,000 bootstraps.

**Fig. 2.** Age-specific survival rate (l_x), age-stage specific fecundity (f_{x3}), age-specific fecundity (m_x), and age-specific net fecundity ($l_x m_x$) of *C. sasakii* at different larval densities per apple.

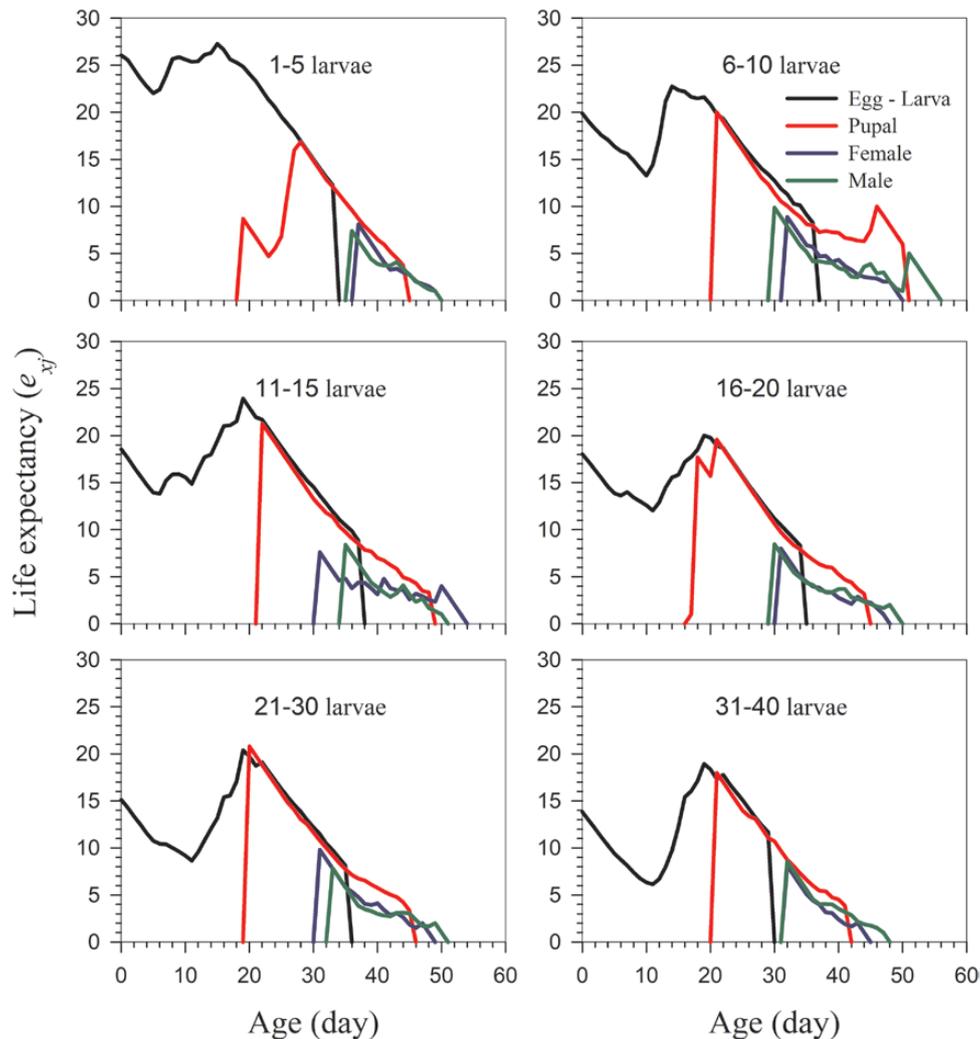
time interval between emergence from the egg and the beginning of oviposition) was significantly affected by the larval density per apple. The TPOP value in the 1–5 larvae/apple density was significantly longer than in other larval densities, whereas the TPOP value at the 31–40 larval density was significantly shorter than in

other larval densities (Table 2). The number of oviposition days (O_d) ranged from 1.9 d (16–20 larvae/apple) to 2.6 d (31–40 larvae/apple), and the daily oviposition rate per oviposition day (E_d) ranged from 31.95 eggs/d in the 6–10 larvae/apple density to 47.99 eggs/d in the 1–5 larvae/apple density (Table 2). There were

Table 2. Mean (\pm SE) of the APOP, TPOP, oviposition days (O_d), and female adult fecundity (F , offspring) of *C. sasakii* reared at different larval densities per apple

Parameter	Density (larvae/apple)					
	1–5	6–10	11–15	16–20	21–30	31–40
APOP (d)	1.4 \pm 0.1a	1.6 \pm 0.1a	1.5 \pm 0.1a	1.5 \pm 0.1a	1.5 \pm 0.1a	1.5 \pm 0.1a
TPOP (d)	42.4 \pm 0.4a	39.3 \pm 0.7b	39.3 \pm 1.0bc	37.5 \pm 0.5cd	38.5 \pm 0.6bc	36.9 \pm 0.5d
Oviposition days, O_d (d)	2.2 \pm 0.1bc	2.4 \pm 0.1ab	2.0 \pm 0.1c	1.9 \pm 0.1c	2.4 \pm 0.1ab	2.6 \pm 0.1a
Fecundity, F (eggs)	104.70 \pm 6.10a	75.88 \pm 3.38b	77.39 \pm 5.27b	60.98 \pm 4.79c	82.53 \pm 4.94b	80.93 \pm 4.36b
Fecundity, F_f (eggs)	104.70 \pm 6.10a	75.88 \pm 3.38c	77.39 \pm 5.27b	62.15 \pm 4.69d	88.43 \pm 2.92b	84.04 \pm 3.12b
Eggs per oviposition days E_d (eggs)	47.99 \pm 1.840a	31.95 \pm 2.51b	38.70 \pm 2.64b	33.32 \pm 2.01b	36.41 \pm 2.44b	32.21 \pm 2.56b

Means followed by different letters in the same row are significantly different between treatments, determined by using the paired bootstrap test ($P < 0.05$). Standard errors were estimated by using 100,000 bootstraps.

**Fig. 3.** Age-stage-specific life expectancies (e_{xj}) of *C. sasakii* at different larval densities per apple.

no significant differences among the 6–10 to 31–40 larvae/apple treatments.

The life expectancy of *C. sasakii* in different treatments is shown in Fig. 3. The life expectancy of a newly laid egg (e_{01}) was 26.06, 19.87, 18.55, 18.02, 15.13, and 13.82 in the 1–5, 6–10, 11–15, 16–20, 21–30, and 31–40 larvae/apple density treatments, respectively. These values are exactly the same as the mean longevity of all individuals in Table 1 (Atlíhan et al. 2017). The life

expectancy of a newly laid egg (e_{01}) decreased with increases in larval density per apple. Due to the high mortality in the egg-larva stage, the life expectancy of the egg-larva stage initially decreased, then later increased. The maximum life expectancy of the egg-larva stage ($e_{xj} = 27.29$ d) occurred at age 15 d in the 1–5 larvae/apple density treatment, whereas the maximum e_{xj} value for pupae (21.28 d) occurred at age 22 d in the 11–15 larvae/apple density (Fig. 3).

The maximum peak for the age-stage-specific reproductive value (v_{xj}) of *C. sasakii* females ($v_{xj} = 116.85$) was at 39 d in the 1–5 larvae/apple density treatment, which was later than the peak observed in the 21–30 larval density ($v_{xj} = 108.40$ at 33 d), and the 11–15 larval density ($v_{xj} = 106.48$ at 32 d) (Fig. 4).

The highest intrinsic rate of increase ($r = 0.0718 \text{ d}^{-1}$), finite rate of increase ($\lambda = 1.0744 \text{ d}^{-1}$), and net reproductive rate ($R_0 = 23.03$ offspring) were all observed in the 1–5 larvae/apple density, whereas the lowest rates were observed in the 31–40 larvae/apple density. There were no significant differences between the 21–30 and 31–40 larvae/apple densities (Table 3). The mean generation times (T) were significantly shorter when larval densities were greater than 5, but no significant differences were found among the 11–15, 16–20, and 31–40 larvae/apple densities. The T value of the 21–30 larvae/apple density was longer than that for 16–20 larvae/apple, but was not different from the 6–10, 11–15, and 31–40 density treatments.

Analysis of Mass-Rearing and Harvest

By using equation 11, the stage structure of a sustainable mass-rearing system that provides 1000 pupae daily is shown in Table 4. To produce 1000 *C. sasakii* pupae, the necessary number of daily recruits needed for the egg-larva stage was 2,148, 4,082, 4,873, 5,468, 12,551, and 23,641 individuals for densities of 1–5, 6–10, 11–15, 16–20, 21–30, and 31–40 larvae/apple, respectively.

The number of apples required daily was 430, 408, 325, 273, 418, and 591 for 1–5, 6–10, 11–15, 16–20, 21–30, and 31–40 larvae/apple densities, respectively. The results demonstrated that the density of 16–20 larvae/apple was the most economical and efficient rearing system. If the goal was to produce 1000 *C. sasakii* pupae daily, the density of 16–20 larvae per apple required the fewest apples among the six densities and the least amount of labor.

To demonstrate the life table variability, the 100,000 bootstrap results of R_0 values in the 16–20 larvae/apple density were plotted in Fig. 5A. Because the bootstrap technique used random sampling with replacement, the R_0 values randomly fluctuated around the mean of R_0 (5.48 offspring). However, when all 100,000 R_0 values were sorted in ascending order, we obtained the smoothed curve (Fig. 5B) and the 2500th and 15866th sorted bootstrap R_0 values represent the 0.025th and 0.1587th percentile of R_0 . The histogram of 100,000 R_0 values showed a normal distribution of bootstrap results (Fig. 5C).

To include the variability of life table data in the mass-rearing procedure, we also used equation 12 and the 0.1587th percentile of R_0 to calculate the conservative harvesting for the production of 1000 *C. sasakii* pupae. The daily recruits needed for the egg-larva stage were 2,168, 4,294, 5,027, 5,697, 14,304, and 29,787 individuals for densities of 1–5, 6–10, 11–15, 16–20, 21–30, and 31–40 larvae/apple, respectively. The number of apples used daily was 434,

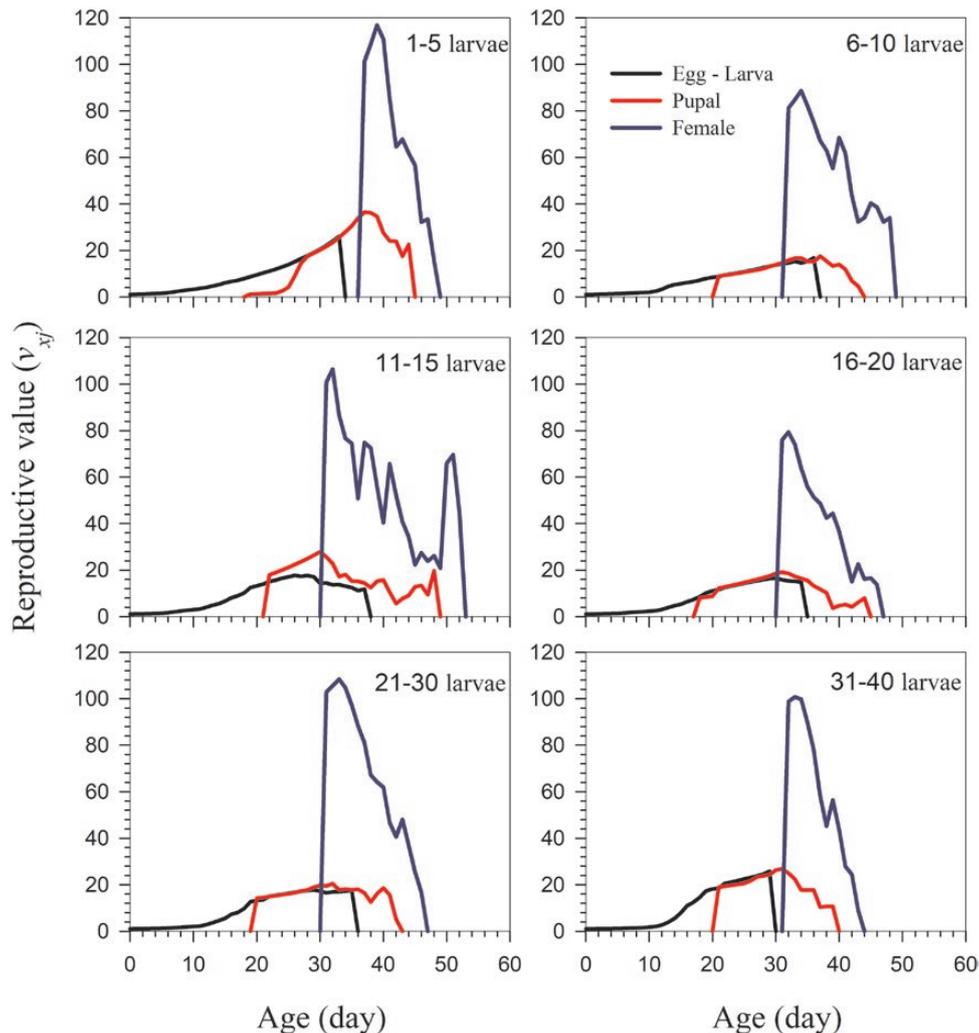


Fig. 4. Age-stage-specific reproductive values (v_{xj}) of *C. sasakii* at different larval densities per apple.

Table 3. Mean (\pm SE) of the intrinsic rate of increase (r), finite rate of increase (λ), net reproductive rate (R_0), mean generation time (T) of *C. sasakii* reared at different larval densities per apple

Parameter	Density (larvae/apple)					
	1–5	6–10	11–15	16–20	21–30	31–40
r (d^{-1})	0.0718 \pm 0.0039a	0.0442 \pm 0.0051b	0.0549 \pm 0.0053b	0.0443 \pm 0.0041b	0.0263 \pm 0.0048c	0.0202 \pm 0.0053c
λ (d^{-1})	1.0744 \pm 0.0042a	1.0451 \pm 0.0054b	1.0564 \pm 0.0056b	1.0453 \pm 0.0043b	1.0266 \pm 0.0049c	1.0204 \pm 0.0054c
R_0 (offspring)	23.03 \pm 3.78a	6.07 \pm 1.21b	8.67 \pm 1.65b	5.48 \pm 0.83b	2.88 \pm 0.54c	2.19 \pm 0.43c
T (d)	43.72 \pm 0.40a	40.84 \pm 0.69b	39.35 \pm 0.85bcd	38.41 \pm 0.42d	40.22 \pm 0.59bc	38.76 \pm 0.48cd

Means followed by different letters in the same row are significantly different between treatments, determined by using the paired bootstrap test ($P < 0.05$). Standard errors were estimated by using 100,000 bootstraps.

Table 4. The stage-specific daily recruit (R_j , the number of individuals recruited to stage j), stage structure (N_j , the total number of individuals in stage j), harvest rate (h , the proportion of pupae harvested), and daily used apples of a stable mass-rearing system of *C. sasakii* with daily harvest rate of 1,000 pupae

Stage structure of mass-rearing system	Density (larvae/apple)					
	1–5 larvae	6–10 larvae	11–15 larvae	16–20 larvae	21–30 larvae	31–40 larvae
Harvest strategy: $R_0(h) = 1$ (using equation 11 and R_j in Table 3)						
Egg-Larva (R_j/N_j)	2148/41733	4082/63091	4873/73791	5468/80781	12551/167579	23641/301187
Pupa (R_j/N_j)	45/447	197/2102	130/1321	223/2253	532/5469	844/8298
Female adult (R_j/N_j)	21/95	54/276	63/292	90/404	152/765	292/1482
Male adult (R_j/N_j)	19/77	121/592	67/301	129/585	329/1496	400/1926
Pupal harvest rate (h)	0.9565	0.8352	0.8846	0.8174	0.6526	0.5423
Daily used apples	430	408	325	273	418	591
Harvest strategy: $R_{0,0.1587}(h) = 1$ (using equation 12)						
$R_{0,0.1567}$	19.25	4.85	7.02	4.65	2.34	1.76
Egg-Larva (R_j/N_j)	2168/42107	4294/66373	5027/76123	5697/84158	14304/190992	29787/379492
Pupa (R_j/N_j)	55/539	259/2766	166/1684	274/2769	746/7669	1323/13011
Female adult (R_j/N_j)	25/115	71/363	80/372	110/497	213/1073	458/2324
Male adult (R_j/N_j)	22/92	159/778	86/384	158/719	462/2097	283/3020
Pupal harvest rate (h)	0.9480	0.7936	0.8575	0.7846	0.5726	0.4304
Daily used apples	434	429	335	285	477	745

429, 335, 285, 477, and 745 for the same densities. Both the number of daily recruits and apples used were higher than that when R_0 was used. Because the $R_{0,0.1587}$ in the 31–40 larvae/apple treatment was less than 2 and the $R_{0,0.1587}$ in the 21–30 larvae/apple treatment was slightly higher than 2, these two densities cannot provide an economical rearing system. The results demonstrated that the 16–20 larvae/apple density was the most economical and efficient rearing system when a conservative harvesting is desired.

Discussion

Density plays an important role in population growth, food utilization, defensive ability, and migration behavior of insects (Kong et al. 2011). For pests that complete their entire larval development within a single fruit, larval density will critically affect the survival, development, and fecundity due to the limited resources provided by the single fruit (Wu et al. 2011). In the present study, the longest egg-larva developmental time (30.00 d) occurred in the 1–5 larval density (Table 1). Ishiguri and Toyoshima (2006) reported a developmental duration for *C. sasakii* larvae of 35.0 d and a survival rate of 6% in unharvested apples, whereas in harvested apples only 18.6 d were needed and the survival rate increased to 85.1%. Therefore, the development of *C. sasakii* is affected by density, fruit growth status, rearing procedures, host plant varieties, environmental conditions, and population variability (Hua et al. 1996).

The shortened TPOP in higher larval densities may be due to intensified intraspecific competition and deteriorating host quality

(Underwood 2010, Cao 2013). Our results showed that the survival rate, fecundity, life expectancy, contributions to reproductive values, and population parameters were significantly affected by larval density. At low larval densities, *C. sasakii* showed an increased preadult survival rate, female adult emergence rate, and fecundity, despite the extended preadult developmental period. The high intrinsic rate of increase, finite rate of increase, and net reproductive rate demonstrated that the *C. sasakii* population grew faster at low larval densities. These results were similar to those noted by Zhang et al. (2006) and Hou and Hua (2004). All the values of the mean fecundity (F) and net reproductive rate (R_0) obtained in all treatments are consistent with the proof of Chi (1988) as $R_0 = F \times (N_f/N)$. Moreover, the peak reproductive value occurred after the first reproductive age and is close to the TPOP as shown by Liu et al. (2018).

Although the differences in adult male and female longevity among larval densities amount to only a few hours and the females mate only once, the significant differences in TPOP, fecundity, survival rate, and other factors were responsible for the differences in the mass-rearing systems calculated for different larval densities. It is obvious that any single statistic, e.g., adult longevity, cannot be used exclusively to determine the correct perspective in mass-rearing programs. Because life tables, by their very nature, include all of the above statistics (i.e., preadult developmental duration, survival rate, and fecundity), they are the most important tool in population ecology studies, which may also include mass-rearing and harvesting.

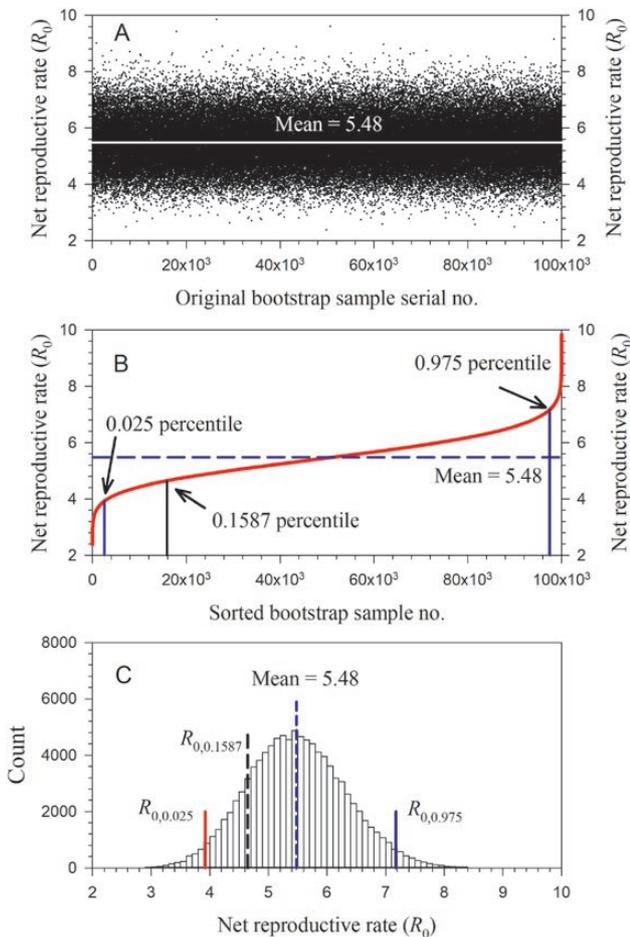


Fig. 5. (A) The original bootstrap results of R_0 . (B) Sorted R_0 . (C) The histogram of R_0 with 0.025th, 0.1587th, and 0.975th percentiles of R_0 .

For successive rearing of *C. sasakii* populations, Zhang et al. (2006) used a density of 11–15 larvae/apple for a shorter larval duration, shorter TPOP, and lower food costs. To maximize rearing efficiency and minimize costs, Chi and Getz (1988) pointed out the necessity of using life tables to take all population characteristics into account, i.e., the developmental rate, survival rate, sex ratio, and fecundity. Although life tables calculated for the 1–5 larvae/apple density generated a higher intrinsic rate of increase (r) and net reproductive rate (R_0), our results showed that the 16–20 larvae/apple density is the optimal density for economically mass-rearing *C. sasakii*. These findings agreed closely to those of Zhang et al. (2006).

To avoid possible collapse of the rearing system due to uncertainties present in the life table, we used the conservatively lower $R_{0,0.1587}$ to calculate the harvest rate. Because we built this safeguard into our analysis, the harvest rates will be lower and more stage recruits will be needed to maintain the mass-rearing system, but the system will be less affected by unpredictable uncertainties present in the life table. The decision to use equation 12 or 13 should be based on the rearing facilities, the required harvest quantity, labor cost, the variability of the life table, etc. To harvest different life stages, researchers can use equations 11–14 to calculate the desired harvest rate and to design a rearing system that meets their specific requirements and saves rearing costs.

Life tables contain realistic “big data”: data for many individuals, sexual composition, development time of each stage, stage

differentiation, and daily fecundity for each female, etc. Because a thorough description of population growth should include all of the above variables, the life table is a critical tool in population ecology and pest management studies (Chi 1988). Due to the variable developmental rate among individuals, overlapping stages were observed in the *C. sasakii* survival rate (Fig. 1), life expectancy (Fig. 3), and reproductive value (Fig. 4). Since stage overlap due to variable developmental rate among individuals is inevitably observed in laboratory and field populations (Liu et al. 1997), the inclusion of this universal phenomenon is important in life table analysis. Because traditional female age-specific life tables ignore the variable developmental rate among individuals and the male individuals, they are unable to accurately describe the stage differentiation in insect life history and the role male individuals play in population growth. Huang and Chi (2012b) discussed the problems of applying female age-specific life tables to two-sex populations. In this study, we analyzed the life table data of *C. sasakii* using the age-stage, two-sex life table, our results showed that including the stage differentiation and both sexes in life table analysis is vital to obtaining an accurate description and interpretation of the survival rate, fecundity, life expectancy, and reproductive value. Our study demonstrated the effect of larval density on insect demography and mass-rearing and harvesting *C. sasakii*. We also demonstrated a method for incorporating the life table uncertainty in the mass-rearing and harvesting system. Because life tables include information on the developmental rate, survival, and fecundity of all individuals, they can be used not only for a lab-based mass-rearing system, but also for the timing of pest management procedures (Chi 1990).

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