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Beneficial Uses of Insects

Comparison of the effect of tea shoots during different seasons in *Arma chinensis* (Hemiptera: Pentatomidae) reared on *Ectropis grisescens* (Lepidoptera: Geometridae) pupae

Qi Liu[1,2,†], Li-Lin Chen[1,2,3,4,†,*], Lin-Lin Wang[1,2,3], Yue Sun[1,2], Yu-Ying Lai[1,2,4], Na-Dang Long[1,2,3], Yi-Han Shi[1,2,3], Li-Fei Quan[1,2,3], Wan-Qiu Feng[1,2,3], Gui-Mei Liang[1,2,3], Jia-Lin Zhao[1,2,3], Zi-Qin Zhou[1,2,4]

[1]State Key Laboratory of Ecological Pest Control for Fujian and Taiwan Crops, College of Plant Protection, Fuzhou, Fujian 350002, China, [2]Institute of China White Tea, Fuding, Fujian 355200, China, [3]Anxi College of Tea Science, Fujian Agriculture and Forestry University, Quanzhou, Fujian 362406, China, [4]China Agricultural Technology Association Anxi Tieguanyin Tea Science and Technology Academy, Quanzhou, Fujian 362406, China [*]Corresponding author, mail: llchen@fafu.edu.cn
[†]These 2 authors contributed equally to this work.

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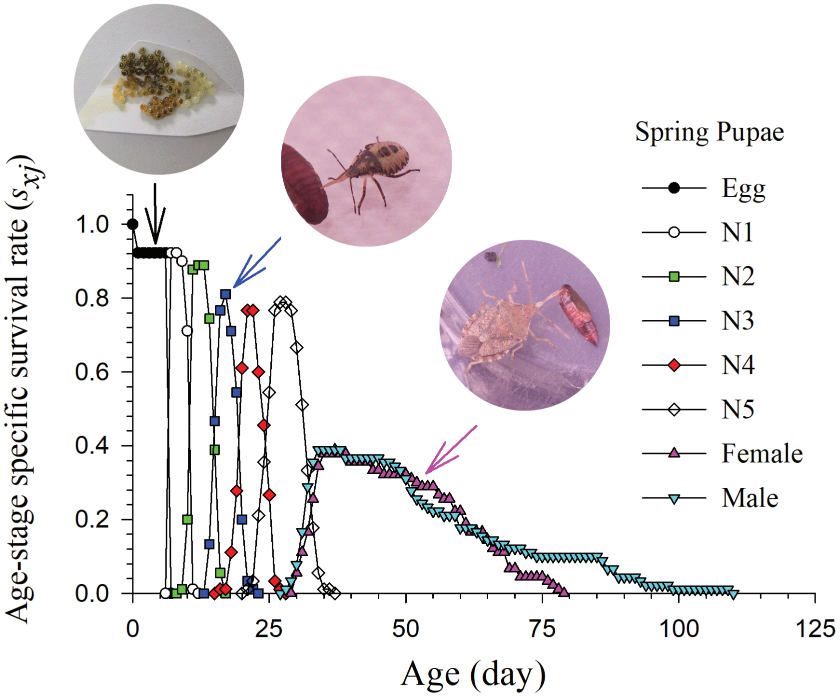
In this study, we compared the growth, development, and fecundity of *Arma chinensis* (Fallou) reared on pupae of the geometrid *Ectropis grisescens* Warren fed on tea shoots during different seasons of the year. The raw data on life history were analyzed using the age–stage, 2-sex life table. When reared on spring or winter geometrid pupae, the duration of the immature stage of *A. chinensis* was significantly longer than in those produced during the summer or autumn. The survival rate of immature *A. chinensis* reared on autumn geometrid pupae was significantly lower compared to other treatments. Reproductive diapause was observed in adult *A. chinensis* reared on winter geometrid pupae. The adult preoviposition period (APOP), total preoviposition period (TPOP), and total longevity were significantly longer in *A. chinensis* reared on winter pupae than in the other treatments. The fecundity of *A. chinensis* reared on spring geometrid pupae was significantly lower than in the other treatments. The higher intrinsic rate of increase of the *A. chinensis* reared on summer pupae ($r = 0.0966$ day^{-1}) and autumn pupae ($r = 0.0983$ day^{-1}) resulted in higher fecundity, shorter immature duration, and shorter TPOP compared to the winter and spring populations. These findings can be utilized to enhance and sustain biological control of *E. grisescens* in tea plantations.

Key words: Arma chinensis, tea geometrid, seasonal effect, age-stage, 2-sex life table, biological control

Graphical Abstract



Introduction

The tea plant, *Camellia sinensis* (L.) O. Kuntze, is an important economic crop in Asia. Because pest infestations remain a major factor in tea production, various approaches have been employed for pest control, including widespread chemical pesticide applications (Chen 2022, Zhou and Gou 2022). The use of chemical pesticides often leads to the "3R" problem, i.e., residue, resistance, and resurgence (Zhou and Gou 2022). The increasing demand for higher tea quality has resulted in recognition of the need to decrease the dependency on chemical control in favor of effective ecological pest management in tea plantations. To achieve this goal, the development and utilization of natural enemies is a vital component in effective pest management programs.

The tea geometrid, *Ectropis grisescens* Warren (Lepidoptera: Geometridae), is one of the most serious pests in tea plantations, which causes severe economic damage worldwide. The predatory stink bug, *Arma chinensis* (Fallou) (Hemiptera: Pentatomidae), feeds on several agricultural pests, including *Dendrolimus punctatus* (Walker) (Lepidoptera: Lasiocampidae), *Spodoptera litura* Fabricius (Lepidoptera: Noctuidae) (Tang et al. 2020), *Tessaratoma papillosa* Drury (Hemiptera: Tessaratomidae) (Gou et al. 2020), and *Ophrida xanthospilota* Baly (Coleoptera: Chrysomelidae) (Chen et al. 2020). *Arma chinensis* has prolonged adult longevity (Shang-Guan 2009), resulting in 3 generations per year in Zhejiang Province (Chai et al. 2000). Shang-Guan (2009) reported that *A. chinensis* is capable of effectively establishing natural populations and providing long-term pest control after being introduced to manage *Parocneria furva* Leech (Lepidoptera: Lymantriidae) in oriental arborvitae (*Platycladus orientalis* (L.) Franco) plantations.

Tea shoots have significant economic importance throughout Asia in every season of the year. Ge et al. (2022) and Ge et al. (2016) demonstrated that *E. grisescens* and *Ectropis obliqua* (Prout) (Lepidoptera: Geometridae) caused substantial damage to tea shoots in every season. Liu et al. (2017a) reported that *A. chinensis* is a natural enemy of *E. grisescens*. Only a few studies have reported the use of *A. chinensis* for controlling geometrids in tea plantations. Therefore, it might be crucial to assess the predatory capacity and suitability of using *A. chinensis* against these pests. Additionally, evaluating the effectiveness of *A. chinensis* in different seasons would provide valuable insights.

Life tables are one of the prime tools in ecological studies. Traditional female-based, age-specific life tables completely ignore the effects attributable to the male population. They are inherently unable to differentiate between the developmental stages that characterize an insect's growth process (Carey 2001, Huang and Chi 2012, Chi et al. 2020, 2023). The age-stage, 2-sex life table, however, is capable of depicting stage differentiation and includes both sexes. It has been widely used in various aspects of ecological research, including predator–prey relationships, biological control, mass rearing of insects, and pest management (Chi and Liu 1985, Chi 1988, Chi et al. 2020). The tea geometrid, *E. grisescens*, causes significant economic losses during each of the 4 seasons (Ge et al. 2016). To mitigate the overuse of chemical pesticides, the development and utilization of natural enemies against *E. grisescens* is of particular importance. The objective of this study was to examine the suitability of *E. grisescens* fed on tea shoots during each season as prey for the predator, *A. chinensis*. The findings of this study will provide valuable insights into the long-term biological control of tea plantation pests using *A. chinensis*.

Materials and Methods

Host Plants

Fresh untreated tea shoots (1 bud and 3-leaf stage) of the host plant, *C. sinensis* (L.) O. Kuntze cv. Huangdan, were collected from the seedling base of Chunlun Tea Garden (26° 08′ 29″ N, 119° 23′ 73″ E), Fujian Agriculture and Forestry University. To determine the possible effects of seasonality on the tea geometrids, tea shoots

Table 1. Developmental duration, APOP, and TPOP of *Arma chinensis* fed on *Ectropis grisescens* pupae developed on tea shoots during 4 different seasons

	Spring geometrid pupae		Summer geometrid pupae		Autumn geometrid pupae		Winter geometrid pupae	
Development stage	*n*	Mean ± SE	*n*	Mean ± SE	*n*	Mean ± SE	*n*	Mean ± SE
Egg (day)	90	7.00 ± 0.00a	90	7.00 ± 0.00a	90	7.00 ± 0.00a	90	7.00 ± 0.00a
First instar (day)	83	3.78 ± 0.05b	82	3.74 ± 0.05b	85	4.01 ± 0.01a	81	3.81 ± 0.04b
Second instar (day)	81	4.55 ± 0.07b	81	4.29 ± 0.06b	81	3.97 ± 0.02b	80	4.89 ± 0.07a
Third instar (day)	75	4.44 ± 0.08a	76	3.80 ± 0.07b	66	3.58 ± 0.08b	74	4.51 ± 0.09a
Fourth instar (day)	73	4.82 ± 0.07a	74	4.58 ± 0.07b	59	3.88 ± 0.09b	74	4.74 ± 0.09a
Fifth instar (day)	72	7.53 ± 0.07a	72	7.37 ± 0.06a	56	7.25 ± 0.11b	74	7.53 ± 0.07a
Total immature duration (day)	70	32.13 ± 0.20a	71	30.76 ± 0.22b	56	29.60 ± 0.15b	73	32.51 ± 0.18a
Immature survival rate (s_a) (%)	90	77.78 ± 4.39a	90	78.89 ± 4.29a	90	58.89 ± 5.21b	90	81.11 ± 4.13a
Adult longevity (day)	70	30.77 ± 1.86b	71	34.00 ± 1.50b	53	29.96 ± 1.99b	73	67.10 ± 1.89a
Total longevity (day)	70	51.62 ± 2.70b	71	53.51 ± 2.63b	53	40.88 ± 2.69b	73	82.38 ± 4.11a
Male adult longevity (day)	35	33.69 ± 3.17b	36	36.11 ± 2.48b	24	29.00 ± 2.60b	40	72.15 ± 2.63a
Female adult longevity (day)	35	27.86 ± 1.87b	35	31.83 ± 1.62b	29	30.76 ± 2.96b	33	60.97 ± 2.32a
APOP (day)	32	8.84 ± 0.39b	34	7.68 ± 0.26c	28	7.32 ± 0.31c	32	37.19 ± 0.85a
TPOP (day)	32	41.56 ± 0.55b	34	38.62 ± 0.34c	28	36.93 ± 0.38c	32	70.12 ± 0.81a
Age of 50% mortality ($A_{0.5}$) (day)	90	56.00 ± 2.68b	90	61.00 ± 2.61b	90	48.00 ± 2.66c	90	93.00 ± 4.09a
Oviposition days (O_d) (day)	32	10.62 ± 0.80b	34	16.74 ± 0.93a	28	15.5 ± 1.51a	32	13.62 ± 1.31a

Means in a row followed by different letters are significantly different at the 5% level using a paired bootstrap test ($P \le 0.05$).

were collected during March–May (spring treatment), June–August (summer treatment), September–November (autumn treatment), and December–February (winter treatment).

Tea Geometrid: *Ectropis grisescens*

Approximately 100 *E. grisescens* larvae used in this study were originally collected from a tea plantation (27° 19′ 92″ N, 119° 57′ 82″ E) at the Fujian Institute of Tea Science, Shekou Town, Fu'an City, Fujian Province, China, in June 2018. Species determinations of the geometrid were conducted using Zhang et al. (2014). The insects were reared in growth chambers set at (26 ± 1) °C, (70 ± 5)% RH, and a photoperiod of L:D = (16:8) h. The larvae were reared on fresh tea shoots collected from tea plants during each of the 4 seasons. No pesticide was applied in the tea plantation during the study period. Pupae of different treatments were used as prey for *A. chinensis*, as discussed in the following section.

Predatory Stink Bug: *Arma chinensis*

Approximately 100 *A. chinensis* adults were obtained in April 2021 from the Institute of Plant Protection, Chinese Academy of Sciences. Insects were reared on *E. grisescens* pupae for more than 1 generation before conducting life table studies. The insects were kept in growth chambers set at the same conditions outlined above. Plastic cups (8 cm bottom diameter, 8.5 cm top diameter, and 15.3 cm height) were used as rearing containers.

Life Table Studies

Ninety *A. chinensis* eggs laid within a 24-h period were randomly selected from more than 20 egg masses at the beginning of the life table study. Newly hatched nymphs were transferred to a plastic cup containing a cotton-wool ball soaked with 10% sucrose solution as food for the first instars. The first instars were group-reared. Beginning with the second instar, stinkbugs were individually kept in plastic cups (replaced as necessary with surplus pupae from the same respective treatment) containing a cotton-wool ball soaked with 10% sucrose. New pupae were supplied daily. The development and survival of stinkbugs were also recorded daily. Newly emerged adults were paired, and each pair was kept in a plastic cup with prey pupae and a piece of folded crumpled white paper. A contingency group of insects was reared separately for each treatment to provide replacement males for mating when necessary. The number of eggs laid by female adults and adult survival rate were recorded daily until all adults had died.

Data Analysis

The life table raw data were analyzed according to the age-stage, 2-sex life table procedure (Chi and Liu 1985, Chi 1988, Chi et al. 2020, 2023) using the Twosex-MSChart program (Chi 2022). Variance and standard error of population parameters N_f/N, R_0, r, λ, T, and others were calculated using the bootstrap technique with 100,000 resampling (Efron and Tibshirani 1991). The paired bootstrap test (Wei et al. 2020) was used to compare the differences among treatments. Life table parameters of *A. chinensis* calculated using the Twosex-MSChart program are shown in Supplementary Table 1. All figures were drawn using SigmaPlot 14.0.

Results

Development Duration, Longevity, and Fecundity

The developmental durations and survival rates of *A. chinensis* are listed in Table 1. *Arma chinensis* could successfully complete its life cycle and produce offspring when reared on geometrid pupae developed during each of the different seasons. The lowest immature survival rate of *A. chinensis* (41.11%) was observed in individuals reared on autumn pupae. The longest female adult longevity (60.97 days), male adult longevity (72.15 days), adult preoviposition period (APOP = 37.19 days), total preoviposition period (TPOP = 70.12 days), and total longevity (99.60 days) was observed in *A. chinensis* reared on winter pupae. When *A. chinensis* was reared on autumn pupae, 50% mortality ($A_{0.5}$) occurred at age 48 days in contrast to the $A_{0.5}$ of 93 days when reared on winter pupae (Table 1; Fig. 2). The lowest fecundity (147.46 eggs/female) was observed in

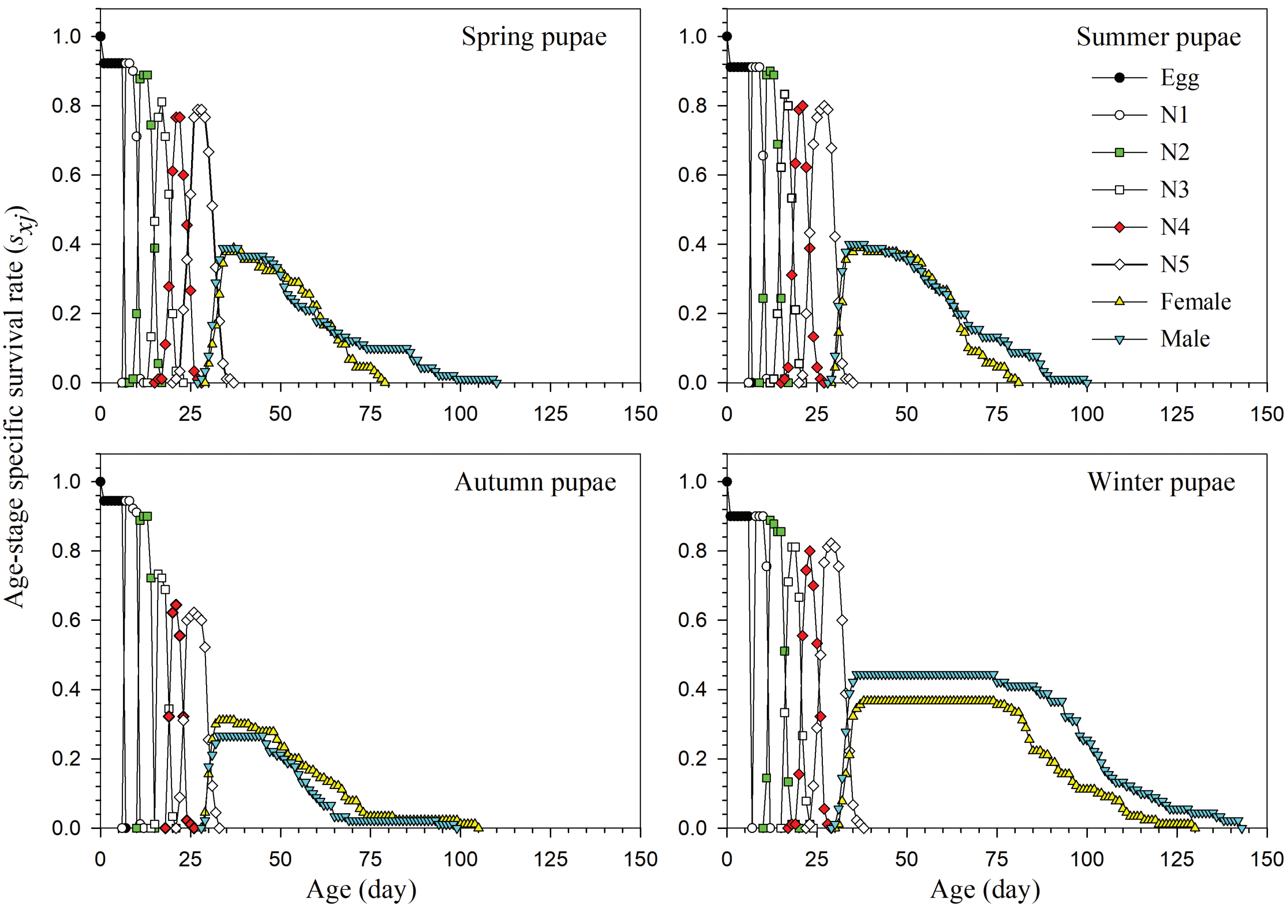


Fig. 1. Age–stage specific survival rate (s_{xj}) of *Arma chinensis* reared on pupae of *Ectropis grisescens* fed with tea shoots in different seasons.

Table 2. Mortality (mean ± SE) of different developmental stages of *Arma chinensis* reared on *Ectropis grisescens* pupae developed on tea shoots during 4 different seasons (%)

Development stage	Spring geometrid pupae	Summer geometrid pupae	Autumn geometrid pupae	Winter geometrid pupae
Egg	7.78 ± 2.82a	8.89 ± 3.00a	5.56 ± 2.41a	10.00 ± 3.16a
First instar	2.22 ± 1.56a	1.11 ± 1.10a	4.44 ± 2.17a	1.11 ± 1.106a
Second instar	6.67 ± 2.63b	5.56 ± 2.42b	16.67 ± 3.93a	6.67 ± 2.63b
Third instar	2.22 ± 1.55a	2.22 ± 1.56a	7.78 ± 2.84a	0.00 ± 0.00b
Fourth instar	1.11 ± 1.11a	2.22 ± 1.55a	3.33 ± 1.89a	0.00 ± 0.00a
Fifth instar	2.22 ± 1.55a	1.11 ± 1.11a	3.33 ± 1.90a	1.11 ± 1.11a
Preadult	22.22 ± 4.38b	21.11 ± 4.29b	41.11 ± 5.18a	18.89 ± 4.13b
Female	38.89 ± 5.13a	38.89 ± 5.13a	32.22 ± 4.94a	36.67 ± 5.08a
Male	38.89 ± 5.11a	40.00 ± 5.14a	26.67 ± 4.64b	44.44 ± 5.24a

Means in a row followed by different letters are significantly different at the 5% level by using a paired bootstrap test ($P \le 0.05$).

A. chinensis when reared on spring pupae. This was significantly lower than in the other 3 treatments (Table 2).

The age-stage specific survival rates of *A. chinensis* are shown in Fig. 1. The overlapping developmental stages were observed in all treatments (Fig. 1). Adults of both sexes of *A. chinensis* had the longest longevity when reared on winter pupae. The age-specific survival rate (l_x), female age-specific fecundity (f_{x7}), age-specific fecundity (m_x), and age-specific net maternity ($l_x m_x$) are shown in Fig. 2. The l_x curve dropped earlier in the cohort of *A. chinensis* reared on autumn pupae, while it was maintained as high as 81.11% until age 73 days in the *A. chinensis* cohort reared on winter pupae (Fig. 2). In general, the life expectancies (e_{xj}) of *A. chinensis* were shorter when reared on autumn pupae than they were in the other 3 treatments. The longest life expectancy was observed in *A. chinensis*, which was reared on winter pupae. The life expectancy of a newly laid egg, i.e., e_{01}, was 51.62, 53.51, 40.88, and 82.21 days when reared on spring pupae, summer pupae, autumn pupae, and winter pupae, respectively. The values of e_{01} are equal to the total longevity of the cohorts (Table 1). The life expectancies of male adults were longer than those of female adults in all treatments (Fig. 3). The age–stage specific reproductive value of a newly laid egg, i.e., v_{01}, was exactly the finite rate of increase (Table 3; Fig. 4). The curves of v_{xj} increased dramatically when the female adults began to produce offspring. The first peak of the v_{xj} curves was close to the TPOP (Fig. 4).

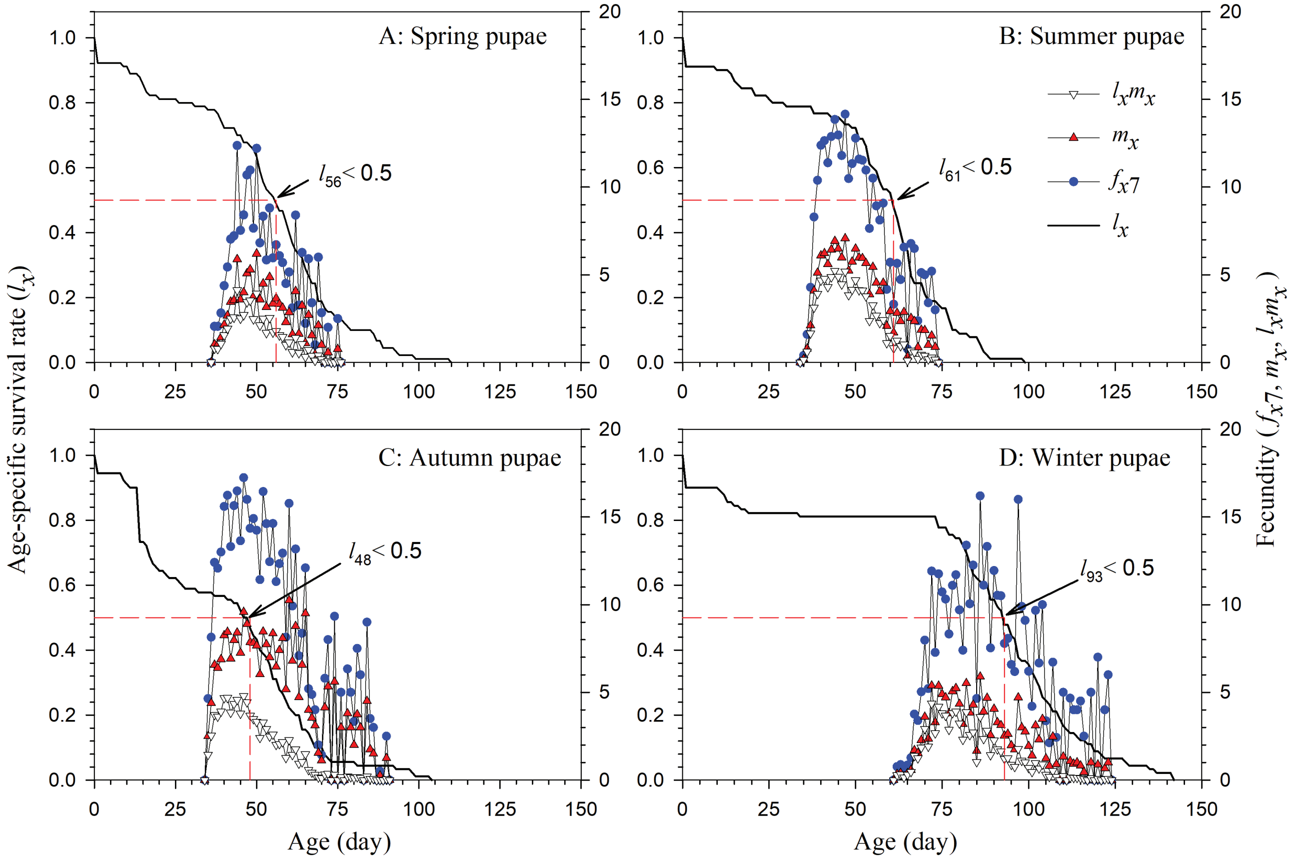


Fig. 2. Age-specific survival (l_x) and fecundity (f_{x7}, m_x, l_xm_x) of *Arma chinensis* reared on pupae of *Ectropis grisescens* fed with tea shoots in different seasons.

Distribution of Mortality

The distribution values of *A. chinensis* preadult mortality are listed in Table 3. When reared on autumn pupae, the mortality occurring in the second instar (16.67%) was the highest among all treatments (Table 2). Consequently, the highest preadult mortality (41.11%) was observed in *A. chinensis* when reared on autumn pupae.

Population Parameters

The net reproductive rate (R_0) of *A. chinensis* was the lowest when reared on spring pupae (R_0 = 57.34 offspring/individual). There were no significant differences among the other 3 treatments. The intrinsic rate of increase (r) and finite rate of increase (λ) of *A. chinensis* reared on summer pupae (r = 0.0966 day^{-1} and λ = 1.1014 day^{-1}) and autumn pupae (r = 0.0983 day^{-1} and λ = 1.1033 day^{-1}) were significantly higher than those reared on spring pupae (r = 0.0826 day^{-1} and λ = 1.0861 day^{-1}) and winter pupae (r = 0.552 day^{-1} and λ = 1.0567 day^{-1}). The mean generation time (T) was 85.62 days when reared on winter pupae, which was significantly longer than that of other treatments. There were no significant differences in the proportion of female adults (N_f/N) among all treatments (Table 3). The stable age–stage distribution (SASD), stable age distribution (SAD), and stable stage distribution (SSD) values are shown in Fig. 5. The proportions of the fifth instar (0.082), female (0.061), and male adults reared on winter pupae (0.086) were significantly higher than in the other treatments.

Discussion

Seasonal variations have a considerable impact on the production and storage of major plant compounds (Dai et al. 2015, Liu et al. 2017b, 2021, Bhardwaj et al. 2019, Yang et al. 2022b, Wang et al. 2023a). The seasonal effects influence crop nutrition, in turn, the population characteristics of pests and their predators (Noriega et al. 1999, Zheng 2020, Boiça Júnior et al. 2022, Li et al. 2023, Wang et al. 2023b, Zhao et al. 2023). Du et al. (2015) reported that the growth and development of the shoots and fruits of peaches and pears in different seasons have a direct impact on *Grapholita molesta* (Busck) (Lepidoptera: Tortricidae). Furthermore, delaying the harvest season of pears can promote an increase in the proportion of *Cydia pomonella* (L.) (Lepidoptera: Tortricidae) larvae entering diapause (Van Steenwyk et al. 2004). In this study, we collected the life table data of *A. chinensis* prey on pupae of *E. grisescens* fed on tea shoots during different seasons. Overall, the current study might be crucial for a tri-trophic relationship.

Development Duration, Longevity, and Fecundity

Previous studies have shown that the developmental period of nymphs and the adult lifespan of the predatory bug *Orius albidipennis* (Reuter) (Hemiptera: Anthocoridae) exhibit pronounced seasonal variations (Chyzik et al. 1995, Anderson 2009). In this study, we observed shorter nymphal development periods in *A. chinensis* reared on summer and autumn pupae of *E. grisescens* compared to those reared on spring and winter pupae. Ge (2022) showed that the developmental period of geometrids reared on tea shoots was not significantly different between spring and winter cohorts. Liu et al. (2017b) reported increased defensive proteins in spring and winter in *E. obliqua* fed on tea shoots. A similar process may occur in its congener, *E. grisescens*, which may be an inhibiting factor affecting the growth of *A. chinensis*. The extended immature developmental period of *A. chinensis* may reflect a possible tri-trophic interaction.

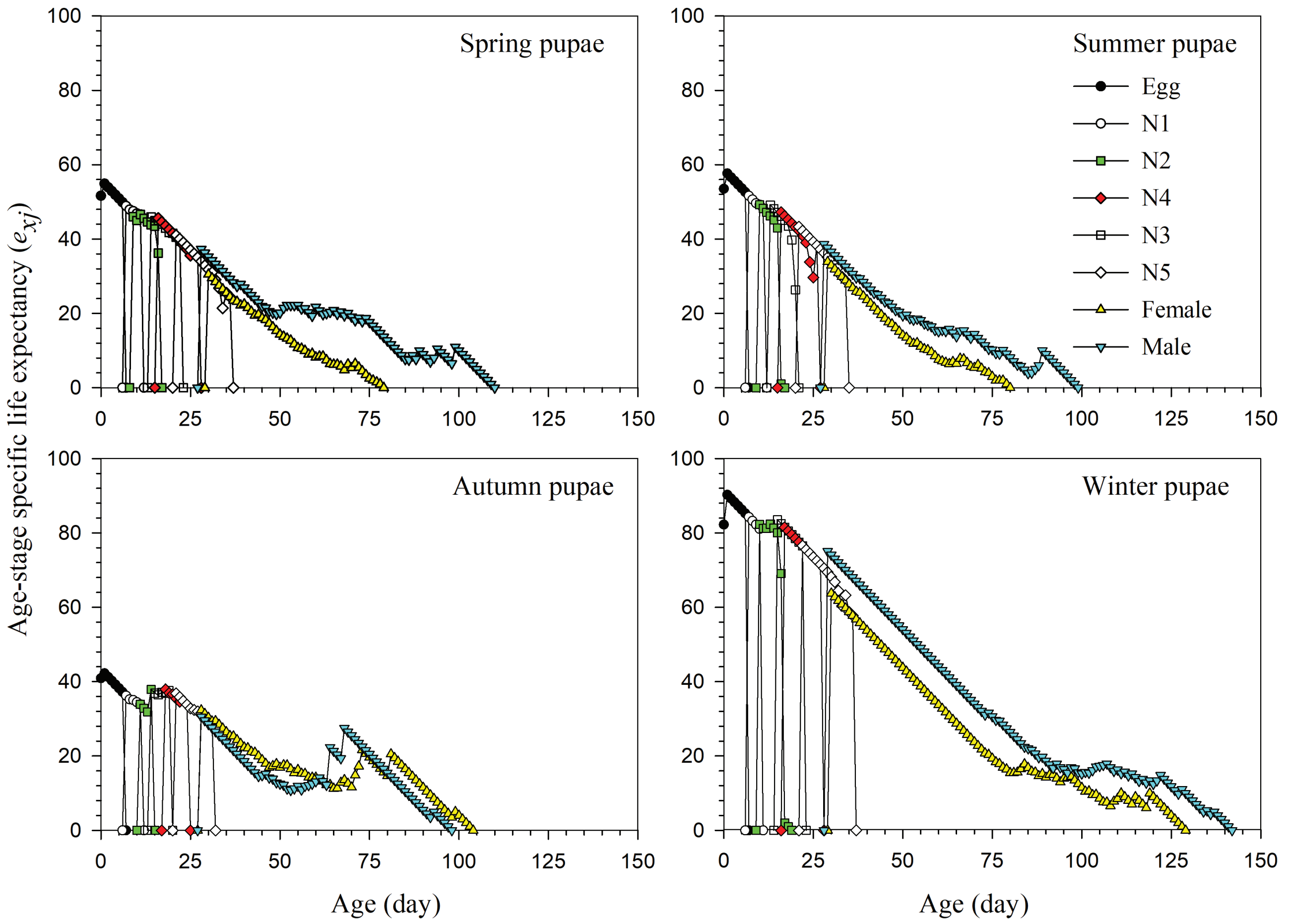


Fig. 3. Age–stage specific life expectancy (e_{xj}) of *Arma chinensis* reared on pupae of *Ectropis grisescens* fed with tea shoots in different seasons.

Table 3. Population parameters (mean ± SE) of *Arma chinensis* reared on *Ectropis grisescens* pupae developed on tea shoots during 4 different seasons

Population parameters	Spring geometrid pupae	Summer geometrid pupae	Autumn geometrid pupae	Winter geometrid pupae
Fecundity (*F*) (offspring/female)	147.46 ± 17.21b	245.11 ± 16.44a	294.52 ± 30.88a	234.27 ± 23.74a
Proportion of female adults (N_f/N)	0.389 ± 0.051a	0.389 ± 0.062a	0.322 ± 0.049a	0.367 ± 0.051a
First reproductive age	37.0 ± 0.10b	35.0 ± 0.58c	35.0 ± 0.03c	62.0 ± 1.26a
Net reproductive rate (R_0) (offspring/individual)	57.34 ± 9.99b	95.32 ± 14.07a	94.90 ± 17.51a	85.90 ± 14.70a
Intrinsic rate of increase (*r*) (day^{-1})	0.0826 ± 0.0037b	0.0966 ± 0.0032a	0.0983 ± 0.0039a	0.0552 ± 0.0021c
Finite rate of increase (*λ*) (day^{-1})	1.0861 ± 0.0041b	1.1014 ± 0.0035a	1.1033 ± 0.0043a	1.0567 ± 0.0022c
Mean generation time (*T*) (day)	49.02 ± 0.69b	47.20 ± 0.47c	46.33 ± 0.78c	80.64 ± 1.12a

Means in a row followed by different letters are significantly different at the 5% level by using a paired bootstrap test ($P \leq 0.05$).

In the present study, the TPOP, APOP, and adult longevities of *A. chinensis* reared on spring, summer, and autumn pupae were similar to those reported by Liu et al. (2023) in *A. chinensis* reared on pupae of *Antheraea pernyi* Guérin-Méneville (Lepidoptera: Saturniidae) at 27 °C. However, when *A. chinensis* adults were reared on winter pupae, the TPOP, APOP, and adult longevities were significantly prolonged. Saulich (2010) suggested that adult diapause is one of the main factors contributing to the extended lifespan exhibited by some insects. Moreover, the occurrence of lower food quality during the winter season may also influence diapause by affecting insufficient production of juvenile hormone and/or negatively impacting ovarian development (Williams and Carroll 1952, Tatar et al. 2001, Denlinger 2003, Short and Hahn 2023). A significant extension of the preoviposition periods (both APOP and TPOP) of *A. chinensis* reared on winter pupae was observed in the present study, which would be consistent with the above findings. Tea plants were grown under cooler climatic conditions during the winter months, resulting in decreased metabolic and chemical compound

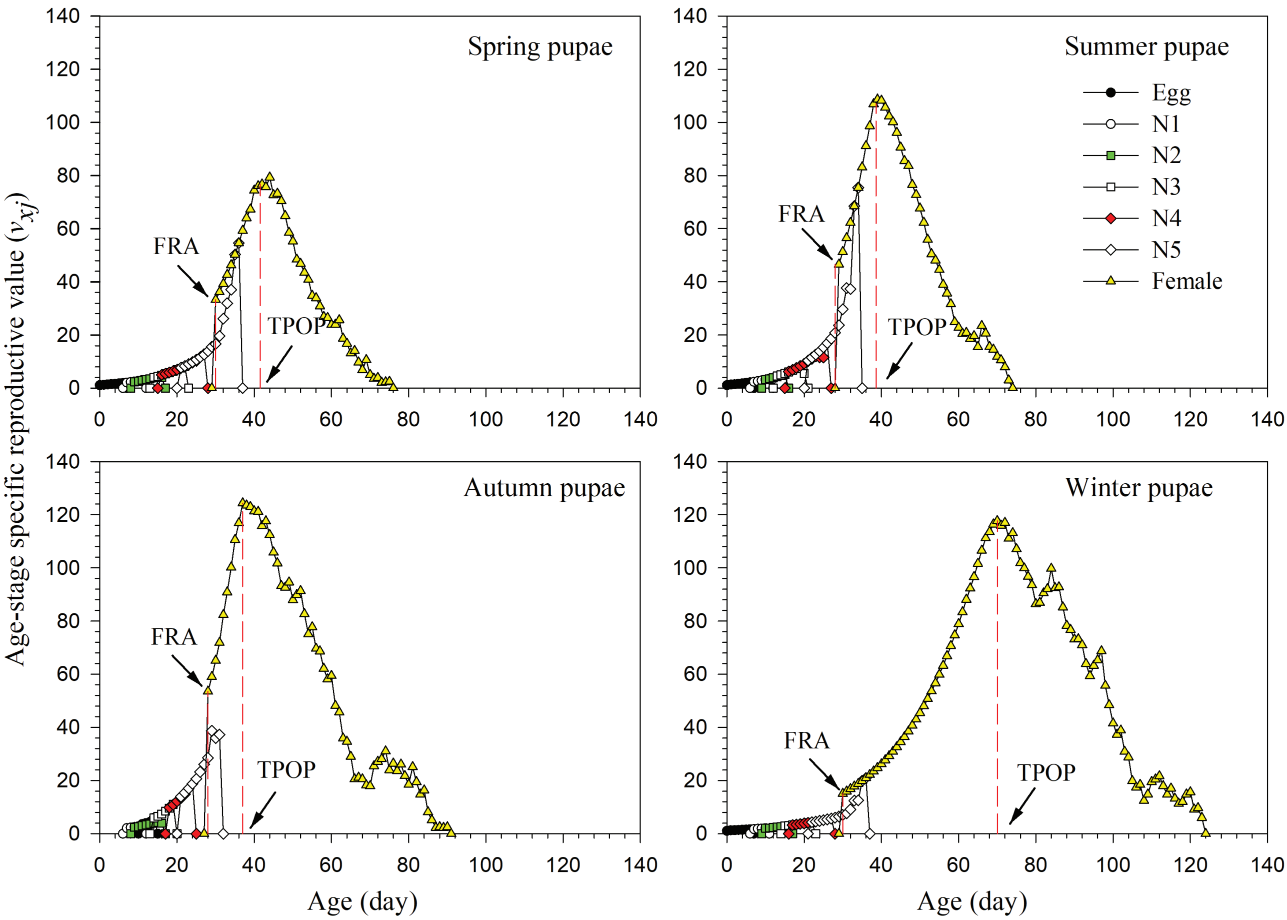


Fig. 4. Age-stage specific reproductive value (v_{xj}) of *Arma chinensis* reared on pupae of *Ectropis grisescens* fed with tea shoots in different seasons. FRA, first reproductive age.

accumulation in the plants, thereby producing lower-quality host plants (Vyas et al. 2007). Likely, the lower-quality nutrients in winter tea shoots would adversely affect the *E. grisescens* pupae, which, in turn, would induce reproductive diapause in *A. chinensis* (Fig. 2). Shintani et al. (2010) found that the adult stage of the predatory stink bug, *Andrallus spinidens* (F.) (Hemiptera: Pentatomidae), underwent diapause during winter as a means of overwintering. Our findings are consistent with these reports.

Distribution of Mortality

Formella et al. (2022) reported that the host plant not only significantly influenced the developmental period of insects but also had a significant impact on their mortality rates. Our results demonstrated that the highest preadult mortality rate was observed in the immature stage of individuals reared on autumn pupae. This may have resulted from the higher caffeine and theophylline levels found in autumn tea shoots (Dai et al. 2015).

Population Parameters

The lowest mean fecundity was observed in *A. chinensis* reared on spring pupae. The variation in nutritional constituents in diet is a crucial element that impacts the reproductive capacity of insects (Zheng 2020). Previous studies have demonstrated that significant variations in the nutritional content of tea shoots occur during different seasons. These include notable differences in total amino acid levels and the presence of different free amino acids and their derivatives, which may, in turn, exert inhibitory effects on insects feeding in plants (Lamberth 2016). The higher concentration of these amino acids and their derivatives, including those with inhibitory effects, occurs in spring tea shoots (Dai et al. 2015, Liu et al. 2017b, 2021, Yang et al. 2022b). The higher amino acid content found in tea shoots during the spring may be responsible for a lower reproduction rate (Ge et al. 2018, 2022, Ge 2022). Ge (2022) indicated that the fecundity of *E. grisescens* fed on winter tea shoots feeding was significantly higher than in those feeding on spring shoots. It may cause *A. chinensis* reared on spring pupae to show lower fecundity than other treatments. Shah et al. (2012) observed a decrease in fecundity in spring adults of the fulgoroid, *Ommatissus lybicus* (de Bergevin) (**Hemiptera: Tropiduchidae**). Our results are consistent with their findings.

Previous studies showed that the temperature or photoperiod that exceeds a specific threshold triggers diapause termination. This leads to restoring normal JH levels and initiating vitellogenesis, resulting in the return of fecundity to normal levels (Tatar et al. 2001, Nielsen et al. 2008, Rice et al. 2014, Yang et al. 2022a). Our study indicated that under constant temperature and lighting conditions, the fecundity of *A. chinensis* reared on winter pupae can recover to normal levels after termination of their diapause. Accordingly, the fecundity of individuals reared on winter pupae was not significantly different from that of summer and autumn pupae. However, it was significantly higher than that of spring pupae.

The first reproductive age and survival rate (l_x) and mean fecundity (f_{x7}) at the first reproductive age are important factors affecting the magnitude of the intrinsic growth rate and finite rate of increase (Lewontin

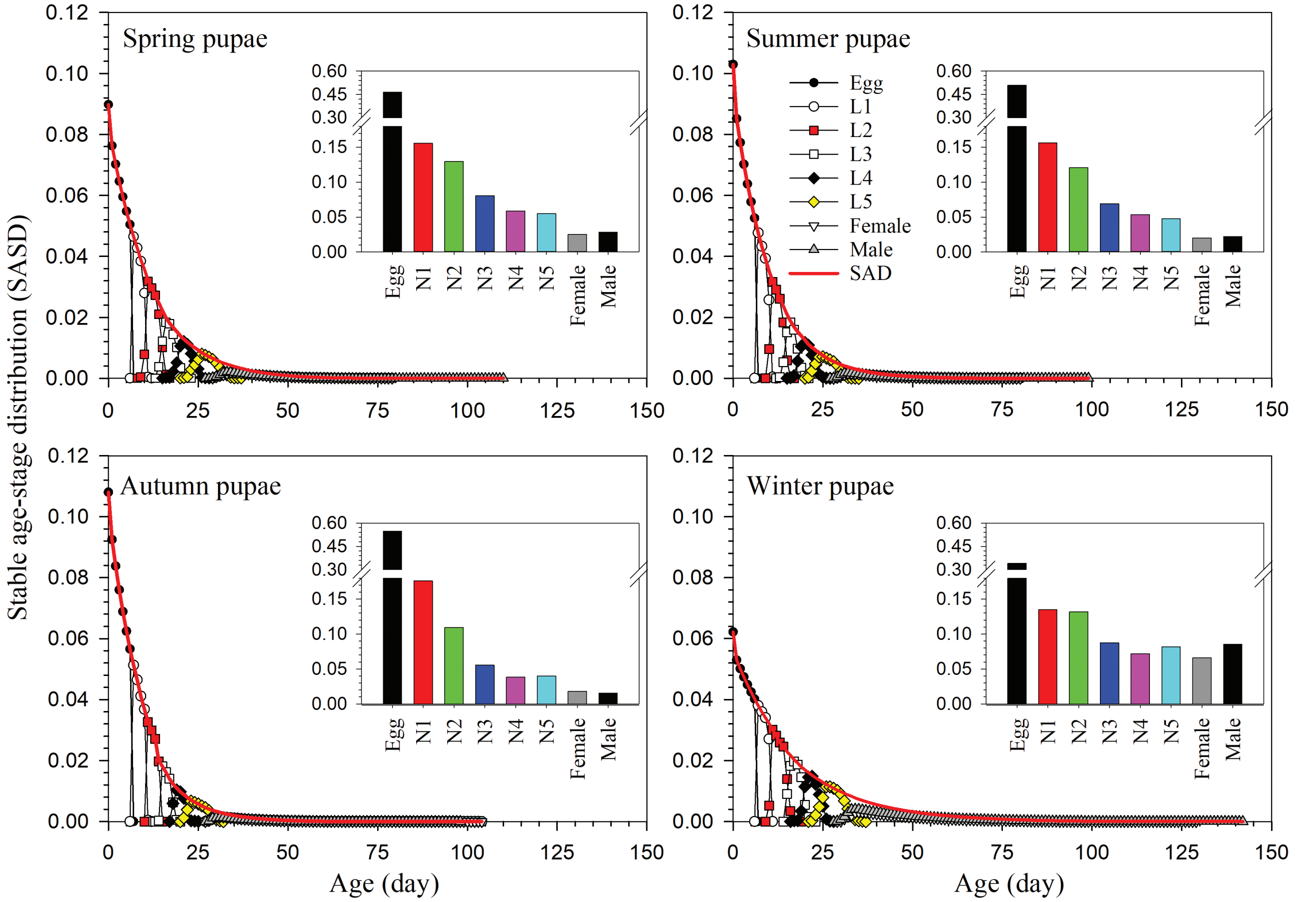


Fig. 5. SASD of *Arma chinensis* reared on pupae of *Ectropis grisescens* fed with tea shoots in different seasons. The thick line without scatter is the SAD. The bar chart embedded in each figure is the SSD.

1964). The first reproductive age of *A. chinensis* reared on winter pupae occurred as late as 62 days. This was the most important factor, resulting in the lowest intrinsic rate of increase and finite rate of increase among all treatments. Gabre et al. (2005) showed that the TPOP was consistent with the first reproductive age. Therefore, compared to the APOP, TPOP is the preferred parameter for demonstrating the effect of reproductive age on the population growth rate.

Because the age–stage, 2-sex life table does consider stage differentiation, we were able to calculate not only the SAD but also the SSD. In a SAD, the proportion of older individuals is less than the younger ages. However, the proportion of adult stages in the SSD can be higher than the younger stages. Due to the longer adult longevity of *A. chinensis* reared on winter pupae, the proportions of female adults (6.61%) and male adults (8.52%) in the SSD were higher than in the 3 other treatments (both female and male adults were less than 3%).

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Author Contributions

Qi Liu (Data curation [equal], Formal analysis [equal], Investigation [equal], Software [equal], Writing—original draft [equal], Writing—review & editing [equal]), Li-Lin Chen (Conceptualization [equal], Data curation [equal], Formal analysis [equal], Funding acquisition [lead], Investigation [equal], Methodology [lead], Project administration [lead], Resources [lead], Supervision [lead], Validation [equal], Visualization [equal], Writing—original draft [equal], Writing—review & editing [lead]), Lin-Lin Wang (Data curation [equal], Formal analysis [equal], Investigation [equal], Writing—original draft [equal]), Yue Sun (Investigation [equal], Writing—original draft [equal]), Yu-Ying Lai (Investigation [equal]), Na-Dang Long (Investigation [equal]), Yi-Han Shi (Investigation [equal]), Li-Fei Quan (Investigation [equal]), Wan-Qiu Feng (Investigation [equal]), Gui-Mei Liang (Investigation [equal]), Jia-Lin Zhao (Investigation [equal]), and Zi-Qin Zhou (Investigation [equal])

Supplementary Material

Supplementary material is available at *Journal of Economic Entomology* online.

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