



Article **Two-Sex Life Table Analysis of the Predator** Arma chinensis (Hemiptera: Pentatomidae) and the Prediction of Its Ability to Suppress Populations of Scopula subpunctaria (Lepidoptera: Geometridae)

Kunqian Cao¹, Rongmeng Lan^{1,2}, Xiuju Yang^{1,3}, Bing Gong¹, Jingjing Zhang¹, Xia Zhou¹ and Linhong Jin^{1,*}

- ¹ National Key Laboratory of Green Pesticide, Key Laboratory of Green Pesticide and Agricultural Bioengineering, Ministry of Education, Guizhou University, Guiyang 550025, China; xzhou@gzu.edu.cn (X.Z.)
- ² College of Agriculture, Guizhou University, Guiyang 550025, China
- ³ College of Tea, Guizhou University, Guiyang 550025, China
- * Correspondence: lhjin@gzu.edu.cn; Tel.: +86-851-3620-521

Abstract: Scopula subpunctaria (Herrich-Schaeffer) (Lepidoptera: Geometridae) is a leaf-eating pest in tea plantations that often causes serious economic losses. Arma chinensis (Fallou) (Hemiptera: Pentatomidae) as a polyphagous insect has become one of the main biological control agents for tea plantation pests due to its wide feeding habit, predatory ability, and adaptability. However, studies related to the predation using A. chinensis on the third instar S. subpunctaria have not been reported. In this study, we used the age-stage, two-sex life table method to analyze the developmental duration and fecundity of S. subpunctaria fed on tea, and A. chinensis fed on third instar S. subpunctaria larvae, under a 25 °C regime. The growth, development, survival, fecundity, and predation rates of the insect populations were investigated. The results showed that the predator and the prey can complete their respective life histories, but the developmental durations at each stage were different, and the developmental stages overlapped significantly. In addition, we used the computer program TIMING-MSChart to project the stage structure and the total population size of A. chinensis and S. subpunctaria. We also simulated the population changes of S. subpunctaria using an A. chinensis intervention. These results showed that S. subpunctaria can support A. chinensis to finish its life history and A. chinensis has great potential to control S. subpunctaria. This study contributes to the understanding of the biological characteristics of S. subpunctaria and provides a theoretical basis for releasing A. chinensis in the field to suppress S. subpunctaria.

Keywords: Arma chinensis; Scopula subpunctaria; two-sex life table; biological control

1. Introduction

Scopula subpunctaria (Herrich-Schaeffer) (Lepidoptera: Geometridae) (Figure 1) is one of the most important pests in tea plantations [1,2] for the concentration of damage phenomena [3]. It mainly occurs in the southern provinces of China, including Guizhou province [4]. According to the field observation, *S. subpunctaria* has six generations per year and its four insect stages can be observed at the same time [5]. The small larvae of *S. subpunctaria* mainly feed on the hypodermis and mesophyll. As their age increases, they cause damage to all the tea leaves. The phenomenon of overlapping generations of *S. subpunctaria* and its overeating characteristics seriously affect the yield and quality of tea, often causing serious economic losses [6,7]. The control of *S. subpunctaria* relies mainly on chemical insecticides [8]. However, the long-term use of chemical insecticides increases their resistance in the field [9]. In the context of the global implementation of chemical pesticide reduction, finding a suitable pest control method for *S. subpunctaria* has become a problem that must be solved.



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Figure 1. Life history of *S. subpunctaria* (including the egg stage, first larva, second larva, third larva, fourth larva, fifth larva, pupa, eclosion of pupa, male adult, and female adult). L1–L5 indicates the first larva to the fifth larva. The scale of the egg was 1 mm and the rest were 1 cm. This unit refers to the length of the insects.

Arma chinensis (Fallou) (Hemiptera: Pentatomidae) (Figure 2) is a predatory natural enemy insect [10]. It is found in northeastern Asia, including Korea, Mongolia, and the Soviet Far East [11], and is also distributed in most provinces of China, including the Guizhou province [12,13]. The continuous improvement of rearing technology [14] and artificial feed [15,16] has enabled *A. chinensis* to expand on a large scale. This provides the basis for releasing *A. chinensis* in the field for biological control [17]. *A. chinensis* can feed on more than 40 species of agricultural and forestry pests, including Lepidoptera, Sphingidae, and Homoptera [18]. For instance, *A. chinensis* predation on the pupa of *Antheraea pernyi* [19], *Mythimna separata* (Walker) [20], *Pyrrhalta aenescens* [21], *Spodoptera frugiperda* [22], and *Ostrinia furnacalis* [23] has been reported. However, studies related to predation by *A. chinensis* on the third instar *S. subpunctaria* have not been reported.



Figure 2. Life history of *A. chinensis* (including the egg stage, first nymph, second nymph, third nymph, fourth nymph, fifth nymph, male adult, and female adult). L1–L5 indicates the first nymph to the fifth nymph. The scale of the insects was 1 mm, and this unit refers to the length of the insects.

Life tables are an important tool for population ecology and pest management [24], and they are a common method for studying the reproductive power of a population [25,26]. Among them, the age-stage, two-sex life table is an effective tool since the development rate, survival rate, reproduction potential, and predation ability are important parameters for evaluating the effectiveness of biological control agents [27–30]. Therefore, in this study, based on the age-stage, two-sex life table method described by Chi [31], we comprehensively investigated the history and fecundity of *S. subpunctaria* on tea. This facilitated an understanding of the ecological habits of *S. subpunctaria* and selected the appropriate pest natural enemies for forest control. Meanwhile, the growth and predation rates of *A. chinensis* were determined when fed on the 3rd instar *S. subpunctaria* since the 2nd instar. In addition, we used the computer program TIMING-MSChart-2022-10-25 B100000.exe to determine the stage structure and the total population size of *A. chinensis* and *S. subpunctaria*. We also predicted the change in the population size of *S. subpunctaria* when *A. chinensis* intervened.

This is the first time that an age-stage, two-sex life table method has been used to synthesize the life histories of *A. chinensis* fed on third instar *S. subpunctaria* and *S. subpunctaria* fed on tea and to study the effects of the intervention of *A. chinensis* on the populations of *S. subpunctaria*. Our study aims to provide a basis for predicting the outbreak of *S. subpunctaria* in tea plantations, releasing *A. chinensis* in the field to control *S. subpunctaria*, and provide a reference for adopting appropriate control strategies to reduce economic losses in agroecosystems.

2. Materials and Methods

2.1. Rearing of Insects

The *A. chinensis* were provided by the natural enemy factory in Zunyi, Guizhou province, China, and fed on the pupa of *Antheraea pernyi* (Guerin-Meneville) in an insect box (20 cm \times 25 cm \times 10 cm). The insect box was maintained in an artificial climate chamber (developed by the Ningbo Jiangnan Instrument Factory) at a temperature of 25 ± 1 °C, a relative humidity (RH) of $75 \pm 5\%$, and a natural photoperiod of 16 h:8 h (L:D). Additionally, *A. chinensis* was fed third *S. subpunctaria* larvae for two generations before the survey. Since *A. chinensis* during the first nymph stage would cluster together and be too small (1.6 mm) to prey on third instar *S. subpunctaria* until they reached the second instar nymph stage, they were supported by 10% hydromel at that age under the same conditions.

The *S. subpunctaria* adults were collected from a tea plantation in Meitan County $(27^{\circ}39'51'' \text{ N}, 107^{\circ}31'59'' \text{ E})$ and identified using external morphology [3,32,33]. The insect colony was reared in an insect cage $(50 \text{ cm} \times 50 \text{ cm} \times 50 \text{ cm})$ for more than one generation. Fresh tea branches were placed in the cage for the feeding and egg laying of *S. subpunctaria*, and the cage was maintained under the above artificial climate conditions.

2.2. Life Table and Predation Rate Studies

2.2.1. Life Table and Predation Rate Study of A. chinensis

The development, fecundity, and predation rates of *A. chinensis* fed on third instar *S. subpunctaria* were determined by observing a cohort of 100 *A. chinensis* eggs (laid within 24 h). *A. chinensis*, once hatched, would cluster together and pierce or suck on its remaining eggs [34]. So, the newly hatched *A. chinensis* were immediately transferred into a separate plastic container (360 mL) covered by 120 mesh nylon net and were provided with a cotton ball soaked with 10% hydromel. New 10% honey in water was added every 24 h until it grew into to the second nymph stage. Then, the third instar of *S. subpunctaria* (attached to fresh tea branches) was supplied as prey for the second nymph *A. chinensis* until the adults died. Fresh tea leaves were replaced each day. The female and male *A. chinensis* that fledged from the fifth nymph on the same day were paired in a separate container with a tiled gauze (4 cm \times 18 cm) for the females to lay eggs. New prey was supplied each day until the female *A. chinensis* died. The highest measured consumption per adult *A. chinensis* was approx. 10 prey of third instar *S. subpunctaria* in a day. Therefore, approx.

ten prey were available every day. The predation ability of the female compared to male adult *A. chinensis* was approximately 1:0.72. Therefore, after being paired, the predation rate of the males and females was assigned according to this ratio. The *S. subpunctaria* that died due to predation could be easily identified for their distinctively shrunken body. When the female *S. subpunctaria* were surplus to the male or the males died before the females, the males that developed from the same batch as the test egg were taken as a supplement. However, their data were not included in the experimental data. The growth, survival, predation, and fecundity of *A. chinensis* were recorded daily and the experiments were conducted until all the adults died.

2.2.2. Life Table Study of S. subpunctaria

Under the above conditions, 100 eggs of *S. subpunctaria* laid within 24 h were observed for the life table data. Each newly hatched *S. subpunctaria* was separated and sheltered in a new tube (50 mL) with a fresh tea branch as food. The bottom of each tea branch was wrapped with a moistened cotton ball to keep it fresh. The living age, survival rate (or mortality), development, and fecundity of *S. subpunctaria* at each stage were recorded daily. After the larvae were pupated, each was transferred into a plastic bowl (360 mL) to develop into adult moths. The male and female adults that hatched from pupae on the same day were paired, and the adult survival, sex ratio, and fecundity were recorded daily until all the adults died.

2.3. Data Analysis

2.3.1. Two-Sex Life Table Analysis

The original data of A. chinensis fed on third instar S. subpunctaria and S. subpunctaria fed on tea branch were analyzed using the age-stage, two-sex life table theory [31,35] and the related software [24]. Firstly, the computer program TWOSEX-MSChart-2022-10-25 B100000.exe [36] was used to calculate the age-stage survival rate (s_{xi}) , age-specific survival rate (l_x), female age-specific fecundity (f_x), age-specific fecundity (m_x), age-specific net maternity $(l_x m_x)$, age-stage-specific life expectancies (e_{xi}) , and age-stage-specific reproductive values (v_{xj}) . The population parameters included the intrinsic rate of increase[®], finite rate of increase (λ), net reproductive rate (R_0), and mean generation time (T). Secondly, the CONSUME-MSChart-2022-10-25 B100000.exe program was used to calculate the age-stagespecific predation rate (C_{xi}), age-specific predation rate (k_x), age-specific net predation rate (q_x) , and stage total predation rates P_i and U_i . Finally, the TIMING-MSChart-2022-10-25 B100000.exe program was used to predict the experimental insect populations N(t) and simulate the control ability of A. chinensis on the S. subpunctaria populations P(t). Among them, the bootstrap method was used to estimate the standard errors of the life table parameters [37,38], and the paired bootstrap method was used to compare the mean values between the different stages (p < 0.05) [39]. The drawing used the SigmaPlot v.14.0 software.

The age-stage survival rate (s_{xj}) is the probability that an individual egg would develop to age *x* and stage *j* [35]. It was calculated using the following.

$$s_{xj} = \frac{n_{xj}}{n_{01}} \tag{1}$$

where n_{01} is the number of individuals used at the beginning of the life table study and n_{xj} is the number of individuals surviving to age *x* and stage *j*.

The age-specific survival rate (l_x) is the probability that a newborn will survive to age x. It was calculated using the following.

$$l_x = \sum_{j=1}^{\beta} s_{xj} \tag{2}$$

where β is the number of stages.

The age-specific fecundity (m_x) of a population is defined as the average number of eggs produced by the entire population at age x. It was calculated using the following.

$$m_{x} = \frac{\sum_{j=1}^{\beta} s_{xj} f_{x}}{\sum_{j=1}^{\beta} s_{xj}}$$
(3)

The intrinsic rate of increase (r) of a population, a life table parameter, was calculated using the binary iteration method, as shown in the following equation.

$$\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1$$
(4)

The finite rate of increase (λ) was calculated using the following.

$$\lambda = e^r \tag{5}$$

The net reproduction rate (R_0), which is the mean number of offspring that an individual could produce during its entire lifespan, was calculated using the following.

$$R_0 = \sum_{x=0}^{\infty} l_x m_x \tag{6}$$

The mean generation time (T) is the time that a population needs to increase its size R_0 -fold at the stable age-stage distribution. It was calculated using the following.

$$T = \frac{\ln R_0}{r} \tag{7}$$

The age-stage-specific life expectancy (e_{xj}) is the duration that an individual of age x and stage j is expected to survive after age x. It was calculated using the following.

$$e_{xj} = \sum_{i=x}^{\infty} \sum_{y=j}^{\beta} s'_{iy}$$
(8)

where s'_{iy} is the probability that an individual of age x and stage j will survive to age i and stage y. It was calculated assuming that $s_{xj} = 1$.

The age-stage-specific reproductive value (v_{xj}) is the contribution that individuals of age x and stage j provide to the future population [40]. It was calculated using the following.

$$v_{xj} = \frac{e^{r(x+1)}}{s_{xj}} \sum_{i=x}^{\infty} e^{-r(i+1)} \sum_{y=j}^{\beta} s'_{iy} f_{iy}$$
(9)

2.3.2. Predation Rate Analysis

The predation rates of all the *A. chinensis* individuals were analyzed using the CONSUME-MSChart-2022-10-25 B100000.exe computer program. The age-stage-specific predation rate (C_{xj}) , age-specific predation rate (k_x) , age-specific net predation rate (q_x) , net predation rate (C_0) , transformation rate (Q_p) , and stage total predation rates P_j and U_j were calculated using the following equations. The age-specific predation rate (k_x) is defined as the number of third instar *S. subpunctaria* consumed by the surviving individuals at age *x*. It was calculated using the following.

$$k_{x} = \frac{\sum_{j=1}^{\beta} s_{xj} c_{xj}}{\sum_{i=1}^{\beta} s_{xj}}$$
(10)

In the above equation, the age-stage-specific predation rate C_{xj} is the mean number of third instar *S. subpunctaria* consumed by individual *A. chinensis* of age *x* and stage *j*, where $d_{xj, i}$ is the recorded predation rate for the *i*th individual at age *x* and stage *j*. It was calculated using the following.

$$c_{xj} = \frac{\sum_{i=1}^{n_{xj}} d_{xj,i}}{n_{xj}}$$
(11)

The age-specific net predation rate (q_x) was the product of the age-specific survival rate $(l_x$ and age-specific predation rate (k_x) . It was calculated using the following.

$$q_x = l_x k_x = \sum_{j=1}^{\beta} s_{xj} c_{xj}$$
(12)

The net predation rate (C_0) is defined as the total number of third instar *S. subpunctaria* consumed by an individual predator averaged from all the *A. chinensis* that died in the preadult stages and those that survived to the adult stage during its lifetime. It was calculated using the following.

$$C_0 = \sum_{x=0}^{\infty} \sum_{j=1}^{\beta} s_{xj} c_{xj} = \sum_{x=0}^{\infty} l_x k_x$$
(13)

The transformation rate (Q_p) is defined as the number of *S. subpunctaria* needed for a predator to produce a single offspring. It was calculated using the following.

$$Q_p = \frac{C_0}{R_0} \tag{14}$$

The stage total predation rate (P_j) of an individual in stage *j*, which represents the number of *S*. *subpunctaria* that a predator needs to consume to complete the development of stage *j*, was calculated using the following.

$$P_j = \frac{\sum\limits_{i=1}^{n_j} p_{ij}}{n_j} \tag{15}$$

where p_{ij} is the total prey killed by individual *i* in stage *j* and n_j is the number of surviving individuals in stage *j*.

The stage total predation rate (U_j) includes all the individuals surviving at the beginning of stage *j* and was calculated using the following

$$U_j = \frac{\sum\limits_{i=1}^{m_j} p_{ij}}{m_j} \tag{16}$$

where m_j is the number of individuals that developed to stage j, although some may die in stage j.

The finite predation rate (ω) was calculated according to Yu [41] using the following equation.

$$\omega = \lambda \psi = \lambda \sum_{x=0}^{\infty} \sum_{j=1}^{\beta} a_{xj} c_{xj}$$
(17)

where a_{xj} is the proportion of individuals belonging to age x and stage j in a stable age-stage distribution and ψ is the stable predation rate.

2.3.3. Population and Predation Projections

The computer program TIMING-MSChart-2022-10-25 B100000.exe [42] was used to show the effect of releasing adults *A. chinensis* on the population growth and control capacity of *S. subpunctaria*.

The total population size at time *t* was calculated using the following.

$$N(t) = \sum_{j=1}^{\beta} \sum_{x=0}^{\infty} n_{xj,t}$$
(18)

where $n_{xj,t}$ is the number of individuals of age *x* and stage *j* at time *t* [43,44]. The predation potential at time *t* use calculated using the following

The predation potential at time *t* was calculated using the following.

$$P(t) = \sum_{j=1}^{\beta} \sum_{x=0}^{\infty} c_{xj} n_{xj,t}$$
(19)

3. Results

3.1. Two-Sex Life Table and Predation Rate

3.1.1. Two-Sex Life Table of A. chinensis Fed on Third Instar S. subpunctaria

The individual number and mean developmental periods of A. chinensis fed on S. subpunctaria in each stage were recorded in the whole living period of 100 A. chinensis eggs at 25 °C. Table 1 summarizes the mortality/survival, developmental duration, adult longevity, female fecundity, and sex ratio of A. chinensis at each age. As a natural enemy, A. chinensis could prey on third instar S. subpunctaria and complete its life history. Including the seven different developmental stages, the maximum life span of A. chinensis was 104 d. The mean developmental period of the early ages (eggs stage to the fourth instar nymph) was nearly the same level (5-8 d), and the adult life period was relatively longer than the life period of the early stages. The mean time for the egg stage was 8 days and 82 eggs survived to the first instar nymph. A total of 61 of them lived through this stage. The first nymph had the shortest developmental period (5.03 d). The developmental durations for the second, third, and fourth instar nymphs were steadily around 7 d. The total preadult stage was accumulated to 45.42 d and was significantly longer than that of the remaining adult stage in the life cycle. The mean living period for the female adults was 26.67 d and was longer than the male adults (19.00 d), though with no significant difference. The sizes of the females were slightly lower and the sex ratio for the adults (female/male) was 0.94.

The adult preoviposition period (APOP) of *A. chinensis* was approx. 13.56 d and the oviposition duration was 5.67 d. Six of the fifteen adult females of *A. chinensis* died before oviposition, so the mean fecundity of *A. chinensis* was 56.60 for the fifteen females and 94.33 for the nine maternal females that completed their reproductive life.

The bootstrapping results of the population parameters of *A. chinensis* from a cohort of 100 eggs are shown in Table 2. The population dynamics of *A. chinensis* were exponential with the intrinsic rate of increase (r = 0.0321), and the values of the finite rate of increase (λ) were 1.0327. The net reproductive rate R_0 is the number of offspring an individual is expected to produce during their lifetime (a net reproductive rate of one means that the population is at its demographic equilibrium). This definition envisions the generation time as a renewal time of the population. The R_0 for *A. chinensis* was 8.49, where 8.49 of the

offspring were expected to produce during the *A. chinensis* lifetime. The mean generation time (*T*) was measured as 66.55, which was the average time between two consecutive generations of *A. chinensis* in this research.

Table 1. Individual number and developmental periods (days) (mean \pm SE) of *A. chinensis* fed on *S. subpunctaria* in each stage (cohort size: 100 eggs).

Stage	n	$\mathbf{Mean} \pm \mathbf{SE}$
Egg	82	$8.00\pm0.00\mathrm{d}$
First nymphs (L1)	61	$5.03\pm0.06 \mathrm{f}$
Second nymphs (L2)	50	$7.00 \pm 0.29 \mathrm{e}$
Third nymphs (L3)	43	7.58 ± 0.40 de
Fourth nymphs (L4)	31	$7.23 \pm 0.37 \mathrm{e}$
Fifth nymphs (L5)	31	$11.26\pm0.74\mathrm{c}$
Preadult	31	45.42 ± 1.29
Female adult longevity	15	$26.67\pm3.82a$
Male adult longevity	16	19.00 ± 3.14 ab
Total longevity of females	15	73.20 ± 4.17
Total longevity of males	16	63.38 ± 3.37
Mean longevity of all the individuals	100	34.02 ± 2.62
Sex ratio (female/male)	0.94 (15/16)	-
Adult preoviposition period (APOP)	15	13.56 ± 1.34
Total preoviposition period (TPOP)	15	61.33 ± 1.94
Oviposition days (O_d)	15	5.67 ± 1.20
Mean fecundity (F) (eggs/female)	15	56.60 ± 16.94

The n means the number of live insects that survived at this stage, and the mean refers to the average number of days of development of all the individuals entering this stage. The mean and standard errors (SE) were estimated using the paired bootstrap test 100,000 times. This means that a column followed by the same letter was not significantly different (p < 0.05). L1–L5 is the nymph stage from the first instar to the fifth instar.

Table 2. Population parameters (mean \pm SE) of *A. chinensis* starting from 100 eggs fed on *S. subpunctaria*.

Population Parameters	$\mathbf{Mean} \pm \mathbf{SE}$
Cohort size (n)	100
Intrinsic rate of increase (r) (d^{-1})	0.0321 ± 0.0066
Finite rate of increase (λ) (d ⁻¹)	1.0327 ± 0.0068
Net reproductive rate (R_0) (offspring/individual)	8.49 ± 3.19
Mean generation time (T) (d)	66.55 ± 0.70

The n means the number of cohort sizes, and the mean refers to the average value of the population. The mean and standard errors (SE) were estimated using the paired bootstrap test 100,000 times.

The expected changes in the survival rate of 100 *A. chinensis* eggs in each stage of the entire lifetime are projected in Figure 3. The line of S_{x1} for the egg stage represented that the cohort hatched or died at day 8 and approx. 82% successfully lived to the first nymph stage. The other s_{xj} curves of each stage climbed from the day of emergence of the *j* stage and were then eliminated in the following time due to the death or stage transition to *j* + 1. Therefore, the overlap of s_{xj} for the different stages indicated the phenomenon of the nymphs of various stages appearing at the same age. For example, nymphs covered the L2–L5 stage on day 27 and the overlap of the L3, L4, and L5 nymphs, and adults could be found during days 33–34. This might have been because the development speeds of the *A. chinensis* individuals were relatively low and different at an older age. The adults, especially the females, possessed a long-term trend of low survival rates (Figure 3A).

Further, the age-specific survival rate (l_x) , female age-specific fecundity (f_x) , agespecific fecundity (m_x) , and age-specific net maternity (l_xm_x) of *A. chinensis* are illustrated in Figure 3B. An overall decreasing trend of l_x during the observed 104 d, however, decreased quickly to 54% on the 15th day. The fecundity is the probability of achieving a live offspring within a single cycle. The female age-specific fecundity (f_x) denotes the number of eggs produced by a female adult (15) at age *x* and the age-specific fecundity (m_x) is the number of eggs produced per individual (31 adults) at age *x*. Both curves showed similar patterns and f_x doubled the value of m_x due to the equal ratio of the sexes (0.94) of *A. chinensis* (Table 1). The reproduction began at age 56 d, and the highest peak (10.67 eggs) was observed at the age of 63 d. The $l_x m_x$ of *A. chinensis* was related to l_x and the peak number was 0.96.



Figure 3. (A) Age-stage survival rate (s_{xj}) ; (B) age-specific survival rate (l_x) , female age-specific fecundity (f_x) , age-specific fecundity (m_x) , and age-specific net maternity (l_xm_x) ; (C) age-stage-specific life expectancies (e_{xj}) ; (D) age-stage-specific reproductive values (v_{xj}) of *A. chinensis* fed on *S. subpunctaria*.

The age-stage-specific life expectancy e_{xj} is mathematically the mean number of subsequent lifetimes for *x*-aged *A. chinensis*, or the time remaining at a given age *x* during stage *j* (Figure 3C). It was acquired by assuming that the age-stage-specific mortality rates remained at the measured level of the observed cohort (Table 1). The e_{xj} of *A. chinensis* was lower at the egg and first nymph stages and higher at the L3, L4, and L5 nymph stages, showing a general decline at each stage *j*. However, there were fluctuations for e_{x3} , e_{x5} , and e_{x7} at the second nymph, fourth nymph, and adult stage, respectively. The life expectancy value of the newly laid eggs of *A. chinensis* was 34.02, representing the mean longevity of the cohort (Table 1) surveyed. The maximum longevity of *A. chinensis* was 104 d. The highest statistical life expectancy of *A. chinensis* was $e_{27.6}$ (40.38), appearing at the 27-day aged fifth nymph stage. The female adult *A. chinensis* had a higher life expectancy and a longer age than the male adults. In addition, there was an obvious overlap e_{xj} for the fourth nymph, fifth nymph, female, and male stages aged 36 to 44 days.

The age-stage-specific reproductive value (v_{xj}) describes the contribution of an individual of age *x* and stage *j* to the future population (Figure 3D). The reproductive value

increased in the successive developmental stages and reached a peak value of 64.40 ($V_{60.7}$) at day 60 for the females. The time for the maximum v_{xj} at the adult stage was naturally close to the time of the TPOP (61.33) (Table 1) [45].

3.1.2. Two-Sex Life Table of S. subpunctaria Fed on Tea

To improve the understanding of the biology of *S. subpunctaria* and assess its damage to the tea plant, we investigated the life table of *S. subpunctaria* fed on the tea branch at 25 °C (Table 3). Similarly, the individual number and mean developmental periods of *S. subpunctaria* in each stage were recorded starting from a cohort of 100 eggs (laid within 24 h). Table 3 summarizes the mortality/survival, developmental duration, adult longevity, female fecundity, and sex ratio of *S. subpunctaria* separately at each age.

Table 3. Individual number and developmental periods (days) (mean \pm SE) of *S. subpunctaria* fed on tea in each stage (cohort size: 100 eggs).

Stage	n	Mean \pm SE
Egg	74	$7.04\pm0.10d$
First larvae (L1)	74	$4.26\pm0.12e$
Second larvae (L2)	74	$3.45\pm0.12\mathrm{f}$
Third larvae (L3)	74	$2.78\pm0.11\mathrm{g}$
Fourth larvae (L4)	74	$1.89\pm0.08 { m h}$
Fifth larvae (L5)	74	$4.38\pm0.17\mathrm{e}$
Pupa	72	$9.25\pm0.14c$
Preadult	72	32.86 ± 0.22
Female adult longevity	36	$28.28 \pm 1.56 \mathrm{a}$
Male adult longevity	36	$22.44 \pm 1.09 \mathrm{b}$
Female adult longevity	36	61.28 ± 1.57
Male adult longevity	36	55.17 ± 1.09
Mean longevity of all the individuals	100	44.53 ± 2.37
Sex ratio (female/male)	1 (36/36)	-
Adult preoviposition period (APOP)	36	5.29 ± 0.40
Total preoviposition period (TPOP)	36	38.15 ± 0.45
Oviposition days (O_d)	36	19.18 ± 1.15
Mean fecundity (F) (eggs/female)	36	200.64 ± 30.45

The n means the number of live insects that survived at this stage, and the mean refers to the average number of days of development of all the individuals entering this stage. The mean and standard errors (SE) were estimated using the paired bootstrap test 100,000 times. This means that a column followed by the same letter was not significantly different (p < 0.05). L1–L5 denotes the larva stage from the first instar to the fifth instar.

A total of 74 of the 100 *S. subpunctaria* eggs hatched and then stably survived to L5 through the whole life cycle, except for the size reduction when transited to pupa (72). The mean developmental period was relatively short in the early age, and the preadult stage lasted for approx. 32.86 d. The female adult *S. subpunctaria* had the longest developmental period (28.28 d) and the fourth instar larva (1.89 d) was the shortest. An exact equal ratio of the sexes was observed where the female and male moths were both 36. However, the females lived longer than the males. The adult preoviposition period (APOP) of *S. subpunctaria* was approx. 5.29 d, the oviposition period was 19.18 d, and the mean fecundity of the 36 female adult *S. subpunctaria* was 200.64.

The population parameters of *S. subpunctaria* are shown in Table 4. The intrinsic rate of increase (*r*) was 0.0951 d⁻¹, and the finite rate of increase (λ) was 1.0998 d⁻¹. The net reproductive rate (R_0) was an average of 72.23 offspring from an individual, and it would take an average of 45 d to complete one generation of *S. subpunctaria*.

The projected age-stage survival curves (s_{xj}) of the *S. subpunctaria* populations in each stage of the survey are illustrated in Figure 4A. The probability of the hatched egg survival to the adult stage of *S. subpunctaria* was stable at around 72–74%. The s_{xj} of the female and male adult *S. subpunctaria* was comparable before 47 days. After that, the females would display a higher survival rate and a longer living period.

Population Parameters	Mean \pm SE
Cohort size (n)	100
Intrinsic rate of increase (r) (d^{-1})	0.0951 ± 0.0053
Finite rate of increase (λ) (d ⁻¹)	1.0998 ± 0.0058
Net reproductive rate (R_0) (offspring/individual)	72.23 ± 14.47
Mean generation time (T) (d)	45.00 ± 0.65

Table 4. Population parameters (mean \pm SE) of *S. subpunctaria* starting from 100 eggs fed on tea.

The n means the number of cohort sizes, and the mean refers to the average value of the population. The mean and standard errors (SE) were estimated using the paired bootstrap test 100,000 times.



Figure 4. (A) Age-stage survival rate (s_{xj}) ; (B) age-specific survival rate (l_x) , female age-specific fecundity (f_x) , age-specific fecundity (m_x) , and age-specific net maternity $(l_x m_x)$; (C) age-stage-specific life expectancies (e_{xj}) ; (D) age-stage-specific reproductive values (v_{xj}) of *S. subpunctaria* fed on tea.

From Figure 4B, the age-specific survival rate (l_x) of *S. subpunctaria* showed an overall decreasing trend. The l_x curve of *S. subpunctaria* dropped rapidly to 74% on day 7 and then remained at a static level of 74% up to the first 37 days. In other words, there were no population losses during this period until the pupa stage. The f_x curve and m_x curve for *S. subpunctaria* showed the same increasing and decreasing trend from 34 to 75 days and reached a maximum value (16 and 7.9) at 40 days. The f_x value based on the female was exactly twice as large as the m_x based on all the adults since the two-sex individuals were equal (37) for *S. subpunctaria* in this surveyed cohort.

The age-stage-specific life expectancies (e_{xj}) of *S. subpunctaria* fed on tea were projected in Figure 4C. Due to the stable survival rate and short stage time during L1–L5, the e_{xj} value decreased continually in the successive developmental stages. The value e_{01} represented the life expectancies of the initial 100-egg cohort and was identical to the mean longevity of all the individuals (44.53) (Table 3). In addition, it was close to the mean generation time (45 d) (Table 4). The life expectancy of all the age stages of *S. subpunctaria* decreased during stage *j* (Figure 4C), and the highest statistical life expectancy of *S. subpunctaria* was $e_{6.2}$ (51.72), appearing at the 6-day aged first larvae stage. Furthermore, the female adult *S. subpunctaria* had a higher life expectancy and a longer age than the male adults. The maximum longevity of *S. subpunctaria* was 76 days, and there was an obvious overlap e_{xj} for the pupa, female, and male stages from ages 32 to 40 days.

Conversely, the reproductive value (v_{xj}) (Figure 4D) increased in the successive developmental stages and peaked at day 38 with a maximum of 100.26 ($V_{38.8}$), with a value close to the TPOP (38.15) (Table 3).

3.1.3. Predation Rate

As shown in Table 5, the stage total predation rate of the *A. chinensis* individuals increased with the developmental stage. In the preadult stage, the total predation rate P_j of the *A. chinensis* individuals was 69.26 prey/predator. However, if the individuals that died in the preadult stage were included, the total predation rate U_j was 26.19 prey/predator. Overall, the predation rates of *A. chinensis* in the adult stage were higher (157.29 prey/predator) than in the preadult stage, and the predation of the females was higher than that of the males.

Table 5. The stage total predation rates (P_j) and (U_j) of *A. chinensis* fed on *S. subpunctaria* (cohort size: 100 eggs).

Stage		P _j		U _j
	n _j	$\mathbf{Mean} \pm \mathbf{SE}$	m _j	$\mathbf{Mean} \pm \mathbf{SE}$
Second nymphs	50	4.60 ± 0.16	61	$4.\ 11\pm0.26$
Third nymphs	43	9.09 ± 0.60	50	8.76 ± 0.59
Fourth nymphs	31	16.77 ± 1.19	43	16.42 ± 1.21
Fifth nymphs	31	39.48 ± 3.33	31	39.48 ± 3.33
Preadult	31	69.26 ± 4.17	100	26.19 ± 3.34
Female adult	15	210.47 ± 3.87	15	210.47 ± 3.87
Male adult	16	107.44 ± 4.00	16	107.44 ± 4.00
Adult	31	157.29 ± 21.56	31	157.29 ± 21.56

 P_j is the stage total predation rate of a predator that successfully survived stage *j* and developed to stage *j* + 1 (sample size n_j). U_j is the stage predation rate of those predators which entered stage *j* but potentially died during stage *j* (sample size m_j). The values are shown as the mean \pm the standard error (SE). The standard errors were estimated using resampling (100,000 times).

From the predation parameters shown in Table 6, it can be found that the net predation rate (C_0) of *A. chinensis* on the populations of third instar *S. subpunctaria* was 74.95, and the finite predation rate (ω) was 0.98 d⁻¹. The transformation rate (Q_p) of *A. chinensis* was 8.83, which was the number of *S. subpunctaria* required for *A. chinensis* to lay one egg.

Table 6. The predation parameters of A. chinensis fed on S. subpunctaria.

Predation Parameters	$\mathbf{Mean} \pm \mathbf{SE}$	
Net predation rate (C_0) (prey/individual)	74.95 ± 12.32	
Finite predation rate (ω) (d ⁻¹)	0.98 ± 0.09	
Transformation rate (Q_p) (C_0/R_0)	8.83 ± 6.79	

Values are shown as the mean \pm the standard error (SE). The standard errors were estimated using resampling (100,000 times).

In the lab survey, *A. chinensis* of first nymph stage was too small to prey on third instar *S. subpunctaria* and was raised using 10% hydromel. Therefore, the age-stage-specific predation rate C_{xj} data was measured from the second instar *A. chinensis* nymph. There was an overall increasing tendency in the predation potential from the second instar nymph to



the adult stage. Specifically, the predation rate of female *A. chinensis* was overwhelmingly higher than that of the males (Figure 5A).

Figure 5. (A) Age-stage-specific predation rate (C_{xj}) ; (B) age-specific survival rate (l_x) , age-specific predation rate (k_x) , and age-specific net predation rate (q_x) of *A. chinensis* fed on *S. subpunctaria*.

The age-specific survival rate (l_x) of *A. chinensis* fed on third instar *S. subpunctaria* decreased dramatically during the early age and continuously declined in the following survey period. The maximum longevity was 104 days (Figure 5B). However, the age-specific predation rate (k_x) increased during all the successive developmental stages and presented a high predation rate during the adult stage. However, when l_x was considered, the age-specific net predation rate (q_x) was much lower than the age-specific predation rate (k_x) (9.5) for *A. chinensis* predation on *S. subpunctaria* occurred on days 91–92 and the age-specific net predation rate (q_x) (1.96) on day 53. There was no overlap during the first 11 days since no predations occurred during the egg stage and the first nymph stage of *A. chinensis*.

3.2. Population Projection

To investigate the population development ability and the population dynamics of *A. chinensis* and *S. subpunctaria*, we conducted a population prediction at a temperature of 25 ± 1 °C and a relative humidity of $75 \pm 5\%$ using the computer program TIMING-MSChart-2022-10-25 B100000.exe.

The predicted population growth with the stage structure of *A. chinensis* fed on *S. subpunctaria* is shown in Figure 6A. The prediction based on five pairs of first-fledged adults *A. chinensis* showed a total 87.92 thousand population of *A. chinensis* by 120 days, and the new eggs and nymphs for the next generation emerged on days 24 and 32, respectively.

The predicted population growth of the stage structure of *S. subpunctaria* fed on tea is shown in Figure 6B. The prediction based on an initial 1000 third instar *S. subpunctaria* larvae showed a total 11.82 billion population of *S. subpunctaria* by 120 days. The females emerged on day 15 and the new eggs for the next generation appeared on day 22.

3.3. Population Growth and Predation Capacity

Under the above conditions, we simulated the variation in population size of *S. subpunctaria* starting with 1000 third instar larvae, and five pairs of first-fledged adults *A. chinensis* introduced on the first day (Figure 7). The results showed that the *A. chinensis* populations were able to consume the population of *S. subpunctaria* on day 17. This indicated that *A. chinensis* has great potential to control *S. subpunctaria*.





Figure 6. Simulated stage structure and total population size: (**A**) *A. chinensis* fed on *S. subpunctaria* starting with five pairs of adults (one-day-old); (**B**) *S. subpunctaria* fed on tea starting with 1000 larvae of third instar.



Figure 7. Simulated population growth of *S. subpunctaria* starting with 1000 third instar *S. subpunctaria* larvae and five pairs of one-day-old *A. chinensis* adults released on the same day. The predation potential is the predation ability of *A. chinensis* to *S. subpunctaria* at time *t*.

4. Discussion

Understanding insect survival, reproduction, and stage information helps with longterm and effective pest control [46]. The program of age-stage, two-sex life tables and predation rates could appropriately estimate the demographic variability of insects, including the age-stage, two-sex life table, survival, reproduction, stage information, predation rate, adaptive ability, and the biological control potential of predators and has been widely applied to the theoretical illustration of predator–prey relationships and the biological control practice [47,48]. With continuous refinement this theory has been recognized and employed by an increasing number of entomologists and ecologists [49].

In this study, we applied the age-stage, two-sex life table to determine the development duration of *A. chinensis* and *S. subpunctaria*. Moreover, predicting the effect of natural enemies on pest control is the basis for the application of biological control agents in the field. Thus, we simulated the control potential of *A. chinensis* as the biological control agent (BCA) on *S. subpunctaria*. From the results of the study, the survival rate of *A. chinensis* before stage three was low, which may be related to the fact that *A. chinensis* was from a natural enemy factory and had population degradation problems. In addition, it was

also related to the feeding of 10% hydromel to the first instar *A. chinensis*. Compared to the existing studies, the developmental duration of *A. chinensis* at the nymph stage differed from the studies on *A. chinensis* predation on *M. separata* [20], where each stage was prolonged, which may have been related to the different nutrients contained in the prey [19]. The longevity of the female adults of *A. chinensis* was higher than that of the male adults (Figure 3A), which may be related to the fact that the female adults were more adaptive than the males [50]. The predation ability for the female adults of *A. chinensis* was higher than that of the male adults (Figure 5A), which may be related to the fact that may be related to the fact that *A. chinensis* live longer in females than in males, and the female adults need to consume more prey and absorb more nutrients to reproduce [51].

Although the *S. subpunctaria* ($R_0 = 72.23$) (Table 4) population seemingly possessed a stronger developmental potential than the population of *A. chinensis* ($R_0 = 8.49$) (Table 2), the simulation showed that *A. chinensis* consumed the population of *S. subpunctaria* in 17 days (Figure 7). This was inextricably linked to the predatory ability of *A. chinensis* ($C_0 = 74.95$) (Table 6) and indicated that *A. chinensis* possessed great control potential on *S. subpunctaria*. In this study, we calculated both the p_j and u_j . However, theoretically, the total stage predation p_j seemed to reflect the true value of the total stage predation of the caterpillars better than the u_j . According to the predation results of *A. chinensis*, we can reasonably infer that the natural enemy *A. chinensis* should be released in tea plantations as soon as possible at the beginning of a *S. subpunctaria* outbreak. The senior (older than the third nymph stage) or adult *A. chinensis* should be selected instead of the egg and other early nymph stages (Table 6).

In this study, our population projection was based on the premise that constant and sufficient prey was provided. However, the predation rate of *A. chinensis* in the field may vary. Further, variable temperatures [52], food availability [53], light [54], and humidity [55] can also affect the population predictions of biological control agents and target pests. We did not consider the effects of the predator density, prey density, and prey stage when conducting the computer simulations. Thus, the population predictions at constant laboratory temperatures may differ from those at naturally fluctuating temperatures [56]. Future research needs to consider applications in various field conditions to achieve more accurate population prediction results [57].

Overall, our results proved that *A. chinensis* has a strong potential to control *S. subpunctaria*. When *A. chinensis* is released into tea plantations, they can effectively control large outbreaks of *S. subpunctaria* and form colonies in the field environment.

5. Conclusions

In this study, to improve the understanding of the life history of A. chinensis and S. subpunctaria, we used the age-stage, two-sex life table method to analyze the developmental duration and fecundity of S. subpunctaria fed on tea branches, and A. chinensis fed on third instar S. subpunctaria larvae starting from the second instar nymph, under 25 °C conditions. The results showed that the predator A. chinensis and the tea plantation pest S. subpunctaria can complete their respective life histories. However, the developmental durations at each stage were different, and the developmental stages overlapped significantly. Other than this, to improve our understanding of the variety of insect populations, we simulated the stage structures and total population sizes of A. chinensis and S. subpunctaria using a computer program. To evaluate the control potential of A. chinensis as a natural enemy against the pest S. subpunctaria, we also simulated the population changes of S. subpunctaria during the A. chinensis intervention. The results showed that the S. subpunctaria population seemingly possessed a stronger developmental potential than the population of A. chinensis, but the predation rate of A. chinensis and the computer simulations inferred that A. chinensis has a strong control potential on S. subpunctaria. This study provides a basis for predicting the outbreak timing of *S. subpunctaria* and provides a reference to achieve effective pest management in tea plantations and to protect the diversity of agroecosystems.

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