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Biocontrol performance and mass production potential of the larval endoparasitoid *Campoletis chlorideae* Uchida (Hymenoptera: Ichneumonidae) against the fall armyworm, *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae)

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Abstract

Background The fall armyworm (FAW), *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae), is an aggressive pest species that causes severe economic losses in outbreak regions. Use of FAW natural enemies, particularly native parasitoids, has been suggested as a promising control strategy. *Campoletis chlorideae* Uchida (Hymenoptera: Ichneumonidae) is a solitary ichneumonid larval endoparasitoid with a broad host range that includes *S. frugiperda*. However, its parasitism rate, developmental stages, and population dynamics during parasitization of *S. frugiperda* remain unclear. A field survey was conducted to determine the emergence rate and sex ratio of *C. chlorideae*, evaluated the biological control performance, and investigated the production potential of it on the individually reared and group-reared *S. frugiperda* through age-stage, two-sex life tables, respectively.

Results The results showed that *C. chlorideae* parasitizing individually reared FAW resulted for the parasitoid in a lifetime total fecundity (F) of 301.5 ± 16.4 eggs/female, a net reproduction rate (R_0) of 62.03 ± 9.07 adult females/female, an overall life span of females of 28.3 ± 0.52 days, and an intrinsic rate of increase (r) of 0.1946 ± 0.0076 day^{-1}. In contrast, the parameters of F, R_0, overall life span of females, and r were 87.71 ± 6.32 pupae/female, 6.02 ± 1.61 adult females/female, 25.21 ± 0.79 days, and 0.0918 ± 0.0148 day^{-1} in group-reared *S. frugiperda*.

Conclusions This study suggests that *C. chlorideae* has a promising biological control potential against *S. frugiperda*. Future research should focus on developing methods to increase the production of *C. chlorideae*.

Keywords *Spodoptera frugiperda*, Field investigation, *Campoletis chlorideae*, Biological control, Mass production, Two-sex life table

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Background

Spodoptera frugiperda (J. E. Smith) (Lepidoptera: Noctuidae) is a pest native to tropical regions of the Americas (Kenis et al. 2023) that has recently spread to Africa, Asia, and Oceania. Since 2019, this pest has rapidly expanded over 1,538 counties in 26 Chinese provinces between 2019 and 2020 (Zhang et al. 2021). This resulted in a significant damage to thousands of hectares of maize (*Zea mays* L.) and other crops, representing a growing threat to agricultural productivity and food security (Wu et al. 2021). Previous reports of maize yield loss from *S. frugiperda* ranged from 40 to 72%, but losses can be as high as 100%, essentially eliminating a season's crop (De Groote et al. 2020). The Centre for Agriculture and Bioscience International (CABI) has reported that if appropriate control measures are not taken, maize yield losses from *S. frugiperda* in 12 African countries could total 8.5 to 21 million tons annually. This could cost around $2.5 billion to $6.3 billion (Day et al. 2017). As a highly polyphagous agricultural pest, *S. frugiperda* can feed on over 185 different plant species across 42 families, with maize, rice (*Oryza sativa* L.), and sorghum (*Sorghum bicolor* (L.) Moench) being particularly preferred hosts (Wu et al. 2021). The reproduction ability and growth rate of *S. frugiperda* are remarkable—females can produce more than 1000 eggs within a life cycle of approximately 30 days (Firake and Behere 2020). Due to the significant risk this pest poses to crops, it was designated among the top 10 most dangerous plant pests in the world by the CABI in 2017 (https://www.cabi.org/isc/fallarmyworm).

Management of the *S. frugiperda* primarily relies on the application of chemical pesticides. However, there is a significant concern regarding the harmful impacts of these compounds on human health, non-target species, and the environment, and overuse/overreliance on chemical pesticides has a high probability of resulting in the selection of insecticide-resistant pest populations (Palma-Onetto et al. 2021). Therefore, alternative control strategies are increasingly needed, with natural enemies potentially being one key biocontrol agent since they have been broadly used both for preventive and curative control of a number of insect pests, including targeting *S. frugiperda* (Kenis et al. 2023). *Campoletis chlorideae* Uchida (Hymenoptera: Ichneumonidae) is an endoparasitic wasp that parasitizes early-stage larvae of more than 30 lepidopteran species, including *Helicoverpa armigera* (Hübner), *H. assulta* (Guenée), *Spodoptera litura* (Fabricius), and *Mythimna separata* (Walker) (Liu et al. 2012). *C. chlorideae* also plays an important role in limiting the population size of lepidopteran pests. Recently, it has been identified as a native parasitoid of FAW larvae in China (Niu et al. 2021) and India (Navik et al. 2021). Previous study has shown that *C. chlorideae* adults prefer to parasitize 2nd–3rd instars of *S. frugiperda* (Tian et al. 2021). Laboratory studies have also found that the parasitism ((number of parasitized hosts/total number of test hosts) × 100%) and eclosion rates ((number of adults after eclosion/total number of cocoons) × 100%) of *C. chlorideae* from *S. frugiperda* 2nd instar can reach 82 and 85%, respectively (Tian et al. 2021). Thus, *C. chlorideae* is a promising natural enemy resource that may be developed as a biological control agent for the control of FAW in the field. However, the biological control capacity of *C. chlorideae* against *S. frugiperda* using it as a host is still unclear. In addition, the use of parasitoids in the field requires reliable and economically feasible mass production (Zang et al. 2021). To improve practical applications, hosts must be mass-reared, and proper mass production techniques are essential to reduce production costs and improve production efficiency (Wang et al. 2020). *S. frugiperda* has a high reproductive capacity and a short life cycle, which suggests it may be an ideal host for mass-produced *C. chlorideae*. However, one potential limitation is that, similar to many other lepidopterans, 4–6th instars *S. frugiperda* exhibit cannibalism when reared in groups (Hou et al. 2022). To overcome this challenge, an artificial diet limiting cannibalism was recently developed (Chen et al. 2022), enabling the potential of group-reared *S. frugiperda* in *C. chlorideae* mass production to be further evaluated.

Here, parasitoid cocoons of *C. chlorideae* were collected from a *S. frugiperda*-infested maize field in Guizhou Province, China, and the species was identified by cytochrome c oxidase subunit I (COI) sequencing through sequence alignment and phylogeny evolution analysis. An age-stage, two-sex life table analysis was then performed on individually reared *S. frugiperda* to estimate the biological control capacity of *C. chlorideae*. In addition, the potential for mass rearing of *C. chlorideae* for release was assessed using an age-stage, two-sex life table when *S. frugiperda* were reared in group conditions. These results showed that *C. chlorideae* has considerable promise as a larval parasitoid of *S. frugiperda*, with favorable biocontrol performance and acceptable mass production potential when the FAW larvae are group-reared on an optimized artificial diet.

Methods

Rearing the host insect, *S. frugiperda*

A laboratory colony of the host insect *S. frugiperda* was started with larvae collected from maize fields in Qiannan Bouyei and Miao Autonomous Prefecture (105.4074° E, 25.0488° N), Guizhou Province, China, and maintained in a climate-controlled room (25 ± 1 °C, 70 ± 5% RH, and 14 L: 10 D). The larvae were maintained in polystyrene Petri dishes and fed an artificial diet (Pinto et al. 2019). To

avoid cannibalism (He et al. 2021), all the 4th instar individuals were reared separately until pupation in 28-compartment boxes (17.5×11×2.5 cm), hereafter called rearing boxes, which is provided by Shenzhen Daji Plastic Packaging Co., Ltd. (Shenzhen, China). *S. frugiperda* pupae were collected and placed into transparent plastic boxes covered with white PP (polypropylene) non-woven fabric as an egg-laying substrate for the emerging adults. A 10% honey solution (v/v) was provided as a food source and replaced daily. After egg laying, substrates with egg masses were collected daily.

Collection and rearing of *C. chlorideae*

To establish *C. chlorideae* population, intact cocoons were collected from a *S. frugiperda*-infested maize field in Huaxi District (106.6776° E, 26.4490° N, 1119 m), Guiyang, Guizhou Province, China, and returned to the laboratory. A survey was conducted to investigate the emergence rate and sex ratio of parasitoid cocoons collected from the field. For rearing of *C. chlorideae*, a pair of newly emerged parasitoids (one female and one male) were placed into transparent plastic boxes (13.5×8.2×6.8 cm) with gauze (200-mesh). A cotton ball soaked in a 10% honey-water solution (v/v) was attached to the inner wall of the box and refreshed every 24 h. Seventy 2nd instar *S. frugiperda* with an artificial diet were transferred into the box for parasitization. After a 24-h exposure, the wasps were removed, and the hosts were separated into multiple rearing boxes until new wasps emerged from parasitized FAW larvae.

Morphology and molecular identification of *C. chlorideae*

For the morphological analysis, twenty 3-day-old *C. chlorideae* females that had mated but not laid eggs were placed into twenty separate glass tubes containing thirty 2nd instar *S. frugiperda* and allowed to lay eggs within 30 min. All these *S. frugiperda* larvae were examined one by one under a stereomicroscope. Briefly, the larvae were placed individually on the stage of the stereomicroscope. The lower light source lamp was turned on, and the body of the larva was gently pressed with a small brush and held in the center of the field of view of the stereomicroscope. The larval body was then gently rolled with a small brush to check for the presence of the light-brown, oval-shaped *C. chlorideae* eggs about 350–400 µm (Fig. A, B) inside the larval body. If eggs were found inside the larvae, parasitism was confirmed. From there, the successfully parasitized larvae were selected and transferred to rearing boxes reared separately. The parasitoid wasp completed the egg to larval stage in the host larvae and then completely replaces the host larvae, after which it transforms into a pupa and then emerges as an adult. In this experiment, 15–20 parasitized larvae were used to dissect for observing the developmental morphology of *C. chlorideae* under a stereomicroscope every 24 h as per the protocol of Pourian et al. (2015) after the parasitoid laid its eggs. The morphology of three-day-old adult females and males was also observed under a stereomicroscope, based on the original description (Uchida 1957).

For COI sequence analysis, the genome of adult parasitoids was extracted using a genomic DNA extraction kit according to manufacturer's instructions (Tiangen, Beijing, China). The genomic DNA was used as a template for polymerase chain reaction (PCR) amplification with the COI primer pair (COI-F: 5′-GGTCAACAAATCATAAAGATATTGG-3′ and COI-R: 5′-TAAACTTCAGGGTGACCAAAAAATCA-3′) (Vrijenhoek 1994) with the following PCR conditions: 94 °C 3 min; 94 °C 30 s, 50 °C 30 s, 72 °C 30 s, 35 cycles; 72 °C 5 min. The PCR products were purified after agarose gel electrophoresis using a gel extraction kit (Tiangen, Beijing, China) before sequencing (Chengdu Sangon Biotech). The sequencing results were analyzed using DNAMAN8.0 and BLAST in National Center for Biotechnology Information (NCBI). A phylogenetic tree based on the partial COI sequences was constructed using MEGA X with Neighbor-Joining method for 1000 bootstrap (Kumar et al. 2018).

Developmental and parasitization parameters of *C. chlorideae* on *S. frugiperda* 2nd instar

In order to determine the pre-adult stage parameters of the two-sex life table of *C. chlorideae* on the individually reared *S. frugiperda*, 70 larvae (2nd instar) were introduced into a box used for parasitism and provided with an artificial diet. A pair (a mated female and a mated male) of 3-day-old *C. chlorideae* were released into the box, allowed to oviposit for 24 h, and then removed. Approximately twenty *S. frugiperda* successfully parasitized by stereoscopic observation without dissection were selected from the box and transferred to individual rearing boxes. Every 24 h, the immatures *C. chlorideae* were checked, and the developmental time was recorded until all *C. chlorideae* had either emerged or died. The experiment was repeated with a total of 10 pairs, resulting in a total of 209 parasitized larvae that were used for experimental observation to record developmental stages and survival rates.

The pre-adult parameters of the two-sex life table of *C. chlorideae* on group-reared *S. frugiperda* were investigated similarly using a separate cohort of *S. frugiperda* reared in group conditions, resulting in a total of 204 parasitized larvae that were investigated. Adult stage parameters, including fecundity, longevity, and parasitism rate of *C. chlorideae* on both individually reared and group-reared 2nd instar *S. frugiperda*, were investigated

using a new cohort of FAW larvae. Specifically, a pair of newly emerged (< 6 h-old) female and male wasps was first allowed to mate in a glass tube (12 × 3 cm) and they placed into transparent plastic boxes (13.5 × 8.2 × 6.8 cm) with 70 2nd instar *S. frugiperda* available for subsequent parasitization. FAW larvae were removed from the tube every 24 h and replenished with 70 larvae until all *C. chlorideae* were dead. During parasitization, if the male wasp died prior to the female, it was replaced with another male. To measure lifetime fecundity, the number of *C. chlorideae* eggs on each *S. frugiperda* larvae was counted and recorded (all the eggs were counted when one larva had several eggs) before each transfer. For each replicate (a pair of *C. chlorideae*), all the parasitized were reared individually as previously described until the larvae died or continued to survive without parasitoid emergence or died with parasitoid emergence. A total of 17 replicates were performed to investigate these adult stage parameters of *C. chlorideae* on individually reared FAW larvae.

The fecundity, longevity, and parasitism rate of adult *C. chlorideae* on group-reared 2nd instar *S. frugiperda* were analyzed similarly, except that the FAW was group-reared after parasitism until the emergence of wasps. The lifetime fecundity data in group-rearing conditions were investigated with the number of parasitoid's pupae rather than the number of *C. chlorideae* eggs and this treatment was performed with 27 replicates.

Data analyses

A bootstrap-match technique developed by Amir-Maafi et al. (2022) for life tables was used to match the data of the pre-adult stage and the adult stage under both individual- and group-rearing conditions, respectively. Life table data (i.e., the developmental duration, survival rate, longevity, and total fecundity) of *C. chlorideae* parasitizing the 2nd instar of *S. frugiperda* were analyzed using the age-stage, two-sex life table method (Chi and Liu 1985; Chi and Su 2006; Tuan et al. 2014; Chi et al. 2020) according to the TWOSEX-MSChart (Chi 2022a). The age-stage-specific parasitism rate (c_{xj}, where x is age and j is stage) was calculated based on the method of Chi and Yang (2003) by using the CONSUME-MSChart computer program (Chi 2022c). The population growth and parasitic capacity of *C. chlorideae* were projected using Timing-MSChart (Chi 2022b). All these formulas and definitions used in this study are shown in Table S1. Unless stated otherwise, some of these formulas and definitions are derived from other works (Goodman 1982; Chi 1990; Farhadi et al. 2011; Huang and Chi 2013; Yu et al. 2013; Mou et al. 2015). The variances and standard errors (SE) of these population parameters were estimated by the bootstrap resampling method with 100,000 re-samplings ($B = 100{,}000$) (Huang and Chi 2011; Li et al. 2022). The 0.025th and 0.975th percentiles of the finite rate of increase (λ) from the sorted 100,000 bootstrap samples were used to represent the variability of population growth and parasitic potential, according to Huang et al. (2018). All figures were created using Sigma Plot 14.0.

Results

Campoletis chlorideae identification, morphology, and field investigations

The ontogenetic development of *C. chlorideae* can be divided into four stages: the egg (embryonic period, Fig. 1A, B), larval (postembryonic development, Fig. 1C–E), pupal (Fig. 1F–H), and adult (Fig. 1O, P). Overall egg dimensions were found to be ~ 50–100 µm × 300–400 µm within the host larvae, and this stage lasted for ~ 2 days before further development was seen. The egg/embryo development proceeded with the emergence (still within the host larvae) of a larva with a light-brown head capsule, a smooth and transparent body about 600–900 µm, an elongated tail, and a pale green gut, occurring over the next 2–3 days (Fig. 1C, D). At the late larval stage (~ 3 days), the wasp morphology changed from caudate type to hymenopteriform (wasp-like) shape, and the intestine changed from pale yellow to pale green (Fig. 1E, G). At ~ 7 days postparasitization the mature larvae emerged from the host and appeared pale pink throughout the sexually dimorphic body. Mature female larvae (Fig. 1H) had three pairs of ova-like depressions on the surface of the ventral segments 10, 11, and 12, whereas mature male larvae had an unpaired ova-like depression near the posterior edge of segment 12. The entire larval stage lasted 6–8 days, with the body length reaching around 1–4 mm.

The cocoon was weaved by the larvae after emergence and appeared white to off-white with small black dots in the cocoon silk, with overall measurements of ~ Ø 2 mm × 6 mm (Fig. 1I). The dissected pupae were long, ovate, and milky white, with colorless compound eyes that gradually turned red and then black, with the color of the emerging insect body also changing from light to dark over time (Fig. 1J–N). Three days into the pupal stage, the ovipositor of female pupa developed at the end of the abdomen (Fig. 1K). The pre-pupal and pupal stages lasted 5–7 d, reaching a body length of about 4–6 mm. Male *C. chlorideae* typically underwent eclosion earlier than females. The body length of male and female adults was around 5–6 mm, both with a pair of long antennae and a yellow, narrow abdomen. Adult males were usually smaller than females, and females displayed a long, pronounced ovipositor (Fig. 1O).

BLAST analysis of the DNA barcode segment of the COI gene using the NCBI database showed 100% query

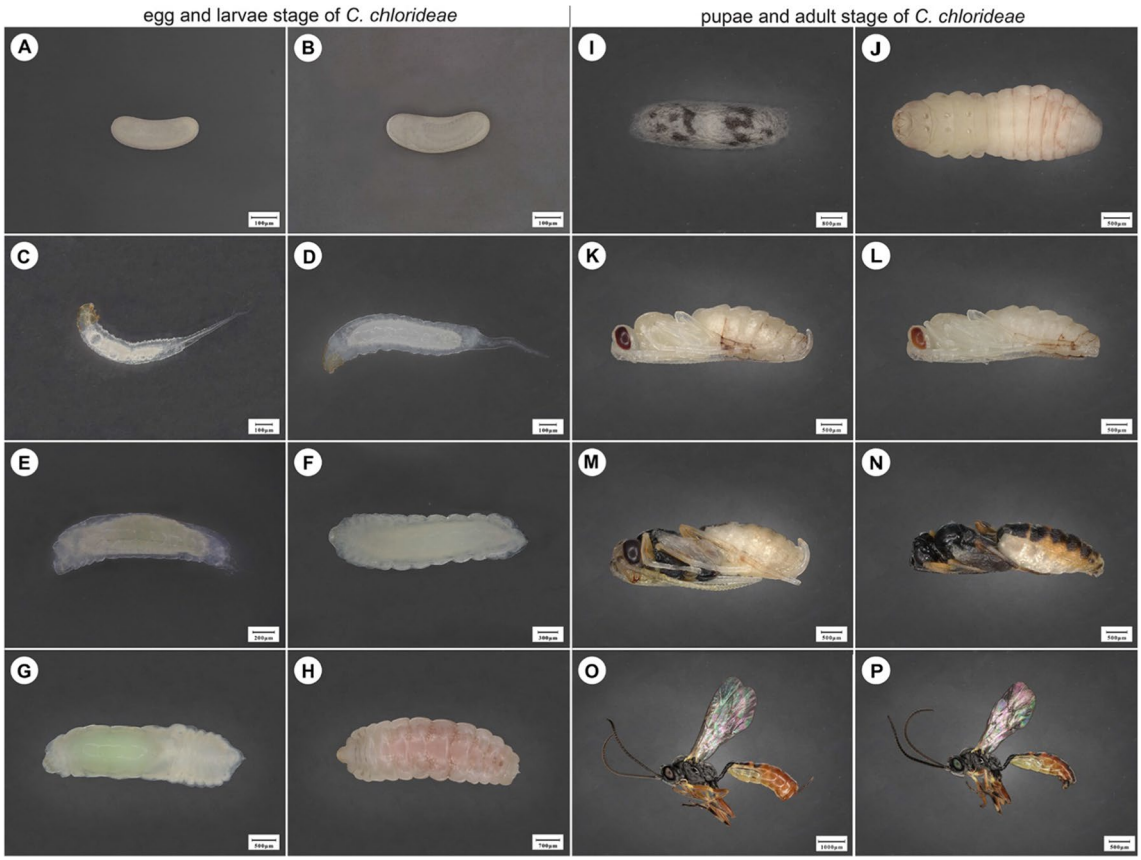

Fig. 1 Morphological changes of *Campoletis chlorideae*. **A**, **B** 1–2-day-old eggs of *C. chlorideae;* **C**–**G** 3–7-day-old larvae of *C. chlorideae;* **H** the mature larvae-female emerged from the host body. **I** cocoon of *C. chlorideae;* **J** prepupae stage of *C. chlorideae*; **K**–**N** pupae stages of *C. chlorideae*; **O** adult female *C. chlorideae*; **P** adult male *C. chlorideae*

coverage and the sequence showed 99.85% identity to *C. chlorideae* voucher sample SCAU 3048973 (GenBank accession number: MW250777). The phylogenetic tree revealed that the COI sequence clustered with the previously identified COI sequences of *C. chlorideae* (Fig. 2). *C. chlorideae* cocoons were collected from a *S. frugiperda*-infested maize field in Huaxi District, a total of 20 cocoons. The emergence rate of *C. chlorideae* from cocoons was 85%, with ~ 30% females.

Longevity and lifetime fecundity of *C. chlorideae* parasitizing *S. frugiperda* larvae

The developmental periods for each stage of *C. chlorideae* from individually reared and group-reared *S. frugiperda* larvae are summarized in Table 1. For individually reared insects, the total pre-adult developmental time was 17.11 ± 0.16 days with an egg–larva and pupa duration of 9.98 ± 0.12 and 7.28 ± 0.08 days, respectively. The proportion of males ($N_f/N = 0.2057 \pm 0.03$ and $N_m/N = 0.3733 \pm 0.03$) was significantly higher than the proportion of females ($P < 0.05$). Mean female adult longevity (11.02 ± 0.49 days) was slightly longer than males (9.04 ± 0.47 days), resulting in a slightly longer overall life span of females (28.3 ± 0.52 days) compared with males (26.05 ± 0.53 days). Females started to lay eggs as soon as they emerged, showing no obvious adult pre-ovipositional period (APOP). Therefore, the total pre-ovipositional period (TPOP) of 17.28 ± 0.26 days was similar to the total pre-adult developmental time. The duration of the ovipositional period was 9.95 ± 0.38 days, with a mean daily ovipositional rate of 30.3 eggs/female and a total fecundity (*F*) of 301.5 ± 16.4 eggs/female. For group-reared *S. frugiperda*, the developmental times for egg–larva, pupa, and pre-adult were 8.82 ± 0.07, 7.02 ± 0.14, and 15.72 ± 0.15 days, respectively. The proportion of males in the group-reared cohort was $N_f/N = 0.0687 \pm 0.02$ and $N_m/N = 0.2452 \pm 0.03$. The average adult longevity of *C. chlorideae* females was 8.79 ± 0.59 days, which was slightly shorter than males (9.54 ± 0.42 days), but the average overall life span between females and males was similar: 25.21 ± 0.79 and 25.06 ± 0.46 days, respectively. There was no obvious APOP for the *C. chlorideae* female

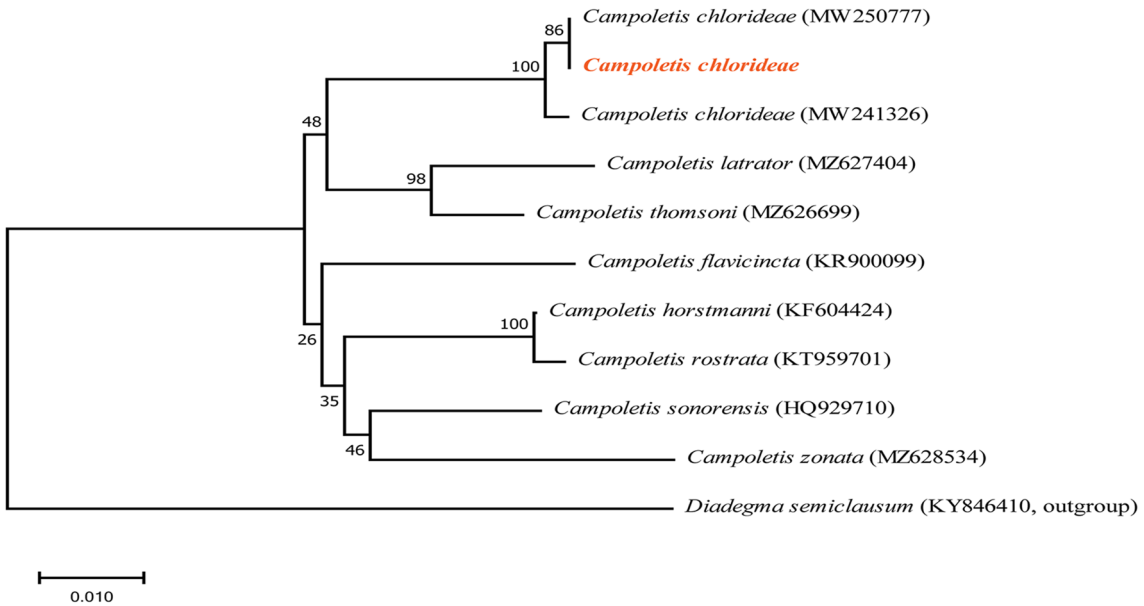

Fig. 2 Phylogenetic analysis of the identified partial COI of *Campoletis chlorideae* and 10 homologies from other species, including nine homologies of *C. chlorideae* and one homology from *Diadegma semiclausum*

Table 1 Means ± SE of developmental times, adult longevity, total longevity, adult pre-ovipositional period (APOP), total pre-ovipositional period (TPOP), ovipositional days, and total fecundity of *Campoletis chlorideae* parasitizing the 2nd instar of *Spodoptera frugiperda* (*2nd Sf*) under individual- and group-rearing conditions

Parameters	*C. chlorideae* on *2nd Sf* in IR[1]		*C. chlorideae* on *2nd Sf* in GR[2]	
	Number of individuals	Means ± SE	Number of individuals	Means ± SE
Egg-larva duration (days)	171	9.98 ± 0.12	146	8.82 ± 0.07
Pupa duration (days)	121	7.28 ± 0.08	64	7.02 ± 0.14
Total pre-adult duration (days)	121	17.11 ± 0.16	64	15.72 ± 0.15
Female adult longevity (days)	43	11.02 ± 0.49	14	8.79 ± 0.59
Female total longevity (days)	43	28.3 ± 0.52	14	25.21 ± 0.79
Male adult longevity (days)	78	9.04 ± 0.47	50	9.54 ± 0.42
Male total longevity (days)	78	26.05 ± 0.53	50	25.06 ± 0.46
Adult pre-ovipositional period (APOP) (days)	43	0.00 ± 0.00	14	0.07 ± 0.07
Total pre-ovipositional period (TPOP) (days)	43	17.28 ± 0.26	14	16.50 ± 0.39
Oviposition days (O_d)	43	9.95 ± 0.38	14	7.21 ± 0.60
Total fecundity (*F*)	43	301.5 ± 16.4	14	87.71 ± 6.32
Proportion of female individuals (N_f/N)	209	0.2057 ± 0.03	204	0.0687 ± 0.02
Proportion of male individuals (N_m/N)	209	0.3733 ± 0.03	204	0.2452 ± 0.03
Proportion of pre-adult mortality (N_n/N)	209	0.4210 ± 0.03	204	0.6862 ± 0.03

SEs were estimated by using the bootstrap technique with 100,000 resampling

[1] Individually-reared *S. frugiperda*, [2]Group-reared *S. frugiperda*

adults (0.07 ± 0.07 days), and they demonstrated similar TPOP (16.5 ± 0.39 days) and total pre-adult development times (15.72 ± 0.15 days). The ovipositional period of *C. chlorideae* females was 7.21 ± 0.60 days, and the total fecundity (*F*) was 87.71 ± 6.32 pupae, with a mean daily ovipositional rate of 12.17 pupae/female.

Age-stage and age-specific survival rate and fecundity of *C. chlorideae* parasitizing *S. frugiperda* larvae

The age-stage-specific survival rate (s_{xj}) is the probability of a newborn offspring surviving to age *x* and stage *j*. Attributable to the developmental time variables among individuals, there were overlaps in the s_{xj} among stages.

For individually reared wasps, the s_{xj} of *C. chlorideae* in the egg-larva stage was high (> 80%) in the first 8 days but decreased sharply as they pupated at 8–10 d (Fig. 3A). The highest number of wasps in the pupal stage (71%) was seen on day 12th. Within ~ 20 days after egg depositing, approximately 33% of the emerging population were males (19 d) and 20% females (20 d), with ~ 47% mortality (i.e., those that did not live to the adult stage) seen. Starting at ~ 24 d, gradual mortality of adult males and females was seen until the population expired at ~ 34–36 d.

For group-reared wasps, egg-larva dynamics were similar to those of the individually reared ones; however, the pupae appeared to emerge faster, with the s_{xj} of an adult male population of ~ 20–25% (16–20 d) and an adult female population of only 7–8%, indicating an overall survival to adult stage of only 28–33%, with 67–72% mortality (Fig. 3B).

The age-specific survival rate (l_x) represents the survival rate from egg to age x, which ignores stage differentiation and is the sum of s_{xj} of all stages at age x. The value of l_x of *C. chlorideae* decreased steadily for individually reared wasps (Fig. 3C). The female age-specific fecundity (f_{x3}) began at day 14, peaked at 19 days (42.41 offspring/female) gradually declined over the next 16 days. The population age-specific fecundity (m_x) and age-specific net maternity ($l_x m_x$) reached their highest values on the 5th day after emergence (i.e., 19 d), and these peaks were 14.14 offspring/female and 7.91 offspring/female, as shown in (Fig. 3C).

In the group-reared condition, the value of l_x decreased fastest at 9–15 days (Fig. 3D). The value of f_{x3} nearly reached its maximum value initially (19.33 offspring/female, 16 d), but it then decreased rapidly with minor fluctuations. The values of m_x and $l_x m_x$ displayed a similar trend as in the individual rearing condition, in which they reached their highest values at 19 days (3.03 offspring/female and 0.95 offspring/female, respectively).

Life expectancy and reproductive value of *C. chlorideae* parasitizing *S. frugiperda* larvae

The life expectancy value (e_{xj}) of a newly laid egg of *C. chlorideae* (age of 0 day) under individual rearing

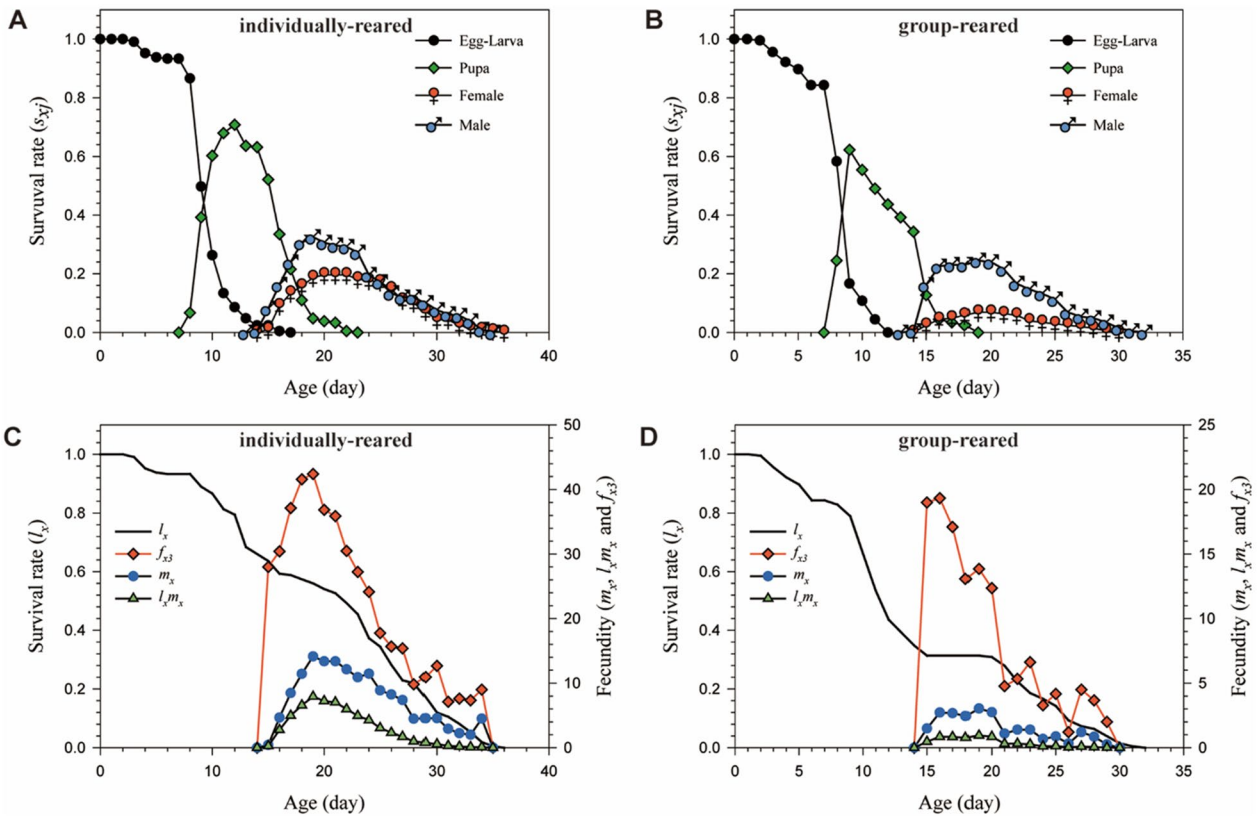

Fig. 3 Age-stage survival rate and age-specific survival rate of *Campoletis chlorideae* parasitizing the individually reared and group-reared *Spodoptera frugiperda*. Age-stage survival rate (s_{xj}) of *C. chlorideae* parasitizing the 2nd instar of *S. frugiperda* in individually rearing (**A**) and group-rearing conditions (**B**). Age-specific survival rate (l_x), female age-specific fecundity (f_{x3}), population age-specific fecundity (m_x), and age-specific net maternity ($l_x m_x$) of *C. chlorideae* parasitizing the 2nd instar of *S. frugiperda* in individually rearing (**C**) and group-rearing conditions (**D**)

conditions was 20.36 days (Fig. 4A). The highest e_{xj} for the *C. chlorideae* pupae was 14.61 days at 8 days postparasitism, while the peak life expectancy of adult females was 13.29 days at 15 days postparasitism. This e_{xj} in female adults was longer than in male adults, which peaked at 11.64 days at 14 days postparasitism. In contrast, the e_{xj} was 14.61 days for newly laid eggs under the group-rearing condition, after which the value of the e_{xj} showed a downward trend (Fig. 4B). The highest e_{xj} for the pupae, adult females, and adult males was 10.11, 10.21, and 11.06 days at the ages of 15-, 15-, and 14-days postparasitism, respectively.

The female-specific reproductive value of (v_{xj}) *C. chlorideae* was 169.07 d^{-1} at 16 days postparasitism when the female adults emerged immediately in the individually reared condition (Fig. 4C). The reproductive value at the age of zero ($v_{0,1}$) was equal to the finite rate of increase (λ), which was 1.2148. On the other hand, the peak age-stage reproductive value (v_{xj}) of *C. chlorideae* occurred at 15 days (87.28 d^{-1}) after parasitization in the group-reared larvae and then gradually decreased (Fig. 4D). The reproductive value at the age of zero ($v_{0,1}$) or finite rate of increase (λ) for this group-reared condition was 1.0961.

Population parameters of *C. chlorideae* parasitizing *S. frugiperda* larvae

The population demographic parameters of *C. chlorideae* parasitizing *S. frugiperda* 2nd instar under individual- and group-rearing conditions were examined (Table 2). Under individual rearing conditions, the R_0 and T (the time required to achieve R_0 when the population reached a steady growth rate ($\lambda = 1.2148 \pm 0.0092$ and $r = 0.1946 \pm 0.0076$) of the *C. chlorideae* population in *S. frugiperda* larvae were 62.03 ± 9.07 females and 21.21 ± 0.27 d. Under group-rearing conditions,

Table 2 Population parameters (means ± SE) of *Campoletis chlorideae* parasitizing the 2nd instar of *Spodoptera frugiperda* under both individual- and group-rearing conditions

Population parameters	*C. chlorideae* on 2^{nd}Sf in IR[1]	*C. chlorideae* on 2^{nd}Sf in GR[2]
Intrinsic rate of increase (r) (day^{-1})	0.1946 ± 0.0076	0.0918 ± 0.0148
Finite rate of increase (λ) (day^{-1})	1.2148 ± 0.0092	1.0961 ± 0.0162
Net reproductive rate (R_0) (adult females/female)	62.03 ± 9.07	6.02 ± 1.61
Mean generation time (T) (day)	21.21 ± 0.27	19.56 ± 0.50

SEs were estimated by using the bootstrap technique with 100,000 resampling. [1] Individually reared *S. frugiperda*, [2] Group-reared *S. frugiperda*

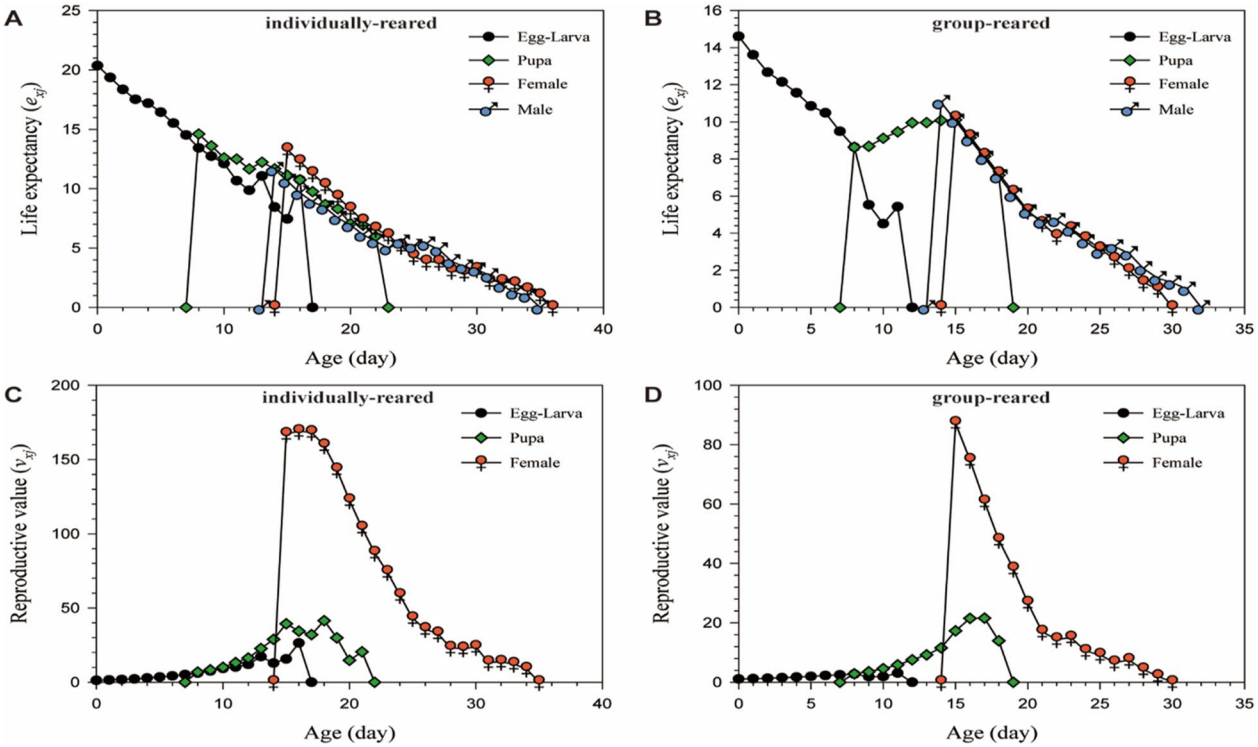

Fig. 4 Life expectancy and reproductive values of *Campoletis chlorideae* parasitizing the individually reared and group-reared *Spodoptera frugiperda*. Life expectancy (e_{xj}) of *C. chlorideae* parasitizing the 2nd instar of *S. frugiperda* in individually rearing (**A**) and group-rearing (**B**). Reproductive values (v_{xj}) of *C. chlorideae* parasitizing the 2nd instar of *S. frugiperda* in individual- (**C**) and group-rearing (**D**) conditions

the intrinsic rate of increase ($r = 0.0918 \pm 0.0148$ d^{-1}) and finite rate of increase of *C. chlorideae* populations ($\lambda = 1.0961 \pm 0.0162$ d^{-1}) were > 0 and > 1, respectively. The net reproduction rate (R_0) was only 6.02 ± 1.61 females. The mean generation time (T) of *C. chlorideae* populations derived from group-reared hosts was 19.56 ± 0.50 days, whereas it was 21.21 ± 0.27 days in the individually reared hosts.

Parasitism rates, population, and parasitism projection of *C. chlorideae* parasitizing individually reared *S. frugiperda* larvae

Since only adult *C. chlorideae* females parasitize and kill *S. frugiperda* larvae, both the age-specific parasitism rate (k_x) and age-specific net parasitism rate (q_x) (representing the mean number of *S. frugiperda* 2nd instar parasitized by *C. chlorideae* at age x and k_x taking the survival rate into consideration, respectively) were 0 before the adult stage (Fig. 5A). These values then peaked at day 19, indicating the parasitizing of 11.99 and 6.71 larvae/parasitoid (at 19 d), respectively, before decreasing over the next 16 d to zero (~ death of the wasp) at 36 d.

The total parasitism rate (i.e., number of host larvae parasitized, except the number of immunized larvae) per adult *C. chlorideae* female was 257.12 ± 12.72, indicating a net parasitism rate (C_0) for *C. chlorideae* of ~ 53 *S. frugiperda* larvae during its lifespan (Table 3). Due to the low survival and parasitism rates after age 26 d, the age-specific cumulative net reproductive rates (R_x) and cumulative parasitism rates (C_x) increased only slightly during the remaining 10 days (Fig. 5B). The finite parasitism rate (ω) and stable parasitism rate (ψ) of *C. chlorideae* were 0.2422 ± 0.0282 d^{-1} and 0.1993 ± 0.0217 d^{-1} under individual rearing conditions, respectively (Table 3). The

Table 3 Parasitism rate parameters (means ± SE) of *Campoletis chlorideae* parasitizing the 2nd instar of *Spodoptera frugiperda* under individual rearing conditions

Parasitism rate parameters	*C. chlorideae* on 2nd *Sf*[1]
Total parasitism rate (host/female)	257.12 ± 12.72
Net parasitism rate (C_0) (host/female)	52.90 ± 7.64
Finite parasitism rate (ω) (d^{-1})	0.2422 ± 0.0282
Stable parasitism rate (ψ) (d^{-1})	0.1993 ± 0.0217

Values are mean standard errors estimated by using 100,000 bootstrap resampling

[1] Individually reared *S. frugiperda*

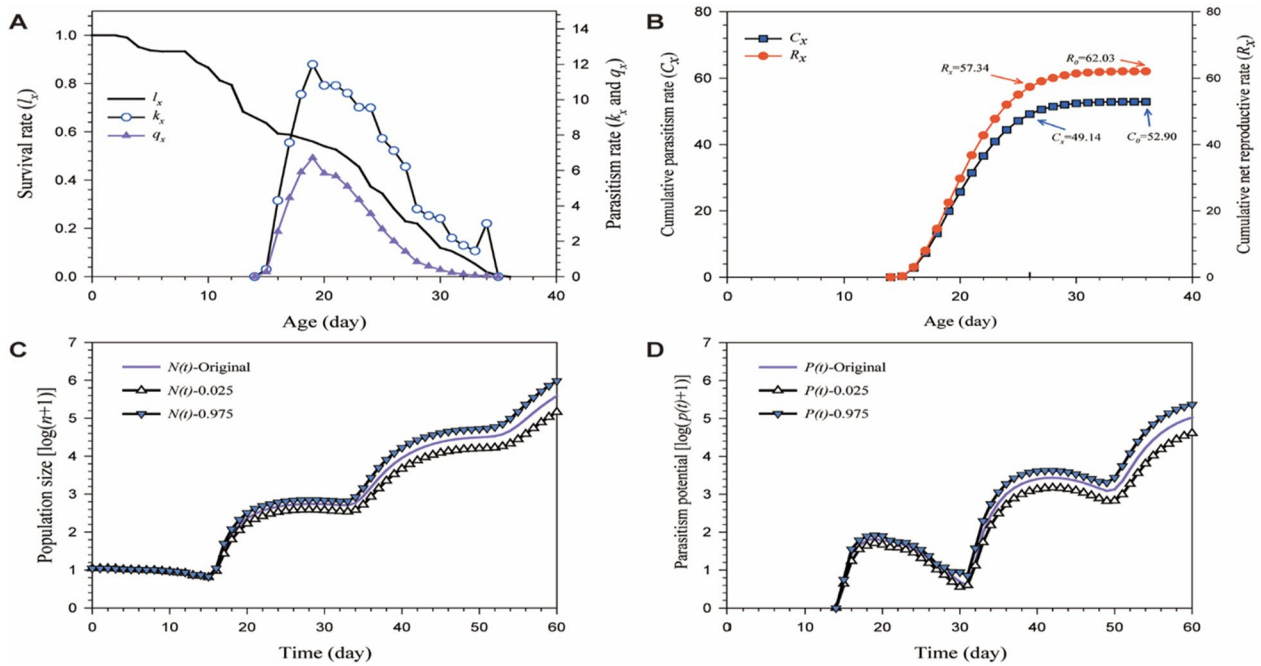

Fig. 5 Population parameters of *Campoletis chlorideae* parasitizing individually reared *Spodoptera frugiperda* larvae. **A** Age-specific survival rate (l_x), age-specific parasitism rate (k_x), and age-specific net parasitism rate (q_x) of *C. chlorideae* parasitizing the 2nd instar of *S. frugiperda* in individual rearing conditions. **B** Age-specific cumulative parasitism rates (C_x) and cumulative net reproductive rates (R_x) of *C. chlorideae* parasitizing the 2nd instar of *S. frugiperda* in individual rearing conditions. Simulated population growth of *C. chlorideae* parasitizing the 2nd instar of individually reared *S. frugiperda* over a period of 60 d. **C** Uncertainty of population projection based on the original, 0.025th percentile, and 0.975th percentile of life tables, starting with an initial population of 10 eggs. **D** Parasitic potential and uncertainty of population projection based on the original, 0.025th percentile, and 0.975th percentile of the life table, starting with an initial population of 10 eggs

predicted total population size of *C. chlorideae* ($N(t)$) and parasitism potential ($P(t)$), beginning with an initial population of 10 eggs assuming an unlimited population of hosts available, including projections using life tables from the 0.025th and 0.975th percentiles of the net reproductive rate, over a time course of 60 days, was modeled (Fig. 5C, D). The projected $N(_t)$ and $P(_t)$ over the same parameters indicated no increase in initial population size and parasitism rates (0–14 d), but periodical bursts of growth in *C. chlorideae* population sizes and parasitic consumptions of *S. frugiperda* by *C. chlorideae* over time (Fig. 5C, D).

Discussion

The aim of the present study was to determine various parameters of the development and parasitization of the parasitoid wasp, *C. chlorideae*, important for determining the potential for its use for pest biocontrol. The parameters included the growth (lengths of time), development, reproduction, and survival of the different stages of *C. chlorideae* (egg, larva, pupa, and adult), including estimation of parasitism rates and population dynamics of *C. chlorideae*. In addition, these parameters were examined as functions of how the host (*S. frugiperda*) was reared, i.e., either individually or group-reared. In related studies, the potential for group rearing is important because this would facilitate mass production of the parasitoid (Wei et al. 2022); however, individual rearing likely better mimics field conditions, where only one larva usually appears in the leaf whorl of maize (Xie et al. 2021). Our data show that *C. chlorideae* targeting individually reared *S. frugiperda* results in a high fecundity (301.5 ± 16.4 eggs/female), a long longevity (~ 28 days), and a high finite rate of increase ($\lambda = 1.2148$), however these parameters of *C. chlorideae* on group-reared *S. frugiperda* (87.71 ± 6.32 pupae/female, ~ 25 days and $\lambda = 1.0961 \pm 0.0162$) indicated a potential bottleneck for mass production.

A previous study found that temperatures < 12 and > 35 °C were detrimental to the survival and development of the larvae of *C. chlorideae,* indicating that temperature fluctuations had a significant effect on the development of parasitic insects (Dhillon and Sharma 2008). The present study was conducted at 25 °C under controlled temperature conditions, and life cycle parameters of *C. chlorideae* derived from individually reared *S. frugiperda* showed that the egg-larval and pupal durations were 9.98 ± 0.12 and 7.28 ± 0.08 days, respectively, slightly longer than *C. chlorideae* growth in *Heliothis armigera* at 27 °C (8.1 to 9.1 days and 6.5 days) (Dhillon and Sharma 2008). The likely changes in temperature would have a great bearing on the effectiveness of natural enemies for pest management, which in turn would affect insect host-natural enemy associations, crop production, and food security. At the same temperature (25 °C), the life cycle of *C. chlorideae* growth in larvae of *S. frugiperda* was about a half shorter than that of *S. frugiperda* (Xie et al. 2021), indicating that the endoparasitoid *C. chlorideae* had a competitive advantage in controlling *S. frugiperda* in the field. The combination of the morphological and developmental parameters established in this work can be used to determine optimal release conditions for *C. chlorideae* that can be coupled to the emergence/detection of *S. frugiperda* in the field.

The present data indicate that the total number of *C. chlorideae* offspring (yield) from individually reared *S. frugiperda* reached 301.5 eggs/female with an emergence rate of ~ 58%, a cumulative parasitism number of 257.12 ± 12.72 host larvae/female *C. chlorideae*, and a finite rate of increase (λ) (day^{-1}) of 1.2148 ± 0.0092. The relatively small parasitism number compared with the offspring numbers could be attributed to the fact that *C. chlorideae* have laid more than one egg in some larvae and because some parasitized larvae can overcome the parasitoids (Poelman et al. 2022). The predicted population size from 10 eggs after 60 days (assuming unlimited hosts) was determined to be 386,764 (rounding causes the sum to differ by "1"), composed of 365,970 egg-larvae, 11,415 pupae, and 3,462 female and 5,916 male adults. Eclosion levels (58%) for *C. chlorideae* produced from individually reared *S. frugiperda* were lower than those reported for *C. chlorideae* in maize-reared *S. frugiperda* (~ 80%) (Tian et al. 2021). This could be a result of the components in the artificial diet, which may have affected the development of *C. chloridea* in the *S. frugiperda* larvae since food source and/or addition of supplements in artificial diets have been shown to affect herbivore performance and defense of host insects (Johnson 2008), impacting the emergence rate of parasitoids grown on various foods (Sarfraz et al. 2009). Similar studies have reported that maize genotypes can also influence the parasitism rate of the related *C. sonorensis* parasitoid wasp on maize-reared *S. frugiperda* (Barreto-Barriga et al. 2021). Although there is a room for improvement, a high fecundity ($F = 301.5 \pm 16.4$ eggs/female) and a 58% eclosion rate should be sufficient to produce adequate populations of *C. chlorideae* for field application purposes over a given period of time under similar conditions.

For *S. frugiperda* hosts derived from group-rearing conditions, the *C. chlorideae* eclosion rate and sex ratios (female: male ratio of 1: 3.6) were low, with each female parasitoid producing about 87.71 pupae/female (~ 64% less). The proportion of N-type parasitic wasps (parasitoids dead before pupae stage) was as high as 69%. These data suggest that despite being fed the "low cannibalism rate" artificial diet, many parasitized larvae were still

consumed by others. These consumed larvae were likely parasitized larvae, as they grow at a slower rate than non-parasitized larvae. Nutrition and larval density are not hypothesized to be the primary causes of such cannibalism, as more than enough food was provided. Additionally, high cannibalism rates have also been reported in larvae kept at very low density (2 per box) (He et al. 2021). Thus, the potential mechanisms underlying this cannibalism as well as optimal artificial diets to reduce it warrant further investigation. Despite this, the population parameter ($\lambda = 1.0961 \pm 0.0162$) indicates this population size can still steadily increase. Overall, however, our data indicate that, under the current state of knowledge, the use of individual rearing techniques is likely a better option than group rearing for effective production of *C. chlorideae* for application purposes. This may not be significantly more costly, as large individual compartment trays can readily be obtained and potentially filled using semi-automated approaches. Parasitization of these cohorts is similar in both circumstances (but much more effective in terms of yield) for individually reared hosts.

Conclusions

Biological control agents are sustainable pest control methods beneficial for biodiversity. This work evaluates the mass production potential and the efficacy of the ichneumonid parasitoid *C. chlorideae* in parasitizing FAW that are reared in both individual and group settings. It highlights the promising biological control potential of *C. chlorideae* against FAW. The endemic status of *C. chlorideae* to China supports its mass production and release as a sustainable and eco-friendly approach for managing the FAW. The age-stage, two-sex life table can provide a description and prediction of parameters such as developmental time, survival, parasitism, and reproductive potential of the parasitoid under field conditions similar to those used in the laboratory. Future research should focus on developing methods to increase the production of *C. chlorideae*, such as using different insect hosts and artificial diets of parasitized *S. frugiperda* that are optimized for low cannibalism under group-rearing conditions or semi-automated approaches to reduce the cost under individually rearing conditions.

Abbreviations

APOP	Adult pre-ovipositional period
CABI	The Centre for Agriculture and Bioscience International
COI	Cytochrome c oxidase subunit I
C_0	Net parasitism rate
C_x	Cumulative parasitism rates
e_{xj}	Life expectancy value
FAW	The fall armyworm
F	Total fecundity
f_{x3}	Female age-specific fecundity
λ	Finite rate of increase
ω	Finite parasitism rate
GR	Group-reared *S. frugiperda*
l_x	Age-specific survival rate
$l_x m_x$	Age-specific net maternity
IR	Individually reared *S. frugiperda*
k_x	Age-specific parasitism rate
m_x	Population age-specific fecundity
NCBI	National Center for Biotechnology Information
$N(t)$	Predicted total population
N_f/N	Proportion of female individuals
N_m/N	Proportion of male individuals
N_n/N	Proportion of pre-adult mortality
O_d	Oviposition days
PP	Polypropylene
PCR	Polymerase chain reaction
$P(t)$	Predicted parasitism potential
q_x	Age-specific net parasitism rate
R_0	Net reproduction rate
r	Intrinsic rate of increase
R_x	Age-specific cumulative net reproductive rates
s_{xj}	Age-stage-specific survival rate
ψ	Stable parasitism rate
TPOP	Total pre-ovipositional period
T	Mean generation time
v_{xj}	Female-specific reproductive value
2nd Sf	2nd instar of *Spodoptera frugiperda*

Supplementary Information

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Supplementary Material 1.

Supplementary Material 2.

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Author contributions

Zhang, W. and Zhang, R. helped in conceptualization, data curation, and methodology; Zhang, R. and Zhao, Q. were involved in formal analysis; Zhang, R, Amr Mohamed, and Zhang, W. investigated the study; Zhang, W. and Liu, C.H. helped in resources; Zhang, R., Zhang, W., Zhao, Q., Amr Mohamed, Nemat O. Keyhani, and Lei X.F. contributed to writing—original draft preparation; Zhang, W., Amr Mohamed, Hathal M. Al Dhafer, and Nemat O. Keyhani helped in writing—review & editing; Zhang, W. supervised the study; Zhang, W administrated the project.

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Availability of data and materials

The data supporting the findings of this study are available within the article [and/or] its supplementary materials.

Declarations

Ethics approval and consent to participate

Not required.

Consent for publication
Not required.

Competing interests
The authors declare that they have no conflict of interest.

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