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Evaluation of *Telenomus remus* (Hymenoptera: Platygasteridae) as a biocontrol agent of *Spodoptera litura* (Lepidoptera: Noctuidae) based on two-sex life table and functional response analyses

Zhen Shen^{1†}, Li-Hui Liu^{2†}, Lian-Sheng Zang¹, Tie-Jun Deng², Zhen-Bao Luo³, Jun-Yi Gao³ and Liang-De Tang^{1*} 

Abstract

Background *Telenomus remus* Nixon is an important egg parasitoid of *Spodoptera* spp. pests and, as such, has potential as a biological control agent. *Spodoptera litura* (Fabricius) is a significant pest of many economically important crops worldwide. This study was conducted to evaluate the demographic parameters and functional response of *T. remus* on the *S. litura* eggs.

Results *T. remus* can lay 186.90 eggs/female in the lifetime, adult preoviposition period was 0 days, total preoviposition period was 10.03 days, and the ratio of female and male offspring was 0.495 and 0.421, respectively. In addition, most females emerged from 24 h-old eggs, whereas most males emerged from 48 h-old eggs. The intrinsic rate of increase, finite rate of increase, net reproductive rate, mean generation time, and population doubling time were 0.3506 d⁻¹, 1.4199 d⁻¹, 92.45 offspring/individual, 12.91 days and 1.98 days, respectively. The net killing rate of *T. remus* on *S. litura* was 101.49 eggs/female, indicating the high capacity of *T. remus* to parasitize *S. litura* eggs. Moreover, the higher the egg density, the higher the parasitism rate by female *T. remus*, although there was a trend of parasitism stabilization at an egg density of 100, indicating a type II functional response curve for this parasitoid.

Conclusion Overall, these findings suggest that *T. remus* can be efficiently reared on *S. litura* eggs and shows potential as biocontrol agent for this economically important pest species.

Keywords Biological control, Functional response, Life table, Mass-rearing, *Spodoptera litura* (Fabricius), *Telenomus remus* Nixon

[†]Zhen Shen and Li-Hui Liu contributed equally to this work.

*Correspondence:

Liang-De Tang
tangldcatas@163.com

Full list of author information is available at the end of the article



Background

Spodoptera litura (Fabricius) (Lepidoptera: Noctuidae) is an insect pest worldwide (Yang et al. 2023; EPPO 2023), with more than 120 host plant species in 48 families, and causes severe economic losses in crop fields (Ravishankar and Venkatesha 2011; Toke, et al. 2016; Shekhawat et al. 2018). Each female can lay more than 2,000 eggs during her lifespan, laying 200–300 eggs in a single egg mass (Ahmad et al. 2013) that are usually covered by a layer of brown abdominal hair-like scales (Li et al. 2023). Thus, control and management of this pest are difficult because of its high fecundity, wide range of host plants (Ahmad et al. 2013), and increased resistance to insecticides (Sreelakshmi et al. 2018; 2019; Babu and Singh 2022). In most current pest control practice, synthetic insecticides are still the most common and effective emergency method for *S. litura* control. However, the adverse effects of synthetic insecticides are significant, such as '3R' (residue, resistance, resurgence) problems, disruption of agroecosystems and killing of nontarget organisms (Ansari et al. 2018; Torres and Bueno 2018) and residual toxicity (Pavela and Sedláč, 2018). Therefore, it is vital to reduce synthetic insecticide use in agriculture. While, parasitoid wasps, offer excellent alternatives for controlling insect pests. Currently, more than 70 species of parasitoids of *S. litura* have been reported (Ranga Rao et al. 1993; Xie et al. 1999).

The efficiency of egg parasitoids as control agents against lepidopterous pests is widely recognized because of their action on early pest stages before any damage occurs to the crop (Parra and Coelho 2019; Zang et al. 2021). The egg parasitoid *Telenomus remus* (Nixon) (Hymenoptera: Scelionidae) is an excellent biological agent not only because of its high fecundity, but also its effective action on layers of *Spodoptera* eggs, even parasitizing eggs located in the inner layers of the egg mass (Hou et al. 2022; Li et al. 2023). Furthermore, its high dispersal (Pomari-Fernandes et al. 2018) and host search capacities (Pomari et al. 2013) support its use in the field. Thus, *T. remus* is widely used in the control of *Spodoptera* spp. It is a parasitoid wasp native to Peninsular Malaysia and Papua New Guinea (Wengrat et al. 2021) and has been released against various pest species of *Spodoptera* (Pomari et al. 2012; Bueno et al. 2010; Ferrer 2001; 2021). *Telenomus remus* was widely released in Venezuela during the 1990s to control *Spodoptera frugiperda* (J. E. Smith) in corn fields (Ferrer 2001) and remains the main measure of integrated pest management (IPM) to control this pest (Ferrer 2021). Its release achieved a control effect of up to 90% and resulted in an overall reduction in insecticide use of 49%–80% against *S. frugiperda* eggs (Hernández et al. 1989; Ferrer 2021). Recently, it was reported that *T.*

remus has established natural populations independent of field release in Brazil (Wengrat et al. 2021). In Ghana, 72–100% of *Spodoptera* egg masses were parasitized in the minor rainy season, compared with 33% during major rainy season (Agboyi et al. 2021). *Telenomus remus* was also considered the egg parasitoid most effective against *S. frugiperda* in its overwintering area in China (Zhao et al. 2023), with a field parasitism rate > 80% (Zhao et al. 2019).

Although *T. remus* can parasitize a variety of *Spodoptera* spp. (Wojcik et al. 1976; Jalali et al. 1987; Wu et al. 2021), most of research has focused on *S. frugiperda* (Colmenarez et al. 2022). However, *S. litura* is also an important natural host of *T. remus* in India, and its eggs were used for the mass-rearing of this parasitoid before being replaced by alternative hosts *Agrotis biconica* Kollar and *Corcyra cephalonica* (Stainton) (Joshi et al. 1976; Gupta and Pawar 1985; Kumar et al. 1986; Gautum and Gupta 1994). This is because alternative hosts can significantly reduce production costs, enabling the economically viable mass-rearing of parasitoids (Queiroz et al. 2017; da Silva et al. 2022). Improvements in the artificial diet of *S. litura* (Cao et al. 2014; Sun et al. 2015), which made its mass-rearing easier and cheaper, subsequently significantly reduced the production cost of parasitoids reared using this species (Chen et al. 2021). Thus, using *S. litura* eggs as a host for mass-rearing *T. remus* is a viable approach. Another important reason is that the alternative host *C. cephalonica* cannot be used to rear Chinese strain *T. remus* (Dai et al. 2019; Chen et al. 2021), whereas eggs of *S. litura* are suitable for mass-rearing *T. remus* (Chen et al. 2021; Wu et al. 2021), including the use of cold-stored *S. litura* eggs (Chen et al. 2022a). The effects of the age and generation of *T. remus* on its mass-rearing on *S. litura* eggs have also been previously evaluated (Chen et al. 2022b, 2023). However, the peak emergence time of male and female parasitoid offspring, and the prediction of the population of *T. remus* reared/parasitized on the *S. litura* have not been reported.

Life tables are a useful tool for researching population ecology as well as pest management because they can accurately reflect the population parameters of the target organisms, such as their survival, development, longevity, and fecundity (Chi and Liu 1985; Chi et al. 2022a). Compared with traditional life tables, the age-stage, two-sex life table integrates data from both age stages and both sexes, which makes the demographic parameters more accurate (AmirMaafi et al. 2022; Chi et al. 2019, 2022a, b). Therefore, age-stage, two-sex life tables are widely used in many studies involving population and community ecology, including pest management, pesticide resistance, predator–prey relationships, biological control, mass-rearing and harvesting of insects, and plant

resistance (Gul et al. 2019; Saeed et al. 2021; Ren et al. 2022; Ullah et al. 2022; Zhu et al. 2022).

Studies on the interaction of natural enemies and their hosts improve understanding of the predation/parasitism dynamics of natural enemies, which can be helpful for formulating IPM programs (Carneiro et al. 2010). Functional response models are important tools to evaluate this interaction. All functional response curves proposed by Holling (1959) stabilize at a certain predation/parasitism rate level, which is related to the maximum number of prey/host attacked per time unit. Three different types (I, II, and III) of functional response can be obtained through mathematic models, represented by discrete curves (Holling 1959). The type II curve is more often related to systems involving arthropods, including predatory and parasitoid insects (Cave and Gaylor 1989). The main characteristic of the type II functional response is a gradual increase in the number of prey consumed up to a density at which the consumption rate stabilizes (Hassel 1978; Hassel et al. 1997). The type II equation was used to build the functional response curves of *T. remus* against *S. frugiperda* eggs (Carneiro et al. 2010).

In this study, we systematically investigated the parasitism, emergence, longevity, and developmental time of *T. remus* on *S. litura* eggs. The resulting demographic parameters generated were analyzed by using age-stage, two-sex life table theory using TWOSEX-MSChart and Cousume (Chi 2021a,b). Moreover, the functional response of *T. remus* against *S. litura* eggs was also evaluated, in terms of the effect of different egg densities of *S. litura* on parasitism by *T. remus*. Whereas a cubic logistic regression model was firstly used to screen the most appropriate functional response model fits for *T. remus* attacking *S. litura*. Such information, in order to provide relevant basis for biological control *S. litura* utilization of *T. remus*.

Materials and methods

Insect colonies

A colony of *T. remus* was collected from the experimental station of South China Agricultural University, Guangzhou, Guangdong Province, China and then reared under laboratory conditions at 28 ± 1 °C, relative humidity (RH) $75\% \pm 5\%$, and a 14 h light:10 h dark photoperiod for more than 20 generations using *S. litura* as the hosts. The same laboratory conditions were used for all experiments described below.

The *S. litura* colony had also been collected from the experimental station of South China Agricultural University and then reared in Guangxi Key Laboratory of Biology for Crop Diseases and Insect Pests, Nanning, China, for more than 2 years. An artificial diet, described by Shu

et al. (2015), was used to rear *S. litura* larvae, using the laboratory conditions described above.

Performance of *T. remus* reared from *S. litura* eggs

Life table study

To investigate the development time and sex ratio of offspring parasitoids, one pair of adult *T. remus* newly emerged from *S. litura* eggs were collected and transferred into a glass tube (1.0 cm diameter \times 10.0 cm height) and allowed to mate for 24 h; the tube also contained 1-day-old *S. litura* egg masses (each containing 100–150 eggs) and filter paper strips contained 30% honey solution. The tube was covered with gauze (100 mesh) to allow air exchange. After 24 h, the parasitized egg masses were transferred to a new test tube and numbered accordingly. The test was repeated ten times. When *S. litura* larvae hatched, they were removed from egg masses with a brush so that they were unable to feed on the remaining eggs. The developmental duration and sex ratio were observed and recorded daily until no more parasitoids emerged. For all eggs without emergence holes, a stereomicroscope (Motic, SMZ-168 BP, Hong Kong, China) was used to check and count the presence or absence of recognizable parasitoid cadavers.

In a parallel experiment, the daily egg production of offspring parasitoids were investigated. One male and one female parasitoid (<6 h old, and unmated) were then matched in a glass tube (1.0 cm diameter \times 10.0 cm height) containing egg masses (\approx 100 eggs) and provided with a few drops (0.1–0.2 mL) of 30% honey water as food. After 24 h, another \approx 100 eggs were placed in the test tube. This cycle was repeated until the female wasp had died. The survival time of female wasp was then recorded. If the male wasp died before the female, its survival time was recorded and it was replaced, ensuring that a male wasp was present until the female had died. The level of parasitism (i.e., the number of black eggs), number of emerged parasitoids, and sex ratio of offspring were observed and recorded daily. The experiment was repeated 15 times. The developmental duration (matched cohort) and daily fecundity (initial cohort) of the female parasitoids were matched by a bootstrap-match based on the life table method as described by Amir-Maafi et al (2022).

Emergence time of *T. remus*

In a parallel experiment, the emergence times of male and female adult *T. remus* were investigated. A pair of newly emerged adult wasps (<6 h old) were randomly collected and transferred to a glass tube (1.0 cm diameter \times 10.0 cm height) and allowed to mate for 24 h; 30% honey solution was provided as a source of food. The male wasp was then removed from the glass tube and

an egg mass (≈ 100 eggs) and a few drops of 30% honey solution were added; the female wasp was allowed to oviposit eggs for 24 h. Then, the female was removed and the parasitized eggs were left in the glass tube, which was covered with gauze. This experiment was repeated ten times. The emerged adult offspring were recorded at 6-h intervals until no further adults emerged.

Effect of host egg age on parasitism by *T. remus*

To evaluate the influence of egg age on parasitism of *T. remus*, ≈ 100 *S. litura* eggs of different ages (24, 36, 48, 60, and 72 h) were provided to each *T. remus* female (mated for 24 h) for 24 h. Eggs of each age were placed in a glass tube (1.0 cm diameter \times 10.0 cm height) containing a female wasp, and each egg age had ten replicates. The parasitism and sex ratio of *T. remus* adults hatching from eggs of different ages were then recorded.

Functional response of *T. remus* parasitizing *S. litura* eggs

Female adults of *T. remus* mated for 24 h were used in this experiment. Each female wasp was introduced into a glass (1.0 cm diameter \times 10.0 cm height) tube, which contained an egg mass of a different density (20, 40, 60, 80, 100, 120, and 140 eggs), and a filter paper strip dipped in 30% honey solution. Each egg density was replicated eight times. After being left to lay eggs for 24 h, the female wasps were removed and discarded. The parasitized egg masses were labeled and the level of parasitism recorded. Newly hatched larvae were counted and withdrawn from the tubes with a brush so they that were not able to feed on parasitized eggs. Such observations were performed in the first 5 days after oviposition at 12-h intervals. Any parasitoids that emerged from the remaining eggs after this time were counted once they had died (Carneiro et al. 2010).

Statistical analysis

TWOSEX-MSChart (Chi 2021a) was used to analyse developmental duration, survival rate, longevity, fecundity (effective parasitism) and parasitism, and CONSUME-MSChart (Chi 2021b) was used to analyse the net killing rate (including effective and non-effective parasitism) data (Chi and Liu 1985; Chi 1988; Chi et al. 2020). The formulas and definitions used in this study are showed in Additional file 1: Table S1. The means, variances, and standard errors (SE) of the life table parameters were estimated with the bootstrap ($B=100,000$) technique (Wang et al. 2016; Zhao et al. 2021). All life table graphs were created using SigmaPlot 12.5 (Systat Software, Inc., San Jose, CA, USA).

Data analyses were performed using the SPSS version 20 software package (SPSS Inc., Chicago, IL, USA). A Shapiro–Wilk test for normality was used to determine if datasets were normally distributed, and a Levene’s test to determine homogeneity of variances. The Shapiro–Wilk test showed that the number of female and male offspring at different time intervals (first sets) and different hosts egg ages (second sets) were not normally distributed, and the Levene’s test for homogeneity of variances showed none of the emergence time or hosts egg ages datasets variance were equal. Datasets had Poisson distributions and therefore this was selected in subsequent analyses. To test first and second sets of null hypotheses, a generalized linear model (GLM) (St-Pierre et al. 2018) was selected. Distribution of residual errors with a logarithm link function were selected. Similarly, when comparing the emergence numbers between females and males with respect to host egg age and time periods, a Poisson distribution was used in the GLM programs. Figures representing the emergence time and parasitism were generated using GraphPad Prism 9.0 (GraphPad Software, Inc., San Diego, CA, USA).

A logistic regression of the proportion of prey consumed (N_e/N_0) as a function of initial density (N_0) was used to determine the shape of the functional response. The type of functional response was determined by fitting data to Eq. 1 (Juliano 2001):

$$N_e/N_0 = \exp\left(P_0 + P_1N_0 + P_2N_0^2 + P_3N_0^3\right) / \left[1 + \exp\left(P_0 + P_1N_0 + P_2N_0^2 + P_3N_0^3\right)\right], \quad (1)$$

where (N_e/N_0) is the proportion of a prey consumed, and P_0 , P_1 , P_2 , and P_3 are the maximum likelihood estimates of the intercept, linear, quadratic and cubic coefficients estimated through the CATMOD procedure in SAS, respectively. The sign of P_1 and P_2 was used to distinguish the shape of the curves. When $P_1 < 0$, the predator/parasitoid displays a type II functional response, indicating that the proportion of prey consumed declines monotonically with host density (De Clercq et al. 2000). When $P_1 > 0$ and $P_2 < 0$, the predator/parasitoid displays a type III functional response (Juliano 2001; Song et al. 2016). Given that our data fitted a type II functional response curve (Table 1), the equation for parasitoids utilized was Eq. 2:

$$N_a = a'T_tN / (1 + a'T_hN), \quad (2)$$

where N_a is the number of parasitized hosts, a' is the parasitoid searching rate, T_t is the total time available for the parasitoid (24 h), N is the host density, and T_h is the handling time.

Table 1 Maximum-likelihood estimates from logistic regressions of the proportion of *Spodoptera litura* eggs parasitized by *Telenomus remus*

Parameter	Estimate	Standard error	Chi-square*	P value
P_0	5.3754	0.6836	61.84	<0.0001
P_1	-0.1271	0.0253	25.31	<0.0001
P_2	0.00106	0.000292	13.24	0.0003
P_3	-3.24E-06	1.05E-06	9.47	0.0021

P_0 , P_1 , P_2 , and P_3 are the maximum likelihood estimates of the intercept, linear, quadratic, and cubic coefficients, respectively. *Chi-square is the value of the likelihood ratio test to determine whether equation coefficients differed significantly from zero

Table 2 Total preadult duration (mean±SE), preadult survival rate, adult longevity, total longevity, adult pre-oviposition period, total pre-oviposition period, fecundity, proportion of female, and oviposition days of *Telenomus remus* reared on *Spodoptera litura* eggs

Parameter	<i>T. remus</i>	
	n	Mean ± SE
Matched cohort size (female:male)	–	94:80
Initial cohort size (female:male)	–	15:15
Preadult duration (days)	174	10.03±0.05
Female preadult duration (days)	94	10.30±0.06
Male preadult duration (days)	80	9.71±0.09
Preadult survival rate (s_a) (%)	190	0.9158±0.020
Adult longevity (days)	174	8.02±0.19
Female longevity (days)	94	8.68±0.32
Male longevity (days)	80	7.24±0.10
Total longevity (days)	174	17.37±0.25
Female total longevity (days)	94	18.98±0.33
Male total longevity (days)	80	16.95±0.13
Adult preoviposition period (days)	94	0.00±0.00
Total preoviposition period (days)	94	10.30±0.06
Fecundity (F) (eggs/female)	94	186.90±2.42
Proportion of female (N_f/N)	190	0.495±0.036
Proportion of male (N_m/N)	190	0.421±0.036
Proportion of female (N_f/N)	190	0.084±0.020
Oviposition days (O_d) (days)	94	7.30±0.23

The standard error (SE) were estimated by using a bootstrap-match technique with 100,000 resamplings

Results

Performance

Life table

Under the matched (female 94: male 80) and initial cohorts (female 15: male 15) of *T. remus*, key demographic parameters, such as the developmental time, adult longevity, total longevity, total preoviposition period (TPOP), adult preoviposition period (APOP), oviposition days, and fecundity, were analyzed (Table 2).

Preadult duration of females, female offspring, and female longevity were 10.30 days, 0.495, and 8.68 days respectively, and males were 9.71 day, 0.421, and 7.24 days, respectively. With a total preadult duration of 10.03 days, and a preadult survival rate (s_a) of 0.9158. With adult longevity and total longevity of 8.02 days and 17.37 days, respectively. The TPOP of *T. remus* was 10.03 days, which was the same as the preadult duration of females because the APOP was zero. Fecundity (F) and oviposition days (O_d) of *T. remus* were 186.90 eggs/female and 7.303 days, respectively.

The age-stage survival rates (s_{xj}) of *T. remus* on *S. litura* eggs showed that the adults began to emerge after 9 days, with obvious overlaps between the stages (Fig. 1a). Adult females of *T. remus* parasitized on *S. litura* eggs survived for 16 days, with s_{xj} peaking at 49.47% at the age of 12 days. Peak s_{xj} of male adults was 42.11% at the age of 12 days. Female adults had a longer longevity than that of male adults of *T. remus* reared on *S. litura* eggs (Fig. 1a).

The age-specific survival rate (l_x), age-specific fecundity (m_x), age-stage specific effective parasitism rate (f_{x2}), and age-specific net maternity ($l_x m_x$) of *T. remus* on *S. litura* eggs are showed in Fig. 1b. The peak m_x and $l_x m_x$ of *T. remus* were 18.70 and 17.12 offspring/female, respectively. The peak f_{x2} of *T. remus* was 50 offspring/female at 9 days of age.

The life expectancy (e_{xj}) of a *T. remus* egg newly laid in *S. litura* eggs was 24 days. The highest e_{xj} of *T. remus* males and females was 9 days (Fig. 2a). The reproductive value (v_{xj}) of *T. remus* peaked at 126.30 d⁻¹ at 9 days of age (Fig. 2b).

The population demographic parameters of *T. remus* on the *S. litura* eggs are showed in Table 3. The gross reproduction rate (GRR), net reproductive rate (R_0), intrinsic rate of increase (r), finite rate of increase (λ), mean generation time (T), and population doubling time (DT) of *T. remus* were 116.42, 92.47, 0.3506 d⁻¹, 1.4199 d⁻¹, 12.91 days, and 1.98 days, respectively.

Pest-killing rate

Given that *T. remus* is an egg parasitoid, only female adult wasps can parasitize, and therefore kill, host eggs; thus, the age-specific *S. litura* eggs-killing rate (k_x), age-specific net killing rate (q_x), and cumulative killing rate (c_x) were all zero before the adult stage (Fig. 3a). Peak k_x of *T. remus* was 20.21 eggs per parasitoid, occurring by 12 days of age. Peak q_x was also reached by 12 days of age (18.51 eggs/parasitoid) (Fig. 3a). Thus, with a starting population of ten *T. remus* eggs, after 30 days, the population reached 74,169 immature individuals, 204 male, and 304 female adults; by day 25, the total killing rate of *T. remus* reared on *S. litura* eggs was 11,816 eggs (Fig. 3b).

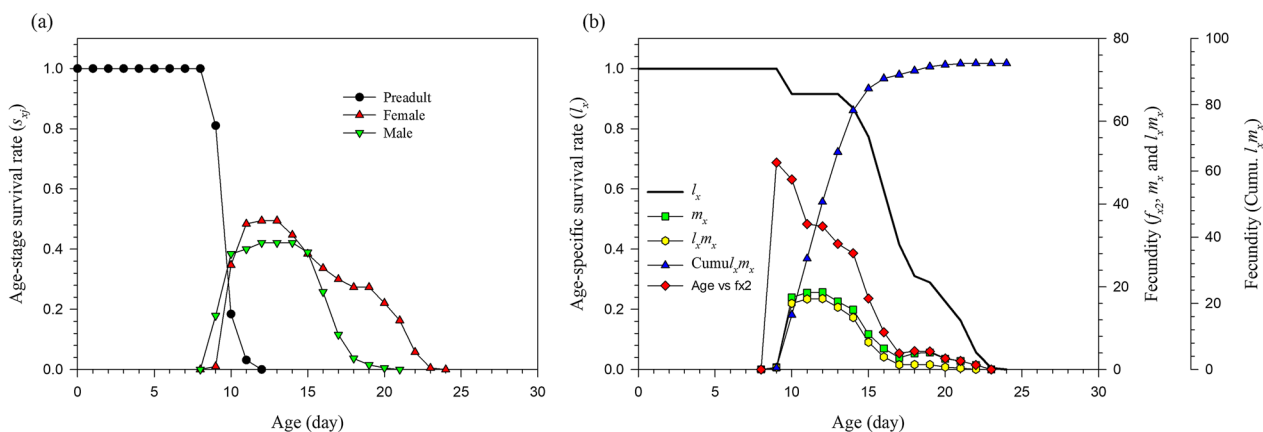


Fig. 1 Age-stage survival rate (s_{xj}) (a), and age-specific survival rate (l_x), female age-specific fecundity (f_{x2}), age-specific fecundity (m_x), and age-specific net maternity rate ($l_x m_x$) (b) of *Telenomus remus* reared on *Spodoptera litura* eggs

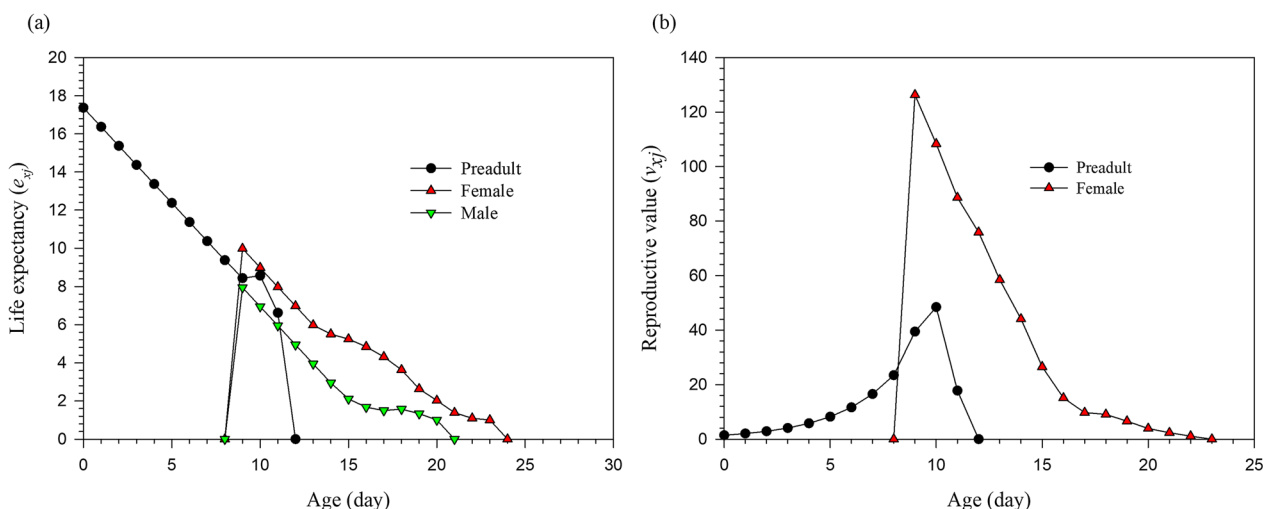


Fig. 2 Age-stage-specific life expectancy (e_{xj}) (a), and age-stage-specific reproductive value (v_{xj}) (b) of *Telenomus remus* reared on the *Spodoptera litura* eggs

Table 3 Population parameters (mean \pm SE) of *Telenomus remus* reared on *Spodoptera litura* eggs

Population parameter	Result
Gross reproduction rate (offspring)	116.42 \pm 7.58
Net reproduction rate (R_0) (offspring)	92.47 \pm 6.88
Intrinsic rate of increase (r) (day^{-1})	0.3506 \pm 0.0062
Finite rate of increase (λ) (day^{-1})	1.4199 \pm 0.0088
Mean generation time (T) (day)	12.91 \pm 0.07
Population doubling time (day)	1.98 \pm 0.04

The standard error (SE) were estimated by using a bootstrap-match technique with 100,000 resamplings

Parameters of *T. remus* parasitism and killing are showed in Table 4. The net non-effective parasitism rate (G_0) was 15.26 offspring/female. The numbers of female and male offspring produced by *T. remus* on *S. litura* eggs were 146.38 and 43.59, respectively. The net killing rate (C_0) of *T. remus* was 101.49 eggs per parasitoid. The stable killing rate (ψ), finite killing rate (ω), and transformation rate (Q_p) of *T. remus* were 0.6541, 0.4606, and 1.0976, respectively.

Emergence time

The emergence of male and female parasitoids was observed over a 6-h period, with significant differences

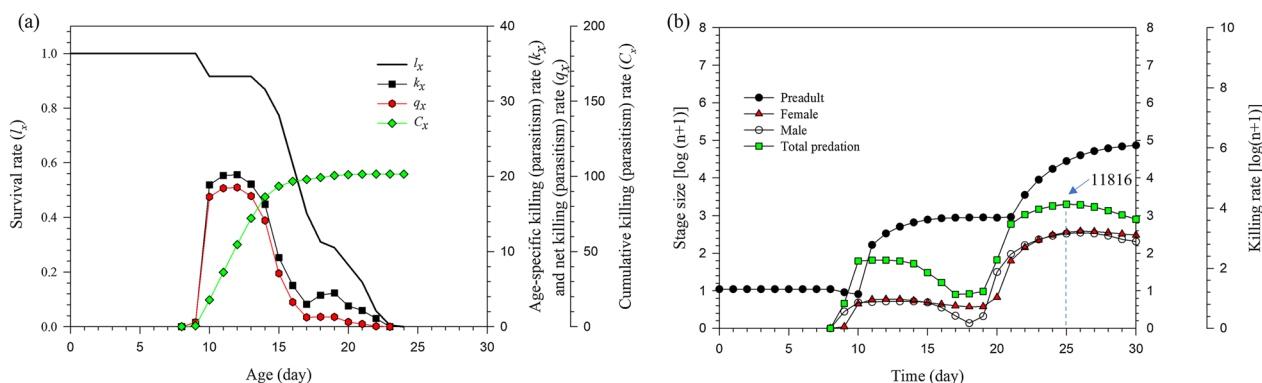


Fig. 3 Age-specific host-feeding rate (k_x), age-specific net host-feeding rate (q_x), and cumulative host-feeding rate (C_x) (a), and population projection of the total killing rate (b) of *Telenomus remus* reared on *Spodoptera litura* eggs. The blue dashed line shows the killing rate on day 25

Table 4 Parameters of parasitism and killing (mean ± SE) of *Telenomus remus*

Parameter	Result
Net non-effective parasitism rate (G_0)	15.26 ± 0.24
R_0 , F (female offspring/individual)	146.38 ± 2.47
R_0 , M (male offspring/individual)	43.59 ± 3.15
Net killing rate (C_0) (eggs/parasitoid)	101.49 ± 7.57
Finite killing rate (ω)	0.6541 ± 0.0261
Stable killing rate (ψ)	0.4606 ± 0.0156
Transformation rate (Q_p)	1.0976 ± 0.0053

The standard error (SE) were estimated by using a bootstrap-match technique with 100,000 resamplings

noted. Male parasitoids emerged in significantly greater numbers than females during the time intervals of 18:00–24:00 h and 0:00–06:00 h (Wald statistic 84.03 df 1, $P < 0.001$; Wald statistic 451.26, df 1, $P < 0.001$). Conversely, the number of female parasitoids was significantly higher than males between 06:00–12:00 h (Wald statistic 151.17, df 1, $P < 0.001$). However, no significant difference was observed between the number of female and male parasitoids emerging during 12:00–18:00 h (Wald statistic 1.50, df 1, $P = 0.221$). Male parasitoids showed a greater emergence pattern during the night (0:00–06:00 h; Wald statistic 360.66, df 3, $P < 0.001$), whereas female parasitoids emerged predominantly during the morning (06:00–12:00 h) (Wald statistic 341.79, df 3, $P < 0.001$) (Fig. 4a).

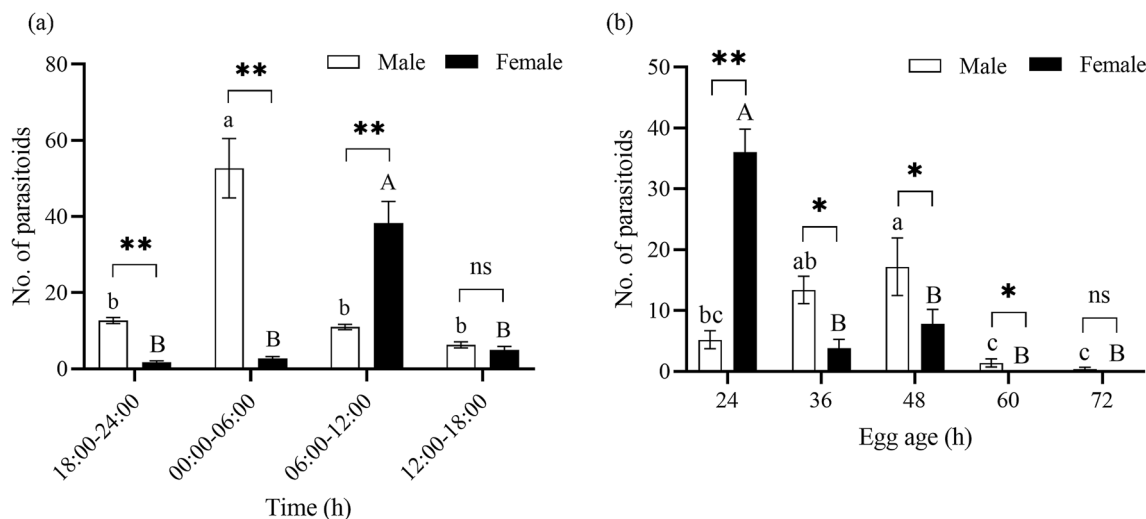


Fig. 4 The emergence time of (a) and time of parasitism (b) by *Telenomus remus* reared on *Spodoptera litura* eggs. Data are mean ± SE; ** $p < 0.001$; ns not significant

Parasitism on host eggs of different ages

The study revealed a significant difference in the emergence of male and female parasitoids across all egg ages tested. The results indicated that 24-h-old host eggs (Wald statistic 230.25, df 1, $P < 0.001$) produced more females than they did males, whereas 36-h, 48-h and 60-h-old host eggs (Wald statistic 53.58, df 1, $P < 0.01$; Wald statistic 35.34, df 1, $P < 0.001$; Wald statistic 5.10, df 1, $P = 0.024$) produced more males than females. However, there was no significant difference in the emergence of male and female parasitoids from 72-h-old host eggs (Wald statistic 2.50, df 1, $P = 0.114$). The results also demonstrated that *T. remus* produced the highest number of females on 24-h-old eggs (Wald statistic 476.00, df 3, $P < 0.001$), whereas the most males were generated on 48-h-old eggs (Wald statistic 305.37, df 3, $P < 0.001$) (Fig. 4b).

Functional response

The results of logistic regression analysis (Table 1) indicated that the linear coefficient (P_1) was negative for parasitism, indicating a type II functional response. The mean number of eggs parasitized by *T. remus* females increased with higher egg host densities, and stabilized at and beyond a density of 100 eggs (Fig. 5). Through disk equation fitting, the instantaneous attack rate (a'), handling time (T_h), and maximum attack rates (T/T_h) were obtained, with values of 0.9764, 0.0066 day, and 152.3 eggs/day, respectively. With the increase of host egg density, *T. remus* showed a decrease in its searching rate (Fig. 5).

Discussion

The life table method is a useful tool for researching population ecology as well as pest management because it can accurately reflect the population parameters of the research organism, such as survival, development, longevity, and fecundity (Chi and Liu 1985; Chi et al. 2022a, b). The life table data showed that the *T. remus* performed well on eggs of *S. litura*, indicating that these eggs could be used to rear increased numbers of parasitoids, in turn controlling the pest itself. Our results were also supported by previous relevant studies (Chen et al. 2021, 2022b, 2023).

Previous studies have showed that some parasitoids can reproduce once they emerge, whereas others need extra nutrients and time to do so (Xu et al. 2015, 2018; Zhao et al. 2021). *Telenomus remus* belongs to the latter group of parasitoids because $APOP = 0$. Generally, parasitism decreased with the increase in female parasitoid age, and female longevity was also limited; thus, the release time (age) of parasitoids becomes important. Some studies showed that 3-day- and 4-day-old parasitoids had higher parasitism performance on all age eggs compared with 1-day- and 2-day-old parasitoids (Chen et al. 2022b), but the total parasitism during the oviposition period was not evaluated. Theoretically, the earlier the release (exposing), the higher the total parasitism would be. In the current study, a total of 186.90 *S. litura* eggs were parasitized by a female *T. remus* during her lifetime, and 70% of eggs were laid during the first 5 days (Fig. 2b), although the age of *T. remus* virgin females did not affect the parasitism of *S. frugiperda* eggs (Queiroz et al. 2019).

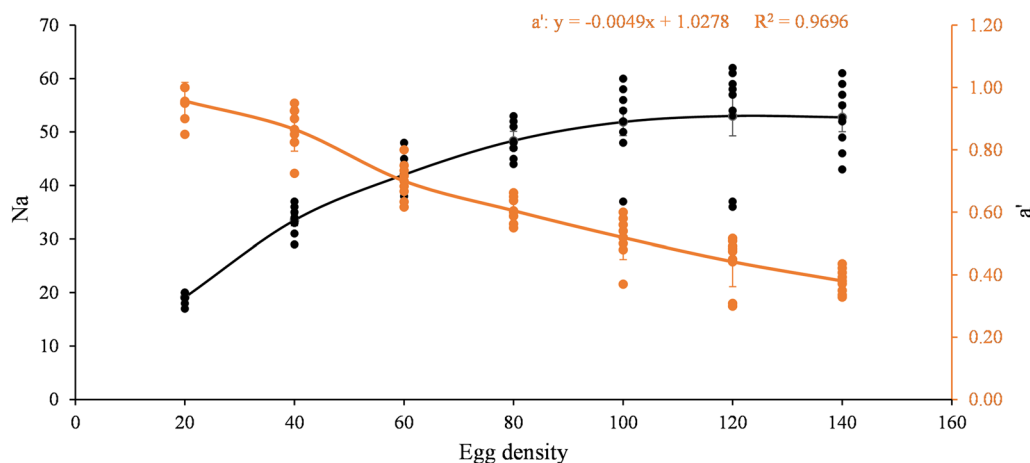


Fig. 5 Functional response of *Telenomus remus* females on *Spodoptera litura* eggs. N_a represents the number of parasitized eggs per day under different host egg densities (black line); a' is the search rate, which represents the proportion of parasitized eggs/available eggs under different host egg densities (orange line). The search rate is reflected by a linear equation, with R^2 as the correlation coefficient

The shorter the longevity of the female, the more APOP should be considered when releasing the parasitoids. The female longevity of *T. remus* reared on *S. litura* eggs was 8.68 days (Table 2), which is relatively longer than that of *T. remus* reared on *S. frugiperda* eggs (8.3 days), but shorter than that of *T. remus* reared on eggs of different generations of *C. cephalonica* (13.1–15.3 days) (Pomari-Fernandes et al. 2015).

Usually, a higher fecundity or faster development rate (lower TPOP) will generate a higher intrinsic rate of increase (r) (Hu et al. 2014), and vice versa. Our results showed a lower fecundity and longer development time of *T. remus* on *S. litura* eggs (186.90 eggs/female and 10.03 days, respectively) (Table 2) compared with those reared on *S. frugiperda* eggs (214.4 eggs/female and 9.0 days, respectively) (Bueno et al. 2014) when the parental generation was reared on their respective primary hosts under the same temperature (28 °C). However, a higher fecundity of *T. remus* was observed when reared on *S. litura* eggs than reared on *S. frugiperda* eggs (174.44 eggs/female) (Chen et al. 2023).

Similar development rates were obtained in another study, in which the development time of *T. remus* was 13.3 days on *S. litura* eggs and 12.2 days on *S. frugiperda* eggs at 26 °C (Li et al. 2023). The longer development time might result from the lower experimental temperature used. However, the fecundity results from different studies vary; for example, 173.5 and 145.8 eggs/female were reported using a field strain and a laboratory-reared strain of *T. remus* reared on *S. frugiperda* eggs, respectively (Naranjo-Guevara et al. 2020), and 140.8 eggs/female was reported by Pomari-Fernandes et al. (2015). Chen et al. (2021) showed that the fecundity of *T. remus* was ≈ 150 eggs/female on *S. litura* eggs among different photoperiods, a slightly longer (≈ 1 day) development time was recorded for *T. remus* on *S. litura* eggs compared with those reared on *S. frugiperda* eggs. In the current study, the r of *T. remus* reared on *S. litura* eggs (0.3506 day^{-1}) (Table 2) was lower than that reported by Chen et al. (2021) ($0.354 \sim 0.463 \text{ day}^{-1}$ among different photoperiods). In our study, a short T and DT were found for *T. remus* reared on *S. litura* eggs (12.91 days and 1.98 days, respectively); thus, the population growth rate was fast, similar to the results of Chen et al. (2023). This result was also been confirmed by a population projection (Fig. 4b).

The parasitic behavior of female parasitoids plays a crucial role in insect pest control, making the determination of the sex ratio a pivotal factor for population dynamics and effective pest management. Numerous studies have identified a range of influential factors, including host quality, host density, female age, and strain differences (Carneiro et al. 2010; Giunti et al.

2015; Chen et al. 2021). In our study, we observed that the proportion of female *T. remus* reared on *S. litura* eggs (N_f/N) was 0.495. This finding deviated from the results reported by Li et al. (2023) (> 0.78 , across different host ages) and Wu et al. (2021) (> 0.9), while it closely resembled the outcome reported by Huo et al. (2019) (0.451). This variability in the sex ratio of *T. remus* on *S. litura* eggs underscores the adaptability and flexibility of this wasp's sex ratio strategy. For instance, Chen et al. (2021) documented that the sex ratio of *T. remus* reared on *S. litura* eggs exhibited a decreasing trend as the parasitoid:host egg ratio increased. In contrast, our research highlights the significant impact of egg age on the sex ratio of *T. remus* (see Fig. 1b). This variation is likely due to changes in nutrient content and chemical defense substances within the eggs as they age (Vinson 2010).

In the context of pest control effectiveness, the net killing rate (C_0) provides a comprehensive measure that accounts for both effective and non-effective parasitism (Zang et al. 2023). Non-effective parasitism, while not contributing to population growth, plays a crucial role in limiting pest population growth. In our study, the net non-effective parasitism rate (G_0) of *T. remus* on *S. litura* eggs was 15.26, surpassing the values reported for *Anastatus* spp. on *Caligula japonica* Moore eggs (0.56–9.11) (Zang et al. 2023). This aligns with our life table results, which indicated a preadult survival rate (sa) of 0.9158 (< 1) (Table 2). Consistently, our findings are supported by emergence rates below 100%, in line with other studies (Wu et al. 2021; Li et al. 2023).

Functional response is an important tool for studying basic aspects of parasitoid–host interactions, with search rates and handling times being particularly important because they can both contribute to the impact of parasitoids on host population dynamics. Previous work reported that *T. remus* spends 40.6 s handling an *S. frugiperda* egg (Carneiro et al. 2010), and 37 s on an *S. littoralis* egg (Schwartz and Gerling 1974), which is significantly lower than that spent on *S. litura* eggs reported by our study (57.0 s/egg). The shorter time required for host recognition and handling means that parasitoids can parasitize more hosts per unit time. Thus, based on the differences in handling time, *S. littoralis* and *S. frugiperda* appear to be suitable for rearing of, and control by, *T. remus*. The way in which females handle host eggs and the time they take to do so are directly related to the number of parasitized eggs. The daily mean parasitism rate of *T. remus* on *S. frugiperda* (Carneiro et al. 2010) was significantly higher than that of *S. litura* (Fig. 5), regardless of host density. However, a higher search rate was recorded at the lowest *S. litura* density (20 eggs:1 parasitoid) (Fig. 5), whereas a higher search rates was found

on both low (25 eggs:1 parasitoid) and medium densities (100 eggs:1 parasitoid) of *S. frugiperda* eggs (Carneiro et al. 2010). A similar result reported that a lower host:parasitoid ratio (14–20:1) was optimal for rearing *T. remus* on *S. litura* eggs (Chen et al. 2021), which was concordant with our study. Our results suggest that the optimal parasitoid-host density was 20:1 for mass rearing or field release (Fig. 5). However, a study showed that an egg:parasitoid ratio of 30:1 and 50:1 achieved the highest rates of parasitism and emergence of *T. remus* reared on *S. litura* eggs (Xie et al. 2021). Thus, functional response studies can provide data for reference decisions related to mass-rearing and field release that depend on density effects.

Conclusion

In the past, *T. remus* was used as a potential dominant parasitoid of *S. frugiperda*. However, our study found, as a natural host of *T. remus*, *S. litura* eggs are suitable for the mass-rearing of this wasp for field release to control this pest, as supported by two-sex life table and functional response data analyses. These findings are helpful to broaden the understanding of *T. remus* against *Spodoptera* spp.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s43170-023-00188-w>.

Additional file 1: Table S1. Definitions and formulas of population parameters estimated in present study.

Author contributions

LDT, LHL, and LSZ designed the experiments, LDT and ZS wrote the manuscript; LHL, ZS and TJD carried out the study, and ZS and LDT analyzed data, LZB and GJY supported funds, LSZ reviewed the manuscript, all authors read and approved the final manuscript.

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Data availability

The datasets are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declared that they have no competing interest in connection with the evaluated manuscript.

Author details

¹National Key Laboratory of Green Pesticide, Key Laboratory of Green Pesticide and Agricultural Bioengineering, Ministry of Education, Guizhou University, Guiyang 550025, China. ²Guangxi Key Laboratory of Biology for Crop Diseases and Insect Pests, Plant Protection Research Institute, Guangxi Academy of Agricultural Sciences, Nanning 530007, China. ³Bijie Tobacco Company of Guizhou Province, Bijie 551700, Guizhou, China.

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