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Evaluation of key factors for mass rearing the egg parasitoid *Telenomus remus* Nixon (Hymenoptera: Scelionidae)

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Abstract

Background *Telenomus remus* is an egg parasitoid used as a biocontrol agent to control the invasive pest *Spodoptera frugiperda*. The use of high-quality factitious hosts is needed for efficient mass rearing of high-fitness parasitoids for biological control releases. To improve the efficiency and quality of parasitoid production for mass rearing, we evaluated host perference, supplemental nutrition, ultraviolet (UV) irradiation, parasitoid density, and exposure duration. Quality control for the mass rearing of *Te. remus* has not been conducted previously. This study determined the conditions and quality control factors necessary for the effective mass rearing of *Te. remus*.

Methods The preferred host of *Te. remus* was determined and the effects of supplemental nutrition on *Te. remus* adults, as well as those of ultraviolet (UV) irradiation on host eggs were evaluated. The subsequent impact on the quality of *Te. remus* were also assessed. The optimal parasitoid-to-host eggs ratio and exposure duration were studied.

Results *Telenomus remus* preferred *S. frugiperda* eggs as the host. Nutrition supplementation prolonged female longevity and increased fecundity of *Te. remus*. UV irradiation caused *S. frugiperda* eggs to shrivel, having a negative effect on *Te. remus* reproduction. When the ratio of *Te. remus* to *S. frugiperda* eggs ranged from 1:4 to 1:10 and the exposure duration was 48 h, a lower wizened egg rate, higher emergence rate, and greater female proportion was obtained.

Conclusions The use of *S. frugiperda* eggs as the host for mass rearing of *Te. remus* was indicated, and it was found *Spodoptera litura* eggs could sever as an alternative host. Nutrition supplementation and non-UV-irradiated *S. frugiperda* eggs should be provided. The suitable ratio of *Te. remus* to *S. frugiperda* eggs ranges from 1: 4 to 1:10, and the exposure duration should be 48 h, as determined by the ratio of parasitoid to host eggs.

Keywords Egg parasitoid wasp, Biological control, Mass reproduction, Quality control

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Background

Since *Spodoptera frugiperda* (J. E. Smith) invaded China, its natural enemies, especially parasitoidwasps, have been widely studied. Egg parasitoid species of *S. frugiperda* including *Telenomus remus* Nixon, *Trichogramma chilonis* Ishii, *Trichogramma minutum* Riley and *Trichogramma pretiosum* Riley, have been reported in the field (Tang et al. 2019; Li et al. 2023a; Kenis et al. 2023). Among these species, *Te. remus* is the primary parasitoid of *Spodoptera* spp. having been first found parasitizing the eggs of *S. frugiperda* in China (Liao et al.

2019; Li et al. 2019a). *Telenomus remus* has previously been used in augmentative biological control programs against *S. frugiperda* and proved to be effective (Colmenarez et al. 2022; Yao et al. 2023; Yuan et al. 2024). It is highly effective at parasitizing the multi-layer and high-scale coverage egg masses of *S. frugiperda* (Beserra et al. 2002; Hou et al. 2022; Li et al. 2023b, 2023c). Even in rainy and humid environments, *Te. remus* can adapt to the conditions and provide a high rate of parasitism. Therefore, studying the large-scale production of *Te. Remus* is necessary. Parasitic wasp quality is an important factor determining their indoor reproduction and the potential effectiveness of field control. The goals are to ensure higher wasp quality at the lowest possible cost in the insectary. Numerous factors can affect the quality of parasitic wasps, including host, temperature, humidity, photoperiod, suitable exogenous nutrients, parasitoid density and exposure duration. Optimal cold storage conditions for storing parasitic wasps and hosts are also important (Böckmann et al. 2012; Abram et al. 2016; Zang et al. 2021).

Host preference and fitness are important components of the mass rearing of parasitoids for biological control (Vinson 1976, 2010; Schmidt 1994). Suitable hosts can ensure the production and quality of a large number of offspring while maintaining rearing costs within an acceptable range. Under laboratory conditions, easy-to-rear alternative hosts are often used for large-scale production of parasitic wasps. However, continuous rearing on alternative hosts can alter the parasitoid's ability to control the target host and affect its preference for the target host (Cobert 1985; van Lenteren and Bigler 2010). Unique factors of host eggs, such as size, color, egg surface structure, age and host quality, can all influence the behavioral responses of parasitic wasps to their hosts and their development (Cônsoli et al. 1999; Wang and Yang 2010). Different species of parasitic wasps exhibit different selectivity toward their hosts, and there are also differences in the selection adaptability of the same species of parasitic wasp to different hosts (Pavlík 1993). Host preference is influenced by the host which the species developed (Stireman et al. 2006; Desneux et al. 2009). The host preference of *Te. remus* is less influenced by the host on which it has developed than *Tr. pretiosum* (Goulart et al. 2011). After continuously rearing on *S. frugiperda* eggs for multiple generations, *Te. remus* preferred *Spodoptera cosmioides* (Walker) eggs over *S. frugiperda* eggs, whereas *Tr. pretiosum* still preferred the original host after switching to *Spodoptera eridania* (Stoll).

Parasitic wasps derive nutrition from hosts and non-hosts. Host nutrition includes host body fluids and tissues (Heimpel and Collier 1996). Non-host nutrition is also called exogenous nutrition or supplementary nutrition. It mainly includes carbohydrates such as nectar (Jervis and Kidd 1986) and plant pollen (Rivero & Casas, 1999). Parasitic wasps can feed on host nutrients in both the larval and adult stages. After emergence, females can obtain host nutrients through direct feeding or parasitism, and leading to the death of the host. This behavior also enhances the adaptability to the host (Zang & Liu 2008; Kaspi et al. 2011; Liu et al. 2014). However, not all adults exhibit host feeding behavior; parasitic wasps cannot rely solely on the host's nutrients. They can feed on plant pollen or nectar, as well as sugars such as a sucrose solution, to meet their energy needs (Jervis and Kidd 1986). Supplemental nutrients can promote the reproduction and development of parasitic wasps, extend their lifespan and minimize the deleterious effects of indoor rearing for multiple generations (Russell 2015; Varennes et al. 2016; Benelli et al. 2017). The parasitism ability of *Te. remus* increased when fed with honey, glucose, fructose, and sucrose solutions after emergence compared to when not provided with supplemental nutrients. In addition, supplemental feeding significantly prolonged the adult lifespan. Females that were only fed with water and lacked nutrients survived only one day, indicating that honey, glucose, fructose, and sucrose are important nutrient sources for *Te. remus* (Meirelles et al. 2008).

Irradiation can ensure that the host does not hatch and some parasitic wasps can successfully develop within irradiated hosts. Irradiation may not significantly affect the quality of the parasitoids and this treatment can facilitate storage, transportation, and release (Cancino et al. 2012; Bachmann et al. 2015). Ultraviolet (UV) radiation has been used in pest control, especially in mass reproduction to preserve host eggs for wasps to parasitize (Tillinger et al. 2004). In biological control programs, UV radiation on host eggs also helps increase parasitic wasp populations. The density, volume, and age of the irradiated host, as well as irradiation time and intensity, are factors that need to be studied and optimized. The suitability of irradiated host eggs for parasitic wasps can be measured by various biological parameters in reproduction, such as adult emergence rate, adult fecundity, longevity, and female proportion. UV irradiation technology is currently primarily employed for rearing *Trichogramma* on *Corcyra cephalonica* (rice moth) eggs (Bigler 1994; Parra 2010; Xu et al. 2016). Yuan et al. (2012) found that UV-irradiated rice moth eggs did not have a negative impact on *Trichogramma* reproduction. UV-irradiated eggs also helped to improve *Trichogramma* reproductive performance. However, the suitability of UV irradiation of host eggs for mass reproduction of *Te. remus* is unknown.

Parasitoid density is important for both indoor reproduction and field release. The appropriate proportion of parasitoid density can enhance the production efficiency, reduce costs, and achieve satisfactory control effects (Wei et al. 2017; Iqbal et al. 2020; Paolo et al. 2020). In indoor reproduction of parasitic wasps, the appropriate exposure duration and proportion can affect the utilization of host eggs. Females cannot parasitize all the host eggs when the exposure duration is insufficient. This leads to low utilization efficiency of host eggs and increases the production cost. Otherwise, a longer exposure duration may lead to superparasitism, reducing the emergence rate and number of offspring produced (Smith 1996). The parasitism rate of *Trichogramma japonicum* Ashmead was relatively high when the ratio of parasitoid to rice moth eggs was between 1:10–20, with a maximum of 91.22%. The appropriate exposure duration increased with the increase in the ratio. In mass reproduction, a 1:20 ratio and exposure for 48 h was optimal (Li et al. 2019b). Chen et al. (2021a) found that the optimal parasitoid-to-host ratio for *Te. remus* reared on *Spodoptera litura* Fabricius eggs was 1:14–20, with an optimal exposure duration of24 h. The highest parasitism rate and female proportion were achieved under these conditions.

Common alternative hosts, such as *Antheraea pernyi* (Guérin-Méneville) eggs, *C. cephalonica* eggs, and *Ephestia kuehniella* Zeller eggs are mainly used as factitious host eggs for mass rearing egg parasitoid wasps. Among them, *Trichogramma* and *Anastatus fulloi* Sheng & Wang have achieved large-scale reproduction and these species have been practically released in the field (Li and Liu 1997; Zang et al. 2021). Previous mass rearing studies on *Te. remus* have utilized the eggs of Noctuidae as hosts. Researchers have successfully used rice moth eggs as factitious hosts in Brazil (Pomari-Fernandes et al. 2016; Queiroz et al. 2017). However, our previous experiments and other studies in China have indicated that *Te. remus* cannot be reared on rice moth eggs (Chen et al. 2021b). At present, a large-scale reproduction system has not been established for *Te. remus* and quality control studies are lacking. The purpose of this study was to clarify the conditions and quality control factors necessary for the large-scale rearing of *Te. remus*. Host selection and preferences of *Te. remus* were determined. The effect of nutritional supplements on wasp reproduction, the effect of UV radiation on host egg quality and the subsequent impact on the quality of parasitic wasps were studied. Finally, the appropriate exposure duration and the optimal ratio of parasitoids to host eggs were investigated.

Methods

Insects

The parasitoid wasp *Telenomus remus* and its host *Spodoptera frugiperda* eggs used in this study were originally collected from a corn field in Huadu of Guangdong province, southern China, in 2020. Pupae of another host, *Spodoptera litura,* were provided by Guangzhou Biological Control Station, Guangzhou, China. A laboratory colony of *S. frugiperda* was established by feeding larvae an artificial diet (Li et al. 2019c) for over 10 generations. Adults of *S. frugiperda* and *S. litura* were fed with 10% honey solution and they laid eggs on paper. The newly laid eggs, within 24 h, were used for subsequent parasitism and rearing experiments. Stock cultures of *Te. remus* were alternately reared on the eggs of both *S. frugiperda* and *S. litura*. The insects were cultured in a climatic cabinet set at 27 ± 1 °C, 75 ± 5% RH and a 16:8 h (L:D) photoperiod.

Experimental setup

Bioassay 1: the preference of *Te. remus* for host species *S. frugiperda* and *S. litura* eggs. To estimate the selectivity of *Te. remus* in the present experiment, newly laid egg masses (~ 100 plump eggs) from both hosts under the same quality conditions (single-layer, low-scale coverage) were used. 1) The selective experiment involved placing an egg mass of *S. frugiperda* and *S. litura* in the same glass tube (3 cm in diameter × 9 cm high) for exposure to a newly emerged and mated *Te. remus* female. 2) In the non-selective experiment: egg masses of *S. frugiperda* and *S. litura* were placed in different glass tubes, each with a mated *Te. remus* female. After 24 h of parasitism, the wasps were removed, and the egg masses of the two hosts were separated into different glass tubes to rear until *Te. remus* emergence. Ten *Te. remus* females and 10 egg masses of each host were used in each treatment.

Bioassay 2: the effect of supplementary nutrition on the reproductive performance of *Te. remus*. Treatments providing supplemental nutrition (10% honey solution) and lacking supplemental nutrition were set up to investigate the longevity and parasitism ability of *Te. remus*. Four treatments (A, not providing host eggs and supplementary nutrition; B, only providing *S. frugiperda* eggs; C, only providing a 10% honey solution; and D, providing both *S. rugiperda* eggs and with a 10% honey solution) were established to investigate *Te. remus* longevity. Ten newly emerged and mated *Te. remus* females were used in each treatment. For treatments B and D, the newly laid single-layer egg masses (~ 100 plump eggs) of *S. frugiperda* were also provided and refreshed every day until the *Te. remus* females died, to investigate the reproductive parameters.

Bioassay 3: the effect of UV-irradiated host eggs on the reproductive performance of *Te. remus*. The newly laid single-layer egg masses (~ 100 plump eggs) of *S. frugiperda* were subjected to 20-W UV irradiation for 20 min or were not exposed to UV irradiation. The distance between the UV light and *S. frugiperda* eggs was

15 cm. Each egg mass was inserted into a different glass tube, and a newly emerged and mated *Te. remus* female was added for parasitism. After 24 h of exposure, the *Te. remus* females were removed, and each of the egg masses was subsequently examined for reproductive parameters. Ten *Te. remus* and 10 *S. frugiperda* egg masses were used in each treatment.

Bioassay 4: the effect of parasitoid-to-host ratio and exposure duration on the reproductive performance of *Te. remus*. The ratios of *Te. remus* to *S. frugiperda* were set to 2:1, 1:1, 1:2, 1:4, 1:6 1:8, and 1:10. The exposure durations were 12 h, 24 h, 36 h, and 48 h. First, the parasitized egg mass (~100 *Te. remus* adults) was placed into a glass tube in advance until emergence. The sex ratio (female to male) of *Te. remus* was approximately 8:1. Subsequently, *S. frugiperda* eggs were prepared according to the parasitoid-to-host ratio. After the *Te. remus* emerged, the prepared host egg masses were provided to the wasps for them to parasitize according to the exposure time. After exposure, each egg mass was inserted into different glass tubes until *Te. remus* offspring emerged. Each tube represented a ratio of *Te. remus* to *S. frugiperda* and exposure duration. Three replicates were set in each treatment.

The climate controlled chambers (Yamato, Tokyo, Japan) in all experiments were set at 27 ± 1 °C, 75% ± 5% RH and a 16:8 h (L:D) photoperiod. When the host eggs hatched into larvae and *Te. remus* adults emerged, the biological parameters were examined using a binocular microscope (Olympus, Tokyo, Japan). All experiments were independently repeated 3 times.

Biological parameters assessed

The number of parasitized egg masses, host eggs, wizened eggs (i.e., no parasitoid emergence and host larvae hatched), hatched/unhatched host larvae, *Te. remus* adults, and male adults were monitored and recorded after observation under a binocular microscope. Considering that the attack of egg parasitic wasps on the host usually results in the partial failure of the development of parasitic wasp offspring and the abortion of host eggs (Abram et al. 2016), the actual number of parasitized eggs included the number of adult emergence and eggs containing developmentally failed wasps. The date of emergence and death of *Te. remus* females were also recorded to calculate their longevity. Fecundity was measured by placing a newly emerged female adult individually for each replicate in a glass tube containing an *S. frugiperda* egg card (~100 eggs for each card) that was refreshed daily until the females died; the number of adults was counted daily. Parasitism rate of egg masses, parasitism rate of eggs, wizened eggs rate, *Te. remus* emergence rate, number of adults produced, and female proportion were calculated as follows:

$$\text{Parasitism rate of egg masses (\%)} = \text{number of parasitized egg masses} / \text{total number of egg masses} \times 100$$

$$\text{Parasitism rate of eggs (\%)} = (\text{number of adults produced} + \text{number of wizened eggs} - \text{number of host larvae unhatched}) / \text{total number of eggs} \times 100$$

$$\text{Wizened eggs rate (\%)} = (\text{number of wizened eggs} - \text{number of host larvae unhatched}) / \text{total number of eggs} \times 100$$

$$\text{Emergence rate (\%)} = \text{number of adults} / \text{total number of parasitized eggs} \times 100$$

$$\text{Female proportion (\%)} = (\text{total number of adults} - \text{number of male adults}) / \text{total number of adults} \times 100.$$

Statistical analysis

One-way analysis of variance (ANOVA) and paired-sample t-tests were used to analyze differences of reproductive parameters between treatments in bioassays 1–3. In bioassay 4, multi-factor analysis of variance was first conducted to evaluate the effect of the parasitoid-to-host ratio and exposure duration and their interaction on reproductive parameters. One-way ANOVA and Tukey's test was used to analyze differences among exposure duration treatments. Before statistical analysis, percentage data were arcsine square root-transformed, while data on the number of adults and longevity were log10-transformed to achieve normal distribution. When means were not normally distributed even when transformed, a nonparametric Kruskal–Wallis ANOVA was used and means were separated using a Mann–Whitney U test. In all experiments, data were analyzed with SPSS 22.0 software (IBM, Armonk, NY, USA), and differences were considered significant at $P < 0.05$.

Results

Preference of Te. remus for S. frugiperda or S. litura eggs

In the selective test, 100% of *Te. remus* chose to parasitize *S. frugiperda* eggs and 93.33% chose to parasitize *S. litura* eggs. Significant differences were observed in the parasitism rate of eggs, emergence rate and the number of adults produced by the two hosts ($U = -3.723, -3.293$, and -4.386, $P < 0.001, = 0.001$, and < 0.01). The performance of *Te. remus* was superior when parasitizing *S. frugiperda*, with a 72.90% parasitism rate of eggs, 53.38% emergence rate and production of 49.00 adults (Fig. 1). In the non-selective test, both host eggs masses were 100% selected by *Te. remus* and the only significant differences were found in the parasitism rate of eggs and female proportion ($U = -4.009$ and 3.744, $P < 0.001$ and 0.01). The parasitism rate of *Te. remus* on *S. frugiperda* was higher, resulting in the production of females (Fig. 2).

Effect of supplementary nutrition on the reproductive performance of *Te. remus.*

The survival data revealed that the longevity of *Te. remus* without supplementary nutrition was only 1.48 d, with only 16.67% of females surviving to 2 d. Longevity was not prolonged by providing *S. frugiperda* eggs (Fig. 3A & B). However, the longevity of *Te. remus* fed a 10% honey solution daily was significantly prolonged, with an average longevity of 11.37 d and a maximum longevity of 24 d ($F_{3, 116} = 52.865$, $P < 0.001$). When both supplemental nutrition and host eggs were provided, the average longevity was not significantly different from that of females provided only with supplementary nutrition. Approximately half of the females survived up to 11 d, but the maximum longevity was 16 d (Fig. 3B).

The reproductive parameters decreased with the extension of longevity during *Te. remus* reproduction. The longevity and oviposition period of *Te. remus* were significantly prolonged by supplementary nutrition. The average number of adults produced during their

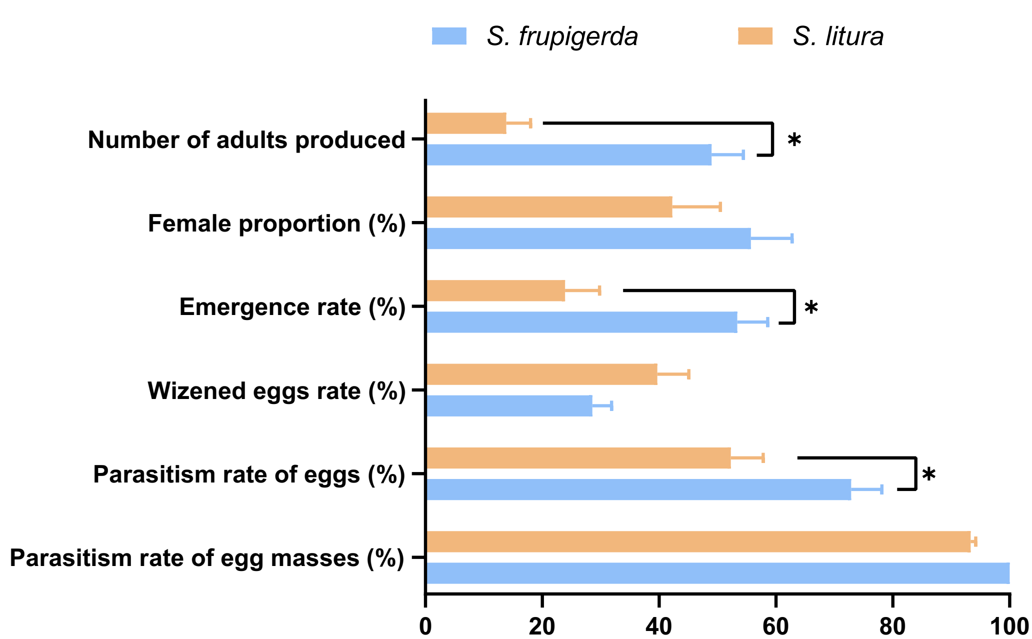

Fig. 1 Reproductive parameters of *Telenomus remus* in the host selectivity test. Means (± SE) were calculated from 30 replicates. Data with an asterisk differ significantly according to Tukey's test at $P = 0.05$

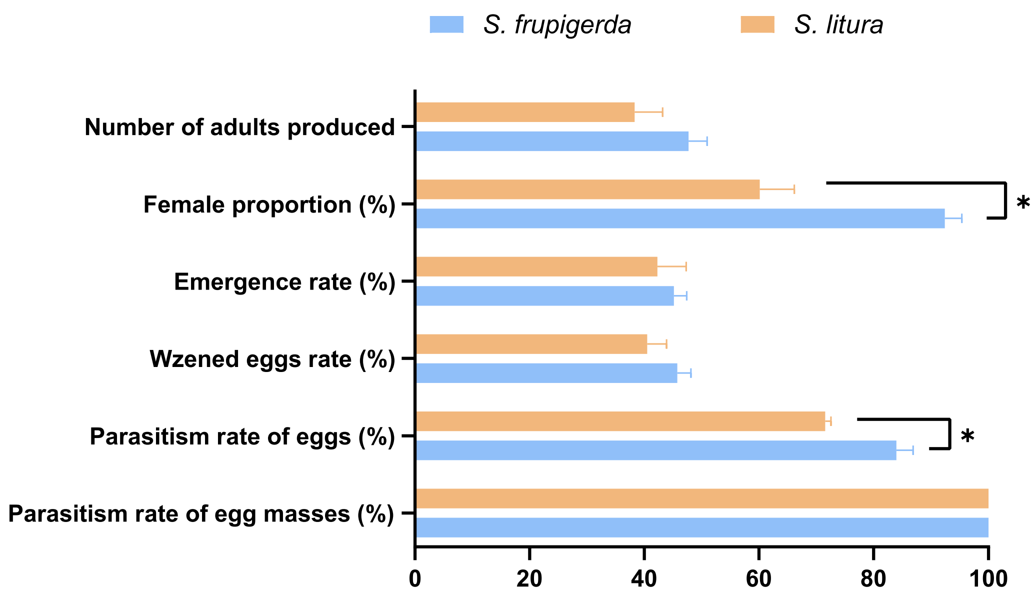

Fig. 2 Reproductive parameters of *Telenomus remus* in the host non-selectivity test. Means (± SE) were calculated from 30 replicates. Data with an asterisk differ significantly according to Tukey's test at $P = 0.05$

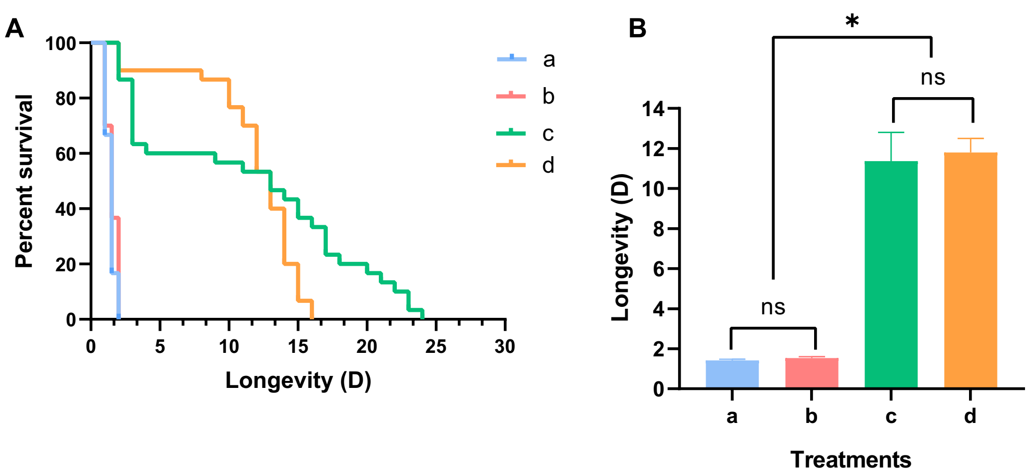

Fig. 3 **A** Survival curves of *Telenomus remus* under different nutritional conditions. **B** Longevity of *Telenomus remus* female under different nutritional conditions. **a** without host egg and supplemental nutrition; **b** only with *Spodoptera frugiperda* eggs; **c** only with supplemental nutrition; **d**, with *Spodoptera frugiperda* eggs and supplemental nutrition. Values were calculated from 30 replicates. Treatments with an asterisk differ significantly according to Turkey's at $P = 0.05$

lifetime reached 117.91 (Fig. 4). However, the average number of adults produced by *Te. remus* without supplementary nutrition was only 47.89, Which was less than half the fecundity of *Te. remus* with supplementary nutrition due to the short longevity (Fig. 5). In addition, although the longevity was extended to 16 d after nutrition supplementation, the oviposition period was only about 10 d, and the number of adults produced was highest on the first day. When comparing the biological parameters on the first day of life, the parasitism rate of *Te. remus* with supplementary nutrition reached 95.10%, producing 61.53 adult wasps. This was significantly higher than that of *Te. remus* without supplementary nutrition ($U = -4.767$, $P = 0.00$; $t = -2.735$, $P = 0.008$) (Fig. 6).

Effect of ultraviolet-irradiated host eggs on the reproductive performance of *Te. remus*

No *S. frugiperda* larvae hatched after UV irradiation of the eggs. The parasitism rate of egg masses, emergence

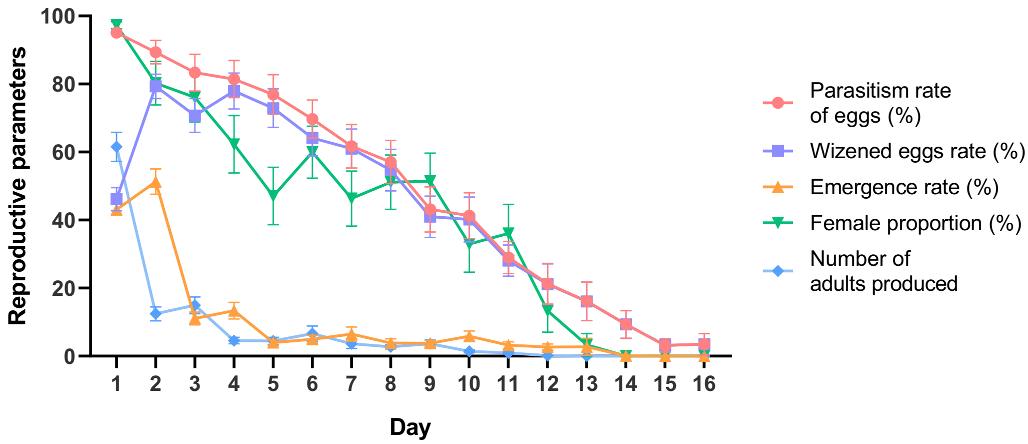

Fig. 4 Dynamics of reproductive parameters of *Telenomus remus* during its lifespan with supplemental nutrition. Means (± SE) were calculated from 30 replicates

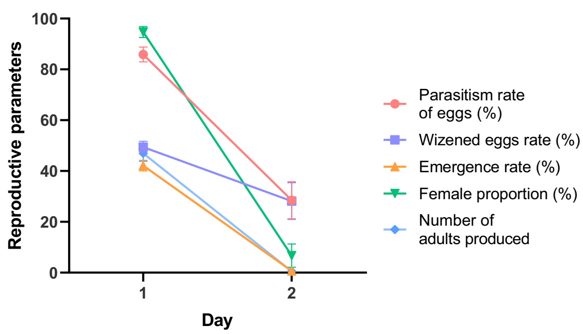

Fig. 5 Dynamics of reproductive parameters of *Telenomus remus* during its lifespan without supplemental nutrition. Means (± SE) were calculated from 30 replicates

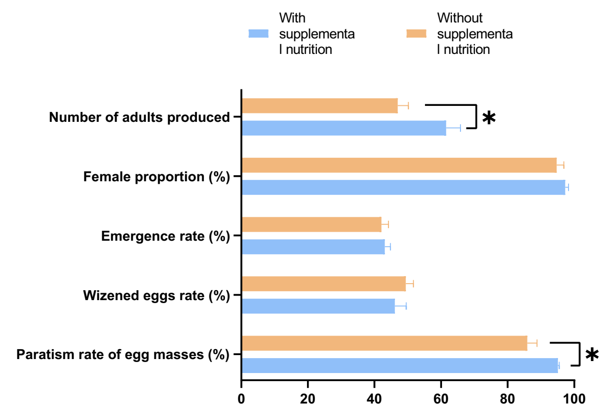

Fig. 6 Biological parameters of the first day of the reproduction period of *Telenomus remus* with/without supplemental nutrition. Means (± SE) were calculated from 30 replicates. Data with an asterisk differ significantly. Tukey's test at $P = 0.05$ were used when means fit a normal distribution, and the Mann–Whitney U test at $P = 0.05$ was used when means were not normally distributed

rate, female proportion and number of adults produced by *Te. remus* reared on fresh *S. frugiperda* eggs were significantly higher than those reared on UV-irradiated *S. frugiperda* eggs ($U = -2.121$, $P = 0.034$; $t = -5.812$, $P < 0.000$; $U = -2.833$, $P = 0.005$; $U = -4.775$, $P = 0.000$) (Fig. 7). Only 76.67% of *Te. remus* preferred to parasitize the UV-irradiated egg masses, causing an 80.47% rate of wizened eggs. The emergence rate, female proportion and number of adults produced on UV-irradiated eggs were less than half the values of *Te. remus* reared on fresh eggs.

Effect of parasitoid-to-host ratio and exposure duration on the reproductive performance of *Te. remus*

Multi-factor variance analysis indicated that exposure duration and the interaction between parasitoid-to-host ratio and exposure duration significantly impacted the wizened eggs rate, emergence rate, female proportion and number of adults produced. However, the wizened eggs rate and emergence rate were not affected by the parasitoid-to-host ratio (Table 1).

The results of one-way ANOVA showed that when the parasitoid-to-host ratio was 2:1, 1:1,1:2 and 1:4,, the female proportion was significantly different ($F = 11.917$, 66.713, 5.636, 5.754, and 3.752, $P = 0.003$, 0.000, 0.023 and 0.021,); when the parasitoid-to-host ratio was 1:8, there were significant differences in the proportion of wizened eggs and emergence ($F = 6.287$ and 6.287, $P = 0.017$ and 0.017); when the parasitoid-to-host ratio was 1:4, there were significant differences in all the biological parameters ($F = 6.621$, 6.621, 5.636, 5.754 and 4.099, $P = 0.015$, 0.015, 0.021 and 0.049); when the host eggs were 10 times the number of parasitoids, there were no significant differences in the biological parameters (Fig. 8). Based on lower wizened eggs rate, higher emergence rate, and

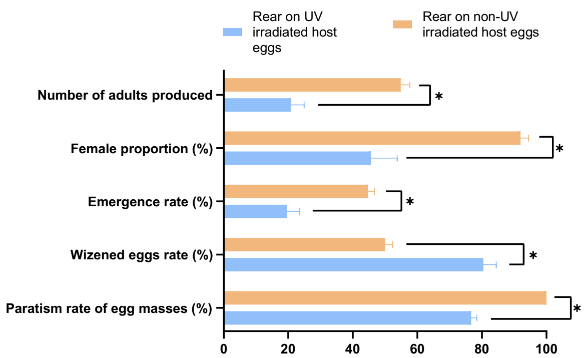

Fig. 7 Biological parameters of *Telenomus remus* reared on UV-irradiated/non-UV-irradiated *Spodoptera frugiperda* eggs. Means (± SE) were calculated from 30 replicates. Data with an asterisk differ significantly. Tukey's test at $P = 0.05$ were used when means fit a normal distribution, and the Mann–Whitney U test at $P = 0.05$ was used when means were not normally distributed

female proportion, the optimal exposure durations were 12 h, 36 h, and 24 h when the ratios of *Te. remus* to *S. frugiperda* were 2:1, 1:1, and 1:2, respectively. The optimal exposure duration was 48 h when the ratio of *Te. remus* to *S. frugiperda* ranged from 1:4 to –10.

Table 1 Multi-factor variance analysis of effects of parasitoid-to-host ratio and exposure duration on reproductive parameters of *Telenomus remus*

Biological parameters	Factors	df	*F*	*P*
Wizened eggs rate (%)	A	3	3.76	0.016
	B	6	2.04	0.076
	A*B	18	2.93	0.001
Emergence rate (%)	A	3	3.75	0.016
	B	6	2.05	0.075
	A*B	18	2.93	0.001
Female proportion (%)	A	3	15.369	0.000
	B	6	16.476	0.000
	A*B	18	5.339	0.000
Number of adults produced	A	3	4.767	0.005
	B	6	468.62	0.000
	A*B	18	2.517	0.004

A, exposure duration; B, parasitoid to host ratio

Discussion

Differences in host species and nutrition can affect the adaptation and preferences of parasitic wasps (Vinson 1976, 2010; Schmidt 1994). Our results demonstrated that *Te. remus* preferred eggs of its natural host, *S. frugiperda,* in both selective and non-selective experiments. This was especially true for the egg parasitism rate, emergence rate and female proportion. However, this result differs from previous studies suggesting that *S. litura* eggs were more suitable for mass rearing *Te. remus* (Huo et al. 2019, 2020; Chen et al. 2021b; Wu et al. 2021). *Te. remus* from field-collected *S. frugiperda* eggs were directly used for host selection experiments without indoor host domestication. Adults of *Te. remus* reared on *S. frugiperda* eggs were larger and the reproductive parameters were higher when using *S. litura* eggs as hosts (Chen et al. 2021b). In addition, using *S. frugiperda* eggs for *Te. remus* rearing was time- and resource-consuming due to *S. frugiperda* larval cannibalism (Perkins 1979). Cannibalism might be minimized by switching to artificial diets or castor oil plants and increasing the separation space for *S. frugiperda* larvae (Glober 2019; Colmenarez et al. 2022). In our study, *Te. remus* showed a stronger preference for *S. frugiperda* eggs, possibly because *Te. remus* were originally field-collected from *S. frugiperda* eggs. In addition, *Te. remus* were reared on *S. frugiperda* eggs for many generations indoors. Although *S. litura* eggs were used as alternative hosts for reproduction, the parasitoids maintained a greater preference for the eggs of *S. frugiperda*. There was little difference in the quality between the two host eggs and this excluded any differences caused by host quality. Goulart et al. (2011) showed that despite *Te. remus* being reared on eggs of *S. frugiperda* for many generations, they exhibited a preference for parasitizing *S. cosmioides* eggs. This disparity in results can also be attributed to our study only examining the reproductive parameters of one generation on two host eggs but without assessing the reproductive fitness of subsequent generations. Therefore, this result only clarifies the host preference for *Te. remus* on two specific host eggs, and it remains unclear whether *S. frugiperda* is a suitable host for mass rearing *Te. remus.* It also emphasizes that the acceptance and preference behavior of female parasitoid wasps toward hosts cannot be simply attributed to the host alone. Correlative factors such as visual, physical and chemical characteristics, as well as nutritive quality, should also be considered (Schmidt 1994; Vinson 1994, 2010). The preference of *Te. remus* for *S. frugiperda* is beneficial for biological control in the field.

In bioassay 1, the female proportion is higher when wasps were reared on *S. frugiperda* eggs than on *S. litura* eggs under non-selective conditions, while there is no significance in the female proportion reared on both host eggs under selective conditions. This may be related to the sex allocation of *Te. remus* during the parasitic process (King and Lee 1994). Sex allocation is influenced by the parasitic experience of parasitic wasps (Liu et al 2017). In the selective experiment, the different oviposition order of *Te. remus* on the two species of host eggs resulted in different sex allocations. This also reflects the determination and selectivity of *Te. remus* towards host eggs, and also indicates that female wasps control

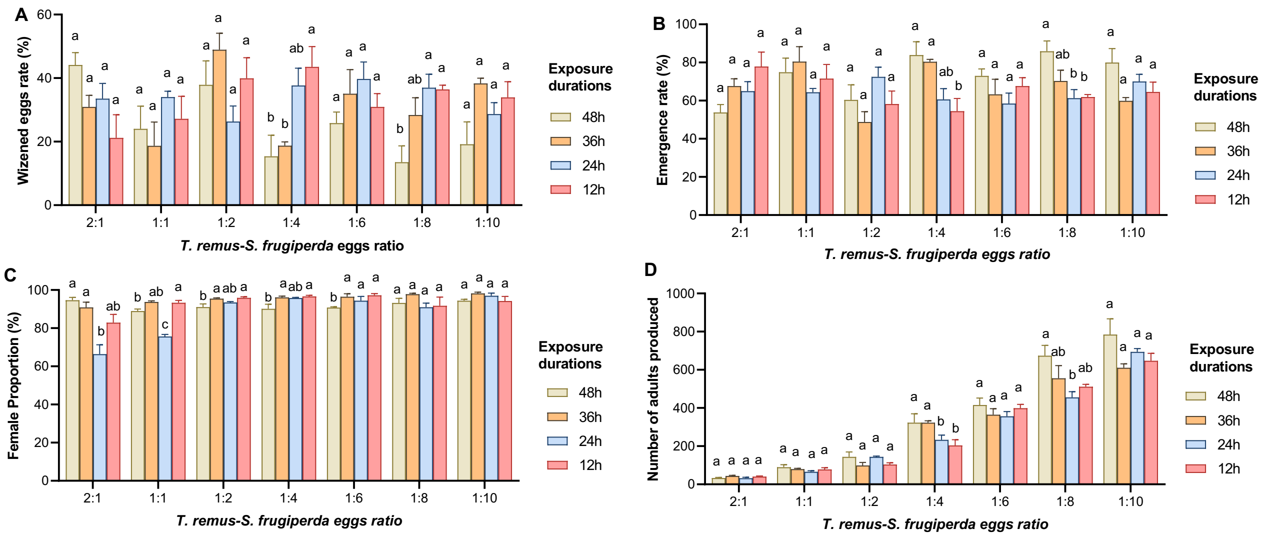

Fig. 8 Biological parameters of *Telenomus remus* under different parasitoid-to-host ratios and exposure durations. **A** Wizened eggs rate; **B** Emergence rate; **C** Female proportion; **D** Number of adults produced. Means (± SE) were calculated from 3 replicates. Exposure duration treatments with a different lower case letter under the same parasitoid-to-host ratio are significantly different using Tukey's test at $P = 0.05$

the progeny sex ratio according to external information, including host size and nutritional status, the age of parasitic wasps and host density (Vinson 1976; King and Napoleon 2006; Heimpel and de Boer 2008).

The results of this study showed that *Te. remus*, like other parasitic wasps, relies on both host and non-host nutrients for development and reproduction. Supplemental nutrients can prolong wasp lifespan and improve reproductive performance (Benelli et al. 2017; Wang et al. 2022). The survival time of *Te. remus* provided with host eggs and honey solution was shorter than that of those provided with only the honey solution. Longevity determines whether parasitoids can successfully search for, and locate, hosts and how effective they are as biological control agents (Roland and Taylor 1997; Wäckers 2004).

In terms of parasitism efficiency, *Te. remus* offered supplementary nutrition was stronger than *Te. remus* only provided with egg masses. This was related to the increased longevity of females provided with supplementary nutrition. When only provided with host eggs, the female longevity was less than 2 d, which was similar to longevity when there was no supplementary nutrition. On the second day, there was little parasitic efficacy, suggesting that *Te. remus* does not feed on the host eggs and mainly supplements its dietary needs by consuming of external nutrients. This is different from female *A. fulloi*, which pierce *Antheraea pernyi* eggs and feed on the egg fluid, as well as on honey solution as a supplementary source of nutrition. The host egg provides nutrition for the larvae of egg parasitoid wasps, while the adults mainly depend on consumption of supplementary nutrients for prolonging their longevity and extending their reproductive duration. This indicates that the growth and reproduction of most egg parasitoid wasps are not entirely dependent on the host eggs (Cônsoli and Grenier 2001). For example, *Trichogramma* must feed on other nutrients when they are newly emerged in order to mature their ovaries and continuously develop eggs (Jervis and Kidd 1986; Heimpel and Collier 1996). We also found that one-day-old *Te. remus* female wasps had the strongest parasitic efficacy and could lay 40–70 eggs, regardless of whether they were fed on supplementary nutrients. This result was similar to Schwartz and Gerling (1974), where one-day-old *Te. remus* females had the highest reproductive capacity. As the age of female increases, the number of offspring produced decreases and the number of male offspring produced increases from the third day on.

Xu et al. (2016) stated that host eggs treated by UV irradiation are the most suitable for rearing parasitic wasps. These eggs not only were affected by hatching host larvae, but also retained better nutrition and may help to increase parasitic wasp populations in biological control. The host quality will be threatened by an unsuitable method of killing the embryo and thus affect the parasitism rate and host selection suitability of parasitic wasps. In our study, we found that 20 watts of UV irradiation for 20 min had a negative effect on the parasitism of *S. frugiperda* eggs by *Te. remus*. Saour et al. (2004) showed that *Trichogramma cacoeciae* and *Trichogramma evanescens* preferred to parasitize the untreated egg masses of *Phthorimaea operculella*. However, *Trichogramma japonicum*, *Trichogramma chilonis* and *Trichogramma* *leucania*e preferred to parasitize rice moth eggs exposed to UV radiation (Xu et al. 2016). These results showed that, compared to the untreated host eggs, the drilling time of *Trichogramma* on the host eggs irradiated by UV radiation was shorter, which can improve the fecundity of the parasitoid wasps (Romeis et al. 1997; Yuan et al. 2012; Yang et al. 2016). This may be related to the changes in the thickness and hardness of the egg shell after the host was irradiated, which would be conducive to oviposition.

Most of the egg masses produced by *S. frugiperda* in the field are multi-layer, while single- and double-layer egg masses were typically produced in the laboratory. Preliminary experiments showed dehydration of surface eggs when the UV irradiation time exceeded 30 min, resulting in the poor reproductive performance of *Te. remus*. When the irradiation time was less than 20 min, the lower layer of eggs did not receive enough UV radiation to allow the larvae to hatch. Therefore, single-layer egg masses were used in this experiment and the UV irradiation time was set at 20 min. The effects of UV irradiation treatment in this experiment need further study. Variation of irradiation time, radiation intensity, distance between host egg and UV lamp are all factors that need to be considered in order to determine an optimal irradiation scheme.

At the lowest ratio of *Te. remus* to *S. frugiperda* eggs (1:10), the exposure duration had no significant effect on the biological parameters. Even with an exposure duration of 12 h, no *S. frugiperda* larvae hatched. Chen et al. (2021a) found that a stable parasitism rate and a female ratio of more than 60% could be obtained when the exposure duration was 24 h and the ratio of *Te. remus* to *S. litura* eggs was 1:14–20. This may be due to the different host eggs. The parasitism efficiency of multi-*Te. remus* females is greater than that of single-female parasitism when tested against *S. frugiperda*, suggesting that the host eggs provided in this experiment had not yet reached the upper limit of *Te. remus* fecundity. Although *Te. remus* usually lays only one egg per host egg, superparasitism can also occur. Superparasitism often produces small, stunted individuals that have difficulty parasitizing hosts (Corrigan et al. 1995) and may even result in no adult emergence. In this study, when *Te. remus* had twice the number of *S. frugiperda* eggs, the reduced emergence rate may be attributed to the wizened eggs caused by superparasitism. The wizened eggs rate was reduced with decreased exposure duration. In contrast, with increased host number and increased exposure duration, the wizened eggs rate can be reduced. It is unclear if the superparasitism of *Te. remus* is due to their weak discrimination of host eggs parasitized by the same or different female wasps.

Conclusions

This study evaluated the effects of host selectivity, nutrition supplementation, UV irradiation of host eggs, ratio of parasitoid to host, and exposure duration for mass production of *Te. remus*. Based on the selection and preference of *Te. remus*, and considering the control efficiency against *S. frugiperda* in the field, the use of *S. frugiperda* eggs as the host for mass rearing *Te. remus* is preferred. *S. litura* eggs are also suitable for mass rearing *Te. remus* and could be used as an alternative host. Alternating the use of two hosts can potentially reduce the reproductive capacity of parasitoid species. Nutrition supplementation had a positive effect on prolonging female longevity and improving fecundity of *Te. remus*. It is considered to be an essential component in mass production. However, UV-irradiated *S. frugiperda* eggs had adverse effects on the reproduction of *Te. remus* and therefore we recommend the use of untreated *S. frugiperda* eggs to rear *Te. remus*. The reproduction efficiency of *Te. remus* was influenced by the parasitoid-to-host ratio and exposure duration. To achieve a low wizened egg rate, high emergence rate and female proportion, it is advisable to provide more than four times the number of *S. frugiperda* eggs for each *Te. remus* and to expose eggs for 48 h. A 24 h exposure duration is suggested when the host egg supply is insufficient. Since the first day is the peak oviposition period of *Te. remus*, it is necessary to increase the parasitoid-to-host ratio appropriately after one day of reproduction.

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Author contributions
Xin Lü and Jun Li conceived the research. Ranran Qiu and Xin Lü prepared the experimental setup. Ranran Qiu and Xin Lü completed the experiments. Xin Lü, Ranran Qiu and Jun Li analyzed the data. Xin Lü, Ranran Qiu, and Xiaofang He wrote the manuscript. All the authors reviewed the manuscript and approved the final version.

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Availability of data and materials
The datasets analyzed during the current study available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publications
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Competing interests

The authors declare that they have no competing interests.

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