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Interspecific Host Discrimination and Competition Between *Telenomus remus* Nixon and *Trichogramma chilonis* Ishii on *Spodoptera frugiperda* (J.E. Smith) Eggs

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Simple Summary

The fall armyworm is one of the most damaging invasive pests of maize in China. Biological control with egg parasitoids offers a promising alternative to chemical insecticides. Two egg parasitoids, *Telenomus remus* and *Trichogramma chilonis*, are being considered for release against this pest, but using them together requires knowing how they interact. Our laboratory study shows that in double-layer egg masses, the two parasitoids divide the egg mass: *Te. remus* attacks the hidden lower layer, while *Tr. chilonis* attacks the exposed upper layer. Furthermore, interspecific discrimination assays on single-layer eggs revealed that only *Te. remus* can recognize eggs already parasitized by the other species. Which species does better also depends on how many individuals are used, with *Te. remus* producing more progeny at low density, whereas *Tr. chilonis* produces more at high density. In practice, this means the two parasitoids may complement rather than compete with each other, as long as parasitoid densities are chosen carefully.

Abstract

Spodoptera frugiperda (J.E. Smith) is a major invasive pest of maize in China. *Telenomus remus* Nixon and *Trichogramma chilonis* Ishii are two promising egg parasitoids, yet their interspecific discrimination and competition remain unclear. Under laboratory conditions, we compared their parasitism on single- and double-layer egg masses and tested bidirectional discrimination, with *Te. remus* against eggs parasitized by *Tr. chilonis* for 0–7 days and *Tr. chilonis* against eggs parasitized by *Te. remus* for 0–10 days, and assessed competition at five parasitoid densities on 100 single-layer host eggs. *Te. remus* parasitized single-layer and double-layer eggs equally, whereas *Tr. chilonis* parasitized single-layer eggs but was restricted to the exposed upper layer in double-layer masses. *Te. remus* rarely oviposited in eggs parasitized by *Tr. chilonis* for 0–3 days and completely avoided those parasitized for 4 days or longer, consistent with strong interspecific host discrimination. In contrast, *Tr. chilonis* oviposited in eggs parasitized by *Te. remus* for 0–6 days, indicating a lack of discrimination. Competition on single-layer eggs was density-dependent: *Te. remus* secured more host eggs at low density, whereas *Tr. chilonis* produced more progeny at high densities. These results indicate that in double-layer egg masses, the two parasitoids partition *S. frugiperda* eggs through niche differentiation and asymmetric discrimination, while under single-layer conditions, their relative performance changes with parasitoid density. These findings provide a basis for evaluating the combined use of these two parasitoids in biological control programs.

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1. Introduction

Spodoptera frugiperda (J.E. Smith) (Lepidoptera: Noctuidae) is a major agricultural pest native to tropical and subtropical regions of the Americas. It is highly polyphagous, migratory, and prone to outbreaks [1,2], feeding on 353 plant species across 76 families, including rice, sugarcane, sorghum, and cotton [3], with maize being one of the most preferred hosts [2]. Since its invasion of Africa in 2016, *S. frugiperda* has rapidly spread to 47 African countries, causing economic losses amounting to billions of dollars [4]. In late 2018, it established a source population in Myanmar and migrated into Pu'er, Yunnan Province, China, where it was first detected in January 2019 [5,6]. Since then, it has spread to many provinces across China, posing a serious threat to maize production and food security [7–9]. Chemical control has been widely used against *S. frugiperda* [10], but intensive and prolonged use has led to rapid development of pesticide resistance and negative impacts on agroecosystems, human and animal health, and environmental safety [10,11]. Environmentally friendly biological control technologies are therefore urgently needed for integrated management of *S. frugiperda*.

Among various natural enemy resources, egg parasitoids have attracted considerable attention because they eliminate pests at the egg stage before feeding damage occurs. In China, 26 parasitoid species associated with *S. frugiperda* have been recorded, among which *Telenomus remus* Nixon (Hymenoptera: Scelionidae) and *Trichogramma chilonis* Ishii (Hymenoptera: Trichogrammatidae) are the two most promising for application [12]. *Te. remus* is an important solitary parasitoid of eggs of various noctuid species, characterized by a short reproductive cycle and high parasitic capacity [13]. This wasp parasitizes 1- to 2-day-old eggs of *S. frugiperda* and can penetrate egg masses to parasitize eggs in double layers, with field parasitism rates of *S. frugiperda* egg masses reaching up to 100% [13,14]. *Tr. chilonis* is a facultative gregarious parasitoid [15–17], with a host range covering at least 60 lepidopteran species [16]. It has been widely applied in the biological control of sugarcane borers and rice leaf rollers [18–20], with an average field parasitism rate of 84.1% on *S. frugiperda* eggs [21]. Recent studies have advanced our understanding of the individual performance of these two parasitoids. Giri et al. systematically compared their parasitism efficiency across egg densities, egg ages, and scale coverings, confirming that *Te. remus* outperforms *Tr. chilonis* on multilayered and scaly egg masses, likely due to its ability to penetrate physical barriers, whereas *Tr. chilonis* has a shorter ovipositor [22]. Under field conditions, Yuan et al. further demonstrated that combined release of the two species as "compound parasitoid balls" improved control efficacy compared to *Tr. chilonis* alone, though not compared to *Te. remus* alone [23]. However, these studies did not directly examine the behavioral and competitive basis of their interaction. These two parasitoid species frequently co-occur and share *S. frugiperda* egg resources in the field [24], making their interspecific interactions an important consideration for combined release programs.

Host discrimination, the ability of female parasitoids to distinguish parasitized from unparasitized hosts, plays a central role in parasitoid coexistence and resource partitioning [25,26]. When a parasitoid discriminates against hosts already parasitized by a heterospecific species, multiparasitism is avoided; when such discrimination is lacking, both species may oviposit in the same host, leading to intrinsic competition whose outcome is influenced by oviposition sequence and developmental rate [25,27]. The physical structure of host eggs, particularly the layering of egg masses, may further shape these interactions by al-

tering host accessibility [28,29]. These structural and behavioral factors together determine whether heterospecific parasitoids encounter and recognize hosts already parasitized by the other species. While interspecific discrimination is most commonly documented between phylogenetically related species [30], evidence also exists for distantly related taxa; notably, *Te. remus* (Scelionidae) discriminates *S. frugiperda* eggs parasitized by *Trichogramma* species (Trichogrammatidae) [29]. Despite the recognized ecological and applied significance of interspecific discrimination and competition, how these interactions play out between *Te. remus* and *Tr. chilonis* remains unclear. In particular, the bidirectional temporal dynamics of interspecific discrimination between *Te. remus* and *Tr. chilonis*, and the density-dependent outcomes of their competition, remain largely unexplored. A recent molecular quantification study showed that *Te. remus* achieves higher parasitism rates than *Trichogramma* species on *S. frugiperda* eggs [31]. Another recent study described the parasitic behavior and intrinsic competition of these two species at different host-to-parasitoid ratios, reporting that *Tr. chilonis* dominated in intrinsic competition at most ratios, while in behavioral interactions *Te. remus* showed a non-significant tendency to continue ovipositing more frequently and leave less often [32]. However, that study focused on behavioral observations and intrinsic competition at several host densities; it did not address how discrimination ability varies with the time elapsed since prior parasitism, nor did it examine whether competitive dominance shifts across a density gradient.

Accordingly, using *S. frugiperda* eggs as a shared host, this study investigated: (1) the parasitic ability of *Te. remus* and *Tr. chilonis* on single-layer and double-layer egg masses; (2) bidirectional discrimination of host eggs parasitized by the other species at different time intervals (0–7 days for *Te. remus*, 0–10 days for *Tr. chilonis*); and (3) interspecific competition across five parasitoid density gradients (1:1 to 17:17). This study aims to clarify the interspecific discrimination and competitive outcomes between *Te. remus* and *Tr. chilonis*, and to provide a basis for evaluating their combined use in *S. frugiperda* biological control.

2. Materials and Methods

2.1. Insect Colonies

S. frugiperda, *Te. remus* and *Tr. chilonis* were originally collected from maize fields in Shoushan, Fuzhou, Fujian Province, China (119° E, 26° N) in October 2019 to establish the initial laboratory colonies; field-collected individuals were added as needed to maintain colony vitality. All colonies were maintained in an insectary at 25 ± 1 °C, 60–80% RH, a 14 L:10 D photoperiod, and had been continuously reared for more than 10 generations. *S. frugiperda* larvae were reared on fresh maize seedlings; both parasitoid species were continuously reared on fresh *S. frugiperda* eggs. All experiments were conducted in an artificial climate chamber under the same conditions, with a light intensity of 1000 lx. After emergence, *Te. remus* and *Tr. chilonis* males and females were paired at a 1:1 ratio in glass finger tubes (4 cm in length, 0.6 cm in inner diameter; Zhangjiagang Fenghuang Hongguang Science and Education Equipment Factory, Zhangjiagang, Jiangsu, China) containing a strip of filter paper soaked in 20% honey water for mating and nutritional supplementation, and were then held for use.

2.2. Experimental Apparatus

Artificial climate chamber (MRX-350B-LED, top-mounted LED, Ningbo Pulangte Instrument Co., Ltd., Ningbo, China); stereomicroscope (SMZ745, Nikon, Tokyo, Japan); and self-made dissecting needles.

2.3. Test Methods

2.3.1. Effects of Single- vs. Double-Layer S. frugiperda Egg Masses on Parasitism Rates of the Two Egg Parasitoids

Fresh *S. frugiperda* egg masses (within 24 h of oviposition) were collected and prepared as either single-layer or double-layer masses. Single-layer masses were standardized to 40 eggs, whereas double-layer masses comprised two layers of 20 eggs each (40 eggs in total). Based on preliminary experiments, the optimal parasitoid-to-host ratios at low host density were 1:5 for *Te. remus* and 1:3 for *Tr. chilonis*; therefore, 8 *Te. remus* females and 13 *Tr. chilonis* females were provided per host treatment, respectively. Five treatments were established: (1) single-layer eggs + 8 *Te. remus*; (2) double-layer eggs + 8 *Te. remus*; (3) single-layer eggs + 13 *Tr. chilonis*; (4) double-layer eggs + 13 *Tr. chilonis*; and (5) double-layer eggs + 8 *Te. remus* + 13 *Tr. chilonis*. Each treatment was placed in a rearing box (32 mm inner diameter, 16 mm height; Zhunya Flagship Store, Tmall, China) and maintained in an artificial climate chamber at 25 ± 1 °C, 60–80% RH, a 14 L:10 D photoperiod, and a light intensity of 1000 lx. After 24 h, the parasitoids were removed, and the host eggs were kept under the same conditions.

Emergence holes on each egg mass were counted for each treatment. For double-layer egg masses parasitized by both species, holes were assigned to species based on developmental time differences, since *Tr. chilonis* develops faster than *Te. remus* and its adults emerged earlier. Egg masses were checked daily; emerging adults and their eggshells were collected and identified to species. Species-specific parasitism rates were then calculated from hole counts. Each female was used once, with five replicates per treatment.

2.3.2. Interspecific Host Discrimination Between *Te. remus* and *Tr. chilonis*

Based on our laboratory's preliminary experiments, the optimal parasitoid-to-host ratios at low host density were 1:5 for *Te. remus* and 1:3 for *Tr. chilonis*. *S. frugiperda* eggs were prepared as single-layer masses. Bidirectional host discrimination assays were conducted in two directions: (1) Discrimination by *Te. remus* of eggs parasitized by *Tr. chilonis*. Eggs were first parasitized by *Tr. chilonis* at a ratio of 17 females:50 eggs per rearing box. After 4 h, all *Tr. chilonis* females were removed. The parasitized eggs were then kept in the boxes for 0, 1, 2, 3, 4, 5, 6, or 7 days after removal. Subsequently, 10 *Te. remus* females were introduced into each box. (2) Discrimination by *Tr. chilonis* of eggs parasitized by *Te. remus*. Following the same procedure, eggs were first parasitized by *Te. remus* at a ratio of 10 females:50 eggs per rearing box. After 4 h, all *Te. remus* females were removed. After 0, 1, 2, 3, 4, 5, 6, 7, 8, 9, or 10 days, 17 *Tr. chilonis* females were introduced into each box. For both assays, the boxes were maintained at 25 ± 1 °C, 60–80% RH, a 14 L:10 D photoperiod, and a light intensity of 1000 lx. After 4 h of exposure to the second parasitoid, the females were removed. After 24 h, ten eggs were randomly sampled from each box using a five-point sampling method and dissected in 0.9% saline. The presence and number of first-instar larvae of the second parasitoid were recorded. The egg and larval morphology of the two parasitoid species follows Tang et al. [33] and Huang et al. [34], and the corresponding photographs we obtained are provided in Figure S1. In the *Te. remus* discrimination assay, the presence/absence of first-instar larvae was recorded per egg. In the *Tr. chilonis* discrimination assay, the number of first-instar larvae was counted in each of the ten eggs, and the mean number of larvae per egg was calculated. To ensure the reliability of the primary parasitism, the nearly 100% baseline parasitism rate (Section 3.1) and the distinct morphological changes during rearing (darkening of parasitized eggs vs. shriveling/hatching of unparasitized ones) were used to verify the parasitism status prior to the second exposure. The remaining eggs were reared until emergence, and the species,

number, and sex ratio of the emerged progeny were recorded. Each parasitoid female was used only once, and each treatment was replicated five times.

2.3.3. Interspecific Competition Between the Two Egg Parasitoids at Different Parasitoid Densities

One hundred fresh *S. frugiperda* eggs (within 24 h of oviposition) were prepared as a single-layer egg mass and provided per rearing box. Five parasitoid density gradients were established: 1:1 (1 *Te. remus* female:1 *Tr. chilonis* female), 2:2 (2:2), 5:5 (5:5), 10:10 (10:10), and 17:17 (17:17). For each gradient, the corresponding numbers of *Te. remus* and *Tr. chilonis* females were introduced into the rearing box. The boxes were maintained in an artificial climate chamber at 25 ± 1 °C, 60–80% RH, a 14 L:10 D photoperiod, and a light intensity of 1000 lx. After 24 h, the parasitoids were removed, and the eggs were kept in the boxes until all *Te. remus* and *Tr. chilonis* adults had emerged. The number, sex, and total progeny of each parasitoid species were recorded. Each parasitoid female was used only once, and each treatment was replicated five times.

2.3.4. Data Analysis

Independent-samples *t*-tests were used to compare the parasitism rates of each parasitoid between single- and double-layer egg masses. Paired-samples *t*-tests were used to compare parasitism rates of *Te. remus* and *Tr. chilonis* on the same egg layer (upper or lower) within double-layer egg masses when both species were released simultaneously. Paired-samples *t*-tests were also applied to compare progeny numbers and female proportions between the two parasitoid species within each time interval in bidirectional host-discrimination assays. Data on interspecific host discrimination and interspecific competition at different parasitoid densities were analyzed using one-way ANOVA in SPSS 21.0 (IBM, Armonk, NY, USA), with significant differences among means separated by the Student–Newman–Keuls (S-N-K) test at $\alpha = 0.05$. Data are presented as mean ± SE. Normality and homogeneity of variance were checked before analysis.

3. Results

3.1. Parasitism of Single-Layer and Double-Layer Egg Masses by the Two Parasitoids

Te. remus exhibited a parasitism rate of 100.0% on single-layer *S. frugiperda* eggs and 97.0% on double-layer eggs, with no significant difference between the two treatments ($t = 1.50$, $df = 8$, $p > 0.05$) (Figure 1A). This indicates that at a parasitoid-to-egg ratio of 1:5, *Te. remus* parasitizes both single-layer and double-layer eggs equally effectively. In contrast, *Tr. chilonis* achieved a parasitism rate of 100.0% on single-layer eggs but only 72.5% on double-layer eggs, showing a significant difference ($t = 13.15$, $df = 8$, $p < 0.05$) (Figure 1B). This suggests that *Tr. chilonis* can fully parasitize single-layer eggs but can only partially parasitize double-layer egg masses.

When both parasitoids were simultaneously introduced to double-layer egg masses, the parasitism of exposed (upper-layer) and unexposed (lower-layer) eggs was compared. *Tr. chilonis* parasitized 61.0% of the exposed eggs, significantly more than *Te. remus* (0.5%) ($t = 10.90$, $df = 4$, $p < 0.05$). Conversely, *Tr. chilonis* did not parasitize any unexposed eggs (0%), significantly fewer than *Te. remus* (23.5%) ($t = 23.50$, $df = 4$, $p < 0.05$) (Figure 2). These results indicate clear niche differentiation between the two parasitoid species within double-layer egg masses: *Tr. chilonis* parasitized only the exposed upper-layer eggs, whereas *Te. remus* was capable of parasitizing the unexposed lower-layer eggs.

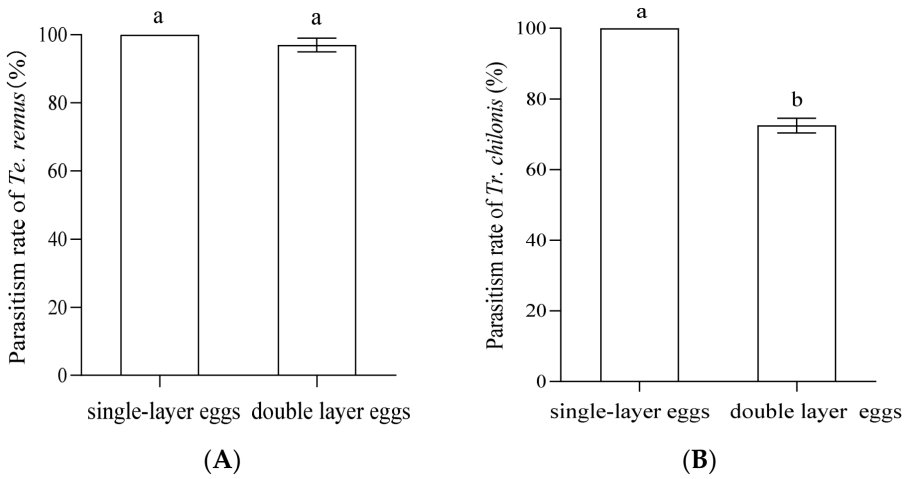


Figure 1. Parasitism rates of *Te. remus* (**A**) and *Tr. chilonis* (**B**) on single-layer and double-layer *S. frugiperda* egg masses. Data are presented as mean ± SE. Different lowercase letters above bars indicate significant differences between treatments ($p < 0.05$). $n = 5$.

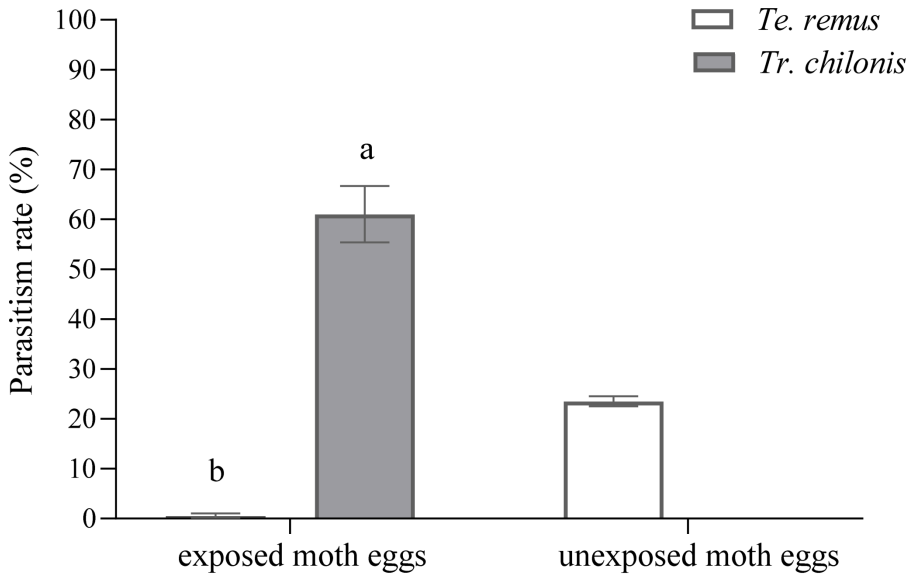


Figure 2. Parasitism rates of *Te. remus* and *Tr. chilonis* on exposed (upper-layer) and unexposed (lower-layer) eggs within double-layer *S. frugiperda* egg masses. Data are presented as mean ± SE. Different lowercase letters above bars indicate significant differences between treatments ($p < 0.05$). $n = 5$.

3.2. Interspecific Host Discrimination Between the Two Egg Parasitoids

3.2.1. *Te. remus* Discrimination of Eggs Parasitized by *Tr. chilonis*

S. frugiperda eggs that had been parasitized by *Tr. chilonis* for 0, 1, 2, 3, 4, 5, 6, and 7 days were exposed to *Te. remus* for parasitism and subsequently dissected. First-instar *Te. remus* larvae were detected in *S. frugiperda* eggs parasitized by *Tr. chilonis* for 0, 1, 2, and 3 days, with proportions of 2.0%, 4.0%, 8.0%, and 6.0%, respectively. No first-instar *Te. remus* larvae were found in eggs parasitized by *Tr. chilonis* for 4, 5, 6, or 7 days. There were no significant differences in the proportion of first-instar *Te. remus* larvae among all time-interval treatments ($F = 0.771$, $df = 7, 32$, $p > 0.05$) (Figure 3). These results suggest that *Te. remus* rarely oviposits in *S. frugiperda* eggs previously parasitized by *Tr. chilonis*, indicating strong interspecific host discrimination.

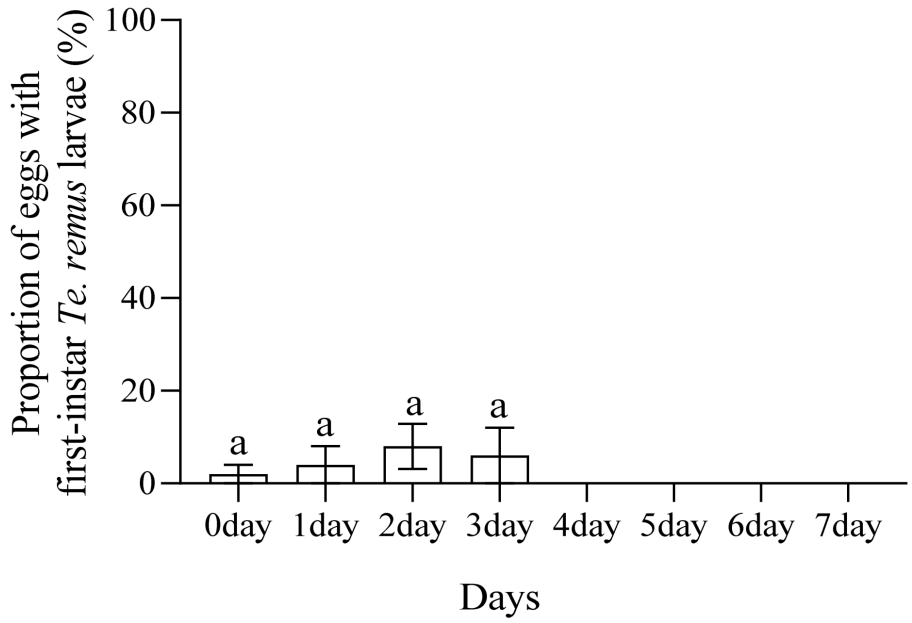


Figure 3. Proportion of first-instar *Te. remus* larvae detected in *S. frugiperda* eggs previously parasitized by *Tr. chilonis* for 0–7 days. Data are presented as mean ± SE. Lowercase letters above bars indicate significant differences among time intervals ($p < 0.05$). $n = 5$.

The remaining *S. frugiperda* eggs were reared until adult emergence, and the F1 progeny were classified and counted. When *Te. remus* was exposed to *S. frugiperda* eggs parasitized by *Tr. chilonis* for 0–7 days, the numbers of *Tr. chilonis* F1 progeny were 47.8, 39.8, 50.2, 22.2, 36.8, 34.2, 37.8, and 37.8, respectively, whereas the numbers of *Te. remus* F1 progeny were 0.2, 0.2, 0, 1.6, 0, 0, 0, and 0, respectively. Because *Te. remus* produced no progeny at 2, 4, 5, 6, and 7 days, statistical comparisons were only performed when both species produced offspring. At 0 and 1 days, the number of *Tr. chilonis* F1 progeny was significantly higher than that of *Te. remus* ($t = 6.962$ and 4.171, respectively, $df = 4$, $p < 0.05$). However, at 3 days, no significant difference was found between the two species ($t = 1.892$, $df = 4$, $p > 0.05$) (Figure 4).

The female proportion of F1 progeny was analyzed for both parasitoid species. Due to the extremely low number of *Te. remus* progeny, a meaningful sex ratio for *Te. remus* could only be calculated at 3 days (17.6%), where it did not differ significantly from that of *Tr. chilonis* (56.2%) ($t = 1.89$, $df = 4$, $p > 0.05$). At 0 and 1 days, only a single *Te. remus* individual emerged (a male at 0 days and a female at 1 day), preventing a meaningful sex ratio calculation. In the remaining treatments (2, 4, 5, 6, and 7 days), no *Te. remus* progeny emerged. Therefore, only the female proportions of *Tr. chilonis* were recorded across the 0–7 day treatments, which were 57.8%, 54.6%, 34.8%, 60.8%, 46.6%, and 37.8%, respectively (Figure 5). Taken together, the dissection and emergence results indicate that *Te. remus* can effectively discriminate *S. frugiperda* eggs already parasitized by *Tr. chilonis* and avoid ovipositing in them.

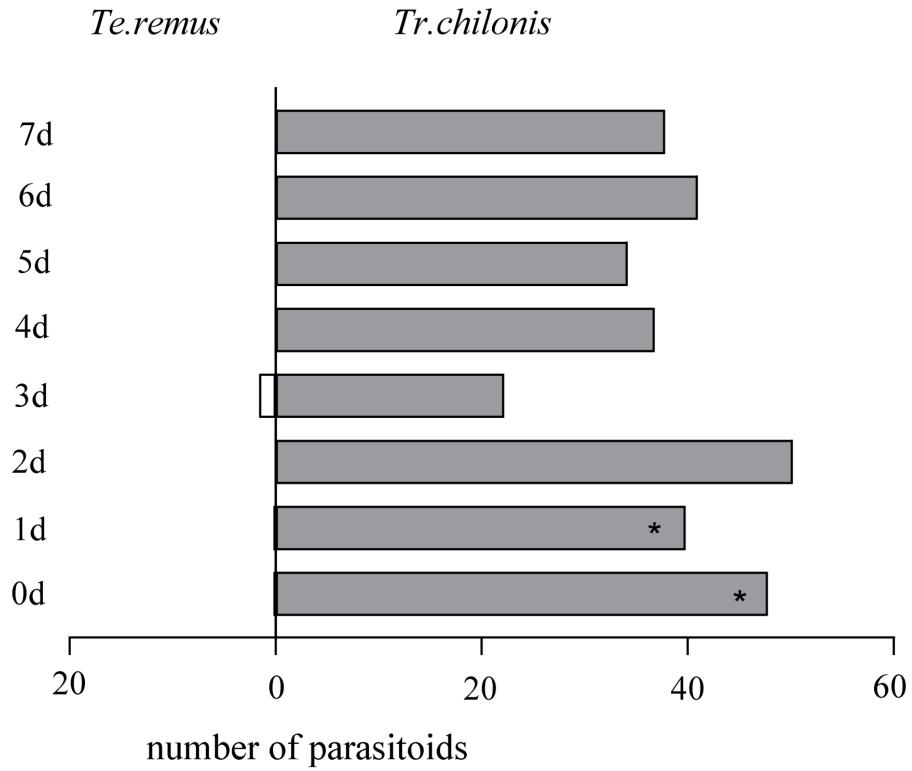


Figure 4. Number of F1 progeny of *Te. remus* and *Tr. chilonis* after *Te. remus* was exposed to *S. frugiperda* eggs previously parasitized by *Tr. chilonis* for 0–7 days. Data are presented as mean ± SE ($n = 5$). Asterisks indicate significant differences between the two species within each time interval ($p < 0.05$). *Te. remus* F1 progeny were nearly absent across all time intervals, except for a small number at 0, 1, and 3 days; therefore, statistical comparisons were only conducted at these three time points.

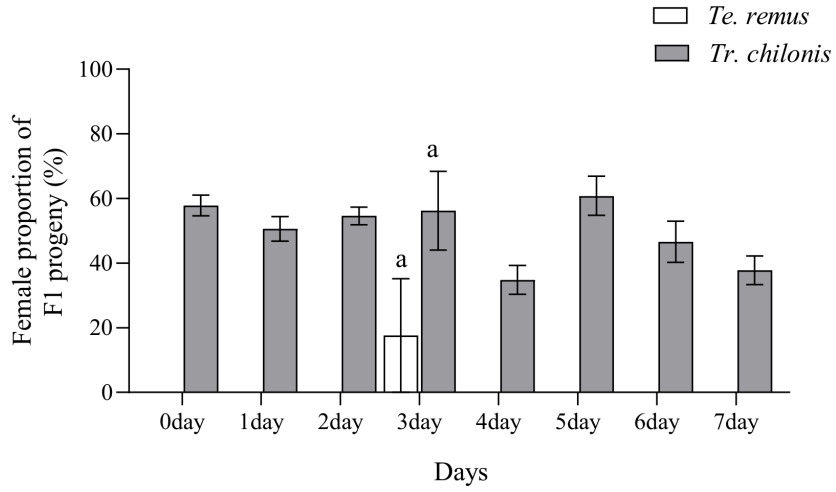


Figure 5. Female proportion of F1 progeny of *Te. remus* and *Tr. chilonis* after *Te. remus* was exposed to *S. frugiperda* eggs previously parasitized by *Tr. chilonis* for 0–7 days. Data are presented as mean ± SE. Lowercase letters above bars indicate significant differences between the two species within each time interval ($p < 0.05$). No *Te. remus* progeny emerged in the 0-, 2-, 4-, 5-, 6-, and 7-day treatments; therefore, female proportions for *Te. remus* are shown only for the 1- and 3-day treatments. $n = 5$.

3.2.2. *Tr. chilonis* Discrimination of *S. frugiperda* Eggs Parasitized by *Te. remus*

S. frugiperda eggs parasitized by *Te. remus* for 0–10 days were provided and exposed to *Tr. chilonis* for discrimination and parasitism, after which the eggs were dissected. First-instar *Tr. chilonis* larvae were detected in *S. frugiperda* eggs previously parasitized by *Te.*

remus for 0–6 days. The mean number of first-instar *Tr. chilonis* larvae per dissected egg was highest on day 1 (1.66 larvae/egg), which was significantly higher than in all other treatments ($F = 12.450$, $df = 10, 44$, $p < 0.05$). On day 2, the mean was 1.06 larvae/egg, which did not differ significantly from the 0.82 larvae/egg recorded in the 0-day treatment ($p > 0.05$). The mean values on days 3, 4, and 6 were 0.34, 0.44, and 0.48 larvae/egg, respectively, none of which differed significantly from the day-0 value ($p > 0.05$). The lowest value (0.04 larvae/egg) was observed on day 5. No first-instar *Tr. chilonis* larvae were detected in eggs parasitized by *Te. remus* for 7–10 days (Figure 6). Because *Tr. chilonis* is a facultatively gregarious parasitoid, the values exceeding 1.0 larva per egg (on days 1 and 2) reflect superparasitism within a single host egg. Taken together, these results indicate that *Tr. chilonis* readily accepts and oviposits into *S. frugiperda* eggs previously parasitized by *Te. remus* for 0–6 days, showing no evidence of interspecific host discrimination over this interval.

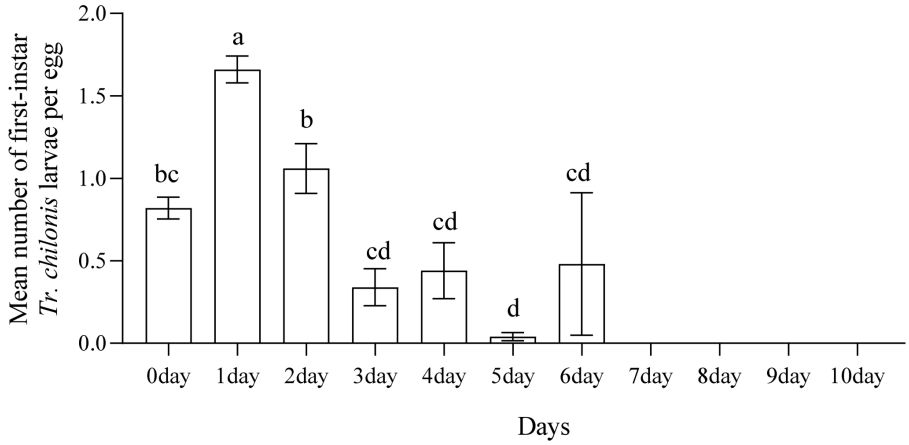


Figure 6. Mean number of first-instar *Tr. chilonis* larvae per dissected *S. frugiperda* egg, after *Tr. chilonis* was exposed to eggs previously parasitized by *Te. remus* for 0–10 days. Data are presented as mean ± SE. Different lowercase letters above bars indicate significant differences among time intervals ($p < 0.05$). $n = 5$.

The remaining *S. frugiperda* eggs after dissection were reared until adult emergence, and the F1 progeny were classified and counted. For *S. frugiperda* eggs parasitized by *Te. remus* for 0 days and subsequently exposed to *Tr. chilonis*, only *Tr. chilonis* progeny emerged (46.8 individuals), whereas no *Te. remus* progeny were recorded. For eggs parasitized by *Te. remus* for 2 and 6 days, the numbers of emerging *Te. remus* (17.2 and 29.6 individuals, respectively) were significantly higher than those of *Tr. chilonis* (6.0 and 2.4 individuals, respectively) (2 days: $t = 3.655$, $df = 4$, $p < 0.05$; 6 days: $t = 14.341$, $df = 4$, $p < 0.05$). For eggs parasitized for 4 days, only *Te. remus* progeny emerged, whereas no *Tr. chilonis* progeny were recorded. For eggs parasitized for 1, 3, and 5 days, there were no significant differences in F1 progeny numbers between the two species ($t < 2.64$, $df = 4$, $p > 0.05$). For eggs parasitized for 7–10 days, only *Te. remus* progeny emerged, with numbers of 26.4, 26.8, 31.4, and 41.2 individuals, respectively (Figure 7).

Analysis of the female proportion of F1 progeny showed that for *S. frugiperda* eggs parasitized by *Te. remus* for 0 days, only *Tr. chilonis* emerged, with a female proportion of 63.8%. For eggs parasitized for 1 day, the female proportions of *Tr. chilonis* and *Te. remus* were 54.2% and 80.0%, respectively, with no significant difference between the two species ($t = 0.812$, $df = 4$, $p > 0.05$). For eggs parasitized for 2, 3, 5, and 6 days, the female proportions of *Te. remus* (98.8%, 55.0%, 93.6%, and 92.3%, respectively) were significantly higher than those of *Tr. chilonis* (49.2%, 43.6%, 71.4%, and 50.6%, respectively) ($p < 0.05$). For

eggs parasitized for 4 days and 7–10 days, only *Te. remus* emerged, with female proportions of 99.1%, 90.2%, 92.2%, 99.3%, and 98.1%, respectively (Figure 8).

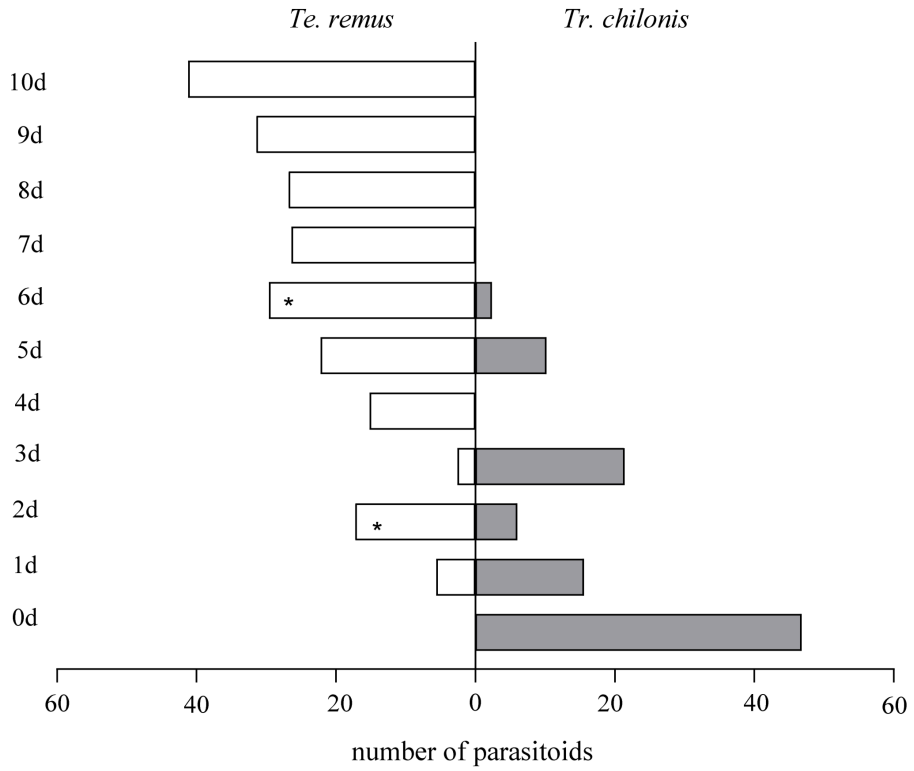


Figure 7. Number of F1 progeny of *Tr. chilonis* and *Te. remus* after *Tr. chilonis* was exposed to *S. frugiperda* eggs previously parasitized by *Te. remus* for 0–10 days. Data are presented as mean ± SE. Asterisks indicate significant differences between the two species within each time interval ($p < 0.05$). Only *Tr. chilonis* progeny emerged in the 0-day treatment, and only *Te. remus* progeny emerged in the 4-day and 7–10-day treatments. $n = 5$.

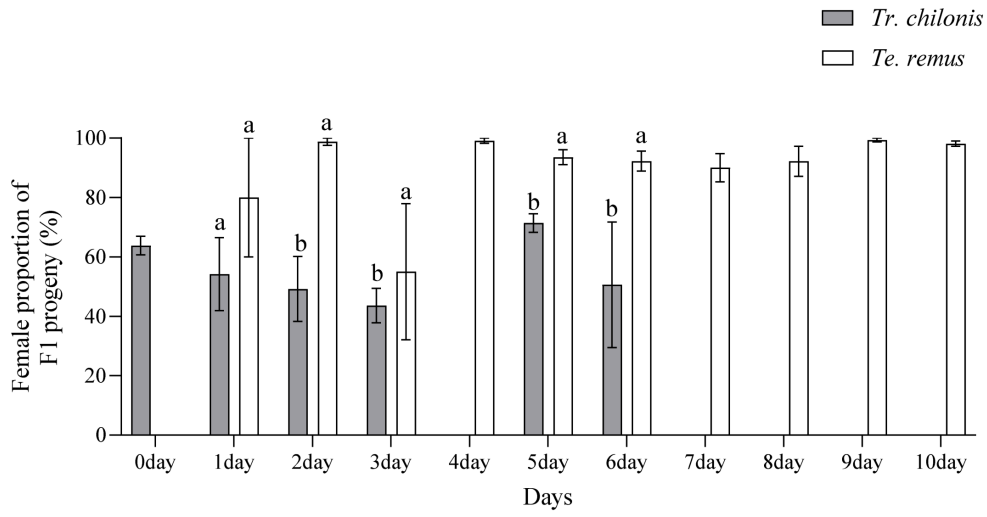


Figure 8. Female proportion of F1 progeny of *Tr. chilonis* and *Te. remus* after *Tr. chilonis* was exposed to *S. frugiperda* eggs previously parasitized by *Te. remus* for 0–10 days. Data are presented as mean ± SE. Different lowercase letters above bars indicate significant differences between the two species within each time interval ($p < 0.05$). Only *Tr. chilonis* progeny emerged in the 0-day treatment, and only *Te. remus* progeny emerged in the 4-day and 7–10-day treatments; therefore, female proportions for both species are not available for these time points. $n = 5$.

In summary, *Tr. chilonis* is unable to discriminate *S. frugiperda* eggs parasitized by *Te. remus* for 0–6 days and can oviposit in them, with successful progeny emergence. For eggs parasitized by *Te. remus* for 7–10 days, no *Tr. chilonis* progeny emerged, likely because *Te. remus* had developed to the pupal stage by this time and the host egg nutrients had been depleted. Our experiments cannot distinguish between host unsuitability and a change in host acceptance behavior at this advanced stage, and we do not interpret this absence as evidence that *Tr. chilonis* has acquired discrimination ability.

3.3. Interspecific Competition Between the Two Egg Parasitoids at Different Densities

Using 100 *S. frugiperda* eggs as a fixed host resource, five parasitoid density gradients of *Te. remus* to *Tr. chilonis* were established: 1:1, 2:2, 5:5, 10:10, and 17:17. The total number of F1 adults increased with increasing parasitoid density ($F = 11.755$, $df = 4, 20$, $p < 0.05$). At the 1:1 density, the total number was 42.6, significantly lower than those at the 2:2 (64.0), 5:5 (69.2), and 10:10 (71.4) densities ($p < 0.05$). At the 17:17 density, the total number reached 108.2 (exceeding the initial 100 host eggs due to the gregarious nature of *Tr. chilonis*), significantly higher than in all other treatments ($p < 0.05$) (Figure 9).

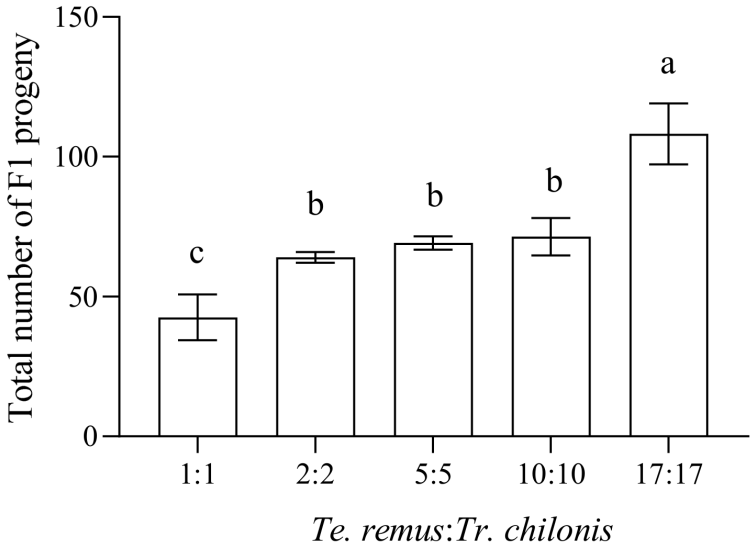


Figure 9. Total number of F1 progeny of *Te. remus* and *Tr. chilonis* combined at five parasitoid density gradients (1:1, 2:2, 5:5, 10:10, and 17:17). Data are presented as mean ± SE. Different lowercase letters above bars indicate significant differences among treatments ($p < 0.05$). $n = 5$.

Comparison of the F1 progeny numbers of each species revealed a density-dependent shift in competitive dominance. At the 1:1 density, the numbers of *Te. remus* and *Tr. chilonis* F1 progeny were 29.6 and 13.2, respectively, with no significant difference ($t = 1.378$, $df = 8$, $p > 0.05$). At the 2:2 density, the number of *Te. remus* F1 progeny (60.0) was significantly higher than that of *Tr. chilonis* (4.0) ($t = 9.108$, $df = 8$, $p < 0.05$), with *Te. remus* producing significantly more progeny. At the 5:5 density, the numbers of *Te. remus* and *Tr. chilonis* F1 progeny were 27.0 and 42.0, respectively, with no significant difference ($t = 1.174$, $df = 8$, $p > 0.05$). At the 10:10 density, the number of *Tr. chilonis* F1 progeny (62.8) was significantly higher than that of *Te. remus* (8.0) ($t = 5.468$, $df = 8$, $p < 0.05$). At the 17:17 density, the number of *Tr. chilonis* F1 progeny (99.4) was significantly higher than that of *Te. remus* (8.4) ($t = 6.954$, $df = 8$, $p < 0.05$) (Figure 10). Because *Te. remus* is a solitary parasitoid, its F1 adult number directly approximates the number of host eggs it secured; this number declined from 60.0 at the 2:2 density to only 8.4 at the 17:17 density, indicating that *Te. remus* secured far fewer host eggs at high wasp density. These results indicate that the two species differ in their density-dependent progeny production: *Te. remus* produced more progeny

and secured more host eggs at low parasitoid density (2:2), whereas *Tr. chilonis* produced more progeny at high parasitoid densities (10:10 and 17:17). We note that, because *Tr. chilonis* is gregarious, its adult progeny number is not directly comparable to that of the solitary *Te. remus*; the latter's egg-securing pattern is therefore a more reliable indicator of competitive outcome.

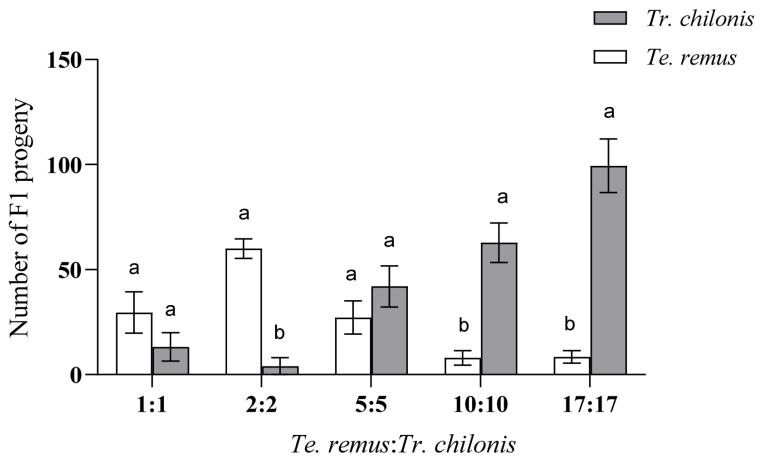


Figure 10. Number of F1 progeny of *Te. remus* and *Tr. chilonis* at five parasitoid density gradients (1:1, 2:2, 5:5, 10:10, and 17:17). Data are presented as mean ± SE. Different lowercase letters above bars indicate significant differences between the two species within each density ($p < 0.05$). $n = 5$.

The female proportions of F1 progeny of *Te. remus* and *Tr. chilonis* were determined separately. At the 1:1, 2:2, and 5:5 densities, the female proportions of *Te. remus* (95.0%, 96.0%, and 92.2%, respectively) were significantly higher than those of *Tr. chilonis* (46.2%, 17.0%, and 74.4%, respectively) (1:1: $t = 2.331$, $df = 8$; 2:2: $t = 4.612$, $df = 8$; 5:5: $t = 2.533$, $df = 8$; $p < 0.05$). At the 10:10 and 17:17 densities, the female proportions of *Te. remus* (74.4% and 75.0%, respectively) did not differ significantly from those of *Tr. chilonis* (66.2% and 58.4%, respectively) (10:10: $t = 0.831$, $df = 8$; 17:17: $t = 0.839$, $df = 8$; $p > 0.05$) (Figure 11).

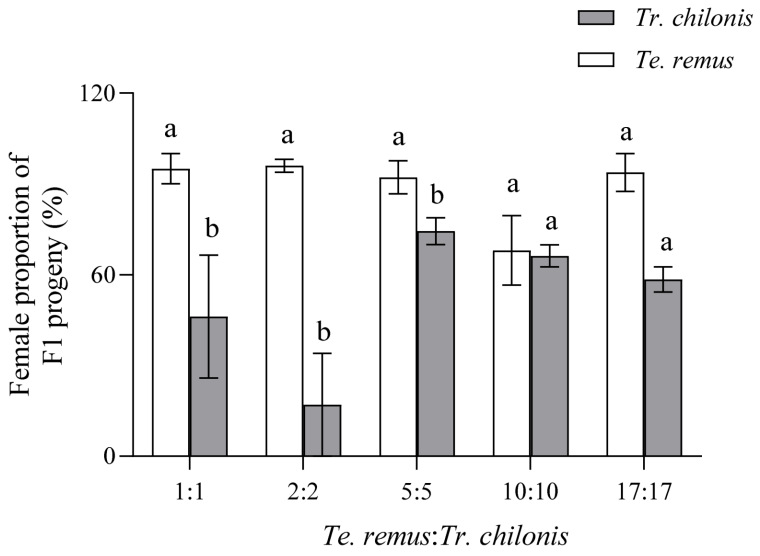


Figure 11. Female proportion of F1 progeny of *Te. remus* and *Tr. chilonis* at five parasitoid density gradients (1:1, 2:2, 5:5, 10:10, and 17:17). Data are presented as mean ± SE. Different lowercase letters above bars indicate significant differences between the two species within each density ($p < 0.05$). $n = 5$.

4. Discussion

In nature, multiparasitism of a single host by parasitoids is common, and the resulting competition can affect the fitness and competitive success of the species involved [27]. When multiparasitism occurs, the progeny of the two species engage in intrinsic competition within the host, the outcome of which is regulated by factors including oviposition sequence, time interval between ovipositions, larval developmental rate, and host developmental stage [27]. Understanding how egg parasitoids discriminate against hosts already parasitized by heterospecifics, and how they compete for shared host resources, is therefore important for evaluating whether two parasitoid species can be used together in biological control programs.

In this study, *Te. remus* parasitized single-layer (100.0%) and double-layer (97.0%) eggs equally well, indicating that it can successfully parasitize eggs in the lower layer of double-layer masses. *Tr. chilonis*, by contrast, parasitized 72.5% of double-layer eggs and was only able to attack the exposed upper layer. When both species were introduced to double-layer egg masses at the same time, *Te. remus* progeny emerged mainly from the unexposed lower-layer eggs (23.5% parasitism), whereas *Tr. chilonis* progeny emerged mainly from the exposed upper-layer eggs (61.0% parasitism; *Te. remus* only 0.5%). This pattern of niche partitioning is consistent with the interspecific interaction between *Te. remus* and *Trichogramma* reported by Carneiro and Fernandes [29]. The two species thus occupy different parts of the same egg mass, and this niche differentiation may arise from the physical barrier imposed by egg layering, from differences in host discrimination ability, or from both. The role of discrimination ability was examined separately.

To test this possibility, we conducted bidirectional assays. *Te. remus* rarely oviposited in *S. frugiperda* eggs parasitized by *Tr. chilonis* for 0–3 days (only 2.0–8.0% of dissected eggs contained first-instar *Te. remus* larvae) and completely avoided eggs parasitized for 4 days or longer. This agrees with Carneiro and Fernandes [29], who reported that *Te. remus* can discriminate both single- and double-layer host eggs parasitized by *Trichogramma pretiosum*. Interspecific discrimination is not uncommon among scelionid parasitoids: *Telenomus isis* discriminates host eggs parasitized by *Lathromeris ovicida* [35]; *Telenomus podisi* discriminates eggs parasitized by *Trissolcus teretis* for intervals ranging from 4 to 192 h [36]. By contrast, some scelionids, such as *Gryon* sp. nr. *gonikopalense* and *Trissolcus hyalinipennis*, avoid conspecific superparasitism but do not avoid multiparasitism [37]. This discriminatory ability enables *Te. remus* to refrain from ovipositing in hosts already parasitized by heterospecifics, thereby lowering the risk of offspring mortality caused by intrinsic competition.

Unlike *Te. remus*, *Tr. chilonis* showed no interspecific discrimination. It readily oviposited in *S. frugiperda* eggs parasitized by *Te. remus* for 1–6 days, and its progeny emerged as adults. Eggs parasitized for 7–10 days, however, were not attacked. By this time, *Te. remus* had reached the pupal stage, and the hemolymph and nutrients in the host egg had been largely depleted, leaving little for *Tr. chilonis* to use. When *Tr. chilonis* attacked eggs that had been parasitized by *Te. remus* on the same day (0-day interval), only *Tr. chilonis* progeny emerged. Strand and Vinson [38] demonstrated that competitive outcomes between *Tr. pretiosum* and *Te. heliothidis* depend strongly on oviposition timing; Tr. pretiosum gains an advantage when ovipositing earlier, likely because gregarious *Trichogramma* consume host egg resources rapidly. This rapid resource exploitation and short developmental time may similarly explain the competitive outcome observed in our 0-day treatment. As *Tr. chilonis* is a primary egg parasitoid with no documented hyperparasitic habits, its successful development in eggs parasitized by *Te. remus* is more likely achieved through larval competition: *Tr. chilonis* develops as a primary parasitoid and competes with *Te. remus* larvae for resources within the same host egg, rather than attacking *Te. remus* larvae directly. This mechanism is distinct from facultative hyperparasitism, whereby a

parasitoid directly attacks the larva of another parasitoid inside an already-parasitized host. The competitive success of *Tr. chilonis* may also reflect traits shared with other *Trichogramma* species, such as a short developmental time and rapid consumption of egg resources [39].

The present study revealed a density-dependent shift in progeny production: *Te. remus* produced more progeny and secured more host eggs at low density (2:2), whereas *Tr. chilonis* produced more progeny at high densities (10:10 and 17:17). At 1:1 and 5:5, neither species produced significantly more progeny than the other. This shift may be related to differences in host-searching efficiency and oviposition rate between the two species. At low density, *Te. remus* may locate and parasitize hosts more efficiently, whereas at high density, *Tr. chilonis* may gain an advantage through its faster oviposition and shorter developmental duration. He et al. [40] studied interspecific competition between *Trichogramma confusum* and *Tr. pretiosum* on *Corcyra cephaloica* eggs and found that *Tr. pretiosum* was the superior competitor, with its advantage remaining stable across host egg densities. This differs from our findings, where dominance between *Te. remus* and *Tr. chilonis* shifted with parasitoid density. Further studies are needed to determine whether this density-dependent shift is driven primarily by extrinsic competition, intrinsic competition, or both.

This study examined interspecific host discrimination and competition between *Te. remus* and *Tr. chilonis* by manipulating host egg layering and parasitoid density. However, several questions remain unresolved. For instance, adult competitive behaviors, such as host-searching efficiency and dispersal ability, were not examined, nor was the precise nature of larval interactions within a single host egg. Furthermore, the physiological or behavioral mechanisms driving the competitive advantage of *Tr. chilonis* require further study. While a parallel unparasitized-host control under identical conditions was not included in this study, the 100.0% baseline parasitism rate (Section 3.1) and our morphological verification during rearing ensured that unparasitized eggs were practically negligible and were excluded from the analysis. Thus, the observed oviposition patterns clearly reflect active behavioral discrimination rather than a general lack of host acceptance. Future assays incorporating naive females and healthy eggs as direct controls would help further quantify these baseline acceptance rates. Notably, we consistently observed first-instar *Tr. chilonis* larvae and *S. frugiperda* larvae coexisting within the same egg during our dissections. This is unexpected, as *Tr. chilonis* is an egg parasitoid, yet the host larvae remained intact alongside its parasitoid larvae. This phenomenon suggests that tritrophic interactions among *Tr. chilonis*, *Te. remus*, and *S. frugiperda* may be more complex than currently recognized and warrant further investigation.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/insects17111205/s1, Figure S1: Morphological comparison of the two parasitoid species. A. *Telenomus remus* egg; B. 24 h post-parasitization by *Telenomus remus*; C. *Trichogramma chilonis* eggs; D. 24 h post-parasitization by *Trichogramma chilonis*.

Author Contributions: Z.W. and T.X. conceived the study. T.X., Z.D. and X.M. collected samples. T.X. and Z.D. conducted lab work and analyzed the data. T.X. and Z.D. wrote the manuscript. Z.D., Z.W. and X.M. revised the manuscript. Z.W. and J.H. edited the manuscript. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: The original contributions presented in this study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Acknowledgments: Please add the corresponding content of this part.

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