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RESEARCH ARTICLE

Performance of *Telenomus remus* (Hymenoptera: Scelionidae), an egg parasitoid of *Spodoptera frugiperda* (Lepidoptera: Noctuidae), under different temperature regimes

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Abstract

Maize fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Noctuidae: Lepidoptera), is a highly destructive and invasive pest of maize, causing havoc in major maize growing states of the country since 2018. Integrated Pest Management (IPM) strategies are being advocated to farmers for the containment of the pest. Among the various IPM components, biological control using the egg parasitoid, *Telenomus remus* (Nixon) (Scelionidae: Hymenoptera) could be considered a promising strategy, as the pest can be managed at a much earlier stage. This study evaluated the influence of five temperature regimes (20, 25, 30, 35 and 40 °C) on the developmental and reproductive performance of *T. remus*. Results indicated that 25-30 °C was optimal, with the highest parasitism (80.70±5.29 eggs/female/24 hrs) and adult emergence (99.51±0.20 %) at 25 °C. Developmental time decreased with increase in temperature, ranging from 8.60 days (35 °C) to 21.95 days (20 °C). Peak fecundity (122.7 ± 3.56 eggs/female) and intrinsic rate of increase (rm = 0.479) occurred at 30 °C. No reproduction occurred at 40 °C. These findings underscore the critical role of temperature in optimizing *T. remus* performance, aiding its effective integration into biological control programs against *S. frugiperda*.

Keywords: biocontrol; fertility life table; parasitization; survivorship curve; thermal tolerance

Introduction

Spodoptera frugiperda J.E. Smith (Lepidoptera: Noctuidae), the fall army worm (FAW), is a highly destructive, polyphagous pest affecting global agriculture by feeding on over 300 plant species including major crops like maize, rice and sorghum. Its invasiveness and adaptability have made it a formidable threat to food security worldwide, particularly due to its rapid spread and capacity for causing extensive crop losses (1, 2). Since its first detection in West Africa in 2016 and subsequent arrival in Asia, including India in 2018, *S. frugiperda* has rapidly expanded its range, becoming a persistent challenge for smallholder and commercial farmers alike (3, 4). Estimates show that annual maize yield losses attributable to *S. frugiperda* could reach between 8.3 and 20.6 million tons, resulting in an economic impact ranging from $2.5 to $6.2 billion if not addressed with timely interventions (5).

While maize plants exhibit some tolerance to leaf feeding, the larval stages of *S. frugiperda* severely damage both vegetative and reproductive tissues, threatening yield and quality (1). Excessive reliance on chemical pesticides has not only increased production costs but has also accelerated the development of insecticide resistance and environmental concerns such as non-target effects and residue problems (6). These issues underscore the urgency for adopting IPM approaches, where biological control leveraging natural enemies remains central to sustainable and environmentally friendly *S. frugiperda* suppression (7).

Among *S. frugiperda* natural enemies, the egg parasitoid *Telenomus remus* (Nixon) (Hymenoptera: Scelionidae) has emerged as a promising biocontrol agent for managing noctuid pests, including *S. frugiperda*, in both the Americas and Africa (8, 9). It is native to Peninsular Malaysia and Papua New Guinea (10, 11). Unlike other egg parasitoids, such as *Trichogramma spp*., which typically parasitize only a portion of the egg mass, *T. remus* is capable of parasitizing the entire egg mass, because S. *frugiperda* deposits eggs in several layers and covers them with scales from her body, which create a barrier for *Trichogramma* females but not for *T. remus* (12). Augmentative releases of *T. remus* in maize fields have demonstrated substantial parasitism rates and enhanced pest suppression, thereby markedly reducing reliance on chemical interventions and supporting the implementation of IPM across diverse agro ecologies (13, 14).

For successful and sustainable use of *T. remus* in IPM, it is essential to understand how environmental factors, especially temperature, influence its development, survival and effectiveness. Temperature is a critical ecological determinant

that regulates insect physiology, behaviour and interactions, shaping both pest outbreaks and the efficacy of biological control agents (15). Climate change, with its associated rise in global temperatures, is expected to alter the population dynamics of both *S. frugiperda* and *T. remus*, potentially shifting their geographic ranges, development rates and interspecific interactions (16). Recent research has shown that *T. remus*'s thermal tolerance, development, parasitism rate and emergence success are all directly affected by the temperature regimes they experience (17), highlighting the need to optimize both laboratory rearing and field release protocols for maximum biocontrol performance.

This study hypothesizes that the biological performance of *T. remus*, including its development, survival and parasitism rates, will exhibit significant variation across a gradient of constant temperatures (20, 25, 30, 35 and 40 °C). Identifying the optimal temperature range for mass rearing in the laboratory will enable effective field deployment and establishment, thereby enhancing the success of IPM programs against *S. frugiperda* under current and future climate scenarios.

Materials and Methods

A laboratory experiment was conducted to assess the influence of temperature on insect growth and development using a completely randomized design (CRD) with five different temperature regimes *viz.,* 20, 25, 30, 35 and 40 °C. These temperature ranges were chosen based on the climatic conditions of major maize-growing districts in Tamil Nadu. Cultures of *S. frugiperda* and *T. remus* are being maintained at the Fall armyworm Laboratory, Department of Agricultural Entomology, Tamil Nadu Agricultural University, Coimbatore, India by following standard protocol (18).

Influence of temperature on *T. remus* parental generation (F0)

The influence of temperature on the growth and development of *T. remus* was evaluated under five constant temperatures (20, 25, 30, 35 and 40°C) at 70% relative humidity in climate-controlled chambers. Fresh (~24 h old) *S. frugiperda* eggs (~150) were pasted onto 1×3cm strips of 144 gsm paper using gum Acacia and air-dried for 5-10 min. A single mated *T. remus* female (~24 h old) was introduced into a labelled test tube (10cm × 1.5cm), covered with nylon mesh and provided a drop of honey on the mesh as food. Females parasitized the eggs for 24 hrs, after which they were removed. The parasitized egg strips were maintained at the respective temperatures for development.

Daily observations were made and *S. frugiperda* neonates hatching from unparasitized eggs were gently removed using a fine camel-hair brush. On the fifth day, blackened eggs were counted to estimate parasitism. The egg strips remained at their respective temperatures until adult emergence. Ten replications were maintained per treatment. From the parental generation, biological parameters such as developmental period (egg to adult), number of eggs parasitized, percent parasitism (Eqn. 1), adult emergence percentage (based on exit holes) (Eqn. 2) and sex ratio (Eqn. 3) of emerged parasitoids were recorded.

$$\% \text{ Parasitism} = \frac{\text{Number of eggs parasitized}}{\text{Total number of eggs exposed}} \times 100 \quad \text{(Eqn. 1)}$$

$$\% \text{ Adult emergence} = \frac{\text{Number of adults emerged}}{\text{Total number of eggs parasitized}} \times 100 \quad \text{(Eqn. 2)}$$

$$\text{Sex ratio} = \frac{\text{Number of female adults}}{\text{Total number of adults}} \quad \text{(Eqn. 3)}$$

Effect of temperature on the offspring (F_1) generation

To study the effect of temperature on the offspring (F_1) generation, a single mated *T. remus* female (24 hrs old) from the parental generation at each temperature regime was selected. Each female was provided with approximately 150 fresh (~24 hrs old) *S. frugiperda* eggs daily, under the same temperature conditions. Ten replications were maintained for each temperature regime. The egg cards were replaced daily until the death of the female to assess parasitism throughout her entire adult lifespan. The parasitized egg cards were then transferred to separate test tubes and maintained under the same temperature conditions as those of the parental generation until no further parasitoids emerged. The biological parameters, *viz.*, total number of eggs parasitized by each female throughout her lifespan, female longevity (days) and percent adult emergence (Eqn. 2) of the resulting progeny were recorded.

Temperature dependent fertility life table and survivorship curve of *T. remus*

The fertility life table of *T. remus* under different temperature regimes was constructed (17). The key biological parameters considered for life table construction included female longevity (days), egg-to-adult developmental duration (days), daily parasitism rate and sex ratio. Based on these parameters, various life table indices *viz.,* net reproductive rate (R_0) (Eqn. 4), approximate generation time (Tc) (Eqn. 5), intrinsic rate of increase (r_m) (Eqn. 7), finite rate of increase (λ) (Eqn. 8) and doubling time (T_D) (Eqn. 9) were calculated using the formulae as follows (19) and survivorship curves were constructed using a previously established method (20).

$$\text{Net reproduction rate } (R_0) = \sum lxmx \quad \text{(Eqn. 4)}$$

$$\text{Approximate generation time } (T_C) = \frac{\sum xlxmx}{\sum lxmx} \quad \text{(Eqn. 5)}$$

$$\text{Corrected generation time } (T) = \frac{\ln R_0}{rm} \quad \text{(Eqn. 6)}$$

$$\text{Intrinsic rate of increase } (r_m) = \ln R_0 / T \quad \text{(Eqn. 7)}$$

$$\text{Finite rate of increase } (\lambda) = e^{rm} \quad \text{(Eqn. 8)}$$

$$\text{Doubling time } (T_D) = \ln 2 / r_m \quad \text{(Eqn. 9)}$$

Where

X: the pivotal age for the age class in units of time (days)

lx: the number of surviving individuals at the beginning of age class

mx: age-specific fertility, the number of living females born per female in each interval class

Statistical analysis

The experimental data on the influence of temperature on both parental and offspring generations were statistically analysed

using SPSS software version 22. To ensure normality and stabilize variance, the data were subjected to appropriate transformations before analysis. A significance level of $p < 0.05$ was adopted for all statistical tests. One-way analysis of variance (ANOVA) was employed to detect significant differences among treatments and where significant effects were found, Tukey's post hoc test was applied to compare the means at a 5 % significance level.

Results and Discussion

Influence of temperature on *Telenomus remus* parental generation (F_0)

Temperature had a significant influence on the biological performance of *T. remus* in the parental generation. Among the five constant temperature regimes tested (20, 25, 30, 35 and 40 °C), the range of 25-30°C emerged as optimal, supporting superior development and reproductive potential (Table 1). The highest parasitism rate was recorded at 25 °C (80.70±5.29 eggs/female/24 hrs), followed closely by 30 °C (74.20±1.37 eggs). In contrast, parasitism dropped drastically at 40 °C (8.90±1.07 eggs), indicating that this temperature is near the lethal threshold for the parasitoid (Fig. 1). A similar trend was observed in adult emergence, which peaked at 25 °C (99.51±0.20 %) and remained high at 30 °C (99.18±0.42 %). These results align with previous findings that reported optimal *T. remus* performance between 20 and 31°C (21).

Although *T. remus* survived at 35 °C, a sharp decline in performance was evident, indicating thermal stress at this level. The upper threshold observed in our study (~35.9 °C) is slightly higher than that reported earlier (22). Comparable findings were reported for *Trichogramma achaeae*, where individuals maintained at 35 °C exhibited wing deformities, severely reduced longevity (<24 h) and absence of parasitism, confirming that this temperature exceeds the upper developmental threshold in some trichogrammatids (23).

The sex ratio of the progeny was also influenced by temperature, with a female-biased proportion recorded at 25 °C (0.81±0.01) and 30 °C (0.78±0.02). Since only females contribute to parasitism, this trend is favourable for biological control programs. Across all tested regimes, the sex ratio remained relatively stable (0.70 to 0.81), suggesting that temperature had minimal effect on sex allocation, in agreement with prior studies (24). However, these findings partially contrast with an earlier report indicating the highest sex ratio (0.94±0.03) at 15 °C (16). Other biotic factors, such as host egg age (18), female parasitoid age (25) and host availability (26), are also known to influence sex determination. Thus, optimizing both biotic and abiotic conditions is crucial for maximizing female-biased progeny and field efficacy (21).

Table 1. Influence of temperature on parental generation

Temperature (°C)	Eggs parasitized in 24h (no.)	% Parasitism	%Adult emergence	Sex ratio
20	56.10±1.92^{b}	37.68±0.76^{b}	44.83±1.73^{c}	0.74±0.02^{bc}
25	80.70±5.29^{a}	47.22±2.05^{a}	99.51±0.20^{a}	0.81±0.01^{a}
30	74.20±1.37^{a}	44.69±0.52^{a}	99.18±0.42^{a}	0.78±0.02^{ab}
35	32.50±1.67^{c}	27.71±0.54^{c}	79.63±2.36^{b}	0.70±0.02^{c}
40	8.90±1.07^{d}	17.09±1.07^{d}	0	0

All values are Mean ± Standard error

Means sharing the same letter do not differ significantly by (Tukey's test, P = 0.05)

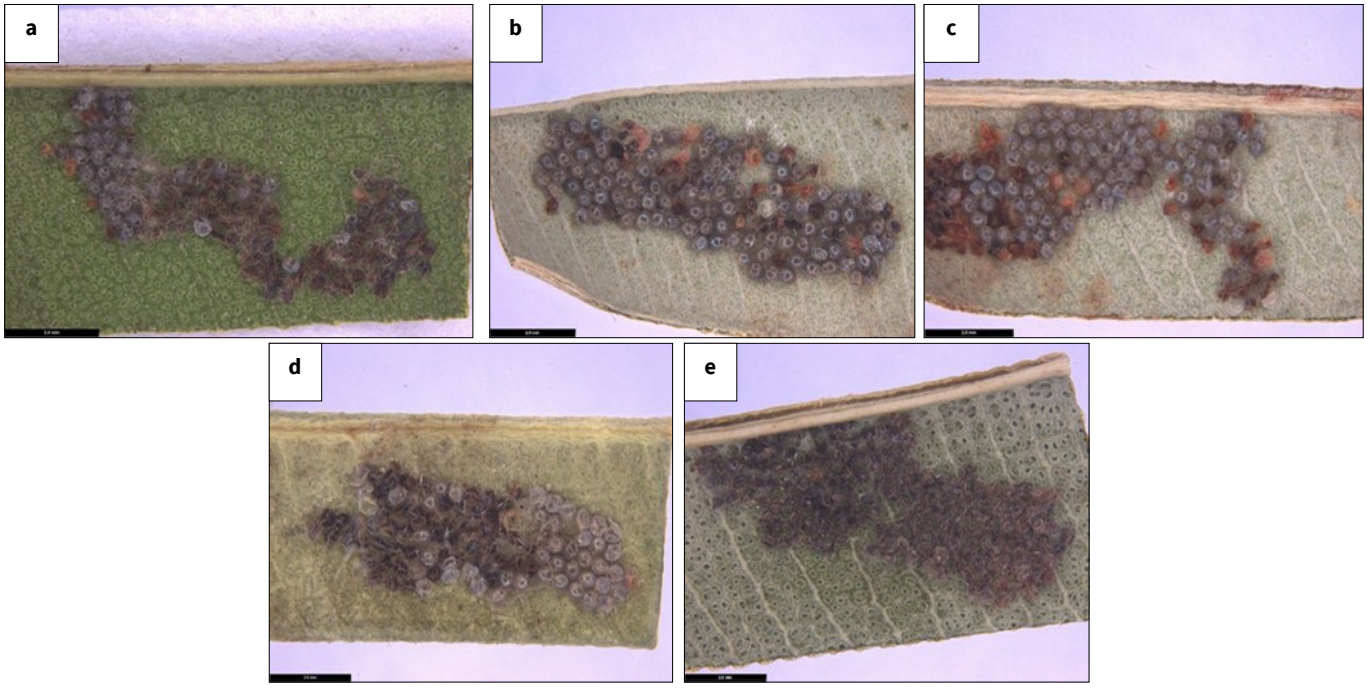

Fig. 1. Number of eggs parasitized under different temperature regimes (a) Parasitization under 20 °C, (b) Parasitization under 25 °C, (c) Parasitization under 30 °C, (d) Parasitization under 35 °C and (e) Parasitization under 40 °C.

Influence of temperature on *T. remus* offspring generation (F_1)

Temperature continued to significantly shape the biological traits of the offspring generation (F_1). The egg-to-adult development period decreased as temperature increased, ranging from 8.60±0.07 days at 35 °C to 21.95±0.23 days at 20 °C (Table 2). This is consistent with the general principle that higher temperatures accelerate metabolic and developmental processes (16). Our results closely align with previous findings that documented a development duration of 8.1 days at 35 °C and up to 52.7 days at 15 °C in *T. remus* (21). A similar developmental range has also been reported for *T. podisi*, which developed in 11.3±0.11 days at 33 °C and 35.4±0.11 days at 16 °C (27).

Lifetime fecundity was highest at 30 °C (122.7±3.56 eggs/female), followed by 25 °C (109.90±2.75 eggs/female), indicating that moderate temperatures enhance reproductive fitness. However, fecundity declined sharply at 35 °C (32.90 eggs/female), likely due to strain-level thermal sensitivity. These findings differ from those of an earlier study where maximum parasitism was recorded at 35 °C (16), suggesting possible population-specific thermal adaptations. Parasitism was concentrated within the first 24 hrs post-emergence, consistent with the pro-ovigenic nature of *T. remus* (28, 29). This observation is supported by other studies that documented similar early reproductive behavior in egg parasitoids (30).

Adult female longevity was inversely related to temperature, with maximum longevity at 20 °C (10.10 days). However, another study reported significantly longer lifespans at the same temperature (40.60 days) (16), suggesting that differences in humidity, strain, or host quality may contribute to variability in longevity.

Temperature-dependent fertility life table and survivorship curve of *T. remus*

The fertility life table parameters varied significantly with temperature, underscoring the role of thermal conditions in population dynamics (Table 3). The net reproductive rate (R_0) was highest at 30 °C (89.4), followed by 25 °C (82.4) and 20 °C (37.7). Values declined substantially beyond the optimal range, indicating that temperature directly impacts reproductive potential and population buildup (17).

The intrinsic rate of increase (r_m) peaked at 30 °C (0.479), followed by 25 °C (0.364). Although *T. remus* was still capable of reproduction at 35 °C (0.361), the lower r_m and fecundity indicate that thermal stress negatively affects fitness. The finite rate of increase (λ) also reached its maximum at 30 °C (1.614 females/day), reinforcing that this temperature is most conducive to rapid population expansion (17).

The population doubling time (TD) was shortest at 30 °C (1.448 days) and longest at 20 °C (4.303 days), while intermediate values were recorded at 25 and 35 °C (~1.92 days). The generation time (Tc) declined from 21.594 days at 20 °C to 8.175 days at 35 °C, indicating faster generational turnover at higher temperatures, although reproductive quality was compromised beyond the optimal limits.

In nature, three primary types of survivorship curves are recognized. Type I features high survival through early and middle life, followed by a sharp decline in older age. Type II exhibits a constant mortality rate across all life stages, while Type III, common in insects, involves high mortality in early stages, with survival stabilizing among the few individuals that reach adulthood (31). In the present study, *T. remus* displayed a pattern between Type I and Type II, characterized by low mortality in early and middle stages, followed by a decline in later stages (Fig. 2). At 20 °C, survival remained high until day 8 and fecundity gradually declined thereafter. At 25 and 30 °C, fecundity peaked on day 1, with survival declining from day 5-6. At 35 °C, both survival and fecundity declined sharply after day 3, indicating accelerated mortality and reduced performance due to thermal stress. These results are consistent with demographic studies that report compromised longevity and fecundity under temperature extremes (32).

Although this study was conducted under constant temperature conditions, recent evidence suggests that fluctuating thermal regimes, which better reflect natural field conditions, may enhance parasitoid performance. Such regimes have been shown to improve development rate, fecundity and longevity in *T. remus* and related species, while also reducing rearing costs (32). Therefore, integrating fluctuating temperatures into mass-rearing protocols may optimize the field performance of *T. remus*, particularly under tropical and subtropical conditions.

Table 2. Influence of temperature on offspring generation

Temperature (°C)	Egg- adult duration (days)	Female longevity (days)	Total Parasitism (no.)	% Adult emergence
20	21.95±0.23^{d}	10.10±0.23^{a}	57.20±1.41^{c}	98.29±0.58^{a}
25	12.75±0.08^{c}	6.30±0.15^{b}	109.90±2.75^{b}	99.65±0.20^{a}
30	9.60±0.07^{b}	6.50±0.17^{b}	122.7±3.56^{a}	99.44±0.16^{a}
35	8.60±0.07^{a}	3.20±0.13^{c}	32.90±1.16^{d}	97.88±0.76^{a}
40	0	0	0	0

All values are Mean ± Standard error

Means sharing the same letter do not differ significantly by (Tukey's test, P = 0.05)

Table 3. Fertility life table of *T. remus* under different temperature regimes

Temperature (°C)	R_0 (Females/female/lifetime)	T_c (days)	r_m	λ (Females/ female/day)	T_D (days)
20	37.7^{c}	21.594^{a}	0.161^{d}	1.175^{d}	4.303^{d}
25	82.4^{b}	12.123^{b}	0.364^{b}	1.433^{c}	1.928^{c}
30	89.4^{a}	9.174^{c}	0.479^{a}	1.614^{a}	1.448^{a}
35	18.9^{d}	8.175^{d}	0.361^{c}	1.434^{b}	1.922^{b}
40	0	0	0	0	0

Means sharing the same superscript letter do not differ significantly (Tukey's test, P = 0.05)

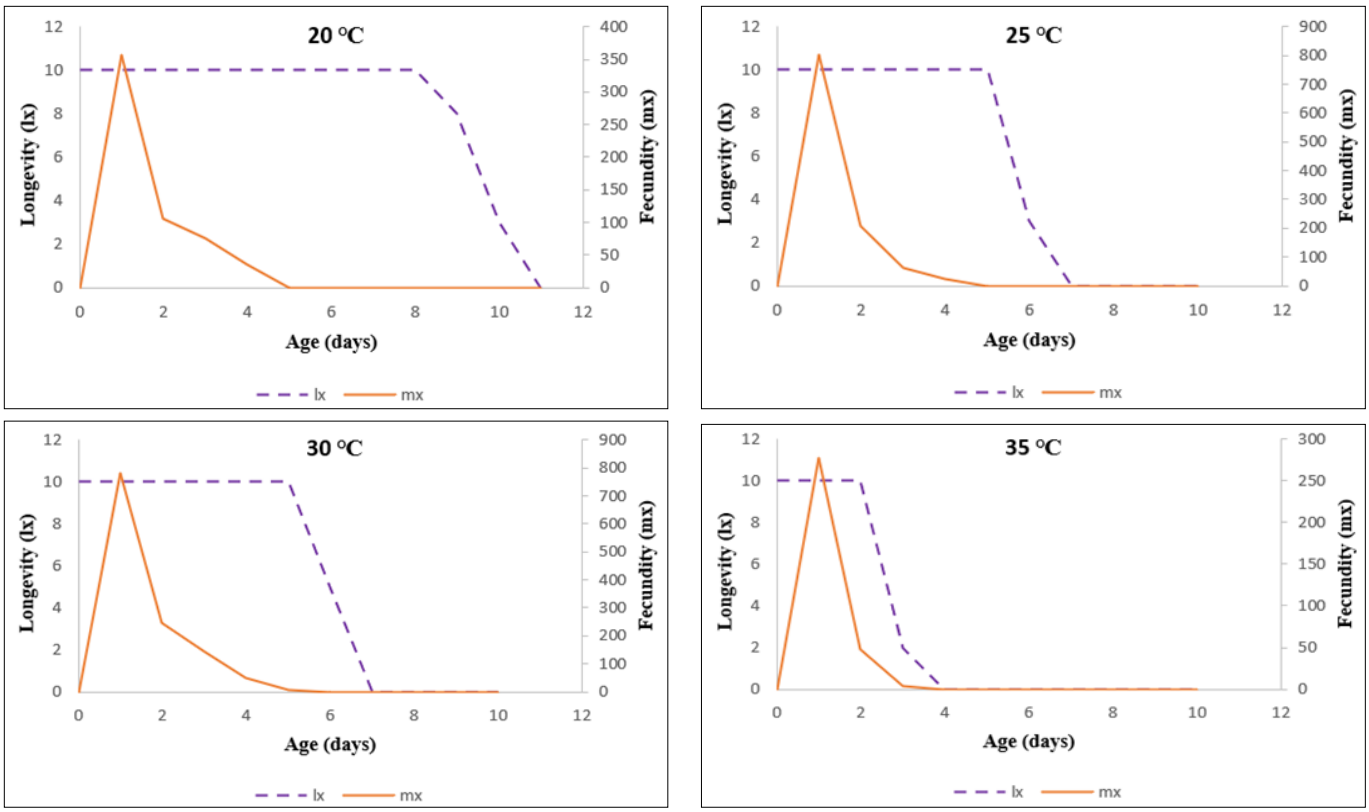

Fig. 2. Survivorship curves under different temperature regimes.

Conclusion

The present study confirms that temperature critically influences the development and reproductive success of *T. remus*. The optimal temperature range of 25-30 °C supported superior biological performance, making it ideal for mass rearing and effective field deployment. In contrast, temperatures above 30 °C or below 25 °C significantly reduced key fitness traits due to thermal stress. Therefore, biological control programs using *T. remus* should be recommended only in regions where ambient temperatures fall within this optimal range. Field release in hotter climates may not provide the expected suppression of the target pests. Future research should focus on evaluating the field performance of lab-reared biocontrol agents under fluctuating temperature conditions, as constant temperatures rarely occur in natural environments. Such studies will help in bridging the gap between laboratory efficacy and field success of parasitoids.

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Authors' contributions

All authors contributed to the study conception, design and manuscript preparation. NMS carried out the experiments, recorded and analysed the data and wrote the manuscript. ST structured and supervised the experiments and edited the manuscript. MM, PSS, KP, RR, SMR and ARR critically reviewed the manuscript. All authors provided feedback on earlier versions of the manuscript and have read and approved the final version.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interests to declare.

Ethical issues: None

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