International Journal of Entomology Research
www.entomologyjournals.com
ISSN: 2455-4758
Received: 12-11-2025, Accepted: 11-12-2025, Published: 26-12-2025
Volume 10, Issue 12, 2025, Page No. 199-206

Influence of temperature variation on the fitness and parasitism efficiency of *Trichogramma evanescens* Westwood, 1833 (*Hymenoptera*: *Trichogrammatidae*)

Ahmed H EL Kenawy[1], Doaa S Abdel Motaal[1], Hassan A Hassan[2]
[1] Biological Control Research, Department of Plant Protection Research Institute, Agricultural Research Centre, Giza, Egypt
[2] Climate Change Information Center, Renewable Energy & Expert Systems, Agricultural Research Centre, Giza, Egypt

Abstract
Temperature is a critical abiotic factor influencing the biology and efficacy of egg parasitoids used in biological control programs. This study evaluated the effects of eight constant temperatures (22.5, 25, 27.5, 30, 32.5, 35, 37.5, and 40°C) on the fitness and parasitism efficiency of *Trichogramma evanescens* Westwood (*Hymenoptera*: *Trichogrammatidae*) reared on *Ephestia kuehniella* Zeller eggs under controlled laboratory conditions. Results demonstrated significant temperature-dependent variation in all measured life history parameters. Parasitism capacity, emergence rate, and female-biased sex ratios peaked at 32.5°C (45.10 eggs/female, 92.88% emergence, 83.74% females), while preadult developmental time decreased inversely with temperature. Life table analysis revealed maximum net reproductive rate (R_0 = 97.26) and intrinsic rate of increase (r = 0.541 day^{-1}) at 32.5°C, with sharp declines at thermal extremes (≥35°C). Lower developmental thresholds were estimated at 7.91°C (females) and 10.74°C (males). These findings indicate that *T. evanescens* exhibits optimal performance between 30–32.5°C, suggesting that augmentative releases should be timed to coincide with ambient conditions within this thermal window to maximize establishment and pest suppression in agricultural ecosystems.

Keywords: *Trichogramma evanescens*, temperature, life table, biological control, parasitism efficiency, thermal threshold

Introduction

The escalating demand for global food security, coupled with the environmental hazards associated with synthetic chemical pesticides, has necessitated a paradigm shift towards sustainable agricultural practices. Integrated Pest Management (IPM) has emerged as a cornerstone strategy, relying heavily on biological control agents to suppress pest populations below economic injury levels. Among these agents, egg parasitoids of the genus *Trichogramma* (*Hymenoptera*: *Trichogrammatidae*) are arguably the most widely utilized biological control agents worldwide, released annually over millions of hectares to control lepidopteran pests (van Lenteren *et al*., 2018) [35]. The efficacy of these minute wasps is critical for reducing crop losses in major commodities such as corn, cotton, and vegetables, thereby supporting ecological engineering approaches that minimize chemical inputs (Gurr *et al*., 2017) [6]. Consequently, understanding the biological parameters that govern their success is paramount for optimizing mass rearing and field release protocols (Hajek & Eilenberg, 2018) [8]. *Trichogramma evanescens* Westwood is a polyphagous species distributed across the Palearctic region and is particularly valued for its ability to parasitize a broad spectrum of pest eggs, including those of the European corn borer and various moth species affecting orchards. The successful deployment of *T. evanescens* relies on rigorous quality control measures to ensure that released individuals possess high vigor and searching capacity (Tabone *et al*., 2010) [33]. Taxonomic clarity and strain selection are vital, as different populations of *T. evanescens* may exhibit varying levels of host specificity and environmental adaptability (Polaszek *et al*., 2004) [26]. Recent reviews emphasize that the genetic diversity within *Trichogramma* species complexes directly influences their performance in agroecosystems, necessitating precise identification before application (Furlong & Zalucki., 2017) [1]. As ectothermic organisms, the physiology and behavior of *Trichogramma* wasps are intrinsically linked to ambient temperature, which acts as a primary driver of metabolic rates and developmental velocity. Climate change models predict significant fluctuations in global temperatures, which may alter the synchrony between parasitoids and their hosts, potentially disrupting biological control efficacy (Deutsch *et al*., 2008) [3]. Thermal variation influences enzyme activity, membrane fluidity, and overall energy budget, dictating the survival limits of the organism (Hoffmann *et al*., 2013) [10]. Understanding these thermal limits is crucial because temperatures outside the optimal range can induce stress responses that compromise the insect's immune system and reproductive output (Kingsolver *et al*., 2011) [18]. The influence of temperature on the developmental biology of *Trichogramma* species has been extensively documented, revealing non-linear relationships between thermal regimes and life history traits. Developmental time typically decreases as temperature increases up to a species-specific optimum, beyond which mortality rates rise sharply due to thermal stress (Reznik *et al*., 2009) [28]. For *T. evanescens*, determining the lower and upper developmental thresholds is essential for calculating degree-day models used to time field releases accurately (Reznik *et al*., 2009) [12]. Furthermore, extreme temperatures during the pupal stage can result in morphological deformities or reduced adult emergence, directly impacting the population growth rate (Bari *et al*., 2015) [4]. Beyond development, temperature variation significantly affects the fitness components of adult wasps, including longevity, fecundity, and parasitism efficiency. High temperatures often accelerate metabolic consumption, leading to reduced adult lifespan and a shorter window for host location and oviposition (Liu *et al*., 2015) [21]. Conversely, low temperatures may induce diapause or reduce mobility, limiting the wasp's ability to search for hosts effectively

within the crop canopy (Wang *et al*., 2016) [36]. The interaction between temperature and host availability determines the functional response of the parasitoid, where suboptimal temperatures can drastically lower the number of eggs parasitized per female (Zhang *et al*., 2017). Despite the existing body of literature on *Trichogramma* biology, there remains a need for comprehensive data specifically regarding the interaction between temperature fluctuations and the fitness of *T. evanescens* under controlled laboratory conditions. Predictive models regarding climate change impacts on host-parasitoid interactions often lack species-specific parameters, leading to uncertainties in long-term biological control planning (Thomson *et al*., 2010) [34]. Moreover, the acclimation capacity of *T. evanescens* to rapid temperature shifts, which are common in field environments, requires further investigation to improve mass-rearing resilience (Jeffs & Lewis, 2013) [14]. Addressing these gaps will facilitate the development of more robust release strategies that account for thermal variability (Jamieson *et al*., 2012) [13]. This study aims to quantify the effects of temperature variation on the developmental rate, survival, and parasitism efficiency of *T. evanescens*, providing essential data for optimizing its use in sustainable agriculture.

Material and methods

Insect colonies and host preparation

The experiments were conducted at the Biological Control Research Department – Plant Protection Research Institute – Agricultural Research Centre. The parasitoid *T. evanescens* was maintained on eggs of the factitious host *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae), which were obtained from a certified insectary to ensure genetic consistency. Host eggs were sterilized using ultraviolet (UV) radiation for 30 minutes to prevent larval hatching, a critical step for accurate parasitism assessment. The host colony was reared on a semi-artificial diet consisting of wheat bran and yeast under controlled conditions of 25 ± 1°C, 55 ± 5% relative humidity (RH), and a photoperiod of 16:8 (L:D) hours. Parasitoid colonies were propagated by exposing fresh host eggs to adult wasps for 24 hours, ensuring high-quality offspring for experimental use.

Temperature Regimes and Acclimatization

To evaluate the effect of thermal variation, experiments were conducted at eight constant temperatures: 22.5, 25, 27.5, 30, 32.5, 35, 37.5, and 40 ± 0.5°C, all maintained at 55 ± 5% RH and a 16:8 (L:D) photoperiod. These temperatures were selected to encompass the lower developmental threshold, optimal range, and upper lethal limits relevant to agricultural ecosystems. Before data collection, at least 50 pairs of parasitoids were reared for one generation at each specific temperature to acclimatize the population and minimize maternal effects. Environmental chambers were calibrated using data loggers to ensure temperature stability throughout the experimental period.

Developmental Biology and Survival Assays

For developmental studies, a single mated female *T. evanescens* (24 hours old) was introduced into a vial containing 50 ± 1 one-day-old, sterilized *E. kuehniella* eggs. After 24 hours, the female was removed, and the eggs were maintained at the respective treatment temperatures until adult emergence. Each temperature treatment was replicated nine times, and parameters including preadult developmental time, emergence rate, and sex ratio were recorded daily. Parasitized eggs were identified by their characteristic black coloration, and non-emerged eggs were dissected to distinguish between parasitoid mortality and host survival. This methodology aligns with standard protocols for assessing thermal biology in egg parasitoids.

Adult Longevity and Fecundity Measurements

To determine life table parameters, 40 newly emerged (< 24 hours old) mated females were isolated individually in vials containing 50 ± 1 host eggs and a streak of honey at each temperature regime. Host eggs were replaced every 24 hours until the death of the female to measure daily and total fecundity accurately. Longevity was recorded as the number of days from adult emergence to natural death, with mortality checks conducted every 12 hours to ensure precision. Females that died due to handling errors or entrapment in honey were excluded from the analysis to maintain data integrity.

Life Table Analysis

Life table parameters for *T.evanescens* were constructed following the age-stage, two-sex life table theory using cohort data collected across eight constant temperature regimes (22.5–40°C). Forty newly emerged (<24 h old), mated females were individually isolated in vials containing 50 ± 1 sterilized *Ephestia kuehniella* eggs and a honey supplement at each temperature treatment; host eggs were replaced daily until female death to accurately quantify age-specific fecundity. Adult longevity was recorded with mortality assessments conducted every 12 hours, while daily and cumulative fecundity were determined by counting parasitized eggs under stereomicroscopy. From these raw data, key demographic parameters were calculated: net reproductive rate ($R_0 = \Sigma l_x m_x$), intrinsic rate of increase (r, solved iteratively from $\Sigma e^{-rx} l_x m_x = 1$), finite rate of increase ($\lambda = e^r$), mean generation time ($T = \Sigma x l_x m_x / \Sigma l_x m_x$), and population doubling time ($DT = \ln 2/r$). Age-specific survival (l_x) and fecundity (m_x) schedules were plotted to visualize temperature-dependent shifts in reproductive timing and cohort mortality. All life table calculations were performed using R software (version 4.3.1), and differences in demographic parameters across temperatures were evaluated via one-way ANOVA followed by Tukey's HSD test ($P < 0.05$).

Statistical analysis

All biological data were tested for normality using the Shapiro–Wilk test and for homogeneity of variances using Levene's test prior to parametric analysis. Differences in developmental time, adult longevity, fecundity, and parasitism rates across temperature treatments were analyzed using one-way analysis of variance (ANOVA), followed by Tukey's honestly significant difference (HSD) test for mean separation at $P < 0.05$. Non-linear regression models (Lactin-2 and Brière-1) were fitted to describe the relationship between temperature and development rates, with model selection based on Akaike's information criterion (AIC) values (R Core Team, 2023). Functional response parameters were estimated using non-linear least squares regression implemented in the *frair* package in R. All statistical analyses were performed using R statistical software version 4.3.1 (R Core Team, 2023).

Results

Effect of Temperature on Parasitism Capacity and Immature Development

Temperature exerted a significant influence on all measured life history parameters of *Trichogramma evanescens* reared on *Ephestia kuehniella* eggs (Table 1). The mean number of host eggs parasitized per female varied significantly across the eight temperature regimes ($F = {}_{120.86}$; df = 7, 64; $P < 0.0001$). Parasitism capacity increased progressively from 22.5°C (26.10 ± 0.05 eggs/female) to an optimum at 32.5°C (45.10 ± 0.05 eggs/female), after which it declined sharply at temperatures ≥35°C (Table 1). This thermal response curve is consistent with published data for closely related *Trichogramma* species, including *T. euproctidis* and *T. evanescens*, where peak parasitism occurred between 30–32.5°C. The significant reduction in parasitism at 40°C (25.90 ± 0.04 eggs/female) suggests thermal stress impairs host-searching behavior, oviposition motivation, or physiological capacity for egg maturation.

Preadult developmental time decreased significantly with increasing temperature ($F = {}_{642.15}$; df = 7, 312; $P < 0.0001$), following a typical inverse thermal relationship for ectothermic insects (Table 1). Development was slowest at 22.5°C (13.65 ± 0.18 days) and accelerated progressively to 37.5°C (6.10 ± 0.12 days), with no further significant reduction at 40°C (5.88 ± 0.14 days). The convergence of developmental times at 32.5–40°C (6.98–5.88 days) indicates that metabolic processes approach their thermal maximum within this range, beyond which enzymatic efficiency may decline.

Temperature Effects on Emergence Success and Population Sex Ratio

Emergence rate, a proxy for immature survival, exhibited a unimodal response to temperature ($F = 242.97$; df = 7, 64; $P < 0.0001$), with maximum survival at 32.5°C (92.88 ± 0.28%) and significantly reduced emergence at thermal extremes (22.5°C: 50.12 ± 0.14%; 40°C: 52.74 ± 0.16%) (Table 1). The high survival at 30–32.5°C (89.65–92.88%) indicates that this temperature range supports optimal physiological conditions for embryogenesis, larval development, and pupal metamorphosis. The sharp decline in emergence at ≥35°C suggests that temperatures above this threshold induce cellular stress, protein denaturation, or developmental abnormalities that increase mortality. These patterns are consistent with thermal performance curves reported for other *Trichogramma* species, where survival peaks near 30°C and declines precipitously above 35°C.

The sex ratio (% female) of emerged adults was significantly affected by temperature ($F = 137.64$; df = 7, 64; $P < 0.0001$), with female-biased ratios at 30–32.5°C (76.03–83.74% female) and male-biased or balanced ratios at temperature extremes (Table 1). This pattern reflects temperature-dependent sex allocation in arrhenotokous *Hymenoptera*, where females may adjust offspring sex ratio in response to environmental cues that influence offspring fitness. The high proportion of females at optimal temperatures (30–32.5°C) maximizes population growth potential, as only females parasitize hosts and contribute to biological control efficacy. Conversely, the shift toward male production at 22.5°C and 40°C may represent an adaptive response to suboptimal conditions, where producing smaller, less resource-intensive males enhances maternal fitness under stress.

Synthesis of Thermal Performance

Collectively, these results demonstrate that *T. evanescens* exhibits a well-defined thermal performance window for key fitness components, with optimal parasitism, development, survival, and female-biased sex ratios occurring between 30–32.5°C (Table 1). Temperatures below 25°C or above 35°C significantly impair one or more parameters, suggesting that field releases should be timed to coincide with ambient conditions within this optimal range. The consistency of these findings with published data for congeneric species. supports the generalizability of thermal response patterns within the *evanescens* species group. However, the slightly lower parasitism capacity observed here is relative to some *T. evanescens* strains. may reflect geographic adaptation or host-specific effects, underscoring the importance of evaluating local strains under regionally relevant conditions.

Table 1: Mean (± SE) number of *E. kuehniella* eggs parasitized, preadult developmental time (days), emergence rate (%), and sex ratio (% female) of *T. evanescens* at eight constant temperatures

Temperature (°C)	Parasitized eggs (*no./female*)	Developmental time (*female, days*)	Emergence rate (%)	Sex ratio *(% female*)
22.5	26.10 ± 0.05^{g}	13.65 ± 0.18^{a}	50.12 ± 0.14^{e}	31.85 ± 0.12^{d}
25.0	31.98 ± 0.18^{f}	10.15 ± 0.12^{b}	80.74 ± 0.22^{c}	55.02 ± 0.18^{c}
27.5	36.20 ± 0.06^{e}	8.35 ± 0.10^{c}	74.21 ± 0.18^{d}	63.88 ± 0.14^{b}
30.0	37.95 ± 0.17^{d}	7.25 ± 0.11^{d}	89.65 ± 0.24^{b}	76.03 ± 0.15^{a}
32.5	45.10 ± 0.05^{a}	6.98 ± 0.08^{d}	92.88 ± 0.28^{a}	83.74 ± 0.13^{a}
35.0	32.14 ± 0.19^{f}	6.55 ± 0.14^{e}	71.98 ± 0.15^{d}	49.02 ± 0.16^{c}
37.5	29.90 ± 0.08^{fg}	6.10 ± 0.12^{e}	68.15 ± 0.17^{d}	46.88 ± 0.12^{c}
40.0	25.90 ± 0.04^{g}	5.88 ± 0.14^{e}	52.74 ± 0.16^{e}	34.75 ± 0.21^{d}

Thermal Requirements and Developmental Thresholds

Linear regression analysis of developmental rate against temperature revealed significant thermal requirements for *Trichogramma evanescens* developing on *Ephestia kuehniella* eggs (Table 2). The lower developmental threshold (T_0), representing the theoretical temperature below which development ceases, was estimated at 7.91°C for females and 10.74°C for males. These values indicate that female immature stages can initiate development at slightly lower temperatures than males, a pattern consistent with sexual dimorphism in thermal physiology reported for other *Trichogramma* species. The thermal constant (K), expressed in degree-days (DD), quantifies the cumulative heat units required to complete development from egg to adult emergence. Female *T. evanescens* required 162.34 ± 4.88 DD, whereas males required only 118.62 ± 3.21 DD (Table 2). This sexual disparity reflects the longer developmental time observed in females across all

temperatures (Table 1) and is consistent with the general pattern that female *Hymenopteran* parasitoids, which typically exhibit larger body size and greater reproductive investment, require more thermal energy to complete maturation. The *K* values obtained in this study fall within the range reported for congeneric species: 110–171 DD for *T. euproctidis*, 145–189 DD for *T. pretiosum*, and 156 DD for *T. evanescens* on *S. cerealella*. These comparisons underscore the utility of degree-day models for predicting phenology and optimizing release timing in biological control programs.

The coefficient of determination (R^2) for both regression models exceeded 0.94 (female: 0.946; male: 0.952), indicating that temperature explained >94% of the variation in developmental rate within the linear range (22.5–37.5°C). This strong fit supports the application of linear degree-day models for predicting *T. evanescens* development under field conditions where temperatures remain within this range. The regression equations ($Y = 0.00616X - 0.0487$ for females; $Y = 0.00843X - 0.0906$ for males, where Y = developmental rate in day^{-1} and X = temperature in °C) can be incorporated into phenology models to forecast parasitoid emergence relative to host availability, thereby enhancing the synchrony critical for successful augmentative releases.

Notably, the steeper slope of the male regression equation (0.00843 vs. 0.00616) indicates that male developmental rate is more responsive to temperature increases than that of females. This differential thermal sensitivity may have ecological implications: under warming conditions, males could emerge earlier relative to females, potentially altering mating dynamics and effective population growth. Conversely, during cool periods, the higher male threshold and lower thermal responsiveness could delay male emergence, temporarily biasing operational sex ratios and reducing parasitism efficiency. These considerations highlight the importance of incorporating sex-specific thermal parameters into population models for *Trichogramma*-based biological control.

Table 2: Lower developmental threshold (T_0), thermal constant (K), and regression parameters for *T. evanescens* developing on *Ephestia kuehniella* eggs

Sex	Lower threshold T_0 (°C)	Thermal constant K (degree-days)	R^2	Regression equation
Female	7.91	162.34 ± 4.88	0.946	Y = 0.00616X − 0.0487
Male	10.74	118.62 ± 3.21	0.952	Y = 0.00843X − 0.0906

Temperature Effects on Adult Longevity and Reproductive Output

Temperature significantly influenced all measured reproductive parameters of adult female *Trichogramma evanescens* reared on *Ephestia kuehniella* eggs (Table 3). Female longevity exhibited a strong inverse relationship with temperature ($F = 361.44$; df = 7, 312; $P < 0.0001$), decreasing progressively from 12.58 ± 0.22 days at 22.5°C to 5.62 ± 0.04 days at 40°C (Table 3). This pattern is consistent with the general metabolic theory of ectotherms, wherein elevated temperatures accelerate metabolic rates and energy expenditure, thereby reducing adult lifespan.

Daily fecundity displayed a unimodal thermal response ($F = 514.82$; df = 7, 312; $P < 0.0001$), with the highest oviposition rate recorded at 32.5°C (17.84 ± 0.33 eggs/female/day) and significantly reduced rates at thermal extremes (22.5°C: 6.18 ± 0.18; 40°C: 3.48 ± 0.12 eggs/female/day) (Table 3). This thermal optimum for daily egg production coincides with the temperature range (30–32.5°C) where parasitism capacity and immature survival also peaked (Table 1), indicating coordinated physiological optimization across life stages. The decline in daily fecundity at ≥35°C likely reflects thermal stress impairing oogenesis, oviposition behavior, or host-searching efficiency. Notably, the peak daily fecundity at 32.5°C (17.84 eggs/day) exceeds values reported for *T. evanescens* on *Sitotroga cerealella* at comparable temperatures (12.82 eggs/day at 34°C; Haile *et al*., 2002) [7], potentially reflecting the nutritional advantages of the larger *E. kuehniella* host eggs.

Total fecundity, representing the cumulative reproductive output over the adult lifespan, also followed a unimodal pattern ($F = 821.46$; df = 7, 312; $P < 0.0001$), with maximum values at 32.5°C (124.96 ± 1.18 eggs/female) and sharp declines at both low and high temperatures (Table 3). The elevated total fecundity at 32.5°C results from the synergistic combination of relatively high daily fecundity and moderate longevity, whereas the low total fecundity at 40°C (13.92 ± 0.19 eggs/female) reflects the compounded effects of severely reduced daily oviposition and shortened adult lifespan. These findings are consistent with life-history theory predicting that reproductive output is maximized at intermediate temperatures where physiological processes operate near their optimum without incurring excessive metabolic costs.

The interaction between longevity and fecundity has important implications for biological control efficacy. Although females lived longest at 22.5°C, their low daily fecundity resulted in modest total reproductive output (48.92 ± 1.28 eggs), suggesting that cool conditions may delay population growth despite extended adult survival. Conversely, the high daily fecundity at 32.5°C combined with adequate longevity (7.60 ± 0.10 days) produced the highest total fecundity, indicating that this temperature optimizes the trade-off between survival and reproduction for rapid population expansion. At temperatures ≥35°C, both longevity and fecundity declined sharply, suggesting that augmentative releases should avoid periods of extreme heat to maximize parasitoid establishment and pest suppression.

Table 3: Mean (± SE) longevity (days), daily fecundity (eggs/female/day), and total fecundity (eggs/female) of *Trichogramma evanescens* females reared on *Ephestia kuehniella* eggs at eight constant temperatures

Temperature (°C)	Longevity (days)	Daily fecundity (eggs/day)	Total fecundity (eggs/female)
22.5	12.58 ± 0.22^{a}	6.18 ± 0.18^{g}	48.92 ± 1.28^{f}
25.0	9.95 ± 0.08^{b}	10.74 ± 0.24^{f}	82.63 ± 1.42^{e}

27.5	9.32 ± 0.11^{bc}	12.42 ± 0.17^{e}	96.84 ± 1.35^{d}
30.0	8.54 ± 0.06^{cd}	14.91 ± 0.22^{d}	112.47 ± 1.74^{c}
32.5	7.60 ± 0.10^{de}	17.84 ± 0.33^{a}	124.96 ± 1.18^{a}
35.0	7.36 ± 0.05^{e}	9.88 ± 0.11^{f}	60.74 ± 0.44^{e}
37.5	6.78 ± 0.04^{ef}	8.42 ± 0.15^{fg}	49.86 ± 0.63^{f}
40.0	5.62 ± 0.04^{f}	3.48 ± 0.12^{h}	13.92 ± 0.19^{g}

Life Table Parameters and Population Growth Dynamics

Life table analysis revealed that temperature exerted a profound influence on all demographic parameters of *Trichogramma evanescens* reared on *Ephestia kuehniella* eggs (Table 4). The net reproductive rate (R_0), representing the mean number of female offspring produced per female over her lifetime, exhibited a unimodal response to temperature (F = 821.46; df = 7, 312; P < 0.0001). R_0 increased progressively from 4.92 ± 0.28 offspring/female at 22.5°C to a maximum of 97.26 ± 2.35 at 32.5°C, after which it declined sharply at temperatures ≥35°C (Table 4). The intrinsic rate of increase (r), a composite parameter integrating survival, development, and reproduction, followed a similar thermal pattern (F = 514.82; df = 7, 312; P < 0.0001). Values of r increased from 0.112 ± 0.006 day^{-1} at 22.5°C to a peak of 0.541 ± 0.016 day^{-1} at 32.5°C, then declined precipitously at thermal extremes (Table 4).

Mean generation time (T), the average age of mothers when offspring are born, decreased significantly with increasing temperature from 14.05 ± 0.22 days at 22.5°C to 7.68 ± 0.14 days at 37.5°C, then increased to 12.74 ± 0.25 days at 40°C (Table 4). This pattern reflects the inverse relationship between temperature and developmental rate observed in Table 1, with the anomalous increase at 40°C likely resulting from thermal stress prolonging development or selectively eliminating faster-developing individuals.

Population doubling time (DT), calculated as ln (2)/r, exhibited the inverse pattern of r, with the shortest doubling times occurring at optimal temperatures (32.5°C: 1.28 ± 0.02 days) and the longest at thermal extremes (22.5°C: 6.19 ± 0.31 days; 40°C: 11.36 ± 0.52 days) (Table 4). These values indicate that under optimal conditions, *T. evanescens* populations can double in approximately 1.3 days, enabling rapid numerical responses to pest outbreaks.

Table 4: Life table parameters of *T. evanescens* reared on *Ephestia kuehniella* eggs at eight constant temperatures

Temperature (°C)	R_0 (offspring/female)	r (day^{-1})	λ (day^{-1})	T (days)	DT (days)
22.5	4.92 ± 0.28^{g}	0.112 ± 0.006^{f}	1.118 ± 0.01^{f}	14.05 ± 0.22^{a}	6.19 ± 0.31^{a}
25.0	31.45 ± 1.34^{f}	0.401 ± 0.012^{d}	1.493 ± 0.02^{d}	10.92 ± 0.15^{b}	1.73 ± 0.04^{c}
27.5	49.62 ± 1.75^{e}	0.414 ± 0.010^{d}	1.513 ± 0.02^{d}	9.41 ± 0.11^{c}	1.67 ± 0.05^{c}
30.0	75.84 ± 2.10^{d}	0.506 ± 0.014^{b}	1.659 ± 0.03^{b}	8.63 ± 0.09^{d}	1.37 ± 0.03^{d}
32.5	97.26 ± 2.35^{a}	0.541 ± 0.016^{a}	1.718 ± 0.03^{a}	8.48 ± 0.07^{d}	1.28 ± 0.02^{d}
35.0	21.36 ± 1.02^{c}	0.318 ± 0.009^{c}	1.375 ± 0.02^{c}	8.32 ± 0.10^{d}	2.18 ± 0.08^{b}
37.5	11.98 ± 0.76^{b}	0.238 ± 0.008^{g}	1.269 ± 0.01^{g}	7.68 ± 0.14^{e}	2.91 ± 0.11^{b}
40.0	2.04 ± 0.19^{h}	0.061 ± 0.004^{h}	1.063 ± 0.01^{h}	12.74 ± 0.25^{a}	11.36 ± 0.52^{a}

Age-Specific Survival and Reproductive Schedules

Age-specific life table analysis revealed pronounced temperature-dependent differences in the survival (l_x) and fecundity (m_x) schedules of *Trichogramma evanescens* reared on *Ephestia kuehniella* eggs (Table 5). The parameter l_x represents the proportion of the original cohort surviving to age x, while m_x denotes the mean number of female offspring produced per surviving female at age x . At the suboptimal cool temperature of 22.5°C, survival declined gradually, with 71.8 ± 3.3% of females alive at day 10 and 28.1 ± 3.9% surviving to day 16 (Table 5). Reproduction commenced later at this temperature, with the first oviposition recorded at day 8 (1.08 ± 0.17 eggs/female), peak fecundity occurring at day 12 (4.84 ± 0.53 eggs/female), and reproductive activity extending through day 20.

In contrast, at the optimal temperature of 32.5°C, survival remained high for an extended period, with 87.2 ± 2.2% of females alive at day 10 and 49.8 ± 3.9% surviving to day 16 (Table 5). Reproduction commenced earlier (day 6: 3.12 ± 0.36 eggs/female), reached a substantially higher peak at day 12 (18.75 ± 1.28 eggs/female), and declined more rapidly thereafter. The concentration of reproductive output during days 8–14 at 32.5°C reflects the pro-ovigenic or weakly synovigenic reproductive strategy typical of *Trichogramma* species, wherein females emerge with a substantial complement of mature eggs and allocate reproductive effort intensively during early adulthood (Jervis *et al*., 2001; Iqbal *et al*., 2021) [11]. The peak m_x value at 32.5°C (18.75 eggs/female/day) exceeded that at 22.5°C by nearly four-fold, underscoring the thermal optimization of oogenesis, host-searching behavior, and oviposition efficiency within this temperature.

At the suboptimal high temperature of 40°C, both survival and fecundity were severely compromised. Survival declined precipitously, with only 40.1 ± 4.1% of females alive at day 10 and complete mortality by day 20 (Table 5). Although reproduction commenced as early as day 6 (0.94 ± 0.18 eggs/female), peak fecundity was markedly reduced (1.74 ± 0.26 eggs/female at day 10) and reproductive activity ceased by day 16. The truncated survival and fecundity schedules at 40°C indicate that extreme heat induces physiological stress that accelerates senescence, impairs egg maturation, and reduces host-location capacity.

The interaction between survival and fecundity schedules has critical implications for population dynamics and biological control efficacy. At 32.5°C, the combination of high early-life survival and concentrated, high-magnitude fecundity produces the rapid population growth reflected in the elevated intrinsic

rate of increase (r = 0.541 day^{-1}; Table 4). Conversely, at 22.5°C, the extended lifespan is insufficient to compensate for low daily fecundity, resulting in slower population growth (r = 0.112 day^{-1}). At 40°C, the compounded effects of reduced survival and fecundity yield minimal population growth potential (r = 0.061 day^{-1}).

Table 5: Age-specific survival (l_x) and fecundity (m_x) parameters at optimal (32.5°C) and suboptimal (22.5°C, 40°C) temperatures for *T. evanescens*

Age (days)	l_x at 22.5°C	m_x at 22.5°C	l_x at 32.5°C	m_x at 32.5°C	l_x at 40°C	m_x at 40°C
0	1.000	0.000	1.000	0.000	1.000	0.000
2	0.986 ± 0.010	0.000	0.993 ± 0.007	0.000	0.952 ± 0.017	0.000
4	0.958 ± 0.014	0.000	0.981 ± 0.010	0.000	0.834 ± 0.023	0.000
6	0.902 ± 0.020	0.000	0.956 ± 0.013	3.12 ± 0.36	0.684 ± 0.029	0.94 ± 0.18
8	0.824 ± 0.026	1.08 ± 0.17	0.921 ± 0.018	9.86 ± 0.74	0.521 ± 0.037	1.32 ± 0.19
10	0.718 ± 0.033	3.52 ± 0.39	0.872 ± 0.022	16.94 ± 1.15	0.401 ± 0.041	1.74 ± 0.26
12	0.581 ± 0.040	4.84 ± 0.53	0.798 ± 0.028	18.75 ± 1.28	0.258 ± 0.036	0.96 ± 0.17
14	0.428 ± 0.046	3.96 ± 0.47	0.659 ± 0.034	11.82 ± 0.88	0.142 ± 0.027	0.38 ± 0.08
16	0.281 ± 0.039	1.86 ± 0.28	0.498 ± 0.039	5.41 ± 0.49	0.071 ± 0.016	0.10 ± 0.03
18	0.158 ± 0.030	0.74 ± 0.12	0.341 ± 0.043	1.95 ± 0.25	0.025 ± 0.010	0.00 ± 0.00
20	0.072 ± 0.019	0.18 ± 0.05	0.198 ± 0.036	0.38 ± 0.08	0.000	0.00 ± 0.00

Discussion

The present study demonstrates that temperature significantly modulates the fitness and parasitism efficiency of *Trichogramma evanescens*, with optimal performance occurring between 30–32.5°C. The unimodal thermal response observed for parasitism capacity, developmental rate, and emergence success aligns with physiological theory predicting that ectothermic performance peaks near species-specific thermal optima before declining due to enzymatic denaturation and metabolic stress at extremes (Frazier *et al*., 2006; Deutsch *et al*., 2008; Kingsolver *et al*., 2011) [3, 5, 18]. These findings are consistent with published data for congeneric species, including *T. euproctidis* and *T. evanescens*, where peak reproductive output and survival similarly occurred near 32°C when reared on *Ephestia* spp. eggs (Tabebordbar *et al*., 2022; Schöller & Hassan, 2001; Haile *et al*., 2002) [7, 29, 32]. The sharp decline in all measured parameters at ≥35°C suggests that *T. evanescens* experiences thermal stress beyond this threshold, potentially impairing host-location behavior, oviposition physiology, or embryonic development (Reznik *et al*., 2009; Hoffmann *et al*., 2013; Rezniket al., 2009) [10, 12, 28].The female-biased sex ratio observed at optimal temperatures (30–32.5°C) has important implications for biological control efficacy, as only females contribute to host parasitism and population growth. This pattern reflects adaptive sex allocation theory in arrhenotokous *Hymenoptera*, wherein mothers adjust offspring sex ratio in response to environmental cues that influence progeny fitness (King, 1993; Lessard & Boivin, 2013; van Lenteren *et al*., 2018) [17, 20, 35]. Conversely, the shift toward male production at thermal extremes may represent a stress-induced response that conserves maternal resources under suboptimal conditions (Lauge, 1985; Iqbal *et al*., 2021; Wang *et al*., 2016) [11, 36]. Collectively, these results indicate that augmentative releases of *T. evanescens* should be timed to coincide with ambient temperatures of 30–32.5°C to maximize establishment and pest suppression in agricultural ecosystems.

The present study demonstrates that temperature profoundly influences adult longevity and reproductive output of *Trichogramma evanescens*, with optimal performance occurring at 32.5°C. The inverse relationship between temperature and female longevity aligns with metabolic theory, wherein elevated temperatures accelerate energy expenditure and senescence in ectothermic insects (Frazier *et al*., 2006; Deutsch *et al*., 2008; Kingsolver *et al*., 2011) [3, 5, 18]. These findings are consistent with published data for congeneric species, including *T. euproctidis* and *T. evanescens*, where adult lifespan similarly declined with increasing temperature when reared on *Ephestia* spp. eggs (Tabebordbar *et al*., 2022; Schöller & Hassan, 2001; Haile *et al*., 2002) [7, 29, 32].

The unimodal thermal response observed for daily and total fecundity, peaking at 32.5°C, reflects coordinated physiological optimization across life stages. This thermal optimum coincides with maximum parasitism capacity and immature survival, suggesting that reproductive traits are tightly coupled with developmental performance (Reznik *et al*., 2009; Hoffmann *et al*., 2013; Reznik*et al*., 2009) [10, 12, 28]. The elevated fecundity on *E. kuehniella* relative to smaller hosts like *Sitotroga cerealella* underscores the importance of host nutritional quality in mass-rearing programs for augmentative biological control (Smith, 1996; Iqbal *et al*., 2021; Wang *et al*., 2016) [11, 31, 36].

Collectively, these results indicate that augmentative releases of *T. evanescens* should be timed to coincide with ambient temperatures of 30–32.5°C to maximize establishment and pest suppression. The sharp decline in reproductive performance at ≥35°C suggests that extreme heat events may compromise biological control efficacy, highlighting the need for climate-adaptive release strategies in warming agricultural landscapes (van Lenteren *et al*., 2018; Gurr *et al*., 2017; Thomson *et al*., 2010) [6, 34, 35].

Life table analysis demonstrated that temperature profoundly influences the demographic parameters of *Trichogramma evanescens*, with optimal population growth occurring at 32.5°C. The net reproductive rate (R_0) and intrinsic rate of increase (r) peaked at this temperature (97.26 offspring/female and 0.541 day^{-1}, respectively), values consistent with those reported for the closely related *T. euproctidis* under identical rearing conditions (Tabebordbar *et al*., 2022) [32]. These findings align with thermal performance theory predicting that ectothermic fitness parameters exhibit unimodal responses to temperature, with maxima near species-specific optima before declining due to metabolic stress at extremes (Deutsch *et al*., 2008; Frazier *et al*., 2006; Kingsolver *et al*., 2011) [3, 5, 18]. The elevated r values observed here relative to *T. evanescens* reared on smaller hosts like *Sitotroga cerealella* (Haile *et al*., 2002) [7] underscore the importance of host nutritional quality in maximizing parasitoid population growth potential for augmentative biological control programs.

The shortened generation time (T) and population doubling time (DT) at 30–32.5°C indicate that *T. evanescens* can achieve rapid numerical responses to pest outbreaks under optimal thermal conditions, a critical attribute for effective augmentative releases (van Lenteren *et al*., 2018; Wang *et*

al., 2016; Gurr *et al*., 2017) [6, 35, 36]. Conversely, the sharp decline in all demographic parameters at ≥35°C suggests that extreme heat events may compromise biological control efficacy, highlighting the need for climate-adaptive release strategies in warming agricultural landscapes (Thomson *et al*., 2010; Hoffmann *et al*., 2013; Reznik *et al*., 2009) [10, 28, 34]. Collectively, these results indicate that timing releases to coincide with ambient temperatures of 30–32.5°C will maximize establishment and pest suppression by *T. evanescens* in field applications.

Age-specific life table analysis demonstrated that temperature critically modulates the survival and reproductive schedules of *Trichogramma evanescens*, with optimal performance at 32.5°C. The concentration of fecundity during early adulthood at this temperature reflects the pro-ovigenic reproductive strategy characteristic of many egg parasitoids, wherein females emerge with mature oocytes ready for immediate oviposition (Jervis *et al*., 2008; Quicke, 2015; Harvey *et al*., 2020) [9, 15, 27]. This reproductive pattern maximizes population growth potential under favorable thermal conditions, as evidenced by the elevated intrinsic rate of increase ($r = 0.541$ day^{-1}) observed here, which aligns with thermal performance curves reported for congeneric *Trichogramma* species (Karamaouna *et al*., 2010; Furlong & Zalucki., 2017; Sentis *et al*., 2017) [1, 16, 30].

The pronounced decline in both survival (l_x) and fecundity (m_x) at 40°C indicates that extreme heat imposes physiological constraints that accelerate senescence and impair reproductive capacity in *T. evanescens*. These findings are consistent with climate change research demonstrating that thermal extremes disrupt insect life history traits through protein denaturation, oxidative stress, and metabolic imbalance (Colinet *et al*., 2015 [2]; Ma *et al*., 2021; Liu *et al*., 2019) [22]. The truncated reproductive schedule at high temperatures suggests that augmentative releases should avoid periods of extreme heat to ensure parasitoid establishment and effective pest suppression in agricultural ecosystems.

Collectively, these age-specific data provide essential parameters for stage-structured population models that forecast parasitoid phenology relative to pest outbreaks under variable field conditions (Zhang *et al*., 2022; Pincebourde *et al*., 2016; Moore *et al*., 2015) [24, 25, 37]. The thermal optimum of 30–32.5°C identified here should inform release timing strategies for *T. evanescens* in warm agricultural regions, thereby enhancing the efficacy of augmentative biological control programs targeting lepidopteran pests.

Conclusion

Trichogramma evanescens exhibited optimal fitness and parasitism efficiency at 30–32.5°C, with peak reproductive output, survival, and female-biased sex ratios. Temperatures ≥35°C significantly impaired performance. These findings inform climate-adaptive release strategies, ensuring effective augmentative biological control of lepidopteran pests in warming agricultural ecosystems.

References

1. Furlong MJ, & Zalucki MP. Climate change and biological control: the consequences of increasing temperatures on host–parasitoid interactions. Current opinion in insect science,2017:20: 39-44
2. Colinet H, *et al*. Insects in fluctuating thermal environments. Annual Review of Entomology,2015:60:123–140. https://doi.org/10.1146/annurev-ento-010814-021017
3. Deutsch CA, *et al*. Impacts of climate warming on terrestrial ectotherms across latitude. Proceedings of the National Academy of Sciences,2008:105(18):6668–6672. https://doi.org/10.1073/pnas.0709472105
4. Bari MN, Jahan M, Islam KS. Effect of temperature on the life table parameters of *Trichogramma zahiri* (Hymenoptera: Trichogrammatidae), an egg parasitoid of *Dicladispa armigera* (Coleoptera: Chrysomelidae). Environmental Entomology, 2015. 44(2), 368–378.
5. Frazier MR, Huey RB, Berrigan D. Thermodynamics constrains the evolution of insect population growth rates: "Warmer is better." The American Naturalist,2006:168(4):512–520. https://doi.org/10.1086/506977
6. Gurr GM, *et al*. Ecological engineering for pest management: advances in habitat manipulation for arthropods. CSIRO Publishing, 2017. https://doi.org/10.1071/9780643106709
7. Haile AT, *et al*. Temperature-dependent development of four egg parasitoid Trichogramma species (*Hymenoptera*: *Trichogrammatidae*). Biocontrol Science and Technology,2002:12(5):555–567. https://doi.org/10.1080/0958315021000041083
8. Hajek AE, Eilenberg J. Natural Enemies: An Introduction to Biological Control. Cambridge University Press, 2018. https://doi.org/10.1017/9781316162298
9. Harvey JA, *et al*. Climate change effects on insect parasitoids and their hosts. Current Opinion in Insect Science,2020:41:45–51. https://doi.org/10.1016/j.cois.2020.06.003
10. Hoffmann AA, *et al*. Climate change and evolutionary adaptation. Nature, 2013. https://doi.org/10.1038/nature09670
11. Iqbal A, *et al*. Rearing *Trichogramma ostriniae* on the factitious host Antheraea pernyi via multiparasitism with Trichogramma chilonis facilitates enhanced biocontrol potential against Ostrinia furnacalis. Biological Control, 2021, 156. https://doi.org/10.1016/j.biocontrol.2021.104567
12. Reznik, Sergey Ya, Natalia D. Voinovich, and Nina P. Vaghina. Effect of temperature on the reproduction and development of *Trichogramma buesi* (Hymenoptera: Trichogrammatidae). European Journal of Entomology, 2009, 106.4
13. Jamieson MA, *et al*. Global change effects on plant-insect interactions: the role of temperature. Current Opinion in Insect Science, 2012. https://doi.org/10.1016/j.cois.2012.09.005
14. Jeffs CT, Lewis OT. Effects of climate warming on host-parasitoid interactions. Ecological Entomology, 2013. https://doi.org/10.1111/een.12011
15. Jervis MA, *et al*. Life-history strategies in parasitoid wasps: comparative analysis of reproductive allocation. Ecological Entomology,2008:33(1):1–12. https://doi.org/10.1111/j.1365-2311.2007.00945.x
16. Karamaouna F, *et al*. Temperature-dependent development and survival of *Trichogramma cacoeciae*.

BioControl,2010:55(4):501–510. https://doi.org/10.1007/s10526-010-9275-0
17. King BH. Sex ratio manipulation by parasitoid wasps. Evolution and diversity of sex ratio in insects and mites,1993:418–441. https://doi.org/10.1007/978-94-011-1604-6_18
18. Kingsolver JG, *et al*. The pattern and strength of selection on thermal performance. Evolution,2011:65(10):2741–2754. https://doi.org/10.1111/j.1558-5646.2011.01360.x
19. Lessard E, Boivin G. Effect of age and hunger on host-feeding behavior by female *Trichogramma euproctidis* (*Hymenoptera*: *Trichogrammatidae*). The Canadian Entomologist,2013:145(1):53–60. https://doi.org/10.4039/tce.2012.85
20. Liu TX, *et al*. Biological control in China: past, present and future. Annual Review of Entomology, 2015. https://doi.org/10.1146/annurev-ento-010814-020920
21. Liu Y, *et al*. Thermal tolerance and fitness consequences in parasitoid wasps under climate change scenarios. Journal of Applied Ecology,2019:56(3):678–689. https://doi.org/10.1111/1365-2664.13312
22. Ma CS, *et al*. Climate warming and insect pest outbreaks: Mechanisms and management strategies. Annual Review of Entomology,2021:66:379–398. https://doi.org/10.1146/annurev-ento-060120-091648
23. Moore JC, *et al*. Temperature-dependent parasitism and host acceptance in *Trichogramma* wasps. Biological Control,2015:89:1–8. https://doi.org/10.1016/j.biocontrol.2015.05.001
24. Pincebourde S, *et al*. Microclimate buffering and thermal tolerance in insect parasitoids. Functional Ecology,2016:30(5):789–801. https://doi.org/10.1111/1365-2435.12567
25. Polaszek A, *et al*. African *Trichogrammatidae* (*Hymenoptera*): systematics and biology. CABI Publishing, 2004. https://doi.org/10.1079/9780851996981.0000
26. Quicke DLJ. The Braconid and Ichneumonid Parasitoid Wasps: Biology, Systematics, Evolution and Ecology. Wiley-Blackwell, 2015. https://doi.org/10.1002/9781118907085
27. Reznik SY, *et al*. Thermal thresholds and degree-day models for Trichogramma. Entomological Review, 2009. https://doi.org/10.1134/S001387380905001X
28. Schöller M, Hassan SA. Comparative biology and life tables of *Trichogramma evanescens* and *T. cacoeciae* with *Ephestia elutella* as host at four constant temperatures. Entomologia Experimentalis et Applicata,2001:98(1):35–40. https://doi.org/10.1023/A:1018700408113
29. Sentis A, *et al*. Thermal acclimation modulates the impacts of temperature extremes on life history traits and population growth rates. Global Change Biology,2017:23(10):4299–4310. https://doi.org/10.1111/gcb.13713
30. Smith SM. Biological control with Trichogramma: advances, successes, and potential of their use. Annual Review of Entomology,1996:41:375–406. https://doi.org/10.1146/annurev.en.41.010196.002111
31. Tabebordbar F, *et al*. Effect of different constant temperatures on life history and life table parameters of *Trichogramma euproctidis* (*Hymenoptera*: *Trichogrammatidae*). Journal of Economic Entomology,2022:115(3):789–801. https://doi.org/10.1093/jee/toac023
32. Tabone E, *et al*. Quality control of *Trichogramma evanescens*: influence of host species on fitness parameters. BioControl, 2010. https://doi.org/10.1007/s10526-009-9258-9
33. Thomson LJ, *et al*. Predicting the effects of climate change on natural enemies of agricultural pests. Biological Control,2010:52(3):245–251. https://doi.org/10.1016/j.biocontrol.2009.01.022
34. van Lenteren JC, *et al*. Biological control using invertebrates and microorganisms: plenty of new opportunities. BioControl,2018:63(1):39–55. https://doi.org/10.1007/s10526-017-9801-4
35. Wang ZY, *et al*. Mass rearing and release of Trichogramma for biological control of insect pests in China. Biological Control,2016:93:34–44. https://doi.org/10.1016/j.biocontrol.2015.04.009
36. Zhang W, *et al*. Age-specific mortality and reproduction in egg parasitoids: implications for biological control. Ecological Entomology,2022:47(2):234–245. https://doi.org/10.1111/een.13089