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## Biological and Microbial Control

# Effect of Different Constant Temperatures on Life History and Life Table Parameters of *Trichogramma euproctidis* (Hymenoptera: Trichogrammatidae)

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### Abstract

Temperature has a profound effect on performance and behavior of egg parasitoids. Egg parasitoids are a well-known alternative for the control of lepidopterous pests. Selected life history parameters of *Trichogramma euproctidis* (Girault) (Hymenoptera: Trichogrammatidae), an established egg parasitoid species in Khuzestan-Southwest Iran, were appraised at eight constant temperatures (22.5, 25, 27.5, 30, 32.5, 35, 37.5, and 40°C) using *Ephesttia kuehniella* Zeller (Lepidoptera: Pyralidae) eggs as the host. We found significant effects of temperature on the number of parasitized eggs, development time, sex ratio, progeny's longevity, and fecundity. *T. euproctidis* developed on *E. kuehniella* eggs at all temperatures tested, but performed best at 32.5°C. At this temperature, they parasitized the most eggs, produced the most female progeny, and had high rates of survival. Our findings revealed that temperature significantly affected the longevity of female progeny and fecundity of *T. euproctidis*. A life table analysis confirmed that temperature resulted in optimal effects on *T. euproctidis* life history. Net reproductive rate ( $R_0$ ) of *T. euproctidis* was different among the temperatures tested. The intrinsic rate of increase ( $r$ ) was positively correlated with temperature from 22.5 to 32.5°C and then decreased from 35 to 40°C. Generation time ( $T$ ) and doubling time ( $DT$ ) decreased as temperature increased from 22.5 to 37.5°C and then increased at 40°C. These data suggest that this strain of *T. euproctidis* is adapted to high temperatures and harsh environmental conditions and has the potential to be used in integrated management programs in Southwest Iran.

**Key words:** egg parasitoid, temperature, development, life table parameter, IPM

Among the different egg parasitoids used as biological control agents, *Trichogramma* wasps are common natural enemies found around the world (Smith 1996, Mills 2010, van Lenteren and Bueno 2003). It is important to select species and strains that are adapted to local environmental conditions to maximize the control of important Lepidopterous pests attacking agricultural crops (Li 1994, Greenberg et al. 1996, van Lenteren 2000). The augmentative release of Trichogrammatid parasitoids can be an effective means of pest suppression. They are used in more than 30 countries including China, Switzerland, Canada, and France, and can reduce pest

damage by as much as 77–92% in crops like sugarcane, wheat, cabbage, and maize (Li 1994).

In recent years, native (or indigenous) *Trichogramma* species are often deployed because they are more adapted to local climatic conditions (Hassan 1994, Hegazi et al. 2012, Wu et al. 2018) and the lack of safety concerns with respect to parasitism of non-pest lepidopterans in landscapes adjacent to agricultural fields (van Lenteren et al. 2003). In Khuzestan (southwestern Iran), farmers grow many crops including sugarcane, maize, tomato, vegetables, and date palm. In each crop, there are several Lepidopteran pests that cause significant economic damage including *Helicoverpa armigera*

(Hübner) (Lepidoptera: Noctuidae), *Tuta absoluta* (Meyrick), and *Autographa gamma* (Linnaeus) (Lepidoptera: Noctuidae). Additionally, there are numerous natural enemies that attack these pests. *Trichogramma euproctidis* (Girault) (Hymenoptera: Trichogrammatidae) (previously identified as *Trichogramma turkestanica* Meyer (Hymenoptera: Trichogrammatidae)) (Sumer et al. 2009) is a native parasitoid that is commonly found in Iran (Modarres Awal 2011) and in other countries like Egypt, Turkey, and Canada (Ferracini et al. 2006, Consoli et al. 2010, Tuncbilek et al. 2012, Hegazi et al. 2019). This species is common in maize fields and date palm orchards in Khuzestan (Tabebordbar unpublished data) and it is mass-reared and used for biological control of a variety of Lepidopterous pests (e.g. *Chilo suppressalis* (Walker) (Lepidoptera: Crambidae), *Tu. absoluta*, *Plodia interpunctella* (Hübner) (Lepidoptera: Pyralidae) and *Cadra cautella* (Walker) (Lepidoptera: Pyralidae)) (Li 1994, Chailleux et al. 2012).

To generate large quantities of individuals for augmentative releases, a mass production system is a prerequisite. Perhaps, *T. euproctidis* could be mass-produced from well-established lepidopteran hosts, i.e., *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) eggs. *Ephestia kuehniella* eggs have been used to mass-produce several commercially available *Trichogramma* species for several decades (Smith 1996). For example, *E. kuehniella* has been used as a factitious host for mass rearing *Trichogramma evanescens* Westwood (Hymenoptera: Trichogrammatidae) and *Trichogramma brassicae* Bezdenko (Hymenoptera: Trichogrammatidae), two closely related species found in Iran (Ebrahimi et al. 1998, Tabebordbar et al. 2020). Because of its larger egg size, *E. kuehniella* rather than *Sitotroga cerealella* (Olivier) (Lepidoptera: Gelechiidae) is preferred as a rearing host (Smith 1996). Larger-sized host eggs contain more nutrients, e.g., egg yolk, to support *Trichogramma* development (Schmidt 1994, Smith 1996) and can yield larger-sized and potentially more fecund *Trichogramma* females (Greenberg et al. 1996, Iqbal et al. 2021). Besides host egg size, the efficacy of biological control agents like *Trichogramma* wasps can be affected by factors such as host age, host species, temperature, humidity, and photoperiod (Noldus 1989, Pratisoli and Parra 2001, Amalin et al. 2005, Pizzol et al. 2012, Tabebordbar et al. 2020).

Temperature is an important environmental factor that influences the biology, survivorship, and demographic parameters of these parasitoids (Messenger 1970, Frazier et al. 2006, Moezipour et al. 2008, Iranipour et al. 2009). Khuzestan has a very hot and dry climate ( $\approx 45^{\circ}\text{C}$ ) from May to late September, and temperatures can even exceed  $48^{\circ}\text{C}$  for short periods of time during the day in the summer. Temperature is the most important limitation in Khuzestan province, and this abiotic condition may affect the activity of *Trichogramma* parasitoids and consequently the efficiency of augmentative releases.

Some of the life history characteristics of *T. euproctidis* have been studied previously (e.g., Silva and Stouthamer 1999, Scholler and Hassan 2001, Haile et al. 2002, Hansen and Jensen 2002, Tuncbilek et al. 2012). Additionally, it has been shown that different strains (also termed races or ecotypes) of *Trichogramma* species that originate from different regions can differ in biological traits that affect their success (Pavlik 1993, Ram et al. 1995, Smith 1996). No information is accessible regarding the biological efficiency of *T. euproctidis* at high temperatures. In order to find a candidate biocontrol agent suitable to be used under these very difficult environmental conditions, we appraised the effect of constant high temperatures on the Iranian strain of *T. euproctidis* collected from a crop-growing area of Khuzestan, and measured immature development, survival, adult longevity and reproduction. This study is important because it defines the temperature range for mass production

of *T. euproctidis* of high quality for augmentation biological control targeting economic pests in crop fields.

## Materials and Methods

### Insect Collection and Rearing

An indigenous colony of *T. euproctidis* was created from parasitoid wasps that were originally collected from a maize field using sentinel *E. kuehniella* eggs during December 2017 in Ahvaz city, Khuzestan province ( $31^{\circ}18'25.3''\text{N}$   $48^{\circ}39'36.1''\text{E}$ ). In this study, we used the "Tricho card" method to collect *Trichogramma* wasps. To prepare Tricho cards, we glued masses of UV-sterilized *E. kuehniella* eggs onto  $3\text{ cm} \times 6\text{ cm}$  cards of paper, which we then hung in maize fields. The *E. kuehniella* eggs used in this study were obtained from Golestan Mooud insectary, Ahvaz, Iran. After 48 h, the Tricho cards were collected and stored in laboratory cabinets at  $25 \pm 1^{\circ}\text{C}$ ,  $55 \pm 5\%$  RH, and a photoperiod of 16:8 h (L:D). We monitored the cards for 3 d. Parasitized eggs were distinguished by their black color. In the laboratory, each card was individually transferred to shell vials (10 cm height and 1 cm diameter) with 50 *E. kuehniella* eggs ( $< 24$  h old) and were sealed with mesh netting. Vials were kept in laboratory cabinets set at the temperature mentioned above. Emerged adults were provided a streak of honey that was smeared in the internal part of the vials. Newly emerged parasitoids (10 ♀ + 10 ♂) were introduced to shell vials (20 cm height and 2 cm diameter) containing a card ( $10\text{ cm} \times 1\text{ cm}$ ) with sufficient number ( $500 \pm 10$ ) of host eggs (*E. kuehniella*). They were reared at last five to six generations prior to setting up the experiments. New emergence Microscope slides for identifying wasp species were prepared according to Platner et al. (1999) and adults were identified with morphological characteristic described in Pintureau (2008). Voucher specimens have been placed in the collection of Shahid Chamran University of Ahvaz, Ahvaz, Iran and the Natural History Museum, London, UK.

### Experimental Procedure

#### Part 1: Biology

The biological characters of *T. euproctidis* were determined at  $22.5, 25, 27.5, 30, 32.5, 35, 37.5,$  and  $40 \pm 0.5^{\circ}\text{C}$  in temperature-controlled cabinets. In the beginning of the experiment, at least 50 pairs (one male and one female) of parasitoids were reared for one generation at each of the above-mentioned temperatures in order to adapt them to that temperature. A single mated female *T. euproctidis* (24 hours), was placed into a vial ( $10\text{ cm} \times 1\text{ cm}$ ) containing  $50 \pm 1$  one-day old of *E. kuehniella* eggs (sterilized with UV light) sprinkled on paper ( $5\text{ cm} \times 1\text{ cm}$ ). The vials were sealed with mesh net. The vials were kept in the cabinets set at the temperatures mentioned above. After 24 hours, parasitoids were removed from their vials using a thin brush and the eggs were maintained at each temperature. Parasitized eggs were followed every day and we recorded the date of adult parasitoid progeny emergence. Each temperature was replicated nine times and the number of parasitized eggs (black eggs), preadult developmental times (female and male), survival rate, and sex ratio (female %) of *T. euproctidis* were recorded.

#### Part 2: Life Table Parameters

To evaluate the life table parameters of *T. euproctidis* females at different temperatures, 40 newly emerged ( $< 24$  h old), mated female parasitoids (obtained from above experiment) were placed individually into vials containing  $50 \pm 1$  one-day old sterilized *E. kuehniella* eggs, and a streak of honey. Every 24 h, egg masses were changed until last female parasitoid died. The vials containing egg papers were kept in cabinets at the temperatures mentioned above. Those

females that were injured during daily handling or those that died because of getting stuck in honey droplets were excluded from data analysis. Longevity and fecundity of female progeny were recorded for each temperature.

### Statistical Analysis

The number of parasitized eggs, preadult developmental time, survival rate, sex ratio, longevity, daily fecundity, and total fecundity of progeny were examined using ANOVA (SAS Institute 2002). Survival rate and sex ratio data were arcsine-transformed before analysis. Means were compared using Tukey's test ( $P < 0.05$ ).

We used linear regression to estimate the lower threshold temperature for development. The number of degree-days (DD) required for development was calculated as:  $DD = Y(T - t)$ , where  $Y$ : is the developmental time (days),  $T$ : is the temperature during development (experimental constant temperature), and  $t$ : is the lower developmental threshold (Arnold 1959).

Life table parameters were estimated by combining data from the preimaginal development and adult survival and reproduction experiment of different treatments. The intrinsic rates of population increase were estimated by iteratively solving the Birch (1948) equation:  $\sum e^{-r_x} l_x m_x = 1$ . Where  $x$  is the mean age class,  $m_x$  is the mean number of female progeny per female of age  $x$ , and  $l_x$  is the probability of survival to age  $x$ . A trial number of values for  $r$  were substituted into the equation until the  $r$  value for which the sum on the left side of the equation approximates unity. The Jackknife procedure was used to estimate an SE for the  $r$  values of different treatments (Maia et al. 2000). Further data were also calculated for each treatment: net reproductive rate ( $R_0 = \sum l_x m_x$ , number of female offspring produced per female), mean generation time ( $T = \ln R_0 / r$ ), doubling time ( $DT = \ln 2 / r$ , number of days required for the population to double in numbers), and finite rate of increase ( $\lambda = e^r$ ), number of times the population will multiply itself per unit of time (Birch 1948). Standard error of the population growth parameters was calculated using the bootstrap technique and multiple comparisons were possible using the paired bootstrap test with 100,000 samples (Maia et al. 2000).

## Results

### Number of Parasitized Eggs

The mean number of *E. kuehniella* eggs parasitized by *T. euproctidis* was significantly influenced by temperature ( $F = 120.86$ ;  $df = 7, 64$ ;  $P < 0.0001$ ). We observed that as temperature increased from 22.5 to

32.5°C, the mean number of parasitized eggs by *T. euproctidis* also increased from 25.85 to 44.85. At higher temperatures (i.e. 40°C) the number of parasitized eggs decreased to 26.14 eggs (Table 1).

### Preadult Developmental Time

Analysis variance revealed that temperature significantly affected the development time of immature *T. euproctidis* (females,  $F = 642.15$ ;  $df = 7, 312$ ;  $P < 0.0001$ ; and males,  $F = 817.42$ ;  $df = 7, 312$ ;  $P < 0.0001$ ). Development times decreased as temperature increased, and were shortest at 35–37.5°C. Development times then increased again as temperatures were raised to 40°C (Table 1).

### Emergence Rate

We found a significant effect of temperature on the rates of emergence (survival) of *T. euproctidis* from parasitized eggs ( $F = 242.97$ ;  $df = 7, 64$ ;  $P < 0.0001$ ). The emergence rate varied from 49.64% for parasitoids reared at 22.5°C to 93.06% for animals reared at 32.5°C. Survivorship also increased with temperature, peaking at 32.5°C, and then declined as temperatures increased towards 40°C (Table 1).

### Sex Ratio (Female %)

We observed significant differences in the sex ratio (percentage of females) of emerged wasps among the temperatures tested ( $F = 137.64$ ;  $df = 7, 64$ ;  $P < 0.0001$ ). The percentage of females increased as temperature increased from 22.5 to 32.5°C, where it peaked at 84%, and then decreased at higher temperatures (Table 1).

### Temperature Threshold

The lower threshold temperature ( $t$ ) and thermal constant ( $DD$ ) for the development of *T. euproctidis* parasitizing *E. kuehniella* eggs at eight constant temperatures are given in Table 2. The lower temperature thresholds for the development from egg to adult female and male *T. euproctidis* were 8.23 and 11.23, respectively. According to these thresholds for female and male *T. euproctidis*, an average of 171.48 and 110.17 day-degrees are required to complete development from egg to adults.

### Longevity of Female Progeny (F1 Generation)

Temperature significantly affected the longevity of female progeny of *T. euproctidis* ( $F = 361.44$ ;  $df = 7, 312$ ;  $P < 0.0001$ ). We observed an inverse relationship between the longevity of female progeny and temperature; as temperatures increased, longevity decreased (Table 3).

**Table 1.** Mean  $\pm$  SE number of parasitised eggs, parasitoid developmental time (days), emergence rate, and sex ratio (percentage of females) of *Trichogramma euproctidis* parasitizing *Ephestia kuehniella* eggs at different constant temperatures

Temperature (°C)	Mean of parasitized eggs	Preadult development time (Female)	Preadult development time (Male)	emergence rate	Sex ratio (% female)
22.5	25.85 $\pm$ 0.04 <sup>e</sup>	13.81 $\pm$ 0.16 <sup>a</sup>	11.68 $\pm$ 0.17 <sup>a</sup>	49.64 $\pm$ 0.12 <sup>e</sup>	32.10 $\pm$ 0.10 <sup>f</sup>
25	32.42 $\pm$ 0.20 <sup>d</sup>	10.00 $\pm$ 0.10 <sup>b</sup>	7.74 $\pm$ 0.11 <sup>b</sup>	81.18 $\pm$ 0.25 <sup>b</sup>	54.39 $\pm$ 0.15 <sup>d</sup>
27.5	35.85 $\pm$ 0.05 <sup>c</sup>	8.28 $\pm$ 0.12 <sup>c</sup>	6.40 $\pm$ 0.11 <sup>c</sup>	73.94 $\pm$ 0.15 <sup>c</sup>	64.57 $\pm$ 0.10 <sup>e</sup>
30	38.42 $\pm$ 0.20 <sup>b</sup>	7.17 $\pm$ 0.10 <sup>d</sup>	5.42 $\pm$ 0.10 <sup>d</sup>	90.01 $\pm$ 0.20 <sup>a</sup>	75.41 $\pm$ 0.12 <sup>b</sup>
32.5	44.85 $\pm$ 0.04 <sup>a</sup>	7.02 $\pm$ 0.06 <sup>d</sup>	4.91 $\pm$ 0.09 <sup>d</sup>	93.06 $\pm$ 0.31 <sup>a</sup>	84.11 $\pm$ 0.11 <sup>a</sup>
35	31.85 $\pm$ 0.20 <sup>d</sup>	6.42 $\pm$ 0.16 <sup>e</sup>	4.68 $\pm$ 0.07 <sup>de</sup>	72.54 $\pm$ 0.12 <sup>c</sup>	48.57 $\pm$ 0.19 <sup>e</sup>
37.5	30.28 $\pm$ 0.09 <sup>d</sup>	6.04 $\pm$ 0.13 <sup>e</sup>	4.37 $\pm$ 0.07 <sup>e</sup>	67.74 $\pm$ 0.19 <sup>d</sup>	47.59 $\pm$ 0.10 <sup>e</sup>
40	26.14 $\pm$ 0.03 <sup>e</sup>		11.32 $\pm$ 0.12 <sup>a</sup>	53.26 $\pm$ 0.13 <sup>c</sup>	35.23 $\pm$ 0.23 <sup>f</sup>

Means in each column followed in the same letter are not significantly different at  $P < 0.05$  (Tukey's test)

### Fecundity of Female Progeny (F1 Generation)

Temperature had a significant effect on the mean daily ( $F = 514.82$ ;  $df = 7, 312$ ;  $P < 0.0001$ ) and total ( $F = 821.46$ ;  $df = 7, 312$ ;  $P < 0.0001$ ) number of eggs laid by the *T. euproctidis* progeny. Across all of the temperatures we examined, the highest and lowest progeny's fecundity was at 32.5°C (121.40 eggs) and 40°C (14.17), respectively.

### Life Table Parameters

Life table parameters of *T. euproctidis* at the different temperatures are presented in Table 4. Analysis of variance revealed that different temperatures significantly affected  $R_0$ ,  $r$ ,  $\lambda$ ,  $T$ , and  $DT$ . Both the net reproductive rate ( $R_0$ ) and intrinsic rate of natural increase ( $r$ ) reached their peaks at 32.5°C and decreased at higher temperatures.

**Table 2.** The lower threshold temperature (t) and thermal constant (DD) for development of *Trichogramma euproctidis* parasitizing *Ephesthia kuehniella* eggs at different constant temperatures

Sex	Parameters			
	Temperature threshold	R <sup>2</sup>	DD ± SE	Regression
Female	8.23	0.943	171	Y = 0.0059x - 0.0486
Male	11.23	0.951	110	Y = 0.0092x - 0.1034

**Table 3.** Mean (± SE) longevity (days), daily fecundity and total fecundity of *Trichogramma euproctidis* female reared on *Ephesthia kuehniella* eggs at different constant temperature

Temperature (°C)	Longevity	Daily fecundity (egg/ days)	Total fecundity (eggs/female)
22.5	12.74 ± 0.19 <sup>a</sup>	6.36 ± 0.15 <sup>f</sup>	50.27 ± 1.16 <sup>f</sup>
25	9.88 ± 0.07 <sup>b</sup>	10.33 ± 0.26 <sup>d</sup>	78.94 ± 1.34 <sup>d</sup>
27.5	9.40 ± 0.09 <sup>bc</sup>	12.15 ± 0.14 <sup>c</sup>	93.97 ± 1.19 <sup>c</sup>
30	8.66 ± 0.05 <sup>c</sup>	14.38 ± 0.20 <sup>b</sup>	108.34 ± 1.80 <sup>b</sup>
32.5	7.68 ± 0.09 <sup>d</sup>	17.20 ± 0.30 <sup>a</sup>	121.40 ± 1.02 <sup>a</sup>
35	7.42 ± 0.04 <sup>de</sup>	9.64 ± 0.09 <sup>d</sup>	58.28 ± 0.38 <sup>e</sup>
37.5	6.85 ± 0.03 <sup>e</sup>	8.65 ± 0.13 <sup>c</sup>	51.68 ± 0.57 <sup>f</sup>
40	5.74 ± 0.03 <sup>f</sup>	3.62 ± 0.13 <sup>e</sup>	14.71 ± 0.16 <sup>e</sup>

Means in each column followed by the same letter are not significantly different at  $P < 0.05$  (Tukey test)

**Table 4.** Life table parameters of *Trichogramma euproctidis* reared on *Ephesthia kuehniella* eggs at different constant temperatures

Temperature (°C)	R <sub>0</sub> (offspring)	r (days <sup>-1</sup> )	λ (days <sup>-1</sup> )	T (days)	DT (days)
22.5	4.75 ± 0.34 <sup>e</sup>	0.108 ± 0.006 <sup>f</sup>	1.11 ± 0.07 <sup>f</sup>	14.34 ± 0.19 <sup>a</sup>	6.34 ± 0.40 <sup>b</sup>
25	30.12 ± 0.51 <sup>d</sup>	0.394 ± 0.002 <sup>c</sup>	1.48 ± 0.01 <sup>c</sup>	11.21 ± 0.07 <sup>c</sup>	1.75 ± 0.01 <sup>c</sup>
27.5	48.15 ± 0.73 <sup>c</sup>	0.403 ± 0.010 <sup>c</sup>	1.49 ± 0.01 <sup>c</sup>	9.59 ± 0.26 <sup>d</sup>	1.71 ± 0.01 <sup>c</sup>
30	73.13 ± 1.21 <sup>b</sup>	0.492 ± 0.004 <sup>b</sup>	1.63 ± 0.07 <sup>b</sup>	8.71 ± 0.06 <sup>e</sup>	1.40 ± 0.01 <sup>c</sup>
32.5	94.08 ± 1.38 <sup>a</sup>	0.532 ± 0.005 <sup>a</sup>	1.70 ± 0.03 <sup>a</sup>	8.54 ± 0.08 <sup>e</sup>	1.30 ± 0.01 <sup>c</sup>
35	20.42 ± 0.13 <sup>e</sup>	0.303 ± 0.004 <sup>d</sup>	1.35 ± 0.06 <sup>d</sup>	8.39 ± 0.09 <sup>e</sup>	2.28 ± 0.02 <sup>d</sup>
37.5	12.15 ± 0.28 <sup>f</sup>	0.297 ± 0.007 <sup>d</sup>	1.34 ± 0.01 <sup>e</sup>	7.65 ± 0.15 <sup>f</sup>	2.33 ± 0.05 <sup>d</sup>
40	1.89 ± 0.07 <sup>h</sup>	0.048 ± 0.003 <sup>e</sup>	1.05 ± 0.00 <sup>e</sup>	13.08 ± 0.06 <sup>b</sup>	14.10 ± 0.93 <sup>a</sup>

Means in each column followed by the same letter are not significantly different at  $P < 0.05$  (Tukey test) (Note: Net reproductive rate ( $R_0$ ), intrinsic rate of increase ( $r$ ), finite rate of increase ( $\lambda$ ), generation time ( $T$ ) and doubling time ( $DT$ )).

Age-specific survival ( $l_x$ ) and fecundity ( $m_x$ ) at each temperature are illustrated in Fig. 1.

### Discussion

Our experiments demonstrate a large effect of temperature on every life history parameters of *T. euproctidis* that we investigated. This is not much published literature regarding the life history traits of *T. euproctidis*. Because *T. euproctidis* and *T. evanescens* are closely related species to the *evanescens* group (Sumer et al. 2009), comparison in the current study be made to *T. evanescens*.

Temperature had a significant effect on the mean number of *E. kuehniella* eggs parasitized by *T. euproctidis*. Scholler and Hassan (2001) reported that at 20, 26, 30, and 35°C *T. evanescens* parasitized mean numbers of 65.7, 53.7, 62.2, and 31.9 *Ephesthia elutella* (Hubner) (Lepidopteazra: Pyralidae) eggs, respectively, which are higher than the results observed in our study. Haile et al. (2002) also founded that at 13, 18, 25, and 34°C *T. evanescens* parasitized a mean of 18.12, 21.97, 50.37, and 12.82 *S. cerealella* eggs, respectively, which are different from our findings. These contrasts may be explained by disparities in *Trichogramma* species (strain or possible species misidentification), host species, and the differences in experimental conditions (temperature, humidity, and photoperiod).

Our finding revealed that at 22.5 and 40°C, the length of preadult development time of *T. euproctidis* took longer than at other temperatures. Also, there was inverse relationship between temperature and the length of preadult developmental time. With increasing temperature from 22.5 to 37.5°C, preadult developmental time of female *T. euproctidis* was reduced from 13.81 to 6.04 d. The current results are in line with the studies on other *Trichogramma* species (Park et al. 2000, Haile et al. 2002, Pratisoli et al. 2005, Melo et al. 2007). Reynolds and Nottingham (1985) suggested that increased the length of developmental time at lower temperatures is due to reduction in metabolic rates, which reduced the rate of conversion of nutrients to energy needed for development.

Our result revealed that the optimum temperature for emergence (survival) of *T. euproctidis* was 32.5°C (90%), and these values are similar to other *Trichogramma* species as reported by Scholler and Hassan 2001, Haile et al. 2002, El-Wakeil 2007 (*T. evanescens*), Bari et al. 2015 (*Trichogramma zabiri* Polaszek (Hymenoptera: Trichogrammatidae)) and Carvelho et al. 2017 (*Trichogramma pretiosum* Riley (Hymenoptera: Trichogrammatidae)). Lessard and Boivin (2013) claimed that suboptimal temperature causes decreased energy, metabolic dysfunction, and mortality in immature stages and consequently had negative effect on the emergence rates of *Trichogramma* wasps.



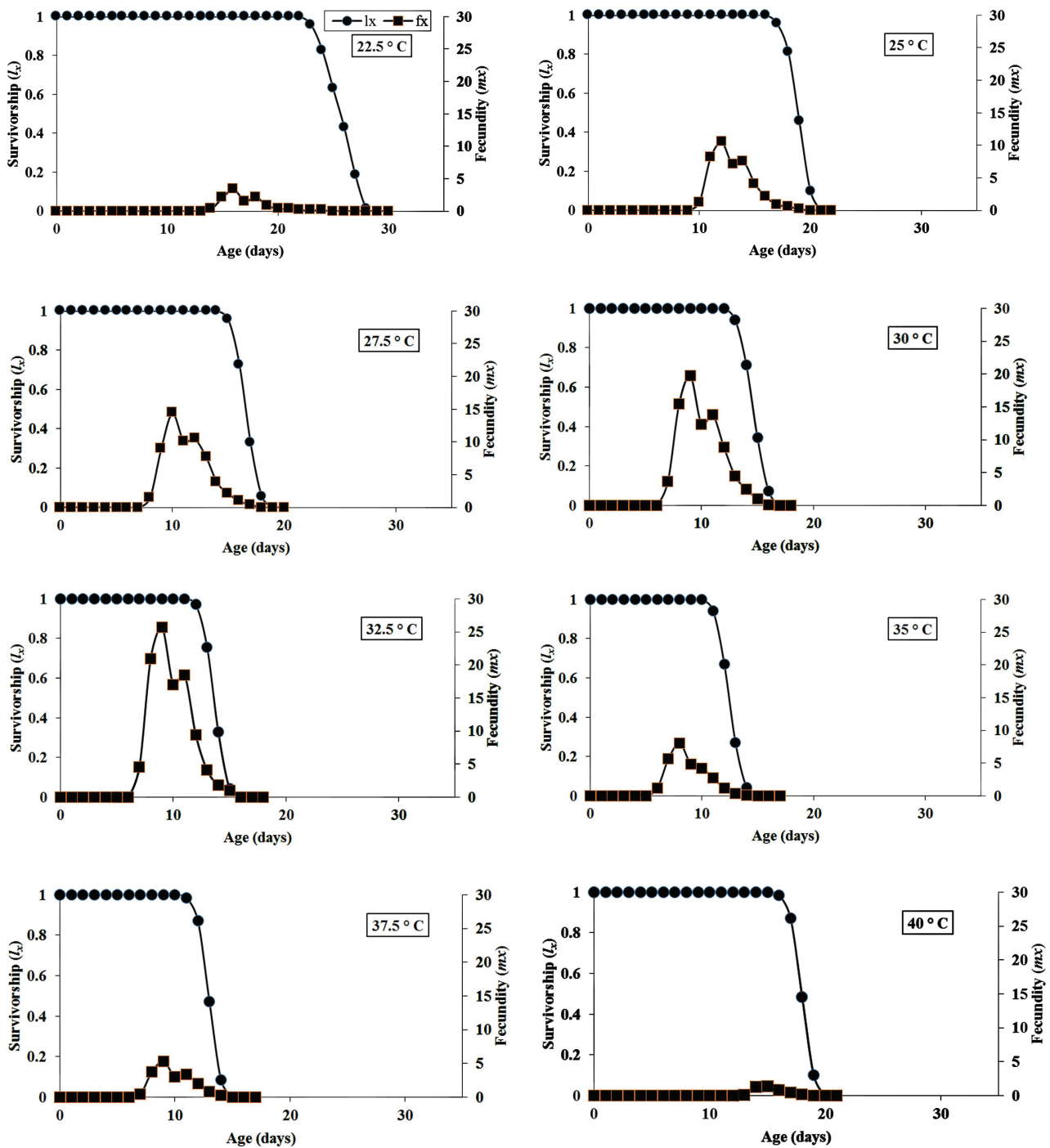


Fig. 1. Survivorship ( $l_x$ ) and Fecundity ( $m_x$ ) of *Trichogramma euproctidis* reared on *Ephestia kuehniella* eggs at different constant temperatures.

In the present study, the sex ratio of *T. euproctidis* was biased for females at 25–32.5°C. Our data are similar with studies of Hansen and Jensen (2002) who reported 61, 59, 70, and 70% females for *T. euproctidis* on the same host eggs at 15, 20, 25, and 30°C, respectively. Scholler and Hassan (2001) also reported a sex ratio of *T. evanescens* on *E. elutella* to be 60, 62, 60, and 70% female at 20, 26, 30, and 35°C, respectively. Similarly, Haile et al. (2002) found sex ratio of *T. evanescens* on *S. cerealella* as 61, 50, 53, and 60% female at 13, 18, 25, and 34°C, respectively. El-Wakil (2007) evaluated the sex ratio of *T. evanescens* on different factitious hosts (*S. cerealella*, *E. kuehniella*, and *Galleria mellonella* (Linnaeus)

(Lepidoptera: Pyralidae) to control *H. armigera*). His results showed female-biased sex ratio for *T. evanescens* for all four species of host eggs examined, ranging from 63 to 74% females. Also, our finding indicated that at low and high temperatures, the ratio of males emerged was higher than females. Similarly, our results have been estimated for *T. pretiosum* and *Trichogramma exiguum* Pinto and Planter (Hymenoptera: Trichogrammatidae) (Harrison et al. 1985). Lauge (1985) claimed that at low and high temperatures, unfavorable environmental conditions (e.g., extreme temperatures, food shortage) and adverse rearing situations can cause shift in sex ratio toward males.

The lower temperature threshold for development of female *T. euproctidis* measured in the present study was 8.23°C, which is close to 9.23°C estimated by Haile et al. (2002) for female *T. evanescens* on *S. cerealella*. However, higher threshold temperatures have been calculated for other *Trichogramma* species e.g. 10–15°C for *T. pretiosum* and *T. exiguum* (Harrison et al. 1985) and 13.6°C for *Trichogramma galloi* Zucchi (Hymenoptera: Trichogrammatidae) (Consoli and Parra 1995).

Our experiments revealed that the longevity of female progeny was also affected by temperature. The present value in longevity of female progeny at 25°C (9.88 d) was similar with estimated with Hansen and Jensen (2002) (8.9 d). However, the longevity of female progeny measured in our study was different from the reported on *T. evanescens* at the same host eggs (*E. kuehniella*) by Ozdar and Kara (2010) (16.94 d). These differences showed that the environmental factor and species of parasitoid are important factors that affect the longevity of female progeny.

We observed that the progeny's fecundity was at highest at 32.5°C (121.40 *E. kuehniella* eggs parasitized by *T. euproctidis*), which is higher than reported by Lund (1938) (17–25 eggs by *T. evanescens* on *S. cerealella* eggs at 25°C), Ram et al. (1995) (17–25 eggs by *T. evanescens* on *S. cerealella* at 27°C), Hansen and Jensen (2002) (82.1 eggs by *T. euproctidis* on *E. kuehniella* at 27°C), Haile et al. (2002) (50.37 eggs by *T. evanescens* on *S. cerealella* at 25°C) and Ozdar and Kara (2010) (87.62 eggs by *T. evanescens* on *E. kuehniella* at 30°C). At all temperatures tested, *T. euproctidis* laid approximately twice the number of eggs in the first 48 h. In fact, some Trichogrammatid species are pro-ovigenic because they emerge as adults with a full or nearly full complement of mature eggs ready for oviposition into suitable hosts; others are synovigenic and emerge with very few mature eggs in ovaries (Jervis et al. 2001). In the presence of an abundance of hosts, recently emerged females could express their potential fecundity in a few days. Thus, understanding the ovarian dynamics of *Trichogramma* females could help explain why some species parasitize more host eggs early in adult life.

All of the temperatures tested have been showed to have a strong effect on the life table parameters of *T. euproctidis*, which is supported by the finding for other *Trichogramma* species (Kalyebi et al. 2006, Bari et al. 2015). The highest intrinsic rate of increase ( $r$ ) value from the present study were calculated at 30°C to 32.5°C, which is consistent with the values reported for *T. evanescens* (Scholler and Hassan 2001) and *T. zahirii* (Bari et al. 2015). The net reproductive rate ( $R_0$ ) changed with temperature variation and decreased at high temperatures. This result was similar to what was reported by Cabello and Vargas (1988) and Pratisoli and Parra (2000). Higher preadult mortality, male production, lower fecundity, and shorter adult longevity are evidence for reduce  $r$  and  $R_0$  at high temperatures in current study.

The findings of the present study indicated that 30–32.5°C is the optimal temperature for development and reproduction of *T. euproctidis*. Similar to our results, optimal developmental temperature near 31°C has been reported for *T. pretiosum* (Butler and Lopez 1980, Calvin et al. 1984) and *Trichogramma bactrae* Nagaraja (Hymenoptera: Trichogrammatidae) (Hutchison et al. 1990, Naranjo 1993). However, an optimal temperature of approximately 25°C has been published for *Trichogramma brevicapillum* Pinto & Planter (Hymenoptera: Trichogrammatidae) (Pak and Oatman 1982), *Trichogramma cordubensis* Vargas & Cabello (Hymenoptera: Trichogrammatidae) (Cabello and Vargas 1988), *Trichogramma ostriniae* Pang et Chen (Hymenoptera: Trichogrammatidae) (Gou 1988), and *Trichogramma cacoeciae* Marchal (Hymenoptera: Trichogrammatidae) (Scholler and Hassan 2001).

In conclusion, our experiments were conducted at broad range of constant temperatures, some of which are typical of a growing season in the southwestern province of Iran. Our results on the number of parasitized eggs, developmental time, emergence rate, sex ratio, and fecundity revealed that this strain of *T. euproctidis*, along with other notable egg parasitoids in Iran, e.g. *T. brassicae* and *T. evanescens*, is adapted to a harsh and hot environment. We found that temperatures ranging from 30 to 32.5°C are optimal for development, survival, and fecundity of this strain of *T. euproctidis*, and it is at these temperatures that we expect it to have the highest efficiency. As temperatures increased from a constant 35 to 40°C, this strain of *T. euproctidis* was able to complete preadult development, but the percentage of females, survival, and fecundity were greatly reduced. Parasitoid performance was reduced at constant temperatures >35°C. However, temperatures in the field are variable throughout the day and night, and we would not expect parasitoids to have to develop under such harsh conditions as constant 35°C. It is unclear what effect host eggs exposed to high temperatures might have on the success of *T. euproctidis*. Our experiments used a thermal maximum of 40°C, and temperatures in southwest Iran can reach as high as 48°C for short periods of time at midday. Presumably, the pests in this region are locally adapted to short bouts of high heat and can withstand it, although additional research is needed to verify that host eggs exposed to high heat are suitable for parasitoid development. Future studies should be focused to the efficacy of this parasitoid outside of laboratory conditions and in semi-field and natural conditions where temperatures will be variable throughout the day, unlike our tests in the laboratory conducted at constant temperatures. Finally, our findings are useful in that they can help predict the correct time of year for release programs, when to appraise the biological efficiency of the parasitoid during growing season, and will provide important information for developing of this strain in mass production and IPM programs.

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## References Cited

- Amalin, D. M., J. E. Pena, and R. E. Duncan. 2005. Effects of host age, female parasitoid age, and host plant on parasitism of *Ceratogramma etiennei* (Hymenoptera: Trichogrammatidae). Fla. Entomol. 88: 77–82.
- Arnold, C. Y. 1959. The determination and significance of the base temperature in a linear heat unit system. Proc. A. Soc. of Hort. Sci. 74: 430–445.
- Bari, M. N., M. Jahan, and K. S. Islam. 2015. Effect of temperature on the life table parameters of *Trichogramma zahirii* (Hymenoptera: Trichogrammatidae), an egg parasitoid of *Di cladispa armigera* (Chrysomelidae: Coleoptera). Environ. Entomol. 44: 368–378.
- Birch, L. C. 1948. The intrinsic rate of natural increase of an insect population. J. Anim. Ecol. 17: 15–26.
- Butler, G. D. Jr., and J. D. Lopez. 1980. *Trichogramma pretiosum*: development in two hosts in relation to constant and fluctuating temperatures. Ann. Entomol. Soc. Am. 73: 671–673.
- Cabello, T., and P. Vargas. 1988. Resistance to high temperatures in the developmental stages of *Trichogramma cordubensis* Vargas and Cabello and *T. pinto* Voegelé (Hymenoptera: Trichogrammatidae). Bol. San. Veg. Plagas. 15: 263–266.
- Calvin, D. D., M. C. Knap, S. M. Welch, F. L. Poston, and R. J. Elzinga. 1984. Impact of environmental factors on *Trichogramma pretiosum* reared on southwestern corn borer egg. Environ. Entomol. 13: 774–780.

- Carvalho, G. D., L. B. Silva, S. S. Reis, M. S. Veras, E. Carneiro, M. L. D. Almedia, A. F. D. Silva, and G. N. Lopes. 2017. Biological parameters and thermal requirements of *Trichogramma pretiosum* reared on *Helicoverpa armigera* eggs. *Pesqu. Agropec. Bras. Brasilia*. 52: 961–968.
- Chailloux, A., N. Desneux, J. Seguret, H. Do Thi Khanh, P. Maignet, and E. Tabone. 2012. Assessing European egg parasitoids as a mean of controlling the invasive South American tomato pinworm *Tuta absoluta*. *Plos One*. 7: e48068.
- Consoli, F. L., and J. R. P. Parra. 1995. Effect of constant and alternative temperatures on *Trichogramma galloi* Zucchi (Hym.: Trichogrammatidae) biology I. Development and thermal requirements. *J. Appl. Entomol.* 119: 415–418.
- Consoli, F. L., J. R. P. Parra, and R. A. Zucchi. 2010. Egg parasitoids in agroecosystems with emphasis on *Trichogramma*. Springer, New York, USA.
- Ebrahimi, E., B. Pintureau, and M. Shojai. 1998. Morphological and enzymatic study of the genus *Trichogramma* in Iran (Hym., Trichogrammatidae). *Appl. Entomol. Phytopath.* 66: 39–40.
- El-Wakil, N. 2007. Evaluation of efficiency of *Trichogramma evanescens* reared on different factitious hosts to control *Helicoverpa armigera*. *J. Pest. Sci.* 80: 29–34.
- Ferracini, C., G. Boivin, and A. Alma. 2006. Costs and benefits of host feeding in the parasitoid *Trichogramma turkestanica*. *Entomol. Exp. Appl.* 121: 229–234.
- Frazier, M. R., R. B. Huey, and D. Berrigan. 2006. Thermodynamics constrains the evolution of insect population growth rate: ‘warmer is better’. *Am. Nat.* 168: 512–520.
- Gou, X. Q. 1988. Bionomics of *Trichogramma ostriniae* Pang et Chen, pp. 191–195. *In* J. Voegele, J. K. Waage, and J. C. van Lenteren (eds.) *Trichogramma* and other egg parasites (Guangzhou, China, 10–15 November 1986). Les Colloques de l’INRA, Paris.
- Greenberg, S. M., D. A. Nordlund, and E. G. King. 1996. Mass production of *Trichogramma* spp.: experiences in the former Soviet Union, China, the United States and Western Europe. *Biocontrol News Inform.* 51–60.
- Haile, A. T., S. A. Hassan, C. K. P. O. Ogo, J. Baumgartner, S. Sithanatham, J. C. Monje, and C. P. W. Zebitz. 2002. Temperature-dependent development of four egg parasitoid *Trichogramma* species (Hymenoptera: Trichogrammatidae). *Biocontrol Sci. Tech.* 12: 555–567.
- Hansen, L. S., and K. M. V. Jensen. 2002. Effect of temperature on parasitism and host-feeding of *Trichogramma turkestanica* (Hymenoptera: Trichogrammatidae) on *Ephesthia kuehniella* (Lepidoptera: Pyralidae). *J. Econ. Entomol.* 95: 50–56.
- Harrison, W. W., E. G. King, and J. D. Ouzts. 1985. Development of *Trichogramma exiguum* and *Trichogramma pretiosum* at five temperature regimes. *Environ. Entomol.* 14: 118–121.
- Hassan, S. A. 1994. Strategies to select *Trichogramma* species for use in biological control, pp. 55–71. *In* E. Wajnberg, and S. A. Hassan (eds.) *Biological control with egg parasitoids*. CAB International, Wallingford, UK.
- Hegazi, E., C. Alder, W. Khafagi, and E. Agamy. 2019. Host preference and parasitic capacity of new candidates of *Trichogramma* species (Hym.: Trichogrammatidae) against some stored products moths. *J. Stored Prod. Res.* 80: 71–78.
- Hegazi, E., W. Khafagi, A. Herz, M. Konstantopoulou, S. Hassan, E. Agamy, A. Atwa, and S. Shweil. 2012. Dispersal and field progeny production of *Trichogramma* species released in an olive orchard in Egypt. *BioControl.* 57: 481–492.
- Hutchison, W. D., M. Moratorio, and J. M. Martin. 1990. Morphology and biology of *Trichogrammatoidea bactrae* (Hymenoptera: Trichogrammatidae), imported from Australia as a parasitoid of pink bollworm (Lepidoptera: Gelechiidae) eggs. *Ann. Entomol. Soc. Am.* 83: 46–54.
- Iqbal, A., Y. M. Chen, Y. Y. Hou, C. C. Ruan, N. Desneux, M. Q. Khan, and L. S. Zang. 2021. Rearing *Trichogramma ostriniae* on the factitious host *Antheraea pernyi* via multiparasitism with *Trichogramma chilonis* facilitates enhanced biocontrol potential against *Ostrinia furnacalis*. *Biol. Control.* 156: 104567.
- Iranipour, S., A. Farazmand, M. Saber, and M. Mashhadi Jafarloo. 2009. Demography and life history of the egg parasitoid, *Trichogramma brassicae*, on two moths *Anagasta kuehniella* and *Plodia interpunctella* in the laboratory. *J. Insect Sci.* 9: 1–8.
- Jervis, M. A., G. E. Heimpel, P. N. Ferns, J. A. Harvey, and N. A. C. Kidd. 2001. Life-history strategies in parasitoid wasps: a comparative analysis of ‘ovigeny’. *J. Anim. Ecol.* 70: 442–458.
- Kalyebi, A., W. A. Overholt, F. Schulthess, J. M. Mueke, and S. Sithanatham. 2006. The effect of temperature and humidity on the bionomics of six African egg parasitoids (Hymenoptera: Trichogrammatidae). *Bull. Entomol. Res.* 96: 305–314.
- Lauge, G. 1985. Sex determination: genetic and epigenetic factors, pp. 295–318. *In* G. A. Kerkut, and L. I. Gilbert (eds.), *Comprehensive Insect Physiology, Biochemistry and Pharmacology*, Vol I. Pergamon Press, Oxford.
- Lessard, E., and G. Boivin. 2013. Effect of age and hunger on host-feeding behavior by female *Trichogramma euproctidis* (Hymenoptera: Trichogrammatidae). *Can. Entomol.* 145: 53–60.
- Li, L. L. 1994. Worldwide use of *Trichogramma* for biological control in different crops, pp. 37–54. *In* E. Wajnberg and S. A. Hassan (eds.), *Biological control with egg parasitoids*. CAB International, Wallingford, UK.
- Lund, H. O. 1938. Studies on longevity and productivity in *Trichogramma evanescens*. *J. Agric. Res.* 56: 421–439.
- Maia, A. H. N., J. B. Alfredo, and C. Campanhola. 2000. Statistical influence on associated fertility life table parameters using Jackknife technique: computational aspects. *J. Econ. Entomol.* 93: 511–518.
- Melo, R., D. Pratisoli, R. Polanczyk, D. Melo, R. Rose, and R. M. Milanez. 2007. Biology and thermal requirements of *Trichogramma atopovirilia* oatman & planter (Hymenoptera: Trichogrammatidae) parasitizing eggs of *Diaphania hyalinata* L. (Lepidoptera: Pyralidae). *Neotrop. Entomol.* 36: 431–435.
- Messenger, P. S. 1970. Bioclimatic inputs to biological control and pest management programs, pp. 84–102. *In* R. L. Rabb, and F. E. Guthrie (eds.), *Concept of pest management*. North Carolina State University, Raleigh.
- Mills, N. 2010. Egg parasitoids in biological control and integrated pest management, pp. 389–412. *In* F. L. Consoli, J. R. P. Parra, and R. A. Zucchi (eds.), *Egg parasitoids in agroecosystems with emphasis on Trichogramma*. Springer, Dordrecht, the Netherlands.
- Modarres Awal, M. 2011. List of agricultural pests and their natural enemies in Iran. Third edition, Ferdowsi University Press, Mashhad, Iran.
- Moezipour, M., M. Kafil, and H. Allahyari. 2008. Functional response of *Trichogramma brassicae* at different temperatures and relative humidities. *Bull. Insectol.* 62: 245–250.
- Naranjo, S. E. 1993. Life history of *Trichogrammatoidea bactrae* (Hymenoptera: Trichogrammatidae), an egg parasitoid of pink bollworm (Lepidoptera: Gelechiidae), with emphasis on performance at high temperatures. *Environ. Entomol.* 22: 1051–1059.
- Noldus, L. P. J. J. 1989. Semiochemicals, foraging, behavior and quality of entomophagous insects for biological control. *J. Appl. Entomol.* 108: 425–451.
- Ozdar, N., and G. Kara. 2010. Comparative biology and life tables of *Trichogramma cacoeciae*, *T. brassicae* and *T. evanescens* (Hymenoptera: Trichogrammatidae) with *Ephesthia kuehniella* and *Carda cautella* (Lepidoptera: Pyralidae) as hosts at three constant temperatures. *Biocontrol Sci. Tech.* 20: 245–255.
- Pak, G. A., and E. R. Oatman. 1982. Biology of *Trichogramma brevicapillum*. *Entomol. Exp. Appl.* 32: 61–67.
- Park, Y., H. Lee, and K. Lee. 2000. Effect of temperature on the biology of *Trichogramma dendrolimi* (Hymenoptera: Trichogrammatidae) reared on a factitious host, *Antheraea pernyi* (Lepidoptera: Saturniidae) egg. *J. Asia-Pac. Entomol.* 3: 65–70.
- Pavlik, J. 1993. Variability in the host acceptance of European corn borer, *Ostrinia nubilalis* Hbn. (Lep.: Pyralidae) in strains of the egg parasitoid *Trichogramma* spp. (Hym.: Trichogrammatidae). *J. Appl. Entomol.* 115: 77–84.
- Pintureau, B. 2008. Les especes europeennes de *Trichogrammes*, ILV ed. *In* *LibroVeritas*, Cergy-Pontoise, France.
- Pizzol, J., N. Desneux, E. Wajnberg, and D. Thiery. 2012. Parasitoid and host egg ages have independent impact on various biological traits in a *Trichogramma* species. *J. Pest Sci.* 85: 489–496.
- Platner, J. D., R. K. Velten, M. Planoutene, and J. D. Pinto. 1999. Slide mounting techniques for *Trichogramma* (Trichogrammatidae) and other minute parasitic Hymenoptera. *Entomol. News.* 110: 56–64.



- Pratissoli, D., and J. R. P. Parra. 2000. Fertility life table of eggs of *Tuta absoluta* and *Phthorimaea operculella* (Lep.: Gelechiidae) at different temperature. *J. Appl. Entomol.* 124: 339–342.
- Pratissoli, D., and J. R. P. Parra. 2001. Selecao de linhagens de *Trichogramma pretiosum* Riley (Hymenoptera: Trichogrammatidae) para o controle das traças *Tuta absoluta* (Meyrick) e *Phthorimaea operculella* (Zeller) (Lepidoptera: gelechiidae). *Neotrop. Entomol.* 30: 277–282.
- Pratissoli, D., J. C. Zanuncio, U. R. Vianna, J. S. Andrade, T. B. M. Pinon, and G. S. Andrade. 2005. Thermal requirements of *Trichogramma pretiosum* and *T. acacioi* (Hym.: Trichogrammatidae), parasitoids of the avocado defoliator *Nipteria panacea* (Lep.: geometridae), in eggs of two alternative hosts. *Braz. Arch. Biol. Technol.* 48: 523–529.
- Ram, P., Tshernyshev, W. B., Afonina, V. M., Greenberg, S. M. 1995. Studies on the strains of *Trichogramma evanescens* weswood (Hym., Trichogrammatidae) collected from different hosts in northern Moldova. *J. Appl. Entomol.* 119: 79–82.
- Reynolds, S. E., and S. F. Nottingham. 1985. Effects of temperature on growth and efficiency of food utilization in fifth-instar caterpillars of the tobacco hornworm, *Manduca sexta*. *J. Insect Physiol.* 31: 129–134.
- SAS Institute. 2002. SAS/STAT User Guide. SAS Institute, Cary, NC.
- Schmidt, J. M. 1994. Host recognition and acceptance by *Trichogramma*, pp. 166–200. *In* E. Wajnberg and S.A. Hassan (eds.), *Biological control with egg parasitoids*. CAB International, Wallingford, UK.
- Scholler, M., and S. A. Hassan. 2001. Comparative biology and life table of *Trichogramma evanescens* and *T. cacoecia* with *Ephestia elutella* as host at four constant temperatures. *Entomol. Exp. Appl.* 98: 35–40.
- Silva, I. M. M. S., and R. Stouthamer. 1999. Do sympatric *Trichogramma* species parasitize the pest insect *Helicoverpa armigera* and beneficial insect *Chrysoperla carnea* in different proportions. *Entomol. Exp. Appl.* 92: 101–107.
- Smith, S. M. 1996. Biological control with *Trichogramma*: advances, success and potential of their use. *Annu. Rev. Entomol.* 41: 375–406.
- Sumer, E., A. S. Tuncbilek, S. Oztemiz, B. Pintureau, P. Rugman-Jones, and R. Stouthamer. 2009. A molecular key to the common species of *Trichogramma* of the Mediterranean region. *Biocontrol.* 54: 617–624.
- Tabebordbar, E., P. Shishehbor, and E. Ebrahimi. 2020. Suitability of different egg ages of *Ephestia kuehniella* (Lep.: Pyralidae) for the development, reproduction and life table parameters of *Trichogramma evanescens* (Hym.: Trichogrammatidae). *J. Crop Protec.* 9: 89–99.
- Tuncbilek, A. S., N. Cinar, and U. Canpolat. 2012. Effect of artificial diets and floral nectar on longevity and progeny production of *Trichogramma euproctidis* Girault (Hymenoptera: Trichogrammatidae). *Turkish J. Entomol.* 36: 183–191.
- van Lenteren, J. C., and V. H. P. Bueno. 2003. Augmentative biological control of arthropods in Latin America. *BioControl.* 48: 123–139.
- van Lenteren, J. C. 2000. Success in biological control of arthropods by augmentation of natural enemies, pp. 77–103. *In* G. Gurr and S. Wratten (eds.), *Biological control: measures of success*. Kluwer Academic Publishers, Hingham, USA.
- van Lenteren, J. C., D. Babendreier, F. Bigler, G. Burgio, H. M. T. Hokkanen, S. Kuske, A. J. M. Loomans, I. Menzler-Hokkanen, P. C. J. van Rijn, M. B. Thomas, M. G. Tommasini, and Q. Q. Zeng. 2003. Environmental risk assessment of exotic natural enemies used in inundative biological control. *BioControl.* 48: 3–38.
- Wu, L. H., M. P. Hill, L. J. Thomson, and A. A. Hoffmann. 2018. Assessing the current and future biological control potential of *Trichogramma ostrinia* on its hosts *Ostrinia furnacalis* and *Ostrinia nubilalis*. *Pest Manag. Sci.* 74: 1513–1523.