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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 *Ephestia 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*

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(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). Lager-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, Pratissoli 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 (≈ 45°C) from May to late September, and temperatures can even exceed 48°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°18'25.3'N 48°39'36.1'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 cm x 6 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 ± 1°C, 55 ± 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 cm × 1 cm) with sufficient number (500 ± 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 ± 0.5°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 cm × 1 cm) containing 50 ± 1 one-day old of *E. kuehniella* eggs (sterilized with UV light) sprinkled on paper (5 cm × 1 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 ± 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

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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: $\Sigma\, e^{-r_x l_x m_x} = 1$. 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 Jacknife 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 ($R_0 = \Sigma\, l_x m_x$, 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 ($\lambda = er$), 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 ± 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 ± 0.04^{e}	13.81 ± 0.16^{a}	11.68 ± 0.17^{a}	49.64 ± 0.12^{e}	32.10 ± 0.10^{f}
25	32.42 ± 0.20^{d}	10.00 ± 0.10^{b}	7.74 ± 0.11^{b}	81.18 ± 0.25^{b}	54.39 ± 0.15^{d}
27.5	35.85 ± 0.05^{c}	8.28 ± 0.12^{c}	6.40 ± 0.11^{c}	73.94 ± 0.15^{c}	64.57 ± 0.10^{c}
30	38.42 ± 0.20^{b}	7.17 ± 0.10^{d}	5.42 ± 0.10^{d}	90.01 ± 0.20^{a}	75.41 ± 0.12^{b}
32.5	44.85 ± 0.04^{a}	7.02 ± 0.06^{d}	4.91 ± 0.09^{d}	93.06 ± 0.31^{a}	84.11 ± 0.11^{a}
35	31.85 ± 0.20^{d}	6.42 ± 0.16^{e}	4.68 ± 0.07^{de}	72.54 ± 0.12^{c}	48.57 ± 0.19^{e}
37.5	30.28 ± 0.09^{d}	6.04 ± 0.13^{e}	4.37 ± 0.07^{e}	67.74 ± 0.19^{d}	47.59 ± 0.10^{e}
40	26.14 ± 0.03^{e}		11.32 ± 0.12^{a}	53.26 ± 0.13^{e}	35.23 ± 0.23^{f}

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

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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, λ, 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 *Ephestia kuehniella* eggs at different constant temperatures

	Parameters			
Sex	Temperature threshold	R^2	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 *Ephestia kuehniella* eggs at different constant temperature

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

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

Age-specific survival (lx) 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 *Ephestia 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, Pratissoli 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 zahiri* 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.

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

Temperature (°C)	R_0 (offspring)	r (days^{-1})	λ (days^{-1})	T (days)	DT (days)
22.5	4.75 ± 0.34^{g}	0.108 ± 0.006^{f}	1.11 ± 0.07^{f}	14.34 ± 0.19^{a}	6.34 ± 0.40^{b}
25	30.12 ± 0.51^{d}	0.394 ± 0.002^{e}	1.48 ± 0.01^{e}	11.21 ± 0.07^{c}	1.75 ± 0.01^{c}
27.5	48.15 ± 0.73^{c}	0.403 ± 0.010^{c}	1.49 ± 0.01^{c}	9.59 ± 0.26^{d}	1.71 ± 0.01^{c}
30	73.13 ± 1.21^{b}	0.492 ± 0.004^{b}	1.63 ± 0.07^{b}	8.71 ± 0.06^{e}	1.40 ± 0.01^{c}
32.5	94.08 ± 1.38^{a}	0.532 ± 0.005^{a}	1.70 ± 0.03^{a}	8.54 ± 0.08^{e}	1.30 ± 0.01^{c}
35	20.42 ± 0.13^{e}	0.303 ± 0.004^{d}	1.35 ± 0.06^{d}	8.39 ± 0.09^{e}	2.28 ± 0.02^{c}
37.5	12.15 ± 0.28^{f}	0.297 ± 0.007^{d}	1.34 ± 0.01^{e}	7.65 ± 0.15^{f}	2.33 ± 0.05^{c}
40	1.89 ± 0.07^{h}	0.048 ± 0.003^{g}	1.05 ± 0.00^{g}	13. 08 ± 0.06^{b}	14.10 ± 0.93^{a}

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 (λ), generation time (T) and doubling time (DT)).

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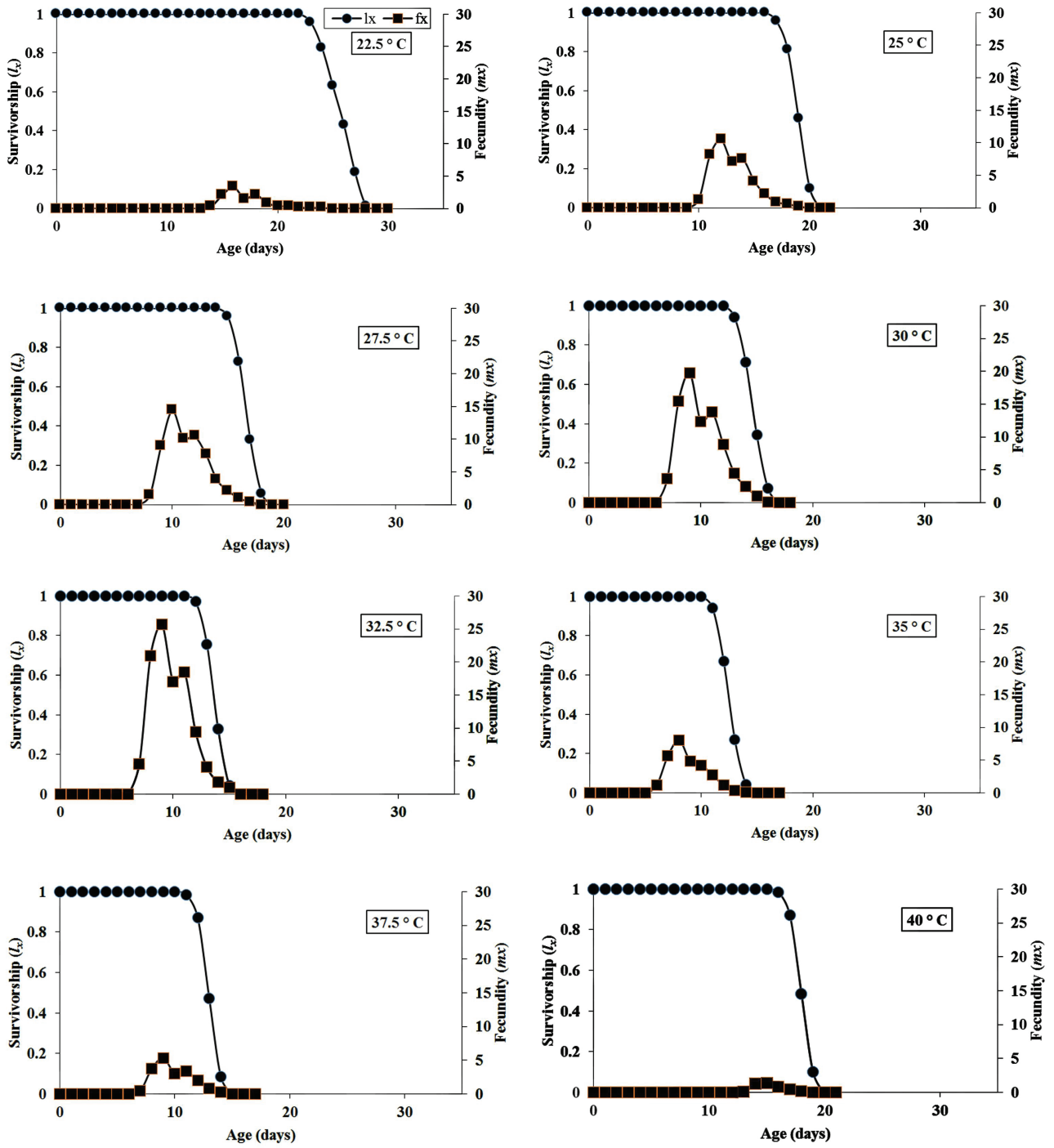

Fig. 1. Survivorship (l_x) and Fecundity (m_x) of *Trichogramma euproctidis* reared on *Ephestia kuehniella* eggs at different constant temperatures.

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.

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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. zahiri* (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 Pratissoli 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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