Phytoparasitica (2024) 52:19
https://doi.org/10.1007/s12600-024-01128-8

The effect of different oviposition and preadult development temperatures on the biological characteristics of four *Trichogramma* spp. parasitoids (Hymenoptera: *Trichogrammatidae*) species

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Received: 31 May 2023 / Accepted: 22 September 2023 / Published online: 14 February 2024

Abstract Trichogramma parasitoids are effective biocontrol agents and a reliable component of integrated strategies against lepidopterous pests. The success of these parasitoids in pest management relies not only on their ability to parasitize their hosts but also on their adaptation to the climatic conditions of the release area, particularly temperature. The expression of life history traits of *Trichogramma* spp. can vary significantly with temperature, depending on the species or strains being tested. *Trichogramma cacoeciae* (Marchal), *T. euproctidis* (Girault), *T. minutum* (Riley), and *T. brassicae* (Bezdenko) (Hymenoptera: Trichogrammatidae) are currently used in biocontrol programs against important lepidopteran pests. We aimed to assess the temperature sensitivity of these parasitoids during oviposition and preadult development, and to identify the most tolerant species to high temperatures conditions commonly encountered in Mediterranean Basin countries during the growing seasons. The biological characteristics of the four species were determined at seven temperature regimes expressed as temperatures during oviposition and preadult development (25/25, 25/30, 25/35, 25/40, 30/30, 35/35 and 40/40 °C), using *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) eggs. *Trichogramma cacoeciae* showed the highest level of parasitism at 30/30 °C, while the other species exhibited the highest levels at 25/25 °C and 25/30 °C. All Trichogramma species were able to develop and survive from 25 °C to 35 °C, but not at 40 °C. Temperature significantly affected the longevity and fecundity of female progeny, with both decreasing when the temperature increased from 25 °C to 35 °C. When exposed to 35/35 °C, *T. cacoeciae* demonstrated the most optimal performance in terms of parasitization efficiency, developmental capacity, progeny longevity, and fecundity.

Keywords Egg parasitoids · *Ephestia kuehniella* eggs · Sex ratio · Emergence · Fecundity · Age-specific survival rate · Biological control · IPM

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Introduction

The Mediterranean region covers approximately 877 million hectares of land, out of which around 28% is allocated to agriculture (Mrabet et al., 2020). This sector plays a crucial role in supporting the socio-economic progress of the area (Ramdani et al., 2009). The specific climatic conditions of the Mediterranean region, characterized by prolonged hot and arid spells during the growing seasons, necessitate highly specialized cropping systems focusing on crops with significant nutritional, commercial, and environmental value (Ramdani et al., 2009; Ukhurebor et al., 2022). Cereals, vegetables, fruits, grapes, olives, and dates are among the most notable crops cultivated in this region (Leff et al., 2004; Mrabet et al., 2020). However, these crops are highly susceptible to damage caused by several harmful insects, including Lepidopteran pests (Abazaid et al., 2021; Caselli & Petacchi, 2021; Dhouibi et al., 2016; Gugliuzzo et al., 2019; Rahouma, 2018). The impact of climate change on Lepidoptera populations in the Mediterranean region has become increasingly apparent in recent years, with some native species expanding their ranges and several non-native species successfully establishing themselves, resulting in significant ecological and economic repercussions (Kocsis & Hufnagel, 2011; Ponti et al., 2016; Uhl et al., 2022).

In order to limit infestations caused by Lepidopteran pests, a diverse range of chemical insecticides has been widely employed in various agro-ecosystems throughout Mediterranean countries (Giorgini et al., 2018; Herz et al., 2005; Pavan et al., 2014; Ugurlu et al., 2013). However, their extensive application has caused several undesirable effects including emergence of pest resistance and resurgence, environmental contamination, and threat to non-target organisms and natural enemies (Carvalho, 2017; Karuppuchamy & Venugopal, 2016). The pursuit of sustainable agriculture and the need to mitigate economic losses caused by pests have led to a growing emphasis on the adoption of integrated pest management (IPM) programs (Karuppuchamy & Venugopal, 2016; Matthews, 2022). Egg parasitoids of the genus Trichogramma (Hymenoptera: Trichogrammatidae) have been proven to be a reliable component of IPM strategies, providing effective control against several lepidopteran pests in numerous agricultural crops and forests (Mills, 2010; Querino et al., 2010; Smith, 1996). The widespread success of Trichogramma parasitoids can be attributed to several key features, including their ease of mass rearing on factitious hosts, short life cycle, broad host range, ease of application as inundative biocontrol agents in both field and greenhouse settings, and their ability to significantly reduce pests egg hatching and subsequent crop damage resulting from larval feeding (Mills, 2010; Smith, 1996; Wu et al., 2015). Each year, over 32 million hectares of land worldwide are treated with Trichogramma spp., leading to a reduced reliance on chemical insecticides (Kumar et al., 2013).

The effective selection and implementation of Trichogramma parasitoids within biocontrol programs hinge upon meticulously considering several critical factors. These factors encompass the inherent capacity of Trichogramma species or strain to thrive within the targeted host, as well as the interplay between various abiotic and biotic factors (Bueno et al., 2012; Oliveira et al., 2017; Pratissoli & Parra, 2000). Notably, temperature emerges as the most preeminent environmental parameter, wielding a profound impact on the biology, survivorship, and distribution of these poikilothermic arthropods (Foerster et al., 2014; Ksentini et al., 2011; Moezipour et al., 2008; Mohammad et al., 2015). In some countries of the Mediterranean region, temperatures can even exceed 45 °C for short periods during the summer days, potentially impacting the activity of Trichogramma parasitoids and, consequently, the efficiency of inundative releases (Ksentini et al., 2010; Melo, 2011). Gaining a thorough and in-depth understanding of the intricate interplay between temperature and the biological parameters of the selected Trichogramma species/strain holds pivotal importance in formulating precise and effective laboratory mass rearing procedures (Greenberg et al., 1996), while also recognizing its potential as a biocontrol agent tailored to address the challenges posed by a particular pest species within a specific geographic region (Pratissoli & Parra, 2000; Pino et al., 2020).

The parasitoids *Trichogramma cacoeciae* (Marchal), *T. euproctidis* (Girault), *T. minutum* (Riley), and *T. brassicae* (Bezdenko) (Hymenoptera: Trichogrammatidae) have gained commercial significance and have been intentionally introduced into various agricultural settings across continents for their effective use as inundative biocontrol agents against important lepidopteran pests (Atashi et al., 2021;

Aubry, 2008; Hegazi et al., 2007; Pease et al., 2016; Renou et al., 1992; Sigsgaard et al., 2017; Zouba et al., 2013a; Zougari et al., 2020). Some of the life history characteristics of these Trichogramma species have been studied previously (Moezipour et al., 2008; Özder & Kara, 2010; Pizzol et al., 2010; Schöller & Hassan, 2001; Tabebordbar et al., 2022a; Yu et al., 1984). However, it has been demonstrated that different strains (ecotypes) of Trichogramma species that originate from different geographic regions may exhibit distinct biological traits that influence their overall success (Pavlik, 1993; Pizzol et al., 2010; Ram et al., 1995; Smith, 1996). To identify a suitable candidate biocontrol agent that can withstand the challenging environmental conditions of the growing season (from May to late September) in Mediterranean Basin countries, we assessed the impact of high temperatures on the biological parameters of the four aforementioned species (originating from different countries) during oviposition and preadult development. This study enables the prediction of the response of these parasitoids to climate changes, and facilitates the identification of the ideal timing for the implementation of inundative release programs during the growing season.

Materials and methods

Parasitoid's origin, culture and maintenance

Trichogramma cacoeciae, a thelytokous species that reproduces independently of Wolbachia symbiotic bacteria (Pintureau et al., 1999), was established as a local population in 2009 by collecting parasitoid wasps from host baits (sentinel eggs of *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae)) in date palm orchards located in southwest Tunisia. Molecular characterization by sequencing of the ITS2 gene was subsequently employed to identify the species (Zouba et al., 2013b). In 2016, this strain of *T. cacoeciae* was introduced into the National Agronomic Institute of Tunisia insectarium for research and conservation purposes. Additionally, three arrhenotokous species, *T. euproctidis* (originated from Egypt), *T. minutum* (originated from Canada), and *T. brassicae* (originated from Iran) were first introduced to Tunisia in 2017 and reared at the National Agronomic Institute of Tunisia insectarium using eggs of the factitious host *E. kuehniella*. These species were sourced from the Earth and Life Institute, Biodiversity Research Center, Université catholique de Louvain, Belgium.

Factitious host eggs used in this study were obtained from a culture of *E. kuehniella* massively reared on a standard diet containing wheat flour, mixed according to the methodology defined by Cerutti et al. (1992). Prior to the experiments, and for at least 15 successive generations, the tested Trichogramma species were maintained on fresh ultraviolet-sterilized eggs of *E. kuehniella* under controlled conditions (25 ± 1 °C, 60–80% RH and 16:8 h L:D photoperiod), as described by Ayvaz et al. (2008). Newly emerged parasitoids (arrhenotokous species: 50 ♀ + 50 ♂/ thelytokous species: 50 ♀) were introduced to glass vials (10 cm height * 1 cm diameter) containing a cardboard card (1 × 5 cm) with sufficient number (≈1000) of *E. kuehniella* eggs. The upper end of vials was covered by a fine mesh net to facilitate air flow. Parasitoids were provided with a honey–water solution (1:1) as a food source, which was smeared onto the internal surfaces of the vials. Afterwards, the parasitized eggs were incubated under the same conditions described above until the emergence of the adult wasps.

Experimental procedure

Part 1: Test on the parental generation

Female wasps of each species were allowed to lay eggs under climatic conditions similar to those used for rearing (25 ± 1 °C, 60–80% RH and 16:8 h L:D photoperiod). One day later, the parasitized eggs were randomly divided into four groups and subjected to different constant temperatures of 25, 30, 35, and 40 ± 1 °C in temperature-controlled cabinets. In parallel, another group of females from each species was allowed to lay eggs under the same temperature conditions used for preadult development of the parasitoids. This experimental design resulted in a total of 7 treatments, representing the temperatures experienced during both oviposition and preadult development: 25/25, 25/30, 25/35, 25/40, 30/30, 35/35 and 40/40 °C. Other climatic conditions were kept similar, i.e. 60–80% RH and 16:8 h L:D photoperiod.

For each treatment, 30 newly emerged females (< 24 h old) of each species were individually isolated in glass vials (5 cm height * 1 cm diameter). Each female was fed with a honey-water solution (1:1) and supplied with fresh eggs of *E. kuehniella* (100 ± 10 one-day old eggs sterilized with UV light) glued on a cardboard card with distilled water (1 × 2.5 cm). Glass vials were covered by a fine mesh net. Each isolated female represented a replicate. After 24 h of exposure, all parasitoids were removed from their vials using a thin brush, and the parasitized eggs were incubated at the respective preadult temperatures. The total number of eggs parasitized by a single female was recorded; successful parasitization could be identified by the blackening of host eggs. The emergence rate was calculated according to the method recommended by Van Driesche (1983) using the following equation:

$$Emergence\ percentage = \frac{Number\ of\ eggs\ with\ emergence\ holes}{Total\ egg\ number} \times 100$$

The egg-to-adult period was measured as the period of time from the day when the females were removed to adult emergence. The sex ratio of the newly emerged adults was determined based on their antennal characters (Bowen & Stern, 1966). The female's percentage was estimated using the following equation:

$$Female's\ percentage = \frac{Number\ of\ females}{Total\ individual\ number} \times 100$$

Part 2: Test on the F1 generation

Females from the F1 generation (obtained from above experiment) were randomly selected at each of the tested preadult temperatures. Since no adult parasitoids emerged at 40 °C in the F1 generation, we focused our investigation on recording the longevity and fecundity of the progeny at 25, 30, and 35 °C, with a 60–80% RH and 16:8 h L:D photoperiod. The selected females were allowed to lay eggs under the same temperature conditions experienced during their preadult development. For each temperature, 20 females less than one day old (< 24 h) of each species were placed individually into glass vials covered with mesh net and a water–honey (1:1) drop for feed. Cardboard cards with 100 ± 10 one-day old sterilized *E. kuehniella* eggs were supplied daily until the natural death of the female parasitoids. The replaced egg cards were kept in cabinets at the corresponding temperatures mentioned above.

Longevity (number of days) until death of the females was recorded. Cumulative female fecundity is defined as the total number of successfully parasitized eggs by a female over the full life span. The number of parasitized host eggs and the number of adults emerging from them were counted for each sample. The following parameters were derived from these records:

- lx: the propotion of females still alive at age x (age-specific survival rate) (Southwood, 1978).
- mx: the number of live female progeny per female at the age x (age-specific fecundity rate) (Southwood, 1978).

Where x is the age of the individuals in days.

Statistical analysis

The number of parasitized eggs, preadult development time, progeny longevity, and fecundity data under different temperature regimes were transformed to log10($x + 1$), while emergence rate and sex ratio data were transformed to arcsine ($\sqrt{}$ (x/100)). All transformed data were analyzed by ANOVA test applying the General Linear Models (PROC GLM) procedure and the average values were compared by Tukey's test ($p = 0.05$) by means of the statistical software IBM SPSS statistics software (Version 20), IBM, USA.

Results

Number of parasitized eggs

The mean number of *E. kuehniella* eggs parasitized by the four Trichogramma species was significantly influenced by temperature ($F_{3.76} = 126.4$; df = 13; p < 0.001) (Table 1). *Trichogramma cacoeciae* exhibited optimal parasitism performance at 30/30 °C, while the other species showed their highest parasitism levels when females laid eggs at 25 °C and preadult development occurred at either 25 °C or 30 °C. All Trichogramma species showed no significant differences in the number of parasitized

Table 1 Mean number (± SEM) of *Ephestia kuehniella* eggs parasitized by four *Trichogramma* species allowed to oviposit and develop under different temperature regimes expressed as temperatures during parasitism/preadult development

Temperature Treatment (°C)	*T. cacoeciae*	*T. brassicae*	*T. minutum*	*T. euproctidis*
25/25	25.3 ± 0.05 Aa	30.5 ± 0.81 Aa	24.35 ± 0.25 Aa	29.2 ± 0.33 Aa
25/30	25.85 ± 0.92 Aa	25.75 ± 0.71 Aa	24.7 ± 1.02 Aa	27.7 ± 0.76 Aa
30/30	33.45 ± 1.10 Ba	17.4 ± 1.07 Bb	16.65 ± 0.75 Bb	17.1 ± 0.30 Bb
25/35	26.8 ± 0.08 Aa	19.4 ± 1.35 Bb	9.55 ± 1.13 Cc	17.85 ± 1.40 Bb
35/35	20.55 ± 0.68 Ca	13.75 ± 0.27 Cb	4.4 ± 0.04 Dc	8.25 ± 0.19 Cd
25/40	14.7 ± 0.29 Da	10.45 ± 0.21 Db	1.3 ± 0.06 Ec	9.05 ± 0.86 Cb
40/40	0.75 ± 0.03 Ea	0.55 ± 0.04 Ea	0.05 ± 0.03 Fa	0.45 ± 0.02 Da

Means followed by the same upper case letter within-column and lower case letter within-rows are not significantly different at $P < 0.05$ (Tukey's test)

eggs between the temperature regimes 25/25 °C and 25/30 °C. *T*richogramma *cacoeciae* was the only species that did not show a significant decrease in parasitism at 25/35 °C when compared to 25/25 °C and 25/30 °C. We recorded a sharp decline in parasitism for all species when the preadult temperature increased to 40 °C (25/40 °C), with *T. minutum* exhibiting the lowest parasitism performance (1.3 ± 0.06 eggs/female/24 h). At 35/35 °C, the number of parasitized eggs was found to be highest in *T. cacoeciae* (20.55 ± 0.68 eggs/female/24 h), while *T. minutum*, *T. euproctidis* and *T. brassicae* demonstrated significantly lower values of 4.4 ± 0.04, 8.25 ± 0.19 and 13.75 ± 0.27 eggs/female/24 h, respectively. Parasitism was further reduced at 40/40 °C, with no significant differences observed among species.

Preadult development time

Analysis of variance revealed that temperature had a significant effect on the development time of immature parasitoids ($F_{2.56} = 329.7$; $df = 14$; $p < 0.001$) (Fig. 1). At 25 °C, all Trichogramma species experienced a significant delay in completing preadult development, taking on average 11–12 days. The shortest developmental times for all species were observed at 35 °C, ranging from 6 to 7 days.

Emergence rate

All four species of Trichogramma were able to complete their immature development and emerge successfully within the temperature range of 25–35 °C (Fig. 2). However, none of them succeeded in reaching adult stage at 40 °C. Temperature had a significant effect on the emergence rates (survival) of *T. cacoeciae* and *T. euproctidis*, with both species showing decreased survivorship as preadult temperature increased towards 35 °C. The emergence rates of *T. brassicae* and *T. minutum* remained statistically similar across all tested temperatures. With the exception of *T. euproctidis*, which only had a 35.2% emergence rate at 35/35 °C, all other Trichogramma species showed high survival rates, exceeding 75% at all temperature regimes.

Sex ratio (Female %)

Trichogramma cacoeciae did not produce males under any of the temperature regimes tested. Temperature had a significant effect on the sex ratio of *T. brassicae* and *T. euproctidis*. In both species, the percentage of females increased as the preadult temperature increased from 25 °C to 30 °C, where it peaked at 69.1% (25/30 °C) and 65.3% (30/30 °C) for *T. brassicae* and 63.2% (25/30 °C) and 62.9% at (30/30 °C) for *T. euproctidis*, and then decreased at 35 °C (Fig. 3). The female-biased sex ratio observed in *T. minutum*

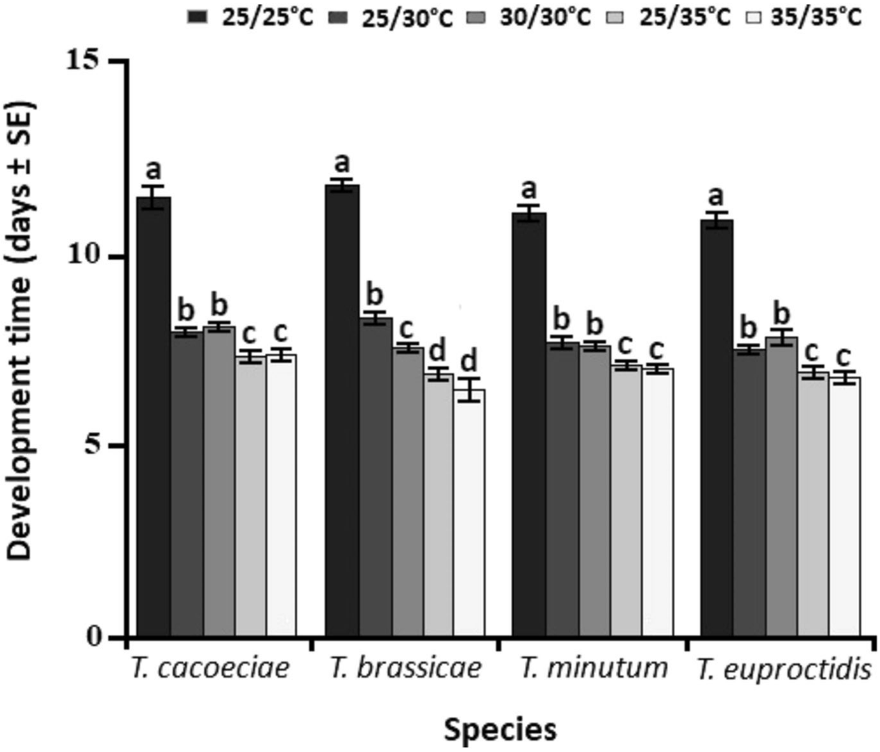


Fig. 1 Development time (days ± SE) of four Trichogramma species allowed to oviposit and developed in *Ephestia kuehniella* eggs under different temperature regimes expressed as temperatures during parasitism/preadult development. Development times (days) followed by the same letter do not differ significantly within the same species (Tukey test, $P < 0.05$)

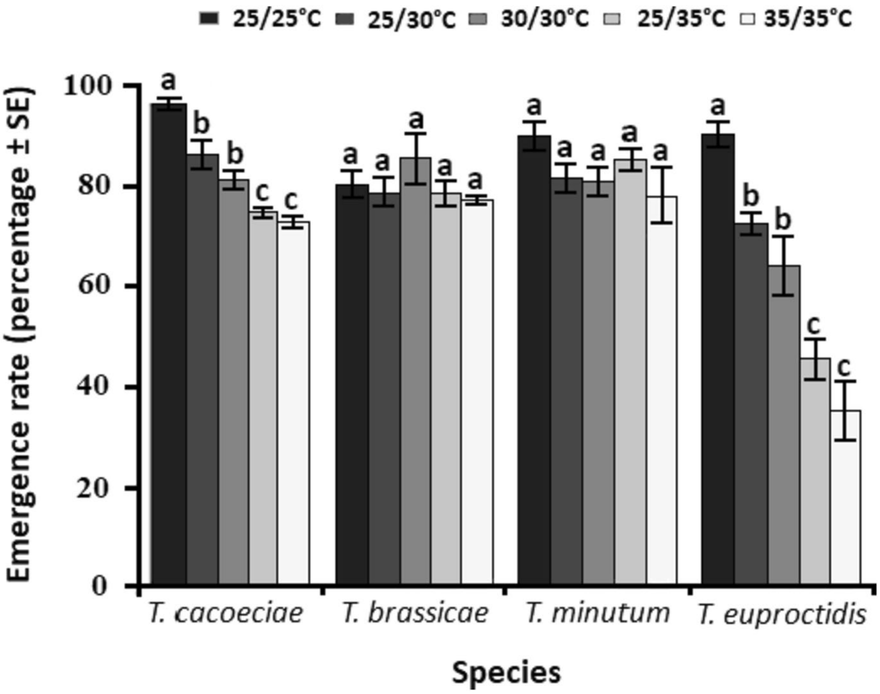


Fig. 2 Emergence rate (percentage ± SE) of four Trichogramma species allowed to oviposit and developed in *Ephestia kuehniella* eggs under different temperature regimes expressed as temperatures during parasitism/preadult development. Emergence rates (%) followed by the same letter do not differ significantly within the same species (Tukey test, $P < 0.05$)

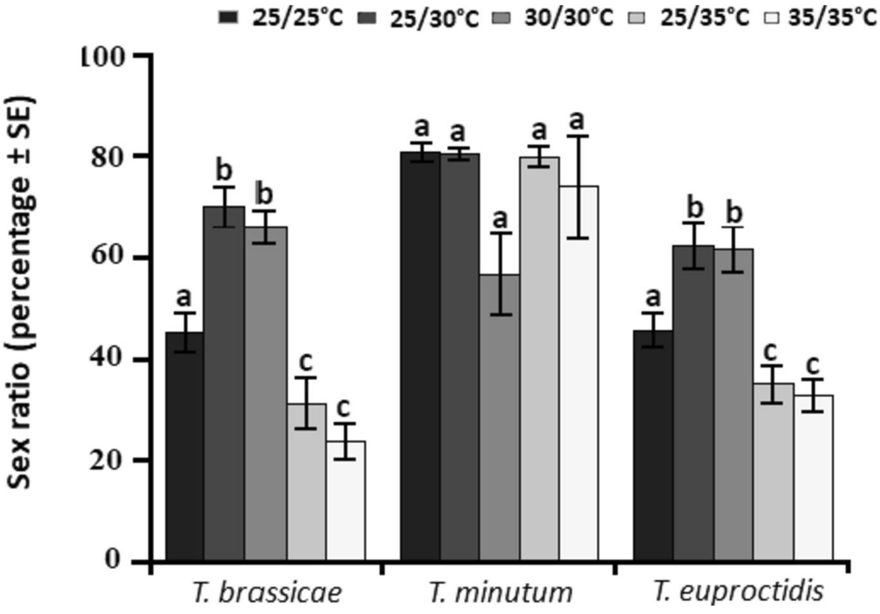


Fig. 3 Sex ratio (percentage of females ± SE) of three Trichogramma species allowed to oviposit and developed in *Ephestia kuehniella* eggs under different temperature regimes expressed as temperatures during parasitism/preadult development. Sex ratios (%) followed by the same letter do not differ significantly within the same species (Tukey test, $P < 0.05$)

(female% > 57%) was not significantly affected by the tested temperatures.

Longevity and fecundity of female progeny (F1 generation)

The age-specific survivorship (l*x*) and the age-specific fecundity (m*x*) of the four Trichogramma species at different levels of temperature are illustrated in Figs. 4 and 5, respectively. They indicate that the F1 female parasitoids can successfully survive and reproduce on *E. kuehniella* eggs between 25 °C and 35 °C. For all Trichogramma species, l*x* and m*x* are inversely proportional to the increase of temperatures; as temperatures increased, survivorship and fecundity decreased. Temperature had a significant effect on the lifespan of F1 female parasitoids (Table 2). Across all studied species, the highest longevity of female progeny was observed at 25 °C. At 35 °C, the F1 female lifespan of *T. cacoeciae* (8.04 days) was significantly longer compared to the other species. As shown in Fig. 5, egg laying is more important during the two first days after female emergence. Temperature significantly affected the total number of eggs laid by F1 female parasitoids (Table 3). *Trichogramma cacoeciae* showed the highest progeny's fecundity at 30 °C, producing an average of 168.03 eggs per female. The total number of eggs parasitized by *T. brassicae*, *T. minutum*, and *T. euproctidis* was highest at 25 °C, with 136.53, 153.03, and 128.24 eggs per female, and lowest at 35 °C, with 25.72, 10.23, and 22.63 eggs per female, respectively. At 35 °C, *T. cacoeciae* showed a significantly higher progeny's fecundity (39.41 eggs/ female) compared to the other species.

Discussion

Our experiments demonstrate a large effect of temperature on all the life history parameters of the investigated Trichogramma species. The study conducted by Yuan et al. (2012) underscores the importance of using Trichogramma species with broad temperature tolerance ranges to achieve effective pest control. According to Samara et al. (2011), temperature is recognized as the primary abiotic factor that directly influences various life history traits of *Trichogramma* spp., including development time, emergence rate, sex ratio, cumulative fertility and adult longevity. However, it is essential to note that the expression of these traits can differ significantly with temperature, depending on the species or strains tested (Foerster et al., 2014; Hassan, 1994; Pizzol et al., 2010; Ram et al., 1995; Tabone et al., 2010). In the context of a warming world (Funes et al., 2016), most insect species are exposed to thermal fluctuations that significantly influence their physiological processes (Feder et al., 1997) and ecological systems (Easterling et al., 2000). Nonetheless, the

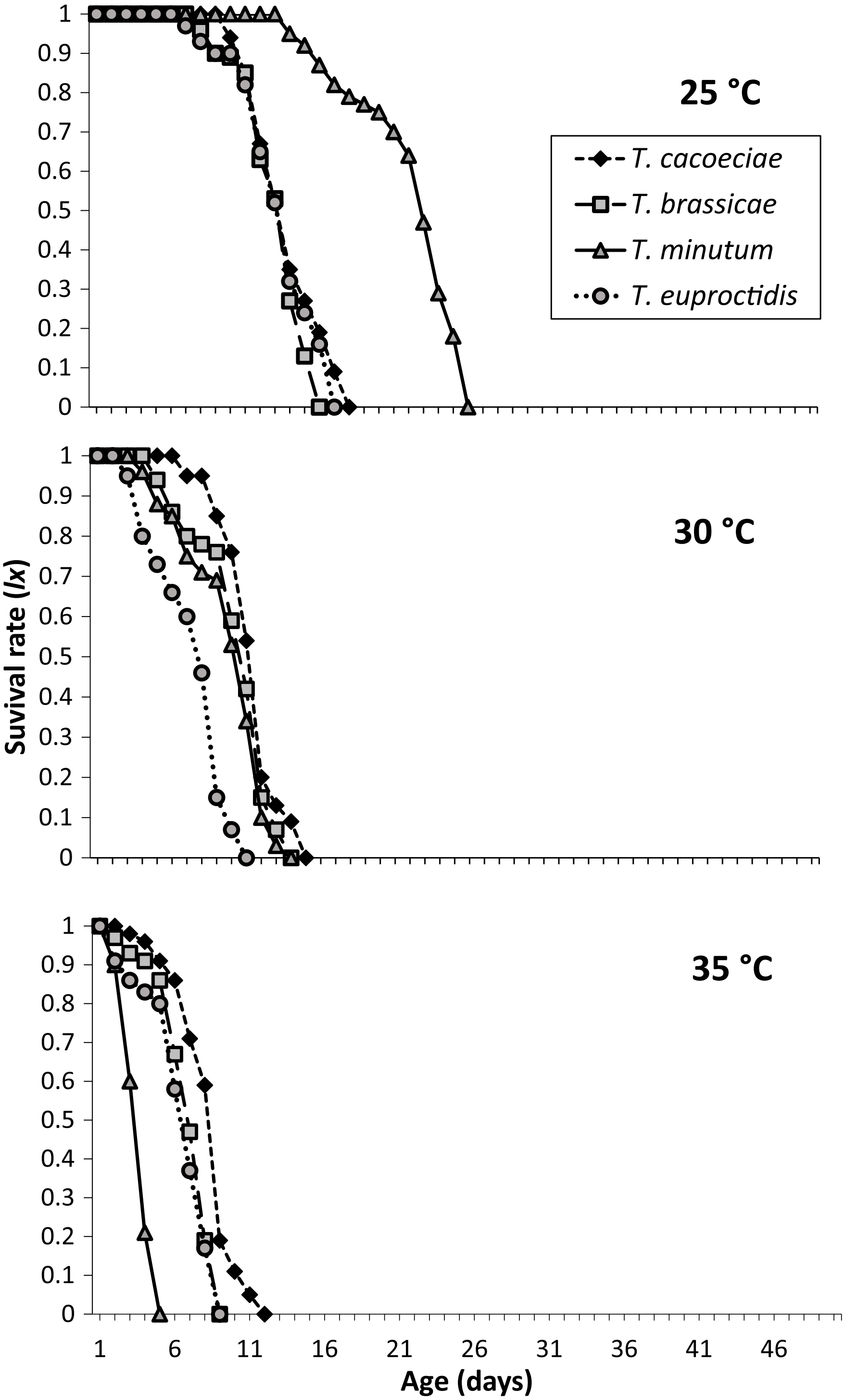
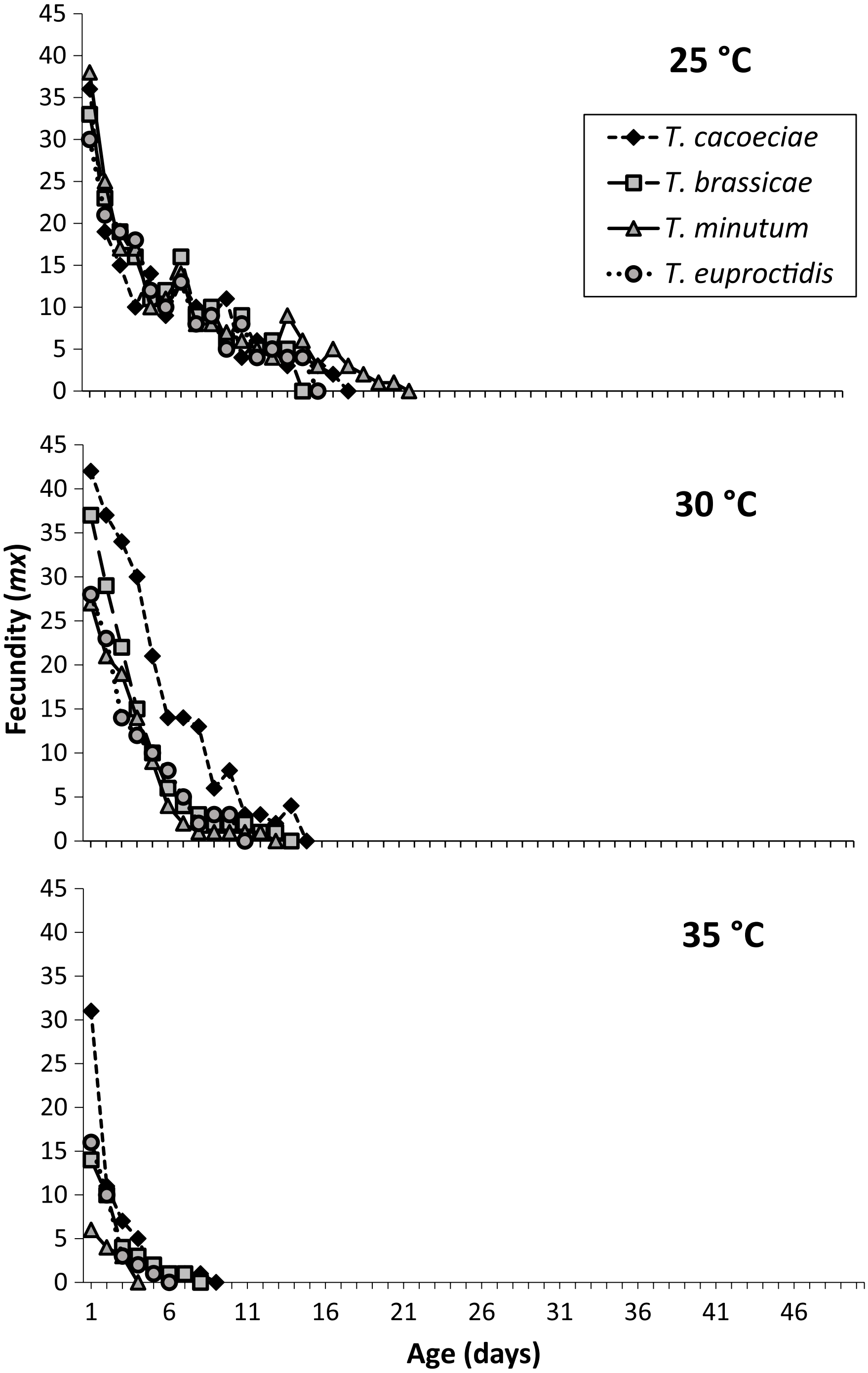


Fig. 4 Age-specific survival rate (l*x*) of four Trichogramma species reared at 25, 30 and 35 °C on *Ephestia kuehniella* eggs

recurring exposure to extreme temperatures may lead to adaptive evolution in insects, facilitated by various mechanisms, including behavioral thermoregulation, phenotypic plasticity, and ontogenetic variations (Scharf et al., 2015). Besides temperature, numerous biological traits of *Trichogramma* spp. are subject to

Fig. 5 Age-specific fecundity (m*x*) of four Trichogramma species reared at 25, 30 and 35 °C on *Ephestia kuehniella* eggs



influence from various factors, encompassing host species, host egg size, host age, nutritional quality of the host egg, spatial density of host eggs, availability of food resources during the adult stage, humidity, and photoperiod (Altoé et al., 2012; Amalin et al., 2005; Atashi et al., 2021; Mashal et al., 2019; Pizzol et al., 2012; Pratissoli & Parra, 2001; Tabebordbar et al., 2022b).

Table 2 Longevity (days) of F1 females (mean ± SE) of four *Trichogramma* species reared on *Ephestia kuehniella* eggs at different constant temperatures under laboratory conditions (60–80% RH and 16:8 h L:D)

Temperature Treatment (°C)	*T. cacoeciae*	*T. brassicae*	*T. minutum*	*T. euproctidis*
25	15.67 ± 0.03 Aa	14.20 ± 0.61 Aa	20.18 ± 0.36 Ab	15.13 ± 0.55 Aa
30	12.07 ± 0.04 Ba	10.55 ± 0.02 Bb	9.97 ± 0.05 Bb	7 ± 0.02 Bc
35	8.04 ± 0.03 Ca	5.33 ± 0.02 Cb	2.31 ± 0.05 Cc	5.07 ± 0.07 Cb

Means followed by the same upper case letter within-column and lower case letter within-rows are not significantly different at $P < 0.05$ (Tukey's test)

Table 3 Fecundity of F1 females (mean ± SE) of four *Trichogramma* species reared on *Ephestia kuehniella* eggs at different constant temperatures under laboratory conditions (60–80% RH and 16:8 h L:D)

Temperature Treatment (°C)	*T. cacoeciae*	*T. brassicae*	*T. minutum*	*T. euproctidis*
25	120.24 ± 16.03 Aa	136.53 ± 12.52 Aa	153.03 ± 18.71 Aa	128.24 ± 13.48 Aa
30	168.03 ± 12.99 Ba	94.07 ± 11.87 Bb	68.20 ± 12.08 Bb	73.84 ± 10.13 Bb
35	39.41 ± 5.51 Ca	25.72 ± 5.62 Cb	10.23 ± 0.07 Cc	22.63 ± 4.42 Cb

Means followed by the same upper case letter within-column and lower case letter within-rows are not significantly different at $P < 0.05$ (Tukey's test)

Temperature had a significant effect on the mean number of *E. kuehniella* eggs parasitized by the four Trichogramma species. *Trichogramma cacoeciae* demonstrated the highest level of parasitism at 30/30 °C, while the other three species showed their optimal parasitism performance at 25/25 °C and 25/30 °C. Although the rate of parasitism peaked at 20/20 °C for some Trichogramma species, such as *T. galloi* Zucchi (Parra et al., 1991) and *T. pretiosum* Riley (Foerster et al., 2014), the majority of studies indicate that the optimal temperature regime for achieving the highest number of hosts parasitized within a specific time period is 25/25 °C (Ayvaz et al., 2008; Kalyebi et al., 2005; Ksentini et al., 2011; Reznik & Vaghina, 2006; Schöller & Hassan, 2001). However, some species, such as *T. chilonis* Ishii (Shirazi, 2006) and *T. nubilale* Ertle & Davis (Russo & Voegelé, 1982), achieve their best parasitism performance at 30/30 °C. Thus, our findings are consistent with the majority of earlier studies. At 35/35 °C, *T. cacoeciae* was able to successfully reproduce on *E. kuehniella* eggs, displaying a significantly higher level of parasitism in comparison to the other species.

The superior parasitism performance exhibited by *T. cacoeciae* at higher temperatures could be attributed to its prior exposure and adaptation to the challenging environmental conditions typically prevalent in southern Tunisia. In contrast, *T. minutum* showed a low parasitism performance at 35/35 °C (4.4 eggs/female), which may be attributed to its Canadian origin, where colder climatic conditions are predominant (Mols & Boers, 2001). According to Yu et al. (1984), *T. minutum* (originated from Canada) has evolved to optimize its reproductive success within a narrower temperature range of 20–25 °C. Our findings are consistent with earlier studies that have shown a correlation between the behavioral variability of Trichogramma species/strains and the climatic conditions of their respective habitats (Andrade et al., 2011; Pizzol et al., 2010; Schöller & Hassan, 2001). The level of parasitism recorded for all Trichogramma species at 40/40 °C was relatively low, with less than 1 egg per female. Reznik and Voinovich (2015) attribute the observed decrease in parasitism, in response to high preadult temperatures, to mortality among immature stages occurring before they reach the third larval stage, which is responsible for the characteristic black pigmentation. Pereira et al. (2007) showed that high temperatures can lead to an increase in turgidity of the host egg, which may impede the successful insertion of the parasitoid ovipositor through the chorion. Furthermore, Shipp and Wang (1998) reported that female parasitoids often show a preference for increased feeding and reduced parasitism at high temperatures to maintain their metabolic activity.

Our findings have shown that all four Trichogramma species were able to complete their egg-to-adult development successfully within a temperature range of 25 °C to 35 °C. Also, we observed an inverse relationship between temperature and preadult development time, with a significant decrease as the temperature increased from 25 °C to 35 °C. The current results are in line with the studies on other Trichogramma species (Altoé et al., 2012; Atashi et al., 2023; Bari et al., 2015; Melo et al., 2007; Negahban et al., 2021; Tabebordbar et al., 2022a). According to Zuim et al. (2017), the observed reduction in development time under high temperature conditions is likely due to a significant increase in metabolic activity during the immature stages, which speeds up the conversion process of reserved nutrients to required energy.

The survival rates of *T. cacoeciae*, *T. brassicae* and *T. minutum* were high (> 75%) at all temperature regimes. However, *T. euproctidis* showed a low emergence rate of 35.2% at 35/35 °C. This finding indicates that high temperatures can have a detrimental effect on the emergence of Trichogramma species, as previously noted by Bari et al. (2015) who reported reduced progeny production of *T. zahiri* Polaszek at 34 °C (6.73 offspring/female), and Nadeem et al. (2009) who observed a low emergence rate of approximately 33% for *T. chilonis* when incubated at 35 °C. Some species, such as *T. brevicapillum* (Pak & Oatman, 1982) and *T. evanescens* (Schöller & Hassan, 2001) did not emerge at all at 35 °C. Our study demonstrated that exposing parasitized eggs to 40 °C resulted in a complete failure of Trichogramma emergence. The eggs turned black and many collapsed, dried, and no viable progeny were observed, indicating a negative effect of the temperature exceeding the upper threshold. Nadeem et al. (2009) did not even observe blackened eggs when exposing a strain of *T. chilonis* from Pakistan to 40 °C. However, Hussain et al. (2013) reported a successful emergence rate of over 66% for the same species from Pakistan under this temperature regime. These contrasting results highlight the potential variation in temperature tolerance among strains of Trichogramma species, even within the same country.

Temperature is a crucial factor that strongly affects the sex ratio in *Trichogramma* spp. (Altoé et al., 2012; Atashi et al., 2023; Negahban et al., 2021; Pratissoli & Parra, 2000; Tabebordbar et al., 2022a). However, the impact of temperature on the sex ratio varies depending on the species/strain of Trichogramma (Bueno et al., 2012). In our study, *T. cacoeciae* did not produce any males across all temperature regimes. This finding corroborates earlier studies (Pizzol et al., 2010; Schöller & Hassan, 2001) that have also documented the stability of the sex ratio in this Trichogramma species. In general, Trichogramma wasps demonstrate haplodiploidy in their sex determination process, wherein unfertilized eggs develop into haploid males, while fertilized eggs give rise to diploid females (Moiroux et al., 2014). However, certain species of Trichogramma, such as *T. cacoeciae*, only produce females without fertilization, in a process known as thelytoky. According to Stouthamer (1993) and Zhou et al. (2020), thelytokous Trichogramma offers several benefits in biological control programs, such as the production of only female offspring, easier colonization without mating, higher efficacy at low host populations, and lower costs for mass rearing. Of the three arrhenotokous species studied, *T. minutum* stood out as the only one consistently exhibiting a female biased sex ratio across all temperature regimes. This finding aligns with previous research conducted on other Trichogramma species, such as *T. evanescens* (Schöller & Hassan, 2001), *T. zahiri* (Bari et al., 2015) and *T. atopovirilia* Oatman and Platner (Melo et al., 2007), which found that temperatures between 20 °C and 35 °C do not significantly affect the predominantly female-biased sex ratio. Our study has revealed a significant effect of temperature on the sex ratio of *T. euproctidis* and *T. brassicae*, with a female bias observed between 25 °C and 30 °C, while at 35 °C, the proportion of male offspring exceeded that of females. This finding is coherent with Harrison et al. (1985) and Cônsoli and Parra (1995), who noticed a bias towards male offspring production in the sex ratios of *T. pretiosum* and *T. galloi*, respectively, at 35 °C. According to Lauge (1985), extreme temperatures, limited food availability, and unfavorable rearing conditions may lead to a shift in the sex ratio towards male biased offspring.

Our experiments revealed that the lifespan of female Trichogramma progeny is highly dependent on temperature. Consistently with prior studies on other Trichogramma species (Ayvaz et al., 2008; Harrison et al., 1985; Schöller & Hassan, 2001), we observed that the mean adult longevity of female parasitoids decreased with increasing temperature, with the highest longevity value was recorded at 25 °C. However, our study uncovered differences in the lifespans of the species we tested, as compared to previous research. For instance, we observed a lifespan of 20 days for *T. minutum* at 25 °C, which is shorter than the lifespan of 28 days reported by Yu et al. (1984) on the same species at 25 °C. Likewise, we found a lifespan of 15 days for *T. cacoeciae* at 25 °C, while Schöller and Hassan (2001) reported a shorter lifespan of only four days for the same species at 26 °C. The above-mentioned dissimilarities underscore the crucial role played by both environmental factors and strains of *Trichogramma* spp. in determining the longevity of female progeny. Our findings have unveiled pronounced variations in the age-specific survivorship (lx) curves of the studied species across the different temperatures. Notably, at 35 °C, all species exhibited the highest mortality rate during the early stages of female life. However, at this temperature, only *T. cacoeciae* demonstrated the capacity to survive for up to eight days, while the other species had had significantly lower lifespans, ranging from 2.31 to 5.33 days. The high mortality rates of Trichogramma parasitoids in the field, caused by extreme temperature conditions, pose a significant obstacle to the success of inundative biological control programs (Zouba et al., 2022). However, a strategic approach involving the organization of successive emergence waves and an increase in the number of released wasps can effectively address this challenge (Wu et al., 2016). Furthermore, the availability of a reliable food source has been identified as a critical factor in promoting the longevity of Trichogramma adults, as it increases their chances of surviving for a longer period and encountering more hosts for egg-laying (McDougall & Mills, 1997). According to Gurr and Nicol (2000), providing food is the most practical and economically feasible approach to enhance the longevity of Trichogramma parasitoids in the field and increase their effectiveness as biocontrol agents.

Across all tested Trichogramma species, our experiments revealed that oviposition reached its peak within the first 24 h after female emergence. Subsequently, oviposition rates steadily declined until female death. This finding aligns with Ventura Garcia et al. (2002), who underscored the critical significance of the number of eggs laid by Trichogramma species during the first 24 h in determining their overall fecundity. Additionally, Bueno et al. (2012) reported that the reduction in the number of parasitized eggs over the female's lifespan is a characteristic commonly observed in pro-ovigenic species, such as the parasitoids of the genus Trichogramma. Our experiments demonstrated that the highest progeny fecundity in *T. brassicae*, *T. euproctidis*, and *T. minutum* was observed at 25 °C. However, at both 30 °C and 35 °C, *T. cacoeciae* parasitized significantly more eggs than the other species, with rates of 168.03 and 39.41 eggs per female, respectively. Notably, these values surpass those reported in previous studies for *T. pretiosum* (106.4 eggs at 30 °C) (Maceda et al., 2003), *T. evanescens* (87.62 eggs at 30 °C) (Özder & Kara, 2010), *T. achaeae* (0 egg at 35 °C) (Pino et al., 2020), *T. evanescens* (17.2 eggs at 35 °C) Schöller and Hassan (2001), and *T. oleae* (5.13 eggs at 35 °C) (Ksentini et al., 2011). Our data revealed a significant decrease in the progeny fecundity of Trichogramma species as the temperature increased from 25 °C to 35 °C. This finding is consistent with studies on other Trichogramma species (Ksentini et al., 2011; Pino et al., 2020; Samara et al., 2011). The adverse impact of high temperatures on fecundity may be attributed to a reduction in female longevity, as reported by Garcia et al. (2001). On the other hand, previous studies references have shown an important variation in fecundity, depending on the Trichogramma strain and rearing host. In our study, we observed that *T. minutum* females parasitized 153.03 eggs of *E. kuehniella* at 25 °C, which is lower than the value of 227.6 eggs reported by Yu et al. (1984) for the same Trichogramma species parasitizing *Anagasta kuehniella* Zeller. Similarly, our results showed that *T. cacoeciae* females parasitized 120.14 eggs at 25 °C, which is higher than the number of eggs parasitized by the same Trichogramma species in studies by Schöller and Hassan (2001) and Özder and Kara (2010) on *Ephestia elutella* Hubner (87.27eggs) and *Cadra cautella* Walker (80.64eggs), respectively.

The assessment of thermal sensitivity among the studied Trichogramma species not only highlights the variability in their susceptibility to high temperatures but also underscores the need for careful species and strain selection to ensure their proper adaptation to the environmental conditions of the release area. In the specific case of the Mediterranean Basin region, *T. cacoeciae* stands out as the preferential choice for mass-rearing and biological control of lepidopteran pests. This preference is attributed to its remarkable ability to survive and develop within the tested temperature range, particularly at high temperatures (30–35 °C). Our findings provide an explanation for the widespread presence and remarkable adaptation of *T. cacoeciae* to the prevailing extreme high temperature conditions in pomegranate and date palm orchards located in southern Tunisia (Ksentini et al., 2010; Zouba et al., 2013a). Furthermore, this species has demonstrated a remarkable ability to withstand the harsh climatic conditions prevalent in olive groves located within the Cairo desert, Egypt (Herz et al., 2007). *Trichogramma cacoeciae* exhibits an extensive worldwide distribution, occurring naturally in diverse regions including North Africa, Europe, Asia, and America (Herz et al., 2007; Pintureau, 2008). Pizzol et al. (2010) have highlighted the species' notable plasticity in terms of temperature tolerance, indicating the presence of multiple populations with finely-tuned biological characteristics adapted to the specific climatic conditions of their respective habitats.

Currently, *T. cacoeciae* is officially listed by the European Plant Protection Organization (EPPO) as a species approved for use in Euro-Mediterranean countries (EPPO, 2002). *Trichogramma cacoeciae* is commercially available and extensively employed as an integral component of integrated pest management strategies for managing the carob moth *Ectomyelois ceratoniae* Zeller (Lepidoptera, Pyralidae) in Tunisia, with studies proving its effectiveness in controlling this pest in pomegranate (Lebdi-Grissa & Ben Ayed 2005; Zougari et al., 2020), date palm (Khoualdia et al., 1996; Zouba et al., 2022), and citrus crops (Dhouibi et al., 2016). Furthermore, *T. cacoeciae* has been recognized as one of the highly efficient Trichogramma species suitable for combating the tomato leaf miner *Tuta absoluta* Meyrick (Lepidoptera, Gelechiidae) in protected and open field tomato crops in Mediterranean Basin countries (Zouba et al., 2013b; Cherif & Lebdi-Grissa, 2013; Cherif & Verheggen, 2019). Additionally, the remarkable potential of *T. cacoeciae* has been demonstrated through successful experimental inundative releases, effectively managing significant pests such as the European grapevine moth *Lobesia botrana* Denis & Schiffermüller (Lepidoptera, Tortricidae) (Hommay et al., 2002; Pizzol, 2004), the apple codling moth *Cydia pomonella* Linnaeus (Lepidoptera: Tortricidae) (Sigsgaard et al., 2017), and the olive moth *Prays oleae* Bernard (Lepidoptera, Plutellidae) (Herz et al., 2007), all of which pose serious threats in the Mediterranean basin region (Coscolla, 1997; Herz et al., 2007).

Conclusions

Through our study, we conducted experiments to investigate the influence of different oviposition and preadult temperatures that reflect the conditions typically experienced during the growing seasons in Mediterranean Basin countries on the biological parameters of four Trichogramma species originating from geographically diverse regions. Our findings have highlighted the notable impact of high temperatures, particularly those reaching 35 °C and 40 °C, on various biological traits exhibited by the studied species. *Trichogramma cacoeciae* showed the best performance in terms of parasitization efficiency, developmental capacity, sex ratio, progeny longevity, and fecundity at 35 °C. However, as temperatures increased from 35 °C to 40 °C, the strain of *T. cacoeciae* was unable to complete preadult development in *E. kuehniella* eggs. It is worth noting that temperatures in the field are subject to fluctuation throughout the day and night, and parasitoids are unlikely to encounter constant temperatures of 35–40 °C. Given these findings, *T. cacoeciae* appears to be a promising candidate for controlling thermophile lepidopteran pests across Mediterranean Basin countries via inundative releases. Nevertheless, to optimize the biological efficiency of *T. cacoeciae* and reduce the growing reliance on synthetic insecticides in diverse cropping systems, it is imperative to integrate this knowledge with other management strategies. Nonetheless, it is important to emphasize that additional efforts are necessary to validate these laboratory observations under natural field conditions.

Acknowledgements Authors are very grateful to Mrs Sonia Jandoubi for her technical assistance in the rearings. This work was supported by the National Agronomic Institute of Tunisia (INAT).

Authors contributions **SZ** conducted experiment. **AZ** and **SZ** contributed equally to the writing of the contents present under different sub-headings of the manuscript. **MM** revised the manuscript. All generated data were statistically analyzed by **SZ** and critically checked and verified by **KGL. NK** help in data entry evaluation. **KGL** and **FBH** supervise. All the authors read and approved the manuscript.

Data availability All data and materials are available on the reasonable request.

Declarations

Competing interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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